An Introduction to Speciation (Evolutionary Process)

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First Edition, 2012

ISBN 978-81-323-3716-4

Published by:
University Publications
4735/22 Prakashdeep Bldg,
Ansari Road, Darya Ganj,
Delhi - 110002
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Introduction to Speciation

Speciation is the evolutionary process by which new biological species arise. The biologist Orator F. Cook seems to have been the first to coin the term 'speciation' for the splitting of lineages or 'cladogenesis,' as opposed to 'anagenesis' or 'phyletic evolution' occurring within lineages. Whether genetic drift is a minor or major contributor to speciation is the subject matter of much ongoing discussion.

There are four geographic modes of speciation in nature, based on the extent to which speciating populations are geographically isolated from one another: allopatric, peripatric, parapatric, and sympatric. Speciation may also be induced artificially, through animal husbandry or laboratory experiments. Observed examples of each kind of speciation are provided throughout.

Natural speciation

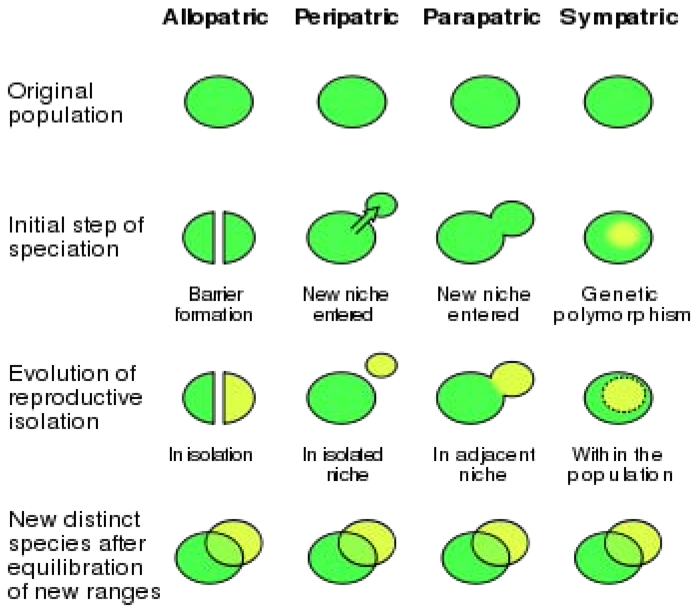
All forms of natural speciation have taken place over the course of evolution; however it still remains a subject of debate as to the relative importance of each mechanism in driving biodiversity.

The three-spined stickleback (*Gasterosteus aculeatus*)

One example of natural speciation is the diversity of the three-spined stickleback, a marine fish that, after the last ice age, has undergone speciation into new freshwater colonies in isolated lakes and streams. Over an estimated 10,000 generations, the sticklebacks show structural differences that are greater than those seen between different genera of fish including variations in fins, changes in the number or size of their bony plates, variable jaw structure, and color differences.

There is debate as to the rate at which speciation events occur over geologic time. While some evolutionary biologists claim that speciation events have remained relatively constant over time, some palaeontologists such as Niles Eldredge and Stephen Jay Gould have argued that species usually remain unchanged over long stretches of time, and that speciation occurs only over relatively brief intervals, a view known as *punctuated equilibrium*.

Allopatric



Comparison of allopatric, peripatric, parapatric and sympatric speciation.

During allopatric (from the ancient Greek *allos*, "other" + Greek *patrā*, "fatherland") speciation, a population splits into two geographically isolated populations (for example, by habitat fragmentation due to geographical change such as mountain building or social change such as emigration). The isolated populations then undergo genotypic and/or phenotypic divergence as: (a) they become subjected to dissimilar selective pressures; (b) they independently undergo genetic drift; (c) different mutations arise in the two populations. When the populations come back into contact, they have evolved such that they are reproductively isolated and are no longer capable of exchanging genes.

Observed instances

Island genetics, the tendency of small, isolated genetic pools to produce unusual traits, has been observed in many circumstances, including insular dwarfism and the radical changes among certain famous island chains, for example on Komodo. The Galápagos islands are particularly famous for their influence on Charles Darwin. During his five weeks there he heard that Galápagos tortoises could be identified by island, and noticed that Mockingbirds differed from one island to another, but it was only nine months later that he reflected that such facts could show that species were changeable. When he returned to England, his speculation on evolution deepened after experts informed him that these were separate species, not just varieties, and famously that other differing Galápagos birds were all species of finches. Though the finches were less important for Darwin, more recent research has shown the birds now known as Darwin's finches to be a classic case of adaptive evolutionary radiation.

Peripatric

In peripatric speciation, a subform of allopatric speciation, new species are formed in isolated, smaller peripheral populations that are prevented from exchanging genes with the main population. It is related to the concept of a founder effect, since small populations often undergo bottlenecks. Genetic drift is often proposed to play a significant role in peripatric speciation.

Observed instances

- Mayr bird fauna
- The Australian bird *Petroica multicolor*
- Reproductive isolation occurs in populations of *Drosophila* subject to population bottlenecking

The London Underground mosquito is a variant of the mosquito *Culex pipiens* that entered in the London Underground in the nineteenth century. Evidence for its speciation include genetic divergence, behavioral differences, and difficulty in mating.

Parapatric

In parapatric speciation, there is only partial separation of the zones of two diverging populations afforded by geography; individuals of each species may come in contact or cross habitats from time to time, but reduced fitness of the heterozygote leads to selection for behaviours or mechanisms that prevent their inter-breeding. Parapatric speciation is modelled on continuous variation within a 'single', connected habitat acting as a source of natural selection rather than the effects of isolation of habitats produced in peripatric and allopatric speciation.

Ecologists refer to parapatric and peripatric speciation in terms of ecological niches. A niche must be available in order for a new species to be successful.

Observed instances

- Ring species
    - The *Larus* gulls form a ring species around the North Pole.
    - The *Ensatina* salamanders, which form a ring round the Central Valley in California.
    - The Greenish Warbler (*Phylloscopus trochiloides*), around the Himalayas.
- the grass *Anthoxanthum* has been known to undergo parapatric speciation in such cases as mine contamination of an area.

Sympatric

Sympatric speciation refers to the formation of two or more descendant species from a single ancestral species all occupying the same geographic location.

In sympatric speciation, species diverge while inhabiting the same place. Often-cited examples of sympatric speciation are found in insects that become dependent on different host plants in the same area. However, the existence of sympatric speciation as a mechanism of speciation is still hotly contested. People have argued that the evidences of sympatric speciation are in fact examples of micro-allopatric, or heteropatric speciation. The most widely accepted example of sympatric speciation is that of the cichlids of Lake Nabugabo in East Africa, which is thought to be due to **sexual selection**.

Until recently, there has a been a dearth of hard evidence that supports this form of speciation, with a general feeling that interbreeding would soon eliminate any genetic differences that might appear. But there has been at least one recent study that suggests that sympatric speciation has occurred in Tennessee cave salamanders.

The three-spined sticklebacks, freshwater fishes, that have been studied by Dolph Schluter (who received his Ph.D. for his work on Darwin's finches with Peter J. Grant) and his current colleagues in British Columbia, were once thought to provide an intriguing example best explained by sympatric speciation. Schluter and colleagues found:

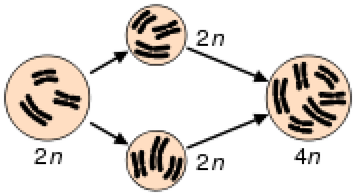
- Two different species of three-spined sticklebacks in each of five different lakes
    - a large benthic species with a large mouth that feeds on large prey in the littoral zone
    - a smaller limnetic species — with a smaller mouth — that feeds on the small plankton in open water
- DNA analysis indicates that each lake was colonized independently, presumably by a marine ancestor, after the last ice age
- DNA analysis also shows that the two species in each lake are more closely related to each other than they are to any of the species in the other lakes
- The two species in each lake are reproductively isolated; neither mates with the other.

- However, aquarium tests showed:
  - the benthic species from one lake will spawn with the benthic species from the other lakes and
  - likewise the limnetic species from the different lakes will spawn with each other.
  - These benthic and limnetic species even display their mating preferences when presented with sticklebacks from Japanese lakes; that is, a Canadian benthic prefers a Japanese benthic over its close limnetic cousin from its own lake.
- Their conclusion: in each lake, what began as a single population faced such competition for limited resources that:
  - disruptive selection — competition favoring fishes at either extreme of body size and mouth size over those nearer the mean — coupled with:
  - assortative mating — each size preferred mates like it — favored a divergence into two subpopulations exploiting different food in different parts of the lake.
  - The fact that this pattern of speciation occurred the same way on three separate occasions suggests strongly that ecological factors in a sympatric population can cause speciation.

However, the DNA evidence cited above is from mitochondrial DNA (mtDNA), which can often move easily between closely related species ("introgression") when they hybridize. A more recent study, using genetic markers from the nuclear genome, shows that limnetic forms in different lakes are more closely related to each other (and to marine lineages) than to benthic forms in the same lake. The three-spine stickleback is now usually considered an example of "double invasion" (a form of allopatric speciation) in which repeated invasions of marine forms have subsequently differentiated into benthic and limnetic forms. The three-spine stickleback provides an example of how molecular biogeographic studies that rely solely on mtDNA can be misleading, and that consideration of the genealogical history of alleles from multiple unlinked markers (i.e. nuclear genes) is necessary to infer speciation histories.

Sympatric speciation driven by ecological factors may also account for the extraordinary diversity of crustaceans living in the depths of Siberia's Lake Baikal.

Speciation via polyploidization



Speciation via polyploidy: A diploid cell undergoes failed meiosis, producing diploid gametes, which self-fertilize to produce a tetraploid zygote.

Polyploidy is a mechanism often attributed to causing some speciation events in sympatry. Not all polyploids are reproductively isolated from their parental plants, so an increase in chromosome number may not result in the complete cessation of gene flow between the incipient polyploids and their parental diploids.

Polyploidy is observed in many species of both plants and animals, and results in rapid speciation since offspring of, for example, tetraploid x diploid matings result in triploid sterile progeny. It has been proposed that many of the existing plant and most animal species have undergone an event of polyploidization in their evolutionary history. However, reproduction is often by parthenogenesis since polyploid animals are often sterile. [needs further editing—not true in plants]. Rare instances of polyploid mammals are known, but most often result in prenatal death.

Hawthorn fly

One example of evolution at work is the case of the hawthorn fly, *Rhagoletis pomonella*, also known as the apple maggot fly, which appears to be undergoing sympatric speciation. Different populations of hawthorn fly feed on different fruits. A distinct population emerged in North America in the 19th century some time after apples, a non-native species, were introduced. This apple-feeding population normally feeds only on apples and not on the historically preferred fruit of hawthorns. The current hawthorn feeding population does not normally feed on apples. Some evidence, such as the fact that six out of thirteen allozyme loci are different, that hawthorn flies mature later in the season and take longer to mature than apple flies; and that there is little evidence of interbreeding (researchers have documented a 4-6% hybridization rate) suggests that sympatric speciation is occurring. The emergence of the new hawthorn fly is an example of evolution in progress.

Speciation via hybrid formation

Reinforcement (Wallace effect)

Reinforcement is the process by which natural selection increases reproductive isolation. It may occur after two populations of the same species are separated and then come back into contact. If their reproductive isolation was complete, then they will have already developed into two separate incompatible species. If their reproductive isolation is incomplete, then further mating between the populations will produce hybrids, which may or may not be fertile. If the hybrids are infertile, or fertile but less fit than their ancestors, then there will be no further reproductive isolation and speciation has essentially occurred (e.g., as in horses and donkeys.) The reasoning behind this is that if the parents of the hybrid offspring each have naturally selected traits for their own certain environments, the hybrid offspring will bear traits from both, therefore would not fit either ecological niche as well as either parent. The low fitness of the hybrids would cause selection to favor assortative mating, which would control hybridization. This is sometimes called the Wallace effect after the evolutionary biologist Alfred Russel Wallace who suggested in the late 19th century that it might be an important factor in speciation. If the hybrid offspring are more fit than their ancestors, then the populations will merge back into the same species within the area they are in contact.

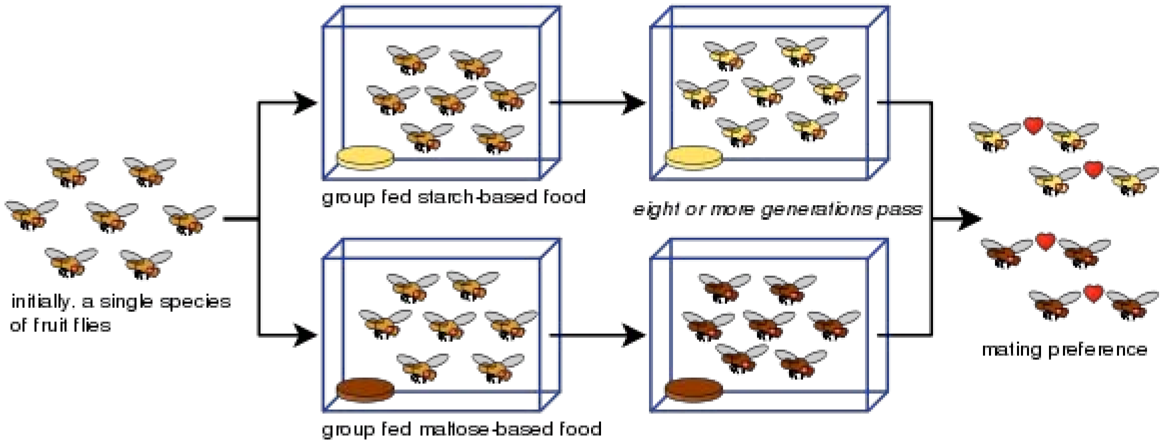
Reinforcement is required for both parapatric and sympatric speciation. Without reinforcement, the geographic area of contact between different forms of the same species, called their "hybrid zone," will not develop into a boundary between the different species. Hybrid zones are regions where diverged populations meet and interbreed. Hybrid offspring are very common in these regions, which are usually created by diverged species coming into secondary contact. Without reinforcement the two species would have uncontrollable inbreeding. Reinforcement may be induced in artificial selection experiments as described below.

Artificial speciation

New species have been created by domesticated animal husbandry, but the initial dates and methods of the initiation of such species are not clear. For example, domestic sheep were created by hybridisation, and no longer produce viable offspring with *Ovis orientalis*, one species from which they are descended. Domestic cattle, on the other hand, can be considered the same species as several varieties of wild ox, gaur, yak, etc., as they readily produce fertile offspring with them.

The best-documented creations of new species in the laboratory were performed in the late 1980s. William Rice and G.W. Salt bred fruit flies, *Drosophila melanogaster,* using a maze with three different choices of habitat such as light/dark and wet/dry. Each generation was placed into the maze, and the groups of flies that came out of two of the eight exits were set apart to breed with each other in their respective groups. After thirty-five generations, the two groups and their offspring were isolated reproductively because of their strong habitat preferences: they mated only within the areas they preferred, and so did not mate with flies that preferred the other areas. The history of such attempts is described in Rice and Hostert (1993).

Diane Dodd was also able to show how reproductive isolation can develop from mating preferences in *Drosophila pseudoobscura* fruit flies after only eight generations using different food types, starch and maltose.



Dodd's experiment has been easy for many others to replicate, including with other kinds of fruit flies and foods.

Genetics

Few speciation genes have been found. They usually involve the reinforcement process of late stages of speciation. In 2008 a speciation gene causing reproductive isolation was reported. It causes hybrid sterility between related subspecies.

Hybrid speciation

Hybridization between two different species sometimes leads to a distinct phenotype. This phenotype can also be fitter than the parental lineage and as such natural selection may then favor these individuals. Eventually, if reproductive isolation is achieved, it may lead to a separate species. However, reproductive isolation between hybrids and their parents is particularly difficult to achieve and thus hybrid speciation is considered an extremely rare event. The Mariana Mallard is known to have arisen from hybrid speciation.

Hybridization without change in chromosome number is called homoploid hybrid speciation. It is considered very rare but has been shown in *Heliconius* butterflies and sunflowers. Polyploid speciation, which involves changes in chromosome number, is a more common phenomenon, especially in plant species.

Gene transposition as a cause

Theodosius Dobzhansky, who studied fruit flies in the early days of genetic research in 1930s, speculated that parts of chromosomes that switch from one location to another might cause a species to split into two different species. He mapped out how it might be possible for sections of chromosomes to relocate themselves in a genome. Those mobile sections can cause sterility in inter-species hybrids, which can act as a speciation pressure. In theory, his idea was sound, but scientists long debated whether it actually happened in nature. Eventually a competing theory involving the gradual accumulation of mutations was shown to occur in nature so often that geneticists largely dismissed the moving gene hypothesis.

However, 2006 research shows that jumping of a gene from one chromosome to another can contribute to the birth of new species. This validates the reproductive isolation mechanism, a key component of speciation.

Interspersed repeats

Interspersed repetitive DNA sequences function as isolating mechanisms. These repeats protect newly evolving gene sequences from being overwritten by gene conversion, due to the creation of non-homologies between otherwise homologous DNA sequences. The non-homologies create barriers to gene conversion. This barrier allows nascent novel genes to evolve without being overwritten by the progenitors of these genes. This uncoupling allows the evolution of new genes, both within gene families and also allelic forms of a gene. The importance is that this allows the splitting of a gene pool without requiring physical isolation of the organisms harboring those gene sequences.

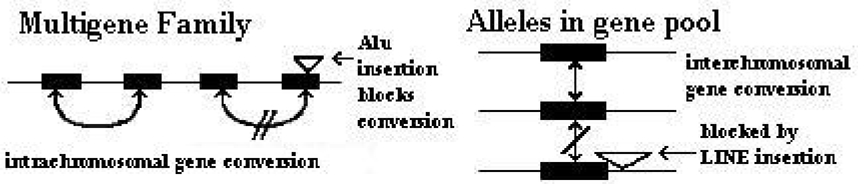
Interspersed repetitive DNA is found in all eukaryotic genomes. Certain classes of these sequences propagate themselves by RNA mediated transposition, and they have been called retrotransposons. Interspersed repetitive DNA elements allow new genes to evolve. They do this by uncoupling similar DNA sequences from gene conversion during meiosis. The recombinational events of meiosis create heteroduplexes composed of strands from each parental chromosome. These heteroduplexes lead to mismatch repair. The net result is the homogenization and elimination of sequence differences during meiosis. Gene conversion can be viewed as the force acting to create sequence identity within the gene pool of a species. This is a cohesive force acting to match up DNA sequences of individual organisms that comprise a species. In effect the gene conversion causes the DNA sequences to *clump together* within a species and by doing so creates the natural boundaries between species. The gene pool of a species consists of DNA sequences linked in a network by gene conversion events.

Intrachromosomal and interchromosomal gene conversion

Gene conversion acts on DNA sequence homology as its substrate. There is no requirement that the sequence homologies lie at the allelic positions on their respective chromosomes or even that the homologies lie on different chromosomes. Gene conversion events can occur between different members of a gene family situated on the same chromosome. When this happens, it is called intrachromosomal gene conversion as distinguished from interchromosomal gene conversion. The effect of homogenizing DNA sequences is the same.

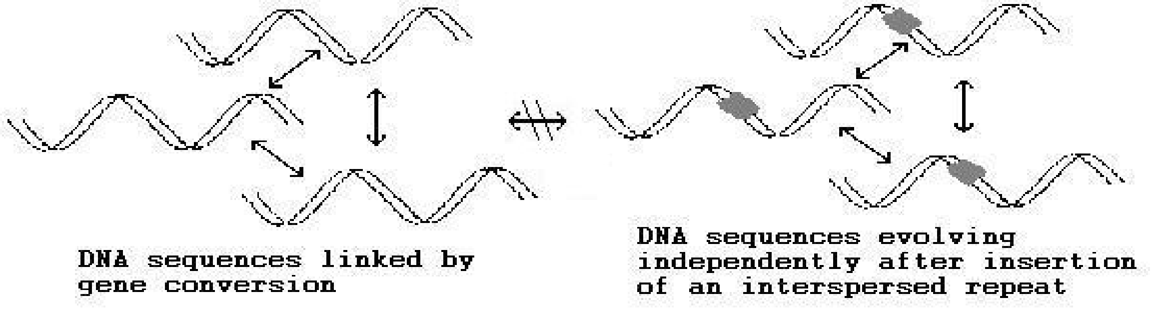
Role of Interspersed Repetitive DNA

Repetitive sequences play the role of uncoupling the gene conversion network, thereby allowing new genes to evolve. The shorter Alu or SINE repetitive DNA are specialized for uncoupling intrachromosomal gene conversion while the longer LINE repetitive DNA are specialized for uncoupling interchromosomal gene conversion. In both cases, the interspersed repeats block gene conversion by inserting regions of non-homology within otherwise similar DNA sequences. The homogenizing forces linking DNA sequences are thereby broken and the DNA sequences are free to evolve independently. This leads to the creation of new genes and new species during evolution. By breaking the links that would otherwise overwrite novel DNA sequence variations, interspersed repeats catalyse evolution, allowing the new genes and new species to develop.



Interspersed DNA elements catalyze the evolution of new genes

DNA sequences are linked together in a gene pool by gene conversion events. Insertion of an interspersed DNA element breaks this linkage, allowing independent evolution of a new gene. The interspersed repeat is an isolating mechanism enabling new genes to evolve without interference from the progenitor gene. Because insertion of an interspersed repeat is a saltatory event the evolution of the new gene will also be saltatory. Because speciation ultimately depends on the creation of new genes, this naturally causes punctuated equilibria. Interspersed repeats are thus responsible for punctuated evolution and rapid modes of evolution.



Human speciation

Humans have genetic similarities with chimpanzees and gorillas, suggesting common ancestors. Analysis of genetic drift and recombination using a Markov model suggests humans and chimpanzees speciated apart 4.1 million years ago.

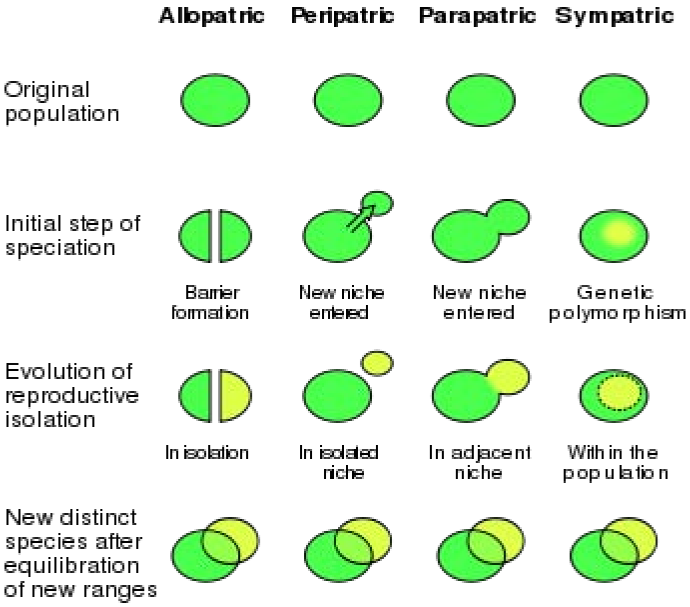
Chapter- 2

Allopatric Speciation

Allopatric speciation (from the ancient Greek allos, "other" + Greek patrida, "fatherland") or **geographic speciation** is speciation that occurs when biological populations of the same species become isolated due to geographical changes such as mountain building or social changes such as emigration. The isolated populations then undergo genotypic and/or phenotypic divergence as: (a) they become subjected to different selective pressures, (b) they independently undergo genetic drift, and (c) different mutations arise in the populations' gene pools.

The separate populations over time may evolve distinctly different characteristics. If the geographical barriers are later removed, members of the two populations may be unable to successfully mate with each other, at which point, the genetically isolated groups have emerged as different species. Allopatric isolation is a key factor in speciation and a common process by which new species arise. Adaptive radiation, as observed by Charles Darwin in Galapagos finches, is a consequence of allopatric speciation among island populations.

Isolating Mechanisms



Comparison of **allopatric**, peripatric, parapatric and sympatric speciation

Allopatric speciation may occur when a species is subdivided into two genetically isolated populations. *Allopatric* and *allopatry* are terms from biogeography, referring to organisms whose ranges are entirely separate such that they do not occur in any one place together. If these organisms are closely related (e.g. sister species), such a distribution is usually the result of *allopatric speciation*. Separation may be attributed to either geological processes or population dispersal.

Geographical isolation

Geological processes can fragment a population through such events as emergence of mountain ranges, canyon formation, glacial processes, the formation or destruction of land bridges, or the subsidence of large bodies of water. On a global scale, plate tectonics is a major geological factor leading to separation of populations and the resulting distribution of species.

Approximately 50,000 years ago, the Death Valley region of the western United States had a rainy climate which produced an interconnecting system of freshwater rivers and lakes. Climatic changes resulted in a drying trend that has continued for the last 10,000 years. As the lakes and rivers shrunk, fish populations became geologically isolated. The few remaining (separated) springs are currently home to a variety of fish, many sharing a close common ancestor; yet each has uniquely adapted to its own particular pool.

The extent to which a geological barrier can effectively isolate a population correlates to the mobility of the organism or its offspring. For example physical barriers such as canyons may effectively block migration and dispersal of small mammals; however, have little impact on flying birds or wind-borne seeds.

Population Dispersal

Population dispersal is used to describe migratory events, either in the form of range expansion (natural movement away from parents) or jump dispersal (crossing of barriers), which may lead to genetic isolation. If the smaller population fragment becomes genetically isolated from the parental group, it may be subjected to its own unique mutations, selection forces, and genetic drift effects; thus, it will follow its own evolutionary pathway. Migrations or accidental relocations (such as birds being blown off course) may lead to population fragments; whereby groups merely become separated by distance. Once gene flow between the two groups is disrupted, speciation becomes a possibility.

Allopatric speciation in peripheral populations

When populations become genetically isolated, heritable variations may accumulate so that they become different from the parental population. Given sufficient time, these variations may lead to reproductive isolation.

Portions of a populations that exist along the edges of the parent population's geographic territory have higher likelihood of developing reproductive isolation. Such peripheral populations are likely to possess genes that are different from the parental population. After isolation, the founding population is less likely to represent the gene pool of the parent population. In addition, peripheral isolates are likely to represent a small number of individuals, meaning their gene pool is more susceptible to the effects of genetic drift (random chance). Furthermore, it is likely that the peripheral population will inhabit an environment different from its ancestral gene pool, likely causing it to be subjected to different selective pressures as it colonizes new areas. The outer periphery of a population's habitat tends to be extreme; hence, the reason range expansion is kept in check. For most peripheral isolates, it is more likely that they die off rather than survive and speciate.

Genesis of reproductive barriers

Adaptive divergence may occur when a population becomes geographically divided: followed by an accumulation of genetic differences as they adapt to their own unique environments. Reproductive barriers do not evolve as a consequence of external forces that drive populations toward speciation. Rather, the evolution of reproductive isolation, leading to speciation, is generally thought to be an incidental by-product of genetic divergence, particularly adaptive changes that evolve through natural selection in response to different environmental conditions in separate geographic areas.

The Biological Species Concept, proposed by Ernst Mayr, in the 1942, emphasizes reproductive isolation as the basis of defining a species. The definition states: "A species is defined as a population or group of populations whose members have the potential to interbreed with one another in nature and to produce viable offspring, but cannot produce viable, fertile offspring with members of other species." Mayr, a proponent of allopatric speciation, hypothesized that adaptive genetic changes that accumulate between allopatric populations cause negative epistasis in hybrids, resulting in sterility of the offspring.

If there is considerable genetic and phenotypic change without the loss of the capacity for interbreeding, then such hybridization is simply prevented by the geographical separation of populations. In this case the populations are normally regarded as subspecies.

The frequency of other types of speciation, such as sympatric speciation, parapatric speciation, and heteropatric speciation, is debated. Proponents of peripatric speciation contend that small population size in the peripheral isolate (sometimes referred to as a "splinter population") increases genetic drift, which can be a more powerful force than natural selection in small populations. It deconstructs complex genotypes, allowing the creation of novel gene combinations. Both forms need not be mutually exclusive. In practice, passive isolation or fragmentation as well as active dispersal seem to play a role in many cases of speciation.

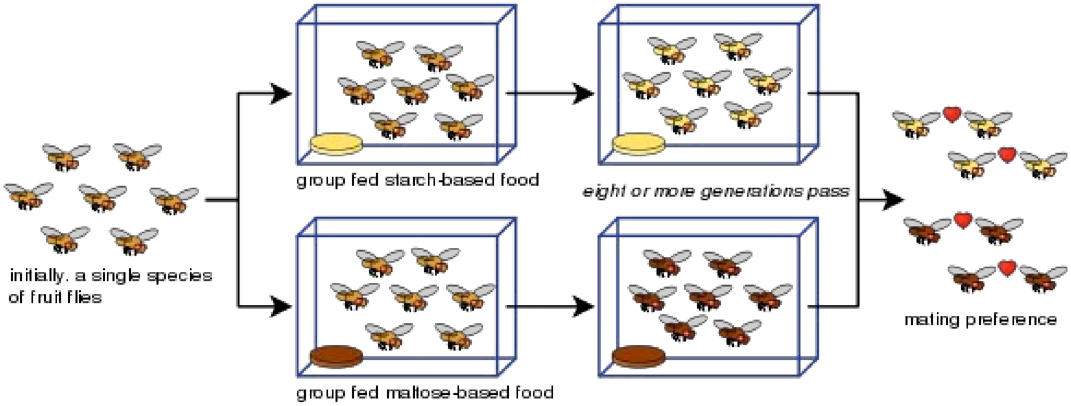
Alternative Modes of Speciation

Sympatric speciation represents an alternative method of speciation that does not require physical separation; instead speciation occurs within a population sharing the same geographic boundaries. For example, the development of polyploidy in plant species can lead to a new species arising within the geographic range of its parent population.

In parapatric speciation there is no physical barrier to gene exchange within the population. Instead, the population is continuous; however, mating is not random. Individuals mate with their closest neighbors rather than with individuals in a more distant location. Divergence may occur as a consequence of both reduced gene flow and natural selection, imposed by the large distance between individuals within a population's habitat.

Allopatric speciation is thought to be the dominant mode of speciation.

Examples



Allopatric speciation among fruit flies

The African Elephant has always been regarded as a single species but, because of morphological and DNA differences, some scientists classify them into three subspecies. Researchers at the University of California, San Diego have argued that divergence due to geographical isolation has gone further, and the elephants of West Africa should be regarded as a separate species from both the savanna elephants of Central, Eastern and Southern Africa, or the forest elephants of Central Africa. A similar situation exists with the Asian Elephant, which has four distinct living sub-species.

Other cases arise where two populations that are quite distinct morphologically, and are native to different continents, have been classified as different species; but when members of one species are introduced into the other's range, they are found to interbreed freely, showing that they were in fact only geographically isolated subspecies. This was found to be the case when the Mallard was introduced into New Zealand and interbred freely with the native Grey Duck, which had been classified as a separate species. It is controversial whether its specific status can now be retained.

Chapter- 3

Sympatric & Peripatric Speciation

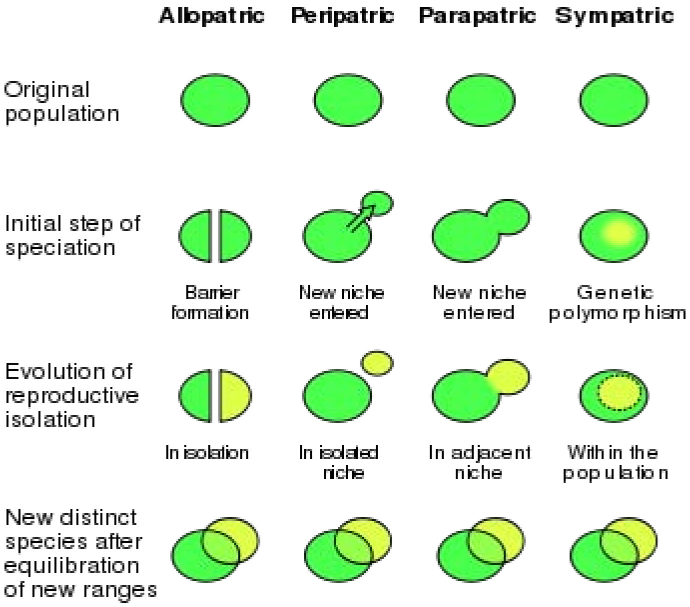
Sympatric speciation

A speciation in which new species evolve from a single ancestral species while inhabiting the same geographic region. In evolutionary biology and biogeography, **sympatric** and **sympatry** are terms referring to organisms whose ranges overlap or are even identical, so that they occur together at least in some places. If these organisms are closely related (e.g. sister species), such a distribution may be the result of **sympatric speciation**. Etymologically, sympatry is derived from the Greek roots *συν* (together, with) and *πατρίς* (homeland or fatherland). The term was invented by Poulton in 1904, who explains the derivation.

Sympatry is one of four theoretical models for the phenomenon of speciation. In contrast to allopatry, populations undergoing sympatric speciation are not geographically isolated by, for example, a mountain or a river.

In multicellular eukaryotic organisms, sympatric speciation is thought to be an uncommon but plausible process by which genetic divergence (through reproductive isolation) of various populations from a single parent species and inhabiting the same geographic region leads to the creation of new species. In bacteria, however, the analogous process (defined as "the origin of new bacterial species that occupy definable ecological niches") is more common and occurs through horizontal gene transfer.

Evidence



Comparison of allopatric, peripatric, parapatric and sympatric speciation.

A number of models have been proposed to account for this mode of speciation. The most popular, which invokes the disruptive selection model, was first put forward by John Maynard Smith in 1966. Maynard Smith suggested that homozygous individuals may, under particular environmental conditions, have a greater fitness than those with alleles heterozygous for a certain trait. Under the mechanism of natural selection, therefore, homozygosity would be favoured over heterozygosity, eventually leading to speciation. Sympatric divergence could also result from the sexual conflict.

Disruption may also occur in multiple-gene traits. The Medium Ground Finch (*Geospiza fortis*) is showing gene pool divergence in a population on Santa Cruz Island. Beak morphology conforms to two different size ideals, while intermediate individuals are selected against. Some characteristics (termed magic traits) such as beak morphology may drive speciation because they also affect mating signals. In this case, different beak phenotypes may result in different bird calls, providing a barrier to exchange between the gene pools.

A well studied circumstance of sympatric speciation is when insects feed on more than one species of host plant. In this case insects become specialized as they struggle to overcome the various plants' defense mechanisms. (Drès and Mallet, 2002)

Rhagoletis pomonella, the apple maggot, may be currently undergoing sympatric or, more precisely, heteropatric speciation. The apple feeding race of this species appears to have spontaneously emerged from the hawthorn feeding race in the 1800 - 1850 AD time frame, after apples were first introduced into North America. The apple feeding race does not now normally feed on hawthorns, and the hawthorn feeding race does not now normally feed on apples. This may be an early step towards the emergence of a new species. Isolated and relatively homogeneous habitats such as crater lakes and islands are among the best geographical settings in which to demonstrate sympatric speciation. For example, Nicaragua crater lake cichlid fishes include at least one species that has evolved by sympatric speciation

Allochrony offers some empirical evidence that sympatric speciation has taken place, as many examples exist of recently diverged (sister taxa) allochronic species.

Sympatric speciation events are vastly more common in plants, as they are prone to developing multiple homologous sets of chromosomes, resulting in a condition called polyploidy. The polyploidal offspring occupy the same environment as the parent plants (hence sympatry), but are reproductively isolated.

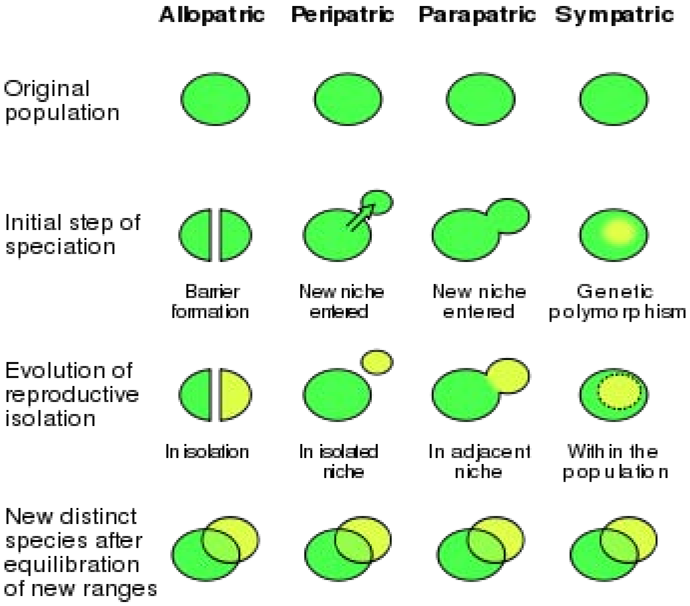
A rare example of sympatric speciation in animals is the divergence of "resident" and "transient" Orca forms in the northeast Pacific . Resident and transient orcas inhabit the same waters, but avoid each other and do not interbreed. The two forms hunt different prey species and have different diets, vocal behaviour, and social structures. Some divergences between species could also result from contrasts in microhabitats.

The polecat *Mustela putorius* exhibited a rare dark phenotype similar to the European mink *Mustela lutreola* phenotype which is directely influenced by peculiarities of forest brooks .

Controversy

Debated almost since the beginning of popular evolutionary thought, sympatric speciation is still a highly contentious issue. By 1980 the theory was largely unfavourable given the void of empirical evidence available, and more critically the conditions scientists expect to be required. Ernst Mayr, one of the foremost thinkers on evolution, completely rejected sympatry outright, ushering in a climate of hostility towards the theory. While still debatable, well documented empirical evidence now exists, and the development of sophisticated theories incorporating multilocus genetics have followed.

Peripatric speciation



Comparison of allopatric, peripatric, parapatric and sympatric speciation.

Peripatric and **peripatry** are terms from biogeography, referring to organisms whose ranges are closely adjacent but do not overlap, being separated by a natural barrier where these organisms do not occur – for example a wide river or a mountain range. Such organisms are usually closely related (e.g. sister species), their distribution being the result of **peripatric speciation**.

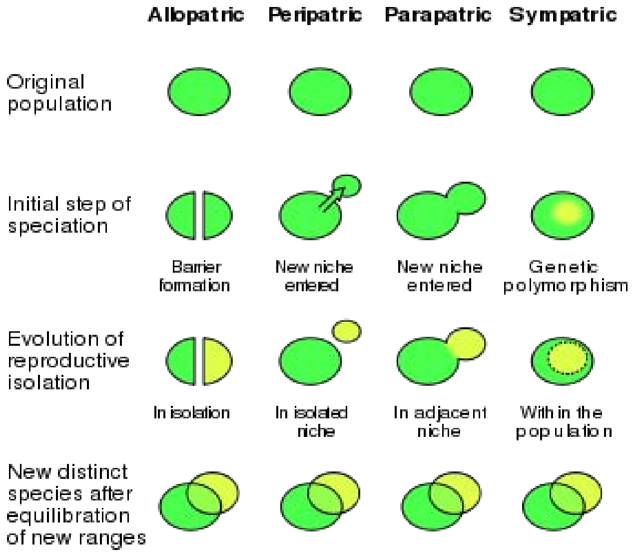
Peripatric speciation is a form of speciation, the formation of new species through evolution. In this form, new species are formed in isolated peripheral populations; this is similar to allopatric speciation in that populations are isolated and prevented from exchanging genes. However, peripatric speciation, unlike allopatric speciation, proposes that one of the populations is much smaller than the other.

Peripatric speciation was originally proposed by Ernst Mayr, and is related to the founder effect, because small living populations may undergo selection bottlenecks. Genetic drift is often proposed to play a significant role in peripatric speciation.

Chapter- 4

Heteropatric Speciation, Parapatric Speciation

Heteropatric speciation



Comparison of allopatric, peripatric, parapatric and sympatric speciation.

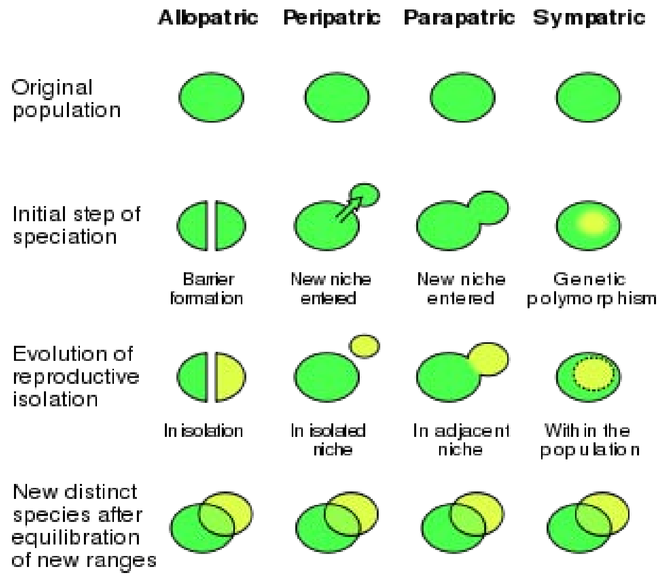
Heteropatric and **heteropatry** are terms from biogeography, referring to organisms whose geographical ranges overlap or are even identical, so that they occur together at least in some places, but which occupy ecological niches distinct enough to prevent frequent hybridization. Such organisms are usually closely related (e.g. sister species), their distribution and ecology being the result of **heteropatric speciation**.

Heteropatric speciation is a special case of sympatric speciation that occurs when different ecotypes or races of the same species geographically coexist but exploit different niches in the same patchy or heterogeneous environment. Thus heteropatric speciation is a refinement of our notion of sympatric speciation in that it represents a behavioral rather than geographic barrier to the flow of genes among diverging groups within a population. The importance of behavioral separation as a mechanism for promoting sympatric speciation in a heterogeneous or patchwork landscape is highlighted in John Maynard Smith's seminal paper on sympatric speciation. In recognition of the importance of this behavioral versus geographic distinction, Wayne Getz and Veijo Kaitala introduced the term heteropatry in their extension of Maynard Smiths' analysis of conditions that facilitate sympatric speciation.

Although some evolutionary biologists still regard sympatric speciation as a highly contentious issue, both theoretical and empirical studies increasingly support sympatric speciation as a likely process in explaining the diversity of life in particular ecosystems. Arguments either implicitly or explicitly implicate competition and niche separation of sympatrically co-occurring ecological variants that through assortative mating ultimately evolve into separate races and then species. Assortative mating most easily occurs if mating is linked to niche preference, as occurs in the apple maggot *Rhagoletis pomonella* where individual flies from different races use volatile odors to discriminate between hawthorn and apple and look for mates on natal fruit.

In essence, the term heteropatry semantically resolves the issue of sympatric speciation by reducing it to a scaling issue in terms of the way the landscape is used by individuals versus populations. Specifically, from a population perspective, the process looks sympatric, but from an individual’s perspective, the process looks allopatric, once the time spent flying over or moving quickly through intervening non-preferred niches is taken into account.

Parapatric speciation



Comparison of allopatric, peripatric, parapatric and sympatric speciation.

Parapatric and **parapatry** are terms from biogeography, referring to organisms whose ranges do not significantly overlap but are immediately adjacent to each other; they only occur together in the narrow contact zone, if at all. Such organisms are usually closely related (e.g. sister species), their distribution being the result of **parapatric speciation**.

Parapatric speciation is a form of speciation that occurs due to variations in the mating habits of a population within a continuous geographical area. In this model, the parent species lives in a continuous habitat, in contrast with allopatric speciation and peripatric speciation where subpopulations become geographically isolated. Niches in this habitat can differ along an environmental gradient, hampering gene flow, and thus creating a cline. In parapatric speciation there is no specific extrinsic barrier to gene flow. The population is continuous, but nonetheless, the population does not mate randomly. Individuals are more likely to mate with their geographic neighbors than with individuals in a different part of the population's range. In this mode, divergence may happen because of reduced gene flow within the population and varying selection pressures across the population's range.

An example of this is the grass *Anthoxanthum*, which has been known to undergo parapatric speciation in such cases as mine contamination of an area. This creates a selection pressure for tolerance to those metals. Flowering time generally changes (tending toward character displacement—strong selection against interbreeding—as the hybrids are generally ill-suited to the environment) and often plants will become self-pollinating.

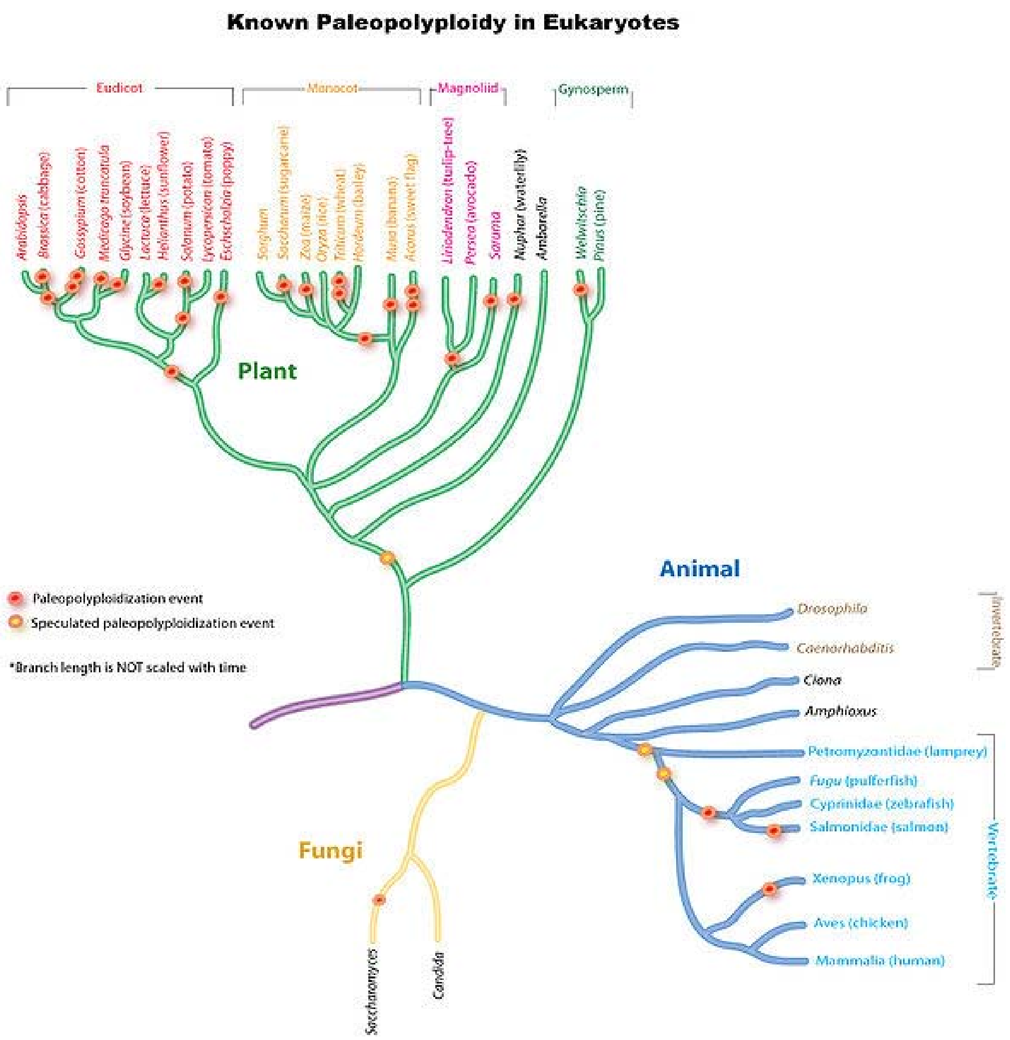
Similarly, a recent study provided evidence for parapatric speciation in Tennessee cave salamanders, involving divergence with gene flow between cave and surface populations.

Another example are ring species.

Chapter- 5

Polyploidy

Polyploidy occurs in cells and organisms when there are more than two paired (homologous) sets of chromosomes.



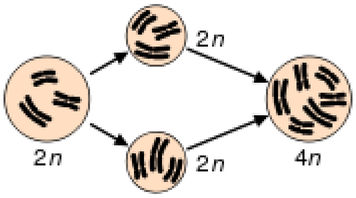
Known paleopolyploidy in eukaryotes

Most organisms are normally diploid, meaning they have two sets of chromosomes — one set inherited from each parent. Polyploidy may occur due to abnormal cell division during metaphase I in meiosis. It is most commonly found in plants. (Haploidy may also occur as a normal stage in an organism's life. A haploid has only one set of chromosomes.)

Polyploidy occurs in some animals, such as goldfish, salmon, and salamanders, but is especially common among ferns and flowering plants, including both wild and cultivated species. Wheat, for example, after millennia of hybridization and modification by humans, has strains that are **diploid** (two sets of chromosomes), **tetraploid** (four sets of chromosomes) with the common name of durum or macaroni wheat, and **hexaploid** (six sets of chromosomes) with the common name of bread wheat. Many agriculturally important plants of the genus *Brassica* are also tetraploids; their relationship is described by the Triangle of U.

Polyploidy also occurs normally in some animal tissues, such as human muscle tissues. This is known as endopolyploidy.

The occurrence of polyploidy is a mechanism of speciation and is known to have resulted in new species of the plant Salsify *(Tragopogon)*.



Speciation via polyploidy: A diploid cell undergoes failed meiosis, producing diploid gametes, which self-fertilize to produce a tetraploid zygote.

Polyploidy can be induced in plants and cell cultures by some chemicals: the best known is colchicine, which can result in chromosome doubling, though its use may have other less obvious consequences as well. Oryzalin also will double the existing chromosome content.

Polyploid types

Polyploid types are labeled according to the number of chromosome sets in the nucleus:

- **triploid** (three sets; 3x), for example seedless watermelons, common in the phylum Tardigrada
- **tetraploid** (four sets; 4x), for example Salmonidae fish
- **pentaploid** (five sets; 5x), for example Kenai Birch (*Betula papyrifera* var. *kenaica*)

- **hexaploid** (six sets; 6x), for example wheat, kiwifruit
- **octaploid** (eight sets; 8x), for example *Acipenser* (genus of sturgeon fish)
- **decaploid** (ten sets; 10x), for example certain strawberries
- **dodecaploid** (twelve sets; 12x), for example the plant *Celosia argentea* and the amphibian *Xenopus ruwenzoriensis*

Polyploidy in animals (non-human)

Examples in animals are more common in the 'lower' forms such as flatworms, leeches, and brine shrimp. Polyploid animals are often sterile, so they often reproduce by parthenogenesis. Polyploid lizards are also quite common and parthenogenetic. Polyploid mole salamanders (mostly triploids) are all female and reproduce by kleptogenesis, "stealing" spermatophores from diploid males of related species to trigger egg development but not incorporating the males' DNA into the offspring. While mammalian liver cells are polyploid, rare instances of polyploid mammals are known, but most often result in prenatal death.

One of the few known exceptions to this 'rule' is an octodontid rodent of Argentina's harsh desert regions, known as the Plains Viscacha-Rat (*Tympanoctomys barrerae*). This rodent is not a rat, but kin to guinea pigs and chinchillas. Its "new" diploid [2n] number is 102 and so its cells are roughly twice normal size. Its closest living relation is *Octomys mimax*, the Andean Viscacha-Rat of the same family, whose 2n = 56. It is surmised that an *Octomys*-like ancestor produced tetraploid (i.e., 4n = 112) offspring that were, by virtue of their doubled chromosomes, reproductively isolated from their parents; but that these likely survived the ordinarily catastrophic effects of polyploidy in mammals by shedding (via translocation or some similar mechanism) the "extra" set of sex chromosomes gained at this doubling. (The closely related Golden Vizcacha Rat, 2n = 96, is thought to have arisen via roughly the same process).

Polyploidy in humans

True polyploidy rarely occurs in humans, although it occurs in some tissues (especially in the liver). Polyploidy refers to a numerical change in a whole set of chromosomes. Organisms in which a particular chromosome, or chromosome segment, is under- or overrepresented are said to be aneuploid (from the Greek words meaning "not," "good," and "fold"). Therefore the distinction between aneuploidy and polyploidy is that aneuploidy refers to a numerical change in part of the chromosome set, whereas polyploidy refers to a numerical change in the whole set of chromosomes.

Polyploidy occurs in humans in the form of triploidy (69,XXX) and tetraploidy (92,XXXX), not to be confused with 47,XXX or 48,XXXX aneuploidy . Triploidy, usually due to polyspermy, occurs in about 2–3% of all human pregnancies and ~15% of miscarriages. The vast majority of triploid conceptions end as miscarriage and those that do survive to term typically die shortly after birth. In some cases survival past birth may occur longer if there is mixoploidy with both a diploid and a triploid cell population present.

Triploidy may be the result of either digyny (the extra haploid set is from the mother) or diandry (the extra haploid set is from the father). Diandry is mostly caused by reduplication of the paternal haploid set from a single sperm, but may also be the consequence of dispermic (two sperm) fertilization of the egg. Digyny is most commonly caused by either failure of one meiotic division during oogenesis leading to a diploid oocyte or failure to extrude one polar body from the oocyte. Diandry appears to predominate among early miscarriages while digyny predominates among triploidy that survives into the fetal period. However, among early miscarriages, digyny is also more common in those cases <8.5 weeks gestational age or those in which an embryo is present. There are also two distinct phenotypes in triploid placentas and fetuses that are dependent on the origin of the extra haploid set. In digyny there is typically an asymmetric poorly grown fetus, with marked adrenal hypoplasia and a very small placenta. In diandry, a partial hydatidiform mole develops. These parent-of-origin effects reflect the effects of genomic imprinting.

Complete tetraploidy is more rarely diagnosed than triploidy, but is observed in 1–2% of early miscarriages. However, some tetraploid cells are commonly found in chromosome analysis at prenatal diagnosis and these are generally considered 'harmless'. It is not clear whether these tetraploid cells simply tend to arise during *in vitro* cell culture or whether they are also present in placental cells *in vivo*. There are, at any rate, very few clinical reports of fetuses/infants diagnosed with tetraploidy mosaicism.

Mixoploidy is quite commonly observed in human preimplantation embryos and includes haploid/diploid as well as diploid/tetraploid mixed cell populations. It is unknown whether these embryos fail to implant and are therefore rarely detected in ongoing pregnancies or if there is simply a selective process favoring the diploid cells.

Polyploidy in plants

Polyploidy is pervasive in plants and some estimates suggest that 30–80% of living plant species are polyploid, and many lineages show evidence of ancient polyploidy (paleopolyploidy) in their genomes. Huge explosions in angiosperm species diversity appear to have coincided with the timing of ancient genome duplications shared by many species. It has been established that 15% of angiosperm and 31% of fern speciation events are accompanied by ploidy increase. Polyploid plants can arise spontaneously in nature by several mechanisms, including meiotic or mitotic failures, and fusion of unreduced (2n) gametes. Both autopolyploids (e.g. potato) and allopolyploids (e.g. canola, wheat, cotton) can be found among both wild and domesticated plant species. Most polyploids display heterosis relative to their parental species, and may display novel variation or morphologies that may contribute to the processes of speciation and eco-niche exploitation. The mechanisms leading to novel variation in newly formed allopolyploids may include gene dosage effects (resulting from more numerous copies of genome content), the reunion of divergent gene regulatory hierarchies, chromosomal rearrangements, and epigenetic remodeling, all of which affect gene content and/or expression levels. Many of these rapid changes may contribute to reproductive isolation and speciation.

Lomatia tasmanica is an extremely rare Tasmanian shrub which is triploid and sterile, and reproduction is entirely vegetative with all plants having the same genetic structure.

There are few naturally occurring polyploid conifers. One example is the giant tree *Sequoia sempervirens* or Coast Redwood which is a hexaploid (6x) with 66 chromosomes (2n = 6x = 66), although the origin is unclear.

Polyploid crops

Polyploid plants tend to be larger and better at flourishing in early succession habitats such as farm fields. In the breeding of crops, the tallest and best thriving plants are selected for. Thus, many crops (and agricultural weeds) may have unintentionally been bred to a higher level of ploidy.

The induction of polyploidy is a common technique to overcome the sterility of a hybrid species during plant breeding. For example, Triticale is the hybrid of wheat (*Triticum turgidum*) and rye (*Secale cereale*). It combines sought-after characteristics of the parents, but the initial hybrids are sterile. After polyploidization, the hybrid becomes fertile and can thus be further propagated to become triticale.

In some situations polyploid crops are preferred because they are sterile. For example many seedless fruit varieties are seedless as a result of polyploidy. Such crops are propagated using asexual techniques such as grafting.

Polyploidy in crop plants is most commonly induced by treating seeds with the chemical colchicine.

Examples of polyploid crops

- Triploid crops: apple, banana, citrus, ginger, watermelon
- Tetraploid crops: apple, durum or macaroni wheat, cotton, potato, cabbage, leek, tobacco, peanut, kinnow, Pelargonium
- Hexaploid crops: chrysanthemum, bread wheat, triticale, oat, kiwifruit
- Octaploid crops: strawberry, dahlia, pansies, sugar cane

Some crops are found in a variety of ploidies: tulips and lilies are commonly found as both diploid and as triploid; daylilies (Hemerocallis cultivars) are available as either diploid or tetraploid; apples and kinnows can be diploid, triploid, or tetraploid.

Terminology

Autopolyploidy

Autopolyploids are polyploids with multiple chromosome sets derived from a single species. Autopolyploids can arise from a spontaneous, naturally occurring genome doubling, like the potato. Others might form following fusion of 2n gametes (unreduced gametes). Bananas and apples can be found as autotriploids. Autopolyploid plants typically display polysomic inheritance, and are therefore often infertile and propagated clonally perfect.

Allopolyploidy

Allopolyploids are polyploids with chromosomes derived from different species. Precisely it is the result of doubling of chromosome number in an F1 hybrid. *Triticale* is an example of an allopolyploid, having six chromosome sets, allohexaploid, four from wheat (*Triticum turgidum*) and two from rye (*Secale cereale*). *Amphidiploid* is another word for an allopolyploid. Some of the best examples of allopolyploids come from the Brassicas, and the Triangle of U describes the relationships among the three common diploid Brassicas (*B. oleracea, B. rapa,* and *B. nigra*) and three allotetraploids (*B. napus, B. juncea,* and *B. carinata*) derived from hybridization among the diploids.

Paleopolyploidy

Ancient genome duplications probably occurred in the evolutionary history of all life. Duplication events that occurred long ago in the history of various evolutionary lineages can be difficult to detect because of subsequent diploidization (such that a polyploid starts to behave cytogenetically as a diploid over time) as mutations and gene translations gradually make one copy of each chromosome unlike its other copy.

In many cases, these events can be inferred only through comparing sequenced genomes. Examples of unexpected but recently confirmed ancient genome duplications include baker's yeast (*Saccharomyces cerevisiae*), mustard weed/thale cress (*Arabidopsis thaliana*), rice (*Oryza sativa*), and an early evolutionary ancestor of the vertebrates (which includes the human lineage) and another near the origin of the teleost fishes. Angiosperms (flowering plants) have paleopolyploidy in their ancestry. All eukaryotes probably have experienced a polyploidy event at some point in their evolutionary history.

Karyotype

A karyotype is the characteristic chromosome complement of a eukaryote species. The preparation and study of karyotypes is part of cytology and, more specifically, cytogenetics.

Although the replication and transcription of DNA is highly standardized in eukaryotes, the same cannot be said for their karotypes, which are highly variable between species in chromosome number and in detailed organization despite being constructed out of the same macromolecules. In some cases there is even significant variation within species. This variation provides the basis for a range of studies in what might be called evolutionary cytology.

Paralogous

The term is used to describe the relationship among duplicated genes or portions of chromosomes that derived from a common ancestral DNA. Paralogous segments of DNA may arise spontaneously by errors during DNA replication, copy and paste transposons, or whole genome duplications.

Homologous

The term is used to describe the relationship of similar chromosomes that pair at mitosis and meiosis. In a diploid, one homolog is derived from the male parent (sperm) and one is derived from the female parent (egg). During meiosis and gametogenesis, homologous chromosomes pair and exchange genetic material by recombination, leading to the production of sperm or eggs with chromosome haplotypes containing novel genetic variation.

Homoeologous

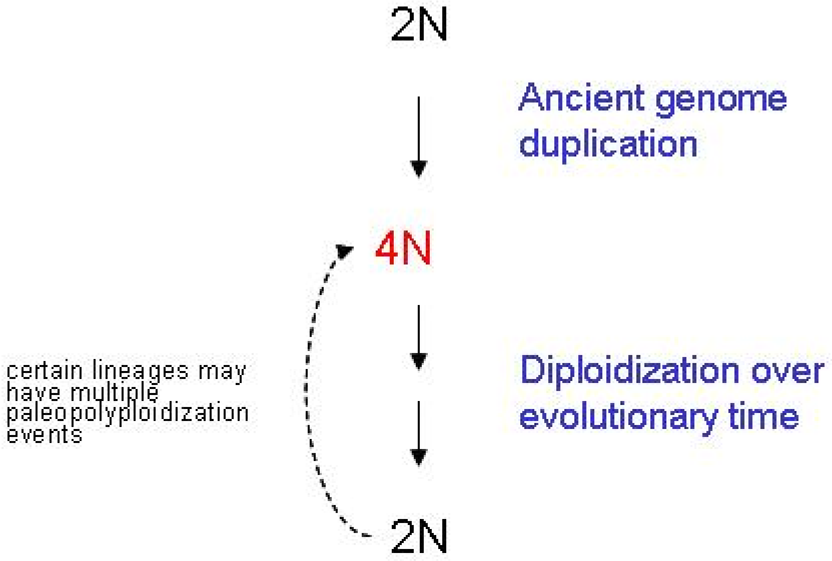
The term *homoeologous*, also spelled *homeologous*, is used to describe the relationship of similar chromosomes or parts of chromosomes brought together following inter-species hybridization and allopolyploidization, and whose relationship was completely homologous in an ancestral species. In allopolyploids, the homologous chromosomes within each parental sub-genome should pair faithfully during meiosis, leading to disomic inheritance; however in some allopolyploids, the homoeologous chromosomes of the parental genomes may be nearly as similar to one another as the homologous chromosomes, leading to tetrasomic inheritance (four chromosomes pairing at meiosis), intergenomic recombination, and reduced fertility.

Example of homoeologous chromosomes

Durum wheat is the result of the inter-species hybridization of two diploid grass species *Triticum urartu* and *Aegilops speltoides*. Both the diploid ancestors had two sets of 7 chromosomes, which were similar in terms of size and genes contained on them. Durum wheat contains two sets of chromosomes derived from *Triticum urartu* and two sets of chromosomes derived from *Aegilops speltoides*. Each chromosome pair derived from the *Triticum urartu* parent is **homoeologous** to the opposite chromosome pair derived from the *Aegilops speltoides* parent, though each chromosome pair unto itself is **homologous**.

Chapter- 6

Paleopolyploidy

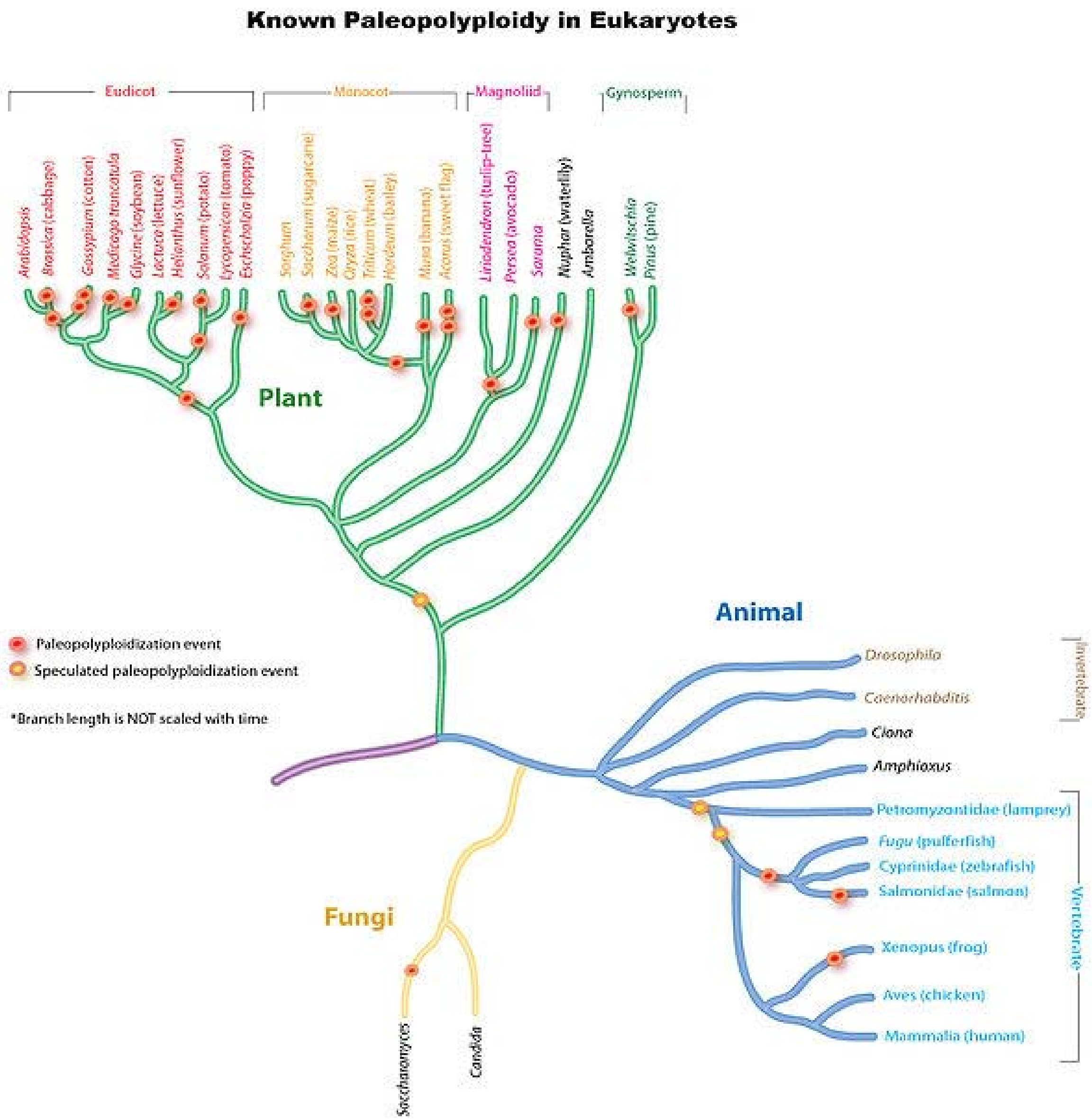


Overview of Paleopolyploidy Process. Many higher eukaryotes were paleopolyploids at some point during their evolutionary history.

Paleopolyploidy refers to ancient genome duplications which occurred at least several million years ago (mya). The genome doubling event could either be an autopolyploidy or an allopolyploidy. Due to functional redundancy, genes are rapidly silenced and/or lost from the duplicated genomes. Most paleopolyploids, through evolutionary time, have lost their *polyploid* status through a process called **diploidization**, and are currently referred to as "diploids" (e.g. baker's yeast, *Arabidopsis*, and perhaps humans).

Paleopolyploidy is extensively studied in plant lineages. It has been found that almost all flowering plants have undergone at least one round of genome duplication at some point during their evolutionary history. Ancient genome duplications are also found in the early ancestor of vertebrates (which includes the human lineage) and another near the origin of the bony fishes. Interestingly, evidence suggests that baker's yeast (*Saccharomyces* *cerevisiae*), which has a compact genome, experienced polyploidization during its evolutionary history.

Eukaryotes



A diagram that summarizes all well-known paleoploidization events.

Ancient genome duplications are widespread throughout eukaryotic lineages, particularly in plants. Almost all important cereal crops are paleopolyploids. Studies suggest that the common ancestor of Poaceae, the grass family, had a genome duplication 50–70 mya. Subsequent genome doublings occurred in maize, and twice in wheat. A duplication which is shared by all eudicots occurred 50-70 mya, and perhaps an earlier duplication affected the ancestor of all the world's flowering plants over 200 mya.

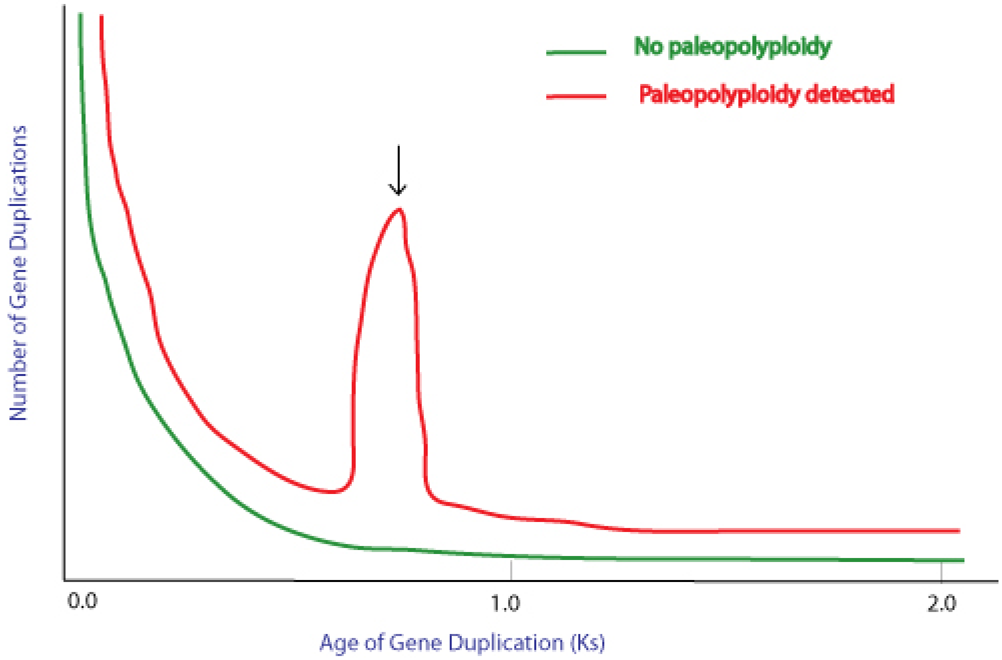
Furthermore, *Arabidopsis thaliana*, which has a small genome for a plant, experienced at least two rounds of paleopolyploidy. The most recent event took place before the divergence of the *Arabidopsis* and *Brassica* lineages, 25–40 mya.

Compared with plants, paleopolyploidy is much rarer in the animal kingdom. It is identified mainly in the amphibians and bony fishes. Although some studies suggested one (some say two) common genome duplications are shared by all vertebrates (including humans), the evidence is not as strong as in the other cases, and it is still under debate. However, many researchers are interested in the reasons why animal lineages had fewer paleopolyploidization events than did plants.

Lastly, a well-supported paleopolyploidy has been found in baker's yeast (*Saccharomyces cerevisiae*), despite its small, compact genome (~13Mbp) after the divergence from *K. waltii*. Through genome streamlining, yeast has lost 90% of the duplicated genome over evolutionary time and is now recognized as a diploid organism.

Detection method

Duplicated genes can be identified through sequence homology on the DNA or protein level. Paleopolyploidy can be identified as massive gene duplication at one time using a molecular clock. To distinguish between whole-genome duplication and a collection of single gene duplication (which is a common phenomenon in the genome) events, the following rules are often applied:



Detection of Paleopolyploidy using Ks.

1. Duplicated genes are located in large duplicated blocks. Single gene duplication is a random process and tends to make duplicated genes scattered throughout the genome.
2. Duplicated blocks are non-overlapping because they were created simultaneously. **Segmental duplication** within the genome can fulfill Rule #1; but multiple independent segmental duplications could overlap each other.

In theory, the two duplicated genes should have the same "age"; that is, the divergence of the sequence should be equal between the two genes duplicated by paleopolyploidy (**homeologs**). Synonymous substitution rate, **Ks**, is often used as a molecular clock to determine the time of gene duplication. Thus, paleopolyploidy is identified as a "peak" on the duplicate number vs. Ks graph (shown on the right).

Duplication events that occurred a long time ago in the history of various evolutionary lineages can be difficult to detect because of subsequent diploidization (such that a polyploid starts to behave cytogenetically as a diploid over time) as mutations and gene translations gradually make one copy of each chromosome unlike its counterpart. This usually results in a low confidence for identifying a very ancient paleopolyploidy.

Evolutionary importance

Paleopolyploidization events lead to massive cellular changes, including doubling of the genetic material, changes in gene expression and increased cell size. Gene loss during diploidization is not completely random, but heavily selected. Genes from large gene families are duplicated. On the other hand, individual genes are not duplicated. Overall, paleopolyploidy can have both short-term and long-term evolutionary effects on an organism's fitness in the natural environment.

- Genome Diversity

  genome doubling provided the organism with redundant alleles that can evolve freely with little selection pressure. The duplicated genes can undergo **neofunctionalization** or **subfunctionalization** which could help the organism adapt to the new environment or survive different stress conditions.

- Heterosis

  polyploids often have larger cell sizes and even larger organs. Many important crops, including wheat, maize and cotton, are paleopolyploids which were selected for domestication by ancient peoples.

- Speciation

  It has been suggested that many polyploidization events created new species, via a gain of adaptive traits, or by sexual incompatibility with their diploid counterparts. An example would be the recent speciation of allopolyploid Spartina

— S. anglica; the polyploid plant is so successful that it is listed as invasive species in many regions.

Human as paleopolyploid

The hypothesis of human paleopolyploidy originated as early as the 1970s, proposed by the biologist Susumu Ohno. He reasoned that the vertebrate genome could not achieve its complexity without large scale whole-genome duplications. The "two rounds of genome duplication" hypothesis (2R hypothesis) came about, and gained in popularity, especially among developmental biologists.

However, the 2R hypothesis has been questioned by many researchers. Based on the theory, the human genome should have a 4:1 gene ratio compared with invertebrate genomes. This did not appear to be supported by findings from various genome projects – the human genome consists of ~35,000 genes while an average invertebrate genome size is about 15,000 genes. However, the recent completion of the amphioxus genome sequence has revealed the presence of a 4:1 ratio of genes, as predicted by the hypothesis. Additional arguments against 2R were based on the lack of the (AB)(CD) tree topology amongst four members of a gene family in vertebrates. However, if the two genome duplications occurred close together, we would not expect to find this topology.

These recent findings have largely supported the 2R hypothesis.

Chapter- 7

Hybrid

In biology and specifically genetics, **hybrid** has several meanings, all referring to the offspring of sexual reproduction.

1. In general usage, **hybrid** is synonymous with heterozygous: any offspring resulting from the mating of two distinctly homozygous individuals
2. a **genetic hybrid** carries two different alleles of the same gene
3. a **structural hybrid** results from the fusion of gametes that have differing structure in at least one chromosome, as a result of structural abnormalities
4. a **numerical hybrid** results from the fusion of gametes having different haploid numbers of chromosomes
5. a **permanent hybrid** is a situation where only the heterozygous genotype occurs, because all homozygous combinations are lethal.

From a taxonomic perspective, hybrid refers to offspring resulting from the interbreeding between two animals or plants of different taxa.

1. Hybrids between different subspecies within a species (such as between the Bengal tiger and Siberian tiger) are known as **intra-specific** hybrids. Hybrids between different species within the same genus (such as between lions and tigers) are sometimes known as **interspecific** hybrids or crosses. Hybrids between different genera (such as between sheep and goats) are known as **intergeneric** hybrids. Extremely rare **interfamilial** hybrids have been known to occur (such as the guineafowl hybrids). No **interordinal** (between different orders) animal hybrids are known.
2. The second type of hybrid consists of crosses between populations, breeds or cultivars within a single species. This meaning is often used in plant and animal breeding, where hybrids are commonly produced and selected because they have desirable characteristics not found or inconsistently present in the parent individuals or populations. This flow of genetic material between populations or races is often called hybridization.

Etymology

According to the Oxford English Dictionary, the word is derived from Latin *hyba* , meaning the "offspring of a tame sow and a wild boar", "child of a freeman and slave", etc. The term entered into popular use in English in the 19th century, though examples of its use have been found from the early 17th century.

Types of hybrids

Depending on the parents, there are a number of different types of hybrids;

- **Single cross hybrids** — result from the cross between two true breeding organisms and produces an F1 generation called an F1 hybrid (F1 is short for Filial 1, meaning "first offspring"). The cross between two different homozygous lines produces an F1 hybrid that is heterozygous; having two alleles, one contributed by each parent and typically one is dominant and the other recessive. The F1 generation is also phenotypically homogeneous, producing offspring that are all similar to each other.
- **Double cross hybrids** — result from the cross between two different F1 hybrids.
- **Three-way cross hybrids** — result from the cross between one parent that is an F1 hybrid and the other is from an inbred line.
- **Triple cross hybrids** — result from the crossing of two different three-way cross hybrids.
- **Population hybrids** — result from the crossing of plants or animals in a population with another population. These include crosses between organisms such as interspecific hybrids or crosses between different races.

Interspecific hybrids

Interspecific hybrids are bred by mating two species, normally from within the same genus. The offspring display traits and characteristics of both parents. The offspring of an interspecific cross are very often sterile; thus, hybrid sterility prevents the movement of genes from one species to the other, keeping both species distinct. Sterility is often attributed to the different number of chromosomes the two species have, for example donkeys have 62 chromosomes, while horses have 64 chromosomes, and mules and hinnies have 63 chromosomes. Mules, hinnies, and other normally sterile interspecific hybrids cannot produce viable gametes because the extra chromosome cannot make a homologous pair at meiosis, meiosis is disrupted, and viable sperm and eggs are not formed. However, fertility in female mules has been reported with a donkey as the father.

Most often other processes occurring in plants and animals keep gametic isolation and species distinction. Species often have different mating or courtship patterns or behaviors, the breeding seasons may be distinct and even if mating does occur antigenic reactions to the sperm of other species prevent fertilization or embryo development. The Lonicera fly is the first known animal species that resulted from natural hybridization. Until the discovery of the Lonicera fly, this process was known to occur in nature only among plants

While it is possible to predict the genetic composition of a backcross *on average*, it is not possible to accurately predict the composition of a particular backcrossed individual, due to random segregation of chromosomes. In a species with two pairs of chromosomes, a twice backcrossed individual would be predicted to contain 12.5% of one species' genome (say, species A). However, it may, in fact, still be a 50% hybrid if the chromosomes from species A were lucky in two successive segregations, and meiotic crossovers happened near the telomeres. The chance of this is fairly high: $(\frac{1}{2})^{(2\times2)} = \frac{1}{16}$(where the "two times two" comes about from two rounds of meiosis with two chromosomes); however, this probability declines markedly with chromosome number and so the actual composition of a hybrid will be increasingly closer to the predicted composition.

Hybrids are often named by the portmanteau method, combining the names of the two parent species. For example, a zeedonk is a cross between a zebra and a donkey. Since the traits of hybrid offspring often vary depending on which species was mother and which was father, it is traditional to use the father's species as the first half of the portmanteau. For example, a liger is a cross between a male lion and a female tiger, while a tiglon is a cross between a male tiger and a female lion.

Domestic and wild hybrids

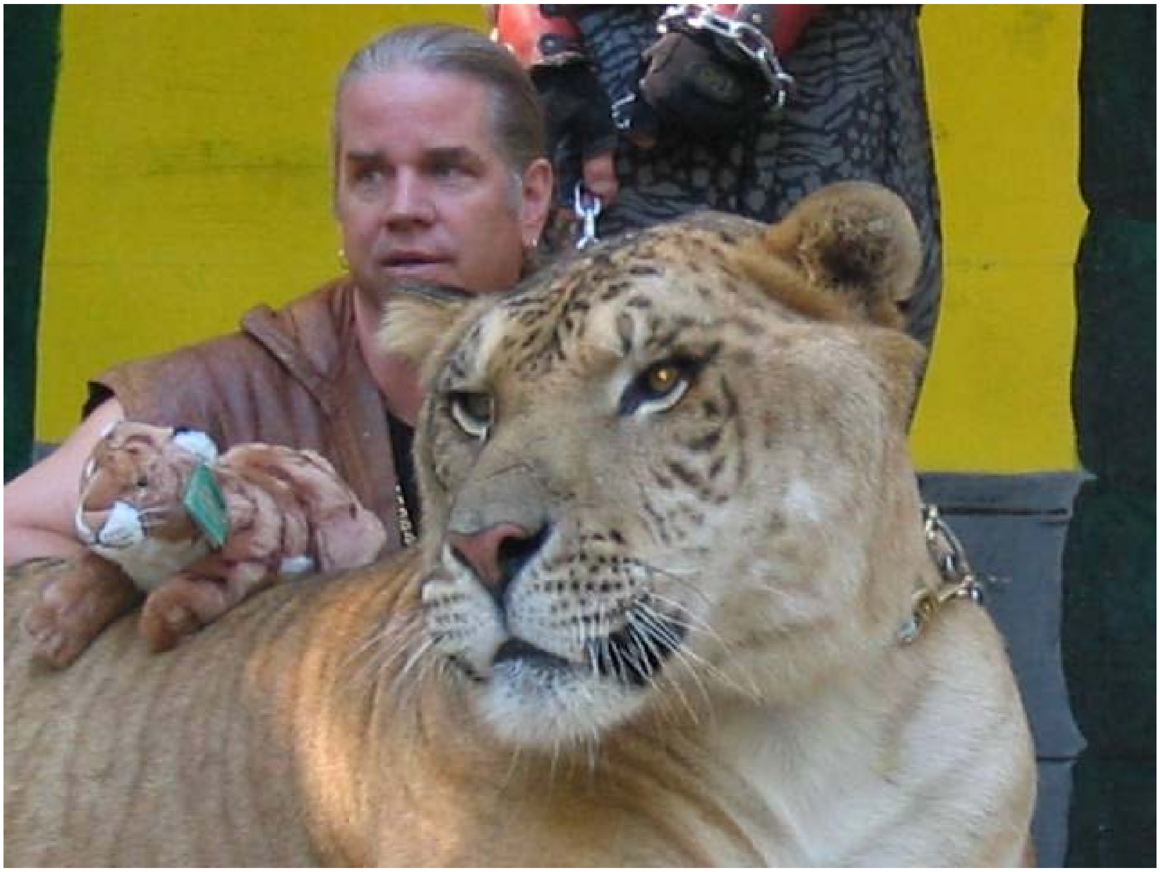
Hybrids between domesticated and wild animals in particular may be problematic. Breeders of domesticated species discourage crossbreeding with wild species, unless a deliberate decision is made to incorporate a trait of a wild ancestor back into a given breed or strain. Wild populations of animals and plants have evolved naturally over millions of years through a process of natural selection in contrast to human controlled selective breeding or artificial selection for desirable traits from the human point of view. Normally, these two methods of reproduction operate independently of one another. However, an intermediate form of selective breeding, wherein animals or plants are bred by humans, but with an eye to adaptation to natural region-specific conditions and an acceptance of natural selection to weed out undesirable traits, created many ancient domesticated breeds or types now known as landraces.

Many times, domesticated species live in or near areas which also still hold naturally evolved, region-specific wild ancestor species and subspecies. In some cases, a domesticated species of plant or animal may become feral, living wild. Other times, a wild species will come into an area inhabited by a domesticated species. Some of these situations lead to the creation of hybridized plants or animals, a cross between the native species and a domesticated one. This type of crossbreeding, termed genetic pollution by those who are concerned about preserving the genetic base of the wild species, has become a major concern. Hybridization is also a concern to the breeders of purebred species as well, particularly if the gene pool is small and if such crossbreeding or hybridization threatens the genetic base of the domesticated purebred population.

The concern with genetic pollution of a wild population is that hybridized animals and plants may not be as genetically strong as naturally evolved region specific wild ancestors wildlife which can survive without human husbandry and have high immunity to natural diseases. The concern of purebred breeders with wildlife hybridizing a domesticated species is that it can coarsen or degrade the specific qualities of a breed developed for a specific purpose, sometimes over many generations. Thus, both purebred breeders and wildlife biologists share a common interest in preventing accidental hybridization.

Examples of hybrid animals

A "Zeedonk", a zebra/donkey hybrid



A "Liger", a Lion/Tiger hybrid

A "Jaglion", a Jaguar/Lion hybrid

- Hybrid Iguana is single cross hybrid, result of natural inbreeding from male marine iguana and female land Iguana since late 2000s.
- Equid hybrids
  - Mule, a cross of female horse and a male donkey.

    - Hinny, a cross between a female donkey and a male horse. Mule and hinny are examples of reciprocal hybrids.
    - Zebroids
        - Zeedonk or Zonkey, a zebra/donkey cross.
        - Zorse, a zebra/horse cross
        - Zony or Zetland, a zebra/pony cross ("zony" is a generic term; "zetland" is specifically a hybrid of the Shetland pony breed with a zebra)
- Bovid hybrids
    - Dzo, zo or yakow; a cross between a domestic cow/bull and a yak.
    - Beefalo, a cross of an American bison and a domestic cow. This is a fertile breed; this along with genetic evidence has caused them to be recently reclassified into the same genus, *Bos*.
    - Zubron, a hybrid between wisent (European bison) and domestic cow.
- Sheep-goat hybrids, such as the Toast of Botswana.
- Ursid hybrids, such as the grizzly-polar bear hybrid, occur between black bears, brown bears, and polar bears.
- Felid hybrids
    - Savannah cats are the hybrid cross between an African serval cat and a domestic cat
    - A hybrid between a Bengal tiger and a Siberian tiger is an example of an **intra-specific** hybrid.
    - Ligers and Tiglons (crosses between a lion and a tiger) and other Panthera hybrids such as the lijagulep. Various other wild cat crosses are known involving the lynx, bobcat, leopard, serval, etc.
    - Bengal cat, a cross between the Asian leopard cat and the domestic cat, one of many hybrids between the domestic cat and wild cat species. The domestic cat, African wild cat and European wildcat may be considered variant populations of the same species (*Felis silvestris*), making such crosses non-hybrids.
- Fertile canid hybrids occur between coyotes, wolves, dingoes, jackals and domestic dogs.
- Hybrids between black and white rhinoceroses have been recognized.
- Hybrids between spotted owls and barred owls
- Cama, a cross between a camel and a llama, also an intergeneric hybrid.
- Wholphin, a fertile but very rare cross between a false killer whale and a bottlenose dolphin.
- A fertile cross between a king snake and an corn snake.
- At Chester Zoo in the United Kingdom, a cross between an African elephant (male) and an Asian elephant (female). The male calf was named Motty. It died of intestinal infection after twelve days.
- Cagebird breeders sometimes breed hybrids between species of finch, such as goldfinch x canary. These birds are known as mules.
- Gamebird hybrids, hybrids between gamebirds and domestic fowl, including chickens, guineafowl and peafowl, interfamilial hybrids.
- Numerous macaw hybrids are also known.

- Red kite x black kite: five bred unintentionally at a falconry center in England. (It is reported that the black kite (the male) refused female black kites but mated with two female red kites.)
- Hybridization between the endemic Cuban crocodile (*Crocodilus rhombifer*) and the widely distributed American crocodile (*Crocodilus acutus*) is causing conservation problems for the former species as a threat to its genetic integrity.
- Blood parrot cichlid, which is probably created by crossing a red head cihclid and a Midas cichlid or red devil cichlid
- The mulard duck, hybrid of the domestic pekin duck and domesticated muscovy ducks.

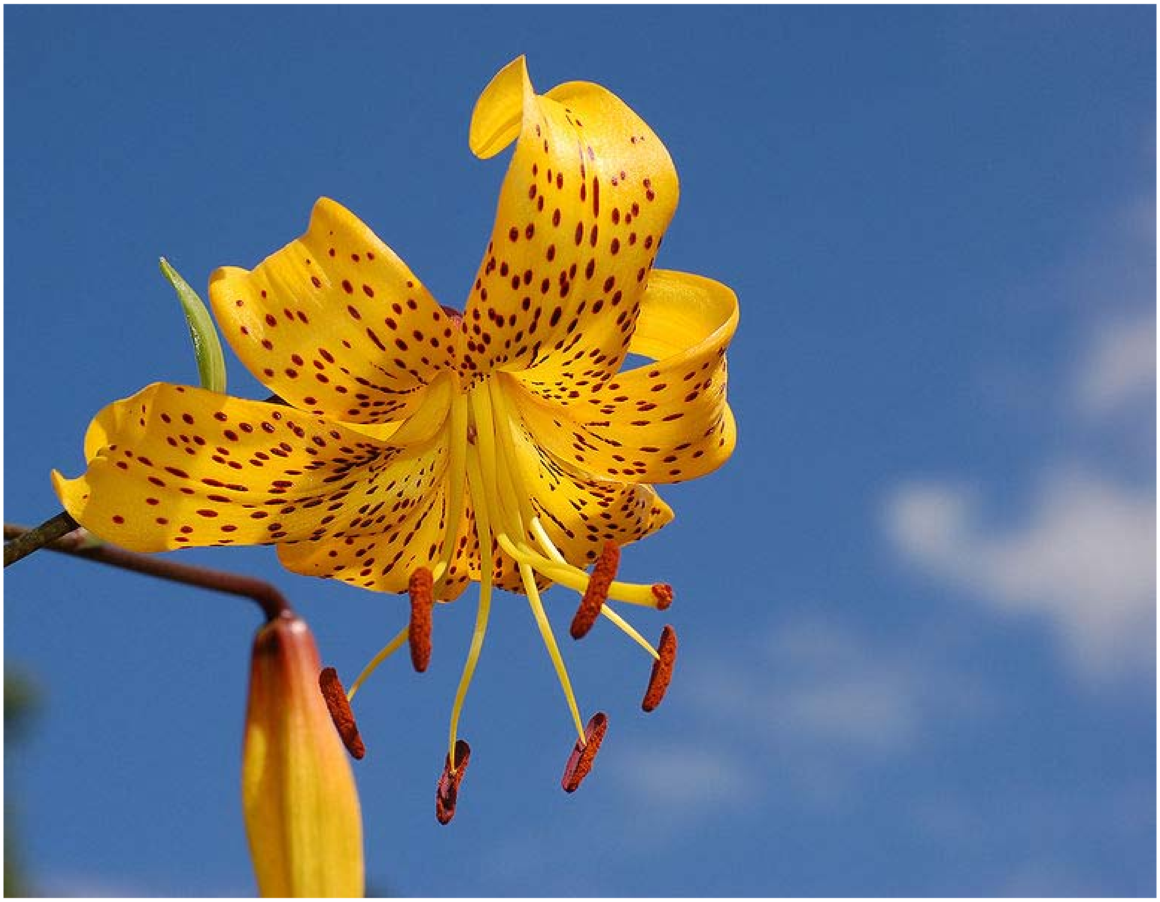
Hybrids should not be confused with genetic chimeras such as that between sheep and goat known as the geep. Wider interspecific hybrids can be made via in vitro fertilization or somatic hybridization, however the resulting cells are not able to develop into a full organism. An example of interspecific hybrid cell lines is humster (hamster x human) cells.

Hybrid plants

Plant species hybridize more readily than animal species, and the resulting hybrids are more often fertile hybrids and may reproduce, though there still exist sterile hybrids and selective hybrid elimination where the offspring are less able to survive and are thus eliminated before they can reproduce. A number of plant species are the result of hybridization and polyploidy with many plant species easily cross pollinating and producing viable seeds, the distinction between each species is often maintained by geographical isolation or differences in the flowering period. Since plants hybridize frequently without much work, they are often created by humans in order to produce improved plants. These improvements can include the production of more or improved; seeds, fruits or other plant parts for consumption, or to make a plant more winter or heat hardy or improve its growth and/or appearance for use in horticulture. Much work is now being done with hybrids to produce more disease resistant plants for both agricultural and horticultural crops. In many groups of plants hybridization has been used to produce larger and more showy flowers and new flower colors.

A sterile *Trillium* hybrid between *Trillium cernuum* and *Trillium grandiflorum*

Many plant genera and species have their origins in polyploidy. Autopolyploidy resulting from the sudden multiplication in the number of chromosomes in typical normal populations caused by unsuccessful separation of the chromosomes during meiosis. Tetraploids or plants with four sets of chromosomes are common in a number of different groups of plants and over time these plants can differentiate into distinct species from the normal diploid line. In *Oenothera lamarchiana* the diploid species has 14 chromosomes, this species has spontaneously given rise to plants with 28 chromosomes that have been given the name *Oenthera gigas*. Tetraploids can develop into a breeding population within the diploid population and when hybrids are formed with the diploid population the resulting offspring tend to be sterile triploids, thus effectively stopping the intermixing of genes between the two groups of plants (unless the diploids, in rare cases, produce unreduced gametes).



An ornamental lily hybrid known as *Lilium* 'Citronella'

Another form of polyploidy called allopolyploidy occurs when two different species mate and produce hybrids. Usually the typical chromosome number is doubled in successful allopolyploid species, with four sets of chromosomes the genotypes can sort out to form a complete diploid set from the parent species, thus they can produce fertile offspring that can mate and reproduce with each other but can not back-cross with the parent species. Allopolyploidy in plants often gives them a condition called hybrid vigour, which results in plants that are larger and stronger growing than either of the two parent species. Allopolyploids are often more aggressive growing and can be invaders of new habitats.

Sterility in a hybrid is often a result of chromosome number; if parents are of differing chromosome pair number, the offspring will have an odd number of chromosomes, leaving them unable to produce chromosomally balanced gametes. While this is a negative in a crop such as wheat, when growing a crop which produces no seeds would be pointless, it is an attractive attribute in some fruits. Bananas and seedless watermelon, for instance, are intentionally bred to be triploid, so that they will produce no seeds. Many hybrids are created by humans, but natural hybrids occur as well.

Heterosis

Hybrids are sometimes stronger than either parent variety, a phenomenon most common with plant hybrids, which when present is known as *hybrid vigor* (heterosis) or heterozygote advantage. A transgressive phenotype is a phenotype displaying more extreme characteristics than either of the parent lines. Plant breeders make use of a number of techniques to produce hybrids, including line breeding and the formation of complex hybrids. An economically important example is hybrid maize (corn), which provides a considerable seed yield advantage over open pollinated varieties. Hybrid seed dominates the commercial maize seed market in the United States, Canada and many other major maize producing countries.

Examples of species hybrids

Some plant hybrids include:

- Leyland cypress, [x *Cupressocyparis leylandii*] hybrid between Monterey Cypress and Nootka Cypress.
- Limequat, lime and kumquat hybrid.
- Loganberry, a hybrid between raspberry and blackberry.
- London plane, a hybrid between *Plantanus orientalis* Oriental plane and *Plantanus occidentalis* American plane (American sycamore). Thus forming [*Plantanus x acerfolia*]
- Peppermint, a hybrid between spearmint and water mint.
- Tangelo, a hybrid of a Mandarin orange and a pomelo which may have been developed in Asia about 3,500 years ago.
- Triticale, a wheat–rye hybrid.
- Wheat; most modern and ancient wheat breeds are themselves hybrids. Bread wheat is a hexaploid hybrid of three wild grasses; durum (pasta) wheat is a tetraploid hybrid of two wild grasses.
- Triangle of U: cabbage, mustard etc.
- Grapefruit, hybrid between a pomelo and the Jamaican sweet orange.

Some natural hybrids are:

- *Iris albicans*, a sterile hybrid which spreads by rhizome division
- Evening primrose, a flower which was the subject of famous experiments by Hugo de Vries on polyploidy and diploidy.

Some horticultural hybrids:

- *Dianthus x allwoodii*, is a hybrid between *Dianthus caryophyllus* × *Dianthus plumarius.* This is an "interspecific hybrid" or hybrid between two species in the same genus.
- *x Heucherella tiarelloides*, or *Heuchera sanguinea* × *Tiarella cordifolia* is an "intergeneric hybrid" a hybrid between two different genera.
- *Quercus x warei* [*Quercus robur* x *Quercus bicolor*] Kindred Spirit Hybrid Oak

Hybrids in nature

Hybridisation between two closely related species is actually a common occurrence in nature. Many hybrid zones are known where the ranges of two species meet, and hybrids are continually produced in great numbers. These hybrid zones are useful as biological model systems for studying the mechanisms of speciation (Hybrid speciation). Recently DNA analysis of a bear shot by a hunter in the North West Territories confirmed the existence of naturally-occurring and fertile grizzly–polar bear hybrids. There have been reports of similar supposed hybrids, but this is the first to be confirmed by DNA analysis. In 1943, Clara Helgason described a male bear shot by hunters during her childhood. It was large and off-white with hair all over its paws. The presence of hair on the bottom of the feet suggests it was a natural hybrid of Kodiak and Polar bear.

In some species, hybridisation plays an important role in evolutionary biology. While most hybrids are disadvantaged as a result of genetic incompatibility, the fittest survive, regardless of species boundaries. They may have a beneficial combination of traits allowing them to exploit new habitats or to succeed in a marginal habitat where the two parent species are disadvantaged. This has been seen in experiments on sunflower species. Unlike mutation, which affects only one gene, hybridisation creates multiple variations across genes or gene combinations simultaneously. Successful hybrids could evolve into new species within 50-60 generations. This leads some scientists to speculate that life is a genetic continuum rather than a series of self-contained species.

Where there are two closely related species living in the same area, less than 1 in 1000 individuals are likely to be hybrids because animals rarely choose a mate from a different species (otherwise species boundaries would completely break down). In some closely related species there are recognized "hybrid zones".

Some species of Heliconius butterflies exhibit dramatic geographical polymorphism of their wing patterns, which act as aposematic signals advertising their unpalatability to potential predators. Where different-looking geographical races abut, inter-racial hybrids are common, healthy and fertile. Heliconius hybrids can breed with other hybrid individuals and with individuals of either parental race. These hybrid backcrosses are disadvantaged by natural selection because they lack the parental form's warning coloration, and are therefore not avoided by predators.

A similar case in mammals is hybrid White-Tail/Mule Deer. The hybrids don't inherit either parent's escape strategy. White-tail Deer dash while Mule Deer bound. The hybrids are easier prey than the parent species.

In birds, healthy Galapagos Finch hybrids are relatively common, but their beaks are intermediate in shape and less efficient feeding tools than the specialised beaks of the parental species so they lose out in the competition for food. Following a major storm in 1983, the local habitat changed so that new types of plants began to flourish, and in this changed habitat, the hybrids had an advantage over the birds with specialised beaks - demonstrating the role of hybridization in exploiting new ecological niches. If the change in environmental conditions is permanent or is radical enough that the parental species cannot survive, the hybrids become the dominant form. Otherwise, the parental species will re-establish themselves when the environmental change is reversed, and hybrids will remain in the minority.

Natural hybrids may occur when a species is introduced into a new habitat. In Britain, there is hybridisation of native European Red Deer and introduced Chinese Sika Deer. Conservationists want to protect the Red Deer, but the environment favors the Sika Deer genes. There is a similar situation with White-headed Ducks and Ruddy Ducks.

Expression of parental traits in hybrids

When two distinct types of organisms breed with each other, the resulting hybrids typically have intermediate traits (e.g., one parent has red flowers, the other has white, and the hybrid, pink flowers). Commonly, hybrids also combine traits seen only separately in one parent or the other (e.g., a bird hybrid might combine the yellow head of one parent with the orange belly of the other). Most characteristics of the typical hybrid are of one of these two types, and so, in a strict sense, are not really new. However, an intermediate trait does differ from those seen in the parents (e.g., the pink flowers of the intermediate hybrid just mentioned are not seen in either of its parents). Likewise, combined traits are new when viewed as a combination.

In a hybrid, any trait that falls outside the range of parental variation is termed heterotic. Heterotic hybrids do have new traits, that is, they are not intermediate. *Positive heterosis* produces more robust hybrids, they might be stronger or bigger; while the term *negative heterosis* refers to weaker or smaller hybrids. Heterosis is common in both animal and plant hybrids. For example, hybrids between a lion and a tigress ("ligers") are much larger than either of the two progenitors, while a tigon (lioness × tiger) is smaller. Also the hybrids between the Common Pheasant (*Phasianus colchicus*) and domestic fowl (*Gallus gallus*) are larger than either of their parents, as are those produced between the Common Pheasant and hen Golden Pheasant (*Chrysolophus pictus*). Spurs are absent in hybrids of the former type, although present in both parents.

When populations hybridize, often the first generation (F_1) hybrids are very uniform. Typically, however, the individual members of subsequent hybrid generations are quite variable. High levels of variability in a natural population, then, are indicative of hybridity. Researchers use this fact to ascertain whether a population is of hybrid origin. Since such variability generally occurs only in later hybrid generations, the existence of variable hybrids is also an indication that the hybrids in question are fertile.

Genetic mixing and extinction

Regionally developed ecotypes can be threatened with extinction when new alleles or genes are introduced that alter that ecotype. This is sometimes called genetic mixing. Hybridization and introgression of new genetic material can lead to the replacement of local genotypes if the hybrids are more fit and have breeding advantages over the indigenous ecotype or species. These hybridization events can result from the introduction of non native genotypes by humans or through habitat modification, bringing previously isolated species into contact. Genetic mixing can be especially detrimental for rare species in isolated habitats, ultimately affecting the population to such a degree that none of the originally genetically distinct population remains.

Effect on biodiversity and food security

In agriculture and animal husbandry, the Green Revolution's use of conventional hybridization increased yields by breeding "high-yielding varieties". The replacement of locally indigenous breeds, compounded with unintentional cross-pollination and crossbreeding (genetic mixing), has reduced the gene pools of various wild and indigenous breeds resulting in the loss of genetic diversity. Since the indigenous breeds are often well-adapted to local extremes in climate and have immunity to local pathogens this can be a significant genetic erosion of the gene pool for future breeding. Therefore, commercial plant geneticists strive to breed "widely adapted" cultivars to counteract this tendency.

Limiting factors

A number of conditions exist that limit the success of hybridization, the most obvious is great genetic diversity between most species. But in animals and plants that are more closely related hybridization barriers can include morphological differences, differing times of fertility, mating behaviors and cues, physiological rejection of sperm cells or the developing embryo.

In plants, barriers to hybridization include blooming period differences, different pollinator vectors, inhibition of pollen tube growth, somatoplastic sterility, cytoplasmic-genic male sterility and structural differences of the chromosomes.

Mythical and legendary hybrids

Ancient folktales often contain mythological creatures, sometimes these are described as hybrids (e.g., Hippogriff as the offspring of a griffin and a horse, and the Minotaur which is the offspring of Pasiphaë and a white bull. More often they are kind of chimera, i.e., a composite of the physical attributes of two or more kinds of animals, mythical beasts, and often humans, with no suggestion that they are the result of interbreeding, e.g., Harpies, mermaids, and centaurs.

Bird hybrid

A **bird hybrid** is a bird that has two different species as parents. The resulting bird can present with any combination of characters from the parent species, from totally identical to completely different. Usually, the bird hybrid shows intermediate characteristics between the two species. A “successful” hybrid is one demonstrated to produce fertile offspring.

A Catalina Macaw - a Blue-and-yellow Macaw x Scarlet Macaw hybrid.

Recognition

The description of bird hybrids results from observations in nature combined with those obtained in captivity such as in zoos per example.

Canid hybrid

Canid hybrids are the result of interbreeding between different species of the canine (dog) family (Canidae)

Genetic considerations

Members of the dog genus *Canis*: wolves, dogs (both common dogs and dingoes), coyotes, and golden jackals cannot interbreed with members of the wider dog family: the Canidae, such as South American canids, foxes, African Wild dogs, bat-eared foxes, or raccoon dogs; or if they could, their offspring would be infertile.

Members of the genus *Canis* species can, however, all interbreed to produce fertile offspring, with two exceptions:the side-striped jackal and black-backed jackal. Although these two could theoretically interbreed with each other to produce fertile offspring, they cannot hybridize successfully with the rest of the genus *Canis*.

The reason for this lies in their genetics. The wolf, dingo, dog, coyote, and golden jackal diverged relatively recently, around 3 to 4 million years ago, and all have 78 chromosomes arranged in 39 pairs. This allows them to hybridize freely (barring size or behavioral constraints) and produce fertile offspring. The side-striped jackal and black-backed jackal both have 74 chromosomes. Other members of the Canidae diverged 7 to 10 million years ago and are less closely related and cannot hybridize with the wolf-like canids: , the red fox has 38 chromosomes, the raccoon dog has 42 chromosomes, and the fennec fox has 64 chromosomes, and the African Wild Dog has 78 chromosomes.

Legal implications of hybrids

Dog hybrids kept as pets are prohibited in certain jurisdictions, or are classed as wild animals and must be housed in the same way as purebred wolves. For example, hybrids of the domestic dog with the wolf, coyote, dingo, jackal, fox, dhole, African Wild Dog, or Raccoon dog are prohibited in the State of Hawaii.

Wolf-dog hybrid

The domestic dog (*Canis lupus familiaris*) is a domesticated form of the Grey Wolf (*Canis lupus lupus*), and therefore belongs to the same species as other wolves such as the Dingo (*Canis lupus dingo*). Therefore crosses between these sub-species are unremarkable, and not a hybridization in the same sense as an interbreeding between different species of *Canidae*.

People wanting to improve domestic dogs or create an exotic pet may breed domestic dogs to wolves. Grey wolves have been crossed with dogs that have a wolf-like appearance, such as Siberian Huskies, and Alaskan Malamutes. The breeding of wolf-dog crosses is controversial, with opponents purporting that it produces an animal unfit as a domestic pet. There are a number of established wolfdog breeds in development. The first generation crosses (one wolf parent, one dog parent) are generally back crossed to domestic dogs to maintain a domestic temperament and consistent conformation. First generation wolf-dog crosses are popular in the USA, but retain many wolf-like traits.

Dingo hybrids

A "dingo" with an unusual colour pattern

The Dingo (*Canis lupus dingo*) breeds freely with other domestic dogs. This is now so widespread that in some areas dingoes are now mostly mixed-breed dogs, crossed in recent times with dogs from other parts of the world. However, DNA study shows that "the dingo originates from domesticated dogs, originally from East Asia" (which reverted back to the wild) and so interbreeding between dingos and other domestic dogs is also not a hybridization in the same sense as an interbreeding between different species of *Canidae*.

Some dingo-mixed-breeds have been deliberately bred as pets, but are turned loose due to behavioural problems. These cross-breeds are accepted back into the wild dingo population where they breed with pure dingoes. In some parts of Australia, up to 80% of dingoes are part domestic dog. Dingoes are distinguishable from domestic dogs through DNA and through having longer teeth and longer muzzles.

The Australian Kelpie sheepdog is widely believed to be the result of crossing dingos with English herding dogs, but this (the dingo blood) is not upheld by breed documentation. The Australian Cattle Dog breed is known to have been influenced by the dingo.

According to the partwork "Animal Life and the World of Nature" (Vol 1, 1902–1903), Lord Walter Rothschild owned a dingo-wolf cross, bred by Mr and Mrs HC Brooke from a tame male dingo and a semi-tame female wolf.

In the United States there is also a dingo known as Carolina Dogs. They are almost identical to the Australian dingos, and were brought over by native peoples migrating from Asia. They used to be very common in the American south, but people started to collect them and breed them for herding. Now they may be extinct in the wild, but there are thousands in captivity, and some of those are crossed with dogs of other breeds to experiment with making them smaller. They seem to be very family dogs and welcome new people into the house without aggression. This makes them bad guard or watch dogs, so either people want American Dingo blood for their small apartment dogs because of their friendly outgoing nature and breed them with smaller lap-dogs, or they want a more aggressive dog with American Dingo blood to guard or protect their houses and property. It's also worth noting that the dog who played Old Yeller (1957 film) in the classic Disney movie had a very high content of American Dingo in him. In the wild both coyotes and wolves have been know to breed with American Dingos, but on a whole they are very different in behaviour and avoid one another.

Dog-fox hybrids

There are no reliable reports or genetic testing that proves the existence of dog-fox hybrids (called **doxes**) although there are many unsubstantiated reports of such hybrids.

An unconfirmed female terrier/fox hybrid was reported, and later euthanized (killed), in the UK. British gamekeeper folklore claims that terrier bitches can produce offspring with male foxes. Other dog breeds claimed to have hybridized with foxes are the Alaskan Malamute, Sheltie, Siberian husky, and most of the hound groups. The supposed hybrids are likely to be natural variation in the domestic dog.

There has been a reported cross between a domestic dog and a South American Maned Wolf, but the Maned Wolf is only a fox like canid not closely related to other canids and is the only member of the genus Chrysocyon.

In Saskatchewan, Canada there was another supposed dox, this time a female miniature Sheltie with a wild fox. There was a litter of three, but only one survived. The surviving (a female) was barren, and looked like an almost pure fox, with slight variations. However, the variability of dogs in appearance makes it impossible to determine whether an animal is hybrid based on looks. In most reported cases the dox had gold or yellow eyes, wired hair, and with black red and gray hairs covering most of the body.

Coyote hybrids

Coyote-Domestic dog hybrid

There is no genetic difference between a male coyote/female dog breeding and a male dog/female coyote breeding, but two separate terms have been invented, *coydog* and *dogote*, as the customary naming for hybrid animals is to derive the first portion of the name from the father and the second from the mother (cf. liger vs. tiglon). A major difference between the two is logically the birthplace of the offspring: a female coyote would give birth in the wild and a female dog, unless feral itself, would give birth domestically.

Coydog

Coydogs (male coyote/female dog) Coydogs were once believed to be present in large numbers in Pennsylvania due to a declining coyote population and a burgeoning domestic dog population. Most supposed hybrids were naturally occurring red or blond color variations of the Coyote or were feral dogs. The breeding cycles of dogs and coyotes are not synchronized and this makes interbreeding uncommon. If interbreeding had been common, each successive generation of the coyote population would have acquired more and more doglike traits.

Coyotes are solitary by nature; this trait is carried across to coyote-dog hybrids. This can result in problematical and unsociable behaviour which makes them generally unsuitable as pets. As a result, they may be abandoned or allowed to stray and be absorbed into the feral dog or coyote population. However if the coyote (or dogote) is found at a very young age and raised properly they can, in fact, become a pet much like some wolf-dogs are kept. Much time and effort must be put into them for this to occur.

Dogote

The mating of a male dog and a female coyote results in a **dogote**. There has been one report of a dogote which arose from a male German shepherd/female coyote mating in the wild. Hybrid pups were found after a female coyote was shot. The adult dogotes resembled German shepherds in color. The dogote displays unsociable behavior much like the coydog but through much time and effort can, like the coydog, become a companion (not pet).Template:Clarification and citation needed

Coyote-wolf hybrid

Hybridization between wolf, and coyote has long been recognized.

The red wolf is considered by some to be a coyote/wolf hybrid

DNA analysis results consistently show that all existing "Red Wolves" carry Coyote genes, though it is not known if this is a result of recent habitat destruction by man, or whether Red Wolves have always been hybrids. This has caused a problem for Canid taxonomy, as hybrids are not normally thought of a species, though the convention is to continue to refer to Red Wolves as a subspecies of wolf, *Canis lupus rufus*, with no mention of the coyote taxon, *latrans*.

In recent history the taxonomic status of the red wolf has been widely debated. Mech (1970) suggested red wolves may be fertile hybrid offspring from grey wolf (Canis lupus) and coyote (C. latrans) interbreeding. Wayne and Jenks (1991) and Roy et al. (1994b, 1996) supported this suggestion with genetic analysis. Phillips and Henry (1992) present logic supporting the contention that the red wolf is a subspecies of grey wolf. However, recent genetic and morphological evidence suggests the red wolf is a unique taxon. Wilson et al. (2000) report that grey wolves (Canis lupus lycaon) in southern Ontario appear genetically very similar to the red wolf and that these two canids may be subspecies of one another and not a subspecies of grey wolf. Wilson et al. (2000) propose that red wolves and C. lupus lycaon should be a separate species, C. lycaon, and their minor differences acknowledged via subspecies designation. A recent meeting of North American wolf biologists and geneticists also concluded that C. rufus and C. lupus lycaon were genetically more similar to each other than either was to C. lupus or C. latrans (B.T. Kelly unpubl.). Recent morphometric analyses of skulls also indicate that the red wolf is likely not to be a grey wolf × coyote hybrid (Nowak 2002). Therefore, while the red wolf's taxonomic status remains unclear, there is mounting evidence to support C. rufus as a unique canid taxon.

Many animals commonly referred to as "Eastern Coyotes" or "Northeastern Coyotes" have wolf and dog genes, a larger size, and a more wolf-like skull shape than other coyotes, and are generally believed by experts to be hybrids. This has become a problem for taxonomists, as it is unclear what new taxon will be used to refer to this new population of animals.

Jackal hybrids

The Wolf plus Jackal can interbreed and produce fertile hybrid offspring, which are sometimes known as huskals. Coyote/Jackal Hybrids have also been bred as pets by Wolf-dog enthusiasts. Dogs have been crossed with golden jackals. It is also thought that Pharoanic Egyptians crossbred domestic dogs with jackals, producing a jackal-dog that resembled the god Anubis.

A Sulimov dog at work

The reason golden jackals differ in chromosome number is most likely because golden jackals have 2 pairs of chromosomes that are twice as long but contain similar gene content as 4 pairs of dog chromosomes. This might reduce fertility but it would not likely completely sterilize golden jackal-dog hybrids.

In *The Variation of Animals and Plants under Domestication* Charles Darwin wrote:

Several years ago I saw confined in the Zoological Gardens of London a female hybrid from an English dog and jackal, which even in this the first generation was so sterile that, as I was assured by her keeper, she did not fully exhibit her proper periods; but this case, from numerous instances have occurred of fertile hybrids from these two animals, was certainly exceptional.

Robert Armitage Sterndale mentioned experimental jackal hybrids from British India in his *Natural History of Mammals in India and Ceylon*, noting that glaring jackal traits could be exhibited in hybrids even after three generations of crossing them with dogs

In Russia, Golden Jackal/Siberian husky hybrids were bred as sniffer dogs because Jackals have a superior sense of smell and Lapponian Herders are good cold climate dogs. Also Fox Terrier, Lunehund, and Spitz blood were bred for over generations and for almost 25 years have been dedicated to the forming and precise genes of the Sulimov dogs. As well as a superior sense of smell, important at low temperatures where substances are less volatile and therefore less pungent, *Sulimov Dogs* are small sized and can work in confined spaces. When tired, their normally curled tails droop, making it clear to the handler that the dog needs to be rested. The jackal hybrids were bred by senior researcher Klim Sulimov, Senior Research Assistant at the D.S. Likhachev Scientific Research Institute for Cultural Heritage and Environmental Protection in Russia. Male jackal pups had to be fostered on a husky bitch in order to imprint the jackals on dogs. Female jackals accepted male huskies more easily. The half-bred jackal-dogs were hard to train and were bred back to huskies to produce quarter-bred hybrids (quadroons). These hybrids were small, agile, trainable and had excellent noses. They are called Sulimov dogs after their creator and may one day be registered as a working breed of dog. Twenty-five jackal-dog hybrids are used by Aeroflot at Sheremetyevo Airport in Moscow, for functions which include bomb-sniffing. Their breeding program dates back to 1975, but was not applied to bomb detection until 2002.

Chapter- 8

Speciation Events

London Underground mosquito

The **London Underground mosquito** is a species of mosquito in the genus *Culex* found in the London Underground. It is thought to have evolved from the overground species *Culex pipiens* recently. Biologists named the London Underground mosquito ***Culex pipiens molestus*** due to its voracious biting. Notably the London *C.p. molestus* assaulted Londoners sleeping in the Underground during the Blitz , although similar populations were already known. The name seems to already have been given to a species of mosquito found in Australia, named as long ago as 1775 . The London Underground mosquito, although first discovered in the London Underground system, has been found in underground systems around the world. It is suggested that it may have adapted to human-made underground systems since the last century from local above-ground Culex pipiens , although more recent evidence suggests that it is a southern mosquito variety related to Culex pipiens that has adapted to the warm underground spaces of northern cities .

The evidence for this mosquito being a different species from *Culex pipiens* comes from research by Kate Byne and Richard Nichols. The species have very different behaviours , are extremely difficult to mate , and with different allele frequency consistent with genetic drift during a founder event. More specifically, this mosquito, *Culex pipiens molestus*, breeds all-year round, is cold intolerant, and bites rats, mice, and humans, in contrast to the above ground species *Culex pipiens* that is cold tolerant, hibernates in the winter, and bites only birds. When the two varieties were cross-bred the eggs were infertile suggesting reproductive isolation .

Since that paper more information has accumulated. The fundamental results still stands: the genetic data indicate that the *molestus* form in the London Underground appeared to have a common ancestry, rather than the population at each station being related to the nearest above-ground population (i.e. the *pipiens* form). Byrne and Nichols' working hypothesis was that adaptation to the underground environment had occurred locally in London once only – since there are many hurdles to jump in order to become adapted to the subterranean environment, it is understandable that it would occur rarely. This hypothesis implies that local adaptation would be expected in different locations around

Europe and beyond, as each local pipiens population evolved an offshoot that overcame the problems of living underground.

However, more recently-collected genetic evidence suggests that a single *molestus* form has spread throughout Europe and beyond, since populations over a large area share a common genetic heritage. These widely separated populations are distinguished by very minor genetic differences, which suggest that the molestus form developed recently: a single mtDNA difference shared among the underground populations of ten Russian cities ; a single fixed microsatellite difference in populations spanning Europe, Japan, Australia, the middle East and Atlantic islands . This worldwide spread might have occurred after the last glaciations or be even more recent, due to the insects hitch hiking on world trade routes. One possibility is the international second-hand tire trade. The tires retain water in which the larvae can survive (Completely removing water from an old tire can be difficult).

What has always been more intriguing about the *molestus* story was that the reproductive isolation in north European populations appears to be almost complete, whereas there is clearly gene flow between them in populations to the south. Byrne and Nichols attributed this pattern to the inability of the underground form (and perhaps their hybrids) to survive above ground in harsh northern winters.

Now it appears that the persistence of hybrids in northern climates may be another evolutionary problem that can be solved but only rarely: the Fonseca paper obtained genetic evidence that the recent colonization of America by *Culex* mosquitoes actually involves a strain derived from a rare successful hybridization between *pipiens* and *molestus*. They suggest that hybridization may explain why the American form bites both birds and humans. The consequences of this more indiscriminate feeding hit the news in 1999 with the outbreak of human encephalitis in New York, caused by West Nile virus. It was the first documented introduction of this virus into the Western Hemisphere; perhaps because in the longer established populations the old world northern above-ground pipiens almost exclusively bite birds, the human biting ones being incarcerated below ground.

Raphanobrassica

Raphanobrassica includes all intergeneric hybrids between the genera *Raphanus* (radish) and *Brassica* (cabbages, etc). The name comes from the combination of the genus names for radish and cabbage. Some botanists prefer to use the name *Brassicoraphanus*, particularly for plants derived from a cross where *Brassica* was the maternal parent (but neither name has been validly published).

The first *Raphanobrassica* or "rabbage", an allopolyploid cross between the radish (*Raphanus sativus*) and cabbage (*Brassica oleracea*), was obtained by the Soviet agronomist Georgi Dmitrievich Karpechenko, in 1928.

Plants of this parentage are now known as radicole. Two other fertile forms of *Raphanobrassica* are known. Raparadish, an allopolyploid hybrid between *Raphanus sativus* and *Brassica rapa* is grown as a fodder crop. "Raphanofortii" is the allopolyploid hybrid between *Brassica tournefortii* and *Raphanus caudatus*.

For gastronomists, (those interested in food) this plant may have seemed a disappointment, since all the resulting hybrids of this crossing have radish leaves and cabbage roots -- the two non-edible parts of its ancestors. For biologists, however, the *Raphanobrassica* is an extremely interesting plant, because - in spite of its hybrid nature - it is not sterile. This led some botanists to propose that the accidental hybridization of a flower by pollen of another species in nature could be a mechanism of speciation common in higher plants. Currently, it is thought that a great part of the flowering plants have some hybridization among their ancestors, particularly in the case of the orchids.

Salsify

Tragopogon, also known as **salsify** or **goatsbeard**, is a genus of flowering plants in the sunflower family Asteraceae that has over 140 species, including the vegetable known as salsify, as well as a number of common wild flowers, some of which are usually regarded as weeds.

Salsifies are forbs growing as biennial or perennial plants. They have a strong taproot and milky sap. They generally have few branches, and those there are tend to be upright. Their leaves are somewhat grass-like. Flower colour varies within the genus, with some yellow species, and some bronze or purple. Seeds are borne in a globe like that of a dandelion but larger, and are dispersed by the wind.

The salsifies are natives of Europe and Asia, but several species have been introduced into North America and Australia and have spread widely there.

Some of the more common species of *Tragopogon* are known, in the regions where they are most common, by the common names goat's beard, goatsbeard, salsify, or common salsify, without further qualification. These names are therefore inherently ambiguous, and best avoided, or reserved for the genus collectively. In the species list below, the first common name given is the one that seems to be most widely used for that species and is not in significant use for any other species.

The vegetable called salsify is usually the root of purple salsify, *Tragopogon porrifolius*; the root is described as having the taste of oysters (hence the alternative common name "oyster plant" for some species in this genus), but more insipid with a touch of sweetness. The young shoots of purple salsify can also be eaten, as well as young leaves . Other species are also used in the same way, including the black or Spanish salsify, *Scorzonera hispanica*, which is closely related though not a member of the genus *Tragopogon*.

Hybridization

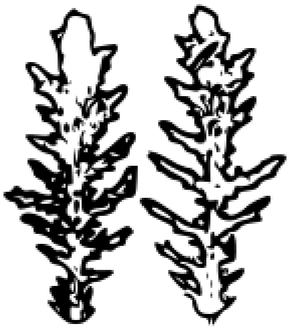
Salsifies are one example where hybrid speciation has been observed. In the early 1900s, humans introduced three species of goatsbeard into North America. These species, the western salsify (*T. dubius*), the meadow salsify (*T. pratensis*), and the oyster plant (*T. porrifolius*), are now common weeds in urban wastelands. In the 1950s, botanists found two new species in the regions of Idaho and Washington, where the three already known species overlapped. One new species, *Tragopogon miscellus*, is a tetraploid hybrid of *T. dubius* and *T. pratensis*. The other species, *Tragopogon mirus*, is also an allopolyploid, but its ancestors were *T. dubius* and *T. porrifolius*. These new species are usually referred to as "the Ownbey hybrids" after the botanist who first described them. The *T. mirus* population grows mainly by reproduction of its own members, but additional episodes of hybridization continue to add to the *T. mirus* population.

Senecio eboracensis

Senecio eboracensis, the **York groundsel** or **York radiate groundsel**, is a self-pollinating hybrid species of ragwort and one of only six new plants to be discovered in either the United Kingdom or North America in the last 100 years. It was discovered in 1979 in York, England growing next to a parking lot and formally described in 2003. Like many of the Senecio genus it can be found growing in urban habitats, such as disturbed earth and pavement cracks and this particular species only in York and between a railway and a parking lot.

Description

York radiate groundsel is a deciduous annual plant that sets its seed within the 3 months that it takes this plant to mature from germination to the upwards of 16 inches (41 cm) high adult plant. With pretty yellow daisy-like flowers from its Sicilian parent (*S. squalidus*) but also with the less-promiscuous habits of its native parent (*S. vulgaris*); this member of the Senecio genus is morphologically distinct from related species.



Leaf shapes of *S. eboracensis*

Leaves and stems

S. eboraccensis have large many lobed leaves divided into slender segments, the clefts not reaching the midrib. The stems are mostly erect to ascending with an occasional horizontal base section up to 2 inches (5 cm) with 'adventitious roots' at base. The upper and lower leaves petiolate and lobes appearing at quarter whole leaf lengths along the midrib. The upper leaves are generally more deeply lobed and in lobed pairs. Leaves on plants grown in fertile soils or in greenhouses can be much more luxurious and more highly dissected (or more finely divided into slender segments) up to 7 inches (18 cm) x 3.5 inches (9 cm) with lobes appearing at fifth whole leaf lengths along the midrib. The plants tip is usually acute with a very small tooth. Leaf edges throughout are dentate or sometimes divided into lobes.

Flowers

York groundsel has showy flower-heads especially when compared to its Common ragwort parent. The flower-head, found at the tips of the plants (apical) appearing in clusters (an inflorescence) usually consists of three to seven florets in a grouped corymb; at first dense and leafy but eventually less dense with peduncles 5 to 20 millimeters (0.2 to 0.8 in) which get longer when fruiting (up to 25 mm (1 in)). The flower-head is broadly cylindrical 10×4 millimeters (0.4×0.16 in), becoming slightly bell shaped) when the bright yellow ray florets open. Involucral bracts sparse (4-8), elongated (3.5–4 mm), usually without black tips. The floret ligules are narrow and long 5 to 7 millimeters (0.2 to 0.24 in) long and 1.5 millimeters (0.06 in) wide), occasionally becoming revolute. Like other Senecios, the 10-30 papilla occur stigmatically into pericarp; each usually with four-pored pollen, the grains in polar view 30-35 micrometers when fully expanded.

Seeds

The umbrella-like achenes can be 2.5 to 3.5 millimeters (0.1 to 0.15 in) long, are straight and shallowly grooved; with hairless smooth ribs while the grooves are covered with hairs. Silky white pappus which readily detach from the fruit when ripe.

Name

The word Eboracum, the classical name of York, was chosen in the year 2000 to describe this tetraploid hybrid derivative informally named 'York radiate groundsel' at the time a formal description was made.

Distribution

This groundsel occurs on disturbed ground, car park perimeters, pavement cracks and other urban/industrial sites; specifically in disturbed areas near to the railways in York, England.

One of the parents *Senecio vulgaris* is a native to the area while the other parent *Senecio squalidus* was introduced from Mount Etna in Sicily in 1690 to the Oxford Botanic

Garden in Oxford, England and was soon spreading happily along the railways and throughout the country.

Evolution

A newcomer to the plant world, *York groundsel* has been used as an example to support macroevolution. The refusal of *S. eboracensis* to breed back to its parents is the main point of contention between the rival parties.

The science of this plant is that it is a hybrid species whose parents are the self-incompatible and promiscuous Sicilian *Senecio squalidus* (also known as Oxford ragwort) and the self-compatible and tenacious *Senecio vulgaris* (also known as Common groundsel). Like *S. vulgaris*, *S. eboracensis* is self-compatible, however, it shows little or no natural crossing with its parent species, and is therefore reproductively isolated, indicating that strong breed barriers exist between this new hybrid and its parents. It is thought to have resulted from a backcrossing of the F1 hybrid of its parents to *S. vulgaris*. *S. vulgaris* is native to Britain, while *S. squalidus* was introduced from Sicily in the early 18th century; therefore, *S. eboracensis* has speciated from those two species within the last 300 years.

Other hybrids descended from the same two parents are known. Some are infertile, such as *S.* x *baxteri*. Other fertile hybrids are also known, including *S. vulgaris* var. *hibernicus* (which has been accepted as a synonym for *S. vulgaris*), now common in Britain, and the allohexaploid *S. cambrensis*, which according to molecular evidence probably originated independently at least three times in different locations. Morphological and genetic evidence support the status of *S. eboracensis* as separate from other known hybrids.

Senecio cambrensis

Senecio cambrensis (**Welsh groundsel** or **Welsh ragwort**) is a flowering plant of the family Asteraceae. It is endemic to the United Kingdom and currently known only from North Wales. It is a recently-evolved plant which arose suddenly as a result of hybridization between two related species.

Origin

Welsh groundsel is an allopolyploid, a plant which contains sets of chromosomes originating from two different species. Its ancestor was *Senecio × baxteri*, an infertile hybrid which can arise spontaneously when the closely-related groundsel (*Senecio vulgaris*) and Oxford ragwort (*Senecio squalidus*) grow alongside each other. Sometime in the early 20th century, an accidental doubling of the number of chromosomes in an *S. × baxteri* plant led to the formation of a new fertile species, Welsh groundsel.

Distribution and habitat

It was first discovered in 1948 by Horace E. Green at Ffrith in Flintshire, north-east Wales. The species was described in 1955 by Effie M. Rosser of Manchester Museum using material from the site. It was later found at a number of sites across the north-east of Wales including Chirk, Brymbo, Queensferry and Colwyn Bay and a herbarium specimen was discovered which had been collected at Brynteg in 1925.

In England it was reported from Shropshire and an introduced population appeared in Wolverhampton. The Shropshire record is now thought to be erroneous and the Wolverhampton plants have disappeared. There are no recent records from England.

In 1982, Welsh groundsel was discovered at several sites around Edinburgh, Scotland. This population arose independently from the Welsh population; it is believed to date from at least 1974 but now appears to have disappeared with no records since 1993.

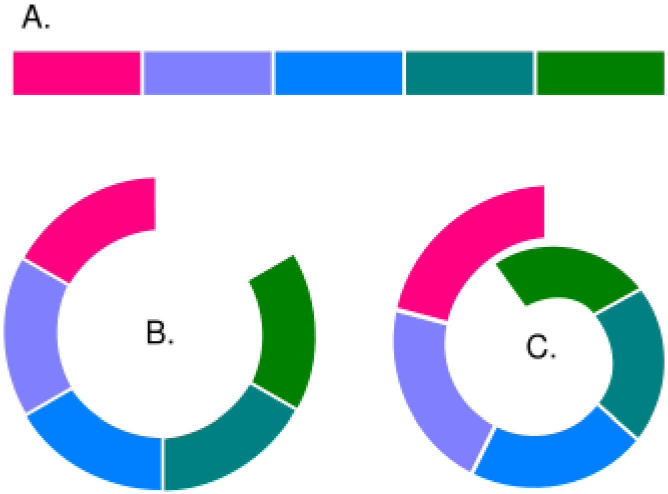
Typical habitats of the species include waste ground, roadsides and cracks in walls and pavements.

Description

The plant is intermediate in appearance between its parents, groundsel and Oxford ragwort. It is an erect annual plant which reaches a height of 30 (sometimes 50) centimetres. The stem and leaves have few or no hairs. The leaves are deeply lobed, the lower ones have stalks while the upper leaves are attached directly to the stem. The flower heads are cylindrical and usually have 8 to 15 yellow ray florets ("petals") although some are rayless. The ray florets vary in length but are most commonly 4 to 7 mm long. The pollen grains are 30 to 36 micrometres across and usually have 4 pores.

Chapter- 9

Ring Species



In this diagram, interbreeding populations are represented by coloured blocks. Variation along a cline may bend right around, forming a ring.

In biology, a **ring species** is a connected series of neighboring populations, each of which can interbreed with closely sited related populations, but for which there exist at least two "end" populations in the series, which are too distantly related to interbreed, though there is a potential gene flow between each "linked" species. Such non-breeding-though-genetically-connected "end" populations may co-exist in the same region thus closing a "ring".

Ring species provide important evidence of evolution in that they illustrate what happens over time as populations genetically diverge, and are special because they represent in living populations what normally happens over time between long deceased ancestor populations and living populations, in which the intermediates have become extinct.

Richard Dawkins observes that ring species "are only showing us in the spatial dimension something that must always happen in the time dimension."

Ring species also present an interesting case of the species problem, for those who seek to divide the living world into discrete species. After all, all that distinguishes a ring species from two separate species is the existence of the connecting populations - if enough of the connecting populations within the ring perish to sever the breeding connection, the ring species' distal populations will be recognized as two distinct species.

Formally, the issue is that *interfertile* "able to interbreed" is not a transitive relation – if A can breed with B, and B can breed with C, it does not follow that A can breed with C – and thus does not define an equivalence relation. A ring species is a species that exhibits a counterexample to transitivity.

Explanation of the diagram

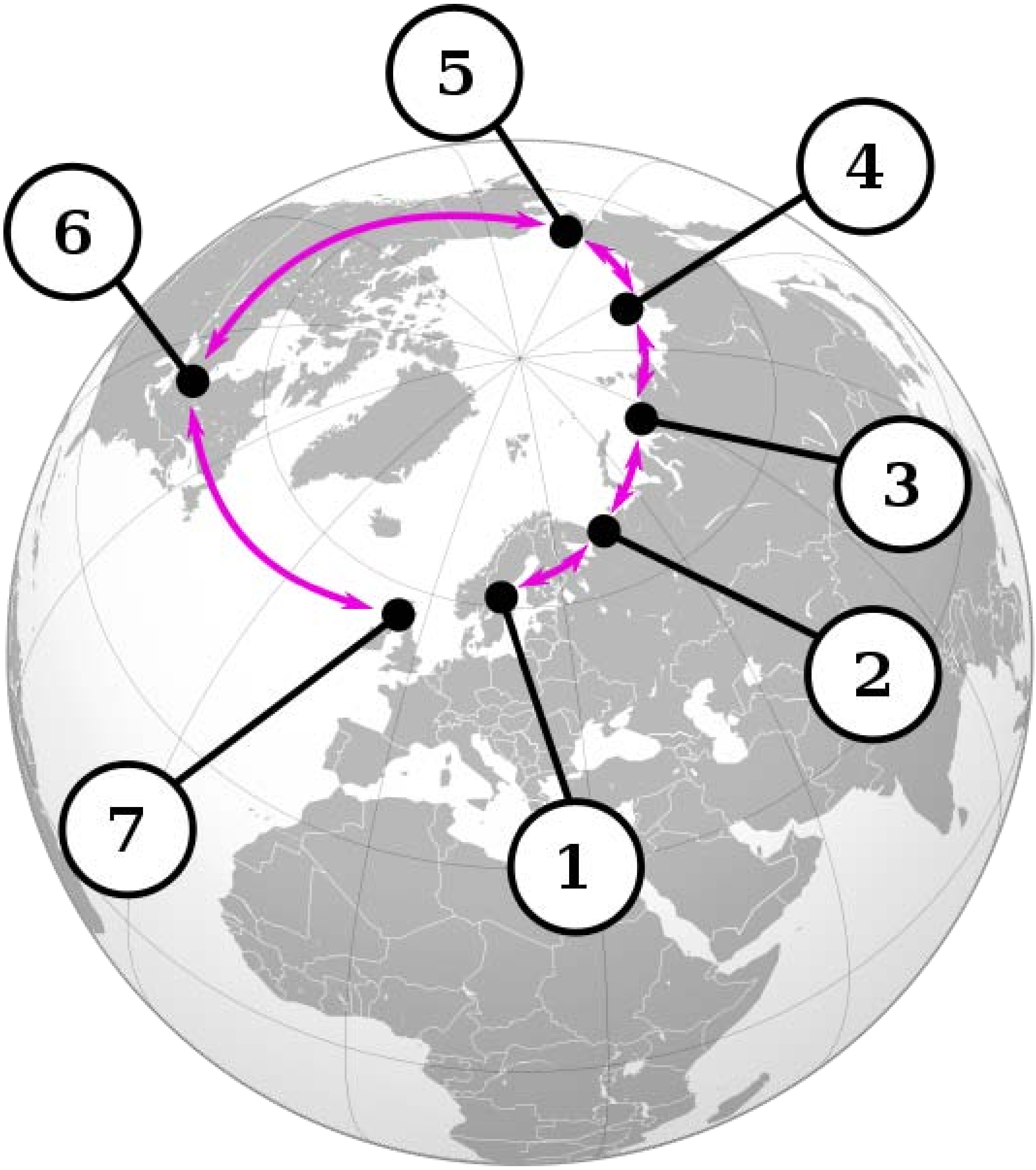
The coloured bar to the right shows a number of natural populations, each population represented by a different colour, varying along a cline (a gradual change in conditions which gives rise to slightly different characteristics predominating in the organisms that live along it). Such variation may occur in a straight line (for example, up a mountain slope) as is shown in *A*, or may bend right around (for example, around the shores of an ocean), as is shown in *B*.

In the case where the cline bends around, populations next to each other on the cline can interbreed, but at the point that the beginning meets the end again, as is shown in *C*, the differences that have accumulated along the cline are great enough to prevent interbreeding (represented by the gap between pink and green on the diagram). The interbreeding populations in this circular breeding group are then collectively referred to as a ring species.

Problem of definition

The problem, then, is whether to quantify the whole ring as a single species (despite the fact that not all individuals can interbreed) or to classify each population as a distinct species (despite the fact that it can interbreed with its near neighbours). Ring species illustrate that the species concept is not as clear-cut as it is often thought to be.

Larus gulls



The *Larus* gulls interbreed in a ring around the arctic
(1 : *Larus argentatus argentatus*, 2: *Larus fuscus sensu stricto*, 3 : *Larus fuscus heuglini*, 4 : *Larus argentatus birulai*, 5 : *Larus argentatus vegae*, 6 : *Larus argentatus smithsonianus*, 7 : *Larus argentatus argenteus*)

A Herring Gull, *Larus argentatus* (front) and a Lesser Black-backed Gull. *Larus fuscus* (behind) in Norway: two phenotypes with clear differences.

A classic example of ring species is the *Larus* gulls' circumpolar species "ring". The range of these gulls forms a ring around the North Pole, which is not normally transited by individual gulls.

The Herring Gull *L. argentatus*, which lives primarily in Great Britain and Ireland, can hybridize with the American Herring Gull *L. smithsonianus*, (living in North America), which can also hybridize with the Vega or East Siberian Herring Gull *L. vegae*, the western subspecies of which, Birula's Gull *L. vegae birulai*, can hybridize with Heuglin's gull *L. heuglini*, which in turn can hybridize with the Siberian Lesser Black-backed Gull *L. fuscus*. All four of these live across the north of Siberia. The last is the eastern representative of the Lesser Black-backed Gulls back in north-western Europe, including Great Britain.

The Lesser Black-backed Gulls and Herring Gulls are sufficiently different that they do not normally hybridize; thus the group of gulls forms a continuum except where the two lineages meet in Europe.

A recent genetic study entitled *The herring gull complex is not a ring species* has shown that this example is far more complicated than presented here (Liebers *et al.*, 2004): this example only speaks to the complex of species from the classical Herring Gull through Lesser Black-backed Gull. There are several other taxonomically unclear examples which belong in the same superspecies complex, such as Yellow-legged Gull *L. michahellis*, Glaucous Gull *L. hyperboreus* and Caspian Gull *Larus cachinnans*.

Other examples

There are other examples. The *Ensatina* salamanders form a ring round the Central Valley in California. The Greenish Warbler (*Phylloscopus trochiloides*) forms a species ring, around the Himalayas (Alström 2006).

Some Specimen of Ring Species: -

Gull

Gulls (often informally called **seagulls**) are birds in the family Laridae. They are most closely related to the terns (family Sternidae) and only distantly related to auks, skimmers, and more distantly to the waders. Until recently, most gulls were placed in the genus *Larus*, but this arrangement is now known to be polyphyletic, leading to the resurrection of several genera.

Gulls are typically medium to large birds, usually grey or white, often with black markings on the head or wings. They typically have harsh wailing or squawking calls, stout, longish bills, and webbed feet. Gull species range in size from the Little Gull, at 120 g (4.2 oz) and 29 cm (11.5 inches), to the Great Black-backed Gull, at 1.75 kg (3.8 lbs) and 76 cm (30 inches).

Biology and habits

Gulls are sociable and often found in groups at rest or when feeding.

Most gulls, particularly *Larus* species, are ground nesting carnivores, which will take live food or scavenge opportunistically. Live food often includes crabs and small fish. Gulls have prophylactic unhinging jaws which allow them to consume large prey. Apart from the kittiwakes, gulls are typically coastal or inland species, rarely venturing far out to sea. The large species take up to four years to attain full adult plumage, but two years is typical for small gulls. Large White-Headed Gulls are typically long-lived birds, with a maximum age of 49 years recorded for the Herring Gull.

Gulls nest in large, densely packed noisy colonies. They lay two to three speckled eggs in nests composed of vegetation. The young are precocial, being born with dark mottled down, and mobile upon hatching.

Gulls—the larger species in particular—are resourceful, inquisitive and intelligent birds, demonstrating complex methods of communication and a highly developed social structure. For example, many gull colonies display mobbing behaviour, attacking and harassing would-be predators and other intruders. Certain species (e.g. the Herring Gull) have exhibited tool use behaviour, using pieces of bread as bait with which to catch goldfish, for example. Many species of gull have learned to coexist successfully with humans and have thrived in human habitats. Others rely on kleptoparasitism to get their food. Gulls have been observed preying on live whales, landing on the whale as it surfaces to peck out pieces of flesh.

Two Western Gulls (adult and juvenile) fight over a freshly killed ground squirrel

A seagull in Aberdeen has been seen repeatedly shoplifting bagged crisps from a shop, apparently displaying a preference for cheese flavour Doritos.

Taxonomy

The taxonomy of gulls is confused by their widespread distribution zones of hybridization leading to geneflow. Some have traditionally been considered ring species, but recent evidence suggests that this assumption is questionable. Until recently, most gulls were placed in the genus *Larus*, but this arrangement is now known to be polyphyletic, leading to the resurrection of the genera *Ichthyaetus*, *Chroicocephalus*, *Leucophaeus*, *Saundersilarus* and *Hydrocoloeus*. Some English names refer to species complexes within the group:

- **Large white-headed gull** is used to describe the 18 or so Herring Gull-like species from California Gull to Lesser Black-backed Gull in the taxonomic list below.
- **White-winged gull** is used to describe the 4 pale-winged, High Arctic-breeding taxa within the former group; these are Iceland Gull, Glaucous Gull, Thayer's Gull, and Kumlien's Gull.

Hybridisation between species of gull occurs quite frequently, although to varying degrees depending on the species involved. The taxonomy of the large white-headed gulls is particularly complicated.

In common usage, members of various gull species are often referred to as *sea gulls* or *seagulls*. This name is used by the layman to refer to a common local species or all gulls in general, and has no fixed taxonomic meaning.

The American Ornithologists' Union combines Sternidae, Stercorariidae, and Rhynchopidae as subfamilies in the family Laridae, but recent research indicates that this is incorrect.

Ensatina

Ensatina eschscholtzii (commonly known by its genus name, ***Ensatina***) is a complex of plethodontid (lungless) salamanders found in coniferous forests, oak woodland and chaparral from British Columbia, through Washington, Oregon, across California (where all seven subspecies variations are located), all the way down to Baja California in Mexico.

As a Ring Species

Monterey Ensatina

The Ensatina salamander has been described as a ring species in the mountains surrounding the Californian Central Valley. The complex forms a horseshoe shape around the mountains, and though interbreeding can happen between each of the 19 populations around the horseshoe, the *Ensatina eschscholtzii* subspecies on the western end of the horseshoe cannot interbreed with the *Ensatina klauberi* on the eastern end. As such it is thought to be an example of incipient speciation, and provides an illustration of "nearly all stages in a speciation process" (Dobzhansky,1958).

Habitat and Description

The Ensatina subspecies *E. e. eschscholtzii*, or Monterey Ensatina, can be found in Santa Cruz, Monterey, and the California coastal mountains. They reach a total length of three to five inches, and can be identified primarily by the structure of the tail, and how it is narrower at the base. This salamander is the only type that has this tail structure and five toes on the back feet.

Males often have longer tails than the females, and many of the salamanders have lighter colored limbs in comparison to the rest of the body. The salamanders lay their eggs underground, often in threes, which then hatch directly into salamanders, skipping the usual aquatic phase.

Human contact

The ensatina can usually be found under logs, brush, by or in streams and lakes, and in other moist places. Because they breathe through their pores, distress in the animal can be caused by improper handling by human hands. They may exude a toxic milky secretion from the tail.

Ensatina eschscholtzii klauberi, the Large-blotched Salamander

Subspecies

- Yellow Blotched Ensatina — *E. e. croceater* (Cope, 1868)
- Monterey Ensatina — *E. e. eschscholtzii* Gray, 1850
- Large Blotched Ensatina — *E. e. klauberi* Dunn, 1929
- Oregon Ensatina — *E. e. oregonensis* (Girard, 1856)
- Painted Ensatina — *E. e. picta* Wood, 1940
- Sierra Nevada Ensatina — *E. e. platensis* (Jiménez de la Espada, 1875)
- Yellow Eyed Ensatina — *E. e. xanthoptica* Stebbins, 1949

Greenish Warbler

The **Greenish Warbler** and **Green Warbler** (***Phylloscopus trochiloides***) are widespread leaf-warblers throughout their breeding range in northeastern Europe and temperate to subtropical continental Asia. This warbler is strongly migratory and winters in India. It is not uncommon as a spring or early autumn vagrant in Western Europe and is annually seen in Great Britain. In Central Europe large numbers of vagrant birds are encountered in some years; some of these may stay to breed, as a handful of pairs does each year in Germany.

Like all leaf-warblers, it was formerly placed in the "Old World warbler" assemblage, but now belongs to the new leaf-warbler family Phylloscopidae.

Description and ecology

Western Greenish Warbler,
P. (t.) viridianus

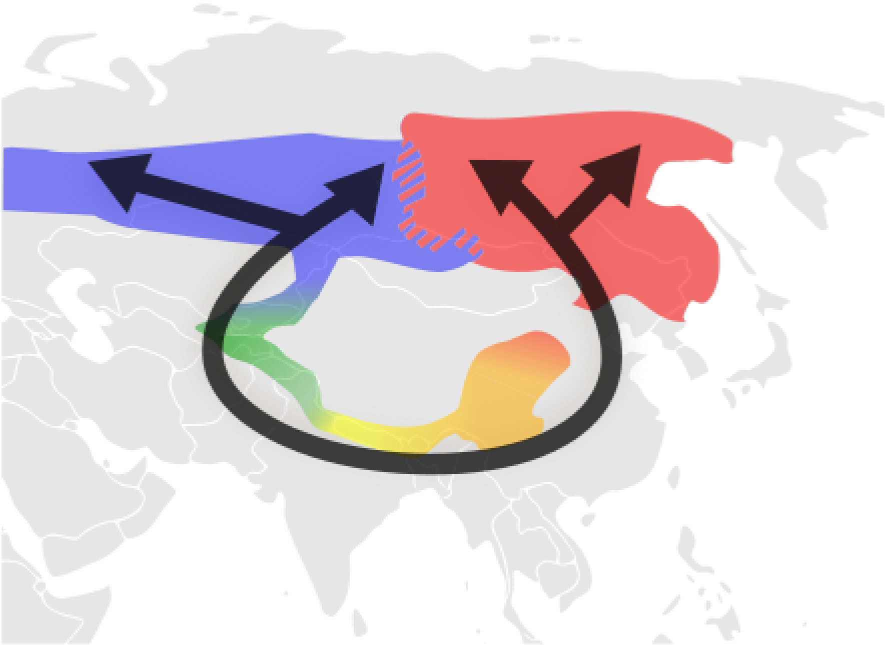
This is a typical leaf-warbler in appearance, grayish-green above and off-white below. The single wing bar found in the southern and western populations distinguishes them from most similar species (except Arctic Warbler *P. borealis*). It is slightly smaller than that species and has a thinner bill, without a dark tip to the lower mandible. A latitude-based analysis of wintering birds indicated that more northerly *P. trochiloides* are smaller, i.e. this species does not seem to follow Bergmann's rule .

Its song is a high jerky trill, in some populations containing a sequence of down- and more rarely up **slurred** notes.

It breeds in lowland deciduous or mixed forest; non-breeding birds in the warmer parts of its range may move to montane habitat in summer. Individuals from southeast of the Himalayas are for example quite often seen in Bhutan during the hot months, typically in humid Bhutan Fir (*Abies densa*) forest up to about 3,800 meters ASL or more, but they do not breed there and return again to the adjacent subtropical lowlands in winter .

The nest is on the ground in low shrub. Like its relatives, this small passerine is insectivorous.

Subspecies and evolution



Presumed evolution around Himalayas.
Yellow: *P. t. trochiloides*
Orange: *P. t. obscuratus*
Red: *P. t. plumbeitarsus*
Green: *P. t. "ludlowi"*
Blue: *P. t. viridanus*
P. t. nitidus of the Caucasus is not shown.

It has a number of subspecies, of which *P. t . viridianus* is the most familiar in Europe. As it seems, it is a ring species, with populations diverging east- and westwards of the Tibetan Plateau, later meeting on the northern side. Their relationships are therefore fairly confusing:

- **Eastern group: Greenish Warblers**
    - *Phylloscopus trochiloides trochiloides*: **Greenish Warbler**
        - Southern rim of the Himalaya eastwards from Nepal into W China.
        - Dusky greyish green above, often traces of second wing bar.
    - *Phylloscopus trochiloides obscuratus*: **Dull-green Warbler**
        - Intermediate between *trochiloides* and *plumbeitarsus*.
        - Gansu and surroundings, China.
    - *Phylloscopus trochiloides plumbeitarsus*: **Two-barred Warbler**
        - Breeds Eastern Siberian taiga.

        - Supercilium more yellow; upperparts more vivid green. 2 well-marked wing bars.
- **Western group: Green Warblers**
    - *Phylloscopus trochiloides viridanus*: **Western Greenish Warbler**
        - Breeds Western Siberia to north-east Europe; at east of range south to NW India.
        - Dull green above, with yellowish supercilium, throat, breast and faint wing bar.
    - *Phylloscopus trochiloides nitidus*: **Green Warbler** or **Bright-green Warbler**
        - Caucasus region.
        - Brighter; underside much more yellow. One strong and one faint wing bar, especially in young birds.

The groups' origin lies probably in the Himalayan region, where *trochiloides* is found. This taxon is close to the parapatric *obscuratus*, and to *plumbeitarsus* which is geographically separated from *obscuratus*; they all can (and in the case of the former two do naturally) hybridize. *P. t. plumbeitarsus* is often split as distinct species, as it does not hybridize with *viridianus* in the narrow zone in the western Sayan Mountains where their ranges overlap.

But phylogenetically, the western taxa are even more distinct. However, there is some gene flow between *trochiloides* and *viridianus* also, with their hybrids being especially common in Baltistan; they were once considered another subspecies *ludlowi*. *nitidus* is a mountain isolate that diverged from ancestral *viridianus*.

Song structure differs mainly between *trochiloides* and *plumbeitarsus*. The former has a fairly uniform, long, and warbling song. Around the Himalayas, song structure is similar, but songs are generally shorter. *plumbeitarsus*, on the other hand, has a long song that can be clearly divided into a warbling part, followed by series of up- and downslurred notes. The songs of *obscuratus*, and, interestingly, *"ludlowi"*, are short, but contain the downslur elements too; in the latter, they uniquely appear at the start of the song.

Chapter- 10

Hybrid Zone

A **hybrid zone** exists where the ranges of two interbreeding species meet. For a hybrid zone to be stable, the offspring produced by the cross (the hybrids) have to be less fit than members of the parent species, although this condition does not need to be met in the very first hybrid generation (F1 hybrid which can exhibit hybrid vigour). Some hybrid zones move, typically at a rate of 0.1-10 metres per year.

Hybrid zones are relatively rare, although a surprising number are now known to science. They present a problem to the taxonomy of the species involved, and the definition of species more generally. They are also important study systems for understanding how new species form (Hybrid speciation), as they are believed to be in transition to reproductive isolation.

These zones are often mapped including the current range of both species, with the overlap ranges highlighted.

Hybrid zones are locations where the hybrid offspring of two divergent populations (sometimes defined as subspecies or races) are prevalent and form a cline (Barton & Hewitt, 1985). Precise definitions of hybrid zones vary, some insist on increased variability of fitness within the zone, others that hybrids be identifiably different from parental forms and others that they represent secondary contact alone (Murray, 1985). They occur at the area of contact between two closely related but genetically different populations, each regarded as parental forms. Reviews of hybrid zones show varying widths between hundreds of metres and hundreds of kilometres and the presence of both gradual clines and stepped clines (Barton & Hewitt, 1985). They present a paradox for the biological definition of a species, usually “a population of actually or potentially interbreeding individuals that produce fertile offspring” (Mayr, 1942). Both parental forms by this definition are one species as they can produce fertile offspring at least some of the time. Despite this, the two populations remain identifiably different, conforming to an alternative definition of species as “taxa that retain their identity despite gene flow” (Barton and Hewitt, 1989). They are useful in the study of the processes of speciation as they provide natural examples of gene flow between populations that are at some point between representing a single species and representing multiple species in reproductive isolation.

The clines of hybrid zones can be observed by recording the frequency of certain diagnostic alleles or phenotypic characteristics for either population along a transect between the two populations. They almost always take the form of a sigmoid curve. They can be wide (gradual) or narrow (steep) depending on the ratio of hybrid survival to recombination of genes (Barton, 1983).

One form of hybrid zone results where one species has undergone allopatric speciation and the two new populations regain contact after a period of geographic isolation. The two populations then mate within an area of contact, producing 'hybrids' which contain a mixture of the alleles distinctive for each population. Thus novel genes flow from either side into the hybrid zone. Genes can also flow back into the distinct populations through interbreeding between hybrids and parental (non-hybrid) individuals (introgression) (Ridley 2003). These processes lead to the formation of a cline between the two pure forms within the hybrid zone.

Hybrid zones and gene flow do not inevitably lead to the recombination of the two populations involved, but can instead continue for thousands of years (White, et al., 1967.). The predominant explanation for this is that the hybrid zone represents a 'tension zone' between the conflicting effects of dispersal of parental forms and selection against hybrids (Bazykin, 1969.). Dispersal of individual parents leads to the creation of more hybrids within the hybrid zone. This results in gene flow between the two populations because of introgression. However, in many cases hybrids are less fit than parental forms because they lack the complete gene complexes of the parentals that make them well adapted to the environments either side of the hybrid zone. The more frequent death and sterility of hybrids forms a barrier to gene flow by making a 'hybrid sink' into which genes from parentals flow but rarely continue into the other population. Statistical models suggest that neutral alleles flow across this barrier very slowly while positively selected alleles will move across quite rapidly (Barton & Hewitt, 1985 p.135). An interesting outcome of this model is that hybrid zones are almost environment independent and can therefore move (Barton, 1979). Hybrids may not always be unfit in the very first generation, which can show hybrid vigour.

Several other models exist to explain hybrid zone stability, although the tension zone model is used in most cases. The dispersal-independent cline model does not consider dispersal at all, with the frequency of alleles finding different equilibria depending on the precise environmental conditions in a particular area. In each location, selection maintains a stable equilibria for each allele, resulting in a smooth cline. (Moore, 1977) The hybrids must therefore be fitter at some point along the cline. The wave of advance model sees multiple clines for individual alleles forming due to the progression of advantageous alleles from one population the other (Pialek and Barton, 1997).

Certain factors contribute to stability and steepness of hybrid zones within these models by reducing the frequency of inter-population mating and introgression. These include positive assortative mating within populations, habitat selection of different populations (examples of both these found in question 1 part B and question 2) and hybrid unfitness. Additionally, it is suggested that individuals in a populations near a tension zone (in which hybrids are less fit), will evolve methods of only mating with their own population to reduce the prevalence of unfit hybrids. This is dubbed reinforcement, and controversy remains as to its importance (Howard, 1993).

Hybrid zones can also occur across regions of primary contact in which parapatric speciation is taking place. As a population spreads across a contiguous area it may spread into an abruptly different environment. The populations will deviate and begin parapatric speciation – those in the new environment adapting to the different conditions. The point of contact between the older population and the newer population will be a stepped cline and a hybridisation zone can form. Despite this, the two populations will never have been fully isolated from one another, unlike in cases of secondary contact. This distinction may not be a very useful one as in practice it can be quite difficult to distinguish between primary and secondary contact (Endler, 1982).

Hybrid Zone Case Study

Mussel populations show extensive hybridisation worldwide and are a well studied example of a marine hybrid zone. There are multiple sites of hybridisation between the species Mytilus edulis, M. trossulus and M. galloprovincialis across the Atlantic, Scandinavian and the Mediterranean Seas. These hybrid zones vary considerably. Some hybrid zones, such as the one in Newfoundland in Canada show remarkably few hybrids, while in Scandinavia most individuals are hybrids to some degree. Morphological and genetic differences are clear between these populations and it is believed that they are close to full speciation. They are probably maintained through a combination of hybrid unfitness, positive assortative mating and habitat segregation. In this summary focus will be on the Canadian hybrid zone in the North Atlantic, particularly that near Newfoundland which has been studied by researchers at Newfoundland Memorial University.

Based on the fossil record and genetic marker studies the following chronology is used to explain the Mussel hybrid zone:

- The genus Mytilus is at one point restricted to the North Pacific but spreads to the Atlantic through the Bering Straight around 3.5 million years ago (Vermeij 1991).
- M. trossulus evolves in the North Pacific and M. edulis in the Atlantic in near allopatry as migration across the Bering Straight is very low.
- Subsequently M. galloprovincialis undergoes cladogenesis from M. edulis in the Mediterranean Sea after it is temporarily isolated from the Atlantic.
- Recently M. trossulus from the Pacific enters the Atlantic and colonises shores on both sides. It spreads and forms secondary contact hybrid zones with M. edulis populations on coasts across Scandinavia and the eastern Atlantic.
- Riginos and Cunningham (2005) includes a suggested pattern of migration of M. trossulus across the ocean based on a review of genetic marker studies.

The Canadian hybrid zone is unusual because both species are found along the entire shore (a mosaic pattern) instead of the typical cline found in most hybrid zones (Bates and Innes, 1995). Studies of mtDNA and allozymes in adult populations show that the distribution of genotypes between the two species is bimodal; pure parental types are most common (representing above 75% of individuals) while backcrosses close to parental forms are the next most prevalent. F1 hybrid crosses represent less than 2.5% of individuals (Saavedra et al., 1996).

The low frequency of F1 hybrids coupled with some introgression allows us to infer that although fertile hybrids can be produced, significant reproductive barriers exist and the two species are sufficiently deviated that they are now able to avoid recombinational collapse despite habitat sharing. Jiggins and Mallet (2000) have found that hybrid zones with low levels of F1 hybrids (bimodal distribution of hybrids) are highly stable and usually the result of assortative mating or fertilization, and not related to gross levels of genetic divergence or intrinsic genomic incompatibility. They hypothesized that such zones occurred between two populations that were close to full speciation and with some reinforcement. Toro et al. (2002) investigated whether different reproductive patterns and behaviour were the cause of this prezygotic isolation and discovered that M. edulis spawned over a 2-3 week period in July, while M. trossulus spawned over a more extensive period between late spring to early autumn. It was also found that hybrids were not infertile and exhibited normal reproductive development, allowing them to introgress with pure species. It was concluded that “differences in reproductive traits may partially explain the maintenance of the mussel hybrid zone in Newfoundland.”

The other likely candidate for hybrid zones stability is species segregation by habitat which has been investigated but not conclusively. Several studies have suggested that M. edulis are found in areas of lower salinity and less wave exposure at the heads of bays more than M. trosullus. M.trosullus appears to be favoured in habitats with higher wave exposure (Bates and Innes, 1995). The one subtidal (low wave action) site sampled by Bates and Innes had just 8% M. trossulus individuals. A similar segregation has been found in the Mediterranean hybrid zone with M. edulis also favouring more sheltered habitats compared to M. galloprovincialis (Bierne et al. 2003). If this is the case, this would provide partial habitat separation and reduce the probability of gametes of two species encountering one another and cross-fertilising. This would increase genetic distinctiveness despite the populations living in sympatry. However, conflicting results have been identified to this trend of habitat segregation and so these results are not conclusive (Riginos and Cunningham, 2005). It is suggested that differences in habitat are what has led to the very different type of hybrid zones in Scandinavia and Canada. Hybrid mussel fitness has not been properly investigated, so it is not possible to judge its effects on postzygotic isolation and whether it could cause reinforcement (Riginos and Cunningham, 2005).