SPECIATION, PROCESS OF

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I. Speciation and Species
II. Reproductive Barriers to Gene Flow and the Evolution of Mate Recognition Systems
III. Two Modes of Speciation
IV. Summary

GLOSSARY

allopatric Populations, species, or taxa occupying different and disjunct geographical areas.
ecotone The boundary or transitional zone between adjacent ecological communities or biomes.
epistasis The interaction of non-allelic genes in which one gene (epistatic gene) masks the expression of another gene at a different locus.
genetic drift The occurrence of random changes in the gene frequencies of small isolated populations not due to selection, mutation, or immigration.
isolating mechanisms Any intrinsic or extrinsic mechanism or barrier that inhibits the free exchange of genes between populations.
plesiomorphic gene A gene that has more than one independent phenotypic effect.
polyplod Having more than one set of homologous chromosomes.
sister species A pair of species that have arisen from a single speciation event; each is the other’s closest relative.
sympatric Populations, species, or taxa that occur together in the same geographical area within the dispersal range of one another.

SPECIATION is the process by which new species are formed. Understanding the origin of species and their contribution to the origin of biodiversity requires an understanding of the process of speciation and an appreciation of the problem of how to define a species.

I. SPECIATION AND SPECIES

A. Speciation
The ultimate source of the earth’s biodiversity is speciation, a process that occurs when gene flow is reduced sufficiently between sister populations to allow each to become irrevocably committed to different evolutionary lineages. Speciation results in the splitting of a lineage into two or more species (cladogenesis). However, when a species is transformed over time (anagenesis) by the acquisition of phenotypic and genetic modification, there is no increase in the number of species and thus no speciation event (Fig. 1a).

B. The Species Problem
Although the end product of speciation seems clear, defining when and under what conditions two popula-
tions become irrevocably committed to different evolutionary lineages has proved to be difficult and controversial. A frequently invoked species definition is the biological species concept (BSC) of Mayr (1942), who proposed that "species are groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups" (p. 120).

However, the BSC and its later modifications have several limitations. It can be applied objectively only to sexually reproducing taxa and to natural populations that are sympatric (i.e., those that occur in the same geographic area) where they have the opportunity to interbreed. Asexually reproducing taxa and fossils must be treated subjectively. A more serious limitation of the BSC is that sympatric taxa that maintain distinct phenotypic and genotypic differences, but sustain some gene flow through interbreeding with close relatives, are generally not recognized as species. Recent molecular studies on closely related sympatric animal and plant taxa recognized as distinct, closely related sister species (the products of one speciation event) reveal that gene flow between them may still occur (Feder et al., 1995; Taylor et al., 1997). Such neospecies have acquired sufficient genetically based differences to maintain independent genotypes and distinct phenotypes but are still capable of sustaining some gene flow as they diverge. Several other species concepts have been proposed (Futuyma, 1998), but all suffer from problems of circularity, inconsistencies, and untestable qualities.

For this reason, the genetic-based species concept of Mallet (1995) provides a useful, less assumption-laden, operational species definition for identifying sister species. Mallet proposed that sister species be recognized only when they maintain distinctly different sym-
patric genotypic clusters. Defining a species based on
genotypic clusters represents the level of differentiation
most interesting to those studying speciation. Gener-
ally, sympatric sister taxa that maintain distinct geno-
typic clusters exploit different habitats or hosts. The
wide use of modern DNA analysis in evolutionary stud-
ies makes this a useful approach particularly when
coupled with sound biological studies. However, as with
the BSC, using genotypic clusters to determine the bi-
ological status of geographically isolated sister popula-
tions without a "test of sympatry" is still a subjective
although somewhat more quantitative call.

II. REPRODUCTIVE BARRIERS TO GENE
FLOW AND THE EVOLUTION OF MATE
RECOGNITION SYSTEMS

A. Reproductive Barriers
The free exchange of genes between populations adapt-
ing to different niches inhibits the evolution of in-
dependent genetic systems. As soon as adaptive gene
combinations are formed, they are broken up by recombina-
tion through interbreeding. There are several
biologically based reproductive barriers or "isolating
mechanisms" that evolve during the course of speciation
which limit gene flow between sister species (Table 1).
These biological barriers constitute components of a
mate recognition system that promotes assortative mat-
ing between individuals adapted or adapting to shared
environmental and reproductive conditions.

III. TWO MODES OF SPECIATION
There are two primary modes of speciation recognized
by most evolutionary biologists (Table II). Allopatric
(geographic) speciation occurs when sister populations
are isolated for a period by a physical barrier such as
a mountain range or an expanse of uninhabitable terrain
or water. In the absence of gene flow, such isolated
populations inevitably accumulate unique mutations
and, over time, may diverge genetically by genetic drift
and in response to divergent selection pressures. If suf-
ficient genetic divergence occurs during isolation to
establish and maintain distinct genotypic clusters, par-
particularly when their ranges later overlap, then the taxa
are regarded as species.

Non-allopatric (ecological) speciation occurs in the
absence of physical barriers to gene flow when sister
populations diverge genetically and become ecologi-
cally and reproductively isolated as they adapt to dif-
ferent habitats. New sister species thus evolve within the
dispersal range of the offspring from a single deme.
Several different patterns of geographic and ecological
speciation are recognized based on the factors involved
in promoting their divergence, such as population

| TABLE I |
| Classification of Reproductive Isolating Mechanisms |

| Prezygotic isolating mechanisms: mechanisms that prevent interspecific mating |
| Temporal isolation (potential mates have overlapping ranges but reproduction occurs at
different times) |
| Habitat isolation (potential mates have overlapping ranges but reproduction occurs in dif-
ferent habitats) |
| Ethological isolation (potential mates meet but do not mate) |
| Mechanical isolation (potential mates attempt to copulate but no sperm is transferred) |
| Mechanism that prevents fertilization |
| Gametic mortality (sperm is transferred but egg is not fertilized) |
| Gametic incompatibility (gametes meet but fertilization is not completed) |
| Postzygotic isolating mechanisms: mechanisms that prevent the development of interspe-
cific hybrids |
| Zygote mortality (eggs fertilized but zygote dies) |
| Hybrid inviability (zygote produces F1 hybrid of reduced viability) |
| Hybrid sterility (F1 hybrid zygote is fully viable but partially or completely sterile or pro-
duces deficient F2 hybrid) |
| Coevolutionary or cytoplasmic interactions (individuals from a population infected by an
endoparasite or with a particular cytoplasmic element are fertile with each other, but fer-
tility and/or viability break down when matings occur between infected and uninfected
individuals) |
structure, habitat specialization, hybridization, and polyploidy.

A. Geography, Geographic Races, and Allopatric Speciation

The process of geographic speciation (often referred to as allopatric speciation) may happen in two ways. Dichopatric or vicariant speciation (Fig. 1b) occurs when a widespread species becomes geographically divided into two or more large subpopulations by an insurmountable or impassable barrier. A second mode of geographic speciation, usually called peripatric or founder event speciation (Fig. 1c), occurs when a geographically isolated population is established by a single fertilized female or a very small number of founding individuals.

However, determining the actual biological status of sister taxa that have arisen in isolation following either a vicariant or a founder event is difficult and controversial. Species can be recognized when artificial hybridization of allopatric taxa in the laboratory reveals post-mating reproductive isolation. If no post-mating incompatibility is noted and mating occurs, then it is necessary to determine if there are factors important in pre-mating isolation not provided in the laboratory environment of the tests. Whether or not such populations are species or geographic races may require an unequivocal “test of sympathy” in which the two taxa coexist without fusing. Only when previously isolated taxa have the opportunity to interbreed under natural field conditions can the species status of closely related taxa lacking post-mating reproductive isolation be confirmed. If they maintain distinct sympatric genotypic clusters, they should be recognized as distinct species. Because such tests cannot often be performed, deciding on whether isolated taxa represent species or geographic races (i.e., subspecies) is a subjective decision. However, it should be stressed that when two taxa overlap naturally (i.e., are parapatric) and do not interbreed, this does not necessarily mean that they speciated sympatrically. This is because it is often impossible to establish if the overlap represents a case of secondary contact following allopatric speciation or if the taxa evolved as the result of non-allopatric divergence.

1. Dichopatric Speciation

When populations of geographically isolated sister taxa remain large during and following geographic subdivision, they will slowly diverge genetically by genetic drift and as they adapt to local conditions in isolation. Over time, they may accumulate sufficient genetic differences to cause negative pleiotropic gene interaction and hybrid incompatibility among genes responsible for proper mate recognition and genome integration. Reproductive isolation therefore occurs by chance as the by-product of genetic divergence in isolation rather than the outcome of natural selection acting directly to promote reproductive isolation.

a. Dichopatric Race Formation and Speciation in Salamanders

The long-term study of evolution in the plethodontid salamander genus *Ensatina* by David Wake and colleagues (Wake and Schneider, 1998; Wake, 1997) provides an excellent example of dichopatric speciation and incipient species formation. The *Ensatina eschscholtzii* complex represents an ancient lineage that has undergone several instances of range contraction, isolation, and expansion and divergence of populations along broad ecological gradients. It is composed of seven contiguous subspecies wrapped in ring-like fashion around the Central San Joaquin Valley of California (Fig. 2). Historically, populations of *Ensatina* slowly differentiated into highly distinct forms from the northern subspecies *E. e. oregonensis* in color and pattern as they expanded southward. Blotched forms occur in the Sierra Nevada and mountains of southern California, whereas unblotched forms are found in the coastal and northern region of their range. The animals, which are long-lived (10–15 years) and take 4 years to mature, are
sedentary and disperse only short distances (home range 10–20 m).

Hybridization and intergradation occur between adjacent subspecies to varying degrees in all except one contact zone. The exception occurs in the Cuyamaca Mountains of San Diego County, in which *E. e. eschscholtzii* and *E. e. klauberi* overlap but rarely interbreed in sympathy and are regarded by some biologists as distinct species. In other areas, the complex includes many geographically and genetically distinct entities, some of which are near the species level of differentiation.
A limited narrow secondary hybrid zone also occurs in Calaveras County between the upland *E. e. platensis* and a coastal, lowland subspecies, *E. e. xanthoptica* that established an outpost in the Sierra foothills sometime in the past. *Ensatica e. platensis* lives in the cool and moist, closed canopy forest at higher elevation than those of *E. e. xanthoptica*, which prefers warmer and drier lower elevations. Hybridization between the pure subspecies is rare, with most hybrids representing progeny from backcrosses or from crosses between hybrid individuals. Hybrid individuals appear to be at a selective disadvantage and thus subject to strong negative selection. They have reduced success in competing for preferred habitats and mates and seem to be more prone to predation. Because little or no gene flow occurs across the narrow hybrid zone, the coastal and Sierra taxa behave as incipient species or taxa in the final stages of speciation. Four other hybrid zones in central California involving *E. e. xanthoptica* have been characterized in detail. The *Ensativa* complex presents a full array of differentiation from geographically variable populations or races to well-marked species. It provides an excellent example of how speciation has progressed slowly by adaptive divergence and stochastic processes during periods of geographic isolation.

2. Peripatric Speciation and the Founder Effect Principle

There are several examples in which species appear to have evolved in small, isolated populations at the periphery of the range of a sister species. Unlike the slow rate of evolution in dichotomous speciation, peripatric speciation is postulated to take a relatively short time. How and how often this divergence occurs is controversial (Barton, 1996; Hollocher, 1996).

Three models, each based on a founder event in which a population is established by only a few individuals, have been proposed to account for the rapid evolution of species observed on islands and elsewhere (Fig. 1c). The founder effect principle was developed by Mayr (1954). It is based on the assumption that reproductive isolation from the parent species can evolve rapidly in a population established by a very small number of founding individuals (i.e., 2–10). He postulated that in such populations a genetic revolution could take place as a by-product of inbreeding, selection, drift, and genome reorganization. While the population is small, these genetic changes may promote substantial morphological and ecological shifts.

A modification of the founder effect principle was proposed by Carson (1975). In his founder-flush model of speciation, isolated populations undergo a series of population expansions and drastic contractions to a very small number of individuals. Carson believes that founder-flush speciation can occur only in certain cross-fertilizing diploid organisms with “open” genetic systems. The genome in such organisms represents a clique of harmoniously collaborating or coadapted genes united by strong epistatic interactions. Their genomes also have abundant pleiotropic interacting genetic polymorphisms and share a high recombination index. Carson hypothesized that these attributes provide great genetic flexibility that predisposes such organisms to speciate by the founder-flush process.

In Carson’s view, the drastic events required to reorganize the original genetic system and restore new balances that are incompatible with ancestors are accomplished during cycles of the founder-flush process. Selection, which is relaxed during the flush phase of population expansion, is greatly intensified as the population crashes. Repeated disorganization and reconstitution of the genome results in the rapid evolution of reproductive isolation.

Templeton (1980) proposed a third modification of founder-induced speciation that involves a genetic transience (Carson and Templeton, 1984). It is similar to Carson’s founder-flush speciation but requires changes in only one or a few segregating units, commonly with epistatic modifiers responsible for reproductive isolation that occurs when a population rapidly passes through an extremely unstable intermediate genetic state. As in the case of the founder-flush model, a genetic transience involves strong inbreeding and large variance in population size. The critical trigger that initiates a transience requires a reweighting of fitness components owing to drift-induced shifts in allele frequencies at one or more major loci that have pleiotropic effects on reproductive isolation.

It seems clear that speciation may occur rapidly following the geographic isolation of a small population. It is not clear, however, whether speciation results from a founder-flush or transience process or solely from natural selection in response to factors such as runaway sexual selection or rapid adaptation to divergent ecological and reproductive conditions. Because conditions required for stochastic transitions are severe and well-documented cases are lacking in which drastic genetic changes caused by founder effects result in speciation, it appears that the process of speciation in small, peripheral populations is the same as that which occurs in dichotomous speciation. Although certain kinds of epistasis can promote strong reproductive isolation, divergence occurs by selection and not random genetic drift (Barton, 1996).
B. Ecology, Ecological Races, and Nonallopatric (Ecological) Speciation

Reproductive isolation between sister populations in cases of allopatric speciation arises as a by-product of genetic changes that originate and accumulate independently in each population during periods of geographic isolation. Speciation may or may not be accompanied by an ecological transformation. In contrast, nonallopatric or ecological speciation inevitably involves a shift to a new niche at the time of speciation, and adaptation to different habitats is the driving force initiating and sustaining genetic divergence (Figs. 1d–1f). Divergent selection on existing genetic variation results in the evolution of reproductive isolation as different suites of genetic variants are favored in each habitat. The emergence of reproductive isolation is also facilitated when mating occurs within a preferred habitat or if mate preference that is based on a phenotypic variant of a sexually selected trait becomes associated with a preferred habitat (Johnson et al., 1996).

A misconception concerning nonallopatric speciation is that it requires a process called reinforcement, which involves the divergence of the mate recognition system between populations during the speciation process as an outcome of selection against hybrids (Butlin, 1987). Because theoretical models suggest that recombination will not allow reproductive reinforcement to develop, critics have argued that parapatric and sympatric speciation are unlikely to occur in nature. These models, however, fail to factor in the role of habitat preference and specialization in speciation and the effects of ecological divergence, which always accompanies sympatric speciation. When habitat choice is taken into consideration, conditions for sympatric speciation are greatly relaxed and its occurrence is probable (Johnson et al., 1996).

Three modes of nonallopatric speciation are generally recognized in sexually reproducing organisms. Parapatric speciation (Fig. 1d) takes place when sister species evolve while adapting to contiguous but spatially segregated habitats or ecotones across a narrow contact zone (Bush, 1994). Sympatric speciation (Fig. 1e) occurs in the absence of geographic segregation when sister species evolve within the dispersal range of the offspring of a single deme. During the course of sympatric speciation, the probability of mating between two individuals depends on their genotypes, and divergence occurs between populations adapting to alternate habitats within the “cruising range” of each other. Parapatric and sympatric speciation actually represent extremes of a continuum in the pattern and extent of habitat and geographic-imposed spatial segregation and gene flow reduction that occurs during nonallopatric divergence. Hybridization (Fig. 1f) is a third mode of nonallopatric speciation. New species rapidly evolve from a mating between individuals of two closely related species by a variety of different processes. It is a frequent mode of speciation in plants but appears to be rare in animals.

1. Parapatric Speciation

This mode of speciation occurs when sister species evolve while adapting to contiguous habitats (or ecotones) along a zone of contact. Examples from nature involve situations in which individuals from a species adapted to one habitat invade and colonize an adjacent habitat. Individuals bearing novel genetic recombinants capable of exploiting and reproducing in the new habitat are the first to invade and colonize the narrow zone where the two habitats meet. As adaptation proceeds, the new colony expands throughout the range of the new habitat. Only along the adjoining borders between the original and new habitat is gene exchange possible between the two populations. As the new population adapts to conditions imposed by the new habitat, divergent selection promotes the evolution of reproductive isolation and eventually parapatric species.

a. Parapatric Speciation in *Mimulus*

An example of rapid parapatric adaptation and speciation of a plant to a newly established vacant niche is that of the monkey flower *Mimulus cupriphilis* in California (Macnair and Gardner, 1998). This species grows only on relatively dry and toxic mine tailings of two small copper mines in California. It grows in close proximity and is recently derived from the widespread hydrophylic *M. guttatus*.

The two species differ in many ways. *Mimulus cupriphilis*, an obligate annual, flowers earlier and produces many small flowers that differ in shape and color from those of *M. guttatus*. *Mimulus cupriphilis* also has higher fitness on the dry tailings of the copper mines and flowers early when pollinators are rare. Because it is self-fertilizing, it is reproducitively isolated from the outcrosser *M. guttatus*, which blooms later when its larger flowers are fertilized by bumblebees. Genetic studies have revealed that the species differ in a few major genes controlling flowering time, flower size, corolla spot number, and general size. Because all the genetic systems are recessive with the exception of flowering time, recessive alleles would be spread by natural selection in the original outbreeding parent spe-
cies. In inbreeders, there is no difference between dominant and recessive alleles.

*Mimulus cuprililis* has evolved recently since the copper mines are less than 150 years old. The shift to the new soils created by the mines involved the development of a copper-tolerant ecotype with a primary semidominant adaptive mutation that shifted flowering time earlier in the plants growing in dry habitats. In the absence of pollinators early in the season, selection favored alleles for self-fertilization. This was accomplished by flower size reduction that brought the stigma and anthers in close proximity. Reduction in size of corolla and associated structures may have also freed up resources for seed production. The result is a new selfing species that has evolved locally in a very short time and that is well adapted to the unique conditions of the mine tailing fields.

There is no evidence of a genetic revolution or reduction in genetic diversity in the new species and F₁ progeny. Nor is there evidence of significant breakdown in so-called gene complexes or major epistatic interactions. Therefore, it is concluded that speciation has been achieved by new selection pressures on normal *M. guttatus* as it colonized a new and unusual habitat. Major genes of large effect that play important roles in reproductive isolation have also been demonstrated in other sister species of *Mimulus* species (Bradshaw et al., 1995). In such cases, new species have the potential to appear nearly full-blown in relatively few evolutionary steps because of changes in a few essential genes.

2. Sympatric Speciation

It is now apparent that sympatric speciation, once thought to be rare in animals and plants, occurs more frequently than previously realized. Because two closely related sympatric sister species cannot share the same resources, nonallopatric speciation is inevitably accompanied by the shift and exploitation of a new habitat by the daughter species. Such habitat or resource shifts reduce competition between sister species. It is for this reason that sympatric speciation is often referred to as ecological speciation.

a. Sympatric Speciation in Cichlid Fish

The important role of ecology in sympatric speciation is exemplified by the study of Schliwien et al. (1994). In a molecular phylogenetic study they discovered that two endemic cichlid fish species flocks (9 and 11 species) in two small, ecologically monotonous volcanic lakes (4.15 and 0.6 km²) in Cameroon speciated sympatrically. Because each crater is isolated from rivers and lacks internal structure, past lake levels are not responsible for physically isolating sister populations during speciation. Field observations, stomach content analyses, and the presence of specialized morphological features related to feeding confirm that the species within each lake have different benthic or pelagic trophic and reproductive ecologies. Although all species nest on the bottom and are capable of encountering one another at moderately high frequencies along ecotones, no hybrids are found because the species mate assortatively and do not interbreed.

Phylogenetic trees were constructed based on an analysis of a 340-base pair fragment of mtDNA cytochrome b and an additional 350 base pairs from the rapidly evolving mitochondrial control region for all 20 species and all tilapine species in neighboring river systems and lakes. This analysis confirmed that the lake species are monophyletic with respect to the river species, i.e., each flock evolved within each lake after a single colonization event.

b. Sympatric Host Race Formation and Speciation in Rhagoletis Fruit Flies

The importance of habitat and resource shifts in the nonallopatric speciation process is exemplified in the case of recent host race formation and speciation in the tephritid fruit fly genus *Rhagoletis* (Bush and Smith, 1998; Feder, 1998). As in other phytophagous and parasitic insects, mating in these flies occurs on the host plant, primarily on the host fruit in which eggs are deposited and larvae develop. *Rhagoletis pomonella*, whose native hosts are fruits of several hawthorn (*Crataegus*) species, colonized apples in approximately 1860, more than 200 years after this fruit tree was introduced to North America by Europeans. Early infestations on apples were restricted to a small area of the Hudson River valley in southern New York where hawthorn is common. The apple flies later spread over the entire northeastern United States and southeastern Canada, where it became a major pest. In a brief span of 150 years, the apple and hawthorn populations diverged in several genetically based traits, such as eclosion time of the adult in summer, and host recognition and acceptance. In addition, strong frequency differences in alleles at several loci coding for proteins are maintained by strong selection and greatly reduced gene flow between the races. The apple and hawthorn races now behave as semispecies or species. All seven members of the *R. pomonella* species group are sympatric in eastern North America and speciation in this species group has always been accompanied by a shift to a new host plant family or genus.
C. Other Modes of Nonallopatric Speciation

1. Spontaneous Thelytokous Speciation
This mode of sympatric speciation occurs when a unissexually reproducing taxa arises spontaneously from an unfertilized egg of a diploid bisexual species. Subsequent reproduction in taxa originating in this way produces only females from unfertilized eggs. Several good examples are provided by White (1978).

2. Autopolyploid Speciation
Occasionally, polyploidization of a diploid species may occur spontaneously in one or more individuals. Because autopolyploid individuals have three or more chromosome sets, each chromosome has more than one homologous pairing partner. During meiosis, multivalents are produced leading to unbalanced gametes and zygotes, sterility, and other problems. Only rarely does autopolyploidy result in the origin of new species, such as in the common potato (Solanum tuberosum) and its relatives (Grant, 1981). These usually originate from crosses between races whose chromosomes differ only slightly.

3. Speciation by Interspecific Hybridization
A new species can arise two ways by interspecific hybridization (Fig. 1f). Homoploid hybrid speciation results in a diploid-derived species, whereas polyploid hybrid speciation produces a species that combines a complete set of chromosomes from each hybridizing parental species. Hybrid species occupy habitats different from those of the parental species, thus reducing competition and the level of gene flow between them. Hybrid speciation, which is far more common in plants than in animals, can occur in at least four ways.

a. Introggressive Hybrid Speciation
Individual gene exchange among closely related species provides recombinant offspring that shift to and exploit a new habitat not utilized by either parental species. The hybrid species may be interfertile with one or both parental species, but it is reproductively isolated from them by premating barriers to gene flow. This mode of speciation has been reported in several plant species (Grant, 1981), but confirmation of this mode of speciation remains controversial and requires definitive experimental and analytical studies.

b. Recombinational Hybrid Speciation
A far more common mode of hybrid speciation involves the formation and establishment in the progeny of a chromosomally sterile or semisterile species hybrid of a new, structurally homezygous recombination type. Individuals are fertile within the line but isolated from other lines and from the parental species by a chromosomal sterility barrier. It is most likely to occur when the hybrid interface is long and the organisms involved are predominantly selfing, relatively fertile, and possess few structural chromosome differences between the parental species.

i. Hybrid Speciation in Wild Sunflowers
A molecular study of hybrid speciation in the wild sunflowers Helianthus by Rieseberg et al. (1995) revealed that F1 hybrids of H. annus and H. petiolaris are semisterile with pollen viabilities less than 10% and seed set less than 1%. F2 pollen viability is highly variable, ranging from 13 to 97%. The two species are distinguished by several morphological and chromosomal features, and based on chloroplast DNA and nuclear ribosomal DNA variation they occur in divergent clades. Although the species are sympatric throughout much of the western United States, they have different ecological requirements. Helianthus annus is restricted to heavy, clay soils, whereas H. petiolaris predominantly inhabits dry, sandy soils.

Helianthus anomalous is a rare endemic to xeric habitats in northern Arizona and southern Utah. It is well within range of parental species and is a recombinational hybrid resulting from a cross between H. annus and H. petiolaris. The F1 hybrids with parental species are partially sterile because chromosomal structural differences enhance reproductive isolation. A preliminary survey of 126 loci in natural populations of the parental species indicated that H. anomalous has loci derived from both H. annus and H. petiolaris. Some blocks of markers, possibly protected from recombination, are transmitted intact.

Helianthus anomalous combines rDNA repeat units and allozymes of H. annus and H. petiolaris as predicted for diploid hybrid species, although individuals possess chloroplast haplotypes of H. annus and H. petiolaris rather than a unique haplotype. Genetic linkage maps generated for all three species using random amplified polymorphic DNA markers reveal loci distributed onto 17 linkage groups corresponding to the haploid chromosome number of the three species. Although levels of polymorphisms vary from 212 in H. annus to 400 in H. petiolaris, map density is similar among species. By comparing genomic location and linear order of homologous markers, chromosomal structural relationships were inferred among the three species. Even though 6 linkage groups showed no changes
in all three species, the remaining 11 linkages were not conserved in gene order. The parental species differ from *H. anomalous* by at least 10 separate structural rearrangements, 3 inversions and a minimum of 7 interchromosomal translocations. The genome of *H. anomalus* is thus extensively rearranged relative to its parents. All 7 novel rearrangements in *H. anomalus* involve linkage groups that are structurally divergent in parental species, suggesting that structural differences may induce additional chromosomal rearrangements upon recombination.

c. Allopolyplid (Amphiploid) Speciation

Interspecific hybridization can also result in combining two or more complete chromosome sets. F1 hybrids produced between two established related species are often sterile because chromosomes lack sufficient homology to pair well at meiosis. Fertility is restored if hybrids persist long enough by asexual reproduction until somatic doubling of the chromosomes can occur in a flower, or until there is a rare union between two unreduced gametes. A new sexually reproducing species is then established that is "instantaneously" isolated from both parental species (Grant, 1981).

i. Allopolyplid Speciation in Spartina anglica

The recent natural rapid evolution of the amphiploid perennial salt marsh grass, *Spartina anglica*, provides an example of allopolyplid speciation (Raybould et al., 1991). This species originated on the south coast of England at the end of the nineteenth century. It arose as a result of chromosome doubling in *S. x townsendii*, a hybrid between the native British *S. maritima* and the North American *S. alterniflora*, introduced by shipping (Fig. 3). *Spartina anglica* is now widespread along the English coast and is highly successful.

Although more than half of all plant species are directly or indirectly the by-products of allopolyplid speciation, allopolyplid speciation is relatively rare in animals (White, 1978).

d. Direct and Reticulate Allogenous Speciation

There are two modes of allogenous speciation (i.e., combining the genomes of two distinct species). In the case of direct allogenous speciation, hybridization between two bisexual, closely related species combines the genomes of two distinct parental species giving rise to a new, unisexual species (Bullini, 1994). The hybridization event produces either an allotriploid or an allotriploid unisexual species that acquires clonal (parthenogenesis) or hemiplanonal (hybridogenesis; i.e., it must mate with males of a bisexual parental species) modes of reproduction. In most such clonal and hemiclonal organisms, the heterozygous genetic structure of the parental species is retained.

In the case of reticulate allogenous speciation, individuals of bisexual hybrid taxon hybridize with a bisexual relative giving rise to new, unisexual species, often with a higher ploidy level than that of the parental species (Bullini, 1994). Most have highly heterogeneous genomes that display heterosis. Clones produced by direct and indirect allogenous speciation exhibit heterosis and demographic advantage over both parental species and individuals.

IV. SUMMARY

After 140 years of speciation research, it is now clear that animal and plant species can originate in a variety of ways. Rapid autopolyplid speciation is common in
plants and accounts for many plant species. In animals, this mode of speciation is relatively rare. Dichopatric speciation gives rise to many, possibly the majority, of the species in some animal groups such as the land vertebrates. In fish, both allopatric and nonallopatric speciation have been reported. The majority of living organisms, however, are insects. Some authorities estimate there are as many as 30–40 million species, and all agree that there are more than 10 million. Approximately 70–75% are highly specialized parasites that feed in or on plant and animal tissue. Although many of these insects probably originated by nonallopatric speciation, it is not clear what percentage have done so. The same is true for the many mites and nematode species that also may number in the millions. Because the mode of speciation in only an extremely small number of animal and plant species has been established, it is impossible to estimate how often each mode of speciation occurs in any particular group of organisms. Such estimates must await research on a great many more taxa.

See Also the Following Articles

CLADOGENESIS • SPECIATION, THEORIES OF • SPECIES, CONCEPT(S) OF • SPECIES DIVERSITY, OVERVIEW

Bibliography


