CHAPTER 24
THE ORIGIN OF SPECIES

OUTLINE

I. What Is a Species?
  - A. The biological species concept emphasizes reproductive isolation
  - B. Prezygotic and postzygotic barriers isolate the gene pools of biological species
  - C. The biological species concept does not work in all situations
  - D. Other species concepts emphasize features and processes that identify and unite species members

II. Modes of Speciation
  - A. Geographical isolation can lead to the origin of species: allopatric speciation
  - B. A new species can originate in the geographical midst of the parent species: sympatric speciation
  - C. Genetic change in populations can account for speciation
  - D. The punctuated equilibrium model has stimulated research on the tempo of speciation

The Origin of Evolutionary Novelty
  - A. Most evolutionary novelties are modified versions of older structures
  - B. Genes that control development play a major role in evolutionary novelty
  - C. An evolutionary trend does not mean that evolution is goal oriented

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Distinguish between anagenesis and cladogenesis.
2. Define morphospecies and explain how this concept can be useful to biologists.
3. Define biological species (E. Mayr).
4. Describe some limitations of the biological species concept.
5. Explain how gene flow between closely related species can be prevented.
6. Distinguish between prezygotic and postzygotic isolating mechanisms.
7. Describe five prezygotic isolating mechanisms and give an example of each.
8. Explain why many hybrids are sterile.
9. Explain, in their own words, how hybrid breakdown maintains separate species even if gene flow occurs.
10. Distinguish between allopatric and sympatric speciation.
11. Explain, in their own words, the allopatric speciation model and describe the role of intraspecific variation and geographical isolation.

12. Explain why peripheral isolates are susceptible if geographic barriers arise.
13. Describe the adaptive radiation model and use it to describe how it might be possible to have many sympatric closely related species even if geographic isolation is necessary for them to evolve.
14. Define sympatric speciation and explain how polyploidy can cause reproductive isolation.
15. Distinguish between autopolyploidy and allopolyploidy.
16. List some points of agreement and disagreement between the two schools of thought about the tempo of speciation (gradualism vs. punctuated equilibrium).
17. Describe the origins of evolutionary novelty.

KEY TERMS

macroevolution	postzygotic barriers	adaptive radiation	allometric growth
speciation	morphological species concept	polyploidy	heterochrony
anagenesis	recognition species concept	autopolyploid	homeosis
phyletic evolution	cohesion species concept	allopolyploid	
cladogenesis	ecological species concept	hybrid zone	
branching evolution	evolutionary species concept	punctuated equilibrium	
species	allopatric speciation	exaptation	
prezygotic barriers	sympatric speciation	paedomorphosis	

LECTURE NOTES

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

The fossil record provides evidence for two patterns of speciation: *anagenesis* and *cladogenesis* (see Campbell, Figure 24.1).

- *Anagenesis (phyletic evolution)* = The transformation of an unbranched lineage of organisms, sometimes to a state different enough from the ancestral population to justify renaming it as a new species.
- *Cladogenesis (branching evolution)* = The budding of one or more new species from a parent species that continues to exist; is more important than anagenesis in life's history, because it is more common and can promote biological diversity.

I. What Is a Species?

Species = Latin term meaning "kind" or "appearance

Linnaeus (founder of modern taxonomy) described species in terms of their physical form (morphology). Morphology is still the most common method used for describing species.

Modern taxonomists also consider genetic makeup and functional and behavior features when describing species.

A. The biological species concept emphasizes reproductive isolation

In 1942, Ernst Mayr proposed the *biological species concept.*

Biological species = A population or group of populations whose members have the potential to interbreed with one another in nature and to produce viable, fertile offspring, but cannot produce viable, fertile offspring with members of other species (see Campbell, Figure 24.2).

- Is the largest unit of population in which gene flow is possible
- Is defined by reproductive isolation from other species in *natural* environments (hybrids may be possible between two species in the laboratory or in zoos)

B. Prezygotic and postzygotic barriers isolate the gene pools of biological species

Any factor that impedes two species from producing viable, fertile hybrids contributes to reproductive isolation.

- Most species are genetically sequestered from other species by more than one type of reproductive barrier.
- Only intrinsic biological barriers to reproduction will be considered here. Geographic segregation (even though it prevents interbreeding) will not be considered.
- Reproductive barriers prevent interbreeding between closely related species.

The various reproductive barriers which isolate the gene pools of species are classified as either prezygotic or postzygotic, depending on whether they function before or after the formation of zygotes.

- *Prezygotic barriers* impede mating between species or hinder fertilization of the ova should members of different species attempt to mate.
- In the event fertilization does occur, *postzygotic barriers* prevent the hybrid zygote from developing into a viable, fertile adult.

1. Prezygotic barriers

a. Habitat isolation

Two species living in different habitats within the same area may encounter each other rarely, if at all, even though they are not technically geographically isolated.

- For example, two species of garter snakes (*Thamnophis*) occur in the same areas but for intrinsic reasons, one species lives mainly in water and the other is mainly terrestrial.
- Since these two species live primarily in separate habitats, they seldom come into contact as they are ecologically isolated.

c. Behavioral isolation

Species-specific signals and elaborate behavior to attract mates are important reproductive barriers among closely related species.

- Male fireflies of different species signal to females of the same species by blinking their lights in a characteristic pattern; females discriminate among the different signals and respond only to flashes of their own species by flashing back and attracting the males.

Many animals recognize mates by sensing pheromones (distinctive chemical signals).

- Female Gypsy moths attract males by emitting a volatile compound to which the olfactory organs of male Gypsy moths are specifically tuned: when a male detects this pheromone, it follows the scent to the female.
- Males of other moth species do not recognize this chemical as a sexual attractant.

Other factors may also act as behavioral isolating mechanisms:

- Eastern and western meadowlarks are almost identical in shape, coloration, and habitat, and their ranges overlap in the central United States (see Campbell, Figure 24.2a).

- They retain their biological species integrity partly because of the difference in their songs, which enables them to recognize potential mates as members of their own kind.

Another form of behavioral isolation is courtship ritual specific to a species (see Campbell, Figure 24.3).

c. Temporal isolation

Two species that breed at different times of the day, seasons, or years cannot mix their gametes.

- For example, brown trout and rainbow trout cohabit the same streams, but brown trout breed in the fall and rainbow trout breed in the spring.
- Since they breed at different times of the year, their gametes have no opportunity to contact each other and reproductive isolation is maintained.

d. Mechanical isolation

Anatomical incompatibility may prevent sperm transfer when closely related species attempt to mate.

- For example, male dragonflies use a pair of special appendages to clasp females during copulation. When a male tries to mount a female of a different species, he is unsuccessful because his clasping appendages do not fit the female's form well enough to grip securely.
- In plants that are pollinated by insects or other animals, the floral anatomy is often adapted to a specific pollinator that transfers pollen only among plants of the same species.

e. Gametic isolation

Gametes of different species that meet rarely fuse to form a zygote.

- For animals that use internal fertilization, the sperm of one species may not be able to survive the internal environment of the female reproductive tract of a different species.
- Cross-specific fertilization is also uncommon for animals that utilize external fertilization due to a lack of gamete recognition.

Gamete recognition may be based on the presence of specific molecules on the coats around the egg which adhere only to complementary molecules on sperm cells of the same species.

- Similar mechanisms of molecular recognition enables a flower to discriminate between pollen of the same species and pollen of different species.

2. Postzygotic barriers

When prezygotic barriers are crossed and a hybrid zygote forms, one of several postzygotic barriers may prevent development of a viable, fertile hybrid.

a. Reduced hybrid viability

Genetic incompatibility between the two species may abort development of the hybrid at some embryonic stage.

- For example, several species of frogs in the genus *Rana* live in the same regions and habitats.
- They occasionally hybridize but the hybrids generally do not complete development, and those that do are frail and soon die.

b. Reduced hybrid fertility

If two species mate and produce hybrid offspring that are viable, reproductive isolation is intact if the hybrids are sterile because genes cannot flow from one species' gene pool to the other.

- One cause of this barrier is that if chromosomes of the two parent species differ in number or structure, meiosis cannot produce normal gametes in the hybrid.
- The most familiar case is the mule which is produced by crossing a donkey and a horse; very rarely are mules able to backbreed with either parent species (see Campbell, Figure 24.4).

c. Hybrid breakdown

When some species cross-mate, the first generation hybrids are viable and fertile, but when these hybrids mate with one another or with either parent species, offspring of the next generation are feeble or sterile.

- For example, different cotton species can produce fertile hybrids, breakdown occurs in the next generation when progeny of the hybrids die in their seeds or grow into weak defective plants.

Campbell, Figure 24.5 summarizes the reproductive barriers between closely related species.

C. The biological species concept does not work in all situations

The biological species concept cannot be applied to:

- Organisms that are completely asexual in their reproduction. Some protists and fungi, some commercial plants (bananas), and many bacteria are exclusively asexual.
  - ⇒ Asexual reproduction effectively produces a series of clones, which genetically speaking, represent a single organism.
  - ⇒ Asexual organisms can be assigned to species only by grouping clones with the same morphology and biochemical characteristics.
- Extinct organisms represented only by fossils. These must be classified by the morphospecies concept.

In some cases, unambiguous determination of species is not possible, even though the populations are sexual, contemporaneous, and contiguous.

- Four phenotypically distinct populations of the deer mouse (*Peromyscus maniculatus*) found in the Rocky Mountains are geographically isolated and referred to as *subspecies*. (see Campbell, Figure 24.6)
- These populations overlap at certain locations and some interbreeding occurs in these areas of cohabitation, which indicates they are the same species by the biological species criteria.
- Two subspecies (*P. m. artemisiae* and *P. m. nebrascensis*) are an exception, since they do not interbreed in the area of cohabitation. However, their gene pools are not completely isolated since they freely interbreed with other neighboring populations.
- This circuitous route could only produce a very limited gene flow, but the route is open and possible between the populations of *P. m. artemisiae* and *P. m. nebrascensis* through the other populations.

- If this route was closed by extinction or geographic isolation of the neighboring populations, then *P. m. artemisiae* and *P. m. nebrascensis* could be named separate species without reservation.

More examples are being discovered where there is a blurry distinction between populations with limited gene flow and full biological species with segregated gene pools.

- If two populations cannot interbreed when in contact, they are clearly distinct species.
- When there is gene flow (even very limited) between two populations that are in contact, it is difficult to apply the biological species concept.
- This is equivalent to finding two populations at different stages in their evolutionary descent from a common ancestor, which is to be expected if new species arise by gradual divergence of populations.

Other species concepts have been developed in an effort to accommodate the dynamic, quantitative aspects of speciation; however, the species problem may never be completely resolved as it is unlikely that a single definition of species will apply to all cases.

D. Other species concepts emphasize features and processes that identify and unite species members

The *morphological species concept* characterizes species on the basis of measurable physical features.

- Can be useful in the field
- Sometimes difficult to apply (e.g., Do physical differences between a set of organisms represent species differences or phenotypic variation within a species?)

In the *recognition species concept*, a species is defined by a unique set of characteristics that maximize successful mating.

- Characteristics may be molecular, morphological, or behavioral in nature
- Characteristics are subject to natural selection

The *cohesion species concept* relies on the mechanisms that maintain species as discrete phenotypic entities.

- Mechanisms may include reproductive barriers, stabilizing selection, and linkages among sets of genes that make a zygote develop into a an adult organism with species-specific characteristics (e.g., sexual reproduction)
- This concept acknowledges that interbreeding between some species produces fertile hybrids (e.g., corn)

The *ecological species concept* defines a species on the basis of where they live and what they do.

The *evolutionary species concept* defines a species as a sequence of ancestral and descendent populations that are evolving independently of other such groups

- Each evolutionary species has its own unique role in the environment; roles are influenced by natural selection.

Campbell, Table 24.1 reviews the species concepts.

II. Modes of Speciation

Reproductive barriers form boundaries around species, and the evolution of these barriers is the key biological event in the origin of new species.

- An essential episode in the origin of a species occurs when the gene pool of a population is separated from other populations of the parent species.

- This genetically isolated splinter group can then follow its own evolutionary course, as changes in allele frequencies caused by selection, genetic drift, and mutations occur undiluted by gene flow from other populations.

There are two general modes of speciation: allopatric speciation and sympatric speciation.

A. Geographical isolation can lead to the origin of species: allopatric speciation

1. Geographic barriers

Allopatric speciation = Speciation that occurs when the initial block to gene flow is a geographical barrier that physically isolates the population

- Geological processes can fragment a population into two or more allopatric populations (having separate ranges).
  - ⇒ Such occurrences include emergence of mountain ranges, movement of glaciers, formation of land bridges, subsidence of large lakes.
  - ⇒ Also small populations may become geographically isolated when individuals from the parent population travel to a new location.
- The extent of development of a geographical barrier necessary to isolate two populations depends on the ability of the organisms to disperse due to the mobility of animals or the dispersibility of spores, pollen and seeds of plants.
  - ⇒ For example, the Grand Canyon is an impassable barrier to small rodents, but is easily crossed by birds. As a result, the same bird species populate both rims of the canyon, but each rim has several unique species of rodents (see Campbell, Figure 24.7).

An example of how geographic isolation can result in allopatric speciation is the pupfish.

- About 50,000 years ago, during an ice age, the Death Valley region of California and Nevada had a rainy climate and a system of interconnecting lakes and rivers.
- A drying trend began about 10,000 years ago, and by 4000 years ago, the region had become a desert.
- Presently, isolated springs in deep clefts between rocky walls are the only remnants of the lake and river networks. Living in many of these isolated springs are small pupfishes (*Cyprinodon* spp.).
- Each inhabited spring contains its own species of pupfish which is adapted to that pool and found nowhere else in the world.
- The endemic pupfish species probably descended from a single ancestral species whose range was fragmented when the region became arid, thus isolating several small populations that diverged in their evolution as they adapted to their spring's environment.

2. Conditions favoring allopatric speciation

When populations become allopatric, speciation can potentially occur as the isolated gene pools accumulate differences by microevolution that may cause the populations to diverge in phenotype.

- A small isolated population is more likely to change substantially enough to become a new species than is a large isolated population.
- The geographic isolation (peripheral isolate) of a small population usually occurs at the fringe of the parent population's range.
- As long as the gene pools are isolated from the parental population, *peripheral isolates* are good candidates for speciation for three reasons:

1. *The gene pool of the peripheral isolate probably differs from that of the parent population from the outset.* Since fringe inhabiters usually represent the extremes of any genotypic and phenotypic clines in an original sympatric population. With a small peripheral isolate, there will be a founder effect with chance resulting in a gene pool that is not representative of the gene pool of the parental population.
2. *Genetic drift will continue to cause chance changes in the gene pool of the small peripheral isolate until a large population is formed.* New mutations or combinations of alleles that are neutral in adaptive value may become fixed in the population by chance alone, causing phenotypic divergence from the parent population.
3. *Evolution caused by selection is likely to take a different direction in the peripheral isolate than in the parental population.* Since the peripheral isolate inhabits a frontier with a somewhat different environment, it will probably be exposed to different selection pressures than those encountered by the parental population.

- Due to the severity of a fringe environment, most peripheral isolates do not survive long enough to speciate.

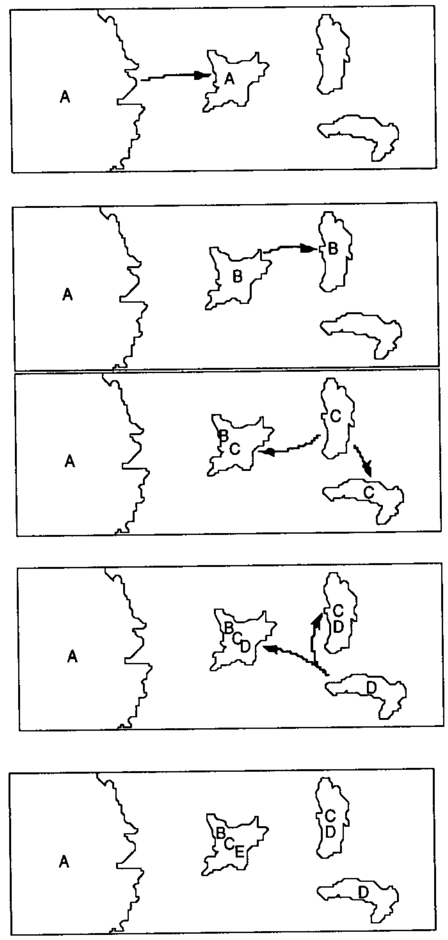
Although most peripheral isolates become extinct, evolutionary biologists agree that a small population can accumulate enough genetic change to become a new species in only hundreds to thousands of generations.

3. Adaptive radiation on island chains

Allopatric speciation occurs on island chains where new populations, which stray or are passively dispersed from their ancestral populations, evolve in isolation.

Adaptive radiation = The evolution of many diversely adapted species from a common ancestor.

Examples of adaptive radiation are the endemic species of the Galapagos Islands which descended from small populations which floated, flew, or were blown from South America to the islands. Darwin's finches can be used to illustrate a model for such adaptive radiation on island chains (see also, Campbell, Figure 24.8).



- A single dispersal event may have seeded one island with a peripheral isolate of the ancestral finch which diverged as it underwent allopatric speciation.
- A few individuals of this new species may have reached neighboring islands, forming new peripheral isolates which also speciated (see Campbell, Figure 24.9).
- After diverging on the island it invaded, a new species could re-colonize the island from which its founding population emigrated and coexist with the ancestral species or form still another species.
- Multiple invasions of islands could eventually lead to coexistence of several species on each island since the islands are distant enough from each other to permit geographic isolation, but near enough for occasional dispersal.

Similar evolutionary events have occurred on the Hawaiian Archipelago. These volcanic islands are 3500 km from the nearest continent.

- Hawaii is the youngest (<one million years old), largest island and has active volcanoes.
- The islands grow progressively older in a northwesterly direction away from Hawaii.
- As each island was formed and cooled, flora and fauna carried by ocean and wind currents from other islands and continents became established.
- The physical diversity of each island provided many environmental opportunities for evolutionary divergence by natural selection.
- Multiple invasions and allopatric speciations have permitted such a degree of adaptive radiation that there are thousands of endemic species on the archipelago which are found no where else on Earth.

In contrast to the Hawaiian Archipelago, islands such as the Florida Keys are close enough to a mainland to allow free movement from the island to the mainland.

- Such islands are not characterized by endemic species since there is no long-term isolation of founding populations.
- Intrinsic reproductive barriers that block gene flow do not develop due to a steady influx of immigrants from the mainland parental populations.

B. A new species can originate in the geographical midst of the parent species: sympatric speciation

Sympatric speciation = Formation of new species within the range of parent populations

- Reproductive isolation evolves without geographical isolation.
- This can occur quickly (in one generation) if a genetic change results in a reproductive barrier between the mutants and the parent population.

Many plant species have originated from improper cell division that results in extra sets of chromosomes—a mutant condition called *polyploidy* (see Campbell, Figure 24.10)

Depending on the origin of the extra set of chromosomes, polyploids are classified in two forms: autopolyploids and allopolyploids.

Autopolyploid = An organism that has more than two chromosome sets, all derived from a single species. For example,

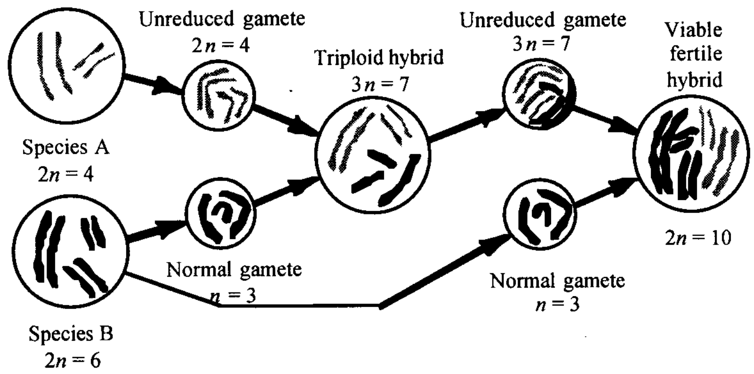
- Nondisjunction in the germ cell line (in either mitosis or meiosis) results in diploid gametes.
- Self-fertilization would double the chromosome number to the tetraploid state.
- Tetraploids can self-pollinate or mate with other tetraploids.
- The mutants cannot interbreed with diploids of the parent population because hybrids would be triploid ($3n$) and sterile due to impaired meiosis from unpaired chromosomes.
- An instantaneous special genetic event would thus produce a postzygotic barrier which isolates the gene pool of the mutant in just one generation.
- Sympatric speciation by autopolyploidy was first discovered by Hugo De Vries in the early 20th century while working with *Oenothera*, the evening primrose.

Allopolyploid = A polyploid hybrid resulting from contributions by two different species.

- More common than autopolyploidy.
- Potential evolution of an allopolyploid begins when two different species interbreed and a hybrid is produced (see Campbell, Figure 24.10b).
- Such interspecific hybrids are usually sterile, because the haploid set of chromosomes from one species cannot pair during meiosis with the haploid set of chromosomes from the second species.
- These sterile hybrids may actually be more vigorous than the parent species and propagate asexually.

At least two mechanisms can transform sterile allopolyploid hybrids into fertile polyploids:

1. During the history of the hybrid clone, mitotic nondisjunction in the reproductive tissue may double the chromosome number (see Campbell, Figure 24.10b).
   - The hybrid clone will then be able to produce gametes since each chromosome will have a homologue to synapse with during meiosis.
   - Gametes from this fertile tetraploid could unite and produce a new species of interbreeding individuals, reproductively isolated from both parent species.
2. Meiotic nondisjunction in one species produces an unreduced (diploid) gamete.



- This abnormal gamete fuses with a normal haploid gamete of a second species and produces a triploid hybrid.
- The triploid hybrid will be sterile, but may propagate asexually.
- During the history of this sterile triploid clone, meiotic nondisjunction again produces an unreduced gamete (triploid).
- Combination of this triploid gamete with a normal haploid gamete from the second parent species would result in a fertile hybrid with homologous pairs of chromosomes.
- his allopolyploid would have a chromosome number equal to the sum of the chromosome numbers of the two ancestral species (as in 1 above).

Speciation of polyploids (especially allopolyploids) has been very important in plant evolution.

- Some allopolyploids are very vigorous because they contain the best qualities of both parent species.
- The accidents required to produce these new plant species (interspecific hybridization coupled with nondisjunction) have occurred often enough that between 25% and 50% of all plant species are polyploids.

Some of these species have originated and spread in relatively recent times and many others are of importance to humans.

- Spartina angelica is a species of salt-marsh grass which evolved as an allopolyploid in the 1870s.
  - ⇒ It is derived from a European species (*Spartina maritima*) and an American species (*Spartina alternaflora*).
  - ⇒ In addition to being morphologically distinct and reproductively isolated from its parent species, *S. angelica* has a chromosome number ($2n$ = 122) indicative of its mechanism of speciation (*S. maritima*, $2n$ = , *S. alternaflora*, $2n$ = 62).
- *Triticum aestivum*, bread wheat, is a 42-chromosome allopolyploid that is believed to have originated about 8000 years ago as a hybrid of a 28 chromosome cultivated wheat and a 14 chromosome wild grass (see Campbell, Figure 24.11).
- Other important polyploid species include oats, cotton, potatoes, and tobacco.
- Plant geneticists are presently inducing these genetic accidents to produce new polyploids which will combine high yield and disease resistance.

Sympatric speciation may also occur in animal evolution through different mechanisms.

- A group of animals may become isolated within the range of a parent population if genetic factors cause them to become fixed on resources not used by the parent population as a whole. For example,
  - ⇒ A particular species of wasp pollinates each species of figs. The wasps mate and lay their eggs in the figs.
  - ⇒ A genetic change causing wasps to select a different fig species would segregate mating individuals of the new phenotype from the parental population.
  - ⇒ Divergence could then occur after such an isolation.
  - ⇒ The great diversity of cichlid fishes in Lake Victoria may have arisen from isolation due to exploitation of different food sources and other resources in the lake.
- Sympatric speciation could also result from a balanced polymorphism combined with assortative mating.
  - ⇒ For example, if birds in a population that is dimorphic for beak size began to selectively mate with birds of the same morph, speciation could occur over time.

While both allopatric speciation and sympatric speciation have important roles in plant evolution, allopatric speciation is far more common in animals.

C. Genetic change in populations can account for speciation

Classifying modes of speciation as allopatric or sympatric emphasizes biogeographical factors but does not emphasize the actual genetic mechanisms. An alternative method which takes genetic mechanism into account, groups speciation into two categories: *speciation by adaptive divergence* and *speciation by shifts in adaptive peaks.*

1. Adaptive divergence

Two populations which adapt to different environments accumulate differences in the frequencies of alleles and genotypes.

- During this gradual adaptive divergence of the two gene pools, reproductive barriers may evolve between the two populations.
- Evolution of reproductive barriers would differentiate these populations into two species.

A key point in evolution by divergence is that reproductive barriers can arise without being favored directly by natural selection.

- Divergence of two populations is due to their adaptation to separate environments, with reproductive isolation being a secondary development.
- Postzygotic barriers may be pleiotropic effects of interspecific differences in those genes that control development.
  - ⇒ Hybrids may not be viable if both sets of genes for rRNA synthesis are not active (e.g., hybrids between *D. melanogaster* and *D. simulans*).
- Gradual genetic divergence of two populations may also result in the evolution of prezygotic barriers.
  - ⇒ For instance, an ecological barrier to inbreeding may secondarily result from the adaptation of an insect population to a new host plant different from the original population's host.

In some isolated populations, reproductive isolation has evolved more directly from sexual selection. For example,

- In *Drosophila heteroneura*, the male's wide head enhances reproductive success with females of the same species while reducing the probability that a male *D. heteroneura* will mate with females of other species.
- Sexual selection, in this case, probably evolved as an adaptation for enhanced reproductive success. A secondary consequence is that it prevents interbreeding with other *Drosophila* species.
- Since reproductive barriers usually evolve when populations are allopatric, they do not function directly to isolate the gene pools of populations.
    - ⇒ For this reason, the emphasis on reproductive isolating mechanisms is one criticism of the biological species concept.

2. Hybrid zones and the cohesion concept of species

Three possible outcomes are possible when two closely related populations that have been allopatric for some time come back into contact:

- The two populations may interbreed freely.
    - ⇒ The gene pools would become incorporated into a single pool indicating that speciation had not occurred during their time of geographical isolation.
- The two populations may not interbreed due to reproductive barriers.
    - ⇒ The gene pools would remain separate due to the evolutionary divergence which occurred during the time of geographical isolation. Speciation has taken place.
- A hybrid zone may be established.

Hybrid zone = A region where two related populations that diverged after becoming geographically isolated make secondary contact and interbreed where their geographical ranges overlap

- For example, the red-shafted flicker of western North America and the yellow-shafted flicker of central North America are two phenotypically distinct populations of woodpeckers that interbreed in a hybrid zone stretching from southern Alaska to the Texas panhandle.
- The two populations came into renewed contact a few centuries ago after being separated during the ice ages.
- The hybrid zone is relatively stable and not expanding.
    - ⇒ The introgression of alleles between the populations has not penetrated far beyond the hybrid zone, although the two populations have been interbreeding for at least two hundred years.
    - ⇒ The genotypic and phenotypic frequencies that distinguish the two populations form steep clines into the hybrid zone.
- Away from the hybrid zone, the two populations remain distinct.

Should two populations which form a hybrid zone be considered subspecies or separate species?

- Some researchers who support species status for such populations, recognize that the presence of stable hybrid zones creates a problem for the biological species concept.
    - ⇒ If the taxonomic identity of two species is maintained, even though they hybridize, there must be cohesive forces other than reproductive isolation that maintain the species and prevent their merging into a single species.

- These researchers favor an alternative known as the *cohesion concept of species*.

The cohesion concept of species holds that the cohesion may involve a distinctive, integrated set of adaptations that has been refined during the evolutionary history of a population.

- Phenotypic variation would be restricted by stabilizing selection to a range narrow enough to define the species as separate from other species.
- In the adaptive landscape view:
  - ⇒ The red-shafted and yellow-shafted flickers are clustered around different adaptive peaks.
  - ⇒ Specific combinations of alleles and specific linkages between gene loci on chromosomes may form a genetic basis for the cohesion of phenotypes.
  - ⇒ The clinal change of genetic structure and phenotype noted in the hybrid zone may be correlated with transitions in environmental factors that help shape the two distinct populations.

3. How much genetic change is required for speciation?

No generalizations can be made about genetic distance between closely related species. Reproductive isolation may result from changes in many loci or only in a few.

- Two species of Hawaiian *Drosophila* (*D. silvestris* and *D. heteroneura*) differ at only one locus which determines head shape, an important factor in mate recognition (see Campbell, Figure 24.12).
  - ⇒ The phenotypic effect of different alleles at this locus is multiplied by epistasis involving at least ten other loci.
  - ⇒ Thus, no more than one mutation was necessary to differentiate the two species.
- Changes in one gene in a coadapted gene complex can substantially impact the development of an organism.

D. The punctuated equilibrium model has stimulated research on the tempo of speciation

Traditional evolutionary trees diagram the descent of species from ancestral forms as branches that gradually diverge with each new species evolving continuously over long spans of time (see Campbell, Figure 24.13a).

- The theory behind such a tree is the extrapolation of microevolutionary processes (allele frequency changes in the gene pool) to the divergence of species.
- Big changes thus occur due to the accumulation of many small changes.

Paleontologists rarely find gradual transitions of fossil forms but often observe species appearing as new forms suddenly in the rock layers.

- These species persist virtually unchanged and then disappear as suddenly as they appeared.
- Even Darwin, who believed species from a common ancestral stock evolve differences gradually, was perplexed by the lack of transitional forms in the fossil record.

Advocates of *punctuated equilibrium* have redrawn the evolutionary tree to represent fossil evidence for evolution occurring in spurts of relatively rapid change instead of gradual divergence (see Campbell, Figure 24.13b).

- This theory was proposed by Niles Eldredge and Stephen Jay Gould in 1972.

- It depicts species undergoing most of their morphological modification as they first separate from the parent species then showing little change as they produce additional species.
- In this theory gradual change is replaced with long periods of stasis punctuated with episodes of speciation.
- The origin of new polyploid plants through genome changes is one mechanism of sudden speciation.
- Allopatric speciation of a splinter population separated from its parent population by geographical barriers may also be rapid.
  - ⇒ For a population facing new environmental conditions, genetic drift and natural selection can cause significant change in only a few hundred or thousand generations.

A few thousand generations is considered rapid in reference to the geologic time scale.

- The fossil record indicates that successful species survive for a few million years on average.
- If a species survives for five million years and most of its morphological changes occur in the first 50,000 years, then the speciation episode occurred in just 1% of the species' lifetime.
- With this time scale, a species will appear suddenly in rocks of a certain age, linger relatively unchanged for millions of years, then become extinct.
- While forming, the species may have gradually accumulated modifications, but with reference to its overall history, its formation was sudden.
- An evolutionary spurt preceding a longer period of morphological stasis would explain why paleontologists find so few transitions in the fossils record of a species.

Because "sudden" can refer to thousands of years on the geological time scale, differing opinions of punctuationalists and gradualists about the rate of speciation may be more a function of time perspective than conceptual difference. There is clear disagreement, however, over how much a species changes after its origin.

- In a species adapted to an environment that stays the same, natural selection would counter changes in the gene pool.
  - ⇒ Once selection during speciation produces new complexes of coadapted genes, mutations are likely to impose disharmony on the genome and disrupt the development of the organism.
- Stabilizing selection would thus hold a population at one adaptive peak to produce long periods of stasis.

Some gradualists feel that stasis is an illusion since many species may continue to change, after they have diverged from the parent population, in ways undetectable in fossils.

- Changes in internal anatomy, physiology and behavior would go unnoticed by paleontologists as fossils only show external anatomy and skeletons.
- Population geneticists also point out that many microevolutionary changes occur at the molecular level without affecting morphology.

It is obvious that additional extensive studies of fossil morphology where specific lineages are preserved should be carried out to assess the relative importance of gradual and punctuated tempos in the origin of new species.

III. The Origin of Evolutionary Novelty

What processes cause the evolutionary changes that can be traced through the fossil record? How do the novel features that define taxonomic groups above the species level arise? The following concepts address the processes relevant to these questions.

A. Most evolutionary novelties are modified versions of older structures

Higher taxa such as families and classes are defined by evolutionary novelties. For example:

- Birds evolved from dinosaurs, and their wings are homologous to the forelimbs of modern reptiles.
- Birds are adapted to flight, yet their ancestors were earthbound.

How could these new designs evolve?

- One mechanism is the gradual refinement of existing structures for new functions.
- Most biological structures have an evolutionary plasticity that makes alternative functions possible.

Exaptation is a term applied to a structure that evolves in one context and becomes co-opted for another function.

- Natural selection cannot anticipate the future, but it can improve an existing structure in context of its current utility. For example,
  - ⇒ The honeycombed bones and feathers of birds did not evolve as adaptations for flight.
  - ⇒ They must have been beneficial to the bipedal reptilian ancestors of birds (reduction of weight, gathering food, courtship), and later through modification, became functional for flying.
- Exaptation cannot be proven, but provides an explanation for how novel designs can arise gradually through a series of intermediate stages, each having some function in the organism.
- The evolution of novelties by remodeling of old structures for new functions reflects the Darwinian tradition of large changes being crafted by natural selection through an accumulation of many small changes.

B. Genes that control development play a major role in evolutionary novelty

The evolution of complex structures (e.g., wings) requires such large modifications that changes at many gene loci are probably involved.

- In other cases, relatively few changes in the genome can cause major modifications in morphology (e.g., humans vs. chimpanzees).
- Thus, slight genetic divergence can become magnified into major differences.

In animal development, a system of regulatory genes coordinates activities of structural genes to guide the rate and pattern of development from zygote to adult.

- A slight alteration of development becomes compounded in its effect on adult *allometric growth* (differences in relative rates of growth of various parts of the body) which helps to shape an organism.
- A slight change in these relative rates of growth will result in a substantial change in the adult (see Campbell, Figure 24.14a).
- Thus, altering the parameters of allometric growth is one way relatively small genetic differences can have major morphological impact (see Campbell, Figure 24.14b).

Changes in developmental dynamics, both *temporal* and *spatial*, have played a major role in macroevolution.

Temporal changes in development that create evolutionary novelties are called *heterochrony*.

Heterochrony = Evolutionary changes in the timing or rate of development

- Genetic changes that alter the timing of development can also produce novel organisms.

Paedomorphosis = Retention of ancestral juvenile structures in a sexually mature adult organism

⇒ Campbell, Figure 24.15 shows the effect of developmental timing on zebra stripes. Figure 24.16 shows paedomorphosis in salamanders.

⇒ A slight change in timing that retards the development of some organs in comparison to others produces a different kind of animal.

- Changes in developmental chronology may have contributed to human evolution.
  - ⇒ Humans and chimpanzees are closely related through descent from a common ancestor.
  - ⇒ They are much more similar as fetuses than as adults.
  - ⇒ Different allometric properties and variations result in the human brain being proportionally larger than that in chimpanzees.
  - ⇒ The human brain continues to grow several years longer than the chimpanzee brain.
  - ⇒ Thus, the genetic changes responsible for humans are not great, but have profound effects.

Equally important in evolution is the alteration of the spatial pattern of development or homeosis.

Homeosis = Alteration in the placement of different body parts (for example, to the arrangement of different kinds of appendages in animals or the placement of flower parts on a plant)

Since each regulatory gene may influence hundreds of structural genes, there is a potential for evolutionary novelties that define higher taxa to arise much faster than would occur by the accumulation of changes in only structural genes.

C. An evolutionary trend does not mean that evolution is goal oriented

Extracting a single evolutionary progression from the fossil record that is likely to be incomplete is misleading.

- For example, by selecting certain species from available fossils, it is possible to arrange a succession of animals between *Hyracotherium* and modern horses that shows a trend toward increased size, reduced number of toes, and modification of teeth for grazing (see Campbell, Figure 24.17 yellow line). Consideration of all known fossil horses negates this trend, and reveals that the line to modern horses is one of a series of species episodes.

Branching evolution (cladogenesis) can produce a trend even if some new species counter the trend.

- There was an overall trend in reptilian evolution toward large size during the Mesozoic era which eventually produced the dinosaurs.
- This trend was sustained even though some new species were smaller than their parental species.

One view of macroevolution, forwarded by Steven Stanley of Johns Hopkins, holds that species are analogous to individuals.

- In this analogy, speciation is birth and extinction is death.
- An evolutionary trend is produced by *species selection*, which is analogous to the production of a trend within a population by natural selection.
- The species that endure the longest and generate the greatest number of new species determine the direction of major evolutionary trends.
- Differential speciation plays a role in macroevolution similar to the way differential reproduction plays a role in microevolution.

Qualities unrelated to the success of organisms in a specific environment may be equally important in species selection.

- The ability of a species to disperse to new habitats may result in development of new "daughter species" as organisms adapt to new conditions.
- A criticism of species selection is the argument that gradual modification of populations in response to environmental change is the most common stimulus to evolutionary trends.

No intrinsic drive toward a preordained state of being is indicated by the presence of an evolutionary trend.

- Evolution is a response to interactions between organisms and their current environments.
- An evolutionary trend may cease or reverse itself under changing conditions. For example, conditions of the Mesozoic era favored giant reptiles, but by the end of that era, smaller species prevailed.

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