Chapter 24: The Origin of Species (Macroevolution)

1. Discuss the biological species concept, including its limitations.

2. Discuss the phylogenetic or evolutionary species concept, including its limitations.

3. Explain what a reproductive isolating mechanism (RIM) is and the difference between prezygotic and postzygotic barriers.

4. Define and give an example of each of the 8 RIMs covered in the notes.

5. Explain the difference between anagenic and cladogenic speciation.

6. Explain the difference between allopatric and sympatric speciation.

7. What is adaptive radiation, and how can it be an example of both allopatric and sympatric speciation?

8. What is the difference between punctuated equilibrium and gradualism?

I. Macroevolution is essentially the formation of new species (speciation) and accompanying events

A. species: “Kind of living thing”; the word “species” is both plural and singular

B. relatively easy to define for sexual organisms, hard for asexual organisms and extinct species

1. biological species concept (for sexual organisms)
   - a species is one or more populations whose members are capable of interbreeding and producing fertile offspring, and whose members are reproductively isolated from other such groups
   - not always clear-cut, because some can interbreed under “artificial” conditions but don’t appear to do so in nature
   - sometimes, “race” and “subspecies” designations are used, but often different specific epithets are used when there are clear morphological differences involved

2. asexual species – definition based on biochemical (think DNA sequence) and morphological differences; no solid rules
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- also includes use of “race,” “subspecies,” and “strain” designations
- in asexual species, microevolution over time directly leads to macroevolution (speciation)

3. phylogenetic species concept or evolutionary species concept

- a species is a single line of descent (lineage with a unique genetic history) that maintains its distinctive identity from other lineages
- this is a more comprehensive concept (it works for both sexual and asexual species)
- but, it can be hard to clearly define and agree upon “distinctive identity”

C. the basis of macroevolution in sexual species is microevolution coupled with reproductive isolation

II. Reproductive isolation can occur in a variety of ways

A. reproductive isolation is any means of preventing gene flow between two species; for a new species to evolve from an existing (sexually reproducing) species, there must be a reproductive isolating mechanism in place

B. reproductive isolating mechanisms can be classified as either prezygotic or postzygotic

1. prezygotic barriers – prevent fertilization (zygote formation) between gametes from two species
   - habitat isolation (or ecological isolation) – isolation by differences in habitat occupied at the time of mating; examples: some garter snakes; some flycatchers
   - temporal isolation – isolation by differences in timing of mating; examples: mating seasons in some skunks; flowering time in some plants; mating time in some fruit flies
   - behavioral isolation – differences in behavior that cause reproductive isolation; examples: mating calls, courtship patterns, and other mating rituals; can be an aspect of sexual selection (selective pressure that comes from mating choices)
   - mechanical isolation – differences in physical aspects make successful mating impossible; examples: many flower species; dragonflies may attempt interspecies mating, but the physical structure of their genitalia prevents successful mating
   - gametic isolation – mating occurs, but the sperm and egg cannot fuse; examples: sperm cannot penetrate the egg of the different species, such as between sea urchins species, as well as in many other animal species; in plants, often pollen grains do not get the proper signal to germinate when on a stigma of a different species

2. postzygotic barriers – reproductive isolation after fertilization has occurred
   - hybrid inviability – (the most common type of postzygotic barrier) normal development of the zygote formed from the mating of two species does not occur and the embryo is aborted, or if development is completed the offspring
is very frail; examples: crosses between different iris species, cross between bullfrog and leopard frog; crosses between some salamander subspecies

- **hybrid sterility** – a zygote of a hybrid proceeds through normal development, but is reproductively sterile
  - sometimes due to other barriers such as behavioral isolation (don't make the right mating call, etc.)
  - most often due to problems in meiosis (example: male donkey \[n=31\] x female horse \[n=32\] generates sterile mule \[2n=63, not an even number, pairing problems during meiosis\])

- **hybrid breakdown** – a zygote of a hybrid proceeds through normal development, and the interspecific hybrid reproduces, but the \( F_2 \) generation and beyond have problems with reproduction; examples: crosses between sunflower species result in 80% hybrid breakdown in the \( F_2 \) generation; crosses between some rice strains

C. the genetic basis for some reproductive barriers have been identified (the basis will vary depending on the species involved)

III. Reproductive isolation is the key to **cladogenic** speciation

A. speciation (the evolution of new species) has two general forms, **anagenic** and **cladogenic**

B. **anagenic speciation** is the gradual change of one species into a new form, with the “new” species form replacing the “old” form; this is essentially microevolution on the whole species level – the number of species does not change

C. **cladogenic speciation**, or branching evolution, occurs when two or more species are present where only one existed before; these species share a common ancestor

  1. a cluster of species that share a common ancestor is a **clade**
  2. cladogenic speciation increases the number of species
  3. two separate species are said to **diverge** from the point where they shared a common ancestor – the gene pools of these species are separated from the point of divergence on

D. cladogenic speciation occurs when a population is different enough from its ancestral species so that no genetic exchange can occur between them

  1. the appearance of a reproductive isolating mechanism produces two or more species where once there was one
  2. The question of macroevolution becomes, what creates reproductive isolation?
  3. there is no easy way to define when cladogenic speciation is complete – often some level of hybridization can persist when there is essentially no gene flow between the “species” or “subspecies” involved

IV. Cladogenic speciation has two modes: **allopatric speciation** and **sympatric speciation**

A. **allopatric speciation** – one population becomes geographically separated from the rest of the species

  1. the separated population encounters different selective pressures from the rest of the species, and also is usually subjected to a genetic bottleneck (thus its gene pool changes due to genetic drift)
2. after a long period of time, the population has diverged enough from the parent species that it is reproductively isolated from the parent species if they come in contact

3. likely the most common means of cladogenic speciation

4. examples of mechanisms for geographic isolation: founders on an island, rivers shifting course, glaciation, land bridge appearance and removal, mountain formation

B. **sympatric speciation** – a species achieves reproductive isolation and evolves in the same geographic location as its ancestral species

1. **polyploidy** (extra sets of chromosomes) is a major factor in sympatric speciation in plants
   - **autopolyploidy** – multiple sets from one parent species; example – plants around Agent Orange sites
   - **hybridization + allopolyploidy** – closely related species produce a hybrid that must double its chromosome number to reproduce successfully; a new, viable hybrid species is thus formed

2. disruptive selection – when disruptive selection occurs, hybrids are selected against
   - there is thus strong selective pressure for the development of reproductive isolation mechanisms
   - example – food preference specializations in Lake Victoria cichlids (over 500 species, likely rapid speciation from a common ancestor less than 13,000 years ago)

C. **adaptive radiation** (rapid production of many species from a common ancestor) is most easily produced by a combination of allopatric speciation and sympatric speciation

1. pioneers on an island, or pioneering fish in Lake Victoria, are separated from their ancestral species allopatrically

2. the presence of a variety of open ecological niches in such regions also gives ample opportunity for sympatric speciation by disruptive selection

3. groups of species that derived by adaptive radiation, like the Lake Victoria cichlids, Galapagos finches, Hawaiian *Drosophila*, and Hawaiian silverswords, thus experience sympatric and allopatric speciation simultaneously

V. **Macroevolution involves both rapid and gradual divergence**

A. Darwin’s original theory suggested that evolution occurs gradually (gradualism model)

1. there is some fossil evidence for this, but in many cases there is a lack of transitional forms

2. the fossil record by its very nature is incomplete, which would explain some of the lack of transitional forms, but there is an alternative: **punctuated equilibrium**

B. **punctuated equilibrium** theory states that evolutionary change can be rapid, and that this rapidity explains much of the lack of transitional forms in the fossil record
1. rapid change means that the transitional forms are around for only a short time (on the order of thousands of years), and thus are far less likely to be preserved as fossils

2. between periods of rapid change are long periods of relative stasis, with little evolutionary change and thus little change in form; these long periods (on the order of millions of years) greatly increase the likelihood of such forms being preserved as fossils

3. first advanced by Stephen Jay Gould and Niles Eldredge in 1972

4. note that "rapid" evolution still takes thousands of years, which in geological time is a relatively short period, but is long in human terms

C. both gradualism and punctuated equilibrium have the same underlying mechanisms (reproductive isolation and genetic divergence); they differ in the rate of genetic divergence predicted

D. there is abundant fossil evidence for both gradualism and punctuated equilibrium; apparently both modes can occur, depending on the situation

E. biologists disagree about the relative importance of gradualism and punctuated equilibrium in evolution, and the clarity of distinction between the two