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From the origin of species to mass extincion.

6

Speciation and Extinction

The process of evolution is most dramatic when entire species originate or go extinct. Evolution can bring about considerable change within species, as the recent rapid evolution of the human brain illustrates. But the appearance and disappearance of entire species, even groups of species, has had immense significance for life on Earth. The extinction of the dinosaurs about 65 million years ago eliminated the dominant terrestrial animals of the Mesozoic. The evolution of flowering plants transformed the relationship between animals and plants, including groups as diverse as insects and birds, roses and camellias. Most people think of these large-scale events when they think of evolution, even though evolutionary processes are not usually so cataclysmic.

The study of the origin and extinction of species is tremendously challenging. Normally, these events occur over thousands or millions of years, making them impossible to study directly. It is unlikely that a scientist will have enough contemporary data to characterize an ongoing speciation event completely. Fortunately the fossil record provides us with some information about the appearance and disappearance of life-forms, as does molecular evolution. In recent times, the pervasive destruction of habitats and rare life-forms by humans has allowed us to observe the extinction of many species directly, a regrettable scientific benefit of the human impact on the biosphere.

We begin with the study of speciation, the origin of species. A problem that was one of the core mysteries of nineteenth-century biology is now a reasonably understood part of twenty-first-century biology. Punctuated equilibrium is one of the more public evolution controversies of recent years, seemingly a challenge to Darwinism itself. The roots of this controversy, however, lie in mainstream evolutionary biology. The subject of extinction has garnered great attention in recent years, thanks to the fascination of scientists with the possibility that mass extinctions have been caused by the collision of large astronomical bodies with Earth. ❖

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Allopatric Speciation

6.1 The biological species concept is based on the reproductive isolation of organisms that are given the opportunity to mate

At the core of the speciation concept is the separation of populations from each other, so that their evolutionary fates become independent. Darwin assumed that this happened, but was usually vague about the biology involved. Ernst Mayr, Theodosius Dobzhansky, and other greats of twentieth-century evolutionary biology wanted to make the crux of speciation clear. They used the **biological species concept** as a way of defining when speciation occurred. This concept makes reproductive isolation the key criterion for the separation of populations into multiple species. **Reproductive isolation** in turn refers to a failure of organisms to reproduce successfully when they are placed together under circumstances in which they would normally mate (Figure 6.1A).

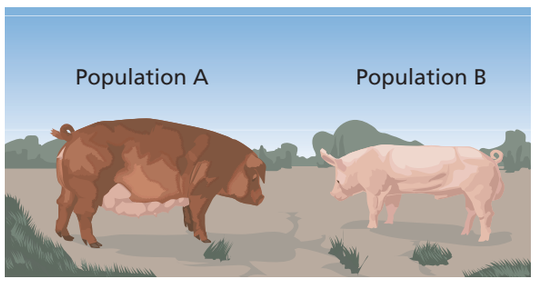
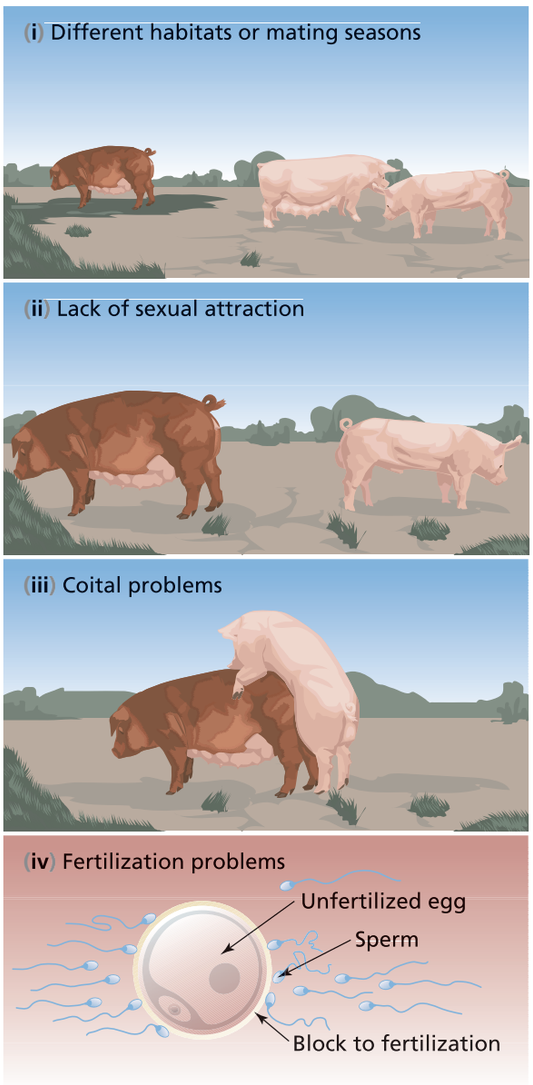


FIGURE 6.1A The Biological Species Concept When members of one population do not mate successfully with members of the other population, no fertile offspring are produced. Mating may never occur, or hybrid offspring may have fitness deficits.





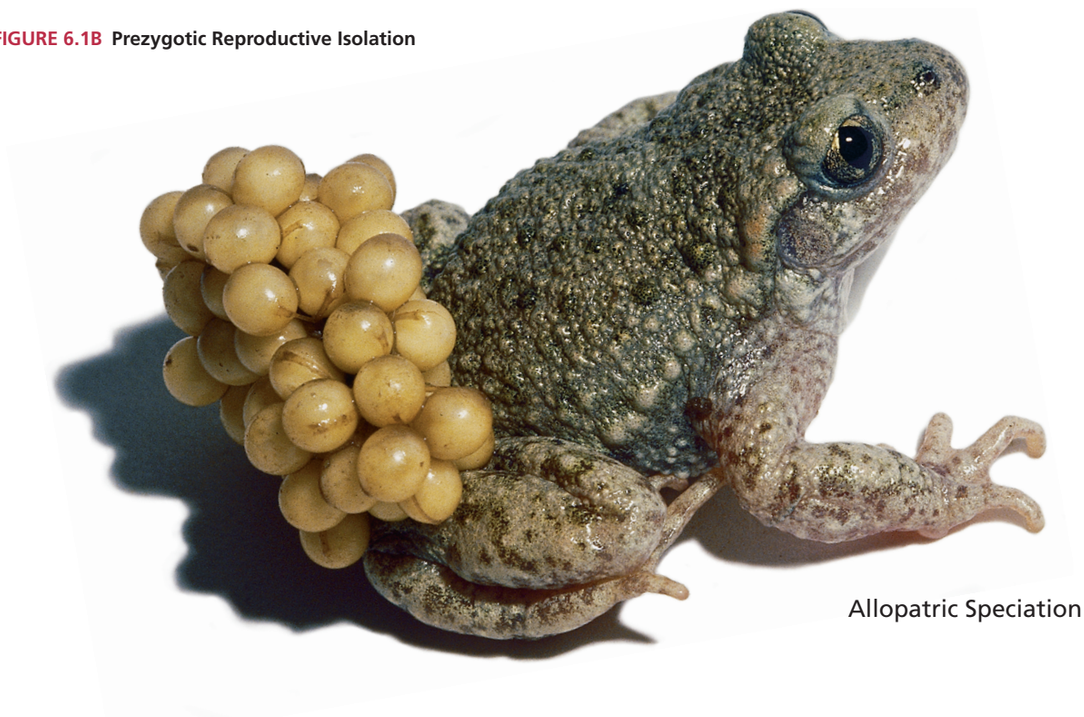
Several features of reproductive isolation need careful thought. Organisms that are being tested should be allowed to develop and produce gametes normally. Mating should not be forced, because part of reproductive isolation is inclination to mate. Indeed, most species are isolated from each other by **prezygotic isolating mechanisms**, as sketched in Figure 6.1B. Even when organisms from two populations are in the same general area, they may not mate because their preferred habitats may be different. These habitat preferences may be specific to the time of mating, with mixing of the populations at other times. Such mating-time preferences can still operate to keep two species isolated from each other.

A common impediment to mating between species is a lack of sexual attraction. This sexual attraction may be mediated by one or several of the sensory modalities: visual appearance, auditory behavior, scent, and so on. Together the senses produce the perception that members of other species are sexually repellent. At least in animals, this may be the single most important factor preventing sex between species.

In a variety of organisms, sex may be attempted between members of different species. In organisms like insects, which use internal fertilization, but have rigid penile and vaginal structures, there may be a lack of "fit" between the genital structures. This can cause a failure of penetration. It can also cause male and female insects to become locked together by their genitals, preventing the reproduction of either. Other species with internal fertilization may achieve ejaculation in hybrid matings, but the sperm of the other species may be expelled after ejaculation.

The final barrier to sex between species arises at the moment sperm come into contact with eggs. Some species have cellular mechanisms that specifically prevent foreign sperm from penetrating their ova. Even in species with external fertilization, like the gamete-shedding sea urchin, mixing sperm from several species will still mostly result in fertilization of eggs by the sperm of the same species. Nature goes to a great deal of trouble to prevent the fertilization of eggs by the gametes of other species.

FIGURE 6.1B **Prezygotic Reproductive Isolation**



6.2 Species may be isolated by a failure to reproduce that occurs after fertilization, which will select for isolation before fertilization

Not all species are isolated from each other by barriers to fertilization. They are instead reproductively isolated because of **postzygotic isolating mechanisms**, which act after fertilization occurs. For example, horses mate with asses and zebras, and hybrids of these equine species with horses are viable. (One example is the zebroid, shown in Figure 6.2A.) In most animal groups, hybrids are typically inviable, sterile, or have greatly reduced fertility, as shown in Figure 6.2B. The lack of fertility of the offspring of hybirds that are not completely sterile is usually attributed to **hybrid breakdown**. Hybrid breakdown occurs due to a failure of the hybrid's genetic system to produce gametes that can successfully combine with the gametes of the parental species, or with the gametes of other hybrids.

The lack of fertility of the offspring of hybirds that are not completely sterile is usually attributed to hybrid breakdown.

Unlike prezygotic reproductive isolation, postzygotic reproductive isolation usually imposes a considerable fitness cost. Males waste their sperm on unproductive matings. Females may waste energy caring for hybrid offspring that will never produce grandchildren. In the case of mammalian hybrids, like those between equine species, the considerable physiological burdens of gestating and nursing a hybrid offspring will fall on females that mate with members of other species. For all these reasons, organisms should be strongly selected to replace postzygotic mechanisms of reproductive isolation with mechanisms of prezygotic reproductive isolation. In other words, natural selection should normally favor the preemption of the fitness costs associated with interspecific fertilization. This point is schematically summarized in Figure 6.2C.



FIGURE 6.2A **A Zebroid: A horse/zebra hybrid together with photographs of its parent species**

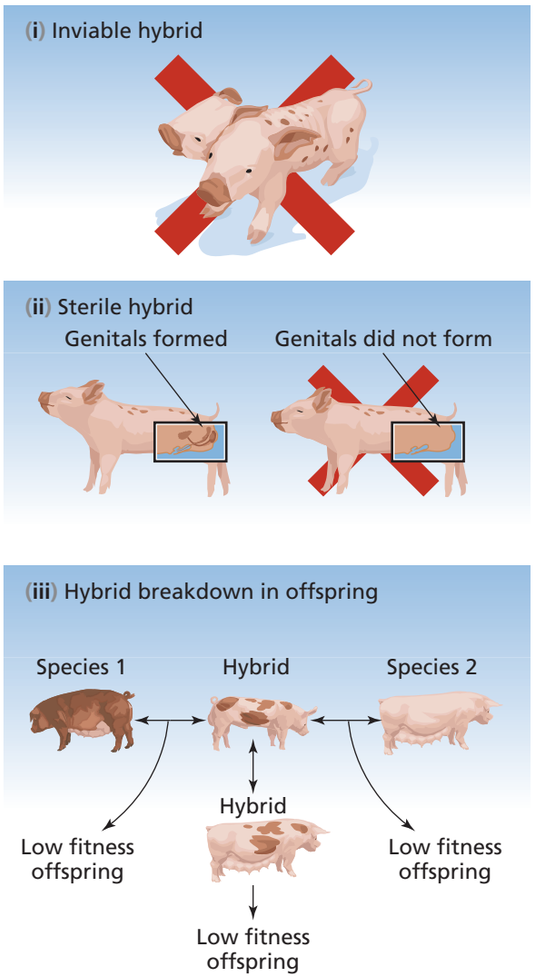


FIGURE 6.2B **Postzygotic Reproductive Isolation**

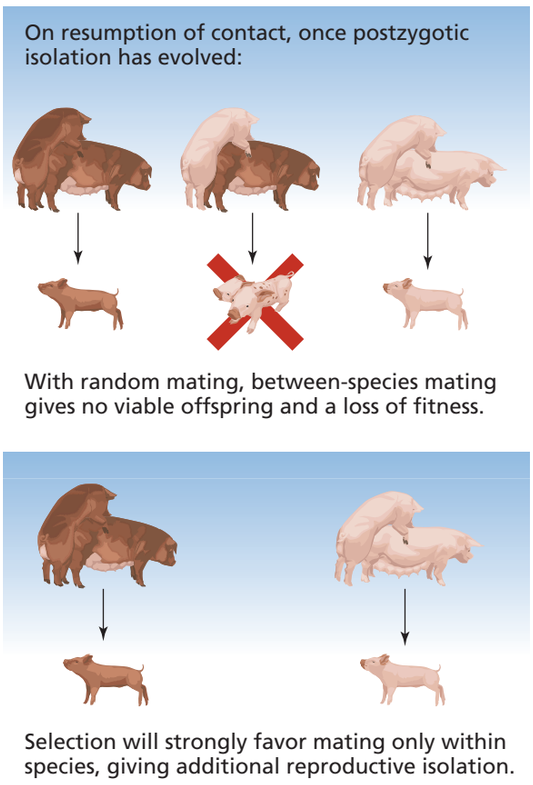


FIGURE 6.2C **Reinforcement of Reproductive Postzygotic Isolation after Postzygotic Isolation Has Evolved**



6.3 Geographical separation of populations fosters speciation

The traditional evolutionary scenario for speciation, developed particularly by Ernst Mayr in the 1940s, is based on geographical migration. Over the course of their evolutionary history, species may split in two because of a major geographical barrier to their migration. What constitutes such a barrier will depend on the mobility of the species. Large ocean-flying birds, like the albatross, are able to range over entire hemispheres (Figure 6.3A). But small cave-dwelling worms may be completely isolated from worms of the same species living in a separate cave just a few yards away. Plants might seem more likely candidates for isolation, because they cannot run or fly. But the wind-borne pollen of pine trees (Figure 6.3B) may disperse for hundreds of miles, as may pollen carried by winged pollinators. The important thing is that most species will have barriers to their dispersal, and when populations are located on either side of such barriers they are evolutionarily independent as long as the barriers are maintained. Such geographically separated populations are called **allopatric**.



FIGURE 6.3A **Albatross**



FIGURE 6.3B **Pine Trees**

The evolutionary situation becomes interesting when allopatric populations evolve separately for a long period. As shown in Figure 6.3C, these populations may diverge from each other, because of selection or because of some other evolutionary mechanism. When they diverge enough, they may become so different from each other that they are separate species when the geographical barrier is removed. Note that there is no necessity to this process. The brief splitting up of a species for a short period of time may not result in speciation. Resumption of contact between populations may lead to their evolutionary reunification. Speciation does not have to occur.

If populations have evolved to be quite different during periods of allopatry, they may have postzygotic reproduction isolation before they ever resume contact with each other. However, these same populations may have no sexual inhibition about mating with members of the separate populations before they resume contact. However, on resuming contact, if there is established postzygotic reproductive isolation, there will immediately be selection on members of the two species to avoid having sex with each other as we have already outlined in the previous module, especially Figure 6.2C.. This effect then tends to reinforce the reproductive isolation of the two populations. An initial degree of reproductive isolation leads to the considerable reinforcement of reproductive isolation by selection on sexual and other reproductive behaviors. For this reason, we expect species to have multiple layers of mechanisms that minimize reproductive interactions with other species. Natural selection actively favors the maintenance of reproductive barriers between species.

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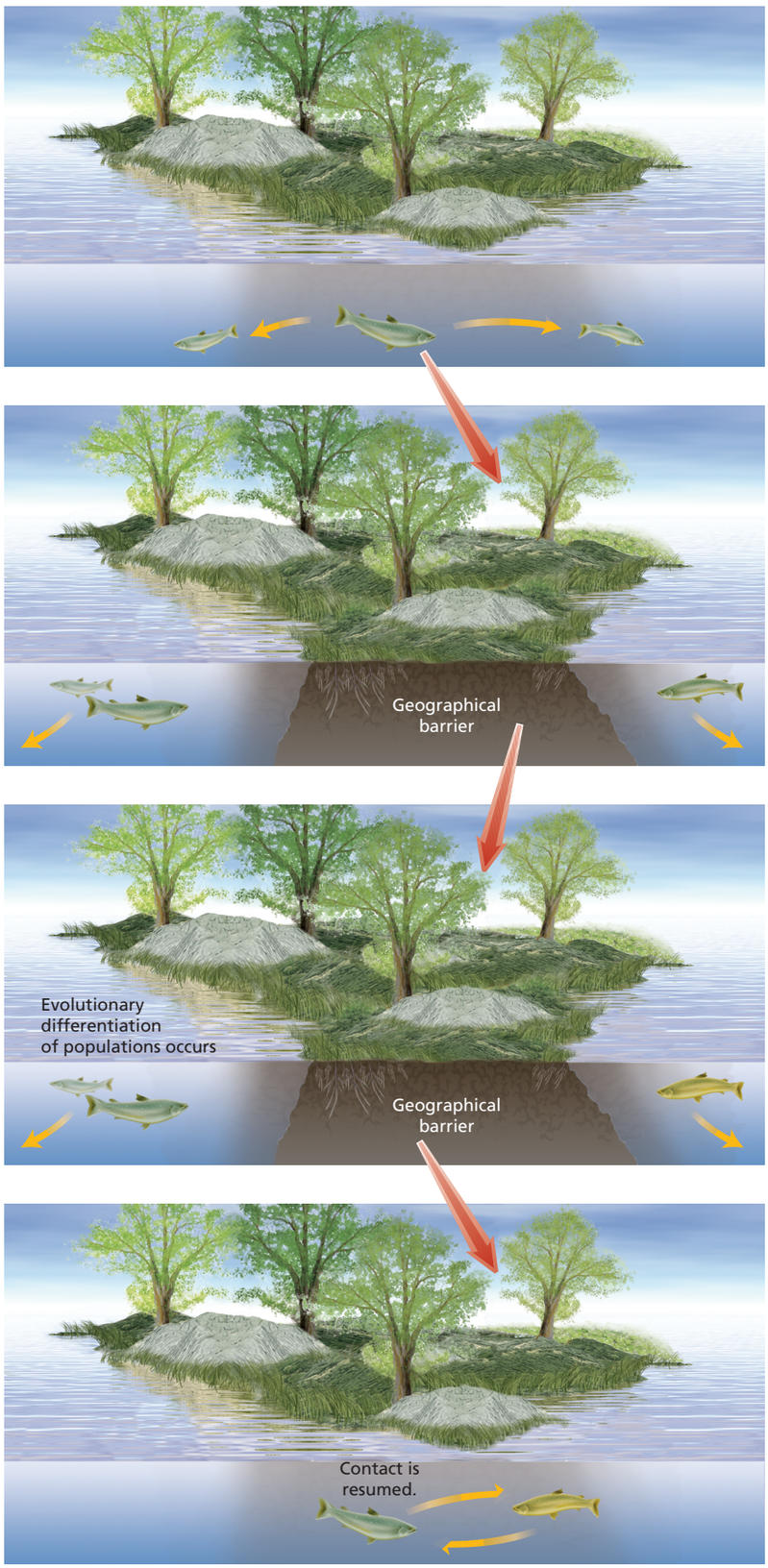


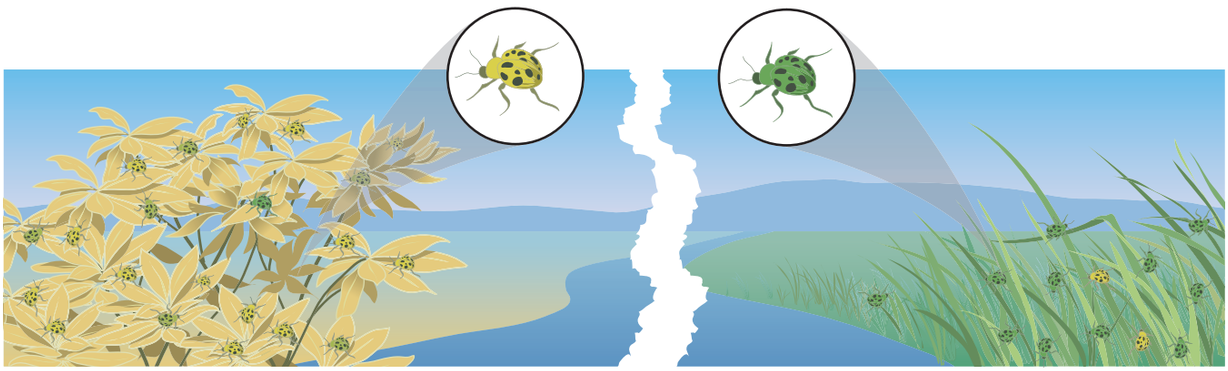
FIGURE 6.3C **Allopatric Speciation**

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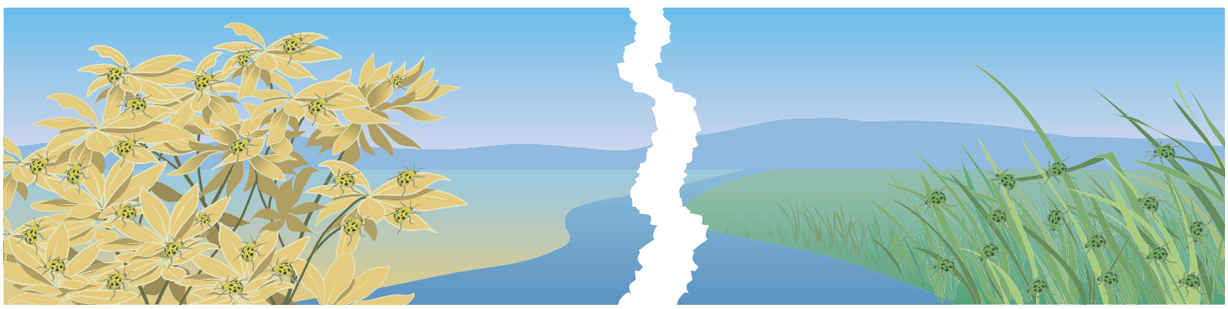
6.4 The genetic mechanisms of allopatric speciation may be adaptive or nonadaptive

In the middle of the twentieth-century, most evolutionary biologists thought the evolutionary changes that bring about speciation arose from adaptation to dissimilar habitats. This basic scenario is illustrated in Figure 6.4A. The idea was that when two populations were separated geographically, they might find themselves in very different habitats, with different kinds of food or, in the case of plants, light levels, among other ecological differences. Many generations in these distinct habitats would lead to contrasting biological adaptation in the separate populations. On resuming contact, members of the two populations might have adaptations that are so different that hybrids between them would have very low Darwinian fitness, and speciation would be achieved.

This is a very plausible scenario. Most evolutionary biologists still suppose that it occurs frequently in evolution. Extensive biological differentiation of allopatric populations has been observed in many organisms. There is a vast body of literature documenting the physiological and genetic differentiation of populations from a number of species, from clines in the frequency of alcohol dehydrogenase alleles in fruit flies to ecological genetic differentiation in clams off the northeastern coast of the United States. Natural selection will



1. Differences between the habitats of the separate areas causes selection for different characteristics.



2. While still separate, the populations become highly differentiated.



3. When the barrier goes away, the populations may now be species.

FIGURE 6.4A Adaptive Differentiation in Allopatry

cause some allopatric populations to differentiate genetically. What has been poorly documented is the association between such allopatric differentiation and the evolution of reproductive isolation.

This is not a trivial question, because there are alternative genetic mechanisms that might bring about speciation—particularly at the level of genomic evolution, described in Chapter 5. Transposable elements can bring about hybrid dysgenesis, even when a single transposable element is involved, as has been shown in *Drosophila*. If allopatric populations undergo multiple, but different, invasions of transposable elements, then it is plausible to suppose that hybrids would cause massive genomic disruption from extensive, unregulated transposition, as shown in part (i) of Figure 6.4B.

An alternative genomic mechanism for speciation is one of structural genome evolution, shown in part (ii) of Figure 6.4B. If one genome becomes very different in structure, then hybrids may be subject to a failure of the genetic mechanism, in both gene transmission and gene expression. The Chinese and Indian muntjacs illustrate this pattern. The muntjac is a small deer that barks. The Chinese species has 46 chromosomes, while the outwardly similar Indian species has 6 chromosomes (Figure 6.4C). During allopatry, it appears, the Indian species has undergone numerous chromosome fusions, end-to-end. Hybrids can be made, but they are infertile, no doubt due to structural incompatibility of the two genomes.

Two important points need to be made about genomic mechanisms of speciation. The first is that they are not fully documented, putting them on the same plane as traditional selective scenarios for speciation. The second is that they do not require natural selection. Transposable elements may spread, genomes may expand in size, and chromosomes may fuse without any action from natural selection at the organismal level. Indeed, natural selection on organisms may oppose such evolutionary processes, perhaps ineffectually.

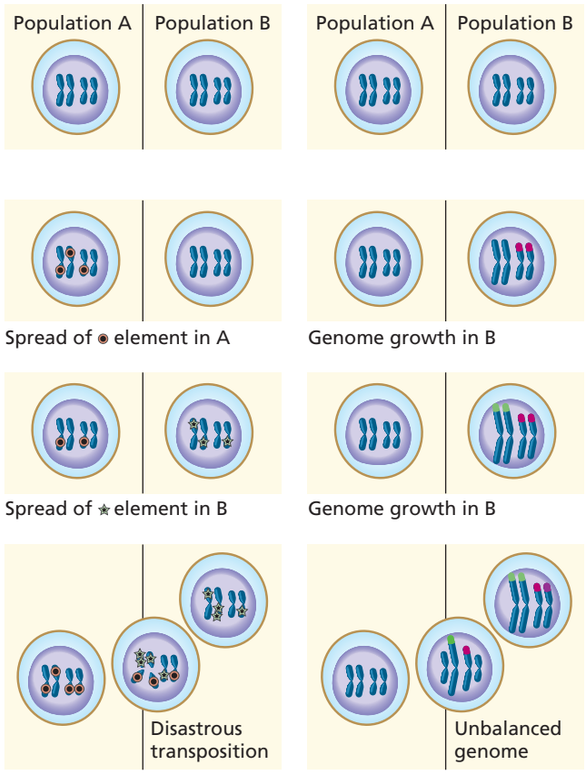


FIGURE 6.4B Genomic Nonadaptive Speciation Note that the opaque bar corresponds to a geographical barrier separating populations.

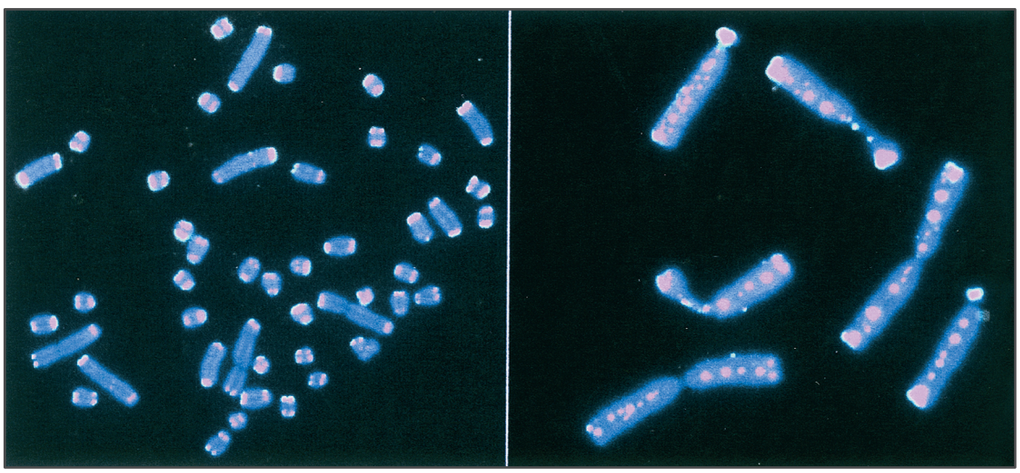


FIGURE 6.4C Reorganization of the Muntjac Genome during Speciation The two staining patterns correspond to two morphologically similar species.

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SYMPATRIC SPECIATION

6.5 Sympatric speciation is difficult due to a lack of evolutionary isolation among groups

Geographical separation provides abundant opportunities for populations to diverge, both accidentally and by natural selection. Is there any possibility for divergence in the absence of allopatry, and can such "sympatric" divergence proceed far enough to produce speciation? (Sympatry is the antonym of allopatry).

In favor of this possibility, there are many known cases of variation within populations. Such variation may even be associated with a geographical pattern, as in the cases of alcohol dehydrogenase alleles and latitude, or sickle-cell anemia and areas with malaria, described in Chapters 4, 5, and 22. Such examples tempt biologists to suppose that humans, for example, might evolve isolation between populations exposed to malaria and populations free of malaria. That way people who are free of malaria, and therefore would not benefit from red blood cell (RBC) sickling, would not inherit the sickling allele.

But there are good reasons for supposing that this isolation will rarely occur. The biggest problem is that any allele that might foster the isolation of group A within a population—call it an "A-barrier" gene—would get into the rest of the population. Then all groups would have the A-barrier gene, and isolation could not evolve (Figure 6.5A).

An evolutionary mechanism that might help **sympatric** speciation along is disruptive selection, discussed in Chapter 4. Suppose that disruptive selection acts to eliminate intermediate individuals, leaving only the extreme genotypes. If successful matings with an individual at one's extreme are the only matings that produce viable offspring, then natural selection will be effectively imposing selection against "hybridizations" between the extremes, as well as selection against intermediate individuals. If such selection is sufficiently intense and sustained for enough generations, then prezygotic isolation might evolve, producing speciation without geographical isolation. Such a disruptive selection process is shown in Figure 6.5B.

Although this type of sympatric speciation could operate in principle, it is unlikely to occur in practice. The problem is that natural selection has to enforce the reproductive isolation of extreme groups. If it relaxes for a generation, there would be abundant gene flow between extreme groups. This relaxation would correspond to a breach in the geographical obstacle separating allopatric populations. Because selection is very rarely rigidly sustained, to our knowledge, it is unlikely to produce sympatric speciation in most species.

However, in a few cases it is plausible to infer that sympatric speciation has occurred, and may occur again. We turn to those cases next.

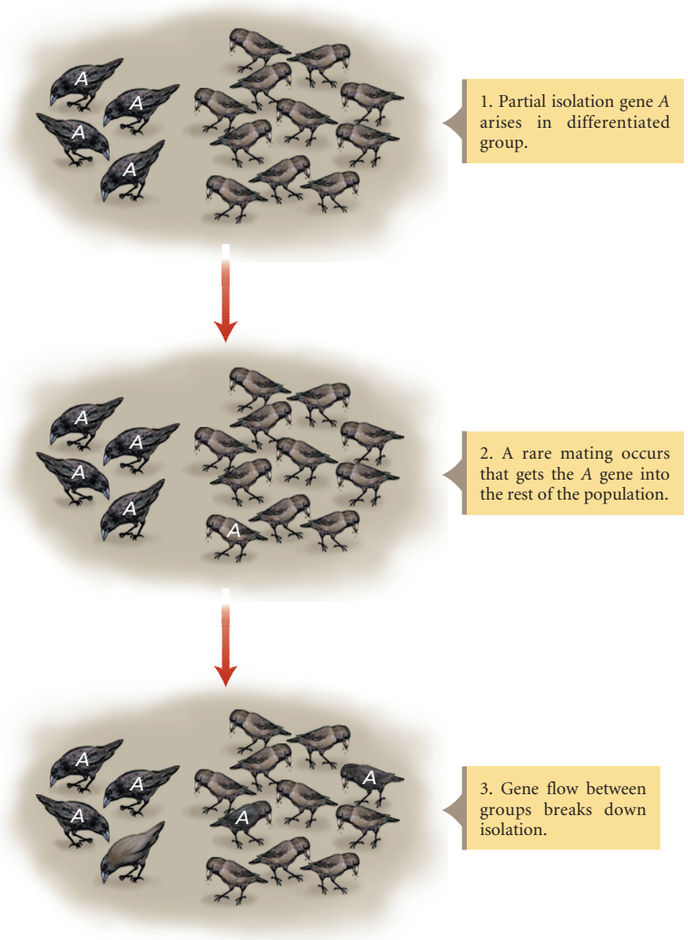


FIGURE 6.5A In sympatry it is difficult for genes that give partial isolation to establish full isolation, because there is no external factor establishing evolutionary separation.

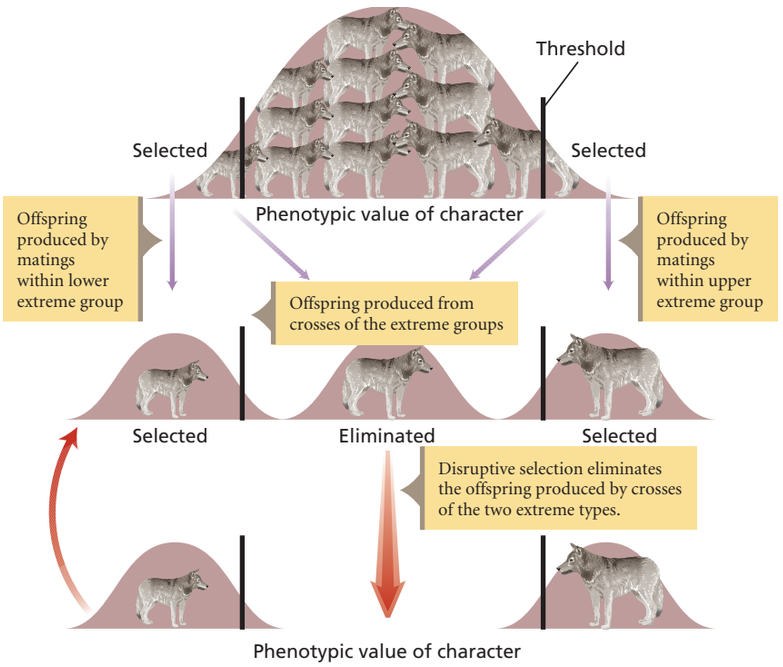


FIGURE 6.5B In principle, disruptive selection could prevent successful reproduction of hybrids between extreme types favored by natural selection, providing that all the hybrid offspring fall between the limits of selection.



6.6 Polyploidization can produce instant sympatric speciation

There are other scenarios for speciation—scenarios that do not require allopatry or disruptive selection. One of these is abrupt genomic reorganization. Plants often undergo spontaneous doubling of chromosome number, which is called **polyploidization**. In angiosperms, for example, up to half of all species have had an evolutionary history of polyploidization. Plants with twice as many chromosomes, however, are often sterile. In some species, these polyploid plants may nevertheless propagate themselves by vegetative reproduction. (This concept is described further in Chapter 18, on the evolution of sex.) Thus the abrupt occurrence of polyploidy may produce a kind of instant speciation, without any geographical isolation.

Figure 6.6A shows how speciation can occur instantly in polyploid plants. Suppose there is a normal, sexual, diploid plant species. From time to time it produces mutant offspring that have twice the normal number of chromosomes, a condition described as *tetraploid*. In many cases, these

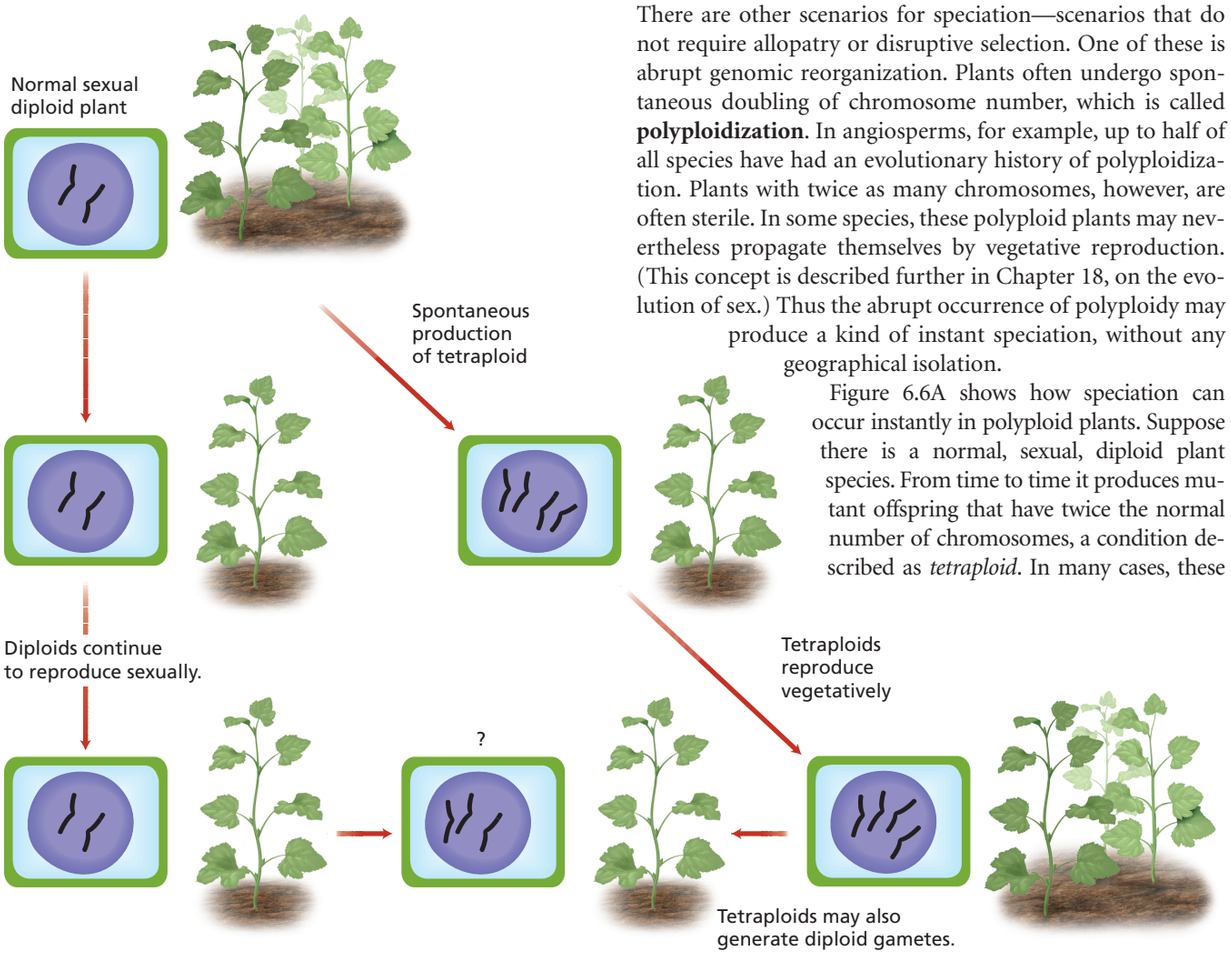


FIGURE 6.6A Speciation by Polyploidy in Plants Speciation hinges on whether triploid hybrids of diploid and tetraploid parents are viable and fertile. If they are, they may establish gene flow between the diploids and tetraploids, preventing speciation. If not, speciation will occur.



FIGURE 6.6B Strawberries spread vegetatively using runners.

tetraploid mutants may be inviable or infertile. Very rarely, however, a viable tetraploid is produced—one that can reproduce without outcrossing, perhaps by selfing. Such selfing may occur by self-fertilization, with the production of diploid gametes. Or the plant might reproduce vegetatively, perhaps through the root system or by "runners," lateral stems that produce new plants as they grow away from parent plants. Strawberries reproduce vegetatively using runners (Figure 6.6B). Many trees use their root systems to produce clonal "stands" of trees. An example of clonal reproduction using roots is the trembling aspen (Figure 6.6C).

An important feature of tetraploid derivatives from diploid species is evident when the tetraploids are exposed to the haploid gametes produced by diploid parents. If the tetraploids produce only diploid gametes, the hybrid zygotes will be triploid. In animals, triploids are not usually viable. But plants are more tolerant of varying ploidies. If successful triploids are generated, and then they successfully mate with diploids and tetraploids, there will be a failure of isolation between diploid and tetraploid plants. Speciation will not occur.

But if there is no successful hybridization between new tetraploids and their parent diploids, the tetraploids will be evolutionarily isolated from the diploids. A new species will have formed almost instantly. Furthermore, tetraploids are usually different from diploids in their patterns of growth, metabolism, and so forth. In such cases, ecological differentiation is achieved instantly as well. This pattern of sympatric speciation is generally accepted as an important mechanism of speciation in plants by biologists. ❖



FIGURE 6.6C A stand of trembling aspen, containing many clonal trees.

6.7 Host-race differentiation might cause sympatric speciation

Another scenario for sympatric speciation involves microgeographical isolation. Some insects, for example, specialize on particular host plants. If mating is associated with plant type, then there is the possibility that the ecology of plant preference could produce pseudo-geographical isolation on a microscale. Different host plants could thereby play a similar role to geographically separate environments.

The true fruit flies of the genus *Rhagoletis* are divided into different **host races** that feed on different types of fruit. Significantly, mating in such species tends to be located at the site of feeding, making the different host races partially isolated from each other (Figure 6.7A). Therefore, this genus seems to fit the pattern expected for sympatric speciation. But what are the specifics of this organism?

The apple maggot fly, *Rhagoletis pomonella*, feeds on several host plants: hawthorn, apple, and cherry. Mating takes place on the plants where the flies feed, and the eggs are laid on the host plants as well. Potentially, there could be isolation between "host races." Is there? Like other flies, *Rhagoletis* disperse readily. There is no physical impediment to switching between host plants. On the other hand, this factor would not matter if the adults always chose the plants on which they had grown.

The genetic evidence suggests there are indeed two races of flies. As shown in Figure 6.7B, there are apple-feeding flies and hawthorn-feeding flies. These flies are not visibly different. Electrophoretic studies (the technology described in Chapter 5) of these flies, however, show that the host races have different allele frequencies. The flies of the two races also prefer their "home" type of host plant. The findings suggest that these flies may be undergoing a process of evolutionary differentiation, despite geographical overlap.

This does not mean that speciation has occurred already. Matings have been observed between the host races, and there is no evidence for postzygotic isolation in laboratory crosses. These fly host races may continue to diverge, and so become species. Or they may continue to exchange genes, remaining part of one species. Evolution is not generally compelled to produce new species. ❖



FIGURE 6.7A Hawthorn and apple trees are distributed throughout eastern North America. True fruit flies can feed on either type of tree. The flies that feed on a particular type of tree, apple or hawthorn, also remain on that tree to mate. Note: Flies and trees are not shown to the same scale or with anatomical precision.

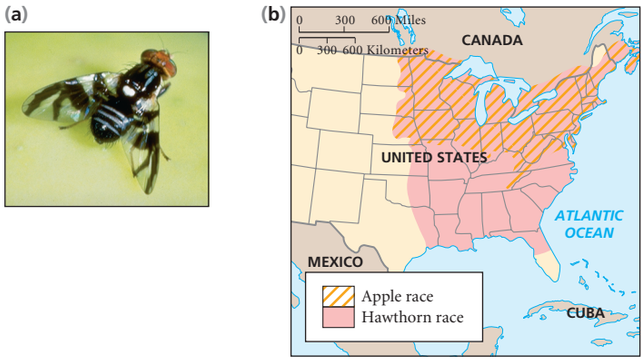


FIGURE 6.7B Apple and hawthorn maggot flies look the same but do not perfectly overlap, because apple trees do not grow in the South.

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6.8 Laboratory experiments show the feasibility of host-race sympatric speciation

One difficulty with the concept of sympatric speciation is that it rests on processes that are not known to work in nature, except for polyploidization. The differentiation of host races has not been observed to evolve to the point where reproductive incompatibility arises. For this reason, sympatric speciation has needed laboratory studies in which evolution can be shown to drive toward reproductive barriers when there is specialization on different hosts.

William Rice performed an ingenious experiment in which host races were allowed to evolve toward separate species. He used two *Drosophila* eye-color mutants, *vermillion* and *raspberry*. He put these flies into a complex laboratory apparatus in which eight different environments were supplied with food, each habitat having one of the eight possible combinations of height (higher, lower), light (bright, dark), and scent (orange, cocoa). The flies were allowed to move through the apparatus as they wished, as adults. But only *vermillion* females that chose the higher, lighted, and orange-scented habitat (habitat 1) were allowed to contribute eggs to the next generation. In parallel, only *raspberry* females that chose the lower, dark, and cocoa-scented habitat (habitat 2) were likewise allowed to contribute eggs to the next generation. Rice imposed these rules as he collected flies for the next generation. The experimental apparatus and rules of culture are diagrammed in Figure 6.8A. (The apparatus and the rules of selection were changed somewhat partway through the experiment, but the basic experimental strategy was preserved.) Although there were opportunities for flies to mate outside of the eight possible habitats, almost all females did not mate until they had reached a habitat with food. In other words, the two types of mutants were analogous to fly host races in nature.

The experimental question was whether these host races would evolve so that they preferred a particular habitat, with mating confined to that habitat. Rice did not force any particular outcome. He merely contrived conditions in which host-race specialization and reproductive isolation might occur.

Figure 6.8B shows the results. At the start of the experiment, the two eye mutants showed no preference for the habitats that allowed them to successfully reproduce. But over 50 generations, strong preferences developed. As shown, *vermillion* flies of both sexes evolved a strong preference for habitat 1, the habitat in which they successfully reproduced. In parallel, the *raspberry* flies evolved a strong preference for their successful habitat for reproduction—habitat 2. (These data are not shown.)

These results show that strong preferences for habitats can evolve in populations that are ecologically successful only if particular genotypes chose particular habitats—even when these habitats are available to all genotypes, and even if there is no genetic bias in favor of choosing the appropriate habitats to begin with. This laboratory experiment was extremely rigorous in destroying flies making the wrong choice. But it did not directly force the evolution of host-race preferences. Those preferences were produced by natural selection acting on its own. Such preferences are a first step in evolution toward reproductive isolation, and thus sympatric speciation.

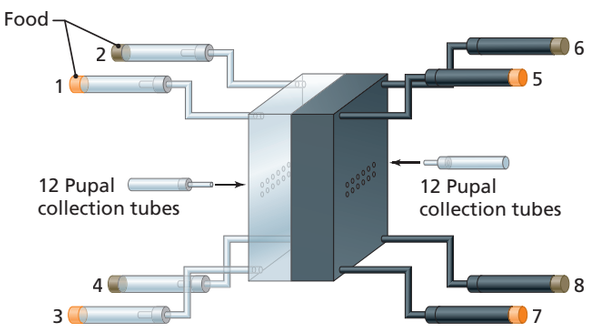


FIGURE 6.8A Habitat Maze Used in the First 24 Generations of the Speciation Experiment Vials with dark medium had cocoa flavoring in the food. Vials with light medium had orange flavoring. Some vials are placed high, others are low. This apparatus let flies choose between habitats (1–8 in the figure). The experimenter then selected the flies by their choices.

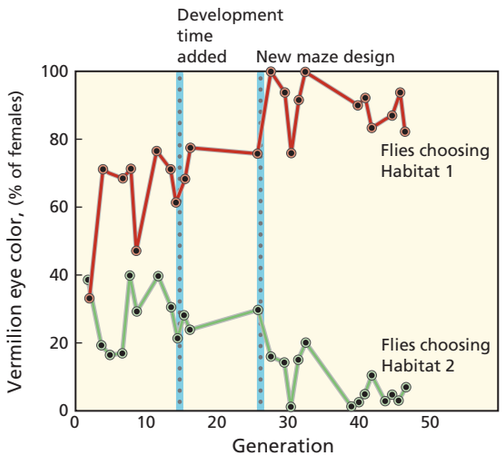


FIGURE 6.8B The results of selection against flies that choose intermediate habitats: Flies make more distinct choices as lab evolution proceeds, resulting in distinct lab species. Flies with *vermillion* eyes become separated from the other flies due to habitat choice.

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HYBRIDIZATION

6.9 Hybridization sometimes occurs in nature

Hybridization occurs when members of one species mate with members of another species and produce offspring. This may lead to (1) alleles spreading from one species to another, or (2) a new hybrid form arising from the cross, or (3) little of evolutionary significance occurring, especially if the matings produce only inviable or infertile hybrids.

In any case, hybridization depends, in the first instance, on enough contact between species that sex happens. Reproductive isolation, and the definition of species as evolutionarily separate, seems to imply that species will not hybridize. However, species may be generally isolated from each other most of the time or over most of their geographical distribution, yet hybridization may still occur under unusual local conditions. When local conditions allow hybridization, the locality is called a **hybrid zone**. This scenario is diagrammed in Figure 6.9A. Hybrid zones may arise, for example, when allopatric speciation has recently occurred and formerly separate populations have resumed contact.

Given that hybridization occurs, several further possibilities arise. One we have already seen—selection for enhanced prezygotic isolation when hybrids are inviable or infertile—"reinforcement" of reproductive isolation. The remaining cases involve fertile hybrids. Some of these scenarios are diagrammed in Figure 6.9B and discussed further here. Later in this module, we describe other scenarios.

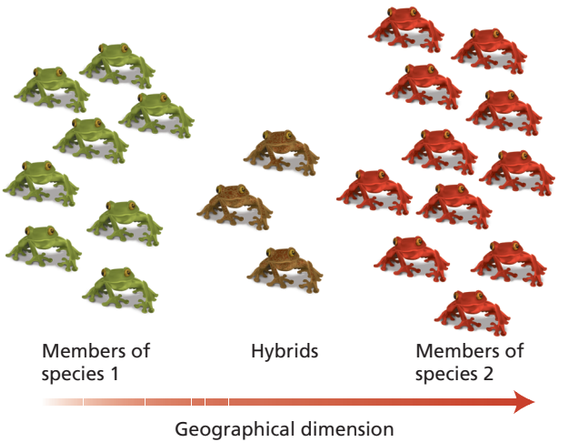
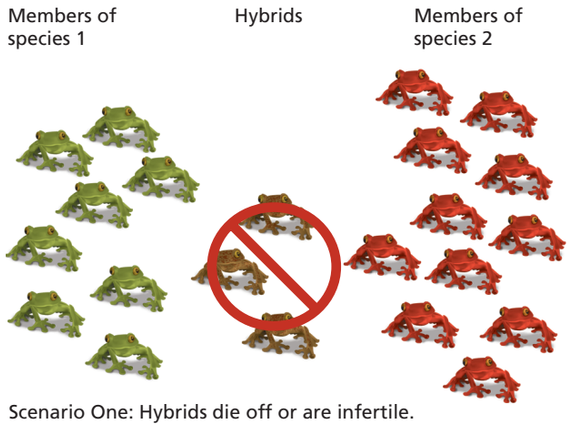


FIGURE 6.9A Hybrid Zone Arising from Sex between Members of Two Distinct Species

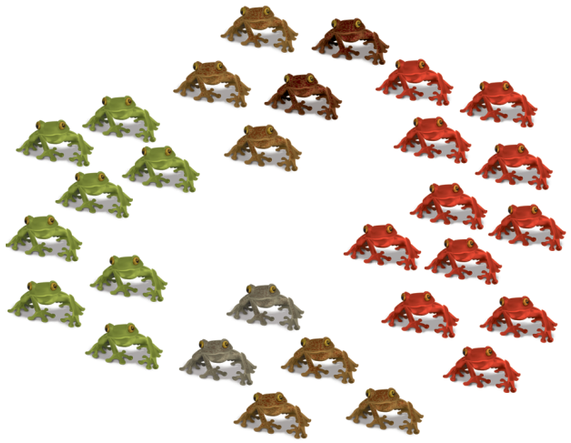
The normal expectation for hybrids between two species is that they will have reduced fitness compared to the two parental species (see Figure 6.9B, Scenario One). Crudely speaking, the hybrids will be dying off soon after they are produced by hybridization. This will tend to produce a narrow hybrid zone, with relatively little evolutionary impact.



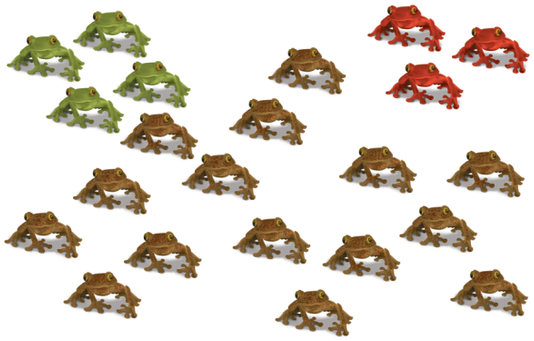
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Scenario One: Hybrids die off or are infertile.



Scenario Two: Hybrids have sex with parental species, causing an exchange of genes between species.

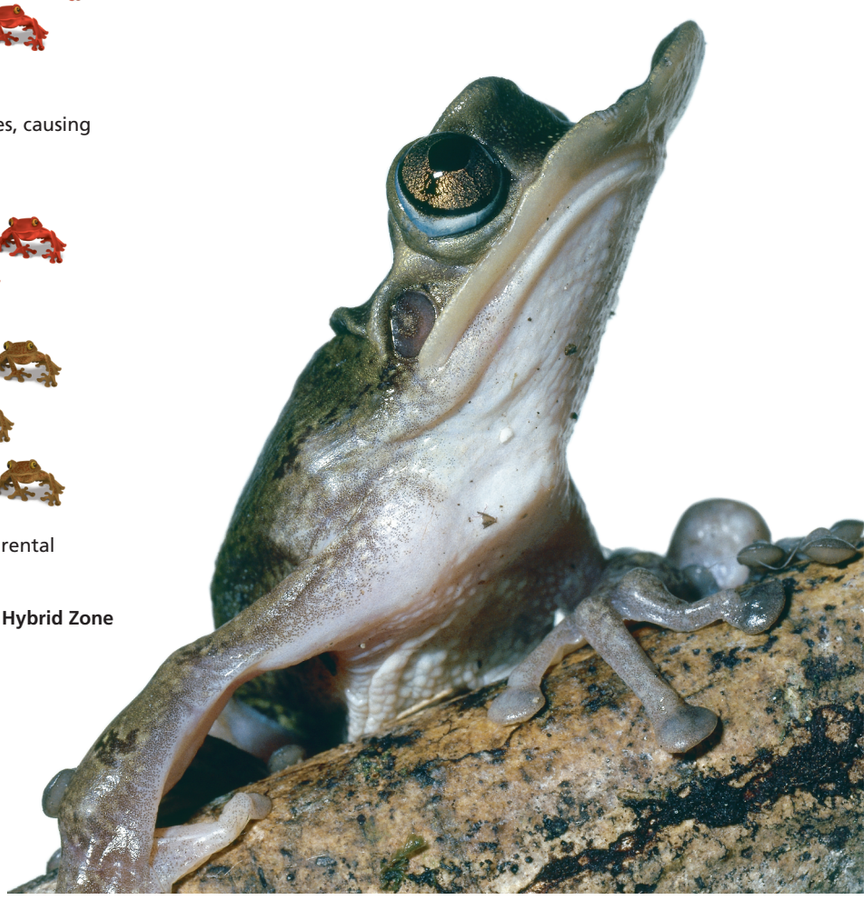


Scenario Three: The hybrids are superior to their parental species, and outcompete them.

FIGURE 6.9B Three Scenarios for Evolution When a Hybrid Zone forms between Two Species

In some species, particularly plants, hybrids may be comparable in fitness to the parental species. Under these conditions, the hybrid zone will be relatively wide (Scenario Two). In rare cases, the proliferation of the hybrid may lead to frequent additional hybridization between the hybrid group and the parental species. Carried to an extreme, this could lead to the disappearance of the evolutionary barrier between the parental species, and the formation of a larger, heterogeneous species made up of the fusion of the two parental species and the hybrid.

Finally, there could be hybrids that have even greater fitness than the parental species (Scenario Three). This superiority might be specific to the hybrid zone habitat, in which case hybrids might be abundant there, but not spread outward. Alternatively, the hybrids could be generally superior to the parental species. Under these circumstances, many outcomes are possible, depending on whether the hybrids evolve independently of the parental species. If a hybrid does so, it might displace the parental forms, even drive them to extinction.



6.10 Hybridization can produce polyploidization and instant speciation

We have already described instant speciation, when plants produce polyploid offspring. Such polyploids are called **autopolyploids**, because all the genetic material comes from one species. Hybridization allows an additional possibility—**allopolyploidization**, in which the extra chromosomes come from hybridization with members of other species. Furthermore, abrogation of normal meiosis is to be expected if chromosomes that lack DNA sequences required for the process are introduced by hybridization (Figure 6.10A). For this reason, the creation of new species with unusual ploidies by hybridization is expected to occur.

Parthenogenetic vertebrate species have apparently been produced by hybridization. (Parthenogenesis is reproduction with unfertilized eggs.) One example comes from the genus *Poecilia*, shown in Figure 6.10B. The species *P. formosa* is an asexual hybrid of two sexual parent species, *P. mexicana* and *P. latipinna*, which live with the asexual species. Other asexual fish are thought to be similar hybrids, particularly species of the related genus *Poeciliopsis*.

An even more interesting example comes from the salamander genus *Ambystoma* (see Figure 6.10B). Two sexual species are known, *A. jeffersonianum* and *A. laterale*, that have two hybrid asexual forms, both successful triploid species. One of the hybrids has two sets of *A. jeffersonianum* chromosomes and one set of *A. laterale* chromosomes. The other hybrid has one set of *A. jeffersonianum* chromosomes and two sets of *A. laterale* chromosomes. In this case, there is no doubt that the new species were produced by hybridization of sexual species that were already established. It is particularly interesting that species formation apparently occurred twice independently, with opposite patterns of chromosomal imbalance. ❖

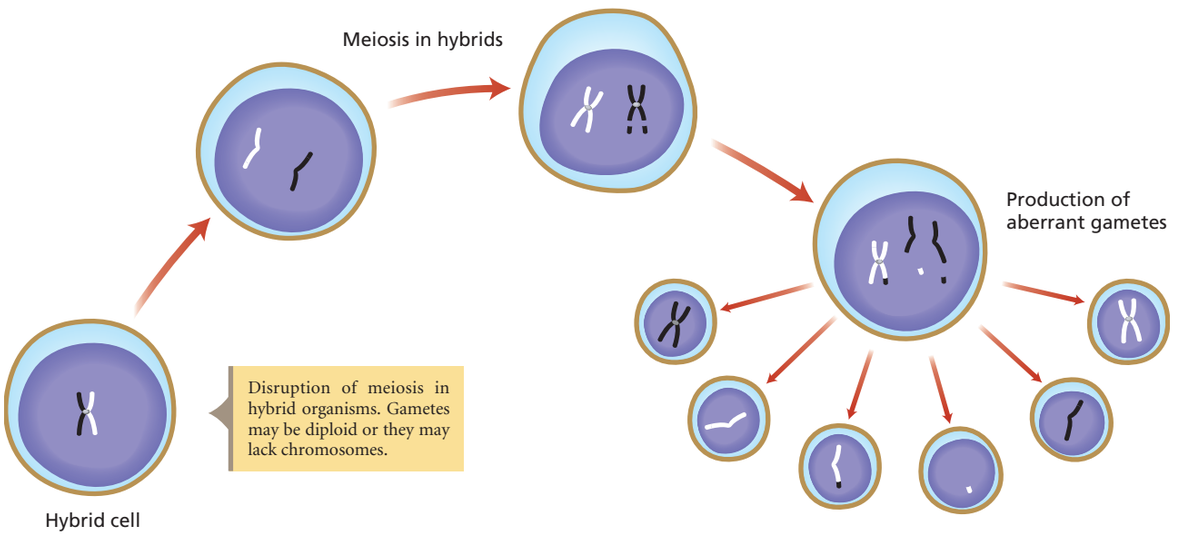


FIGURE 6.10A Aberrant Meiosis in Hybrids Black chromosomal material comes from one species; white chromosomal material comes from the other species.



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(**i**) Mollies and guppies from the genus *Poecilia*



(**ii**) Juvenile (above) and adult (below) salamanders from the genus *Ambystoma*.

FIGURE 6.10B Two groups of animals that form triploid hybrid species: (i) killifish (the poecilids); (ii) ambystomatid salamanders.

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Species Radiations

6.11 The Cambrian explosion was a spectacular radiation of animal species

From time to time, a large number of species come into existence in a short period of geological time. (A few million years would be a brief period on this timescale.) This type of proliferation of species is called a **species radiation**, or an *adaptive radiation*. The most spectacular of all species radiations is that which occurred during the **Cambrian** period, 510–543 million years ago. At that time, land was colonized by multicellular plant and animal species. Many animal taxa appear in the fossil record for the first time during the Cambrian. Essentially all the major animal body plans evolved in an explosion of diversification, including the chordate body plan that was the basis of human evolution.

The Cambrian explosion is documented in the **Burgess Shale**, one of the greatest of all fossil finds. Located on the side of a mountain in the Canadian Rockies, the Burgess Shale contains fossils of whole aquatic animals, not just fossils of bones and shells. For some reason, soft-bodied animals were trapped in sediment that did not crush them immediately, allowing slow mineralization to preserve their anatomy in some detail. Over hundreds of millions of years of geological churning, the sediment was transported en masse from the bottom of a body of water to the side of a mountain.

Figure 6.11A shows photos of some of the fossils found in the Burgess Shale. Figure 6.11B displays drawings of biologists' best guesses as to what these animals looked like. What is striking is that these animals often do not resemble the fossil species that we know from the 500 million years since the Cambrian period. That is, there appears to have been a Cambrian explosion of diversity, which was then cropped back. The Burgess Shale ecosystem is reconstructed in the illustration used for the cover of this book.

Some of these unusual animals have been placed in modern-day taxonomic groups, especially the arthropods. Other Cambrian fossils do not fit in any known taxonomic group. Indeed, some of these animals seem virtually impossible. When it was first found, it was not clear how to orient a fossil called *Hallucigenia* (shown on the book cover). Which side was the bottom and which was the top? Further research also changed the identification of the head end. Yet this fossil animal has been placed in a surviving taxon—the Phylum Onychophora, the velvet worms. ❖

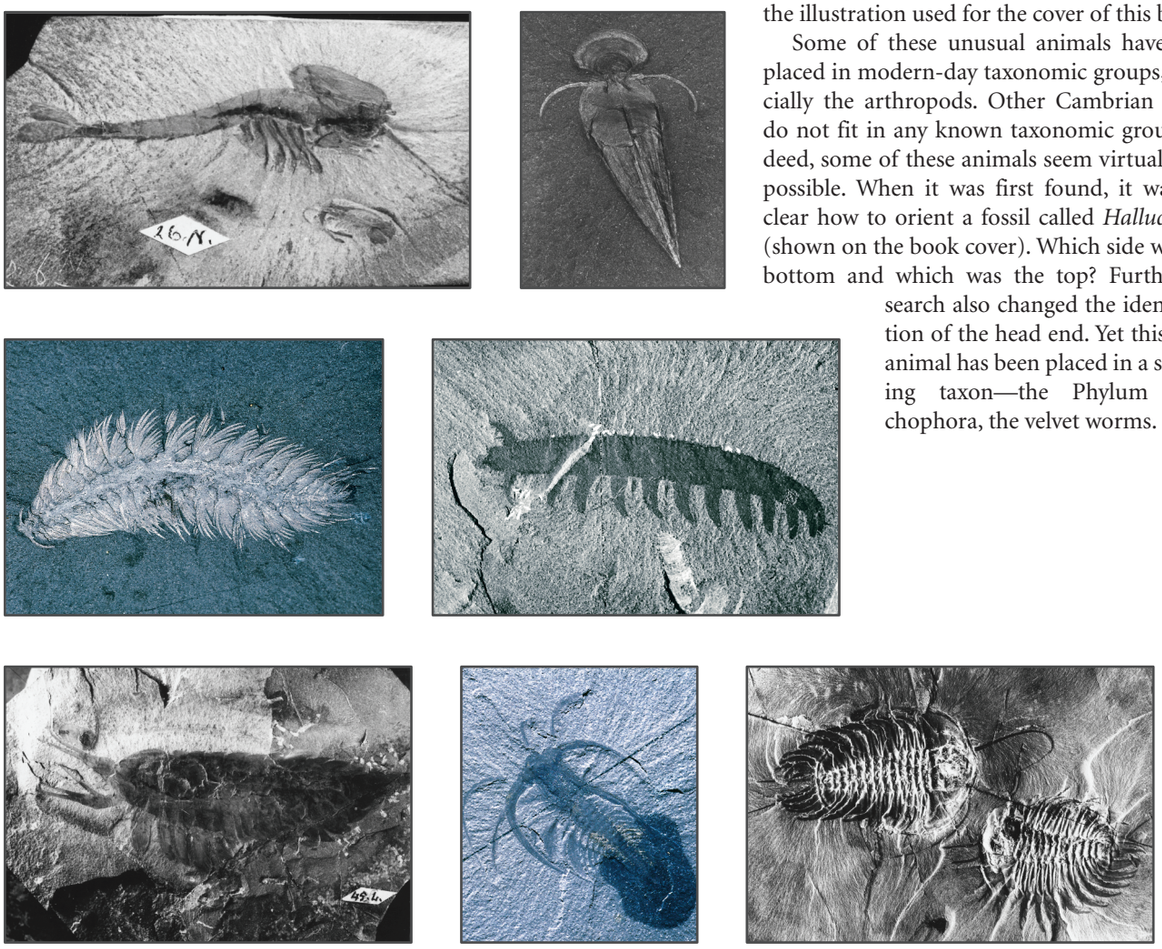


FIGURE 6.11A Fossils from the Canadian Burgess Shale, about 500 Million Years Old See the front endpapers for the names of these fossil life-forms.

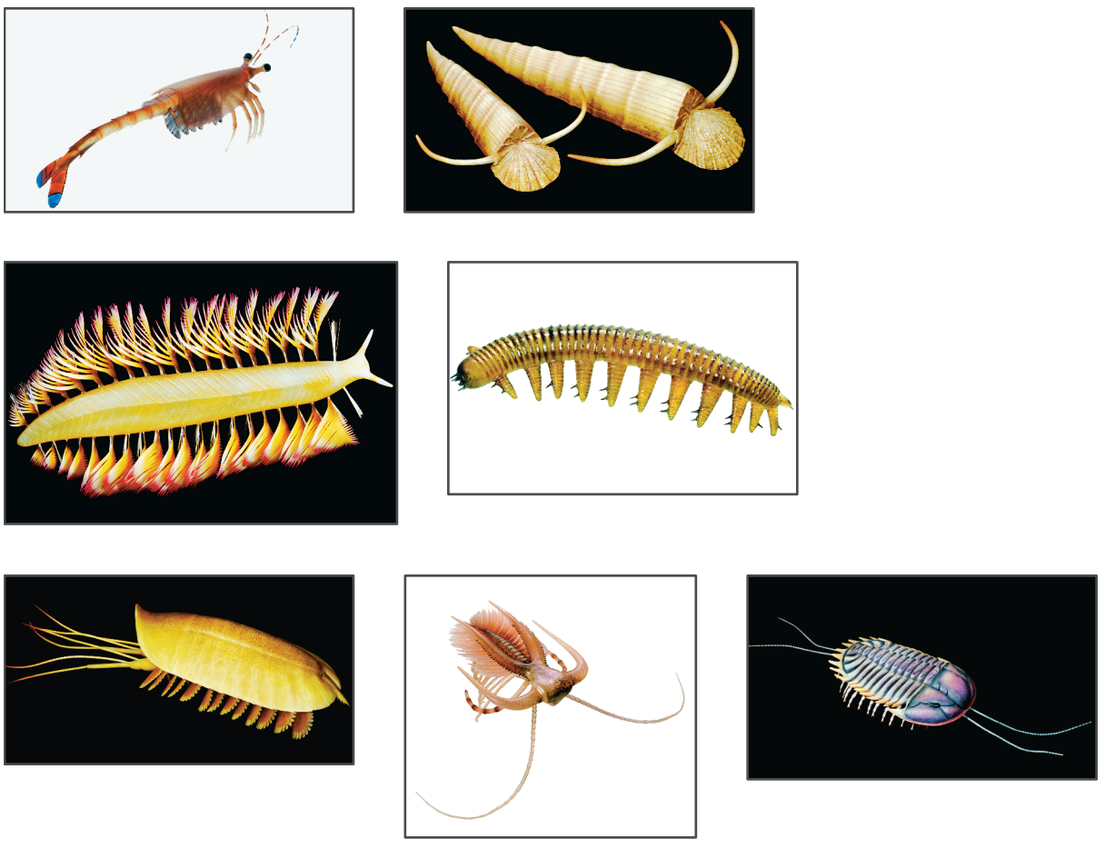


FIGURE 6.11B Reconstructions of the Animals Whose Fossils Are Shown in Figure 6.11A



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6.12 The colonization of the Galápagos Archipelago by finches led to an adaptive radiation

After the Cambrian explosion, one of the best-known examples of adaptive radiation is the colonization of the **Galápagos Islands** by bird species, especially **finches** and mockingbirds. The thirteen finch species of the genus *Geospiza*, known as Darwin's finches, have been best studied. The diversity of species is shown in Figure 6.12A (see Chapters 1 and 4 also).

Figure 6.12B shows one theory for the evolutionary tree connecting these finch species. The most important idea presented by this tree is that all these species descend from a single founder species. This founder is generally thought to have arrived from the South American mainland some thousands of years ago. Presumably, that founding event was a flock of finches blown west into the Pacific. This is not entirely groundless speculation. Exotic birds and plants still appear on the Galápagos Islands, blown in by wind, or floating in on tides.

Once they got to the Galápagos, Darwin's finches evolved into a number of different species. Some have evolved into insect eaters. Other species eat seeds. Some live on the ground, while others live primarily in trees. The finches are not that different from each other in anatomy. Some are obviously

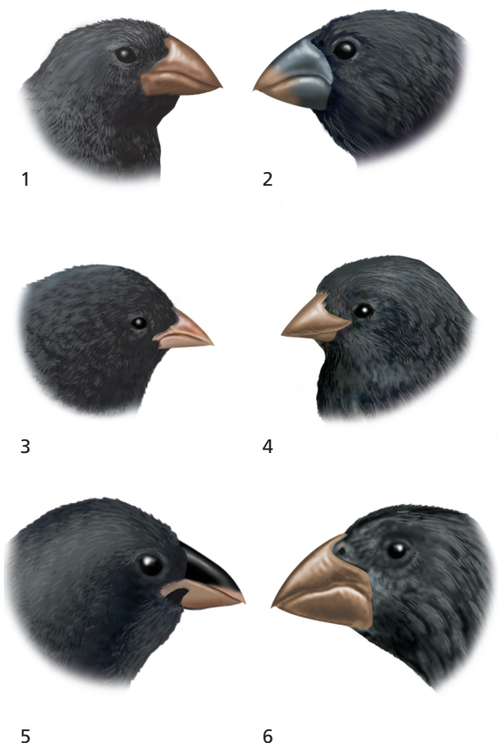


FIGURE 6.12A Heads of Some of Darwin's Ground Finches





larger. The central feature in their evolution has been their beaks. Some of the finches have beaks twice the size of the smallest finches, and the shape of the beaks varies a lot. Some finches have beaks that are short but deep; others have pointed beaks that project sharply outward from the bird's face. This variation in beaks corresponds to variation in diet. The birds with large, powerful beaks are able to eat hard-shelled seeds. Cactus finches have long beaks that enable them to forage for food between the spines of cacti. A simple evolutionary inference is that these finches would never have become so diverse if the Galápagos Islands had already been colonized by a full range of bird species before the finches arrived. But because the islands were likely free of most bird species when the first finches arrived, the finches were free to evolve and speciate, filling up a greater number of ecological niches than they would have otherwise. This is a species radiation that occurred to fill an ecological vacuum.

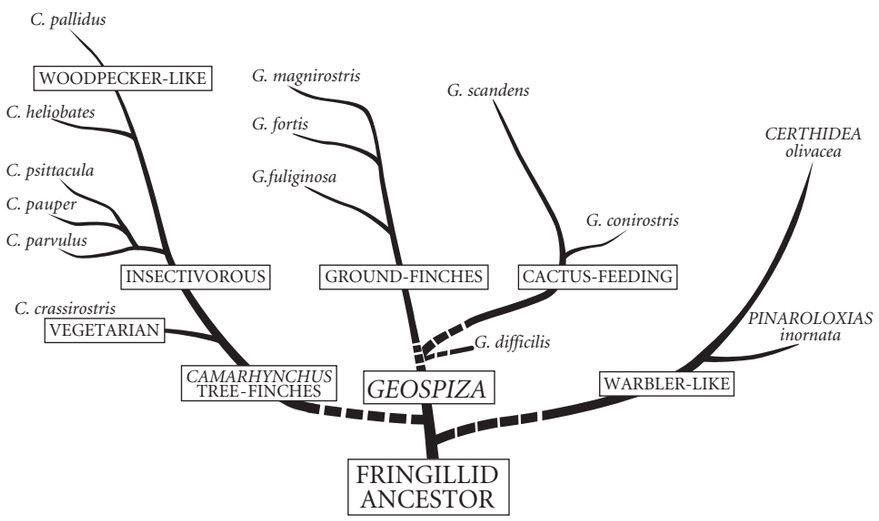


FIGURE 6.12B **An Evolutionary Tree for Darwin's Finches**

PUNCTUATED EQUILIBRIUM

6.13 Mayr's speciation model implies punctuated equilibrium

Many scientists have thought that Darwin's theory of evolution means that species should gradually change in the fossil record. Sometimes they do. Since the start of the **Tertiary** period, terrestrial mammalian species like horses, bears, and pigs have gotten larger, or smaller, fairly smoothly. This pattern, called **phyletic gradualism**, is shown in Figure 6.13A. The doctrine of phyletic gradualism leads paleontologists to look for "missing links" when there seems to be an abrupt change in the fossil record of evolution. This search for missing links is inspired by the assumption that when there is a missing link, it is only because of a failure to find an intermediate fossil that is in fact out there. The most famous missing link, that between ape and human, is discussed in Chapter 21.

There is an alternative interpretation to phyletic gradualism and missing links. This is the view that there really are abrupt changes in evolution. In this theory, species are normally at evolutionary equilibrium, with little evolutionary change. But when speciation occurs, evolutionary equilibrium undergoes rapid change. This theory is called **punctuated equilibrium**. The evolutionary pattern that arises with punctuated equilibrium is shown in Figure 6.13B. The horizontal branching of the evolutionary process signifies evolutionary change during speciation, while the vertical lines denote unchanging species between speciation events.

How can evolutionists explain punctuated equilibrium? One explanation comes from a theory of speciation developed first by **Ernst Mayr**, but since elaborated by many evolutionary theorists, especially **Stephen Jay Gould** and **Niles Eldredge**. Mayr's original idea was that small **peripheral** populations might be more likely to undergo the kind of **genetic revolution** required to produce a new species. Among other things, such small populations would have a much greater speed of **genetic drift.** This has two consequences: (1) The large populations that make up the bulk of a species may be relatively static evolutionarily; and (2) the processes that produce new species may typically occur in populations so small that they would not be represented in the fossil record. As shown in Figure 6.13C, these processes tend to make the appearance of new species in the fossil record abrupt. Evolution may thereby proceed by normal processes of speciation, but the resultant pattern may resemble punctuated equilibrium more than it conforms to the idea of phyletic gradualism. ❖

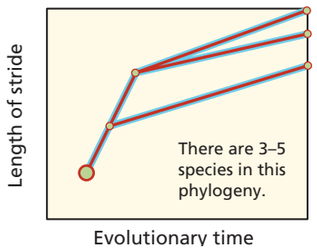


FIGURE 6.13A The Traditional View by Paleontologists of Macroevolution From this viewpoint, the pattern of evolution among species follows that within species with no discontinuities. (New species occur when the phylogeny branches *and* during evolution between branching events.)

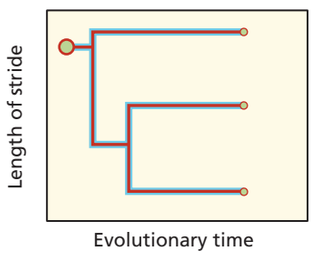


FIGURE 6.13B The Punctuated Equilibrium View of Macroevolution From this viewpoint, the pattern of evolution among species does not follow that within species. It is supposed that most evolutionary change occurs when new species are produced. (New species occur only when the phylogeny branches.)

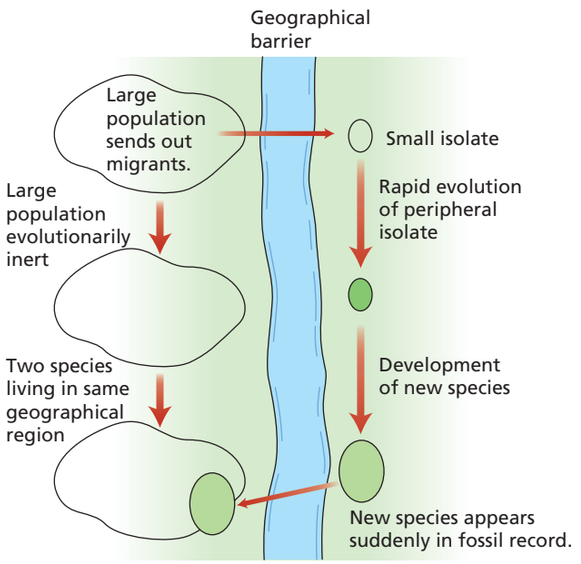


FIGURE 6.13C Mayr's scheme, in which small, isolated populations evolve rapidly and form new species that appear abruptly in the fossil record of evolution. (The scale of the blobs roughly indicates the population size of the organisms they represent.)

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6.14 Hopeful monsters can escape evolutionary stasis, in theory

When the idea of punctuated equilibrium was first proposed, it was an application of Mayr's speciation model. Mayr's model in turn was a special case of the type of speciation process that evolutionary biologists have generally accepted. However, in the hands of Gould, the idea became more extreme. Gould went from using Mayr's Darwinian model of speciation to the idea that speciation might occur as a result of almost instantaneous genetic upheavals. Coupled with this was an emphasis on the idea that normal species are locked into **evolutionary stasis**, with little change possible until speciation occurs. Both of these ideas were major challenges to the Darwinian tradition.

There are three main scenarios by which species may show evolutionary stasis. These scenarios are illustrated in Figure 6.14A. The first is a *lack of genetic variation*. If species are genetically uniform, there is little prospect that natural selection will change their phenotypes. This is a straightforward application of the basic features of natural selection, described at the start of Chapter 4. However, surveys of genetic variability indicate that most plants and animals have abundant genetic variation. A lack of genetic variation is not a viable explanation for the stasis of most species during evolution.

The second scenario is **stabilizing selection**. Stabilizing selection undoubtedly can prevent evolutionary change. But it is not clear that all, or even most, characters of most species undergo stabilizing selection. Evidence for such an extreme assumption is lacking. Furthermore, the ease with which artificial and laboratory selection can change biological characters, a point that Darwin himself emphasized, suggests that the phenotypes of organisms are not generally "locked down" by stabilizing selection.

The third scenario is **fluctuating selection**. If selection has no long-term focus, then evolving characters may move back and forth during the course of evolution, without the kind of trend that is expected from the perspective of phyletic gradualism. The problem with this view is that it is a kind of selective drift, which should eventually lead to a breakdown of stasis within species evolving according to this scenario.

If it is not easy to see why most species should show evolutionary stasis, the problem of abrupt speciation may also be difficult. We have already considered polyploidy and hybridization as mechanisms for instantaneous speciation, in which asexual forms are derived from sexual species. The problem is that speciation by spinning off asexual forms is not common across the evolutionary spectrum. Other species that might undergo instant speciation have a major problem: the **hopeful monster**. A newly tetraploid plant that reproduces vegetatively does not have to find a mate. But most species do not produce asexual offshoots. Therefore a sexual organism that has undergone a radical transformation to become a monster from a new species needs to mate with another of its kind, which is the hopeful part. Frankenstein's monster needed a bride made for him. In a real biological setting, which this cartoon does not show, the genetic upheaval required to produce one monster is rare, so producing two or more monsters is still less likely. This problem is diagrammed in Figure 6.14B. ❖

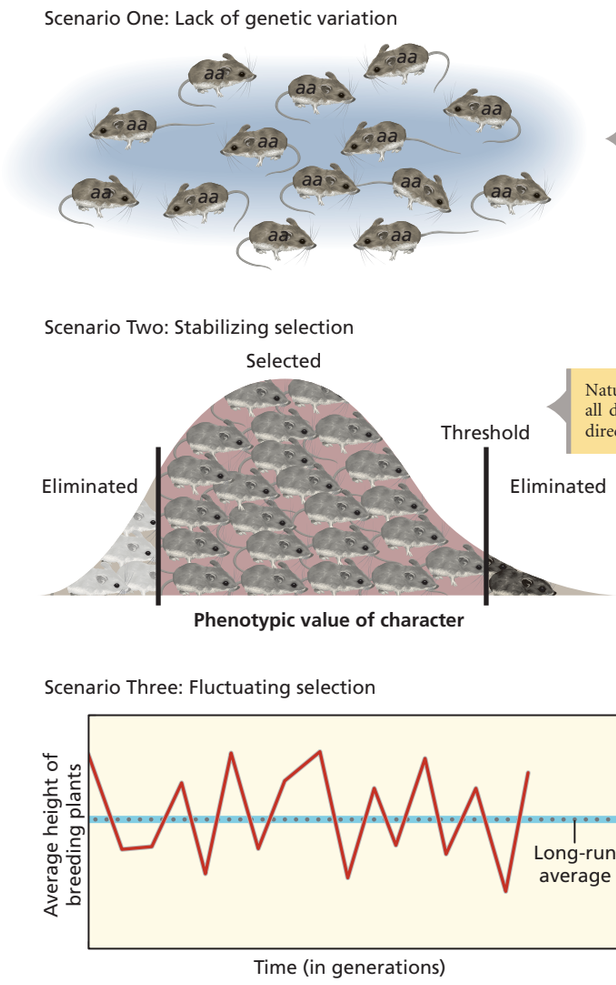


FIGURE 6.14A Three Explanations of Evolutionary Stasis

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FIGURE 6.14B **The Hopeful Monster Needs a Bride** A major mutant (i.e., a monster) can start a new species only if it reproduces asexually, or if a sexually compatible similar mutant is improbably produced.

RETAIL EXTINCTION

6.15 Extinctions destroy unique products of biological evolution

People may complain that things never seem to last anymore—things like marriage or audience attention spans—but one thing is really forever: **extinction**. Parallel evolution does occur, and such parallels can produce rough "repeats" in evolution. One example is the fusiform body shape of sharks, ichthyosaurs, and dolphins. This body shape has evolved repeatedly in diverse phylogenies, and quite independently, as shown in Figure 6.15A.

But we can be confident that these repeats were not complete reincarnations of earlier species. Comparing shark and dolphin DNA would reveal a vast number of evolutionary differences between these forms, differences that instead would ally them with other fish and other mammals, respectively. That is, they are on very different branches of the evolutionary tree of vertebrates, as shown in Figure 6.15B. In the parallel evolution of streamlined shapes for rapid swimming, natural selection has produced a similar result starting from dissimilar evolutionary backgrounds.

Comparing shark and dolphin DNA would reveal a vast number of evolutionary differences between these forms, differences that instead would ally them with other fish and other mammals, respectively.

Therefore, even though dolphins are similar to some aquatic **dinosaurs**, they are not themselves dinosaurs. All aquatic dinosaurs have gone extinct, and they will never come back. Evolution does not supply complete repetitions, only repeated parallels. Once we lose a species, we do not get it back again.

Another way to understand this concept is that the evolutionary tree introduced in Part One directly implies that each species is an historically unique entity. Species are not functional categories like table, knife, or car. You can always make a new knife. Species are like the paintings of Van Gogh—each species a remarkable masterpiece, unique in itself, produced at a singular point in time by a process of speciation that we have yet to understand fully. When such species are lost, they are virtually irreplaceable. The one mitigation is that there may be other, similar species, just as there are several Van Gogh paintings of sunflowers. ❖



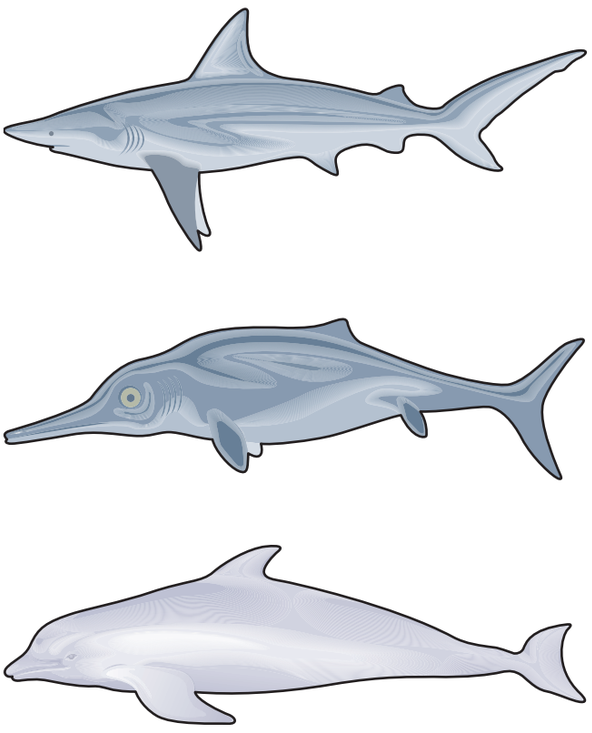


FIGURE 6.15A Body Outlines for Sharks, Ichthyosaurs, and Dolphins, Showing Parallel Evolution for Fast Underwater Swimming

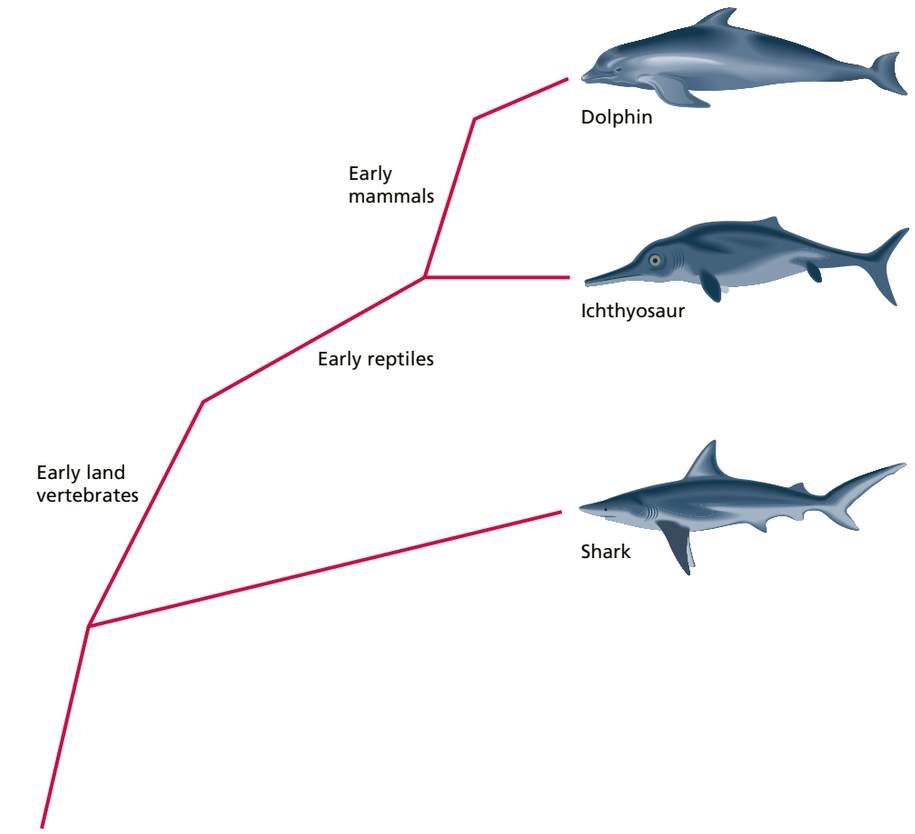


FIGURE 6.15B **Evolutionary Tree Showing Evolutionary Relationships of Sharks, Ichthyosaurs, and Dolphins**



6.16 Normal biotic diversity is the result of a balance between the processes of speciation and extinction

It is a cliché of evolution that the dinosaurs went extinct 65 million years ago, and then the mammals evolved. This suggests that extinction got the dinosaurs, and the mammals then went from success to success. Such an interpretation, however, falsifies what really happens in evolution. All major taxonomic groups undergo repeated extinctions, as well as repeated speciation events.

One well-studied example of this is mammalian evolution since the extinction of the dinosaurs. During these 65 million years, many successful forms of mammalian life evolved. But even more prominent in the fossil record is the repeated extinction of mammalian species. The evolutionary ancestry of the modern horse, for example, is full of examples of species and genera going extinct, as shown in Figure 6.16A. Usually we do not know why these forms went extinct. It would not be correct to assume that species less like modern horses were always the ones that went extinct, compared to a "horsier" ancestor. Such patterns are occasionally found in mammalian evolution, but are by no means the rule. Figure 6.16B shows some examples of the various mammalian species that went extinct in the last 60 million years. Even though the mammals were an extremely successful animal in this period, a large number of mammalian species went extinct, even as new mammalian species evolved.

One way to understand this situation is illustrated in Figure 6.16C. Think of species as molecules of water. At any time, species are doing one of three things. First, some of them are evolving from other species, joining the basin of living species. This process is like water dripping from a tap into a basin. Second, there are the species going about their business as living things, increasing or decreasing in numbers temporarily, but otherwise floating in the basin of the living. Third, because the basin is plugged, the water in the basin tends to overflow, letting water drip out. The water dripping out is the normal process of extinction, by which species are being lost at all times. This metaphor is a bit misleading, though: Water in a plugged basin with a dripping faucet will maintain the same level, but the number of species in the world does not stay strictly constant. The important point is that there are three kinds of species: those being created by speciation; those merely existing; and those going extinct. The total number of species at any one time reflects the balance between these three types of species.

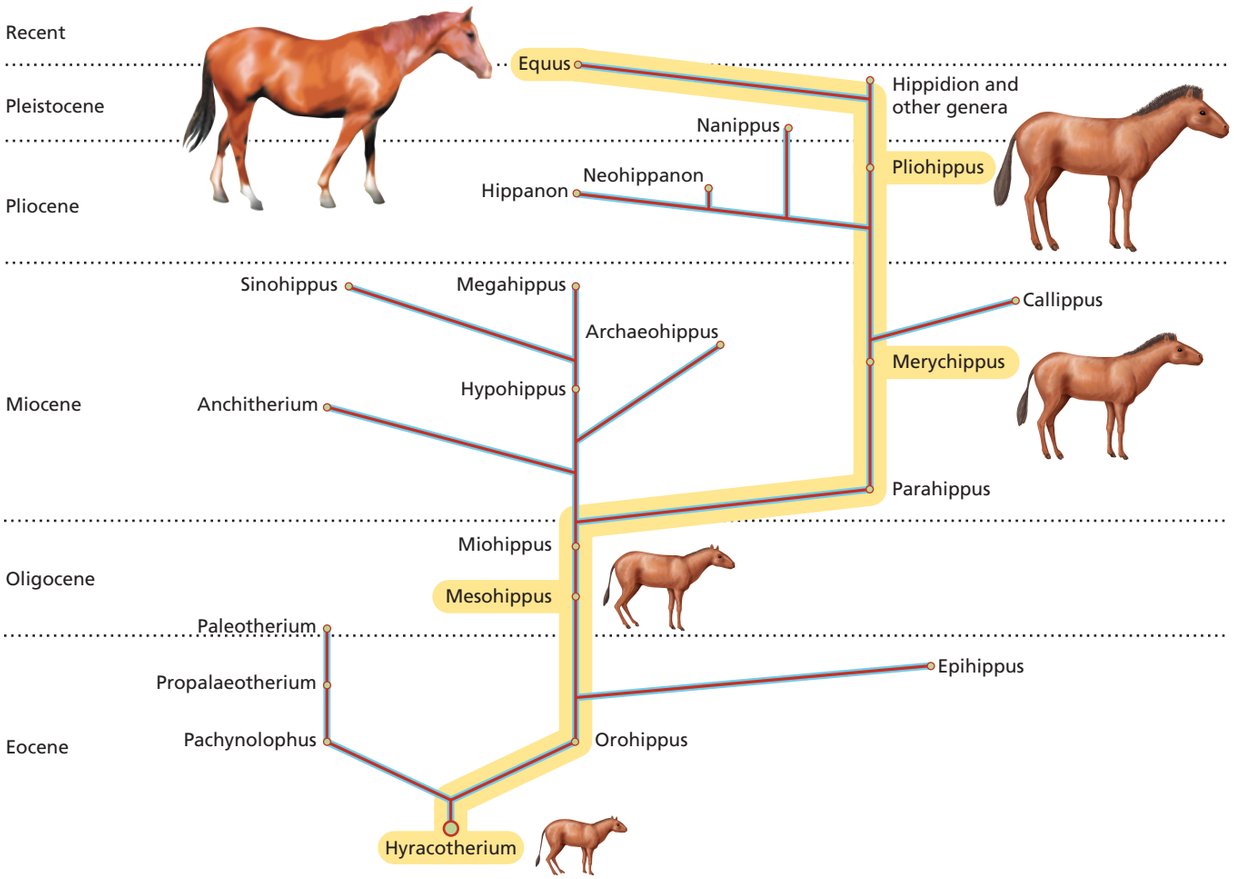


FIGURE 6.16A The Evolution of Horses, Showing Repeated Extinctions



(i) Nesodon of South America



(ii) Giant kangaroo of Australia



(iii) Woolly mammoth of Eurasia and North America



(iv) Giant ground sloth of North America

FIGURE 6.16B **Extinct Pleistocene Mammalian Megafauna**

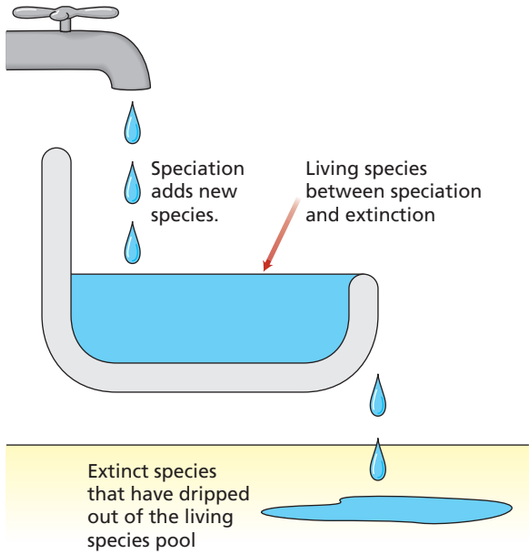


FIGURE 6.16C **Balance Between Ordinary Extinction and Speciation Controls Diversity**



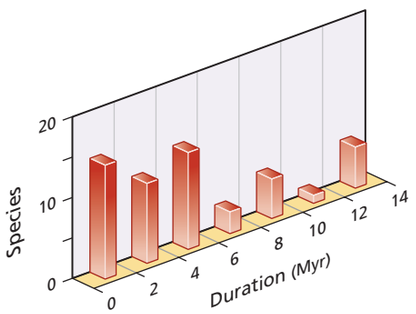
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6.17 Species that escape extinction tend to disperse widely over large geographic ranges

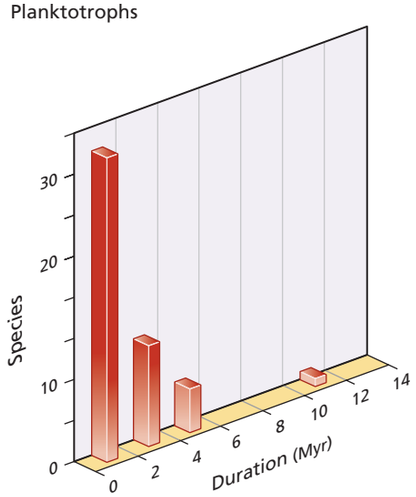
Many factors influence whether or not a species goes extinct. Extinction is primarily a matter of too many deaths among both juveniles and adults. The normal causes of death are also factors in extinction. Disease, predation, or competition are all biotic factors that must kill organisms at all times. A new deadly disease may pose a threat to the survival of an entire species. Potentially, the human immunodeficiency virus (HIV) could kill off our entire species, because the recently successful drugs only slow the progress of the disease rather than curing it. Dramatically virulent pathogens, like the Ebola virus, conceivably could accomplish quickly what HIV is doing only slowly, providing efficient world travel spreads these pathogens faster than they can kill all available victims. The recent rapid spread of the severe acute respiratory syndrome (SARS) virus illustrates the potential for disaster with disease transmission arising from intercontinental travel. Abiotic factors, like excessive heat, desiccation, or salinity, will kill some organisms that are in the wrong place at the wrong time. The aptly named Death Valley in eastern California embodies this principle. Tourists who visit the locale, especially those from Europe, frequently suffer exposure, heat stroke, and death. When there is a major climate change, such as an ice age, many species may freeze to death and thus become extinct. Too much death, however caused, must foster extinction.

The effects of the recent human population explosion have revealed one particularly important point of vulnerability where extinction is concerned—loss of habitat. It is often difficult for humans and other predators to destroy all members of a species, if only because most species are distributed somewhat broadly. But if the habitat of the species is greatly reduced, or cut up by roads, railways, and canals, then it may have few resources with which to produce young or hide from predators. And this vulnerability to loss of habitat is as true of a small plant as it is of a small butterfly. Furthermore, if one species is extinguished, then other species that depend on it for their food or other functions may go extinct themselves. Plants that depend on specific pollinators probably will not survive the extinction of their pollinator species. A number of parasite species are vulnerable to the extinction of just one or two host species: Insect parasitoids are one example; and pathogens like smallpox, which infects only humans, are another. In a sense, the "bumping boxcar" extinction (one extinction causing another, which causes another, etc.) of these additional species is a continuation of the problem of loss of habitat, because the species they depend on are in a sense part of their habitat.

There is extinction data that supports the importance of habitat loss, although it is a bit indirect. Species that have a local distribution, with one or just a few suitable habitats, are inherently more vulnerable to habitat loss than are species that disperse widely and have a broad geographic range. Therefore, if habitat loss is generally important, then

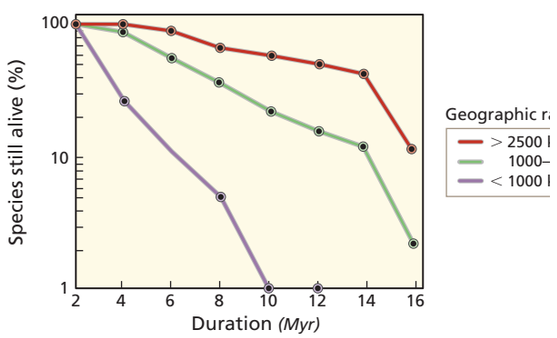


Planktotrophs



Nonplanktotrophs

(i) Comparison of species duration among marine species



(ii) Comparison of species duration among mollusks

FIGURE 6.17A (i) Planktonic species disperse more widely than nonplanktotrophs. Planktotrophic species also last longer before extinction. (Myr is millions of years) (ii) Mollusk (snails, clams, etc.) species last longer when they have a wider geographic range. (Myr is millions of years.)

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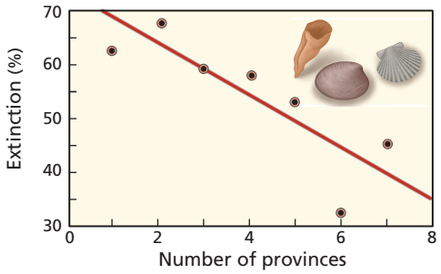


FIGURE 6.17B Marine bivalve genera that inhabited more oceanic regions, or "provinces," were less likely to go extinct at the K-T boundary.

we should see an inverse correlation between breadth of distribution and likelihood of extinction. The broadly distributed species should go extinct less often. For example, marine invertebrates that have a planktonic larval form, which floats long enough to be distributed widely across an ocean, should go extinct less often than forms without a planktonic phase. Figure 6.17A shows that this pattern does exist in studies of planktonic life history and geographic range, at least during normal extinction periods. This pattern also shows up in data from large-scale extinctions, as shown in Figure 6.17B for the extinctions at the end of the **Cretaceous** period. With respect to avoiding extinction, spreading out is better.



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Mass Extinction

6.18 Mass extinctions have intermittently eliminated a large proportion of living species

Influenced by Darwin, most evolutionary biologists have thought of the broad evolution of life in terms of the slow production of new species, together with their steady extinction, as discussed in the preceding modules. Most of the time, so far as we can tell from the fossil record, this is correct. More than 90 percent of extinctions occur in this unspectacular fashion. But at a few points of time, this pattern is annihilated by massive levels of extinction.

The most extensive **mass extinction** is the one that happened at the end of the **Permian** period, which was also the end of the **Paleozoic** era, the first of the three major eras comprising the eon of multicellular life known as the **Phanerozoic**. This mass extinction wiped out about 50 percent of all known taxonomic families and an even larger percentage of species—about 90 percent of all species then living. This massively catastrophic event marks the transition between the Paleozoic and the **Mesozoic** eras.

Dinsoaurs would dominate the large fauna of the Mesozoic before they too would be wiped out at the end of the Cretaceous, the **K-T boundary**, a point in time that is also the end of the Mesozoic and the start of the **Cenozoic** period. Since then mammals and birds have dominated the large fauna populations of the world. The Cretaceous is the most recent mass extinction event, visualized in Figure 6.18A. The overall sequence of mass extinctions is shown in Figure 6.18B.

Two major scientific issues arise from the phenomenon of mass extinction. First, do species levels recover, or has the Earth been progressively losing species because of mass extinctions? It turns out that species numbers recover from mass extinction events, as if evolution tends to return to a "set point" for species numbers. The causes of this pattern are not fully understood, but some hint of explanation is provided by such events as the mammalian recovery of many large-animal niches, after the dinosaurs went extinct.



FIGURE 6.18A Pictoral Visualization of the Large-Body Impact That is Thought to Have Ended the Cretaceous and Killed Off the Dinosaurs This is explained further in Module 6.19.

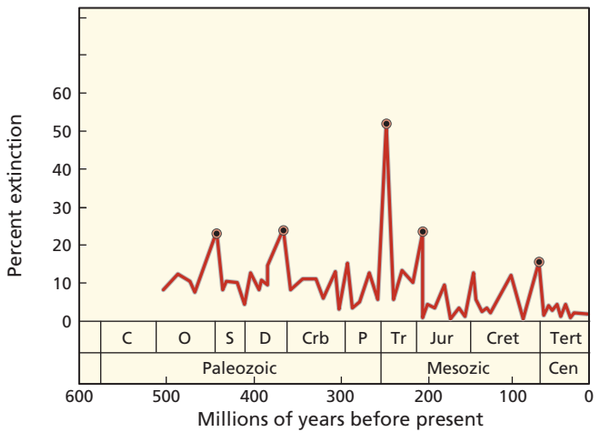
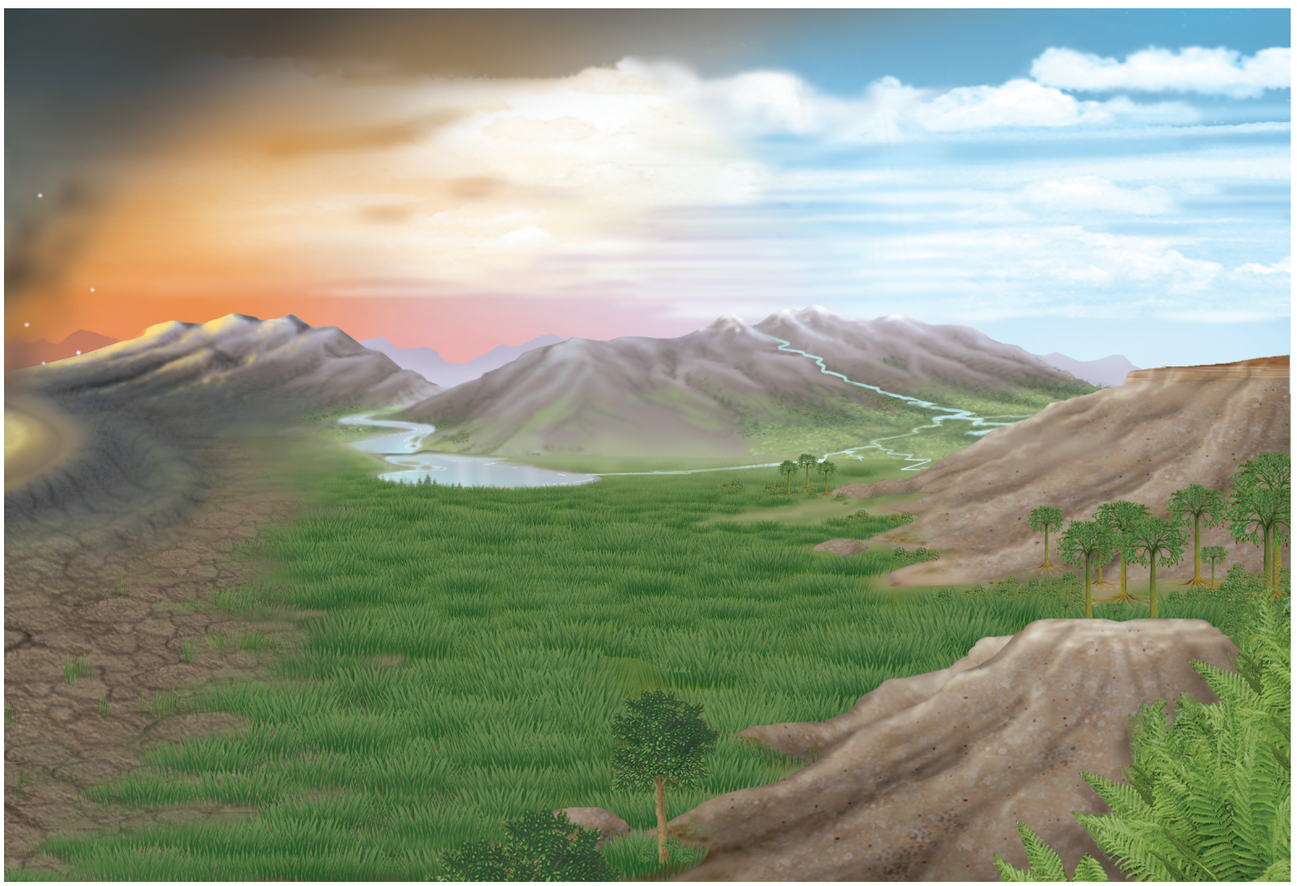


FIGURE 6.18B Patterns of Extinction among Taxonomic Families Since the Cambrian, Showing the Mass Extinctions The rate of extinction of individual species was far higher.

It may be that evolution tends to fill up "vacated" ecological niches after mass extinctions. However, there are many dinosaur features that have not been emulated in the course of mammalian evolution, so this theory is unlikely to be the whole truth.

The second major scientific issue is the cause(s) of mass extinctions. Figure 6.18A depicts one possible cause: the impact of a large astronomical body, such as a comet or large meteorite. This idea is discussed further in Module 6.19.



6.19 The mass extinctions probably arose from large-body impacts

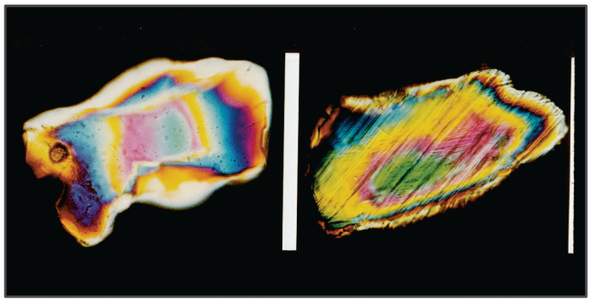
What causes mass extinctions? Geologists once believed that such normal processes as volcanic activity or climate change caused mass extinction. Some still do.

Since 1980, however, an alternative theory has been proposed that has excited the scientific community. The theory is that moderately large astronomical bodies, either comets or meteors, have intermittently hit the Earth with explosive forces equal to those of many exploding thermonuclear weapons. The best evidence for this **large-body impact** theory has come from the most recent mass extinction, 65 million years ago, at the end of the Cretaceous. At that point in the geological sediment, there are many indications of an extraterrestrial impact: High levels of **iridium**, which is common in meteorites; "shocked" glass over wide areas, like the effect produced by thermonuclear weapons; and extensive ash and soot deposits in the proposed impact sediment. These phenomena are shown in Figure 6.19A.

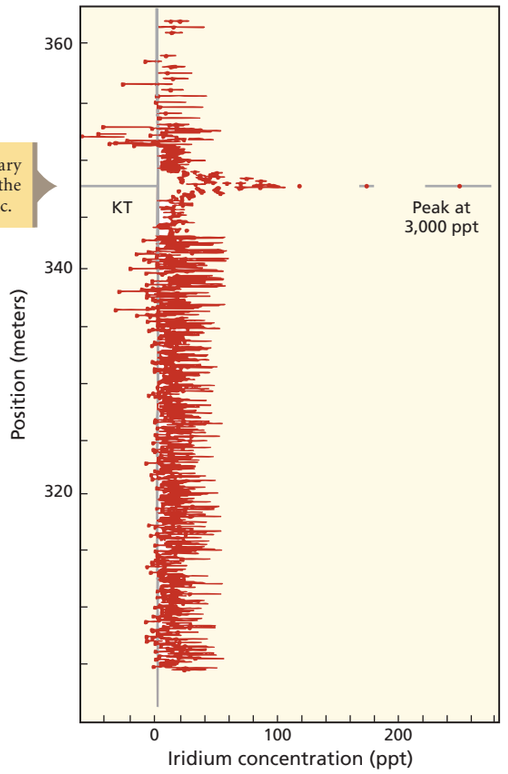
Most important is the fact that all these geological features are concentrated in a very narrow band. In the sediment just inches away from this band, they are not found. Many geologists and evolutionary biologists now accept the theory that at least some mass extinctions, and almost certainly the one at the end of the Cretaceous, were caused by the impact of a large comet or meteor. As shown in Figure 6.19B, geologists now think that they have found the site where this large object hit the Earth—Chicxulub, at the tip of the Yucatán peninsula, in Mexico.



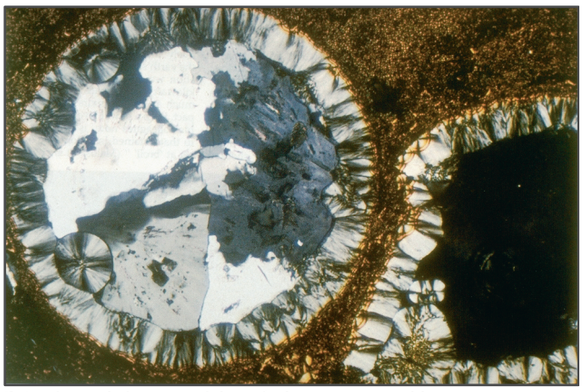
(i) Dark band of clay at K-T boundary, suggesting abrupt release of soot and other debris.



(ii) Shocked quartz on the right, normal quartz on the left; shocked quartz is often found near meteorite strikes.



(iii) The spike in iridium concentration at the K–T boundary sediment layer.



(iv) Microtektites, particles of glass generated by meteorite impacts.

FIGURE 6.19A **Four pieces of evidence for a large-body impact collected from Cretaceous-Tertiary (K-T) boundary sediment. See Alvarez (1997).**



FIGURE 6.19B Location of the Chicxulub crater, which is below ground and partly below water, at the tip of the Yucatán peninsula. This crater may have been produced by the same astronomical body that caused the K-T mass extinction.

SUMMARY

1. Species are defined according to reproductive isolation: Organisms are members of different species if they do not mate when they live in the same area. Speciation is thus the process by which populations develop reproductive isolation. Prezygotic reproductive isolation may be established by a failure to produce zygotes, which may involve a lack of sexual attraction, for example. Postzygotic reproductive isolation may occur when hybrid zygotes do not develop into fertile adults. In some species, both types of reproductive isolation may occur.
2. Geographical separation of populations, called allopatry, plays an important role in speciation. Allopatric populations may evolve distinct mating adaptations that create prezygotic reproductive isolation when they resume contact. Allopatric populations may also develop postzygotic reproductive isolation when they evolve distinct genomic features that render hybrids inviable or infertile. When postzygotic reproductive isolation evolves allopatrically, contact with closely related species may select for prezygotic reproductive isolation, to avoid wasted reproductive activity.
3. Speciation also occurs without allopatry, by a process called sympatric speciation. One evolutionary process that produces speciation sympatrically occurs when genomes are increased in ploidy by a failure of meiosis or by hybridization. Another evolutionary process that may create new species is local mating of specialized fruit eaters.
4. New species sometimes originate in rapid radiations. The most spectacular example of species radiation occurred around 500 million years ago, when most groups of animals and plants evolved. Less dramatic examples of species radiation are known, such as the radiation of finch species on the Galápagos Islands.
5. The fossil record often shows a pattern of intermittently abrupt evolution called punctuated equilibrium. Punctuated equilibrium can be explained in terms of normal Darwinian processes.
6. Extinction occurs frequently. The diversity of living species is the result of a balance between speciation and extinction. Dispersed species tend to go extinct less often.
7. Mass extinctions have occurred at least five times during the last 500 million years. Mass extinctions involve the abrupt loss of the majority of living species—sometimes more than 80 percent. Many biologists and geologists now think that mass extinctions are caused by the collision of large asteroids and comets with the Earth, including subsequent disruptions to the Earth's atmosphere.

REVIEW QUESTIONS

1. What is a biological species?
2. What is the difference between sympatry and allopatry?
3. Does speciation increase the level of adaptation in the new species?
4. Why is allopatric speciation more likely than sympatric speciation?
5. Name one biological process that might produce new species sympatrically.
6. Explain why the evolution of mammals over the last 65 million years could be called an adaptive radiation.
7. Which theory would Darwin have preferred, phyletic gradualism or punctuated equilibrium?
8. What is the normal fate of a species?
9. What kinds of species are more likely to go extinct when mass extinctions occur?
10. What kinds of species are humans driving to extinction?
11. Propose a scenario for the extinction of the human species.

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KEY TERMS

allopatry
allopolyploid
autopolyploid
biological species concept
Burgess Shale
Cambrian
Cenozoic
Cretaceous
dinosaurs
Eldredge, N.
evolutionary stasis
extinction
fluctuating selection
Galápagos Islands
genetic drift
genetic revolution
Gould, S. J.
hopeful monster
host race
hybrid breakdown
hybridization
hybrid zone
iridium
K-T boundary
large-body impact
mass extinction
Mayr, E.
Mesozoic
Paleozoic
parthenogenesis
Permian
Phanerozoic
phyletic gradualism
polyploidization
postzygotic isolating mechanism
prezygotic isolating mechanism
punctuated equilibrium
reproductive isolation
species radiation
stabilizing selection
sympatry
Tertiary

FURTHER READINGS

Alvarez, W. 1997. *T. Rex and the Crater of Doom*. Princeton, NJ: Princeton University Press.

Briggs, D.E.G., D. H. Erwin, and F. J. Collier. 1994. *The Fossils of the Burgess Shale*. Washington, DC: Smithsonian Institution Press.

Dobzhansky, T. H. 1937. *Genetics and the Origin of Species*. New York: Columbia University Press.

Mayr, E. 1942. *Systematics and the Origin of Species*. New York: Columbia University Press.

———. 1963. *Animal Species and Evolution*. Cambridge, MA: Harvard University Press.

Otte, D., and J. Endler. 1989. *Speciation and its Consequences*. Sunderland, Massachusetts: Sinauer.

Raup, David M. 1991. *Extinction, Bad Genes or Bad Luck?* New York: W.W. Norton.

Rice, W. R., and E. E. Hostert. 1993. "Laboratory Studies on Speciation—What Have We Learned in 40 Years?" *Evolution* 47: 1637–1653.

Weiner, J. 1994. *The Beak of the Finch: A Story of Evolution in Our Time*. New York: Knopf.

White, M.J.D. 1978. *Modes of Speciation*. San Francisco: W.H. Freeman.

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