The Origin of New Species

Gillia tenuiflora, a member of the phlox family, and Oligoderanes sp. in the family of bee flies, Bombyliidae—the most numerous and effective pollinator in a population near Creston, California. (Based on illustrations in Grant and Grant 1995)

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Summary
Darwin's (1872) model of speciation must be teased out of his extensive discussion on the subject, but a careful reading reveals a rather simple view of the mechanism involved with the evolution of new species. First a species spreads out over a large area (see Figure 3-4). Then environmental variation within this area produces different variations in the populations of different environments. Restricted movement of individuals between environments results in independent natural selection and finally a new species in each environment.

Hybrid zones give rise to maladapted individuals that survive poorly in both parental environments. Because environments are not completely discrete, variation between species is continuous. The hybrid populations are small and must compete with parental populations; they are likely to eventually go extinct.

It will be interesting to keep Darwin's model in mind and compare it with other speciation models that developed subsequently.

5.1 GEOGRAPHIC SPECIATION, OR ALLOPATRIC SPECIATION

After Darwin's time, a major building block of the modern synthesis was Mayr's model of geographic speciation, or allopatric speciation. The biological species concept serves as an essential component of geographic speciation, for it explains how two or more populations that once shared a common gene pool become reproductively isolated. Mayr's view that the speciation process is almost exclusively geographic has been largely accepted. As we shall see, alternative mechanisms are also important, and views on the relative contributions of those mechanisms to the diversity of life on earth are shifting. Even textbooks on evolution debate the validity of modes of speciation other than geographic speciation. Clearly, no consensus has been reached (cf. Cockburn 1991, Futuyma 1986, Minkoff 1983, Ridley 1993, Strickberger 1990, and this chapter).

We may call Mayr's views on geographic speciation the classic model of speciation, as they were largely accepted in the 1940s and are still intact. The classic model invokes a geographic barrier as an essential part of the scenario (Figure 5-1). A geographic barrier divides a population, gene flow between the two parts stops, each new population evolves independently of the other, and differences accumulate until the members of one population cannot breed with members of the other even when the ranges again overlap. Thus, two new species have evolved.

Allmon (1992) emphasizes the need for a more detailed mechanistic understanding of each phase of allopatric speciation. He notes that the process can be divided into three stages: the formation of an isolated population, the persistence of that population, and the differentiation of the population from the parental stock. The heuristic value of this subdivision lies in the increased focus on each phase. For example, in isolate formation, what are the relative roles of extrinsic mechanisms, such as glaciation effects, and intrinsic mechanisms, especially dispersal ability or vagility? Does isolate persistence depend on population size and stability, ecological amplitude or specialization, environmental rigor, niche space, or adaptation? What are the key processes in isolate differentiation? Keeping Allmon's arguments in mind will help us assess the thoroughness with which scientists have described each process of speciation discussed in this chapter.

Speciation in Warblers

Mengel (1964) developed an example of geographic speciation involving northern wood warblers (in North America) that divided into two large populations. In the black-throated green warbler group are one eastern species, the black-throated green warbler, *Dendroica virens*, and three western species with extensive distributions (Figure 5-2): Townsend's, hermit, and black-throated gray. Mengel argued that the parental species with a southeastern distribution adapted to coniferous forest during the Pleistocene Nebraskan glaciation, which compressed vegetation toward the south. During the interglacial period, the warblers expanded north and west with the conifers. The next glaciation, the Kansan, reached its southern extremity in central North America and constituted a geographic barrier separating the eastern parental species from a western population. Speciation occurred. The process was repeated in the next interglacial period, the Yarmouth, and the Illinoian glaciation, cutting off a second western species. A third warbler species in the West originated in a similar manner after the Sangamon interglacial period and the Wisconsin glaciation. This scenario also fits the distribution of species in the Nashville warbler group, reinforcing the view that large-scale geographical barriers formed by glaciation caused similar patterns of warbler distribution and (avoiding complexities not to be discussed here) explaining why three species of the black-throated green warbler group occur in the West and only one occurs in the East.

Speciation in Darwin's Finches

Alternatively, only one inseminated female or a very few individuals may colonize a new locality—perhaps an oceanic island 500 miles off the mainland—
and found a new population. The founder effect, discussed in Section 5.4, can be defined as the founding of a new population by one or a few individuals, which carry only a small proportion of the genetic variation of the parental population. With the founder effect, sampling error becomes an important influence in evolutionary change, as Section 5.5 and Chapter 15 discuss. The new population evolves independently of the parent population and eventually becomes reproductively isolated from it.

Because the ocean is so effective as a geographic barrier, such colonization events are extremely rare. We find an example in the original colonization of the Galapagos Archipelago by a South American finch, the formation of a new species, and subsequent speciation as new islands were colonized. The species now called Darwin's finches (Figure 5-3) are the result.

**Geographic Barriers**

Thus, geographic barriers may take very different forms. For large mammals and birds, they may be large expanses of ocean, high mountain ranges, or
FIGURE 5-2
Allopatric speciation of *Dendroica* warblers, based on Mengel's (1964) argument that major glaciations produced geographic barriers, resulting in a new species of warbler in western North America after each event. Note that another glaciation event is likely to compress the distribution of *D. virens* to the south and cut off another species in the west. The additional bird illustrated is Wilson's warbler (*Wilsonia pusilla*), which has a trans-American range, posing the question of how this species escaped the geographic barrier of an ice cap and consequent speciation.

Reproductive Isolating Mechanisms, or Reproductive Barriers

Reproductive isolating mechanisms are the properties of individuals, populations, and species that constrain gene flow between populations and species. These properties evolve during geographic isolation and may take many different forms. Mayr (1963, 91) defined reproductive isolating mechanisms as "biological properties of individuals that prevent the interbreeding of populations that are actually or potentially sympatric." His classification scheme illustrates the great diversity of the mechanisms that are potentially involved in reproductive isolation (Table 5-1). Note that in hybrid sterility, so long as the $F_1$ hybrid has a lower fitness than either of the parental types, the two populations remain isolated. Also, there are considerable differences between premating and postmating barriers. In the case of the former, no loss of time, energy, or gametes occurs in seasonal or habitat isolation or in ethological isolation, and some loss of time and energy may occur in mechanical isolation. Postmating mechanisms, however, waste...
time, energy, and gametes, and so these mechanisms are particularly inefficient in terms of energetics and reproductive effort. Although natural selection may be expected to increase efficiency in energy and gamete allocation and effect a transition from postmating to premating mechanisms as populations and species diverge, researchers have had difficulty finding good evidence for reinforcement of premating isolation (Butlin 1989).

One can develop a legitimate argument that isolating mechanisms are actually a whole set of characteristics that usually facilitate reproduction within a species, as Chapter 4 discusses (Paterson 1985, Templeton 1989). The emphasis should therefore be on the positive mechanisms involved with mate recognition, acceptance, and interfertility rather than on the resultant reproductive isolation between species. That is why Paterson (1985) emphasized his recognition species concept. Attention to positive mechanisms may suggest a term such as reproductive barrier rather than reproductive isolating mechanism. However, a geographic obstacle can also act as a reproductive barrier, and so our preference is to keep the two terms distinct: a geographic barrier is a property of the environment, as described earlier, and a reproductive isolating mechanism is a property of individuals, as just explained.

Secondary Contact
After geographic isolation and the divergence of populations, secondary contact may be established. The results of such contact vary depending on the duration of isolation, the effectiveness of the geographic
Table 5-1 Reproductive isolating mechanisms proposed by Mayr (1963)

<table>
<thead>
<tr>
<th>Type</th>
<th>Mechanism and Example</th>
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<tbody>
<tr>
<td><strong>A. Premating mechanisms</strong></td>
<td></td>
</tr>
<tr>
<td>1. Seasonal and habitat isolation</td>
<td>Transfer of gametes is prevented. Potential mates do not meet; e.g., small-mouthed salamander, <em>Ambystoma texanum</em>, breeds in ponds, but <em>A. barbouri</em> breeds in streams (Kraus and Petranka 1989).</td>
</tr>
<tr>
<td>2. Ethological isolation</td>
<td>Potential mates meet but do not mate. Some species of <em>Allonemobius</em> crickets (see Chapter 4), leopard frogs (Hillis 1988). In pollination systems, a pollinating insect may carry pollen but does not deposit it on the stigma.</td>
</tr>
<tr>
<td>3. Mechanical isolation</td>
<td>Copulation is attempted, but no transfer of sperm takes place. Many insect genitalia require precise lock-and-key link for transfer of sperm (cf. Eberhard 1985).</td>
</tr>
<tr>
<td><strong>B. Postmating mechanisms</strong></td>
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<tr>
<td>1. Gametic mortality</td>
<td>Sperm transfer takes place but egg is not fertilized. Pseudogamy in parthenogenetic <em>Poeciliopsis</em> related, for example, to the Sonoran topminnow (e.g., Vrijenhoek 1984), plants, and nematodes.</td>
</tr>
<tr>
<td>2. Zygotic mortality</td>
<td>The egg is fertilized but the zygote dies. Some leopard frogs in the <em>Rana pipiens</em> complex (Hillis 1988).</td>
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<tr>
<td>3. Hybrid inviability</td>
<td>Zygote produces an F₁ hybrid of reduced viability, or hybrid recombinations are less viable—e.g., frogs in the genus <em>Pseudophryne</em> (Woodruff 1979).</td>
</tr>
<tr>
<td>4. Hybrid sterility</td>
<td>F₁ hybrid is fully viable but partially or completely sterile, or it produces a deficient F₂. Crosses between horses and donkeys produce mules, which are sterile. Some hybrids in the <em>Rana pipiens</em> complex (Hillis 1988).</td>
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</table>

Barrier, and ultimately the degree to which reproductive isolating mechanisms have evolved.

Let us call one scenario case 1. After very effective and long-term isolation, on secondary contact populations have diverged into discrete ecological niches and reproductive isolation is complete. New species become sympatric without any mutually induced evolutionary change (Figure 5-4).

Case 2 may occur after less prolonged geographic isolation or because of slower evolutionary rates, such that ecological divergence may be less complete, although reproductive isolation may be complete. During secondary contact, competition between the two new species is likely to result in mutually induced divergence in ecologically relevant traits (Figure 5-4). This process, which Darwin (1859) called character divergence and Brown and Wilson (1956) called character displacement, need not involve morphological characteristics. Rather, it can involve only characteristics of behavior, habitat use, and food choice. (Since the 1950s, the term “character displacement” has broadened to include character divergence, convergence, and parallel characteristic shifts in zones of sympatry [cf. Taper and Case 1992].)

In case 3, after shorter periods of geographic isolation that result in incomplete reproductive isolation, hybridization may occur between the two incipient species during secondary contact. One possibility in case 3, which Figure 5-4 illustrates, is that hybrids have equal or greater fitness than either of the parental populations. The result is complete introgression, or the incorporation of genes of one species into the gene pool of another. Any differences between the populations that evolved during geographic isolation would be swamped, and something akin to the old parental species would be reinstated (Figure 5-4). Another possibility is that hybrids may have low fitness, and thus introgression does not occur. Theoretically, natural selection might then improve the reproductive isolating mechanisms so that hybridization would diminish, although the reality of this process, called the Wallace effect, has been questioned (e.g., Butlin 1989).

Thus, the model of geographic speciation accounts successfully for many characteristics observed when species coexist, from lack of interbreeding and the presence of distinct ecological niches all the way to considerable introgression and strongly overlapping ecological niches.
Three possible cases during geographic isolation. **Case 1**: After prolonged geographic isolation, reproductive isolating mechanisms (RIMs) are complete and ecological divergence (ED) is complete. **Case 2**: RIMs are complete but ED is incomplete. **Case 3**: RIMs are incomplete. SC indicates time of secondary contact between diverging populations. Time passes from top to bottom in each case, and the parental species occupies niche A. **Case 1** in the left-hand population illustrates ecological divergence into niche B.

### 5.2 SYMPATRIC SPECIATION

Mayr (1963) pointed out that the concept of speciation without geographic isolation was much older than his geographic speciation model, as Darwin's eventual speciation model suggests. Mayr gave a brief historical account of other concepts and the negative criticism they had received. One concept seemed more viable than most others. It concerns the speciation process in rather specialized groups of insects and the evolution of new species within one locality. This **sympatric speciation model** can be defined as "the establishment of new populations of a species in different ecological niches within the normal cruising range of the individuals of the parental population" (Mayr 1963, 449) accompanied by rapid development of reproductive isolation between members of the populations in different niches.

Two points relating to specialized, or monophagous, insect groups are worth noting. First, plant-feeding monophagous insects frequently belong to large genera. Thus, their apparently rapid speciation is unlikely to have occurred during prolonged geographic isolation. For example, Ross (1962) reported that the *Erythroneura* group of leafhoppers (Cicadellidae) includes approximately 500 species, and speciation has involved about 150 shifts from utilization of one host plant species to another. Such extensive
speciation is likely where many new niches exist, and with high food specificity, ecological barriers to introgression are likely to be very effective. Second, it seems unlikely that a geographically isolated monophagous species would repeatedly split into two species, each with a different host food plant. In many cases we should expect retention of the ancestral food plant by both species, but this is not common.

An Allopatric Alternative
In defense of the allopatric speciation model, Mayr (1963) pointed out that peripheral populations are likely to be exceedingly important in the speciation process. We can call this view the marginal-population allopatric speciation model (Figure 5-5). In a marginal population, a subsidiary host species may become the primary host because it is more abundant than the major host or is favored in other ways. (This scenario assumes that the so-called specialized insect species is not strictly monophagous but utilizes more than one host plant species, which is commonly the case.) Such a shift in hosts results in rapid adaptation to the new conditions and rapid genetic change in the small isolated population. At the same time, reproductive isolation from the parental population may develop. On secondary contact, the new species on its new host plant remains sympatric with the parent species, and the history and mechanism of the speciation process are obliterated. Thus, the marginal-population allopatric model is a special case of the geographic speciation model.

Mayr (1963) also noted problems with applying the geographic speciation model to animal parasites. For example, a sympatric model for speciation of the human louse into the body louse and the head louse need not be complex (cf. Price 1980). Mayr, however, argues that the current species probably diverged allopatrically, the body louse evolving on the bodies of heavily clothed people such as Eskimos and the head louse on people clothed only in breechclouts and grass skirts or less.

Any discussion on speciation processes will fail to prove either the allopatric or the sympatric model beyond a doubt unless the actual process of speciation can be studied in ecological time, over a few decades or years. This kind of study, of course, is difficult to carry out, and it has seemed that speciation is such a gradual and rare event—relative to the 130 or so years since Darwin—that the issues will remain tantalizing but unresolved. Yet increasing evidence forces us to consider sympatric speciation as a reality. Because this kind of speciation can occur rapidly, we may indeed observe the process in ecological time.

**FIGURE 5-5**
Mayr's (1963) marginal-population allopatric speciation model.
Others in addition to Mayr (e.g., Futuyma and Mayer 1980) have criticized the evidence for sympatric speciation and other modes of nonallopatric speciation. We discuss these modes here because they offer explanations of how speciation can result in very closely related sibling species, an event that would not be expected to result from allopatric speciation (cf. Bush and Howard 1986, Tauber and Tauber 1989, Cockburn 1991).

Speciation in Rhagoletis Fruit Flies

In the light of tantalizing debates and the skepticism of entomologists and botanists about the universality of the geographic speciation model, Guy Bush in the 1960s undertook a study of host-specific true fruit flies in the genus Rhagoletis and family Tephritidae. He knew that several species in this genus had recently established new host races on introduced commercial fruits. The apple maggot, R. pomonella, had moved from its native host, hawthorn (Crataegus sp.), to introduced apples in the Hudson River Valley, New York, in 1864. Then it had shifted from apples to cherries in Door County, Wisconsin, as recently as 1960 (Bush 1974, 1975a). Another host race of R. pomonella occurs on wild and cultivated plums, but less is known of its biology. In western North America, the western cherry fruit fly, R. indifferens, in Oregon, Washington, and British Columbia, shifted from the native bitter cherry, Prunus emarginata, to the domesticated cherries, P. avium and P. cerasus, a little before 1913, only 89 years after cherries were introduced into the region. Where bitter cherry and domestic cherries grow close together in California, R. indifferens occasionally attacks domestic cherries as if establishing a new host race. However, the California Department of Agriculture quickly expunges these populations.

It became evident that much information—behavioral, ecological, and genetic—was needed to establish the likelihood of sympatric speciation. Bush and his coworkers have provided such information. Figure 5-6 summarizes much of the behavior of Rhagoletis fruit flies in relation to host selection and mating behaviors. Note that a female fly finally accepts a fruit based on a chemical cue, which must be received by her chemoreceptor. A mutation in the fly could therefore affect the amino acid composition of a receptor protein and radically change the fly’s response to a specific host-plant chemical. Also, courtship and mating occur on the host fruit, and fruits are essential to fly reproduction. Thus, host shifts often result in fly populations that are allochronic, or chronologically out of phase. Once a host shift has occurred, allochronic isolation can become a factor in limiting gene flow.

For example, the two emergence patterns of R. pomonella in Door County, Wisconsin, are so different that the hawthorn and cherry races of flies show practically no overlap (Figure 5-7). Emergence time is under genetic control (Smith 1988). T. K. Wood and his associates have explored in detail the processes involved in allochronic isolation in the herbivorous membracid treehopper genus Enchenopa (Wood and Keese 1990, Wood et al. 1990, and references therein).

The shift of R. indifferens from native cherry to the introduced Prunus avium in California involves both temporal and spatial factors. On Mount Shasta, for example, the two tree species overlap in a zone from 3,500 to 5,000 feet above sea level, but their fruiting times are so different that there is only a 2-week period in July and August in which R. indifferens populations overlap (Figure 5-8).

At least two genes must be involved in a host shift by an insect: one for host recognition and selection and another for larval survival once the egg is deposited. Huettel and Bush (1971) have indeed shown, in a related species of tephritid, that a single major locus controls host selection. In addition, Hatchett and Gallun (1970) found that a gene-for-gene relationship exists between host resistance and parasite survival in the hessian fly, which attacks wheat. Genes for plant resistance to the fly are matched by genes for virulence in the fly population, as described in Section 19.2. Apparently, such relationships between plant pathogens and their hosts are common (Day 1974). Thus, a shift from one host to another of similar chemistry may involve only two genes, and, because of allochronic isolation and mating on the fruit, a shift causes ecological isolation, strongly reduced gene flow between host races, and essentially instantaneous and sympatric speciation. Isolation of races is followed by changes in other loci to adapt the new race to new conditions. Thus, a factor such as larval survival may become polygenetically controlled once evolution of the new race has progressed.

Bush (1975a, 199) stated,

It is now quite clear that host races of phytophagous parasitic insects have evolved sympatrically. Furthermore, these host races are undoubtedly the progenitors of the many reproducively isolated sibling species so frequently found coexisting sympatrically on different host plants.

Even Mayr in 1970 accepted the real possibility of incipient sympatric speciation in Rhagoletis.

Bush (1975a) observed that sympatric speciation probably has been common in monophagous and stenophagous parasitic insects, but certain qualities of species predispose them to host shifting. (1) Mating
occurs on or near the host plant. (2) The adult female selects the host; the larvae have no choice. (3) The parasitic species is specialized, attacking groups of closely related host plant species. (4) Host selection and larval survival are under genetic control; other factors reinforce reproductive isolation and accelerate the speciation process. (5) As Smith (1988) demonstrated, univoltinism (a single generation per year) with genetic control of emergence time increases the probability of allochronic isolation. (6) If genetic
control of host-plant induction or conditioning is present, where an adult insect is induced or conditioned to return to the same host from which it emerged, fidelity to the specific ecological niche increases.

**The Genetic Model**

Bush (1974, 1975a) based his proposal for a generalized genetic model of sympatric speciation on the shift of *R. pomonella* from apples to cherries in Door County, Wisconsin. For a host shift to occur, mutations must produce new host selection (H) and survival (S) alleles in a race—e.g., the apple race of flies—that are homozygous at those loci: $H_1H_1S_1S_1$. $H_2$ and $S_2$ can then symbolize the mutations, which enable the bearer to select and survive on a new host—such as cherry. The new alleles might remain in the population for a variety of reasons, but certain combinations would be lethal in the older race. For instance, all $H_1H_1$ and $H_1H_2$ would probably oviposit on apple, but any $S_2S_2$ larvae would die on apple. $H_2H_2$ females would oviposit on cherries, but their $S_2S_1$ progeny would die (Figure 5-9). Heterozygous $H_1H_2$ individuals could oviposit on both plant species. However, Huettel and Bush (1971) found that individuals were conditioned by larval food and tended to oviposit on the species from which they had emerged. This factor together with allochronic isolation would inhibit random mating, and $H_1H_2$ individuals would be most likely to remain on apple, where coadapted induction genes would operate effectively. Only few $H_2H_2$ flies that emerged early in the season would mate and oviposit on cherry (cf. Figure 5-7).

Shifts in emergence time of the new race would increase the separation of races in time. An occurrence of spread to other areas might cause divergence from a purely sympatric distribution of the new species. Investigators have documented genetically distinct host races of *R. pomonella* on sympatric hawthorn and apple (Feder et al. 1988, McPheron et al. 1988, Smith
1988). The most likely mechanisms maintaining significant genetic differences are genetic control of allochronic emergence times and at least partial premating reproductive isolation because of host-plant fidelity. Diehl and Bush (1989) provide the theoretical basis for this divergence: habitat preferences of individuals and mating within habitats (see also Bush 1992, 1994).

No doubt, endless natural "experiments" in host race and species formation have taken place in wild populations, and the successes must constitute a very small fraction of the total. However, when one considers the vast number of highly specialized parasitic organisms on this earth, many of which are liable to sympatric divergence of populations (Price 1980), we must wonder about the extent to which sympatric speciation has been more common than allopatric speciation, especially when we include plant speciation, discussed later in this chapter (see also Bush and Howard 1986). As Barton et al. (1988, 14) stated, may help to explain the origins of the tens of millions of species estimated to be alive today. Perhaps the patron saint of evolution is, after all, sympatric.

5.3 PARAPATRIC SPECIATION

White (1968, 1978) advanced a third mode of speciation that he called stasipatric speciation; Bush (1975b) called it parapatric speciation. This model defines the mechanism that accounts for a pattern of closely related species contiguously distributed in space with narrow zones of overlap (Figure 5-10). Basically, a certain set of ecological factors may limit the range of a species. A new chromosomal rearrangement or gene combination may enable a few members to colonize the unexploited habitat. Heterozygotes between the parental and progeny types are well adapted for neither the original environment nor the colonists' conditions and are rapidly selected out of the population. Premating isolating mechanisms evolve rapidly, and the new species occupies a range contiguous with that of the parental species. The new species is likely
FIGURE 5-9
Bush's (1975a) genetic model of sympatric speciation, based on a shift by apple maggots in Door County, Wisconsin, from apple hosts to cherry hosts. H is the host selection gene (H₁ for apple, H₂ for cherry), and S is the survival gene (S₁ for apple, S₂ for cherry). (After Bush 1975a)

FIGURE 5-10
A general view of parapatric speciation.

Speciation in Morabine Grasshoppers
One example of this stasipatric or parapatric model concerns the Australian morabine grasshoppers in the genus Vandiemella. (The name "morabine" comes from another genus, Morabic.) These are all wingless grasshoppers with low vagility; consequently, they move little over a lifetime. They feed mainly on shrubs in the family Asteraceae. All the species have parapatric distributions. No two species, or even races within species, are sympatric over much of their range (Figure 5-11). Zones of hybridization are only 200 to 300 meters wide in several cases.

About 240 species of morabine grasshoppers occur in Australia. Because most of the species recognized by Key (1974) and White (1968, 1974, 1978) have not been formally described and assigned specific names, they are designated P for provisional species.
In southern Australia they are numbered P24, P25, P45b, and so on (Table 5-2). The distributions of species and races are almost mutually exclusive (Figure 5-11). Each race has a unique karyotype, meaning a unique set of chromosomal morphologies. Figure 5-11 shows the haploid karyotype, its distribution of metacentric, acrocentric, and telocentric chromosomes demonstrating considerable variation in chromosome structure. A metacentric chromosome has the centromere in its middle. An acrocentric chromosome has one arm off the centromere. A telocentric chromosome has two arms extending asymmetrically off the centromere. For example, the karyotype of Vandiemenella viatica, race 19, has 9 autosomes in the haploid state and 18 in the diploid state plus one sex chromosome, the X, adding up to 19 chromosomes. No Y chromosomes exist in this race, and so the race is designed an XO type of race (cf. Table 5-2). The nine autosomes comprise one telocentric and eight acrocentric chromosomes.

On Kangaroo Island, the distributions of Vandiemenella species seem very strange until one realizes that, during the Pleistocene Epoch, solid land filled what are now the channels and bays between the mainland and the island. This pattern suggests that the parapatric distributions have been remarkably stable over the past 10,000 years.

Given the lack of geographic barriers between species—indeed, the lack of any distinct factor limiting distribution—and the very local distribution of species with almost exclusive distributions of species within genera, neither the allopatric nor the sympatric model accounts adequately for the distributions of Vandiemenella. The parapatric model accounts for the pattern, but more research is needed on what defines the limits of species ranges.
5.4 SPECIATION MECHANISMS AND THE KINDS OF SPECIES INVOLVED

The allopatric, sympatric, and parapatric mechanisms of speciation are so different mechanistically and in the species distribution patterns they are likely to cause that we should expect rather different kinds of organisms to engage in each. Bush (1975b) reviewed the general attributes of the species that are likely to be generated by each mode of speciation.

Allopatric Speciation

Allopatric speciation should be subdivided into the classic model, involving speciation by subdivision of large populations, and speciation by the founder effect, in which a very small subsample of a population founds a new population in a geographically isolated area. In the classic model, an extrinsic barrier between two or more relatively large populations interrupts gene flow. In large populations evolution is likely to be slow, as many genetic changes must accumulate during geographic isolation (see Chapter 15). Thus, speciation is a long-term, gradual process. Relatively large animal species with high vagility are probably restricted to this mode of speciation. For example, the vetebrate carnivores, many birds, certain reptiles and amphibians, and most marine, lacustrine and riverine fish probably speciate slowly in geographic isolation.

Chromosomal evolution, which is a good indicator of rapid speciation (see Chapter 14), is minimal in animals with extensive ranges, such as the cats and dogs. Cats (*Felis*) in the Northern Hemisphere all have a chromosome number $2n = 38$. All dogs (*Canis*) have $2n = 78$, whereas animals such as foxes (*Vulpes* and other genera) with smaller home ranges show considerable chromosome evolution ($2n = 38, 40, 64$, and $78$ in four species). As movement becomes more local, the chance that a chromosome rearrangement will become fixed increases, and the second type of allopatric speciation becomes more likely.

The Founder Effect

Speciation by the founder effect may be more rapid and possibly more frequent than speciation by subdivision. A novel environment disrupts coadapted gene complexes in the parental population, and rapid evolution is likely to build to a new adaptive peak, resulting in a speciation event (Carson and Templeton 1984). Mutations in an almost empty and perhaps novel environment are more likely to be adaptive and to generate novel evolutionary steps than those in the old environment. Advantageous changes in the gene pool become fixed much more rapidly in a small population than in the original, larger one (see Chapter 15). Major adaptive chromosome rearrangements may readily become fixed in the homozygous condition.

Organisms with moderately low vagility are susceptible to speciation by the founder effect, although it can also be effective in some very vagile animals, such as birds colonizing oceanic islands (see Chapter 8). Even subsocial or social mammals, such as primates and ungulates that typically form small, cohesive bands, can exist in a sufficiently fractionated population structure so that founder effects become important. Cave-dwelling animals with homing behavior, such as bats, are liable to found new colonies distant from parental groups. Carson (1973, 1975) suggested that speciation of some Hawaiian *Drosophila* is most likely to be by the founder effect, and many other insects must surely be equally likely candidates.

The opportunities for chromosomal evolution during this mode of speciation are great. Such rearrangements as fusions, fissions, whole-arm translocations, and pericentric inversions may cause rapid reorganization of regulatory mechanisms and thus drastic changes in the developmental process without a genic change (see also Chapters 12 and 14). Such radical changes may permit the exploitation of a set of ecological conditions or resources very different from conditions in the parental environment. Major shifts in the adaptive mode may occur during speciation by the founder effect.

Parapatric Speciation

Parapatric speciation differs from speciation by the founder effect in several important ways (Bush 1975b). No spatial isolation occurs. The involved organisms are exceptionally sedentary. Selection activates reproductive isolating mechanisms at the same time as individuals with new, highly adaptive gene combinations move into and exploit a new habitat. The organisms are sedentary enough that 100 to 1,000 meters may be the limit of movement of an individual or its progeny. Plants, terrestrial snails, pocket gophers and other fossorial rodents, morabine grasshoppers, small mammals such as *Peromyscus* species and shrews, certain lizards, mole crickets, stick insects, and many other flightless insects are likely to speciate parapatrically.

Sympatric Speciation

Sympatric speciation differs from parapatric speciation in three ways. (1) Premating reproductive isolation develops before the shift to a new niche because the new variant gene for habitat and host selection
arises within the parental population. (2) Chromosomal rearrangements do not seem to be involved. (3) Speciation is likely to occur at the center of the species range instead of the periphery and thus can lead to the evolution of many sympatric sibling species.

Sympatric speciation is common among parasites of plants and animals, which constitute a very species-rich and diverse group of taxa.

**Additional Speciation Mechanisms**

Other common and important modes of speciation include interspecific hybridization and polyploidy, which occur frequently in plants. Association with symbionts commonly adds to the complexity of intraspecific interactions and the development of reproductive isolation, as is the case with symbiotic sterility factors in *Drosophila* (e.g. Ehrman 1983) and other pathogens that induce hybrid inferiority between host populations (Thompson 1989, 1994). Developmental pathways may change because of mutations or environment so that the timing or rates of developmental events differ from those of the same events in the parental population. The general term for developmental change that results in new morphology, life history, or behavior is heterochrony, meaning literally “different time” (McKinney and McNamara 1991). Clearly, the timing of events such as reproduction of morphological changes may contribute to reproductive isolation, and speciation and higher levels of macroevolution may result, as McKinney and McNamara (1991) discuss. (See also Chapter 18, “Rates of Evolution,” especially Sections 8.5 through 8.7.)

Plants are so different from animals in many ways that we should examine the extent to which the modes of speciation found in these two kingdoms are similar or disparate. Grant (1971) distinguished between primary and secondary forms of speciation in plants. By *primary speciation* he meant the origination of new species from one common ancestral species, as we have discussed in the three modes of speciation—allopatric, sympatric, and parapatric (Figure 5-12). In *secondary speciation*, good biological species produce new species rather rapidly or even instantaneously—for example, by hybridization or polyploidy or by a shift from an outcrossing to an amictic system of reproduction. Researchers have studied such secondary speciation extensively in plants because it has been so common. Their accumulated knowledge about plant speciation can enrich our appreciation of the speciation process as a whole.

### 5.5 PRIMARY SPECIATION IN PLANTS

**Quantum Speciation**

Grant classified primary speciation into geographic, quantum, and sympatric modes (Figure 5-13). Geographic speciation is the classic model of speciation. Grant (1971, 114) defined *quantum speciation* “as the budding off of a new and very different daughter species from a semi-isolated peripheral population of the ancestral species in a cross-fertilizing organism.”
In contrast with geographic speciation, quantum speciation is rapid and results in major shifts in phenotype and genotype. Two mechanisms seem to play roles in quantum speciation.

In the first mechanism, a shift from an outcrossing mode of reproduction to an inbreeding mode seems to be the major factor. A large central population of individuals is adapted for outcrossing by having genes that can effectively interact in the genome with new genes brought in during gene flow throughout the population. In this central population, inflow of new genes tends to swamp idiosyncratic variation. Once a few individuals become isolated in a peripheral population, however, inbreeding becomes common among them, with drastic genetic and phenotypic effects. Most of the change to inbreeding has strong negative effects on fitness and may cause extinction of the local population. However, in many peripheral populations, radical changes in genotype produce a few individuals with highly adaptive traits. This outcome occurs especially in peripheral locations where the parental species has presumably been an unsuccessful colonizer. Thus, the mechanism of quantum speciation fits within the umbrella of allopatric speciation by the founder effect.

Verne and Alva Grant's (Grant and Grant 1960) work on the genus Gilia in California (Figure 5-14) provides an example of the pattern expected from this first mode of quantum speciation, in which the shift to inbreeding is important. Gilia tenuiflora is a wide-ranging, predominantly outcrossing species. Two other species, G. austrooccidentalis and G. jacens, have smaller, peripheral ranges and are autogamous, or self-fertilizing. Apparently, chromosomal changes have not been important in speciation. The fact that the peripheral species live in more arid habitats than does G. tenuiflora, the apparently parental species, suggests that a physiological shift in the adaptive mode of the species during speciation enabled a range extension beyond the parental species.

A second mechanism that Grant regards as quantum speciation fits into the parapatric model. A com-
Comparison between *Clarkia biloba* and *C. lingulata* suggests *C. biloba* as the parental species and *C. lingulata* as the derived species (Table 5-3; see also Figure 4-7 on left). A chromosomal sterility barrier, resulting apparently from an original reciprocal translocation involving two chromosomes, and a subsequent translocation in the *C. lingulata* line reproductively isolate the species. Thus, *C. lingulata* is an aneuploid of *C. biloba*, meaning that its chromosome number is not a multiple of the parental haploid number. Because *C. biloba* is self-compatible, speciation occurred through chromosomal repatterning rather than through a shift from outcrossing to inbreeding. Lewis (1966) called this form of speciation **speciation by saltation**.

In addition to the factors already mentioned as contributing to the two mechanisms of quantum evolution, populations are likely to be very unstable. At marginal sites in severe conditions, mortality is high and population size fluctuates dramatically through bottlenecks of low numbers and rapid increases during favorable years. Thus, as Carson (1975) envisioned, populations are likely to pass through flush-crash cycles, with a founder effect after each crash stimulating rapid genetic drift and evolutionary change (Figure 5-15). (Lewis [1962] emphasized this evolutionary pattern in the genus *Clarkia*, arguing that catastrophic selection was an important ingredient in the evolutionary divergence of species.) Genetic drift is the alteration of gene frequencies through sampling error (see Chapter 15 for more detail). When populations become very small, as after a population crash, the few remaining individuals usually contain only a small proportion of the genes that were present in the largest population. Just as two crayons sampled at random from a 20-color crayon box cannot represent the color diversity in the box, so a few individuals cannot usually contain the genetic diversity of a large population. Repeated episodes of the founder effect with genetic drift result in change in gene frequencies—or evolutionary change—even in the absence of natural selection.

**The Wallace Effect**

Another potential factor in rapid divergence of populations during primary speciation is the **Wallace effect**. In his book *Darwinism: An Exposition of the Theory of Natural Selection*, Wallace (1889) stated that crossing between populations in the same area or adjacent areas that resulted in inferior-quality individuals would select directly for reproductive isolating mechanisms. As Grant (1971, 136-137) put it, “Those individuals in two sympatric populations which produce inviable or sterile hybrids will contribute fewer offspring to future generations than sister individuals in the same parental populations which do not hybridize.” Therefore, natural selection reinforces reproductive isolating mechanisms, and speciation by reinforcement occurs (Butlin 1989). Grant (1971) argued that the Wallace effect is most likely to be important in annual plants, since reduced seed production is much more catastrophic in them than in a long-lived species with many years for seed production and many chances for crossing with compatible genotypes.

A nice example of the Wallace effect comes from Grant’s (1966) studies on *Gilia*. The leafy-stemmed

<table>
<thead>
<tr>
<th>Characteristic</th>
<th><em>Clarkia biloba</em></th>
<th><em>Clarkia lingulata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Relationship</td>
<td>Presumed parental species</td>
<td>Derived species</td>
</tr>
<tr>
<td>Geographical range</td>
<td>Large area of northern Sierra Nevada and adjacent California</td>
<td>Very small area in one river canyon on southern periphery of <em>C. biloba</em></td>
</tr>
<tr>
<td>Chromosome number</td>
<td>$n = 8$</td>
<td>$n = 9$</td>
</tr>
<tr>
<td>Pollination</td>
<td>Self-compatible</td>
<td>Self-compatible</td>
</tr>
<tr>
<td>Habitat</td>
<td>Moist, closer to ancestral habitats for <em>Clarkia</em></td>
<td>Drier</td>
</tr>
<tr>
<td>Morphology</td>
<td>Petals heart-shaped</td>
<td>Petals tongue-shaped</td>
</tr>
</tbody>
</table>

See Figure 4-7.
Gilias can be divided into two major groups, and all are annuals. The distributions of the five foothill and valley species in California overlap extensively, with individuals of two or more species growing and flowering together in many localities. Very strong incompatibility barriers separate these species. The degree of separation can be measured conversely by the number of hybrid seeds per flower produced as a result of cross-pollination between species. In Grant’s study, seed output in this group ranged from 0 to 1.2 seeds per flower and averaged 0.2 seeds per flower. Four maritime species are completely allopatric in distribution, occurring on coastal strands in North and South America. The maritime species cross-fertilize easily, yielding 7.7 to 24.8 hybrid seeds per flower, with an average of 18.1 seeds per flower.

Grant noted that in other characteristics the inland and maritime species had similar amounts of divergence between species, suggesting that the evolution of fertility barriers has accelerated greatly where species are sympatric. Butlin (1989) discusses problems with interpretation of evidence for the Wallace effect.

Sympatric Speciation
Grant (1971) found no evidence for primary sympatric speciation. However, one case suggested that detailed studies might reveal more frequent instances of the process. Gottlieb (1973) argued for the sympatric origin of a species derived from the parental stock of an annual plant, Stephanomeria exigua. The parental species was an obligate outcrosser with eight chromosomes \( (n = 8) \). Reproductive isolation of the new species developed sympatrically when an individual carried a new chromosomal arrangement such that hybrids had reduced pollen viability and seed set and natural selection favored the evolution of a self-pollinating breeding system.

5.6 SECONDARY SPECIATION IN PLANTS

Hybrid Speciation and Amphiploidy
The major forms of secondary speciation in plants involve a sympatric origin of new species. Hybrid speciation, the origination of new species directly from a natural hybrid (Grant 1971), is a secondary mode of speciation because no divergence from a common parental stock occurs. One of the problems with hybrid speciation is that two genomes must be integrated. Commonly, this occurs because segregation stops in the \( F_1 \) generation, although a great diversity of mechanisms is involved, resulting in many different kinds of genetic systems. Some methods of stabilization in hybrid reproduction include vegetative reproduction, agamospermy (the production of seeds without fertilization of the ovule), permanent odd polyploidy, and amphiploidy, or allopolyploidy. An amphiploid, or allopolyploid, is “a polyploid that originated by the doubling of the chromosomes of a zygote with two unlike chromosome sets, usually owing to hybridization of two species” (Mayr 1963, 663). Polyploidy is the “condition in which the num-
ber of chromosome sets in the nucleus is a multiple (greater than 2) of the haploid numbers" (Mayr 1963, 671).

The most common barrier to hybridization in viable plants is that, during meiosis, chromosomes cannot pair up because they are not homologous (Figure 5-16). Thus, hybrid species originate where this problem is circumvented by various means. In vegetative reproduction and agamospermy, meiosis is completely absent, and mitosis proceeds normally to produce vegetative individuals or to mitotically produce viable seeds. These kinds of uniparental reproduction are likely to give rise to microspecies. The development of amphiploidy results in good biological species that maintain effective sexual reproduction (Figure 5-16). Amphiploidy produces a second version of each chromosome, and so homologous chromosomes are available for normal pairing, and sexual reproduction is reestablished.

Clearly, hybrid speciation can result in very different kinds of species. Some examples follow. Common hemp-nettle, Galeopsis tetrahit, is a naturally occurring biological species (2n = 16), and Müntzing (1932, 1938) reproduced this species by crossing two diploid species of hemp-nettle (2n = 16), Galeopsis pubescens and G. speciosa (Figure 5-17). Despite considerable sterility between the two diploid species, Müntzing obtained F₁'s, one of which was a triploid individual. He backcrossed it to the parent G. pubescens, which yielded a tetraploid G. tetrahit-like plant.

Karpechenko (1927) produced a totally artificial species by crossing the radish, Raphanus sativus, with cabbage, Brassica oleracea, to form a tetraploid, Raphanobrassica. Initially a diploid hybrid was formed from the parental genera. Then, this largely sterile hybrid apparently gave rise to Raphanobrassica after the union of two diploid gametes. Natural hybridization may produce a hybrid complex in which "the morphological discontinuities between the originally divergent ancestral forms" are obscured, giving rise to a species group in which discrete species are hard to identify (Grant 1971, 296).

**Autopolyploidy**

Another form of polyploidy in addition to amphiploidy is autopolyploidy, in which the same chromosome set is doubled, tripled, and so on, giving rise to new species. For example, native species of Dahlia have 2n = 32, whereas the cultivated Dahlia variabilis, grown for show in flower gardens, has 2n = 64 and is a tetraploid. Further multiples of chromosome number can occur, as in Triticum, the genus to which common wheat belongs, where 2n = 14, 28, and 42, the last being a hexaploid (n = 7, 6 x n = 42). In Chrysanthemum, which includes Shasta daisies and marguerites, 2x, 4x, 6x, 8x, and 10x levels of ploidy are represented. Odd numbers of chromosome sets can maintain themselves if asexual reproduction or some degenerate form of sexual reproduction occurs and meiosis is avoided. The Rosa canina group of dog roses in Europe has diploids (2n = 14), tetraploids (2n = 28), pentaploids (2n = 35), and hexaploids (2n = 42). The Crepis occidentalis group among the plants commonly called hawk's-beards has 2x, 3x, 4x, 5x, 7x, and 8x levels of ploidy.

Many other forms of polyploidy can occur, since the presence of at least a duplicate copy effectively buffers change in chromosome number. Hence, chromosomes can be lost or added by ones and twos as well as in whole haploid sets. As a result, an almost infinite variety of karyotypes is possible in plants, and polyploid complexes are relatively common.

**Frequency of Polyploid Plant Species**

Polyploidy is so frequent in plants that it is a major form of speciation. Grant (1963) constructed a frequency distribution of chromosome numbers in flowering plants and developed the argument that many plant taxa have polyploidization events in their phylogenetic histories, resulting in chromosome numbers greater than n = 13. He found a modal distribution around n = 7, 8, and 9 and suggested that the original basic number in the angiosperms lay in this range. Then, chromosome numbers of n = 14 and above would all be polyploids.
Using Grant's estimate, Goldblatt (1980) suggested that many families of monocotyledons comprise entirely polyploid species—for example, the Bromeliaceae (1,700 species), Agavaceae (300 species), and Lemnaceae (30 species). And some very large families have more than 50 percent of species that are polyploids: Cyperaceae, 73% (4,000 species), Poaceae, 60% (10,000 species), and Orchidaceae, 94% (18,000 species). In all, we regard 55 percent of monocotyledonous species as polyploids on the basis of chromosome numbers greater than $n = 13$. Lewis (1980) called this an estimate of paleopolyploids, meaning that polyploidization has occurred in the phylogenetic background of a species. An estimate of intrageneric polyploid species illuminates more recent speciation events, because the polyploids have arisen since the genus evolved. For monocotyledons, the paleopolyploid estimate is therefore 55 percent of species, and the intrageneric polyploid estimate is 36 percent of species (Goldblatt 1980). Both estimates illustrate the impressive impact of polyploidy in plant speciation. In the dicotyledons, similar proportions of species are polyploid (Lewis 1980).

Polyploidy is certainly less common in animals than in plants; it occurs in only some 30 species of reptiles and amphibians (Bogart 1980) and is rare in insects (Lokki and Saura 1980). Schultz (1980) regards polyploidy in fishes, however, as a mechanism that has provided the extra genetic material for major adaptive breakthroughs. Perhaps all the salmonids and catostomids are tetraploids, for example. But it is not yet clear how important polyploidy is in animals in terms of speciation and macroevolution.

5.7 AGAMIC SYSTEMS

In addition to hybridization and polyploidy, loss of gamete fusion has occurred many times. Such agamic systems of reproduction result in immediate repro-
productive isolation from the parental stock, independent divergence of lineages, and the emergence of new species. Sympatric speciation is likely to occur. Because the nomenclature of agamic systems in plants has developed independently from that in animals, some definitions are in order (see Chapter 14). Apomictic reproduction, or apomixis, is asexual reproduction in plants in general, which may involve development of a new individual from an unfertilized egg or from a somatic cell of the parent. Agamospermy is seed formation without fertilization by pollen. Vegetative reproduction is the production of new individuals from somatic cells, not cells related to gametes. A clone consists of all individuals derived by uniparental reproduction from a single parental individual, the genet being the genotype of all individuals and the ramet being one individual in the clone (Harper 1977). Uniparental reproduction is reproduction involving one parent by vegetative means or by a degenerate form of sexual reproduction such as agamospermy. Pseudogamy is the necessity of pollination for seed formation in an apomictic species. (These genetic systems are discussed more in Chapter 14.)

Agamospermy is very common in plants; perhaps the best-known cases are in the family Asteraceae, in the genera Hieracium, the hawk weeds, and Taraxacum, the dandelions. It is common to find apomictic and automictic (self-pollinating) or amphimictic (outcrossing) forms of the same morphospecies. Taraxacum officinale, the common dandelion, has populations of apomicts and automicts in the same general locality. Most agamospermous species are the results of hybridization, and so speciation by hybridization goes hand in hand with agamospermous species. Once each lineage is reproductively isolated, the opportunities for development of many microspecies are extensive, since clones in the same locality can diverge through somatic mutations.

Overall, speciation mechanisms are very diverse in detail, although in general they may be distributed among the allopatric, sympatric, and parapatric forms of primary speciation and the hybridization, polyploidy, and agamic systems of secondary speciation (Table 5-4). Each form of speciation results in a discrete genetic system. Chapter 14 will explore the consequences of each of these genetic systems.

One of the great accomplishments of the theory of evolution is that it describes mechanisms to account for the great diversity of species on this planet. Otte and Endler (1989) and references therein discuss recent developments in the fascinating field of speciation. The question of how life originated is more difficult, but the next chapter will attempt to answer it.

### Table 5-4

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Allopatric</th>
<th>Parapatric</th>
<th>Sympatric</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population size</td>
<td>Large</td>
<td>Very small</td>
<td>Very small</td>
</tr>
<tr>
<td>Major processes</td>
<td>Small genic differences accumulate</td>
<td>Genetic drift, shift in adaptive peak</td>
<td>Very rapid</td>
</tr>
<tr>
<td>Speciation rate</td>
<td>Slow</td>
<td>Faster</td>
<td>Very rapid</td>
</tr>
<tr>
<td>Speciation location</td>
<td>Allopatry</td>
<td>Allopatry</td>
<td>Center of parental range</td>
</tr>
<tr>
<td>Reproductive barrier</td>
<td>Any</td>
<td>Any</td>
<td>Premating</td>
</tr>
<tr>
<td>Examples</td>
<td>Dendroica warblers (Mengel 1964)</td>
<td>Darwin's finches (Grant 1986)</td>
<td>Morabine grasshoppers (White 1968, 1978)</td>
</tr>
<tr>
<td></td>
<td><em>Gilia tenella</em> and relatives (Grant and Grant 1960)</td>
<td>Clarkia biloba (Lewis and Roberts 1956)</td>
<td><em>Rhagoletis fruit flies</em> (Bush 1975a)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Galeopsis</em> (Müntzing 1932, 1938)</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Stephanomeria (Gottlieb 1973), hybrid species (Grant 1971)</td>
</tr>
</tbody>
</table>
SUMMARY

Darwin’s model of speciation lacked as an ingredient geographic barriers that isolate populations and cause them to evolve independently. The model of geographic, or allopatric, speciation emphasizes the importance of geographic isolation during which properties of populations evolve, ultimately leading to reproductive isolation and the evolution of new species. An illustration of this mechanism involved Dendroica warblers and glaciation acting as a geographic barrier. When one or a few individuals found a new population in isolation, as happened in the case of Darwin’s finches, allopatric speciation by the founder effect may occur.

Geographic isolation results from environmental characteristics, such as mountain ranges, that prevent movement of individuals between populations. Reproductive isolation results from properties of species that constrain gene flow between populations, preventing the production of fully fertile progeny, even when the populations occur in the same locality. After geographic isolation, secondary contact between populations may indicate that the new species are fully developed in terms of both reproductive isolating mechanisms and ecological divergence into different ecological niches. If reproductive isolation is incomplete, however, secondary contact may result in introgression and the blending of the diverging populations.

Sympatric speciation may occur in one locality, especially if parasitic organisms, such as Rhagoletis fruit flies, shift to a new host. Allopatric speciation in marginal populations may account for the patterns of overlap in the distributions of many closely related species, although it would not lead us to expect the common occurrence of sibling species. Host shifting between closely related plant species may require only small differences involving the genes for host selection and survival of larvae in the host. The timing of fruiting and the partial overlap of host species in space may result in narrow windows in space and time for host shifts to be made, even though they occur within the cruising range of a parental population.

In parapatric speciation, a chromosomal mutation enables carriers to invade new territory beyond the parental range, and adjacent distributions of parental and derived species develop. Morabine grasshoppers in Australia demonstrate patterns of distribution and karyology that are best accounted for by this speciation model.

Each mode of speciation may apply to a particular set of species characteristics. For example, allopatric speciation involving extensive geographic barriers probably applies to highly mobile organisms such as birds and large mammals; sympatric speciation is likely to be common among parasitic species; and highly sedentary organisms have the potential for speciating parapatrically.

Among plants, we distinguish between primary speciation, involving divergence from a common stock, and secondary speciation, by hybridization or polyploidy or both, involving coalescing of genomes or multiplication of genomes. In primary speciation, quantum speciation—rapid divergence from a parental stock in a peripheral population—may include elements of the founder effect and parapatric speciation. The Wallace effect may promote the rapid evolution of reproductive isolation.

Secondary speciation in plants results from hybrid speciation usually coupled with amphi-ploidy, a form of polyploidy that stabilizes sexual reproduction by providing homologous sets of chromosomes. Auto-polyploids are also reproductively isolated from parental diploid stock and can give rise to new species. Polyploidy has provided the basis for probably more than half the angiosperm species when the estimate includes paleopolyploids. Polyploidy, although a mechanism of secondary speciation, is a sympatric mode. Agamic systems of reproduction automatically cause reproductive isolation among lineages and the potential for evolutionary divergence until stocks can be recognized as separate species.

QUESTIONS FOR DISCUSSION

1. In your estimation, do methods exist for objectively defining or discovering the mode or modes of speciation involved with the development of a set of related species?

2. This chapter attempted a balanced view on alternative modes of speciation. Has this been a truly balanced view, or do you think that preconceived ideas and biases molded the development of this chapter?

3. Do you think that modes of speciation in plants and animals are basically the same, and should they be treated as such?

4. An enigmatic aspect of morabine grasshopper distributions is the lack of any clear physical feature at the edge of a range that may be involved in limiting dispersal. What research would you plan in order to understand the reasons for parapatric distributions in these species?
5. Do you agree that organisms that habitually live in or on other species, such as parasites, small herbivores, and mutualists, are likely to come under strong influences from the host population during the speciation process?

6. Many evolutionary biologists have expressed concern about the sympatric model of speciation and its reality in nature, because it is relatively difficult to understand how reproductive isolation could develop without some kind of physical isolation between divergent populations. What kinds of research would you propose to clarify this debate?

7. Is it possible that new modes of speciation will be discovered when we better understand the nature of the fungal and bacterial species?

REFERENCES


