3 Preamble to Speciation and Adaptation

"It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us" (Darwin 1872:403). This sentence, with its evocation of a diverse, intertwined web of life, can never fail to rouse even the most reductionist of biologists.

The "question of diversity" has been approached on two levels by evolutionary ecologists: description and explanation. Descriptions of diversity are concerned with the total number of species and the relative abundance of species in a given area. These descriptions, in turn, rest upon our ability to perceive, collect, and classify organisms and to depict the data mathematically in the form of diversity indices. Explanation, or the search for processes underlying observed biological diversity, is in itself a complicated process that has blazed a trail of discovery and controversy through the ecological literature. Evolutionary ecologists originally attempted to incorporate both population-level and community-level factors into their explanations of ecological structure. They examined biotic interactions based on traits that were fixed within each species but **variable among** species. This permitted researchers to filter out the confounding influence of intraspecific variability and thus formulate hypotheses concerning the influence of species composition on differences in interspecific interactions. General rules for the production and structuring of diversity were sought by investigating (1) specific components of the system, such as patterns of colonization and extinction of species (MacArthur 1965; MacArthur and Wilson 1967); the age (Wallace 1878), productivity (Connell and Orias 1964; Brown 1973; Connell 1978), structural complexity (Hutchinson 1959), and stability (Slobodkin and Sanders 1969) of the system under investigation; predation (Paine 1966; Parrish and Saila 1970); and interspecific competition (Dobzhansky 1951; Williams 1964); (2) patterns of energy flow through the system (Lindeman 1942; Odum 1969; Brown 1981; Wright 1983; Glazier 1987); (3) organism/environment

as an inseparable whole (Patten 1978, 1982); and (4) the impact of "stochastic factors" (Simberloff 1971). All approaches have contributed some pieces to the intricate puzzle of biological diversity (for excellent reviews see Brown 1981; McIntosh 1987).

In the past two decades, however, the amount of confounding complexity has led an increasing number of evolutionary ecologists to abandon the search for multispecies, large-scale regularities in favor of single-species studies. This has produced a research program founded on the assumption that an understanding of the population biology of each species within a biota will lead to an understanding of the evolution of that biota. As population studies gained increasing ascendancy, the research emphasis shifted to traits that are variable *within* species. These studies have contributed a wealth of detailed information concerning microevolutionary oscillations at the demic level.

Two things are now required: an equivalent data base for ecological systems at the macroevolutionary level and a way to incorporate information from both levels into a comprehensive theory of evolution. We will thus confine our discussions to characters that are relatively fixed within species. This does not mean that variable intraspecific traits are uninteresting or even without phylogenetic components. On the contrary, in chapter 9 we will discuss the potential for dovetailing historical ecology with an emerging research program that uses a combination of phylogenetic and statistical information to discern phylogenetic constraints on the evolution of variable life-history traits. Overall, it is our contention that contemporaneous ecological complexity is embedded in a well-organized historical matrix and that, as a consequence, much of the confounding data compiled by evolutionary ecologists is due to the inability to distinguish between effects stemming from historical background and those stemming from proximal dynamics.

Historical ecologists examine diversity from an explicitly phylogenetic, or historical, perspective. In chapters 4 and 5 we are going to investigate the influence of two evolutionary processes, speciation and adaptation, on the diversification of individual clades. We believe that if some aspects of diversity represent persistent ancestral conditions, then the study of diversity is inherently a macroevolutionary research program. The term "macroevolution," like many terms in science, is the multifaceted result of contributions from many different people. Of these facets, Cracraft's (1985b) distinction between the "transformational view" and the "taxic view" of macroevolution (see chapter 1) is especially helpful in understanding this section. The transformational approach emphasizes the origin of key innovations and adaptive radiations, and the evolution of large-scale trends in character modifications. The taxic view, by contrast, is concerned with uncovering patterns in the distribution of numbers of species, then examining the underlying mechanisms controlling rates of speciation and extinction. We believe that the phylogenetic analysis of speciation approaches macroevolution from the taxic

perspective, whereas the phylogenetic analysis of adaptation represents the transformational view. Although we are presenting them separately, using somewhat different approaches in each case, we hope to show that these two aspects of macroevolution complement each other well, and that robust macroevolutionary explanations often require information about both speciation and adaptation.

In chapter 4 we will address macroevolutionary questions concerning the numbers of species in clades, both total and relative. To understand this, we must investigate the ways in which new species come into existence; this, in turn, means that we must first know something about the nature of species (Wiley 1981; Cracraft 1989; Nelson 1989; Templeton 1989).

Speciation

What Is a Species?

Speciation has always been a central process in evolutionary theory. If follows, then, that if speciation is a "real" process, species must be "real" in some sense relevant to evolution. Nineteenth-century philosophers of science argued that the only "real" entities were those that had immutable spatiotemporal existence. Because of their unchangeable nature, such bits of reality could be grouped into "classes" defined by the fixed properties of their components. Classic examples of such "real" entities, sometimes called "species," are "hydrogen" and "gold." Darwin (1859) threw a monkey wrench into this system by suggesting that organisms could be grouped into biological species, but that these species were not immutable. Although this proposal is not considered controversial today, it took two major philosophical revolutions to forge an understanding of just what a biological species really is. The first step was the emergence of what Mayr (1963, 1988) has called "population thinking" as opposed to "typological thinking." Proponents of the typological approach treat biological species as classes, groups of organisms sharing unique features that define the species. In other words, just as one atom of gold is interchangeable with any other atom of gold, one tiger is interchangeable with any other tiger. This static concept of species makes it difficult to understand how biological species can evolve. In order for speciation to occur, an ancestral species must be variable, and in order for variation to occur, the species must include organisms that do not conform completely to the "definition" of the species. Each new variant that arises in a species must therefore create its own class, so we must either equate "species" with "individual organism," in which case we equate evolution with development, or we must give up the notion of species as real evolutionary entities, if we adopt this perspective.

Advocates of populational thinking treat species as assemblages of orga-

nisms held together by reproductive bonds that are exclusive to them, that can develop like an individual organism (but do not have to die of old age), and that can "reproduce" by something analogous to binary fission. This approach allowed biologists to slip comfortably into a transformational or evolutionary mode, because it viewed species as collections of organisms characterized by both common traits and variable traits. Mayr (1942, 1963) called this the biological species concept. The first major step towards an evolutionary species concept had been taken. The next step awaited resolution of the observation that, although species cohesion is provided by reproductive bonds, reproductive structure in many species lies at the level of local breeding units (demes). This leads us in a completely different direction conceptually, to a worldview in which only demes and populations are real, and species are relegated to the role of artificial constructs. Two problems arise from this perspective: demes and populations might be typological constructs themselves, and, if species are not real, then neither is speciation, and evolution is reduced solely to processes involved in reproductive exchange within individual demes. This purely populational view equates evolution with changes in gene frequencies in populations, and this, in turn, construes evolution as a reversible phenomenon, in contrast to all of our empirical evidence to the contrary. Interestingly, speciation, like evolution, is irreversible. It is a property of collections of demes that is not manifested by the demes themselves because, although changes are always occurring within populations, the coherent structure of the species is not affected unless gene flow is severed between populations (fig. 3.1). Not surprisingly, then, the collection of demes construed as representing a species often exhibits more geographical and ecological coherence than the demes themselves (i.e., demes can disappear and re-form without destroying the species).

For those, like Mayr, who have always felt that species and speciation were important aspects of evolution, the biggest problem has been to determine just how to consider those groups of demes as real without being typological. Michael Ghiselin (1974) provided the solution to the problem by considering species as if they were individual, rather than collective, entities (see also Hull 1976, 1978, 1980; Wiley 1978, 1980a,b; Mishler and Donoghue 1982; Cracraft 1983; Donoghue 1985; McKitrick and Zink 1988). Biological species are real, but not in the same sense that "hydrogen" is real. A molecule of hydrogen found anywhere, and formed at any time, in the universe would be a member of the class hydrogen. By contrast, an organism that looks like a tiger on this planet would not be part of the same species as an organism that looks like a tiger on another planet unless the two organisms shared a common ancestor. Viewed in this way, we can see that classes are defined by convergences, whereas individuals are defined by homology. So the typological view and the purely populational view of species are nonevolutionary,
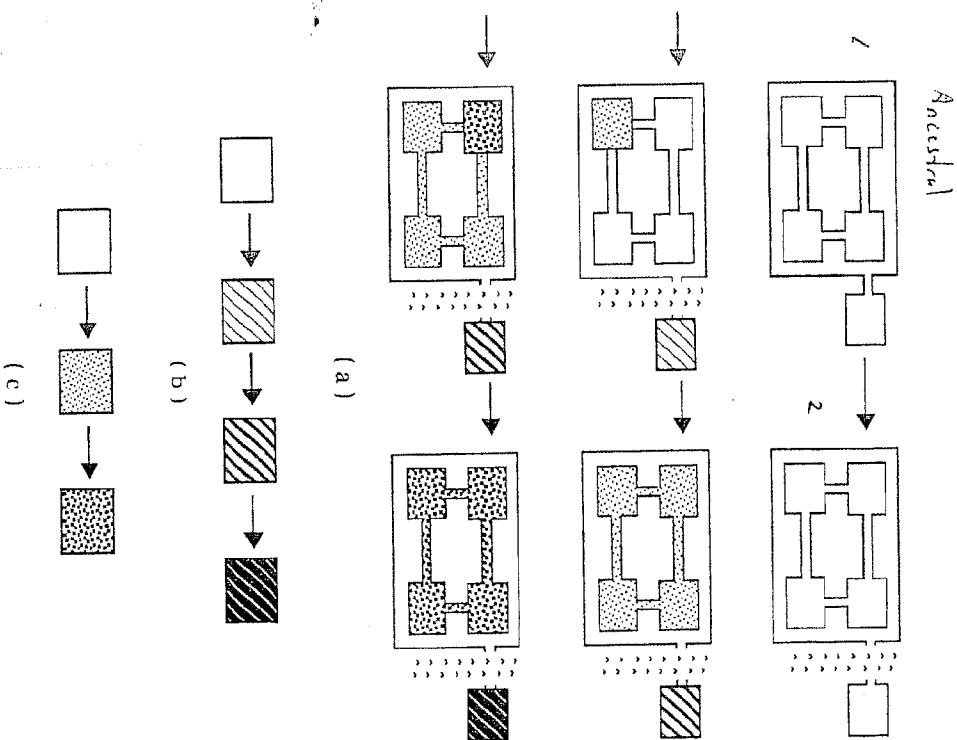

Ancestral

(a)

(b)

(c)

Fig. 3.1. Heuristic diagram depicting the difference between speciation and population differentiation. (*a*) The ancestral species is initially composed of five populations (represented by small boxes) connected by some level of gene flow. One population is isolated (gene flow is severed or severely restricted); the remaining populations continue to experience gene flow. Character changes, depicted by *different patterns in the boxes*, occur in both the ancestral populations and the isolated population. (*b*) Character changes in the isolated population. It is impossible to determine which scenario, *b* or *c*, represents the speciation event *without reference to other ancestral populations*. In this situation, the isolated population has established an independent evolutionary trajectory (speciated), while the remaining populations, although they have changed, remain part of the original evolutionary lineage.
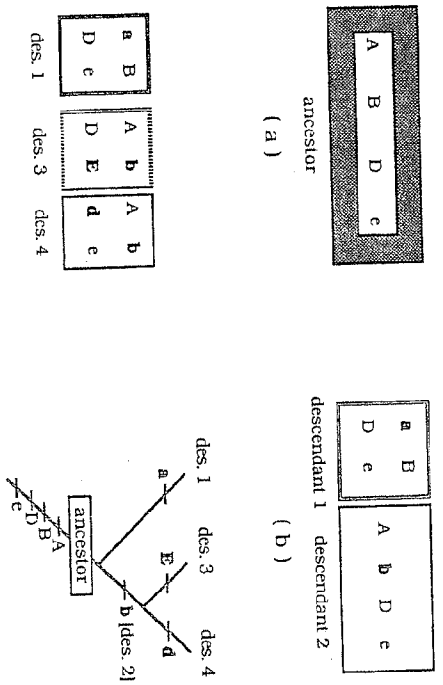
(a)

(b)

(c)

(d)

Fig. 3.2. Species are a mosaic of ancestral and derived traits, but only synapomorphies distinguish phylogenetic relationships. *Bold letters* = derived traits. (*a*) Ancestral species. (*b*) Ancestral species divided, descendant species 1 and 2 produced. (*c*) Descendant species 2 divided, descendant species 3 and 4 produced. (*d*) Phylogenetic tree depicting the relationships among the ancestor and all its descendants. Notice that descendants 1 and 2 are sister species (possession of character e); descendants 3 and 4 are sister species (possession of character b). Autapomorphies (a, d, E) distinguish individual species, but not phylogenetic relationships.

because they are based on homoplasy and evolutionary descent involves homology (common ancestry; Wiley 1989).

Under this "*species as individuals*" view, the most important characteristic of a species is that its members are bound together by unique common ancestry, and not that its members are reproductively isolated from members of other species. The evolution of a single species is analogous to the development of a single organism; just as an organism changes its appearance without losing its identity during development, so a species can change its appearance without losing its identity during evolution (fig. 3.1a and c). The formation of new species is analogous to asexual reproduction, in which new individuals are distinct from the old individual because they form independent evolutionary lineages (fig. 3.1a and b). Over time, distinct historical trajectories emerge from the speciation process, each differing to some degree from its ancestor and closest relatives, but retaining some of its ancestry in the form of synapomorphies. We take advantage of this historical mosaic nature of the attributes of organisms that comprise species when we use synapomorphies to reconstruct phylogenetic trees (fig. 3.2). The adoption of the evolutionary species concept (Wiley 1978, 1980a) appears to have finally exorcised the persistent spector of typology and also freed us from a reductionist view of species concept (Wiley 1978, 1980a) appears to have finally exorcised the persistent spector of typology and also freed us from a reductionist view of

evolution (Mishler and Donoghue 1982; Cracraft 1983b; Donoghue 1985; McKitrick and Zink 1988). All species that conform to the biological species concept are evolutionary species, but not all evolutionary species need conform to the biological species concept (see also Endler 1989; Templeton 1989).

Understanding what species are conceptually remains an interesting issue in the philosophy of biology (see, e.g., articles in *Biology & Philosophy*, vol. 2, 1987 and for an enlightening counter-point, see Powers 1909). What is important to most biologists, however, is not definition but identification. Wiley (1981) discussed a series of criteria that can be used to make decisions about species membership. Despite these empirical tools, delimitation of species boundaries remains a problem in some groups, and may limit our ability to study speciation processes in those organisms. Nonetheless, students of such groups should take heart. As David Hull (pers. comm.) has pointed out, if all species had sharply distinct boundaries, we would have no reason to suppose that any of them could evolve into other species. Hence, those groups for which it is difficult to delimit boundaries represent some of the strongest evidence we have for the evolutionary potential of biological species.

How Species Are Produced: Uncovering Patterns and Processes of Speciation

Mayr (1963) recognized three general classes of speciation. The first is *reductive speciation*, in which two existing species fuse to form a third. Harlan and DeWet (1963) proposed the term "compilo-species" for cases in which one species absorbs another; however, examples of this phenomenon have not been documented to date. The second is *phyletic speciation*, in which a gradual progression of forms within a single lineage is assigned species status at different points in time. As noted above, we consider each individually evolving lineage to be a single species; therefore, phyletic speciation represents evolutionary change within a single species, usually termed **anagenesis**, rather than a mode of species formation, or **cladogenesis.** The third class, *additive speciation*, is characterized by an increase in the number of species. The majority of speciation models, although based on several different mechanisms, are models of additive speciation. The most important thing to remember about speciation is not that it produces species, but that it produces *sister species*, so you cannot formulate explanations about speciation modes based on analysis of a single species. Rather, you need to examine sister species and clades.

Wiley (1981; see also Felsenstein 1981; Templeton 1982; Wiley and Mayden 1985) suggested that various models of additive speciation could be studied if phylogenetic, biogeographic, and population biological data were avail-

able, and if three assumptions could be met. First, character evolution must provide a reliable basis for reconstructing sequences of speciation events; that is, speciation has left a trace of its actions that we can detect. This assumption requires the operation of one of two processes, character evolution tightly coupled with speciation, or character evolution occurring at the same or higher rate than lineage splitting. So long as one of these processes is operating, even if the divergence of particular characters is not driving the divergence of the lineages, there will be a historical trail of character transformation highlighting speciation events. The second assumption is that there have been no extinctions in the clade. If we are to use phylogenetic trees to study particular modes of speciation, we must have confidence that sister species are each other's closest relatives and not, in reality, more distantly related due to the extinction of several unknown intermediate species.

The third assumption postulates that, if speciation has been associated with geographical changes, then we can reconstruct the original background of speciation events because the current distributions of descendant species do not differ dramatically from their original distributions. In other words, we assume that the dispersal of descendant species has not obscured the geographical context of the speciation events. This assumption requires closer inspection because of the confounding ways in which the movements of organisms and populations have been described in evolutionary biology. One of the most contentious words in biogeography and speciation has been *dispersal*. To some, the word refers to localized movements of organisms during short periods of time and is associated with concepts such as home range. To others, dispersal refers to the expansion and contraction of populations and species over longer periods of time. This form of dispersal is a necessary part of one class of speciation model (what we will call "allopatric speciation mode I" in chapter 4), because range expansion results in the widespread distribution of a species through space. This, in turn, increases the probability that geological changes will isolate large enough populations to form descendant species. A third meaning of the term dispersal is associated with another class of speciation models (what we will call "allopatric speciation mode II" in chapter 4), in which speciation is initiated by the dispersal of organisms into new areas. Thus, in some cases dispersal is not associated with speciation, in other cases it establishes the conditions under which speciation can be initiated, and in still other cases it is responsible for initiating speciation.

This highlights an important and often misconstrued aspect of the relationship between speciation and dispersal. The third assumption does not state that dispersal is unimportant, only that postspeciation dispersal does not overwhelm speciation patterns. Like many biological assumptions, this is a necessary starting point because without it we have no a priori justification for attempting to reconstruct speciation patterns, and thus no hope of studying speciation.

the process. Unlike many biological assumptions, data are available to examine the validity of this supposition. For example, Lynch (1989) examined the distributions of sixty-six pairs of sister species and concluded that since "only 3–5 cases out of 66 possibilities reflect appreciable dispersal, then significant dispersal should not be envisioned as an important hypothesis [in studies of speciation]."

Speciation processes can be characterized in a number of ways. At the coarsest level there are two categories of models, those involving the physical disruption of gene flow by geographical isolation (allopatric modes), and those which do not require isolation for speciation to occur (nonallopatric modes). The allopatric category can be further subdivided depending on whether disruption of gene flow is accomplished through geological alteration (passive allopatric, or vicariant, speciation) or through movements of members of the ancestral species that eventually result in their geographical isolation (active allopatric speciation). In a different, but complementary, vein adaptive changes within populations play different roles in each of these three general classes of speciation processes. Adaptive changes are not required to initiate passive allopatric speciation, although they may accompany such speciation events; conversely, adaptive changes are often postulated to accompany active allopatric speciation and are a necessary component in initiating nonallopatric speciation.

In chapter 4 we will use "passive allopatric speciation" as the null hypothesis because, being independent of any particular underlying biological properties, it is a mode of speciation that could occur in any group of organisms. All that is required is for an ancestral species to "get separate and get different." Since most models were developed to explain the breakdown of a single ancestral species into descendants, an entire clade is not necessarily expected to be the product of a single speciation process, unless it is the "null" mode. From a conceptual standpoint then, uncovering incidents of active allopatric and nonallopatric speciation is just cause for celebration, because these modes represent departures from the historical background of vicariance and give us insights into the possible roles of a variety of environmental processes in speciation. As a consequence, historical ecological researchers must delve into the minutest details of each putative case of speciation within a clade in the quest to delineate and understand the patterns and processes composing the important evolutionary force of "speciation."

The Frequency of Different Speciation Modes

Theoretical studies of speciation have produced a plethora of models that are variations on the three themes of passive allopatric, active allopatric, and nonallopatric speciation. Now that theoretical biologists have delineated these models by mathematical and deductive reasoning, the next question is, How

often does each of these speciation modes actually occur in nature? Unfortunately, investigating this question is hampered by the paucity of explicit species-level phylogenetic hypotheses. There has been only a single such study undertaken to date, but, as we will discuss in chapter 4, the results of that study are intriguing. In brief, Lynch (1989) discovered that vicariance (passive allopatric speciation), the most plausible speciation mode on theoretical grounds, also seems to have been the most prevalent on empirical grounds. Vicariant speciation requires only the physical disruption of gene flow; it does not require that speciation be initiated by adaptive processes (although it may be accompanied by such responses). Speciation modes, such as parapatric and sympatric speciation, that require adaptive changes to initiate and/or complete the process are relatively unlikely on theoretical grounds, and very few putative examples of these modes have been documented. This implies that speciation and adaptation need not always be tightly coupled evolutionarily. If that is true, the relationship between speciation, adaptation, and diversity may not be as straightforward as previously thought.

Macroevolutionary Trends in Diversity: Species Numbers

Other questions concerning numbers of species in evolutionary ecology have been formulated within two contexts. The first of these is comparison of species numbers in different environments; for example, Why are there more species in the tropics than in the polar regions? The second involves comparison of species numbers between different groups of organisms; for example, Why are there more species than species of birds? The first approach has generally sought nonhistorical explanations, so there are, at present, no empirical studies available for discussion in a book dedicated to "historical ecology," although we will discuss a phylogenetic perspective on the question in chapter 4. We hope researchers will eventually become interested in examining the phylogenetic component of species distribution in different environments (see also Ricklefs 1989). The second question has traditionally incorporated some minimal concept of "taxonomic relatedness" into its explanations. The goal of research comparing species numbers between groups has been to determine if there are clades of "unusually high" or "unusually low" species number, and to attempt to explain those unusual groups. Although there have been numerous discussions of this problem, the lack of rigorous, objective criteria has proved to be a major impediment to its resolution. For example, how much asymmetry in species numbers can be considered unusually high or unusually low? Or, since the "number" of species within a given clade is strongly dependent upon the window of time through which one is viewing, on what temporal scale should an investigation be conducted? Answering this question may require more information than is

readily available for most clades; therefore, there has been a tendency to focus only upon the diversity of extant species. Nonetheless, there is a perception that some groups are "more species-rich" than other groups that are somehow "equivalent," and that there is an evolutionary explanation for this difference. It is tempting to postulate that highly species-rich groups are, or have been, "better" or "more successful" than average, whereas groups of low species number are, or have been, somehow "less successful" than average.

Mayden (1986) took the first steps towards establishing a more rigorous foundation for assessing differences in species number between or among groups. He suggested that two standards were required. First, each group under examination must be monophyletic, and second, the groups being compared must be of equal antiquity. Because phylogenetic systematics stresses the recognition of monophyletic groups, an appropriate starting point for investigations into this component of diversity should be a phylogenetic analysis of the study organisms. A number of methods have been proposed for documenting the relative ages of clades. Stratigraphic and biogeographic analyses attempt to use environmental parameters as independent indicators of age. The use of "genetic distances" attempts to use a hypothetical "internal clock" that is universally informative about evolutionary rates. Phylogenetic systematics uses yet another criterion, sister-group relationships, because, by definition, each of two sister groups is the same age. If Mayden's conditions are met, groups of equal age may differ in species number either because of unequal rates of speciation or because of unequal rates of extinction. Assessing this component of diversity requires comparative analysis of speciation patterns and mechanisms.

Adaptation

We will address macroevolutionary questions concerning the degree of functional (ecological and behavioral) differentiation within and among groups of species in chapter 5. Since the beginning of modern evolutionary theory, this aspect of diversity, traditionally examined within a nonhistorical framework, has been a central focus of adaptation theory. We hope to show that there is generally a coherent phylogenetic sequence by which complex behaviors and ecologies are "assembled." Rarely do these character complexes arise de novo in the "lifetime" of any single species. We will also show, as a correlate, that current data suggest that ecological and behavioral diversification within groups is generally more conservative than morphological diversification and speciation. As a consequence, we will begin to view adaptation as a conservative, or cohesive, influence on evolution, complementing rather than causing diversification.

Contemporary adaptive explanations refer to an individuals' response to some problem set by nature. Adaptation is thus related to notions of a function

Historical ecologists have a perspective that speciation does not just produce species, it produces **sister species**. Since this irreversible production of groups that are each other's closest relatives introduces a historical component into the process, speciation cannot be studied without first determining the sister-group relationships within the system of interest. Assuming that two species are or are not "closely related," and basing hypotheses of the speciation model involved in their production on this assumption, will, in most cases, ultimately lead to confusing and contradictory results.

Mayr (1963) recognized three general classes of speciation. In *reductive speciation* two existing species fuse to form a third. In *phyletic speciation* a gradual progression of forms through a single lineage (anagenesis) is assigned species status at different points in time. Although the endpoints of such a continuum may be recognizably "different," separation of the intermediate forms into distinct groups is an inherently arbitrary exercise (Hennig 1966; Wiley 1981). Additionally, since we consider each individually evolving lineage to be a single species, "phyletic speciation" can only represent intraspecific evolutionary change, that is, change preceding or following, but not correlated with, speciation. *Additive speciation* involves lineage splitting (cladogenesis) and reticulate evolution. The majority of examples of speciation represent cases of additive speciation. No single mechanism is responsible for the initiation of additive speciation (Wiley 1981). Several mechanisms have been proposed, and we will consider each as a distinct "model" of speciation. Our discussion will rely heavily on the methodological framework incorporating phylogenetic patterns with biogeographic and population work incorporating phylogenetic patterns with biogeographic and population information provided by E. O. Wiley (see especially Wiley 1981; Wiley and Mayden 1985). Wiley's evolutionary detective work, in turn, has been based on the pioneering studies of Mayr (e.g., 1954, 1963), Bush (1975a,b), Endler (1977), White (1978), Wright (1978b), Lande (1980a, 1981), Templeton (1980, 1981, 1982), and Felsenstein (1981).

Assumptions of a Speciation Study

Wiley (1981; see also Wiley and Mayden 1985) suggested that the various models of additive speciation could be studied by establishing phy-

logenetic, biogeographic, and population biological predictions corresponding to each model. In order to begin such extensive studies, three assumptions concerning the nature of the data must be satisfied. First, character evolution must provide a reliable basis for reconstructing sequences of speciation events, that is, speciation has left a trace of its actions that we can detect. This assumption requires that one of two processes is occurring: either character evolution is tightly coupled with speciation, of character evolution occurs at the same or higher rate than lineage splitting. Thus, even if the divergence of particular characters is not driving the divergence of the lineages, there will be historical trail of character anagenesis highlighting speciation events. Although the second condition represents the traditional perspective of evolutionary biologists, the recent advent of punctuated equilibrium models (Eldredge and Gould 1972) has strengthened the proposition of a causal relationship between character modification and speciation. The first assumption is violated if gene flow is halted permanently between populations at a faster rate than character change is occurring. If this happens, the traits present in each species will represent a combination of (1) characters that existed prior to the isolation of the populations, providing information about common ancestry (symplesiomorphies), and (2) evolutionary modifications that occurred subsequent to the population's isolation, providing information about the unique status of the population (autapomorphies). Since derived traits are not shared between populations under these circumstances, sequences of speciation events will be difficult or impossible to determine (we will discuss this more in a later section) (fig. 4.1).

The second assumption is that there have been no extinctions in the clade. If we are to use phylogenetic trees to study particular modes of speciation, we must have confidence that sister species are each other's closest relatives and not, in reality, more distantly related due to the extinction of several unknown intermediate species. Consider the following hypothetical example. Two groups of fish, demonstrated to be sister species on the basis of a phylogenetic analysis, are located on either side of a mountain range (fig. 4.2a). Based on these observations, we might hypothesize that the disjunct distribution was caused when the upheaval of the mountains separated the ancestral species into two populations, which subsequently diverged in isolation (fig. 4.2b). Unfortunately for our theory, a group of enthusiastic paleontologists discover an abundance of fossil evidence suggesting that at least two other species fall between the extant representatives (fig. 4.2c). Hence, the current disjunction of fishes B and C was probably derived through a series of speciation and extinction events, only one of which need have been associated with the tectonic activity (fig. 4.2d).

The third assumption postulates that the influence of geographical separation during the evolutionary divergence of a clade has not been obscured by rampant dispersal of the descendant species (fig. 4.3). Pairs of sister species
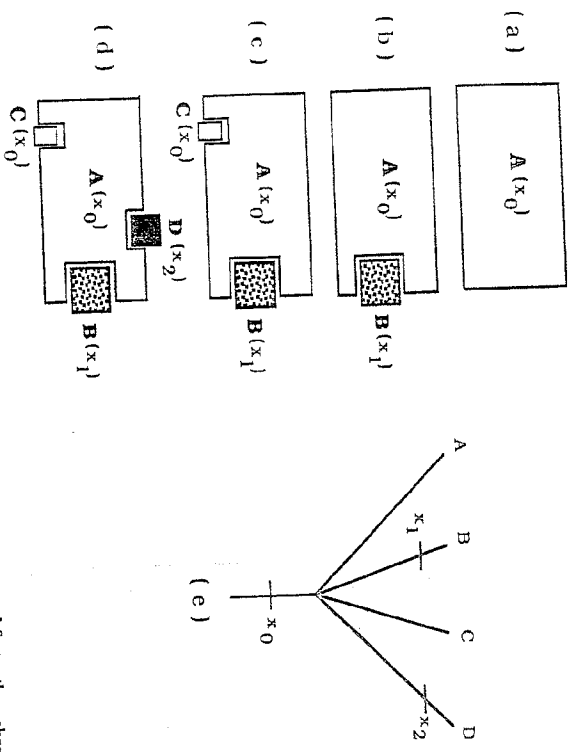
(a)

(b)

(c)

(d)

(e)

Fig. 4.1. Problems arising when gene flow between populations is severed faster than character change occurs. (a) Ancestral species A bearing character state x_0. (b) Speciation producing B accompanied by the divergence of x_0 to x_1. (c) Speciation of C, no character change. (d) Speciation of D accompanied by the divergence of x_0 to x_2. (e) Phylogenetic tree reconstructed by changes in character x. Note that there is no way to differentiate between A and C, and that it is impossible to reconstruct the temporal sequence of speciation because the derived characters x_1 and x_2 are autapomorphies.

or clades that show such dissemination may be identified by large-scale sympatry; however, uncovering such sympatry creates a problem because it is difficult to determine whether the current distribution pattern existed during the speciation of the group, or whether it represents widespread dispersal following speciation in isolation.

It is probably true that many groups will not satisfy all the assumptions; however, until a larger data base is established, it is impossible to determine whether these nonconformists need be accorded the status of an overwhelming majority or a confounding minority. We are confident that numerous clades will emerge in which phylogenetic patterns and distribution patterns are congruent with predictions from particular speciation models.

Phylogenetic Patterns of Speciation

Allopatric Speciation

"Allopatric" speciation is a generic term for models that invoke the complete geographical separation of two or more populations of an ancestral spe-
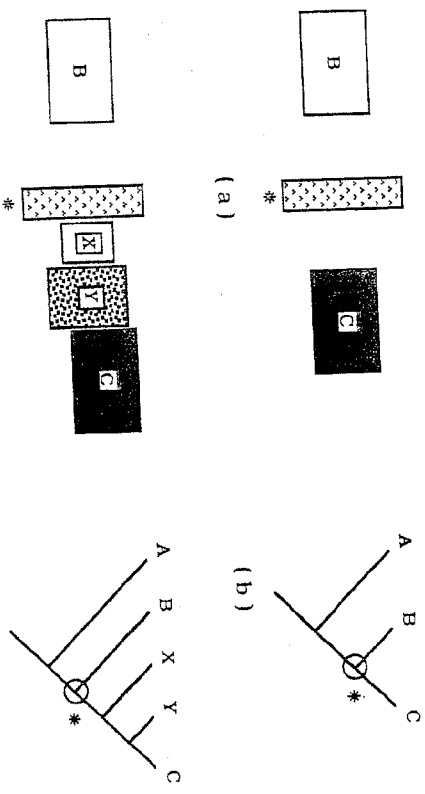
(a)

(b)

(c)

(d)

Fig. 4.2. Problems arising from extinctions. (a) Two fishes, B and C, are located on either side of a mountain range. (b) Phylogenetic tree for the genus containing species B and C. Open circle = the speciation event; * = the upheaval of the mountains. (c) Fossil evidence of extinct species X and Y on the same side of the mountains as extant species C. (d) New phylogenetic tree incorporating fossils. According to this new hypothesis, the mountains may have played a role in the production of species B and the ancestor of the X + Y + C clade.
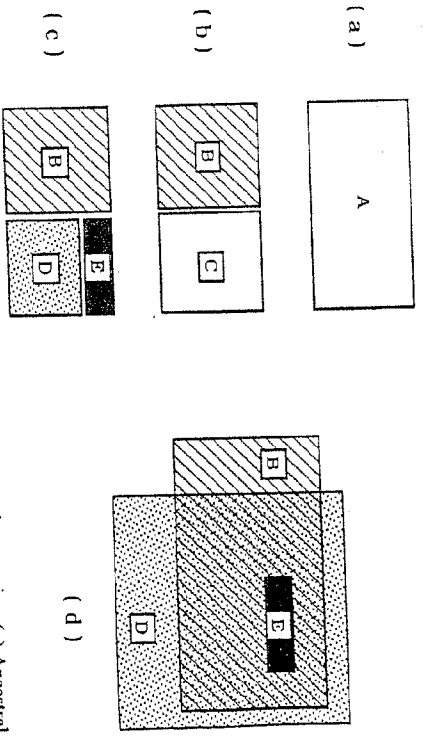
(a)

(b)

(c)

(d)

Fig. 4.3. Problems arising from widespread dispersal of descendant species. (a) Ancestral species A. (b) Geographic separation of A produces descendant species B and C. (c) Geographic separation of C produces descendant species D and E. (d) Rampant dispersal of descendants ? and D produces a current distribution pattern of widespread sympatry and obscures the origin... pattern of geographic disjunction.

(a)

(b)

(c)
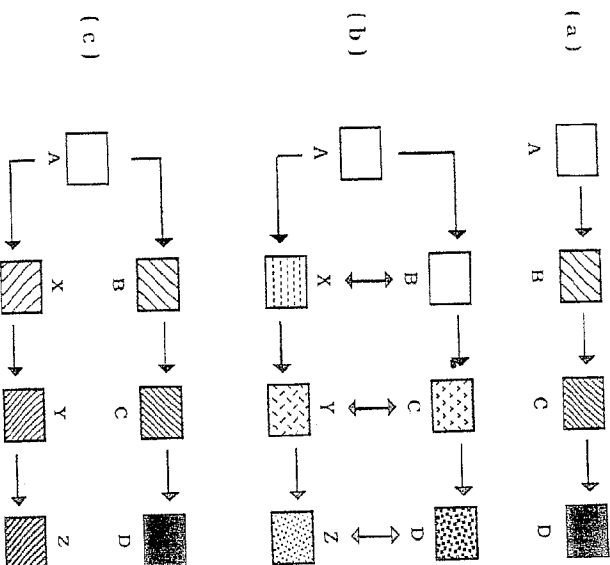
t.4. Three types of population structure. (*a*) A single deme evolving through time. (*b*) Two s, linked by gene flow, evolving through time. (*c*) Two demes with no gene flow, evolving gh time.

to initiate speciation. Distinguishing the allopatric models from one an-
r requires that we answer three questions: (1a) Were the disjunct pop-
llations created by the actions of geological processes (*passive role for the
ancestor*) or by the dispersal of some ancestral individuals over preexisting
barriers (*active role for the ancestor*)? (2) Was gene flow among ancestral pop-
ulations *present* (fig. 4.4a and b) or *absent/rare* (fig. 4.4c) prior to the [s]e-
ating event? This is an important question because the rate of speciation will
be affected by the interaction between local differentiation in response to se-
ction, which tends to promote speciation (e.g., Fisher 1930; Wright 1931,
0, 1978a; Haldane 1932; Lande 1980a, 1981; Templeton 1980, 1981,
2; Coyne and Kreitman 1986), and the *cohesive* forces of persistent an[d]
ral traits and gene flow among demes, which tend to inhibit speciation
ley 1981; Wiley and Brooks 1982; Brooks and Wiley 1986, 1988; Temple
on 1989). (3) Was the ancestral population equally subdivided, or was only
r a very small part of the ancestral range "budded off" from the rest of
ne species range (or was the division somewhere between these two extre
ies)?
eating these questions in mind, let us examine the phylogenetic patterns

93   Speciation

predicted by the three allopatric models (as summarized by Wiley 1981;
Wiley and Mayden 1985; Funk and Brooks 1990).

Allopatric speciation mode I

Usually called **vicariance**, or **geographic speciation**, allopatric speciation
mode I combines gene flow among populations prior to separation with a
passive role for range changes in the ancestral species. It occurs when an
ancestral species is geographically separated into two or more relatively large
and isolated populations, with subsequent lineage divergence by the isolated
descendant populations (fig. 4.5). The speciation rate will depend on the
degree of variation in the ancestral species prior to isolation and the rate of
origin of evolutionary novelties in the subdivided populations. Three predic-
tions from this model are of interest to students of speciation: (1) The phy-
logenetic tree for the group will be predominantly dichotomous because the
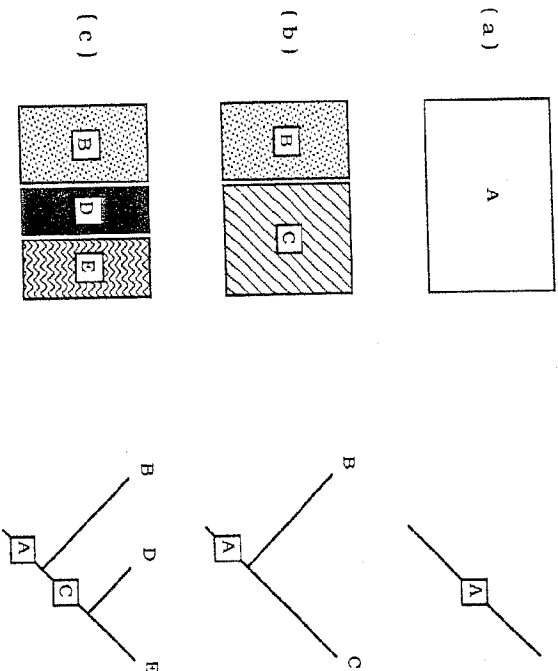fragmentation of the ancestral species and concomitant interruption of gene

(a)

A

(b)

B

C

(c)

B

D   E

B

D   E

A

C

A

Fig. 4.5. Allopatric speciation mode I. (*a*) Species A extends throughout a geographical area.
(*b*) The species is divided by the appearance of some geographical barrier preventing gene flow;
the two populations continue to evolve independently of one another, producing new species B
and C. (*c*) Species C undergoes another geographical upheaval, gene flow is eliminated, and
changes continue in isolation, leading to the eventual production of new species D and E. The
outcome of this division of space through time is the production of three extant species (B, D,
and E) and the extinction through total speciation of two ancestors (A and C).

flow among the isolated populations makes it unlikely that either of the descendant species will be identical to the ancestor or to each other. In this case, the ancestor experiences "extinction through total speciation." (2) The points of geographical disjunction between sister species will correspond to the historical boundaries established by the geological changes. Based on this, the ancestral range may be estimated by combining the distributions of the descendant species, assuming no substantial range expansion or contraction following speciation (fig. 4.3). (3) A multitude of ancestral species, could all theoretically speciate in the same way by the same geological event, because the mechanism initiating speciation is independent of any particular biological system. Hence, we would expect to find the same biogeographical distribution pattern shared by a number of different clades. The research program called "vicariance biogeography" relies on this mode of allopatric speciation to detect episodes of parallel biological and geological evolution (see chapter 7).

Allopatric speciation mode II

Allopatric speciation mode II, more commonly known as **peripheral isolates allopatric speciation** or **peripatric speciation**, postulates that a new species arises from a small, isolated population usually, but not always, on the periphery of the larger central ancestral population. Gene flow between the peripheral and central populations contributes to species cohesion, because it is initially sufficient to keep novel traits from being fixed; however, it is not strong enough to prevent the establishment of novel phenotypes in the peripheral population. The foundation and final disjunction of the peripheral population that initiates speciation may involve either a passive or active role for the ancestor. When the new species arises in a geographical locality not previously occupied by the ancestor, an active role in invoked. Once geographic separation is complete, gene flow from the central population is stopped. This could happen rapidly, as in founder-effect phenomena (Carson 1975, 1982; Templeton 1980; Lande 1981; Carson and Templeton 1984; Goodnight 1987; Charlesworth and Rouhani 1988; Barton 1989), or it could be a relatively gradual process, such as a gradual environmental change in the peripheral area (Mayr 1954, 1963, 1982; Patton and Smith 1989). Unlike allopatric speciation mode I, this model predicts that the ancestor will persist after the speciation event, because its fragmentation was so asymmetrical. When we say that the ancestor "survives," we mean that it does not exhibit any evolutionary change correlated with the speciation event (i.e., the peripheral descendant shows all the divergence). Because the peripheral population is small and thus released somewhat from the homeostatic constraints of large-scale gene flow, the peripheral descendant will exhibit more autapo-

How to distinguish from higher rank?

morphic traits than the central population, even if that central population experiences its own anagenetic events or eventually speciates again. Hennig (1966) termed the general observation that one of two descendants tended to be more divergent from the ancestor than the other his "deviation rule."

There are three different pathways to this speciation mode, so there are several predicted phylogenetic and biogeographic patterns. In "classic" peripheral isolation (Wiley and Mayden 1985), there are both ecological and phylogenetic components to speciation, and the ancestor is accorded an active role. The assumption is that populations in peripheral habitats are initially free to diverge evolutionarily from their ancestor because of reduced gene flow (Mayr 1963; Hennig 1966; Brundin 1966), and that this divergence, in turn, may be reinforced by local adaptive responses to the new habitat (Hennig 1966) and/or genetic drift and founder effects. Proponents of this speciation mode often assume that peripheral habitats are necessarily marginal in composition. Lynch (1989) pointed out the dangers in equating "different" with "marginal." This is an important distinction because it allows the potential for evolutionary change to occur in response to the presence of a new selective regime, without invoking the assumption that the habitats occupied by the central populations are somehow "better" than the habitats occupied by their peripheral counterparts. If peripheral isolation is due to random settlements of ancestral individuals around the margins of the species' range, we expect to find phylogenetic trees comprising polytomies in which the number of terminal taxa equals the number of peripheral descendants "budded off" from the ancestor, plus the ancestor itself (fig. 4.6). Biogeographically, we would expect to find similar patterns of distribution only among clades with similar ecological requirements.

If isolation is due to ancestral individuals dispersing into a new habitat, experiencing peripheral isolation, and speciating, followed by movement of some members of the new species into another peripheral area, repeating the process, we would expect to find dichotomous phylogenetic patterns reflecting the alternating episodes of dispersal and isolation (Hennig's "progression rule"; fig. 4.7). An excellent example of this type of pattern might be found among organisms that have speciated repeatedly during progressive colonization of island archipelagos. Unlike allopatric speciation mode I, which predicts that all clades segregated by a vicariance event could theoretically show the same biogeographical patterns, similar patterns are expected here only for clades demonstrating analogous ecological requirements and dispersal abilities.

The final form of peripheral isolates allopatric speciation, "vicariant" peripheral isolation (Wiley and Mayden 1985), invokes a passive role for the ancestral species. Specifically, when large chunks of ancestral populations are subdivided geographically, we speak of vicariant speciation (allopatric spe-
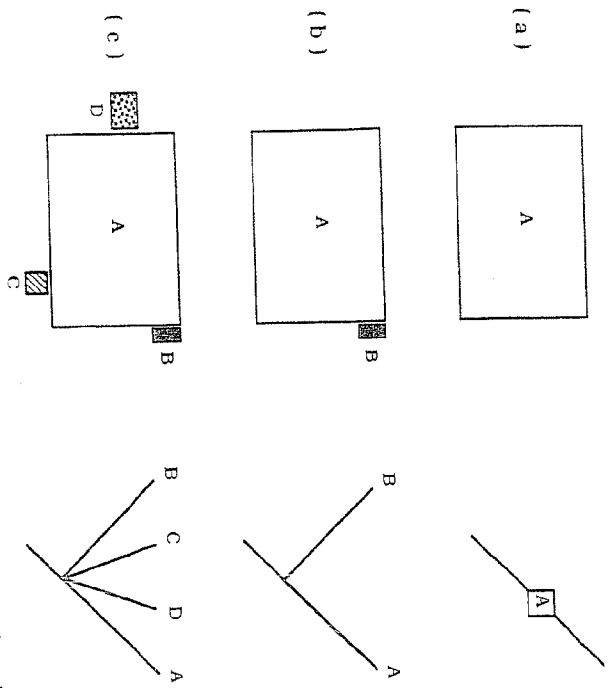
ig. 4.6. Allopatric speciation mode II, peripheral isolates allopatric speciation via random dispersal. (a) Species A extends throughout a geographical area. (b) Some individuals disperse into a new area; gene flow is severed, producing species B. (c) Random dispersal and severing of gene flow results in the budding off of descendant species D and C. The traits present in each species represent a combination of characters that existed prior to the isolation of the population (symplesiomorphies) and evolutionary modifications that occurred subsequent to the isolation (autapomorphies). Since derived traits are not shared between populations under these circumstances, sequences of speciation events will be impossible to determine, and the resultant phylogenetic pattern will be a polytomy.

iation mode I), and when small chunks are subdivided, we speak of this orm of peripheral isolates speciation (fig. 4.8). Lynch (1989) has termed this 'microvicariance.'

"Since the mechanism initiating speciation (vicariance) is independent of any particular biological system, there is a phylogenetic component to speciation (the relationship between ancestor and descendant) but not necessarily an ecological one. If more than one small group is isolated by the vicariance events, we would expect phylogenetic patterns showing polytomies, and would expect to find similar biogeographical distribution patterns only for other species that were fragmented by the same geographic events.

The peripheral isolates model is the traditional favorite of evolutionary biologists (Mayr 1963) because it combines geographically restricted gene flow with the exposure of small populations to new selection pressures from

---

the peripheral habitats, which, in turn, is postulated to reinforce evolutionary divergence. However, Barton and Charlesworth (1984; see also Barton 1989) have recently questioned the likelihood of this mode of speciation. Biologists have been particularly interested in the possibility that an ancestor occupying a large central range can remain relatively unchanged for a long period of time, become extinct, and, in a relatively short time, have its range reclaimed by descendant species that have been evolving in peripheral areas. If this happens, the fossil record will show the long-term persistence of a "static" ancestral species, followed relatively quickly by its extinction and replace-
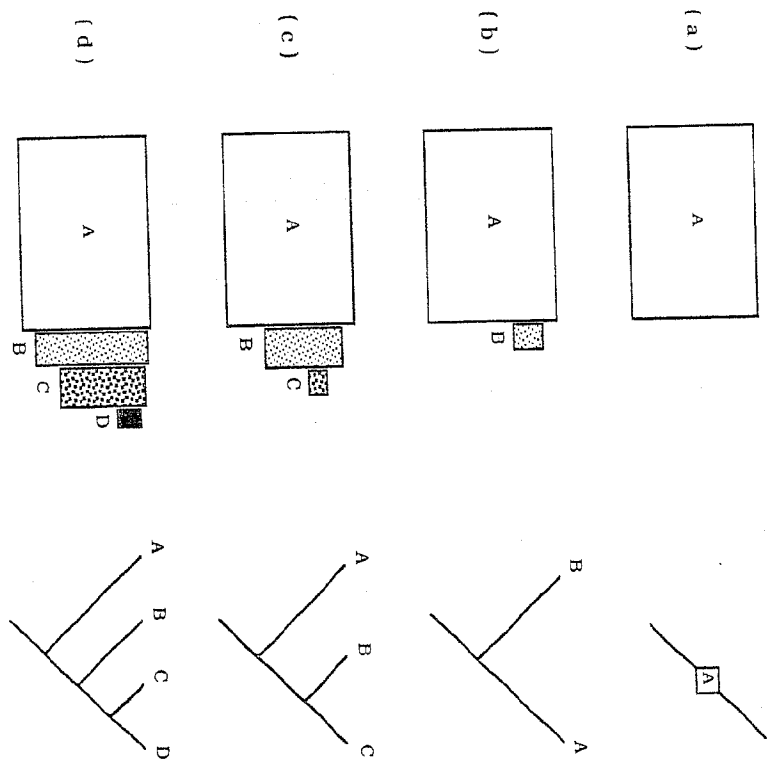
Fig. 4.7. Allopatric speciation mode II, peripheral isolates allopatric speciation via sequential dispersal. (a) Species A extends throughout a geographical area. (b) Some individuals disperse into a new area; gene flow is severed, producing species B. (c) Individuals from species B disperse into a new area; gene flow is severed, producing species C. (d) Individuals from species C disperse into a new area; gene flow is severed, producing species D. In this case, sister species can be identified by the presence of shared derived traits; therefore the resultant phylogenetic pattern will be dichotomous.
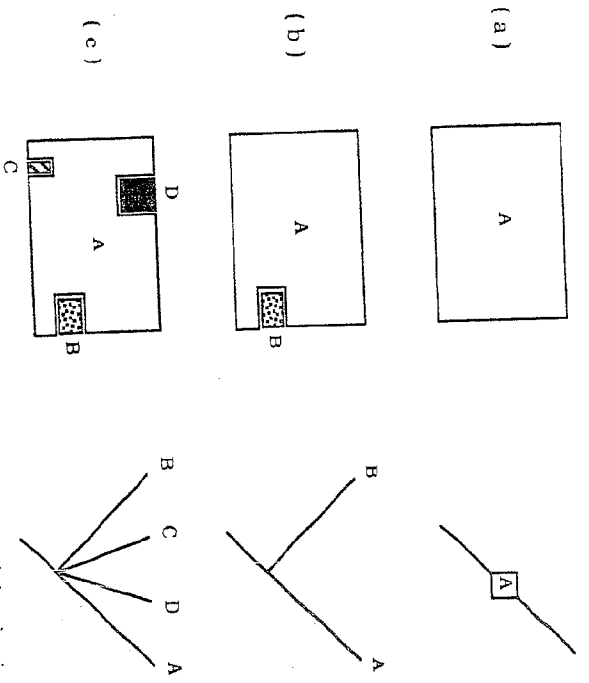
(a)

A

(b)

A

B

(c)

C

D

A

B

B C D A

Fig. 4.8. Allopatric speciation mode II, peripheral isolates speciation via microvicariance. (a) Species A extends throughout a geographical area. (b) Gene flow is severed in a small area, producing species B. (c) Severing of gene flow by a series of microvicariance events results in the budding off of descendant species D and C. The traits present in each species represent a combination of characters that existed prior to the isolation of the population (symplesiomorphies) and evolutionary modifications that occurred subsequent to the isolation (autapomorphies). Since derived traits are not shared between populations under these circumstances, sequences of speciation events will be impossible to determine, and the resultant phylogenetic pattern will be a polytomy.

ment by a descendant bearing novel traits (Mayr 1954). This combination of peripheral isolates allopatric speciation, extinction of the ancestor, and range expansion of the descendant has come to be known as "punctuated equilibrium" (Eldredge and Gould 1972; see also Futuyma 1986) because it looks like rapid speciation pulses are occurring sporadically throughout evolutionary time. In fact, it is the disappearance of the ancestor, not the appearance of the descendant, that is sudden and unexpected.

Allopatric speciation mode III

Some species exist as several disjunct populations without appreciable gene flow among them. Under these circumstances, species cohesion is provided only by the constraining influences of developmental homeostasis (Eld-

redge and Gould 1972; Gould and Eldredge 1977), as evidenced by the persistence of ancestral traits in the populations. Depending upon the strength of these constraints, the species may remain in a state of relative evolutionary stasis for long periods of time. Speciation occurs whenever a deme becomes fixed for a novel phenotype; therefore, phylogenetic trees will be composed of one branch for each ancestral deme that speciates, plus a branch for the collection of unmodified ancestral demes (fig. 4.9).

Stasipatric speciation (White 1978; see also Key 1968; Patton and Sherwood 1983; Thompson and Sites 1986) is a special case of allopatric speciation mode III that invokes a specific genetic mechanism to explain population differentiation. More particularly, population differentiation is hypothesized to occur via chromosomal mutations, coupled with genetic drift or meiotic drive to fix the mutation in the population. Although Futuyma and
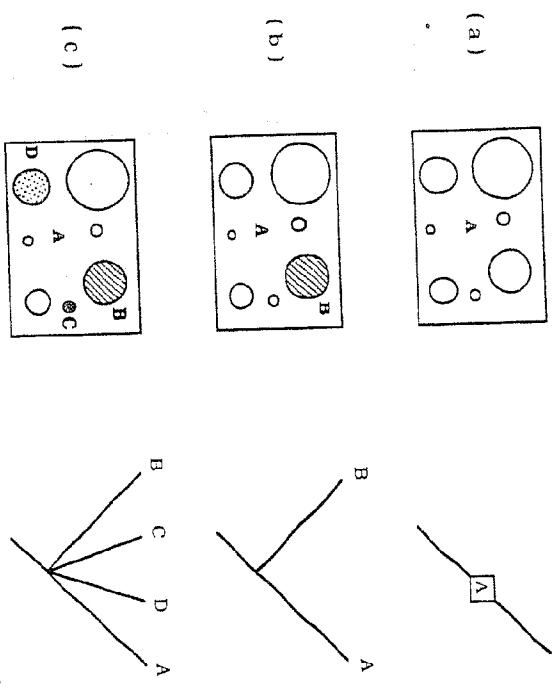
(a)

A

(b)

A B

(c)

A B C D

B C D A

Fig. 4.9. Allopatric speciation mode III. (a) Species A extends throughout a geographical area and comprises several populations. Gene flow among the populations is either insignificant or absent. (b) Evolutionary change in one of the populations at any position in the species range, due to chance (genetic drift) or selection, produces species B. (c) Evolutionary change in two of the populations, due to chance (genetic drift) or selection, produces species D and C. The traits present in each species represent a combination of symplesiomorphies and autapomorphies. Since derived traits are not shared between populations under these circumstances, sequences of speciation events will be impossible to determine, and the resultant phylogenetic pattern will be a polytomy.

Mayer (1980) have questioned the reality of this model, based on population genetical arguments, groups that are suspected of having been produced by stasipatric speciation have not yet been investigated phylogenetically.

Aside from the recognition that the ancestral species is a collection of allopatric demes, there are no biogeographical correlates for this model, because speciation occurs within demes that are already disjunct. If the ancestral species is geographically widespread, the distance between disjunct populations, combined with their phenotypic similarity, is guaranteed to provide an inordinate number of sleepless nights for systematists. For example, despite having no demonstrable qualitative or quantitative phenotypic differences, two species of tropical plants, *Acacia heterophylla* in the Mascarene Islands and *A. koa* in the Hawaiian Islands, have been assigned separate species status on the basis of their vast geographical separation (see Geesink and Kornet 1989 for a discussion of this and other examples). Although some sexually reproducing species may show this type of spatially disjunct population structure, this is primarily a speciation model for asexual organisms. Given the number of asexual species on this planet, it is unfortunate that studies based on allopatric speciation mode III are so scarce.

Parapatric and Alloparapatric Speciation

Parapatric speciation (see Endler 1977; Lande 1982; Barton and Charlesworth 1984) occurs when two populations of an ancestral species differentiate into descendant species despite the maintenance of some gene flow and geographical overlap during the process (fig. 4.10). Stochastic events (e.g., drift) and/or adaptive responses to local selection pressures initiate the differentiation, which is then promoted by low vagility among members of the populations (decreasing gene flow even when sympatric) and/or a decrease in heterozygote/hybrid fitness leading to positive assortative mating.

A related mode, alloparapatric speciation (Mayr 1942; Dobzhansky 1951; Key 1968; Endler 1977), occurs when allopatric populations of an ancestral species begin to differentiate during the period of allopatry, become sympatric
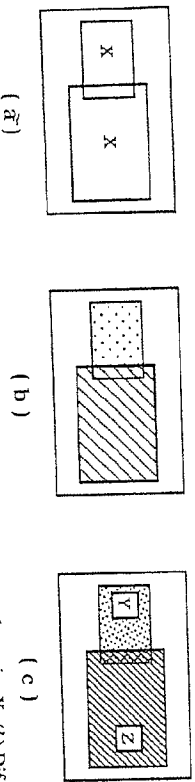
Fig. 4.10. Parapatric speciation. (*a*) Overlap of two populations of ancestral species X. (*b*) Differentiation of populations begins while they are still in contact. (*c*) Speciation of Y and Z is completed despite maintenance of the contact area.
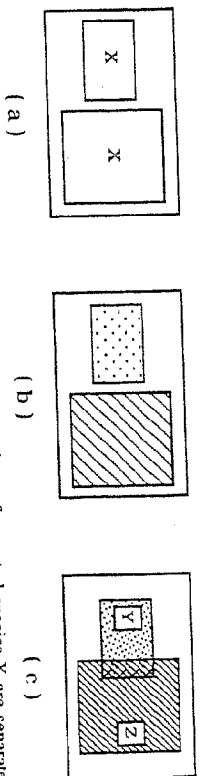
(*a*) (*b*) (*c*)

(a) (b) (c)

Fig. 4.11. Alloparapatric speciation. (*a*) Two populations of ancestral species X are separated geographically. (*b*) Differentiation of populations begins while they are allopatric. (*c*) Speciation of Y and Z is completed when contact is established between the diverging populations.

over a limited area, and complete their divergence because of interactions between the differentiated populations in the zone of sympatry that reinforce the differentiation (fig. 4.11).

These two speciation modes differ primarily in two ways. First, in parapatric speciation the zone of sympatry between two sister species is a primary zone of contact (i.e., the species have always been in contact at that point), whereas in alloparapatric speciation the zone of sympatry is an area of secondary contact. Second, in the parapatric model, population differentiation begins *in spite of* any interactions between populations, while in the alloparapatric model, differentiation begins in isolation. Once contact is established, both models postulate that speciation is completed *because of* the interactions among the differentiating populations in the areas of overlap. These models are difficult to study because, with the exception of the zone of sympatry, their phylogenetic and biogeographic predictions do not differ from those for allopatric speciation.

Endler (1977) presented a detailed defense of parapatric speciation in his extensive treatise on the microevolutionary aspects of geographical and clinal variation. He suggested that members of (1) the anuran *Rana pipiens* group, (2) the mosquito-fish genus *Gambusia*, (3) the fruit-fly genus *Drosophila*, (4) the plant genus *Gilia*, (5) the frogs *Hyla ewingi* and *H. verreauxi*, and (6) the frogs *Pseudophryne dendyi*, *P. bibroni*, and *P. semimarmorata* might all be examples of parapatric speciation. In the case of *H. ewingi* and *H. verreauxi*, hybrids from the zone of sympatry showed depressed fitness relative to hybrids from parents taken from allopatric portions of the species population. This satisfies one of the conditions of both parapatric speciation models; however, since Endler did not present evidence of the phylogenetic relationships of the groups under investigation, we are not certain that any of the species pairs are sister species. There are also inherent problems in attempting to discern primary from secondary contact zones. For example, Woodruff (1972) suggested that the three species of *Pseudophryne* frogs originated allopatrically and became secondarily parapatric. In this case it is difficult to ascertain whether the parapatric contact had anything to do with the comple-
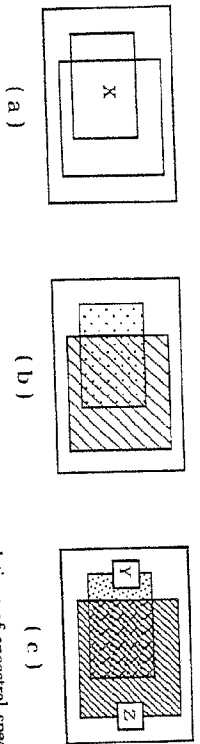
Fig. 4.12. Sympatric speciation. (a) Extensive overlap of two populations of ancestral species X. (b) Differentiation of populations begins while they are still in contact. (c) Speciation of Y and Z is completed despite maintenance of the contact area.

tion of speciation. If it did, this favors an interpretation of alloparapatric, rather than parapatric, speciation.

Sympatric Speciation

Sympatric speciation (Maynard Smith 1966; Dickinson and Antonovics 1973; Felsenstein 1981; Gittenberger 1988) occurs when one or more new species arise without geographical segregation of populations (fig. 4.12). Unlike the allopatric models, which postulate that gene flow between populations is initially severed by factors extrinsic to the biological system, sympatric speciation requires the involvement of biological processes intrinsic to the system, for example, hybridization, ecological partitioning, the evolution of asexual or parthenogenetic populations, or a change in mate recognition. Additionally, differentiation must occur "within the dispersal area of the offspring of a single deme [the cruising range]" (Mayr 1963:257).

Although this was the mode originally preferred by Darwin (1859), support for sympatric speciation wavered when population geneticists demonstrated that the effects of gene flow among populations would tend to swamp out or homogenize any novel traits arising within a population. If gene flow were restricted or interrupted, as in the allopatric or parapatric speciation models, the novel trait would have a better chance of becoming fixed within a deme, and the whole process would operate much more smoothly. The work of the population geneticists was coupled with the earlier recognition that most "related" species (this usually meant members of the same genus) exhibited allopatric distributions (e.g., Mayr 1942; Wallace 1955), and this combination provided a strong foundation for the hypothesis that most speciation was allopatric. However, in recent years there has been a revival of interest in the possibility of sympatric speciation modes, as researchers have intensified investigations of mechanisms of phenotypic plasticity, disruptive selection, and chromosomal divergence (see, e.g., discussion and references in West-Eberhard 1989), papers in Otte and Endler 1989). One of the most eloquent supporters of this and other nonallopatric models has been Guy Bush (e.g.,

1975a,b, 1982; Diehl and Bush 1989), who suggested that it is unnecessary to postulate a link between speciation and adaptation in allopatric speciation models, while in nonallopatric models (Bush 1982),

speciation is the direct outcome of adaptation, and divergence occurs as a product of selection for habitat preference, competition, and selection to enhance reproductive isolation.

Sympatric speciation requires observations of the sympatric distribution of sister species that differ in some special ecological or genetic characteristics that could, in themselves, produce independent species. Phylogenetic trees reflecting incidents of sympatric speciation may be either dichotomous or polytomous, depending on how many species have been produced sympatrically from the same ancestor, and depending on whether or not the ancestor persists. Biogeographically, this mode requires that sister species be broadly sympatric today and at the time of speciation. Observing that the two species are sympatric today is not sufficient evidence of either sympatry in the past or a sister-group relationship.

Sympatric speciation by ecological segregation

The most controversial form of sympatric speciation proposes that evolutionary divergence has been driven solely by ecological segregation, usually studied in terms of host (habitat) switching (see, e.g., Diehl and Bush 1989; Grant and Grant 1989; Tauber and Tauber 1989). This mode of speciation is problematical because it is at once theoretically attractive and perplexingly paradoxical. The attraction lies in the models' invocation of adaptive processes to drive speciation. The paradox is twofold. First, once colonization of a new type of resource (habitat or host) within the ancestral-species range has occurred, the probability that the new resource will exert strong directional selection pressure on the colonizing population should be higher for species displaying pronounced habitat specificity. These species are more tightly coupled to their resource bases and thus should be more sensitive evolutionarily to changes in that component of their environment than their generalist counterparts. However, the likelihood of a habitat change occurring in the first place is decreased for species that respond to only a small number of cues. Therefore, the species least likely to colonize new habitats (specialists) are the ones most likely to speciate as a result of any such switch, while the species most likely to colonize new habitats (generalists) are the least likely to speciate as a result of the interaction.

The second dilemma arises because, when habitat switching means host switching, the switches can occur only while the hosts (and thus, the initial associate population) are sympatrically distributed. However, speciation may

speciation) or after the hosts have been separated (*allopatric speciation*). When sister species are associated with allopatric hosts, it is often impossible to determine whether the actual speciation event producing those species occurred before or after the hosts's isolation. Just as the observation of current sympatric overlap between two "related" species is a weak test of sympatric speciation without the relevant phylogenetic information (i.e., Are the taxa sister species?), knowledge that two sister species show evidence of host switching in their evolution is not sufficient to invoke sympatric speciation in the absence of current sympatric overlap between them. Of course, it is always possible to invoke the effects of "sympatric speciation in the past," followed by vicariance, to explain the observed disjunct distribution, but this is a weak hypothesis at best. Overall then, the strongest evidence for speciation via host switching is provided by situations in which a sympatric overlap of associate sister species can be demonstrated (fig. 4.13).

There are a variety of population genetical models explaining the origins of reproductive isolation under a host-switching regime (see, e.g., Maynard Smith 1966; Dickinson and Antonovics 1973; Caisse and Antonovics 1978; Wood and Gutman 1983; Sturgeon and Mitton 1986; Thompson 1988). Futuyma and Mayer (1980) explored putative examples of sympatric speciation by host switching within this genetical framework and concluded that these examples were not particularly convincing. They focussed their attention on two paradigm cases involving predatory lacewings of the genus *Chrysopa* (see Tauber and Tauber 1977a,b) and true fruit flies of the genus *Rhagoletis* (see also Bush 1966, 1969, 1974, 1975a,b; Berlocher and Bush 1982). In the lacewing example, there are two species, *Chrysopa downesi* and *C. carnea*, the first a specialist feeder on conifers and the second a generalist feeder in meadows. There is no phylogenetic evidence that they are sister species, or biogeographic evidence that they are primarily sympatric. Hence, the traits by which these species can be distinguished and by which they are ecologically segregated today may, or may not, have evolved in a single ancestral species under conditions of sympatry. The fruit-fly example is somewhat more complex because it is purportedly an example of sympatric speciation in progress. The debate centers on the association of the North American *Rhagoletis pomonella* "host race" complex with hawthorn, apple, and cherry hosts. Futuyma and Mayer amalgamated the results from a variety of studies and concluded that there was no evidence that the putative host races were existing in either behaviorally or genetically differentiated forms. This, however, does not detract from the exciting discovery that the researchers have potentially tapped into an actual speciation event rather than, as is generally the case, being restricted to documenting the historical traces of the process. Determining that the "races" are not genetically distinct at this point in time does not rule out a role of sympatric speciation. There is really nothing to do at the moment but sit back and watch the process.
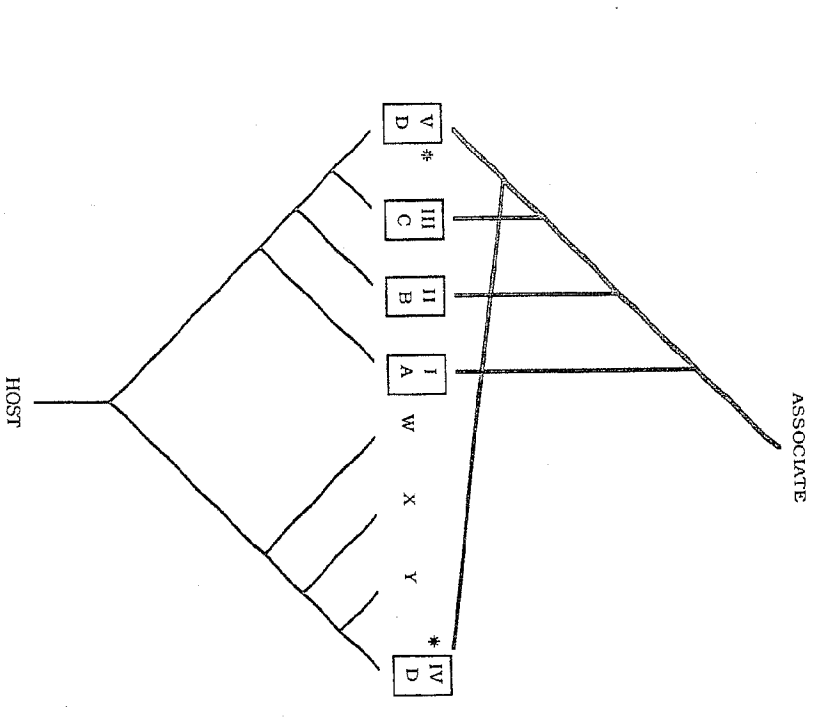
Fig. 4.13. The "best case" scenario for postulating the existence of sympatric speciation via host switching. The *letters* on the host tree refer to the areas where the hosts are found; thus the two different host species marked with *asterisks* inhabit the same area (area D). When the phylogeny for the associates is compared with the phylogeny for the hosts, we find that all the branches match except the relationship between associate IV and its host. Branches that are "out of synch" represent cases of cospeciation between the associate and its host. Branches that match represent cases of cospeciation (this will be explained in detail in chapter 7). In this case, the switch and subsequent speciation occurred in a host that was sympatric with the historical host group. The observation of sister species in sympatric hosts is strong evidence for sympatric speciation.

Sympatric speciation by hybridization

Regardless of the outcome of the preceding studies of ecological segregation, there are other mechanisms of genetic change that can result in sympatric speciation. One of these, speciation by hybridization (see Harrison and Rand 1989; Hewitt 1989; Wake, Yanev, and Frelow 1989), is a phenomenon of particular importance to diversification among plant groups, certain groups
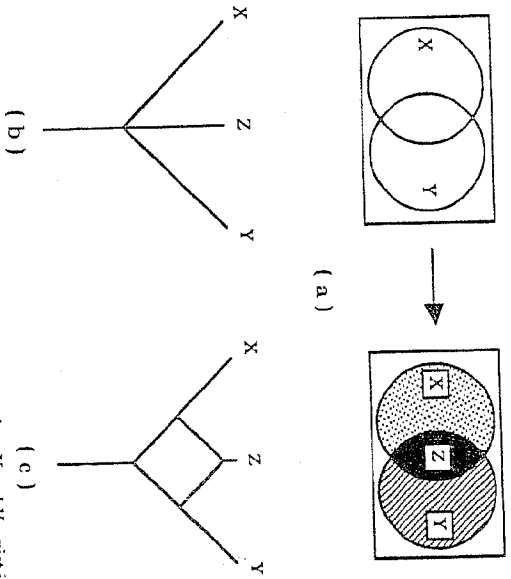
X   Y

(a)

X   Z   Y

X   Z   Y   Y

(b)

X   Z   Y   Y

(c)

Fig. 4.14. Sympatric speciation by hybridization. (*a*) Two species, X and Y, exist in sympatry in a portion of their range. In this area of sympatry, a third species, Z, arises due to hybridization between X and Y. (*b*) Branching pattern expected if X, Y, and Z are not related by hybridization. (*c*) Reticulate branching pattern that arises when Z is a hybrid of species X and Y.

of freshwater fishes, and lizards (fig. 4.14a; Grant 1981). This mode of speciation produces reticulate (fig. 4.14c) rather than hierarchical (fig. 4.14b) patterns of phylogenetic relationships for a group of species, one of which is a hybrid of two others. (See Funk 1985 and Funk and Brooks 1990 for detailed discussion of phylogenetic protocols for detecting species of hybrid origin and depicting their relationships on a phylogenetic tree.)

1) One of the most intriguing aspects of speciation by hybridization is that it may lead to three different classes of phenotypic and ecological outcomes. In the first case the hybrids segregate phenotypically and ecologically with one of the parents and are thus subjected to the same selection regime as that parent. Since the parent is already surviving in the environment, it is likely that the hybrids will survive as well, assuming that necessary resources are not limiting. Mixed stands of such "species groups" have been documented. It is also possible that, under conditions of limited resources, interspecific competition will occur, since new genetic information has been added to the 2) system without enlarging the available resource base. In the second case the hybrids display a mixture of parental attributes, some of which may be intermediate in nature. If such hybrids are capable of living in a wider range of habitats than either parent, they should have a good chance of survival because, although subject to a wider range of selection pressures, their flexibility will reduce the likelihood of competition with each parent. If adaptive

processes in evolution tend to promote specialization, this is an evolutionary mechanism for producing new generalists. Finally, the hybrids could represent a unique phenotypic and ecological system. In this case survival will be more problematical because the new combination must correspond to one allowed by un- or underexploited resource bases in the local environment. However, such hybrids, if they survive, should face no competition from either parent. Each of these three survival pathways open to species of hybrid origin implies different microevolutionary scenarios. Testing these scenarios requires knowledge of parental identity as well as the degree of phenotypic and ecological similarity between parental and hybrid species.

Sympatric speciation by shifts in sexuality

Another plausible mechanism for sympatric speciation is the evolution of genetic changes resulting in the production of asexual lineages from a sexually reproducing ancestral species. Mechanisms that may be involved in such changes include apomixis, parthenogenesis, and ploidy shifts (Felsenstein 1981; Barrett 1989). Support for this class of explanations requires that we find asexual and sexual sister species occurring sympatrically. Wiley and Mayden (1985) discussed three unisexual fish species that have apparently evolved via a combination of hybridization and subsequent genetic alteration: the gynogenetic species *Poecilia formosa*, found in northern Mexico and southern Texas, is thought to be a result of hybridization between *P. latipinna* and either *P. sphenops* or *P. mexicana*; *Menidia clarkhubbsi*, a unisexual species, is postulated to have arisen from hybrid-producing interactions between *M. beryllina* and *M. peninsulae*; and finally there are at least five parthenogenetic "forms" of unclear phylogenetic status within the topminnow genus, *Poeciliopsis*, which are potentially the byproducts of hybridization events (see Vrijenhoek 1989). In none of these cases were the parental species each other's closest relatives. This suggests that, while the production of the asexual hybrid species might well have occurred in sympatry, some degree of geographical dispersal was involved in getting the parental species together in the first place.

Sympatric speciation and sexual selection

The observation that some species possess sexually dimorphic traits that appear to decrease the survivability of their bearers was problematical for the theory of natural selection. Darwin sought a way out of this dilemma by reasoning that such extreme characters must confer some sort of advantage to their bearers, which at least balanced, or at best outweighed, their deleterious effects on survival. He looked for this advantage in the second component of

natural selection—production of offspring—and proposed from this his theory of sexual selection (Darwin 1872:64).

This form of selection depends, not on a struggle for existence in relation to other organic beings or to external conditions, but on a struggle between the individuals of one sex, generally the males, for the possession of the other sex.

Fisher (1930, 1958) examined sexual selection in genetic terms and formulated the implications of this selective regime to speciation (Fisher 1930).

It is, of course, characteristic of unstable states that minimal causes can at such times produce disproportionate effects; in discussing the possibility of the fission of species without geographic isolation, it will therefore be sufficient if we can give a clear idea of the nature of the causes which condition genetic instability.

Sexual selection has been examined from two perspectives, interactions between members of one sex (usually males) to acquire mates (intrasexual selection) and interactions between the sexes to choose mates (intersexual selection). Investigations of the relationship between sexual selection and speciation have generally focussed on the latter form and have followed three pathways. Dobzhansky (1940) emphasized the role of mate discrimination in reinforcing speciation once populations that had diverged in allopatry came back into contact (alloparapatric speciation mode; see reviews in Dobzhansky 1970; Mayr 1970). Muller (1942; see also Paterson 1985) proposed that the appearance of divergent mate-recognition systems could occur and complete the speciation process in allopatry without the need for reinforcement via secondary contact of the diverging populations (allopatric and alloparapatric modes; see discussion in Kaneshiro 1980). Lande (1981, 1982) was the first researcher to develop explicitly genetical models that demonstrated the potentially powerful nature of sexual selection as a mechanism of sympatric speciation (see also West-Eberhard 1983). He concluded (1982),

Incipient speciation in a population occupying a continuous range is modeled as the joint evolution of geographic variation in female mating preferences and a quantitative secondary sexual character of males. Even in the absence of genetic instability, the evolution of female mating preferences can greatly amplify large-scale geographic variation in male secondary sexual characters and produce widespread sexual isolation with no geographical discontinuity.

The proposal that intersexual selection is a strong driving force in sympatric speciation is a promising new line of research because the theoretical framework is well developed and a plethora of sexual selection studies exist for individual species (see articles and references in Bateson 1983; Thornhill

and Alcock 1983; Bradbury and Andersson 1987). What is needed now is an examination of these data within a phylogenetic context. In order to do this, we require three pieces of information: a phylogeny for the group of interest, biogeographical data, and experimental evidence for intersexual selection. Remember, the comparisons of changes in female mating preference and changes in the male character must be made between sympatric sister species.

A Comment on Sympatric Speciation

Although it appears that sympatric speciation often requires unusual genetic and/or ecological circumstances (Futuyma and Mayer 1980), there is evidence that those circumstances occur regularly in some restricted groups of plants and animals. In chapters 7 and 8 we will discuss a number of examples in which host switching is associated with speciation. To some, this might be seen as de facto evidence of sympatric speciation, in which case approximately half of the host-parasite and phytophagous insect-plant associations for which there is phylogenetic information are the result of this speciation mode. However, in the majority of cases we do not know if the host switch had anything to do with the speciation event, because we are not certain that the colonization events represented the invasion of a new resource base or the expansion of an old one. In many cases there is biogeographic evidence suggesting that passive allopatric speciation accounts for the speciation events and that host switching is not coupled with speciation. In any event, we think it is apropos to close this section with the statement by Bush (1982) that

the future holds many surprises. . . . I suspect that macromutations and rapid nonallopatric mechanisms of speciation will prove to be far more important in many groups of organisms than previously imagined.

Some Sample Studies

Freshwater Fishes of the Mobile basin and the Interior Highlands of southeastern North America

The freshwater stream fishes of southeastern North America represent an excellent model system for studying speciation in a historical ecological framework. Detailed distributional data are available, and explicit phylogenetic hypotheses have been published and are being reinforced or upgraded on a regular basis. Although there is a plethora of examples, we will discuss only a few of these from each region (for a more extensive discussion see Wiley and Mayden 1985 and examples in Mayden 1988, in press; also example in chapter 7).

Darters are small, bottom-dwelling percids. Although distributed in fresh-water throughout the Northern Hemisphere, approximately 90% of the species are restricted to locations east of the Rocky Mountains (Moyle and Cech 1982). Killifish are small, brightly colored cyprinodontids that are both geographically and ecologically diverse. They can tolerate a wide variety of habitats, from freshwater streams and desert springs to salt marshes and mangrove swamps. This discussion will focus on speciation patterns within one group of sand darter (*Ammocrypta*; fig. 4.15) and one group of killifish (*Fundulus*; fig. 4.16).

Examination of the disjunct distribution patterns of these fishes reveals that vicariant speciation (allopatric speciation mode I) has been the predominant mode in these groups. Within the sand darters (fig. 4.15), geographic division of ancestor x into two populations produced *Ammocrypta clara* and its sister species, ancestor y, with some apparent extinction of *A. clara*, leaving two disjunct populations of the species today. In addition, geographic division of ancestor y into populations east and west of the Mobile drainage system produced *A. beani* and *A. bifascia*.

The killifish pattern (fig. 4.16) is slightly more complicated. Production of sister species p and q is problematical because, since they no longer exist, we can obtain only an estimate of their distribution by combining the ranges of their descendants. This method assumes that there has not been any widespread extinction or dispersal in the area, assumptions that are tenuous at best for these fishes. The results of such an analysis indicate that the ranges of p and q potentially overlapped near the mouth of the Mobile drainage area. Although fossil evidence of overlap would be illuminating, it would not resolve this quandary because, since p and q are extinct, we can no longer test for the presence or absence of interpopulation interactions in the parapatric area. So, for the present, this speciation event must be tentatively assigned an indeterminate status (parapatric mode?). Division of ancestor p producing *Fundulus blairae* and *F. dispar*, division of ancestor q producing *F. lineolatus* and ι, and division of ancestor r into populations east and west of the Mobile drainage system, producing *F. nottii* and *F. escambia*, all represent apparent examples of vicariant speciation (allopatric speciation mode I). Although suggestive of sympatric speciation, the observation that *F. nottii* is located almost entirely within the range of *F. blairae* is not important to a study of speciation modes, because the two fishes are not sister species (see also the slight overlap between *F. escambia* and *F. lineolatus*). It is important to remember that there is a fundamental difference between models of speciation and mechanisms of speciation. Speciation models describe different original conditions, which set the stage for the subsequent divergence of ancestral populations. This divergence, in turn, may be accomplished by a variety of biological processes. For example, it could be envisioned that once ancestor
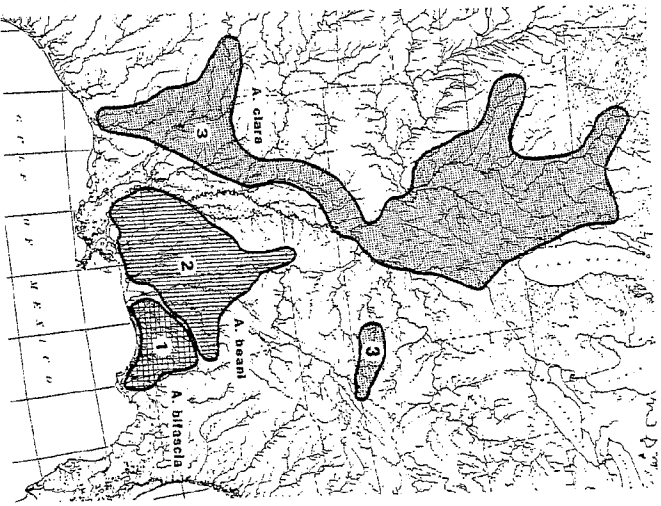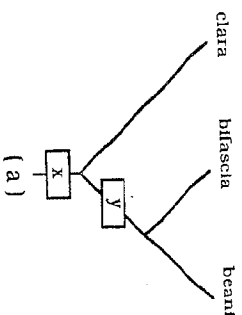
Fig. 4.15. Speciation of sand darters. (a) Phylogenetic tree for sand darters in the *Ammocrypta beani* group. *Names* = species; *letters* = ancestral species. (b) Distribution map for three *Ammocrypta* species. (Modified from Wiley and Mayden 1985.)

r was separated on either side of the Mobile River, interactions between *F. blairae* and the population of ancestor r, isolated on the west side of the basin, were involved in driving the population along the pathway to "specieshood." Nevertheless, these interactions have no effect on the original event that established the potential for the speciation of ancestor r that is, its separation into two disjunct populations.
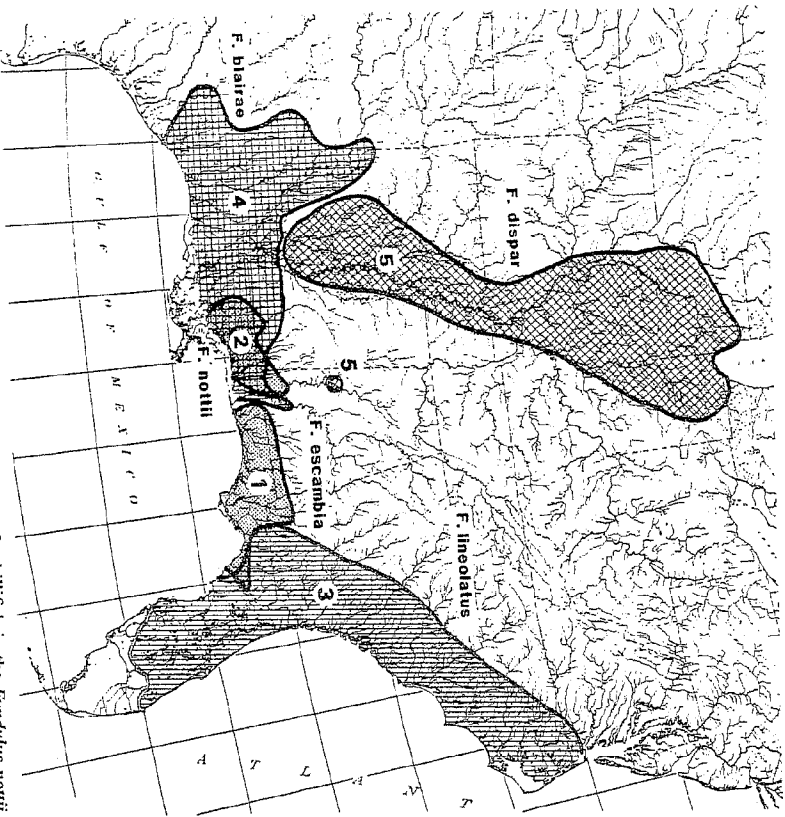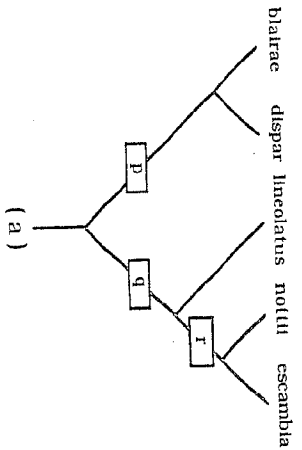
Examples of allopatric speciation mode I are widespread among fishes inhabiting the central areas of the Mississippi drainage from the Ozark Plateaus and Ouachita Highlands in the west to the Interior Low Plateau, Ridge and Valley Province, and Blue Ridge Province in the east. Darters are well represented in this area, as are the small, species-rich, silvery cyprinids aptly referred to as shiners. During the breeding season many shiner species don flamboyant red, orange, and/or yellow breeding liveries, and because of this, they have drawn the attention of many researchers. This discussion will be restricted to speciation patterns within two groups of shiners (*Notropis*; figs. 4.17 and 4.18) and one group of darters (*Etheostoma*; fig. 4.19).

Examination of the distribution patterns of these fishes reveals that, like the situation in the Mobile drainage system, vicariant speciation (allopatric speciation mode I) has been the predominant speciation mode in these groups. The simplest pattern occurs in the *Notropis rubillus* clade (fig. 4.17), where two speciation events associated with geographical vicariance have been coupled with the apparent loss of one species' (*N. rubilus*) central populations.

The second *Notropis* example (fig. 4.18) is equally straightforward. The distributions and phylogenetic relationships support the proposal that the four putative speciation events within this clade have been vicariant, via the geographical divisions of (1) ancestor o, possibly through a vicariance event eliminating the central populations, producing sister species p and q; (2) ancestor p producing *N. pilsbryi* and *N. zonatus*; (3) ancestor q producing *N. cerasinus* and ancestor r; and finally (4) ancestor r producing *N. coccogenis* and *N. zonistius*.

The pattern depicted for the darters (fig. 4.19) is slightly more problematical because the current pattern appears to have resulted from a combination of two and possibly three speciation modes. First, there is the possible asymmetrical division of ancestor u, producing *Etheostoma blennius* and ancestor v, plus the asymmetrical division of v, producing *E. sellare* and ancestor w, both examples of allopatric speciation mode II, either peripheral isolates or microvicariance. Second, there are three putative speciation events that indicate vicariant speciation (allopatric speciation mode I): the division of ancestor w, associated with extinction of central populations, producing ancestors x and y; the division of ancestor x, producing *E. tetrazonum* and *E. euzonum*; and the division of ancestor y, producing *E. variatum* and ancestor z. Finally, there is the potential parapatric speciation involving ancestor z, producing *E. osburni* and *E. kanawhae*. The case for parapatric speciation in this instance would be strengthened if interactions between the two species could be documented in the region of overlap.
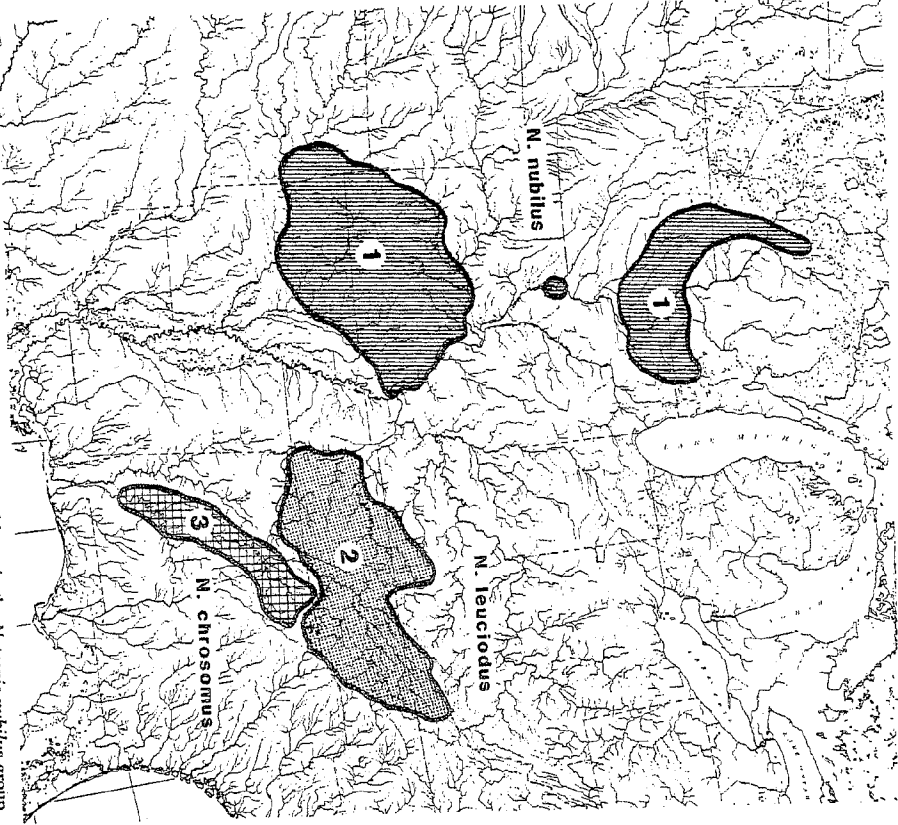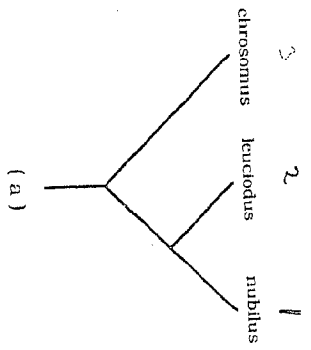

Fig. 4.16. Speciation of topminnows. (*a*) Phylogenetic tree for killifish in the *Fundulus nottii* group. *Names* = species; *letters* = ancestral species. (*b*) Distribution map for five *Fundulus* species. (Modified from Wiley and Mayden 1985.)

(a)

chrosomus 3
leuciodus 2
nubilus 1

Fig. 4.17. Speciation of shiners. (a) Phylogenetic tree for shiners in the *Notropis nubilus* group. *Names* = species. (b) Distribution map for three *Notropis* species. (Modified from Wiley and Mayden 1985.)
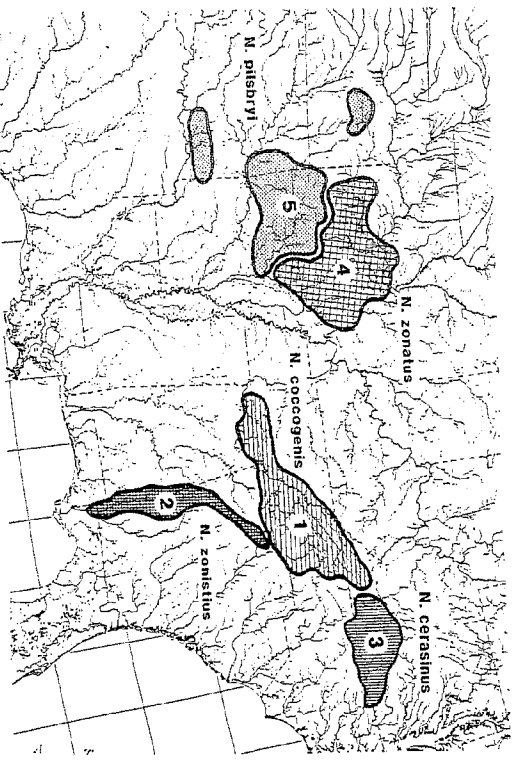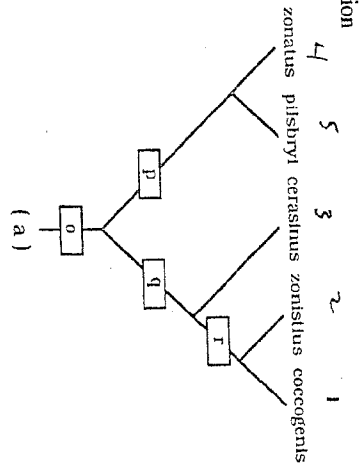

(a)

zonatus 4
pilsbryi 5
cerasinus 3
zonistius 2
coccogenis 1

o p q r

Fig. 4.18. Speciation of more shiners. (a) Phylogenetic tree for shiners in the *Notropis zonatus coccogenis* group. *Names* = species; *letters* = ancestral species. (b) Distribution map for five *Notropis* species. (Modified from Wiley and Mayden, 1985.)

South American horned frogs

One of the most diverse and widespread of all frog groups is the family Leptodactylidae. Among South American leptodactylids, the subfamily Ceratophryinae comprises two genera, *Lepidobatrachus*, with three species, and *Ceratophrys*, with six species. *Ceratophrys* species are boldly colored, voracious predators that are well known to aquarists and tropical hobbyists as "horned frogs." They dwell in a variety of different habitats, ranging from neotropical rainforests (*C. aurita* and *C. cornuta*) through grasslands (*C. ornata*) to semixeric (*C. calcarata*) and xeric regions (*C. stolzmanni* and *C. cranwelli*). Lynch (1982) presented a phylogenetic analysis of the six species
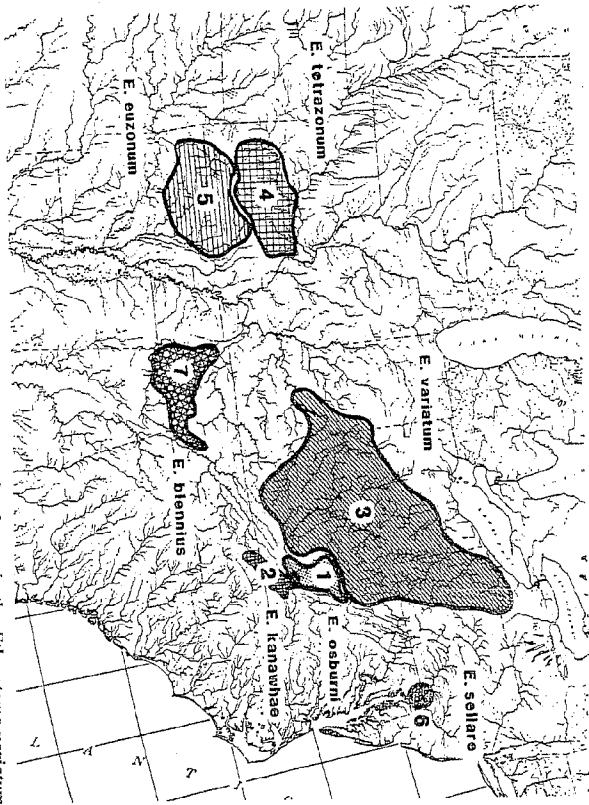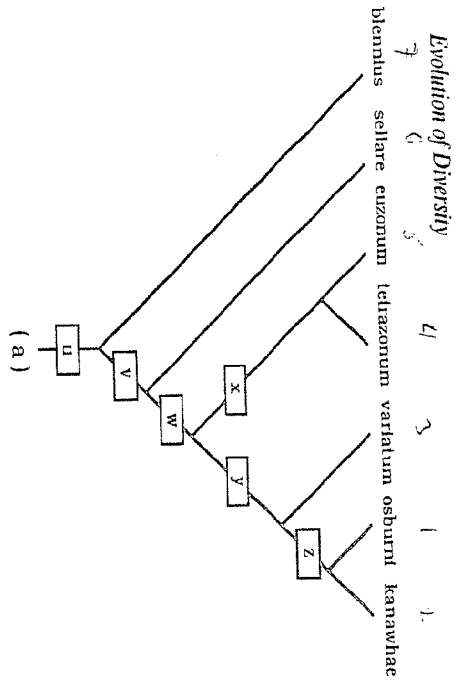
blennius sellare euzonum tetrazonum variatum osburni kanawhae

(a)

u v w x y z

Fig. 4.19. Speciation of darters. (a) Phylogenetic tree for darters in the Etheostoma variatum group. Names = species; letters = ancestral species. (b) Distribution map for seven Etheostoma species. (Modified from Wiley and Mayden 1985.)

of Ceratophrys, using the monophyletic sister group of Ceratophrys, the genus Lepidobatrachus, as the outgroup. Lynch's resulting phylogenetic tree (fig. 4.20a) has a consistency index of 87.5%.

The geographical distribution of the six species is shown in figure 4.20. The genus comprises two clades of three species each, one occurring from just north of the central Amazon northwards (C. stolzmanni, C. calcarata,

E. tetrazonum
E. euzonum
E. variatum
E. blennius
E. kanawhae
E. osburni
E. sellare

LEPIDOBATRACHUS — | CERATOPHRYS —

asper laevis llanensis cranwelli ornata aurita stolz. calcarata cornuta

(a)

6-7
1-2
3-5
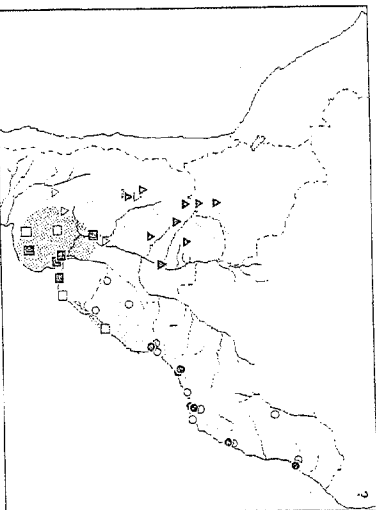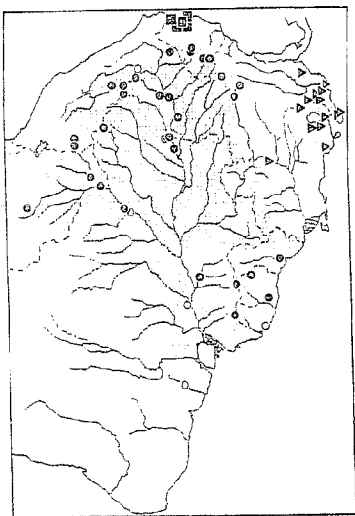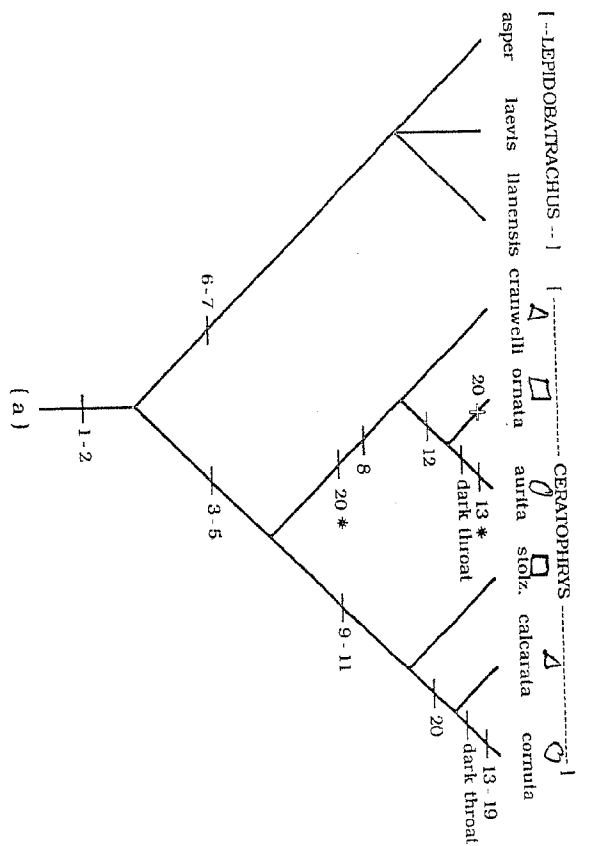20*
20*
8
12
13*   dark throat
20
13-19   dark throat
9-11

Fig. 4.20. Speciation of frogs. (a) Phylogenetic tree for the frog genus Ceratophrys, based on eighteen adult morphological characters (1-6, 8-11, 13-20), one larval morphological character (7), and one karyotypic character (12). Names in lowercase letters = species; stolz. = C. stolzmanni. # = homoplasious characters. Figures b and c are distribution maps for these frogs. Continuous distributions are estimated using stippling. Black symbols = specimens examined; white symbols = specimens in literature and/or museum records. (b) Frogs in the subgenus Stombus. Triangles = C. calcarata; circles = C. cornuta; squares = C. stolzmanni. (c) Frogs in the subgenus Ceratophrys. Triangles = C. cranwelli; circles = C. ornata.? ria; squares = C. ornata; cranwelli; circles = C. ornata.? = an unidentified taxon. (From Lynch 1982.)

C. cornuta: fig. 4.20b) and the other associated with the Paraná River system and coastal areas of southeastern Brazil, Uruguay, and Argentina (*C. cranwelli*, *C. ornata*, *C. aurita*; fig. 4.20c). The three species in the "northern" clade are all allopatric. At first glance, their distributional pattern conforms to a classical peripheral isolates scenario of a widespread central species, *C. cornuta* (black circles), with two smaller species located on the periphery of its range. However, Lynch's analysis uncovered the one phylogenetic pattern that specifically refutes this hypothesis of allopatric speciation mode II. The large central species cannot be considered ancestral because *C. cornuta* is not the sister group of the other two members of the clade, conflicting with the phylogenetic pattern predicted if speciation were due to a repeated cycle of sequential dispersal, isolation, and speciation (fig. 4.7). Nor does *C. cornuta* occur in a polytomy with *C. stolzmanni* and *C. calcarata*, conflicting with the phylogenetic pattern predicted if speciation were due to random settlements of individuals around the margins of the ancestral species' range (fig. 4.6), or to a series of microvicariance events (fig. 4.8). In addition, it is *C. cornuta*, and not the peripheral species, that is the most divergent member of the clade (i.e., it exhibits the largest number of autapomorphies). This pattern, however, does support the hypothesis that evolutionary diversification in this clade has been associated with two vicariance events (allopatric speciation mode I: fig. 4.5). The sundering of the first ancestral species resulted in the appearance of *C. stolzmanni* and the ancestor of the *C. calcarata* + *C. cornuta* clade, while the second vicariance event fragmented that ancestor, resulting in the emergence of *C. calcarata* and *C. cornuta*.

The situation is complex for the species composing the "southern" clade. The ranges of these species are relatively equal in size and overlap in two areas. Although *C. ornata* and *C. cranwelli* are parapatric, they are not sister species, so their zone of contact might initially be regarded as unimportant to speciation studies. However, this interpretation changes somewhat after a more detailed examination of the relationships depicted in figure 4.20a. The sister species of *C. cranwelli* was the ancestor (x in fig. 4.21) of the clade *C. ornata* + *C. aurita*. Both of these descendant species display autapomorphies; therefore, neither of them can immediately be identified as a persistent ancestor. However, the autapomorphy for *C. ornata* is the postulated second-ary loss of character 20 (eyelid tubercles), and there are three equally parsimonious interpretations of the transformation series for this character (fig. 4.21).

Since the transformation shown in figure 4.21a eliminates the only autapomorphy postulated for *C. ornata*, we cannot eliminate the possibility that this species might, in reality, be ancestor x, based upon the information we have to date. If this possibility is realized, then the overlap between *C. ornata* and *C. cranwelli* represents a parapatric speciation event in which both spe-
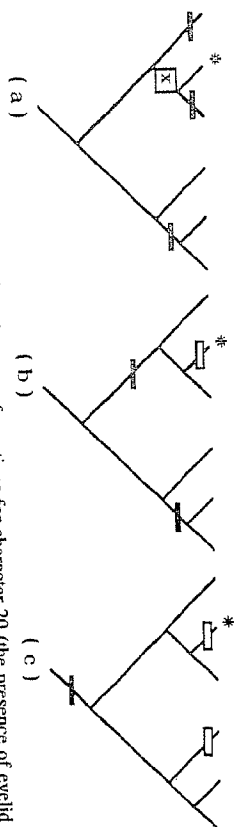
Fig. 4.21. Three equally parsimonious transformations for character 20 (the presence of eyelid tubercles) mapped onto the phylogenetic tree for the frog genus *Ceratophrys*. *White bars* = secondary loss of eyelid tubercles; *black bars* = presence of tubercles. * = the species of interest in this discussion, *C. ornata*; x = the ancestor of *C. ornata* and *C. aurita*.

cies are still extant, and thus within the scope of ongoing research. However, if future investigations uncover a solid autapomorphy for *C. ornata*, then the origins of *C. cranwelli* and the ancestor of the *C. aurita* + *C. ornata* clade are embedded deeper within the phylogenetic tree and are no longer subject to experimental investigation. *C. cranwelli* and *C. ornata* are ecologically (xeric versus grasslands) and karyotypically (both *C. ornata* and *C. aurita* are octoploid, while *C. cranwelli* is diploid) distinct. It is possible, therefore, that the ecological and/or the chromosomal change may have been associated with the parapatric speciation of *C. cranwelli* and ancestor x.

Equally exciting is the discovery that the ranges of the sister species *C. ornata* and *C. aurita* overlap in one locality. Both these species are ecologically isolated (Lynch 1982), *C. ornata* in the grasslands and *C. aurita* in the southern subgenera, there has been a movement, correlated with speciation, towards the rainforests. In the northern clade this change in habitat preference is associated with two vicariance events, and thus is not the driving force behind the initiation of speciation. In the southern clade the change in habitat preference may have been associated with two parapatric speciation events. If ecological segregation has been the motivating force behind the *C. ornata* and *C. aurita* (and *C. cranwelli*-ancestor x) differentiation, then we would expect to find evidence of ecological interactions between overlapping populations of these species. Total ecological and behavioral segregation will not provide support for the parapatric model, nor will it refute it; this type of "absence of data" can only fail to refute the hypothesis, leaving us still partially in the dark.

Overall, then, researchers interested in studying parapatric speciation should focus their attention on the two areas of overlap in the southern clade, between *C. ornata* and *C. cranwelli* and between *C. ornata* and *C. aurita*. Since several critical pieces of information are lacking, involving the status

f *C. ornata* as a species independent from its ancestor (x) and the interactions, if any, between species in the areas of parapatry, the opportunities for future research are intriguing.

South American plants: *Lepechinia* section *Parviflorae*

Lepechinia is a group of small, white-flowered shrubs distributed mainly throughout tropical and subtropical Latin American highlands. Within this range, the section *Parviflorae*, comprising twelve weedy species living at altitudes of 1,700–3,900 meters in Andean shrub/forest zones, shows complicated latitudinal and altitudinal distribution patterns. Hart (1985a) analyzed the phylogenetic relationships in this group, using the sections *Speciosae* and *Salviifoliae* as the outgroups. The resultant tree (fig. 4.22a), based on twenty-four morphological characters, has a consistency index of 95.8%.

Figure 4.22b depicts the geographic distribution of these twelve species. The six oldest species in this section are allopatrically distributed with respect to the appropriate sister species. *Lepechinia graveolens*, the sister species to the rest of the section, occurs in northern Chile and southern Bolivia. *L. bullata* is widely disjunct in Columbia and Venezuela. Finally, *L. heteromorpha* ranges from eastern Ecuador to southern Peru and Bolivia, while *L. radula* is distributed throughout southwestern Ecuador and northern Peru, and *L. conferta* is widespread throughout Columbia and Venezuela. Although *L. bullata* and *L. conferta* occur in moist, upper Andean forests at similar altitudes in Columbia and Venezuela, they are not sister species, so their potential geographical overlap is not pertinent to speciation studies. At the moment, the relationships in this portion of the phylogenetic tree are not strongly delineated (Hart 1985a). Further resolution of this problem is required before it will be possible to hypothesize about the type(s) of allopatric speciation mode(s) involved in these speciation events.

The remaining six species, *L. betonicaefolia*, *L. paniculata*, *L. scobina*, *L. dioica*, *L. mutica*, and *L. mollis*, from a clade united by a change in ovarian fertility (character 22; see also chapter 5). In contrast to the widespread distributions of their higher elevation, forest-dwelling relatives (five of the six preceding species in the section and all species in the outgroup), all members of this clade are locally endemic with very small ranges and are found only in lower-elevation, dry habitats (fig. 4.22a). Additionally, they all appear to be more apomorphic than their common ancestors. The distributions, habitat preferences, and hypothesized patterns of phylogenetic relationships among these six species can be explained by repeated incidents of peripheral isolates allopatric speciation by means of sequential colonization and speciation (fig. 4.7). Since this portion of the phylogenetic tree is not an unresolved poly-
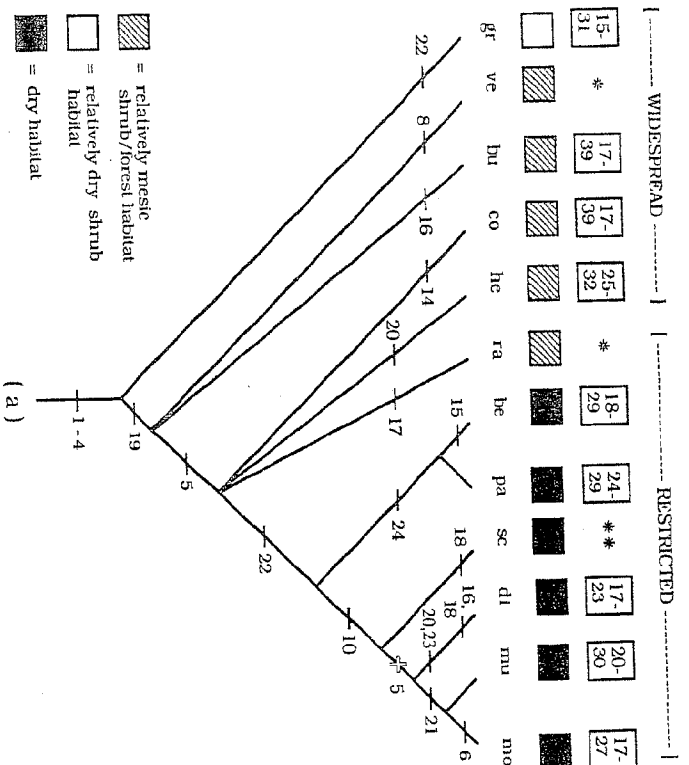

Fig. 4.22. Speciation of plants. (*a*) Phylogenetic relationships within *Lepechinia* section *Parviflorae* based on twenty-four morphological characters. Details of the characters used are provided in Hart 1985a. Habitat preferences are depicted in the bottom line of boxes above the species names. Range of inhabited altitudes, in hundreds of meters, is depicted in top line of boxes above species names, and geographical distribution is listed as either widespread or restricted. *be* = *Lepechinia betonicaefolia*; *bu* = *L. bullata*; *co* = *L. conferta*; *di* = *L. dioica*; *gr* = *L. graveolens*; *he* = *L. heteromorpha*; *mo* = *L. mollis*; *mu* = *L. mutica*; *pa* = *L. paniculata*; *ra* = *L. radula*; *sc* = *L. scobina*; *ve* = *L. vesiculosa*. Asterisks refer to incomplete data: * = "high" altitudes, ** = "low" altitudes. (*b*) Distribution map for twelve species of *Lepechinia* section *Parviflorae*. (From Hart 1985a.)
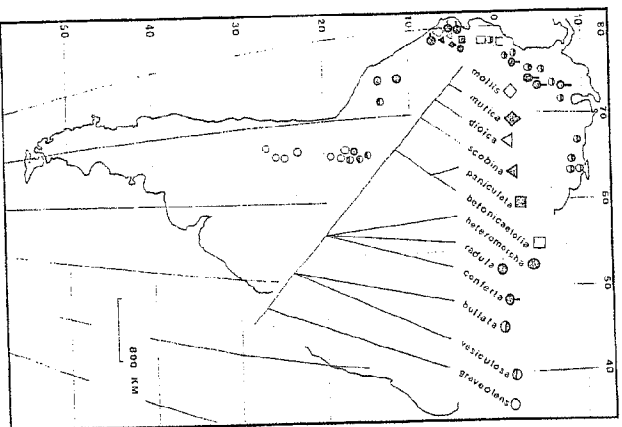
tomy, the microvicariant splitting of one ancestral species into several periph-erally isolated populations (fig. 4.8) seems not to have been the initial con-dition for the evolutionary diversification of these plants. Hart proposed that a series of forest expansions and contractions during the ebb and flow of the Pleistocene glacial periods produced a repeating cycle of ancestral range ex-pansion, range contraction accompanied by peripheral isolation, and specia-tion of the isolate. The members of this clade are located within the Huan-cabamba Deflection region of southern Ecuador and northern Peru. Unlike the usual north-south orientation of the Andean mountain range, this area is characterized by low mountain chains, bisected by deep, dry, east-west-running valleys. These topographical differences, then, set the geographical stage on which the following scenario is hypothesized to have been enacted (Hart 1985a).

Forests in the higher mountains were reduced and the eastern and western slopes separated by the lowering snow line during the cold, wet glacial peri-ods (van der Hammen and Gonzales 1960; van der Hammen 1972; Geel and van der Hammen 1973). The Pacific side of the Andes was colder and wetter, so forests forced down the mountainsides and to the east were more likely to find refuge than their western counterparts (Hastenrath 1971a,b; Simpson 1975). Interestingly, this scenario, based upon a variety of geological data, is supported by the extant distributions of *L. vesiculosa* and *L. heteromorpha* in eastern-slope forest habitats. Within the Huancabamba Deflection, the de-crease in mountain size and the communication between the eastern and west-ern slopes through valleys is postulated to have allowed a westerly expansion of the eastern-slope forests. Following this expansion, the climate gradually shifted towards a drier state, driving the forests back up the mountainsides following the retreating ice fields. This movement, combined with the com-plex geography in the area, left populations isolated within moister refugia. Increasing xeric conditions, small population size, and severed gene flow eventually resulted in a series of peripheral isolates allopatric speciation events.

At the moment, the evolutionary diversification of the *Parviflorae* section of *Lepechinia* appears to have resulted from a combination of vicariance events in the older members of the clade and a sequence of peripheral isola-tions in xeric environments in the more recently derived species. The pro-posal that the older species appeared following large-scale geographical split-ting of the ancestral range is predicated on the assumption that the polytomies shown in the current phylogeny will be resolved when more data are collected and examined phylogenetically. If, in fact, such data *support* the polytomies, a new explanation, based on peripheral isolation, must be adopted. The pro-posal that diversification in the *L. betonicaefolia, L. paniculata, L. scobina, L. dioica, L. mutica,* and *L. mollis* clade has been driven by sequential pe-

ripheral isolation could be examined by comparing this pattern with phylo-genies for other groups in the area. Given this mode of speciation, we would expect to find congruent phylogenetic patterns only in clades containing spe-cies adapted to xeric conditions.

Although Hart's scenario is enticing, it needs to be corroborated by an independent estimate of the age of the clade, which is difficult based on the current information. For example, the Huancabamba Deflection is associated with Miocene uplifting of the Andes that resulted in the reversal of the Ama-zon River so that it no longer flowed into the Pacific Ocean (see also chapter 7). If, in fact, this group is older than the Pleistocene, this does not rule out a role for peripheral isolates allopatric speciation. Investigating this requires that we delve deeper into the biogeography of the area. It is possible, for example, that the Pleistocene glaciation dissected an already established flora, leaving the distributions that we see today and possibly obscuring the evidence for the speciation events that occurred prior to glaciation. This is apparently what happened with respect to the freshwater fish fauna of North America (see Wiley and Mayden 1985; Mayden 1988). Lynch (1986) dis-cussed the origins of the high Andean herpetofauna (amphibians and rep-tiles), concluding that the current phylogenetic data base was inadequate to provide robust explanations, but that the available data supported an expla-nation that the assemblage of the Andean herpetofauna began with the origins of the Andes themselves. Because amphibians and reptiles do not exist in the absence of vegetation, we might well conclude that at least part of the flora of the Andes predates the timing of the scenario proposed by Hart. We do not know yet if *Lepechinia* section *Parviflorae* is part of the old assemblage or a relative newcomer.

The Frequencies of Different Modes of Speciation

To date, very few studies have been published that examine specia-tion using phylogenetic evidence. Development of this depauperate data base is vitally important to the future of speciation research because this is the only known way to assess the relative frequencies of different speciation modes based on evidence rather than on theory. Lynch (1989) has begun such an investigation, with intriguing results. He examined species ranges for members of a number of clades for which phylogenetic trees and extensive distributional data were available, estimating ancestral ranges by the sum of all descendants' ranges. Based on an analysis of sixty-six documented cases of vertebrate speciation, he suggested that 71% of the speciation events were due to vicariance (allopatric speciation mode I), 15% of the cases resulted from a combination of the three forms of peripheral isolates allopatric specia-tion (allopatric speciation mode II), and 6% of the evolutionary divergence

ble 4.1 Frequencies of speciation modes within seven different clades.

	N	Allopatric		Sympatric	Unknown[a]
		I	II		
ogs					
Rana	22	17	1	1	3
Ceratophrys	6	5	1	0	0
Eleutherodactylus	8	5	1	1	1
shes					
Fundulus	4	4	0	0	0
Heterandria	8	5	3	0	0
Xiphophorus	13	7	4	1	1
irds					
Poephila	5	4	0	1	0
requencies		71.2%	15.1%	6.1%	7.6%

[a] Unknown cases represent potential sympatric events buried deep within the phylogenetic tree. The species in question are now extinct (in the sense that ancestral species "go extinct" when hey speciate), making it difficult to obtain distribution patterns and measurements of interpopulation interactions. Inclusion of these cases in the sympatric category boosts its frequency to 3.7%.

ulfilled the requirements of sympatric speciation (table 4.1). In the other 8% of the cases, Lynch discovered dichotomies buried deep within the phylogenetic trees that explained significant geographical overlap between more highly derived sister groups. Because of the age of these speciation events, his could be explained either as sympatric speciation, because of the putative widely sympatric distributions of the ancestral sister species, or as allopatric speciation followed by dispersal. If these cases represent instances of sympatric speciation, it would increase the possible frequency estimate for sympatric speciation to 14%.

Lynch's study and other examples we have discussed in this chapter (see examples in chapters 7 and 8; also Weitzmann and Fink 1983; Weitzmann and Fink 1985, using the species of *Paracheirodon* [neon tetras] and some of the Xenurobryconine fishes in South America) support the major contention of evolutionary theorists, such as Mayr (1963) and Futuyma and Mayer (1980), that sympatric speciation does not seem to occur very often. However, these studies do not support the traditional perspective that peripheral isolates allopatric speciation has been the major speciation mode on this planet; rather, it supports the view presented by Barton and Charlesworth (1984) that peripheral isolates allopatric speciation is not likely on theoretical grounds. In fact, it would seem to be as rare as sympatric speciation. Contrary to many early theoretical predictions, the predominant mode appears to be vicariant speciation, in which the roles of adaptation and speciation need

not be coupled (see also Butlin 1987; Futuyma 1989). We will examine the implications of these findings in subsequent chapters.

Documenting the Influence of Microevolutionary Processes

Population biologists have documented the existence of numerous processes that might be involved in speciation, once particular sets of initial conditions have been established. Mechanisms resulting in the divergence of ecological characters correlated with speciation events are of particular importance for nonallopatric speciation models, because these models invoke a close tie between adaptation and speciation. We have already discussed some ecological factors that might be important in sympatric speciation, and we will expand upon the relationship between adaptation and evolution more fully in chapter 5. Another important aspect of microevolutionary theories about speciation concerns the role of reproductive isolation in initiating and completing the process.

Mayr (1963) emphasized the importance of postzygotic isolating mechanisms (i.e., reduction in hybrid fitness) as strong selection pressures promoting the spread of prezygotic isolating mechanisms (i.e., mate recognition) through the speciating populations. According to this scenario, the loss of fitness associated with the production of genetically and developmentally unstable hybrids precedes the appearance of behavioral isolating mechanisms; so, while reproductive isolation over a contact zone does not initiate speciation, it does complete the process. Paterson (1985) stood the problem on its head and argued that the evolution of mate recognition, driven by an individual mating advantage, precedes genetic and developmental changes; thus, such changes can be viewed as by-products rather than causes of speciation. Here, the origin of isolating mechanisms is associated with the initiation of speciation. Investigations reporting the existence of premating (e.g., studies by Ohta 1978; McLain and Rain 1986; Stratton and Uetz 1986; Moore 1987; Butlin 1989) and postmating (e.g., studies by Vigneault and Zouros 1986; Zouros 1986; Christie and MacNair 1987; Coyne and Orr 1989) isolating mechanisms appear regularly in the evolutionary biology literature, attesting to the importance of the concepts. Rarely, however, are those mechanisms examined within a phylogenetic framework.

In order for isolating mechanisms to be causally involved in the speciation event, both of these scenarios require an area of contact between two diverging populations (nonallopatric speciation modes), either following secondary contact between incompletely speciated populations (alloparapatric mode), or through parapatric or sympatric speciation. Neither of these scenarios is causally involved in allopatric speciation because in those modes **the disjunct populations speciate independently of one another.** Therefore, in order to

investigate the temporal sequence of prezygotic versus postzygotic isolating mechanisms within a group of organisms, we must first differentiate between the contributions of allopatric and nonallopatric speciation events to the evolutionary diversification of the clade.

Once incidents of nonallopatric speciation have been identified, phylogenetic analysis can be used to determine whether the evolution of mate recognition systems precedes or follows the evolution of postzygotic isolating mechanisms. Investigating this requires an explicit phylogenetic tree based on characters other than those postulated to be part of the interaction between the origins of isolating mechanisms and the speciation event: Neither type of isolating mechanism is associated with speciation (fig. 4.23a); both mechanisms are associated with speciation (fig. 4.23b). This configuration does not support or refute either of the two scenarios because phylogenetic analysis cannot
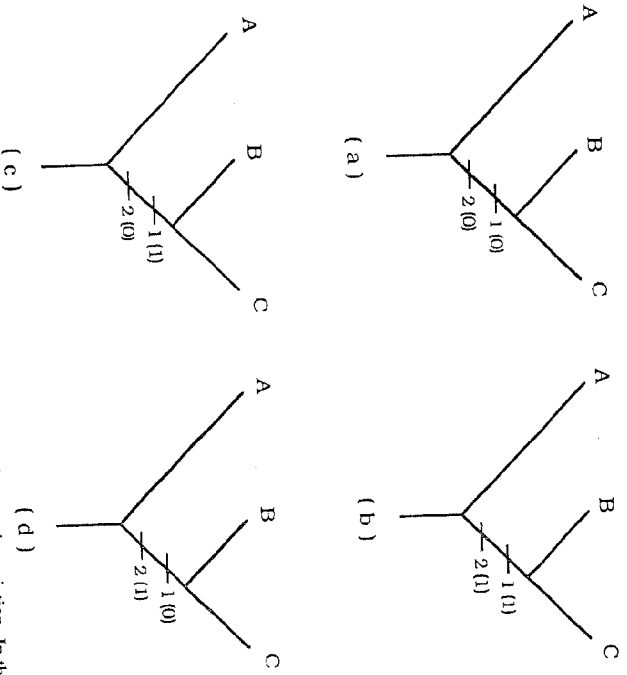

Fig. 4.23. Association between two types of isolating mechanisms and speciation. In this hypothetical example, distributional and experimental data have verified that the production of taxa B and C involved sympatric speciation. Character states: $1(0)$ = postzygotic isolating mechanisms absent; $1(1)$ = postzygotic isolating mechanisms present; $2(0)$ = prezygotic isolating mechanisms absent; $2(1)$ = prezygotic isolating mechanisms present. (a) Neither mechanism present. (b) Both mechanisms absent. (c) Postzygotic isolating mechanisms associated with speciation. (d) Prezygotic isolating mechanism associated with speciation.

untangle the sequence of appearance of autapomorphic characters; postzygotic fitness depression is associated with speciation (i.e., it precedes the appearance of prezygotic isolating mechanisms: fig. 4.23c). This pattern supports Mayr's hypothesis; prezygotic isolating mechanisms are associated with speciation (i.e., it precedes the appearance of postzygotic fitness depression: fig. 4.23d). This pattern supports Paterson's hypothesis.

Macroevolutionary Trends in Diversity: Species Number

As we discussed in chapters 1 and 3, the term "diversity" has been used in a variety of ways by biologists. One major usage is associated with the number of species in a group, the number of individuals in a population, or the relative number of individuals of different species in a given community or ecosystem. In this section we will address macroevolutionary questions concerning the number of species in different groups. This question falls within the domain of the "taxic approach" to macroevolutionary studies, an approach concerned with the analysis of phylogenetic patterns resulting from processes controlling the rates of speciation and extinction (Cracraft 1985a,b). The goal of this research is to separate groups that are more species-rich from other "equivalent" groups and to distinguish between clades of "unusually high" or "unusually low" species number.

It is difficult to generalize across studies in the absence of rigorous definitions of "unusual" and "equivalent." Mayden (1986) suggested that two criteria must be satisfied before any conclusions about differences in species number, between or among groups, can be drawn. First, all groups under examination must be monophyletic. Because phylogenetic systematics stresses the recognition of monophyletic groups, it is an appropriate starting point for studies of this component of diversity. Second, the groups being compared must be of equal antiquity. A number of methods have been proposed for documenting the relative ages of clades. Stratigraphic and biogeographic analyses (see chapter 7) attempt to use environmental parameters as independent indicators of age. The use of "genetic distances" is based on the existence of a hypothetical "internal clock" that is universally informative about evolutionary rates. Phylogenetic systematics uses yet another criterion, sister-group relationships. Remember that sister groups are the descendants of a common and unique speciation event. Hence, by definition sister groups must be of equal age.

Once these criteria have been satisfied, any disparity in diversity between sister groups may be due to unusually high or unusually low speciation or extinction rates in one of the sister clades. Delineation of these influences still leaves the underlying mechanism enclosed within a black box. The "transformational" component of macroevolution is concerned with exploring

this black box is an attempt to uncover attributes associated evolutionarily with the existence of species-rich or depauperate clades. Extinctions or unusually low speciation rates will produce depauperate clades, while unusually high speciation rates will produce species-rich clades. It has been tempting to think that species-rich groups are somehow "better" or "more successful" than average, whereas groups of low species number are somehow "less successful" than average. Hence, a taxic macroevolutionary study of diversity is necessary for robust transformational macroevolutionary studies of diversity.

Unusually Low Diversity Groups

Simpson (1944) was among the first modern evolutionary biologists to consider general explanations for groups of unusually low species numbers. He considered all such groups *relicts* of one form or another and postulated that different processes could produce different kinds of relictual groups. We will be concerned with two major types of relicts. **Phylogenetic relicts** are "living fossils," members of groups that have existed for a long time without speciating very much. Such low speciation rates could result from phylogenetic or developmental constraints on phenotypic diversification, and/or from unusually pronounced ecological specialization (i.e., ecological constraints due to the effects of strong, long-term stabilizing selection from the specialized habitat). **Numerical relicts**, by contrast, are the surviving members of once more species-rich groups that have been depleted by extinction.

Brooks and Bandoni (1988) suggested that a combination of phylogenetic, biogeographical, and ecological information could be used to distinguish between phylogenetic and numerical relicts. Establishing a group's relictual status first requires methods for determining that the group is old enough to be highly diverse. There are a number of methods available for estimating the ages of clades, including molecular-clock criteria, paleontological data, and biogeographical analysis (see also chapter 7). Second, it must be established that the group is in fact unusually depauperate. As suggested above, this can be established by comparing sister groups (Mayden 1986). Brooks and Bandoni further suggested that phylogenetic relicts should be ecologically conservative, whereas numerical relicts should be ecologically diverse.

For example, ratfish (chimaeroids) are the sister group of sharks, skates, and stingrays (elasmobranchs). There are 25 species of ratfish, compared with approximately 625 species of elasmobranchs. Ratfish occur worldwide in mid-to-deep-water marine habitats, and forage on benthic invertebrates. The fossil record indicates that ratfish have been in existence for a considerable period of time but have never been highly diverse. Both the fossil evidence and the ecological homogeneity of contemporaneous species suggest that ratfish are phylogenetic relicts. Now, consider the crocodilians (Crocodilia), the

sister group of the species-rich clade, the birds (Aves). Living crocodilians, numbering about 22 species, inhabit a variety of estuarine to freshwater habitats throughout the tropical and subtropical regions of the world. They prey on a wide variety of vertebrates and some invertebrates. The fossil record indicates that crocodilians were once a species-rich group, including many fully marine species; in addition, the earliest known crocodilian fossils suggest a terrestrial origin for the group. Hence, the current diversity of crocodilians represents only a fraction of the species number and ecological diversity once encompassed by the group, so we consider crocodilians to be numerical relicts.

Unusually High Diversity Groups

According to the taxic view of macroevolution, unusually species-rich groups have experienced higher speciation rates than their sister groups. However, as we have discovered in the preceding paragraphs, speciation results from a complex interaction of a variety of processes. In general, unusually high speciation rates can be attributed to three influences.

1. Cracraft (1982a,b, 1985a) suggested that the key to understanding taxic macroevolutionary patterns for any clade lay in the history of geological change and accompanying vicariant speciation. This suggestion is supported by three lines of evidence. First, since speciation is an irreversible phenomenon, it should be most strongly affected by irreversible environmental factors. Paleoecological studies indicate that most climatic changes are cyclical, so this would argue against a strong role for climate in the speciation process. However, geological evolution is an irreversible phenomenon and probably the only environmental process that is irreversible on time scales long enough to affect species. Second, biological diversity tends to be clumped in "hot spots" corresponding to areas with historically high rates of geological change, rather than being uniformly distributed across a given habitat or zone. For example, tropical diversity is clumped in South America and in the Indo-Malaysian region (named Wallacea, after Alfred Russell Wallace, co-discoverer of the theory of natural selection), two areas whose geological history is extremely complicated. And finally, most documented speciation patterns correspond to the predictions of vicariant (and microvicariant) speciation.

2. Certain types of habitat may support higher diversity than others. For example, the observation that diversity in the tropics is higher than diversity in the temperate or arctic regions is often attributed to differences in speciation rates. From this perspective, the greater energy budget in the tropics allows a finer partitioning of the environment to occur, permitting more species to evolve. Cracraft (1985a) approached the problem from a different

angle. He suggested that the critical comparison should be the rates of extinction, rather than the rates of speciation, in the different areas. From this perspective, extinction rates in temperate to arctic habitats have been higher than extinction rates in the tropics, due to historical increases in environmental harshness in the colder areas. To study the influence of habitat on speciation rates, it is necessary to filter out the effects of vicariant speciation and then search for conditions of uniformly high (or low) diversity in a given habitat.

3. A particular group of organisms might exhibit unusually high speciation rates because they possess attributes that allow them to invade and exploit new habitats. The extent to which this influence has affected species richness will be reflected in the amount of peripheral isolates, parapatric, or sympatric speciation that has occurred in a clade. Many authors have therefore sought specific attributes or "key innovations" or "key adaptations" whose origin in an ancestor increased the likelihood of nonvicariant modes of speciation (see also chapter 5). Vrba (1980, 1983) recognized two classes of key innovations that could affect speciation and extinction rates. Species selection involves studies of traits that emerge in an evolving lineage (i.e., in an ancestral species) that directly affect the way organisms interact with their environments. By contrast, effect macroevolution involves studies of traits that emerge in an evolving lineage that have an effect on speciation and extinction rates regardless of the environment (for further discussions, see Mayr 1963; Jackson 1974; Jablonski 1982; Hansen 1983; Valentine and Jablonski 1983).

As an example of the difference between these two classes of key innovations, let us consider the evolutionary diversification of the passeriform birds, a monophyletic group that is commonly perceived as unusually species-rich. One explanation of this diversity is that songbirds, as a group, possess some "key adaptation" that has allowed them to become "more successful" evolutionarily than other birds (but see Raikow 1986). Kochmer and Wagner (1988) suggested that the small size of passeriforms relative to other birds was the key adaptation. They argued that small organisms should speciate more often because of their greater success at carving up environmental resources. If this is true, then passeriforms should be ecological specialists. Fitzpatrick (1988) also suggested that small size was a key adaptation, but attributed the evolutionary success of songbirds to their role of ecological generalists. Although this conflicted with Kochmer's and Wagner's prediction, both of these explanations fall within the domain of "species selection" because the success of the key innovation is attributed to an enhanced interaction with the environment (foraging success; see also Vermeij 1988 for a discussion of diversity in male courtship songs).

From a historical ecological perspective, the question of whether passeriforms are specialists or generalists is secondary to the question, Are their

foraging habits apomorphic or plesiomorphic with respect to their sister group, which is not so species-rich? Two steps are required for the clarification of this problem: first, a refinement of the data base for foraging habits within the passeriforms and, minimally, their sister group and, second, a phylogenetic analysis of the relationships within the passeriforms and, minimally, their sister group. From this, we can determine whether the foraging mode displayed by the songbirds is a plesiomorphic (ancestral) trait or a derived trait. The discovery that passeriforms display a derived feeding mode will support the hypothesis that a shift in foraging strategies associated with a change in size represented a "key adaptation" in these birds. On the other hand, the discovery that songbirds display the ancestral foraging strategy does not support a species-selection hypothesis of the relationship between body size and foraging success. For example, suppose the passeriforms are ecological generalists. If the sister group of the passeriforms includes species that are also generalists (at least primitively within the group), then the presence of that foraging mode among songbirds is not a unique attribute of those birds. Rather, the propensity to be an ecological generalist has been inherited from some common ancestor that gave rise to groups some of which are, and others of which are not, unusually species-rich.

An alternative perspective, more similar to effect macroevolution than to species selection, also assumes that "being small" is the key innovation. Regardless of the environmental context, we might expect that species of small organisms would (1) have higher reproductive rates (and hence higher probabilities of producing new variants) than their larger relatives; (2) occupy less geographic territory, and hence be more likely to speciate as a result of relatively small-scale geographic subdivision, than populations of larger organisms (see "geological change," above); and (3) require less energy to survive than species of large organisms, giving them a greater probability of survival during periods of environmental stress (see "habitat," above; see also Schmidt-Nielsen 1984 for a more detailed discussion of possible evolutionary advantages in being small). Maurer (1989) produced a mathematical model demonstrating the potential significance to speciation and extinction rates of different persistent ancestral population dynamics, regardless of the environment in which those population dynamics are manifested.

Summary

Researchers studying macroevolutionary patterns of species number have become increasingly aware of the effects of geological activity (vicariance) on speciation rates. However, what is often overlooked is that vicariant speciation also affects extinction rates because every vicariant speciation event results in the "extinction" of the ancestor giving rise to the sister species.

ies. If Lynch's (1989) estimates of the frequencies of speciation modes is representative of diversity as a whole, then as many as 71% of extinctions are due to vicariant speciation and not to the irreplaceable loss of an evolving lineage. This is an important point, because it emphasizes the dangers of letting our perceptual biases color our evolutionary explanations. "Extinction" is generally associated with destructive influences; it eliminates biological entities. "Speciation," on the other hand, is generally associated with productive influences; it creates new biological entities. Because of the special, and probably subliminal, connotations of these terms, we have overlooked the dual nature of vicariant speciation. And this, in turn, is rather a catastrophic prospect, because if roughly three-quarters of past extinctions have simply been a by-product of biological creation through speciation, where does that leave a global ecosystem in which most of the current extinctions are not accompanied by such productive processes?

5   Adaptation

The search for a functional (adaptive) fit between an organism and its environment is one of the dominant themes in evolutionary biology (see, e.g., Lewontin 1978; Dunbar 1982; Coddington 1988). There are three components to adaptation: origin, diversification, and maintenance of characters.

Microevolutionary studies concentrate on the maintenance of traits in current environments where the processes shaping the interactions between the organism and its environment can be observed and measured directly. Having untangled this complicated web, these researchers then extrapolate backwards to the processes involved in the character's initial appearance in, and subsequent spread through, the ancestral species.

Historical ecology complements these studies by providing direct estimates of phylogeny, which can be used as a template for reconstructing the historical patterns of character origin and diversification. Such a template can help ecologists to focus their search for the processes underlying adaptation. For example, consider an interesting (but improbable) group of species with the following characteristics (table 5.1) and phylogenetic relationships (fig. 5.1).

In this group the relationship between a character and the environment in which it originated can be investigated for only one taxon and one character, namely, the evolutionary increase in size (big) in species D (fig. 5.1). Researchers interested in the processes involved in character origin and adaptive success, if any, should concentrate their efforts on this species. The presence of small, blue, and square in species A, small, red, and square in species B, small, red, and round in species C, and red and round in species D are all ancestral legacies. Studies of these species will uncover the processes involved in character maintenance. Combining the results from all these studies will provide us with a more direct estimate of the relationship among the processes underlying the origin, spread, and maintenance of potentially adaptive traits. The incorporation of both the patterns of the past and the processes of the present into our framework of evolutionary explanations will thus strengthen our hypotheses of adaptation.

In this chapter we are going to examine the types of questions about adaptation that can be investigated from a historical ecological perspective. In