INTRODUCTION

The study of speciation is an ad hoc science. No one has yet observed the development from beginning to end of a new plant or animal species in nature. The fossil record, so useful in painting a broad picture of long-term evolutionary trends, lacks the temporal and biological sensitivity to dissect the multitude of processes involved in speciation. Population genetics, the extreme opposite of paleontology in its ability to measure and model gene frequency changes and stability, has also failed to provide much insight into the genetics of speciation (110).

At the molecular level, proteins used in the current flush of allozyme studies (110, 158, 174) have almost no direct bearing on speciation. Estimates of genetic differentiation based on allozyme data alone (i.e. 147, 189), therefore, provide only crude indexes of genetic divergence between species and so-called semispecies, most of which could easily be regarded as species (178). Moreover, animals used in these studies have often long since passed through the critical “point of no return,” at which hybridization will no longer result in fusion of two races (24, 29, 110). They tell us little about how many or what kind of genes are directly implicated in speciation itself. Thus we are still forced to reconstruct events surrounding speciation from observations on extant species, a task that has fallen almost exclusively to the naturalist (see 44, 69, 72, 124 for historical aspects).

Speciation is ultimately an adaptive process that involves establishment of intrinsic barriers to gene flow between closely related populations by development of reproductive isolating mechanisms. A study of speciation is, to a considerable extent, a study of the genetics and evolution of reproductive isolating mechanisms. Most evolutionists therefore generally accept as a working definition the biological species concept: species represent groups of interbreeding natural populations reproductively isolated from other such groups (125). Although it has its weak points (44), alternatives (e.g. 65, 164) impose more problems than they solve.

Selection for reproductive isolation between closely related populations is fundamentally different from the process involved in local adaptation (28, 109, 181). The latter entails only minor genetic adjustments, whereas speciation frequently involves a reorganization of some crucial component in the genetic system that results in a
quantum step toward the origin of interspecific differences (109, 181). Although the genetic system embraces a constellation of biological properties, those most pertinent to modes of speciation to be discussed are presented in Table 1.

In this review, I show that the ways in which various groups of animals differ in these properties determine, to a great extent, the mode of speciation they are most likely to follow. I also reexamine the conventional wisdom that new species of sexually reproducing animals arise only after a period of complete geographic isolation and gradual genetic change, a viewpoint long held by most evolutionary biologists. Major advances in our understanding of the relationship between the structure and function of genetic systems and mechanisms of speciation in different animal and plant groups now make it almost impossible to accept the universality of allopatric speciation.

MODES OF SPECIATION AND THE GENETIC SYSTEM

Almost all evolutionary biologists agree that, in order to speciate, gene flow between diverging populations must be reduced to a level where "foreign" genes entering the population as a result of hybridization can be eliminated by natural selection. Disagreement arises, however, on whether this is accomplished by strictly extrinsic barriers (i.e. geographic isolation) or by intrinsic barriers arising within a population as certain members bearing unique genotypes shift into a new environment while still in contact with the parental population.

Three broad patterns of speciation involving either allopatric, parapatric, or sympatric development of reproductive isolation have been invoked to explain the origin of new species of sexually reproducing animals (44, 69, 124, 179, 181, 182). Others have been suggested—saltational or catastrophic speciation (66, 109); centrifugal speciation (17, 20, 40); stasipatric speciation (179); cascading speciation, etc (162); allelic contracomplementation (141)—but they all appear to represent only modifications of the three basic types.

Properties of the genetic system appear to restrict each group of animals to predominantly one mode of speciation. Although I recognize that some attributes may be relatively unimportant for certain animals, the combinations provided in Table 1 are those most frequently encountered in animal speciation by one of the modes discussed below.

ALLOPATRIC SPECIATION (TYPES Ia and Ib)

Without a doubt, allopatric (geographic) speciation is very common in almost all groups of sexually reproducing animals. Examples of ecogeographic races existing in various states of geographic speciation are so common that it is hardly necessary to discuss them here. Dobzhansky (44, 45), Grant (69, 72), Mayr (124), and others treat the subject thoroughly; here I touch only on features relevant to later topics.

Allopatric speciation, regarded by many evolutionary biologists as the major means of generating new species in sexually reproducing animals, can occur in basically two different ways (Type Ia and Type Ib, Table 1).
**Type Ia: Speciation by Subdivision**

In this classic model, a widely distributed species becomes subdivided into two or more relatively large populations (Figure 1). After gene flow is interrupted by some extrinsic barrier, genetic differences begin to accumulate between isolates as each population responds to its own array of selective forces and tracks its ever-changing environment. Any barriers to gene exchange that develop are usually the result of these fortuitous adaptive genetic changes \((44, 72, 124, 128, 178)\). Populations will not fuse once they reestablish contact if enough genetic differences have accumulated during isolation to ensure that hybrids between them are of such low fitness that they are strongly selected against or eliminated. Reproductive isolation is therefore frequently incomplete between closely related allopatric populations, although genetical analyses and ecological studies necessary to demonstrate this quantitatively have not been made \((110, \text{ but see } 50, 51)\).

Premating reproductive isolating mechanisms are usually perfected first in the zone of contact so that hybrids eventually become rare or absent altogether \((13, 44, 115, 128)\). This final stage in the speciation process is called the *Wallace effect* \((72, 128)\). Although examples in nature are difficult to substantiate \((68, 177)\), it has been convincingly demonstrated in frogs \((111)\) and in lizards \((81, 82)\). The process has been reproduced experimentally using various mating and selection schemes on sibling species (or so-called semispecies) of *Drosophila* \((48, 70, 71, 93, 99, 101)\). It can occur very rapidly \((\text{e.g. } 90)\), or occasionally may establish a more or less permanent narrow hybrid belt \((124)\). Because this last stage of speciation requires accumulation of many genetic changes during the period of complete geographic isolation, allopatric speciation by subdivision is necessarily a relatively long-term process.

Speciation through subdivision is commonly regarded as widespread in animals and certain large animal species of high vagility that are typically *K*-selected \((4)\), as defined by several authors \((62, 115, 137, 138)\), are probably limited to this mode of speciation. This is apparent in vertebrates, such as the Carnivora, whose reproductive strategies are better known and hence more easily correlated with speciation.

Chromosomal evolution, a good indicator of rapid speciation (see below), is minimal in such wide-ranging groups \((181)\). All cats (*Felis*) in the northern hemisphere are \(2n = 38\) and true dogs (*Canis*) all have \(2n = 78\). In both genera, speciation appears to have been slow relative to that of foxes, which have a wide range of chromosome numbers \((2n = 38, 40, 64, \text{ and } 78 \text{ in } 4 \text{ species})\). The reason for karyotype stability in dogs and not in foxes is related to their ecology and social structure. Most large carnivores, for instance, must space themselves out to ensure an adequate food supply; as a result, selection favors dispersal accomplished by defense of territory, by formation of small closed social groups with annual juvenile dispersal, or by pronounced natural avoidance. Diurnality and utilization of an open habitat in many species also favor group formation (*Canis, Panthera, etc*) and is accompanied by high mobility with extensive home ranges. Foxes are an exception in that they do not form cohesive units beyond a permanent pair association. Their home range is thus relatively much more restricted than canids, which often form
Table I Some correlates in the properties of the genetic systems and other attributes of species undergoing allopatic, parapatric, and sympatric speciation. These relationships pertain only to individuals within related taxonomic groups or ecological guilds (i.e., large carnivores or a guild of parasitic insects)

<table>
<thead>
<tr>
<th></th>
<th>Allopatric Type Ia</th>
<th>Allopatric Type Ib</th>
<th>Parapatric Type II</th>
<th>Sympatric Type III</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reproductive strategy</td>
<td>Low reproductive rate; late sexual maturity, few offspring, long lifespan, high competitive ability (K-strategist)</td>
<td>High reproductive rate; early sexual maturity, large number of offspring, short lifespan, low competitive ability (r-strategist)</td>
<td>Same as Type Ib (r-strategist)</td>
<td>Same as Type Ib (r-strategist, but see text)</td>
</tr>
<tr>
<td>Vagility</td>
<td>High</td>
<td>High</td>
<td>Low</td>
<td>High (but niche limited) to low Variable</td>
</tr>
<tr>
<td>Initial population size</td>
<td>Large</td>
<td>Small</td>
<td>Small</td>
<td>As in Type II</td>
</tr>
<tr>
<td>Ecological amplitude</td>
<td>Mostly broad, Environment utilization fine grained, i.e., generalized feeding habits</td>
<td>Type Ia or Type II</td>
<td>Mostly narrow, Environment utilization coarse grained i.e., specialized feeding habits</td>
<td>As in Type II</td>
</tr>
<tr>
<td>Change in niche</td>
<td>Speciation involves no radical shift to new niche</td>
<td>Type Ia or Type II</td>
<td>Speciation accompanied by shift to new niche</td>
<td>As in Type II</td>
</tr>
<tr>
<td>Mate selection</td>
<td>Not closely linked with niche selection</td>
<td>Same as Type Ia</td>
<td>As in Type Ia or III</td>
<td>Closely linked to niche selection</td>
</tr>
<tr>
<td>Breeding system</td>
<td>Normally outbreeding</td>
<td>Normally inbreeding or facultatively inbreeding</td>
<td>As in Type Ib</td>
<td>As in Type Ib</td>
</tr>
<tr>
<td>Selection</td>
<td>Heteroselection level high</td>
<td>Homoselection level high</td>
<td>As in Type Ib</td>
<td>As in Type Ib</td>
</tr>
<tr>
<td>Chromosome rearrangements</td>
<td>Little or no chromosome evolution; chromosome rearrangements if present not associated with speciation</td>
<td>Chromosome rearrangements may or may not be associated with speciation</td>
<td>Chromosome rearrangements frequently associated with speciation ('negative heterosis')</td>
<td>As in Type Ib</td>
</tr>
</tbody>
</table>
Table 1 (Continued)

<table>
<thead>
<tr>
<th></th>
<th>Allopatric Type Ia</th>
<th>Allopatric Type Ib</th>
<th>Parapatric Type II</th>
<th>Sympatric Type III</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genetic changes</td>
<td>Speciation results from cumulative adaptive changes at structural and regulatory genes</td>
<td>Speciation may or may not be associated with radical alterations in structural and regulatory genes</td>
<td>Speciation frequently associated with radical alterations of regulatory systems, but minor structural gene mutation</td>
<td>Speciation frequently results from only minor changes in both regulatory and structural genes</td>
</tr>
<tr>
<td>Nongenetic DNA</td>
<td>Relatively large amounts of nongenetic DNA; genome size large.</td>
<td>Comparatively small amounts of nongenetic DNA; genome size small.</td>
<td>Same as Type Ib</td>
<td>Same as Type Ib</td>
</tr>
<tr>
<td>Evolution of reproductive isolating mechanisms (RIM)</td>
<td>Postmating RIM fortuitous result of long term adaptive genetic changes during isolation. Premating RIM perfected in and limited to hybrid zone.</td>
<td>Same as Type I but genetic changes occur rapidly; RIM widespread.</td>
<td>Premating and/or postmating RIM directly selected for during or soon after shift to new niche and widespread.</td>
<td>Premating RIM directly selected for and precedes shift to new niche.</td>
</tr>
<tr>
<td>Gene flow</td>
<td>None.</td>
<td>None.</td>
<td>Some initially</td>
<td>Some initially</td>
</tr>
<tr>
<td>Distribution of semispecies and sibling species</td>
<td>Usually allopatric or parapatric; niche requirements similar; interspecific competition high in zone of contact.</td>
<td>Usually allopatric or broadly sympatric; niche requirements vary.</td>
<td>Usually parapatric</td>
<td>Usually sympatric</td>
</tr>
<tr>
<td>Speciation rates</td>
<td>Slow.</td>
<td>Rapid, sometimes passing through critical stages which guarantee speciation within a few generations.</td>
<td>As in Type Ib</td>
<td>As in Type Ib</td>
</tr>
<tr>
<td>Stage</td>
<td>Extrinsic Origin of Barriers to Gene Flow</td>
<td>Intrinsic Origin of Barriers to Gene Flow</td>
<td></td>
<td></td>
</tr>
<tr>
<td>-------</td>
<td>------------------------------------------</td>
<td>------------------------------------------</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Freely interbreeding population</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Establishment of barriers to gene flow, development of RIM's</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Expansion of range; perfection RIM's</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Species distribution after stabilization of ranges</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

**Figure 1** Diagrammatic representation of three basic modes of speciation. Post-mating reproductive isolating mechanisms (RIM's) arise after geographic isolation in Types Ia and Ib situations; pre-mating RIM's are perfected once contact is reestablished. In Type Ib situations, populations of daughter species may still be small at time of contact. Pre- and postmating RIM's are therefore fully developed over the entire range of the daughter species. Niche preferences may also be somewhat different between recently evolved Type Ib species that may permit broad sympathy. Type Ia species are likely to share very similar ecologies and are rarely broadly sympatric; pre-mating reproductive isolating mechanisms are usually restricted to or just beyond the zone of overlap. In parapatric and sympatric speciation pre- and postmating RIM's are developed during or before a shift to a new niche. In both modes, daughter species are never geographically isolated from parental species during speciation. Consequently, reproductive isolating mechanisms are fully developed throughout the range of daughter species. Sympatric speciation normally involves radical shifts in niche preferences. Competition is greatly reduced between the old and new species, which inevitably remain broadly sympatric. The ecologies of species that have undergone parapatric speciation are generally more similar. This fact, coupled with their low vagility, usually results in very narrow zones of overlap. See text for details.
wide-ranging packs (53). Other small carnivores have similar reproductive strategies and dispersal characteristics (118). The chance of a chromosome rearrangement becoming fixed in a small, isolated population founded by a single pair of foxes is considerably increased over wide-ranging carnivores, such as cats and dogs and constitutes a different kind of allopatric speciation (Type Ib).

Felids and canids represent the extreme opposite of the genetic system encountered in small, short-lived fossorial species of rodents, many of which have more typically r-selected strategies of reproduction. As a group they are the most diverse and dominant of all vertebrates (161) and are represented by many cryptic or sibling species and races distinguishable only on the basis of their karyotypes (181).

Many birds (157), certain reptiles (138) and amphibians (18), and most large marine (119), lacustrine, and riverine fish (113) would also share similar biological attributes with the large mammals. Most birds are highly vagile, have extensive ranges, and show remarkably little variation in chromosome number, form, or DNA content (8, 181). Speciation in birds is almost invariably by geographic speciation, with many species resulting from populations isolated in refugia established by climatic events of the Pleistocene (157), although founder events may also be important in some groups (124, 125). One case of sympatric speciation has recently been suggested in Darwin’s finches (59), but the evidence is inconclusive.

From an ecological standpoint, many Type Ia species treat the environment in a fine-grained manner (107, 159). Their high vagility and relatively broad niche requirements ensure that suitable resources will be encountered frequently. When the distributions of such wide-ranging species are broken up into two or more populations, environmental conditions within each refugium remain similar (124, 125). Unless population size is greatly restricted, relatively high heteroselection levels (selection for heterozygosity) will be maintained.

Genetic changes in such species will occur slowly as such tightly integrated coadapted polymorphic systems exert considerable speciational inertia (27, 124). These populations rarely tolerate the levels of inbreeding necessary to go through a genetic bottleneck typically experienced in Type Ib speciation events. Many of the same coadapted gene complexes will be retained in large isolated populations. Most genetic changes therefore probably occur in structural genes rather than through any major reorganization of the regulatory system.

This view is supported by the fact that Type Ia mammalian species have undergone much less chromosomal evolution and also have retained relatively larger amounts of nongenetic DNA than have rapidly evolving rodents (127). Recent investigations have found that large amounts of nongenetic DNA prolong cell generation and life, minimize chromosomal errors during cell division, protect genes from mutagenic agents, and are essential for structural organization, functional relationships, and regulation of the cell nucleus (8, 56, 176, 181, 184, 185, 187, 188). DNA also plays a special inhibitory role on speciation. Small genome size is associated with rapidly evolving, specialized, short-lived groups (168). Accumulation of nongenetic DNA may actually be a form of evolutionary senescence that, unless reversed, might eventually contribute significantly to extinction.
Type Ib: Speciation by the Founder Effect

Probably a much more common form of geographic speciation occurs by way of the establishment of a new colony by a small number of founders (Figure 1) (121, 123, 124). What kind of species are most likely to provide founders that can survive the rigors of colonization and go on to evolve into new species? Carson (29, 30), who has studied the pattern of rapid speciation in Hawaiian *Drosophila* (600+ spp.), provided rather convincing evidence that small propagules—sometimes represented by only a single fertile female—coming from small semi-isolated peripheral populations, are most likely to be preadapted as colonists. These populations are usually adapted to some degree of inbreeding and are often products of a population “flush,” a period of rapid population increase wherein natural selection is temporarily relaxed (26, 30). Such populations usually exist in peripheral habitats and are under relatively intense r-selection regimes (115). By existing at the periphery, they also are most likely to become permanently isolated from the parent population or to be close to an unexploited area suitable for invasion. Homoselection (selection for homozygosity) may also be more common in marginal environments, as less of the genome is tied up in elaborate coadapted complexes characteristic of large, stable central populations with high heterozygosity (29, 30, 44, 115, 124). Speciation under these conditions may occur rapidly (27, 45, 103, 123, 124, 157).

In endemic Hawaiian *Drosophila*, there has been little chromosome evolution and no evidence for a major genetic revolution during speciation by founder effects. A number of related species are homosequential (i.e. banding patterns of polytene chromosomes are identical) (29), and what little variation does exist involves paracentric inversions that are normally not involved in speciation. Only four of the many species examined cytologically have undergone chromosome fusions, although many have different levels and distributions of heterochromatin (181). Regulatory rather than structural gene changes may therefore be important in speciation in these animals. Allozyme variation suggests that species differ in gene frequency rather than allele form (88, 151). What little change has occurred involved enzymes like esterases and phosphotases, which are affected by changes in substrates and probably have no direct bearing on reproductive isolation separating closely related species (R. H. Richardson, personal communication). There has also been very little ecological divergence (29).

The major differences are in premating isolating mechanisms (28, 29, 37, 38). Carson proposed a plausible explanation for these differences, involving isolation of a fertile female on an unexploited kipuka, or island, followed by random genetic drift and abrupt nonadaptive changes in the gene pool following the founder event; Richardson (146) and Craddock (38) have suggested alternative means for some species. As the population size increases, normal interdemic processes of mutation, recombination, and selection take over.

In other invertebrate and vertebrate groups, chromosome evolution may be an important factor in speciation by the founder effect. Species of mammals of moderately low vagility that are subsocial or social frequently form small cohesive closed bands or small family groups (primates), harems, herds (some ungulates), or family
groups with permanent pair bonds (e.g. foxes). Others are solitary, flightless, or cave-dwelling with homing behavior similar to that of bats (40). Most have fairly restricted home ranges, and a single pair or small group existing near the species' border may frequently become isolated from the parental population for a time. Many of these temporarily isolated populations either become extinct or are reabsorbed into the parental population. If the isolated population, however, includes an individual (possibly an α-male in a small herd, or one member of a pair) bearing a major adaptive chromosome rearrangement, conditions are ideal for its rapid fixation in homozygous condition within the small isolated group (181).

Major chromosome rearrangements (i.e. fusions, fissions, whole arm translocations, and pericentric inversions) provide one way whereby rapid reorganization of regulatory mechanisms can take place; their importance in speciation has been demonstrated experimentally in animals (102) and plants (72). They may cause enormous changes in the developmental process without a genic change (8, 19, 91, 92, 185), and may permit a population homozygous for the new karyotype to penetrate and exploit a new and previously unsuitable habitat at the periphery of a species' range. These rearrangements therefore appear to play a special role in speciation, as reorganization of control systems provides, more than genic changes, major innovation and novelty. Such rearrangements are essentially the systematic mutations, or macromutations, of Goldschmidt (66).

Some groups with highly variable karyotypes, such as certain carnivores (foxes, \(2n = 38-78\)), artiodactyles (horses, \(2n = 44-64\); pigs, \(2n = 30-38\); deer, \(2n = 6-68\)), and certain primate groups, including man (\(2n = 20-80\)) appear to fit this Type Ib mode of allopatric speciation. McFee et al (116), for instance, reported a case of Robertsonian fusion in a semi-isolated herd of wild pigs in Tennessee, introduced from Europe in 1912. The Tennessee populations have \(2n = 36-37\), and the wild and domesticated pig have \(2n = 38\). These three orders also represent the most widespread and successful groups of large mammals (161, 169).

In Type Ib speciation, incipient reproductive isolation arises fortuitously, just as in the Type Ia case, after the founders have established themselves in a new territory. If chromosome rearrangements are involved, as they frequently appear to be, then some postmating reproductive isolation will occur with the fixation of the new arrangement. There is, however, no direct selection for intrinsic barriers to gene flow, as hybrids are never produced between the parent and daughter populations.

If, as in the case of the homosequential Hawaiian Drosophila, no chromosomal changes are involved, rapid development of reproductive isolation is more difficult to explain. Carson (29, 30) suggested that this process is accomplished as a by-product of a "genetic revolution," although in this case it appears to be more of a local disturbance than a revolution. In an unsaturated island environment, minor genetic changes may permit new founder populations to exploit unoccupied niches and, in turn, promote some form of reproductive isolation. Perfection of postmating reproductive isolating mechanisms and selection for premating mechanisms in Type Ib speciation, as in Type Ia, will generally occur only if and when the sister populations reestablish contact (the Wallace effect). In Type Ib speciation, this may occur rapidly, as the new species is likely to reestablish contact with the parent population.
within a short time. The budded-off species will therefore carry fully developed reproductive isolating mechanisms with it as it expands its range into unoccupied territory (178), thus possibly accounting for the frequent lack of evidence for the Wallace effect [i.e. character displacement of Brown & Wilson (21)] in natural populations.

PARAPATRIC SPECIATION (TYPE II)

Parapatric speciation occurs whenever species evolve as contiguous populations in a continuous cline. White (179, 181, 182), who called this stasispatric speciation, and Murray (128) have offered interesting evaluations of the criteria necessary for parapatric speciation. Other authors have recently analyzed specific examples (34, 40, 87, 130, 131, 135, 156, 170, 175, 179, 180, 182) or presented theoretical models and experimental evidence (33, 54, 75, 140, 149, 150). Parapatric speciation superficially resembles speciation by the founder effect, but differs in three major ways: 1. no spatial isolation is required during speciation, 2. the level of vagility in the animals undergoing parapatric speciation is exceptionally low, and 3. reproductive isolating mechanisms arise by selection simultaneously with the penetration and exploitation of a new habitat by genetically unique individuals.

In general, all species implicated in parapatric speciation possess the combination of properties listed in Table 1. They are typically $r$-selected species existing in many small to medium sized semi-isolated peripheral populations, and thus adapted to some inbreeding. Although chromosome rearrangements frequently are responsible for initiation of speciation by altering major regulatory pathways, little or no genic differentiation occurs even after speciation has been completed (131, 132, 160). Populations also have relatively low levels of heterozygosity and are normally under regimes of homoselection (131).

Parapatric divergence and speciation are always associated with animals and plants of low vagility (72, 109, 128, 179, 181, 182). Adjacent populations in new habitats are established as an animal acquires the genetic tools to enter and exploit a new environment [Ludwig effect (114)]. No long-range dispersal takes place, and diverging populations are in constant contact. They are therefore never strictly geographically isolated from one another. Although some gene flow occurs initially only at the borders between adjacent populations, introgressing genes may penetrate no more than a few feet as observed in some natural populations of morabine grasshoppers (179, 181), snails (33, 34), and plants (3). Furthermore, a growing body of evidence suggests that effects of this gene flow on differentiation and parapatric speciation may be small (49, 54).

Note that some authors have regarded this as a case of disruptive selection (173) when in fact the majority of individuals in the two populations are under strong directed selection in different habitats (126). Only a few individuals at the borders may experience some disruptive selection, but even at this point gene flow from allopatric members of their population would tip the balance of selection in favor of one or the other (43). Disruptive selection may rarely be associated with speciation in nature.
Sessile animals share many features with annual plants (cf 72, 109). Dispersal powers of adults and young in snails, fossorial rodents, and some flightless insects may frequently be no greater than seed and pollen dispersal in annual plants. They also have similar reproductive strategies and genetic systems (76, 139). Many models proposed for the genetic differentiation of parapatric plant populations (3, 39, 43, 83), therefore, are applicable to these animals with low vagility.

Another attribute that differentiates parapatric speciation from allopatric modes is that both postmating and, more importantly, premating reproductive isolating mechanisms arise by selection as individuals penetrate a new habitat. A typical case that has been thoroughly studied in plants is the rapid evolution of heavy metal (copper, lead, zinc)-tolerant races of plants growing on contaminated mine tip soils (3, 83). Within a relatively short span of time, strong barriers to gene flow between the races have been erected, involving a shift in flowering time and increased selfing, even though individuals have always existed within only a few feet of one another at the racial border. Extensive studies on *Clarkia* by Lewis and his co-workers (109) and Gottlieb on *Stephanomeria* (67) are also pertinent here.

A very similar case of parapatric differentiation of adjacent populations in snails of the genus *Partula* has been investigated by Clarke (33, 34). Certain features of the *moorea-olympia-tohiveana* series on the island of Moorea in the Pacific suggest that reproductive isolation has evolved parapatrically around vertical overhanging cliffs. The observed morph-ratio clines have probably resulted from sharp discontinuity between two incompatible coadapted gene complexes.

Even though these sharp genotypic changes do not necessarily coincide with an easily defined environmental change, morph-ratio clines ultimately depend on a change in some important environmental gradient. If the gradient is smooth, then an animal of low vagility will retain a coadapted gene complex until selective coefficients become so great that a complete reordering of the genome is necessary in order to cope with any further environmental changes. Because hybrids occurring at the morph-ratio cline interfaces are of reduced fitness, selection favors the evolution of reproductive isolation. More detailed accounts of this process can be found in Clarke (33), Murray (128), and Cook (35), and the subject is treated in a somewhat different way, using fitness sets and environmental grains, by Levins (107).

Other investigations into the genetic structure of natural animal populations reveal similar patterns of rapid differentiation over very short distances. Borisov (15) has found that there are urban and rural ecological races of *Drosophila funebris* clearly demonstrating ecogeographic divergence in inversion frequencies. Evidence of strong local parapatric racial differentiation for alcohol tolerance was found by McKenzie & Parsons (117) in a wine cellar population of *D. melanogaster*. However, the relatively high vagility of these flies probably precludes speciation unless a major chromosome rearrangement could become established, an unlikely possibility given the apparent low rate of incorporation of major chromosome rearrangements in this group of flies (181).

If sharp discontinuities in sedentary species can evolve by genic reorganization alone, any intrinsic factor that would reduce gene flow between parapatric races, such as a chromosome rearrangement, would be strongly selected for (186). The two
most thoroughly studied examples of parapatric speciation involving chromosome rearrangement are a group of flightless morabine grasshoppers (179, 181, 182) and a fossorial group of mole rats of the genus Spalax (129, 133, 175).

The great majority of Australian morabine grasshopper species and races (300+) have unique karyotypes. The most conspicuous chromosome rearrangements involve fusions, dissociations, and pericentric inversions. The latter exist in several species as floating polymorphisms. Fusions or dissociations, on the other hand, are never found in the polymorphic state except in narrow hybrid zones existing between two chromosome races. It is unlikely any of these fusions and dissociations ever existed as balanced polymorphisms. They are therefore divisive rather than cohesive factors in phylogeny, and play important roles in speciation of these insects (182).

White (179, 181, 182) outlined step-by-step the way in which parapatric speciation occurred in these grasshoppers. Formation and fixation of these divisive rearrangements, which give adaptively superior homozygotes but inferior heterozygotes (negative heterosis), comprise the essential first step. Such rearrangements simultaneously permit the population to shift into a new niche and erect a strong postmating barrier to gene exchange. White considered it possible for this to happen most frequently well within the population range, rather than at the periphery where populations are smaller and ecologically more restricted. Yet, as pointed out by Lewis (109), rearrangements arising at the center of the range are the most likely to be lost, as there is little chance for the heterozygotes to mate before the rearrangement is eliminated by strong negative selection and chance. Only on the periphery, where inbreeding is high, do such rearrangements stand a chance to survive through the negative heterosis barrier. On the other hand, species existing in a patchy environment may have many populations that are internally parapatric or stasipatric (182). The possibility that an individual could shift to a new niche well within the range of the animal is still an open possibility warranting further study.

Key (94, 95) argued that all such rearrangements arise first in a propagule well beyond the general range of the parental species. He asserted, without presenting evidence, that all hybrid zones between chromosome races in morabines are the result of secondary range expansions of previously isolated populations, that the rearrangements act only as gene filters, and that introgression of some genes will occur.

His argument seems to pivot on whether small populations existing at the periphery of species range are allopatric or parapatric. To a morabine grasshopper, a snail, or a fossorial rodent, 100–1000 m is a formidable distance. Such distances may exist temporarily at the extreme limits of a species range when population densities become low during adverse years. Small, highly localized, and inbred family groups would be common under these circumstances. It seems realistic to envision a situation in which fixation of the new arrangement in only a few generations could occur in a small colony established by a single fertile female bearing a major chromosome rearrangement located only a few hundred meters from other members of her population. As most animals undergo similar density cycles without speciating, it seems rather arbitrary to single out these grasshoppers as unique. In the light of the
genetic evidence from morph-ratio clines, even this degree of isolation is probably not essential.

Fixation of the new karyotype brings about major changes in regulatory function and a release from the ecogeographic restraints that the genetic architecture placed on the parental population (181). The new chromosome races are then free to expand into the unoccupied area to which they were previously poorly adapted. Hybridization might occur at the border between the old and new populations, but if a large enough reservoir of homozygotes with the new rearrangement existed beyond the hybrid zone, gene flow would be eliminated by selection. Furthermore, it is unlikely that much, if any, introgression would occur as proposed by Key (95), because of the high selective coefficients that act in the hybrid zones, and because invading genes between chromosome races are likely to be poorly coadapted.

The case of parapatric speciation in the mole rats Spalax is somewhat similar. Four chromosome races of mole rats in Israel have arisen by a series of dissociations (129, 132, 175). Races are distributed in a more or less north-south cline, with higher chromosome races clearly adapted to more arid zones. As in the case of Partula, the environmental gradient is a smooth one and no specific attribute of the habitat is correlated with the shift from one chromosome race to another (133). The same sort of negative heterosis found in the morabines accompanies heterokaryotypes that occur at low frequency at the boundaries of the parapatrically distributed races of species.

Many other animal species with low vagility appear to have speciated by the same parapatric process. Parapatrically distributed chromosomal forms of species or so-called semispecies have been reported in a wide range of fossorial mammals and insects reviewed by White (181). More recently, other examples have appeared involving pocket gophers (131, 135, 170), Peromyscus (156), shrews (64), Sceloporus lizards (74, 112), mole crickets (130), and stick insects (36), for which parapatric speciation has been invoked or is likely because of their population structure and other features of their genetic system.

One group in particular, the cichlid fish of the great lakes of East Africa, is of special interest. These animals have formed many huge endemic species flocks in short periods of time. In Lake Victoria more than 150 endemic species of Haplochromis evolved in less than 750,000 years (73). Lake Nabugabo, cut off from Victoria about 3500 years ago, contains five endemic species (61, 73). Without a doubt, all species have arisen by intralacustrine speciation. Both Greenwood (73) and Fryer & Iles (61) argue with good evidence that allopatric speciation by the founder principle augmented by strong predation can probably account for most species, although some forms may have speciated parapatrically. No chromosome studies have been published thus far, so little more can be said at this point.

SYMPATRIC SPECIATION (TYPE III)

Mayr (124) has defined sympatric speciation as the “origin of isolating mechanisms within the dispersal area of the offspring of a single cline.” Superficially, there appears to be a fuzzy line between parapatric and sympatric speciation and, indeed,
at least one author (128) regards the former to be a special case of the latter. On closer examination, the two are qualitatively different in several important features; probably the most important one is the way in which reproductive isolating mechanisms are established. In cases of parapatric speciation, strong pre- and postmating reproductive isolation develops as the population penetrates a new niche. In sympatric speciation, premating reproductive isolation arises before a population shifts to a new niche. Chromosome rearrangements appear to be rarely involved in the examples thus far studied. Furthermore, speciation frequently occurs at the center of the species range in a patchy environment rather than at the periphery, which results in the rapid generation of many sympatric sibling species.

Several authors have developed realistic mathematical models for sympatric speciation based on selection in a heterogenous environment (10, 114, 120). The first stage in sympatric speciation, development of a stable polymorphism, is easily attained in populations adapting to different niches in the absence of heterozygotic advantage. Maynard Smith (120) found that if such a polymorphism were accompanied by an assortative mating gene (i.e. individuals best adapted to a particular niche tend to mate with one another) and if there were some degree of habitat selection, then two reproductively isolated populations would evolve.

Attempts have been made to simulate sympatric speciation in the laboratory under different levels of artificial selection and isolation. Of those carried out with Drosophila melanogaster under disruptive selection regimes (32, 146–148, 152–155, 171, 172), only the one by Thoday & Gibson (171) was successful. Others were able to demonstrate that populations can undergo rapid divergence in the face of massive gene flow, but found little evidence for the development of strong reproductive isolation between lines. These results are not surprising. Most Drosophila possess a constellation of biological traits, particularly in female reproductive behavior (148), which make them unlikely to speciate sympatrically, especially under laboratory conditions and with the small population sizes used in the experiments.

Sympatric speciation appears to be limited to special kinds of animals, namely phytophagous and zoophagous parasites and parasitoids. However, this group encompasses a huge number of species (well over 500,000 described insects alone). A few other animals with special biological features may also speciate sympatrically, but they represent a small number of the world’s fauna and are discussed later. The basic question is how can reproductive isolation arise before some barrier to gene flow is erected? Because parasites and parasitoids constitute the vast majority of animals speciating sympatrically, I examine them first.

Many parasites use their hosts as a rendezvous for courtship and mating (5, 22–24, 144). Mate selection in many of these groups therefore depends upon host selection (5, 22–24, 97, 134, 190). The principal isolating mechanism is ecological, not ethological, and postmating isolating mechanisms do not seem to be involved. Closely related sympatric sibling species of Tephritidae, for instance, can frequently be hybridized, and fertile F1, F2, and backcross progeny produced in the laboratory (14, 80; G. L. Bush unpublished). Under certain conditions, a shift to a new host can therefore have a profound effect on mate selection and provide a strong barrier to gene exchange between the parental and daughter populations.
The appearance of new host races of insects on introduced and native plants provides the best examples of this process. Some shifts such as the hawthorn fly, *Rhagoletis pomonella*, to apple in 1864, and later to cherries in Wisconsin in about 1960, have been studied in considerable detail (see 23, 24 for summaries). Similar cases of rapid sympatric host race formation have been reported for diptonid sawflies (97) and the codling moth, *Laspeyresia pomonella* (16, 136). Even some plant-infesting *Drosophila*, such as those associated with cacti (96) and certain endemic Hawaiian trees (38, 146), may have speciated sympatrically, but probably only in a few instances (78).

Genetics of host race formation and speciation has been reviewed by Bush (22–24) and Huettel & Bush (80). Two genetic components appear to play a primary role in many parasitic host shifts: 1. gene(s) controlling host recognition and selection and 2. genes involved with survival. Two other genetic factors may be of considerable importance: 3. those genes that determine to what degree insects can be induced to distinguish one host plant from another, and 4. in insects of temperate climates, those gene(s) that regulate diapause. They are not essential for sympatric speciation to occur, but serve to reinforce ecological isolation.

The number of major genes controlling host selection and survival may be relatively few (24, 106) and involved for the most part with chemoreception, as host discrimination is often determined by chemical rather than physical cues (42, 183).

No one has reported a case of genetic polymorphism for host selection within a natural population of parasites. Evidence that allelic variation is involved in host shifts comes from a few studies made on interspecific hybrids. The most extensive are those of Huettel & Bush (80). In the gall-forming fruitfly *Procecidochares*, one locus controls host plant recognition in males and females (80). Minor changes resulting from single mutations in receptor proteins of a chemoreceptor or decoding pathways in the central nervous system of the type demonstrated by Ferkovich & Norris (55) in roaches and Bentley (11) in crickets, respectively might well be involved.

The ability of a parasite to survive on a new host may also require the alteration of alleles at only a few minor loci (23, 24, 41, 63, 77, 106). A gene-for-gene relationship between host-resistant genes and parasite survival genes usually exists, and has been extensively studied in a wide range of coevolutionary associations between domesticated crops and their pest species (41). When the formal genetics of the relationship has been established, alleles for resistance are usually found to be dominant over those for susceptibility, and survival genes in the animal are frequently recessive (41). Genetic modifiers and epistatic interactions are also involved (106), but their relationship to speciation is not understood.

A shift to a new host, if it is to be permanent, must be preceded by the establishment of a new host recognition allele (or alleles), which permits the parasite to recognize and, preferentially, move to the new host. If the mortality level induced by the new host is not too high, further genetic changes are not initially required to establish a new host race. Mayr (124) has argued that it is "typological" to assume that a single gene could preadapt an individual to a new niche and lead to speciation. Such a gene, he contended, "would require a veritable 'systemic' mutation that
simultaneously results in 1) a change in host preference; 2) a special adaptation to a new niche; and 3) a preference for mates with similar niche preferences.” Yet, contrary to Mayr, there is strong evidence that a single allele substitution either in structural or regulatory genes can indeed fulfill all of these criteria.

If the new host has a radically different chemistry, new survival genes must also be incorporated into the genome of those parasites switching to the new host. A genetic model based on host recognition and survival genes has been proposed by Bush (22–24). It closely resembles the model of sympatric speciation rejected by Mayr (122, 124) as biologically untenable for reasons that no longer seem objectionable. There is now no question that host and mate selection are often closely linked and genetically controlled. It is also likely that the genetic variation needed to establish a new host race is present in the parent population even before the new host appears on the scene. This is evident in the speed at which phytophagous parasites can adapt to new insecticides and new plants to which they have never been previously exposed (23, 106).

Bush (23, 24) also pointed out that host shifts are most likely to occur when the original and new hosts occur together within the dispersal range of the parasite. In this situation, new genotypes can constantly be tested until the right combination results in a successful shift. New recombinants would statistically stand a much better chance of survival in an area where both host and parasite occur together in high densities along with the new host. Thus peripheral populations may be of less importance than in the other modes of speciation. It is improbable that random long-range dispersal of a few individuals beyond the normal range of the species would enable them to find a new host with which they are genetically compatible.

Another objection expressed by Mayr (124) against sympatric speciation by way of host race formation is that parasites are seldom truly monophagous, but often have secondary hosts. He contends that specialization occurs over a period of time in different areas as one host or the other becomes extinct. Specialization in isolation eventually results in the development of sufficient genetic divergence to guarantee speciation, even if the population becomes sympatric. Such a pattern of geographic isolation has undoubtedly occurred. Ample opportunity for such events have arisen during the Pleistocene.

However, the majority of parasites are, in fact, host specific (6, 57, 58, 144). In one well-studied dipteran family, the Agromyzidae, 73% are monophagous, 12% oligophagous, and 5% polyphagous (166). In light of the fact that parasites are probably the most abundant of all eukaryotes, sympatric divergence seems an equally probable, and possibly even the normal, mode of speciation in many groups. The number of zooephagous and phytophagous parasites is staggering. Price (144 and personal communication) estimated that about 72.1% of the British insects (among the best known in the world) are parasitic on plants or animals. Two species of oaks (Quercus robæae and Q. petraea) alone sustain 284 species of parasites (herbivores) (165). If we consider that there are already 750,000 described species of insects worldwide (125), over 525,000 of these are parasites, a conservative figure as at least three times this number remains undescribed. This amounts to more than all other plant and animal species combined. It is difficult to believe that all of these speciated allopatrically.
When comparing the reproductive strategies of parasites and parasitoids with vertebrates and some large flying insects, it is clear that all possess many of the biological correlates generally attributed to $r$-strategists (6, 57, 58, 142, 143). Frequently they have very high reproductive rates, small body size, and short life spans; their mortality is likely to be density independent. However, when comparisons are made within a complex of parasitic or parasitoid species, sequential series of $r$- and $K$-strategists relative to one another within the same guild have obviously evolved (6, 57, 58, 142–144). This is the case with certain insect-host-parasitoid communities, such as the one consisting of the gall-forming midge (*Rhopalomyla californica*) and some 10 species or more of its hymenopterous parasitoids. Even more elaborate complements involving 30–40 parasitoids per host species are known (6).

Studies by Force (57, 58) and Askew (6) show that within such groups the $r$-strategists are the opportunists best able to penetrate and adapt to new environments. They have: 1. greater physiological tolerances to withstand physical perturbations, 2. greater dispersal capabilities so that new host populations can be located in case of local disaster, 3. high reproductive capacity, 4. adaptiveness to a variety of conditions, but 5. low competitive ability, and are 6. characterized as being monophagous. Parasites with these credentials are obviously the most likely to speciate sympatrically.

In sawflies and parasitoids such as the Chalcidoidea, host specificity is high and mating frequently occurs on the host. Sib-mating and inbreeding are common, and females usually mate only once. Furthermore, the haplodiploid genetic system exposes unfavorable genes directly to selection in the male and unfertilized females produce male progeny that will tend to increase the frequency of new host selection genes. Thus adaptation to a new host would occur rapidly (5, 97). Most parasitic species also appear to belong to groups that have small genome size (12), a feature associated with rapid speciation (168, 187).

High reproductive rates and other $r$-selected traits are also common to many other phytophagous insect parasites and to most other parasitic groups of animals. In many, a sequential series of $r$- to $K$-strategists exists similar to the ones found in hymenopterous parasitoids, but no relevant studies seem to have been published. Reproductive strategies, however, are probably less important to speciation in parasitic forms than other aspects of the genetic system, such as the amount of inbreeding, level of heterozygosity, the mode of host and mate selection, host specificity, and the distribution of potential host plants. $K$-selected species, which are also frequently host specific, might be capable of shifting just as readily to a new host under certain stable environmental conditions such as those encountered in the tropics (84–86).

Other Patterns of Sympatric Speciation

At least five other patterns of divergence involving temporal, chemical (pheromone), symbiotic factors, hybridization, and polyploidy suggest a sympatric origin of species. Examples of allochronic divergence in breeding time have been discussed for diprionid sawflies (97, 98), field crickets (1, 2), *Rhagoletis* fruit flies (22–24), and char (60). In some cases, allochronic isolation has apparently led to speciation (1, 2, 24, 60), whereas in others it appears to have occurred along with a shift.
to a new host, thus serving to reinforce reproductive isolation (22–24, 98). All of these examples are as feasible as any allopatric explanation thus far offered (124).

Laven (104, 105) outlined a mechanism for sympatric speciation based on a cytoplasmic incompatibility system caused by an independent factor he called a plasmon. A similar case has been observed in Australian Aedes (163). A series of hybridization studies has revealed 20 “crossing types” representing different geographic races of Culex pipiens. Crosses between races are fertile in one direction, but sterile in the other. Caspari & Watson (31) pointed out that such a system would not necessarily lead to speciation because only the cytoplasm of one race would replace that of another, whereas genotypes would be mixed. A similar pattern of incipient speciation has been reported in semispecies of Drosophila paulistorum, caused by a mycoplasma-like intracellular symbiont (46–48, 52), and in D. equinoxialis [see (7)]. Lewis (108) has suggested that symbiosis of this type might permit exploitation of a marginal habitat.

Dobzhansky & Pavlovsky (47, 48) found that one laboratory strain of D. paulistorum had undergone speciation while in laboratory culture over a period of a few years. This phenomenon of symbiotic sterility interactions may be much more widespread in insects than is now recognized and deserves more attention. Its role in speciation, however, is still poorly understood, but may be more important in parapatric than in sympatric divergence.

Another possible mechanism for sympatric speciation is through a change in mating pheromones (145). Two pheromone “races” are known to exist in the European corn borer, Ostrinia nubilalis. The males of the eastern population are attracted to the natural female lure consisting of trans-11-tetradecenyl acetate (96%) and cis-11-tetradecenyl acetate (4%). Males of the western strain are attracted to the same isomers but in the reverse concentrations (3 and 97%). Kochansky et al (100) correctly regarded these two forms, which occur sympatri-ically in Pennsylvania without interbreeding (25), as distinct species. Both species have slightly different biological traits and may represent separate introductions into North America from Europe. Irrespective of the origin of the two species in North America, a change in responsiveness could have arisen here or in Europe by only two independent mutations, one in the male altering a trans receptor protein to a cis receptor, and the second occurring in an enzyme used by the female to produce the cis rather than the trans form of the pheromone. Such a system could only arise successfully at the periphery of a large population. A more detailed study of these two populations and the forms from which they came is obviously warranted. The host plant may also alter sex pheromones and reinforce incipient isolation (79).

Interspecific hybridization and polyploidy, of major importance in plant speciation (72), appear to have played an insignificant role in animal speciation. The most clear-cut example of interspecific hybridization leading to speciation is that described by Johnston (89). He has presented convincing evidence that the Italian sparrow arose as the result of the hybridization of the house and willow sparrows some 3500 years ago. The final development of complete reproductive isolation
appears to have occurred 300–400 years ago during the “Little Ice Age,” and may well have involved a period of complete geographic isolation.

The only legitimate examples of polyploidy in bisexual species are in the cerato-phyrid Amphibia and two species of hylid frogs, a few teleost fishes, and possibly a few hermaphroditic turbellaria and annelids [(181), but see (9)]. Cases of polyploidy in asexual forms are more common, but because of the nature of sex chromosome mechanisms, the high frequency of cross fertilization, and the overall cellular complexity of animals, the phenomenon is rare in sexual forms.

CONCLUDING REMARKS

The mode of speciation adopted by a species or group of related species of animals (or plants) is clearly determined to a considerable extent by the architecture of their genetic systems. We still have only fragmentary information on many aspects of the biological properties of most animals. Yet the emerging picture in recent years, gathered from independent molecular, organismal, and population studies, clearly indicates that a reconsideration of some long held attitudes toward the way animals speciate is warranted. A multidisciplinary approach to speciation problems is obviously needed if we are ever to construct realistic models of speciation.

Genetic revolution and geographic isolation may not be required for speciation in many animals. Single gene substitution or a chromosome rearrangement can initiate speciation, if they have a drastic and permanent effect on gene flow between diverging populations. Reproductive isolation can arise during (parapatric) or even before (sympatric) new populations become adapted to new niches; such populations can speciate without loss of contact with parent populations. Based on new evidence, old models of sympatric and parapatric speciation are now being dusted off and reexamined.

Even the view of Goldschmidt (66) that a “hopeful monster,” a mutation that, in a single genetic step, simultaneously permits the occupation of a new niche and the development of reproductive isolation, no longer seems entirely unacceptable. In discussing the population size necessary for fixation of chromosomal rearrangements in parapatrically distributed European newts, Spurway (167) remarked: “The population size N of Wright should be so small that it may be profitable to think of some species originating from a single pair in a new Eden. Being an Adam and Eve gives a monster a chance to hope.”

Because of the possibility that the number of animals that may be speciating sympatrically or parapatrically (i.e. rodents, parasites, flightless insects, etc) might exceed or at least equal the number of those speciating allopatrically, more emphasis should be placed on biological studies involving Types II and III species in the future for both academic and practical reasons. Included in this group of animals are almost all of the major pests of plants, animals, and man. We need, therefore, an emphasis on applied evolutionary biology. From an agricultural and medical standpoint, an understanding of speciation mechanisms is essential to the development of realistic pest control programs. It is time that more applied evolution be incorporated into this essential field of biology.
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Literature Cited


54. Endler, J. A. 1973. Gene flow and popu-
100. Kochansky, J., Cardé, R. T., Liebherr, J., Roeofs, W. L. 1975. Sex pheromones of the European corn borer (*Oe-


