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Observed Instances of Speciation

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1.0 Introduction and Acknowledgements

This FAQ discusses several instances where speciation has been observed. It also discusses several issues related to speciation.

I have divided this FAQ into several sections. Part 2 discusses several definitions of what a species is. Part 3 explains the context in which observations of speciation are made. Part 4 looks at the question, "How can we tell when a speciation event has occurred?" Part 5 describes a number of observed speciation events and several experiments which (in my opinion) failed to produce speciation. Part 6 is a list of references.

Other Links:

Some More Observed Speciation Events
A group of articles originally posted to the talk.origins newsgroup that provides some instances of speciation not covered by this document.

The descriptions of each observation come from the primary literature. I went back to this literature for two reasons. First, many of these observations are not discussed (or not discussed in much detail) in secondary sources such as reviews, texts and popular articles. Second, it is difficult, if not impossible, to evaluate what a piece of research actually established without looking at the methods and data. Secondary sources rarely give this information in any detail. Anyway, I have included only those observations that I have been able to find the original sources for.

I consider this FAQ incomplete. One reason for this is that I am still chasing references (I still have a list of over 115 to find). More important is the fact that observations of speciation are buried in papers on a number of topics. If you know of observations that I should include, let me know and I will chase down the reference, read it and modify the file (assuming that the data are the least bit convincing). I ask that you try to give me as complete a reference as possible to aid me in finding the original source.

1.1 Acknowledgements

Back in April of 1993, Rich Fox asked a series of questions related to species and speciation events. These questions got me interested in the topic. I hope that I have, at least, provided grist for the mill that will grind out an answer to Rich's questions. In any case, Rich deserves the credit (or blame :-)) for inspiring me to write this. My starting point was the references contained in the old speciation FAQ. I wish to thank the authors of this, Chris Stassen, James Meritt, Anneliese Lilje and L. Drew Davis. Tom Scharle and Simon Clippingdale sent a couple of references my way. Finally, John Edstrom sent me considerable information on symbiosis in Amoeba. While I have not had a chance to get all the references that he has sent me, he has given me a great deal to think about over the role of symbiosis in speciation. Many thanks to all.

2.0 Species Definitions

A discussion of speciation requires a definition of what constitutes a species. This is a topic of considerable debate within the biological community. Three recent reviews in the Journal of Phycology give some idea of the scope of the debate (Castenholz 1992, Manhart and McCourt 1992, Wood and Leatham 1992). There are a variety of different species concept currently in use by biologists. These include folk, biological, morphological, genetic, paleontological, evolutionary, phylogenetic and biosystematic definitions. In the interest of brevity, I'll only discuss four of these -- folk, biological, morphological and phylogenetic. A good review of species definitions is given in Stuessy 1990.

2.1 The Folk Concept of Species

Naturalists around the world have found that the individual plants and animals they see can be mentally grouped into a number of taxa, in which the individuals are basically alike. In societies that are close to nature, each taxon is given a name. These sorts of folk taxonomies have two features in common. One aspect is the idea of reproductive compatability and continuity within a species. Dogs beget dogs, they never beget cats! This has a firm grounding in folk knowledge. The second notion is that there is a discontinuity of variation between species. In other words, you can tell species apart by looking at them (Cronquist 1988).

2.2 The Biological Species Concept

Over the last few decades the theoretically preeminent species definition has been the biological species concept (BSC). This concept defines a species as a reproductive community.

2.2.1 History of the Biological Species Concept

The BSC has undergone a number of changes over the years. The earliest precursor that I could find was in Du Rietz 1930. Du Rietz defined a species as

> "... the smallest natural populations permanently separated from each other by a distinct discontinuity in the series of biotypes."

Barriers to interbreeding are implicit in this definition and explicit in Du Rietz's dicussion of it.

A few years later, Dobzhansky defined a species as

> "... that stage of evolutionary progress at which the once actually or potentially interbreeding array of forms becomes segregated into two or more separate arrays which are physiologically incapable of interbreeding." (Dobzhansky 1937)

It is important to note that this is a highly restrictive definition of species. It emphasizes experimental approaches and ignores what goes on in nature. By the publication of the third edition of the book this appeared in, Dobzhansky (1951) had relaxed this definition to the point that is substantially agreed with Mayr's.

The definition of a species that is accepted as the BSC was promulgated by Mayr (1942). He defined species as

> "... groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups."

Note that the emphasis in this definition is on what happens in nature. Mayr later amended this definition to include an ecological component. In this form of the definition a species is

> "... a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature."

The BSC is most strongly accepted among vertebrate zoologists and entomologists. Two facts account for this. First, these are the groups that the authors of the BSC worked with :-). (Note: Mayr is an ornithologist and Dobzhansky worked extensively with Drosophila). More importantly, obligate sexuality is the predominant form of reproduction in these groups. It is not coincidental that the BSC is less widely accepted among botanists. Terrestrial plants exhibit much greater diversity in their "mode of reproduction" than do vertebrates and insects.

2.2.2 Criticisms of the Biological Species Concept

There has been considerable criticism of the theoretical validity and practical utility of the BSC. (Cracraft 1989, Donoghue 1985, Levin 1979, Mishler and Donoghue 1985, Sokal and Crovello 1970).

The application of the BSC to a number of groups, including land plants, is problematical because of interspecific hybridization between clearly delimited species (McCourt and Hoshaw 1990, Mishler 1985).

There is an abundance of asexual populations that this definition just doesn't apply to (Budd and Mishler 1990). Examples of taxa which are obligately asexual include bdelloid rotifers, euglenoid flagellates, some members of the Oocystaceae (coccoid green algae), chloromonad flagellates and some araphid pennate diatoms. Asexual forms of normally sexual organisms are known. Obligately asexual populations of Daphnia are found in some arctic lakes. The BSD can be of no help in delimiting species in these groups. A similar situation is found in the prokaryotes. Though genes can be exchanged among bacteria by a number of mechanisms, sexuality, as defined in eukaryotes, in unknown in the prokaryotes. One popular microbiology text doesn't even mention the BSC (Brock and Madigan 1988).

The applicability of the BSC is also questionable in those land plants that primarily self-pollinate (Cronquist 1988).

A more serious criticism is that the BSC is inapplicable in practice. This charge asserts that, in most cases, the BSC cannot be practically applied to delimit species. The BSC suggests breeding experiments as the test of species membership. But this is a test that is rarely made. The number of crosses needed to delimit membership in a species can be astronomical. The following example will illustrate the problem.

Here in Wisconsin we have about 16,000 lakes and ponds. A common (and tasty ;-)) inhabitant of many of these bodies of water is the bluegill sunfish. Let's ask a question -- do all these bluegill populations constitute one species or several morphologically similar species? Assume that only 1,000 of these lakes and ponds contain bluegills. Assuming that each lake constitutes a population, an investigator would have to perform 499,500 separate crosses to determine whether the populations could interbreed. But to do this right we should really do reciprocal crosses (i.e. cross a male from population A with a female from population B and a male from population B with a female from population A). This brings the total crosses we need to make up to 999,000. But don't we also need to make replicates? Having three replicates brings the total to 2,997,000 crosses. In addition, you just can't put a pair of bluegills into a bucket and expect them to mate. In nature, male bluegills excavate and defend nests in large mating colonies. After the nests are excavated the females come in to the colony to spawn. Here the females choose among potential mates. This means that we would need to simulate a colony in our test. Assume that 20 fish would be sufficient for a single test. We find that we would need about 60,000,000 fish to test whether all these populations are members of the same species! (We would also need a large number of large aquaria to run these crosses in). But bluegills are not restricted to Wisconsin...

I could go on, but I think the point is now obvious. The fact of the matter is that the time, effort and money needed to delimit species using the BSC is, to say the least, prohibitive.

Another reason why using the BSC to delimit species is impractical is that breeding experiments can often be inconclusive. Interbreeding in nature can be heavily influenced by variable and unstable environmental factors. (Any angler who has waited for the bluegills to get on to the beds can confirm this one). If we can't duplicate natural conditions of breeding, a failure to breed doesn't mean that the critters can't (or don't) interbreed in the wild. The difficulties that were encountered in breeding pandas in captivity illustrate this. In addition, experimentally showing that A doesn't interbreed with B doesn't preclude both interbreeding with C. This gets even more complicated in groups that don't have nice, straightforward sexes. An example of this occurs in a number of protozoan species. These critters have numerous mating types. There can be very complicated compatability of mating types. Finally, breeding experiments can be inconclusive because actual interbreeding and gene flow among phenetically similar, genetically compatible local populations is often more restricted than the BSC would suggest (Cronquist 1988).

In practice, even strong adherents of the BSC use phenetic similarities and discontinuities for delimiting species. If the organisms are phenotypically similar, they are considered conspecific until a reproductive barrier is demonstrated.

Another criticism of the BSC comes from the cladistic school of taxonomy (e.g. Donoghue 1985). The cladists argue that sexual compatibility is a primitive trait. Organisms that are no longer closely related may have retained the ability for genetic recombination with each other through sex. This is not a derived characteristic. Because of this it is invalid for defining monophyletic taxa.

A final problem with the BSC is that groups that do not occur together in time cannot be evaluated. We simply cannot know whether two such groups would interbreed freely if they came together under natural conditions. This makes it impossible to delimit the boundaries of extinct groups using the BSC. One question will illustrate the problem. Do Homo erectus and Homo sapiens represent the same or different species? This question is unresolvable using the biological definition.

Several alternatives to the biological species concept have been suggested. I will discuss two.

2.3 The Phenetic (or Morphological) Species Concept

Cronquist (1988) proposed an alternative to the BSC that he called a "renewed practical species definition". He defines species as

> "... the smallest groups that are consistently and persistently distinct and distinguishable by ordinary means."

Three comments must be made about this definition. First, "ordinary means" includes any techniques that are widely available, cheap and relatively easy to apply. These means will differ among different groups of organisms. For example, to a botanist working with angiosperms ordinary means might mean a hand lens; to an entomologist working with beetles it might mean a dissecting microscope; to a phycologist working with diatoms it might mean a scanning electron microscope. What means are ordinary are determined by what is needed to examine the organisms in question.

Second, the requirement that species be persistently distinct implies a certain degree of reproductive continuity. This is because phenetic discontinuity between groups cannot persist in the absence of a barrier to interbreeding.

Third, this definition places a heavy, though not exclusive, emphasis on morphological characters. It also recognizes phenetic characters such as chromosome number, chromosome morphology, cell ultrastructure, secondary metabolites, habitats and other features.

2.4 Phylogenetic Species Concepts

There are several phylogenetic species definitions. All of them assert that classifications should reflect the best supported hypotheses of the phylogeny of the organisms. Baum (1992) describes two types of phylogenetic species concepts.

1. A species is the smallest cluster of organisms that possesses at least one diagnostic character. This character may be morphological, biochemical or molecular and must be fixed in reproductively cohesive units. It is important to realize that this reproductive continuity is not used in the same way as in the BSC. Phylogenetic species may be reproductive communities.

Reproductively compatible individuals need not have the diagnostic character of a species. In this case, the individuals need not be conspecific.

2. A species must be monophyletic and share one or more derived character. There are two meanings to monophyletic (de Queiroz and Donoghue 1988, Nelson 1989). The first defines a monophyletic group as all the descendants of a common ancestor and the ancestor. The second defines a monophyletic group as a group of organisms that are more closely related to each other than to any other organisms. These distinctions are discussed in Baum 1992 and de Queiroz and Donoghue 1990.

A recently offered hypothesis suggests that phylogenetic species concepts and the biological species concept may be highly, if not completely, incompatible. "Parallel speciation " has been defined as the repeated independent evolution of the same reproductive isolating mechanism (Schluter and Nagel 1995). An example of this may occur when a species colonizes several new areas which are isolated from, but environmentally similar to, each other. Similar selective pressures in these environments result in parallel evolution among the traits that confer reproductive isolation. There is some experimental evidence that this might occur (Kilias, et al. 1980; Dodd 1989). The implication of this is that biological species (as defined by the BSC) may often be polyphyletic. If this occurs in nature, it could undermine the usefulness of phylogenetic species concepts.

2.5 Why This is Included

What is all of this doing in a discussion of observed instances of speciation? What a biologist will consider as a speciation event is, in part, dependent on which species definition that biologist accepts. The biological species concept has been very successful as a theoretical model for explaining species differences among vertebrates and some groups of arthropods. This can lead us to glibly assert its universal applicability, despite its irrelevance to many groups. When we examine putative speciation events, we need to ask the question, which species definition is the most reasonable for this group of organisms? In many cases it will be the biological definition. In many other cases some other definition will be more appropriate.

3.0 The Context of Reports of Observed Speciations

The literature on observed speciations events is not well organized. I found only a few papers that had an observation of a speciation event as the author's main point (e.g. Weinberg, et al. 1992). In addition, I found only one review that was specifically on this topic (Callaghan 1987). This review cited only four examples of speciation events. Why is there such a seeming lack of interest in reporting observations of speciation events?

In my humble opinion, four things account for this lack of interest. First, it appears that the biological community considers this a settled question. Many researchers feel that there are already ample reports in the literature. Few of these folks have actually looked closely. To test this idea, I asked about two dozen graduate students and faculty members in the department where I'm a student whether there were examples where speciation had been observed in the literature. Everyone said that they were sure that there were. Next I asked them for citings or descriptions. Only eight of the people I talked to could give an example, only three could give more than one. But everyone was sure that there were papers in the literature.

Second, most biologists accept the idea that speciation takes a long time (relative to human life spans). Because of this we would not expect to see many speciation events actually occur. The literature has many more examples where a speciation event has been inferred from evidence than it has examples where the event is seen. This is what we would expect if speciation takes a long time.

Third, the literature contains many instances where a speciation event has been inferred. The number and quality of these cases may be evidence enough to convince most workers that speciation does occur.

Finally, most of the current interest in speciation concerns theoretical issues. Most biologists are convinced that speciation occurs. What they want to know is how it occurs. One recent book on speciation (Otte and Endler 1989) has few example of observed speciation, but a lot of discussion of theory and mechanisms.

Most of the reports, especially the recent reports, can be found in papers that describe experimental tests of hypotheses related to speciation. Usually these experiments focus on questions related to mechanisms of speciation. Examples of these questions include:

- Does speciation precede or follow adaptation to local ecological conditions?
- Is speciation a by-product of genetic divergence among populations or does it occur directly by natural selection through lower fitness of hybrids?
- How quickly does speciation occur?
- What roles do bottlenecks and genetic drift play in speciation?
- Can speciation occur sympatrically (i.e. can two or more lineages diverge while they are intermingled in the same place) or must the populations be separated in space or time?
- What roles do pleiotropy and genetic hitchhiking play in speciation?

It is important to note that a common theme running through these questions is that they all attempt to address the issue of how speciation occurs.

4.0 Telling Whether a Speciation Event Has Occurred

What evidence is necessary to show that a change produced in a population of organisms constitutes a speciation event? The answer to this question will depend on which species definition applies to the organisms involved.

4.1 Cases Where the Biological Species Concept Applies

One advantage of the BSC is that it provides a reasonably unambiguous test that can be applied to possible speciation events. Recall that under the BSC species are defined as being reproductively isolated from other species. Demonstrating that a population is reproductively isolated (in a nontrivial way) from populations that it was formerly able to interbreed with shows that speciation has occurred. In practice, it is also necessary to show that at least one isolating mechanism with a hereditary basis is present. After all, just because a pair of critters don't breed during an experiment doesn't mean they can't breed or even that they won't breed. Debates about whether a speciation event has occurred often turn on whether isolating mechanisms have been produced.

4.1.1 Isolating Mechanisms

Mechanisms which produce reproductive isolation fall into two broad categories -- premating mechanisms and postmating mechanisms.

Premating isolating mechanisms operate to keep species separate before mating occurs. Often they act to prevent mating altogether. Examples of premating mechanisms include ecological, temporal, behavioral and mechanical mechanisms.

Ecological isolation occurs when species occupy or breed in different habitats. It is important to be careful when claiming ecological isolation. For example, I have a population of Dinobryon cylindricum (a colonial algal flagellate) growing in a culture tube in an environmental chamber. It's been there for three years (which is a lot of time in flagellate years! :-)). Even though there is no possibility that they will mate with the D. cylindricum in Lake Michigan, it would be silly to assert that they therefore constitute a separate species. Physical isolation alone does not constitute an isolating mechanism with an hereditary basis.

Temporal isolation occurs when species breed at different times. This may be different times of the year or different times of day.

Behavioral isolating mechanisms rely on organisms making a choice of whether to mate and a choice of who to mate with. Differences in courtship behavior, for instance, may be sufficient to prevent mating from occurring. A behavioral isolating mechanism should result in some sort of positive assortative mating. Simply put, positive assortative mating occurs when organisms that differ in some way tend to mate with organism that are like themselves. For example, if blonds mate exclusively with blonds, brunettes mate exclusively with brunettes, redheads mate exclusively with redheads (and those of us without much hair don't get to mate :-() the human population would exhibit a high degree of positive assortative mating. In most examples in the literature when positive assortative mating is seen it is not this strong. Positive assortative mating is especially important in discussions of sympatric speciation.

Mechanical isolating mechanisms occur when morphological or physiological differences prevent normal mating.

Postmating isolating mechanisms prevent hybrid offspring from developing or breeding when mating does occur. There are also several examples of postmating mechanisms.

Mechanical postmating isolating mechanisms occur in those cases where mating is possible, but the gametes are unable to reach each other or to fuse. Mortality acts as an isolating mechanism when the hybrid dies prior to maturity. Sterility of hybrids can act as an isolating mechanism. Finally a reduction in the fitness of the hybrid offspring can isolate two populations. This happens when the F1 hybrid is fertile but the F2 hybrid has lower fitness than either of the parental species.

4.2 Cases Where the Biological Species Concept Does Not Apply

There is no unambiguous criterion for determining that a speciation event has occurred in those cases where the BSC does not apply. This is especially true for obligately asexual organisms. Usually phenetic (e.g. phenotypic and genetic) differences between populations are used to justify a claim of speciation. A few caveats are germane to this. It is not obvious how much change is necessary to claim that a population has speciated. In my humble opinion, the difference between the "new species" and its "ancestor" should be at least as great as the differences among recognized species in the group (i.e. genus, family) involved. The investigator should show that the change is persistent. Finally, many organisms have life cycles/life histories that involve alternative morphologies and/or an ability to adjust their phenotypes in response to short term changes in ecological conditions. The investigator should be sure to rule these things out before claiming that a phenetic change constitutes a speciation event.

5.0 Observed Instances of Speciation

The following are several examples of observations of speciation.

5.1 Speciations Involving Polyploidy, Hybridization or Hybridization Followed by Polyploidization.

5.1.1 Plants

(See also the discussion in de Wet 1971).

5.1.1.1 Evening Primrose (Oenothera gigas)

While studying the genetics of the evening primrose, Oenothera lamarckiana, de Vries (1905) found an unusual variant among his plants. O. lamarckiana has a chromosome number of 2N = 14. The variant had a chromosome number of 2N = 28. He found that he was unable to breed this variant with O. lamarckiana. He named this new species O. gigas.

5.1.1.2 Kew Primrose (Primula kewensis)

Digby (1912) crossed the primrose species Primula verticillata and P. floribunda to produce a sterile hybrid. Polyploidization occurred in a few of these plants to produce fertile offspring. The new species was named P. kewensis. Newton and Pellew (1929) note that spontaneous hybrids of P.

verticillata and P. floribunda set tetraploid seed on at least three occasions. These happened in 1905, 1923 and 1926.

5.1.1.3 Tragopogon

Owenby (1950) demonstrated that two species in this genus were produced by polyploidization from hybrids. He showed that Tragopogon miscellus found in a colony in Moscow, Idaho was produced by hybridization of T. dubius and T. pratensis. He also showed that T. mirus found in a colony near Pullman, Washington was produced by hybridization of T. dubius and T. porrifolius. Evidence from chloroplast DNA suggests that T. mirus has originated independently by hybridization in eastern Washington and western Idaho at least three times (Soltis and Soltis 1989). The same study also shows multiple origins for T. micellus.

5.1.1.4 Raphanobrassica

The Russian cytologist Karpchenko (1927, 1928) crossed the radish, Raphanus sativus, with the cabbage, Brassica oleracea. Despite the fact that the plants were in different genera, he got a sterile hybrid. Some unreduced gametes were formed in the hybrids. This allowed for the production of seed. Plants grown from the seeds were interfertile with each other. They were not interfertile with either parental species. Unfortunately the new plant (genus Raphanobrassica) had the foliage of a radish and the root of a cabbage.

5.1.1.5 Hemp Nettle (Galeopsis tetrahit)

A species of hemp nettle, Galeopsis tetrahit, was hypothesized to be the result of a natural hybridization of two other species, G. pubescens and G. speciosa (Muntzing 1932). The two species were crossed. The hybrids matched G. tetrahit in both visible features and chromosome morphology.

5.1.1.6 Madia citrigracilis

Along similar lines, Clausen et al. (1945) hypothesized that Madia citrigracilis was a hexaploid hybrid of M. gracilis and M. citriodora As evidence they noted that the species have gametic chromosome numbers of $n = 24$, 16 and 8 respectively. Crossing M. gracilis and M. citriodora resulted in a highly sterile triploid with $n = 24$. The chromosomes formed almost no bivalents during meiosis. Artificially doubling the chromosome number using colchecine produced a hexaploid hybrid which closely resembled M. citrigracilis and was fertile.

5.1.1.7 Brassica

Frandsen (1943, 1947) was able to do this same sort of recreation of species in the genus Brassica (cabbage, etc.). His experiments showed that B. carinata ($n = 17$) may be recreated by hybridizing B. nigra ($n = 8$) and B. oleracea, B. juncea ($n = 18$) may be recreated by hybridizing B. nigra and B. campestris ($n = 10$), and B. napus ($n = 19$) may be recreated by hybridizing B. oleracea and B. campestris.

5.1.1.8 Maidenhair Fern (Adiantum pedatum)

Rabe and Haufler (1992) found a naturally occurring diploid sporophyte of maidenhair fern which produced unreduced (2N) spores. These spores resulted from a failure of the paired chromosomes to dissociate during the first division of meiosis. The spores germinated normally and grew into diploid gametophytes. These did not appear to produce antheridia. Nonetheless, a subsequent generation of tetraploid sporophytes was produced. When grown in the lab, the tetraploid sporophytes appear to be less vigorous than the normal diploid sporophytes. The 4N individuals were found near Baldwin City, Kansas.

5.1.1.9 Woodsia Fern (Woodsia abbeae)

Woodsia abbeae was described as a hybrid of W. cathcariana and W. ilvensis (Butters 1941). Plants of this hybrid normally produce abortive sporangia containing inviable spores. In 1944 Butters found a W. abbeae plant near Grand Portage, Minn. that had one fertile frond (Butters and Tryon 1948). The apical portion of this frond had fertile sporangia. Spores from this frond germinated and grew into prothallia. About six months after germination sporophytes were produced. They survived for about one year. Based on cytological evidence, Butters and Tryon concluded that the frond that produced the viable spores had gone tetraploid. They made no statement as to whether the sporophytes grown produced viable spores.

5.1.2 Animals

Speciation through hybridization and/or polyploidy has long been considered much less important in animals than in plants [[[refs.]]]. A number of reviews suggest that this view may be mistaken. (Lokki and Saura 1980; Bullini and Nascetti 1990; Vrijenhoek 1994). Bullini and Nasceti (1990) review chromosomal and genetic evidence that suggest that speciation through hybridization may occur in a number of insect species, including walking sticks, grasshoppers, blackflies and cucurlionid beetles. Lokki and Saura (1980) discuss the role of polyploidy in insect evolution. Vrijenhoek (1994) reviews the literature on parthenogenesis and hybridogenesis in fish. I will tackle this topic in greater depth in the next version of this document.

5.2 Speciations in Plant Species not Involving Hybridization or Polyploidy

5.2.1 Stephanomeira malheurensis

Gottlieb (1973) documented the speciation of Stephanomeira malheurensis. He found a single small population (< 250 plants) among a much larger population (> 25,000 plants) of S. exigua in Harney Co., Oregon. Both species are diploid and have the same number of chromosomes (N = 8). S. exigua is an obligate outcrosser exhibiting sporophytic self-incompatibility. S. malheurensis exhibits no self-incompatibility and self-pollinates. Though the two species look very similar, Gottlieb was able to document morphological differences in five characters plus chromosomal differences. F1 hybrids between the species produces only 50% of the seeds and 24% of the pollen that conspecific crosses produced. F2 hybrids showed various developmental abnormalities.

5.2.2 Maize (Zea mays)

Pasterniani (1969) produced almost complete reproductive isolation between two varieties of maize. The varieties were distinguishable by seed color, white versus yellow. Other genetic markers allowed him to identify hybrids. The two varieties were planted in a common field. Any plant's nearest neighbors were always plants of the other strain. Selection was applied against hybridization by using only those ears of corn that showed a low degree of hybridization as the source of the next years seed. Only parental type kernels from these ears were planted. The strength of selection was increased each year. In the first year, only ears with less than 30% intercrossed seed were used. In the fifth year, only ears with less than 1% intercrossed seed were used. After five years the average percentage of intercrossed matings dropped from 35.8% to 4.9% in the white strain and from 46.7% to 3.4% in the yellow strain.

5.2.3 Speciation as a Result of Selection for Tolerance to a Toxin: Yellow Monkey Flower (Mimulus guttatus)

At reasonably low concentrations, copper is toxic to many plant species. Several plants have been seen to develop a tolerance to this metal (Macnair 1981). Macnair and Christie (1983) used this to examine the genetic basis of a postmating isolating mechanism in yellow monkey flower. When they crossed plants from the copper tolerant "Copperopolis" population with plants from the nontolerant "Cerig" population, they found that many of the hybrids were inviable. During early growth, just after the four leaf stage, the leaves of many of the hybrids turned yellow and became necrotic. Death followed this. This was seen only in hybrids between the two populations. Through mapping studies, the authors were able to show that the copper tolerance gene and the gene responsible for hybrid inviability were either the same gene or were very tightly linked. These results suggest that reproductive isolation may require changes in only a small number of genes.

5.3 The Fruit Fly Literature

5.3.1 Drosophila paulistorum

Dobzhansky and Pavlovsky (1971) reported a speciation event that occurred in a laboratory culture of Drosophila paulistorum sometime between 1958 and 1963. The culture was descended from a single inseminated female that was captured in the Llanos of Colombia. In 1958 this strain produced fertile hybrids when crossed with conspecifics of different strains from Orinocan. From 1963 onward crosses with Orinocan strains produced only sterile males. Initially no assortative mating or behavioral isolation was seen between the Llanos strain and the Orinocan strains. Later on Dobzhansky produced assortative mating (Dobzhansky 1972).

5.3.2 Disruptive Selection on Drosophila melanogaster

Thoday and Gibson (1962) established a population of Drosophila melanogaster from four gravid females. They applied selection on this population for flies with the highest and lowest numbers of sternoplural chaetae (hairs). In each generation, eight flies with high numbers of chaetae were allowed to interbreed and eight flies with low numbers of chaetae were allowed to interbreed. Periodically they performed mate choice experiments on the two lines. They found that they had produced a high degree of positive assortative mating between the two groups. In the decade or so following this, eighteen labs attempted unsuccessfully to reproduce these results. References are given in Thoday and Gibson 1970.

5.3.3 Selection on Courtship Behavior in Drosophila melanogaster

Crossley (1974) was able to produce changes in mating behavior in two mutant strains of D. melanogaster. Four treatments were used. In each treatment, 55 virgin males and 55 virgin females of both ebony body mutant flies and vestigial wing mutant flies (220 flies total) were put into a jar and allowed to mate for 20 hours. The females were collected and each was put into a separate vial. The phenotypes of the offspring were recorded. Wild type offspring were hybrids between the mutants. In two of the four treatments, mating was carried out in the light. In one of these treatments all hybrid offspring were destroyed. This was repeated for 40 generations. Mating was carried out in the dark in the other two treatments. Again, in one of these all hybrids were destroyed. This was repeated for 49 generations. Crossley ran mate choice tests and observed mating behavior. Positive assortative mating was found in the treatment which had mated in the light and had been subject to strong selection against hybridization. The basis of this was changes in the courtship behaviors of both sexes. Similar experiments, without observation of mating behavior, were performed by Knight, et al. (1956).

5.3.4 Sexual Isolation as a Byproduct of Adaptation to Environmental Conditions in Drosophila melanogaster

Kilias, et al. (1980) exposed D. melanogaster populations to different temperature and humidity regimes for several years. They performed mating tests to check for reproductive isolation. They found some sterility in crosses among populations raised under different conditions. They also showed some positive assortative mating. These things were not observed in populations which were separated but raised under the same conditions. They concluded that sexual isolation was produced as a byproduct of selection.

5.3.5 Sympatric Speciation in Drosophila melanogaster

In a series of papers (Rice 1985, Rice and Salt 1988 and Rice and Salt 1990) Rice and Salt presented experimental evidence for the possibility of sympatric speciation. They started from the premise that whenever organisms sort themselves into the environment first and then mate locally, individuals with the same habitat preferences will necessarily mate assortatively. They established a stock population of D. melanogaster with flies collected in an orchard near Davis, California. Pupae from the culture were placed into a habitat maze. Newly emerged flies had to negotiate the maze to find food. The maze simulated several environmental gradients simultaneously. The flies had to make three choices of which way to go. The first was between light and dark (phototaxis). The second was between up and down (geotaxis). The last was between the scent of acetaldehyde and the scent of ethanol (chemotaxis). This divided the flies among eight habitats. The flies were further divided by the time of day of emergence. In total the flies were divided among 24 spatio-temporal habitats.

They next cultured two strains of flies that had chosen opposite habitats. One strain emerged early, flew upward and was attracted to dark and acetaldehyde. The other emerged late, flew downward and was attracted to light and ethanol. Pupae from these two strains were placed together in the maze. They were allowed to mate at the food site and were collected. Eye color differences between the strains allowed Rice and Salt to distinguish between the two strains. A selective penalty was imposed on flies that switched habitats. Females that switched habitats were destroyed. None of their gametes passed into the next generation. Males that switched habitats received no penalty. After 25 generations of this mating tests showed reproductive isolation between the two strains. Habitat specialization was also produced.

They next repeated the experiment without the penalty against habitat switching. The result was the same -- reproductive isolation was produced. They argued that a switching penalty is not necessary to produce reproductive isolation. Their results, they stated, show the possibility of sympatric speciation.

5.3.6 Isolation Produced as an Incidental Effect of Selection on several Drosophila species

In a series of experiments, del Solar (1966) derived positively and negatively geotactic and phototactic strains of D. pseudoobscura from the same population by running the flies through mazes. Flies from different strains were then introduced into mating chambers (10 males and 10 females from each strain). Matings were recorded. Statistically significant positive assortative mating was found.

In a separate series of experiments Dodd (1989) raised eight populations derived from a single population of D. Pseudoobscura on stressful media. Four populations were raised on a starch based medium, the other four were raised on a maltose based medium. The fly populations in both treatments took several months to get established, implying that they were under strong selection. Dodd found some evidence of genetic divergence between flies in the two treatments. He performed mate choice tests among experimental populations. He found statistically significant assortative mating between populations raised on different media, but no assortative mating among populations raised within the same medium regime. He argued that since there was no direct selection for reproductive isolation, the behavioral isolation results from a pleiotropic by-product to adaptation to the two media. Schluter and Nagel (1995) have argued that these results provide experimental support for the hypothesis of parallel speciation.

Less dramatic results were obtained by growing D. willistoni on media of different pH levels (de Oliveira and Cordeiro 1980). Mate choice tests after 26, 32, 52 and 69 generations of growth showed statistically significant assortative mating between some populations grown in different pH treatments. This ethological isolation did not always persist over time. They also found that some crosses made after 106 and 122 generations showed significant hybrid inferiority, but only when grown in acid medium.

5.3.7 Selection for Reinforcement in Drosophila melanogaster

Some proposed models of speciation rely on a process called reinforcement to complete the speciation process. Reinforcement occurs when to partially isolated allopatric populations come into contact. Lower relative fitness of hybrids between the two populations results in increased selection for isolating mechanisms. I should note that a recent review (Rice and Hostert 1993) argues that there is little experimental evidence to support reinforcement models. Two experiments in which the authors argue that their results provide support are discussed below.

Ehrman (1971) established strains of wild-type and mutant (black body) D. melanogaster. These flies were derived from compound autosome strains such that heterotypic matings would produce no progeny. The two strains were reared together in common fly cages. After two years, the isolation index generated from mate choice experiments had increased from 0.04 to 0.43, indicating the appearance of considerable assortative mating. After four years this index had risen to 0.64 (Ehrman 1973).

Along the same lines, Koopman (1950) was able to increase the degree of reproductive isolation between two partially isolated species, D. pseudoobscura and D. persimilis.

5.3.8 Tests of the Founder-flush Speciation Hypothesis Using Drosophila

The founder-flush (a.k.a. flush-crash) hypothesis posits that genetic drift and founder effects play a major role in speciation (Powell 1978). During a founder-flush cycle a new habitat is colonized by a small number of individuals (e.g. one inseminated female). The population rapidly expands (the flush phase). This is followed by the population crashing. During this crash period the population experiences strong genetic drift. The population undergoes another rapid expansion followed by another crash. This cycle repeats several times. Reproductive isolation is produced as a byproduct of genetic drift.

Dodd and Powell (1985) tested this hypothesis using D. pseudoobscura. A large, heterogeneous population was allowed to grow rapidly in a very large population cage. Twelve experimental populations were derived from this population from single pair matings. These populations were allowed to flush. Fourteen months later, mating tests were performed among the twelve populations. No postmating isolation was seen. One cross showed strong behavioral isolation. The populations underwent three more flush-crash cycles. Forty-four months after the start of the experiment (and fifteen months after the last flush) the populations were again tested. Once again, no postmating isolation was seen. Three populations showed behavioral isolation in the form of positive assortative mating. Later tests between 1980 and 1984 showed that the isolation persisted, though it was weaker in some cases.

Galina, et al. (1993) performed similar experiments with D. pseudoobscura. Mating tests between populations that underwent flush-crash cycles and their ancestral populations showed 8 cases of positive assortative mating out of 118 crosses. They also showed 5 cases of negative assortative mating (i.e. the flies preferred to mate with flies of the other strain). Tests among the founder-flush populations showed 36 cases of positive assortative mating out of 370 crosses. These tests also found 4 cases of negative assortative mating. Most of these mating preferences did not persist over time. Galina, et al. concluded that the founder-flush protocol yields reproductive isolation only as a rare and erratic event.

Ahearn (1980) applied the founder-flush protocol to D. silvestris. Flies from a line of this species underwent several flush-crash cycles. They were tested in mate choice experiments against flies from a continuously large population. Female flies from both strains preferred to mate with males from the large population. Females from the large population would not mate with males from the founder flush population. An asymmetric reproductive isolation was produced.

In a three year experiment, Ringo, et al. (1985) compared the effects of a founder-flush protocol to the effects of selection on various traits. A large population of D. simulans was created from flies from 69 wild caught stocks from several locations. Founder-flush lines and selection lines were derived from this population. The founder-flush lines went through six flush-crash cycles. The selection lines experienced equal intensities of selection for various traits. Mating test were performed between strains within a treatment and between treatment strains and the source population. Crosses were also checked for postmating isolation. In the selection lines, 10 out of 216 crosses showed positive assortative mating (2 crosses showed negative assortative mating). They also found that 25 out of 216 crosses showed postmating isolation. Of these, 9 cases involved crosses with the source population. In the founder-flush lines 12 out of 216 crosses showed positive assortative mating (3 crosses showed negative assortative mating). Postmating isolation was found in 15 out of 216 crosses, 11 involving the source population. They concluded that only weak isolation was found and that there was little difference between the effects of natural selection and the effects of genetic drift.

A final test of the founder-flush hypothesis will be described with the housefly cases below.

5.4 Housefly Speciation Experiments

5.4.1 A Test of the Founder-flush Hypothesis Using Houseflies

Meffert and Bryant (1991) used houseflies to test whether bottlenecks in populations can cause permanent alterations in courtship behavior that lead to premating isolation. They collected over 100 flies of each sex from a landfill near Alvin, Texas. These were used to initiate an ancestral population. From this ancestral population they established six lines. Two of these lines were started with one pair of flies, two lines were started with four pairs of flies and two lines were started with sixteen pairs of flies. These populations were flushed to about 2,000 flies each. They then went through five bottlenecks followed by flushes. This took 35 generations. Mate choice tests were performed. One case of positive assortative mating was found. One case of negative assortative mating was also found.

5.4.2 Selection for Geotaxis with and without Gene Flow

Soans, et al. (1974) used houseflies to test Pimentel's model of speciation. This model posits that speciation requires two steps. The first is the formation of races in subpopulations. This is followed by the establishment of reproductive isolation. Houseflies were subjected to intense divergent selection on the basis of positive and negative geotaxis. In some treatments no gene flow was allowed, while in others there was 30% gene flow. Selection was imposed by placing 1000 flies into the center of a 108 cm vertical tube. The first 50 flies that reached the top and the first 50 flies that reached the bottom were used to found positively and negatively geotactic populations. Four populations were established:

Population A + geotaxis,	no gene flow
Population B - geotaxis,	no gene flow
Population C + geotaxis,	30% gene flow
Population D - geotaxis,	30% gene flow

Selection was repeated within these populations each generations. After 38 generations the time to collect 50 flies had dropped from 6 hours to 2 hours in Pop A, from 4 hours to 4 minutes in Pop B, from 6 hours to 2 hours in Pop C and from 4 hours to 45 minutes in Pop D. Mate choice tests were performed. Positive assortative mating was found in all crosses. They concluded that reproductive isolation occurred under both allopatric and sympatric conditions when very strong selection was present.

Hurd and Eisenberg (1975) performed a similar experiment on houseflies using 50% gene flow and got the same results.

5.5 Speciation Through Host Race Differentiation

Recently there has been a lot of interest in whether the differentiation of an herbivorous or parasitic species into races living on different hosts can lead to sympatric speciation. It has been argued that in animals that mate on (or in) their preferred hosts, positive assortative mating is an inevitable byproduct of habitat selection (Rice 1985; Barton, et al. 1988). This would suggest that differentiated host races may represent incipient species.

5.5.1 Apple Maggot Fly (Rhagoletis pomonella)

Rhagoletis pomonella is a fly that is native to North America. Its normal host is the hawthorn tree. Sometime during the nineteenth century it began to infest apple trees. Since then it has begun to infest cherries, roses, pears and possibly other members of the rosaceae. Quite a bit of work has been done on the differences between flies infesting hawthorn and flies infesting apple. There appear to be differences in host preferences among populations. Offspring of females collected from on of these two hosts are more likely to select that host for oviposition (Prokopy et al. 1988). Genetic differences between flies on these two hosts have been found at 6 out of 13 allozyme loci

(Feder et al. 1988, see also McPheron et al. 1988). Laboratory studies have shown an asynchrony in emergence time of adults between these two host races (Smith 1988). Flies from apple trees take about 40 days to mature, whereas flies from hawthorn trees take 54-60 days to mature. This makes sense when we consider that hawthorn fruit tends to mature later in the season that apples. Hybridization studies show that host preferences are inherited, but give no evidence of barriers to mating. This is a very exciting case. It may represent the early stages of a sympatric speciation event (considering the dispersal of R. pomonella to other plants it may even represent the beginning of an adaptive radiation). It is important to note that some of the leading researchers on this question are urging caution in interpreting it. Feder and Bush (1989) stated:

> "Hawthorn and apple "host races" of R. pomonella may therefore represent incipient species. However, it remains to be seen whether host-associated traits can evolve into effective enough barriers to gene flow to result eventually in the complete reproductive isolation of R. pomonella populations."

5.5.2 Gall Former Fly (Eurosta solidaginis)

Eurosta solidaginis is a gall forming fly that is associated with goldenrod plants. It has two hosts: over most of its range it lays its eggs in Solidago altissima, but in some areas it uses S. gigantea as its host. Recent electrophoretic work has shown that the genetic distances among flies from different sympatric hosts species are greater than the distances among flies on the same host in different geographic areas (Waring et al. 1990). This same study also found reduced variability in flies on S. gigantea. This suggests that some E. solidaginis have recently shifted hosts to this species. A recent study has compared reproductive behavior of the flies associated with the two hosts (Craig et al. 1993). They found that flies associated with S. gigantea emerge earlier in the season than flies associated with S. altissima. In host choice experiments, each fly strain ovipunctured its own host much more frequently than the other host. Craig et al. (1993) also performed several mating experiments. When no host was present and females mated with males from either strain, if males from only one strain were present. When males of both strains were present, statistically significant positive assortative mating was seen. In the presence of a host, assortative mating was also seen. When both hosts and flies from both populations were present, females waited on the buds of the host that they are normally associated with. The males fly to the host to mate. Like the Rhagoletis case above, this may represent the beginning of a sympatric speciation.

5.6 Flour Beetles (Tribolium castaneum)

Halliburton and Gall (1981) established a population of flour beetles collected in Davis, California. In each generation they selected the 8 lightest and the 8 heaviest pupae of each sex. When these 32 beetles had emerged, they were placed together and allowed to mate for 24 hours. Eggs were collected for 48 hours. The pupae that developed from these eggs were weighed at 19 days. This was repeated for 15 generations. The results of mate choice tests between heavy and light beetles was compared to tests among control lines derived from randomly chosen pupae. Positive assortative mating on the basis of size was found in 2 out of 4 experimental lines.

5.7 Speciation in a Lab Rat Worm, Nereis acuminata

In 1964 five or six individuals of the polychaete worm, Nereis acuminata, were collected in Long Beach Harbor, California. These were allowed to grow into a population of thousands of individuals. Four pairs from this population were transferred to the Woods Hole Oceanographic Institute. For over 20 years these worms were used as test organisms in environmental toxicology. From 1986 to 1991 the Long Beach area was searched for populations of the worm. Two populations, P1 and P2, were found. Weinberg, et al. (1992) performed tests on these two populations and the Woods Hole population (WH) for both postmating and premating isolation. To test for postmating isolation, they looked at whether broods from crosses were successfully reared. The results below give the percentage of successful rearings for each group of crosses.

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WH × WH - 75%
P1 × P1 - 95%
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P2 × P2 - 80%
P1 × P2 - 77%
WH × P1 -  0%
WH × P2 -  0%
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They also found statistically significant premating isolation between the WH population and the field populations. Finally, the Woods Hole population showed slightly different karyotypes from the field populations.

5.8 Speciation Through Cytoplasmic Incompatability Resulting from the Presence of a Parasite or Symbiont

In some species the presence of intracellular bacterial parasites (or symbionts) is associated with postmating isolation. This results from a cytoplasmic incompatability between gametes from strains that have the parasite (or symbiont) and stains that don't. An example of this is seen in the mosquito Culex pipiens (Yen and Barr 1971). Compared to within strain matings, matings between strains from different geographic regions may may have any of three results: These matings may produce a normal number of offspring, they may produce a reduced number of offspring or they may produce no offspring. Reciprocal crosses may give the same or different results. In an incompatible cross, the egg and sperm nuclei fail to unite during fertilization. The egg dies during embryogenesis. In some of these strains, Yen and Barr (1971) found substantial numbers of Rickettsia-like microbes in adults, eggs and embryos. Compatibility of mosquito strains seems to be correlated with the strain of the microbe present. Mosquitoes that carry different strains of the microbe exhibit cytoplasmic incompatibility; those that carry the same strain of microbe are interfertile.

Similar phenomena have been seen in a number of other insects. Microoganisms are seen in the eggs of both Nasonia vitripennis and N. giraulti. These two species do not normally hybridize. Following treatment with antibiotics, hybrids occur between them (Breeuwer and Werren 1990). In this case, the symbiont is associated with improper condensation of host chromosomes.

For more examples and a critical review of this topic, see Thompson 1987.

5.9 A Couple of Ambiguous Cases

So far the BSC has applied to all of the experiments discussed. The following are a couple of major morphological changes produced in asexual species. Do these represent speciation events? The answer depends on how species is defined.

5.9.1 Coloniality in Chlorella vulgaris

Boraas (1983) reported the induction of multicellularity in a strain of Chlorella pyrenoidosa (since reclassified as C. vulgaris) by predation. He was growing the unicellular green alga in the first stage of a two stage continuous culture system as for food for a flagellate predator, Ochromonas sp., that was growing in the second stage. Due to the failure of a pump, flagellates washed back into the first stage. Within five days a colonial form of the Chlorella appeared. It rapidly came to dominate the culture. The colony size ranged from 4 cells to 32 cells. Eventually it stabilized at 8 cells. This colonial form has persisted in culture for about a decade. The new form has been keyed out using a number of algal taxonomic keys. They key out now as being in the genus Coelosphaerium, which is in a different family from Chlorella.

5.9.2 Morphological Changes in Bacteria

Shikano, et al. (1990) reported that an unidentified bacterium underwent a major morphological change when grown in the presence of a ciliate predator. This bacterium's normal morphology is a short (1.5 um) rod. After 8 - 10 weeks of growing with the predator it assumed the form of long (20 um) cells. These cells have no cross walls. Filaments of this type have also been produced under circumstances similar to Boraas' induction of multicellularity in Chlorella. Microscopic examination of these filaments is described in Gillott et al. (1993). Multicellularity has also been produced in unicellular bacterial by predation (Nakajima and Kurihara 1994). In this study, growth in the presence of protozoal grazers resulted in the production of chains of bacterial cells.

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