CHAPTER **5**

SPECIATION AND TAXONOMIC DECISIONS

Demeke13

Ecological niche = fit of sp. living under specific environmental conditions

What taxonomists encounter in nature are concrete things: individuals and populations. The taxonomist knows that they belong to species, and the first task is to assemble populations in a way that leads to the best delimitation of species taxa. If species had been created according to a plan, this task might be easy. However, it is not, for species are the product of the opportunistic process of evolution. Two aspects of evolution in particular are responsible for the difficulties the taxonomist encounters in trying to delimit species: variability within populations and the existence of incipient species, that is, populations that have evolved only part of the way toward species status. Infrapopulational variation is discussed in Chapter 4. The emphasis in this chapter is on the consequences of the fact that species are the product of evolution. In order to be able to interpret correctly the difficulties created by opportunistic evolution, it is necessary to analyze the process by which new species taxa originate.

THE ORIGIN OF NEW SPECIES TAXA

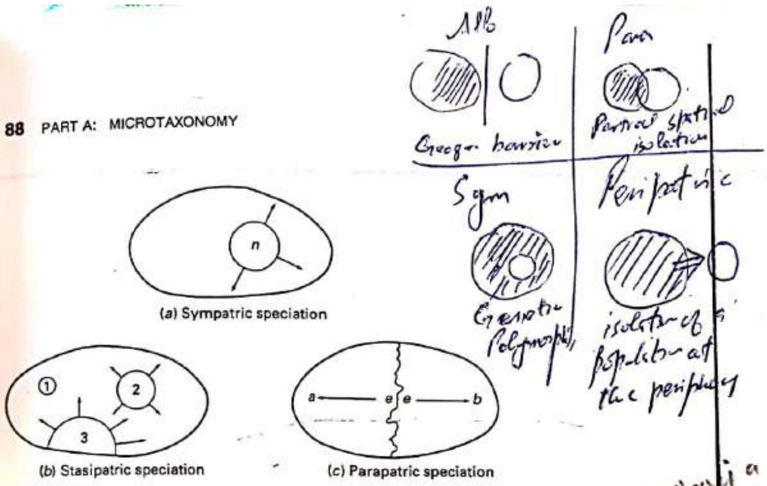
Although it is now universally believed that geographic or *allopatric* speciation is the most common process by which new species of animals originate, other modes have been proposed. It is still controversial how frequent these modes are and indeed whether some of them occur at all.

Many of the controversies concerning speciation are due to the fact that the opponents did not see clearly that speciation has two aspects, genetic and populational. Contrary to the beliefs of some authors, these two aspects are not mutually exclusive alternatives; both are always involved simultaneously.

As far as the genetics of speciation is concerned, the evolutionist is compelled to confess that more than 80 years after the rediscovery of Mendel's laws, there is still almost complete uncertainty regarding its mechanisms (Barigozzi 1982). Chromosome structure is sometimes involved in speciation, but in other cases it is not. The best understood of all categories of genes, the enzyme genes, seem to be minimally involved in episodes of speciation. What other kinds of DNA are causally connected with the acquisition of isolating mechanisms is completely unknown. Regulatory genes are sometimes suspected, but there is no solid evidence for this. It is only in polyploidy that the genetic situation is reasonably well understood. In this case the doubling of the chromosomes—or in the case of triploidy the addition of a third set of chromosomes—may induce instantaneous *speciation,* that is, the production of a reproductively isolated individual. As deplorable as this ignorance of the genetic mechanisms of speciation is in regard to evolutionary studies, it seems to raise no major difficulties for the taxonomist.

Speciation, however, is not only a genetic but also a populational phenomenon, allowing for two very different processes.

1 New species may originate by the instantaneous production of a reproductively isolated individual within a population, as in *polyploidy*. This process may raise two problems. First, the new species individual, owing to polyploidy or another form of chromosomal restructuring, may have acquired total cross-sterility with the parent species but no morphological difference. Its recognition as a biological species will thus be very difficult except when artificial breeding or cultivation is possible. Sexually reproducing polyploid species occur in turbellarians, oligochaetes, leeches, pulmonate mollusks, some groups of insects, fishes, and anurans, but except in oligochaetes, polyploidy is a relatively rare phenomenon in animals. A second difficulty exists when the new karyotype does not produce complete sterility in crosses with individuals of the parent karyotype. White (1978) postulated that new species can originate under these conditions within the parental species population by means of a process he called *stasipatric speciation,* but this possibility has been questioned by Key (1981), Mayr (1982*b*), and others. There is no sound evidence for such a process. (Figure 5-1*b*).



(a) Sympatric speciation

(b) Stasipatric speciation

(c) Parapatric speciation

FIGURE 5-1
Models of gradual nonallopatric speciation. (a) *Sympatric speciation.* A new species originates within the range of the parental species through development of different mate preferences and/or ecological segregation. (b) *Stasipatric speciation.* New species populations originate within the range of the parental species through chromosomal mutation and subsequent displacement of the parental species. (c) *Parapatric speciation.* An intrinsic species barrier within the originally contiguous species *ab* evolves along the ecological escarpment *ee*, resulting in the two species *a* and *b*.

Contiguous = sharing a common border
Touching each other

Natural selection / gene drift

2 Speciation may result from a gradual genetic reconstruction of populations. By and large the various possibilities under this heading can be assigned to six postulated classes:

a *Sympatric speciation:* This can be defined as the origin of a new, reproductively isolated species population within the dispersal area of the offspring of the parental deme (Bush 1975) (Figure 5-1*a*). How frequent sympatric speciation is—indeed, whether it occurs at all (Futuyma and Mayer 1980; Paterson 1982; Barigozzi 1982)—is still controversial. The most probable cases involve host-specific plant feeders and host-specific parasites. Since a switch to a new host is most easily accomplished in a small founder population, the origin of most host-specific species may well be due to peripatric speciation (see below) not requiring sympatric speciation.

evolution in a shared space

b *Parapatric speciation:* In this mode of speciation, it has been postulated (Endler 1977) that isolating mechanisms build up in a cline, along an ecological escarpment, until the two adjacent populations finally are reproductively isolated (Figure 5-1*c*). All the observed cases of more or less drastic belts of intergradation between two subspecies or semispecies known to us are far better explained as zones of secondary contact of two formerly isolated populations.

Evolution in contiguous niches

steep slope separating two land areas at diff. heights

Nevo (1982), in an analysis of such "tension zones," found no evidence whatsoever for a reenforcement of isolating mechanisms; neither have Butlin (1986), Hewitt (1989), and several other recent authors. For these and other reasons, the occurrence of parapatric speciation is unlikely (Mayr and O'Hara 1986).

c *Geographic or allopatric speciation:* This term designates cases in which reproductive isolation is gradually (at a minimum over several generations) acquired in spatially isolated populations. Within allopatric speciation two subtypes can be distinguished:

Selection of gene drift

(1) *Traditional allopatric speciation (dichopatric speciation):* According to this theory, a reasonably large distributional area is divided by a newly arising barrier (geological, geographic, vegetational), which secondarily splits the previously continuous range into two isolated groups of populations (Figure 5-2).

(2) *Peripatric speciation by primary isolation:* Here a new population is founded outside the continuous species range by a single colonist (a fertilized female) or a small founder group and remains isolated long enough to acquire the genetic basis for reproductive isolation (Figure 5-3).

evolution in isolated niche

d *Speciation in time:* Those who believe that speciation in time can occur postulate that a species (phyletic lineage) may change genetically in the course of time to such a degree that the descendants will be reproductively isolated from their own ancestral population if the two could meet. If no appreciable morphological change has occurred during the same period, there will be sibling species in time. The practicing paleotaxonomist has no choice but to ignore such a possibility. However, if morphological change has occurred over time, the taxonomist must decide how much change indicates the attainment of species level. As with geographically isolated populations, it is not possible to provide reliable proof of the species status of *allochronic* populations.

All six of these possible modes of speciation can create situations that make the delimitation of species taxa difficult. This is true even for instantaneous speciation, because individuals with a new karyotype may be reproductively isolated but phenotypically identical. In each of the other five processes of speciation taxonomists assume the existence of incipient species, that is, of populations in the process of genetic reconstruction and a gradual acquisition of isolating mechanisms. The decision whether to designate such incipient species as full species or subspecies is of necessity sometimes arbitrary. The application of the biological species concept helps one make a decision in most difficult cases. For a more detailed treatment of speciation, see Mayr (1970).

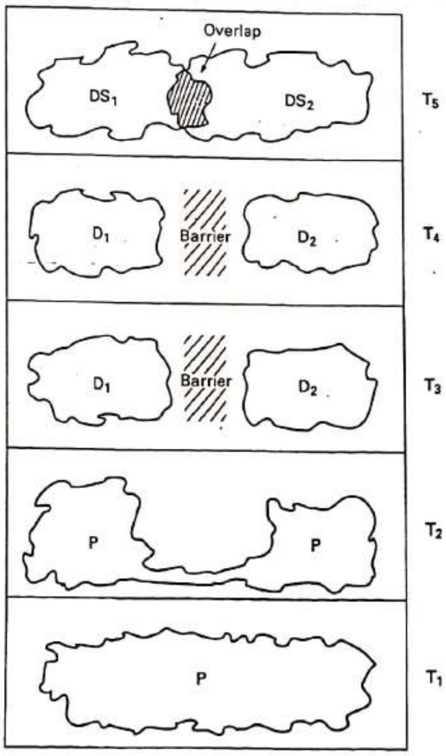


FIGURE 5-2
Dichopatric speciation (speciation by splitting). The parental species P is separated at time 3 (T_3) by a barrier into two daughter populations D_1 and D_2. During their isolation (times T_3 and T_4) these separated populations evolve into two independent species, DS_1 and DS_2, which at time T_5 can overlap without interbreeding.

DECISIONS IN DIFFICULT CASES

The working taxonomist generally encounters two categories of practical problems. Decisions must be made about which individuals encountered in a given locality belong to a single interbreeding population (hence are conspecific) or belong to sympatric species and about which populations, different in space and time, which belong to the same species (see above).

Analysis of Sympatric Samples

On the whole, three very different kinds of situations are responsible for difficulties with sympatric samples:

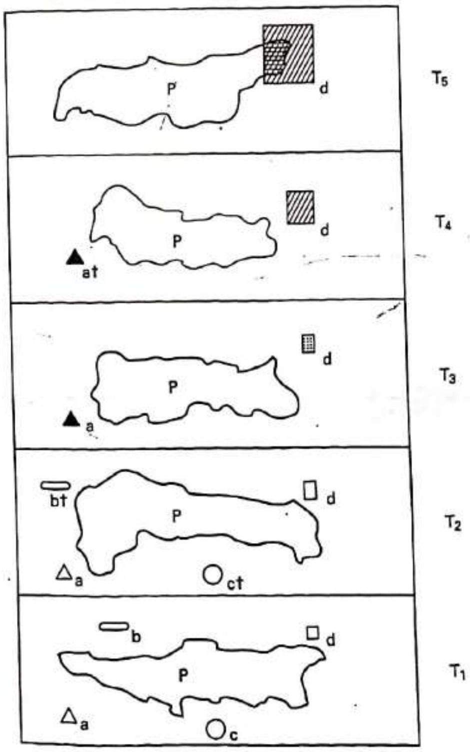


FIGURE 5-3
Peripatric speciation (speciation by budding). Parental species P with four peripheral isolates (a, b, c, d) at time 1 (T_1). Isolates b and c become extinct at time 2 (T_2), isolate a at time 4 (T_4). Isolate d becomes a different species and has overlapped the range of the parental species P at time 5 (T_5).

1 Extreme difference among phena belonging to a single species. The analysis of this situation and methods of resolving it taxonomically are discussed in Chapter 4.

2 Extreme similarity of good biological species (sibling species).

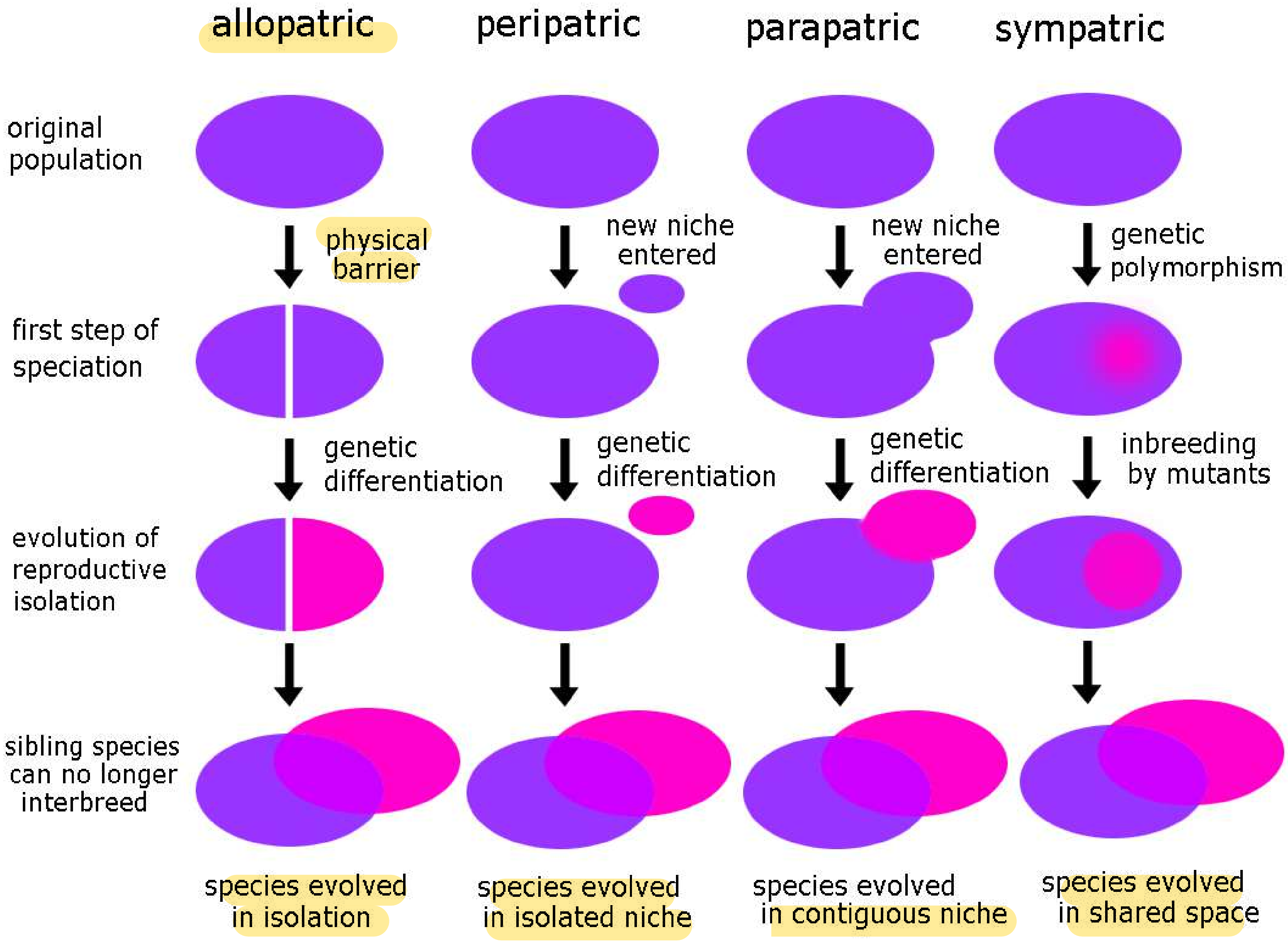
3 Wide variability and phenotypic overlap of two species (discussed in this chapter).

Sibling Species Biological species are reproductively isolated *gene pools* (Chapter 2). When two populations (gene pools) become geographically isolated, they diverge genetically and may eventually acquire isolating mechanisms. As a by-product of the genetic divergence during this process, most species also acquire morphological differences that are suitable for diagnostic purposes, but a few species fail to acquire such differences. Such very similar species are called *cryptic or sibling species*. All the available evidence indicates that they differ from ordinary species only by the minuteness of the morphological difference, not by other biological criteria. They are merely species which are near the invisible end of the spectrum of morphological species differences. Sibling species grade imperceptibly into species that are morphologically more and more distinct from one another. However, once discovered and thoroughly studied, they are usually found to have at least a few previously overlooked morphological differences.

Sibling species are not recent species or incipient species. For several pairs of sibling species the date of speciation has been determined, ranging from several million to 18 million years ago (Bullini et al. 1978). If within a single genus both sibling species and morphologically distinct species occur, the latter tend to be older.

Mayr (1963:33–58) has shown how widespread sibling species are in the animal kingdom. Most of them were discovered not during routine taxonomic analysis but during the study of species that are medically (e.g., *Anopheles*), genetically (e.g., *Drosophila, Paramecium*), cytologically, or agriculturally of special importance. It is therefore impossible to indicate what percentage of species are sibling species. In the case of North American crickets, about 50 percent of the species were discovered through differences in their sounds (Walker 1964), and in certain genera of protozoans (e.g., *Paramecium*), the percentage of cryptic species seems to be even higher.

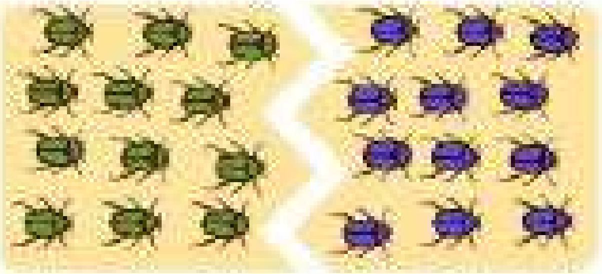
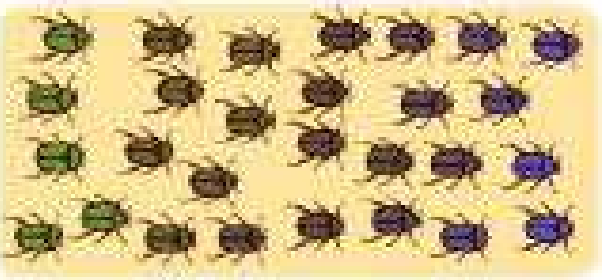
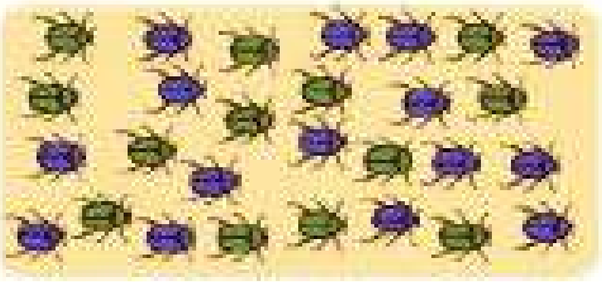
Sibling species can be discovered because they differ in various other attributes even when they are extremely similar in the morphological characteristics normally employed in taxonomic analysis. Mayr (1963:50) listed a number of characteristics that facilitate the recognition of sibling species. Precise measurements sometimes reveal bimodal characteristics, and the two modes can be correlated with additional characters. There are often differences in the number or structure of the chromosomes, a fact which has led to the recognition of sibling species in *Drosophila, Sciara, Chironomus, Prosimulium,* and other dipterans as well as in orthopterans, beetles, and other insects. Various aspects of behavior—such as differences in visual and vocal displays, nest construction, breeding season, migratory behavior, prey selection, and host preference—have perhaps led to the discovery of more sibling species than have any other type of characteristic. Sibling species may differ in their pathogenicity (e.g., *Anopheles*) or in their susceptibility to parasites and suitability to serve as hosts. Various biochemical methods, particularly

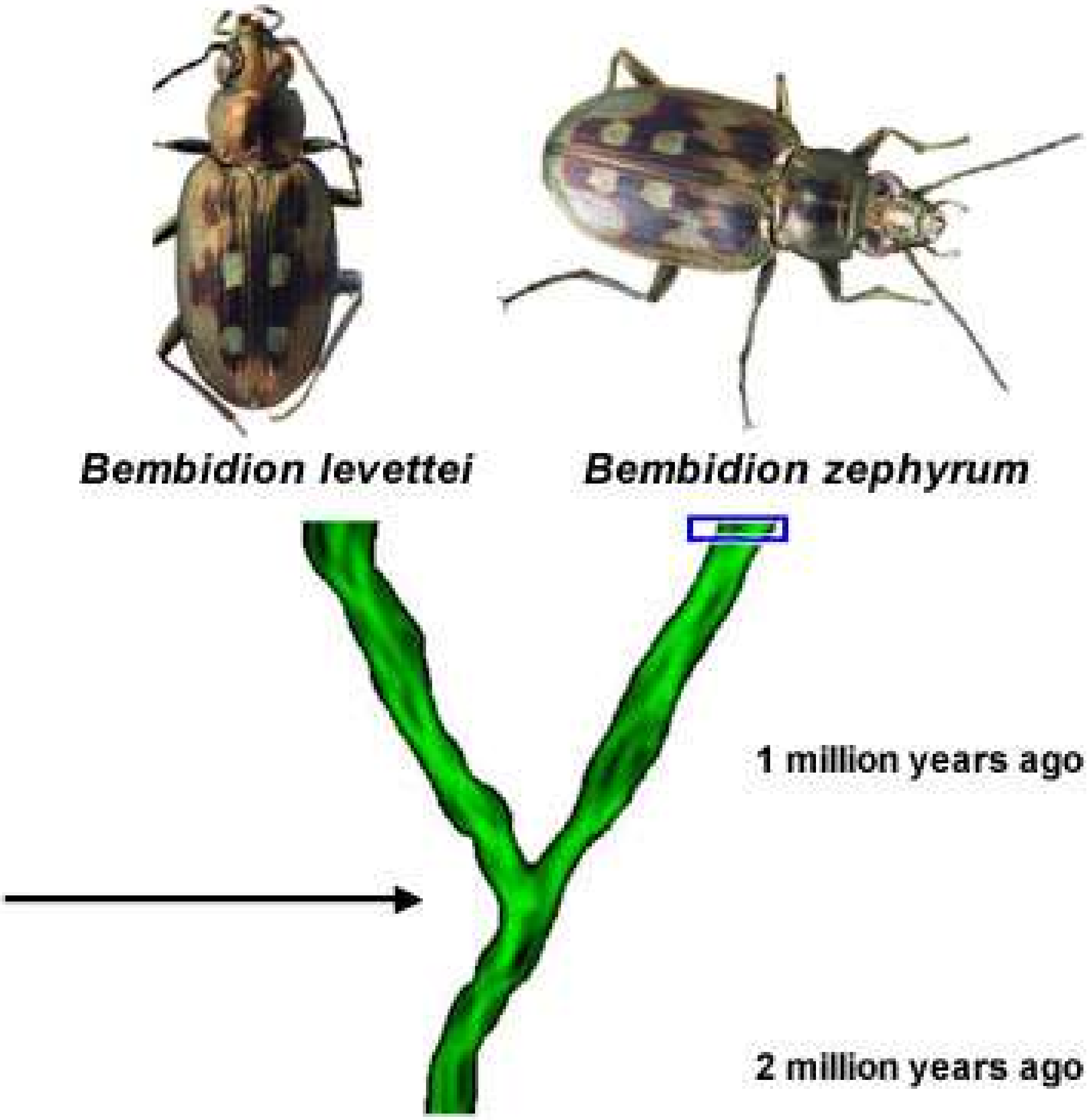

allopatric
peripatric
parapatric
sympatric
original population
physical barrier
new niche entered
new niche entered
genetic polymorphism
first step of speciation
genetic differentiation
genetic differentiation
genetic differentiation
inbreeding by mutants
evolution of reproductive isolation
sibling species can no longer interbreed
species evolved in isolation
species evolved in isolated niche
species evolved in contiguous niche
species evolved in shared space

Modes of Speciation

The key to speciation is the evolution of genetic differences between the incipient species. For a lineage to split once and for all, the two incipient species must have genetic differences that are expressed in some way that causes matings between them to either not happen or to be unsuccessful. These need not be huge genetic differences. A small change in the timing, location, or rituals of mating could be enough. But still, some difference is necessary. This change might evolve by natural selection or genetic drift.

Reduced gene flow probably plays a critical role in speciation. Modes of speciation are often classified according to how much the geographic separation of incipient species can contribute to reduced gene flow. The following table compares some of these speciation modes.

Mode of speciation	**New species formed from...**	
Allopatric (allo = other, patric = place)	geographically isolated populations	
Peripatric (peri = near, patric = place)	a small population isolated at the edge of a larger population	
Parapatric (para = beside, patric = place)	a continuously distributed population	
Sympatric (sym = same, patric = place)	within the range of the ancestral population	


Bembidion levettei
Bembidion zephyrum
1 million years ago
2 million years ago