

# Allopatric and sympatric modes of speciation: examples from *Drosophila*

B. N. Singh\*

Genetics Laboratory, Department of Zoology, Institute of Science, Banaras Hindu University, Varanasi 221 005, India

**Basically, there are two different ways by which new species are created: anagenesis and cladogenesis (true speciation). During anagenesis, one species is transformed into new one so there is a phyletic change in the course of time and there is no involvement of reproductive isolation. Cladogenesis is considered as true speciation during which new species originate through splitting of pre-existing ones. Different models have been proposed from time to time to explain the modes of speciation. There are two important modes of speciation which are primarily based on geographic factors: allopatric (dichopatric and peripatric) and sympatric. In this article, both allopatric and sympatric modes of speciation are briefly described with the help of suitable examples from *Drosophila*.**

**Keywords:** Allopatric, *Drosophila*, speciation, sympatric.

SPECIES is a taxonomic rank and it is also the basic unit of binomial classification. There are a large number of concepts of species which define them in different ways<sup>1,2</sup>. Linnaeus (1707–1778), a prominent taxonomist suggested the binomial nomenclature and was a strong supporter of typological species concept (essentialism). Mayr and Ashlock<sup>3</sup> have described four species concepts: typological, nominalistic, biological and evolutionary species concepts in their book *Principle of Systematic Zoology*. The most widely accepted concept is biological species concept (BSC) which has been elaborated in detail by Jordan, Mayr and Dobzhansky<sup>2</sup>. Different species concepts and modes of speciation have also been discussed by Singh<sup>2</sup>. Coyne and Orr<sup>4</sup> suggested that definitions of species have been historically controversial but one of the most widely accepted concept is BSC. According to Castillo and Barbash<sup>5</sup>, BSC works well for *Drosophila* for the study of evolution of reproductive isolation, but other species concepts may have more utility for taxonomic and systematic studies. Mayr<sup>6</sup> defined a species as ‘Group of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups’. Dobzhansky was a population geneticist and introduced the term gene pool to the definition of

species, which was ‘Reproductive community of sexually or cross fertilizing individuals which share in a common gene pool’<sup>7</sup>. Evolutionary species concept was suggested by Simpson<sup>8</sup> who considered species as a lineage (ancestral-derived relationship), but it was criticized by Mayr<sup>9</sup> who denied it as the definition of species, but that of phyletic lineage which was also applicable to incipient species. There are more than twenty species concepts suggested by naturalists, evolutionary biologists and taxonomists<sup>1,2,10</sup>. Darwin<sup>11</sup> who proposed the natural selection theory of evolution to explain the mechanisms of evolution, was initially a supporter of BSC but later supported morphological species concept which was related to his theory of natural selection<sup>12</sup>. Mayr<sup>13</sup> introduced the concept of sibling species for those species which were morphologically similar but reproductively isolated. In *Drosophila*, a large number of sibling species (pairs or groups) showing evolutionary significance have been reported<sup>14</sup>. Cook<sup>15</sup> coined the term speciation during which new species of organisms arise. Different evolutionary biologists have suggested different modes of speciation<sup>3,4,13,16–21</sup>. The terms used in this article are explained, which are: Allopatry – species living in different geographical areas; Sympatry – species living in the same geographical area; Genetic drift – random fluctuation in allele frequency in small populations; Founder effect – when a daughter species arises from a few individuals (in extreme case a single gravid female), there will be a larger founder effect; Asymmetrical mode of sexual isolation – between two species when sexual isolation is one-sided, it is called asymmetrical isolation, and when sexual isolation is two-sided, it is called symmetrical isolation; Ancestral-derived species – when the original species giving rise to another (new) species, the former is ancestral species and the new one is derived species; Stabilizing, centripetal or normalizing selection – it signifies selection for intermediate phenotypes and elimination of extreme phenotypes, which leads to reduction in the degree of genetic variability; Disruptive selection or diversifying selection is, when a population is subjected within a single generation to various environments to which different genotypes are most suited and this leads to sustain the genetic variability. Different factors have been considered important in the process of speciation such as mechanisms generating genetic variability, origin of reproductive isolating mechanisms and geographical

\*e-mail: bnsingh@bhu.ac.in

factors. On the basis of these factors, White<sup>16</sup> proposed different models to explain the modes of cladogenesis (true speciation) like: (i) Strict allopatry without a narrow population bottleneck, (ii) Strict allopatry with a narrow population bottleneck (founder effect), (iii) Extinction of intermediate populations in a chain of races, (iv) Clinal speciation, (v) Area effect speciation (primarily genic), (vi) Stasipatric speciation (primarily chromosomal), and (vii) Sympatric speciation. White<sup>16</sup> considered polyploidy which is basically a chromosomal model separately, and comes under sympatric mode of speciation that commonly occurs in plants. Mayr<sup>13</sup> gave much emphasis on geographic speciation (allopatric) which is an important mode of speciation. Thus, two speciations are primarily important namely, allopatric and sympatric, during which new species of organisms arise due to origin of reproductive isolating mechanisms which are considered a pre-requisite for speciation<sup>22</sup>. Sexual isolation which is a prezygotic (pre-mating) isolation has been extensively studied in *Drosophila*, and the asymmetrical mode of mating preference is considered to discuss ancestral-derived relationship between species which are primarily based on allopatric and sympatric modes of speciation<sup>23,24</sup>. Nanda and Singh<sup>25</sup> discussed the behavioural reproductive isolation and speciation in different species groups of *Drosophila* including Hawaiian species along with origin of sexual isolation, genetics of pre-mating isolation, asymmetrical mode of mating preference, and the direction of evolution. In this article, both allopatric and sympatric modes of speciation are discussed briefly with suitable examples from *Drosophila* which is considered as an interesting and important biological model.

### Allopatric mode of speciation

Based on geographical distribution of species/populations, different terms are used such as sympatric, allopatric, parapatric and peripatric. To explain the mechanism of speciation, geographical component is very important. It may range from absence (sympatric) to complete separation (allopatric). Allopatric mode of speciation was initially called geographic speciation by Mayr<sup>13,18</sup> who believed that it was the most important mode of speciation. Whereas other evolutionists used the term 'allopatric' mode of speciation<sup>4,16,21</sup>. Basically allopatric speciation is of two types: dichopatric or dumbbell model and peripatric speciation. There is a sharp difference between these two types. In dichopatric, there is no role of genetic drift or population bottleneck or founder principle. However, in the peripatric speciation, there is a profound effect of genetic drift/population bottleneck/founder principle. In dichopatric mode of cladogenesis, a population of species splits into two subpopulations which are of large size separated by geographical/ecological barriers having no contact and no gene flow

between them. Both subpopulations which are allopatric in distribution, evolve independently due to the action of different evolutionary forces such as mutation, natural selection, genetic drift, migration, etc. and accumulate micro-evolutionary changes in the long course of time. Because of geographic isolation, gene flow between them is completely prevented and they become genetically different. In the long run, they develop genetically based mechanisms of reproductive isolation and acquire the status of two separate allopatric species. If the geographic barrier is removed, they become two sympatric species but interbreeding is prevented between them since they would have already developed reproductive isolating mechanisms. Thus, allopatric species become sympatric species due to removal of geographical barrier, and still maintain their own gene pool due to prevention of interbreeding. Thus, allopatric species originating through dichopatric mode of speciation (dumbbell model) become sympatric because of the developing zone of contact resulting from the removal of geographical barrier. One example of dumbbell model of allopatric speciation is provided in Hawaiian *Drosophila* when the population existing at low elevation had been split into two by the separation of two islands Molokai from Maui due to rise in sea level<sup>16</sup>.

In the allopatric mode of speciation (with a narrow population bottleneck), which is also known as peripatric mode of speciation, a small number of individuals (in extreme case a single gravid female) migrate from the original population to a new area and evolve into a new species in the long course of time. It becomes genetically different from the original population as it passes through population bottleneck/founder effect/flush crash cycle. It has also been suggested that the rate of evolution is faster in such cases because of the action of genetic drift and genetic differences. This is the basic difference between dichopatric and peripatric modes of speciation although broadly both come under allopatric mode. Carson<sup>26-29</sup> did extensive work on Hawaiian species of *Drosophila* and explained their evolution by peripatric mode of speciation involving population bottleneck, founder principle, random genetic drift and flush crash cycles. In the Hawaiian Islands, there are more than 500 species of *Drosophila* distributed on different islands and their evolution has been explained by founder principle. There are about 100 picture winged *Drosophila* species which have been utilized for evolutionary, behavioural and cytogenetic studies<sup>23,30,31</sup>. Kaneshiro<sup>23,32</sup> studied certain aspects of behavioural isolation in certain species of picture winged Hawaiian *Drosophila*. Based on asymmetrical mode of sexual isolation (one-sided sexual isolation), Kaneshiro<sup>23</sup> suggested the direction of evolution among the species of *D. planitibia* subgroups: *D. differens*, *D. planitibia*, *D. heteroneura* and *D. silvestris*. Based on the asymmetrical mode of mating preference, he suggested that the ancestral females discriminate against derived males because

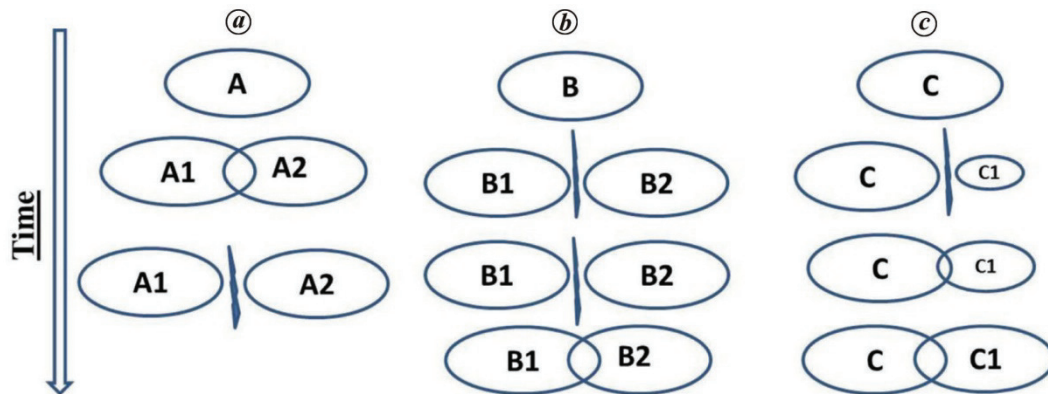
of loss of certain courtship elements of males due to random genetic drift. His model is also based on genetic drift (founder effect) causing allopatric mode of speciation. Origin of asymmetrical sexual isolation in drift lines with varying number of founders has been reported in *D. ananassae*<sup>33</sup>. The phylogenetic relationship between the species/strains based on asymmetrical mode of mating preference has also been suggested to support Kaneshiro's model<sup>34–38</sup>. Thus, the findings on these species support the role of genetic drift in speciation extending evidence for allopatric mode of speciation.

### Sympatric mode of speciation

Sympatric mode of speciation has been explained by different evolutionary biologists<sup>4,16,20,21</sup>. Singh<sup>2</sup> also reviewed species concepts and modes of speciation with the help of various examples. In the same geographical area, new species originates from the segments of the original population through instantaneous origin of reproductive isolation. Both species remain in the same geographical area and maintain their integrity. These species are called sympatric species. However, when they are separated, and one or both species move to other areas, they are called allopatric species. Thus, in the sympatric mode of speciation, the most important factor is the instantaneous origin and development of certain reproductive isolating mechanisms between the segments of original population and parental population in the same geographical area. Hence, it has been stated that the reproductive isolating mechanisms are pre-requisites for speciation<sup>22</sup>. Several examples demonstrating the occurrence of sympatric mode of speciation are described by White<sup>16</sup>. Polyploidy, which is a more common means of speciation in plants also comes under this mode. As far as *Drosophila* is concerned, a very good example was cited from the laboratory experiments on disruptive selection in *D. melanogaster*<sup>39</sup>. Selection was done for high and low number of sternopleural bristles in *D. melanogaster* for several generations. In each generation, tests were carried out to determine the type of progeny produced by forced high–high, high–low and low–low matings. It was confirmed by these tests that the absence of flies with intermediate number of sternopleural bristles after several generations was due to reproductive isolation between two types of flies. It was an interesting experiment demonstrating the occurrence of sympatric speciation in a laboratory. Disruptive selection for sternopleural bristle number in *D. melanogaster* produced divergence for both sexual isolation and the bristle number simultaneously. Thus, the development of sexual (behavioural or ethological) isolation due to disruptive selection in the laboratory demonstrated the role of sympatric speciation in *D. melanogaster*<sup>16</sup>. Nanda and Singh<sup>40</sup> conducted similar experiments in *D. ananassae* for 12 generations, but disruptive selection for sternopleural

bristle phenotypes did not produce ethological isolation between high and low lines' flies, as the pattern of mating between the two types was random. However, this affected the mating propensity of flies in different selection lines, i.e. high line flies had high mating propensity and the low lines showed low mating success. Thus, the results of *D. ananassae* did not support the observation reported in *D. melanogaster*<sup>39</sup>.

Watanabe and Kawanishi<sup>24</sup> suggested a hypothesis which was just opposite to that of Kaneshiro's, to explain the direction of evolution based on asymmetrical mode of mating preference. They studied sexual isolation among *D. melanogaster*, *D. simulans* and *D. mauritiana* and found one-sided sexual isolation between them. According to their model, the derived females discriminated against the ancestral males<sup>24</sup>. The concept<sup>24</sup> given by them has been used to discuss the evolutionary sequence of species in different species groups of *Drosophila*. Watanabe and Kawanishi<sup>24</sup> proposed that the failure of mating between females of new species and males of ancestral species was the first step in developing reproductive isolation and creation of incipient species favouring sympatric mode of speciation<sup>41</sup>. They also suggested that the genes of new populations, if found in ancestral populations due to some matings between females of ancestral species with the males of derived ones, are eliminated through the action of stabilizing selection<sup>24</sup>. One-sided mating preference has been found between *D. bipectinata* and *D. parabipectinata*, where *D. bipectinata* is considered ancestral to *D. parabipectinata* because females of *D. parabipectinata* discriminate against the males of *D. bipectinata*. This favours Watanabe and Kawanishi's hypothesis<sup>42,43</sup>. Asymmetrical mating preference between isofemale lines of *D. ananassae*<sup>44</sup> as well as light (*pallidosa*) and dark (*ananassae*) forms of *D. ananassae*<sup>45,46</sup> have also been explained by Watanabe and Kawanishi's model, as derived females discriminate against ancestral males<sup>41</sup>. Thus *D. ananassae* (dark form) is considered ancestral to *D. pallidosa* (light form). Both these species are sympatric in distribution and their separation is maintained by ethological isolation. *D. ananassae* is a cosmopolitan and domestic species whereas its sibling *D. pallidosa* has localized distribution in south central Pacific islands of Samoa and Fiji<sup>46</sup>. These examples support the sympatric mode of speciation<sup>41</sup>. Dobzhansky<sup>47</sup> gave importance to natural selection in sympatric populations for genetic divergence of incipient species. Figure 1 depicts the different modes of speciation during which new species originate in the course of time due to the origin of genetically based reproductive isolating mechanisms. A population of a species may give rise to two separate species characterized by prevention of gene flow which may be sympatric or allopatric depending upon their geographical distribution. During the process of cladogenesis (true speciation), all the three components are important namely, geographical factor, genetic variability and



**Figure 1.** Schematic representation of (a) Sympatric, (b) Allopatric without a narrow population bottleneck and (c) Allopatric with a narrow population bottleneck (peripatric/founder effect) modes of speciation (modified from Bush<sup>20</sup> and Savage<sup>48</sup>). The geographical component and development and perfection of reproductive isolating mechanisms are important for the origin of species.

origin of reproductive isolating mechanisms causing prevention of gene flow between the species.

## Conclusion

There are interesting examples known from *Drosophila* in support of these two modes of speciation. Studies on *Drosophila* demonstrate that new species may originate through both these modes of speciation. In both these cases, the role of reproductive isolating mechanisms are important because it has been observed that without isolation evolution is not possible. The basic difference between the two is geographical factor. In sympatric situation, new species arises from the parental species through the instantaneous origin of reproductive isolating mechanisms and later on when one or both species move to new area, they become allopatric species. On the other hand, in allopatric situation when speciation occurs between two subpopulations of a species which are geographically isolated and new species after acquiring certain mechanisms of reproductive isolation become allopatric species. When the geographical barrier is removed, the two allopatric species become sympatric. Thus sympatric species after moving to new area become allopatric species and allopatric species become sympatric after developing contact zone due to removal of geographical barrier and there is no gene flow between them because they had already developed certain mechanisms of reproductive isolation. In this context, the different models demonstrating the direction of evolution between species based on one-sided sexual isolation (asymmetrical mode of mating preference) are also important because they are based on sympatric and allopatric modes of speciation<sup>41</sup>.

1. Mallet, J., Species, concepts of. In *Encyclopedia of Biodiversity* (ed. Levin, S. A.), Elsevier, Oxford, 2007, pp. 1–15.

- Singh, B. N., Concepts of species and modes of speciation. *Curr. Sci.*, 2012, **103**, 784–790.
- Mayr, E. and Ashlock, P. D., *Principles of Systematic Zoology*, McGraw Hill Int. Edn, Singapore, 1991.
- Coyne, J. A. and Orr, H. A., *Speciation*, Sinauer Associates Inc. Sunderland, Massachusetts, USA, 2004.
- Castillo, D. M. and Barbash, D. A., Moving speciation genetics forward: modern techniques built on fundamental studies on *Drosophila*. *Genetics*, 2017, **207**, 825–842.
- Mayr, E., Speciation phenomena in birds. *Am. Nat.*, 1940, **74**, 249–278.
- Dobzhansky, Th., Mendelian populations and their evolution. *Am. Nat.*, 1950, **84**, 401–418.
- Simpson, G. G., *Principles of Animal Taxonomy*, Columbia University Press, New York, 1961.
- Mayr, E., *The Growth of Biological Thoughts*, Harvard University Press, Cambridge, USA, 1982.
- Mayden, R. L., A hierarchy of species concepts, the development in the saga of species problem. In *Species: The Unit of Biodiversity* (eds Claridge, M. F., Dawah, H. A. and Wilson, M. R.), Chapman and Hall, London, UK, 1997, pp. 381–424.
- Darwin, C., *On the Origin of Species by Means of Natural Selection*, John Muray, London, 1859.
- Mallet, J., A species definition for the modern synthesis. *Trends Ecol. Evol.*, 1995, **9**, 175–180.
- Mayr, E., *Systematics and the Origin of Species*, Columbia University Press, New York, 1942.
- Singh, B. N., The genus *Drosophila* is characterized by a large number of sibling species showing evolutionary significance. *J. Genet.*, 2016, **95**, 1053–1064.
- Cook, D. F., Evolution without isolation. *Am. Nat.*, 1906, **42**, 727–731.
- White, M. J. D., *Modes of Speciation*, W.H. Freeman and Company, San Francisco, 1978.
- Huxley, J., *Evolution: The Modern Synthesis*, Allen and Unwin, London, 1942.
- Mayr, E., *Animal Species and Evolution*, The Belknap Press of Harvard University Press, Cambridge, 1966.
- Wright, S., Population structure in evolution. *Proc. Am. Philos. Soc.*, 1949, **93**, 471–473.
- Bush, G. L., Modes of animal speciation. *Ann. Rev. Ecol. Syst.*, 1975, **6**, 339–364.
- Hartl, D. L. and Clark, A. G., *Principles of Population Genetics*, Sinauer and Associates, Sunderland, Massachusetts, 2007, 4th edn.



## REVIEW ARTICLES

---

22. Singh, B. N., Reproductive isolating mechanisms: prerequisite for speciation. *J. Exp. Zool. India*, 2014, **17**, 23–31.
23. Kaneshiro, K. Y., Ethological isolation and phylogeny in the *Drosophila planitibia* subgroup of Hawaiian *Drosophila*. *Evolution*, 1976, **30**, 740–745.
24. Watanabe, T. K. and Kawanishi, M., Mating preference and the direction of evolution in *Drosophila*. *Science*, 1979, **205**, 906–907.
25. Nanda, P. and Singh, B. N., Behavioural reproductive isolation and speciation in *Drosophila*. *J. Biosci.*, 2012, **37**, 359–374.
26. Carson, H. L., Chromosome tracers of the origin of species. *Science*, 1970, **168**, 1414–1418.
27. Carson, H. L., Speciation and the founder principle. *Stadler Genetics Symposium*, 1971, vol. 3, pp. 51–70.
28. Carson, H. L., Ancient chromosomal polymorphism in Hawaiian *Drosophila*. *Nature*, 1973, **241**, 200–202.
29. Carson, H. L., Pattern of speciation in Hawaiian *Drosophila* inferred from ancient chromosomal polymorphism. In *Genetic Mechanisms of Speciation in Insects* (ed. White, M. J. D.), Australia and New Zealand Book Co., Sydney, Australia, 1987, pp. 81–93.
30. Carson, H. L., Hardy, D. E., Spieth, H. T. and Stone, W. S., Evolutionary biology of the Hawaiian Drosophilidae. In *Essays in Evolution and Genetics in Honour of Theodosius Dobzhansky* (eds Hetch, M. K. and Steere, W. C.), Appleton Century Crafts, New York, 1970, pp. 437–443.
31. Kaneshiro, K. Y., Carson, H. L., Clayton, F. E. and Heed, W. B., Nitch separation in a pair of homosequential *Drosophila* species from Islands of Hawaii. *Am. Nat.*, 1973, **107**, 766–774.
32. Kaneshiro, K. Y., Sexual isolation, speciation and the direction of evolution. *Evolution*, 1980, **34**, 437–444.
33. Nanda, P. and Singh, B. N., Origin of sexual isolation in *Drosophila ananassae* due to founder effect. *Genetica*, 2011, **139**, 779–787.
34. Arita, L. H. and Kaneshiro, K. Y., Ethological isolation between two stocks of *Drosophila adiastola*. *Proc. Hawaii Entomol. Soc.*, 1979, **23**, 31–34.
35. Ahearn, J. N., Evolution of behavioural reproductive isolation in a laboratory stock of *Drosophila silvestris*. *Experientia*, 1980, **36**, 63–64.
36. Kaneshiro, K. Y. and Kurihara, J. S., Sequential differentiation of sexual isolation in populations of *Drosophila silvestris*. *Pac. Sci.*, 1981, **35**, 177–183.
37. Dwivedi, Y. N., Singh, B. N. and Gupta, J. P., One-sided sexual isolation between *Drosophila takahashii* and *D. pseudotakahashii*. *Experientia*, 1982, **38**, 318.
38. Ramachandra, N. B. and Ranganath, H. A., Mating preference between *Drosophila nasuta nasuta* and *Drosophila nasuta albomicans*. *Indian J. Exp. Biol.*, 1987, **25**, 55–57.
39. Thoday, J. M. and Gibson, J. B., Isolation by disruptive selection. *Nature*, 1962, **193**, 1164–1166.
40. Nanda, P. and Singh, B. N., Disruptive selection for sternopleural bristle phenotypes in *Drosophila ananassae*. *Genome*, 2011, **54**, 845–851.
41. Singh, B. N., Mode of mating preference and the direction of evolution in *Drosophila*. *Indian J. Exp. Biol.*, 1997, **35**, 111–119.
42. Singh, B. N., Dwivedi, Y. N. and Gupta, J. P., Sexual isolation among three species of the *Drosophila bipectinata* species complex. *Indian J. Exp. Biol.*, 1981, **19**, 898–900.
43. Banerjee, P. and Singh, B. N., Interspecific sexual isolation and phylogeny among different members of the *Drosophila bipectinata* species complex. *Genetica*, 2012, **14**, 75–81.
44. Singh, B. N. and Chaatterjee, S., Symmetrical and asymmetrical sexual isolation among laboratory strains of *Drosophila ananassae*. *Can. J. Genet. Cytol.*, 1985, **27**, 405–409.
45. Futch, D. G., A study of speciation in South Pacific populations of *Drosophila ananassae*. *Univ. Texas Publ.*, 1966, **6615**, 79–120.
46. Futch, D. G., On the ethological differentiation of *Drosophila ananassae* and *D. pallidosa*. *Evolution*, 1973, **52**, 456–467.
47. Dobzhansky, Th., *Genetics of the Evolutionary Process*, Columbia University Press, New York, 1970.
48. Savage, J. M., *Evolution*, Holt, Rinehart and Winston, Inc., New York, 1963.

ACKNOWLEDGEMENT. I thank the anonymous reviewer for helpful comments on the original draft of the manuscript.

Received 15 January 2021; revised accepted 2 April 2021

doi: 10.18520/cs/v121/i1/56-60

---