# Ring Species and Speciation

**Heath Blackmon,** *The University of Texas at Arlington, Arlington, Texas, USA*

**Jeffery P Demuth,** *The University of Texas at Arlington, Arlington, Texas, USA*

*Based in part on the previous version of this eLS article 'Ring Species and Speciation' (2005) by Jeffery P Demuth and Loren H Rieseberg.*

A ring species is a monophyletic group whose range has extended around a geographic barrier to produce a ring-shaped distribution. The populations that make up the ring should be contiguous and without barriers to gene flow anywhere in the ring except where the terminal populations are sympatric but reproductively isolated from one another. Few, if any of the species that have been described as ring species, actually meet all of these requirements. The best documented example of a species that exhibits all of these traits is the greenish warbler complex (*Phylloscopus trochiloides*). However, even species like the herring gull complex or *Ensatina* salamanders that fail to exhibit some of the characteristics of a true ring species offer opportunities to study important evolutionary processes. These species are particularly helpful in understanding how microevolutionary changes can create two unique species, how speciation can occur in spite of gene flow, and how geographic speciation with or without adaptive divergence can occur.

## What is a Ring Species?

The perfect demonstration of speciation is presented by the situation in which a chain of intergrading subspecies forms a loop or overlapping circle of which the terminal links have become sympatric without interbreeding, even though they are connected by a complete chain of intergrading or interbreeding populations (i.e. 'ring species') (Mayr, 1963).

Most organisms designated as ring species do not adhere to the rigorous definition suggested by Mayr. If examined on a coarse geographical scale, they typically do have the requisite circular distribution of morphologically intergrading populations except in one area, where a sharp morphological discontinuity is found. However, closer scrutiny almost inevitably leads to the discovery of gaps in the distribution of populations around the ring. Moreover, deoxyribonucleic acid (DNA) and protein analyses often detect cryptic barriers to gene flow, suggesting that speciation is complete despite continuous morphological gradation. Mayr (1963) recognised that many examples of ring species did not fit his definition 'in the most diagrammatic manner'. However, he maintained that it was the ability to follow the process of speciation step by step that made ring species such a convincing demonstration of geographic speciation. **See also**: Species and Speciation: An Overview

The term ring species persists primarily because most authors have adopted an implicit definition of ring species that describes taxa in which intergrading geographic varieties are distributed in a ring with overlapping ends. In the area of overlap, two sympatric forms maintain their distinct phenotypes. This is similar to the definition of Mayr (1963) but allows for more than one species to be recognised in the ring, and for discontinuity in the distribution of populations. Ring species is often used synonymously with 'circular overlap' in the literature. The term 'rassenkreis' is also sometimes used in the context of ring species (Stebbins, 1949); however, rassenkreis is more appropriately synonymous with 'polytypic species', which does not imply anything pertaining to geographic distribution. Finally, it deserves emphasis that the importance of studying ring species is not that they demonstrate a particular mode of speciation such as allopatric or parapatric. Rather, they provide natural evidence that speciation has occurred and offer a means for reconstructing the process through study of extant members of the ring. **See also**: Speciation: Introduction; Sympatric Speciation

## Examples of Ring Species

In the following section the authors describe some classic examples of ring species and some more recent ones. The cases reviewed include classic examples outlined by Mayr (1963) in *Animal Species and Evolution*, newer examples reviewed by Irwin *et al.* (2001), and the first example of a

possible Coleopteran ring species. Of the original 22 proposed ring species, 15 were birds. Mayr (1963) attributes this to the maturity of avian taxonomy. In recent years, the bias has been towards mammals. This taxonomic skew is reflected in the examples discussed below.

## *Ensatina* salamanders

### Early hypotheses

The salamanders of the genus *Ensatina* are probably the best known and most thoroughly studied of all ring species. Prior to 1949, *Ensatina* contained four species (*Ensatina eschscholtzii*, *Ensatina sierrae*, *Ensatina croceater* and *Ensatina platensis*) of fully terrestrial, lungless salamanders (family Plethodontidae). Beginning with a comprehensive study of colouration and morphology by Stebbins (1949), *E. eschscholtzii* has been subdivided into seven subspecies. The seven subspecies encircle the Central Valley of California. Three unblotched subspecies (*oregonensis*, *xanthoptica* and *eschscholtzii*) ring the coastal side of the valley, three blotched subspecies (*platensis*, *croceater* and *klauberi*) complete the ring along the interior Sierra Nevada Mountains and an intermediate 'mottled' subspecies (*picta*) is found north of the valley along the California–Oregon coast (**Figure 1**). In addition to the obvious morphological gradation, extensive collecting (Stebbins, 1949) demonstrated that subspecies freely interbreed in northern California, but hybridise only occasionally where *xanthoptica* crosses the valley in central California (**Figure 1**). Where the two subspecies *eschscholtzii* and *klauberi* meet in southern California they occur microsympatrically without interbreeding. Based on this information, Stebbins (1949) hypothesised that (1) the species originated in forests near the California–Oregon border from a *picta*-like ancestor; (2) populations dispersed southwards along both sides of the Central Valley during times of increased humidity; (3) interior populations of *xanthoptica* were the result of a Pleistocene transvalley invasion from coastal



**Figure 1** Distribution of taxa identified by Stebbins (1949), but with ranges based on molecular evidence (Wake, 1997).

*xanthoptica* and (4) coastal and interior populations followed different patterns of divergence in response to different ecological factors.

### New evidence

Based on Stebbins' observations, Dobzhansky (1958) concluded that virtually the entire process of speciation was evident in *Ensatina*, but that completion of speciation was inhibited by continued gene flow through the continuous string of interbreeding subspecies. Morphological, behavioural, biochemical and molecular measures from extensively surveyed locations throughout the *Ensatina* complex range have since shown that Stebbins' (1949) biogeographical hypothesis is too simple, and speciation is no longer prevented by persistent gene flow (Brown, 1974; Wake and Yanev, 1986; Moritz *et al.*, 1992; Jackman and Wake, 1994; Wake, 1997; Wake and Schneider, 1998; Pereira *et al.*, 2011). However, Stebbins' hypothesis has not been falsified in a general sense. For example, allozyme variation is highest in the northern part of the range and genetic distances between pairs of populations from across the Central Valley generally increase from north to south (Wake and Yanev, 1986), both of which are predicted by Stebbins' hypothesis. Additionally, phylogenetic analysis of cytochrome *b* (cyt *b*) haplotypes showed that *croceater*, *klauberi* and southern populations of *platensis* form a monophyletic group (i.e. a group that includes all descendants of a common ancestor), as do *xanthoptica* and *eschscholtzii*. Monophyly of these southern segments of the ring is consistent with independent southward dispersal along opposite sides of the valley (Moritz *et al.*, 1992). **See also**: Biogeographical Regions; Speciation: Genetics

Although the predicted correlation of geographic distance with genetic and morphological divergence largely holds at a macrogeographic scale, exceptions are found at a finer scale (Jackman and Wake, 1994). Perhaps the most striking exception involves populations from the northern part of the *platensis* range. Specifically, in the area near Lassen Peak (**Figure 1**) there is a sharp transition in the genetic and morphological data between the unblotched and blotched forms. There is also a morphologically cryptic boundary to gene flow that separates northern *platensis* from southern *platensis* populations. Jackman and Wake (1994) interpret this genetic structure, which contradicts the classical model of steady north to south population expansion, as evidence that northern *platensis* is the product of introgression between southern *platensis* and *oregonensis*. In their view, the southern boundary is due to ancient vicariance; whereas, the presently distinct transition between *oregonensis* and northern *platensis* is due to geologically recent volcanism and glaciations that caused repeated extinction and recolonisation.

Historical biogeography also poses a problem for Stebbins' classical hypothesis. Molecular clock and fossil evidence estimate the divergence time of the coastal clade containing *xanthoptica* and *eschscholtzii* to be 8.9–10 million years (Parks, 2000; Kuchta *et al.*, 2009), far earlier than
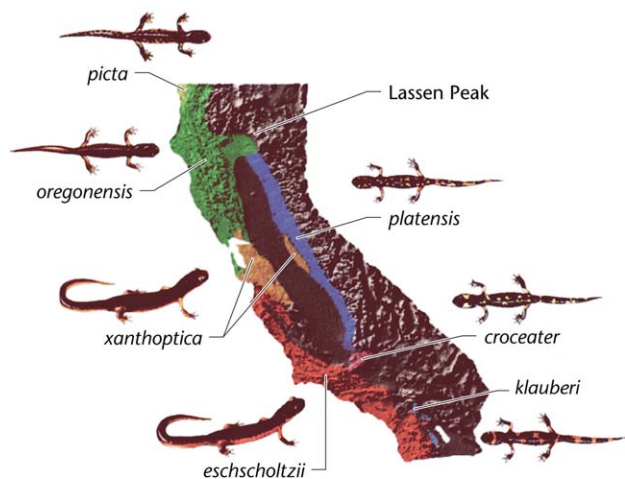
the coastal range became a contiguous landmass. The central valley of California was a marine embayment that drained into Monterey Bay until approximately 600 000 years ago (Kuchta *et al.*, 2009). These results have led to alternative hypotheses that involve the dispersal of a *xanthoptica* and *eschscholtzii* ancestor dispersing to an archipelago and then later invading the mainland with *xanthoptica* spreading north and *eschscholtzii* spreading south to close the ring (Wake, 2006).

Analysis of 13 overlap zones found that mitochondrial DNA (mtDNA) divergence and ecological adaptation, measured by the climatic an vegetative dissimilarity of the parent populations, do not predict the degree of reproductive isolation, but nuclear genes do (Pereira *et al.*, 2011). This suggests that ecological adaptation in *Ensantina* not only directly leads to reproductive isolation; but also that reproductive isolation is not strictly necessary for genetic and ecological divergence among subspecies to occur. In *Ensatina*, reproductive isolation may be a result of extended periods of geographic isolation rather than selection in different ecological contexts.

### Current status

The same continuity of the speciation process that makes ring species like *Ensatina* valuable study systems also tends to make them taxonomic quandaries. The extent of morphological and genetic divergence across some contact zones, such as that between *oregonensis* and northern *platensis*, has led some researchers to suggest that *Ensatina* be broken into several species. For example, Highton (1998) reanalysed published data and concluded that *Ensatina* was a superspecies comprising 11 allopatric and parapatric species and semispecies. Based on his reanalysis of the data, Highton (1998) suggests that the ancestor of the present complex was widely distributed throughout the current range. Subsequent periods of aridity caused the groups that he recognises to diverge in allopatry. Wake and Schneider (1998) disagree with Highton's (1998) conclusions and advocate maintaining the current taxonomy until ongoing studies are complete. The difference between Wake's and Highton's (1998) conclusions are superficially related to the application of species criteria, but are probably rooted in more philosophical views about what constitutes a species. Highton (1998) uses genetic distance data to cluster groups of populations into proposed independent lineages (i.e. species). Wake and Schneider (1998) espouse a more phylogenetic approach that emphasises the importance of monophyly in naming species. **See also**: Speciation: Allopatric; Species Concepts; Variation, Within Species: Introduction

In sum, increasingly detailed studies reveal significant complexity in the relationships and interactions of populations. There also appears to be increasing momentum towards breaking *E. eschscholtzii* into at least two or three species. However, doing so will not diminish the opportunity this group affords researchers to study one of the great examples of recent and (or) ongoing speciation.

## Song Sparrow

The song sparrow *Melospiza melodia* is a wide-ranging species with between 25–52 subspecies described. The subspecies that occur in western North America have been suggested to form a ring species. The terminals of this ring species are in southern California where the subspecies *fallax* and *heermanni* overlap in the southern Coachella Valley. The other subspecies are arranged in a ring with the deserts of eastern California and southern Nevada providing the barrier to range expansion. The subspecies that complete the ring are *gouldii, cleonensis* and *montana*. The subspecies *santaecrucis, ingersolii* and *virginis* are the intergrade forms found between each primary subspecies. In the south the terminal taxa exhibit assortative mating. Females show preference for their own taxon's plumage and song, and males show assortative agonistic singing behaviour (Patten and Pruett, 2009).

## European gulls

Herring gulls (*Larus argentatus*) and lesser black-backed gulls (*Larus fuscus*) are the widely cited examples of the terminal ends of a ring species. The taxa are sympatric and reproductively isolated in northern Europe, but are connected by several intergrading subspecies that encircle the north temperate zone. There are distinct differences between the colouration, ecology and behaviour of the two species where they are sympatric, but the differences are blurred in populations from around the ring. Detailed surveys of distribution and morphology from the late 1940s through early 1960s showed that the ring was not completely continuous and suggested that the 'Larus argentatus complex' (including *L. fuscus* at that time) should be divided into three species, *L. argentatus*, *L. fuscus* and *Larus cachinnans* (reviewed in Mayr, 1963). More recent work on the cyt *b* gene in this group indicates that gene flow between the three gull species must be negligible and that they represent rather young species, perhaps diverging 100 000–500 000 years ago (Wink *et al.*, 1994). The cyt *b* data support recognition of *L. cachinnans* as a species distinct from *L. fuscus* and *L. argentatus* and suggests that *L. cachinnans* is more closely related to *L. fuscus* than to *L. argentatus*. This corresponds well with the original phylogeographic hypothesis suggesting that *L. argentatus* is the end result of circumpolar eastwards colonisation of Europe from North America and *L. fuscus* is the result of colonisation from the Caspian Sea region into the eastern north Atlantic with *L. cachinnans* being nearest to the ancestor of all three species (reviewed in Mayr, 1963). However, additional molecular data, including mtDNA sequences, suggest that *L. argentatus* and *L. cachinnans* are closest descendants of gulls from two different, isolated glacial refugia (Liebers *et al.*, 2004). The *L. argentatus* refugium is proposed to have been in the eastern north Atlantic and the *L. cachinnans* refugium near the Caspian Sea. Liebers *et al.* (2004) propose that current reproductive isolation in sympatry between *L. fuscus* (descended from the Caspian

refugium) and *L. argentatus* is a result of divergence during allopatry not isolation by distance as is supposed to occur in ring species. It is noteworthy that *Larus* gulls may yet provide an example of true ring species, because the range of *L. fuscus* continues to expand westward and they may soon colonise North America (Liebers *et al.*, 2004). If colonisation occurs, it will be interesting to see whether *L. fuscus* and the American Herring Gull (*Larus smithsonianus*), which both descend from the Caspian refugium will be reproductively isolated from each other. **See also**: Aves (Birds)

## Greenish warblers

*Phylloscopus trochiloides*, the greenish warbler, is perhaps the best remaining example of a ring species. Greenish warblers have six named subspecies. In central Siberia the ranges of two widely distributed northern forms, *P.t. plumbeitarsus* and *P.t. viridanus*, overlap and the two live sympatrically without interbreeding. However, a ring consisting of *P.t. obscuratus*, *P.t. trochiloides* and *P.t. ludlowi* connects the two northern subspecies as one travels clockwise around the Tibetan Plateau. Based on the Himalayas being the centre of *Phylloscopus* species diversity, as well as on molecular and historical climate data, the ancestral range of greenish warblers was likely located in the Himalayas (Price *et al.*, 1997; Irwin, 2000). Subsequent differentiation into the subspecies recognised today occurred as the *P. trochiloides* range expanded along the eastern and western sides of the plateau. There is a large gap in the ring distribution in northeastern China. However, this is likely a result of recent deforestation and the individuals on either side of this gap show strong similarity in all traits examined (Irwin, 2002).

In one of the best examples of how ring species can inform studies of speciation, Irwin (2000) used song variation among *P. trochiloides* populations to investigate the microevolutionary factors involved in their divergence. The study found that song structure diverges gradually around the ring and is substantially different between the two reproductively isolated Siberian subspecies. Additionally, singing behaviour is simplest in the Himalayas and increases along two different axes of complexity as the ranges move north along opposite sides of the Tibetan Plateau (Irwin, 2000). Irwin argues that the increased song complexity in northern ranges is due to clinal variation in ecological factors (e.g. forest density and food availability). Therefore, he concludes that, 'Ecological differences influence the balance between sexual and natural selection, leading to divergence'. Given that *P.t. plumbeitarsus* and *P.t. viridanus* have converged ecologically and share habitats (Irwin, 2000), it would not be obvious that ecological factors have played a role in their divergence were they not the ends of a ring species. **See also**: Bird Song: Steroid Hormones and Plasticity

## Titmice

Three groups of titmice are distributed in a somewhat similar fashion to the greenish warblers summarised above.

Around the Tibetan Plateau titmouse colouration grades from green back with yellow abdomen in the *Parus major* group, to green back with white abdomen in the *Parus minor* group, to grey back with white abdomen in the *Parus cinereus* group. Rensch (1933) (cited in Mayr, 1963) hypothesised that all three groups evolved from the great titmouse (*P. major*) during the Pleistocene, and that subsequent recession of Pleistocene glaciers resulted in intergradation in zones of secondary contact except where the hypothetical ends of the ring overlap in the upper Amur Valley of eastern Asia. A more recent analysis of mtDNA indicates that the three groups diverged in allopatry between .5 and 2 mya and then towards the end of the Pleistocene experienced a range expansion with secondary contacts in the hybrid zones. Despite limited hybridisation there is no sign of broad scale gene flow or genetic swamping. This data as well as analysis of song data prompted Päckert *et al.* (2005) to recommend the recognition of three distinct species.

## Pocket mice

The pocket mice *Perognathus amplus* and *Perognathus longimembris* are morphologically similar species that Hoffmeister (1986) hypothesised were actually a single ring species in the southwestern United States. The two species are allopatric except where they meet in La Paz county, Arizona. In the area of overlap *P. longimembris* is smaller than *P. amplus* except in tail length; however, in northern Arizona the two species are divided by the Colorado River and are nearly indistinguishable morphologically. Hoffmeister (1986) proposed that *P. amplus* might be one divergent end of a continuous chain where the relatively large *P. longimembris* crossed the Colorado River and spread through Arizona becoming progressively larger until we see the distinction between small *P. longimembris* and large *P. amplus* in sympatry.

McKnight (1995) has since refuted the ring species hypothesis for this species pair based on cyt *b* sequences. It appears that *P. amplus* and *P. longimembris* completed speciation in allopatry. Although the molecular evidence points to a northern origin for both lineages, with increasing divergence southward, McKnight (1995) concludes that, 'due to the incompleteness of the ring of subspecies and the apparent timing of evolutionary events in this group… *P. amplus* and *P. longimembris* are distinct lineages that have completed the speciation process'.

## House mice

The house mouse, *Mus musculus*, has been suggested to contain a possible ring species covering much of Europe and Asia (Din *et al.*, 1996). The three main subspecies, *M.m. domesticus* (distributed through Europe, Africa and Australia), *M.m. musculus* (northern Asia) and *M.m. castaneus* (southeastern Asia), each have some gene exchange. *M.m. domesticus* and *M.m. musculus* meet in Europe and form a narrow hybrid zone; *M.m. musculus* and *M.m.*

*castaneus* intergrade in southern China and are completely admixed in the main Japanese islands. Further, there is evidence of both *M.m. domesticus* and *M.m. castaneus* genes in California and Hawaii (Din *et al.*, 1996). Although *M. musculus* is one of the best genetically characterised mammals for populations on the periphery of its range, less was known about the central part of the species range until Din *et al.* (1996) studied the genetic structure of populations in northern and southern India, Pakistan and Iran. Their results suggest that *M. musculus* originated from the Indian subcontinent and potentially forms two rings: a western ring that appears to overlap in Europe where *domesticus* and *musculus* meet and an eastern ring that overlaps at the *musculus–castaneus* boundary (Din *et al.*, 1996). However mitochondrial and nuclear data support continued gene flow between the terminal populations in both rings. In fact, even the X chromosome which would be expected to diverge more quickly than other portions of the genome still shows the signs of gene flow between distant populations within and between rings (Bonhomme *et al.*, 2007).

### Darkling beetle

The tenebrionid beetle *Mimopeus elongatus* is a polymorphic species that lives under creeping plants in coastal habitats in New Zealand. The external morphology and genitalia are distinctly different when individuals from the east and west coast near Auckland are compared. However, these distinct forms are connected by a series of intermediates that occur northward up the east coast to Doubtless Bay and then back southward on the west coast. Reproductive isolation may not be complete since occasional specimens with traits that are intermediate have been found in the south near Orua Bay (Watt, 1983).

### Solitary bees

Five subspecies of the solitary bee *Hoplitis producta* surround the great basin of the western United States. *H.p. gracilis* is distributed from southern California to northern Oregon. In northern Oregon, *gracilis* intergrades with *H.p. subgracilis*, which ranges north through Washington and east into Idaho and Montana. Along the eastern part of its range *subgracilis* intergrades with *H.p. interior*, which ranges south almost into Mexico. *H.p. interior* has twice reinvaded across the great basin into southern California each time establishing a distinct subspecies, *H.p. panamintana* and *H. p. bernardina*. The two subspecies derived from *H.p. interior* exist in sympatry with *gracilis* without interbreeding (Mayr, 1963).

## African Acacia

The African acacia is a polymorphic species that can range in height from 1 to 30 m and has a ring-shaped distribution encircling the Drakensberg massif in southern Africa.

Brain (1989) proposed that it was a ring species based on the gradual variation in allozyme frequencies across most portions of the ring with the exceptions of two small regions on the eastern side of the distribution that showed distinct and sharp gradients in changes of allozyme frequency. It remains unclear whether there is any location where two divergent forms are sympatric. Phenotypically divergent plants have been documented less than 12 km apart but no data on the genetic relatedness of such plants is available (Ward, 2011).

## Why Are Ring Species Rare?

Simply put, ring species are rare because they have an unlikely geographic distribution. Only rarely is appropriate habitat distributed in a circular manner (i.e. an area that serves as a complete barrier to gene flow must be surrounded by habitat that the species is able to invade). In addition to the odd habitat distribution requirements, migration rates must fall within a fairly narrow window to balance the requirements for dispersal and isolation by distance. Some dispersal capability is required because the ring species must somehow colonise new habitat as it slowly moves around the circle. However, if movement is too great, differences between populations will not accumulate. Given these criteria, it is not surprising that ring species are uncommon; however, reasons for their rarity in some taxa but not others remain unclear. In particular, the absence of plant examples is intriguing. **See also**: Geographical Variation

Ring species may also be rare because they are unstable and therefore short lived. McKnight (1995) points out that the characteristics that favour the formation of ring species are the same ones that make them most likely to undergo allopatric speciation. Gavrilets *et al.* (1998) used a theoretical model to study the likelihood of rapid speciation in sequentially founded subpopulations that were allowed to diverge through mutation and drift. Approximately 75% of their simulations with eight subpopulations resulted in isolation between neighbouring subpopulations within 3000 generations. In the remaining 25%, sufficient divergence accumulated between populations 1 and 8 to produce isolation if they came in contact. Gavrilets *et al.* (1998) further add that continuing the runs for more generations 'would almost definitely result in speciation (among neighbouring subpopulations) in all runs'. Therefore, ring species are expected to be rare because they comprise a limited subset of speciation events, which are further limited by duration and by peculiar geographical distribution. **See also**: Drift: Introduction; Drift: Theoretical Aspects

## Relevance to How Geographic Variation Promotes Speciation

Because speciation occurs predominantly on a geological time scale rather than human generations, it is difficult to

study the chain of events leading to the formation of new species. This difficulty has led to a debate among evolutionary biologists as to the importance of ecological versus purely genetic causes of speciation. There is a general consensus among speciation geneticists that the role of geographic separation is to inhibit or prevent gene flow. Lack of gene flow provides an opportunity for different mutations to become fixed in different populations. To couch the standard speciation genetics model in terms of a classic ring species hypothesis, suppose that a single panmictic population begins to disperse along two sides of a central barrier. On one side there is a mutation at the *A* locus (**Figure 2**). Along the opposite side there is a mutation at the *B* locus (**Figure 2**). As populations continue to disperse around the ring, the allele frequencies of the new mutations increase until, in the area of overlap, the two populations are fixed for alternative mutations (**Figure 2**). The newly sympatric populations may be partially reproductively isolated if the mutated 'a' and 'b' alleles are incompatible. In this example, ring species provide a means to investigate factors responsible for driving 'a' and 'b' to fixation. **See also**: Sympatric Speciation

Ring species can be valuable tools for disentangling the roles of ecological and geographic isolation in speciation. In *Ensatina* there is some evidence that ecology contributes to isolation of the most divergent populations (Wake and Schneider, 1998). Further, Irwin's (2000) study of greenish warblers illustrates how ring species can help elucidate a role of ecology in speciation that would be obscured if only the ends of the continuum remained.

Ring species will continue to attract attention from evolutionary biologists because they demonstrate unequivocally that the accumulation of variation among populations with limited gene flow is leading to reproductive isolation (speciation with gene flow). Although not as clearly indicative of particular modes of speciation as originally hypothesised, studying ring species remains useful for our understanding of speciation. By studying the build-up of divergence in space, researchers are able to reconstruct the history of variation in time and thereby observe the processes that lead to speciation.

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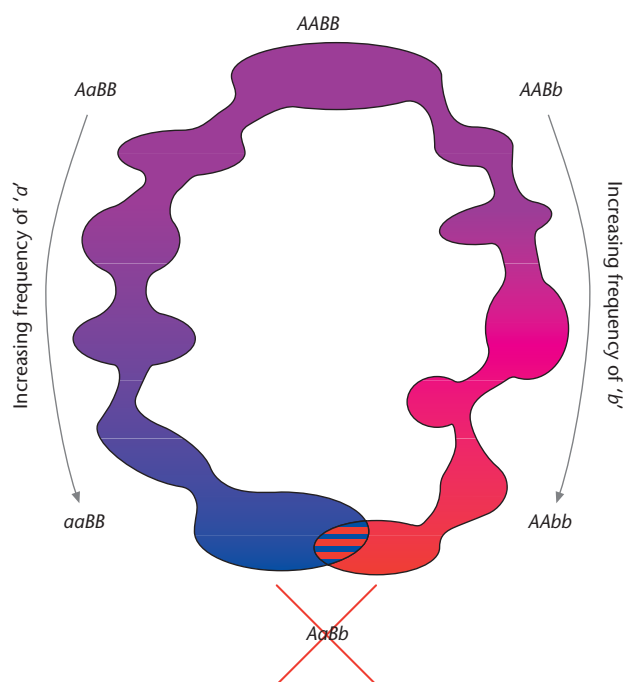
**Figure 2** Diagrammatic representation of the origin of genetic incompatibility in a ring species. The ancestral population (purple) disperses southwards along both sides of a barrier. A mutation at the *A* locus occurs on one side of the barrier, whereas a mutation at the *B* locus occurs on the other side. The frequency of the mutant 'a' allele (blue colouration) and 'b' allele (red colouration) increases as populations disperse southward. Since 'a' and 'b' alleles are incompatible, sympatric populations fixed for them do not exchange genes (striped region).

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