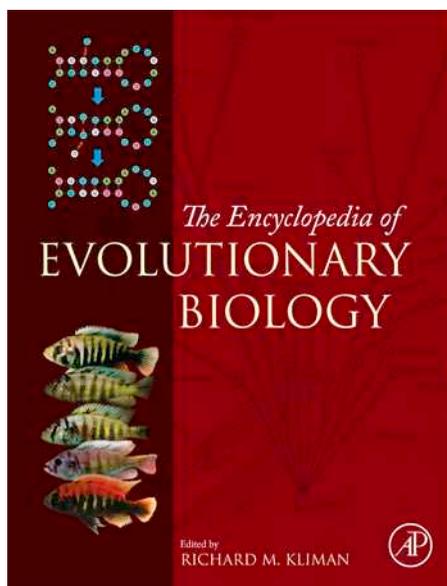


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Ring Species

DE Irwin, University of British Columbia, Vancouver, BC, Canada

DB Wake, University of California, Berkeley, CA, USA

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The perfect demonstration of speciation is presented by the situation in which a chain of intergrading subspecies forms a loop or an overlapping circle, of which the terminal forms no longer interbreed, even though they coexist in the same localities. (Mayr, 1942, p. 180)

With the above quote, the great evolutionary biologist Ernst Mayr concisely described the phenomenon now termed 'ring species' (Cain, 1954) and pointed out their importance to the study of speciation, the process by which one species evolves into two or more. Ring species are fascinating to biologists because they illustrate in geographic space a central principle of evolutionary biology that we usually conceive of occurring in time: that species can evolve via small, stepwise changes into new species (Figure 1). In a ring species, two distinct forms can be found in the same geographic region, such that most biologists would consider them different species; yet these forms are connected by a chain of populations through which traits change gradually from one species to the other (Mayr, 1942; Cain, 1954; Moritz *et al.*, 1992; Wake, 2001; Irwin *et al.*, 2001b). The two forms can be considered simultaneously as members of the same species (if one looks at the chain of intergrading populations) and as two distinct species (if one looks at the reproductive isolation in the overlapping region). As Mayr (1942, p. 180) stated, ring species are "disturbing to the orderly mind of the cataloguing systematist, but they are welcome to the student of speciation." The ring species concept has inspired much thought about speciation, both with regard to specific case studies (see below) and in development of theory (Gavrillets *et al.*, 1998; Ashlock *et al.*, 2010; Martins *et al.*, 2013).

A wide variety of ring species have been proposed (reviewed by Mayr, 1942, 1963, 1970; Irwin *et al.*, 2001b; Irwin and Irwin, 2002; see also Bowen *et al.*, 2001; Bensch *et al.*, 2009; Mulcahy and Macey, 2009; Patten and Pruett, 2009; Cacho and Baum, 2012; Eastwood *et al.*, 2014), but there is controversy over whether specific cases should be described as

ring species. This is a result of wide variation among biologists in concepts both of what a ring species is and of how they form, and ultimately in the ways ring species are used as evidence for various evolutionary processes. Here we review these distinct uses of the ring species concept, discuss the various types of ring species and the ways they could form, examine two ring species in depth, and then look toward future investigations of ring species.

Uses of the Ring Species Concept

The literature reveals a striking characteristic of the history of thought on ring species: the basic concept has been used as illustrations of and support for evolutionary processes in at least four distinct ways:

Illustrating the Fact that Species Evolve

Ring species are often used as a simple yet powerful illustration that distinct species can be connected by a series of small stepwise changes. While ring species provide a taxonomic conundrum (should we call a ring species a single species or two (or more) species?), they in fact illustrate in space the fundamental way that a single species can evolve into two over time (Figure 1). It is primarily for this reason that ring species are used so often in textbooks on evolution: they illustrate the continuity between evolution within species and between species so clearly.

Showing the Importance of Geography in Speciation

In the earliest apparent clear articulation of the ring species concept, in a quote attributed to Leonhard Stejneger (as reported by Jordan, 1905), the concept is used to explain how two closely related forms might come to live in the same area,

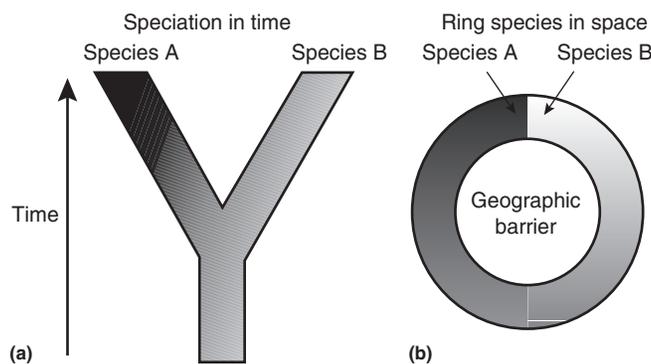


Figure 1 Speciation (a) is the process by which a single species diverges into two (or more) over time. Ring species (b) show a similar pattern over space, allowing geographic variation to serve as a possible proxy for divergence from a common ancestor over time.

by expansion from an ancestral area in two directions around a geographical barrier, the end points coming into contact and behaving as distinct species. In this context, the concept was first developed as support for the idea that geographic differentiation plays a key role in speciation: closely related species may be found living in the same area, but they diverged in different geographical areas and then expanded into the same region. Mayr (1942, 1963, 1970), who did much to popularize the concept, also emphasized this aspect of ring species, writing that “a more dramatic demonstration of geographic speciation than cases of circular overlap cannot be imagined” (Mayr, 1970, pp. 292–293; see also Cain, 1954). More recently, Newton (2003), Price (2008), and Coyne and Orr (2004) also emphasized ring species as illustrating various forms of geographic speciation.

Reconstructing the History of Changes During Speciation

Geographic variation in a ring species can sometimes be used to reconstruct how speciation occurred in time (Wake, 2001; Irwin *et al.* 2001a,b). This requires several assumptions: (1) the ancestral population is well represented by one of the intermediate forms in the ring, (2) we have a good idea which population is that source ancestral population, and (3) the current pattern of variation well represents the changes that occurred in time. A variety of genetic and biogeographic analyses can in some cases provide support for these assumptions, increasing confidence that such reconstruction of the history of speciation is valid.

Illustrating that Speciation Can Occur Despite Gene Flow

Finally, and more controversially, the ring species concept has sometimes been considered to demonstrate that speciation can occur without complete geographic and genetic isolation. The standard model of ‘allopatric speciation’ holds that speciation occurs following division of a single population into two geographically separated populations that do not exchange genes. Another theoretical possibility is ‘speciation by distance,’ in which divergence to the point of species occurs between the end points of a long chain of populations – gene

flow can occur between neighboring populations, but the distance between the end points is so much greater than the movement of individuals that the two end populations are effectively isolated. Mayr (1942) initially emphasized both the geographic-speciation and speciation-by-distance aspects of the ring species concept, but later abandoned the speciation-by-distance idea as an important part of his concept of circular overlaps, given the “major gaps in nearly all of these chains of populations or at least evidence for the former existence of such gaps” (Mayr, 1970, p. 320). Nonetheless, he continued to hold up circular overlaps as prime examples in which “the process of geographic speciation can be followed step by step” (Mayr, 1970, pp. 292–293).

Dobzhansky went further than Mayr in emphasizing gene flow as an important feature of ring species, describing the chain of populations as a ‘genetic bridge’ between forms that are otherwise reproductively isolated (Dobzhansky, 1958; Dobzhansky *et al.*, 1964). His prime example, however, was based on various forms within the *Drosophila paulistorum* complex, in which gene flow was inferred using laboratory breeding experiments, and he acknowledged that “it is questionable whether [gene flow] is actually taking place” (Dobzhansky *et al.*, 1964).

Given these varying ways that the ring species concept has been used, it is unsurprising that there is debate over proposed cases in terms of whether they can be described as ring species. The debate can be simplified by clearly separating questions about pattern from questions about process. We can organize our thinking by considering two basic questions: First, what patterns have been described as ring species? Second, what processes lead to their formation?

Types of Ring Species

Scenarios described as circular overlaps or ring species come in a wide variety of flavors. The ideal case is illustrated in Figure 2(a), in which there is a complete ring of gradually varying populations, the end points of which (in blue and red) act as reproductively isolated species where they meet. There have never been actual proposed examples that fit such an ideal scenario; rather all cases that have been proposed (reviewed by

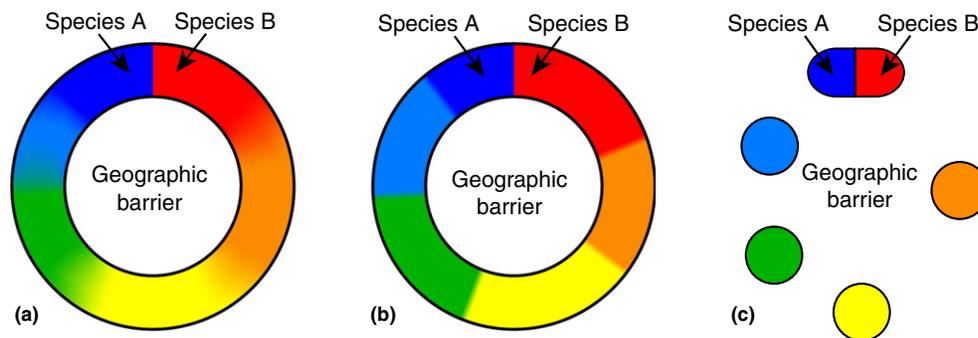


Figure 2 The types of situations that have been described as ring species. The ideal situation (a) is one in which a continuous ring of populations, through which traits and genes change gradually, except at a single location where distinct forms live side-by-side. All known cases of ring species fit less ideal situations in which there are stepwise, rather than completely gradual changes around the ring (b) and/or large gaps in distribution around the ring (c). Nonetheless, those situations illustrate the central concept of a ring species: a single species boundary through a ring of populations.

Mayr, 1942, 1963, 1970; Stebbins, 1949; Irwin *et al.*, 2001b; see also Bowen *et al.*, 2001; Bensch *et al.*, 2009; Mulcahy and Macey, 2009; Patten and Pruett, 2009; Cacho and Baum, 2012; Eastwood *et al.*, 2014) have imperfections of one sort or another. These real-world cases usually have a mixture of two other patterns, illustrated in Figures 2(b) and 2(c). In these cases, variation around the ring is not completely gradual (2(b)) and/or continuous (2(c)). Nonetheless, the overall pattern is one in which a series of progressively intermediate forms is arranged in a rough geographic order between the co-occurring and most divergent terminal forms (shown in blue and red). Another common complication is that reproductive isolation between the terminal forms can be incomplete, with some direct hybridization and introgression occurring between them (Brown, 1974; Wake *et al.*, 1989; Devitt *et al.*, 2011; Alcaide *et al.*, 2014). However, it is now generally accepted that reproductive isolation between distinct species is often incomplete (Coyne and Orr, 2004), such that a small amount of direct introgression is not inconsistent with the ring species description. The unifying characteristic common to all of these types of ring species is that there is a single species boundary around the ring: species A and B are considered two species where they meet, but there is no species boundary through the chain of populations connecting them around the ring (Cain, 1954).

How Do Ring Species Form?

Because ring species have generally been used as evidence for evolutionary processes, we have a fairly good understanding of various authors' ideas regarding how ring species form. In the ideal scenario (Figure 3(a)), which could be used for all of the purposes referred to above, an ancestral form expands from one side of the ring along two pathways around a geographic barrier, with progressive differentiation occurring before the terminal forms meet each other on the other side of the ring, where they are reproductively isolated. During this differentiation process, individuals can move a short distance during their lives in any direction, such that gene flow is continuous,

although low in magnitude, throughout the ring. As mentioned above, we have no good examples of fully gap-free and completely gradual rings, so empirical evidence for such an ideal scenario is lacking. However, there is much evidence for cases in which populations expanded from a common ancestor along two pathways, colonizing a series of habitat patches in each pathway, with the final colonization event in each chain bringing the end points together again (Figure 3(b)). Such a scenario was outlined for many of the examples provided by Mayr (1942, 1963, 1970), as well as the recently proposed example in plants (Cacho and Baum, 2012). Finally, such a colonization process can be followed by expansion of each population into the gaps in the ring (Figure 3(c)), resulting in contact between previously separated populations and resulting in broad blending (Figure 2(a)) or the formation of narrow hybrid zones (Figure 2(b)).

In reality, most species complexes have had very complex histories, involving periods of geographic isolation and re-expansion as well as divergence-with-gene-flow (Mayr, 1942, 1963, 1970; Wake, 1997; Alcaide *et al.*, 2014), such that particular ring species may have formed via a complex mix of the processes illustrated in Figure 3. Regardless, the resulting pattern of two mostly reproductively and co-occurring forms being connected by a chain of progressively intermediate forms illustrates the evolutionary continuity between species and in some cases allows the inference of processes important in the generation of reproductive isolation.

Example Ring Species

There have been a large number of proposed ring species, but evaluating many of them is difficult due to lack of detailed research on specific cases as well as to the variety of ring species concepts. We propose that the emphasis should be not on declaring whether particular cases are or are not ring species, but rather on understanding the particulars of each proposed case and what we can learn from it. Specific cases should be viewed as lying somewhere on a spectrum between the ideal ring species (Figures 2(a) and 3(a)) and clear examples of non-ring species.

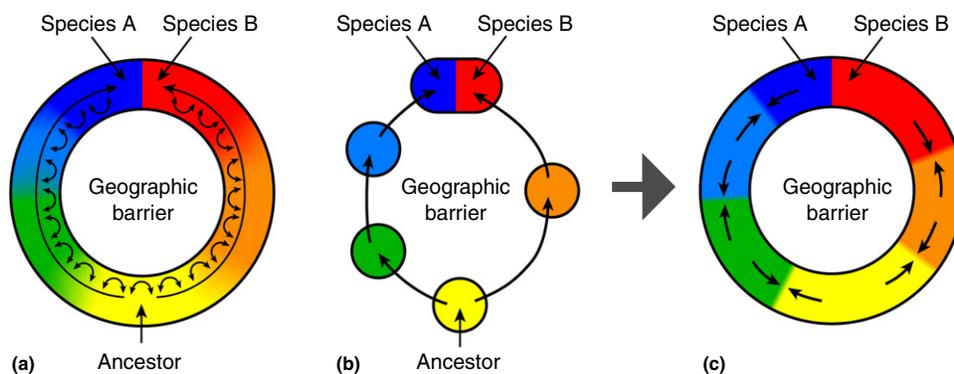


Figure 3 Scenarios by which ring species might form. In (a), an ancestral form expands around a geographic barrier, diverging gradually despite continuous gene flow at all stages of the process. In (b) populations colonize new areas and differentiate in a stepwise manner but there are major gaps in distribution, and divergence eventually proceeds through the chain of populations to the level of distinct species. In (c), the populations expand to meet each other again in narrow zones of intergradation. In each case, divergence to the level of distinct species has occurred only between the terminal forms.

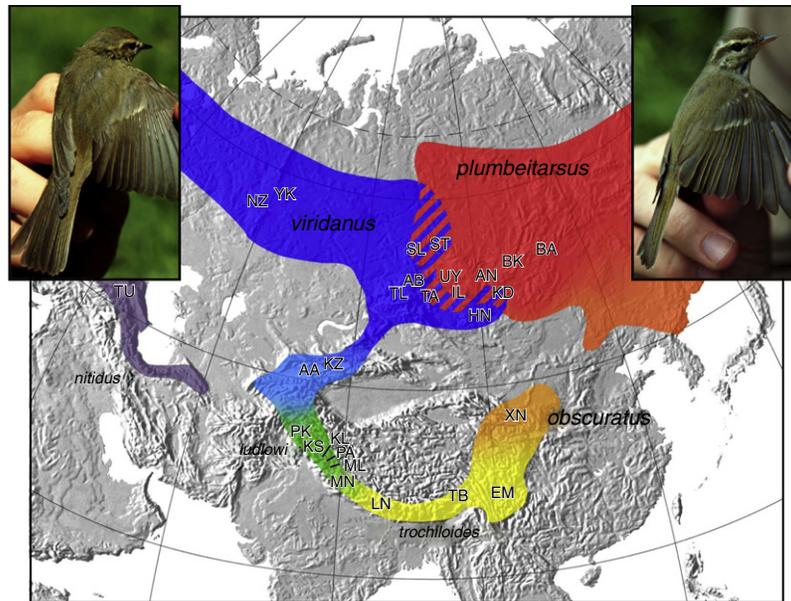


Figure 4 The breeding range of greenish warblers (*Phylloscopus trochiloides*) in Asia. Subspecies designations according to Ticehurst (1938) are shown with different colors: *viridanus* in blue, *ludlowi* in green, *trochiloides* in yellow, *obscuratus* in orange, *plumbeitarsus* in red, and *nitidus* (outside of the main ring) in purple. Photos show the difference in wing bars between *viridanus* (upper left, with a single wing bar) and *plumbeitarsus* (upper right, with two wing bars).

Of all of the cases that have been proposed, two in particular, the greenish warblers in Asia and the *Ensatina* salamanders in California, have stood out as meeting the ring species definition fairly well in terms of being a chain of intergrading forms with distinct coexisting terminal forms. We discuss each in some detail, before mentioning other proposed cases.

Greenish Warblers

In 1938, Claude Ticehurst conducted a detailed taxonomic reassessment of the *Phylloscopus* genus of Old World warblers (Ticehurst, 1938), based on examination of morphological variation in museum skins (e.g., body shape and size, as well as plumage color variation). He provided an intriguing description of six subspecies within the greenish warbler (*Phylloscopus trochiloides*) species complex: two subspecies, *viridanus* in west Siberia and *plumbeitarsus* in east Siberia, differed in plumage but co-occurred in central Siberia without intermediates there, suggesting reproductive isolation. But these forms were apparently connected by a ring of progressively changing forms: *viridanus* extended south into central Asia, where it met *ludlowi*, which Ticehurst described as a transitional form leading to *trochiloides*, the southern form spanning across the Indian and Nepali Himalayas and into southern China. Next came *obscuratus* in central China, which appeared intermediate between Himalayan *trochiloides* and east Siberian *plumbeitarsus*. Based on this description, Mayr (1942) featured the greenish warblers as an illustrative example of circular overlap. Ticehurst hypothesized that the situation arose when an ancestral species in the Himalayas (i.e., in the south) expanded along two pathways northward, separated by the high-altitude Tibetan Plateau.

Both the ring-species description and the proposed parallel northward expansion have now been tested by examining a variety of genetic, morphological, and behavioral traits, and the patterns are broadly consistent with Ticehurst's hypothesis (Figure 5; Irwin, 2000; Irwin *et al.*, 2001a, 2005, 2008; Wake, 2001; Alcaide *et al.*, 2014). Vocalizations (both songs and calls), plumage characteristics (mainly wing bar size), and genetic markers (including mitochondrial DNA, microsatellites, AFLPs, and genomic SNPs) differ strongly between *viridanus* and *plumbeitarsus*, supportive of there being strong reproductive isolation between them in central Siberia. Genetic data are supportive of two northward expansions into Siberia, as west Siberian *viridanus* is most related genetically and phenotypically to central Asian *viridanus* and *ludlowi*, and east Siberian *plumbeitarsus* is most related to *obscuratus* in China and *trochiloides* in the eastern Himalayas. Phenotypic traits such as songs, plumage, and migratory behaviors show gradual change around the ring (Figure 5). The pattern of song variation is particularly interesting: songs are simple in the south but become increasingly long and complex toward the north, but the form of complexity that has evolved during the two northward expansions differs dramatically between them, resulting in highly divergent songs in west and east Siberia (Irwin, 2000; Irwin *et al.*, 2008), where songs appear to play a role in reproductive isolation (Irwin *et al.*, 2001a).

Complicating the ring species scenario is evidence for a zone of steep genetic transition in the western Himalayas near the boundary between Kashmir and Himachal Pradesh, in a region where there is little change in song or plumage. This genetic transition was first observed as a narrow overlap area between the two major mitochondrial clades (Irwin *et al.*, 2001a). Later, patterns in AFLP markers were interpreted as supportive of gradual genetic variation through this region as

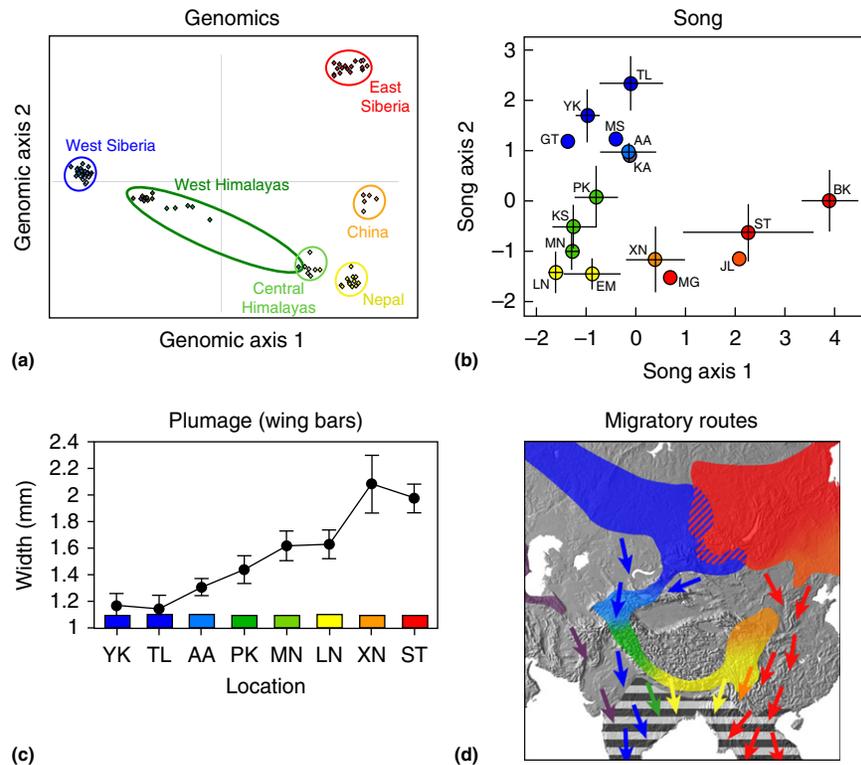


Figure 5 Patterns of genomic and phenotypic variation in greenish warblers. Colors correspond to the subspecies groups in [Figure 4](#). Genomic variation (based on 2334 single nucleotide polymorphisms; [Alcaide et al., 2014](#)), songs ([Irwin, 2000](#); [Irwin et al., 2008](#)), wing bars ([Irwin et al., 2001a,b](#)), and migratory routes ([Irwin and Irwin, 2005](#)) all show strong differences between the two Siberian forms (*viridanus* and *plumbeitarsus*), but gradual or stepwise variation through the chain of populations to the south. These patterns are supportive of [Ticehurst's \(1938\)](#) and [Mayr's \(1942\)](#) description of the greenish warbler as a ring species, with two separate expansions northward into Siberia.

well as the entire ring, except between the highly divergent *viridanus* and *plumbeitarsus* ([Irwin et al., 2005](#)), and this interpretation of isolation-by-distance was confirmed in subsequent analyses of the same data by [Novembre and Stephens \(2008\)](#), [Zhang et al. \(2009\)](#), and [Martins et al. \(2013\)](#). Finally, analysis of thousands of markers spread throughout the genome has revealed strong evidence for secondary contact in the western Himalayas of previously separated populations ([Figure 5\(a\)](#); [Alcaide et al., 2014](#)), within the range that Ticehurst described as the subspecies *ludlowi*. A further complication is that the genomic data shows strong evidence for a small amount of hybridization and introgression between *viridanus* and *plumbeitarsus*, such that reproductive isolation between those forms is not absolute ([Alcaide et al., 2014](#)). There is also evidence for some individuals in central Siberia singing songs that mix elements of the songs of *viridanus* and *plumbeitarsus* ([Irwin et al., 2012b](#); [Kovylov et al., 2012](#)). Nonetheless, those forms display highly divergent genetic clusters, indicating that the limited hybridization has not blended the two forms and suggesting that there is selection against introgressed genes.

The greenish warblers display the essential characteristics of a ring species: two highly differentiated forms that co-occur in one region (central Siberia) while being connected by a long chain of forms through which traits change gradually (e.g., song) or in a more stepwise fashion (e.g., genetics). However, the evidence for periods of geographic separation and secondary contact implies that greenish warblers do not provide a

clear example of speciation by distance ([Alcaide et al., 2014](#)), counter to a previous interpretation based on more limited genetic data ([Irwin et al., 2005](#)).

Ensatina Salamanders

In 1949 R.C. Stebbins at the University of California, Berkeley, published a monograph on the *Ensatina* genus of salamanders that had a surprising conclusion: what had been treated as a genus with four distinctively colored species distributed along the west coast of North America was reduced by Stebbins to a single species comprised of 7 subspecies distributed in the form of a geographic ring ([Figure 6](#); [Stebbins, 1949](#)). The subspecies all occur in California, where they are wrapped around the inhospitable Great Central Valley and extend southward both along the coast and inland into northern Baja California, Mexico. A form with the most generalized color pattern occurring in the historically most stable part of the overall range, in northwestern California, was hypothesized to have spread inland and southward through the Sierra Nevada, in one leg of its distribution, and separately along the coast southward through diverse coastal uplands. The forms were thought to have adapted to local and regional habitats and climates as they migrated southward, with coastal forms becoming more or less uniformly, and brightly, colored, and in the central coastal area they became aposomatically colored as part of a mimicry complex involving the dangerously poisonous newts, *Taricha* ([Kuchta, 2005](#); [Kuchta et al., 2008](#)). In contrast, in the inner mountains

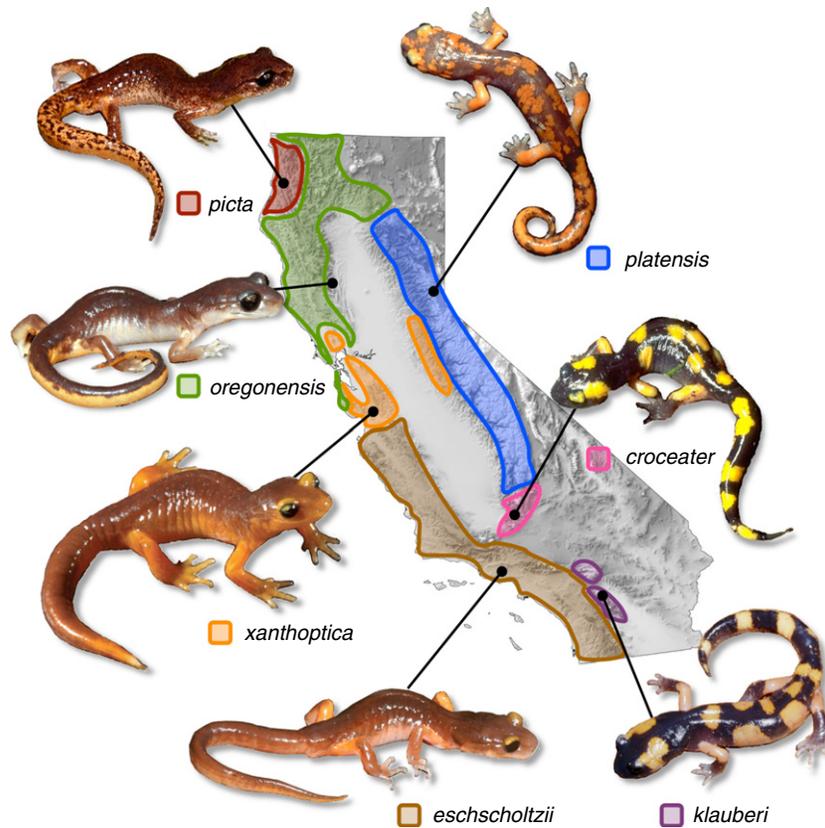


Figure 6 Geographic variation among races in the *Ensatina eschscholtzii* ring species in California. Reproductive isolation is stronger between the southern forms *klauberi* and *eschscholtzii* than elsewhere around the ring. Reproduced from Pereira, R.J., Monahan, W.B., Wake, D.B., 2011. Predictors for reproductive isolation in a ring species complex following genetic and ecological divergence. *BMC Evolutionary Biology* 11, 194, with permission from BMC Evolutionary Biology.

the salamanders evolved cryptic coloration and behavior, becoming spotted and blotched (such that they match the leaf litter well). The end points of these adaptively divergent pathways appeared to be different species.

Stebbins, who was renowned for his artistic abilities as a painter as well as being a serious scientist, argued that the forms intergraded with each other at various points in the ring. His critical insight was that the two major types came into near sympatry in Southern California, and he recognized signs of hybridization and intergradation between forms elsewhere around the ring. Nowhere was the ring hypothesis seen in more vivid detail than in the central Sierra Nevada, where two remarkably distinct forms, the aposematically colored *Ensatina eschscholtzii xanthoptica* and the cryptically colored, blotched, *Ensatina eschscholtzii platensis*, met and hybridized extensively, the result of a 'mid-valley leak' that had brought coastal forms into contact with Sierran forms (essentially a 'test' of the ring species concept mid-way through the ring); this contrasted with the much stronger reproductive isolation between distinct forms *Ensatina eschscholtzii klauberi* and *Ensatina eschscholtzii eschscholtzii* at the southern end of the ring. Stebbins did not think that the ring resulted from smooth expansion without any geographic breaks in continuity around the ring, but rather as something that had developed in fits and starts, with many interruptions and long periods during which regional adaptation occurred.

Subsequent research has added much detail and texture to the *Ensatina* example, and in recent years a heavy emphasis on molecular traits has shown that the ring of forms is old (millions of years) and deeply differentiated (Wake and Yanev, 1986). Both intergradation (based originally on color analysis, now backed up by allozyme data) and hybridization are well documented at various places around the ring (Wake and Schneider, 1998; Kuchta *et al.*, 2009). It is now thought (Jackman and Wake, 1994; Pereira and Wake, 2009; Pereira *et al.*, 2011) that the blotched forms were separated from other members of the complex for a long time before moving back northward and meeting the unblotched forms in secondary intergradations north and west of Lassen Peak, in northeastern California. Some hybridization has been observed between the terminal forms in southern California (Brown, 1974; Wake *et al.*, 1989; Devitt *et al.*, 2011), but it is more restricted than in the central Sierra Nevada (Alexandrino *et al.*, 2005), and at the southern-most possible point of meeting of the two main lineages, in the Cuyamaca Mountain of inner San Diego County, California, there is sympatry with no evidence of local hybridization (Wake *et al.*, 1986). While some have questioned the ring species description of the *Ensatina* complex (e.g., Highton, 1998) no primary researchers focused on the group has felt their results constituted a refutation of Stebbins' original hypotheses concerning intergradation, hybridization, and sympatry at different places within the ring,

nor, especially, of his broad biogeographical hypothesis. Despite the complexities, there is a single place in the ring where genetic and phenotypic differentiation are much stronger than elsewhere around the ring.

Other Proposed Cases

At least two dozen species complexes have been described as 'circular overlaps' or 'ring species' at one time or another (Mayr, 1942, 1963, 1970; Bowen *et al.*, 2001; Irwin *et al.*, 2001a,b; Patten and Pruett, 2009; Cacho and Baum, 2012; Eastwood *et al.*, 2014), but many of these are far from the ideal. Most of them are cases cited by Mayr (1942, 1963), containing large geographic gaps in distribution (e.g., similar to Figure 2(c)). Several cases that have been commonly used as example ring species in the popular literature have recently been called into question; these include the herring gull (*Larus argentatus*) complex surrounding the Arctic Ocean (Crochet *et al.*, 2002; Irwin and Irwin, 2002; Liebers *et al.*, 2004), the great tit (*Parus major*) complex (Kvist *et al.*, 2003; Päckert *et al.*, 2005), and the crimson rosella (*Platycercus elegans*) complex (Joseph *et al.*, 2008; Ribot *et al.*, 2009). In each of these cases, molecular analysis has revealed sizeable discontinuities and a lack of support for previously articulated biogeographic scenarios, leading some authors to declare that they are not ring species. During the same period of time that these classic cases were being called into question, a few other potential cases have been proposed. These include the first convincing example of a possible ring species in plants, in the Caribbean slipper spurge (*Euphorbia tithymaloides*; Cacho and Baum, 2012), the ring-like evolutionary pattern described for Night Snakes (*Hypsiglena*) around the Gulf of California (Mulcahy and Macey, 2009), an apparent 'incipient ring species' in willow warblers (*Phylloscopus trochilus*) surrounding the Baltic Sea (Bensch *et al.*, 2009; Irwin, 2009), a possible although complex example in song sparrows (Patten and Pruett, 2009), and a case in trumpetfish (*Aulostomus* sp.), although in the latter case the terminal forms of the ring appear to be blending together (Bowen *et al.*, 2001). Particularly intriguing is the first proposed case of a ring species in a pathogen (Eastwood *et al.*, 2014), in beak and feather disease virus infecting the crimson rosellas, which have themselves been proposed as ring species (see above). Most of these cases have strong discontinuities around the ring, such that the cases recently proposed as ring species ironically have many of the characteristics of those recently declared not to be ring species. This is a reflection of the fact that biologists use a variety of meanings of the word 'ring species,' and why we advocate that the term be used for any current situation in which a loop of populations has a single species boundary, avoiding definitions that include a statement about the process of formation of such a situation.

Conclusion

Both the greenish warblers and *Ensatina* salamanders are ring species in the sense that two forms that have diverged to the species level are connected by a chain of populations in which there is gradual or stepwise change, such that there is no clear

species-level boundary through that chain. They both beautifully illustrate the first two purposes for which ring species have been used: as demonstrations that species differences are a result of evolution and that geography often plays an important role in the evolution of separate species. Species are not fixed entities, and the barriers between them are fluid and context-dependent. These cases also have been used to infer the history of changes during speciation. This is perhaps most clear in song variation of greenish warblers (Figure 5(b)), which provoked the working hypothesis that short, simple ancestral songs gradually evolved into the long, complex, and divergent songs of the two Siberian species. Both cases are however not good examples of speciation by distance, and the quest will have to continue for any examples that fit the ring species concept in that most ideal form (Figures 2(a) and 3(a)). We note however that there is strong evidence from a variety of other sources for divergence-with-gene-flow (Pinho and Hey, 2010), and increasing evidence for speciation-with-gene-flow (Martin *et al.*, 2014), such that evidence for these phenomena from ring species is not essential to the validity of those ideas. In most of the literature on speciation-with-gene-flow, however, reproductive isolation is envisioned as evolving directly within the chain of populations connecting the diverging forms. The ring species concept differs in that reproductive isolation evolves not within the chain but rather between the overlapping end points.

One reason that the ideal ring species scenario (Figures 2(a) and 3(a)) has proven so elusive is that it requires an unusual geographic arrangement of ecologically suitable and unsuitable areas of just the right geographic sizes, such that the central barrier is large enough to prevent movement of individuals across it while the ring is small enough for gene flow to keep neighboring populations similar. Furthermore, a period of ecological stasis long enough for the ring to form is necessary. It is likely this last requirement that is not often satisfied on this complex Earth with its frequent climatic shifts. Divergence to the level of species tends to occur on a scale of hundreds of thousands to millions of years, whereas climate shifts occur on a scale of hundreds to thousands of years, such that species distributions are undergoing frequent shifts. Hence it may be unlikely that we will find any cases that fit the most ideal scenario, but the search should still go on, as the Earth is filled with many possible barriers around which ring-like distributions may form (Irwin, 2012a; Monahan *et al.*, 2012).

See also: Speciation Continuum. Speciation-with-Gene-Flow

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