

Modes of Peripheral Isolate Formation and Speciation

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Peripheral isolates are relatively small isolated or semiisolated populations distributed around the periphery of a large central portion of a species' range. Range maps typically show the distribution of a species to be continuous (Udvardy, 1969; Hengeveld, 1990). However, close examination of the distribution of a species or monophyletic group will likely reveal peripheral isolates (Mayr, 1963). Peripheral isolates have been regarded as important units of evolutionary divergence (e.g., Mayr, 1963; Bush, 1975; Mayr and Ashlock, 1991). This idea stems from early observations of "differences between central and peripheral populations" (Mayr, 1963:386) and the tendency for taxonomic recognition of these populations. Advocated most strongly by Ernst Mayr, the importance of peripheral isolates has become almost dogma in the evolutionary literature. The traditional mode of speciation relegated to peripheral isolates is the peripheral isolates model (PIM) of allopatric speciation (=peripatric and founder sensu Mayr, 1963; model 1B sensu Bush, 1975; model II allopatric sensu Wiley, 1981), and this mode has been regarded as the dominant mode of animal speciation (Bush, 1975).

The traditional treatment of peripheral isolates suffers from two major problems. First, although it might seem reasonable to suppose that the process of peripheral isolate formation should not influence the pattern of evolutionary descent, this is not the case (Wiley, 1981; Brooks and McLennan, 1991). However, alternative modes of peripheral isolate formation rarely have been addressed, or when addressed, all possible modes typically have not been included. For example, in one of the most recent treatments, Brooks and McLennan (1991:95) outlined three pathways to the PIM, including random settlements, alter-

nating episodes of dispersal and isolation, and "vicariant" peripheral isolation. An additional and important mode of peripheral isolate formation is through range retraction of a species, although this mode rarely has been recognized (but see Brown, 1957). Thus, the first objective of this paper is to examine alternative modes of peripheral isolate formation.

The second problem with the traditional view of peripheral isolates is that the PIM is not the only allopatric speciation model that specifically involves these isolates. An alternative model that involves peripheral isolates is the centrifugal speciation model (CSM) proposed by Brown (1957). Since first proposed, this speciation model has been largely ignored in the evolutionary literature. A striking exception is a series of papers by Bowers et al. (1973), Lawlor (1974), Baker et al. (1975), and Greenbaum et al. (1978), which discussed the possibility that the deer mouse (*Peromyscus maniculatus*) and its peripheral isolates (including *P. melanotis* and *P. polionotus*) evolved through centrifugal speciation. Wiley (1981) and subsequently Wiley and Mayden (1985) and Brooks and McLennan (1991) outlined the assumptions and specific phylogenetic and biogeographic predictions of the PIM. However, specific phylogenetic and biogeographic predictions following the logic of Wiley (1981) have not been constructed for the CSM. Predictions of the CSM differ from those of the PIM and depend on the mode of peripheral isolate formation. Thus, the second objective of this paper is to outline specific phylogenetic and biogeographic predictions of the CSM and to explore the predicted evolutionary consequences of alternative modes of peripheral isolate formation within both speciation models.

Predictions of speciation models make

no attempt to implicate specific mechanisms (Wiley, 1981). In addition, the predictions are dependent on the following assumptions: character change is fast enough to reconstruct the history of speciation, there have been no extinctions, and rampant dispersal has not obscured the sequence of speciation (Wiley and Mayden, 1985; Brooks and McLennan, 1991). Wiley (1981) noted that specific predictions of speciation models could be used to distinguish among modes of speciation in a particular situation. Speciation within South American frogs of the subgenus *Stombus* (genus *Ceratophrys*) will be discussed in light of modes of peripheral isolation and speciation.

MODES OF PERIPHERAL ISOLATE FORMATION

Waif Dispersal

Waif dispersal is long-distance movement of organisms across a barrier of inhospitable habitat that results in the establishment of a new population. This is the classic mode of peripheral isolation in the PIM (Wiley and Mayden, 1985). Waif dispersal is dependent on a species' biology and may involve either active movement, whereby organisms move under their own power, or passive movement, whereby organisms are carried by another organism or physical agent (Brown and Gibson, 1983).

Although formation of a peripheral isolate via waif dispersal probably occurs infrequently, it becomes inevitable over a long period of time (Brown and Gibson, 1983). For example, terrestrial organisms have colonized volcanic oceanic islands, such as the Hawaiian and Galapagos archipelagos, exclusively by dispersal. Organisms differ in their abilities to disperse long distances and establish colonies. Flying organisms, such as some birds, bats, and insects, and organisms with special adaptations for long-distance passive dispersal (e.g., coconut [*Cocos*] fruits and brine shrimp [*Artemia*] eggs), are relatively more capable of establishing peripheral isolates through dispersal. Species also differ in their ability to withstand competition and predation pressures during establishment

of an isolated population subsequent to dispersal. In some circumstances, it is difficult to envision a scenario in which long-distance dispersal could occur except for a "freak accident." Thus, 20th century biogeographers are often reticent to invoke dispersal in the distributions of species and often make an initial assumption that it has not occurred (Humphries and Parenti, 1986). However, even in circumstances where dispersal seems an unlikely event, the propagule necessary to establish a peripheral isolate may consist of a single individual or seed of asexual, hermaphroditic, self-compatible, or parthenogenic species or a single pregnant female in sexually reproducing species. Thus, in considering the origin of a peripheral isolate, dispersal should not be a priori discredited as a viable alternative.

Microvicariance

Vicariance is the physical division of a previously continuous distribution through forces such as orogenic uplift, continental drift, changing sea levels, and glacial tongues. Microvicariance is the formation of a peripheral isolate through a vicariance event (Lynch, 1989; also termed vicariant peripheral isolation by Wiley and Mayden, 1985). Microvicariance "invokes a passive role for the ancestral species" (Brooks and McLennan, 1991:95) and is independent of the species' biology. Thus, species that inhabit the area will be divided by the vicariance event, and depending on the nature of the vicariance event and distributional patterns of the species, many if not all species will form peripheral isolates in the same geographic region. These events are essentially range retractions through extirpation at the disjunction, but all species, regardless of their environmental adaptations, will be affected.

Range Retraction

A species' range is a composite reflection of the species' biology. The highest density is assumed to be in the center of a species' range, where environmental conditions are most favorable, with decreasing densities towards the range margins, where condi-

tions are increasingly suboptimal, until the range is limited by environmental conditions to which the species is not adapted (Brown, 1984; Hengeveld, 1990). If environmental conditions change, particularly near the margins of a species' range, the range of a species may change in concert. Local range expansions are vastly more common than long-distance dispersal (Brown and Gibson, 1983). Furthermore, Frey (1992) demonstrated that relatively dramatic changes of species' ranges can occur in a short time span (ca. 20 years) as a result of minor climatic changes.

Peripheral isolates form when tolerable environmental conditions degrade, resulting in the retraction of the species' range. Range retractions result from extirpation or from the movement of individuals away from the deteriorating conditions. However, even in a generally degrading environment, certain peripheral areas will often maintain conditions or habitats suitable to the species. The species will persist in these patches but will become isolated by the retracting range of the adjacent populations. For example, 76% of the peripheral subspecies of mammals in North America are south of their central ranges (Rapoport, 1982). Most of these subspecies were presumably isolated in patches of suitable habitat when their range shifted northward due to climatic warming at the end of the Pleistocene. Formation of peripheral isolates through range retractions is the classic mode specified by the CSM (Brown, 1957).

Although peripheral isolate formation through waif dispersal is largely random as a result of the independent probabilities of each species crossing a barrier to colonize a new area (Brown and Gibson, 1983), changing environmental conditions that result in range retractions may produce similar patterns of peripheral isolate formation among species. Species that occur in similar habitats and have similar geographic ranges (i.e., members of the same floral or faunal element) can experience similar changes in range as a result of changing environmental conditions (Frey, 1992). Thus, it is possible for species that

occur in similar habitats to become isolated in the same peripheral areas by concordant retractions of their ranges. However, unlike traditional vicariance events (i.e., physical division) that affect many, if not all, species of an area, range retractions are expected to result in concordant biogeographic patterns only among species with similar environmental requirements and distribution patterns.

MODES OF SPECIATION

Peripheral Isolates Model

The PIM postulates a distributional pattern of a widespread central species with one or more peripheral isolates. Assumptions of the PIM are based on differences in gene flow between the central and peripheral populations. The model assumes that gene flow at the center of a species' range is great enough to prevent differentiation of central demes, whereas weak or absent gene flow among peripheral isolates allows a relatively high frequency of new characters to become established or fixed. Thus, the PIM predicts that the most apomorphic populations are peripheral isolates, whereas the central population is relatively plesiomorphic.

Phylogenetic and biogeographic predictions of the PIM under alternative modes of peripheral isolate formation (except through range retraction) have been variously treated by Wiley (1981), Wiley and Mayden (1985), and Brooks and McLennan (1991; see Table 1 for summary). The formation of peripheral isolates through independent dispersal to random geographic regions (first pathway discussed by Brooks and McLennan, 1991:95, fig. 4.6), microvicariance (third pathway discussed by Brooks and McLennan, 1991:95-96, fig. 4.8), or retraction of a species' range results in a polytomous pattern of evolutionary descent as revealed by cladistic analysis because synapomorphies are lacking. Because the rate of character change is assumed to be much higher in peripheral populations, peripheral isolates possess only symplesiomorphic characters that were present in the original population be-

TABLE 1. Predicted phylogenetic and biogeographic patterns of the peripheral isolates model (PIM) and centrifugal speciation model (CSM) of allopatric speciation. Predictions depend on the mode of peripheral isolate formation.

	Phylogenetic pattern	Phylogeny reflects sequence of speciation	Plesiomorphic population	Apomorphic population	Rate of change in peripheral populations	Biogeographic congruence among species
PIM						
Dispersal						
Independent	polytomous	no	central	peripheral	fast	no
Sequential	dichotomous	yes	central	peripheral	fast	no
Range retraction	polytomous	no	central	peripheral	fast	no ^a
Microvicariance	polytomous	no	central	peripheral	fast	yes
CSM						
Dispersal						
Independent	dichotomous	yes	peripheral	central	slow	no
Sequential	polytomous	no	peripheral	central	slow	no
Range retraction	dichotomous	yes	peripheral	central	slow	no ^a
Microvicariance	dichotomous	yes	peripheral	central	slow	yes

^a Congruence is expected only among taxa with similar distributional patterns and environmental requirements.

fore the isolations and autapomorphic characters that arise in each peripheral isolate independently of other populations. Thus, the phylogeny will not reflect the sequence of peripheral isolate formation and cladogenesis except when two or more peripheral isolates form simultaneously. Furthermore, biogeographic patterns among different species inhabiting the area are not expected to be congruent (i.e., no congruence of tracks), except in a case of microvicariance or range retraction that involves more than one species with similar distributions and habitat requirements.

Conversely, in the special case of sequential dispersal through time and space (i.e., the peripheral isolation, divergence, and subsequent dispersal of the new species to a new area), the phylogenetic pattern will be dichotomous (second pathway discussed by Brooks and McLennan, 1991: 95, fig. 4.7) because newly diverged peripheral isolates will share apomorphies with subsequently formed peripheral isolates. The phylogeny will reflect the sequence of speciation, with the central population most plesiomorphic and the most recently formed peripheral isolate most apomorphic. However, congruence of tracks is not expected among different

clades because of differences in biology and dispersal capabilities.

Centrifugal Speciation Model

The CSM has the same distributional prerequisite as the PIM, but predictions are contradictory because of different assumptions. Assumptions of the CSM are based on the different frequencies with which characters arise in either the central or peripheral populations. The CSM assumes that the center is "the principal source of evolutionary change leading to 'potent' new species" (Brown, 1957:248). New phenotypes are most likely to become established in the center of the range because (1) of the relatively greater number of new mutations that arise in a large population, (2) individuals in the central area have a better chance of gaining new characters as they spread from various points of origin within the species, (3) variability is maintained because of a large number of niches, and (4) the center of the range is the "most dependable refugium" for the species (Brown, 1957). Thus, the CSM predicts that peripheral isolates will remain relatively plesiomorphic while the large central population becomes highly derived (Table 1) and that the central population will be more

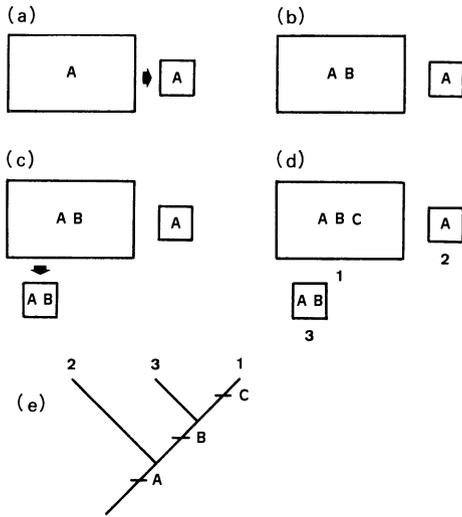


FIGURE 1. Centrifugal speciation model where peripheral isolates are formed by independent dispersal to random geographic areas. (a) Individuals disperse to a new geographic area. (b) A new character B develops in the rapidly evolving central population. (c) Dispersal to another geographic area. (d) A new character C develops in the rapidly evolving central population. (e) Cladogram depicting relationships among populations 1, 2, and 3. The central population (1) is relatively autapomorphic.

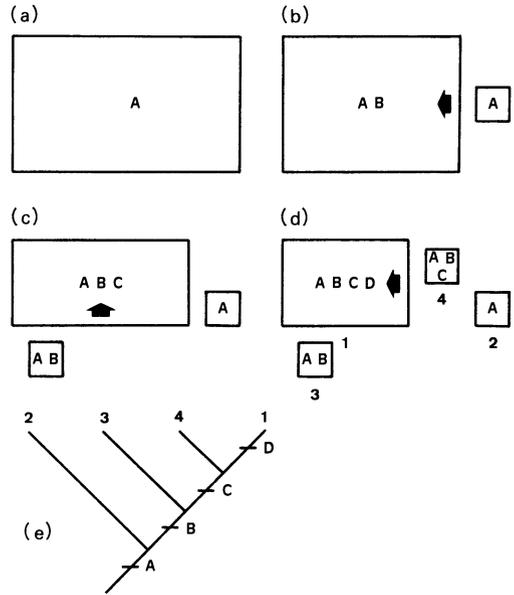


FIGURE 2. Centrifugal speciation model where peripheral isolates are formed by retraction of a species' range or by microvicariance (not illustrated). (a) The organism occupies the ancestral range. (b) A peripheral isolate forms through a range retraction or by microvicariance, and a new character B subsequently arises in the central population. (c) Further range retraction or a second incidence of microvicariance forms a second peripheral isolate. The peripheral isolate shares the characteristics of the central population at the time of its isolation. A new mutation C arises in the central population. (d) Further range retraction or a third incidence of microvicariance creates a third peripheral isolate and the central population subsequently acquires a new character D. (e) Cladogram depicting relationships among populations 1, 2, 3, and 4.

variable than the peripheral isolates (Greenbaum et al., 1978).

Formation of peripheral isolates through independent dispersal to different geographic areas (Fig. 1), microvicariance, or range retraction (Fig. 2) results in a dichotomous pattern of evolutionary descent. Peripheral isolates share the characteristics of the rapidly evolving central population at the time in which they are formed. Thus, a newly formed peripheral isolate will share synapomorphies with the central population and with previously formed peripheral isolates in a nested hierarchy. The phylogenetic pattern will reflect the sequence of cladogenesis, but the first formed peripheral isolate will be most plesiomorphic and the central population will be most apomorphic. Congruence of tracks is expected only in the case of microvicariance and only for species with the same distributional patterns and habitat requirements when peripheral isolates form through range retraction.

Conversely, if peripheral isolate formation is due to sequential dispersal, the resulting phylogenetic pattern will be polytymous (Fig. 3). Peripheral isolates maintain characteristics of the central population at the time of dispersal while the central population develops autapomorphies. If individuals of the original peripheral isolate disperse into a new area, the new peripheral isolate will also share the primitive characters. Thus, synapomorphies will be lacking but the central population will be highly autapomorphic. The phylogenetic pattern will not reflect the sequence of speciation. Congruence of tracks is not expected among different species because of

differences in biology and dispersal capabilities.

SPECIATION IN *STOMBUS*

The alternative phylogenetic and biogeographic predictions of the different models of speciation (Table 1) can be used to distinguish the mode of speciation operating in a particular situation (Wiley, 1981). I examined speciation in South American frogs of the subgenus *Stombus* (genus *Ceratophrys*, family Leptodactylidae) using Lynch's (1982) analysis of phylogenetic relationships. *Stombus* is a well-defined monophyletic group consisting of three species: *C. cornuta*, broadly distributed in rainforest habitat of the Amazon Basin, and the peripheral species *C. calcarata*, inhabiting semixeric habitats in northern Colombia and eastern Venezuela, and *C. stolzmanni*, inhabiting xeric habitats in southwestern Ecuador (Lynch, 1982). Lynch's cladistic analysis resulted in a sister-group relationship of the peripheral species *C. stolzmanni* with a clade consisting of *C. calcarata* and the central *C. cornuta* (i.e., *C. stolzmanni* + [*C. calcarata* + *C. cornuta*]). Lynch (1982:178) also examined the distribution of autapomorphies and found that the widely distributed central *C. cornuta* is highly autapomorphic, whereas the peripheral species exhibit no known autapomorphies.

Lynch (1982) and Brooks and McLennan (1991) noted that the geographic distribution of the subgenus *Stombus* suggests divergence by the PIM. Under the PIM, a dichotomous branching pattern such as that found in *Stombus* is predicted only in the special case of sequential dispersal through time and space. However, the geographic distributions of the three species do not suggest that sequential dispersal has occurred; the peripheral species are relatively close to *C. cornuta* (*C. stolzmanni* occurs approximately 175 km west of *C. cornuta* and *C. calcarata* occurs approximately 100 km north of *C. cornuta*), and the distance between the peripheral species is relatively great (approximately 1,325 km). Furthermore, the relatively plesiomorphic

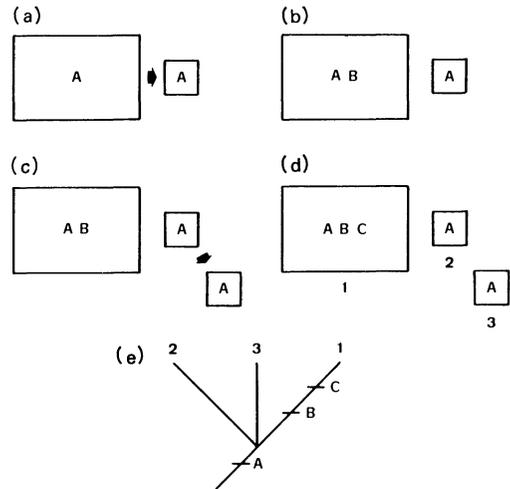


FIGURE 3. Centrifugal speciation model where peripheral isolates form by sequential dispersal through space and time. (a) Individuals disperse to a new geographic area. (b) A new character B develops in the rapidly evolving central population but new characters are not expected to arise in the peripheral isolate. (c) Individuals from the newly formed peripheral isolate disperse to another new area. (d) An apomorphy C develops in the central population. (e) Cladogram depicting relationships among populations 1, 2, and 3.

condition of the peripheral species *C. stolzmanni* in relation to the central species (*C. cornuta*) and the highly autapomorphic nature of the central species are inconsistent with the predictions of the PIM (Lynch, 1982; Brooks and McLennan, 1991).

These violations of the predictions of the PIM require consideration of alternative modes of speciation. Lynch (1989) and Brooks and McLennan (1991) did not consider the CSM as a possible alternative and subsequently concluded that speciation within *Stombus* was due to vicariance (allopatric speciation model I sensu Wiley, 1981). However, Lynch (1989) based his decision on the actual size of the peripheral species but concluded that speciation fit the PIM based on the relative size differences of the distributions of *C. cornuta* and the peripheral species. No explanation was provided for the highly autapomorphic nature of the central species *C. cornuta* and lack of autapomorphies in the periph-

eral species. Brooks and McLennan suggested no specific vicariance events, but Lynch (1982:176) noted that "one might be tempted to implicate the emerging Andes as a causal force in the fragmentation of the ancestral stock of the subgenus *Stombus*." Although the fossil record is inadequate to support any hypothesis, vicariance is discredited by the presence of *C. calcarata* on both sides of the Andes (Lynch, 1982). Duellman (1979) distinguished major and minor physiographic barriers to dispersal of Andean herpetofauna that may act as dispersal corridors through the Andes for low-elevation species such as *Stombus*. All of these corridors are located in proximity to the peripheral species. The Huancabamba depression in southern Ecuador could provide a major dispersal corridor for *C. stolzmanni*, and corridors between the Sierra Nevada de Santa Maria, Cordillera Oriental de Colombia, Merida Andes, and Cordillera de la Costa could allow dispersal through the Andes for *C. calcarata*.

Lynch (1982:176) concluded that the distributions of these species "suggest contractions of formerly more broad distributions." Speciation in this group is best supported by the centrifugal speciation model, where peripheral isolates form through range retraction. As predicted by this mode of peripheral isolate formation and speciation, the phylogenetic pattern is dichotomous, the peripheral species are relatively plesiomorphic with no known autapomorphies, and the central species is relatively apomorphic (i.e., highly autapomorphic) with respect to the peripheral species.

Haffer (1969) hypothesized that forest habitats in South America were restricted to refugia during the Pleistocene. Lynch (1982) rejected this hypothesis as an explanation for the distribution and divergence of *Stombus*. However, the Pleistocene forest refugium hypothesis may indirectly have played a role in speciation within *Stombus*. Based on a phylogenetic analysis of the subfamily Ceratophryinae utilizing *Lepidobatrachus* as the outgroup, Lynch (1982:176) concluded that

the most parsimonious explanation is that the non-forest (or dry forest) environment is the aboriginal environment for frogs of the subfamily Ceratophryinae, and the forest-dwelling habits evolved independently in *C. aurita* and *C. cornuta* (eight evolutionary shifts in habitats preference are required if one considers forest-dwelling as primitive as opposed to three if forest-dwelling is derived).

Thus, the ancestral species of *Stombus* may have been widely distributed throughout xeric nonforest habitats in northern South America during the Pleistocene. At the end of the Pleistocene with the onset of more mesic conditions, the range of the ancestral species would have retracted. The geographic areas currently occupied by the peripheral species have maintained arid conditions, allowing the persistence of the ancestral populations. *Ceratophrys stolzmanni* was isolated west of the Andes as the central range retracted through the Huancabamba depression. The presence of *C. calcarata* on both sides of the Andes indicates that the formation of the Andes (vicariance) was not responsible for the separation of the peripheral species *C. calcarata* and the central population (*C. cornuta*). Rather, it suggests that the separation of *C. calcarata* and the central population occurred on the east side of the mountains through further retraction of the range of the central population. Further expansion of rainforest from Pleistocene refugia continued to eliminate xeric habitats from the Amazon Basin where *C. cornuta* occurs.

CONCLUSIONS

The peripheral isolates model of allopatric speciation traditionally has been regarded as a dominant mode of evolutionary divergence and has received considerable attention. However, Lynch (1989) empirically determined that the PIM was a relatively infrequent mode of speciation. The prevalence of published cladograms with dichotomous branching patterns suggests that centrifugal speciation may be more common than the peripheral isolates model. The CSM predicts that a dichotomous branching pattern will be produced

through cladistic analysis except when peripheral isolates form through sequential dispersal. In contrast, the PIM results in polytomous phylogenies in all cases except for sequential dispersal. Changes in the margin of a species' range (which may lead to the formation of peripheral isolates) are vastly more common than dispersal events (Brown and Gibson, 1983). Furthermore, sequential dispersal is probably relatively common only when there is a cluster of islands (oceanic or habitat) or a stepping-stone arrangement of islands away from a mainland because these patterns increase the probability of dispersal (MacArthur and Wilson, 1967).

The analysis of patterns of species' distributions and phylogenetic descent has been regarded as useful in determining modes of speciation (Wiley, 1981; Wiley and Mayden, 1985; Lynch, 1989; Brooks and McLennan, 1991). The analysis of the distribution of apomorphic characters on a phylogenetic tree also is useful in determining these modes. Lynch (1989) suggested that the distribution of apomorphic characters would be useful in determining peripheral isolates speciation if the pattern (i.e., central population relatively plesiomorphic, peripheral isolates highly autapomorphic) were consistent. However, he considered this to be an unreliable characteristic for determining peripheral isolates speciation because in his example (Lynch, 1982) the central population, *C. cornuta*, rather than the peripheral species, was relatively apomorphic and highly autapomorphic. As has been demonstrated, the highly apomorphic nature of *C. cornuta* is interpretable as a result of centrifugal speciation rather than peripheral isolates speciation. Thus, the pattern of distribution of apomorphies within a monophyletic lineage is of use in distinguishing among modes of speciation.

In discussing modes of allopatric speciation, careful distinction must be made between vicariance and the vicariance speciation model (VSM). Vicariance, in a narrow sense, is a physical division (usually physiographic; does not include range

retraction) of the range of a taxon and may result in large-scale subdivision into two (or more) populations of large size (vicariance) or small-scale subdivision into one (or more) peripheral isolates (microvicariance). However, the relative and absolute size distinction between large-scale and small-scale subdivision has been arbitrary (e.g., Lynch, 1989). Microvicariance is one of three modes of peripheral isolate formation (the others are waif dispersal and range retraction) that may be involved in either the PIM or CSM of allopatric speciation. Vicariance, however, is the mode of geographic subdivision often invoked in the VSM. However, discussions of the VSM often consider that geographic subdivision can occur through physical division or range retraction (vicariance in a broad sense) without distinguishing between the two modes; waif dispersal is not a likely mode of geographic subdivision because the VSM involves relatively large populations. In this discussion of the VSM, geographic subdivision is considered to occur only through physical division (vicariance in a narrow sense). Vicariance speciation is the attainment of lineage independence of two relatively large, geographically isolated populations. The prediction is that cladistic analysis will produce a dichotomous branching pattern that accurately reflects the sequence of subdivision and speciation.

Given the arbitrary size distinction between large-scale and small-scale subdivision and the often unclear distinction between vicariance (including microvicariance) and range retraction, additional ways to distinguish the VSM from other modes of allopatric speciation are needed. The distribution patterns of autapomorphic characters on the organism's phylogeny are useful for this endeavor. The CSM and PIM make clear-cut predictions as to which populations (central or peripheral) will be relatively apomorphic and highly autapomorphic. In contrast, the VSM makes no such predictions; the larger of the two populations may be relatively apomorphic or plesiomorphic, but autapomorphies should

be relatively equally distributed on the tree. Biogeographic patterns of other organisms inhabiting the same area may be of limited use. Modes of speciation that involve geographic subdivision through physical division (including the PIM and CSM where peripheral isolates form through microvicariance and the VSM) predict that most if not all species inhabiting the area should have the same biogeographic pattern (i.e., there is congruence of tracks). Conversely, in the PIM and CSM, where geographic subdivision is through waif dispersal, biogeographic patterns will not be congruent. The confounding factor is how to distinguish the VSM from the PIM or CSM when geographic subdivision occurs through range retraction. In the case of geographic subdivision through range retraction, it is possible for some taxa with similar habitat requirements and distributions to show similar biogeographic patterns. The three modes of allopatric speciation may form a continuum in terms of relative size differences among populations and relative rates of evolutionary change, with the VSM intermediate between the PIM and CSM, or one or more modes of allopatric speciation may be special cases of another.

ACKNOWLEDGMENTS

I thank J. H. Brown, T. K. Lowrey, J. B. M. Miyashiro, R. E. Palma, J. Salazar-Bravo, and T. L. Yates for comments on an earlier version of this manuscript. J. D. Lynch and an anonymous reviewer provided helpful criticisms, which improved this paper.

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Received 2 October 1992; accepted 1 February 1993