Geographic Differentiation, Cladistics, and Vicariance Biogeography: Reconstructing the Tempo and Mode of Evolution

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SYNOPSIS. Although the literature on speciation is large, surprisingly little attention has been paid to methodological considerations. If there is a general methodology within this literature, it consists of delimiting taxa and their distributions, describing patterns of phenotypic (and occasionally genotypic) variation, noting contact zones and hybridization, reviewing information on past climates and vegetations, and from these constructing a narrative scenario of the pathway of speciation. However, two kinds of knowledge, essential for reconstructing speciation, are typically lacking: a genealogical hypothesis of the relevant taxa based on cladistic analysis, and a hypothesis of the interrelationships of areas of endemism based on vicariance biogeography. Both are necessary to develop and test alternative hypotheses about the mode of taxonomic differentiation. A model of speciation analysis is constructed using taxa of Australian birds as the empirical data base. Cladistic relationships among taxa and vicariance patterns among areas of endemism reveal a specific, nonrandom historical relationship among the areas of differentiation for Australian birds and suggest that type 1a allopatric speciation (of Bush, 1975) is more common than type 1b, that peripheral isolates are less important than previously maintained, and that parapatric speciation is rare. The model can also be used to examine the patterns of concordance between phenotypic and genotypic characteristics during geographic differentiation and to investigate their relative and absolute rates of change.

INTRODUCTION

The investigation of the patterns and processes of evolution can be organized in terms of three hierarchical levels of analysis: microevolution (within- and between-population phenomena), speciation (the differentiation of new taxa), and macroevolution (supraspecific patterns of diversity within and between monophyletic groups). A unified conceptualization of evolution will emerge not only from intense study within each level but also at the two interfaces. Taxonomic differentiation (speciation) is the link between population-level patterns and processes and the among-species patterns and processes constituting macroevolution (see Eldredge and Cracraft, 1980).

The literature on speciation is enormous, but curiously there has been very little discussion about the methodology of speciation analysis. For example, in his major summary, Mayr (1963) does not address specific problems of methodology: How do we reconstruct the patterns of differentiation, and how do we come to have knowledge of the processes that may have produced those patterns? Virtually all recent discussions of evolution in general (e.g., Dobzhansky et al., 1977; Futuyma, 1979) or of speciation in particular (Bush, 1975; Endler, 1977; White, 1978) merely describe how speciation is thought to occur but do not treat in any detail the problem of how that knowledge was obtained. Now certainly imbedded in the literature on speciation are statements about methodology, but as I hope will emerge in this paper, a more specific concern in the future with problems of methodology will greatly increase our understanding of speciation.

At this point it is worthwhile to distinguish between pattern and process and to comment on their conceptual interaction. In the case of speciation analysis, pattern includes the distribution of the relevant taxa (of whatever categorical level) in space and time as well as the distribution of the phenotypic and genotypic similarities and

differences among those taxa, all interpreted within the framework of a hypothesis of the genealogical relationships of the included taxa. It should be obvious that one can build up a rather complete picture of pattern without allegiance to any specific assumptions about the processes that may have produced those patterns ( Eldredge and Cracraft, 1980; Nelson and Platnick, 1981). When speaking of processes we may want to mention those that have produced spatial patterns, such as dispersal or vicariance of a once continuous distribution by geographic or climatic events, or we may want to focus on genetic, developmental, or even ecological processes. The important point is that our knowledge of patterns may be independent of our notions of process, and that knowledge of patterns is necessary to test or evaluate alternative hypotheses of process; alternative hypotheses of process should make different predictions about the patterns we can expect to see in nature.

In the first part of this paper I will discuss some of the requirements for constructing hypotheses of pattern within the context of speciation analysis. It will then be shown how some of those patterns might be used to evaluate certain process-level phenomena within speciation analysis. Following this more general, theoretical discussion I want to construct a model of speciation analysis using a continental avifauna as the empirical data base. Finally, I will discuss how this model might be used to investigate a series of general questions within evolutionary biology.

Reconstructing Speciation: The Component of Pattern

Within the large literature on speciation, it was noted earlier, workers rarely discuss the methodology of reconstructing speciation. If that literature is examined, however, a relatively consistent methodology emerges; Vuilleumier (1980) has summarized these methods and has identified, correctly I think, the major stages of speciation analysis followed in the large proportion of these papers, particularly those which approach speciation from a systematic point of view.

1. The taxa in question (usually species and subspecies) are chosen or delimited and their geographic distributions are mapped.

2. Particular attention is paid to phenotypic variation of geographic isolates and to the structure of any cline. Zones of presumed secondary contact are discovered and any hybridization is described. Vuilleumier (1981) has called this phase “the fundamental datum of speciation analysis.”

3. The literature on the present ecological characteristics of the taxa is reviewed (perhaps supplemented by field work) as is that on Plio-Pleistocene palynology, palaeoclimatology, and paleogeography, to suggest times of isolation, barrier formation, or secondary contact.

4. Finally, all these data are synthesized into a narrative scenario that attempts to be internally coherent and in accord with our current notions of speciation (generally as described by Mayr, 1968).

In recent years some investigators have begun to collect “genetic” data more directly rather than infer it from morphological data (see especially White, 1978, pp. 11–12). In most of these cases the methodological sequence is the same, and this “genetic” analysis merely extends the description of the phenotype (data on allelic, genotypic, or karyotypic frequencies are themselves “phenotypic,” and as such they also form patterns in need of explanation).

I suggest that there are two fundamental kinds of information missing from the above methodological sequence and that without them one cannot gather the type of evidence needed to test hypotheses of speciation or to investigate questions of the tempo and mode of differentiation. That both types of information are lacking from the majority of speciation studies implies serious gaps in our knowledge of taxonomic differentiation. Interestingly, I can find no specific mention of their necessity or importance in the current major works on speciation (e.g., Mayr, 1963; Bush, 1975; Endler, 1977; White, 1978: see especially chapter 1).

The first, and perhaps most important, information needed is a corroborated hy-
hypothesis of the genealogical relationships of all the differentiated taxonomic units considered relevant for the study (Eldredge and Cracraft, 1980; Wiley, 1981). Because of variation in taxonomic philosophy these units might be classified as species or as subspecies; or because most present-day classificatory schemes are non-phylogenetic, many relevant taxa may have been elevated to separate generic status as a result of emphasizing a large morphological discontinuity (see Yates et al., 1979, for an example). If we are to have a testable assessment of rates of morphological and genetic differentiation, then taxonomic ranks assigned by traditional, nonphylogenetic systematists cannot be taken at face value.

I know of no speciation study within birds in which a corroborated hypothesis of relationships among the taxa is the cornerstone of the analysis. Indeed, there are only a few studies in which such relationships are postulated, and in these cases the relationships were determined essentially ex post facto, not as a basis for inferring the history of speciation but as a conclusion of the speciation scenario. The importance of a phylogenetic analysis cannot be overestimated, for it is the genealogical history of the differentiated taxa in space and time which we are trying to reconstruct. Systematists typically use geographic distribution itself, or the presence of zones of hybridization, to make inference about relationships, and, accordingly, about the pattern of speciation. But an independent estimate of relationships, based on a cladistic analysis of the phenotype or genotype, is required to make an unbiased assessment of the pattern of differentiation through space and time. The genealogical pattern itself is crucial for evaluating alternative hypotheses about the mode of speciation, and therefore the use of geographic distribution to infer relationships prevents us from evaluating modes of speciation with geographic patterns that are defined in terms of genealogy. Similarly, hybridization cannot be employed to assess hypotheses of relationship. The literature is full of references to the assumption of a sister-group relationship among taxa that are in contact and hybridize, and many decisions as to specific status are based on this ability to hybridize (Mayr, 1969, p. 195). But as Rosen (1979) has argued, hybridization is a primitive retention within a lineage and as such cannot constitute evidence of genealogical relationship and, therefore, methodologically cannot contribute much to assigning taxonomic rank (several clade-genetic events may separate two taxa that hybridize, and other, more closely related taxa produced by those events may be distinct and isolated genetically; see Rosen, 1979, for an example).

In any speciation analysis it may be that one of the included species was ancestral to one or more of the other taxa. Corroborated phylogenetic hypotheses are necessary to formulate and test hypotheses about ancestry and descent (Eldredge and Cracraft, 1980; Nelson and Platnick, 1981). A rigorous methodology to address the issue of ancestry and descent is typically missing from contemporary speciation analysis.

A second kind of information needed in speciation analysis is that provided by vicariance biogeography (Rosen, 1978; Platnick and Nelson, 1978; Nelson and Platnick, 1981). We must estimate to what extent the genealogical relationships of the taxa under study, as translated in space, are concordant with the patterns of other taxa distributed in the same areas. Only in this way can we discover whether our taxa are part of a more generalized pattern of speciation or whether the history of this isolated group is largely unique and not explainable by the causes of some more general pattern. In a real sense we must know the generality of the distribution patterns of groups other than the one we are studying before we can test hypotheses about the history of speciation of any specific group. And, as we shall see, vicariance biogeography is necessary to assess questions about rates of morphological and genetic differentiation during speciation.

That cladistic analysis and vicariance biogeography have been absent from virtually all previous speciation analyses means that we cannot fully assess the value of their conclusions. Their absence cer-
tainty means that such studies primarily have taken the form of narrative scenarios. The next section will explore some of the ways in which cladistics and vicariance can be used to evaluate modes of speciation.

**Modes of Speciation and Their Evaluation**

Given some set of distribution patterns and a series of geographic and climatic events thought to influence the isolation and evolution of the disjunct populations, there are any number of speciation "scenarios" or hypotheses that would be more or less consistent with the data. Cladistic analysis and vicariance biogeography can be used to falsify one or more of these hypotheses. In this section I want to discuss some of the modes of speciation that are thought to characterize vertebrates such as birds in order to point out the critical importance of cladistic analysis and vicariance biogeography. Because of space limitations, this discussion is directed primarily toward patterns that will be exemplified in the next section (see also Eldredge and Cracraft, 1980; Wiley, 1981).

Several general modes of speciation have been recognized (Bush, 1975). In type 1a allopatric speciation a broadly distributed ancestral species is subdivided by an isolating barrier, and the two isolates are assumed to change by phyletic evolution to an extent such that if they became sympatric they would maintain their separate specific identities. Given the nature of the process, the ancestral species is by definition assumed to go extinct at the time of geographic separation, although one of the descendant species may remain very similar to the ancestral species for a varying length of time; clearly one of the descendants must diverge sufficiently for speciation to be completed. The type 1b allopatric speciation mode involves the origination of one or more small peripheral isolates from a large ancestral species which is assumed to persist relatively unchanged; it is the peripheral isolate which is thought to diverge in phenotype and/or genotype.

How might these two modes be distinguished? The relative sizes of the distri-

butions of the two sister-taxa have been the traditional criteria. If the two ranges are about equal in size, then type 1a speciation is suggested; if a peripherally located taxon has a much smaller range than its sister-taxon, then type 1b is implied. But as most workers realize, following geographic isolation the distributions of taxa might expand or contract substantially, therefore the relative sizes of ranges are not critical tests of speciation mode. Without a dense fossil record that is also widely distributed geographically—a situation lacking for virtually all terrestrial organisms—there would be no way of knowing whether present ranges are similar to those at or near the time of speciation.

Cladistics per se cannot falsify either model, except in the trivial case in which the two taxa are shown not to be sister-taxa. But cladistics associated with vicariance biogeography can provide a basis for evaluating these two modes (see also Wiley, 1981). A type 1a mode implies the appearance of a geographic or climatic barrier. Such a barrier would be expected to influence the vicariance patterns of numerous taxa, and we would predict that there should be concordant pairs of sister-taxa on either side of this barrier. The ranges of all these taxa would not necessarily be expected to be of the same size—some might have enlarged or contracted—but we might predict that a sample would show sister-taxa with distributions of relatively the same size. Given this vicariance pattern within a biota, we probably would be justified in invoking type 1a speciation.

Vicariance biogeography can likewise be used to evaluate type 1b speciation, but several patterns are possible depending upon the way in which peripheral isolation comes about. Type 1b speciation typically is viewed as being initiated by a founder population, thus implying a dispersal event by one or more individuals to a peripheral area (Bush 1975, p. 346). As such, type 1b speciation is seen to be largely random, and we would not expect highly concordant vicariance patterns to develop from one clade to the next. If we observe a situation in which peripheral taxa have small ranges relative to their sister-taxon,
and we fail to find concordant vicariance patterns, type 1b speciation might be assumed. It must be emphasized, however, that peripheral isolation of taxa with small distributions can come about by vicariance, that is, by the establishment of a geographic or climatic barrier. In such cases we might predict that concordant vicariance patterns across a number of clades would be observed, with the peripheral sister-taxa all showing a small, and generally overlapping, distribution.

Parapatric speciation is said to occur by differentiation of contiguous populations without there being allopatric disjunction: isolation comes about primarily by distance (vagility is generally assumed to be low), some abrupt change in the genetic structure of the peripheral population is thought to occur, and strong directional selection within new adjacent habitats is postulated (Bush, 1975). By the nature of the way in which parapatric speciation is hypothesized to happen, one would not expect concordant cladistic-vicariance patterns to develop. Although some authors have inferred the occurrence of parapatric speciation from parapatric distribution patterns (see below), it is obvious that such distributions cannot provide a critical test because both modes of allopatric speciation can also result in parapatry. On the other hand, cladistics and vicariance biogeography can provide such tests. In Figure 1, three closely related parapatric species are shown, each endemic to its own area. Three cladistic hypotheses, 1a–c, and their corresponding area-cladograms, would be inconsistent with an interpretation of parapatric speciation. Hypothesis 1a would imply either the allopatric disjunction of the common ancestor of A and C from B, with the subsequent dispersal of B into the area between A and C, or the extinction of relatives of A and C from other areas. Hypotheses 1b and 1c imply allopatric disjunction (with the early vicariance of A or C respectively), particularly if the area-cladogram is repeated in other groups (see Discussion). If either hypothesis is unique with respect to other clades endemic in these areas, then parapatric speciation might be surmised. The hypo-

![Figure 1](image-url) (A-C). There are four possible area cladograms (a-d); the first three imply allopatric differentiation, whereas the last is consistent with parapatric differentiation. See text.

Because parapatric speciation is hypothesized to produce unique cladistic and vicariance patterns, it is essential to verify whether common patterns are in fact absent. If present, then allopatric modes were probably operating. Parapatric speciation has been invoked (or implied) for birds, but as will be discussed below, cladistic and vicariance data appear to falsify that hypothesis. Bush (1975, p. 348) cites a number of examples of parapatric speciation, but in none were cladistic and vicariance patterns examined; I suspect that most, but possibly not all, of these will prove to be instances of allopatric differentiation.

A CLADISTIC-VICARIANCE MODEL OF GEOGRAPHIC DIFFERENTIATION

The purpose of this section is to develop a model of speciation analysis using the methods of phylogenetic (cladistic) systematics and vicariance biogeography. The model will be presented in terms of a preliminary hypothesis specifying the patterns
of geographic differentiation of the Australian avifauna. Because of space limitations, speciation in the Australian avifauna cannot be described in detail, but some of the better corroborated systematic data available will be used to illustrate the major patterns and to construct testable hypotheses about avian evolutionary history on that continent (many other data that could have been included are compatible with those chosen for illustrative purpose). The patterns that are described do not convey the complexities that exist, but again this discussion is not meant to be a definitive analysis of avian speciation in Australia. By design, this section illustrates a method. My interpretations of systematic relationships are based on an evaluation of the literature and study of specimens in the American Museum of Natural History (New York) and Field Museum of Natural History (Chicago) and were derived using conventional cladistic methodology ( Eldredge and Cracraft, 1980). Although citations to the relevant literature are included here, a more complete documentation of the systematic conclusions will be presented elsewhere.

Areas of differentiation and endemism

Gentilli (1949), Serventy (1953), Ford (1974), and especially Keast (1960, 1961, 1974) have discussed the broad patterns of Australian avian speciation. All have emphasized areas of endemism and the geographic and climatic barriers assumed to define them. Figure 2 depicts ten areas of endemism considered in this paper (for this analysis all of New Guinea is taken—clearly incorrectly—to represent one area). All of these areas of endemism are well known in the literature, although my own studies suggest some slight modifications in their boundaries; in any case, the distributions of isolates rarely are precisely concordant with the distributions of other taxa in the same region, and the areas of Figure 1 should be viewed as abstractions of collective areas of differentiation.

Generally speaking these areas of endemism have been characterized in terms of the increasing isolation of taxa in peripheral refuges of more moist environments as the climate deteriorated during the Plio-Pleistocene (e.g., Keast, 1961). Although mesic refuges do exist, the situation is complicated by the fact that the arid interior can itself be viewed as consisting of several areas of endemism (Ford, 1974) and that some of the mesic centers of isolation on the eastern and northern coasts have historical relationships with other mesic areas rather than to the arid interior. Thus, although previous workers sometimes called attention to similarities among areas, none developed a general hypothesis about the historical interrelationships of these areas of endemism (primarily because they did not use corroborated phylogenetic hypotheses as their basic biogeographic data). On the other hand, these workers cannot be faulted for not applying a systematic-biogeographic theory and method that has been developed only recently, and a comparable situation exists for all continental biogeographic patterns; there is as yet no comprehensive hypothesis, based on the systematics of any group of organisms, for the interrelationships of the areas of endemism of any continent.

Areas of endemism can be established by inspection of the distributions of monotypic genera, species, and infraspecific taxa. Once these areas are defined, one then seeks to construct a hypothesis about
their historical interrelationships based on the phylogenetic patterns of the taxa differentiated in those areas. The extent to which concordant vicariance patterns can be established from clade to clade defines the degree to which we can reconstruct a general pattern of speciation, and consequently identify and describe the differentiation of taxa whose history is unique, in whole or in part, from that of the more general pattern.

Phylogenetic patterns of differentiation and Australian vicariance relationships

An analysis of genealogical relationships within a series of Australian taxa suggests a major vicariance pattern between the avifauna of the interior and southern portions of the continent and that of the northern and eastern regions. Two genera in particular provide evidence for the interrelationships of the interior and southern areas of endemism. The emu-wrens (Stipiturus) have four major isolates on the continent (Fig. 3A): S. malachurus has endemic subspecies in the southwest (7) and the southeast (5a), whereas the sister-group of S. malachurus consists of two taxa, S. ruficeps in the western desert (8) and S. mallee in the eastern mallee (6). The latter two taxa have been treated as subspecies or as species, but in either case they are now generally agreed to be sister-groups (Ford, 1970, 1974; Ford and Parker, 1974).

A genus of finches, Emelea, also has four isolated forms all of which have distributional and geological patterns similar to those of Stipiturus (Fig. 3B). In the southwest (7) is E. oculata, whereas its sister-species, E. bella, is in the southeast (5a). There are two other well-defined isolates, one (E. picta) in the western interior (8) and the other (E. guttata) in the eastern interior (6). The latter two species are postulated to be sister-taxa on the basis of hypothesized derived characters in their plumage patterns (Cracraft, in preparation).

Both these clades imply the following vicariance hypothesis: (1) an ancestral species was distributed over most of south-
ern Australia, (2) a broad vicariance event separated a central form from one distributed along the southern and southeastern coasts, and (3) subsequent disjunctions took place that separated both central and southern forms into eastern and western isolates. This vicariance pattern is corroborated by the genealogical history of other clades, but in the next example to be discussed an eastern component has been added.

The whipbirds and wedgebills, genus Psophodes, exhibit six endemics (Fig. 4A). Their genealogical and distributional patterns are very similar to those of Stipiturus and Emblemata except that a more extensive eastern distribution is seen for P. olivaceus. The relationships shown in Figure 4A are supported by morphological and behavioral data (Ford, 1971; Ford and Parker, 1973). Psophodes, then, seems to confirm the vicariance relationship between the central and southern areas. The biogeographic meaning of the eastern distribution of P. olivaceus, on the other hand, can be clarified only by comparison with other clades.

Some of the geographical components seen in Psophodes are paralleled in the flycatcher genus Eopsaltria (Fig. 4B). There is a genealogical connection between the southwest (7) and southeast (5b) in E. griseogularis, which in turn is related to E. australis in the east. Unlike Psophodes olivaceus, E. australis has not differentiated into distinct isolates but rather appears to show clinal variation (Ford, 1979). That there may have been older patterns of vicariance along the southern coast is suggested by the presence of E. georgiana in the southwest (7); alternatively, E. georgiana may represent an example of dispersal followed by differentiation. It will take analysis of additional clades to decipher this history.

The vicariance history of the eastern re-
regions is ambiguous. Both Psophodes olivaceus and Eopsaltria australis imply a vicariance pattern between the east and south, but other evidence suggests these elements may have attained this disjunction by northward dispersal. The areas of endemism in the east, particularly areas 3a and 3b of Figure 2, have well-corroborated vicariance relationships to areas in the north. This is exhibited within the genus Eopsaltria in which E. leucops is differentiated in New Guinea (9) and the York Peninsula (1) and its sister-species, E. capito, is differentiated in areas 3a and 3b of the east (Fig. 4B). This pattern of relationships is repeated in other clades.

The finch genus Poephila shows the general vicariance patterns connecting the north and east (Fig. 5A). One species, P. personata, has two differentiated isolates uniting area 4 with 1 + 2. This pattern is repeated, but with further differentiation, within the other lineage of Poephila. Area 4 is seen to consist of two centers of endemism (Ford, 1978) as evidenced by the differentiation of P. acuticauda. The latter is the sister-group of P. cincta, which is differentiated in the York Peninsula (area 1 + 2) and in the east (area 3).

The patterns of speciation within other genera can be used to further clarify and corroborate vicariance relationships of the north and east. For example, within the birds-of-paradise genus, Ptiloris, one species (P. magnificus) is differentiated in New Guinea and the York Peninsula, whereas its sister-taxon consists of two closely related species, P. victoriae in area 3a and P. paradiseus in area 3b (Fig. 5B).

**Australian speciation patterns: A general hypothesis**

Using the patterns of differentiation discussed above and those for other taxa of Australian birds, it is possible to construct a hypothesis of the historical interrelationships of the areas of endemism. It must be stressed that this is a very preliminary hypothesis, one that will certainly be modified as the phylogenetic and distributional patterns of additional clades are analyzed. Nevertheless, if we are eventually to understand avian speciation in Australia, we must investigate these general historical
patterns. The question is not whether exceptions to this pattern can be found—of course they can—but whether an altogether different general pattern exists.

Figure 6 depicts a vicariance hypothesis for the Australian avifauna. This general hypothesis postulates not only the interrelationships of the areas of endemism but also proposes a historical sequence for the relative ages of the vicariance events (isolating barriers). The hypothesis implies a major separation (F) between a northern and eastern avifauna from that of the central and southern portions of the continent. It also postulates the existence of a broad barrier (G) between the central arid region and the entire southern mesic fauna. Some previous workers have pointed to the apparent historical unity of the arid interior (Ford, 1974), but none have suggested a vicariance relationship to the southern avifauna (discussions are generally in terms of dispersal from the south into dry interior habitats). Postdating barrier G two other vicariance events (H and I, respectively) divided the central avifauna and the southern mesic fauna. Further analysis may show that more than one barrier developed in the region of I at different times.

In the north the barrier at the head of the Gulf of Carpentaria (D) apparently split a western avifauna (4) from a northeastern and eastern one (1–3, 9). Subsequent to D, these two regions were further vicariated by other isolating barriers.

Previous students of Australian speciation have pointed out that most of these barriers are related primarily to climatic deterioration during the Pleistocene and to present habitat discontinuities (see especially Keast, 1961; Ford, 1974, 1978). Because these studies were not interpreted within a cladistic-vicariance framework, little attention was paid to the relative ages of these barriers. The predictions of the hypothesis of Figure 6 are subject to testing by geological and paleobotanical data.

**Discussion**

**Speciation and general vicariance history**

The general vicariance hypothesis is an abstraction of the speciation patterns of many clades and cannot be taken as a representation of the pathway of differentiation for any specific group: the areas of endemism frequently do not correspond exactly to the distributions of the taxa under consideration, and patterns of variation, zones of primary or secondary contact, areas of sympatry, and precise locations of disjunctions are not specified by the vicariance hypothesis. Nevertheless, a general vicariance pattern is a prerequisite for reconstructing the history of speciation of specific groups. The primary reason for this has been mentioned already: the vicariance hypothesis allows us to specify the general component of a clade's pattern of differentiation, and thereby helps us identify any unique characteristics. For example, we need a vicariance hypothesis in order to determine whether a disjunct is the result of a vicariance event or of differentiation following dispersal. The geographic, climatic, and biotic histories implied by these two alternatives are completely different, and only
the general vicariance hypothesis will enable us to discriminate between them.

The above comments point to a fundamental conclusion regarding speciation analysis, one that has obviously been overlooked in most of the literature: one cannot reconstruct the history of speciation of any designated group if the analysis is restricted to just that group; one must have some notion of general vicariance patterns for the geographic areas in question. If this conclusion is admitted, it clearly has implications not only for our interpretation of the literature but also for the design of future analysis of speciation.

**Modes of speciation in Australian birds**

The results of this study enable us to assess the relative frequency of different modes of speciation (Bush, 1975) as they apply to the Australian avifauna. Based on these preliminary data, it would appear that type 1a allopatric speciation is more common than type 1b. Although this study focused on taxa with concordant distributions, and thus would bias the sample toward type 1a, an examination of the patterns of variation of a large sample of Australian birds (see also Keast, 1961) suggests that most isolates are concordant with the areas of endemism of Figure 2. Type 1b allopatric speciation implies a largely random component, and this seems small compared to the nonrandom vicariance component. Distribution patterns within South America are also decidedly nonrandom in their appearance (Haffer, 1974), thus indicating that type 1a differentiation has been frequent.

It may be that contemporary speciation analysis overemphasizes the concepts of peripheral isolate and founder populations. Certainly this mode of speciation is implicated in many studies of avian speciation, but in continental situations type 1a may be decidedly more common than previously realized. This conclusion arises primarily from the methods of analysis: because a cladistic-vicariance approach has not been used in previous studies, there was no incentive to search for nonrandom patterns from clade to clade. Each taxon was investigated on its own, and patterns of differentiation were typically interpreted within the predominant paradigm of

the time—dispersal. This work is clearly in need of re-evaluation.

Endler (1977, pp. 7-12, see especially table 1.2) has made the observation that in Australian birds, species in contact show more differentiation than those which are allopatric. From this he implies that parapatric speciation may be more common than previously realized. This suggestion can be evaluated by comparing the cladistic and geographic patterns of individual taxa with the general vicariance hypothesis. When this is done the available data strongly indicate that avian differentiation does not take place parapatrically. In most cases parapatric taxa are not sister-groups, thus indicating an allopatric mode of differentiation. In those instances in which parapatric distributions involve sister-taxa, two observations indicate that the mode of differentiation was predominantly allopatric. First, such parapatric distributions seem to be concordant from clade to clade, thus suggesting the presence of a barrier that caused spatial disjunction. Second, parapatric speciation would be expected to produce concordant vicariance patterns only if the taxa in numerous clades showed a parallel clinal response to a sharp increase in some environmental parameter. Current data indicate this is not significant in producing taxonomic differentiation in Australian birds. For example, vicariant taxa have developed in the adjacent Kimberley Plateau and Arnhem Land (4b and 4a, respectively, of Figure 6) and are now parapatric, but concordant patterns of clinal variation are absent; rather, the disjunction appears due to geographic and climatic factors (Ford, 1978). Clinal variation exists in many Australian birds (Keast, 1961), but there does not appear to be much concordance in these patterns of variation. Current evidence suggests, therefore, that parapatric speciation is not important in Australian birds, and certainly it would not be prudent to invoke its presence from geographic data alone.

**Vicariance hypotheses and the genetics of differentiation**

It is a curious observation that despite the rather large amount of genetic data on populations, we know exceedingly little
about the genetics of speciation (Lewontin, 1974). Recent investigators seemingly have been guided by Lewontin’s (1974, p. 160) perception of the problem: “The problem of making quantitative statements about the multiplication of species has been that we have been unable to connect the phenotypic differentiation between populations, races, semispecies, and species with particular genetic changes.” Thus, virtually the entire literature on the “genetics of speciation” consists of making comparisons of genetic distance among taxa that are classified at various levels of taxonomic differentiation (populations, subspecies, semispecies, sibling species, nonsibling species; the underlying assumption, of course, being that phenotypic differentiation is directly proportional to changes in structural genes). These results have been summarized by Lewontin (1974), Ayala (1975), and Avise (1976).

There are various problems with these types of data, many of which are well-known: (1) it is uncertain to what degree electrophoretic data estimate the genetic structure of populations, (2) there remains the question of whether estimates of genetic composition should be based primarily on estimates of structural genes, (3) the validity of comparisons among different taxa are extremely suspect because taxonomic ranks are not “equal” from one taxon to the other, and (4) even within a single group, taxonomic ranks are essentially meaningless as far as examining the question of genetic changes associated with differentiation (in many, if not most, groups current taxonomic rankings are largely arbitrary). But perhaps the major problem is that none of these studies have had a genealogical control, that is, there has been no corroborated genealogical hypothesis for the taxa being investigated.

The methods outlined in this paper for analyzing the geographical pattern of differentiation provide a powerful research strategy for investigating the correlation between genetic change and phenotypic differentiation (a causal relationship between the two is a problem for developmental genetics). First, these methods require a corroborated phylogenetic hypothesis for all the taxa, regardless of their present taxonomic status. Differentiated isolates are the basic taxonomic units of the analysis, and their taxonomic rank is not emphasized. Second, within the context of the phylogenetic hypothesis the degree of phenotypic differentiation along each line potentially can be estimated (by primitive-derived character analysis), and it is this measure which can be compared with estimates of genetic differentiation. Although this method is not free of problems, it offers a more “direct” investigation of the “genetics of differentiation” than making “genetic distance” comparisons within taxa of the same rank. Third, within the context of concordant vicariance patterns it is possible to compare genetic and phenotypic differentiation from one clade to the next. This comparison is possible because of the parsimonious assumption that if numerous clades show concordant vicariance patterns, they can be taken to have had the same temporal history. Indeed, it would seem impossible to make inter-cladal comparisons of the correlation of genotypic and phenotypic differentiation without applying vicariance biogeography. This method allows us to investigate, more or less “directly,” the degree to which genotypic and phenotypic differentiation are coupled or decoupled. In summary, then, it would seem important for those biologists interested in the genetics of speciation to incorporate recent advances in systematic theory and methodology, namely cladistics and vicariance biogeography, into their research programs.

Vicariance hypotheses and rates of evolution

It should be clear that the above analysis of genotypic-phenotypic differentiation offers the potential to investigate rates of evolution in a strikingly different way. Concordant vicariance patterns imply the same tempo of differentiation from clade to clade. If we can date vicariance events by geological techniques, we can place the degree of differentiation from one clade to the next within a common time-frame. Moreover, rates of differentiation can be
compared among those clades showing either complete, or in some cases partial, congruence in vicariance pattern. This method of analysis provides a way in which absolute rates of differentiation might be investigated, but even in the absence of geological data the method would allow comparisons of relative rates to be examined because the internodes of the congruent phylogenetic hypotheses establish a relative time-scale. Finally, given a sufficiently complex vicariance pattern (i.e., fairly large clades), it may be possible to investigate the correlation between rates of cladogenesis and genotypic and phenotypic differentiation from one clade to another. This would be possible if within each clade one lineage had vicariated disproportionately more than its sister-lineage.

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