CHAPTER 2

SPECIATION AND ITS ONTOLOGY: The Empirical Consequences of Alternative Species Concepts for Understanding Patterns and Processes of Differentiation

Joel Cracraft

INTRODUCTION

Biology has long endured arguments over species concepts. The reasons for this contentiousness are not simple, but the willingness of biologists to engage in continued intellectual debate underscores the critical importance placed on species and the fact that no solution to the "species problem" has been generally accepted. Species concepts have assumed this role as instigators of debate largely because biologists have used species with two different objectives in mind. First, species have served as the basis for describing and cataloging biotic diversity and for our attempts to represent the historical relationships of that diversity in a hierarchical manner. Species are thus taken to be the primary taxa of systematic biology. Second, species have also been employed as basic entities of evolutionary theory. They are said to be the things produced by the process called speciation and the entity that speciates.

It may seem that these two roles are not disparate enough to require different conceptions of species, but biologists have found it difficult to reconcile them. At the center of this dialogue is the biological species concept (Mayr 1942, 1963, 1969), which has a wide following within evolutionary biology (Dobzhansky et al. 1977; Futuyma 1986), particularly in those disciplines concerned with processes operating at the microgeographic level of demes and populations. Thus, population geneticists and ecologists have generally embraced the biological species concept (BSC) even though most of their studies are not directly concerned with species-level taxa (e.g., Lewontin 1974; Endler 1977; Nei 1987).

In spite of this general acceptance, controversy over species concepts has arisen because many evolutionary biologists and systematists have found the BSC to be untenable in theory and unworkable in practice. The list of critiques of the BSC is long indeed, emanating from both botanists (Cronquist 1978; Levin 1979; Raven 1980; Mishler and Donoghue 1982; Donoghue 1985; Ehrendorfer 1984) and zoologists (Ehrlich 1961; Sokal and Crovello 1970; Rosen 1978, 1979; Cracraft 1983, 1987, 1988; McKitrick and Zink 1988). The majority of this criticism, however, has gone unanswered by supporters of the BSC and has been overlooked or discounted by those many evolutionary biologists who endorse biological species in their work. This is perplexing because most botanists, and an increasing number of zoologists, have chosen to abandon the BSC (Donoghue 1985:173).

One theme of this chapter is that systematic and evolutionary biologists can no longer afford to ignore this body of criticism. Use of the BSC presents fundamental obstacles to describing and interpreting patterns and processes of evolutionary differentiation. At present, many biologists have not realized the depth of these difficulties, which suggests that further dialogue is desirable. The ensuing discussion will deemphasize the theoretical reasons for abandoning the BSC as these have been treated in detail elsewhere (see especially Rosen 1978, 1979; Cracraft 1983, 1987; Rosenberg 1985; Donoghue 1985; McKitrick and Zink 1988). Instead, the focus will be on the empirical consequences of using the BSC in evolutionary studies. A major conclusion will be that evolutionary biologists should abandon the BSC. No doubt this will be a radical proposal to some, yet if the BSC obscures our ability to reconstruct evolutionary history accurately and to investigate the processes responsible for evolutionary differentiation, then abandoning that definition is a decision having strong scientific justification.

A decision such as this necessitates adopting an alternative definition that does not possess the difficulties of the BSC. One viable candidate is the phylogenetic species concept (Rosen 1978, 1979; Nelson and Platnick 1981; Cracraft 1983, 1987, 1988; McKitrick and Zink 1988). It will be argued that, compared to the BSC, the phylogenetic species concept is more successful at unifying the two roles of species, namely serving as the entity of evolutionary theory and as a basis for describing the historical pattern of taxonomic diversity and reflecting that pattern in biological classifications.

BIOLOGICAL AND PHYLOGENETIC SPECIES: CONCEPTUAL CONTRASTS

Speciation is the process whereby new species originate. Species are speciated; they are effects of lower level processes. From this perspective, a theory of speciation has as its units entities we call species. Species must be treated as discrete real entities because all theories require this (Hull 1976, 1977, 1978; Gaukroger 1978): empirical theories cannot be about unreal, arbitrarily delimited entities and it would be biological nonsense to say "species are speciated" if they were not real things. Entities chosen to function in a particular theory, moreover, must be irreducible to other units that serve a similar role within the domain of that theory. This means that if we are to compare these entities, or use them in descriptions of pattern, or perhaps as participants in processes specified by some theory, then they must be the same kind of entity (Gaukroger 1978; Cracraft 1987). These simple requirements of every theory have been largely overlooked by evolutionary biologists. "Biological species" are often delimited subjectively, many are clearly reducible to other discrete entities, and they frequently lack comparability among themselves as basal evolutionary taxa (Rosen 1978, 1979; Cracraft 1983, 1987). In numerous instances, moreover, "biological species" are not the entities that result from "speciation" (taxonomic differentiation).

These introductory remarks emphasize the utmost importance of a species definition within evolutionary theory: that definition establishes a particular ontology for the theory itself. If the ontology specified by the definition fails to match the real entities participating in or produced by natural processes, then not only will nature be described incorrectly, but it will be difficult to evaluate any theory that makes use of those entities. Such is the effect of the BSC, for it does not describe a correct ontology for theories about species origins. To appreciate this more fully, we need to identify the characteristics of entities presumably produced by the process of speciation (hereafter, these entities will be termed *evolutionary taxa*).

First and foremost, the speciation process produces differentiated taxa, that is, populations of interbreeding (reproductively cohesive) organisms having one or more evolutionary novelties distinguishing this new unit from all other similar units. These novelties could be any intrinsic attribute, from fixed differences at the genomic level to new morphological, biochemical, or behavioral characters. Whatever the novelty, populations are delineated as new taxa when they are, in principle, 100% diagnosable (see below). Many populations exhibit quantitative differences from other populations, but recognizing them as a taxon means that a biologist would have to apply some subjective criterion to subdivide continuous variation. In these instances, however, the taxa of our theories would be individuated arbitrarily and would not have ontological status as discrete entities.

Evolutionary taxa (as discrete entities) are also basal in the sense that none of them can be further subdivided into smaller populations that are themselves discrete, diagnosable units. Speciation theory does not specify the sizes of differentiated populations, and some can clearly be quite small (many founder populations, for example). Thus, size is irrelevant to the question of whether a population is a basal, differentiated taxon; what is important is whether that population can be recognized as being distinct.

Finally, the entities of speciation theory would be expected to have some degree of geographic integrity if reproductive cohesion is to be maintained over time. An essential element of current speciation theory is that an incipient new taxon will have some degree of spatial disjunction from its ancestral population (or sister taxon) so that reproductive cohesion can be disrupted, thereby allowing differentiation to take place. Note that this does not necessarily imply *reproductive isolation* (in the sense of the BSC), only that the loss of cohesion through spatial isolation leads to differentiation.

These are the minimal characteristics seemingly possessed by entities that are produced by processes of differentiation. If this is an accurate representation of current knowledge about the origin of evolutionary taxa, how well do existing definitions of species facilitate our understanding of these events?

The biological species concept

As noted earlier, a major contributor to controversies over species concepts has been the conceptual antagonism between seeing species as taxonomic entities or as evolutionary entities. The biological species concept has exacerbated that antagonism through the use of a plethora of subsidiary concepts, including nondimensional, multidimensional, and polytypic species, which ostensibly enable application of the BSC to biologically disparate situations. Of these, the polytypic species concept has had the widest influence.

Polytypic species are taxonomic, not evolutionary, constructs, and gained broad acceptance in the 1930s and 1940s as a response to what was perceived to be a pernicious trend within taxonomy: the tendency to name differentiated isolates as distinct species (what Mayr calls "typological-morphological species," e.g., 1963:338). As an alternative, it was proposed that diagnosable, or nearly diagnosable, taxa which replace one another spatially be united into a single "polytypic species." Historically, the main function of this procedure was to simplify classification and reduce the number of species names (Mayr 1942:126; 1969:38). As Mayr (1942:127) noted about the advantage of polytypic species within birds: "The total number of species to be memorized by the taxonomist has thus been cut by two-thirds."

Although the notion of polytypic species may be thought beneficial for taxonomists' memories, it unfortunately has canalized thinking about the historical pattern of speciation. Species are envisioned to be subdivided into numerous geographic races or subspecies. These taxonomic units exhibit a broad range of phenotypic differentiation, from being barely distinct quantitatively from their neighbors to being diagnosably distinct populations. The glue uniting all these units into a single polytypic species is the presumption of potential interbreeding; that is, it is assumed they are not reproductively isolated, no matter what their degree of differentiation. If a population is so markedly different that a taxonomist would judge it could not interbreed with other closely related taxa if they were in sympatry, then it is treated as a separate biological species. Speciation, under this ontology, is a process whereby these populations become more and more differentiated, so much so that they eventually cross the line of reproductive compatibility with the other populations of the same polytypic species.

The fact that the biological polytypic species concept was created to solve what was felt to be an undesirable glut of species names has had a profound affect on our attempts to describe and explain evolutionary pattern and process. Given this ontology, what is the unit of evolution? What entity speciates? Certainly it is not the polytypic species itself. Most workers seem to think it is the subspecies that is differentiating and becoming a new taxonomic unit, and Mayr himself held this view until recently. Now he considers subspecies as merely "pigeon-holing" devices for taxonomists (Mayr 1982:289). Unfortunately, subspecies names are frequently applied to a population showing any degree of differentiation deemed worthy of recognition by a taxonomist. This contributes to a classificatory system that is meaningless for describing evolutionarily relevant variation (see below). Given that many subspecies are themselves arbitrary subdivisions of continuous variation, it seems inescapably clear that many subspecies could hardly be considered units of evolution inasmuch as they do not qualify as objective units in the first place. Indeed, it can only be concluded that under the biological polytypic species concept there is no consistent, objective unit of evolution and, as such, the concept does not provide an empirically sound ontology for studying the origin of species.

It is essential for evolutionary biology to have an objective ontology

with which to individuate the entities relevant to our theories. The biological species concept is frequently characterized as an objective or nonarbitrary descriptor of taxonomic diversity (Mayr 1969:27; Sudhaus 1984; Willmann 1987). In fact, in all situations that are critical for evolutionary analysis, the biological species concept can be applied only subjectively. The sole case in which the BSC can be said to be objective is in spatially restricted areas in which two diagnosably distinct taxa are in sympatry and reproductively isolated. But this is also a case in which all other species concepts currently in use would treat this situation in precisely the same manner. Cases of sympatry, therefore, do not speak for the objectivity of the BSC any more than for other concepts of species.

There are, however, two situations in which we would expect different species concepts to provide alternative interpretations of species limits. In both the BSC can be applied only subjectively and inconsistently. The first case involves two largely allopatric taxa that hybridize in a zone of contact. A decision as to whether a systematist recognizes one or two species depends on a personal assessment of the amount of hybridization and the width of the hybrid zone. Cases of this kind cannot be resolved in a straightforward manner using the BSC, as even proponents of that concept readily admit.

The second situation involves decisions about the specific status of differentiated populations that are entirely allopatric. As Mayr notes (1969:196), the criterion of reproductive isolation cannot be directly applied to these taxa, and all surrogate criteria used to evaluate potential reproductive isolation also fail the test of objectivity. These solutions generally include extrapolations from comparisons of morphological, behavioral, and ecological differences in closely related species that are sympatric or parapatric (e.g., Mayr 1963:31). But morphological differentiation among populations is not always closely correlated with their genetic compatibility, even among closely related taxa, therefore a solution such as this would require acceptance of numerous untested and untestable assumptions. Perhaps the most important requirement for this methodology is approval of the proposition that morphological, behavioral, and genetic rates of differentiation have been constant across the taxa being compared. Only if rates are constant can assessments between the amount of morphological differentiation and reproductive isolation in one group be used to guess at this relationship in allopatric taxa in other groups. Ironically, the hypothesis of constant rate cannot be examined *unless* the biological species concept is abandoned and a corroborated phylogenetic hypothesis for all the differentiated taxa is obtained.

Decisions about the species status of hybridizing taxa or differentiated allopatric taxa are critical in any analysis of speciation. Because the criterion of reproductive isolation cannot be applied in a uniform and objective manner, the ontological status of the units identified by the biological species concept must always be in doubt. This point requires emphasis: the ability to interbreed—*reproductive cohesion*—by itself cannot establish those populations as a discrete, evolutionary unit (contra Ayala 1981:46), because reproductive cohesion, which manifests a primitive morphogenetic organization, can transcend well-defined species boundaries. *Reproductive disjunction,* on the other hand, reflects evolutionary changes that signify the presence of discrete taxonomic entities, but so too do other changes that fail to affect reproductive isolation. This is one reason why the BSC cannot establish a consistent ontology for evolutionary theory. Similarly the recognition concept of species (Paterson 1981, 1982, 1985) possesses many of these same difficulties. Although the evolution of a new "specific-mate recognition system" could be used to diagnose an evolutionary unit, many evolutionary taxa obviously are capable of sharing these systems. Thus, the recognition concept of species, like the BSC, has the potential to confound the historical analysis of taxonomic diversification.

Many investigators have stressed that the biological species concept confounds the causal analysis of differentiation because the historical pattern of differentiation will not always be congruent with the historical pattern of reproductive isolation. Worse still, the BSC can lead to incorrect conclusions about the causal relationship between morphological (and genetic) differentiation and reproductive disjunction. Thus, Mayr (1963:31) claims that "The degree of morphological difference displayed by a natural population is a by-product of the genetic discontinuity resulting from reproductive isolation." In fact, however, reproductive isolation is itself a by-product of genetic differentiation following isolation and not causal of any accompanying morphological differentiation (e.g., Levin 1979:383). Reproductive isolation, therefore, is merely a subset of the numerous possible consequences of the more general process of differentiation, as many biologists have realized.

Phylogenetic species concept

The preceding section outlines some conceptual difficulties of the biological species concept that impair its effectiveness in evolutionary analysis. This raises the question of whether an alternative species concept can provide a better ontological foundation for evolutionary theory and at the same time satisfy the needs of systematic biology. In this regard, it has been suggested that a phylogenetic species concept constitutes a solution to the problems presented by the BSC (see discussions of Rosen 1978, 1979; Nelson and Platnick 1980; Cracraft 1983, 1987; McKitrick and Zink 1988; Zink 1988).

A phylogenetic species is an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent (Cracraft 1983, 1987; see also Rosen 1978, 1979; Nelson and Platnick 1980). The phylogenetic species concept circumvents all of the difficulties of the BSC because, as defined here, species are equivalent to evolutionary taxa in the sense they were portrayed earlier. Phylogenetic species are, therefore, basal, differentiated, evolutionary taxa. In the majority of cases, phylogenetic species will be demonstrably monophyletic; they will never be nonmonophyletic, except through error. Some phylogenetic species may be diagnosably distinct from other such units and yet not possess characters that can be hypothesized to be derived. In some instances, these species may be truly monophyletic but evidence of that fact has remained undiscovered. Or their historical status may be unresolved because relative to their sister species they are primitive in all respects. Whether they might be the "ancestor" of that species, and therefore be truly paraphyletic with respect to the historical structure of their populations, is probably unresolvable.

The phylogenetic species concept emphasizes the most general aspect of taxonomic diversification, namely differentiation. Some differentiation results in reproductive isolation and some does not. By relying solely on reproductive isolation as the central criterion for species status, the BSC precludes recognition of a very large class of evolutionary taxa, namely that constituting all instances of diagnostically distinct populations that are not reproductively isolated from other such populations. The BSC relegates this ubiquitous phenomenon to a position of secondary importance, and this is a primary reason why so many botanists in particular have not found the BSC useful in evolutionary analysis (Cronquist 1978; Levin 1979; Raven 1980; Donoghue 1985; Ehrendorfer 1984). The phylogenetic species concept, in contrast, views reproductive isolation as an important, but not necessarily predominant subset of effects produced by the process of differentiation. Reproductive isolation signifies the evolution of diagnostic characters, but not all newly evolved characters necessarily affect reproductive isolation.

The phylogenetic species concept, as all species concepts must, recognizes the critical importance of reproductive cohesion. This component of the definition is required if we wish to avoid assigning species status to individual organisms, to different sexes and morphs, or to developmental stages. In this sense, then, reproductive cohesion is a trivial component of all species concepts, including those that are purely morphological.

Because phylogenetic species are equivalent to basal evolutionary taxa, their use at once unifies the notion of species as it is applied to evolutionary theory, and as it is used in taxonomic practice. This concept thus provides a theoretically coherent ontology for systematic and evolutionary biology. The phylogenetic species concept emphasizes *diagnostic* character variation for individuating basal evolutionary taxa, thereby allowing nondiagnostic character variation to be partitioned into its evolutionary relevant intra- and interspecific components. Because the biological species concept does not necessarily divide nature at its true historical "joints" (Rosenberg 1985:197), there will always be the possibility of confounding within- and among-taxon patterns of variation.

The phylogenetic species concept is not a resurrected version of the so-called morphological species concept. Diagnostic characters can be represented by any intrinsic attribute of organisms, from the genome level on up. Determining whether character variation is diagnostic or not is decidedly more objective than assessing whether allopatric populations might hybridize or whether hybridization is sufficiently extensive to recognize a single biological species (contra Coyne and Barton 1988). In principle, populations should be 100% diagnosable, that is, all of the individuals will have the relevant diagnostic character(s). But realistically, the biological situation will almost always call for deeper analysis (see McKitrick and Zink 1988). Diagnostic characters may be restricted to males, to females, or perhaps to a particular ontogenetic stage; some individuals, moreover, may exhibit variation that obscures recognition of diagnostic characters. It is because of situations such as these that understanding the reproductive relationships of individuals within populations is often critical for delineating species correctly. In spite of potential difficulties, assigning a differentiated population to species rank under the phylogenetic species concept is still a hypothesis whose verification or rejection will always be dependent on the data available and the thoroughness with which they are interpreted.

It was noted earlier that some diagnosable populations may be quite small. This is not an arbitrary artifact of the phylogenetic species concept (Coyne and Barton 1988) but simply a reflection of natural processes of taxonomic differentiation: populations of all sizes can become isolated and then differentiate. If the delineation of species were based on the relative degree of similarity or dissimilarity, as is effectively the case with the BSC (direct application of reproductive disjunction being relatively rare in practice), then species limits inevitably will be arbitrary in many cases. The polytypic species concept has sought to unite many small differentiated populations into larger ones to "simplify" taxonomy. Yet, this too is arbitrary, and it confounds an accurate description and causal analysis of evolutionary diversity. Because the phylogenetic species concept recognizes the evolutionary singularity of diagnosably distinct populations—of whatever size—it offers the ontological foundation on which we can begin to understand any historical pattern underlying population differentiation.

The preceding sections indicate that the conceptual differences between biological and phylogenetic species are profound. It remains to be seen how these concepts have different consequences for interpretation of real-world data.

EMPIRICAL CONSEQUENCES OF ALTERNATIVE SPECIES CONCEPTS

The analysis of evolutionary pattern and process begins with an established species ontology derived from a theoretical expectation of how nature is organized and from previous empirical experience. In speciation analysis, for example, observational data on patterns of character variation and spatial distribution, along with perhaps a theoretical model of speciation, are used to individuate species-level taxa *prior* to subsequent investigations into their history. Within this context, then, species might be considered units of evolution and might be expected to exhibit a pattern of phylogenetic deployment through space and time. These elementary precepts can be used to compare the empirical consequences of applying biological and phylogenetic species concepts.

The historical pattern of taxonomic diversification

Different concepts of species influence analysis in several ways. The most important of these will be considered first: different species concepts often imply different ontologies and this results in misinterpretations of the historical pattern of differentiation. The following examples illustrate this influence.

Example 1. Speciation in *Cinclosoma*. The quail-thrushes (*Cinclosoma*) of Australia consist of six well-defined taxa distributed allopatrically and parapatrically in central and southern Australia (Figure 1). Considerable controversy regarding species limits has arisen because various authors have not been able to apply the biological species concept in a consistent manner. Table 1 summarizes ornithologists' attempts to assign species status to these taxa. Within the context of the BSC, conspecificity is typically decided on the basis of relative phenotypic similarity, which functions as a surrogate for a direct measure of reproductive compatibility (Mayr 1942, 1963, 1969). In the quail-thrushes, this procedure has failed because estimating relative similarity has been subjective at best.

These different judgments of species limits within *Cinclosoma* have obvious implications for speciation analysis. Taken at face value, each implies a different history for the pattern of differentiation. More importantly, each of these different estimates of species limits influences our ability to reconstruct that historical pattern accurately, because if biological species are real entities in nature and these are our best interpretations of those

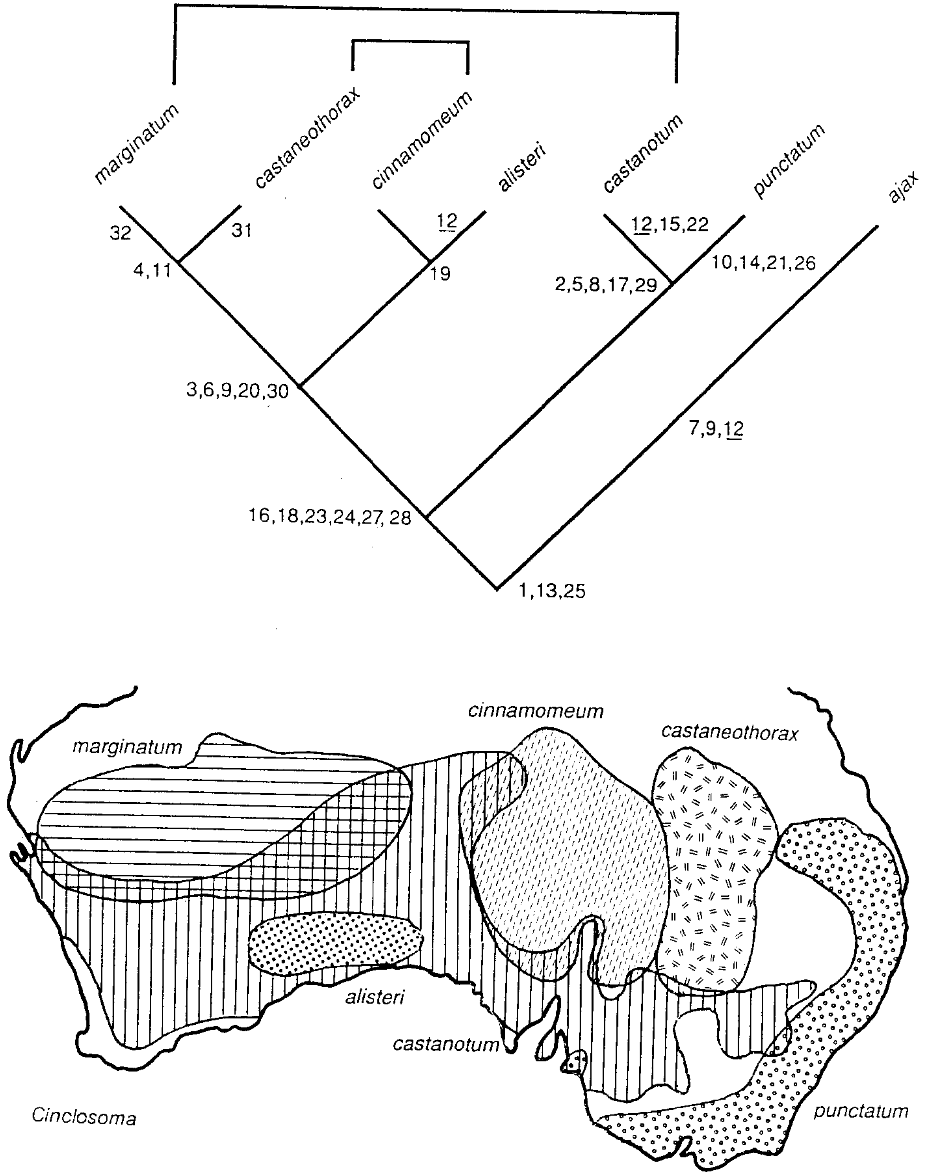

FIGURE 1. Distribution and phylogenetic hypothesis for the phylogenetic species of Australian quail-thrushes (*Cinclosoma*). An analysis of 32 ordered characters (Table 2) produced a best-fit tree of 35 steps (consistency index = 0.914). The tree was rooted using the outgroup taxa, *Ptilorrhoa castanota* and *P. leucosticta*. Underlined characters identify parallelisms and brackets link taxa that are known to hybridize. Distributions are after Ford (1983).

TABLE 1. Historical summary of species limits among the quail-thrushes (*Cinclosoma*) of Australia.

Campbell and Campbell (1926)	Condon (1962)	Ford (1974, 1976)	Ford (1983)
1. *punctatum* 2. *castanotum* 3. *alisteri* 4. *cinnamomeum* 5. *marginatum* 6. *castaneothorax*	1. *punctatum* 2. *castanotum* 3. *alisteri* 4. *cinnamomeum* 5. *marginatum* 6. *castaneothorax*	1. *punctatum* 2. *castanotum* 3. *cinnamomeum* (*marginatum*) (*castaneothorax*)	1. *punctatum* 2. *castanotum* 3. *cinnamomeum* (*alisteri*) 4. *castaneothorax* (*marginatum*)

MacDonald (1968, 1973)	Deignan (1964)	Pizzey (1980)	Wolstenholme (1926)
1. *punctatum* 2. *castanotum* (*alisteri*) 3. *cinnamomeum* (*castaneothorax*) (*marginatum*)	1. *punctatum* 2. *castanotum* 3. *cinnamomeum* (*castaneothorax*) (*alisteri*) (*marginatum*)	1. *punctatum* 2. *castanotum* 3. *cinnamomeum* (*castaneothorax*) (*marginatum*) 4. *alisteri*	1. *punctatum* 2. *castanotum* 3. *cinnamomeum* 4. *castaneothorax* (*marginatum*) 5. *alisteri*

entities, then clearly many of these sets of postulated species limits will lead us astray as we attempt to recover the one true history. Reproductive isolation is not an intrinsic attribute, but a relational concept, and thus does not constrain biological species to be strictly monophyletic. By definition, nonmonophyletic species imply history has been misrepresented.

These problems do not exist with the phylogenetic species concept. When this concept is applied, minimally six phylogenetic species are recognized in Australia (diagnoses are contained in the data of Table 2). A hypothesis of their phylogenetic relationships can then be generated by cladistic analysis of a set of discrete character data derived from external morphology (Table 2). The hypothesis of Figure 1, for example, is the most parsimonious tree for the data (length = 35 steps; consistency index = 0.914) and represents our current best estimate of the historical pattern of taxonomic differentiation (see also Cracraft 1986).

This phylogenetic hypothesis also permits analysis of patterns of hybridization in a way that is not possible when employing the BSC. The species pairs, *castanotum–marginatum* and *cinnamomeum–castaneothorax*, hybridize sporadically in zones of overlap (Ford 1983). Hybridization is apparently not extensive because of habitat segregation of the

TABLE 2. Character-state data for the genus *Cinclosoma*.[a]

Taxa	Characters																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
P. leucosticta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. castanota	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. ajax	1	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
C. punctatum	1	1	0	0	1	0	0	1	0	1	0	0	1	1	0	1	1	1	0	0	1	0	1	1	1	1	1	1	1	0	0	0
C. castanotum	1	1	0	0	1	0	0	1	0	0	0	1	1	0	1	1	1	1	0	0	0	0	1	1	1	0	1	1	1	0	0	0
C. castaneothorax	1	0	1	1	0	1	0	0	1	0	1	0	1	0	0	1	0	1	0	1	0	1	1	1	1	1	1	1	0	1	1	0
C. cinnamomeum	1	0	1	0	0	1	0	0	1	0	0	0	1	0	0	1	0	1	1	1	0	0	1	1	1	0	1	1	0	1	0	0
C. marginatum	1	0	1	1	0	1	0	0	1	0	1	0	1	0	0	1	0	1	0	1	0	0	1	1	1	0	1	1	0	1	0	1
C. alisteri	1	0	1	0	0	1	0	0	1	0	0	1	1	0	0	1	0	1	1	1	0	0	1	1	1	0	1	1	0	1	0	0

[a] Outgroups include *Ptilorrhoa castanota, P. leucosticta,* and C. ajax, all distributed in New Guinea. Key for characters (0, primitive and absent; 1, derived and present, in all cases): 1, male throat blue-black; 2, female throat gray; 3, female throat buff or cream; 5, female breast solid gray; 6, female breast light brown to brown; 7, female breast reddish chestnut; 8, feathers at sides of breast and upper throat solid gray; 9, feathers at sides of breast brown to rufous; 10, male breast solid gray; 11 male breast with extensive chestnut or rust-red patch; 12, male breast extensively blue-black; 13, male flanks with spotting; 14, female flanks with spotting; 15, male flanks gray-brown; 16, male with white spots on lesser primary coverts; 17, crown and forehead gray; 18, crown light brown; 19, crown light cinnamon or rufous cinnamon; 20 upperparts cinnamon to light rufous cinnamon; 21, upperparts heavily streaked; 22, male back and rump deep rufous; 23, primaries light brown; 24, tertials rufous to cinnamon with dark central streak; 25, male white malar streak not extending onto throat; 26, male malar streak reduced anteriorly; 27, male light eye stripe; 28, relative bill size decidedly reduced; 29, ear coverts gray-brown; 30, ear coverts rufous or cinnamon; 31, male upper breast rich rust-red; 32, male upper breast pale chestnut.

parental forms. It might be imagined, however, that if climate changed, and these habitat differences were abolished, then hybridization could become rampant. Given that this might occur, use of the BSC would imply these species pairs are conspecific. The problem, however, is that these differentiated evolutionary taxa are not sister groups but are each separated by three and four speciation events. In fact, sister species within this complex are typically widely separated geographically. Application of the BSC has created paraphyletic taxa and has hindered recognition of this historical pattern, but it is easily revealed when the phylogenetic species concept is employed.

Example 2. Speciation in *Daphoenositta.* A classic and frequently mentioned example of avian speciation used to illustrate the biological species concept involves the sittellas of Australia (e.g., Keast 1961; Mayr 1963:372–373). Five well-differentiated taxa are distributed peripherally around northern, eastern, and southern Australia (Figure 2). At one time the five forms were thought to be essentially allopatric, and some authors (e.g., McGill 1948) considered them to be distinct species. With more extensive collecting and examination of specimens, it soon was realized that these taxa have much larger ranges than previously thought. Individuals of these taxa exhibit a substantial capacity to disperse, and the result has been hybridization in zones of contact. Indeed, there is evidence for hybridization among all the forms in parts of Queensland (Ford and Parker 1974; Ford 1980; Short et al. 1983a, 1983b).

Documentation of hybridization has led most workers to recognize a single polytypic biological species (Mayr 1950; Keast 1961; Ford 1980; Short et al. 1983a, 1983b), with each form being ranked as a subspecies or even something called a "megasubspecies" (Short et al. 1983a). The conventional story about speciation is that the ancestor of the five parental forms was once distributed broadly across Australia, with the five populations becoming isolated in relatively more humid refuges during a time of increased aridity. With amelioration of the climate, these populations, now differentiated, spread outward from these refuges to eventually hybridize in areas of overlap (Keast 1961; Mayr 1963:372; Ford 1980).

At first it might appear that the sittellas provide a clear example of the success of the biological species concept. Yet, application of the BSC in this and many other similar cases raises some serious difficulties. The first is ontological in nature: what is the unit of evolution in a situation such as this? The single global biological species is certainly not the unit that was speciated: it possesses no singularity as a differentiated taxon that is not shared by any monophyletic group. Instead, virtually all workers have treated the subspecies as the unit of evolution, because each of these populations is interpretable as having evolved its own characters in isolation.

Ironically, if subspecies are only "a unit of convenience for the tax-

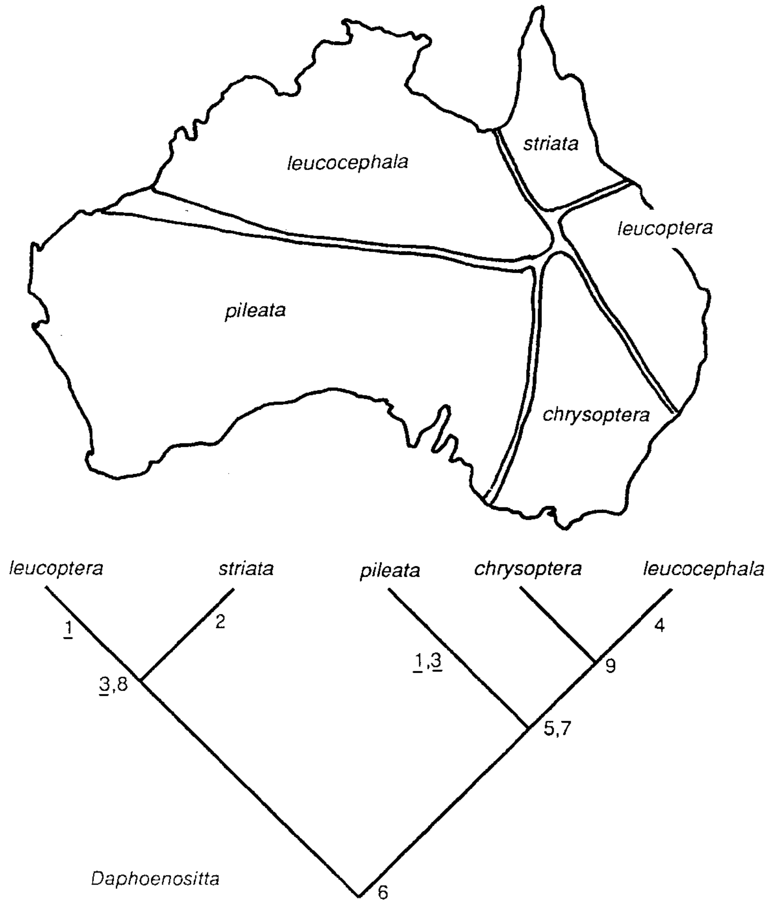

FIGURE 2. Distribution and phylogenetic hypothesis for the phylogenetic species of Australian sittellas (*Daphoenositta*). An analysis of nine ordered characters (Table 3) produced a best-fit tree of 11 steps (consistency index = 0.818). The tree was rooted using the outgroup taxon, *Daphoenositta papuensis*. Underlined characters signify parallelisms. Distributions after Ford (1980) and Short et al. (1983a).

onomist, but not a unit of evolution," as Mayr has stressed (1982:289), then seemingly we are left without taxa that could be called evolutionary units. To deny these well-defined entities a unitary evolutionary role merely to satisfy the sanctity of a particular species definition is to cast doubt on the usefulness of that definition. If evolutionary theory is supposed to be generally applicable across organisms, there cannot be ontological confusion about the identity of its units. Are they species, subspecies, megasubspecies, or what? The biological species concept does not make this clear nor is it capable of a consistent answer.

The sittellas raise another problem for the biological species concept. If the five forms are considered to be phylogenetic species (diagnoses in Table 3) and their character variation is tabulated, then cladistic procedures can be used to generate a hypothesis of their history. This hypothesis (Figure 2) proposes a very specific pattern of relationships with the northeastern form, *striata*, being the sister species of the northwestern form, *leucoptera*. These, in turn, are the sister group of the other species. This latter group includes the sister pair, *chrysoptera* (Southeast) and *leucocephala* (East), and their sister species, *pileata* of southwestern Australia. This pattern of historical and spatial relationships is markedly congruent with speciation patterns in other Australian birds (Cracraft 1982, 1986).

This hypothesis indicates a complex history of differentiation within sittellas. The forms are not of the same ages, as is often implied in the scenarios associated with the biological species concept. Placing all these evolutionary taxa in a single biological species obfuscates this historical pattern, because the ability to hybridize merely signifies the retention of a primitive morphogenetic milieu.

TABLE 3. Character-state data for the genus *Daphoensitta*.[a]

	Characters								
Taxa	1	2	3	4	5	6	7	8	9
D. albifrons	0	0	0	0	0	0	0	0	0
D. papuensis	0	0	0	0	0	0	0	0	0
D. pileata	1	0	1	0	1	1	1	0	0
D. chrysoptera	0	0	0	0	1	1	1	0	1
D. leucocephala	0	0	0	1	1	1	1	0	1
D. striata	0	1	1	0	0	1	0	1	0
D. leucoptera	1	0	1	0	0	1	0	1	0

[a] Outgroups include two taxa in New Guinea (*albifrons*, *papuensis*), both usually placed in a single species, *D. papuensis*. Key for characters (0, primitive and absent; 1, derived and present): 1, male with white breast and belly (unstreaked); 2, female throat black; 3, crown jet glack; 4, male with white crown; 5, reduction in melanin deposition in feathers and upperparts (streaks and background less dense); 6, wing patch on primaries; 7, cinnamon wing patch on primaries and secondaries; 8, white wing patch on primaries; 9, bill virtually all black (without extensive yellow).

Example 3. Speciation in the *Pipilo fuscus* complex. The brown towhees of the southwestern United States and Mexico include four differentiated taxa (Figure 3). Two of these, *P. aberti* and *P. albicollis*, are moderately distinct, whereas *P. fuscus* and *P. crissalis* are very similar, differing primarily in the presence (*fuscus*) or absence (*crissalis*) of a breast spot. Virtually all workers have united these latter two taxa into the same biological species on the assumption that if they were in contact, they would probably interbreed (Davis 1951; Marshall 1960, 1964; Mayr and Short 1970; AOU 1983). Eight subspecies have been described within the *crissalis* group and 11 within the *fuscus* group (Davis 1951). Populations of *crissalis* from southern Baja California are said to bridge the morphological gap between more typical *crissalis* and populations in the *fuscus* group. None of these subspecies is apparently diagnosably distinct.

Placing *fuscus* and *crissalis* in the same biological species, even though they are diagnosably different, has clearly seemed like a reasonable decision to many biologists. Yet, it constrains our view of speciation within the brown towhees. Such a decision implies *fuscus* and *crissalis* are more closely related to each other than either is to *albicollis* or *aberti*. The analysis of speciation has effectively been reduced to a three-taxon statement.

The history of these taxa has recently been reevaluated by Zink (1988). Using variation at 39 presumptive loci and 29 skeletal measurements, he was able to demonstrate, first, that *P. fuscus* and *P. crissalis* are not closest phenetically given either data set. Furthermore, cladistic analysis of Rogers' genetic distances (Zink 1988:76, Table 3) suggests that *P. crissalis* is the sister species of *P. aberti*, and *P. fuscus* is the sister species of *P. albicollis* (Figure 3), although the data are by no means unambiguous.

Assuming that this historical hypothesis will be substantiated by future work, the similarities that led workers to unite *fuscus* and *crissalis* in the same biological species are easily interpretable as retentions of primitive characters. Even if *fuscus* and *crissalis* are eventually shown to be each other's closest relative, they still remain diagnosably distinct, evolutionary taxa. Research undertaken within the context of the biological species concept has led to misunderstandings about the evolutionary roles of these taxa and their history, whereas use of the phylogenetic species concept can avoid these misinterpretations.

Example 4. Speciation in the *Thomomys umbrinus* complex. Use of the biological species concept often results in species taxa that lack a unitary historical role. This is illustrated by the pocket gophers of central Mexico that are currently placed in the biological species, *Thomomys umbrinus*. Patton and Feder (1978) and Hafner et al. (1987) have shown that at the gross level of chromosomal variation, this species can be subdivided into

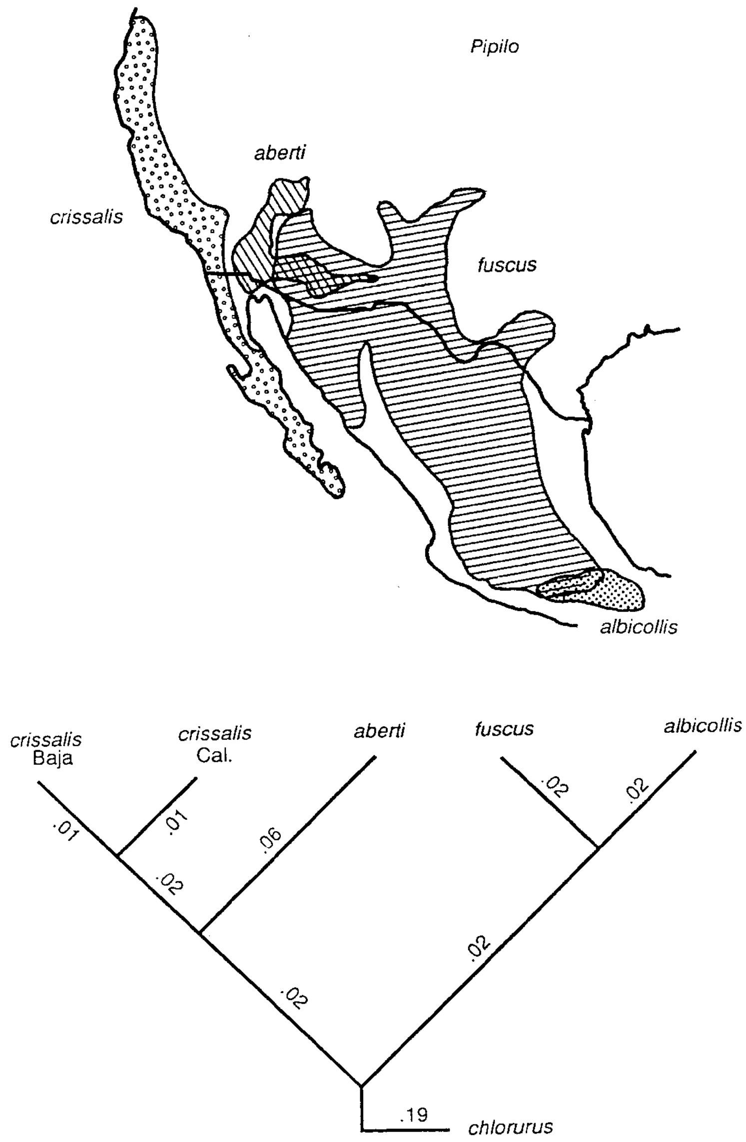

FIGURE 3. Distribution and phylogenetic hypothesis for four phylogenetic species in the North America sparrow genus *Pipilo*. The Fitch–Margoliash tree based on Rogers' genetic distances (data from Zink 1988) is rooted using the outgroup species *P. chlorurus*. Distributions are from Hubbard (1973).

two karyotypic groups, one of $2N = 76$ and the other $2N = 78$. Hafner et al. (1987) present arguments and evidence to suggest that populations in each group are reproductively isolated from populations in the other. Taken at face value, these observations would seem to suggest that minimally two biological species are involved instead of one. The situation is more complex, however, for each of these karyotypic entities is paraphyletic and is comprised of sets of populations having closer phyletic relationships to populations with a different karyotype than to populations within the same karyotypic group.

The biological species concept cannot be applied to the *Thomomys umbrinus* complex unless one is willing to accept paraphyletic species, and to do that would be a de facto admission that biological species are not units of evolution. Hafner et al. (1987:18) conclude that "paraphyletic species may be common, perhaps the rule, in naturally occurring organisms" (see also Patton 1981, and Patton and Smith 1981, for similar observations). To the extent this is true, the biological species concept will fail to provide an accurate trace of the history of taxonomic differentiation. The phylogenetic species concept, on the other hand, does not present this difficulty, because it identifies the unit of evolution to be differentiated evolutionary taxa.

Species concepts and the analysis of geographic variation

Evolutionary biologists have long known that the study of geographic variation is central to understanding the patterns and processes of speciation (e.g., Dobzhansky 1937; Mayr 1942), and countless studies have been undertaken over the last half century (for reviews of only a small portion of this extensive literature see Mayr 1963; Gould and Johnston 1972; Endler 1977; Zink and Remsen 1986). Much of this research has been motivated by two important goals: first, to elucidate the causal agents responsible for spatial patterns of phenotypic or genotypic variation, and second, to identify those microevolutionary processes by which new species arise. It is clear the second problem cannot be solved without having answers to the first, yet the observation that variation can often cut across species boundaries indicates that an investigator could pursue facets of the first problem without necessarily directly being concerned with the second. Thus, although some evolutionary biologists have treated these two problems as inseparable, this need not be so.

There has been very little discussion about the influence that different species concepts might have on the analysis of geographic variation (but see Zink and Remsen 1986). For certain kinds of questions, it may not matter how species are defined or how that concept is applied to natural situations. Thus, a causal analysis of a well-defined cline that trends across two taxa may be of interest regardless of whether the two taxa are considered subspecies of a single biological species or two sister species. Nevertheless, an interpretation of any pattern of variation is predicated upon a correct description of the pattern itself, and sometimes the latter is influenced by the choice of species boundaries. Sensitivity to this influence is particularly important when the impetus for an analysis of geographic variation is the study of speciation. In this case, the investigator is presumably interested in the processes that apportion variation within an ancestral population into variation between descendant populations. If this is the case, then application of the biological species concept to this problem would seem to require an emphasis on variation that is considered of importance for reproductive isolation (e.g., Frost and Platz 1983; Nevo et al. 1987; Zink and Remsen 1986:33), whereas use of a phylogenetic species concept, in contrast, would focus attention on those aspects of variation that are relevant to the origin of any evolutionary novelty (including those affecting reproductive isolation). Of more importance for the present discussion is a consideration of the ways in which alternative species concepts might cause us to resolve patterns in different ways.

Some of the potential influences of species concepts can be illustrated by the following hypothetical situation. Consider three parapatric populations (call them A, B, C) distributed along a latitudinal transect. Assume that each is weakly differentiated but still diagnosably distinct and that some hybridization is observed between each adjacent pair of populations (A × B, B × C). Finally, assume that the population means for some attribute, say body size, exhibit a pattern of clinal variation, with size increasing with latitude. Many such cases have been described in the literature. The standard interpretation would be to treat these populations as subspecies of a single biological species (e.g., Mayr 1942, 1963; Endler 1977). Defined as a single species, the task at hand would be to find an explanation for the trend in size, employing perhaps correlation analysis with a suite of environmental variables. In this case, the biological species concept predisposes us to look at and attempt to explain an *intraspecific* pattern of variation, and, as Endler (1977:7) noted for similar situations, this type of variation is generally not deemed important from the standpoint of speciation because the populations in these cases are neither strongly allopatric nor strongly differentiated.

The use of a phylogenetic species concept compels us to investigate this same problem in a different way. Even though weakly differentiated, the presence of diagnostic characters implies that we are dealing with three evolutionary taxa. As such, both intra-and interspecific patterns of variation are potentially of interest and therefore must be defined. In this example, it is entirely possible that intraspecific size patterns will *not* be concordant with the interspecific pattern: variation within each species might show a decrease in body size as latitude increases even as the population means themselves increase. Such an observation might caution us against accepting an explanation for the interspecific trend when that explanation is based only on a correlation with some environmental variable that also happens to show a trend across the distributions of the species.

This example can be made still more complex, and once again species concepts are important in the resolution of pattern. An historical analysis of geographic variation requires a phylogenetic hypothesis for the entities under study (Straney and Patton 1980). If Mayr's (1982:289) assessment that subspecies should not be interpreted as units of evolution is correct, then application of the biological species concept to situations such as this implies that historical analysis will be at an impasse. In contrast, the phylogenetic species concept compels us to ask how the three evolutionary taxa—A, B, C—might be interrelated. If there is reason to believe they form a monophyletic group, then there are three relevant phylogenetic hypotheses that could be considered. Two of these hypotheses, in which the centrally distributed taxon is more closely related to either adjacent taxon [i.e., (A + B) + C and A + (B + C)], would imply concordance between the historical pattern of speciation and the size trend. As a consequence, either (or both) environmental causation and historical constraint could be important in explaining the observed trend. The third hypothesis, in which the northernmost and southernmost taxa are sister groups [i.e., (A + C) + B], would suggest that differentiation associated with body size is not related to phylogenetic history, which strengthens the case for seeking a causal relationship with some environmental factor (see Straney and Patton 1980; and below).

Although the preceding example is hypothetical, many published studies of geographic variation illustrate instances in which the description of intra-and interspecific patterns of variation could potentially be misinterpreted by application of the BSC. Some aspects of the problem will be illustrated by the following examples using data from natural situations.

Geographic patterns of morphological differentiation. One important component of the study of geographic variation is the most elementary: to describe and explain spatial patterns of differentiation. In this type of analysis, it is of interest to explore whether the spatial patterns of variation are correlated with spatial patterns of environmental variation or with the phylogenetic pattern of the entities being studied. Each type of correlation implies a different underlying causal fabric for the observed pattern of differentiation (Straney and Patton 1980). Resolution of the phylogenetic pattern itself is strongly influenced by decisions about species limits. This influence can be illustrated by again considering variation within the brown towhee complex (Zink 1988).

The question to be investigated is whether patterns of morphological variation are congruent with phylogenetic pattern. If they are, this suggests

differentiation has a strong historical component that is related to divergence following cladogenesis; if patterns of variation exhibit congruence with environmental patterns but not with phylogenetic history, then adaptive or epigenetic determinants on variation might be interpreted as being more important (see Straney and Patton 1980, for detailed discussion).

The best available estimate of phylogenetic pattern for the brown towhees is a cladistic analysis of Rogers' genetic distances (data from Zink 1988; Figure 3). These results can be compared to an estimate of phenetic relationships that has been calculated using the standardized group means of six external dimensions for each of 46 populations (data taken from Davis 1951). A phenogram was generated using UPGMA on a matrix of taxonomic distances (Sneath and Sokal 1973), and this has been mapped onto the phylogenetic hypothesis (Figure 4, left). Given these data and the simple approach used to analyze them, patterns of morphological variation across space are not very congruent with the phylogenetic pattern. Thus, *Pipilo crissalis* is generally phenetically more similar to *P. albicollis* and *P. fuscus* than to *P. aberti.*

This relationship between the two patterns would be altered if the species limits themselves were modified. Previous workers, using phenetic assessments of plumage, ecology, and behavior to judge the extent of reproductive isolation, have considered *crissalis* and *fuscus* to be parts of a single biological species. Rearranging the phyletic pattern to reflect this conception of species limits, and then juxtaposing that with the phenetic pattern, reveals a new set of relationships (Figure 4, right). Now there is somewhat more congruence between the two patterns, particularly as they are expressed between *crissalis* and *fuscus.*

The purpose of this exercise is to show that the perceived pattern of geographic variation is in part dependent on prior judgments about species limits. The decision to place *P. crissalis* and *P. fuscus* in the same biological species has been based on overall resemblance. If, hypothetically, they happened to be sympatric and hybridize, this would seemingly strengthen and justify this interpretation. Yet, they are apparently distantly related geographically and do not comprise an evolutionary unit with a singular history. Only be treating them as if they were phylogenetic species can the historical pattern be resolved. And if it is necessary to treat them as phylogenetic species for analytical purposes, then it makes scientific sense to call them phylogenetic species. The biological species concept is superfluous in this case.

Clinal variation across evolutionary taxa. Uniting evolutionary taxa into a single biological species may cause us to describe a pattern of clinal variation where one does not exist. Two evolutionary taxa within the galliform

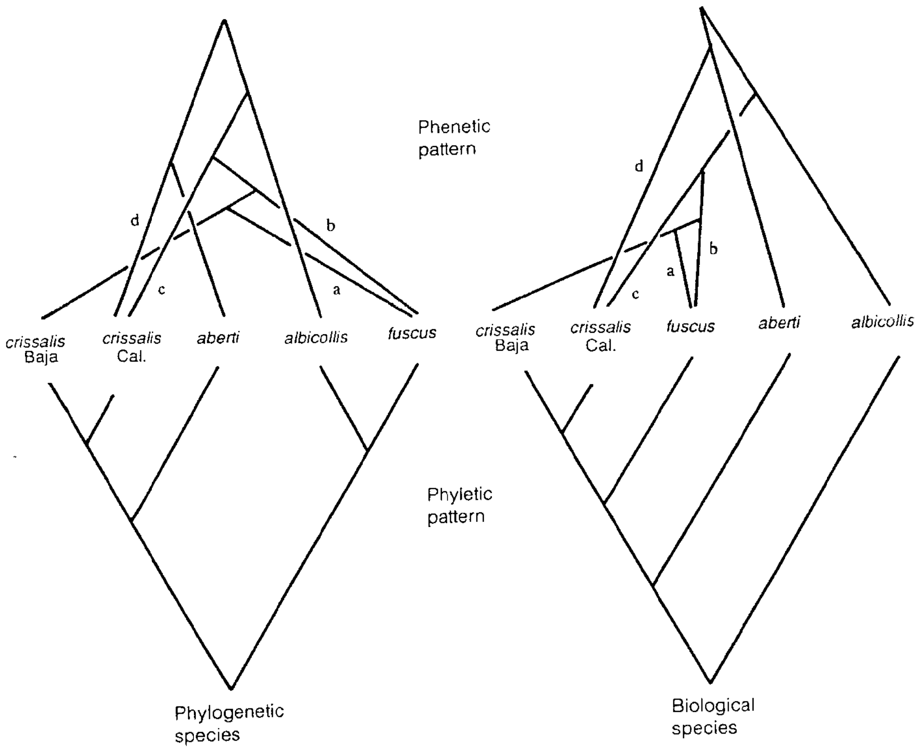

FIGURE 4. Comparison of the congruence between phenetic and phylogenetic patterns using phylogenetic species (left) and biological species (right). The phenetic pattern was generated as discussed in the text.

family Cracidae, *Ortalis cinereiceps* and *O. garrula*, are often placed in a single biological species on the basis of their potential to hybridize (Vaurie 1965, 1968). Although recognizing these two taxa as phylogenetic units, Vaurie (1965) described a size cline across them. *Ortalis cinereiceps* exhibits a cline of decreasing size from Nicaragua south to northwestern Colombia. *Ortalis garrula*, which is distributed across northern Colombia to the east of *O. cinereiceps*, is smaller still but shows no noticeable size variation across its range. It is doubtful that there is any significant gene flow between these two forms: only one specimen seems to be intermediate, and the taxa themselves are allopatric (Delacour and Amadon 1973:95). Within the context of a single biological species, there is a strong predilection to describe and seek a causal explanation for intraspecific clinal variation, even when it extends across two or more evolutionary taxa.

Because these two forms of *Ortalis* are diagnostically distinct, however, the transspecific trend may be spurious. There exists the possibility that *O. garrula* may be more closely related to a third species of *Ortalis* than it is to *O. cinereiceps*. If such is the case, the small size of *O. garrula* might be a primitive character shared with that other species. Use of phylogenetic species and a search for their relationships could help solve this problem.

Geographic variation and the historical analysis of hybridization. Within the context of a biological species concept investigators rarely make a distinction between diagnostic and nondiagnostic components of variation. The history of speciation can thereby be obscured. In those cases in which differentiated isolates have presumably come into geographic contact and hybridize, the usual procedure is to unite these taxa into a single biological species. From this perspective, subsequent analysis of geographic variation focuses almost entirely upon nondiagnostic variation because the problem of interest is to document character variation through the zone of intergradation. Indeed, under the aegis of the biological species concept, the study of hybridization has taken center stage in the analysis of geographic variation in contrast to those investigations that emphasize the historical analysis of taxonomic diversification. Without an understanding of the historical pattern of taxic origins, however, it is very likely that the causal dynamics of hybridization itself will be misconstrued. This general point can be illustrated by one example from Haffer's (1974) classic study of geographic variation and hybridization in the toucans of Amazonia.

Haffer's (1974:265–284) study included an analysis of variation within an entity said to be a biological species. Thus, ***Ramphastos vitellinus*** is distributed across much of Amazonia, but is subdivided into three well-marked evolutionary taxa (assigned subspecific rank by Haffer) that broadly hybridize north and south of the Amazon, although apparently not across the lower Amazon (Figure 5). Haffer examined patterns of variation in a number of variables, only one of which will be considered here. Haffer (1974:274, Figure 16.34) demonstrated a zig-zag cline in the width of the red breast band, first decreasing from the population in the Guianas and Venezuela (*R. v. vitellinus*) toward that in eastern Ecuador and Peru (*R. v. culminatus*) and then increasing again toward the population of central and southeastern Brazil (*R. v. ariel*). These and other clines are interpreted by Haffer (1974) as the result of gene flow within hybridizing populations that have come into secondary contact.

Haffer's general interpretation appears correct. Yet, interpreting patterns of variation *within* what is taken to be a single biological species has made it conceptually more difficult to examine that same variation from

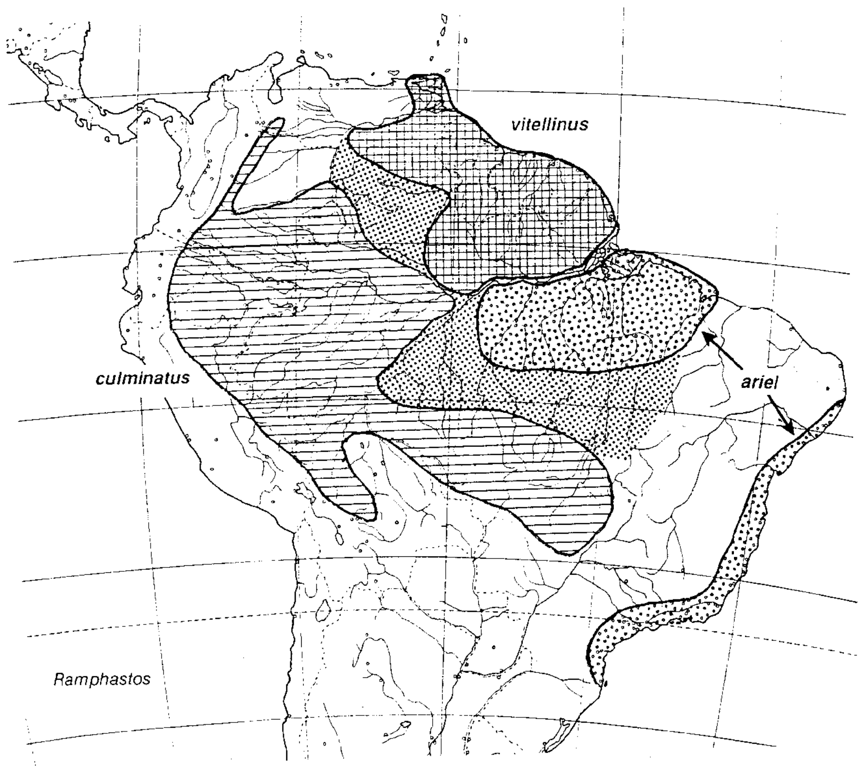

FIGURE 5. Distribution of three phylogenetic species in the toucan genus *Ramphastos.* Distributions of hybrids between *R. vitellinus* and *R. culminatus* and between *R. culminatus* and *R. ariel* are shown by black dots. *Ramphastos vitellinus* and *R. ariel* are apparently sister species (Prum 1982). Distributions from Haffer (1974). See text.

the perspective of historical patterns that may have arisen *among* differentiated taxa. The three taxa of toucans in this example are well-defined evolutionary units, or phylogenetic species. Prum (1982, 1988) has proposed that *vitellinus* of the Guianas is the sister species of the south Amazon form, *ariel,* and that both comprise the sister group of *culminatus* from upper Amazonia. Consequently, historical analysis indicates that the sister species of this clade do not hybridize and that all hybridization is taking place among taxa separated by at least two speciation events. Whether the sister species *vitellinus* and *ariel* are capable of hybridizing is conjecture at this point, for in spite of having an ability to fly long distances, they are isolated by the Amazon.

Two important conclusions can be drawn from this historical hypothesis. First, the patterns of variation resulting from gene flow must be the result of secondary contact and hybridization and not primary intergradation because the hybridizing taxa are not sister groups. Second, the clines themselves must be younger than the speciation event that gave rise to *vitellinus* and *ariel.* If that event could be dated in some manner, either by a geological or biological clock, then it would establish a time constraint on any analysis that attempted to describe or reconstruct the dynamics of this hybridization.

The preceding example is also similar in some ways to the situation described earlier for the Australian sittellas (*Daphoenositta*). Using hybridization as a criterion for uniting all these taxa into a single biological species clearly impairs the historical analysis of hybridization itself: even though two differentiated taxa hybridize, they may not be sister species (Rosen 1978, 1979). In the sittellas (Figure 2), patterns of hybridization are expressed across a complex pattern of historical interrelationships. These examples illustrate the point that as long as hybridization is used as a criterion to define species limits, those limits cannot then be used to study the degree of concordance between phylogenetic history and the ability to hybridize. This circularity is not confronted when using phylogenetic species.

It might be argued that these observations and conclusions could be studied within the context of the biological species concept. One response to this is that if investigations of history were an integral part of the application of the biological species concept to speciation analysis, then we might expect to see many examples. We do not, however, and it is only necessary to inspect the major texts on speciation to document what little role historical analysis has played (e.g., Mayr 1942, 1963, 1969; Endler 1977; White 1978). This situation has begun to change, primarily because workers are seeing the benefits of treating differentiated taxa as evolutionary units having a unique historical pattern of interrelationships. As this work continues, more and more patterns of variation and hybridization will be found to transcend the boundaries defined by speciation events. When this occurs, the biological species concept not only becomes inapplicable, it carries with it the potential to complicate evolutionary analysis.

Species concepts and the genetics of speciation

Evolutionary geneticists, operating within the framework of the biological species concept, have viewed the genetic analysis of speciation and differentiation as two separate problems, what Templeton (1981:25) calls the genetics of speciation versus the genetics of species differences. To most evolutionary geneticists, probably, the genetics of speciation is essentially equivalent to the genetics of reproductive isolation (Ayala 1975; Bush

1975; Avise 1976; Templeton 1981, 1982; Nei et al. 1983; Rose and Doolittle 1983; Barton and Charlesworth 1984; Barton and Hewitt 1985; Krieber and Rose 1986), and the research protocol is one of searching for the kinds of genetic changes that bring about reproductive disjunction. As Templeton (1981, 1982) notes, however, generalities have failed to emerge from this work.

Acceptance of a phylogenetic species concept implies a shift in perspective: the genetics of speciation now becomes one component of a causal chain that seeks to explain the origin of evolutionary novelties in populations. Once again, we assume these novelties can be any intrinsic attribute as long as it characterizes the existence of an evolutionary taxonomic unit. To simplify the problem, we can envision the contribution of evolutionary genetics to be twofold:

1. to propose causal explanations for the origin of these novelties within the ontogenies of individual organisms within a population, and
2. to propose causal explanations for the spread and fixation of those novelties in the population, thus characterizing the latter as a new, differentiated taxon.

The first contribution appears to reside within the realm of developmental molecular genetics and the second within population genetics and ecology.

Seeing speciation from the standpoint of phylogenetic species thus calls for a new emphasis on the genetics of species differences, but not in the way this subject has sometimes been studied in the past. Attempts to relate genetic distance to taxonomic rank (Ayala et al. 1974; Ayala 1975; Avise 1976; Zimmerman et al. 1978) are unlikely to lead to useful generalizations because within the context of current widely accepted methods of classification, any correlations might well be spurious (see also Patton 1981:286–287). Given the methods of evolutionary classification, in which taxonomic rank is often a subjective assessment of the degree of phenotypic divergence, there is no reason to expect that taxa assigned to ranks such as subspecies, semispecies, sibling species, or nonsibling species will be internally homogeneous with respect to age or be comparable phylogenetically. Many so-called subspecies or semispecies, for example, might be as old as, if not older than, entire clades of species.

This cautionary note implies that studies on species differences should have a strong measure of phylogenetic control. By definition, sister taxa, whatever taxonomic rank they might be given, are of the same age, and comparisons between sister groups offer a wealth of opportunities to explore the relationships between genetic differences, on the one hand, and phenotypic divergence or relative differences in diversity, on the other.

In one sense, it is possible to remain pessimistic regarding the possibility of finding general explanatory laws relating genetic divergence and speciation. Many different kinds of genetic change appear responsible for perturbations of developmental pathways and hence contribute to the origin of novelties. Moreover, many of these processes have a strong stochastic component, which contributes even more to the state of pessimism about the generation of deterministic laws. Yet, at an idiographic level, at least, population genetics has contributed substantially to our understanding of differentiation, including the origin of reproductive isolation. From a systematic viewpoint, however, there seems to be a need for more discussion about the exact nature of the problems facing those biologists interested in the genetics of speciation and what the major questions might be. Only by defining the problems more precisely are we likely to develop major explanatory generalizations.

CONCLUSIONS

Carson (1985:380) has recently argued that evolutionary biology suffers from "a regrettable lack of unification of theory relating to the modes or processes involved in the origin of new species." One primary reason for this, he contends, is the biological species concept, which Carson sees as having been particularly unsuccessful in plants. The examples discussed in this chapter demonstrate that the difficulties of the biological species concept are much more general and extend to animals as well. Even in the two groups most often associated with the biological species concept, birds and mammals, these difficulties are commonplace. As Hafner et al. (1987) note, many biological species are likely to be paraphyletic. If so, then it will not be possible to recover the true history of speciation, and all results based on these taxa will be misleading. Moreover, even so-called "monophyletic" biological species will obscure historical reconstruction because they mask the true number of differentiated evolutionary taxa and their genealogical relationships. Given these difficulties, nothing is served by using the biological species concept.

Equating differentiated evolutionary taxa with species at once provides a basis for unifying the description of evolutionary pattern in both plants and animals. Phylogenetic species are basal taxonomic units, and as such are broadly comparable. Although many different processes may underlie evolutionary change, a constant outcome is the origin of evolutionary taxa. The phylogenetic species concept recognizes this, and consequently provides a powerful ontological framework for systematic and evolutionary biology.

ACKNOWLEDGMENTS

I want to thank the authorities of the American Museum of Natural History, New York, and the Museum of Zoology, University of Michigan, for permitting me to study specimens in their care. I am grateful to Drs. Thomas E. Dowling, Robert M. Zink, and Mary C. McKitrick for their comments on the manuscript. This work was supported by a grant from the National Science Foundation.

LITERATURE CITED

American Ornithologists' Union. 1983. *Check-list of North American Birds,* 6th ed. American Ornithologists' Union, Lawrence, Kansas.

Avise, J. C. 1976. Genetic differentiation during speciation. Pp. 106–122 in: F. J. Ayala (ed.), *Molecular Evolution.* Sinauer Associates, Sunderland, Massachusetts.

Ayala, F. J. 1975. Genetic differentiation during the speciation process. Evolution. Biol. 8:1–78.

Ayala, F. J. 1981. Speciation: Stages, modes and genetic analysis. Pp. 45–67 in: O. A. Reig (ed.), *Ecology and Genetics of Animal Speciation.* Univ. Simon Bolivar, Decanato Invest., Caracas, Venezuela.

Ayala, F. J., M. L. Tracey, D. Hedgecock, and R. C. Richmond. 1974. Genetic differentiation during the speciation process in *Drosophila.* Evolution 28:576–592.

Barton, N. H., and B. Charlesworth. 1984. Genetic revolutions, founder effects, and speciation. Annu. Rev. Ecol. System. 15:133–164.

Barton, N. H., and G. M. Hewitt. 1985. Analysis of hybrid zones. Annu. Rev. Ecol. System. 16:113–148.

Bush, G. L. 1975. Modes of animal speciation. Annu. Rev. Ecol. System. 6:339–364.

Campbell, A. J., and A. G. Campbell. 1926. A review of the genus *Cinclosoma.* Emu 26:26–40.

Carson, H. L. 1985. Unification of speciation theory in plants and animals. System. Bot. 10:380–390.

Condon, H. T. 1962. Australian quail-thrushes of the genus *Cinclosoma.* Records South Aust. Mus. 14:337–370.

Coyne, J. A., and N. H. Barton. 1988. What do we know about speciation? Nature (London) 331:485–486.

Cracraft, J. 1982. Geographic differentiation, cladistics, and vicariance biogeography: Reconstructing the tempo and mode of evolution. Am. Zool. 22:411–424.

Cracraft, J. 1983. Species concepts and speciation analysis. Curr. Ornithol. 1:159–187.

Cracraft, J. 1986. Origin and evolution of continental biotas: Speciation and historical congruence within the Australian avifauna. Evolution 40:977–996.

Cracraft, J. 1987. Species concepts and the ontology of evolution. Biol. Philos. 2:63–80.

Cracraft, J. 1988. Species as entities of biological theory. In M. Ruse (ed.), *What the Philosophy of Biology Is.* D. Reidel, Dordrecht. In press.

Cronquist, A. 1978. Once again, what is a species? Beltsville Symp. Agricult. Res. 2:3–20.

Davis, J. 1951. Distribution and variation of the brown towhees. Univ. Calif. Publ. Zool. 52:1–120.

Delacour, J., and D. Amadon. 1973. *Curassows and Related Birds.* American Museum of Natural History, New York.

Diegnan, H. G. 1964. Subfamily Orthonychinae. Pp. 228–240 in: E. Mayr and R. A. Paynter, Jr. (eds.), *Check-list of Birds of the World.* Museum of Comparative Zoology, Harvard University.

Dobzhansky, Th. 1937. *Genetics and the Origin of Species.* Columbia University Press, New York.

Dobzhansky, Th., F. J. Ayala, G. L. Stebbins, and J. W. Valentine. 1977. *Evolution.* W. H. Freeman, San Francisco.

Donoghue, M. J. 1985. A critique of the biological species concept and recommendations for a phylogenetic alternative. The Bryologist 88:172–181.

Ehrendorfer, F. 1984. Artbegriff und Artbildung in botanischer Sicht. Z. zool. System. Evolution. 22:234–263.

Ehrlich, P. R. 1961. Has the biological species concept outlived its usefulness? System. Zool. 10:167–176.

Endler, J. A. 1977. *Geographic Variation, Speciation, and Clines.* Princeton University Press, Princeton, N.J.

Ford, J. 1974. Taxonomic significance of some hybrid and aberrant-plumaged quail-thrushes. Emu 74:80–90.

Ford, J. 1976. Systematics and speciation in the quail-thrushes of Australia and New Guinea. Proc. 16th Int. Ornithol. Congr. 542–556.

Ford, J. 1980. Hybridization between contiguous subspecies of the Varied Sittella in Queensland. Emu 80:1–12.

Ford, J. 1983. Evolutionary and ecological relationships between quail-thrushes. Emu 81:57–81.

Ford, J., and S. A. Parker. 1974. Distribution and taxonomy of some birds from south-western Queensland. Emu 74:177–194.

Frost, J. S., and J. E. Platz. 1983. Comparative assessment of modes of reproductive isolation among four species of leopard frogs (*Rana pipiens* complex). Evolution 37:66–78.

Futuyma, D. J. 1986. *Evolutionary Biology.* Sinauer Associates, Sunderland, Massachusetts.

Gaukroger, S. 1978. *Explanatory Structures.* Humanities Press, Atlantic Highlands, N.J.

Gould, S. J., and R. F. Johnston. 1972. Geographic variation. Annu. Rev. Ecol. System. 3:457–498.

Haffer, J. 1974. Avian speciation in tropical South America. Publ. Nuttall Ornithol. Club 14:1–390.

Hafner, M. S., J. C. Hafner, J. L. Patton, and M. F. Smith. 1987. Macrogeographic patterns of genetic differentiation in the pocket gopher *Thomomys umbrinus.* System. Zool. 36: 18–34.

Hubbard, J. P. 1973. Avian evolution in the aridlands of North America. Living Bird 12:155–196.

Hull, D. L. 1976. Are species really individuals? System. Zool. 25:174–191.

Hull, D. L. 1977. The ontological status of species as evolutionary units. Pp. 91–102 in: R. Butts and J. Hintikka (eds.), *Foundational Problems in the Special Sciences.* D. Reidel, Dordrecht-Holland.

Hull, D. L. 1978. A matter of individuality. Philos. Sci. 45:335–360.

Keast, A. 1961. Bird speciation on the Australian continent. Bull. Mus. Comp. Zool. 123:303–495.

Krieber, M., and M. R. Rose. 1986. Molecular aspects of the species barrier. Annu. Rev. Ecol. System. 17:465–485.

Levin, D. A. 1979. The nature of plant species. Science 204:381–384.

Lewontin, R. C. 1974. *The Genetic Basis of Evolutionary Change.* Columbia University Press, New York.

MacDonald, J. D. 1968. Notes on the genus *Cinclosoma.* Emu 67:283–289.

MacDonald, J. D. 1973. *Birds of Australia.* A. H. & A. W. Reed, Sidney, Australia.

Marshall, J. T., Jr. 1960. Interrelations of Abert and Brown towhees. Condor 62:49–64.

Marshall, J. T., Jr. 1964. Voice in communication and relationships among brown towhees. Condor 66:345–356.

Mayr, E. 1942. *Systematics and the Origin of Species.* Columbia University Press, New York.

Mayr, E. 1950. Taxonomic notes on the genus *Neositta.* Emu 49:282–291.

Mayr, E. 1963. *Animal Species and Evolution.* Harvard University Press, Cambridge.

Mayr, E. 1969. *Principles of Systematic Zoology.* McGraw-Hill, New York.

Mayr, E. 1982. *The Growth of Biological Thought.* Harvard University Press, Cambridge.

Mayr, E., and L. L. Short. 1970. *Species Taxa of North American Birds.* Publications of the Nuttall Ornithological Club No. 9, Museum of Comparative Zoology, Harvard University, Cambridge.

McGill, A. R. 1948. A distributional review of the genus *Neositta.* Emu 48:33–52.

McKitrick, M. C., and R. M. Zink. 1988. Species concepts in ornithology. Condor 90:1–14.

Mishler, B. D., and M. J. Donoghue. 1982. Species concepts: A case for pluralism. System. Zool. 31:491–503.

Nei, M. 1987. *Molecular Evolutionary Genetics.* Columbia University Press, New York.

Nei, M., T. Maruyama, and C. Wu. 1983. Models of evolution of reproductive isolation. Genetics 103:557–579.

Nelson, G. J., and N. I. Platnick. 1981. *Systematics and Biogeography: Cladistics and Vicariance.* Columbia University Press, New York.

Nevo, E., G. Heth, A. Beiles, and E. Frankenberg. 1987. Geographic dialects in blind mole rats: Role of vocal communication in active speciation. Proc. Natl. Acad. Sci. U.S.A. 84:3312–3315.

Paterson, H. E. H. 1981. The continuing search for the unknown and unknowable: A critique of contemporary ideas on speciation. South African J. Sci. 77:113–119.

Paterson, H. E. H. 1982. Perspective on speciation by reinforcement. South African J. Sci. 78:53–57.

Paterson, H. E. H. 1985. The recognition concept of species. Transvaal Mus. Monograph No. 4:21–29.

Patton, J. L. 1981. Chromosomal and genic divergence, population structure, and speciation potential in *Thomomys bottae* pocket gophers. Pp. 255–295 in: O. A. Reig (ed.), *Ecology and Genetics of Animal Speciation.* Univ. Simon Bolivar Decanato Investigaciones, Caracas, Venezuela.

Patton, J. L., and J. H. Feder. 1978. Genetic divergence between populations of the pocket gopher, *Thomomys umbrinus* (Richardson). Z. Saugetier. 43:17–30.

Patton, J. L., and M. F. Smith. 1981. Molecular evolution in *Thomomys* pocket gophers: phyletic systematics, paraphyly, and rates of evolution. J. Mammal. 62:493–500.

Pizzey, G. 1980. *A Field Guide to the Birds of Australia.* Princeton University Press, Princeton, New Jersey.

Prum, R. O. 1982. Systematics and biogeography of the family Ramphastidae (Aves). Unpublished Senior Honors Thesis, Harvard University, Cambridge, Massachusetts.

Prum, R. O. 1988. Historical relationships among avian forest areas of endemism in the neotropics. Proc. 19th Int. Ornithol. Congr., Ottawa, Canada.

Raven, P. H. 1980. Hybridization and the nature of species in higher plants. Can. Bot. Assoc. Bull. Suppl. 13:3–10.

Rose, M. R., and W. F. Doolittle. 1983. Molecular biological mechanisms of speciation. Science 220:157–162.

Rosen, D. E. 1978. Vicariant patterns and historical explanation in biogeography. System. Zool. 27:159–188.

Rosen, D. E. 1979. Fishes from the uplands and intermontane basins of Guatemala: Revisionary studies and comparative geography. Bull. Am. Mus. Nat. Hist. 162: 267–376.

Rosenberg, A. 1985. *The Structure of Biological Science.* Cambridge University Press, New York.

Short, L. L., R. Schodde, and J. F. M. Horne. 1983a. Five-way hybridization of Varied Sittellas *Daphoenositta chrysoptera* (Aves: Neosittidae) in central Queensland. Aust. J. Zool. 31:499–516.

Short, L. L., R. Schodde, R. A. Noske, and J. F. M. Horne. 1983b. Hybridization of 'White-headed' and 'Orange-winged' Varied Sittellas, *Daphoenositta chrysoptera leucocephala* and *D. c. chrysoptera* (Aves: Neosittidae), in eastern Australia. Aust. J. Zool. 31:517–531.

Sneath, P. H. A., and R. R. Sokal. 1973. *Numerical Taxonomy.* W. H. Freeman, San Francisco.

Sokal, R. R., and T. J. Crovello. 1970. The biological species concept: A critical evaluation. Am. Natur. 104:127–153.

Straney, D. O., and J. L. Patton. 1980. Phylogenetic and environmental determinants of geographic variation of the pocket mouse *Perognathus goldmani* Osgood. Evolution 34:888–903.

Sudhaus, W. 1984. Artbegriff und Artbildung in zoologischer Sicht. Z. zool. System. Evolution. 22:183–211.

Templeton, A. R. 1981. Mechanisms of speciation—a population genetic approach. Annu. Rev. Ecol. System. 12:23–48.

Templeton, A. R. 1982. Genetic architectures of speciation. Pp. 105–121 in: D. Barigozzi (ed.), *Mechanisms of Speciation.* A. R. Liss, New York.

Vaurie, C. 1965. Systematic notes on the bird family Cracidae. No. 4. *Ortalis garrula* and *Ortalis ruficauda.* Am. Mus. Novitates 2237:1–16.

Vaurie, C. 1968. Taxonomy of the Cracidae (Aves). Bull. Am. Mus. Nat. Hist. 138: 131–260.

White, M. J. D. 1978. *Modes of Speciation.* W. H. Freeman, San Francisco.

Willmann, R. 1987. Missverständnisse um das biologische Artkonzept. Paläontol. Z. 61:3–15.

Wolstenholme, H. 1926. *Official Checklist of the Birds of Australia,* 2nd ed. H. J. Green, Melbourne.

Zimmerman, E. G., C. W. Kilpatrick, and B. J. Hart. 1978. The genetics of speciation in the rodent genus *Peromyscus.* Evolution 32:565–579.

Zink, R. M. 1988. Evolution of brown towhees: Allozymes, morphometrics and species limits. Condor 90:72–82.

Zink, R. M., and J. V. Remsen, Jr. 1986. Evolutionary processes and patterns of geographic variation in birds. Curr. Ornithol. 4:1–69.