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Choosing among Alternative "Phylogenetic" Species Concepts

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ABSTRACT. Several different "phylogenetic" species concepts have been proposed, and we consider how to choose among them. There appear to be two main approaches. "Character-based" concepts define species on the possession of characters, whereas "history-based" concepts are based on historical relatedness. Under the latter view, characters may be used to discover species in practice but they are not viewed as defining attributes of species. To illustrate the distinction we discuss a character-based approach utilizing "diagnostic" characters and a history-based approach using genetic coalescence. We argue that the choice between character- and history-based concepts is primarily determined by one's understanding of systematics. If the goal of systematics is simply to describe the hierarchical distribution of characters ("pattern cladistics"), a character-based definition of species is required. In contrast, if systematics is concerned with inferring the evolutionary relationships of organisms ("evolutionary phylogenetics"), a history-based definition of species is needed. We hold the view that phylogenetic systematics is concerned with evolutionary history and therefore we maintain that a phylogenetic species concept should be history-based.

The rise of phylogenetic systematics resulted in dissatisfaction with prevailing species concepts. In particular, the biological species concept (e.g., Mayr 1942) was called into question because it emphasized a property (the capacity to interbreed) that is not necessarily a good guide to relationships (Rosen 1979; Cracraft 1983; Donoghue 1985). In response to the perceived incompatibility of this and other species concepts (e.g., the "ecological," "cohesion," and "recognition" concepts) with the principles of phylogenetic systematics, a number of alternative approaches have been proposed. However, despite being motivated by a concern with defining the species category in a manner compatible with phylogenetic systematics (broadly construed), there are significant differences among so-called "phylogenetic" species concepts. Our aim is to characterize these different concepts and discuss how a choice might be made among them.

It appears to us that the most fundamental division among different phylogenetic species concepts is that some define species on the basis of characters, whereas others define species in terms of historical relationships or ancestry.

Under "character-based" concepts, an organism is a member of a given species if and only if it possesses some character (i.e., an observable organismal attribute) or combination of characters. Generally, the origins of these characters are ignored (e.g., whether they are ancestral or derived) as is the actual genealogy of the organisms in question. In contrast, "history-based" concepts consider an organism a member of a given species if and only if it is historically related to other organisms in the species. It is important to appreciate that although history-based concepts view characters as irrelevant to the **definition** of species, characters generally are needed to **recognize** species and assign organisms to species in practice. Thus, under both history-based and character-based concepts, characters provide the main source of evidence in species delimitation. However, whereas history-based concepts view characters as (fallible) **evidence** of species existence, character-based concepts view characters as **defining attributes** of species.

A first step in deciding among "phylogenetic" species concepts is to understand clearly the distinction between history- and character-based

concepts. This entails a careful evaluation of the consequences of adopting one approach or the other. To do this we will describe and contrast one character-based and one history-based species concept. We will focus on the most completely explicated character-based approach, that formulated by Cracraft (1983, 1989) and extended by Nixon and Wheeler (1990, 1992) and Davis and Nixon (1992). Similarly, we will focus on one of the many history-based approaches, that developed by Baum and Shaw (1995). It should be stressed, however, that there are other character- and history-based concepts besides these two, and the fact that we focus attention on two concepts does not mean we advocate these over the alternatives. Rather, we use them simply to illustrate the two basic approaches to defining phylogenetic species, and to raise general concerns pertinent to the choice between them. This choice, we will argue in the second half of the paper, is guided primarily by one's view of the aim of systematics.

CHARACTER-BASED APPROACHES

The character-based concept we will consider defines a species as "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)" (Nixon and Wheeler 1990, p. 218). This concept is called "the phylogenetic species concept" or PSC by its proponents, but to avoid confusion with other phylogenetic species concepts (e.g., Rosen 1979; Mishler and Donoghue 1982; Donoghue 1985; Mishler and Brandon 1987) we will refer to it as the "diagnostic approach."

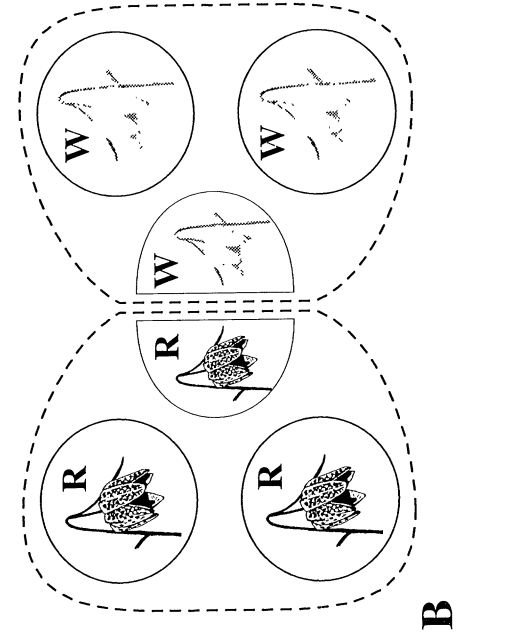
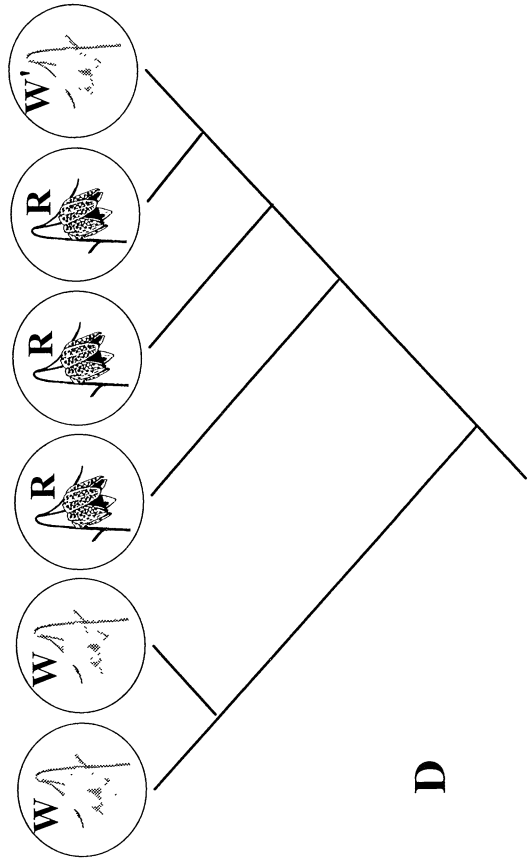
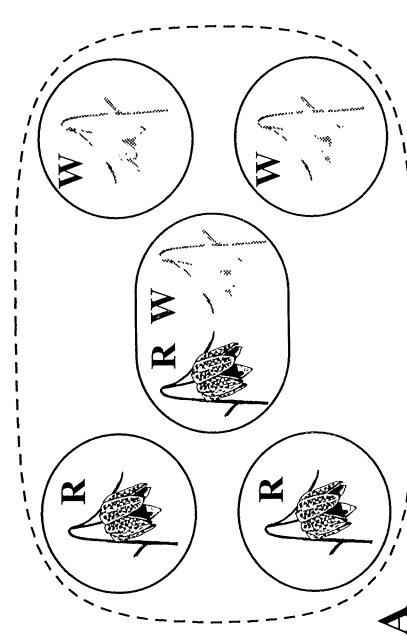
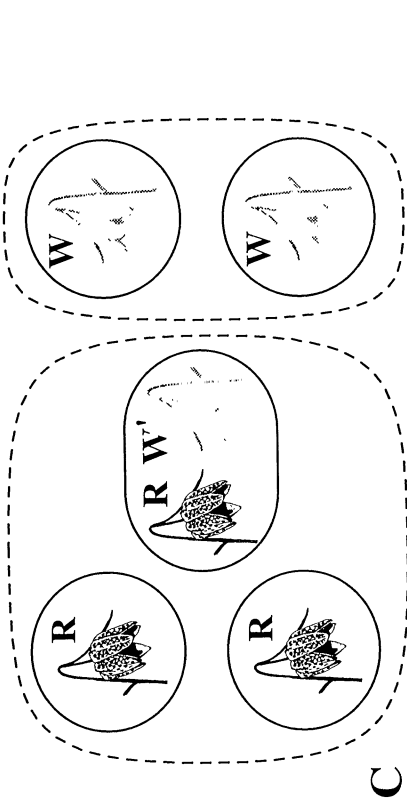
The diagnostic approach is clearly character-based, inasmuch as the definition rests on the possession of characters (specifically "diagnostic" characters), with considerations of organismal history or relatedness playing a subordinate role. This dependence on characters can be seen by considering a hypothetical example. Consider a situation in which four populations of *Fritillaria* exist, two of which are composed entirely of red-flowered individuals and the other two of white flowered individuals. Perianth color is the only attribute that distinguishes the populations. In this situation two diagnostic species exist, one comprising the two white-flowered populations and the other com-

prising the red-flowered populations. As this example shows, species limits are determined, and organisms are assigned to species, based solely upon the distribution of characters, without reference to evolutionary history. However, although character-based, the diagnostic approach requires additional information aside from characters, as shown by further examples.

Imagine that *Fritillaria* were found growing in a fifth locality, but at this site both red and white perianths occurred (Fig. 1). This finding is subject to two alternative interpretations: 1) the new locality constitutes a single population and perianth color is a polymorphic trait [i.e., not a "character" in the sense of Nixon and Wheeler (1990)]; hence, all five populations are members of the same diagnostic species (Fig. 1A), or 2) the newly discovered site is not a single population but two sympatric populations, one composed of the red-flowered species and the other of the white-flowered species (Fig. 1B). Clearly, the choice between these alternatives rests on what is meant by the term "population."

It should be obvious that a "population" is not simply a group of organisms living in one place, because this would result in distantly related organisms (e.g., oak trees and squirrels) being assigned to the same population and thus species. Traditionally, population definitions rest on interbreeding or reproductive cohesion (e.g., Dobzhansky 1950). Davis and Nixon (1992, p. 430) adopted this view stating that, when considering the local units aggregated into species, populations are "the arenas in which most genetic recombination occurs." Thus, application of the diagnostic approach to sexual organisms implies knowledge of patterns of gene flow in nature.

This concept of population clearly applies only to sexual organisms, and a different approach must be taken for asexuals. Nixon and Wheeler (1990) used "lineage" in place of "population" when applying their species definition to asexuals. By "lineage," they mean a group of organisms that has a unique combination of characters, whether or not they comprise all the descendants of an ancestral organism. Thus, despite the connotation of history implied by the term "lineage" the diagnostic approach as applied to asexuals is also character-based. Delimiting "lineages" is the same as delimiting diagnostic species, which in turn is the same as



finding any discrete character variation: "when unique character combinations occur in asexual or clonal forms, these forms should be recognized as distinct species" (Nixon and Wheeler 1990, p. 219).

The reason we bring up the issue of the treatment of asexual organisms is not because we have a problem with a species concept that applies only to sexuals (or conversely to asexuals), and not because of worries about there being "too many" species. Rather, we wish to clarify that although minimal "diagnostic" groups can be delimited in principle in both sexual and asexual organisms, species status is achieved in different ways under the different circumstances and, therefore, "species" are not comparable entities (e.g., Frost and Hillis 1990). In sexual organisms breeding relations are critical whereas in asexuals all that is needed is the possession of similar characters. What unites these both as "species" is not some underlying biological property, but simply the fact that they pass some operational test ("diagnosability").

Returning now to the hypothetical *Fritillaria* example, if it is decided that the fifth site is indeed a single population that is polymorphic for flower color, then, at least under early versions of the diagnostic approach (Cracraft 1983, 1989; Nixon and Wheeler 1990), one would recognize only a single species. However, Davis and Nixon (1992) proposed a modification of the concept of "character." They retained the view of a diagnostic character as a fixed attribute but noted that "by 'fixed' we do not mean that the character is necessarily observed as monomorphic but that it occurs in all individuals of the lineage, in either its original or in a transformed state" (p. 424). Thus, in the *Fritillaria* example, two species would exist if, for example, the white flowers in the polymorphic pop-

ulation were derived from the red flowers in that population rather than being derived from white flowered individuals of the other "species" (Fig. 1C). This is an issue of homology assessment, which can be resolved by determining the historical relations among the character-states (Fig. 1D). Although this may be difficult to unravel in practice (especially in cases involving reversal or parallel loss of a state), in principle it provides a criterion for determining whether an attribute is diagnostic. However, there are complications that Davis and Nixon (1992) have not adequately addressed.

To illustrate one such problem, imagine two populations differing only in the alleles they manifest at a particular allozyme locus. Population 1 has alleles **a** and **b**, whereas population 2 has alleles **c** and **d**. Assume that allele **d** was derived from **c** which was derived from **b** which was, in turn, derived from **a**. If the approach advocated by Davis and Nixon (1992) is applied consistently, population 2 would be judged to be fixed for the diagnostic character (**c,d**) because it contains all organisms with either the original state (**c**) or the derived state (**d**). In contrast, population 1 is not fixed for any diagnostic character, because it contains no character that does not also occur (in the derived state) in population 2. If diagnostic species must have fixed characters, then is population 1 a species? In the spirit of Nixon and Wheeler (1990), population 1 should be considered a diagnostic species, but to do so seems contrary to the historical conception of characters promoted by Davis and Nixon (1992). If one followed Nixon and Wheeler (1990) and considered both populations diagnosable species then, in effect, one is applying two definitions of "fixation." Population 2 is "fixed" because it has a unique historical character, whereas population 1 is

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FIG. 1. A hypothetical example to illustrate the application of the diagnostic species concept. The boundaries of diagnostic species are marked with a dashed line. A-C. Two red-flowered and two white-flowered *Fritillaria* populations are depicted and a fifth site that contains both red- and white-flowered individuals. A. If the fifth site is a single population, then only one *Fritillaria* species exists. B. If the fifth site contains two populations, one comprising red-flowered plants only and the other comprising white-flowered plants only, then two diagnostic species would be recognized. C-D. If the fifth site is judged a single population, then two species can still be recognized if the white-flowered individuals there (W') are found to be derived from red flowers independently of the white flowers in the other two populations (W). D. A character-state tree (for example, derived from a molecular phylogeny of the genes controlling flower pigmentation) in which W' and W are shown to be non-homologous.

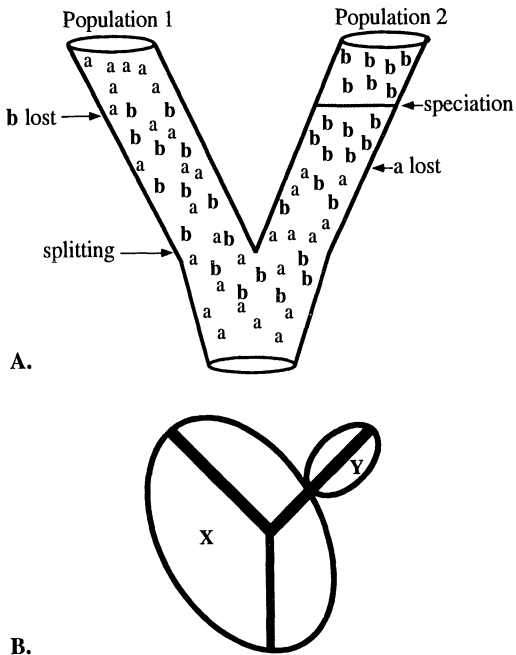


FIG. 2. Diagnostic species through time. A. The events leading to the formation of a descendant species, Y, from an ancestral species, X, are shown. The ancestral lineage, comprising a single population, is polymorphic for an ancestral trait, a, and a derived trait, b. The population splits into two isolated populations (1 and 2). Population 2 then loses a and some time later, population 1 loses b. Speciation of population 2 as species Y occurs with loss of the derived trait in population 1 and is not coincident with character fixation in population 2. B. The temporal boundaries of diagnostic species X and Y on the population tree.

"fixed" because the organisms in it bear characters absent from population 2. Again, as in the cases of sexual vs. asexual "species," such "species" share no substantive properties; they are equivalent only in the sense of having passed an operational test.

So far our discussion of the diagnostic approach has focused on its application at a point in time. However, Nixon and Wheeler (1992) explore its implications for time extended lineages. For them, character-fixation (i.e., the extinction of an ancestral trait) is synonymous with speciation and therefore all character fixation entails "speciation," regardless of proximity to lineage-branching events. In other words, "speciation" occurs in unbranching lineages each

time the last organism bearing an ancestral trait dies. When branching is involved, "speciation" is not linked with the branching event *per se* but occurs as soon as the two (or more?) lineages become diagnosably distinct (Fig. 4). This can occur through fixation of a derived trait in the speciating population (Nixon and Wheeler, 1992), or alternatively, a population can speciate when it is already fixed for a derived trait and that trait goes extinct in all other lineages (Fig. 4).

The time extended model of speciation proposed by Nixon and Wheeler (1992) is consistent with the diagnostic approach, but has several worrisome implications (in addition to effectively ignoring the distinction between anagenesis and cladogenesis). For example, if one considers a "trait" to be any heritable feature of an organism, then each organism has a potentially huge number of traits. This means that each organismal death is likely to cause at least one ancestral trait to become extinct and, hence, one derived trait to become fixed (the expected number will depend upon the number of traits per genome and the population size). Thus, in many plausible demographic situations, Nixon and Wheeler's (1992) approach will imply "speciation" more than once per generation. While it is important to recognize conflicts with prevailing views, such as those we have just described, such conflicts are not by themselves grounds for rejecting this or any other "phylogenetic" species concept. We could choose to revamp existing speciation theory instead. Rather, we must compare this approach to alternative species concepts and then choose among them based on consistency with the perceived goals of systematics.

HISTORY-BASED APPROACHES

A variety of history-based definitions of species are possible and several of these have been proposed. For example, it is clear that Hennig (1966) considered genealogical relationships to be the main concern in defining species (and other taxa), with characters being viewed merely as the evidence by which one could infer relationships (e.g., pp. 30, 79–80). It is noteworthy, for example, that in his frequently reproduced Figs. 4 and 6, both depicting speciation, no characters are shown. Likewise, several recent attempts to formulate phylogenetic spe-

cies concepts granted primacy to history over characters (e.g., Mishler and Donoghue 1982; Donoghue 1985; Mishler and Brandon 1987; de Queiroz and Donoghue 1988, 1990; Frost and Hillis 1990).

In order to highlight the basic issues that any history-based approach must confront, we have chosen to focus on just one such concept, the gene coalescence view outlined recently by Baum and Shaw (1995). In doing so, our purpose is not to promote their "genealogical species concept" as **the** solution. In fact, whereas the two of us agree completely on the need for a history-based species concept (see below), we do not agree entirely on which of these concepts is best.

The central aim of a history-based species concept is to define species based on historical relationships. However, the notion of historical relationship needs clarification. Especially critical here is the need to identify concepts that are sensitive to the fact that within populations of biparental organisms relationships are reticulate whereas between higher taxa they are divergent (Hennig 1966). There must be a boundary between these two types of relationship, and it is at this boundary that history-based species concepts have generally attempted to locate species. An obstacle that needs to be overcome is to develop a history-based concept of "relationship" that can potentially apply both within and among populations.

The concept of monophyly, as currently defined by many systematists (a single ancestral species and all of the species descended from it), cannot logically apply to species themselves or to entities below that level (Hennig 1966; de Queiroz and Donoghue 1988; McKittrick and Zink 1988; Wheeler and Nixon 1990). For this reason, de Queiroz and Donoghue (1988) suggested an expansion of the concept of monophyly to allow entities other than "species" to be ancestors, including individual organisms or breeding pairs (a possibility hinted at by Hennig 1966, e.g., p. 209; also see Donoghue 1985; Mishler and Brandon 1987). In principle, this broader definition of monophyly permits species to be monophyletic. However, because this concept of monophyly extends down to the level of mating pairs and their offspring, species concepts based on monophyly have tended to add "ranking" criteria such as the ability to interbreed (e.g., Mishler and Brandon 1987). If

one wishes to define species without such non-historical criteria, however, it is necessary to base the definition on a historical attribute other than monophyly.

The historical property we will focus on here is "exclusivity," where an exclusive group of organisms is one whose members are more closely related to each other than they are to any organisms outside the group (de Queiroz and Donoghue 1990; Baum 1992; Baum and Shaw 1995). Before continuing to discuss the implementation of exclusivity in a definition of species it is necessary to clarify the origin of the concept, because there has been some confusion on this point.

As well as presenting his well known definition of monophyly (see above), Hennig (1966) also stated another definition of the concept: "a group of species in which every species is more closely related to every other species than to any species that is classified outside the group" (p. 73). Apparently he recognized that when a phylogeny is strictly divergent, the two definitions of monophyly would always apply to the same groups, and in view of this synonymy he evidently saw no need to coin a new term for the property described by the alternative definition. In broadening the concept of monophyly to include descent from any common ancestor, de Queiroz and Donoghue (1988, 1990) noted that a strict correspondence between the alternative aspects of monophyly broke down. That is, the descendants of a particular ancestor may not form a group all of whom are each others closest relatives (e.g., within a population of sexually reproducing organisms). For this reason they suggested that the term "exclusivity" be used for the property analogous to Hennig's alternative version of monophyly (de Queiroz and Donoghue 1990). It should be noted, however, that the concept of "exclusivity" is not identical to either of Hennig's definitions of monophyly, because it may apply to groups of organisms rather than only to groups of species. Furthermore, whereas monophyly (in the standard usage) cannot logically apply to species (McKittrick and Zink 1988; Wheeler and Nixon 1990), exclusivity can (see below). Thus, even if the broadened definition of monophyly (de Queiroz and Donoghue 1988) were rejected (which would, incidentally, require some other term to be developed for the general phenomenon of descent from a common an-

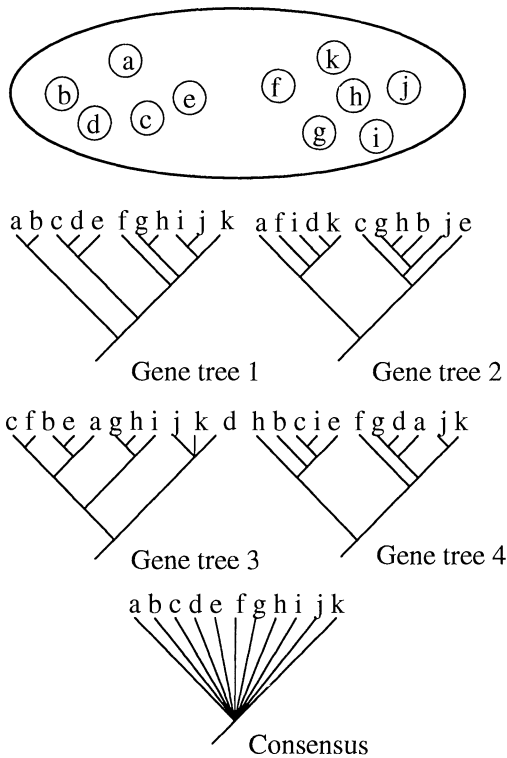


FIG. 3. The relationship among phylogenies of different unlinked genes from 11 organisms (a-k) within a single panmictic population (note only one allele of each organism is considered for each locus). Four gene trees are shown and their consensus. No groups of organisms are clades on all four gene trees.

cestor), the concept of exclusivity is still a valuable one, distinct from any developed by Hennig.

Under the species concept of Baum and Shaw (1995), species are viewed as basal, exclusive taxa; that is, taxa containing within them no subgroups that are themselves exclusive. In order to decide whether a group is exclusive the degree of relatedness of its constituent organisms, and between these organisms and other organisms outside the group, must be evaluated. The novel feature of this genealogical species concept is that, rather than being based on descent from an ancestral organism, relatedness is viewed in terms of the genealogical descent of the genome as a whole. This can be accomplished within the conceptual framework of the recently developed branch of population ge-

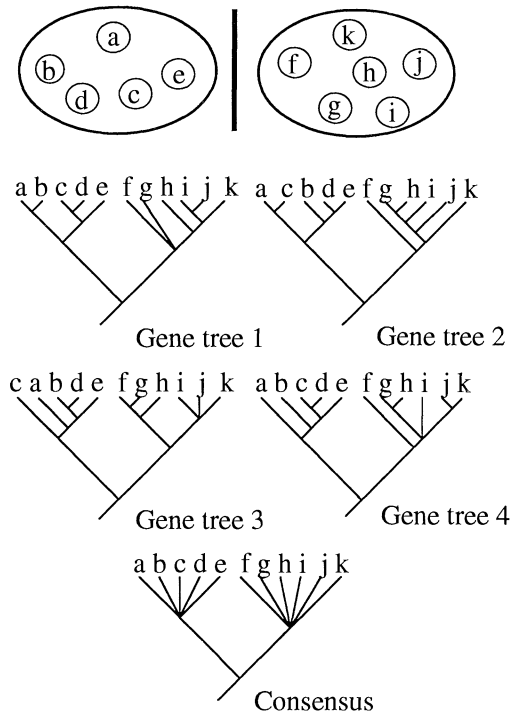


FIG. 4. The relationship among phylogenies of different unlinked genes from 11 organisms in two populations that have been genetically isolated for a long time. Four gene trees are shown and their consensus. Organisms in population 1 (a-e) and those in population 2 (f-k) always appear as distinct clades.

netics named "coalescent theory" [see Hudson (1990) for an introduction to the field, and Maddison (1995) for a discussion of its relevance to phylogenetic systematics]. To illustrate this approach it is easiest to go through a hypothetical example.

Imagine 11 sexual organisms in the same panmictic population (Fig. 3). The copies of a homologous gene (i.e., a piece of DNA inherited from a common ancestral gene and small enough not to have recombined) present in each of the 11 organisms will have a tree-like history (the gene-tree). Looking, for example, at gene 1 in Fig. 3, the alleles possessed by organisms **A** and **B** trace back to a common ancestral gene (i.e., "coalesce") more recently than either coalesces with **C**. Another gene, unlinked to the first, will have its own independent gene tree, which is likely to show a pattern of coalescence that is somewhat different from that of the first gene.

For example, in Fig. 3, gene 2 shows more recent coalescence between organisms **B** and **C** than between either of these and **A**. In such a panmictic population, there should be no groups of organisms that form a clade in all of the gene-trees (Avice and Ball 1990). Under the concept of exclusivity, as applied by Baum and Shaw (1995), there are, thus, no exclusive groups within the population.

Imagine now that this population had split very recently into two genetically isolated populations. The pattern of coalescence will not be any different from that found in the panmictic population, namely, the organisms of both populations will together constitute a single exclusive group without any exclusive subgroups. However, if these two populations continue to be genetically isolated, many of the gene lineages present at the time of the split will become extinct in one or the other population (or both). Eventually, if the populations remain isolated long enough, all copies of any gene present in one population will coalesce with each other before coalescing with copies in the other population (Fig 4; see Avice and Ball 1990). At this point the two populations each constitute an exclusive group of organisms and, assuming that they contain no exclusive subgroups, are "genealogical species" (Baum and Shaw 1995).

Extrapolating from this example, we may insert the coalescent view of relatedness into the concept of exclusivity and define a species as: a basal group of organisms all of whose genes coalesce more recently with each other than with those of any organisms outside the group. Notice that this concept is history-based because species are defined solely on genealogical history rather than on characters. As explained earlier, this certainly does not prevent characters from being used to infer history, and reference to characters will almost certainly be necessary in practice. However, whether a group of organism is a species is determined by the genealogical history of their genes, and gene trees exist regardless of whether that history can be reconstructed by reference to characters.

Many systematists are uncomfortable with a species definition that precludes knowing with certainty whether a group of organisms is a species. However, the act of describing a species can be viewed, and often has been, as the formulation of an hypothesis that a group of or-

ganisms has some special property (such as genetic isolation, or even independent creation). A species concept then is seen as guiding taxonomists as to the criteria that are relevant in testing a species hypothesis. However, it need not provide a prescribed set of operations by which "species" are discovered (Frost and Hillis 1990). The genealogical approach to defining species provides a concept of what a species is [contrary to the claim of Frost and Kluge (1994)] and, thus, suggests methods (e.g., gene tree analysis) by which particular species hypotheses can be tested rigorously.

As we have shown, the genealogical concept defines species based solely on the historical relationships of their constituent organisms [contrary to the implication in O'Hara (1992) that all species concepts must be prospective]. However, the genealogical species concept does have some implications that conflict with taxonomic tradition, of which three are worth briefly summarizing. We refer the reader to Baum and Shaw (1995) for discussion of other implications of the coalescent approach.

If the two populations shown speciating in Fig. 4 were unequal in size, coalescent theory predicts that the smaller population would become exclusive before the larger. Therefore, there will be a period of time during which the smaller population is a genealogical species, but the organisms of the larger population are not members of any genealogical species [see Fig. 5 in Baum and Shaw (in press)]. The larger population in this example has no history that is not also shared with the small population. However, to reflect the likelihood that its descendants become a distinct exclusive group, it and analogous groups of organisms may be termed "metaspecies" (Donoghue 1985; de Queiroz and Donoghue 1988). This poses a problem due to the traditional requirement that all organisms be ascribable to a species. However, it may well be that history-based concepts of taxa (at any level) will conflict with existing taxonomic conventions (de Queiroz and Gauthier 1992).

Another issue raised by the coalescent approach, which we think will apply to other history-based concepts, is "fuzziness." Because different genes coalesce at different rates the boundary between reticulate and divergent genealogy is not sharp. We believe that this fuzz-

iness is an inherent feature of such systems rather than a result of the particular definitions of reticulation and divergence advocated by Baum and Shaw (1995). Thus any concept aiming to place species limits at the reticulate/divergent boundary must accept a certain fuzziness. However, it should be noted that, provided a single historical criterion is applied (e.g., exclusivity), fuzziness reflects the way the world is rather than a lack of conceptual clarity. Thus, whereas fuzziness may complicate the act of delimiting species in practice, it need not undermine the theoretical utility of a history-based species concept.

Finally, it should be noted that the definition of genealogical species given above applies to the organisms living at one point in time. Baum and Shaw (1995) suggested two alternatives for dealing with this fact. First, basal exclusive groups can be equated with species, meaning that species would not be seen as persisting through time (analogous to semaphoronts; Hennig 1966). Alternatively, basal exclusive groups could be equated with the temporal cross-sections of species, which would therefore be equated with time-extended lineages. Future discussions of history-based species definitions (and other types of species definition) will need to address the issue of temporal extent.

CHOOSING BETWEEN A CHARACTER-BASED AND HISTORY-BASED APPROACH

We have described both a character-based and a history-based species concept and have shown that these approaches are quite distinct and that they each appear to be internally consistent. They differ in the ways they conflict with current ideas in evolutionary biology and taxonomy, but this, we would argue, should not be the basis on which to choose between them. Similarly, the choice should not be achieved by comparing the species delimited under each concept with the "species" that a "good taxonomist" recognizes. Instead, we think that the choice between alternative species concepts must be discussed in the context of the overall aims and rationale of systematics. Thus, it is necessary to characterize alternative versions of phylogenetic systematics and examine their compatibility with character-based and history-based species concepts.

As we see it, among the systematists who consider themselves to be descendants of Hennig, there are currently two poles, which de Queiroz and Donoghue (1990) termed "cladistics" and "phylogenetic systematics." These designations are, however, potentially confusing (e.g., because the methods referred to as "cladistics" are used by proponents of both views) so we will use modifiers that we hope will minimize misunderstanding: "pattern cladistics" and "evolutionary phylogenetics." Under the pattern cladistic view, systematics is concerned with providing a theory-neutral description of the hierarchic distribution of characters, whereas under the evolutionary phylogenetic view it is concerned with reconstructing descent relationships (de Queiroz 1992; de Queiroz and Gauthier 1990). We believe that the choice between the pattern cladistic and evolutionary phylogenetic views is critical in choosing between alternative phylogenetic species concepts.

Species from a Pattern Cladistic Perspective. The pattern cladistic view [perhaps best exemplified by Patterson (1988) and Nelson (1989)] argues for the primacy of "observation" (characters) over "theory" (evolutionary history). Thus, cladograms are viewed as summaries of character distributions rather than depictions of evolutionary history. Following from this, taxa are seen as being properties of characters rather than the reverse (Nelson 1989), and monophyletic higher taxa are implicitly or explicitly defined as groups of species having shared **characters**. It is, therefore, internally consistent to define species on the basis of characters. There are, however, two alternative character-based species concepts that are compatible with the pattern cladistic view of systematics, depending upon whether one assumes that there is a lower boundary below which cladistic methods are invalid. Denying such a boundary leads to species being viewed as operational taxa composed of those individual organisms that, in a given analysis, are identical for all the characters under consideration (Vrana and Wheeler 1992). However, most proponents of the cladistic view assume that there is a lower bound below which characters are not distributed hierarchically [i.e., the boundary between phylogenetic and tokogenetic relationships (Hennig 1966)] and, thus, they consider species to be the least inclusive groups

that show hierarchic character distributions. This perspective seems to have led to the diagnostic approach discussed above, perhaps using the following reasoning. 1) Organisms are inappropriate as terminals in cladistic analyses (at least for sexuals) and, therefore, some collection of organisms ("population" or "lineage") must be used instead. 2) Only populations/lineages possessing fixed differences can be assumed to be hierarchically related. 3) Therefore, populations/lineages can be aggregated together until each aggregation has a fixed difference from all other such aggregations (e.g., Davis and Manos 1991; Davis and Nixon 1992). 4) Because these aggregations cannot be broken up using the evidence at hand, they are appropriate basal taxa, that is, species.

It seems that a character-based approach is consistent with the pattern cladistic view of systematics, but would a history-based species concept also be acceptable? Clearly, the answer is "no." A history-based definition, such as the genealogical species concept, makes a number of assumptions; for example, it assumes that evolution occurred and that we can use evolutionary theory to devise methods for reconstructing phylogenetic history. This conflicts with the pattern cladists' attempt to avoid assumptions and use only "theory-neutral" methodologies. The incompatibility of history-based concepts and pattern cladistics is amply demonstrated by the fact that history-based approaches imply the existence of species that cannot be discovered by reference to characters, which is unthinkable under pattern cladistics. Furthermore in pattern cladistics, taxa, and hence species, are defined based on operations performed on the data at hand (i.e., characters) and therefore, if they are to be delimited consistently, it is important that only one "discovery procedure" (parsimony) be admitted (Nelson 1989). In contrast, history-based species concepts permit evidence other than characters to enter into decisions about species delimitation. For example, information on the vagility of organisms and biogeography might be brought to bear in assessing whether an individual variant in a population originated in that population or represented gene flow from another population (i.e., distinguishing between the alternatives in Fig. 1). Furthermore, even when only characters are used, diverse methods of analysis can contribute to the evaluation of

a species hypothesis (e.g., maximum likelihood).

Species from an Evolutionary Phylogenetic Perspective. Under the evolutionary phylogenetic view [as exemplified by de Queiroz and Donoghue (1990), de Queiroz and Gauthier (1990), and de Queiroz (1992)] the goal is to discover historical entities that exist in the real world (i.e., have causes or are effects; Ereshefsky 1992) as inferred within an external theoretical framework including, but not limited to, current evolutionary theory. Taxa (including species) are viewed as monophyletic or exclusive groups of organisms and thus, by virtue of ancestry and descent and extinction of lineages, they exist independently of the occurrence of synapomorphies. Characters, under this view, are seen as a basis for hypothesizing taxon status and testing such hypotheses. Exactly how species and other taxa are to be defined historically remains to be seen, but the point here is that history-based species concepts are in principle compatible with an evolutionary phylogenetic approach to systematics.

Is a diagnostic or other character-based species concept compatible with phylogenetics? We think the answer is "no." Under an evolutionary phylogenetic perspective, systematists are concerned with describing evolutionary history and, therefore, it follows that the entities defined are those that gain their existence by virtue of history. Character-based approaches define species based on the distribution of characters among organisms (and/or populations) rather than on historical relationships and therefore must be rejected.

It could perhaps be argued that since the distribution of characters among organism is a product of evolutionary history, species concepts such as the diagnostic approach are in some sense history-based and therefore compatible with evolutionary phylogenetics. This argument is, however, fallacious because it is characters that give diagnostic species their existence, not history. Nonetheless, if it were the case that the diagnostic criterion succeeded infallibly in delimiting historically meaningful groups, then this point would be a mere philosophical quibble. If, on the other hand, diagnostic species can be shown to be non-historical groups in some cases, then an evolutionary phylogeneticist would have practical as well philosophical grounds for rejecting the diagnostic

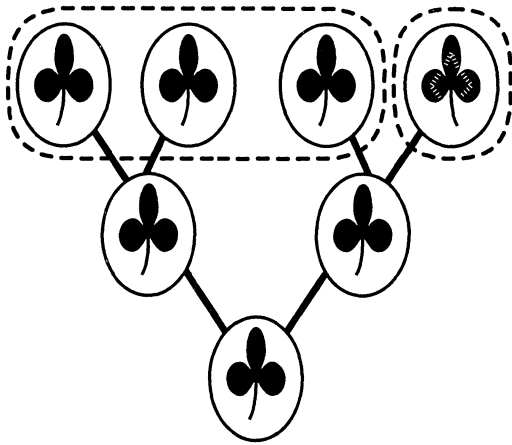


FIG. 5. A hypothetical example to illustrate the non-historical nature of diagnostic species. An ancestral *Trifolium* population has undergone a series of cladogenetic events. One of the four extant populations has become fixed for the presence of a light v-shaped mark on the leaves. Two diagnostic species must be delimited among the extant populations, one comprising individuals with marked and the other with unmarked leaves.

approach. For this reason it is important to evaluate the claim by Davis and Nixon (1992, p. 429) that: "if every phylogenetic species exhibits a unique combination of characters, each is an extended genealogical population, all of whose constituent individuals are historically related." This can be achieved by considering two examples.

Imagine an ancestral population of *Trifolium* with unmarked leaves, which gives rise to a number of isolated daughter populations through a series of cladogenetic events that are not marked by any discrete character evolution (Fig. 5). Note that the previous statement is possible only from an evolutionary phylogenetic perspective because, under pattern cladistics, cladogenesis does not occur without character evolution (Nixon and Wheeler 1992). Suppose that in one of the descendant populations a mutation occurs for the presence of a v-shaped mark on the leaves and that this mutation goes to fixation in this population (Fig. 5). Applying the diagnostic criterion described above, two *Trifolium* species would be recognized among the extant populations, one comprising all the unmarked clover populations (of which three are shown in Fig. 5) and the other comprising only the population with v-marked leaves.

In claiming that all individuals in diagnostic species are "historically related," Davis and Nixon (1992) are arguing that both the marked and unmarked clover "species" are composed of organisms that are "historically related" to each other. However, while it may be true that the members of the marked clover species are historically related (more information would be needed to apply the coalescent approach discussed above), it is clear that individuals with unmarked leaves are not historically related. The unmarked populations have no common history that is not also shared with the marked population and thus they constitute a group that is analogous to a paraphyletic higher taxon. Phylogenetic systematists should therefore agree that the unmarked clover "species" is not composed of "historically related" organisms under any substantive definition of that phrase.

A second example serves to emphasize further the possible non-historical nature of diagnostic species. Imagine an ancestral population of *Senecio* containing individuals with both rayed and rayless capitula (Fig. 6). This splits into two similarly polymorphic populations, but these daughter populations give rise to populations all of which are fixed for either the rayed or rayless form. Applying the diagnostic definition to the extant populations, two diagnostic species would have to be recognized, one composed entirely of rayed and the other of rayless individuals (Fig. 6). However, neither the rayed nor rayless species are composed of historically related individuals, each being analogous to a polyphyletic higher taxon (further information would be needed to determine which groups of populations, if any, are species using the coalescent approach presented above). It should be noted that recognition of two diagnostic species rests on the distribution of characters in the current populations and ignores information on when those characters became fixed. Thus, even if we had full knowledge that lineage sorting had occurred as depicted in Fig. 6, we would nonetheless have to recognize two species.

These two examples illustrate that, notwithstanding claims to the contrary, the diagnostic approach can lead to the recognition of species that lack historical meaning. This should not be surprising because there are many biological situations in which character distributions fail to track history. As well as the retention of ancestral characters and lineage sorting (illustrat-

ed with our hypothetical examples), strong local adaptation and introgressive hybridization can lead to groups that are historically unrelated but nonetheless manifest diagnostic characters. When such conflicts arise between history and characters, the diagnostic approach would give primacy to characters and, as a result, groups with fundamentally different historical structure (e.g., the "paraphyletic" and "monophyletic" *Trifolium*) are not conceptually discriminated. Since evolutionary phylogenetics is above all interested in reconstructing history, this view of systematics is incompatible with the diagnostic approach.

How To Choose a Species Concept. It should be clear from the foregoing arguments that we think the choice between history- and character-based species concepts rests critically on whether one takes a pattern cladistic or evolutionary phylogenetic view of systematics. Pattern cladistics demands a character-based concept (e.g., the diagnostic approach), whereas evolutionary phylogenetics demands a history-based concept (e.g., the coalescent approach).

We hold an evolutionary phylogenetic view, and therefore favor a history-based concept of species. Faced with the fact that we cannot know evolutionary history with certainty, we think that our concepts should at least be designed to inspire us to learn as much as possible about that history. The alternative reaction to this uncertainty—the one taken by pattern cladists—is to retreat to the false certainty of operationalism. Under this view we "know" only what we observe, and furthermore only those things that can be "observed directly" are admitted to exist at all. Retreats such as this have happened before in the history of systematics (e.g., phenetics), and in other branches of science, but these have ultimately seemed unsatisfactory (Hull 1968). We think that the reason for this is that scientists are interested in more than surface appearances, and instead want to learn how the world works. The decision not to look beyond the immediately observable is, in our view, fundamentally a decision not to engage in the scientific enterprise. We think that operational definitions of key terms such as species, by discouraging the attempt to penetrate surface appearances, impede our ability to learn about the world. They are simply not bold enough. Physicist have not been content to define electrons as clicks emitted by a Geiger-

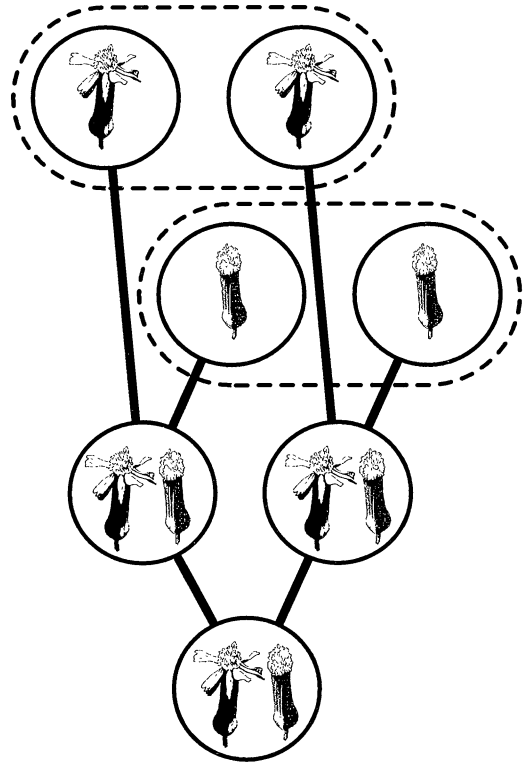


FIG. 6. A hypothetical example to illustrate the non-historical nature of diagnostic species. An ancestral *Senecio* population polymorphic for the presence of ray florets gave rise to two daughter populations each, likewise, polymorphic. These in turn gave rise to the four extant populations, all of which have become fixed for either rayed or rayless forms. Two diagnostic species must be delimited among the extant populations, one comprising individuals with rayed and the other with rayless capitula.

counter and neither should systematists be satisfied with defining species as things discovered using a particular procedure.

Notwithstanding our own preference for evolutionary phylogenetics, the main point of our paper is simply that one's general philosophy of systematics is the major consideration guiding the choice between alternative "phylogenetic" species concepts. In fact, we think the choice among species-concepts is made more-or-less automatically by deciding on the overall rationale for systematics. It is quite obvious, however, that many find it difficult to make **that** choice.

We suspect that many systematists hold no particular view of the philosophy of systemat-

ics, or hold a composite view to the effect that characters and history tend not to conflict in practice, so there is no need to decide which is more important. However, this inclination to "sit on the fence" in the debate between pattern cladistics and evolutionary phylogenetics certainly does not imply that such a position is tenable in the long run. In fact, because historical groups and character-based groups may often fail to coincide in nature, an intermediate or mixed position will serve only to perpetuate confusion about the ontology of taxa. The debate over alternative species concepts, while perhaps unseemly at times, is ultimately beneficial if it leads to a clarification of alternative philosophies of systematics and if systematists are compelled to confront the broader question of what they are trying to achieve.

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