

## Are many plant species paraphyletic?

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### *Summary*

Rieseberg, L. H. & Brouillet, L.: Are many plant species paraphyletic? – *Taxon* 43: 21-32. 1994. – ISSN 0040-0262.

The phylogenetic status of plant species has become a critical issue in systematic and evolutionary botany, due in part to the influence of Hennigian principles on organismal classification. This paper reviews various modes of speciation and their frequency in plants, and discusses predicted phylogenetic consequences of different modes of speciation. The classic model of allopatric speciation by subdivision will typically generate monophyletic daughter species, whereas most geographically local models of speciation (e.g., the founder effect model), will produce a paraphyletic progenitor and monophyletic derivative species. Due to the theoretical difficulty of transforming widespread population systems through gene flow or selection, allopatric speciation by subdivision is likely to be less frequent than geographically local models of speciation. Low levels of gene flow will also increase the time required for the progenitor species to achieve monophyly. Thus, many plant species are likely to be paraphyletic, and predictably a species classification based on the criterion of monophyly is unlikely to be an effective tool for describing and ordering biological diversity.

### *Introduction*

Species are fundamental entities in biology. They are the basic units of plant taxonomy and classification (Greuter & al., 1988; Davis & Heywood, 1963). Conservation biologists focus their efforts on species (e.g., Falk & Holsinger, 1991), as they are often considered to form the basis of biodiversity. To evolutionists, they represent a critical evolutionary unit, the genesis of new species, or speciation, constituting the only way to bring about the diversification of lineages (Mayr, 1969), while intraspecific processes foster adaptation and maintenance (Grant, 1963). The converse process, the winnowing of lineages or extinction, acts through disappearance of species, since genera and families go extinct when their last species disappears. Species also represent the basic unit of phylogenetic studies. Even where the phylogeny addresses higher categories (genera and above), cladistic analysis fundamentally reduces to determining the order of origin of ancestral species of the groups studied. There have been arguments concerning the monophyletic nature of species (e.g., Masters & Spencer, 1989; Frost & Hillis, 1990; Beckstrom-Sternberg & al., 1991), particularly in the cladistic literature (e.g., Cracraft, 1987; Mishler & Brandon, 1987; De Queiroz & Donoghue, 1988; Nelson, 1989; Theriot, 1992). Thus, it is pertinent to review briefly these arguments in light of the speciation patterns known to occur in nature. Our thesis is that species are often paraphyletic, speciation being fundamentally a paraphyletic process, and that operational assumptions should not be confused with biological reality. Only one or two decades ago this question may have been irrelevant in practice since the phylogenetic resolution provided by the characters in use at the time was insufficient for verifying the monophyly of most plant species. Due to the population-level resolution recently provided by molecular characters, however,

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it is now imperative to develop species concepts that integrate both biological and operational reality. We recognize, of course, that cladistic methods and cladistic terminology may be inappropriate below the species level for sexual taxa due to non-hierarchical patterns of evolution (Nixon & Wheeler, 1990). We have employed the terms herein (Table 1), however, in order to explore the effectiveness of phylogenetic methods for species circumscription.

### *Species concepts*

From an operational standpoint, the question of whether or not species are paraphyletic will depend on the species concept employed by the workers asking the question. If the autapomorphic species concept is accepted (Table 2), then a requirement for species status is monophyly, and the answer to this question must be no. For species concepts based on other criteria (Table 2), however, we can ask whether or not species will be monophyletic based on these criteria, although advocates of the phylogenetic species concept (Table 2; Cracraft, 1989) argue that the terms and concepts of monophyly, paraphyly, and polyphyly are not relevant when discussing single species (e.g., Nixon & Wheeler, 1990).

Several species concepts are based on interbreeding, reproductive isolating barriers or both (e.g., the biological, recognition, and unitary species concepts). The ability to interbreed, however, represents the plesiomorphic condition in most taxa (Donoghue, 1985), although components of isolating barriers may represent apomorphies. Thus, species defined on the basis of monophyly (i.e., synapomorphies) may not correlate well with species circumscribed based on the ability of populations to interbreed. Likewise, employment of species concepts based on morphological similarities or differences (e.g., the taxonomic and phenetic species concepts) may or may not result in monophyletic entities since no consideration is given to whether the morphological characters uniting or differentiating groups of populations are plesiomorphic or apomorphic. Species based on ecological differentiation (e.g., the ecological species concept) are unlikely to be monophyletic for these same reasons, as well as for the fact that parallel ecological adaptations appear to occur frequently among closely related plant populations, likely leading to polyphyletic ecospecies. Because the cohesion species concept incorporates aspects from most of the species concepts listed above, its use is unlikely to result always in the circumscription of monophyletic groups of populations. In contrast, the phylogenetic and evolutionary species concepts, like the autapomorphic species concept, recognize the importance of common descent as an important cohesive force, and many but not all species based on these concepts are likely to be strictly monophyletic.

Thus, it would seem that to answer correctly the question of whether or not species are often paraphyletic, we must first understand the nature of species and determine which species concept or concepts best describe the organization of biological diversity. This is not a simple question, given that some workers doubt whether species actually exist (e.g., Levin, 1979; Nelson, 1989), suggesting instead that species are purely conceptual and disconnected from nature. However, just because taxa are often difficult to define and circumscribe does not prove their non-existence in nature. Furthermore, most biologists appear to agree that there are real discontinuities in nature that can be designated as species (e.g., Gould, 1992; Mayr, 1988). In this paper, we assume that species are biologically real entities (Mayr, 1969, 1988) and feel they should be treated as such unless proven otherwise. Thus, we accept the

Table 1. Terminology

Term	Definition	Reference
monophyletic group	a group which includes an ancestor and all of its descendents	Donoghue & Cantino, 1988
metaphyletic group	an unresolved or undifferentiated group; i.e., a group which is neither paraphyletic or monophyletic	Donoghue & Cantino, 1988; Mishler, pers. comm.
paraphyletic group	a group which includes an ancestor and some but not all of its descendants	Donoghue & Cantino, 1988
polyphyletic group	a group in which the most recent common ancestor is assigned to some other group and not to the group itself	Ferris, 1974

view that species represent more natural or cohesive units than higher taxonomic categories (e.g., Mayr, 1942; Huxley, 1940; Dobzhansky, 1941), and believe that this argument is well-founded due to the larger number and greater strength of integrative evolutionary forces at the species level (e.g., gene flow, selection, drift, common descent, developmental constraints, etc.) than at higher taxonomic levels (but see Mishler & Donoghue, 1982, and Nelson, 1989, for alternative viewpoints).

Even if species are assumed to be real, the best way to “discover” or “characterize” them conceptually and operationally remains controversial. In general, workers have been searching for those evolutionary mechanisms that serve to integrate species. Thus rises the argument over whether gene flow/reproductive barriers or ecological similarities are more critical in maintaining species (e.g., Ehrlich & Raven, 1969; Van Valen, 1976; Andersson, 1990; Grant, 1992). It has been recognized recently that many species, particularly autogamous or asexual taxa, represent cohesive biological units due to descent from a common ancestor (monophyly) (e.g., Mishler & Budd, 1990; Levin, 1993; Theriot, 1992). Ironically, as pointed out by Mishler & Donoghue (1982) and Templeton (1989), all of these views are probably partially right, and a large number of evolutionary factors are likely responsible for species cohesion, with these factors varying in terms of their relative influence (or even existence) in different taxa. This has led to the development of the cohesive species concept (Templeton, 1989), which has attempted to integrate these different views. This concept is clearly difficult to implement from an operational standpoint and is unlikely to produce a universally consistent species classification in different groups because of this difficulty. Nonetheless, the recognition of the variety of different evolutionary forces responsible for species cohesion and their integration into working species concepts are important first steps toward a universal species concept.

### *Modes of speciation*

Modes of speciation traditionally have not been considered critical to the discussion or formulation of species concepts because it has generally been agreed that species must be definable on the basis of current patterns of variation and that knowledge of the evolutionary processes responsible for their origin should not be required for species circumscription. However, consideration of mode and frequency of speciation can lead to a better understanding of the nature of species and perhaps

Table 2. Species Concepts

Type	Definition	Reference
Biological	species are groups of interbreeding natural populations that are reproductively isolated from other such groups	Mayr, 1969: 314
Cohesion	the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability	Templeton, 1989: 25
Ecological	a species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from other such lineages	Van Valen, 1976: 233
Evolutionary	a single lineage of ancestral-descendent populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate	Wiley, 1978: 18
Phenetic	dense regions within a hyperdimensional environmental space	Sokal & Crovello, 1970: 150
Phylogenetic	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, 1989: 35
Autapomorphic	the least inclusive taxon recognized in a classification, into which organisms are grouped because of evidence of monophyly..., that is ranked as a species because it is the smallest 'important' lineage deemed worthy of formal recognition	Mishler & Brandon, 1987: as quoted in Mishler & Budd (1990)
Recognition	the most inclusive population of individual biparental organisms which share a common fertilization system	Paterson, 1985: as quoted in Templeton (1989)
Taxonomic	species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means	Cronquist, 1988: 71
Unitary	the most extensive units in the natural economy such that reproductive competition occurs among their parts	Ghiselin, 1974: 538

to the support or rejection of some species concepts, or even lead to the formulation of new definitions of species. Furthermore, the implementation of certain recent species concepts (e.g., the evolutionary and autapomorphic species concepts) requires some knowledge of the evolutionary history of populations. The purpose of this section is to review briefly the various modes of speciation in plants and to discuss the potential impact of this knowledge on current species concepts, the autapomorphic species concept in particular.

There is no single way in which speciation occurs, and many models of speciation have been developed. Nevertheless, modes of speciation are most frequently defined in terms of geographic distribution – allopatric, parapatric, and sympatric speciation being the most commonly discussed modes. Allopatric and parapatric speciation refer to differentiation between geographically separated and geographically con-

tiguous populations, respectively, whereas sympatric speciation refers to differentiation of a population completely within the dispersal range of the parent species.

Mayr (1942) argued that all speciation is allopatric, and this view has profoundly influenced the development of conceptual models for speciation. Although other modes of speciation are considered to be significant, allopatric speciation is generally considered to be the prevalent mode of speciation in plants (e.g., Grant, 1981; Stebbins, 1950) and animals (Mayr, 1963; White, 1978). There are three basic models of allopatric speciation. The best-known is allopatric speciation by subdivision (geographic speciation; Grant, 1981), where a population or population system is subdivided due to the development of geographic barriers. The geographically isolated population systems genetically diverge over time, sometimes resulting in reproductive isolation. A second type of allopatric speciation occurs via the extinction of intermediate populations in a chain of races. From a biological standpoint, however, this is not different from allopatric speciation by subdivision. A third model of allopatric speciation, which is profoundly different biologically from the first two, is allopatric speciation by founder effect (Carson, 1968; Templeton, 1980) or quantum speciation (Lewis, 1966; Grant, 1981). In this model, a small peripheral population undergoes a population crash, or a new area is colonized by one or several founding individuals. Inbreeding and genetic drift lead to the fixation of alleles different from those found in the parental populations, or at least lead to different allele frequencies.

The relative frequency of allopatric speciation by subdivision (the first two models) versus founder effect speciation is not clear. Both models appear plausible in plants. However, Raven (1980, 1986) suggests that gene flow is often too restricted to allow the transformation of geographic races as required for most models of geographic speciation (allopatric speciation by subdivision). This view is expanded by Levin (1993), who argues that geographically local speciation (founder effect, parapatric, sympatric) is the rule rather than the exception. He presents convincing evidence that the transformation of widespread geographic races of plants through either gene flow or uniform selection is theoretically difficult and thus unlikely. This view appears to contradict evidence from geographic distribution (Grant, 1981) and phylogenetic reconstructions (Lynch, 1989; Cracraft, 1982; Wiley & Mayden, 1985), which suggest that allopatric speciation by subdivision (or vicariance) is the predominant mechanism of speciation. As reasoned by Levin (1993), however, speciation in geographically marginal or disjunct isolates followed by range expansion could easily result in distribution patterns identical to those predicted by geographic speciation. Nonetheless, Levin (1993) does not rule out geographic speciation, and it seems likely that species with high effective population sizes and efficient mechanisms of seed or pollen dispersal, such as long-lived woody perennials (especially those with intercontinentally disjunct distributions), may often speciate by geographic subdivision, whereas local speciation is likely to be the rule for taxa with smaller effective population sizes and lower levels of gene flow, such as annual plants as well as perhaps entire island floras.

Other modes of speciation may be less common in plants, but should not be ignored. Parapatric speciation, for instance, has received relatively little consideration from botanists, but may play a significant role in speciation in some groups. White (1978) has proposed two models of parapatric speciation: clinal and area effect speciation. Clinal speciation is defined as differentiation between contiguous populations in a continuous cline and assumes that all geographic variation is distributed in

a clinal fashion. However, we know that this is not the case. In fact, many genetic investigations of wide ranging species with moderate or low dispersability have revealed the existence of area effects areas in which the genetic composition of the population or populations is strikingly different from that in the surrounding contiguous areas (e.g., Adams, 1975; Liston & al., 1989, 1992). Area effects appear to arise by population subdivision or by founder effect and subsequent range expansion. Thus, area effect speciation is mechanistically comparable to the two models of allopatric speciation discussed above and Levin's arguments in favor of local (founder effect) speciation versus speciation by geographic subdivision should be applicable here as well. The primary evidence for clinal and area effect speciation are the numerous examples of clines or area effects in plants. In addition, there are numerous instances where two species or geographic races are parapatric and hybridize or interbreed in areas of contact. We often do not know, however, whether the parapatric populations were once geographically isolated. Thus, it is difficult to estimate the actual frequency of these modes of speciation.

The third category of speciation, sympatric speciation, is undoubtedly the most controversial. In fact, some question its existence. For example, Mayr (1963) writes, "The same old arguments are cited again and again in favor of sympatric speciation, no matter how decisively they have been disposed of previously... Sympatric speciation is like the Lernaean Hydra which grew two new heads whenever one of its old heads was cut off...; the hypothesis is neither necessary nor supported by irrefutable facts." Botanists appear to share a similar opinion as indicated by Grant (1971): "Biogeographic evidence for primary sympatric speciation, unlike that of geographic quantum speciation, is lacking." A similar sentiment was held by Stebbins (1950) who writes, "The available factual evidence points toward the rarity of speciation without previous geographic isolation ... in plants just as in animals."

Nonetheless, a theoretical model for sympatric speciation based on strong disruptive selection was developed by Maynard-Smith (1966) and Dickinson & Antonovics (1973), and experiments with heavy metal tolerant plants have demonstrated that the model is theoretically feasible (Antonovics & Bradshaw, 1970). Unfortunately, proposed examples of this model in nature are difficult to verify. There is actually more evidence for other types of sympatric speciation, such as sympatric host race formation, allochronic speciation, the pollinator constancy model (Grant, 1949; Straw, 1955), breeding system changes, and hybridization and polyploidy. Host race formation has been studied primarily in animals (e.g., Bush, 1975a, 1975b), although it may occur infrequently in plants. The other four models of speciation are feasible in plants (e.g., Grant, 1949), but only the latter two have been verified (Gottlieb, 1973; Gallez & Gottlieb, 1982; Ownbey, 1950). Clearly, the most common of these is polyploid speciation, given that over 50 % of angiosperm species are thought to be polyploid (Grant, 1981). Although this number is not equivalent to the frequency of polyploid speciation, it does suggest polyploid speciation is a frequent and important component of plant evolution. The frequency of diploid hybrid speciation is much less clear, although a number of recent studies attest to the fact that this mode of speciation is important in some plant groups (e.g., *Helianthus*, Rieseberg, 1991; *Iris*, Arnold & al., 1990, 1991; *Stephanomeria*, Gallez & Gottlieb, 1982). Thus sympatric speciation cannot be considered a rare form of speciation in plants.

A final type of speciation that cannot be categorized in a geographical sense is asexual speciation. Asexual speciation has often been considered a contradiction in

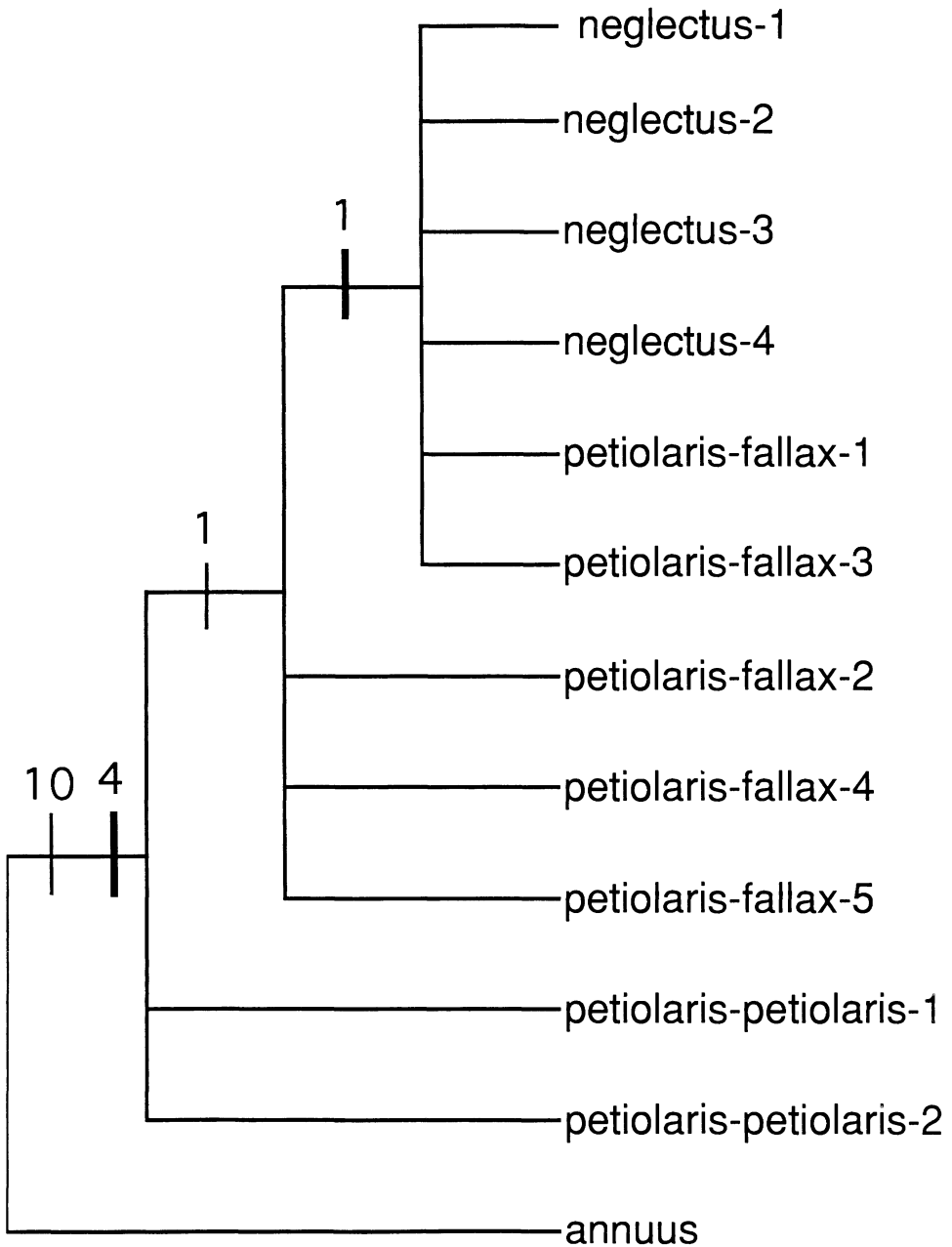


Fig. 1. Single shortest Wagner tree for populations of *Helianthus petiolaris* and its derivative species, *H. neglectus*, based on chloroplast and nuclear ribosomal DNA restriction site mutations (from Rieseberg & al., 1990; Rieseberg, 1991). *H. annuus* was employed as an outgroup. Chloroplast DNA mutations are indicated by the thick vertical bars, whereas ribosomal DNA mutations are indicated by thin vertical bars. Numbers above vertical bars indicate number of mutations represented by each bar. Consistency index = 1.0.

terms since many species concepts define species in terms of reproductive isolation or the ability to exchange genes. Asexual speciation is important, however, in certain groups of plants such as *Crepis*, *Poa*, *Rubus*, *Taraxacum*, etc., and this mode of speciation must be considered in discussions of species concepts. The actual significance of asexual speciation in angiosperms as a whole is more difficult to assess because so many plant species reproduce both sexually and asexually.

Although some modes of speciation are considerably more frequent than others in plants, all possibilities must be considered in terms of evaluating current concepts of species. The lack of sexual reproduction in asexual plants and the extensive hybridization observed in certain highly outcrossing plant groups immediately invalidate species concepts which rely wholly on interbreeding or reproductive barriers as species criteria. However, species concepts that are based on assumptions of common ancestry are also impacted by knowledge of speciation modes. Founder effect, area effect, and most models of sympatric speciation by definition generate a monophyletic derivative species and a paraphyletic or at least metaphyletic progenitor. That is, the derivative species is likely to share one or several apomorphies with the local population(s) from which it was derived. One example involves the origin of *Helianthus neglectus* from *H. petiolaris* (Rieseberg & al., 1990; Beckstrom-Sternberg & al., 1991). *H. petiolaris* is a widespread polytypic species occurring commonly in dry, sandy soils in the western U.S. and less frequently eastward. By contrast, *H. neglectus* is a rare taxon restricted to sandy soils in southeastern New Mexico and adjacent Texas. The two species can be distinguished by several morphological and chemical characters (Spring & Schilling, 1989) and are reproductively isolated due to a chromosomal sterility barrier (Heiser, 1958). Yet, *H. neglectus* possesses a subset of the allozymes and rDNA genotypes of *H. petiolaris* and has the same cpDNA haplotype as that found in two populations of *H. petiolaris* subsp. *fallax* – data suggesting that *H. neglectus* may be a recent derivative of *H. petiolaris* subsp. *fallax* so that *H. petiolaris* would be clearly paraphyletic (Fig. 1). In contrast, much of the lineage sorting (or lineage extinction) eventually leading to monophyly has probably been already completed in geographic speciation (Neigel & Avise, 1986). Diploid hybrid species and allopolyploids are classic examples of polyphyletic species in the sense that they combine the genomes of two differentiated species. One could speculate that at least 50 % of all plant species and, if Levin (1993) is correct, almost all plant species are products of geographically local speciation, and that close to one half of these are likely not to be monophyletic. Moreover, this figure does not include taxa which are polyphyletic in the classical sense. That is, species that originated on more than one instance (e.g., Soltis & Soltis, 1989, 1991), a phenomenon that is probably relatively common for all of the modes of speciation discussed here. Although the concept of a polyphyletic species is difficult to accept for most phylogenists, the recognized operation of cohesive forces other than common descent within species is consistent with the polyphyletic origin of a species. Thus, we argue that species concepts that insist on monophyly are inadequate for a significant proportion of plant species.

#### *Time to monophyly*

If most plant speciation represents some type of progenitor/derivative situation, then the ancestor and in the short term, the derivative species will not represent

monophyletic lineages (Neigel & Avise, 1986). Monophyly may be obtained over time, however, via the sorting and extinction of lineages. The question that needs to be addressed then is how long will it take the two taxa to achieve monophyly (Levin, 1993). This situation has been modelled for the maternally inherited cytoplasmic genomes (mtDNA and cpDNA) by Neigel & Avise (1986) based on different modes of speciation. As predicted, mode of speciation did influence the phylogenetic status of related species. Related species generated by the geographic speciation model (modes 2a and 2b in Neigel & Avise, 1986) were likely to be monophyletic, whereas speciation by founder effect (mode 1 speciation; Neigel & Avise, 1986) followed a common time-course of change subsequent to speciation of polyphyly->paraphyly->monophyly. For a short time period ( $N$  generations; where  $N$  = the carrying capacity of the larger daughter species) the two species would be polyphyletic in terms of maternal ancestry, whereas, after an intermediate period of time ( $N$  to  $4N$  generations), paraphyly is likely. A much greater period of time would be required for both species to achieve monophyly in terms of maternal ancestry ( $4N$  generations). It should be pointed out that the time to achieve monophyly would be even greater for nuclear genes, whose effective population size is four times that of cytoplasmic genes (Birky, 1988). A number of other factors will affect time to monophyly in the progenitor species, including geographic range, levels of geographic differentiation, selection, levels of gene flow, rate of population extinction, rate of population expansion, etc. Given the low levels of gene flow (Levin, 1984) and significant geographic differentiation reported for many plant species (Crawford, 1990), monophyly for most nuclear genes is predicted to be difficult to achieve in all but the most ancient progenitor species, which may partially explain the difficulty of finding species-specific nuclear markers in sister species of plants (e.g., Rieseberg & al., 1991). Species monophyly will not be attained until at least one detectable nuclear apomorphy is fixed in all populations. Although this is somewhat difficult theoretically, it is even more difficult operationally due to sampling limitations. Finally, predictions of paraphyly in the progenitor of known progenitor/derivative species pairs have been documented empirically based on isozyme markers (e.g., Gottlieb, 1973, 1974; Crawford, 1985; Rieseberg & al., 1987), as well as in terms of maternal ancestry (e.g., Rieseberg & al., 1990; Fig. 1). These paraphyletic situations are likely to be discovered for much more ancient progenitor/derivative species pairs as nuclear sequence data are obtained from low-copy-number nuclear genes.

### *Conclusions*

Proponents of the autapomorphic species concept are well aware of the problem of progenitor or ancestral taxa (e.g., Mishler & Brandon, 1987; Donoghue & Cantino, 1988). They note that ancestral populations will often lack autapomorphies and thus will not be assignable to a species. To remedy this problem, they propose that these unresolved entities of unknown phylogenetic status be termed "metaspecies" (Table 1). Demonstrably paraphyletic ancestral populations or species are considered to be very rare, although their existence is recognized (Donoghue & Cantino, 1988). Advocates of the autapomorphic species concept differ with regard to how demonstrably paraphyletic ancestral populations or taxa should be classified.

As discussed above, we clearly disagree with the view that paraphyletic species are uncommon in plants. Rather, we argue that species derived through some type of

local speciation will follow a common sequence of polyphyly->paraphyly->monophyly. Only ancestral species with extremely high gene flow levels and/or little to no differentiation among populations (a rare situation in plants as noted by Levin, 1984) will be truly unresolvable. In almost all other cases, given adequate study of sufficiently rapidly evolving gene sequences, the actual stage in a species route from polyphyly to monophyly should be diagnosable (e.g., Fig. 1). Thus, rather than insisting on a criterion of monophyly for species recognition, it would be more logical to view the phylogenetic status of a species as a property that will vary over time. For example, although *Helianthus petiolaris* (Fig. 1) is currently a paraphyletic species, if examined 100,000 years from now it might very well have achieved monophyly. From our perspective, the efforts of species biologists would be better spent studying the evolutionary and historical forces that lead to variation in the phylogenetic status of species within and among major taxonomic groups rather than arguing about whether species are monophyletic groups.

#### Acknowledgements

We wish to thank P. Fritsch, E. Knox, B. Mishler, C. T. Philbrick, Ward Watt, and two anonymous reviewers for constructive comments (not necessarily favorable) on an earlier version of this manuscript. The research on *Helianthus* discussed in this paper was supported by grants to LHR from the National Science Foundation.

#### Literature cited

- Adams, R. P. 1975. Gene flow versus selection pressure and ancestral differentiation in the composition of species: analysis of populational variation of *Juniperus ashei* Buch. using terpenoid data. *J. Molec. Evol.* 5: 177-185.
- Andersson, L. 1990. The driving force: species concepts and ecology. *Taxon* 39: 375-382.
- Antonovics, J. & Bradshaw, A. C. 1970. Evolution in closely related plant populations, VIII: Clinal patterns at a mine boundary. *Heredity* 25: 349-362.
- Arnold, M. L., Buckner, C. M. & Robinson, J. J. 1991. Pollen-mediated introgression and hybrid speciation in the Louisiana irises. *Proc. Natl. Acad. Sci. U.S.A.* 88: 1389-1402.
- , Hamrick, J. L. & Bennett, B. D. 1990. Allozyme variation in Louisiana irises: a test for introgression and hybrid speciation. *Heredity* 65: 297-306.
- Beckstrom-Sternberg, S. M., Rieseberg, L. H. & Doan, K. 1991. Gene lineage analysis in populations of *Helianthus niveus* and *H. petiolaris*. *Pl. Syst. Evol.* 175: 125-138.
- Birky, C. W. 1988. Evolution and variation in plant chloroplast and mitochondrial genomes. Pp. 23-53 in: Gottlieb, L. D. & Jain, S. K. (ed.), *Plant evolutionary biology*. London.
- Bush, G. L. 1975a. Modes of animal speciation. *Annual Rev. Ecol. Syst.* 6: 364-399.
- 1975b. Sympatric speciation in phytophagous parasitic insects. Pp. 187-296 in: Price, P. W. (ed.), *Evolutionary strategies of parasitic insects and mites*. London.
- Carson, H. L. 1968. The population flush and its genetic consequences. Pp. 123-137 in: Lewontin, R. C. (ed.), *Population biology and evolution*. Syracuse, NY.
- Cracraft, J. 1982. Geographic differentiation, cladistics and biogeography: reconstructing the tempo and mode of evolution. *Amer. Zoologist* 22: 411-424.
- 1987. Species concepts and the ontology of evolution. *Biol. & Philos.* 2: 329-346.
- 1989. Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. Pp. 28-59 in: Otte, D. & Endler, J. A. (ed.), *Speciation and its consequences*. Sunderland, MA.
- Crawford, D. J. 1985. Electrophoretic evidence and plant speciation. *Syst. Bot.* 10: 405-416.
- 1990. *Plant molecular systematics*. New York.
- Cronquist, A. 1988. *The evolution and classification of flowering plants*, ed. 2. New York.
- Davis, P. H. & Heywood, V. H. 1963. Principles of angiosperm taxonomy. London.

- De Queiroz, K. & Donoghue, M. J. 1988. Phylogenetic systematics and the species problem. *Cladistics* 4: 317-338.
- Dickinson, H. & Antonovics, J. 1973. Theoretical considerations of sympatric divergence. *Amer. Naturalist* 107: 256-274.
- Dobzhansky, T. 1941. *Genetics and the origin of species*, ed. 2. New York.
- Donoghue, M. J. 1985. A critique of the biological species concept and recommendations for a phylogenetic alternative. *Bryologist* 88: 172-181.
- & Cantino, P. D. 1988. Paraphyly, ancestors, and the goals of taxonomy: a botanical defense of cladism. *Bot. Rev. (Lancaster)* 54: 107-128.
- Ehrlich, P. R. & Raven, P. H. 1969. Differentiation of populations. *Science* 165: 1228-1232.
- Falk, D. A. & Holsinger, K. E. (ed.) 1991. *Genetics and conservation of rare plants*. New York.
- Farris, J. S. 1974. Formal definitions of paraphyly and polyphyly. *Syst. Zool.* 23: 548-554.
- Frost, D. R. & Hillis, D. M. 1990. Species concepts and practice: herpetological applications. *Herpetologia* 46: 87-104.
- Gallez, G. P. & Gottlieb, L. D. 1982. Genetic evidence for the hybrid origin of the diploid plant *Stephanomeria diegensis*. *Evolution* 36: 1158-1167.
- Ghiselin, M. T. 1974. A radical solution to the species problem. *Syst. Zool.* 23: 536-544.
- Gottlieb, L. D. 1973. Genetic differentiation, sympatric speciation and the origin of a diploid species of *Stephanomeria*. *Amer. J. Bot.* 60: 545-553.
- 1974. Genetic confirmation of the origin of *Clarkia lingulata*. *Evolution* 28: 244-250.
- Gould, S. J. 1992. What is a species? *Discover* 1992(Dec.): 40-42.
- Grant, V. 1949. Pollination systems as isolating mechanisms. *Evolution* 3: 82-97.
- 1963. *The origin of adaptations*. New York.
- 1971, 1981. *Plant speciation*, ed. 1, ed. 2. New York.
- 1992. Comments on the ecological species concept. *Taxon* 41: 310-312.
- Greuter, W., Burdet, H. M., Chaloner, W. G., Demoulin, V., Grolle, R., Hawksworth, D. L., Nicolson, D. H., Silva, P. C., Stafleu, F. A., Voss, E. G. & McNeill, J. (ed.), 1988. International code of botanical nomenclature, adopted by the Fourteenth International Botanical Congress, Berlin, July-August 1987. *Regnum Veg.* 118.
- Heiser, C. B. 1958. Three new annual sunflowers (*Helianthus*) from the southwestern United States. *Rhodora* 60: 272-283.
- Huxley, J. S. 1940. *The new systematics*. Oxford.
- Levin, D. A. 1979. The nature of plant species. *Science* 204: 381-384.
- 1984. Immigration in plants: an exercise in the subjunctive. Pp. 242-260 in: Dirzo, R. & Sarukhan, J. (ed.), *Perspectives on plant population ecology*. Sunderland, MA.
- 1993. Local speciation in plants: the rule, not the exception. *Syst. Bot.* 18: 197-208.
- Lewis, H. 1966. Speciation in flowering plants. *Science* 152: 167-172.
- Liston, A., Rieseberg, L. H. & Elias, T. S. 1989. Molecular divergence and morphological stasis in the intercontinental disjunct, *Datisca* (*Datisceae*). *Aliso* 12: 525-542.
- , – , & Hanson, M. A. 1992. Geographic partitioning of chloroplast DNA variation in the genus *Datisca* (*Datisceae*). *Pl. Syst. Eol.* 181: 121-132.
- Lynch, J. D. 1989. The gauge of speciation: on the frequencies of modes of speciation. Pp. 527-553 in: Otte, D. & Endler, J. A. (ed.), *Speciation and its consequences*. Sunderland, MA.
- Masters, J. C. & Spencer, H. G. 1989. Why we need a new genetic species concept. *Syst. Zool.* 38: 270-279.
- Maynard-Smith, J. 1966. Sympatric speciation. *Amer. Nat.* 100: 637-650.
- Mayr, E. 1942. *Systematics and the origin of species*. New York.
- 1963. *Animal species and evolution*. Cambridge, MA.
- 1969. The biological meaning of species. *Bot. J. Linn. Soc.* 1: 311-320.
- 1988. *Toward a new philosophy of biology*. Cambridge, MA.
- Mishler, B. D. & Brandon, R. N. 1987. Individuality, pluralism and the biological species concept. *Biol. & Philos.* 2: 397-414.

- & Budd, A. F. 1990. Species and evolution in clonal organisms – Introduction. *Syst. Bot.* 15: 79-85.
- & Donoghue, M. J. 1982. Species concepts: a case for pluralism. *Syst. Zool.* 31: 491-503.
- Neigel, J. E. & Avise, J. C. 1986. Phylogenetic relationships of mitochondrial DNA under various demographic models of speciation. Pp. 515-534 in: Karlin, S. & Nevo, E. (ed.), *Evolutionary processes and theory*. New York
- Nelson, G. 1989. Species and taxa: systematics and evolution. Pp. 60-81 in: Otte, D. & Endler, J. A. (ed.), *Speciation and its consequences*. Sunderland, MA.
- Nixon, K. C. & Wheeler, Q. D. 1990. An amplification of the phylogenetic species concept. *Cladistics* 3: 201-209.
- Ownbey, F. M. 1950. Natural hybridization and amphiploidy in the genus *Tragopogon*. *Amer. J. Bot.* 37: 487-499.
- Paterson, H. E. H. 1985. The recognition concept of species. Pp. 21-29 in: Vrba, E. E. (ed.), *Species and speciation*. [Transvaal Museum Monograph, 4.] Pretoria.
- Raven, P. H. 1980. Hybridization and the nature of plant species. *Bull. Canad. Bot. Assoc. Suppl.*: 13, 3-10.
- 1986. Modern aspects of the biological species in plants. Pp. 11-29 in: Iwatsuki, K., Raven, P. H. & Bock, W. J. (ed.), *Modern aspects of species*. Tokyo.
- Rieseberg, L. H. 1991. Homoploid reticulate evolution in *Helianthus* (*Asteraceae*): evidence from ribosomal genes. *Amer. J. Bot.* 78: 1218-1237.
- , Beckstrom-Sternberg, S., Liston, A. & Arias, D. M. 1991. Phylogenetic and systematic inferences from chloroplast DNA and isozyme variation in *Helianthus* sect. *Helianthus* (*Asteraceae*). *Syst. Bot.* 16: 50-76.
- , Carter, R. & Zona, S. 1990. Molecular tests of the hypothesized hybrid origin of two diploid *Helianthus* species (*Asteraceae*). *Evolution* 44: 1498-1511.
- & Peterson, P. M., Soltis, D. E., & Annable, C. R. 1987. Genetic divergence and isozyme number variation among four varieties of *Allium douglasii* (*Alliaceae*). *Amer. J. Bot.* 74: 1614-1624.
- Sokal, R. R. & Crovello, T. 1970. The biological species concept: a critical evaluation. *Amer. Naturalist* 104: 127-153.
- Soltis, P. S. & Soltis, D. E. 1989. Allopolyploid speciation in *Tragopogon*: insights from chloroplast DNA. *Amer. J. Bot.* 76: 1119-1124.
- & – 1991. Multiple origins of the allotetraploid *Tragopogon mirus* (*Compositae*): rDNA evidence. *Syst. Bot.* 16: 407-413.
- Spring, O. & Schilling, E. E. 1989. The sesquiterpene lactone chemistry of *Helianthus* (*Asteraceae*). Part II: The annual species of *Helianthus*. *Biochem. Syst. Ecol.* 17: 535-539.
- Stebbins, G. L. 1950. *Variation and evolution in plants*. New York.
- Straw, R. M. 1955. Hybridization, homogamy, and sympatric speciation. *Evolution* 9: 441-444.
- Templeton, A. R. 1980. The theory of speciation via the founder principle. *Genetics* 94: 1011-1038.
- 1989. The meaning of species and speciation: a genetic perspective. Pp. 3-27 in: Otte, D. & Endler, J. A. (ed.), *Speciation and its consequences*. Sunderland, MA.
- Theriot, E. 1992. Clusters, species concepts, and morphological evolution of diatoms. *Syst. Biol.* 41: 141-157.
- Van Valen, L. 1976. Ecological species, mutispecies, and oaks. *Taxon* 25: 233-239.
- White, M. J. D. 1978. *Modes of speciation*. San Francisco.
- Wiley, E. O. 1978. The evolutionary species concept reconsidered. *Syst. Zool.* 27: 17-26.
- & Mayden, R. L. 1985. Species and speciation in phylogenetic systematics, with examples from the North American fish fauna. *Ann. Missouri Bot. Gard.* 72: 596-635.

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