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## The Morphological, Developmental, and Phylogenetic Basis of Species Concepts in Bryophytes

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**Abstract.** *This paper examines the theoretical and practical status of species relative to two major issues: the recognition of the importance of epigenetic constraints in evolution and the rise of Hennigian phylogenetic systematics (cladistics). Theories advanced to explain the origin and maintenance of basic morphological clusters of organisms (species) have usually involved two main classes of causal factors: selection (ecological constraints) and gene flow (breeding barriers vs. the integrating effect of gene exchange). However, in many plants non-correspondence of patterns of discontinuities among basic morphological, ecological, and breeding groups has been noted. The “biological species concept” is flawed because it is biased towards explanations at the genetic level. A third class of causal factors (epigenetic constraints) has come into favor as an explanation for the distinctness of higher-level morphological clusters, but the relevance of epigenetic factors as primary constraints on morphological variation at the species level remains to be examined. A phylogenetic species concept is advocated, which views species as monophyletic groups of organisms, the smallest such groups recognized in a formal classification. Assignment of species rank to a particular group should depend on the causal factors acting to maintain that group as an independent lineage. Epigenetic constraints may prove to be the most important factor producing and maintaining species lineages. Bryophytes are useful organisms for investigating this question because they are readily manipulated under experimental conditions, both sexual and asexual species exist, and a diversity of ecological and geographic specificities are known.*

What are basic kinds in systematic and evolutionary biology? Since the Darwinian Revolution, biologists have been struggling to arrive at a concept of species in order to explain morphological discontinuities in terms of the dynamic process of evolution. This debate has not been resolved. Botanists and zoologists, phyleticists and pheneticists, paleontologists and population geneticists, philosophers and practitioners have yet to reach a consensus.

Simple observation shows that the diversity of the natural world is not continuous. Organic variation usually falls into clusters or nodes, which are often structured hierarchically into progressively more inclusive clusters. The central problem of systematic biology is to document these patterns; the central problem of evolutionary biology is to determine what processes are responsible for stasis or change in these nodes. Clearly, the units recognized by systematists must be the units involved in processes studied by evolutionists if the work of these two fields is to be mutually relevant. Therefore, it is important to examine carefully the status of species, a category often held to be unique and fundamental by both systematists and evolutionists.

A diversity of views on the meaning of species exists (for reviews see Mayr 1957; Wiley 1978). Yet it seems that the prevailing species concept among

systematists, ecologists, and evolutionists (especially zoologists) is some version of the biological/evolutionary species concept (Simpson 1961; Mayr 1970) or the “species as individual” concept as developed by Ghiselin (1974) and Hull (1976, 1980). In this view species taxa are seen as fundamentally and universally different from taxa at all other levels: real, genetically integrated, cohesive, and comparable units of evolution.

The acceptance of the biological or evolutionary species concept has certainly not been universal among botanists (Mishler & Donoghue 1982). Some botanists, especially cytologists (e.g., Stebbins 1950, 1979) advocate a biological species concept based on discontinuities in gene flow. However, many botanists favor a morphological (i.e., phenetic) species concept (e.g., Cronquist 1978; Levin 1979). However, neither of these concepts is appropriate for recognizing theoretically meaningful taxa.

Mishler and Donoghue (1982) presented empirical and theoretical arguments to indicate that current biological or evolutionary species concepts are oversimplified (see also Donoghue, this symposium). They concluded that no single and universal basic evolutionary unit exists and that in most cases species taxa have no special reality in nature. Furthermore, criteria for what constitutes an “impor-

tant" discontinuity appear to depend on differences in the biology of different groups of organisms. Causal factors responsible for the existence of morphologically distinct species seem to be fundamentally different in different groups. It was suggested that a more pluralistic concept of species is needed to reflect adequately the variety and complexity of "species situations."

In the present paper I attempt to weave together two theoretical strands. The first relates to the general debate in systematics over what taxonomic names should represent. Even among Hennigian phylogenetic systematists a diversity of species concepts has been or is being espoused. While this school of thought is presenting a strong challenge to traditional "evolutionary systematics," there has been inadequate discussion of the fundamental taxonomic level of species. The second strand involves the debate over the relative importance of various evolutionary forces acting to constrain morphological variation over time. Growing realization of the importance of epigenetic constraints in evolution is another element in an increasingly coherent challenge to the neo-Darwinian "modern synthesis." However, whether epigenetic factors act as constraints on morphological variation at the species level remains to be examined.

This discussion will of necessity be generalized because the application and meaning of the species category remains problematical in all major groups of organisms. However, in keeping with the theme of the symposium, I will refer primarily to bryophytes (especially to the moss *Tortula*) for examples. What is special about the species situation in bryophytes? Conversely, how can bryophytes illustrate issues of general biological interest with respect to the species problem?

#### THE SPECIES CATEGORY AND HENNIGIAN PHYLOGENETIC SYSTEMATICS: ONTOLOGY AND PHYLOGENY

The past two decades have seen the rise of Hennigian phylogenetic systematics or cladistics. This method arose as a reaction to the traditional, subjective "evolutionary systematics" and to the more recent indiscriminate grouping by overall similarity advocated by the numerical phenetics school. The application of Hennigian cladistics to bryology was discussed by Mishler and Churchill (1984); see Wiley (1981) for further details.

Two important ideas contributed by Hennig (1966) were the recognition of the importance of using shared derived characters for reconstructing phylogeny and the restriction of the concept of

monophyly to those groups that contain all and only descendants of a common ancestor.

Within the Hennigian school a diversity of species concepts are advocated, none of which fully deals with the application of Hennigian ideas such as monophyly to the species category. Hennig (1966) advocated the biological species concept in his work. As expressed by Mayr (1970), biological species "are groups of interbreeding natural populations that are reproductively isolated from other such groups."

Nelson and Platnick (1981) devoted only a few paragraphs to the species category. They define species as "simply the smallest detected samples of self-perpetuating organisms that have unique sets of characters," then go on to stress that a species need not have any single unique trait—only a unique, diagnosable combination of characters. They make a distinction between "species" and "groups of species." As Platnick (1985) has elaborated, the latter *do* need to have apomorphies. However, a basic concept (such as "species") that fills an ontological role in a theoretical system cannot be chosen arbitrarily and independent of the theoretical system in which it occurs. Since Nelson and Platnick are not enthusiastic about current evolutionary theory, it is perhaps understandable that they do not frame and justify their species concept in terms of that theory. However, their concept seems inadequately justified even in terms of the theoretical system in which they work. There is no explicit connection to the general concept of taxa as lineages, and there is also nothing to distinguish their concept from those proposed by pheneticists. The use of phenetic species in cladistic and biogeographic analyses is an important internal conflict. A phenetic species concept at best can serve as a first approximation of basal cladistic units in a phylogenetic analysis, but the concept of species needed for phylogenetic systematics must be richer in content.

Rosen (1979) has defined species as a "population or group of populations defined by one or more apomorphous features . . . the smallest natural aggregation of individuals with a specifiable geographic integrity that can be defined by any current set of analytical techniques." This definition, in contrast to that of Nelson and Platnick is consistent with the systematic and biogeographic theories of the author. However, it is atomistic, tending towards the recognition of individual organisms or family groups as Linnaean species (Hill & Crane 1982; Mishler & Donoghue 1982). It is important to recognize that concepts of phylogenetic taxa (including species) must include two components, a grouping criterion (e.g., monophyly) *and* a ranking criterion (see Donoghue, this symposium). Rosen's definition has a criterion that can be used to group

organisms, but the criterion for ranking is vague. I will return later to this distinction and to the question of just what these ranking criteria should be in phylogenetic systematics.

Eldredge and Cracraft (1980) defined species as: "a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind." While this definition out of context may not be clear, since all would accept that there *is* a pattern of ancestry and descent beyond the species level, reference to the discussion in Eldredge and Cracraft (1980) will show that the concept being advocated is more or less the standard biological species concept. However, Cracraft (1982) has more recently presented a view of species similar to that of Nelson and Platnick (1981).

As a modification of Simpson's (1961) evolutionary species concept Wiley (1981: 25) has presented the following species definition: "a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." I find this concept to be the most compelling so far advocated by cladists because it provides an explicit statement of species as lineages. However, this concept is similar to the biological species concept in its usual emphasis on genetic discontinuity and in that it views the species category as unique and fundamental (a view that I argue is not generally the case).

Taken as a whole, the various concepts of species held by cladists span almost the whole range of diversity of species concepts held by systematists generally. However, these cladistic species concepts have features in common. All (except for Rosen's concept) make a clear distinction between species and groups of species (i.e., higher taxa) and do not apply an unequivocal, cladistic concept of monophyly (i.e., the recognition of monophyly by apomorphies) to the species level. This distinction is also made by Hill and Crane (1982) who contrast cladistic species (as evidenced by apomorphies) with "real" species (as evidenced by genetic isolation) and point out that there is no necessary congruence between the two.

There are also substantial differences among the species concepts discussed above. What species concept is adopted matters theoretically because of the central role of the species concept and of species in biology and practically because systematists with differing views of species will often treat the same situation in different ways. Terms such as "species" have a necessary relationship to theories in which they are embedded (Hull 1981). As Hull (1968,

1981), Beatty (1982), Lewontin (1974), Hennig (1966), and others have pointed out, progress in understanding the world comes as we build an elaborate theoretical structure by iteratively matching together lower-level theories (such as species concepts and classifications) with higher-level theories (such as evolutionary theory). The question of definition or meaning of a basic term such as species is thus embedded in both lower-level and higher-level causal theories. Empirical considerations enter in the low-level matching of observation and theoretical concept; ontological considerations enter in because of the function of such basic terms in higher-level explanatory theories.

Despite the many problems with details, the theory of evolution (descent with modification) unquestionably remains the primary overarching theoretical structure for comparative biology and provides both the justification and motivation for the development of phylogenetic systematics. Concepts of species must be evaluated in terms of the role these concepts play in evolutionary theory as well as by their fit to observed patterns of variation among organisms.

The evolutionary species concept as developed by Wiley and others fails to fit observed empirical patterns in many groups of organisms (Mishler & Donoghue 1982). There are two main conclusions drawn by Mishler and Donoghue which, if true, have important implications for phylogenetic systematics. The first is the notion that species often have no special reality as compared to taxa at other levels within a clade. The second is that the causal factors responsible for differentiation at the species level seem to be fundamentally different in different groups.

The first conclusion conflicts with the current distinction between "species" and "groups of species," which figures importantly in cladistic concepts of monophyly, ancestor-descendant relationships, and the supposed difference between cladograms and trees. Since (contrary to Wiley 1981) species cannot be taken as a priori monophyletic, cladistic theory must expand and develop meaningful concepts of monophyly at the species level. The task of developing a revised definition of monophyly that is applicable to the species category (which is necessary because Hennigian monophyly is traditionally defined with reference to origin of a taxon in a single species) is beyond the scope of the present paper. In short monophyly should be viewed as involving a single origin of a taxon. In the case of species this means single origin in one population or even one individual organism.

Particularly controversial situations that must be faced by a strict phylogenetic species concept are

the apparently frequent cases of incongruence between cladistically discrete groups and genetically discrete groups (biological species) (Bremer & Wanntorp 1979; Hill & Crane 1982). As pointed out by Rosen (1979), biological species may often be united only by a plesiomorphy, reproductive compatibility. A solution favored in these situations by Wiley (1981, and pers. comm.) and Hill and Crane (1982) is to name as species the genetically interconnected groups. In my opinion, however, this would obscure the important pattern. The fact that cladistic structure can be observed in the face of potential or actual gene flow is an indication that other causal factors are operating and a good reason to name as species the cladistically distinct groups. I favor applying Hennigian principles of classification to the use of Linnaean binomials, reserving the formal taxon, species, for minimally "important" phylogenetic units as evidenced by apomorphies. In this context "important" refers to ranking criteria.

The generally unrecognized distinction between the grouping and ranking components of a species concept is critical (see also discussion by Donoghue, this symposium). All species concepts have both components. For example, in the biological species concept the grouping criterion is having the ability to interbreed; the ranking criterion is being the most inclusive group having that ability. Even when monophyletic groups (*sensu* Hennig) are delimited the problem of ranking remains because monophyletic groups can be found at many levels within a clade. Species *ranking* criteria could include morphological gap size (i.e., morphological distinctiveness), ecological or geographical criteria, degree of intersterility, and possibly others. The general problem of ranking is presently unresolved. I contend that an absolute and universally applicable criterion is not possible and that criteria will have to be developed on a group by group basis with reference to causal factors that are important in maintaining lineages in particular groups. The *grouping* concept, monophyly, should be retained as a universal component of the species concept until it can be shown empirically that other concepts of grouping are needed (which may indeed be the case in groups such as bacteria).

#### AN EPIGENETIC VIEW OF THE SPECIES CATEGORY: ONTOGENY AND PLURALITY

A renewal of interest in the relationship between development and evolution has taken place in evolutionary biology. Darwin's mysterious "laws of correlation of characters" did not figure prominently in the modern synthesis of evolutionary theory fashioned in the 1930s and 40s despite Waddington's (1957) striking analogy of a developmental

landscape. [See Gould (1980) for a general discussion of current challenges to the "modern synthesis," which hardened in the late 1940s and 50s into a strongly reductionistic, genetically based theory.]

Of particular relevance here are recent attempts to discover and define developmental or epigenetic constraints on patterns of morphological form (Ho & Saunders 1979; Alberch 1980, 1982; Rachootin & Thomson 1981; Oster & Alberch 1982). The general theme of these investigations is the existence of complex epigenetic programs that translate the genotype into the phenotype. These epigenetic rules insure that a one-to-one matching between a particular sequence of DNA and a particular phenotypic feature is unusual. Thus, certain phenotypes are prohibited or are unlikely, and continuous genetic change can result in discontinuous epigenetic changes.

The possible role of epigenetic factors as primary constraints on morphological variation at the species level has only been mentioned in passing (Eldredge & Gould 1972). In my opinion an important internal conflict is created when workers such as Gould (1979) and Eldredge and Cracraft (1980) defend the strongly reductionistic, genetically based biological species concept at the same time they are advocating a critical reexamination of the modern synthesis. The newly developing macroevolutionary theory relies strongly on a hierarchical view of evolution (Gould 1980; Eldredge & Cracraft 1980), but the biological species concept is not necessary (in fact, it may even be harmful) for this view.

The debate about the differentiation or stasis of populations and species has so far primarily been a comparison of two classes of causal factors, gene flow and selection (Ehrlich & Raven 1969; Jackson & Pounds 1979; Ehrlich & White 1980; Pounds & Jackson 1982). Neither position seems to provide a satisfactory explanation for many situations in plants. As pointed out by Grant (1980: 167), "the homogeneity of species is due more to descent from a common ancestor than to gene exchange across significant parts of the species area." Of course, this well-justified conclusion by itself does not provide an explanation for the homogeneity of species; the addition of a third class of causal factors, epigenetic constraints, is necessary.

It is well known that morphological variation is often poorly connected to genetic variation in plants. In some cases small genetic changes can lead to major morphological changes (Gottlieb 1984); in other cases large genetic changes result in little or no morphological difference. Examples of the latter are provided by single morphological species with a variable chromosome number (e.g., *Sedum moranense*, Uhl 1983; and *Tortula princeps*, Steere, Anderson & Bryan 1954) or the widely recognized

existence of high levels of genetic polymorphism (as revealed by electrophoresis) within and between single populations (Lewontin 1974; reviewed for bryophytes by Wyatt 1982).

Examples of noncorrespondence between morphological, breeding, and ecological discontinuities in plants are numerous (see literature cited in Mishler & Donoghue 1982), but one example from bryophytes is instructive. My studies of the moss *Tortula* (Mishler 1984) illustrated the sorts of noncorrespondence that have caused dissatisfaction with the prevailing view of gene flow and selection as the only major causal factors in the homogeneity or divergence of species and have prompted a search for another explanation.

*Tortula* contains both sexual and asexual species, a spectrum of sexual conditions from dioecy to synoecy in the sexual species, and several types of specialized asexual propagules. *Tortula* includes species that are narrowly endemic, others that are cosmopolitan, and some that are intermediate. Ecologically, both specialized and generalized species are represented. This diversity can allow comparative study of topics of current interest, such as punctuated morphological change and the relative importance of gene flow, selection, developmental constraints, and historical factors in producing and maintaining discontinuities in morphological variation.

The 21 species of *Tortula* recognized for Mexico (Mishler in press a) do not form a monophyletic group, but they represent a cross-section of the diversity of species within the genus. These species can be divided into four discrete categories: sporophytes always present (7 species); sporophytes infrequent but produced in a roughly equal frequency throughout the range of the species (6 species); sporophytes infrequent but produced only in a small part of the total range, the species thus asexual throughout most of their ranges (5 species); and sporophytes absent and the species thus apparently wholly asexual (3 species). The lack of certain expected correlations with the frequency of sporophyte production (and hence the opportunity for reproducing via sexually produced propagules) is striking. The size of a species' geographic range or its frequency of occurrence within it (as judged from herbarium specimens and my extensive field studies in Mexico) is not correlated with the frequency of sporophyte formation. Furthermore, the distinctiveness of a particular species (i.e., the possession of a set of unique characters) is not correlated with either sporophyte frequency or the occurrence of specialized asexual propagules.

The evident importance of asexual reproduction in many species of *Tortula* and the occurrence of widespread species that are nonetheless constant

morphologically seem to eliminate gene flow as a likely integrating factor. Stabilizing selection may be acting to maintain the morphologically distinctive features of each species of *Tortula* in Mexico. But this explanation seems unlikely because while each species has a rather restricted set of preferred habitats, the various species overlap in their preferences, and a single species may have a considerable ecological amplitude without concomitant morphological variation. For example, *T. quitoensis* Taylor occurs disjunctively from the northern Andes to the subalpine and alpine zones of the high volcanoes of Mexico. Plants of this species produce sporophytes infrequently but asexual reproduction is possible via the easily detachable leaves. The species maintains its distinctive morphology while occurring on soil of disturbed trail banks, on the bark of trees in shaded situations, and on moist rocks near streams—a broad habitat preference for any moss, let alone a species with a restricted disjunct distribution. The question remains: if neither patterns of gene flow nor a specifiable ecological “niche” appear to cause the morphological coherence of species, what does?

While not yet well-known in a mechanistic sense, a compelling answer to this question is the notion of epigenetic constraints on species. A species in this sense is a monophyletic lineage (recognized as such by the possession of a set of unique characters), buffered against small amounts of gene exchange because of the action of homeostatic epigenetic programs. Such a lineage might be fuzzy at the edges, but still be recognizable as a lineage, just as the Gulf Stream is recognizably a current (and has causal efficacy for the climate of Britain) despite the loss and gain of some water molecules along the way. Biological examples are many North American oak species, which seem to maintain their integrity despite some inter-crossing and apparent ecological overlap.

Just how much genetic intermixing causes a blending of two lineages (as defined above) appears to depend on what other processes are operating in a particular case. This returns the discussion to pluralism and the distinction between grouping and ranking criteria. The grouping criterion in the species concept advocated here remains monophyly. Various causal factors (epigenetic constraints, discontinuities in gene flow, or stabilizing selection) may figure in the ranking criterion needed in particular cases. This distinction is important because, as noted by several authors, the action of epigenetic constraints can lead to a strong bias towards parallelism. In other words organisms with similar developmental programs may independently undergo channelized morphological changes, thus independently gaining similar phenotypes. How-

ever, using the grouping criterion of monophyly requires one to make every attempt to distinguish polyphyletic from monophyletic groups and formally name only the latter.

The concept of epigenetic constraints remains suggestive and is imperfectly known, but it is an exciting field for future research. The full importance of such constraints will only become clear with a greater understanding of development than is currently present. Further study is needed to discover patterns of continuity and discontinuity in the transition from genes through epigenetic programs to phenotypes.

Bryophytes appear to be an advantageous group of organisms for experimentally examining these questions because of the ease with which clones can be replicated and because a large number of plants can be cultured in a small space. Their development is rather simple and yet a considerable morphological, reproductive, and ecological diversity is present. The work of Basile and Basile (1983, 1984) has demonstrated the feasibility of documenting and experimentally manipulating morphogenetic processes in liverworts. Wettstein's early experimental work with mosses (reviewed by Anderson 1963) likewise shows great promise.

#### IMPLICATIONS OF A PHYLOGENETIC CONCEPT OF SPECIES

The phylogenetic concept of species developed in this paper and in Donoghue (this symposium) has both theoretical and practical implications. Usefulness is often taken to be an important virtue of a classification. As discussed above, an important part of the usefulness of taxa (including species) resides in their ontological role in causal theories meant to explain them. Taxa that are monophyletic in the Hennigian sense are necessary for more than purposes of phylogenetic reconstruction. Species that are historical (i.e., monophyletic) entities are necessary if meaningful studies of biogeography, speciation, historical ecology, or comparative morphology are to be carried out. Phenetic species are unsuitable for these purposes because grouping by overall similarity will only sometimes recognize monophyletic lineages.

The phylogenetic species concept seems to fit the theoretical uses to which botanists have always applied their species. Traditional studies of phyto-geography, speciation, and evolution have treated species as "things" (i.e., historical entities with many of the attributes of individuals in the philosophical sense; Ghiselin 1974; Hull 1976, 1980). The concept of species advocated here merely provides an explicit connection between the concept and the uses to which it is put.

In a practical sense usefulness has been claimed

for phenetic taxa (including species, e.g., Levin 1979) without challenge until recently. As discussed by Farris (1983), many measures of information content are satisfied better by cladistic classifications than by phenetic ones. Therefore, not only do cladistically defined taxa have the primary benefit of theoretical meaningfulness, they are also more informative about known and predicted biological information than phenetically defined taxa. Thus phylogenetic species are more practical in the sense botanists have used the term when advocating phenetic concepts.

What are the taxonomic implications of the phylogenetic species concept advocated here? How does a practicing systematist proceed in a group such as the bryophytes that is little known biologically? One proceeds using the method of reciprocal illumination (Hennig 1966) to study morphology and produce a hypothesis of basic monophyletic groups (i.e., species) evidenced as groups by apparent apomorphies and perhaps initially ranked as species only because of the size of morphological gaps. One then progressively adjusts the circumscription of species as more becomes known about gene flow, ecological relationships, and the genetic and epigenetic basis of characters.

The astute bryological taxonomist will realize by this point that many species especially in taxonomically difficult groups such as the *Tortula ruralis* complex, *Bryum*, or *Brachythecium* cannot currently be defined by the possession of autapomorphies. However, considerable lumping may be required to recognize species in these groups that are characterized by autapomorphies. This may be precisely why these groups are taxonomically difficult; current taxonomic work is below the level at which clearly monophyletic lineages can be recognized. An analogy may be in order: the situation in such difficult groups is rather like trying to read a book with a microscope—the very quality of "letterness" disappears into blobs of ink and fibers of paper. Meaningful letters come into focus only when examined with less magnification.

If it is accepted that a species should be named formally only when a hypothesis is made that it is a historically discrete, monophyletic entity, then specific and infraspecific taxa characterized only by shared primitive characters (plesiomorphies) are not satisfactory. In such cases attempts should be made to find characters that either demonstrate the monophyly of the taxon or conversely demonstrate how the taxon could be broken up into monophyletic groups. Such attempts may fail, since "paraphyletic" speciation is a real possibility, as in the case of a widespread species that gives rise to other species through peripheral isolation (Bremer & Wanntorp 1979; Mishler & Donoghue 1982; Donoghue this

symposium). Ackery and Vane-Wright (in press) and Donoghue (this symposium) discussed this important problem in the application of monophyly to species. Donoghue noted that some species have an intermediate status between monophyly and paraphyly, in having no autapomorphies and yet with no characters that demonstrate paraphyly. Such a group of uncertain monophyly can be recognized formally under the phylogenetic species concept advocated here (as long as the group is not demonstrably paraphyletic), but should be distinguished in some way from demonstrably monophyletic species. [See further discussion of this topic by Donoghue, this symposium.]

Clearly, the recognition of polyphyletic taxa at or below the level of species, as for example in the naming of taxa on the basis of a few, environmentally labile characters or a simple genetic polymorphism, is unsatisfactory. Such ecological modifications (or even minor genetical variants) are likely to appear independently many times within a single, monophyletic species and should be given at most only informal recognition.

Examples of these considerations are provided by biosystematic studies of the *Tortula ruralis* complex (Mishler 1984, and in press b). *Tortula ruralis* itself as currently circumscribed is problematical because it appears to have no unique characters to define it as a species, there are elements within it that appear to be defined by unique characters, and some elements of it share possibly unique characters with other species. This "species" is thus likely to be paraphyletic. Examples of currently recognized species in the complex that are likely to be polyphyletic are *T. ruraliformis* and *T. intermedia*. Preliminary culture studies of these "species" indicate that characters held to distinguish them are quite plastic phenotypically and thus not reliable indicators of monophyly.

I contend that formal infraspecific names should be subject to the same criteria as species names in order to have a taxonomic system that is completely consistent and theoretically meaningful. The former should be used only if a hypothesis of monophyly is made and if there is some reason why the taxa recognized are not ranked at the species level.

If formal taxonomic names are used exclusively for phylogenetically discrete units at all taxonomic levels, then of course, many other biologically important units (such as physiognomic types, ecological guilds, ecophenotypes, cytotypes) will not be formally named. Nothing need be lost, however, and much may be gained. These units can be described informally and placed in overlapping, non-hierarchical arrangements as required. As such they will be clearly distinguished from monophyletic groups that bear formal names.

To summarize, I have advocated the proposition that species should be viewed as monophyletic groups of organisms, recognized as lineages on the morphological basis of the possession of shared, derived characters and ranked as species because of causal factors (perhaps especially epigenetic constraints) that maintain the lineage as the smallest important monophyletic group recognized in a formal classification. Such a view of species, while "morphological" in an important sense, is different than previous morphological or phenetic species concepts. It can provide species that are theoretically meaningful for biogeographic, ecological, and evolutionary studies and that have the practical virtues of consistency and predictiveness.

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#### LITERATURE CITED

- ACKERY, P. R. & R. I. VANE-WRIGHT. 1984. Milkweed Butterflies: Their Cladistics and Biology. Cornell Univ. Press, Ithaca, New York.
- ALBERCH, P. 1980. Ontogenesis and morphological diversification. *American Zoologist* 20: 653-667.
- . 1982. Developmental constraints in evolutionary processes, pp. 313-332. In J. T. Bonner (ed.), *Evolution and Development*. Springer-Verlag, Berlin.
- ANDERSON, L. E. 1963. Modern species concepts: Mosses. *THE BRYOLOGIST* 66: 107-119.
- BASILE, D. V. & M. R. BASILE. 1983. Desuppression of leaf primordia of *Plagiochila arctica* (Hepaticae) by ethylene antagonist. *Science* 220: 1051-1053.
- & ———. 1984. Probing the evolutionary history of bryophytes experimentally. *Journal of the Hattori Botanical Laboratory* 55: 173-185.
- BEATTY, J. 1982. Classes and cladists. *Systematic Zoology* 31: 25-34.
- BREMER, K. & H.-E. WANNTORP. 1979. Geographic populations or biological species in phylogeny reconstruction? *Systematic Zoology* 28: 220-224.
- CRACRAFT, J. 1982. Are cladistic species biological, evolutionary, or phylogenetic? A discourse on the kinds of cladists. Third Annual Meeting of the Willi Hennig Society, College Park, Maryland.
- CRONQUIST, A. 1978. Once again, what is a species?, pp. 3-20. In J. A. Romberger (ed.), *Biosystematics in Agriculture*. Allanheld & Osmun, Montclair, New Jersey.
- EHRlich, P. R. & P. H. RAVEN. 1969. Differentiation of populations. *Science* 165: 1228-1232.
- & R. R. WHITE. 1980. Colorado checkerspot butterflies: Isolation, neutrality, and the biospecies. *American Naturalist* 115: 328-341.
- ELDRIDGE, N. & J. CRACRAFT. 1980. *Phylogenetic Patterns and the Evolutionary Process*. Columbia Univ. Press, New York.
- & S. J. GOULD. 1972. Punctuated equilibria: An



- alternative to phyletic gradualism, pp. 82–115. In T. J. M. Schopf (ed.), *Models in Paleobiology*. Freeman, Cooper & Co., San Francisco.
- FARRIS, J. S. 1983. The logical basis of phylogenetic analysis, pp. 7–36. In N. D. Platnick & V. A. Funk (eds.), *Advances in Cladistics*, Vol. 2. Columbia University Press, New York.
- GHISELIN, M. T. 1974. A radical solution to the species problem. *Systematic Zoology* 23: 536–544.
- GOTTLIEB, L. D. 1984. Genetics and morphological evolution in plants. *American Naturalist* 123: 681–709.
- GOULD, S. J. 1979. A quahog is a quahog. *Natural History* 88: 18–26.
- . 1980. Is a new and general theory of evolution emerging? *Paleobiology* 6: 119–130.
- GRANT, V. 1980. Gene flow and the homogeneity of species populations. *Biologisches Zentralblatt* 99: 157–169.
- HENNIG, W. 1966. *Phylogenetic Systematics*. Univ. Illinois Press, Urbana, Illinois.
- HILL, C. R. & P. R. CRANE. 1982. Evolutionary cladistics and the origin of angiosperms, pp. 269–361. In K. A. Joysey & A. E. Friday (eds.), *Problems of Phylogenetic Reconstruction*. Academic Press, London.
- HO, M. W. & P. T. SAUNDERS. 1979. Beyond neo-Darwinism—an epigenetic approach to evolution. *Journal of Theoretical Biology* 78: 573–591.
- HULL, D. L. 1968. The operational imperative: Sense and nonsense in operationism. *Systematic Zoology* 17: 438–457.
- . 1976. Are species really individuals? *Systematic Zoology* 25: 174–191.
- . 1980. Individuality and selection. *Annual Review of Ecology and Systematics* 11: 311–332.
- . 1981. The principles of biological classification: The use and abuse of philosophy. *PSA [Philosophy of Science Association.]* 1978(2): 130–153.
- JACKSON, J. F. & J. A. POUNDS. 1979. Comments on assessing the de-differentiating effect of gene flow. *Systematic Zoology* 28: 78–85.
- 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.
- MAYR, E. 1957. Species concepts and definitions, pp. 1–22. In E. Mayr (ed.), *The Species Problem*. American Association for the Advancement of Science Publ. 50, Washington, D.C.
- . 1970. *Populations, Species and Evolution*. Harvard University Press, Cambridge, Massachusetts.
- MISHLER, B. D. 1984. Systematic studies in the genus *Tortula* Hedw. (Musci: Pottiaceae). Ph.D. thesis, Harvard University.
- . (in press a). *Tortula*. In A. J. Sharp & H. A. Crum (eds.), *A Manual of Mexican Mosses*.
- . (in press b). Biosystematic studies of the *Tortula ruralis* complex. I. Variation of taxonomic characters in culture. *Journal of the Hattori Botanical Laboratory*.
- & S. P. Churchill. 1984. A cladistic approach to the phylogeny of the “bryophytes.” *Brittonia* 36: 406–424.
- & M. J. DONOGHUE. 1982. Species concepts: A case for pluralism. *Systematic Zoology* 31: 491–503.
- NELSON, G. & N. PLATNICK. 1981. *Systematics and Biogeography: Cladistics and Vicariance*. Columbia University Press, New York.
- OSTER, G. & P. ALBERCH. 1982. Evolution and bifurcation of developmental programs. *Evolution* 36: 444–459.
- PLATNICK, N. 1985. Philosophy and the transformation of cladistics revisited. *Cladistics* 1: 87–94.
- POUNDS, J. A. & J. F. JACKSON. 1982. Gene flow and differentiation: The isolated populations of checkerspot butterflies in Colorado. *American Naturalist* 120: 280–281.
- RACHOOTIN, S. P. & K. S. THOMSON. 1981. Epigenetics, paleontology, and evolution, pp. 181–193. In G. G. E. Scudder & J. L. Reveal (eds.), *Evolution Today*. Carnegie-Mellon University, Pittsburgh.
- ROSEN, D. E. 1979. Fishes from the uplands and intermontane basins of Guatemala: Revisionary studies and comparative geography. *Bulletin of the American Museum of Natural History* 162: 267–376.
- SIMPSON, G. G. 1961. *Principles of Animal Taxonomy*. Columbia Univ. Press, New York.
- STEBBINS, G. L. 1950. *Variation and Evolution in Plants*. Columbia University Press, New York.
- . 1979. Fifty years of plant evolution, pp. 18–41. In O. T. Solbrig, S. Jain, G. B. Johnson & P. H. Raven (eds.), *Topics in Plant Population Biology*. Columbia University Press, New York.
- STEERE, W. C., L. E. ANDERSON & V. S. BRYAN. 1954. Chromosome studies on California mosses. *Memoirs of the Torrey Botanical Club* 20: 1–75.
- UHL, C. H. 1983. Chromosomes of Mexican *Sedum*. IV. Heteroploidy in *Sedum moranense*. *Rhodora* 85: 243–252.
- WADDINGTON, C. H. 1957. *The Strategy of the Genes*. Allen & Unwin, London.
- WILEY, E. O. 1978. The evolutionary species concept reconsidered. *Systematic Zoology* 27: 17–26.
- . 1981. *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. John Wiley, New York.
- WYATT, R. 1982. Population ecology of bryophytes. *Journal of the Hattori Botanical Laboratory* 52: 179–198.