An Essay on Species Concepts Developed During Revisionary Studies

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The International Code of Botanical Nomenclature carefully avoids incorporation of a species concept in the promulgated rules. We are given, instead, a structure of ranks with that of species as basal. A nomenclaturally correct name may have various degrees of biological substance, however, and only rarely is such a name based on qualitative or quantitative studies demonstrating that it represents a valid inference of the existence of a more or less clearly differentiated group of individuals in nature.

The period of exploratory botany of the last two hundred years resulted in many geographic species names with little species concept associated with them other than that their authors could not remember seeing anything quite like the representative specimens before, at least from that area of the world. The writers of floristic manuals and world revisions recognized that many species names from the exploratory effort must be relegated to synonymy because they are represented by specimens that intergrade on a morphological continuum that is called variability. This variation is generally supposed to have a biological explanation. Nevertheless, acceptance that an intergrading spectrum of morphotypes requires synonymy of names is basically a philosophical stance on the part of the taxonomist. Seldom is there any experimental demonstration of biological continuity between morphotypes. In fact some taxonomists are apparently able to tell when the continuum is too broad and surely cannot represent only one species. Local floristic manuals may accept taxa that were not previously recognized in world revisions (e.g., Crum & Anderson 1981 versus Zander 1972 regarding synonymy of Leptodontium excelsum Sull.). This may be because certain taxa are more clearly distinguishable in some areas of the world than in others or are supposedly distinguishable if one looks close enough. Also, the descriptions and circumscriptions of species and supraspecific taxa in regional treatments may be different from those of the same taxa in world revisions in that the former are often based solely on the local representation. These problems, and still others, are characteristic of the period of revisionary studies when synthetic species concepts begin to be established.

One of the tenets of herbarium taxonomy is that much can be discovered about bryophyte biology without recourse to a more lengthy experimental approach. Herbarium taxonomy contributes to an understanding of the biology of a group through evaluations based on long familiarity (through observation in the herbarium and in the field) with morphological and phenological variation and their associated habitat and distribution. Thus, taxonomic study itself reveals biological facts about organisms. But, because alpha-taxonomy is, for the most part, simply well informed opinion, species concepts of taxonomists may differ according to differences between the taxonomists themselves: by how well-informed they are, how much weight they give new data, how inclined they might be to introduce novelties, and various other tendencies and attitudes. Given this situation, practical bryophyte taxonomists generally do not espouse a “best” species concept, or even assume such exists, but show a tolerance and acceptance of other workers’ attempts to present their admittedly subjective studies as contributions towards a useful taxonomic framework.

A species definition is a piece of guesswork—a hypothesis that ties together observations and which might be tested by future study with appropriate controls. It is not a thing in nature that can be measured or studied. To demonstrate how species concepts are important in representing the results of herbarium study at the alpha-taxonomic level, I will review how my own concepts have developed over 15 years of work with the Pottiaceae and then discuss the various papers in the symposium with this experience in mind. It will be evident that my greatest concern is with the way nomenclature deals or, more often, avoids dealing with species concepts.

Presentation of nomenclatural novelties. New taxa I have described have been conceptualized in contexts of both splitting and lumping. Names in the genera Fissidens (Zander 1969), Desmatodon (Zander & Crum 1977), Tortula (Zander & Steere 1978) and Splachnobryum (Norris & Zander 1981) were offered based on apparently unique combinations of character states but without evaluation of the value of such characters in general taxonomy of the groups, which would be impossible in any case without extensive revision. Names in Leptodontium (Zander 1972) and Trichostomum (Zander 1982c) were published for taxa that proved clearly distinctive in the context of regional revisions. New names, combinations and statuses were also given under...
narrow, conservative species concepts in poorly understood genera: e.g., Didymodon (Zander 1978b), Tortella (Zander & Hoe 1979); and, in somewhat better known or recently revised situations: Didymodon (Zander 1982b), Oxystegus (Zander 1982a, 1983c), and Hyphila and Leptodontium (Zander 1983b). The genus Pseudocrossidium was emended (Zander 1979a) to include species previously in Barbula and Tortula in order to recognize what was hypothesized to be a monophyletic group evolving towards morphological modifications for photosynthesis. Clearly, the sophistication of the species definitions offered in the papers cited above depended on the extent of knowledge of the group.

**Morphological variation.** Noguchi's (1956) paper offering extensive synonymy for species of Scopelophila was the conceptual model at the species level for my treatment of this genus in the New World (Zander 1967). The two species recognized (S. ligulata (Spruce) Spruce, S. cataractae (Mitt.) Broth.) are easily distinguished but are rather variable with respect to several characters. I pointed out two extremes of morphological variation in S. ligulata: a "hydric" form with loosely pulvinate habit and flaccid, spreading leaves with the upper leaf cells thinly walled and the enlarged basal cells often extending more than half way up the leaf, and a "montane" form with a densely pulvinate habit and narrow, firm, appressed leaves with the upper cells mostly thick-walled and the enlarged basal cells mostly confined to the lower third of the leaf. The existence of intra-specific intergradation between morphological extremes is discussed in succeeding papers on other genera as part of a "species concept" that recognized this as a common occurrence in the Pottiaceae. Species definitions incorporating a gradual change in several character states—this often correlated with plant stature—were recognized in the genera Leptodontium (Zander 1972), Gymnostomum, Hymenostylum, and Molendoa (Zander 1977, Zander & Eckel 1982), Didymodon (Zander 1978b, 1982b), Bryoerythrophyllum (Zander 1978a), and Neohyphila (Zander 1983a).

Leptodontium viticulosoides (P. Beauv.) Wijk & Marg. var. viticulosoides and L. viticulosoides var. sulphureum (Lor.) Zand. (as var. panamense (Lor.) Zand.) are very close morphologically but differ (Zander 1972) in sexuality (monoicous, including apparent rhizautoicy, vs. dioicus) and spore size (anisosporous vs. isosporous). For Leptodontium, these are rather important characters, and the two taxa may have been recognized at the specific level were it not for the fact that collections of the two taxa are generally sterile and the gametophytes are for the most part indistinguishable. To avoid labelling the many sterile collections simply "Leptodontium sp.,” an appellation that conveys little information, the taxa were distinguished at the infraspecific level, a solution that better represents the perceived biological relationship. Sterile specimens can then be annotated “Leptodontium viticulosoides sensu lato.” A fact supporting this resolution is that a third variety, var. exasperatum (Card.) Zand., based on differences in laminal papillae morphology, is represented by both anisosporous and isosporous collections. This is an example of a species concept tailored in part to optimize the biological significance of its associated name.

The Code requires, through the principle of nomenclatural priority, that taxa be discontinuous, at least to the extent that the taxonomist must be able to refer type specimens to the appropriate taxonomic group. For groups that appear to be nondiscontinuous, but very distinctive at the morphological extremes, I at first (Zander 1978a, 1982d) used a taxonomically informal way of designating the extreme morphotypes (the species name sensu lato, followed by the term "facies" and the name of the earliest or the most familiar synonym, the type specimen of which approximated the extreme morphotype). This proved ungainly. Informal names for bryophyte morphological variants, such as the "Idealtypen" of Herzog (1907) or the "modificatio" system of Buch (1922), have certainly never proved popular. I then (Zander 1981, 1982b, 1983a; Zander & Eckel 1982) decided that non-discontinuous but distinctive infraspecific variants are better named using standard nomenclature. I used a method that assigned a particular varietal name to a distinctive morphotype at one end of a perceived continuum of variation using the earliest type specimen (of available names at the varietal level, including that of the typical variety) that was clearly representative of that morphotype. Once all varieties were named, all remaining heterotypic names were assigned to synonymy under the species name sensu lato. This contravenes no nomenclatural rules and provides taxonomically acceptable varietal names without having to invent an artificial boundary with which to segregate all type specimens included in the species sensu lato. Identifications of specimens may now well represent the species concept in that the species name sensu lato can be used for specimens of intermediate morphology.

**Name enhancements.** As I have previously pointed out (Zander 1982b), the Code does not provide for different names for different species concepts that include the same type specimen, and, through the requirement of the type method for working with the nomenclature of infraspecific taxa, it at least implies that all taxa are discontinuous. I have attempted to deal with this in several ways, none of which is completely satisfactory.

The terms "columbarium" and "parochialis" were
introduced in a treatment of Didymodon (Zander 1978b). The former was appended to the names of taxa to identify those suspected to be pigeonhole species definitions, i.e., segregates on a continuum of morphological variation. The latter was used for geographic or otherwise narrowly conceived species with practically nothing known, or at least inferable, about their biology and for which a previously published synonym probably already exists.

Because there are sometimes more than one different species definition attached to particular species names by various authors, I have recommended (Zander 1982d) that the phrases sensu lato, sensu stricto and emendavit (with author's name and date of publication) be more commonly used to better indicate exactly what an author or annotator of a specimen means in using such names.

Parallel trends. In a treatment of Didymodon (Zander 1978b), I presented a chart that demonstrated possible parallel trends in speciation among several taxa in three sections of the genus. Certain slots remained empty: a hygrophylic species for sect. Vineales and a species with a propaguloid apex in sect. Fallaces (as sect. Graciles). Although it is well known that it is dangerous to assume that species concepts useful in one group can be expected to apply in another, the discovery of collections with one or the other morphological features given above would certainly encourage recognition of a species along the same lines as in the other, assumably parallel evolving sections.

Introducing new characters. Bryologists often search for new characters that might help distinguish taxa that are similar, at least when sterile. The genera of Pottiaceae proved to have rather distinctive leaf color responses to various reagents (Zander 1980, 1983c), and characteristic dates of sporophyte maturation (Zander 1979b) that proved helpful in placing Tortula plinthobia (Sull. & Lesq.) Broth., at least, in the correct genus.

Growth studies. Behavior in cultivation was significant in uncovering heterophyllly in Tortella fragilis var. tortelloides (Greene) Zand. & Hoe (Zander & Hoe 1979). This threw light on a similar situation (Zander unpublished) in the var. fragilis (detailed below). A common garden comparing Tortula cainii Crum & Anderson and the similar T. norvegica (Webr.) Lindb. demonstrated (Zander & Eckel 1980) the apparent permanency of certain features of the former.

In sum, my species definition is not one “form” or model of what a species is supposed to be but instead attempts to represent what is known about a group biologically through appropriate nomenclature and discussion, and, although based largely on morphological observation of herbarium specimens, is refined through simple biosystematic studies and inferences about population biology and the sources of variability. I am an unabashed adherent of “general purpose taxonomy” (for instance, as is discussed by Raven 1974), and I think this attitude may be characteristic of how other herbarium taxonomists of my generation have developed species concepts. Given this, how might the new taxonomic emphases of the symposium speakers contribute to taxonomy for its own sake and for its contribution to biological understanding of the Bryophyta?

**Commentary**

Donoghue’s “Critique ...” clarifies the problems associated with the “biological species concept,” and his proposal for a “phylogenetic species concept” is certainly challenging. I have in the past generally avoided discussion of phylogenetic relationships in my papers because assignment of traits to “primitive” or “advanced” status seems either arbitrary or extremely problematical. The only way it appeared to me that one can infer an evolutionary relationship with any confidence is to assume that a morphologically, and therefore probably evolutionarily, complicated trait, for example, the chorate eye, the feather, or the seed habit, has a very small chance of evolving twice in unrelated groups. I have not pursued this since I have not found many complicated traits in mosses below the family level that cannot be considered possibly being due to parallel evolution. Also, I can identify few transformation series that are probably irreversible and are uncomfortable with the idea of regarding rare or unique characters as almost surely apomorphic.

There is no reason why morphologically generalist daughter species cannot be derived from a species with a few rare characters, especially in bryophytic taxa with morphological variation characterized by extreme reduction of the gametophyte. The appearance of a particular character state in a group is not necessarily through selection for a new character but can also occur through selection against genes masking an old character. If the plesiomorphic character is also masked in related groups (but is perhaps present but masked in other members of the original group), the outgroup comparison is invalid. For instance, leaves of Barbula unguiculata Hedw. are denticate in cultured specimens (D. Basile & R. Zander unpublished). “Leaves denticate” is a rare character in the genus and might be expected to be derived. Thus, what may be a plesiomorphic character can be “advanced” through desuppression into false apomorphy. How common is this? Could the well-known Weissia-Astomum and Pottia-Tortula transformation series actually be caused by gradual desuppression of peristome characters rather than the more common interpretation of these
as reduction series (through suppression or loss of traits)?

The absence of a mutation ("leaves smooth") has quite different phylogenetic significance than does the masking of a character ("leaves lacking papillae"). One or more mistakes in this fashion in evaluating character states might be multiplied into a series of spurious assignments of plesiomorphy and apomorphy through cladists' method of "reciprocal illumination." Little is known about the genetic basis of character expression in the bryophytes, and simple features dependent on one or few alleles are, in any case, little liable to obey a rule of parsimony. This is not to say that tentative assignment of advanced and primitive character states is not usually well-informed and of inferential value, since we all make some hypotheses about phylogeny and this influences our taxonomy, but to what extent should we base our systematics on it? The first step in phylogenetic analysis is surely the longest.

Cladistics probably will have much to offer when it has passed through its difficult quasi-ideological phase. I look forward to classifications of bryophyte groups advanced through cladistic studies. Unfortunately, the present bryophyte genera and species are mostly artificial constructs and probably not very valuable for use in developing cladograms. Bryophyte taxa may not only be groups of rather unrelated organisms, but morphological terminology is inexact and misleading. For instance, taxa described as "dioicus" may include all or many rhizatoucous species. Cladistic work based solely on information from the literature involving bryophyte groups that have not been monographed or otherwise recently revised ought to be viewed with much reservation. Even the word "character" has all the vagueness of definition as have "species" and "population."

The "phylogenetic species concept" has much to recommend it. Its success in bryology, I believe, will depend on how convenient cladistically derived species concepts are for use by bryologists in general. As to ranking, a classification based entirely on genealogical principles will remain of interest only to specialists in phylogeny unless it has the utility of the present phenetic system. It remains cloudy, for many taxonomists at least, just how certain one can be that clades—constructed through the intuitive processes of (1) selecting the proper outgroup and (2) correct assignment of advanced and derived characters—reflect actual ancestry. Any amount of uncertainty in cladistic techniques must be weighed against whatever uncertainties are involved in using phenetic principles to group and rank taxa.

Mishler's contribution introduces a somewhat more complicated species concept involving both phylogenetic and epigenetic evaluations. In general, I find his species concept attractive and certainly worth testing. His suggestion that developmental events may strongly affect the phenotype is worthwhile. I agree with his estimate that much present taxonomic study is "below the level" at which good taxonomic judgments can be made. In fact, I think there are many papers in the literature that attempt to solve problems in genetics and population biology quite inappropriately using the techniques of alpha taxonomy. Mishler's advocacy of many criteria for evaluating species ranking is admirable. I do not feel, however, that "simple observation" is sufficient to show that diversity in nature is discontinuous. He may be confusing language with perceived phenomena. Perceptions are more easily dealt with if comprehended as relationships between discrete objects, but the phenomena represented by linguistic abstractions like "species" and even many "real" things (like the "upper part" of this page) are quite vague in circumscription. I ascribe to a kind of nominalism that recognizes the value of inference and the mere convenience of abstract terms. Mishler promotes an across-the-board realism (in the philosophical sense) that I do not think is widely shared among taxonomists. I, for one, infer that species of various sorts exist, being aggregations of biologically related individuals in nature for which our species definitions (developed as hypotheses based on observations of comparatively few representative individuals) serve as models; but I have faith in the expected utility of that inference, not in the concept of "species" itself. Mishler's requirement of the recognition of "theoretically meaningful taxa" seems to make theory itself the test of the validity of the species concept.

Mishler's discussion of the lack of correlation between reproductive method and range in Tortula may not demonstrate a noncorrespondence, since spores may be little more genetically heterogeneous than other diaspores. As I have previously noted (Zander 1984), crossing between two different gametophytes, even in dioicus species, may simply involve crossing between the products of the same sporangium. This is equivalent to rather close inbreeding in the flowering plants. Also, one might expect that crossing between gametophytes is almost always within one microhabitat because of the short sperm gene flow distance, which inhibits hybridization between different ecotypes. This assumes that spores of different ecotypes seldom produce sexually mature gametophytes in environments other than those for which they are adapted. Thus, spores may be seen as numerous, small propagula of value for fitness in habitats with much available colonizable surface, while asexual species are adapted for reasons of atelochozy (Zander 1979a)
"patchy" or narrowly circumscribed habitats, or for conservation of biomass in harsh environments. In any case genetic variability of diasporas may play little part in determining range differences in species of Tortula.

Wyatt's paper discussing recent discoveries from population biology brings the sibling species problem to bryology with a vengeance. I am happy to see that he does require morphological markers for the recognition of genetically diverse but morphologically similar taxa. Likewise, I appreciate reading that "the naming of . . . all genetic variants as species should be avoided" and that the evaluation of a monographer of the level of morphological difference that constitutes a species within a group should be respected. I have no argument with most of what Wyatt has written but hope that future systematic studies involving non-morphological variation will be reflected in only those nomenclatural changes that preserve the convenience of scientific names in representing important biological differences at a level useful to most biological researchers. Whether electrophoretic analyses demonstrate real biological differences or are essentially neutral in regard to evolution, their taxonomic value ought to be weighted in respect to other characters so as not to compromise a generalist taxonomy.

Stark's case study of phenology (and reproductive morphology and branching patterns) is an excellent example of the refinement of species concepts with additional biological knowledge. The fact that the two species studied show clear differences in reproductive behavior and morphology gives more value to the morphological characters used in their taxonomy. Because characters associated with reproduction directly influence fitness, Stark's treatment is a contribution to understanding of species as biological entities. Because this study was done at only one site, however, the conclusions reached in the paper may not apply equally across the distributional range of the taxa discussed.

Of the symposium papers, Shaw's discussion of the relevance of ecology to species concepts is probably the most apropos to the interests of the practical taxonomist. The use of ecological data is common among monographers and revisionists in developing species concepts, and Shaw provides a sensible perspective and details some interesting techniques. I applaud Shaw's assertion that classifications cannot be proven or disproven, and agree that classifications that reflect evolutionary history would be more apt to group genetically related organisms, which heightens the predictive value of the classification. Agreeably, he does not state that cladistics is the best or only way to determine genealogy. His statement that it is important to demonstrate some biological individuality for species that have been construed on phenotypic grounds is, in my opinion, true but idealistic. There is a time for putting forward a biologically based species definition just as there is a time for the geographic species of exploratory floristics and those developed in revisionary studies.

The "reverse geographic argument," as shown for Mielichhoferia species, is very interesting, and rates being pursued for other similar pairs or series as floristic information is amassed for them. Regarding this, I once wondered if there was not a genetic relationship between Tortella tortuosa (Hedw.) Limpr. and T. fragilis in view of a somewhat similar habitat and range match, and the fact that fragile-leaved variants of the former are apparently common in northern North America. A close study (Zander unpublished) of herbarium specimens, however, demonstrated that young plants of T. fragilis lack the bistratose apex with elongate marginal cells found in the upper leaves of mature plants. If this developmental variation is taken into account, the two species are quite distinct when mature and can always be separated when immature by the appearance of the leaf apex, which in T. tortuosa has a short awn several cells in length, and in T. fragilis has an apiculus of one to three cells. This is supported by culture experiments demonstrating similar heterophylly in T. fragilis var. tortelloides (Greene) Zand. & Hoe (Zander & Hoe 1979).

Summary

With the appearance of monographic and revisionary works over time, it is becoming possible to do studies that link biological facts of phenology, development, ecology, and population biology to species concepts, and to use such knowledge in evaluating the degree to which particular species definitions are useful for the purposes of biological study as a whole. The implications of the theoretical ideas advanced by the symposium participants are far reaching, but their value to practicing taxonomists and biologists in general can only be assessed through our application of the described techniques to actual problems. The Symposium does well in promoting and regularizing species concepts as tools in taxonomy.

The drafts of the papers upon which I base this commentary give the reader the impression that each author has one species concept that they personally feel is "best." This is surely not the case. During the question and answer session of the symposium, Donoghue suggested that different disciplines may require different species concepts, and because he is interested in phylogeny, he is concerned primarily with a phylogenetic species concept. But, he explained, if we are clear in discussing
correspondences between phylogeny, ecology and so forth, there would be no real problem dealing with discipline-oriented species concepts. Later, Stark went further with this in suggesting that different taxa may also require different species concepts. This flexibility on the part of our best modern bryological theorists is comforting.

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