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Autor(en): **Wagner, W.H. Jr.**

Objekttyp: **Article**

Zeitschrift: **Botanica Helvetica**

Band (Jahr): **97 (1987)**

Heft 2

PDF erstellt am: **27.04.2024**

Persistenter Link: https://doi.org/10.5169/seals-67865

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Botanica Helvetica 97/2, 1987

0253-1453/87/020195-11 $ 1.50+0.20/0
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Some questions about natural hybrids in ferns

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Manuscript accepted July 14, 1987

Abstract

Wagner, W.H., Jr. 1987. Some questions about natural hybrids in ferns. Bot. Helv. 97: 195–205.

The questions of the status, evolutionary importance, and sterility vs. fertility of fern nothospecies (interspecific hybrids) are discussed. Further problems touched upon are: i.a., What is the connection between genetic affinity and hybridability? Are hybrids concentrated in disturbed sites? Why are there so few hybrids of epiphytic ferns? Is the morphology of a nothotaxon of known parentage predictable? How should hybrid species be treated in a phylogenetic analysis? What are the best solutions for problems pertaining to the nomenclature and classification of intergeneric and interspecific hybrids? The emphasis is on posing the questions, rather than on offering the answers.

Key words: nothospecies – hybrid reproduction – names and taxonomic status of hybrids.

Professor T. Reichstein is one of our leaders in the complicated study of the role of hybridization in the systematics of ferns. Through his many contributions he has helped us to place the concepts of reticulate evolution on a firm basis. In the past this approach to pteridology was largely ignored by many workers, and in North America some fern taxonomists recognized interspecific crosses not as hybrids but rather as varieties of one of the parents, sometimes on the grounds that the hybrids "look more like one parent than the other." The hybrids were treated in other ways as well – as separate normal species, or correctly, as crosses. Either formulae or binomials were used for the latter. The multiplication sign was placed before the epithet in binomials, e.g., *Asplenium* ×*ebenoides,* or sometimes in front of the whole name, ×*Asplenium ebenoides.* Practically all monographic work seemed to be based on the postulate that fern diversity could be explained by divergence or cladogenesis. Indeed, strange to say, many taxonomists were *opposed* to hybrids. They did not want to see them or hear about them. Hybrids were contaminated, bad, and difficult to key out because they obscured the best key characters. I remember one authority pleading with me after I turned up a hybrid asplenium in Guam, "Please don't have hybrids in tropical ferns!" Now, through the works of persons like Reichstein and other researchers in all parts of the world, the role of hybridization in creating the patterns of fern diversity has become

Dedicated to Prof. Reichstein on the occasion of his 90th birthday

well accepted, and new techniques are being applied to the study of hybrids that additionally confirm that reticulation is of great importance in pteridology. In North America I estimate that between 20 and 25% of all known taxa are of interspecific hybrid origin.

I have been somewhat out of line in my efforts to make a strong distinction between normal divergent species and reticulate hybrids. I recognize that to some extent the distinction may be a matter of degree, but I have dealt almost exclusively with "real hybrids," those involving very distinct species. If two taxa are recognized by all hands as entirely distinct species, then their cross is an interspecific hybrid. If two groups of species are similarly recognized as entirely distinct genera, then a cross between a member of one group and a member of the other group is an intergeneric hybrid. To be true, all ferns are, or once were, hybrids in the strictly genetic sense, including intraspecific hybrids at the populational level. But as one of my students bluntly put it (in words best appreciated by speakers of idiomatic English) "All plants are hybrids, but some are greater bastards than others." I am writing about the "real bastards," those ferns that came into being by fertilizations between thoroughly differentiated species or genera. Involved here is "super-miscegenation."

The problem of not recognizing hybrids as different from normal species is exacerbated by the droll efforts of certain cladists to equate them in phylogenetic analysis. In my opinion, because of the special combinatorial nature of reticulate evolution, every effort should be made to remove hybrids prior to phylogenetic analysis. Otherwise the character polarity interpretations will be fouled up in a network of compromises and blends. As I shall point out below, some cladists do not agree with me on this. In fact, at a larger level, some pteridologists do not even agree that hybrids are different in nature from normal species, so long as they can reproduce sexually. It is with such thoughts in mind that I have prepared this informal essay to pose some questions about fern hybridization. It is surprising how many points of view there are. There are many areas of disagreement, and we are by no means settled in our attitudes toward intertaxon hybridization and how we manage it in our thinking and our classification. Readers may examine one or more of the questions given below and say "We already know the answer to that!" However, I must point out that in my experience all of the questions given are still more or less controversial, and that is why I have enumerated them here.

One of the primary contributions of investigations of reticulation has been to explain baffling taxonomic situations. The holly ferns, *Polystichum,* of western North America were in a state of taxonomic chaos until we were able to show that several original species through their hybrids, allopolyploids, and backcrosses, have produced a hybrid "mess". Once we determine the basic pattern, the classification becomes obvious. In Hawaii where the great floristician Hillebrand a century ago recognized a welter of confusing aspleniums, we are now gaining more and more evidence that hybridization and polyploidy are strongly involved, and that there are fewer basic species than he supposed.

For purposes of this essay I shall use the word *orthospecies* (normal, divergent species) to contrast with *nothospecies* (a taxon derived originally from interspecific hybridization). It does not matter in either orthospecies or nothospecies what the mode of reproduction is, whether apomictic or sexual. Many widespread plants traditionally classified as orthospecies reproduce by apomixis. In North American ferns, *Pellaea atropurpurea* and *Asplenium resiliens* reproduce by apogamy, but there is no good evidence that they are interspecific hybrids. Sometimes asexual forms occur side-by-side with sexual forms of the same species, as in *Pellaea glabella.* The point is that repro-

ductive method is not a hard-and-fast way of distinguishing between orthospecies and nothospecies. Orthospecies form the basic framework of plant diversity, while the nothospecies form connections between them, reticulations. Nothospecies have genetic materials of two (sometimes three or more) orthospecies, combined in them, and are thus genetically more complex, having the alleles of different orthospecies together.

How significant are nothospecies in the broad picture of pteridophyte evolution? Pteridologists differ widely in their responses. Some workers believe that nothospecies are of major importance; others that they have little to do with the broad picture. One group of researchers, for example, points out that the majority of fern species are diploid and apparently orthospecies, and that, if nothospecies had been important, they would be a lot more common than they are. Other researchers believe that they are very important, and that they have given rise to all or most of the polyploids among ferns. According to this view, all polyploids are actually allopolyploids, i.e., nothospecies that doubled their chromosome numbers and became sexual. Taxonomic autopolyploids are disallowed.

A related question is: *How often do allopolyploids give rise to new lines of evolution?* Such allopolyploids as *Asplenium* × *adiantum-nigrum* or *A.* × *pinnatifidum* illustrate the problem. Are such allopolyploids potential sources for new orthospecies, or are they simply dead-ends that, in spite of their wide ranges and importance in floras, will go nowhere? On the contrary, one may consider the high chromosome base numbers of ferns as demonstrating that multiple hybridizations in the early history of these plants gave rise to polyploids which then went on to evolve into the various lines of ferns we know today. In other words, the sequence is read as follows: (1) original fern stocks were made up of orthospecies that had low numbers; (2) hybridization took place resulting in reticulate evolution, and the formation of paleopolyploids; and (3) subsequently the different paleopolyploids generated new lines of evolution by orthospeciation and by genetic diploidization.

The same inquiry may be raised about such fertile allohomoploids as *Pteris otophora* or some of the cyatheas. (Similar conditions exist in the *Lycopodium complanatum* group of non-fern pteridophytes). In contrast to allopolyploids, these hybrids maintain the same chromosome number as their parents but nevertheless have normal sexual life cycles. *How often do allohomoploids give rise to new lines of evolution?* According to classical theories of introgression, gene exchange by hybridization and backcrossing can substitute for mutation, and thus make possible new lines of orthospeciation. The theory is an intriguing one, but we need to have a lot more information about allohomoploidy in ferns and other pteridophytes before we can declare that new lines of evolution have actually resulted from allohomoploid nothospecies. To be true, hybrid conditions can be preserved if homoploid nothospecies undergo strict intragametophytic mating in subsequent generations. Allohomoploidy can be preserved by gametophytic selfing. But the question of whether such allohomoploids can then proceed to produce new lines of evolution is not answered by this.

Returning to polyploids, we may ask: *Do allopolyploids arise only once or repeatedly?* Workers with allozymes conclude on the basis of heterozygosity of certain alleles that there have been repeated origins of allopolyploids. However, critics observe that the diversity of enzyme alleles may be due instead to repeated mutations within the nothospecies, and that allopolyploid nothospecies may arise only once. In other words, the critics argue that the mutations may have taken place after the allopolyploid was formed rather than earlier, in the respective parental orthospecies. Those who hold that allopolyploids arise only once seem to have an antipathy to the idea that the same

taxon can arise several times from different combinations of the same parental orthospecies; the idea smacks of polyphylesis – the *bête noire* of phylogeneticists.

One of the most perplexing inquiries is: *Why are some hybrids so rare and others so common?* Such orthospecies as *Osmunda regalis* and *O. claytoniana* occur together in extraordinary abundance in eastern North America, yet their hybrid is known from only two localities. In the Old World tropics, *Odontosoria chinensis* and *Lindsaea ensifolia* are weedy ferns that occur side-by-side in many sites over an enormous range, but their hybrid is known only from one spot on the island of Kauai in Hawaii. On the contrary, some hybrid combinations are extremely common: In Hawaii the hybrid of *Thelypteris dentata* and *Th. parasitica* is everywhere that the orthoparents co-occur. In North America, *Dryopteris marginalis* and *D. filix-mas* apparently never fail to produce hybrids when they grow together, as do *D. marginalis* and *D. goldiana.* The controls are clearly not all-or-nothing. There are various degrees of hybridability, depending on subtle factors in the parents that are still unknown.

Sometimes the presence of a large number of hybrids may be due to factors other than repeated *de novo* hybridizations. It has long been suspected that sterile hybrids may indeed have methods of reproducing by spores in nature. *How often do sterile nothospecies reproduce by unreduced spores?* It is hard to imagine the products of meiosis in most sterile fern nothospecies involving many "good" spores because of the unequal distribution of chromosomes in irregular meiosis. As workers have found in laboratory culture experiments, the majority, if not all, of sterile nothospecies have the ability to produce numerous gametophytes from spores, and these presumably unreduced. If we assume that these gametophytes can proliferate directly by apogamy, then we have a mechanism for reproduction for sterile hybrids. But does this take place in nature?

As we move toward better understanding of breeding systems in ferns, ortho- as well as nothospecies, an interesting question has arisen regarding the formation of hybrids in relation to inbreeding vs. outbreeding. The question is: *Why do pteridophytes that are mainly selfers seem to produce just as many nothospecies as those that are mainly outcrossers?* Recent work suggests, for example, that pteridophytes with mycoparasitic subterranean gametophytes among the clubmosses, whiskferns, and ferns produce as many hybrids as those with photosynthetic surficial gametophytes. Of special interest is the finding that allozymic studies in the genus *Botrychium* indicate very strong evidence for intragametophytic selfing, yet roughly a dozen different combinations of orthospecies have been encountered. Can this mean that intragametophytic mating is preferred, but when the prothallia of two different species co-exist, intergametophytic matings take place? A related question, still not satisfactorily answered, is: *Do pteridophytes with subterranean mycoparasitic gametophytes produce fewer nothospecies than those with surficial autotrophic gametophytes?* The evidence quoted above would seem to answer this in the negative, but a number of students of fern reproductive biology still maintain that the subterranean habitat militates against cross-fertilization. They assert that hybrids are much more rare in subterranean than in surficial gametophytes. We need more evidence to solve this controversy one way or the other.

Traditionally biosystematists have used experiments on hybridability as a test of relationships between orthospecies. Until recently most workers have accepted this procedure as a reliable test, but there is now a tendency away from this. In the ferns, relatively little experimental hybridization has been carried out, in contrast to seedplants, so most of our evidence is based upon field observations. The problem remains, however: *Is there any connection between hybridability and genetic affinity or phylogenetic relationship?* There are serious pitfalls involved in answering this question. For

example, what is genetic affinity? Can simple genetic factors influence compatability and thus obscure the true genetic affinity, whatever that is? As to phylogenetic relationship, there are different kinds – evolutionary and cladistic. Evolutionary relationship involves both cladogenesis and anagenesis, and so the test of extent of relationships depends on total phyletic distance. Cladistic relationships are concerned merely with branchings. Two closely related sister groups are just as "close" as two distantly related sister groups. Authors dealing with the question of hybridability must define exactly what they are referring to when they speak of genetic affinity or phylogenetic relationship.

A fairly new field of investigation on nothospecies involves their ecology and geography in comparison with related orthospecies. One impression that many workers have is that fertile nothospecies tend to be more successful than their parental orthospecies. My question is: *Are nothotaxa on average more common and widespread or less common and widespread than orthospecies?* To deal with this, one has to be concerned with incidence, i.e., local abundance, dispersion (local vs. generalized), as well as geographical pattern, including latitudinal vs. longitudinal distribution, and altitudinal distribution. No one doubts that sterile nothospecies tend to be less common than their parental orthospecies, even though some of them may become common locally. In general, sterile nothospecies tend to be confined to the contact between the occurrences of the fertile parental orthospecies (but this is not always so, as is evidenced in *Dryopteris* × *boottii* [*D. cristata* × *intermedia*] in western Minnesota, where we have found it in the absence of *D. intermedia*). Fertile nothospecies may have ranges that extend beyond those of one or both parents. The apogamous *Asplenium* × *heteroresiliens* occurs well north of the range of one of its parents, *A. heterochroum.* The sexual *A.* × *pinnatifidum* occurs far to the west of one of its parents, *A. montanum.* We usually assume that hybrids are better adapted to their habitats and more flexible than their parents, but this may not be so.

The matter of disturbed habitats has long intrigued hybridists, because it is assumed that crossing takes place more readily in upset than in settled conditions. *Do hybrids form more readily in disturbed sites than in settled communities?* It is somewhat difficult to answer because many of nature's successional phases can be classified as "disturbed" such as marshes, prairies, savannas, swamps, rock cliffs, and so on – habitats that normally host species of ferns. In general, roadsides, edges of pathways, openings in the forest, old rotting tree trunks, talus slopes, and a variety of other, more or less transient situations do seem to stimulate hybridization. In Florida we find *Pteris* × *delchampsii* (*P. bahamensis* × *vittata*) where disturbances occurred, and in Hawaii *Thelypteris* × *palmeri* (*Th. cyatheoides* × *dentata*) the same. In both of these cases, it should be noted that the first parent is a native species, the second one an adventive weed that normally occurs in strongly disturbed habitats. As regards ferns, the question of disturbance stimulating hybridization must be approached carefully because so many fern habitats where orthospecies concentrate are actually stages in succession toward a climax community.

Tropical pteridologists have long been concerned with the differences between epiphytic and terrestrial ferns. In some localities as many as one-third of the species may be epiphytes, often including all the members of certain genera or families. It is usually assumed that epiphytes have different germination requirements from terrestrial species (although some species may be both epiphytic and terrestrial). A problem greatly needing study is: *Do epiphytic pteridophytes cross less readily than epipetric or terrestrial pteridophytes?* So far the information suggests that they do cross less readily;

the number of epiphytic fern nothospecies is smaller than that of terrestrial fern nothospecies. Practically all of the hybrids in Hawaii and Costa Rica that are known so far are terrestrial or between epiphytic and terrestrial orthospecies. The recent discovery of various *Elaphoglossum* hybrids in Mauritius was interesting because the orthospecies involved are terrestrial, rather than epiphytic, the usual state for the genus. If it does indeed prove to be the rule that epiphytic fern hybrids are less common than terrestrial ones, an intriguing further question is Why.

A number of botanists believe that nothospecies should be ignored when analyzing species associations. I ask: *Should nothospecies be included in community and floristic studies?* And I answer: Why not? There are various kinds of nothospecies, including asexual *de novo* hybrids, asexual apomicts that reproduce by vegetative means or by apogamy (or by unreduced spores? See above), or sexually (allohomoploid or allopolyploid). In the case of asexual *de novo* hybrids, or what we believe to be these, their presence is often almost as characteristic of a given community or flora as any sexual orthospecies. For example, it is difficult to find a swamp community in Michigan, U.S.A., that lacks *Dryopteris* × *boottii* (*D. cristata* × *intermedia*) or *D.* × *triploidea* (*D. carthusiana* × *intermedia*). These sterile nothospecies are much more common over-all than is the fertile allopolyploid nothospecies, *D.* × *clintoniana* (*D. cristata* × *goldiana*). Certainly *D.* × *boottii* and *D.* × *triploidea* are much more common and characteristic of swamps in Michigan than are certain well known orthospecies, such as various ferns (e.g., *Dryopteris goldiana*) or orchids (e.g., *Corallorhiza trifida*).

Closely related to the above is the following: *Should nothospecies be given the same attention as orthospecies in analyses of rare and endangered species?* Practically all of the compilers of rare and endangered species leave out nothospecies. It you ask them why, they state that they are interested only in "true species" (i.e. orthospecies). But how can this be? Well known American taxa, *Dryopteris* × *celsa, Asplenium* × *bradleyi, A.* × *ebenoides, Aspidotis* × *carlotta-halliae* – all of these and many more are hardly orthospecies or "true species." They originated, without doubt, through reticulation between parental orthospecies; they are probably no different, except for becoming amphidiploid, from their sterile antecedents. All of the evidence now coming from allozyme electrophoretic techniques supports this conclusion. For that matter, what of the numerous nothospecies that reproduce by apomictic methods such as rhizome or root proliferation or by spore apomixis? Many orthospecies are apomictic just as are nothospecies. Why should nothospecies be treated differently? I am in the dark about why conservationists should want to ignore taxa of hybrid origin, but I am in the minority, and would appreciate learning more about the reasons underlying the seeming paradox.

With increasing interest in phyletic methods of recent years there has been increasing interest in the study of hybrid characters, especially in reference to phylogenetic analysis and how hybrids fit into the over-all scheme of things. Quite a few workers still doubt whether our methods of detecting hybrids are valid, in spite of repeated confirmations of our conclusions. They argue that the only way to be sure that a plant is a hybrid is to recreate the taxon by experimental hybridization. *Are our indirect tests for diagnosing hybrids (such as morphological intermediacy, chemical additivity, disturbances in the life cycle, chromosome pairing, association with parents) reliable?* For those still reticent about accepting our indirect tests, I recommend reading the excellent paper of Professor Reichstein's on "Hybrids in European Aspleniaceae" in Botanica Helvetica 91: 89–139 (1981). It nicely summarizes our knowledge of European spleenwort hybrids, but also gives references to the huge corpus of experimental and circumstantial evidence that has been acquired over the years.

There seems to be some confusion about what we mean when we say "morphological intermediacy." *What do we mean by intermediacy – having character states anywhere between those of the parents, or in the middle between the parents?* For some reason, not clear to me, a number of workers have come to the conclusion that hybrid intermediacy must mean precisely in the middle between the parents. In actuality, most hybridists accept as intermediate any stage in the sequence between the character state of one parent and that of the other. In total, and on the average, the nothospecies lies approximately in the middle between the two parental orthospecies, i.e., over-all, the hybrid is near the middle between the parents, but the individual characters that make up the whole fluctuate from nearer one parent or nearer the other. A related question is: *In the character states of nothotaxa, what causes intermediate vs. dominant vs. transgressive expressions?* My impression is that certain character states such as venation free tend to be dominant over others such as venation reticulate. Transgressive character states, those that are not intermediate between the parents, are especially fascinating, and they bring up the whole question, for example, of the nature of heterosis or hybrid vigor. Often, hybrids tend to be larger and (or) more vigorous than their parents, but sometimes (perhaps more often than is generally realized) they are smaller and (or) less vigorous than their parents. In hybrids between diploids and tetraploids, all nothospecies tend to be closer to the tetraploids.

A very enticing problem related to the foregoing now comes up: *Is intermediacy more consistently medial (close to the middle) the more closely related are the parental orthospecies?* This is a question that has not been stressed in the past, but one that can perhaps be answered statistically by using measures of difference between the orthospecies characters and the nothospecies characters and correlating these with the totals of differences between the parents. If the answer to this query is positive, then we may expect much more irregular distribution of intermediacy in intergeneric or intersectional nothospecies than within intrageneric or intrasectional nothospecies.

Irregular or asymmetrical expressions of characters of meiosis and morphogenesis have long been taken as tokens of hybridity. *Are irregular expressions of meiosis and morphogenesis altogether dependable indicators of hybridity?* Meiotic irregularity is well known in cases of hybridization between different ploidal forms of the same orthospecies. Probably other factors beside hybridization can cause meiotic irregularity but in such cases the individuals showing it will not have the other features of nothospecies. Irregular morphogenesis results in commonly striking deviations from symmetry, and is well known, for example, in hybrids between simple- and compound-bladed orthospecies. Often taxa with strongly different patterns of soriation display soral irregularity. However, irregularity is also well known among ferns that are evidently orthospecies. Some of the forms of the diploid Hawaiian *Pteris irregularis* are noted for their irregular frond cutting. The Fijian *Syngramma pinnata* and the Costa Rican *Pleopeltis gomeziana* both illustrate striking irregularities of soriation more or less combining coenosori with schizosori. The very distinctive Hawaiian *Grammitis tenella* has, among its other peculiarities, very irregularly scattered sori, unlike other grammitids with neat rows of sori on either side of the midrib. All of these examples are apparently "true species," not nothospecies. Their irregularity should not be used as a diagnosis of hybridity.

Can we predict what a given nothotaxon will look like before it is produced in the laboratory or found in nature? This question is, of course, closely related to some of the foregoing ones. For any given character, and assuming perfect mediality for the hybrid expression, we can quantify the situation as follows: Let A be character state value for

orthospecies 1, and B be character state for orthospecies 2. The formula for X, the character state value for their hybrid, then, would be

$$(A+B)/2=X$$

For all the differing characters in orthospecies 1 and 2, the same formula is used, and theoretically all the characters can be combined to describe the hybrid. Unfortunately, as indicated above, intermediacy is not usually completely medial, so that some characters will be mispredicted. By and large, however, a fairly close approximation can be made for the majority of hybrids of which I am aware. The formula is also useful for predicting a parent, given the nothospecies and the other parent.

Where the parental orthotaxa differ in character states, are the primitive states likely to be expressed more strongly than the advanced ones (i.e., plesiomorphy dominant over apomorphy)? I do not know the answer, or any answers, but I suspect that there may be some difference in inheritence. Of nothotaxa I have studied, free venation dominates over reticulate, and the free condition is generally considered to be primitive. Examples are *Asplenium* × *Camptosorus* and *Lindsaea* × *Odontosoria.* Glandularity is dominant in American hybrids involving *Dryopteris intermedia* with species that lack glands. The presence of abundant acicular hairs is dominant in hybrids involving the glabrous Hawaiian *Thelypteris cyatheoides* and the hairy introduced *Th. dentata.* However, we do not yet know the polarities involving these indument characters.

The highly vocal cladists who are concerned primarily with producing cladograms or branching diagrams have made every attempt to accomodate nothotaxa in their graphs, using strictly cladistic techniques for accomplishing this. They tend to believe that nothotaxa are no different from orthotaxa in making their trees. Let us ask: *Should nothospecies be treated the same as orthospecies in phylogenetic analysis?* Evolutionists (as opposed to cladists) tend to agree with me that hybrids should be recognized and withdrawn from any phylogenetic analysis beforehand. The analysis can then be made using divergent orthotaxa, and only after it is made can the hybrid attachments be accomplished. This question can be resolved only after the "schools" of phylogenetics have calmed down, and the pros and cons can be evaluated eclectically and thoughtfully.

One of the most serious objections to treating nothotaxa as the same as orthotaxa in making cladistic analyses is that many of the practitioners do not distinguish between hybrid character states and divergent species character states. *Can nothospecies characters be scored in a phylogenetic analysis as 0 for primitive and 1 for advanced, or is it necessary to include hemiapomorphic states scored as 1/2?* Having two extreme conditions, the plesiomorphic and the apomorphic, gives an easy contrast. Unfortunately, most hybrid characters are intermediate, if not medial. Thus character analysis that involves both ortho- and nothospecies requires a careful evaluation of to what extent the apomorphic state is expressed. It is not fair to say that the parents have pinnate blades and simple blades respectively, and the hybrid also has simple blades, when in fact it has the intermediate condition, i.e., pinnatifid blades. Thus if pinnate is primitive and simple is advanced, the hybrid is only partially advanced, i.e. hemiapomorphic. Others (obviously) handle the matter of scoring differently, so that we must await for consensus in the future.

How can nothospecies be separated from orthospecies prior to a phylogenetic analysis? Many workers, especially cladists, feel that they cannot be separated *a priori,* but only after a cladistic routine is followed, *a posteriori.* Nevertheless, taxonomists have for many generations learned to spot hybrids by simply recognizing numerous hemi-

apomorphies. As the specimens are sorted, certain ones turn out to be intermediate in numerous characters, and by using the mind and the eye it is readily feasible to detect nothospecies and to check their parents. This method can and has been converted to computer hybrid detection methods which make all possible triplets in the study collection and find those which have two extremes and one intermediate.

Patently it is illogical to present hybrids as orthotaxon branches. The only scientific way to express nothotaxa is to place them on the phylogenetic graph as connections (which is what they are) between separate orthotaxa. The answer to *How should nothotaxa be expressed in phylogenetic graphs* is nevertheless controversial. Some cladists prefer to make a trichotomy, the hybrid "line" between the two parental lines. In other words, the nothotaxon is expressed as an unresolved clade together with its two parents.

Taxonomists have had trouble with hybrid nomenclature since the inception of the binomial system. They have had difficulties in finding a place to put them in the herbarium and in monographs. They are often hard to key out, especially in groups that have undergone extensive reticulate evolution. Some authors have argued that sterile hybrids should always be expressed as formulae, e.g. *Asplenium montanum* × *platyneuron*. Unfortunately, the same diploid combination may also be represented by a tetraploid combination, the former sterile, the latter fertile. Also, a formula is really not a name; it is a taxonomic statement about the origin of a particular plant. In spite of the serious efforts of the Committee on Hybrid Nomenclature of the International Association for Plant Taxonomy, there are still problems, most of them having to do with taxonomic consistency and logic rather than the nomenclatural procedures themselves.

One of our biggest problems has to do with using the varietal category in place of the hybrid category. In North America this has been a very serious problem because some workers believe that hybrids should be treated as orthovarieties and not as nothospecies. We may inquire: *Should a hybrid be treated as a variety of the parental orthospecies to which it bears or seems to bear the greatest resemblance?* Well known examples are *Pellaea ternifolia* var. *wrightiana* (= *P. mucronata* × *ternifolia*) and *Dryopteris cristata* var. *clintoniana* (= *D. cristata* × *goldiana*). Dozens of others can be quoted, of which most are treated by the majority of workers as nothotaxa, although some diehards persist in the use of variety for hybrid.

One of the most surprising uses of nomenclature is to treat the sterile forms of hybrids as nothospecies but the fertile forms as orthospecies. Thus the sterile form of *Polystichum dudleyi* × *munitum* would be *P.* × *californicum* and the fertile form *P. californicum* (i.e., without the × sign, the indicator of nothospecies). Another good example from the North American flora is *Asplenium platyneuron* × *Camptosorus rhizophyllus*. This genotype occurs in two forms, sterile diploid and fertile tetraploid. The hybrids are placed in the hybrid genus × *Asplenosorus*. However, the fertile form, for consistency, is placed in the non-hybrid genus *Asplenosorus*. Somehow, the concept of hybridity of many taxonomists is confused with sterility. If sterile, it is a hybrid (nothospecies); if fertile it is a normal species (orthospecies). It has always seemed to me that the designation intended by the multiplication sign, ×, classifies the taxon as a hybrid, and that it is therefore a very useful device. It is my opinion that all taxa for which there is sufficient evidence for interspecific hybrid origin should be so designated by the use of the × sign. My answer to the question *Should allopolyploids be treated as orthospecies or nothospecies?* is that they should be treated as nothospecies using the × sign. But there is not wide agreement on this point.

One of the questions that constantly arises is the following: *Can the presence of intergeneric hybrids (nothogenera) be used as a basis for evaluating whether two genera should be merged or not?* Most of us know what answer the orchidologists would give to this question. In ferns, however, there is less agreement. Indeed, some of the situations are amusing. The same author may use intergeneric hybridization as a basis for merging some genera and ignore it in other cases. One might say that the presence of intergeneric hybrids is an indication that recognition of two genera may not be warranted, but each situation needs to be carefully evaluated on its own.

Is the present Code's requirement that nothogeneric names be formed from the names of the parent orthogenera the best procedure? On the face of it, this procedure seems to be ideal, but there are some problems. The outstanding problem has to do with genus names. Not only are generic definitions rapidly changeable during periods of taxonomic upheaval, but failure of conservation may bring new names to apply. To give a crude example, if *Aspidium hawaiiense* hybridized with *Phegopteris honolulensis* and the nothogeneric name ×*Aspidopteris* were created for it in 1920, today the Hawaiian parent species are known as *Dryopteris hawaiiensis* and *Ctenitis honolulensis* respectively, so the nothogeneric name loses its relevance. This leads to an additional question: *If a name already exists for a nothogenus, should it be rejected in favor of a compound nothogeneric name?* The spectacular hybrid of *Dictyoxiphium panamense* with its "upside down" marginal coenosorus and *Tectaria incisa* with ordinary dorsal discrete sori, should according to the Code be named something like ×*Tectaroxiphium.* However, this hybrid already has a time-honored name, ×*Pleuroderris michleriana.*

An interesting problem recently arose when an author published a sectional classification of a well known genus, and included in his treatment some intersectional hybrids (i.e., hybrids between species respectively in two different sections). *Should intersectional hybrids within genera be placed in the section of one of the parents, or in a special nothosection?* Logically, only one answer seems possible: a special nothosection must be created, because the nothospecies cannot rationally be placed in the section of only one of its parents. Nevertheless, the author in question did just this.

One of the worst taxonomic mix-ups comes about because of the following apocryphal situation:

Dryopteris cristata × *D. carthusiana* var. *carthusiana* = *D.* × *uliginosa*

D. cristata × *D. carthusiana* var. *intermedia* = *D.* × *boottii*

I pick up a manual and find that two wholly separate nothospecies binomials are applied to hybrids that have the same species are parents, but differ in that one of the parents involves different varieties. The question is: *Should nothotaxa that differ only in having different varieties of one of the parents involved be treated at the species or the varietal level?* I submit that the most logical treatment would be for the nothotaxa to be dealt with as varieties, as follows: *D.* × *uliginosa* var. *uliginosa* and *D.* × *uliginosa* var. *boottii* respectively. However, many traditionalists would disagree.

The above questions deal with a wide range of problems ranging from broad evolutionary significance and character analysis of hybrids to the formalistic procedures involved in nomenclature. To me, nothotaxa are very different from orthotaxa, and the recognition of this difference is fundamental to clear taxonomic and evolutionary understanding. Typically, nothotaxa in ferns differ from orthotaxa in many ways: geography, population structure, abundance, ecology, duration in time, process of origin, number of generations required to produce them, cladistics, phylesis, gradistics, apomorphy, symmetry, chemical profiles, experimental synthesis, and comparative value for the study of character polarities. The investigation of hybrids in nature has be-

come a whole field in itself, one that I have named "reticulistics," because so many of the ground rules are different from those pertaining to organisms with normal, divergent origins. It is delightful that finally in the history of pteridology, practically all workers accept the importance of hybrids in the study of free-sporing plants, and we have now succeeded in building up a body of hypotheses that will keep us busy for many years to come. It is my hope that the assortment of questions asked here may be of some value in helping to align our research and to recognize where work is most needed. There are probably many others I have missed. The most important question about fern hybrids that we can ask is: *Which questions are the most important?*