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| <b>PROPOSALS TO AMEND THE CODE</b> |
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**(13) Proposal to designate reproductively competent species of hybrid origin by an  $\times$  placed in brackets (reword Article H.3 *Note 1*)**

Interspecific hybridization, a prevalent and problematic aspect of plant diversification, is dealt with in the present Code of Botanical Nomenclature (ICBN, 1988) under the rules for nothotaxa. The majority of interspecific hybrids that form in nature are of isolated and ephemeral occurrence, and are either sexually sterile or otherwise disadvantaged. However, a significant fraction of natural hybrids do become reproductively competent and form populations, thus giving rise to species of hybrid origin that differ significantly from orthospecies that arise through the more usual processes of mutation, recombination, isolation, selection, and drift. Perhaps the most frequent class of taxa of hybrid origin is that of sexual allopolyploids. However, other classes are known (see below), including stabilized species of allohomoploid origin. In addition, reproductive competence of hybrids may be effected by various avenues of apomixis, including several modes of vegetative reproduction (see Grant, 1981, for a review of the role of hybridization in plant evolution).

For the purposes of the present discussion, the immediate products of interspecific hybridization (i.e., usually sterile  $F_1$  hybrids) will be referred to as initial nothospecies, and any taxa derived from these that are reproductively competent will be referred to as reproductive nothospecies. Only in certain cases are initial hybrids immediately reproductively competent (fertile allohomoploids and certain types of apomicts particularly). Reproductive nothospecies share most of their features with the initial nothospecies that are their progenitors, but also differ from them in important ways. Both types may be thought of as hybrids, because there is a direct lineage from the initial nothospecies to the reproductive nothospecies. Moreover, the hybrid genotypes of initial nothospecies are usually perpetuated more or less intact by the derivative reproductive nothospecies (cf. Roose and Gottlieb, 1976; Werth et al., 1985a). This is underscored by the contemporaneous occurrence of some allopolyploids with their allodiploid progenitors, whereby their close phenotypic and genotypic similarities are readily apparent. However, in nature, reproductive nothospecies function ecologically much as do the more usual taxa of divergent origin by forming populations and becoming permanent and perhaps important components of natural ecosystems. These nothospecies may evolve through mutations (for example allopolyploids may experience silencing of duplicate genes—Werth et al., 1985b) and thereby acquire novel genotypes (and phenotypes) that are somewhat different from those of their initial nothotaxon ancestors. There is also evidence that reproductive nothotaxa may undergo orthospeciation, thus becoming the nodes from which future clades arise (Werth and Windham, 1990).

The present Code provides for indicating hybridity of a taxon by use of a multiplication sign  $\times$  (H.1.1), used either in a formula (H.2.1.) or placed before the collective specific epithet of the hybrid (or genus name in the case of an intergeneric hybrid) (H.3.1.). A distinction between initial and reproductive nothospecies is implied under *Note 1* of Article H.3 which reads "Taxa which are believed to be of hybrid origin need not be designated as nothotaxa." Unfortunately, in many cases this provision presents a dilemma for the treatment of reproductive nothospecies. To designate a reproductive nothospecies as a hybrid by use of the unbracketed  $\times$  equates it to an initial nothospecies, failing to recognize the intervening evolutionary history of the taxon. On the other hand, omitting the  $\times$  results in a failure to communicate an extremely important attribute of the reproductive nothospecies, i.e., that it is biologically a hybrid, and equates such taxa to those that have arisen through divergent orthospeciation, even though that is not the case. The problem becomes especially acute when both an initial nothotaxon and its derivative reproductive nothotaxon are contemporaneous (and even syntopic), where a choice must be made between treating both as equivalent nothospecies, or treating the reproductive nothospecies as a non-nothotaxon, resulting in confusion. In cases where the distinction between initial and reproductive nothospecies is not clear cut, such as allohomoploids and hybrids that are sexually sterile but reproduce *via* apomixis, the choice must be made either to treat the taxon as a nothotaxon, or treat it erroneously as an orthospecies with no hybrid history. Thus, the designation of reproductive nothotaxa by the use of the  $\times$  has been inconsistent. The following proposal is a simple way to alleviate this problem:

(13) Proposal to reword Article H.3 *Note 1*:

"Note 1. For reproductively competent taxa known to be of hybrid origin, hybrid ancestry may be indicated by placing an  $\times$  in brackets immediately before the epithet or genus name."

Use of brackets rather than round parentheses is preferred because of remotely possible confusion with procedures adopted in the International Code of Nomenclature for Cultivated Plants (Brickell et al., 1980). Under "Collective Names, Article 14" it states: "The formula designating derivatives of an interspecific or intergeneric somatic cross, obtained by a parasexual process such as protoplast fusion, consists of the botanical names of the parents connected by a multiplication sign within parentheses (round brackets). Example: *Nicotiana glauca* ( $\times$ ) *N. langsdorffii*."

Such a procedure allows for distinguishing immediate hybrids from their reproductively competent derivatives. In some borderline cases, such as certain vegetatively reproducing hybrids, there would be justification for using either the initial or reproductive nothospecies designation, depending on their success. In such cases, we recommend in general the use of [ $\times$ ]. Usage will no doubt vary among taxonomists, but the decision will be less drastic than the all-or-none hybrid designation of the present Code. It is *not* recommended that the [ $\times$ ] designation be used for strongly introgressed taxa that have hybrid ancestors but retain only a small portion of the contribution of one of the parental taxa.

One of us (Wagner, 1983) has repeatedly stressed the need to distinguish all taxa of hybrid origin from normal, divergent taxa. The basic phylogenetic framework of plants is produced by divergence, involving amount, direction, and sequence of evolutionary changes. Hybrids, unlike orthotaxa, bring together different lines or clades. They are mostly intermediate and additive in their character states, including all levels—geography, ecology, morphology, anatomy, cytology, chemistry, and molecular biology. It is a serious mistake to confuse reticulistic mixing with gradistic and cladistic divergence. Some authors in the past have even included taxa of hybrid origin together with normal divergent species in their phylogenetic analyses! However, such analyses were never designed to accommodate hybrids, and the results can be extremely distorted. For this, as for other reasons given above, the use of [ $\times$ ] is strongly supported.

Examples to illustrate this proposed usage are widespread among the classes of higher plants. Rather than indicate precise wording of examples to be included in the Code at this point, we present for consideration a number of cases with which we have become familiar. The final wording in the Code might include some of these as well as others that might be offered as especially illustrative. In flowering plants, the Droseraceae provide a classic example. The hybrid sundew *Drosera*  $\times$  *anglica* Hudson is a circumpolar fertile allotetraploid derived from *D. linearis*  $\times$  *rotundifolia*. It occurs even in the Hawaiian Islands. Yet, in the Great Lakes region of North America, the reproductively competent form grows side-by-side with new sterile diploids and the parents (Voss, 1985). These two kinds of hybrids are indistinguishable morphologically, except that the initial hybrids have abortive seeds and fruits. Voss gives them the same binomial, but he calls the allotetraploid "*D. anglica*" and the allodiploid "*D.  $\times$  anglica*." We propose that, instead of the above procedure, the two forms be designated respectively *D.* [ $\times$ ] *anglica* and *D.*  $\times$  *anglica*, thus recognizing their close taxonomic and genetic affinity and at the same time indicating the difference in reproductive potential.

In ferns, the Appalachian *Asplenium* complex (Wagner, 1954) provides some very appropriate examples. *Asplenium*  $\times$  *ebenoides* R. R. Scott, the sterile hybrid of *A. platyneuron* and *A. rhizophyllum* arises at numerous localities. The fertile allotetraploid derived from this hybrid, *A.* [ $\times$ ] *ebenoides*, is also known, but only from a single locality (Hale County, Alabama). Conversely, while the fully reproductive allotetraploid *A.* [ $\times$ ] *bradleyi* (derived from *A. montanum*  $\times$  *platyneuron*) is widespread, the sterile initial nothospecies *A.*  $\times$  *bradleyi* is known from only two localities (Wagner et al., 1973; Werth and Evans, unpublished). The initial nothospecies corresponding to the fertile allotetraploid *A.* [ $\times$ ] *pinnatifidum* (*A. montanum*  $\times$  *rhizophyllum*) is still unknown but could be very easily overlooked in the field because of its confusion with the reproductive form.

The clubmosses provide interesting examples of widely different reproductive competencies in hybrids. In the gemma fir-mosses of the genus *Huperzia* there occur numerous sexually sterile crosses, some of them surprisingly frequent and widely distributed. Beitel (unpublished) finds extreme spore abortion in these hybrids, but they are nevertheless widely propagated and dispersed (in nature) by elaborate gemmae—highly modified samara-like shoots that abscise and are spread by wind. These reproductively competent nothospecies may occur in large colonies at some distance from the parents, for example the frequently occurring *H.* [ $\times$ ] *bartleyi* Cusick (*H. lucidula*  $\times$  *porophyllum*) of the Appalachian region of eastern United States.

In flat-branched clubmosses, *Diphasiastrum*, in contrast, the homoploid initial hybrids are evidently fully sexual immediately, undergoing normal meiosis and producing healthy spores. These hybrids can reproduce in two ways: locally by extensively branching rhizome systems that sometimes form huge colonies tens of meters in diameter, and presumably by allohomoploid spores that provide dispersal over much longer distances and the formation of new clones. Both of these reproductive means are believed to account for the wide distribution, over a large area of eastern North America, of the well-known reproductive nothospecies *Diphasiastrum* [ $\times$ ] *habereri* (House) Holub, the hybrid of *D. digitatum*  $\times$  *tristachyum* (F. Wagner, unpublished).

Among scouring rushes, Equisetaceae, there are a number of examples of sexually sterile nothospecies rendered reproductively competent by vegetative reproduction from nodes of stem fragments. *Equisetum* [ $\times$ ] *iferissii* Clute is the sterile-spored hybrid of *E. hyemale*  $\times$  *laevigatum*. This taxon occurs well beyond the range of one of its parents, demonstrating that vegetative reproduction by fragmentation can be effective in accomplishing long distance dispersal of the hybrid, especially along lake shores and rivers (Hauke, 1963; Wagner and Hammitt, 1970). Although it is a sexually sterile hybrid, it is common enough to be reckoned with over an extensive area of North America.

Thus reproductive competence in nothospecies is accomplished over a broad spectrum of vascular plants and via a wide array of mechanisms, including allopolyploidy, fertile allohomoploidy, gemma production, and fragmentation. Not the least of the methods is one still to be cited, namely apomixis by seeds or spores. In the ferns, the plant that we wish to designate *Asplenium* [ $\times$ ] *heteroresiliens* W. Wagner is an apogamous derivative of the hybrid *A. heterochroum*  $\times$  *resiliens*. The former is a tetraploid sexual species limited to Florida, the latter a triploid agamosporous species widespread in southern United States and Mexico. Their hybrid ranges in the eastern Coastal Plain from Florida to North Carolina, and it is a pentaploid that inherited the apogamous life cycle of *A. resiliens* rather than the sexual cycle of *A. heterochroum* (Morzenti, 1966; Wagner, 1966). *Asplenium* [ $\times$ ] *heteroresiliens* is thus a reproductively competent nothospecies. Similar conditions involving seed apomixis of various types occur in flowering plants and are apparently important in some genera, e.g., *Amelanchier* (Campbell, Greene, and Bergquist, 1987) and *Crataegus* (Dickinson and Phipps, 1986).

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