

An Intersectional Point of View

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I would like to use my column this time to share some of my thoughts on the new book by Josef Halda, which was reviewed by Bill Countryman in the June issue of *The APS Bulletin*.

In his review of The Genus Paeonia, Bill Countryman deemed Josef Halda's new book as a worthy successor to the famous and most widely recognized monograph on *Paeonia*, A Study of the Genus Paeonia. Although I agree with many of the glowing remarks praising this book, I do not accept it as the successor to the Stern monograph. In the next few paragraphs, I will give the reasons why.

Let me start by briefly discussing the Stern monograph. Stern studied and classified the genus *paeonia* in his monograph, A Study of the Genus Paeonia published in 1946 by the Royal Horticultural Society. Stern divided the genus into three sections, one for the American species, *Onaepia*; one for the rest of the herbaceous species, *Paeonia*; and one for the woody types (tree peonies), *Moutan*. He further divided two of these sections, *Moutan* and *Paeonia*, into two sub-sections each. For example, section *Paeonia* was split into sub-sections, *Paeonia* and *Foliolatae*, according to the degree of foliage dissection. All things considered, this classification of the genus *Paeonia* has stood up very well for more than 50 years. Recently, in a series of seminal DNA studies on peonies by Sang, *et al* the authors concluded that many species in section *Paeonia* are of hybrid origin and that a third sub-section in section *Paeonia* was probably required to taxonomically accommodate these various hybrid species. This aside, Stern's classification of the genus appears to have held up quite well when examined under the light of these modern DNA studies.

Halda has suggested in his new book that Stern's analysis was incomplete because his results were based primarily on examination of foliage with little attention to other plant characteristics, such as roots, flowers and seeds. Halda attempts to correct this deficiency and improve on the Stern treatment by studying a broader range of plant characteristics including roots, flower structure, fruits, seeds as well as leaves. The assumption being that the more information collected and analyzed, the better the result will be. However, this may not always be true. Sometimes, there can be too much information, especially if different data sets are inconsistent and/or contradictory. In such cases, it is possible to arrive at erroneous or illogical conclusions. Furthermore, it is likely that some morphological characteristics are far more useful and reliable than others as taxonomic indicators in plants. Including more, but possibly less reliable, factors in the analysis, therefore, can ultimately produce a less reliable result. This may be what happened here. It is hard to tell from the book or from his earlier publications just where Halda went wrong, but his conclusions are fairly radical and appear to be inconsistent with both Stern and the recent studies of Sang and others mentioned above.

The most serious deficiency of the Halda book is that it ignores virtually all of the work published by others on peonies over the last 12-15 years. This includes at least a dozen missing references to recent work by Tao Sang, *et al* and De-yuan Hong, *et al* that include several landmark publications (by Sang) which document the extensive natural hybridization found in the evolution of the genus *Paeonia*. In fact, other than references to the author's own work (1997-1999), there is only one reference after 1992.

The grouping together of related species into sections and subsections based on plant morphology has always been a complex and difficult scientific task that is inevitably accompanied by some degree of controversy and disagreement. The recent application of molecular markers, however, has greatly facilitated the detection of hybridization as well as the recognition of allopolyploids

in many plant groups. This is especially true in *Paeonia*, where several recent landmark studies by Tao Sang, *et al* (1995, 1997) have clearly established that reticulate evolution has played a primary role in speciation in peonies. These studies have concluded that the majority of the species in section *Paeonia* of the genus are of hybrid origin. This extensive natural hybridization in section *Paeonia* has made classification of the genus extremely difficult. Without the ability to recognize and detect where hybridization has occurred, it is nearly impossible to accurately reconstruct the very complex reticulate evolution patterns within section *Paeonia* of the Genus. In the midst of these new discoveries, Halda presents a new classification that represents a radical departure from the currently accepted classification of the genus. Unfortunately, this classification is in serious disagreement with Stern and nearly every other classification of the genus as well. More importantly, Halda supports his hypothesis by referencing only his own work while ignoring virtually all other work on the genus published during the last 15 years. This includes the series of seminal studies published since 1995 on the DNA analysis of peony species by Tao Sang, *et al* mentioned above. Halda can, of course, choose to dispute the validity of these studies, but he cannot choose to simply ignore them. It is important to note that these modern studies generally confirm the conclusions draw by Stern from the leaf morphology while lending little or no support to the conclusions put forth by Halda.

The problems with the Halda treatment and conclusions are many. Probably the most troubling and difficult to understand is the assignment of *Albiflora* (which in Halda's study contains only one species, *lactiflora*) as a subgenus. Halda's classification divides the genus into four subgenera: *Moutan* (which includes all the woody species), *Onaepia* (which includes the two American herbaceous species), *Paeonia* (which includes all of the other herbaceous peonies except *lactiflora*) and *Albiflora* (*lactiflora*). It is the separation of *lactiflora* from all of the other herbaceous species and its elevation to the subgenus level that represents the greatest departure from other previous classifications. Unfortu-

nately, Halda presents no real explanation or justification for such a radical reassignment, nor does he discuss or deal with the significant implications of his new assignments. As pointed out by Bill Countryman in his review, accepting this new assignment has major implications for the "Itoh" hybrid group that are now widely referred to as "intersectional" hybrids. Accepting Halda's classification would elevate these hybrids to the level of "intersubgeneric" hybrids thus making them even more important and unusual than they already are. In my opinion, Countryman's review did not carry this argument nearly far enough. Accepting Halda's classification also has major implications for the nomenclature of virtually every hybrid group within the genus. For example, Halda's classification also requires that the vast majority herbaceous hybrids in existence also be classified as "intersubgeneric" hybrids, since they are largely hybrids between various herbaceous species (all from subgenus *Paeonia*) and lactiflora (subgenus *Albiflora*). Considering just how uncommon "intersubgeneric" hybrids are throughout the rest of the horticultural world I find this radical new assignment of the genus *paeonia* too much for me to accept without compelling new evidence. Unfortunately, no such evidence has been presented. In the final analysis, I believe this book represents a major opportunity lost. As a replacement for the Stern monograph as the definitive work on the genus, I am sorry to report that in my opinion this book short of the mark.