

## Part 4F

# *Hosta* Species: Breeding Systems, Reproductive Organs and Fertility

By W. George Schmid ©2006 for the Hosta Library

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**Hosta Flower  
Showing 6 Anthers and 1 Pistil**

***Breeding Systems:*** Like all other living species on Earth, the survival of the species of the genus *Hosta*, depends on their ability to reliably produce offspring. In fact, hostas are quite successful in that regard. No doubt, hostas are a prolific bunch. Many plant species in different genera will refuse to make hybrids with another species, but, as many a hosta hybridizer can attest, the cultivated species of the genus *Hosta* are a rather indiscriminate bunch when it comes to keeping “pure lineage.” In the wild as well as in gardens, different species will interbreed with abandon. There is no doubt that one of the classic definitions of a species (as a population of similar individuals that in nature breed only with each other) just does not apply to the genus *Hosta*.

Nevertheless, many of the species do behave like species, as long as they are reproductively isolated.

This reproductive isolation can be caused by geographical, seasonal, ecological or other non-genetic factors. *H. yingeri*, for example, speciated on a remote island off the coast of Korea and evolved into a distinct species, which breeds relatively true,



**Hachijojima Island with Mount Hachijo-fuji  
Home of *H. rupifraga***



**Female Style (left) with Stigma  
Male Filaments (right) with Anthers  
(usually 6 ▪ only 3 shown)**

when carefully selfed under protected conditions. This is also true (to a lesser extent) with *H. rupifraga*, another species that evolved in relative isolation on Hachijojima, a remote island in the Pacific Ocean 220 miles south of Tokyo. Its speciation into a thick-leaved, short-scaped species was primarily caused by ecological factors, namely its adaptation to a changing, inhospitable habitat on the top of Hachijo-fuji Mountain. Still another, *H. venusta*, speciated from *H. minor* remnants deposited on mountainous Cheju Island after the last Ice Age. In order to survive, those pitiful remnants had to change into another species rather quickly, much smaller and more adapt to life on top of a mountain. I mention this to show that *Hosta* species are survivors and the species will interbreed or speciate if they have to.

***Male and Female Reproductive Organs:*** All flowers in the genus *Hosta* are bisexual, meaning they contain both male and female reproductive organs.

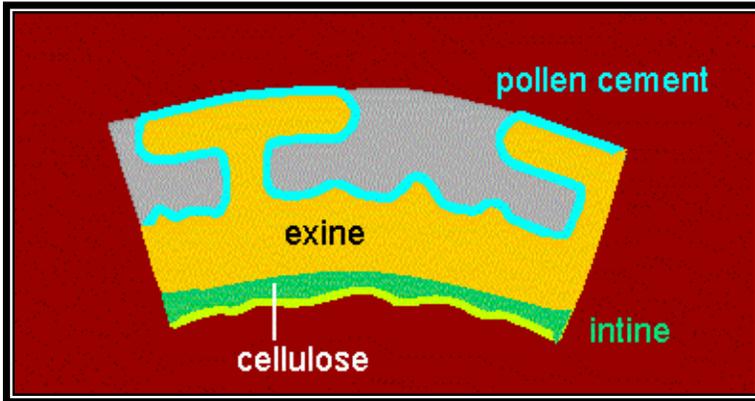


***H. montana* Seed Pods • Hosta Hill (W.G.Schmid Photo)**  
Fertile Bracts Remain and the Spent White Tepals Remain Attached to the Pods

***The female reproductive organ*** is a compound type pistil fused together from 3 parts (*carpels*) and comprising the ovary located at the base of the flower, a long, tubular, usually up-curving style with a 3-lobed stigma, which receives the pollen. As can be seen in the photo on Page 2 (above), frequently, the 3 stigma lobes are not fully developed and appear to be a ball-shaped structure. Notwithstanding, in some species, the stigma is distinctly 3-lobed. The ovary has 3 cavities (*locules*) in which the ovules are arranged in 2 rows attached to the central axis of the ovary. The ovary develops into a seed capsule which, when it becomes dry, splits open starting at the tip in 3 parts progressively curving away from the initial point and finally being individually attached to the pedicel only.

***The male reproductive organs*** are the stamens consisting of the filaments, long, slender stalks, usually up-curving, 6 in the genus and the 6 anthers. In most species the filaments are attached below the ovary but in *H. plantaginea* they are attached to the lower inside of the tepals above the ovary. The anthers are pollen sacks, 6 in *Hosta*, which are bilocular, meaning each anther is composed of 2 pollen sacks. In the cavity (*loculus*) of each sack mother cells undergo meiosis which eventually results in the production of pollen grains. In the genus *Hosta* the anther surface cells have characteristic coloration and patterns which are useful in classifying the species.

Fertilization is accomplished through pollination, the process of depositing pollen on the stigma which is usually carried out by insects (*entomophily*), wind (*anemophily*), by gravity, or through human intervention. Once deposited a pollen tube grows from the stigma towards the eggs in the ovary. This tube is an outgrowth of the inner pollen grain wall (*intine*) which pushes through the outer pollen wall (*exine*) (see cross section of pollen wall below) and carries the male gametes with it as it grows through a canal in the style (*stylar canal*). This growth is fast in species reaching 3 mm/hr.



**Pollen Wall Schematic  
Showing Exine and Intine**

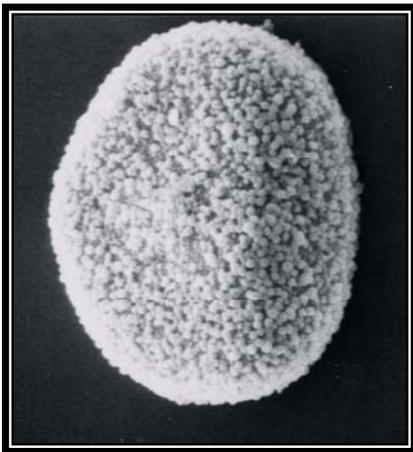
Once the eggs are reached the pollen tube discharges its contents resulting in fertilization, which is the fusion of haploid male and female gametes to form a diploid zygote from which seed develops.

***Fruiting (Seed Set):***

Species obviously must be fertile to procreate.

Unfortunately, this matter is not a simple one. In the genus *Hosta*, a number of breeding factors are

involved. In actuality, there is one species, which does not “breed” at all. *H. clausa* extends from Chungchongnam-do and Chungchongbuk-do in central Korea to north of the Yalu River in Liaoning and Jilin provinces of northeastern China. This extremely variable species has undergone substantial changes responding to environmental conditions. Some populations grow along river banks and are exposed to periodic flooding brought about by typhoons. Frequently, this happens during the time of flowering and seed maturation so severely disturbing normal, sexual



**Pollen of *H. 'Undulata'*  
Subtype RG IV • Polar View  
SEM × 650**

propagation. In response to this, the populations underwent evolutionary changes from the impaired mode of sexual propagation to a more efficient vegetative method by way of extensively creeping rhizomatous root systems. This adaptation is known as *H. clausa* var. *stolonifera* and occurs under the dense cover of native willows (*Salix*) in areas of frequent floods. Thus, it never develops flower stalks which would be useless in the dense cover. Its rhizomes compete aggressively with the willow roots and perpetuate the species. In cultivation, some species are very fertile, while others produce viable seed only when carefully hand-pollinated.

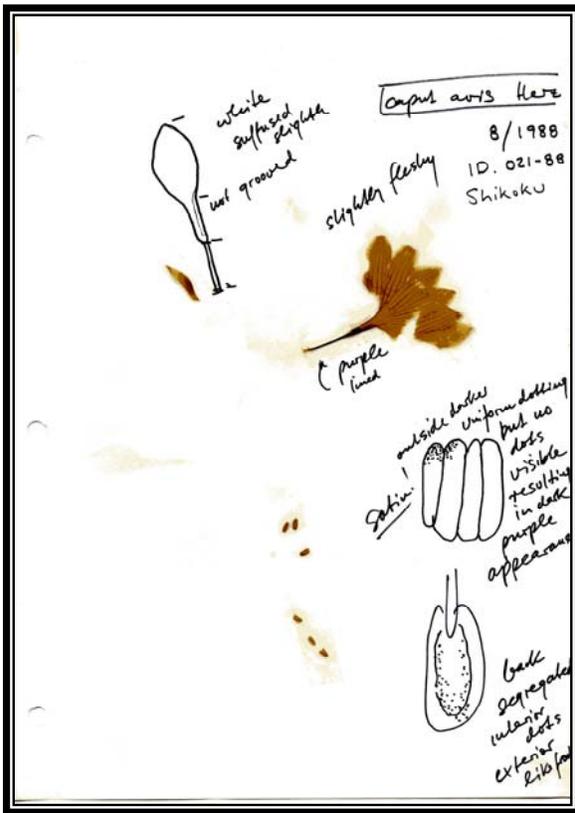
Occasionally, plants in cultivation produce seed capsules in abundance, giving the appearance of being fertile, but their capsules are filled with aborted or

undeveloped ovules and no viable seed is to be found. Viable seeds are ovoid, black with winged appendages.

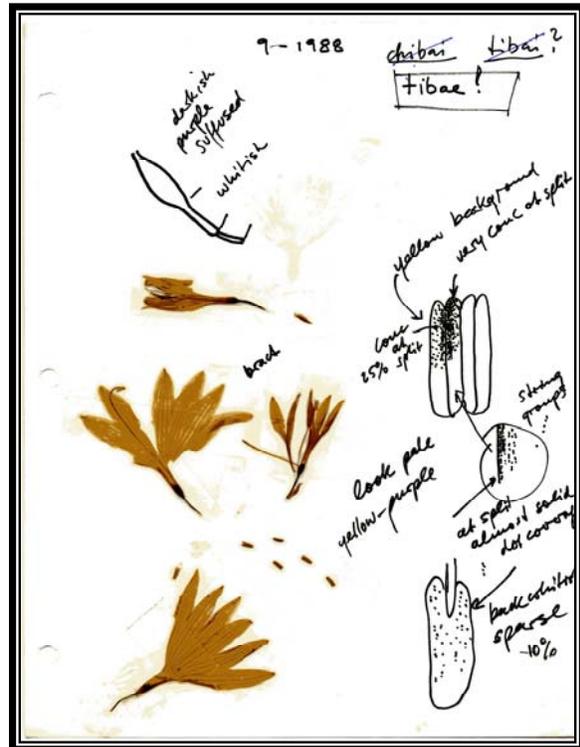
Sometimes, late-blooming species in cultivation species are quite fertile, but fail to set seed in northern latitudes, due to the shortness of the growing season. A few, such as the night-blooming *H. plantaginea* require narrowly defined climatic and environmental prerequisites to produce seed. In these cases, production of seed is impaired because the species are grown in unsuitable environmental conditions.

I have assumed that under cultivation opportunities for pollination are abundant and will additionally be helped along by careful human hands and with the aid of unnatural, but helpful circumstances, such as growing in greenhouses. Under these conditions, I have found that many a “misplaced” (out of its natural envelope) species produces viable seed, albeit in a rather sporadic fashion.

**Anther Coloration:** My study of anther coloration (Schmid, 1986–1989) was conducted on 351 specimens of species and cultivar anthers. It consisted of excising the anthers from the unopened



Study Sheet *H. kikutii* var *caput-avis*



Study Sheet *H. tibae*

flower in a non-dehisced state and examining both anterior and posterior surfaces for color, distribution of spotting and other visible differences. To illustrate this, I am showing two of the several hundred record sheets of this study. My examination confirms that anther coloration is an important characteristic

for classification. Judging of color must be done before the anthers dehisce and release their yellow pollen, thereby masking the true anther color. Examination is best accomplished with a 30-power microscope on anthers removed from an un-opened flower. *Hosta* anthers have two oblong, parallel pollen sacks, which open at the dividing line and dehisce introversely which obscures the exterior coloration. Preliminary results indicate that true species have either pure yellow or uniformly purple dotted anthers, while interspecific hybrids have non-uniform purple dotting with several dot sizes, or irregular dot patterns, or have one locule yellow colored and the other purple dotted to varying degrees and this condition is called "bi-color anthers" in the descriptions. Anther color has been added to the macromorphological features in Part 4A, Table 1.

**Note:** The following discussion deals with the several mechanisms involved in *Hosta* species breeding systems. It is perhaps a bit too technical for some readers, but I encourage all to "give it a glance."

## *Hosta* BREEDING SYSTEMS



Breeding systems have been linked directly with genetic variation so it is important to determine the several mechanisms active in the genus. The spatial separation of mature anthers and stigmas varies considerably with the species (Shown in the photo of *H. laevigata* to the left). Chung (1990) has shown that there is considerable distance between the sexual organs in the Korean taxa and this separation is also seen in most Japanese populations but not all of them. Impeding self-pollination, this separation fosters entomophily (insect pollination) and promotes outcrossing

(outbreeding) with the resulting fusion of distantly related gametes. Preliminary tests show little fruit set in the screened greenhouse with a lack of congruous pollinators. According to my own studies the distance between anthers and stigma in some lines of interspecific and horticultural hybrids seems to diminish with succeeding generation so favoring self-pollination and eventual back-crossing to a parental species. Inbreeding reduces genetic variability and increases the number of lethal and semi-lethal recessive genes produced in successive crosses. Eventually, the vigor of a particular natural group undergoing intensive inbreeding is sufficiently weakened so as to result in declining membership which may be an evolutionary mechanism to eliminate natural hybrid populations. The breeding system in most natural populations of confirmed *Hosta* species appears to support outcrossing but, undoubtedly, other mating mechanisms are at work. If it can be shown that over a

protracted period of time heterozygosity affects the distance between anthers and the stigma this feature may eventually become a diagnostic tool for the detection of hybrids but further studies are needed. In some Japanese natural populations the spatial anther/stigma separation is relatively small and these species are intensely self-fertile but due to persistent and early entomophily (insect pollination) most of these populations still outcross to a high degree. This should make it obvious that lack of congruent pollinators will to some degree reduce or prevent outcrossing. Many of the cultivars formerly considered species have very little anther/stigma separation (*H. `Crispula'*) and inbreed profusely occasionally even self-fertilizing within the unopened flower. Clever hybridizers have taken note and remove the anthers and all perianth lobes, leaving only the ovary with pistil and stigma attached to be fertilized when ready. True out-crossing appears to be active only in populations where reproductive isolation is sustained by geographical, seasonal and ecological factors. Japan has many species populations of mixed specific origin with attendant favorable pollination systems and as a consequence interspecific hybridization is rapid but mixed mating systems also occur in these groups. *H. capitata* has bi-color anthers and according to Chung (1990) shows patterns of fixed heterozygosity along with little spatial anther/stigma separation. As a consequence self-pollination occurred under screened greenhouse conditions pointing to possible tendencies for inbreeding. Field studies show that the Korean natural populations of *H. capitata* are very small and few pollinators exist in the habitat so the disposition for self-pollination may be an evolutionary adaptation which, incidentally, is also coupled with a proclivity for clonal reproduction also observed by Chung under screened greenhouse conditions. The in-breeding may explain why some of the natural populations of *H. capitata* are in a recessive state caused by a loss of vigor and consequent failure to adapt to new environments. Some horticultural hybrids, for example *H. `Honeybells'* have extreme anther/stigma separation and the significance of this is not fully understood, but in this case the hybrid is sterile which may be partially due to morphological barriers. The diploid number for *Hosta* was determined by Kaneko (1968a) and Chung and Chung (1982) to be  $2n = 60$ . Rare triploid ( $2n = 90$ ; *H. clausa* var. *clausa*, *H. clausa* var. *stolonifera* nom. nud., and *H. alismifolia*) and tetraploid ( $2n = 120$ ; *H. ventricosa*) forms have also been found. The diploid number of  $2n = 60$  has been confirmed for the Korean taxa, including the recently named *H. jonesii* and *H. yingeri*, by M. G. Chung (1990) using the colchicine-aceto-orcein squash method of Smith described in Jones and Luchsinger (1968). Chung also determined that gene duplications exist and this knowledge together with the confirmed and relatively high diploid number point to a polyploid origin for *Hosta*.

## Interbreeding Species

As pointed out in the beginning of this discussion, some species have reproductive isolation, as in *H. rupifraga* and *H. yingeri*. Other speciated and adapt to new environments, as for example *H. venusta*. Still other species are “created” by nature due to interspecific hybridization. We know for a fact that the cultivated species of the genus *Hosta* hybridize rather abundantly. As stated under *Breeding Systems* above, high diploid number seen in the genus point to a polyploid origin for *Hosta*.

Most species may be allopolyploids, which behave like diploids. As a consequence, one of the classic definitions of a species, that it is a population of similar individuals—that in nature breed only with each other—is of limited value when applied to the genus *Hosta*.

It must be recognized that even these relatively “pure” species will interbreed in gardens, particularly when coaxed by a determined hybridizer. Seasonal isolation



### Interspecific Hybrid at Hosta Hill

*H. rectifolia* ♀ × *H. yingeri* ♂  
(W.G.Schmid Photo • 2006)

may work in the wild, but hybridizers think nothing of storing pollen in the freezer to overcome such problems. Hybridizers also found out very early on, that a species requirement once put forth stating that hybrids between species be sterile, simply does not apply in the genus *Hosta*. They have also discovered that the pollen viability may be low in hybrids between species but, at the same time, it is quite easy to overcome such difficulties in their hybridizing efforts. When considering these conundrums further, we find that what we have considered *Hosta* “species” may in fact be isolated local hosta “races” of the same species, differentiated by local circumstances and habitat. *H. rupifraga*, mentioned earlier, represents a good variant of *H. longipes* that migrated south along the chain of the seven Izu Islands.

It is possible that some hosta populations classified as species are hybrid swarms, i.e., hybrids between species. These are populations of natural hybrids made by interbreeding species populations when reproductive isolation is discontinued, either by natural events or human interference. Botanists refer to

the phenomenon of hybrid swarms as “intergradation of phenotypes.” Simply put, *phenotype* means “the expressed characteristics of a species,” i.e., what it looks like.

Hybrid swarms are frequently quite fertile and maintain themselves in the wild as hybrid populations that interbreed freely with each other and often backcross to one of the parental types. This process of backcrossing, called *introgression*, greatly increases the riddle of what a species is and what it is not. Frequently, the genes from one of the parent species of the hybrid swarm are gradually absorbed into the other species, resulting in many intermediate types among a natural, intergrading population. Obviously, local circumstances, like the habitat, the overall environment and human interference, often affect the final outcome.

Most gardeners know that hybridizing creates many new, attractive hosta cultivars. To define a new cultivar, all that is required is a new name, a description and, preferably, registration. Much less known to gardeners, however, is the fact that our species have done a bit of their own “mixing up” in the wild. Long before humans made an impact on the evolution and speciation of natural *Hosta* populations, changes in the environment or other natural events caused species to interbreed. These interspecific groups, or hybrid swarms, do, after adaptation, behave like species. When classified under the interbreeding species concept, hybrid swarms can be considered species and that is the most logical solution to the conundrum we are faced with. If it comes out of the wild, it is a species, whether hybrid or not.



*H. laevigata* • Seed Collected on Taehuksan Island  
A Natural Interspecific Hybrid: *H. yingeri* ♀ × *H. sieboldii* ♂ (?)  
W.G.Schmid Photo • Hosta Hill 1993