



Peony Flower Anatomy Part I

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Synopsis of Part I

Although cultivated peonies are descended from natural species having as few as five petals, the preservation of natural mutations has resulted in garden forms having hundreds of petals per flower. These variations commonly seen in peony flower anatomy have led to the standard American Peony Society flower form classifications currently in use. A glossary of terms has arisen for purposes of name registration description, for the identification of individual cultivars and in evaluation and selection by breeders, both for commerce and end users. Terminology related to the Singles form is defined and illustrated. Although similar variations of flower form will be seen in some tree peonies, this series is specifically applicable to herbaceous peonies.

What Makes a Peony Flower Luxurious?

Rich luxury of the flowers explains why peonies are wanted, why loved and why known in history of their cultivation for many centuries. In our day we choose them for their ability to produce abundant large and lovely flowers in a wide range of showy colors. Yet, also in our time we know the natural species ancestors of our favorite flower are quite likely to have as few as five petals per flower. So, how has the peony come from a natural species five petals to the sometimes hundreds of petals seen in heavy flowers, such as the peony 'MOTHER'S CHOICE'? The short answer is human intervention, this having been enabled by showy mutations of flower parts leading to distinct variations. During the many centuries of peony cultivation, desirable changes have been accumulated and preserved. Using deliberate plant breeding efforts and selection among seed-grown plants, such desirable natural mutations have been combined in peony breeding to create the range of ornamental variation now in peonies commerce. This process continues to our time in history of peony breeding.

Details of flower form are especially important in providing clues by which to verify cultivated variety (**cultivar, cv.**) identity. Experienced peony growers recognize the plant state of growth also dictates variations in the size of a flower and the volume of its parts. Botanists have long recognized, however, the sexual parts tend to remain constant irrespective of state of growth; therefore these parts of the flower are especially important for diagnosis of identity. The purpose of this article is to increase awareness of how data on peony differences can empower peony growers to verify plants received are correct for the cultivar name. In this spirit I will describe and illustrate the anatomical features seen in peony flowers.

Because of length, this article will be published in installments. The first installment considers the peony species flower form, followed by illustration and discussion of major heritable characters leading to increased fullness seen in the flowers of most modern peony cultivars. The overall plan is to compile and illustrate a glossary of terms useful for cultivar description and the identification of unique characteristics to assist in verifying cultivar identities and as tools useful to breeders. In recent decades it has been a principal goal of the APS nomenclature function to establish and publish sufficient data as new peonies names are registered to enable verification of

correct cultivar identity. This will be seen in the current edition of APS “Cultivar Registration Form Explained” at www.americanpeonysociety.org. Look in the drop down list under the “Cultivar Reg.” tab. One may compare flowers of available peonies with the registration form schedule of items as a further exercise in building increased awareness as to how the study of peony flower anatomy may be personally useful.

Peony Flower Glossary — the Singles Form

The American Peony Society formal classification **Single** (“Simple” in France) applied to cultivars is also generally applicable to flowers of the botanical species. The most obvious difference is seen in the increased number of flower segments that typically characterize modern cvs.

Receptacle (not shown) — a slightly domed and flared area at the flower base accommodates the points of attachment and the vascular connections through which the flower parts beyond receive their life support. The fuller the flower with multiple segments, the larger is the receptacle.



LAVENDER Saunders, 1939 [Herbaceous Hybrid]

The terms listed here are presented as they occur in the flower — starting from the bottom, then upwards.

Sepals (not shown) — these tough green, sometimes stained red, floral segments will be seen merged at base of the opened flower. The sepals extend to include the bud covers, these being critical protection for the more fragile inner parts until the latter are mature and the flower ready to open. The outer (lowest) sepals are leafy or have leaf-like extensions. The extensions repeat inward becoming progressively smaller until absent. Innermost sepals become progressively expanded, ending as the flower bud covers. The quantity of sepals and the frequency of the leaf-like appendages vary between species and their derived cultivars, in some instances

assisting identification. Plant taxonomists note sepals are naturally fewest in the more evolved peony species native to Southern Europe, also reflected in their hybrids; more abundant in Lactiflora species and cultivars. Peony bud-cover sepals may also have nectar-producing glands (**nectaries**) the sugary output attracting sweet-eating ants.

Guard Petals — The large outer petals, always present in cultivated sorts, variously colored, these impart a major showy quality to the opened flower of all peonies, normally free of green pigments, sometimes more or less deeply notched at the outer margin. The typical quantity of guard petals may be as few as five in species, but commonly no less than nine to 13 in cultivated varieties. The guards may open widely into a flat shape, form a saucer shape or remain strongly cupped to a more or less extent and in some kinds will close and reopen as temperatures rise and fall. For our purposes it is important to consider guard petals as distinct from the inner petals commonly occurring in peony cultivars, the latter not treated in this installment.



CAMPAGNA Saunders, 1941 [Herbaceous Hybrid]
Single peony flower form.
[photo: Hidden Springs Flower Farm]

Stamens — The sperm carrying organs, these pollen-bearing structures arise in bundles from the receptacle, together forming a band of contrasting color, the band width extending from the guard petals inward to the **staminal disc**. Natural stamens of peony flowers have two well-defined parts, the **filament** (stem) and the **anthers**, one on each side at the upper end of the filament, capsules enclosing the pollen.

These **anther capsules** are almost always creamy to yellow in color, yet in certain lineages of *Paeonia delavayi* their outer sheath is sometimes the same deep red as the petals. **Filaments** may be a translucent light yellow color or furnished with reddish pigments from the base, extending variably upwards. Occasionally the reddish pigment extends the entire length of the filament; for example, see a flower of Burma Ruby.

Disc (also, **Staminal Disc**) — this may be seen as an inconspicuous ring of tissue found at inner margin of the stamens band, encircling the **carpels**, often furnished with irregularly spaced **nodules**. When present, these nodules (or **kernels**) are sometimes seen to be the chief evidence of the organ. The nodules may contain reddish pigment, but are often creamy white in color. In *delavayanae* species, the nodules sometimes include **nectaries**, by which insects are attracted to the opened flower. In most woody peony flowers and their Itoh Group hybrid descendants, the disc is expressed as a variously colored **sheath**, partially or fully enclosing the carpels.

Carpel — the principal part of this organ is the **ovary** of the peony flower, a capsule protecting the ova, (eggs) leading to a pod bulging with seeds when ova are successfully fertilized. In peony flowers, carpels normally occur in clusters, but remain separate, not united (each is pollinated separately). The outer surface at flower opening varies in depth of color from creamy white to green, but may develop darker, reddish-purple pigments as the flower ages in sunlight. The outer surface varies from smooth to being covered with fuzz or small hairs of various lengths and densities in different cultivars. **Pistils** is an alternate name for carpels, now generally fallen into disuse.

Style (not labeled) — in technical botanical anatomy, the style is the upper part of the carpel, beginning with the short “neck” at the top of the ovary chamber, the size enlarging above, which part varies in color among cultivars. However, for capturing data wanted for identification, our common practice is to include **as one** the style and stigmatic surface (the latter is a small space on the style where pollen grains are enabled to germinate). We thus apply the term **stigma** to the whole of style and stigma for our convenience in specifying the variations of color and shape.

Stigma — specifically, this is the slightly swelled, moist, sticky, nutrient surface at the edge of the style upon which the pollen grain comes into active growth. The style provides the channel through which the growing pollen tube reaches the ovary for delivery of the male germ cell. As set forth in **Style**, above, for recording data on peony flower differences we commonly include as stigma all of the upper extension of the carpel. Differences in color and shape of these parts tend strongly to remain constant regardless of the plant’s state of growth. When the organ is present, it can help to separate one cultivar from another. In sum, stigma means all of the carpel anatomy from top of the ovary chamber to the stigmatic surface.

Nevertheless, for purposes of controlled crosses in peony breeding it is important to know the pollen can only be effective when applied to the moist stigmatic surface, an area to be found somewhere at outer edge of the organ. Depending on the characteristic shape of the seed parent style arm, the stigmatic surface may be found at top, to the side or turned somewhat down-facing.



VIVID GLOW Cousins/Klehm, R.G., 1986 [Herbaceous Hybrid] Single peony flower form. [photo: www.songsparrow.com]

Peony Flower Anatomy Part II

Synopsis of Parts I and II

The heritable differences of form commonly seen in modern peony cultivars have resulted from mutations noticed over the centuries by interested observers and preserved in cultivation. These variations in peony flower anatomy have led to the standard American Peony Society flower classifications—Single, Japanese, Anemone, Bomb, Semi-double and Double. A vocabulary of descriptive terms has arisen for purposes of name registration and cultivar description, for use in the diagnosis of individual cultivar identities, and, in the evaluation and selection of cultivars for both commerce and for end users. Terms describing the basic elements of herbaceous peonies’ floral anatomy are described and illustrated in Parts I and II. Please note that information in this series pertains specifically to herbaceous peonies. While analogous variations of flower anatomy will be seen among woody peony cultivars, some are expressed differently.

Additional Factors of Peony Flower Doubling

In addition to the **Single** flower form classification already treated, the American Peony Society flower classifications currently in use for herbaceous peonies are **Japanese, Anemone, Bomb, Semi-double** and **Double**. These APS classifications result from the outward expression of different underlying genetic factors. To the extent variations in petals expression among the standard classifications are the result of inherited factors, these variations have constancy, repeating in all plants of a particular cultivar.

Nevertheless, different seasonal growing conditions and site limitations may lead to additional variation in the outward expression of the underlying genetics. When variations due to both heritable and environmental influences are understood, they empower useful description and identification. We make use of this understanding to describe a cultivar such that it can be identified in general and often can be reliably separated from other quite similar cultivars. This installment will deal with the transformation of the normal pollen-bearing stamens into petals or petal-like structures.



KAREN GRAY Krekler, 1965 (Lactiflora Group)



MAHOGANY Glasscock, 1937 [Herbaceous Hybrid]



WALTER MAINS Mains, 1957 [Herbaceous Hybrid]



LE CHARME Eliason, 1964 (Lactiflora Group)



BELLVILLE Wolfe / Hollingsworth 1998 (Lactiflora Group)



LAUREN Niva / Snelson, 1999 (Lactiflora Group)

Two distinctly different patterns of stamen transformation are seen among different cultivars. For purposes of this discussion we will term them: **All-over stamen transformation** for one and **Progressive stamen transformation** for the other.



RED GRACE Glasscock / Klehm, R. G., 1980 [Herbaceous Hybrid]

All-over transformation leads to obvious contrasts in the flower. The contrasts are in form, color or both, being expressed in different cultivars to different degrees; in their differences continuously variable across the spectrum, ranging from minimal change of the natural stamens, advancing in size and texture to inner petals quite alike in color and texture to the larger guard petals. For purpose of assigning the standard flower form classifications, the graduated segment series is arbitrarily divided into three more or less definable structures: staminodes, petalodes and inner petals. These names coincide with the classification Japanese, Anemone and Bomb, respectively. The degree of all-over transformation may be quite uniform across the space from guard petals to the inner margin. However, when inner segments are not of uniform size it is unique to all-over

transformation the larger, more advanced segments are found at the inner margin (next to the carpels), sometimes of a contrasting, inner petals form, called **flag** petals. Also, there may be seen a band of smaller segments forming a distinctive **collar** next to the guard petals.

Staminodes are the closest in form to the natural stamens from which they derive, usually showing the **filament** color, always accented by lumpy texture, these most often including pollen grains, the color reminiscent of the natural pollen capsules. Peony cultivars producing the distinctive staminode form were first received from Japan, resulting in the flower type class name: **japanese** (Imperial, in the UK). Transformed stamens become petalodes when their changes have progressed to the point where all visible evidence of stamen origin, except for sometimes yellow color, has disappeared.

Petalodes are always of smoother texture compared to that of staminodes, absent the lumpy remnants of pollen capsules, in color ranging from a pale contrast to the guard petal hue. Compared to the guard petals and inner petals, petalodes may be of thinner texture, somewhat translucent and always smaller, taken together resulting in the **Anemone** class flower, appearing as a **center ball** of contrasting size segments resting on a flat or cupped **saucer** formed by the guard petals.



ANGEL CHEEKS Klehm, Carl G., 1970 (Lactiflora Group)



MONS. JULES ELIE Crousse, 1888 (Lactiflora Group)

Inner Petals constitute the most advanced petal form resulting from all-over stamen transformation, being similar in color and texture to guard petals, but narrower and, in some cultivars, capable of growing to substantial length as the flower matures. This inner petal form leads to the flower class **Bomb**, characterized by a large center ball, sometimes growing so large as to diminish the effect of the guard petals, for example, 'Mons. Jules Elie'. The name Bomb is said to have been adapted from "bombe", the name of a molded frozen desert popular in the 1920s.

Progressive stamen transformation is not as obvious, the changes more subtle, lacking the sharper contrasts afforded by all-over transformation; the changed stamen segments being entirely inner petals, echoing the guards in color and texture. Unlike all-over transformation, the inner petals' size will be graduated, largest next to the guards, grading smaller inward along a spiral ending either at a remnant of stamens or, less obvious, continues with complete transformation of all natural stamens. When a remnant of stamens is obvious in



KIMSUE Hollingsworth, 2019 [Herbaceous Hybrid]



PINK VANGUARD Seidl / Hollingsworth, 2005
[Herbaceous Hybrid]

the opened flower the standard classification will be **Semi-double**. The amount of stamen segments converted to petals is variable, the quantity subject both to the underlying genetics and to the flowering stem state of growth. The remnant of stamens will be seen to range in quantity among flowers of the same cultivar from quite obvious to obscure. When stamens are obscure it may lead to uncertainty at competitive exhibitions whether the specimen is most suitably staged as a Double or a Semi-double. The competitive flower show answer lies with the individual flower specimen under consideration, not with the published description of the cultivar.

Progressive transformation is not present in the 'KimSue' image. The petals seen are all guard petals, the extra quantity of them attributable to **multipetally**, the term applied for this heritable state, understood to vary in its expression by cultivar, but in

general contributing added fullness in any of the standard flower classifications. The 'Pink Vanguard' image illustrates progressive stamen transformation, clearly apparent in the short sequence of inner petals, the largest adjacent to the guards and grading smaller inward. The 'Cherry Ruffles' image shows a near maximum extension of progressive transformation, the few remaining stamens evident adjacent to the carpels. For the interest of breeders, the two types of stamen transformation are inherited separately, not as alleles (alleles being alternate genes at the same location). All-over stamen transformation appears to be inherited as a simple recessive character, meaning both parents must be carriers of the controlling form of the gene(s). Nevertheless, the extent of transformation in an individual flower is expected to also be subject to influence of additional genetic factors ("modifier" genes), as well as varying in concert with plant maturity and growing conditions.

The inheritance of progressive stamen transformation appears to be more complex, possibly inherited as a partially dominant complex of genes. As with all-over transformation, in an individual flower the extent to which the stamen cluster is changed may be modified under influence of both other genetic factors and the state of growth.

Yes, an individual cultivar can carry the genetic basis of both transformation types and will manifest both in the same flower. In fact, this dual condition is common in some flowers shown in the Full Doubles classes. It is most easily recognizable when the all-over transformation is at the staminodes or petalodes level and providing a color contrast. With this makeup a band of yellow petalodes is normally apparent between layers of petals as seen in novelty Doubles, such as: 'Golly', 'Feather Top', 'Lavon' and 'LaDonna'.



CHERRY RUFFLES Hollingsworth, 1996 [Herbaceous Hybrid]

Further discussion and illustration of doubling anatomy will be treated in the next installment. The variations in flower anatomy outlined herein are, when known, especially useful for purposes of verifying the identity of the correct plant for a peony cultivar name. For additional discussion of these factors, study the “Cultivar Registration Form Explained” at the American Peony Society web site, www.americanpeonysociety.org under the “Registration” tab (can be printed).

More Peony Flower Glossary –

All-over stamen transformation — denotes the pattern of stamen transformation seen in peony flowers wherein petal-like segments of different form replace the natural, pollen bearing-stamens; no natural stamens remain. This is a heritable state specifically leading to the standard flower forms classifications Japanese, Anemone or Bomb.

Collar — a constricted band noticeable in the silhouette of a peony flower, resulting from a layer of reduced size petalodes encircling the lower margin of the center ball (adjacent to the guard petals. Some cultivars normally produce flowers having a noticeable collar. Others may tend to do so only on less than typical size flowers of the cultivar.

Flag petal — a large inner petal occasionally seen arising at inner margin of the stamens, outside the carpels, but not enclosed by them. This is thought to reflect the of the all-over stamen transformation pattern in which inner segments are showing tendency to change from petalodes to the larger inner petals. When similar petals arise instead from between the carpels, this is thought suggestive of genetic tendency for two-stage doubleness of flower and in breeding for the Doubles class might represent a degree of gain toward the end goal.

Multipetally — the heritable increase in quantity of floral parts beyond the minimums seen in the natural species, generally much sought in breeding peonies for new cultivated varieties. Recognizing multipetally as seen in existing sorts varies from a few extra rows of guard petals to the very large amount of all petals segments seen in the most massive Doubles. Both between different individual cultivars and among flowers of the same cultivar, the increased quantity will be seen in a continuously variable range rather than as an exact quantity per cultivar, well grown mature plants giving maximum expression of the inherent capability of a particular cv.

Petalodes — a petals segment form seen in the all-over stamen transformation series, the name denotes the middle size range of petal like segments, more advanced toward petal form than staminodes, less advanced than inner petals. The segments may be larger than staminodes, smoother and of evenly distributed coloration, yet do not have the color and texture of inner petals. The form of petalodes will generally be strap-like and show no obvious evidence of their stamen origin, no yellow lumps on the edges of petals, no remnant of the filament stalk being apparent. When a cultivar typically produces petalodes the standard flower classification is Anemone. However, in its lesser flowers such cultivar may also produce staminodes.

Progressive stamen transformation — denotes the distinctive change of the natural stamens cluster in which the altered segments always become inner petals, while a remnant of natural stamens may remain next to the disc and carpels. The resulting inner petals are largest next to the guards and usually grade noticeably smaller inward, smallest near any remaining normal stamens or at the inner margin when no stamens remain. The

extent of change produced in an individual flower will be seen in a range from only a small portion of the stamen cluster changed to all stamens having become inner petals. This is a heritable state seen in the standard flower classifications Semi-double and Double.

Stamen boss — a term sometimes seen in peony literature, designating the stamen cluster as a whole, the usage adapted from the vocabulary of ornamentation design, denoting a central prominence.

Staminodes — when all-over stamen transformation is present, the term that is applied to the altered segments nearest in form to the natural stamens from which they derive. The texture will be uneven, the coloration variable, reflecting the underlying filament color and including edge contrasts from embedded remnants of the pollen capsules. See also petalodes and inner petals. Cultivars which typically produce the staminodes form of inner segments belong to the standard flower class Japanese.

Peony Flower Anatomy Part III

FLOWER-IN-FLOWER FORM: THE APS DOUBLES FLOWER CLASS

Usage of “double” in English language has many faces. My desk dictionary requires half a column to present the choices. For our purposes, however, the distinction to be made is between the **peony flower** class name **Double** (also “Full Double”) and other ways the term is used in conversation about flowers in general— often used to denote any increased quantity of petal-like floral segments. To earn the classification Double the peony flower anatomy is almost always physically doubled; having a flower-in-flower structure (also called a two-stage double form), not usually just showing the large quantity of floral parts. This means there is a repeat flower of the same organization and form in its constituent parts, which arises from the very center of the lower flower. The upper flower will often be smaller, as may contribute to a relatively seamless transition at the boundary between the two when fully opened.

The margin between the lower and upper repeat is generally preferred for to be obscure upon casual observation. Like other anatomy variables described herein, flower-in-flower form is expressed in a graded series. The range of expression will vary from a few petals and a vestige of sexual parts embedded within carpels of the lower flower, leading to only a center tuft when the flower has fully opened, ranging to the full blown, most wanted model. When visible stamens are an obvious feature of the opened flower, the standard classification is Semi-double. Thus, the Semi-double class form is more broadly defined than is Double, not limited to specimens having the higher degree of fullness.

What remains to complete our sequence of articles on flower anatomy is to define and illustrate physical characteristics of the flower-in-flower anatomy and variations of its expression. All flower images following have flower-in-flower form, and including various combinations of the other doubling traits.

'Pfeiffer's Red Triumph' is illustrative of the APS historical ideal for a fully doubled peony flower, **all** floral segments expressed as petals and with flower-in-flower form, the transition between the two parts being near seamless, even to a practiced eye. This flower classification is Double. Older cultivar name descriptions when published, especially before 1950, often used the now generally abandoned descriptors "Rose Double" vs. "Semi-Rose Double", the latter used for the comparable Double form in which could be found a thin ring of natural stamens obscured from view by petals. (Visible stamens lead to the standard classification: Semi-double.)



PFEIFFER'S RED TRIUMPH Pfeiffer, 1937 (Lactiflora Group)



Unnamed Seedling

An unnamed Herbaceous hybrid seedling; this one has the flower-in-flower genetic factor clearly expressed, uncluttered by other significant doubling elements. The only other doubling factor apparent is a minimal measure of multipetally expressed in guard petals of the lower flower. While a flower of this makeup is unlikely to be put in commerce, because of clearly evident stamens the standard flower classification would be Semi-double.

Another unnamed herbaceous hybrid seedling, center flower remains in bud, lower flower fully open, some multipetally and progressive stamen transformation is expressed, stamens expected to remain prominent when fully opened. The standard flower classification would be Semi-double.



Unnamed Seedling



Unnamed Seedling

Herbaceous hybrid seedling, center flower beginning to open, a medium degree of multipetally plus progressive stamen transformation is expressed, stamens somewhat obscured at the stage of opening and well obscured in other flowers of the same plant. Flower class when determined on mature plants in a favorable state of growth expected to be Double, although staging for exhibition will nevertheless depend on the character of the individual flower specimen, whether best exhibited in Semi-double or Double classes.

'Maestro', pictured as the upper stage flower is opening; a relatively large degree of multipetally is expressed in the lower flower, not so in the upper flower, does not have all-over stamen transformation (stamens are present). While the stamen ring is not large, due to the relatively small center flower, it is expected the stamens will almost always be evident in the opened flower. Thus the standard classification is Semi-double.



MAESTRO (Auten, 1955)]



JUNE ROSE Jones, 1938 (Lactiflora Group)

'June Rose' specimen has flower-in flower form, apparently with all-over stamen transformation (no stamens), possibly progressive transformation, as well. Center flower is partly open, its larger outer petals apparent, owing to the stage of expansion when pictured. Inner petals of the lower flower are relatively large, multipetally moderate. This subject was produced on a third spring plant; considerably more petals expected when plant is mature. Standard flower classification is Double.



LADONNA Hollingsworth, 1997 (Lactiflora)

'LaDonna' is a flower-in-flower example, genetically carrying both progressive stamen transformation and all-over stamen transformation, (this writer knows from the plant those are staminodes, not stamens, between the lower and upper flowers, repeated at center). Lesser specimens of its flowers will express a wider band of staminodes. Under current APS exhibition specifications no natural stamens being present defaults this form to the standard classification: Double.

Among Lactiflora Group cultivars 'Frances Mains' is notably capable of making a large, exhibition quality flower that is uncommonly packed with petals. Pictured here at a half opened state, note the guard petals of the inner flower are yet to unfurl. The smooth area seen at center is the outer boundary of the inner flower. This flower was produced on fourth spring growth—the plant having grown three seasons from division. Multipetally approaches maximum, the inner petals' size and distribution typically leading to a smooth transition over the top of the finished flower. Standard flower classification is Double.



FRANCES MAINS Mains, 1955 (Lactiflora Group)



MY LOVE Hollingsworth, 1992 (LactifloraGroup)

This flower pictured fully open—the unusual profile illustrates a form sometimes manifested in cultivars having both types of stamen transformation, plus two-stage doubling. We recognize this 'My Love' flower form is governed by all-over stamen transformation because a band of smaller transformed segments, but never natural stamens, is sometimes seen. We also see the form is governed by progressive transformation, because the center petals size is sometimes seen to grade smaller inward. Side bud flowers of this cultivar on established plants and terminal flowers produced on young plants will sometimes be seen to form pale yellow staminodes inward, the contrast noticeable where they form a visible contrast. The degree of multipetally is substantial. Standard flower classification is Double.