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Redbuds and Legumes Subfamilies

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Conserving wild flowers and wild places

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First Legume WOY

Redbuds and Legume subfamilies

Although legumes constitute one of the largest families of flowering plants in the world, and despite 25 years of celebrating Virginia's wildflowers, redbud (*Cercis canadensis*) is the first legume to be recognized as a VNPS Wildflower of the Year. This article addresses the relationships of *Cercis* with the rest of the legumes (family Fabaceae, or Leguminosae in older literature).

In general, legumes can be recognized by their usually compound, stipulate leaves bearing hinge-like swollen pulvini on petioles and petiolules (leaflet stalks); floral details vary from group to group (see below), but there is always a single pistil with a superior ovary that matures into a dry fruit that is usually flattened, elongate, multi-seeded, and dehiscent along both sides. The characteristic fruit is known botanically as a legume—which leads me to the nearly tautological truism, "Legumes make legumes." Traditionally, legumes (the plants) have been partitioned into three well-defined subfamilies—Mimosoideae, Caesalpinioideae, and Papilionoideae—distinguished largely by details of floral structure.

Mimosoid legumes are most diverse in the tropics and subtropics, but at least one member of this subfamily

should be familiar to most readers of the VNPS Bulletin, the so-called mimosa, *Albizia julibrissen*, native to western Asia, but now widespread in much of North America. Most mimosoid legumes are woody plants of the tropics and subtropics; relatively few occur in temperate regions. Leaves are often bipinnate with

numerous small leaflets. Further, mimosoid flowers are individually small and radially symmetric (Figure A), but they are most easily recognized by their occurrence in tight head-like clusters dominated by numerous elongate styles and stamens—the overall effect resembling a powder puff. There

(See *Redbud*, page 4)



Pea pods? Well, sort of... You are looking at the seed pods of the VNPS 2013 Wildflower of the Year, redbud. (Photo courtesy John Hayden)

•Redbud

(Continued from page 1)

are two mimosoid legumes native to Virginia: *Aeschynomene virginica*, sensitive or Virginia jointvetch, a rare plant of freshwater tidal marshes, and *Mimosa* (*Schrankia*) *microphylla*, littleleaf sensitive-briar, a species of the Southeast that reaches its northern limit in Virginia where it, too, is considered rare.

Papilionoid legumes are cosmopolitan, well developed and diverse from the tropics to temperate regions. All growth habits are well represented among the papilionoid legumes, but herbaceous forms are especially common in temperate regions. Leaves are mostly once-pinnate or trifoliate. Flowers are bilaterally symmetric with two keel petals that enclose 10 stamens and the pistil, two laterally divergent wing petals, and an erect standard (or banner) petal (Figure C). Further, the 10 stamens can be completely separate from each other, fused in a ring, or, most frequently, nine are fused along their filaments forming a partial tube surrounding the pistil, with the 10th stamen separate from the rest, extending parallel to the upper edge of the pistil. There are many papilionoid legumes native to Virginia. A few of the more familiar genera include *Desmodium* (beggar's ticks), *Robinia* (locusts), *Trifolium* (clovers), *Vicia* (vetches), and *Wisteria*.

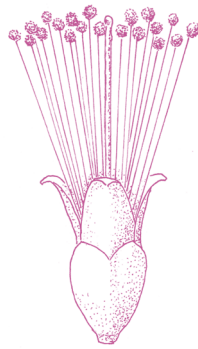
The traditional definition of **caesalpinoid legumes**—to which redbuds belong—suggests some degree of intermediacy between the other two subfamilies. Like the mimosoids, most are woody and tropical or subtropical, but there are temperate zone examples, including some herbs. Floral symmetry varies from radial to extremely bilateral; in some cases, redbud being a good example, flowers appear superficially very much like papilionoid flowers. However, when possessing bilateral symmetry, caesalpinoids always differ from papilionoids in one respect: the uppermost petal (standard or banner) is covered by the two wing petals in flower buds whereas among papilionoids the uppermost petal is always outermost in the bud (Figure B). Another interesting characteristic of many caesalpinoid le-

gumes is that roots lack the nodules containing nitrogen-fixing symbiotic bacteria that are widespread among other legumes.

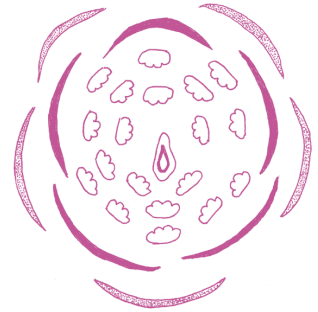
In addition to redbuds, some prominent caesalpinoid legumes to be found in Virginia include species of

Chamaecrista (partridge pea), *Senna*, *Gleditsia* (honey locust), and *Gymnocladus* (Kentucky coffee tree). Though few in number, the Virginia caesalpinoids form a heterogeneous group: *Chamaecrista* species have
(See *Redbud*, page 5)

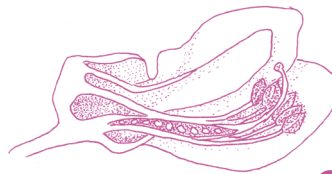
A. Subfamily Mimosoideae



Acacia



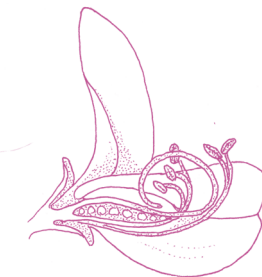
B. Subfamily Caesalpinioideae



Cercis



C. Subfamily Papillioideae



Cytisus



Sketches and diagrams of legume flowers representing the three traditionally recognized subfamilies. Key to floral organs in the diagrams (right hand side of figure): calyx/sepals are shaded, corolla/petals are black, stamens are 4-lobed and white, pistils are the centermost element of each diagram; note that papilionoid stamens are linked indicating fusion; sepals in each subfamily may be fused at the base, a detail not depicted in these diagrams. Redrawn by Nicky Staunton from images on the Watson and Dallwitz web site (<http://delta-intkey.com/angio/>).

• Redbud

(Continued from page 4)

symbiotic nitrogen fixation in root nodules, while the others do not; *Chamaecrista* and *Senna* are herbaceous, but the others are woody; and flower symmetry varies from essentially radial in *Gleditsia* and *Gymnocladus* to slightly bilateral in *Chamaecrista* and *Senna* to extremely bilateral in *Cercis*

Within Caesalpinioideae, *Cercis* is classified in tribe Cercideae (Wunderlin 2010), a group of 12 genera that, except for the redbuds, are native to tropical regions of South America, Africa, and Australia. To most Virginians, these redbud relations are obscure plants but some readers may be familiar with the large genus *Bauhinia* (so-called orchid trees), frequently seen as ornamentals in conservatory collections and tropical landscapes.

The preceding sketch of legume relationships will almost certainly undergo some revision in the not too distant future. Molecular genetic studies confirm, at least in broad outline, the composition of subfamily Mimosoideae, subfamily Papilionioideae, and tribe Cercideae. However, subfamily Caesalpinioideae, as traditionally defined, is untenable in the light of current knowledge. The problem is that caesalpinoid legumes do not

form a single distinct lineage. Rather, subfamily Caesalpinioideae is composed of six (maybe more) discrete lineages, several of which (for example, tribe Cercideae) form the lowermost branches of the legume evolutionary tree, while the remaining branches are interspersed among the well-defined mimosoids and papilionoids. By the modern philosophy of systematics, this situation is a mess . . . but exactly how best to resolve it is not yet clear. One may expect proposals to define additional subfamilies that will, in effect, dismantle the traditional broad definition of Caesalpinioideae. In all likelihood, a much more narrowly defined Caesalpinioideae will emerge, and *Cercis* will be placed elsewhere. Stay tuned!

It may be disconcerting to learn that classification of eastern redbud, a plant named by Linnaeus more than two and a half centuries ago, is currently in flux. There are lessons to be learned here. The first lesson is that naming a plant and placing that plant in a classification are two different enterprises. While many of the names coined by Linnaeus are considered valid and enjoy widespread use today, the very concepts of plant family and subfamily that are such integral parts of modern plant taxonomy do not appear at all in the formal classifications of Linnaeus. Naming and classifying are not the same. The second lesson is that all classifications are hypotheses. The traditional definition of legume subfamilies arose during the

19th century, a time when gross morphology dominated how botanists perceived relationships. Nowadays much more data are available to systematists; it is now commonplace to integrate traditional gross morphology with microscopic structure, comparative chemistry, and vast amounts of gene sequence data in order to generate classifications. Not only is there much more information available, but the principles of cladistics, now firmly ascendant in systematics, alter how hypotheses about relationships are evaluated. As it turned out, the morphology used by 19th-century botanists to distinguish mimosoid and papilionoid legumes correlates well with patterns revealed via gene sequence data and the principles of cladistic classification, confirming, at least in broad overview, these two very old hypotheses of legume relationships. The problem with the caesalpinoids is not simply failure of morphological characters to define the subfamily. The problem stems from the very fine resolution of relationships revealed by gene sequence data coupled with the relatively new requirement that taxonomic groups be monophyletic (not merely descended from a common ancestor but also including *all* descendants of that ancestor) that makes the subfamily problematic. Finally, there is a third lesson to be taken from the impending failure of traditional Caesalpinioideae: we just don't know everything there is to know about biodiversity. That's true for plants in general and the legumes in particular. Yes, *Cercis*, the redbuds, are reasonably well known plants, but to place them properly in a robust classification (a hypothesis likely to withstand rigorous testing), requires that we also know all the potential redbud relatives, i.e., all the caesalpinoids, equally well. We are not there yet! So, for now, redbuds are classified in subfamily Caesalpinioideae, but that is a temporary situation, an old concept retained out of expediency for lack of a better alternative.

Wunderlin, R. P. 2010. Reorganization of the Cercideae (Fabaceae: Caesalpinioideae). *Phytoneuron* 2010-48: 1-5.

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