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Sepals and Petals and Stamens—Oh, My! Or, a brief discourse on putative homologies of perianth elements of Common Black Cohosh

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Or, a brief discourse on putative homologies of perianth elements of Common Black Cohosh

By W. John Hayden, Botany Chair

I encountered some contradictory information while preparing to write the 2017 Wildflower of the Year brochure: some sources describe flowers of *Actaea racemosa*, Common Black Cohosh, as having petals, while others say petals are absent. How can that be? How could there be such uncertainty about this common plant, one known to science since before the time of Linnaeus? After a little research, I decided to describe Black Cohosh flowers as having a series of organs interpretable either as staminodes (nonfunctional stamens) or as petals located between its sepals and stamens (Figure 1). Frankly, I waffled on the petal issue, and this article explores why.

Petals are the floral organs situated between sepals and stamens, usually distinctively pigmented, and functioning to attract potential pollinators. At some fundamental level, all floral organs are interpreted to be modified leaves attached to the end (receptacle) of the flower-bearing stem (pedicel)—an idea first articulated by the German poet Goethe (1790). But the diversity of flowering plants is profound, and there are lots of variations in floral organography. Certain flowers challenge simplistic interpretation, and the structural details of petals and petallike organs have led botanists to ponder whether the petals of all flowers are fundamentally the same.

Comparative morphologists have developed two models for the origin of petals. One model posits that petals represent stamens that lost the capacity to form anthers and pollen as they became larger and pigmented; these modifications mark a shift away from a direct role in reproduction to the equally important supporting role of enhancing pollinator attraction. Flowers believed to have produced petals via sterilization of stamens are said to possess *andropetals*. This model involves a somewhat round-about path: leaflike organs bearing anthers and pollen first became stamens, and then some stamens became petals of this sort. An alternative model suggests that petals originated more directly from a leaflike ancestral condition simply by loss of chlorophyll and enhancement of other pigments; such petals are termed *bracteopetals*. For any species, either the andropetal or the bracteopetal model could be correct, but not both. For flowering plants as a whole, however, both models could be valid; some plants may have andropetals while others may have bracteopetals.

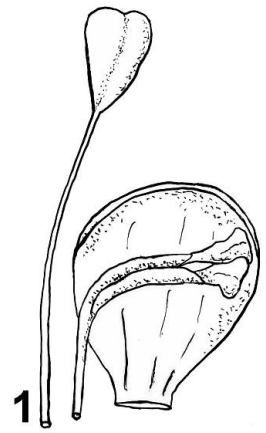

Figure 1 Stamen (left), petal/staminode (right front), and sepal of *Actaea racemosa*. Illustration by Sheila Hayden.

Multiple tools are available for addressing which model of petal origin applies for a given species. From the realm of morphology, an andropetal originates as a slender bump (resembling the first visible stages of a stamen primordium), and at maturity it has a narrow base and a single vascular trace, just like a stamen. In contrast, a bracteopetal originates on the floral meristem as an arclike bulge, retains a relatively wide base at maturity, and

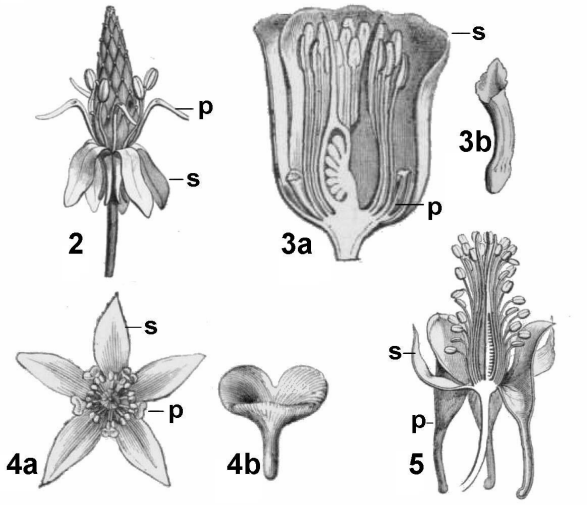

Figure 2 *Myosurus minimus*; **3a**. *Helleborus foetidus*, flower, longitudinal section; **3b.** *Helleborus foetidus*, petal; **4a**. *Xanthorhiza simplicissima* flower, top view; **4b.** *Xanthorhiza simplicissima*, petal; **5.** *Aquilegia vulgaris,* flower, longitudinal section. Images from H. Baillon. 1867–1869. *Histoire des plantes,* vol. 1. Hachette, Paris.

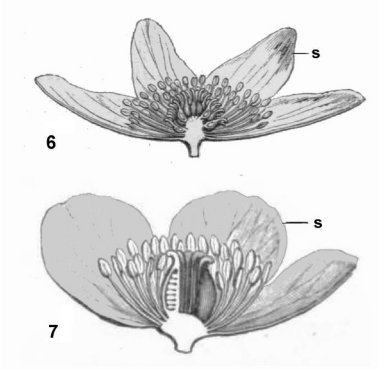

Figure 6 *Anemone nemorosa*, flower longitudinal section. **7.** *Caltha palustris*, flower, longitudinal section. Images from H. Baillon. 1867–1869. *Histoire des plantes*, vol. 1. Hachette, Paris.

has three (or more) vascular traces. In these features, bracteopetals are essentially like differently pigmented versions of sepals. Further, determination of which genes are active during initiation and early development of floral organ primordia can help resolve the question. Finally, phylogenetic perspective provides insight to petal organ identity by mapping morphological characteristics on well-resolved evolutionary trees. For a long time, based only on morphological evidence, many botanists subscribed to the andropetal model for all eudicots (traditional dicots minus basal angiosperms). But this paradigm of petal origin has been overturned by de Craene (2007, 2008), whose analyses support the bracteopetal model for core (i.e., most) eudicots.

And this is where the story returns to *Actaea*. Black Cohosh is classified in Ranunculaceae, the Buttercup Family, which, along with Poppies, Barberries, and several other families, constitutes the basal eudicots, distinct from most (or core) eudicots now modeled to possess bracteopetals. So what's the story with petals in Ranunculaceae—and in *Actaea*? Morphology, development, developmental genetics, and phylogenetic perspective support the idea that petals, when present in Ranunculaceae, were derived from stamens. That is, petals in Ranunculaceae are andropetals and thus fundamentally different from bracteopetals of core (i.e., most) eudicots. Further, when present, petals in the Buttercup Family often bear nectar-secreting glands; classical-era German morphologists called these unusual nectar-bearing petals *Hönigblatter* (honey-leaves) (Figures 2-5). These nectary-bearing petals can be downright odd: in Mousetail (*Myosurus*, Figure 2), they are extremely narrow, flexed structures with a nectary located at the point of flexure; in Hellebores (*Helleborus*, Figures 3a, 3b), they are tubular; in Yellowroot (*Xanthorhiza*, Figure 4), they are stubby and bilobed; and in Columbine (*Aquilegia*, Figure 5), nectary-bearing petals form distinctive elongate spurs. In Buttercups (*Ranunculus*), nectary-bearing petals look like ordinary petals that just happen to have a glandular region toward their base.

Other familiar plants in the Buttercup Family possess just a single perianth whorl that is brightly pigmented; further, these floral organs have relatively wide bases and three vascular traces, but not the vestige of a nectary. If we apply the criteria articulated above, these members of the Buttercup Family have sepals that have taken on the pollinator-attraction function of petals. Examples include Anemone (*Anemone*, Figure 6), Marsh Marigold (*Caltha palustris*, Figure 7), and Clematis (*Clematis*). The showy sepals in flowers of these members of Ranunculaceae are commonly referred to as petaloid sepals, but they also fit well the distinguishing features of bracteopetals. The point is that, regardless of what morphological terms we choose to apply, the things that look like petals in flowers of Anemone, Marsh Marigold, and Clematis are not the same as the things that look like petals in Buttercups—and the things that look like petals in Buttercups are fundamentally similar to the oddly shaped organs illustrated in Figures 2–5 and to the odd organs located between sepals and stamens in flowers of *Actaea* (Figure 1).

My decision to waffle about the petal/staminode organ of *Actaea racemosa* emerged from within the framework of issues outlined above. Including both interpretations for this organ in the Wildflower of the Year brochure provided an opening for this article and the opportunity to interpret floral morphology of *Actaea* in the context of Ranunculaceae in particular and eudicots at large. There is not much that is petallike about the petal/staminodes of *Actaea racemosa* (Figure 1). To interpret these organs as staminodes emphasizes their similarities with stamens: small size, narrow filamentlike base, and a bilobed apex that suggests a pair of anther sacs. On the other hand, though they would be decidedly odd in any plant family other than Ranunculaceae, these organs are not particularly unusual for the nectary-bearing andropetals of the Buttercup Family. So, good reader, take your pick, call them petals, andropetals, *Hönigblatteren*, or staminodes, but whatever you call them, know that the choice is a complicated one. Who would have imagined that these graceful forest herbs stood at the crux of such basic, yet complicated, issues of plant morphology? All petals are not the same! ❖

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