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## **Recommended** Citation

Hayden, W. John. "Unique Features of *Ceanothus* Trace to Earliest Stages of Flower Development." *Sempervirens Quarterly* Spring 2019, 6-7.

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## Unique Features of Ceanothus Trace to Earliest Stages of Flower Development

Articles by W. John Hayden, Botany Chair

The basics of flower structure L are straightforward. A "typical" flower (Figure 1) has four whorls of floral organs arranged in stereotypical order: sepals (lowermost and outermost), petals, stamens, and, finally, one or more carpels (pistils)located in the innermost (or uppermost) position. This is not rocket science. Names of these floral organs and their relative placement within the flower can be grasped readily by schoolchildren. Also "typical" but seldom emphasized in elementary lessons is the fact that theorgansofeachsuccessivewhorl occupy alternate radii; i.e., petals are routinely positioned between sepals, and stamens (if only one whorl) are positioned between petals. Said another way, successive floral organs typically occur on alternate radii. Thus, for example, in most flowers, sepals and stamens occur on the same radii. "Typical" flowers are straightforward.

But what does typical mean? There are more than 350,000 extant species of flowering plants, and, to some degree, it is the details of how their flowers are constructed that make each one different from all others. The typical flower is really just a convenient starting point for learning about the immense full spectrum of floral diversity that exists in the natural world. One or more floral organs may be completely absent, or some organs may be present in multiple whorls. Numbers, sizes, shapes, and degrees of fusion between and among the floral organs can vary widely. Sepals may look like petals. Sometimes stamens and pistils

can be present in nonfunctional states, known, respectively, as staminodes and pistillodes. The ovary portion of carpels (pistils) may be located above or below the other floral organs. A flower can be as small and simple as a single stamen, as in, for example, *Euphorbia*, or as large and complex as the massive flowers of Rafflesia, from the jungles of Indonesia, which can exceed one meter in diameter. Variations on the typical flower theme go on and on. To really understand flower structure requires familiarity with plant diversity on a global scale. While the typical flower is pretty straightforward, the full spectrum of floral diversity is mindbogglingly complex.

Thankfully, there is a saving grace for those who study plant diversity: these myriad variations of flower structure fall into discrete patterns. And it is these patterns that allow us to recognize, on sight, species, genera, and families. These patterns are the raw material upon which classification, taxonomy, and systematics are built. Fundamentally, knowledge of biodiversity, as summarized by taxonomy and systematics, grows from the bottom up; patterns seen among organisms define species, patterns among species define genera, and so on, up the taxonomic hierarchy.

Our 2019 Wildflower of the Year, *Ceanothus americanus*, provides an interesting case in point. In some respects, flowers of New Jersey Tea are quite straightforward (Figure 2): five sepals, five petals, five stamens, and three carpels making up a compound pistil with a superior ovary.

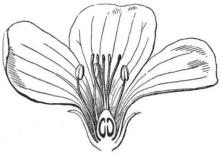


Figure 1. Flower of *Linum* (Flax), partly dissected to reveal all four floral organs. From Gray, A. 1868. Gray's School and Field Book of Botany. Ivison, Blakeman, & Co., New York.

Lots of dicots classified in a number of different families have the same general formula. But there is one detail by which Ceanothus departs radically from the common pattern of flower construction: rather than occupying alternate positions, petals and stamens occur on the same radii. Further, the petals are somewhat spoon-or hoodlike, and, in the bud, these hooded petals fit tightly over the pollen-bearing anthers. This is odd, and therefore noteworthy, but not unique. The character of hoodlike petals aligned with stamens is one of the distinguishing features of the plant family Rhamnaceae, in which Ceanothus is classified. If you spot a flower with hoodlike petals aligned with the stamens, you can confidently pronounce that plant as rhamnaceous!

Fifty-five genera and 950 species of plants are classified in Rhamnaceae. That is a mere one-half of one percent of all flowering-plant genera, and one-quarter of one percent of all flowering-plant species. Why is it that this small slice of biodiversity departs from the usual pattern of flower construction? Study of flower development provides the clue. In flowers of Rhamnaceae: 1) sepals start

to form first, as little bumps on the sides of the floral meristem; 2) then, instead of petals, which would be the usual second organ to appear, stamens take form, also as small bumps, alternating with the already formed sepal primordia; and 3) petals don't maketheirappearanceuntilafterthe stamens - and the first sign of petals is a series of small bumps on the outer flanks of the stamen primordia. In other words, the odd pattern of rhamnaceous petals and stamens traces back to the earliest stages of floral organ initiation. But why aren't these organs initiated in the usual sequence (sepals, then petals, then stamens)? One interpretation is that distant ancestors of Rhamnaceae, most likely, lacked petals entirely, and that petals were "reinvented" by proliferation of stamen primordia in the lineage leading to modern day Rhamnaceae.

Good stories have distinctive plot twists. Great pieces of music have memorable themes. In similar fashion, each flowering-plant family has its own unique pattern of distinctive features, prominent among

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which are the particulars of how its flowers depart from so-called typical structure. In essence, the plot twist or dominant theme for recognizing Rhamnaceae is that the petals develop from the flanks of the stamens, resulting in radial alignment of these organs. And flowers of Ceanothus americanus (Figure 2) represent just one of 950 variations on that general theme. No, knowing biodiversity is not rocket science, but knowing what makes families, genera, and species unique across the full spectrum of biodiversity is, easily, as complex. ↔