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Upside-down Anthers of *Clethra* Stand Out

W. John Hayden
University of Richmond, jhayden@richmond.edu

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Upside-down Anthers of *Clethra* Stand Out

By W. John Hayden, Botany Chair; illustrations by Sheila M. Hayden

For the most part, the flowers of the 2015 VNPS Wildflower of the Year, *Clethra alnifolia* (Sweet Pepperbush), are unremarkable. Five separate sepals, 5 separate petals, 10 stamens in 2 whorls, and a 3-carpellate superior ovary—an organization that can only be considered prosaic among the dicots. One floral feature, however, stands out: the anthers in the open flowers are upside-down! (See Figure 1A.) Further, these upside-down anthers open by pores (Figures 1B, 1C) rather than longitudinal slits, as in most flowering plants. These pores initially form on what would normally be the lowermost extremity of the anther, the inversion of which brings the pores to a forward position in the open flower. The significance of these acrobatic anthers—found not just in Sweet Pepperbush but through all 65 members of the genus *Clethra*—is twofold: anther inversion is essential to the plant's pollen-presentation strategy, and the odd morphology taxonomically links *Clethra* with the large and diverse heath family (Ericaceae).

Barnes (1880) provided one of the first descriptions of anther inversion in *Clethra*. In flower bud stages, the anthers of *Clethra alnifolia* take on a sagittate shape (Figure 1A), narrower at the apex and flared outward toward the base. Before the flower bud opens, the future pore for pollen release is located on the external (petal) side of the anther, a position technically described as extrorse. As the bud opens, the staminal filaments rapidly elongate, pushing the anthers past the opening petals. At the same time, the anthers begin to invert, quickly becoming horizontal, with their tips temporarily pointing toward the center of the flower. From the rapidly achieved horizontal position, complete inversion proceeds a bit more slowly (over the course of a few minutes), so that the narrow tip of each anther now points toward the base of the flower (Figures 1C, 1D). An additional consequence of anther inversion is that the pores for pollen release, formerly extrorse in orientation, become introrse, i.e., positioned on the stigma side of the now fully inverted anther.

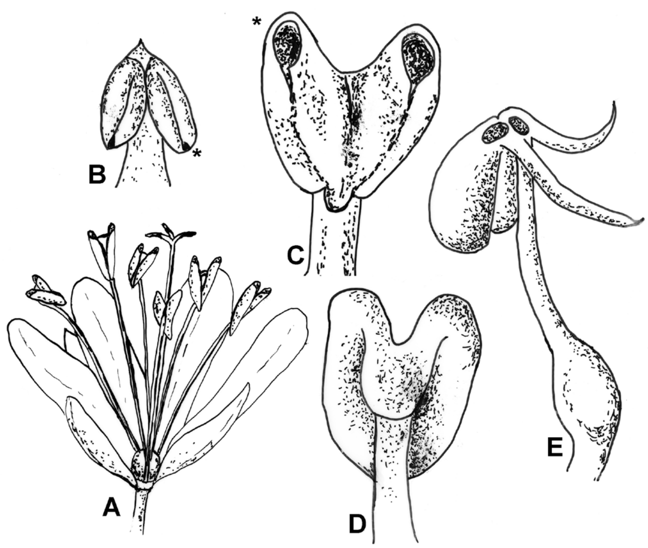

Fig. 1. (A) Flower of *Clethra alnifolia*. (B) Immature anther of *Clethra*, before inversion, as viewed from external (petal) side; asterisk (*) indicates initial basal position of dehiscence pore. (C) Mature anther of *Clethra*, after inversion, as viewed from internal (stigma) side; asterisk (*) indicates ultimate terminal position of dehiscence pore. (D) Mature anther of *Clethra*, after inversion, as viewed from external (petal) side. (E) Mature inverted anther of *Arctostaphylos uva-ursi*, with appendages.

How do these anthers invert? Barnes (1880) attributes the anther acrobatics of *Clethra* to cellular processes in the connective, the tissue located at the apex of the filament that serves to attach (connect) anther and filament together. In most plants, connective cells are uniform, but in *Clethra*, connective cells vary from longer, thin-walled cells containing oil droplets to shorter, thick-walled cells devoid of oil. In unopened flower buds, before anther inversion, the

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long, thin-walled cells are located on the petal side of the connective. As described by Barnes, bud opening brings relatively dry air into contact with the thin-walled connective cells, which collapse, presumably from evaporative water loss. This collapse of these thin-walled cells pulls the tip of the anther downward, accomplishing anther inversion as the bud opens.

So, if the anthers of *Clethra* did not invert, pollen would be shed extrorsely (petal side) from the anther bottoms. But since they do invert, pollen is shed introrsely (stigma side) from the original bottom of the anther that in open flowers occupies the extreme tip of the stamen. Arguably, pushing the pollen-releasing pores to a foremost position makes sense for efficient transfer to pollinators. In *Clethra alnifolia,* pollen is shed soon after flowers open. In other species, for example *Clethra acuminata,* pollen is shed before the flowers are fully open. In either case, these flowers are protandrous, shedding pollen before stigmas become receptive, an adaptation that promotes cross-pollination. Later, styles elongate, pushing stigmas beyond the level occupied by the anthers (Figure 1A), at which point stigmas become receptive to pollen. Presumably, introrse orientation of the inverted anthers allows for self-pollination, which has been documented, should cross-pollination fail.

Inverted porous anthers also occur in the heath family, and the shared presence of this unusual character is part of the evidence indicating a close relationship between these two families. See, for example, the stamen of *Arctostaphyllos uva-ursi* (Bearberry) in Figure 1E. But the anthers of Ericaceae are not identical to those

Clethra alnifolia in flower. (Photograph by W. John Hayden)

of *Clethra*. In most Ericaceae, anther inversion takes place much earlier in flower development, when flower buds are still quite small (Hermann and Palser 2000). Further, anthers of Ericaceae are usually equipped with slender appendages (Figure 1E) that are absent in *Clethra*. These anther appendages come in two forms: awns (as defined in this context) are hollow, elongate extensions of the pollen-bearing region, whereas spurs are solid and develop independently of the pollen-bearing anther sacs.

Regardless of their internal structure and how they originate, anther appendages in Ericaceae are critical for pollination. Typical ericaceous flowers are urceolate (urnlike) and pendent, which forces pollinators to probe the flower from below. As the insect, typically a bee, rummages around, it inevitably contacts one or more anther appendages, which act as tiny levers, causing pollen to sift out of the porous anthers onto the probing pollinator; when it moves on to another flower, some of that pollen will be deposited on its stigma.

As is often the case in comparative biology, the details are a little more complicated than the simple overview described above. Ericaceae is a large family, and intermediate states of anther modifications have been documented. For example, in *Arbutus* and *Enkianthus,* anther inversion happens late, as the flower buds open, pretty much as in *Clethra*. In *Cassiope,* partial anther inversion happens a little earlier, shortly before bud break (Hermann and Palser 2000) and reaches completion as the flower becomes fully open. Anthers of *Enkianthus* also differ from those of all other Ericaceae in that they open by longitudinal slits, not pores. And some of the most familiar members of Ericaceae have nonurceolate corollas; examples are *Rhododendron* (azaleas and rhododendrons) and *Kalmia* (Mountain Laurel). These genera have completely different pollen-presentation strategies and, correlated with that fact, they have no anther appendages. So the situation regarding anther structure and development is relatively complicated in Ericaceae. Nevertheless, the acrobatic anthers of *Clethra* provide—conceptually—a reasonable starting point for interpreting ericaceous anther diversity and the peculiar pollination mechanism characteristic of those members of the family that possess urceolate corollas.

Prosaic flowers? *Clethra*? Hardly! Its acrobatic inverted anthers earn Sweet Pepperbush a place of distinction among flowering plants, and a noteworthy addition to our Society's roster of beloved native plants. ❖