What Good Is A Sterile Stamen?

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Penstemons are one of our favorite and most familiar groups of native plants. That's understandable because there are lots of them and most have colorful, showy flowers. In fact, *Penstemon* is the largest genus of plants among those found only in North America. Of the 250 species, the majority occur in the western U.S. The great diversity of penstemons makes them a great group for gardening, but it also allows us to study how flowers evolve without having to go too far from home.

Beardtongue is the common name applied to many members of the genus *Penstemon*. It refers to the fact that all penstemons have a sterile stamen called a "staminode" that is hairy to some extent in the majority of species. Penstemon flowers are pretty simple, so the staminode is easy to see. Just peel open the corolla. There are six slender, whitish stalks inside. Four have elongate sacs at their tips; these are the fertile stamens, and the sacs contain pollen. One of the two remaining stalks comes from the top of the ovary; this is the style that carries pollen tubes to the young seeds. The other sacless stalk is the staminode.

Evolutionary biologists believe that the pollen-bearing function of the staminode was lost during the evolution of penstemon's two-sided, two-lipped flower from more primitive, radially symmetrical tube flowers. Flowers of these less advanced groups have five functional stamens. But five doesn't divide evenly into the two halves of the bilaterally symmetrical penstemon flower, so apparently the function of one of the five stamens was lost as flowers evolved toward being two-lipped.

Organs that no longer serve their primary function are called vestigial. Vestigial organs eventually meet one of two fates: they cease to be produced (like the tail

in humans), or they evolve to serve a new function. An example of a novel function for a vestigial character is facial hair in humans. Facial hair undoubtedly serves a protective function in most mammals, but it is not needed for this in humans. It has been lost in females but served a signaling function in males—white-bearded males have seniority, and, of course, a mustache is rakish and debonair.

There has been a good deal of speculation about the function of penstemon's staminode. Some researchers considered it useless, while others felt it prevented nectar robbing or otherwise facilitated pollination. Recently two biologists from Calgary sought evidence for staminode function in two hummingbird and two bee-pollinated penstemons. Lawrence Harder and his student Jennifer Walker-Larsen removed the staminode in some flowers through a small slit they cut at the base of the corolla. In red, bird-pollinated penstemons there was no difference in pollination between flowers with and without a staminode. However, the bee-pollinated species were a different story. In the narrowly tubular flowers of *Penstemon ellipticus*, a common species in northwest Montana, the staminode impeded visiting bees. They spent more time in the flower and consequently went away with more pollen on their bodies. Walker-Larsen and Harder also looked at *P. palmeri*, a species with a pouch-shaped corolla, very similar to our common fuzzy-tongue, *P. eriantherus*. In these species the staminode acts like a lever, causing the style to be pressed against the back of the bees when they land in the spacious flower. The long hairs help ensure contact, and the bees deposit more pollen on the stigma than in flowers with the staminode removed.

The results of Walker-Larsen and Harder's study suggest that the evolution of the staminode is taking several different directions within the genus *Penstemon*. All red, hummingbird-pollinated flowers in the Intermountain Flora (6 species) have glabrous staminodes. It appears they serve no function in pollination, so we might expect them to be reduced or lost in the future. On the other hand, the staminode in bee-pollinated flowers has evolved to enhance pollination, and it is

hairy to some extent in most of these species. Staminodes of narrowly tubular flowers act as a barrier, while those of pouch-like flowers have evolved to be levers. The vestigial staminode has taken on a secondary function, and even within a single genus, evolution of the staminode has gone in different directions depending on the shape and color of the flowers.

Additional reading:

Walker-Larsen, J. And L. D. Harder. 2001. Vestigial organs as opportunities for functional innovation: the example of the *Penstemon* staminode. *Evolution* 55: 477-487.