ACANTHACEAE, AN ADDITIONAL FAMILY OF ANGIOSPERMS WITH STAMINAL LEVERS

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Abstract. We report for the first time the occurrence of a staminal lever mechanism in Acanthaceae. Pressing the staminal appendage in two species of *Justicia* causes the anther to descend in a manner similar to the genus *Salvia*. Anther movement via a lever may affect where pollen is deposited on the body of potential pollinators. Acanthaceae are one of only a few families where staminal levers have been reported, and most of those families are in the order Lamiales.

Keywords: anther appendage, convergent evolution, *Justicia*, Lamiaceae, Linderniaceae, Plantaginaceae, Zingiberaceae

Resumen. Reportamos por primera vez un mecanismo de palanca staminal en Acanthaceae. Presionar el apéndice staminal en dos especies de *Justicia* causó que la antera descendiera en una forma similar al género *Salvia*. Movimiento de las anteras con una palanca puede afectar donde el polen es depositado en el cuerpo de potenciales polinizadores. Acanthaceae es una de las pocas familias donde se han reportado palancas estaminales, y la mayoría de las familias están en el orden Lamiales.

Palabras claves: apéndice de la antera, convergencia evolutiva, *Justicia*, Lamiaceae, Linderniaceae, Plantaginaceae, Zingiberaceae

The stamen is the pollen producing and presenting structure in flowers. Consisting of a filament or stalk and the pollen-bearing anther, stamens show remarkable diversity in shape, size, color, and number per flower. When an anther consists of two pollen sacs (thecae), the portion of the filament between them is known as the connective. The connective can be enlarged and highly modified into structures that aid in their interactions with floral visitors, including pollinators. In the genus *Salvia* L. (Lamiaceae), for example, the connective is modified into a long structure, which, when pressed by a potential pollinator, acts as a lever mechanism to lower the anther for precise pollen placement (Fig 1A; Claßen-Bockhoff et al. 2003). It has been suggested that the evolution of the lever has been a key innovation in *Salvia* that led to species diversification (Claßen-Bockhoff et al. 2004).

Staminal levers are rare in plants and known mainly in the families Lamiaceae and Zingiberaceae (Zhang et al. 2010). The similarity between levers in species of these two distantly related families has long been recognized (Lynch, 1882). The lever in Zingiberaceae differs from that of *Salvia*, the primary genus of Lamiaceae with staminal levers, in that it is produced by a variously modifed thecal appendage instead of an expanded connective tissue (Zhang et al. 2010; Paudal and Li, 2020). Another family where staminal levers have been documented is the Linderniaceae. For example, in the genus *Torenia* L., the thecal wall has a lateral flange-like outgrowth that functions as a lever (Armstrong, 1992). The fourth family that has a lever mechanism is the Plantaginaceae, where the staminode in some species of *Penstemon* Schmidel helps lever the stamens and style (Walker-Larsen and Harder, 2001).

Thecal appendages of various shapes and sizes occur in another family, the Acanthaceae, including species in subfamilies Thunbergioideae (Borg et al., 2008) and the mega-diverse Acanthoideae (e.g., tribes Acantheae, Justicieae, and Ruellieae; Manzitto-Tripp et al., 2022). Among Justicieae, thecal appendages and variously elongated connectives are common in the genus *Justicia* L. (Graham, 1988), in which appendages were found to have evolved at least twice (Kiel et al., 2017, 2018). Thecal appendages have been widely used as taxonomic characters among Acanthaceae, but their function remains unknown.

We hypothesize that at least some thecal appendages in *Justicia* are part of a lever mechanism that most likely functions in the placement of pollen onto floral visitors. This hypothesis is supported by manipulations and observations on two Mexican species described below. As in species of *Salvia*, such as garden sage (*S. officinalis* L., Fig. 1A), the appendages/levers in these species of *Justicia* are positioned such that an insect visitor seeking nectar at the base of the corolla tube would contact them. Using plants of two species of *Justicia* from Michoacán, Mexico, *J. salviiflora* Kunth (*Daniel 11917cv* grown from seeds of *Daniel & Steinmann 11917*) and *J. wilburii* T.F. Daniel (*Daniel 11919cv* grown from seeds of *Daniel & Steinmann 11919*), with all voucher specimens at CAS, we experimented with their flowers by contacting the appendage with the blunt bottom end of a paper clip and forceps. Contact of the appendage on one or both anthers by either instrument causes the stamen to move downward, confirming the lever-like function (Fig. 1C–F). Pollen from dehisced thecae was deposited onto the instrument used. As in *Salvia*, once pressure is no longer applied to the appendage, the stamen with anthers returns to its original position. The anther displacement via the lever mechanism was possible multiple times.

Previous observations on *Justicia salviiflora* noted that "the androecium conforms to the back and sides of a visiting

We are grateful to Emily Magnaghi for help with imaging the lever mechanism. We also thank the editor and reviewers for their input and Bryan Drew and Carrie Kiel for their comments.

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Harvard Papers in Botany, Vol. 29, No. 1, 2024, pp. 97–99.

ISSN: 1938-2944, DOI: 10.3100/hpib.v29iss1.2024.n11, Published online: 30 June 2024

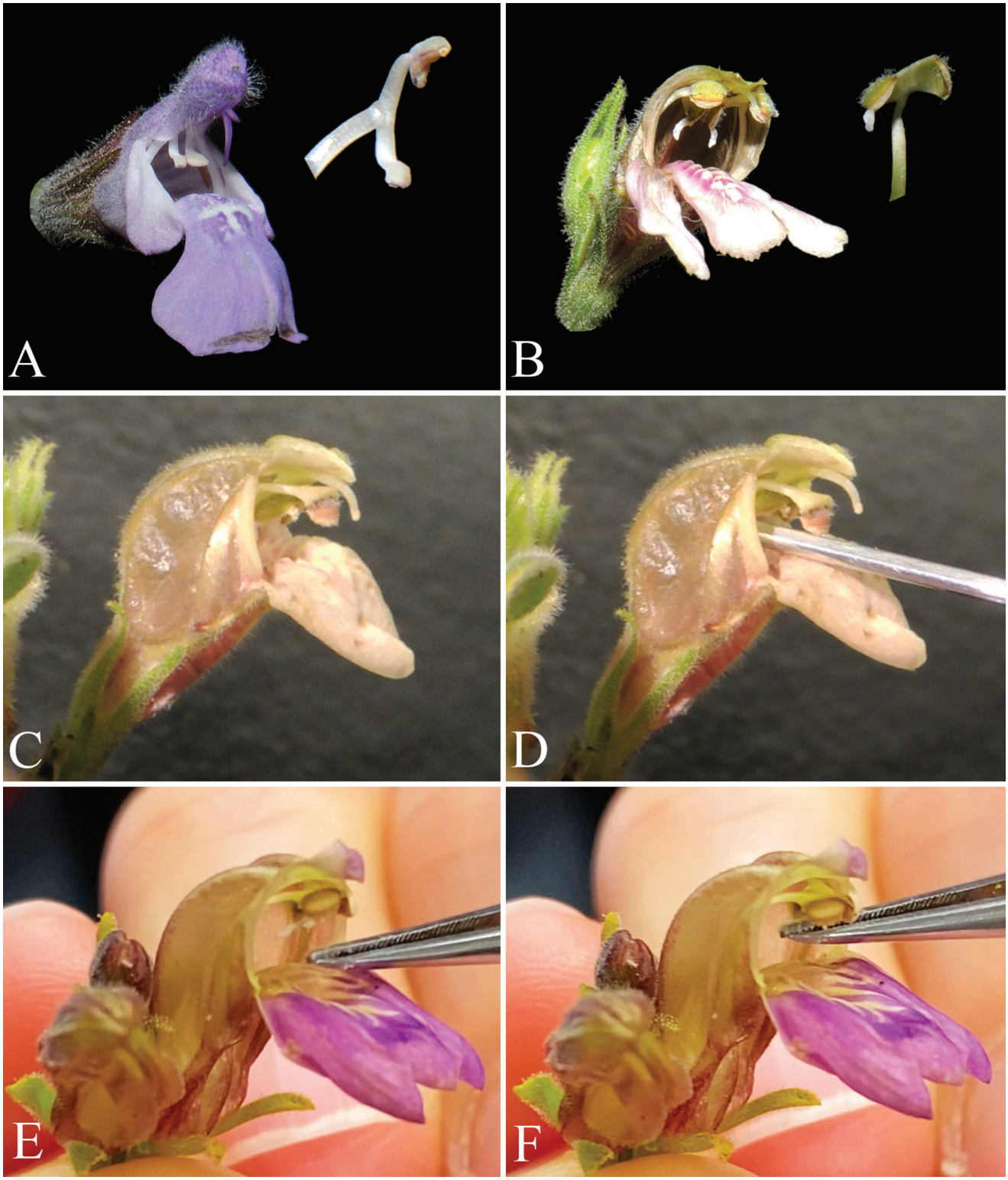

FIGURE 1. **A**, *Salvia officinalis* and close-up of one of its stamens. **B–D**, *Justicia salviiflora*. **B**, View of the corolla showing the stamens and their respective appendages and close-up of a stamen. **C**, Lateral view of the corolla, stamens and style. **D**, Lateral view of the corolla, stamens, and style with a pin inserted into the corolla and touching the anther appendages, causing the anther to lever down. **E–F**, *J. wilburii*. **E**, Lateral view of the corolla, stamens and style. **F**, Lateral view of the corolla, stamens, and style with a pin inserted into the corolla and touching the anther appendages, causing the anther to lever down.

bee as it enters the mouth and throat of the corolla, seeming to clamp onto the bee's body" (Kiel et al., 2023: 55). The authors hypothesized "that this mechanism deposits pollen on bees' bodies in locations where it cannot be reached by the grooming bee" and suggested that experiments would shed light on the function of this thecal shape variation. Our experiments indeed confirmed a function for the asymmetric thecae with an elongated connective and a basal appendage on the lower theca: a lever mechanism that assists in the deposition of pollen onto a floral visitor.

Among species of *Justicia* in the New World, basal appendages are rarely more than one millimeter long. Those of *J. salviiflora* and *J. wilburii* vary from 0.8 to 1.5 mm in length. Whereas there is only moderate elongation of the connective (e.g., to 0.5 mm) in these two species, other species of *Justicia* have stamens bearing more elongated anther connectives (e.g., Graham, 1988, Fig. 2; Kiel et al., 2017, Fig. 4, 2018, Fig. 2) that more closely resemble those in *Salvia*. These may also serve as levers in the absence of basal appendages or assist in levering of pollen placement when basal appendage functioning as levers are present. Hopefully, our observations will stimulate future investigations on the evolution and morphological diversification of thecal appendages and staminal levers among Acanthaceae and their impacts on evolution within the family.

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