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THE NATURE OF THE FLORAL APPENDAGES IN FOUR SPECIES OF *DICHELOSTEMMA* (LILIACEAE)

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All species of *Dichelostemma* have at the mouth of the perianth tube conspicuous appendages which taxonomists have described differently. Transections of flowers of four of the species show that while these appendages appear very much alike they have three modes of origin.

In the flower of *Dichelostemma pulchellum* (Salisb.) Heller there are six more or less triangular strips of tissue which together form a somewhat protective covering over the anthers. These structures have been interpreted in various ways. Jepson (1922) described them as, "filaments opposite the inner perianth segments with a broad membranous wing extending beyond the anthers as two lanceolate appendages." According to Hoover (1940) the "stamens opposite the inner segments with filaments entirely adnate, bearing a narrowly triangular wing 4-6 mm long on either side of the anther." According to Munz and Keck (1959), "those [filaments] opposite the inner segments adnate but extending beyond the anthers as 2 lanceolate appendages." Keator (1968) stated that the "stamens opposite the inner segments with filaments adnate to the perianth tube, producing two triangular wing-like processes 4-6 mm long behind the anther. . . ." None of these statements describes correctly the nature of these appendages.

Transections of the flower toward the base of the perianth tube show the filaments of three stamens adnate to the perianth tube (Fig. 1). At the level where the three outer segments become free it can be seen (Fig. 2) that the adnate filaments are attached to what will become the three inner perianth segments and the stamens those of the inner whorl. At the level where all six perianth segments have become free (Fig. 3) there exists a central cylinder of tissue with the filaments of the stamens opposite the inner whorl of perianth segments still adnate to the inner wall of the cylinder (Fig. 3b). At a still higher level (Fig. 4) the filaments of the stamens become free (Fig. 4a) and the central cylinder of tissue is interrupted. When all six stamens are free, all that remains of the original cylinder are six segments of tissue that at a lower level connected the filaments of the six stamens. These segments of tissue extend upward and form six lanceolate appendages; each appendage is opposite two anther sacs, one from a stamen opposite the outer perianth segment and one opposite the inner perianth segment (Fig. 5).

The short cylinder of tissue of which the filaments are a part should perhaps be termed a staminal tube and the 'appendages' as extensions of the tissue of the staminal tube. A similar condition exists in species of *Dandya*, *Bessera*, and *Behria*, all of which have staminal tubes but lack the extensions of the tube in the form of appendages.

Taxonomic statement: Filaments of the six stamens united at the base and forming a short staminal tube; connective tissue between the filaments extending upward as six triangular appendages.

In *Dichelostemma multiflorum* (Benth.) Heller there are three appendages described by Jepson (1922) as "staminodia entire, broad, obtuse, involute-cylindric, equalling or slightly exceeding the anthers." Hoover (1940) also called them staminodia, "Staminodia usually white but more or less violet-tinged, broad, involute, 5-6 mm long, entire at the apex: filaments entirely adnate, without appendages." Munz and Keck (1959), under the name *Brodiaea multiflora* Benth. likewise termed them staminodia, "staminodia white to violet, 5-6 mm long, entire; filaments adnate, not appendaged. . . ." Keator (1968), using the name *Dichelostemma parviflorum* (Torr.) Keator, stated "fertile stamens 3, the outer row entirely lacking, the filaments adnate to the tube, . . . the anther appendages coalescent to an inner and outer perianth segment and forming a corona."

Transections of the flower of *D. multiflorum* show that the three appendages are formed of tissue derived from the adaxial side of each of the perianth segments (Fig. 6). Each individual appendage being made up of tissue from one of the outer perianth segments (Fig. 6a) and tissue of the proximal half of the two adjacent perianth segments (Fig. 6c). Since the appendages are derived wholly from perianth tissue (Fig. 7c) and are not provided with a vascular strand there are no grounds for referring to them as staminodia. Although one might wish for a better term since the term 'corona' has been rather loosely used, it appears that the appendages in the flowers of *D. multiflorum* can be referred as a corona on the basis of Jackson's (1928) definition of the term as "any body which intervenes between the corolla and stamens."

Taxonomic statement: Flowers with a three-parted corona equalling or slightly exceeding the stamens.

The floral anatomy of *Dichelostemma volubile* (Kell.) Heller, while less misunderstood than it has been in the two species previously discussed, has still suffered from differing interpretations. *Dichelostemma volubile* is the only species in the genus possessing true staminodia opposite the three outer

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Figs. 1-4. *Dichelostemma pulchellum*.—1. a. Portion of perianth tube which will become inner segment.—b. Filament adnate to perianth tube.—c. Portion of perianth tube which will become outer perianth segment.—d. Vascular strand for stamen opposite the outer segment.—2. a. Outer perianth segments.—3. a. Inner perianth segments.—b. Filament of stamen opposite the inner perianth segment attached to central cylinder of tissue.—4. a. Filaments of stamens opposite the inner perianth segments.—b. Filaments of stamens opposite the outer perianth segments.—c. Connective tissue between filaments of stamens opposite the outer perianth segments.

Fig. 5. *Dichelostemma pulchellum*.—a. Six floral appendages, each opposite an anther sac of a stamen from the inner whorl and one from the outer whorl. Figs. 6–7. *Dichelostemma multiflorum*.—6. a. Perianth segments of the outer whorl.—b. Perianth segments of the inner whorl.—c. Tissue which will become one of the coronal segments, free from the inner perianth segment but still adnate to the outer perianth segment.—7. a. Outer perianth segments.—b. Stamens.—c. Segments of the corona.

perianth segments and these have been recognized by all recent authors. It is the so-called appendages that have received differing interpretations. Jepson (1922) wrote, "stamens 3, ... their filaments short with lanceolate appendages nearly or quite as long as the anthers. ..." According to Hoover (1940) the "filaments [are] entirely adnate to perianth, at apex bearing two oblong white appendages which nearly equal the anthers. ..." A similar explanation is given by Munz and Keck (1959) who wrote, "fils. adnate, apically bearing 2 oblong appendages ca. as long as anthers. ..." According

Figs. 8-10. *Dichelostemma volubile*.—8. a. Vascular strand for inner perianth segment.—b. Vascular strand to the anther.—c. Vascular strand for the outer perianth segment.—d. Vascular strand to the staminodia.—9. a. Outer perianth segment.—b. Inner perianth segment with filament still partially adnate.—10. a. Staminodia.—b. Stamen showing winglike filament.—c. Wings of filament free. These will extend upward as floral appendages.

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Fig. 11. *Dichelostemma ida-maia*.—a. Outer perianth segment.—b. Inner perianth segment.—c. One segment of the corona.—d. Stamen filament still partially attached to one of the coronal segments which in turn is still partially attached to an outer perianth segment. Flower somewhat compressed during preparation.

to Keator (1968) the “fertile stamens 3, the filaments adnate to the tube the anthers 3–4 mm. long, the appendages whitish, about 3–4 mm. long, bifid into two wings so folded in as to hide the anthers.” Only Jepson recognized that the filaments were not entirely adnate.

A transection of the perianth tube near its base shows the filaments of the three stamens opposite what will be the inner segments adnate to the walls of the tube (Fig. 8). At that point there are two vascular strands, one which will supply the anthers (Fig. 8b) and the other which will become the inner perianth segments (Fig. 8a). Alternating with these are two closely associated vascular strands the outer of which will supply the outer perianth segments (Fig. 8c) and the inner the staminodia (Fig. 8d). At the point where the six perianth segments are free, the three staminodia have separated from the adaxial surface of the outer segments (Fig. 10a) whereas the filaments of the three stamens are still adnate to the adaxial surface of the inner perianth segments (Fig. 9b). At the time that the filaments of the

stamens become free they bear wide lateral flanges that could be described as wings (Fig. 10b). Shortly thereafter the wings become free from the central portion of the filament and extend upwards as two appendages (Fig. 10c). Above the level of the perianth segments the anthers are surrounded by three staminodia alternating with three pairs of appendages, extensions of the winged filaments of the three stamens.

Taxonomic statement: Flower with three staminodia alternating with three stamens; basal portion of the short filaments winged; wings soon free and extending upward as six oblong appendages as long as the anthers.

In *Dichelostemma ida-maia* (Wood) Greene there are three appendages that Munz and Keck (1959) described as "staminodia white, involute, apically rounded, 3–4 mm long, somewhat wider." Jepson (1922) merely described them as "staminodia 3, white." According to Hoover (1940) the "staminodia [are] white, broader than long, involute, rounded at apex. . . ." Keator (1968) correctly described them saying "the appendages [are] coalescent with an inner and outer perianth segment to form a conspicuous white corona . . . involute and rounded."

Transections of the flower of *D. ida-maia* (Fig. 11) shows that the three appendages (Fig. 11d) are formed as in *D. multiflorum*—of tissue derived from the adaxial side of each of the perianth segments. Each individual appendage is made up of tissue from one of the outer perianth segments (Fig. 11a) and tissue of something more than the proximal half of the two adjacent inner perianth segments (Fig. 11b). The result is an overlapping of adjacent coronal segments. In this, *D. ida-maia* differs from *D. multiflorum* where the coronal segments are made up of the proximal half of the adjacent inner perianth segments and there is no overlapping of the coronal segments. Figure 11d shows a stamen filament, one half of which is attached to one coronal segment, and the other half with the adjacent coronal segment which is still partially attached to the outer perianth segment. At the time the filaments become free they possess a V-shape (Fig. 11d).

Taxonomic statement: Flowers with a conspicuous three-parted, involute and rounded, white corona.

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