Anatomy and Pollination of Cleistogamous Flowers of Benghal Dayflower (*Commelina benghalensis*)

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The anatomy and pollination of subterranean cleistogamous flowers of Benghal dayflower (*Commelina benghalensis*) is described as a contribution to understanding its reproductive biology. Subterranean stems bear one spathe per node, each enclosing a single cleistogamous flower. Only the three anterior stamens produce functional pollen; the posterior three stamens are staminodes. Tapetum is amoeboid and endothecium is present. The three-carpellate superior ovary bears five dimorphic orthotropous ovules. Nearly mature flowers have straight to somewhat curved styles; at maturity, styles elongate and coil. Our observations indicate that coiled style growth causes rupture of anthers and brings pollen into contact with stigmas. Pollen tubes were observed in styles that had previously undergone coiling, located within mucilaginous secretions of the mature stylar canal. The subterranean cleistogamous flowers of Benghal dayflower and their apparently unique mode of pollination, viewed together with reproductive capacity of its aerial chasmogamous flowers, underscore the complexity and flexibility of the reproductive biology of this noxious weed species.
Nomenclature: Benghal dayflower, *Commelina benghalensis* L., COMBE.
Key words: Tropical spiderwort, Commelinaceae.

Benghal dayflower is an Old World species characterized as one of the world's worst weeds (Holm et al. 1977). This weed is distinguished by production of chasmogamous flowers borne near aerial stem tips and cleistogamous flowers borne on basal, often subterranean, branches (Faden 1993). Range expansion of this federally listed noxious weed in agricultural settings of the southeast United States has been documented by Krings et al. (2002) and Webster et al. (2005); Benghal dayflower is also known from southern California and Hawaii (Faden 1993). A small population of Benghal dayflower was discovered among landscape plants on the University of Richmond campus, in Richmond, VA, in October 2012 (Hayden 2013)—underscoring the warning articulated by Sermons et al. (2008) about the potential northward spread of this aggressive weed. The senior author collected three flowering plants and a dozen seedlings from this only known Virginia colony (now believed to be extirpated), simultaneously preserving specimens for the anatomical studies reported here.

Standard floristic and systematic works (e.g., Faden 2000a,b) present overviews of the morphology of the aerial chasmogamous flowers of Benghal dayflower, and Maheshwari and Maheshwari (1955)

offer baseline morphological data on its cleistogamous flowers. No previous studies describe the microscopic anatomical structure of cleistogamous flowers of Benghal dayflower, which is one goal of this report. The other goal is to provide observations on the process of pollination in the underground cleistogamous flowers of this troublesome weed. Sound management of noxious weeds depends on full understanding of their reproductive capacity, which, for Benghal dayflower, includes both chasmogamous and cleistogamous flowers.

Materials and Methods

Anatomical specimens were collected on October 19, 2012 and preserved in formalin : acetic acid : 70% ethanol (5 : 5 : 90). This collection is vouchered by *Hayden 5688* (URV); multiple duplicate herbarium vouchers were distributed to FARM, JMU, LYN, MARY, NCU, ODU, VCU, VPI, WILLI, and WVA (herbarium acronyms follow Index Herbariorum 2015). Standard techniques were employed to make slides for light microscopy (Johansen 1940); in summary, this involved dehydration via a graded series of ethanol and tert-butanol, sectioning at 10 μm on a rotary microtome, staining with a combination of hematoxylin and safranin, and mounting with Cytoseal® resin. In order to preserve crystals in tissues, several slide sets were stained in 0.05% aqueous aniline blue before being deparaffinized and mounted in resin. Microscope slides provided a continuum of

Figure 1.   Subterranean stems with a single spathe at each node, each bearing a single cleistogamous flower.

developmental stages from early stages of anther and ovule differentiation to early stages of fruit and seed formation; sections of 25 subterranean cleistogamous flowers and one aerial cleistogamous flower were studied in detail. Photomicrographs were made with a Nikon CoolPix 990 digital camera fitted with a Martin Microscope S/N 0120 adapter on a Nikon Optiphot microscope. For scanning electron micrographs, five dissected gynoecia were dehydrated in ethanol, critical point dried with CO_2 as the transitional solvent, sputter coated with a gold–palladium mixture, and observed and imaged via JEOL JSM6360LV scanning electron microscope (SEM) (Parsons et al. 1974). Unless explicitly stated otherwise, all descriptions that follow pertain to subterranean structures of Benghal dayflower.

Results and Discussion

Cleistogamy in *Commelina*. *Commelina* is a genus of ca. 170 species (Faden 2000a). In addition to Benghal dayflower, two additional species are known to produce cleistogamous flowers: *Commelina forskalii* Hochst. ex C. B. Clarke (Maheshwari and Baldev 1958), and *Commelina indehiscens* E. Barnes (Barnes 1949; Faden 2000b). This large genus is taxonomically difficult, and cleistogamy has been erroneously attributed to two additional taxa cited in Lord's (1981) review of cleistogamic reproduction in plants. As noted by Faden (1993), Uphof's (1938) study of *Commelina virginica* L. was based on misidentified specimens of *C. benghalensis*; further, *Commelina nudiflora* L., studied by Calvino (1922, 1923), is now known as *Murdannia nudiflora* (L.) Brennan. Anatomy and embryology of chasmogamous flowers of *Commelina forskalii* have been described by Maheshwari and Baldev

(1958), but their study includes only peripheral mention of its cleistogamous flowers. Although cleistogamy is also known in three other genera of Commelinaceae (viz., *Murdannia* Royle, *Plowmanianthus* Faden & C. R. Hardy, and *Tinantia* Scheidw.), Hardy and Faden (2004) characterize its occurrence in the family as rare. Reproductive effort and sex allocation strategies in cleistogamous and chasmogamous flowers of Benghal dayflower have been studied by Kaul et al. (2002).

Anatomy and Morphology of Subterranean Axes. Cleistogamous spathes (Figures 1 and 3A) arise from lower nodes of the plant and usually, though not always, penetrate the soil surface and, when fully subterranean, are achlorophyllous throughout. We found some green cleistogamous spathes on the soil surface, but only subterranean spathes were studied in detail. Green aerial spathes bearing chasmogamous flowers are clustered on short branches in the axils of photosynthetic leaves; in contrast, the pale white subterranean cleistogamous spathes occur singly in the axils of reduced bracteal leaves. Further, cleistogamous spathes bear a single bisexual flower (Figure 2); in contrast, aerial spathes bear multiple flowers, usually interpreted to represent a pair of scorpioid cymes, the upper or distal cyme reduced to a single staminate flower, and the lower or proximal cyme consisting of several bisexual flowers, a pattern common in the genus (Faden 2000a). The sole flower present in subterranean spathes (Figure 2) is reasonably viewed as an element of the lower (abaxial) reduced cyme, an interpretation consistent with that applied to the cleistogamous flowers of *Commelina forskalii* by Maheshwari and Baldev (1958). Midline of the sole flower, defined by the posterior sepal and anterior petal, is rotated approximately 20 degrees relative to the midline of the enclosing spathe (Figure 2).

Distal internodes of subterranean axes are sufficiently short that one or two younger nodes may be enclosed within the bract of the most recently expanded cleistogamous spathe. In sections it can be challenging to distinguish basal regions of subterranean stem bracts from spathes, because both take the form of closed loops of tissue enclosing other structures (Figures 3B and 3C). Bracts always enclose a segment of the subterranean stem and spathes enclose a single flower, its pedicel, or in its distal extremity, nothing at all. Also, spathes exhibit folded margins (Figure 2), a feature that can be pronounced distally, but which is never present in bracts. Finally, spathes can be readily recognized in
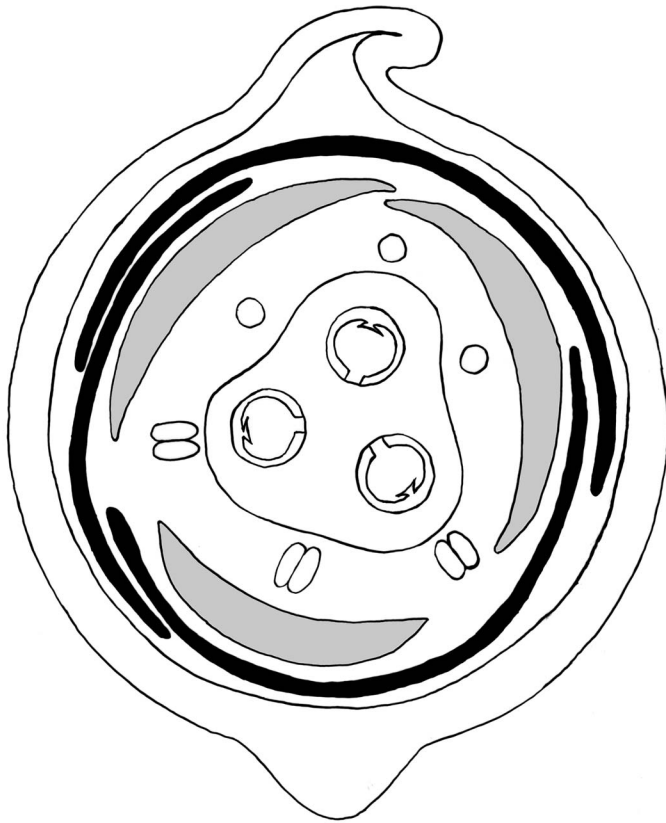
Figure 2. Floral diagram of the subterranean cleistogamous flower of Benghal dayflower. Floral midline is rotated ca. 20 degrees relative to the spathe in which it remains enclosed; anterior stamens bear fertile anthers, posterior staminodes lack anthers. Spathe, white; sepals, black; petals, gray.

sections by their distinctively differentiated epidermides (see below).

Figure 3A illustrates a longitudinal section through the base of a single cleistogamous spathe and its flower, permitting visualization of the subterranean stem, a bract and its associated axillary branch stem terminating in a single spathe, within which the cyme peduncle, flower pedicel, and flower (in longitudinal section) can be distinguished.

Spathe. Axillary branch stems below spathes are vascularized by a ring of usually 12 regularly spaced bundles that enclose an additional group of six somewhat irregularly spaced bundles (Figure 3B). The spathe has 3 major veins that arise from 3 evenly spaced bundles from the outer ring of 12; each of these is joined promptly by branches from the adjacent peduncle bundles. The result is nine bundles that vascularize the spathe, seven of which are approximately of equal size; development of the two bundles adjacent to the midvein, however, remains rudimentary. Epidermis on both surfaces is uniseriate (Figure 3A). Adaxial (inner) epidermal

cells are larger than ground tissue cells of the spathe and are also somewhat elongated in the anticlinal direction. In contrast, abaxial (outer) epidermal cells are cuboidal, about the same size as adjacent ground tissue cells, and include short antrorsely flexed uniseriate trichomes. Mesophyll consists of three to four layers of tightly packed cells, i.e., intercellular spaces are not prominent.

Pedicel and Vasculature to the Floral Organs. Cyme peduncle and flower pedicel feature nine vascular bundles, six forming an exterior ring enclosing the remaining three (Figure 3C); these supply the floral organs, either by direct divergence of the entire bundle into the organ, or by branching, with one branch supplying the organ, the other contributing vasculature to the next organ above. Sepals are vascularized by three traces each, as are the lateral petals; the anterior petal (homologous with the small, nonpigmented anterior petal of chasmogamous flowers) bears just a single vascular bundle. At their point of insertion, all six stamens are of similar size, each bearing a single strand of procambium or vascular tissue. Within a mere 50 to 70 μm above their bases, however, differences between the fertile anterior stamens and the posterior staminodes become apparent (Figure 3D): Stamen vasculature extends through the full length of the anterior filaments, whereas the posterior staminodes greatly diminish in size and no longer show any evidence of procambium nor of a vascular strand. Each of the three carpels exhibits a dorsal midvein located in the ovary wall, and a pair of laterals located in the axial position. We found vascular anatomy of the subterranean cleistogamous flowers of Benghal dayflower to be similar to that of the aerial chasmogamous flowers as described by Murty et al. (1974) with just one exception—whereas perianth elements of chasmogamous flowers were described to be supplied with three traces each, we observed only single traces. Reduction of vascular supply to perianth of subterranean cleistogamous flowers may be reasonably attributed to the fact that water stress should be minimal in organs that are never exposed to the atmosphere.

Perianth. Perianth consists of three separate sepals and three separate petals (Figures 2 and 3D); perianth elements remain closed through all stages examined in this study. In cross sections, the posterior sepal is large, spanning approximately half of the flower bud diameter and overlapping approximately one quarter of the two lateral sepals in their posterior portions. Each sepal has a

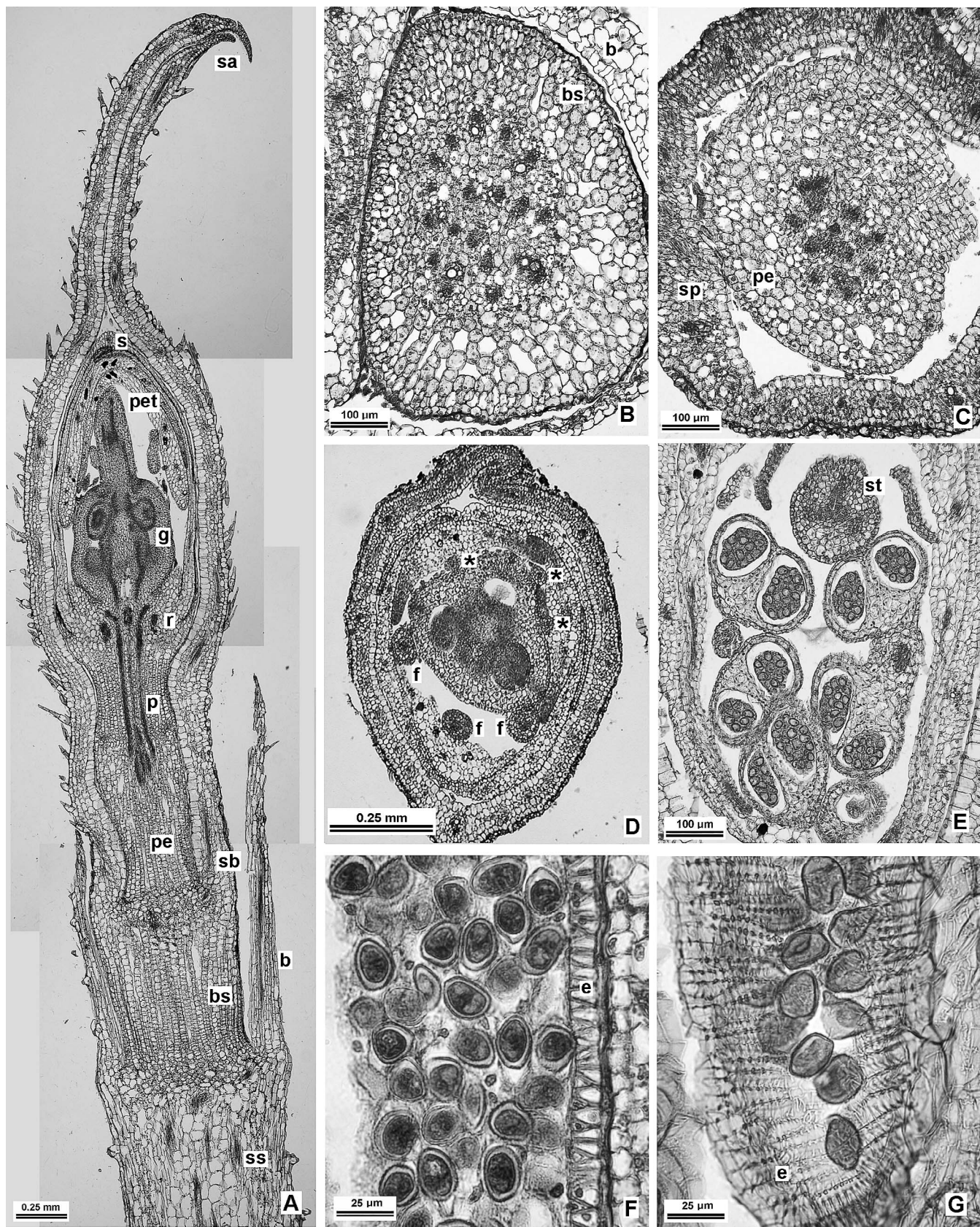Hayden and Fagan: Cleistogamous flowers of Benghal dayflower • 457

Figure 3. (A) Overview of structures bearing subterranean cleistogamous flowers, longitudinal section. (B) Branch stem below spathe, cross section. (C) Pedicel (center) enclosed by spathe, cross section. (D) Flower cross section enclosed within spathe. (E) Immature anthers of the three anterior (fertile) stamens, and style, cross section. (F) Amoeboid tapetum between developing pollen grains. (G) Mature pollen and endothecium, longitudinal section. Abbreviations: b, bract; bs, branch stem; e, endothecium; f, filament; g, gynoecium; p, pedicel; pe, peduncle; pet, petal; r, receptacle; s, sepal; sa, spathe apex; sb, spathe base; sp, spathe; ss, subterranean stem; st, style; *, staminode.

prominent midvein and a pair of smaller lateral veins. Sepal epidermides are uniseriate. Sepal mesophyll is about three cells thick across most of its width, but tapers to two, then one cell thick at the margins. Sepal mesophyll cells are parenchymatous and tightly packed. Petals are narrower but have a greater radial dimension than sepals. Petal epidermides are also uniseriate; lateral petals have a midvein and a pair of smaller lateral veins; the anterior petal bears a single vein. Petal mesophyll is parenchymatous and approximately six cells thick near the midvein, tapering to a single cell thick at the margin.

Stamens. Subterranean cleistogamous flowers of Benghal dayflower bear six stamens. Three stamens located in the posterior (adaxial) position are mere staminodes without distinguishable anthers; in contrast, only the three anterior (abaxial) stamens bear anthers with functional pollen grains (Figures 2 and 3D). Androecium of these cleistogamous flowers represents a simplification of the pattern found in chasmogamous flowers of Benghal dayflower and many other congeners. As documented in chasmogamous flowers of several species of *Commelina,* all stamens produce at least some viable pollen (Faden 2000a; Hrycan and Davis 2005); the three posterior stamens produce little viable pollen and are interpreted to function mainly to provide attraction and reward for pollinators; of the three anterior stamens, the two laterals produce abundant viable pollen and anthers are well exserted, presumably positioned to promote outcrossing; the median anterior stamen also produces functional pollen but it is much shorter, dehisces late in anthesis, and is interpreted to allow self-pollination if the flower has not already been pollinated in early anthesis. Reduction of the posterior stamens and their total lack of pollen in cleistogamous flowers of Benghal dayflower is consistent with overall reduction in floral organs and production of fewer pollen grains per flower that is commonly observed in cleistogamous flowers relative to chasmogamous flowers in the same or closely related species (Lord 1981).

The three functional anterior anthers are tetrasporangiate (Figure 3E) and tapetum is amoeboid, forming a periplasmodium that surrounds developing microspores (Figure 3F), similar to descriptions of the chasmogamous anthers of *Commelina forskalii* (Maheshwari and Baldev 1958). A single layer of endothecium develops as pollen grains reach maturity (Figure 3F and 3G); endothecium cells bear band-like thickenings of wall material on their anticlinal and inner periclinal walls; external periclinal walls lack band-like thickenings; endothecial thickenings fail to exhibit birefringence in plane-polarized light. In flowers of most plants, endothecial thickenings promote anther dehiscence as a result of forces that develop when surface layers of the anther wall respond to drying that occurs as the flower opens (Fahn 1982). In contrast, because these buds are subterranean and never open, anthers in cleistogamous flowers of Benghal dayflower are not likely to experience desiccation-induced dehiscence. Maheshwari and Singh (1934) reported raphide crystals in tapetum cells of Benghal dayflower; we have not been able to confirm raphides in tapetum of cleistogamous flowers, but we did observe a few scattered styloid crystals ca. 5 µm long among mature pollen grains in sections prepared to preserve their presence.

Gynoecium. Gynoecium consists of a three-carpellate superior ovary bearing a single unbranched style (Figures 2, 3A, 3D, and 4A); stigma is simple (unlobed). Ovaries contain a total of five ovules. As previously noted by Maheshwari and Maheshwari (1955), ovules and the seeds they produce are dimorphic; each of the two anterior carpels bears two small ovules and the posterior carpel bears a single large ovule. Dimorphism is also present in seeds produced by aerial flowers; Faden (2000a) reports large seeds from the adaxial carpel as 1.7 to 2.5 mm long, and small seeds are roughly two-thirds the size of large seeds, but are otherwise of similar morphology. Despite having five ovules per flower, we observed only three seeds per fruit in cleistogamous spathes, one seed per locule; Maheshwari and Maheshwari (1955) also reported three seeds per locule as the usual case, with two to four seeds occurring on occasion.

Despite size differences, all ovules are orthotropous, bitegmic, crassinucellate, and include a nucellar beak, a projection of megasporangium cells into the micropylar region. Maheshwari and Maheshwari (1955) also interpreted the ovules to be orthotropic; nevertheless, ovules of *Commelina forskalii* are described as amphitropous by Maheshwari and Baldev (1958). In early stages, the style is straight to gently curved downward (Figure 4A) and cellular throughout (Figure 4B). Styles were consistently observed to be cellular (not hollow) in 13 out of 14 flowers sectioned prior to the rupture and release of pollen from anthers (see below). Solid styles consistently show a three-lobed zone of densely cytoplasmic (darkly staining) cells at the center (Figure 4B). The one exceptional style that
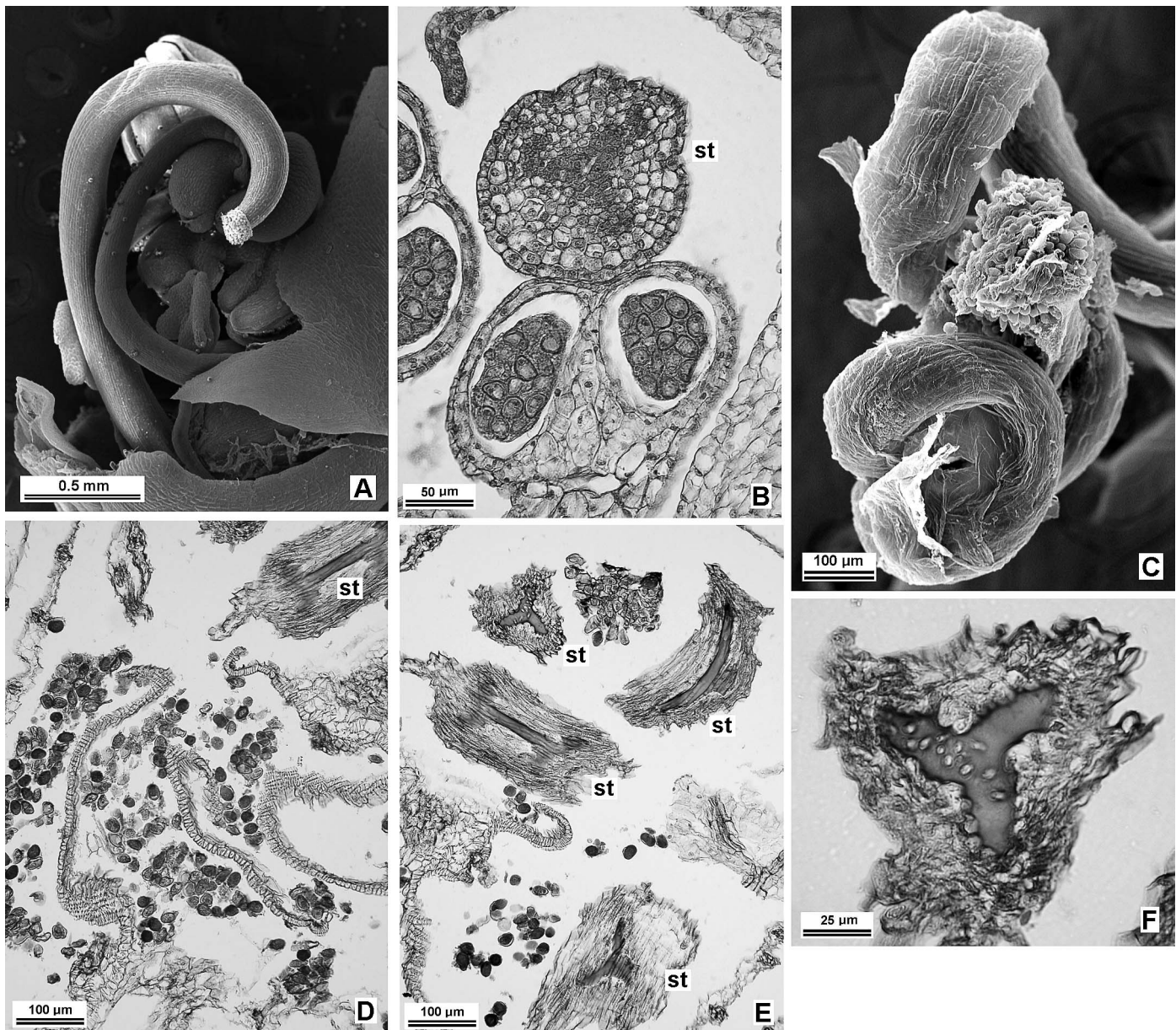
Figure 4. (A) Dissected gynoecium with style before helical elongation, scanning electron microscopy (SEM). (B) Immature style prior to formation of schizogenous central canal. (C) Dissected gynoecium after helical elongation of style, SEM. (D) Anthers after disintegration by helical elongation of style. (E) Multiple sections through helically coiled style. (F) Postpollination style with acellular mucilage-filled canal containing pollen tubes. Abbreviation: st, style.

we observed bore a schizogenous three-lobed central canal. We interpret canalization of the formerly solid style to occur immediately before the style's active role in pollination of these cleistogamous flowers (see below). The stigmatic surface can be recognized in sections because the surface cells bear convex outer periclinal cell walls, resulting in a somewhat irregular, convoluted, surface.

Cleistogamous Pollination. From dissected material, Maheshwari and Maheshwari (1955) observed pollen grains germinating on stigmas and further described these postpollination styles as having

elongated into a helical shape; these investigators did not, however, comment on how pollen grains exited anthers and came to be positioned on styles. We confirm that older cleistogamous flowers contain coiled styles (Figure 4C). Further, every older flower with coiled styles that we observed in sections was associated with grossly distorted and fragmented anthers (Figures 4D and 4E). Because these anthers are still tightly enclosed within the perianth (which is enclosed by a spathe, located underground), we doubt that any appreciable drying of the endothecium takes place, rendering

ineffective the usual mechanism of anther dehiscence. We propose that style coiling in the confines of mature cleistogamous buds is an adaptation to rupture anthers, liberate the pollen grains, and bring them into contact with the style. Maheshwari and Baldev (1958) reported no observations on pollination in cleistogamous flowers of *C. forskalii.*

We note some parallels between our proposed mechanism for pollination in subterranean cleistogamous flowers of Benghal dayflower with self-pollination mechanisms described for chasmogamous flowers of *Commelina.* As described and illustrated by Hrycan and Davis (2005; see their Figure 7K), the style of late anthesis chasmogamous flowers curves slightly and comes into direct contact with the short median anterior stamen (which, being exposed to dry air, dehisces without assistance from the style/stigma), and proximity of the two organs is sufficient to result in self-pollination. We view the autogamous process described by Hrycan and Davis (2005) as a preadaptation for the evolution of the much more pronounced stigma coiling and consequent crushing of anthers in cleistogamous flowers of Benghal dayflower.

Further, we note that an intermediate pollination mode exists between that described above for *Commelina* at large and the special situation in Benghal dayflower. Maheshwari and Baldev (1958) indicate that styles of seemingly ordinary aerial chasmogamous flowers of *Commelina forskalii* routinely contact and receive pollen from dehisced anthers of anterior stamens while still in unopened flower buds. In the terminology of Lloyd and Schoen (1992), this process would be neither straightforward cleistogamy nor chasmogamy, but "prior [to anthesis] self-pollination." Thus, potential steps for the evolution of cleistogamous pollination observed in Benghal dayflower might include late anthesis self-pollination (delayed self-pollination of Lloyd and Schoen 1992) that seems to be widespread in *Commelina,* followed by routine prior self-pollination via stylar contact with dehisced anthers in flower buds as described by Maheshwari and Baldev (1958) for *Commelina forskalii,* culminating in active rupture of anthers by coiled growth of styles within the confined space of cleistogamous flower buds as per our observations in Benghal dayflower.

Available literature on pollination mechanisms in cleistogamous flowers suggest that active rupture of anthers by coiled growth of styles observed in Benghal dayflower may be unique. In most cleistogamous flowers, pollen grains germinate while still enclosed within the anther, the pollen tubes growing just a short distance to contact the stylar surface (Lord 1981). For example, according to Parks (1935), pollination in cleistogamous flowers of *Commelinantia pringlei* involves spontaneously dehiscing anthers, but with few pollen grains escaping the anthers; further, "pollen grains germinate wherever they lie and the pollen tubes make their way to the stigma" (Parks 1935). Careful observations of pollination in other cleistogamous flowers of Commelinaceae would be interesting, especially for the cleistogamous flowers of *Commelina forskalii* and *Commelina indehiscens.*

At the cellular level, several changes occur during style coiling. Before coiling, styles are cellular and solid throughout (Figures 3E and 4B); cells of coiled styles appear disorganized (Figure 4F). In addition to becoming longer and taking on a coiled three-dimensional shape, styles expand somewhat radially, forming a tri-lobed schizogenous intercellular canal; this space accumulates mucilaginous material. Numerous pollen tubes were observed in this mucilage-filled intercellular canal throughout the length of mature coiled styles (Figure 4F), and even into upper regions of the ovary.

The material at our disposal provided limited observations of reproductive events within the ovule. We observed, for example, some evidence of female gametophyte structure, including cells of the egg apparatus, a presumptive polar nucleus, and antipodals. Our observations are consistent with cleistogamous seeds forming as a result of sexual processes but are certainly not conclusive of that interpretation.

Acknowledgments

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