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RESEARCH PAPER:

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RESEARCH PAPER:

**Unraveling the development and secretory structures of the atypical flowers of *Dalea purpurea*
(Leguminosae: Papilionoideae)**

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ABSTRACT

Dalea purpurea, an herbaceous papilionoid legume of the North American Great Plains, has floral characteristics that are highly atypical within subfamily Papilionoideae, such as organs reduction, low differentiation among petals, with keel absence, adnation between petals and stamens and presence of anther glands. This study aims to elucidate the ontogenetic processes responsible for its atypical architecture. Floral buds and flowers were processed by scanning electron microscope (SEM) and light microscope (LM). Five sepals initiate in a modified unidirectional order, followed by five petals simultaneously. The five antesealous stamens initiate in a bidirectional order. No antepetalous stamens primordia were initiated, suggesting that the presumed evolutionary reduction from ten to five stamens in *Dalea* was due to ontogenetic pathway organ absence since the initiation. The single and central carpel is precocious, emerges concomitantly with the first stamen primordium. The hypanthium is short, and the ovary is superior, with a short stipe. The five anthers are dorsifixed and rimose, with elongated glandular dorsal and apical appendages. The petals are clawed, and positioned like a hood above the reproductive whorls during development. We found an adnation of the basal region of the filaments to the petal claws, forming a stemonozone. The structure, on the abaxial side, forms an elongated sheath through the adnation of the stamens to four weakly differentiated petals to the height of the calyx lacinia. The adaxial petal (banner) is free for the most part, with adnation only at the base of the stemonozone, forming the apron. The peculiar feature absence of the typical staminal tube seems to be circumvented by the adnation of the five stamens to the five petals and the position of the adaxial petal in *D. purpurea*, which looks like it performs a similar function to that of the diadelphous staminal tube of other Papilionoideae. The diversity and distribution of floral secretory structures indicate that this species, which lost part of its floral specialization, might be using chemical defenses as protection against the predation of the reproductive organs. Thus, we conclude that the atypical *Dalea purpurea*'s floral architecture is due to some ontogenetic events associated with evolutionary and environmental pressures.

Key words: floral architecture; stamens; Fabaceae; anther glands; floral ontogeny; organ reduction; synorganization.

Introduction

The flower has several characteristics specialized in protecting and attracting pollinators or presenting reproductive whorls (Richard, 1997). In addition, the large number of characters considered conserved places the flower in prominence to elucidate the evolutionary history of the groups (Soltis et al., 2009; Teixeira et al., 2015). Thus, the floral organs development deserves attention because it provides subsidies to understanding the floral diversification that leads to floral architectures that deviate from the pattern of some taxonomic groups (Tucker, 2003; Pedersoli et al., 2010; Paulino et al., 2013; Teixeira et al., 2015). Floral ontogeny and morphology, associated with information from phylogenetic analyzes, improve our understanding of the morphological patterns and evolutionary changes that culminate in floral diversification (Fougère-Danezan et al., 2010, Nogueira et al. 2013).

Among the floral whorls, the androecium deserves attention because it is responsible for producing, storing, and releasing pollen grains. The stamens have elongated filaments, which expose the anthers (the unit that produces and shelters the pollen grains) and carry water and nutrients to them (Scott, 2004). The study of the androecium is highly relevant in Papilionoideae since the arising of specialized floral architecture involving the fusion of filaments in a tube around the carpel resulted in the formation of the reproductive column (staminal tube + central carpel). A structure sheltered and fitted in the wing-keel complex is directly related to the pollen grain release mechanisms in this group, which are involved in optimizing the pollen transfer (Westerkamp, 1997; Galloni et al., 2007).

Further studies on the development of unusual conditions in the androecium are important because it is a whorl that is directly related to sexual reproduction in plants (Richards 1997). For example, the androecium of *Lupinus* “The Governor” and *Cytisus scoparius* (L.) Link., two species of Papilionoideae, in which distinct ontogenetic pathways lead to the formation of the heteromorphic androecium with the division of labor between the two distinct morphs, as an evolutionary strategy to circumvent the excessive loss of pollen grains destined for pollinator feeding (Paulino et al., 2016). Thus, understanding patterns of floral development, both from a genetic and morphological perspective, can be crucial to unraveling how changes in floral architecture arise and broaden our understanding of evolutionary trends in the history of Leguminosae (Soltis et al. 2002, Soltis et al. 2009), besides to understanding how such changes interfere with floral functionality, revealing characteristics that mediate the relationship between flowers and pollinators (Teixeira et al. 2014).

In this context, *Dalea* Mill. stands out, the most species-rich genus of the tribe Amorpeae (Cardoso, 2013), with more than 180 species (World Flora Online, 2022). This genus displays an androecium varying

between ten (pattern) and five stamens per flower, and more rarely nine; the species known as prairie clovers (section *Kuhnistera*) have strictly five stamens per flower (Barneby, 1977). It has a mostly North American distribution, with many species occurring in Mexico. However, some species are found in Argentina (such as *D. ornata* (Douglas) Eaton & Wright and *D. boliviana* Britton). Representatives of the genus are herbs and low shrubs, with imparipinnate leaves containing subepidermal secretory cavities, which are also found on branches and, occasionally, on flowers (Turner, 1986). The inflorescences are spikes or racemes, with varying levels of flower density. The petals are mostly white or various shades of purple, but there are also species with yellow and/or orange petals (Barneby, 1977).

Dalea purpurea Vent. has a wide range in central North America, distributed in a variety of open habitat types (League, 2004) in the Great Plains, where it constitutes the small non-grassy percentage of the local flora (Zajicek, 1986). It is classified as a hemicryptophyte, according to Raunkiaer (1934), and resistant to fire (Towne and Knapp, 1996; Ritchie, 2020). It is a forage species for native and domestic animals, important because of its high protein content in vegetative organs (National Academy of Sciences, 1971; Posler, 1993). For humans, it has different traditional uses reported by Native North American ethnicities, from medicinal uses to the manufacture of domestic utensils (Gilmore, 1919).

Dalea purpurea, and some closely related species, arouse special interest for presenting unusual characteristics in their floral architecture (McMahon and Hufford, 2002), which have already led to different organogenetic interpretations of the mature flower (Barneby, 1977). The typical flower of Leguminosae is pentamerous and zygomorphic, formed by 21 floral organs: five sepals, five petals, two whorls of five stamens, and a single carpel (Tucker, 2003). *D. purpurea*, with other prairie clovers, differ from this pattern by presenting only five stamens adnate to the petals forming a stemonozone (Faegri and Van Der Pijl, 1979). The abortion or absence of floral organs since their initiation is considered rare, especially in Papilionoideae, occurring only sporadically in some lineages, such as the reduction of petals number in Swartzieae and Amburaneae (Tucker, 1987; Leite et al., 2014). The flower of *D. purpurea* also differs from the typical floral architecture of Papilionoideae by its poorly differentiated petals and without apparent structural specialization. The papilionaceous flower keeps the reproductive organs (i.e., androecium and gynoecium) enclosed and protected by the keel petals, especially to avoid excessive pollen collection (Westerkamp, 1997), given that the keel is an additional barrier to pollen access by floral visitors. Such modification in the corolla of *D. purpurea* may indicate a pollination strategy that differs from the other Papilionoideae (Westerkamp, 1997), in which the presence of the papilionaceous flower is directly related to the specialized mechanisms of pollen grain release:

mainly, the piston, valvular, explosive, and style brush types (Galloni et al., 2007). It is worth mentioning that *D. purpurea* is mainly a xenogamous species with highly diverse insect visitors, specially, a guild of native bees. Self-fertilization may also occur (Robson, 2014; Cane, 2006).

Thus, this work aimed to elucidate the floral development of *Dalea purpurea*, to understand: (i) which ontogenetic pathway gives rise to the reduction of stamens in *D. purpurea*; (ii) how atypical floral traits are settled during developmental processes. We also explore histological aspects of floral secretory structures commonly found in the Amorpheae tribe and discuss whether the change in floral architecture has ecological implications.

Materials and methods

Inflorescences with floral buds at different stages of development and flowers of *Dalea purpurea* were collected in the United States (Figs. 1A-F), and the voucher specimen is deposited at the Missouri Botanical Garden Herbarium, MO (acronym according to Thiers, 2016), under the number Davidse, Gerrit – 39547.

Samples were fixed in FAA 50 (formalin: acetic acid: alcohol – Johansen, 1940) for 24 h, gradually dehydrated in an ethanol series, and stored in 70% ethanol, or in some cases, they were fixed and stored directly in 70% ethanol. They were then dissected and prepared for subsequent analyses.

For surface analysis (SEM), samples were dissected using a Leica SAPO stereoscopic microscope, dried in a Bal-Tec CPD 030 critical point dryer (Bal-Tec AG, Liechtenstein) and in an EM-CPD300 (Leica, Germany) instruments, mounted on aluminum stubs, placed on carbon adhesive tape and then coated with gold in an Emitech K550X sputter coater (Ashford, UK) and a Balzers Union FL 9496 sputter coater (Balzers, Liechtenstein). Observations and illustrations were performed using a QUANTA 250 (CENABIO) and JEOL JSM-6490LV (CBPF) scanning electron microscope at 15, 20 or 30kv.

For anatomical analysis (LM), samples of developed flowers and buds at a stage immediately preceding anthesis were embedded in historesin (Gerrits and Horobin 1991), and transversely and longitudinally sectioned (2 to 5 μ m thick) with a rotary microtome (Leica RM 2245, Wetzlar, Germany). Sections were stained with 0.05% Toluidine Blue in phosphate buffer (pH = 4.4) (O'Brien et al., 1964). Histochemical tests were performed to detect carbohydrates using PAS (Jensen, 1962) and for the detection of reducing sugars with Fehling's Reagent (Purvis et al., 1964). Appropriate controls were conducted simultaneously with the tests. Histological sections were observed, and photomicrographs were obtained using a light microscope (Eclipse 50i, Nikon) coupled to a digital camera (Sight DS-5M-L1).

The images obtained were analyzed and processed using Adobe Photoshop CS5. The terminology used to describe the floral ontogeny followed Tucker (1987, 1997, 2003b), Klitgaard (1999), and Prenner (2004a, b, 2013a). The term stemonozone refers to the region of petal-stamen synorganization, below the insertion points of the petals and above the rim of the hypanthium (McMahon and Hufford, 2002), and apron refers to the tissue continuous with that of the staminal tube located at the adaxial region, where the banner claw is inserted (*sensu* Wemple and Lersten, 1966).

Results

Organography

The flowers of *Dalea purpurea* are purple, petiolate, pentamerous, perfect, and complete, with moderate zygomorphy (Figs. 2A-B), they are arranged in racemes, which range from 2-6 cm long, and are found on the top of long erect peduncles. Each flower is subtended by an angled bract, with dense brown pigmentation in the upper third. Bracteoles are absent in this species.

The calyx is gamosepalous, composed of five sepals, ca. 4 mm long, covered with simple trichomes and sparse stomata on the adaxial surface, and simple trichomes arranged on the abaxial surface, especially at the apex of the lacinia. The fused region (calyx tube) reaches about three-quarters of the length of the calyx (Fig. 2B, 2K, and 2L).

The corolla and androecium are adnate, and the petal claws and the basal portion of the filaments are fused, forming a sheath called stemonozone (Figs. 2C-D). The stemonozone follows the carpel on the abaxial side as a staminal sheath until the opening of the calyx lacinia (Fig. 2D). In contrast, on the adaxial side, it surrounds only the lower region of the ovary, forming the “apron” (Fig. 2E).

The corolla is purple, composed of five clawed petals fused with the filaments, forming the stemonozone. The standard, adaxial median petal, is the slightly differentiated petal: it varies from reniform to sagittate and has a longer claw due to the lower height reached by the stemonozone on the adaxial side, the apron, where the claw of this petal is inserted. (Fig. 2J). The other four petals, spatuliform (two lateral and two abaxial), have the basal region (claws) intercalated and fused with the stamen filaments, forming the columnar portion of the stemonozone (Figs. 2F-I).

The androecium is formed by five stamens that are characterized its adnation to the petals, comprising the stemonozone, with the free apical portion of the filaments (Figs. 2C-D). The filaments are linear and weakly

pigmented. The anthers are rimose-dehiscent, dorsifixed, linear-oblong with truncated base, appendiculate, and sporadically show stomata in the connective, close to the region of filament insertion (Fig. 2O).

The gynoecium is monocarpellate. The superior carpel is elongated and recurved with short stipe (Fig. 2P); the ovary is ca. 1.5 mm long, is oblong, unilocular, with anomocytic stomata both in the outer and inner ovary epidermis, and trichomes are positioned in a semicircle on the adaxial surface, associated with the carpel cleft; the style is glabrous, ca. 6.8 mm long; the stigma is terminal and punctiform. The hypanthium is short and narrow.

Organogeny

The floral meristems are initiated in acropetal order on the inflorescence (Fig. 3A). An abaxial bract subtends each floral meristem. The floral meristems have a slightly ovate shape due to the angular pressure exerted by the bracts at the beginning of development (Fig. 3B). There is no initiation of bracteoles. Floral organs initiate in mixed acropetal succession. The order of initiation of the floral whorls follows this sequence: sepals, petals, carpel + antesealous stamens.

The sepals initiate in modified unidirectional order, with the median abaxial primordium formed first, followed by the two lateral primordia, then the first adaxial primordium, and finally the second adaxial primordium (Figs. 3C-D). The position and development of the sepals allied to the pressure of the bracts give the floral bud a pentagonal shape at this stage (Fig. 3B).

After the initiation of the sepals, the five petal primordia begin in simultaneous order, in an alternate position to the sepals (Figs. 3E-F). The petal primordia become quite evident early in development, with prominent axillary space between two sepals. (Fig. 3G).

The five stamen primordia arise in the antesealous whorl, alternating with the petal primordia in bidirectional order (Fig. 3F). No antepetalous stamen primordia were observed, with a reduction of five stamens by the developmental pathway absence of organs since initiation.

Carpel initiation is precocious, concomitant with the first stamen primordia (Figs. 3F-H). The central carpel becomes prominent in the early stages (Fig. 3H). The plicated carpel cleft appears after all the organs are formed (Fig. 3I).

Intermediate and final stages of development

Sepals enlarge following their initiation order but ultimately attain similar sizes. During elongation, the sepals fuse, forming the gamosepalous calyx (Fig. 4A). With the development of adjacent buds, there is a compression given the high density of flowers per inflorescence, which results in the formation of an exceptionally thinner basal region (pedicle + receptacle) compared to the rest of the floral structure (Fig. 4B). The sepals enclose and protect the developing internal organs since the beginning of their elongation. During the differentiation and elongation of the sepals, stomata form on their adaxial surfaces (Fig. 4C). Subsequently, the already differentiated petals displaying cochlear aestivation begin to enclose the stamens and carpel (Fig. 4E), a phase in which the calyx lacinia are free, exposing the internal organs in the apical portion of the floral bud (Fig. 4F). Simple trichomes appear first on the apical portions of the sepals, and then on the entire abaxial surface, forming a densely hairy calyx (Figs. 4B, F).

After each of the five petals develops a narrow base (claw) and laminar apex, the five antesepalous stamens develop filaments and anthers (Fig. 4D). Subsequently, the adnation of the base of the petals to the filaments occurs, forming a tube around the carpel, called the stemonozone (Figs. 4E, 5A, 4H, 6C-E). The distal portion of the petal's claw and the filaments remain free (Figs. 2C-D, 5A). The stemonozone at the end is longer in the abaxial region and shorter in the adaxial region, forming the apron, where the standard insertion occurs (Figs. 2C-E, 4E, 5A-B). The adaxial median, the banner (Fig. 4D) is the first petal to show marginal expansion. As the petals marginally expand, they assume cochleate-descending aestivation, covering and protecting the reproductive whorls (Figs. 4E-F). The growth of the petals is mainly marked by the great elongation of the claws and by their position, alternating with the stamens in the stemonozone (Figs. 2C-D, 5H, 6A-E).

Elongation of the stamen primordia occurs previous to the elongation of the petals. The differentiation of the anthers begins soon after the formation of the carpel cleft and before the formation of the stemonozone (Fig. 3I). The five stamens show rapid differentiation between filament and anther, with the formation of theca concurrent with the beginning of the marginal expansion of the petals before they assume the characteristic aestivation. (Fig. 4D). At the end, the anthers take a linear-oblong shape with a truncated base. They are dorsifixed, rimose-dehiscent, and have apical glands (Fig. 5E-F). Pollen grains occur in monads, are tricolpate, and have perforate ornamentation (Fig. 5G). Elongation is also rapid and pronounced in this whorl, resulting in the compacted and twisted filaments in the floral buds at the final stages of development, i.e., pre-anthetic buds.

After the formation of the carpel cleft, the carpel assumes a hemispherical shape and elongates rapidly (Fig. 3I). Then, the apical portion extends, forming the style which initiates a curvature towards the adaxial region (Fig. 5D), culminating in a carpel with a long style and a terminal punctiform stigma (Fig. 5I, 6A). The

mature ovary contains two ovules (Fig. 5H-I). The mature carpel is elevated above the short hypanthium by a short stipe of ca 3 mm in length (Fig. 5I).

Floral Secretory Structures

The flowers of *Dalea purpurea* present a great diversity of secretory structures, such as phenolic idioblasts, mucilaginous cells and secretory cavities, distributed in all floral whorls.

Phenolic idioblasts are distributed in the receptacle, sepals, stamens, and carpels (Figs. 7A, E, G-I, K). In the sepals, they are voluminous, distributed in great quantity, and located in the subepidermal layers, mainly close to the abaxial surface, forming an almost continuous layer with interruptions close to the vascular bundles (Fig. 7A). In the stamens, they surround the anther glands (Fig. 7G-H). In the carpels, they are distributed mainly on the ovary wall and along the style, in the external subepidermal region (Figs. 7E). In the receptacle, the phenolic idioblasts are in the subepidermal region and surrounding the vascular bundles (Fig. 7I).

Secretory cavities were found in the ovary wall close to the outer epidermis, between the phenolic idioblasts (Figs. 7E). The anther's glandular appendage, positioned in the dorsal and apical region, is elongated and easily observable with the naked eye, given its brownish solid color (Figs. 2O, 5D-F). This appendix has an apical secretory cavity, with one layer of epithelial cells surrounding an oval lumen. The secretory cavity is surrounded apically and laterally by a layer of phenolic cells and a much thicker zone of phenolic cells at its base. The secretory cavity occupies about a third of and layers of phenolic cells two-thirds of the appendix (Figs. 6B, 7G-H).

Bulky mucilaginous cells were found in the petals and sepals. However, they are more evident and voluminous in the petals. In this species, the petals are thin, and the mucilaginous cells make up almost the entire mesophyll volume (Fig. 7B-C). In the sepals, they occur sparsely in the mesophyll and have a smaller diameter, similar to the other parenchymatic cells.

No structured nectary or nectariferous disc was evidenced in histological sections in the region of the hypanthium base (Fig. 7I-K). The apron's inner epidermis shows some stomata, but no structured nectary was observed in this region (Fig. 7D). Cells with moderately dense cytoplasmic content were found to be associated with the vascular bundles of the stemonozone (Fig. 7K), and starch granules were found at the base of the ovary (Fig. 7J). However, tests with Fehling and PAS reagents did not detect sugars in these regions.

Discussion

Unraveling the ontogenetic pathways that lead to the atypical floral architecture in a papilionoid species

The unusual floral morphology of *Dalea purpurea* is the product of a series of special events observable during development. The first morphological peculiarity worth mentioning is the reduced number of stamens. The reduction of organs in the flower of *D. purpurea*, which leads to significant changes in floral architecture, is due to the absence of the five antepetalous stamens primordia since their initiation. The complete reduction of floral whorls is a rare feature in Papilionoideae (Tucker, 2003). The reduction of the antepetalous stamens, and not the antesealous stamens, might be associated with the position of the former whorl closer to the apex of the floral meristem (Ronse De Craene, 2018) and the short plastochron between the initiation of whorls, considering that the carpel appears right after the initiation of the petal primordia and overlaps with the initiation of the first primordia of the antesealous stamens. It is worth mentioning that, in general, organs of the same whorl have very short or null plastochrons, with simultaneous or rapid sequence organ initiation; however, the plastochron between different whorls is usually longer (Endress and Doyle, 2007; Smyth, 2018). This contrasts with the pattern observed in *D. purpurea*, whose plastochron is short between the whorls of petals, antesealous stamens, and the carpel. Therefore, the precocious initiation of the central carpel, likely as an outcome of the shortening of plastochrons between whorls, integrated into the rapid development of the carpel may result in a spatial limitation, an ontogenetic contingency culminating in the absence of the internal whorl of stamens (Ronse De Craene, 2016; Ronse De Craene, 2018; Bull–Hereñu et al., 2022). Space availability has been considered to be a critical factor in guiding development (Ronse De Craene, 2018). This hypothesis was inferred to explain the reduced number of petals in the Swartzoid clade of Papilionoideae, in which the spatial restriction is imposed by the presence of a ring meristem, which forms the polyandrous androecium (Paulino et al., 2013). The rapid expansion of the carpel imposed a spatial constraint, possibly associated with the evolutionary loss of the antepetalous whorl of stamens, which leads us to hypothesize that there is a selection to reduce the antepetalous whorl as a thrift in the floral development.

Stamen reduction in Papilionoideae is a rare phenomenon and manifests differently in a few lineages. In *Abrus precatorius* L., a reduction by absence since initiation occurs only in the adaxial stamen of the antepetalous whorl, resulting in an adaxially open sheath (Prenner, 2013). In *Leptosema chaapmani* Crisp. late abortion of a variable amount of the stamens of the antepetalous whorl occurs. Evolutionary reduction to five fertile stamens appears to have occurred in *Biserrula* L. and *Robynsiophyton* Wilczek (Crisp, 1999) and in the

species *Ormosia semicastrata* Hance, which has at least some of the reduced stamens present as staminodes (Merrill & Chen, 1943; Torke et al. 2022). However, the nature of the reductions in these genera has not been subject to developmental studies. These observations highlight the peculiarity of the complete absence of the antepetalous stamen whorl in *D. purpurea* and likely the other prairie clovers – *Dalea* section *Kuhnistera* (McMahon and Hufford, 2002) – in the evolutionary history of Leguminosae.

In addition to the five stamens, their adnation to the five petals (which leads to the formation of a sheath, the staminal zone) raised questions about the nature and origin of the organs that form such a synorganized structure. Previous debates on this topic mainly involved groups that mentioned that the position of organs was a more significant consideration than their function, associated with a lack of ontogenetic information guiding the argument. The first ontogenetic evidence to unravel the nature and origin of the synorganized structure was obtained by McMahon and Hufford (2002) in a study involving *Dalea candida*. However, this is the first work that elucidates the organogenesis in *Dalea*, showing a whorl appearing in an alternating position with sepal primordia, then developing in cochlear aestivation, and the subsequent whorl arising in an anternipetalous position, the antesepalous stamens. Such evidence corroborates the reduction of organs in the androecium (antepetalous whorl), in agreement with the findings for other Daleoids previously studied (McMahon and Hufford, 2002).

Structural aspects of Dalea purpurea flower and its ecological implications

The many unusual floral characteristics in the flower of *D. purpurea* lead us to questions about possible functional implications. First and most uncommon in the evolutionary context of the subfamily is the loss of the typical papilionaceous flower. The papilionaceous flower presents a structural specialization with a wings-keel complex to ensure more limited contact of the floral visitors with the reproductive whorls. This specialization results in specialized pollination for the visitors mechanically able to deal with the floral structure (usually hymenoptera) while mitigating excessive pollen predation (Westerkamp, 1997). By presenting the four petals corresponding to the weakly differentiated wings-keel complex and the exposed reproductive whorls, we can make two considerations about the pollination of *D. purpurea*: 1- this species probably underwent selection directed towards generalist pollination to add a diverse range of pollinators; since keel-flowers morphology acts effectively as a pollinator filter (Kooi et al., 2021), however field studies in prairie clovers, including keel flower species would be useful to test this hypothesis; 2- some new route must do protection against pollen predation, or it has been completely abandoned. The generalist visiting of this species is easily attested in field observations. It

can be argued to be an advantage compared to species with typical papilionaceous flowers in the same environments (Reed, 1995).

The presence of phenolic idioblasts in the glandular appendages of anthers may suggest an alternative defense route to pollen predation. These cells are involved in the accumulation of unpalatable substances, thus acting in the plant's defense against herbivory (Fahn, 1979; Lattanzio, 2013). Adnation between petals and stamens, on the other hand, also has significant implications for the functionality of this flower, and the original debate about the nature of organs provides an exciting starting point for this discussion. Considering that the stemonozone has already been interpreted as a sheath of stamens, its structural function analogous to conventional structures, which form the reproductive column in the papilionaceous flower, is evident (Westerkamp, 1997). Suppose the corolla and the androecium are considered a structural unit; the connection between the position of the floral pieces in the stemonozone of *D. purpurea* and the position of the stamens in a typical diadelphous androecium, where the claw of the standard of *D. purpurea* would correspond to the adaxial median stamen filament of a papilionaceous flower. Therefore, stemonozone may be responsible for amalgamating functions between two distinct whorls.

The absence of a structured and evident nectary at the base of the carpel is a puzzling question. As evidence in favor of the presence of nectar as a floral resource in *D. purpurea*, we have the very structure analogous to a diadelphous androecium, the great diversity of floral visitors, including specialist species (Reed, 1995), and reports of the possible presence of nectar in pollination studies (Cane, 2006). Against the presence of nectar, we have the absence of an evident nectariferous disc around the carpel, as commonly found in flowers of Papilionoideae (Waddle and Lersten, 1974, Tucker, 2003), the congested arrangement of the floral parts up to the height of the stemonozone, making it difficult to access of pollinators to a possible nectariferous disc, absence of modified stomata in this region and lack of an evident histological region that refers to a structured nectary, with epidermis, nectariferous parenchyma and vascular bundles (Fahn, 1979), in addition to negative reactions with Fehling's reagent and PAS, indicating the absence of sugars in this region. But it is worth mentioning that the absence of evident floral nectaries may be because of the presence of substitute nectaries (*sensu* Vogel, 1997), as in *Anadenanthera colubrina* (Vell.) Brenan (Borges et al., 2017). Regardless of the presence or absence of nectar as a floral resource, it is important to mention that the general appearance of the flowers and inflorescences of *D. purpurea*, with a purplish color and evident stamens, are similar to other species from North American prairies, such as *Amorpha canescens* Pursh, another Leguminosae of the tribe Amorphaeae; and species of Asteraceae such as those of the genus *Liatris* Gaertn. ex Schreb, which to some degree are

involved in sharing pollinators. Assuming the absence of nectar, it is possible that *D. purpurea* takes advantage of the visual and, possibly, chemical similarity with other species and behaves as a decoy flower for exclusively nectariferous visitors (Jersáková et al., 2009). Comparative works with access to field observations and detailed floral anatomy are necessary to search for possible substitutive nectary. They may provide more conclusive data on the presence or absence of nectar, expanding the understanding of numerous ecological relationships of *D. purpurea*.

Some aspects of the interaction between *D. purpurea* and the occasional natural fires characteristic of grasslands are also known (Bidwell 1990, League, 2004). Some floral characteristics may be directly or indirectly related to this environmental factor. Knowing that *D. purpurea* can regrowth through the destruction of the shoot with the passage of fire (Towne, 1996, Ritchie 2020), we can understand some aspects of the floral structure and biology as ways to circumvent this event and favor plant reproduction. We have the two most peculiar characteristics of the floral structure: the loss of the antepetalous stamens whorl and the fusion between antesealous stamens and petals, leading to a reduction in the number of floral parts and subsequent amalgamation of functions in a common structure. This amalgamation can simplify the development process and lower energy costs per flower. The “discount” promoted by the loss of whorl may indirectly contribute to the high density of flowers per inflorescence and allow a relative speed in floral development after a fire. After the fire, there is competition among the colonizing plants due to the reduced amount of nitrogen available in the soil (Ojima, 1994), giving an advantage to those capable of nitrogen fixation, such as *D. pupurea*. Another interesting feature is that there is only one viable seed per fruit in all species of the Amorpheae tribe. In general, the limitation of ovules per carpel, only two (McMahon and Hufford, 2004) and only one viable seed per pollinated flower (Cardoso, 2013), could be interpreted as disadvantageous in the rapid recruitment of new individuals. A reduced number of ovules requires less maternal allocation, avoiding the waste of maternal resources with unpollinated or even aborted ovules (Lloyd, 1980). Furthermore, the large number of flowers per raceme of *D. purpurea* can compensate for the low production of eggs per flower, allowing efficient recruitment.

Aspects of the floral structures of Dalea purpurea

Phenolic idioblasts were the most abundant floral secretory structures, especially in the sepals, anthers, and carpel. They are commonly found in Leguminosae flowers (Judd et al. 2009) and are generally responsible for protecting against herbivory due to the accumulation of unpalatable substances (Castro and Demarco, 2008). Its presence in the sepals might reinforce its protective function since these are the most

external floral organs. Therefore, they are the first to suffer attacks by herbivores, corroborating cases described in the literature (Nakano et al. 2020). This same type of cell covering the anther glands probably has a similar function since the anthers are located in the floral apical region, deprived of the protection of the calyx. In *Dalea purpurea*, they are also unprotected by the absence of the wing-keel complex, which promotes the reproductive column's shelter in keel flowers (Westerkamp, 1997), making them more susceptible to herbivores.

Mucilaginous cells, found mainly in petals, can have different functions, such as carbohydrate sources, water retention, and filtering light (Gregory and Bass, 1989; Matthew and Endress, 2006). In *D. purpurea*, the additional function of mechanical protection is considered; given the rapid elongation of the stamens and carpel, such mucilaginous cells in the overlapping petals in cochlear aestivation can act in a similar way to a "waterbed", avoiding more intense friction between the elongating organs. This hypothesis is supported by the fact that the mucilaginous cells occupy almost the entire thickness of the petal mesophyll and the folded shape that the elongating organs assume in pre-anthesis.

The presence of a glandular appendage with a secretory cavity in the anther of *D. purpurea* is an intriguing feature as it is the first report for Papilionoideae outside the initial branching group (Leite et al. 2022), previously seen only for species from the subclades Amburaneae and Dipterygeae (Leite et al. 2019; Leite et al. 2022), suggesting a convergent evolution (Cardoso et al., 2013; Choi et al. 2022). The record of secretory cavities in the anthers of *D. purpurea* (clade Amorpheae) (Cardoso et al., 2013; Choi et al. 2022), suggests two possible causes: (i) it is a rare event in the subfamily outside the ADA clade; or (ii) the observations of anther glands may be neglected, deserving more attention in the works of floral morphology and anatomy.

In *D. purpurea*, the covering of the secretory cavity by a thick layer of phenolic compounds in the glandular appendage suggests its involvement in defense against herbivory, as mentioned above (Fahn, 1979; Lattanzio, 2013). On the other hand, the content of secretory cavities may be related to pollination, acting on the attraction of pollinators through odors (Fahn, 1979) or on the release of oleoresins and polysaccharides, favoring the adhesion of pollen grains to the body of visitors (Leite et al 2019). Pollination studies combined with histochemical tests of the secretory cavities' exudate are needed to confirm this function.

The carpel cavities, which usually occur in pairs in the ovary wall cross sections, are of unknown function. For *Dalea candida*, a closely related species (McMahon and Hufford, 2004), similar cavities were observed in the calyx in an intercostal position (personal observation). In addition, cavities or glandular structures are described for several species of the genus in different organs, both reproductive and vegetative (Barneby, 1977; Turner, 1986; Piñeros-U and González, 2020). Given the lack of recent works that address the

anatomy of *Dalea* species, we hope for future research to show the function of this and other floral secretory structures and its distribution in other representatives of the genus.

Conclusions

The atypical floral architecture of *Dalea pupurea* is the result of ontogenetic events possibly motivated by evolutionary and environmental pressures. There is a complete absence of the antepetalous stamen whorl. Also, the adnation to the stamens of the four non-specialized petals in a stemonozone originates from an intercalary growth. The reduction in the number of floral organs from 21 (typical of Leguminosae flowers) to 16 occurs through the ontogenetic pathway absence of organs since the initiation. It is noteworthy that this is the first report of a secretory cavity in the anther outside the initial branching group of Papilionoideae (Leite et al., 2022), indicating the convergent evolution of the trait in Papilionoideae. Finally, anatomical analyses suggest that this species uses chemical defenses against predation, and it may not offer nectar as a floral resource, suggesting an attraction of the pollinator by deception or by exclusive supplying of pollen as a reward. Research with an ecological focus, approaching the biology of pollination may expand our understanding of floral specializations and correlate with the species' evolutionary success.

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AUTHOR CONTRIBUTIONS: S.M.M., V.G.L. performed the experiments and analyzed the data. J.V.P. and V.F.M. contributed to the study conception and design. All authors contributed to the writing of the manuscript.

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Figure captions:

Figure 1 – Drawing of *Dalea purpurea* flowers. A: Overview of the *D. purpurea* individuals in the field; B-C: Detail of the inflorescence; D: An inflorescence sectioned in half, E-F: Detail of individualized flowers, showing its uncommon floral architecture. Scale bar: A = 5 cm; B-C = 2,5 cm; D-F = 4 mm.

Figure 2 – Drawing of floral structures in *Dalea purpurea*: A: frontal view of the flower, showing moderately zygomorphic symmetry; B: lateral view of the flower; C: flower in frontal view, showing reproductive column, petals, and the stemonozone in detail; D: flower in lateral view, showing reproductive column, petals, and the stemonozone in detail; E: the apron of the stemonozone, note the adaxial petal inserted in this region; F-I: weakly differentiated petals (wings and keel); J: adaxial petal (banner); K: calyx (note height of lacinia); L: internal view of the calyx tube; M-O: stamens in lateral, ventral and dorsal views, respectively; P: carpel. Illustration by Maria Alice de Rezende.

Figure 3 – Organogeny in *Dalea purpurea*: A: general view of the inflorescence and the apical meristem of the inflorescence; B: floral meristem and bracts; C-E: sepal and petal initiation; F: bidirectional order of stamens initiation and the central carpel primordium; G: petal development in the space left by two contiguous sepal primordia; H: early carpel expansion; I: formation of carpel cleft and the onset of anther differentiation (im = inflorescence meristem, fm = floral meristem, br = bract, s = sepal, p = petal, ss = antesealous stamen, c = carpel) Scale bar: A = 250µm; B-I = 50 µm.

Figure 4 – Intermediate and final stages of development in *Dalea purpurea*: A: Elongation of the sepals and the calyx tube formation; B: floral bud in lateral view (note the density of simple trichomes in the apical portion of the calyx); C: stomata on the adaxial face of the sepal (arrowhead); D: differentiation of petals and elongation of the stamens filaments and petals' claws; E: floral bud showing in lateral view, showing the stemonozone (calyx removed), note in the detail (square) the insertion of the banner in the stemonozone (F); G: frontal view of a floral bud, showing the cochlear petals aestivation and the open calyx. (s = sepal, p = petal, ss = antesealous stamen, c = carpel) Scale bar: A = 100 µm; B, F = 500 µm; C = 50 µm; D = 150 µm; E = 1mm.

Figure 5: Intermediate and final stages of development, showing details of developed floral structures in *Dalea purpurea*: A: stemonozone and carpel; B: apron, banner insertion zone (petal removed - arrow) and

ovary; C: petal in socket in the stemonozone; D: reproductive whorls in elongation (petals and sepals removed); E-F: dorsal and ventral views of the anther, respectively; G: pollen grain in polar axis view (asterisk), note the perforated ornamentation of the exine, arrows indicating the colpi; H: floral bud in cross section, showing shape and undulations in the stemonozone; I: floral bud in longitudinal section showing the short hypanthium. (ap = apron, ag = anther gland, pk = pollenkit, p = petal, ov = ovary, stl = style, stz = stemonozone) Scale bar: A, D, H = 500 μ m; B, E, F = 250 μ m; C = 50 μ m; G = 10 μ m; I = 1mm.

Figure 6: Schematic drawing of the flower in lateral view and cross-sections at different heights, showing the floral vascularization: Green dots: calyx vascular bundles. Red dots: corolla vascular bundles. Yellow dots: androecium vascular bundles. Blue dots: carpel vascular bundles (ap = apron, ag = anther gland) Scale bar = 100 μ m.

Figure 7: Distribution of floral secretory structures in *Dalea purpurea*: A: phenolic idioblasts in the calyx, showing the interruption close to the vascular bundles; B: overlapping petals, showing the distribution of mucilaginous cells; C: detail of mucilaginous cells; D: detail of apron, showing parenchymatic cells in the mesophyll, and one stoma on the inner epidermis (arrow); E: calyx, stemonozane and carpel wall in cross-section, showing the phenolic idioblasts. Note the ovary cavity in formation (square). F: detail of ovary cavity note their secretory epithelium and the lumen; G: longitudinal section of the anther gland, showing the apical secretory cavity, with an oval lumen, surrounded by one layer of epithelial cells, and a thick layer of phenolic cells; H: detail of the epithelial layer and the outer phenolic layer of the anther gland; I: short hypanthium and phenolic idioblasts centralized and close to the epidermis; J-K: detail of the hypanthium, showing the region of usual presence of nectary (asterisk). Note the starch grains in the ovary (arrows) (J) (ag = anther gland, ca = cavity, hp = hypanthium, lu = lumen, mc = mucilaginous cells, ov = ovary, ph = phenolic idioblasts, s = sepal, stz = stemonozone, cell, vb = vascular bundle) Scale bar A, E-G, I-K = 100 μ m, B, D = 50 μ m; C, H = 20 μ m.



Figure 1.

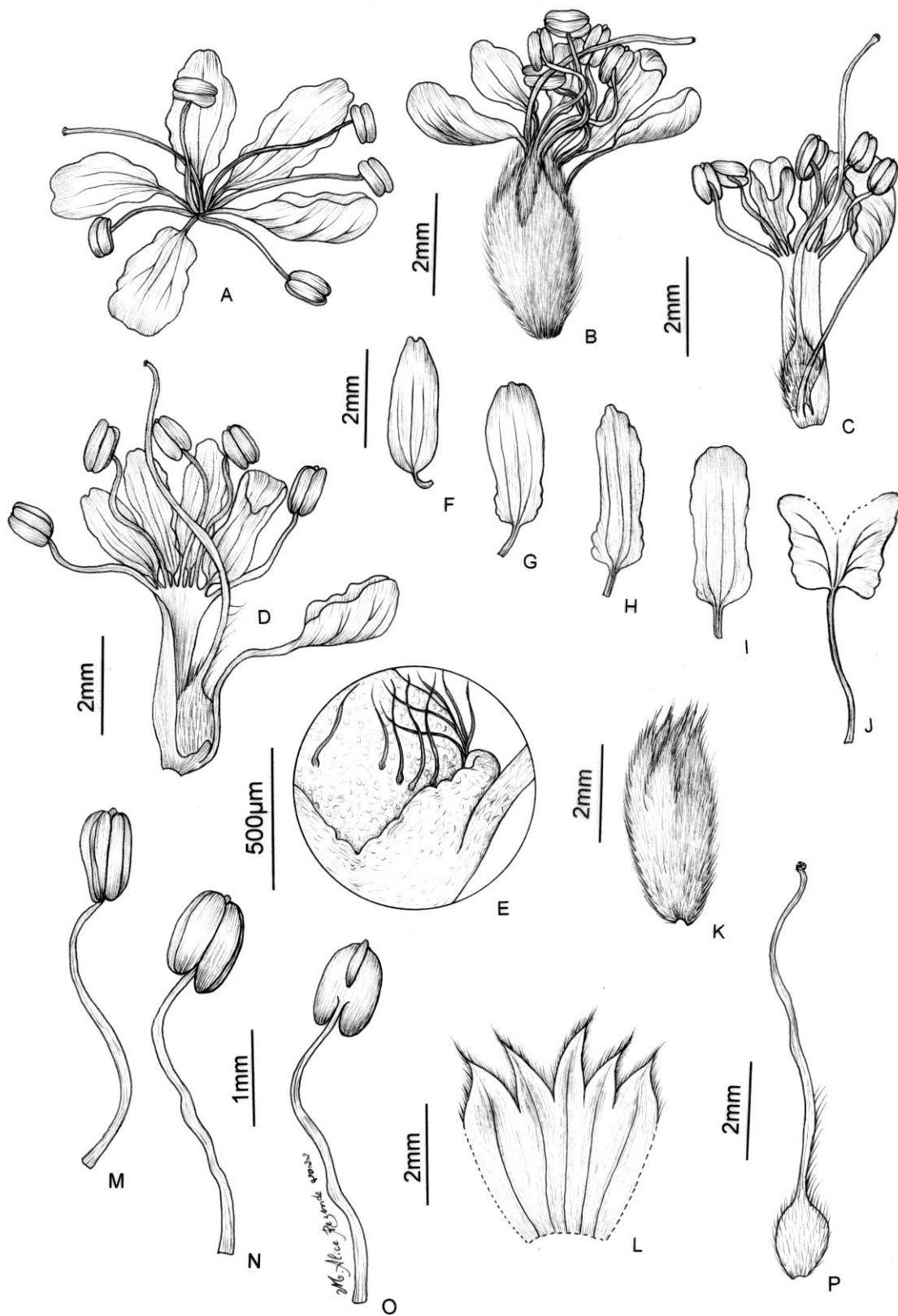


Figure 2.

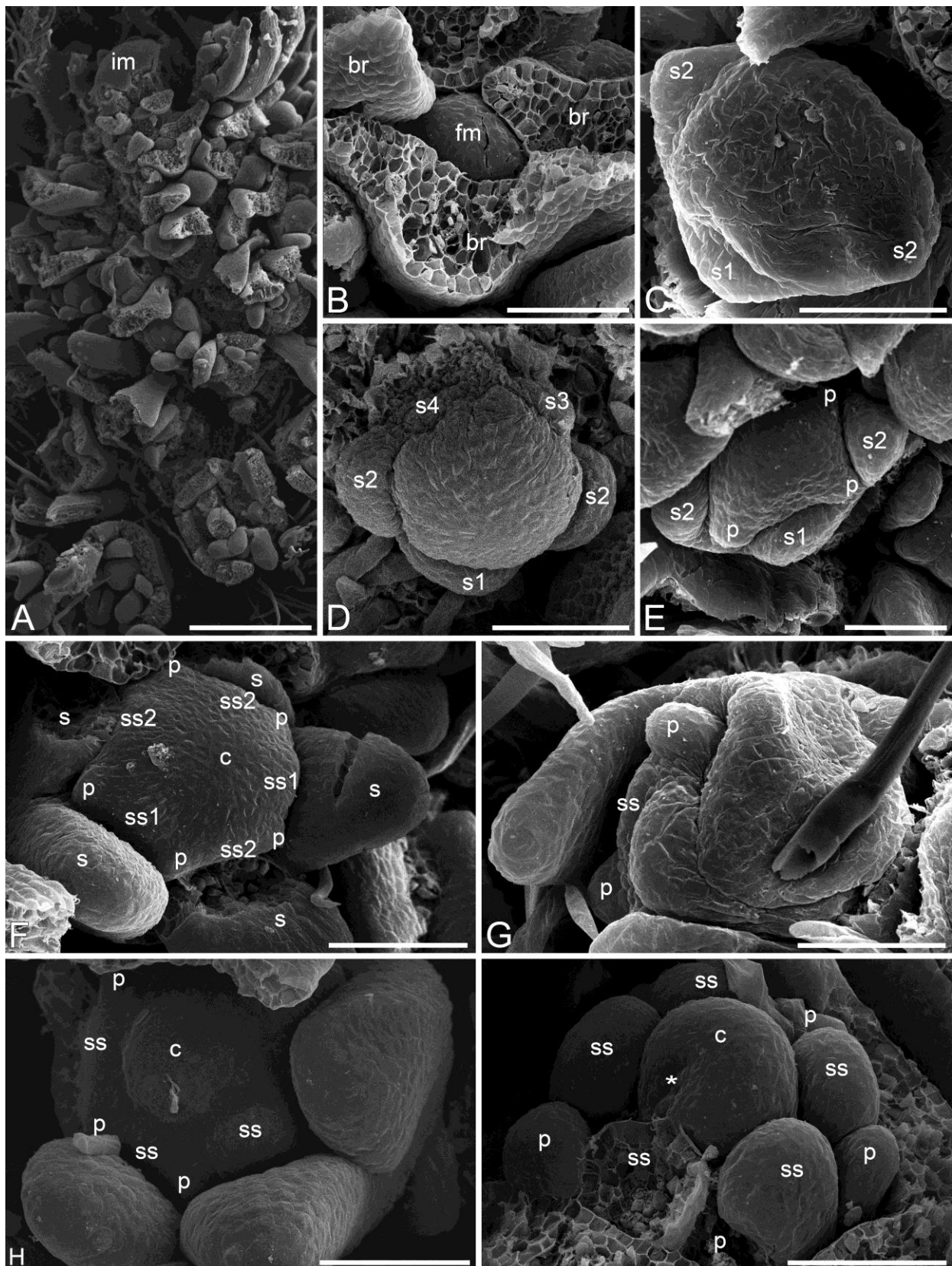


Figure 3.

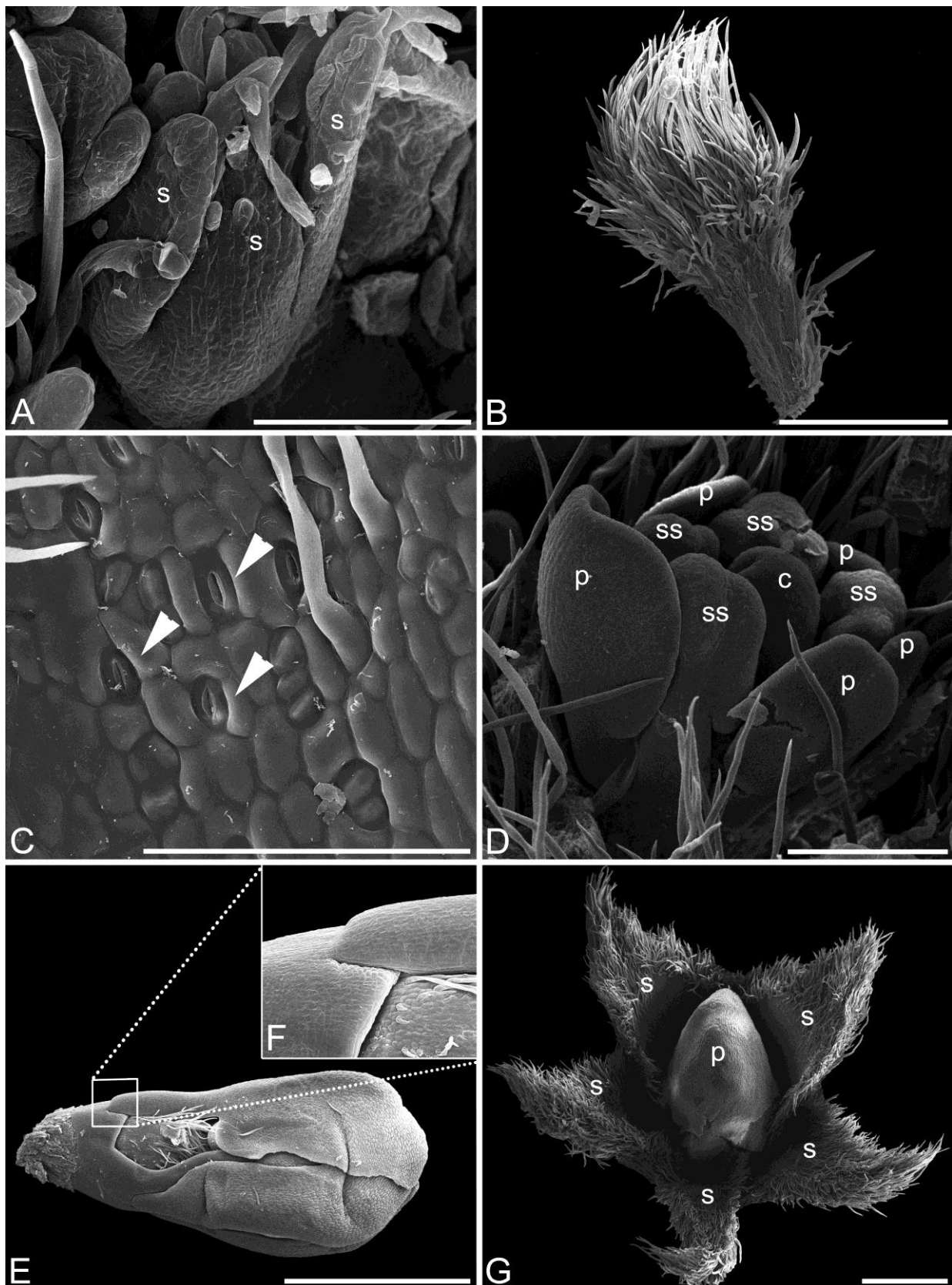


Figure 4.

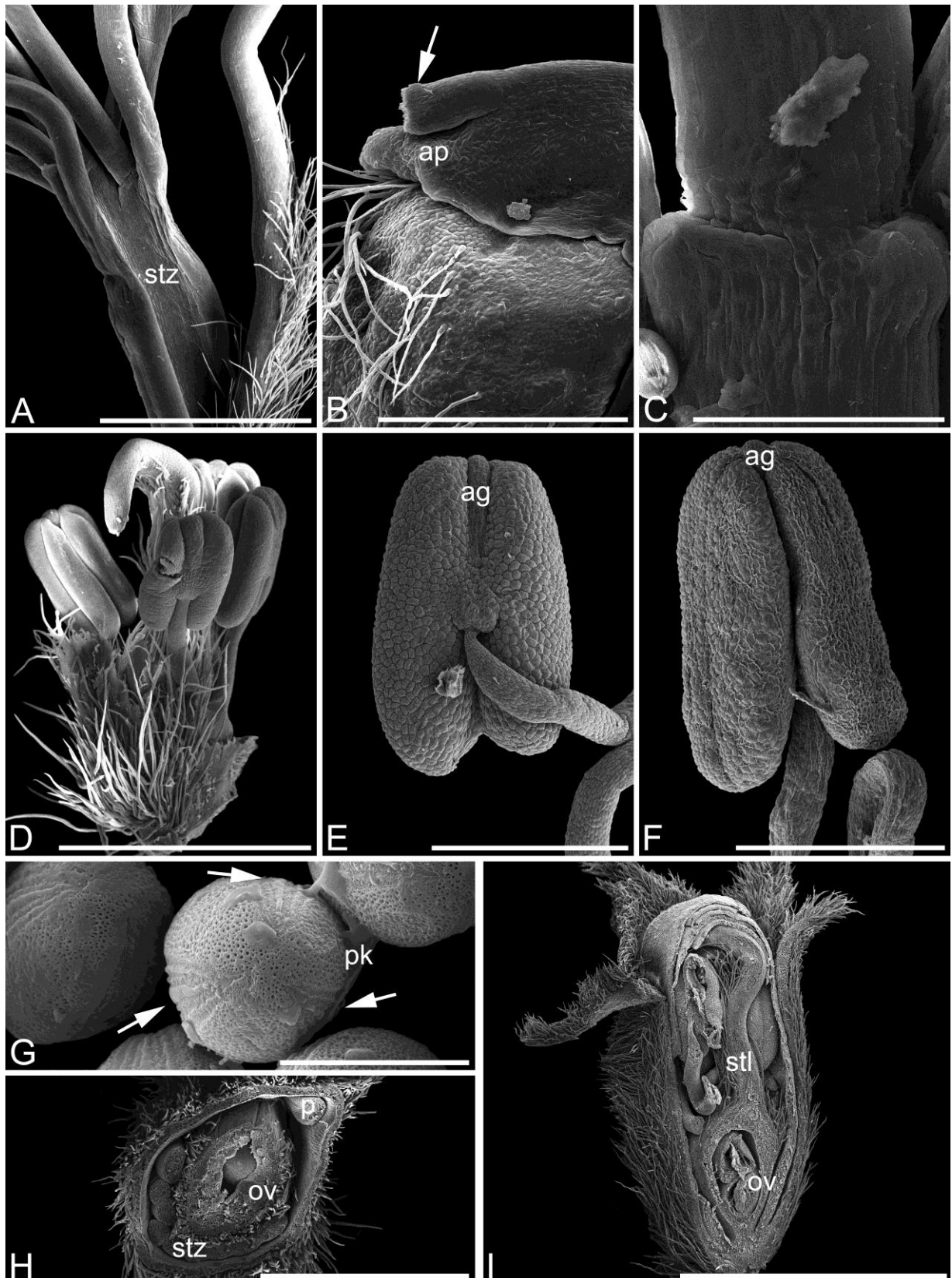


Figure 5.

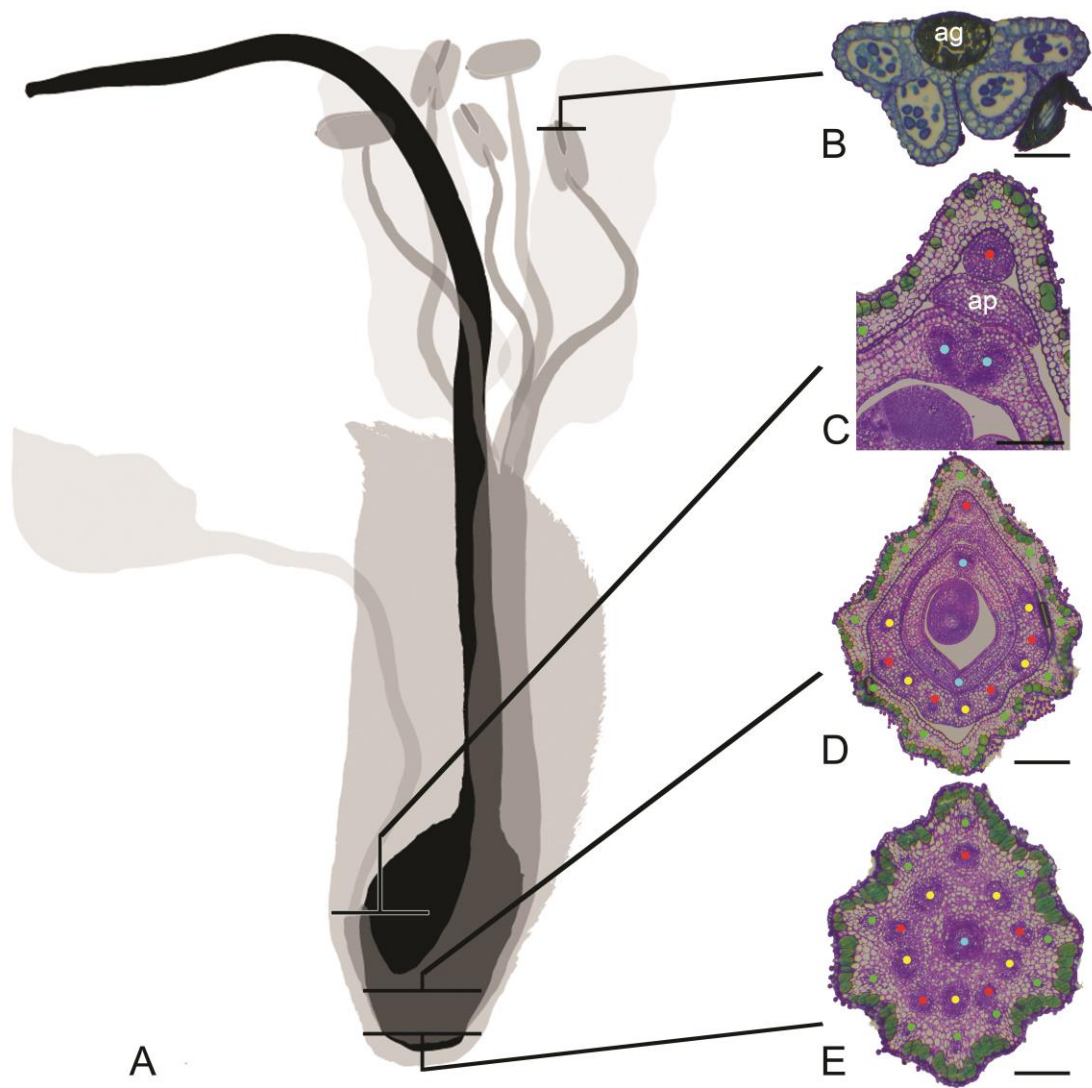


Figure 6.

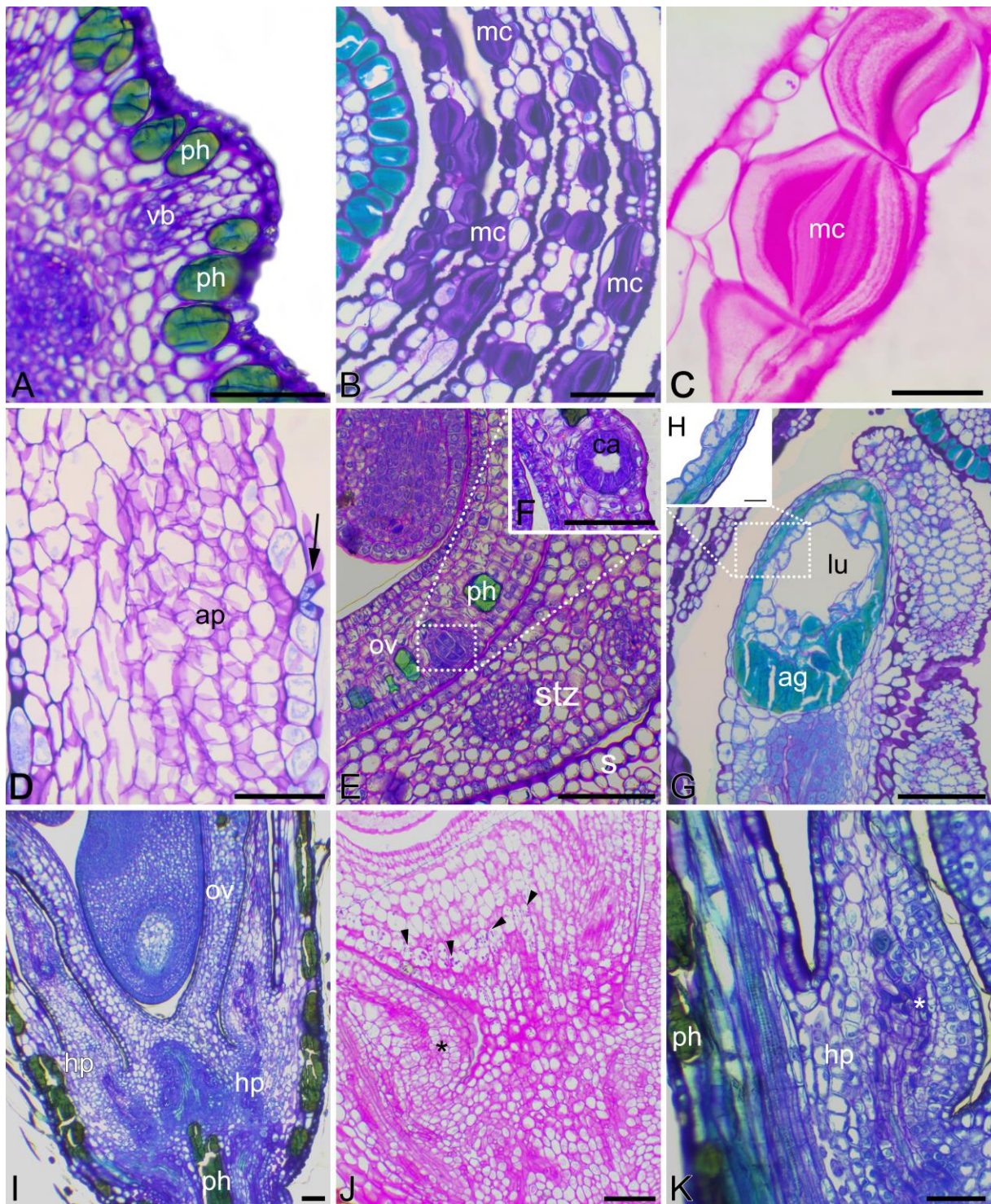


Figure 7.