Developmental morphology and structural homology of corolla-androecium synorganization in the tribe Amorpheae (Fabaceae: Papilionoideae)[1]

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Comparative developmental morphology was used to assess structural homology of flowers in *Dalea*, *Marina*, and *Psorothamnus* of the tribe Amorpheae (Fabaceae: Papilionoideae). *Dalea*, *Marina*, and some species of *Psorothamnus* have an unusual petal-stamen synorganization (stemonozone) in which free petals are inserted on a region that is continuous with fused stamen filaments. Developmental studies of these three genera demonstrated similarity during organogenesis. Zonal growth results in several synorganized regions, including the stemonozone of *Dalea*, *Marina*, and some *Psorothamnus*. *Psorothamnus* species that lack a stemonozone have fused stamens and free petals inserted on the hypanthium, as in most other papilionoid legumes. We concluded that the stemonozone is not strictly homologous to either androecium or receptacle, but that it is the product of a modified androecial developmental program. In the prairie clover daleas, petaloid structures positioned between the stamens have been variously interpreted as petals or as staminodes; we infer that they have an extreme form of the daleoid stemonozone, on which five petals (no staminodes) and five stamens are inserted. Assessing structural homology of these flowers allows us to characterize accurately daleoid morphology for evolutionary studies in the tribe Amorpheae.

Key words: Amorpheae; corolla; Fabaceae; flowers; homology; Papilionoideae; stamens; synorganization.

The evolutionary unification of historically separate parts is a major mode of floral morphological diversification (Robinson, 1985; Endress, 1994; Raven and Weyers, 2001), which we will discuss as synorganization (Hufford, 1996). Examples include the evolution of the corolla tube from separate petals in the asterid clade and the evolution of syncarpy from separate carpels among early eudicots. Although understanding the evolution of synorganized structures is critical to understanding the diversification of floral form, synorganization can obscure structural homology, making inferences about evolutionary diversification problematic. When the synorganization involves dissimilar structures, such as adnation among floral whorls, homology can be particularly difficult to assess.

Some aspects of synorganization are well known in papilionoid legumes, which include the tribe Amorpheae. For example, the fusion of stamen filaments that results in various conditions ("monadelphy," "diadelphy," and others) has commonly been used in classifications and identification keys for the group. Synorganization between abaxial lateral petals forms the distinctive papilionoid "keel"; synorganization among sepals forms the calyx tube. Less commonly recognized in papilionoid flowers is a region of synorganization below the perianth and androecium, i.e., an hypanthium or floral cup, that surrounds the base of the superior ovary. Some members of Amorpheae have, in addition to these regions, an unusual example of synorganization involving petals and stamens. In *Dalea* and *Marina*, the four lateral petals (wing and keel petals) appear attached to the fused filament tube (Bentham, 1865; Hutchinson, 1964; Barneby, 1977). Although homology of the tissue below the insertion points of the petals has not been explicitly assessed, Barneby (1977, p. 1), in his monograph of four Amorpheae genera, suggests that "the daleoid petal . . . appears to be elevated on an outgrowth of receptacular origin."

Our study of the petal-androecium synorganization in Amorpheae is important for several reasons. First, it is a unique arrangement of floral organs; although petal-stamen synorganization is common (e.g., the epipetalous stamens of sympetalous Asteridae), cases in which free petals apparently attach to fused stamens are extremely rare (although a similar-appearing condition occurs in Linaceae [Sharsmith, 1961]). Second, the synorganization is important to taxonomy within the tribe: species assigned to *Dalea* and *Marina* have been described as having petals inserted above the rim of the hypanthium, whereas the remaining taxa are said to have all petals inserted on the hypanthium (Hutchinson, 1964; Barneby, 1977). Petal-stamen synorganization, therefore, could be a synapomorphic innovation. Finally, accurate statements of homology are prerequisites for meaningful characterization of floral diversity in Amorpheae.

Definitions of homology have long been debated (e.g., Donoghue, 1992; Hall, 1994 and references therein). Here we use homology to mean similarity by descent, rephrasing Lankester's (1870) homogeny, defined as similarity due to inheritance from a common ancestor (Donoghue, 1992). We choose this definition because of our interest in the processes of evolution, of which inheritance is central. Additionally, defining homology as "similarity by descent" allows us to be explicit about

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criteria that we use to assess homology. For structures to be comparable among taxa, they need to pass the two tests implied by this definition. First, the structures need to be similar, or structurally homologous. To assess structural homology, we can apply the three principal criteria of Remane (1952): correspondence of position, correspondence of special attributes, and the presence of intermediates (Riedl, 1978). Special attributes could include, e.g., histological characteristics, surface features, or gene expression data. Second, these similarities must have arisen by the process of descent (with or without modification), i.e., they must be phylogenetically homologous. To assess phylogenetic homology we can apply the single criterion of having been inherited from a common ancestor (the congruence test of Patterson, 1988). To understand the evolution of floral form in Amorpheae, we first need to assess structural homology in order to make correct comparisons of attributes; this is the focus of the current paper. Next we need a phylogenetic hypothesis, in order to assess phylogenetic homology of those attributes found to be structurally homologous; this will be the focus of future work.

Amorpheae comprises eight genera, about 240 species, and is thought to be monophyletic, based on the presence of several morphological characteristics (Barneby, 1977) and preliminary phylogenetic analyses (McMahon and Hufford, 2000; McMahon, 2002). Flowers of Amorpheae demonstrate notable variation, particularly in the context of the fairly conserved papilionoid floral form. Within Amorpheae, only the small genus *Psorothamnus* has flowers that are typically papilionoid, having five petals, strong bilateral symmetry, and reproductive organs enclosed by the postgenitally fused keel petals. Other genera in Amorpheae have flowers that are open and nearly radially symmetric (most *Errazurizia*, *Eysenhardtia*, and *Apoplanesia*), and still others have flowers with one petal (*Amorpha*) or no petals (*Parryella* and *Errazurizia* in part). Most species in the remaining two genera, *Dalea* and *Marina*, have flowers that appear papilionoid but for the synorganization described above.

The goals of this paper are to present the morphology, development, and distribution of the petal-stamen synorganization in Amorpheae and to assess structural homology of the floral parts involved. In particular, we will address three interrelated questions: (1) In the flowers that have petal-stamen synorganization, what is the region below the insertion points of the petals and above the rim of the hypanthium? For ease of discussion, we will refer to flowers that have this condition as "daleoid" and this region as the "stemonozone," a term also applied to petal-stamen synorganization in mimosoid legumes (Lewis and Elias, 1981). Narrowing our focus to *Dalea* subgenus *Kuhnistera* ("prairie clovers," about 22 species), in which five fertile stamens alternate with four sterile, laminate structures, we will ask, (2) Do the prairie clovers have staminodes, i.e., are these sterile structures homologous to stamens or to petals in other daleas? Finally, we wish to pursue a suggestion made by Barneby (1977) that the daleoid flowers may be the result of a secondary derivation of the papilionoid form. The range of variation among all Amorpheae flowers includes corolla forms that are not papilionoid; this led to a concern about corolla form polarity in the group. Therefore, we will ask, (3) Are daleoid flowers structurally homologous to other papilionoid flowers, or is there structural evidence to suggest non-homology, i.e., a secondary derivation of the general papilionoid form?

MATERIALS AND METHODS

Terminology—Synorganization (Endress, 1990, 1994) is here used to denote an evolutionary process in which the condition of fused organs is derived from the ancestral condition of free organs (Hufford, 1996). Developmentally, the condition of fusion can occur two ways: postgenitally or congenitally. During postgenital fusion, organs that were free at the start of development become fused; this process generally involves epidermal contact between structures (Cusick, 1966; Sattler, 1978). During congenital fusion, growth occurs under individual organs or their primordia, raising the organs together (Sattler, 1978). This process is more descriptively called zonal growth and involves no observable contact among organs (Cusick, 1966).

Sampling—We selected three taxa, exemplifying different floral forms, for morphological and developmental study. For each taxon we dissected at least 75 flowers at various stages of ontogeny. For the purpose of comparison, we will first describe the adult morphology of a flower with no corolla-androecium synorganization, exemplified by *Psorothamnus kingii*. Second, a flower is described with corolla-androecium synorganization, exemplified by *Marina maritima*. Finally, we include a prairie clover, *Dalea candida*, to allow discussion of homology for this floral form in the context of the other two floral forms (with and without a stemonozone). Following the descriptions of the adult morphologies, we characterize floral development of these species. Adult flowers of other Amorpheae are briefly compared to these three species in order to describe the distribution of the stemonozone, including its presence in species of *Psorothamnus* for which no such synorganization had been reported previously. For a list of species examined and voucher information, see the Botanical Society of America website (http://ajbsupp.botany.org/v89/).

Morphology—We studied early ontogeny and major structures in later ontogeny primarily using scanning electron microscopy (SEM), and we observed details of mid-stage and late stage ontogeny primarily through serial sections. Inflorescences bearing anthetic and pre-anthetic flowers were collected from natural populations and preserved in FAA (37% formalin, glacial acetic acid, absolute ethanol, and water, 5 : 5 : 45 : 45). Flowers and flower buds were dissected in 50% ethanol, dehydrated in a graded ethanol series, critical point dried, and examined using a scanning electron microscope at 10–20 kV. Whole flowers and flower buds were dehydrated in a graded tertiary butanol series, embedded in Paraplast, and serially cross and longitudinally sectioned at 8–20 μm for anthetic flowers or 6–12 μm for buds, mounted on glass slides, and stained with safranin and fast green. To determine the order of initiation of zonal growth, we examined cross and longitudinal sections and documented the presence of observable tubes, i.e., the products of zonal growth. If a particular structure is observed without other structures present (and never the reverse) that structure is the first to begin developing. For example, if some buds had only a calyx tube and others had a hypanthium as well as a calyx tube, we considered this to be evidence that the calyx tube initiates earlier than the hypanthium.

RESULTS

Anthetic floral morphologies—Psorothamnus kingii—The flower of *Psorothamnus kingii* is similar in overall form to that of a "typical" papilionaceous legume (e.g., *Pisum*): the flower is pentamerous, having five calyx lobes, five petals, ten stamens, and a single carpel, and is strongly zygomorphic, having a banner petal, two wing petals, and two keel petals (Fig. 1). The calyx is synsepalous, with five unequal deltate lobes. Each petal consists of a laminate distal portion (blade) and a narrow proximal portion (claw) (Fig. 2). All petals are free except the distal portion of the keel blades, which are fused to one another along their adjacent and distal margins, thereby enclosing the anthers and style (Fig. 1). The proximal half of the stamen filaments form a sheath, c-shaped in cross section, open on the adaxial side of the flower (Fig. 13). The abaxial antesepalous stamen is medial, but the adaxial ante-
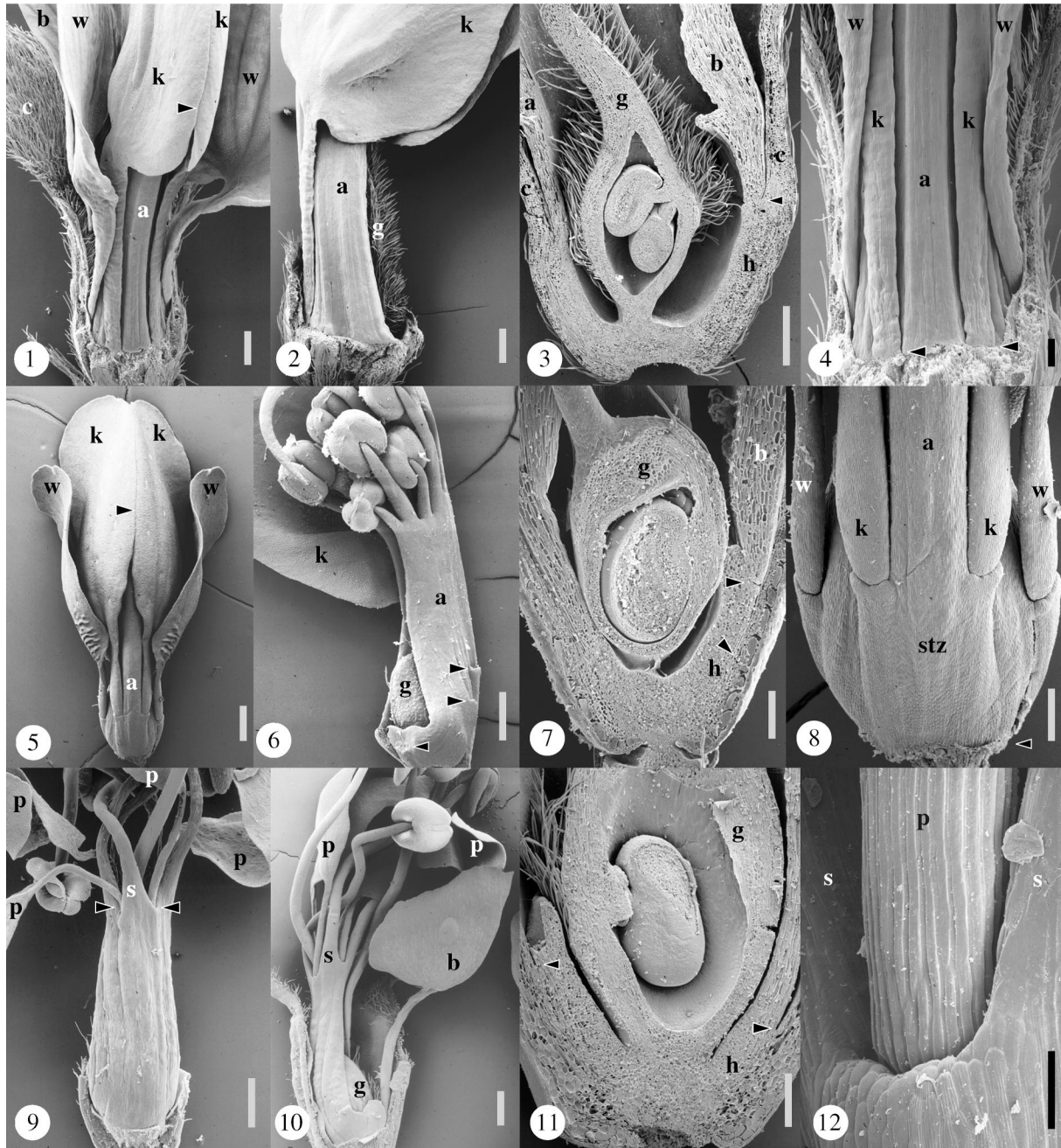
Figs. 1–12. Anthetic flowers of *Psorothamnus*, *Marina*, and *Dalea*. Figs. 1–4. *Psorothamnus kingii*. **1.** Oblique abaxial view showing marginally fused (arrowhead) keel petals of flower from which part of the calyx has been removed. **2.** Lateral view, showing petal insertion and staminal sheath of flower from which the banner, one wing petal, and part of the calyx have been removed. **3.** Bisection showing hypanthium and banner petal attachment (arrowhead). **4.** Abaxial view of flower from which the calyx has been removed, showing keel petals attached at the same level as the calyx tube (arrowheads). Figs. 5–8. *Marina maritima*. **5.** Abaxial view of flower from which the calyx has been removed, showing marginal fusion (arrowhead) of the keel petals. **6.** Oblique lateral view of flower from which the calyx and all but one keel petal have been removed, showing staminal sheath and three petal insertion points (arrowheads). **7.** Bisection showing the banner petal attachment (upper arrowhead) and the top of the hypanthium, at the point of calyx attachment (lower arrowhead). **8.** Abaxial view of flower from which the calyx has been removed showing insertion of the wing and keel petals in sockets above the point of calyx tube attachment (arrowhead). The region between petal insertion and calyx insertion is the stemonozone. Figs. 9–12. *Dalea candida*. **9.** Abaxial view showing insertion of petaloid structures (arrowheads) between stamen filaments on a flower from which the calyx has been removed. **10.** Lateral view showing insertion of banner petal. **11.** Bisection showing short hypanthium (arrowheads at calyx attachments). **12.** Insertion of the petaloid structure in a socket between the free stamen filaments. Scale bars = 0.5 mm in Figs. 1–3, 5, 6, 9, and 10; = 0.2 mm in Figs. 4, 7, 8, and 11; = 50 μm in Fig. 12.

Figure Abbreviations: a, androecium; b, banner petal; be, bracteole; br, bract; c, calyx lobe or tube; f, floral meristem; g, gynoecium; h, hypanthium; k, keel petal; p, petaloid structure; s, stamen; stz, stemonozone; w, wing petal.
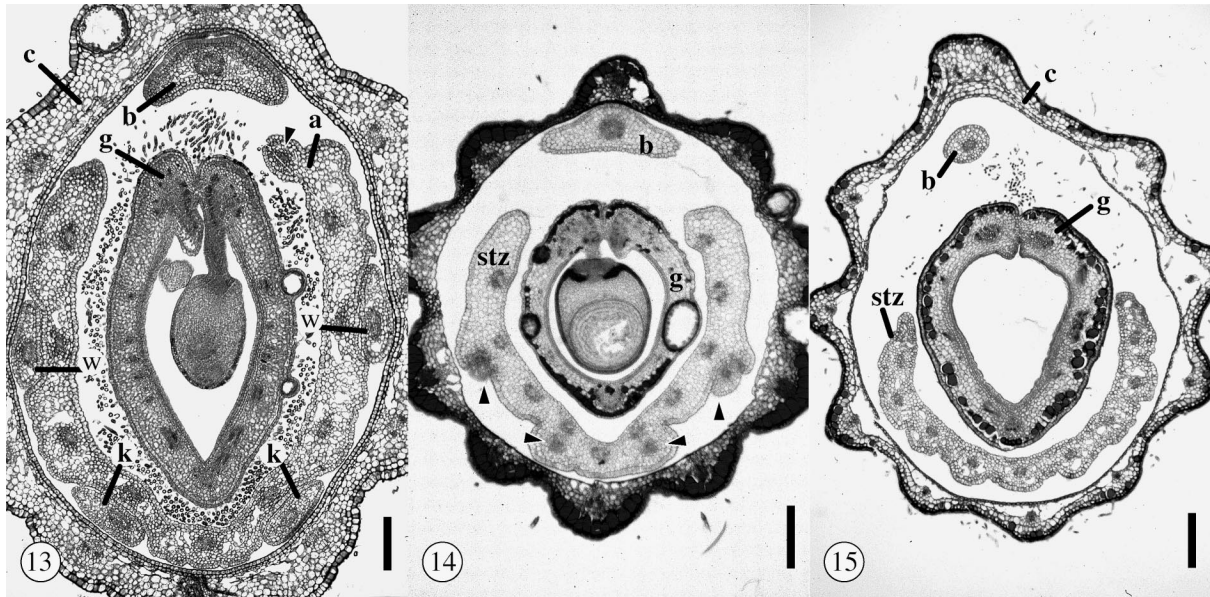
Figs. 13–15.   Cross sections of anthetic flowers of *Psorothamnus*, *Marina*, and *Dalea*. Adaxial side of flower is towards top in all sections. **13.** *Psorothamnus kingii*. Section showing part of the calyx tube, the five separate petals, the gynoecium, and the androecium. At this level in the flower, the androecium is a sheath, discontinuous on the adaxial side. Ten stamen vascular bundles are visible; the adaxial antepetalous stamen bundle is to the right of the banner petal (arrowhead). **14.** *Marina maritima*. Section showing calyx tube, gynoecium, banner petal, and stemonozone, at the level of insertion of the wing petals (vertical arrowheads). In the stemonozone, vascular bundles leading to the petals are separate from the associated antepetalous staminal bundles; this is visible here for the bundles leading to the keel petals (horizontal arrowheads). **15.** *Dalea candida*. Section showing calyx tube, gynoecium, banner petal, and the sheath of tissue below the petaloid structures and the five stamens, labeled as stemonozone for convenience. In the stemonozone, ten vascular bundles are visible, alternately leading to stamens and to petaloid structures. Scale bars = 0.2 mm.

petalous stamen is not; therefore the open sheath is not precisely symmetrical (Fig. 13). The ovary is shorter than the long arching style and contains two ovules (Fig. 3). The ovary is inserted on the receptacle and surrounded by a cup-like structure, on the rim of which the perianth and stamens are inserted (Fig. 3). We will refer to this as hypanthium, i.e., a region of tissue that is below the separately inserted calyx, corolla, and androecium but not the ovary ("perigynous hypanthium" of Leins, Merxmüller, and Sattler, 1972). Petals of *P. kingii* are inserted directly on the rim of the hypanthium (Figs. 3 and 4).

Marina maritima—As in *Psorothamnus kingii*, the general form of the *Marina maritima* flower resembles a "typical" papilionaceous flower, with the same number of organs in each whorl as above, and similarly strong zygomorphy (Fig. 5). The androecium of *M. maritima* has all ten filaments fused for about two-thirds of their length in a slightly asymmetrical open sheath (Fig. 6), as in *P. kingii*. Aside from differences such as petal color, relative petal sizes (the banner is proportionally smaller in *M. maritima*), and ovule orientation, the primary differences between the flowers of *M. maritima* and *P. kingii* lie in proximal regions of the androecium and corolla. The base of the ovary is surrounded by a small hypanthium (Fig. 7) similar to, although shorter than, that seen in *P. kingii*. The calyx tube extends from the rim of the hypanthium as in *P. kingii*. However, in *M. maritima*, the petals are not situated on the hypanthium; instead, a second tube of tissue extends from the hypanthium rim. This second tube of tissue has the appearance of androecial sheath and, for a short distance (about 0.5 mm), it is a complete tube (Figs. 6 and 7). More distally, it is a sheath, discontinuous on the adaxial side (Fig. 14). Petals, as well as stamens, are inserted on this sheath. The banner

petal attaches near the apex of the short closed tube (Figs. 6 and 7), the wing petals attach on the sheath more distally, and the keel petals attach to the sheath still more distally (Fig. 6). The stemonozone, i.e., the region between the petal attachments and the calyx attachment, is more extensive abaxially than adaxially. The claws of the petals are inserted in sockets on this structure (Figs. 8 and 14), from which they abscise following anthesis.

Dalea candida—The general form of the *Dalea candida* flower, in contrast to the forms of the previous two species, does not resemble a "typical" papilionaceous flower (Fig. 9). The androecium and corolla are similar to neither *P. kingii* nor *M. maritima*. The androecium of *D. candida* has only five fertile stamens, fused for about one-half of their length in a symmetrical open sheath (Figs. 10 and 15). The free portions of the stamens alternate with four petaloid structures at the apex of the sheath (Figs. 9 and 10). The banner petal is medial and adaxial and shaped similarly to the banners of the previous two species, with a narrow claw and a laminate, cucullate, distal portion. The four petaloid structures also have narrow proximal portions and laminate distal portions. However, these laminate blades are dissimilar to the blades of the wing and keel petals of the other two species described: the blades of *D. candida* are flat, with no proximal auricle nor sculpturing (as in wing petals), no marginal fusion (as in keel petals), and all four are similar to one another, not distinguishable as wings and keels. The placement of the four petaloid structures is exactly between the five stamens; the claws attach to the top of what appears to be androecial column, in the sinuses between the free stamens (Figs. 9, 10, and 12). We will refer to the region between the insertion of the petaloid structures and stamens and the hypanthium as stemonozone (Fig. 15), al-
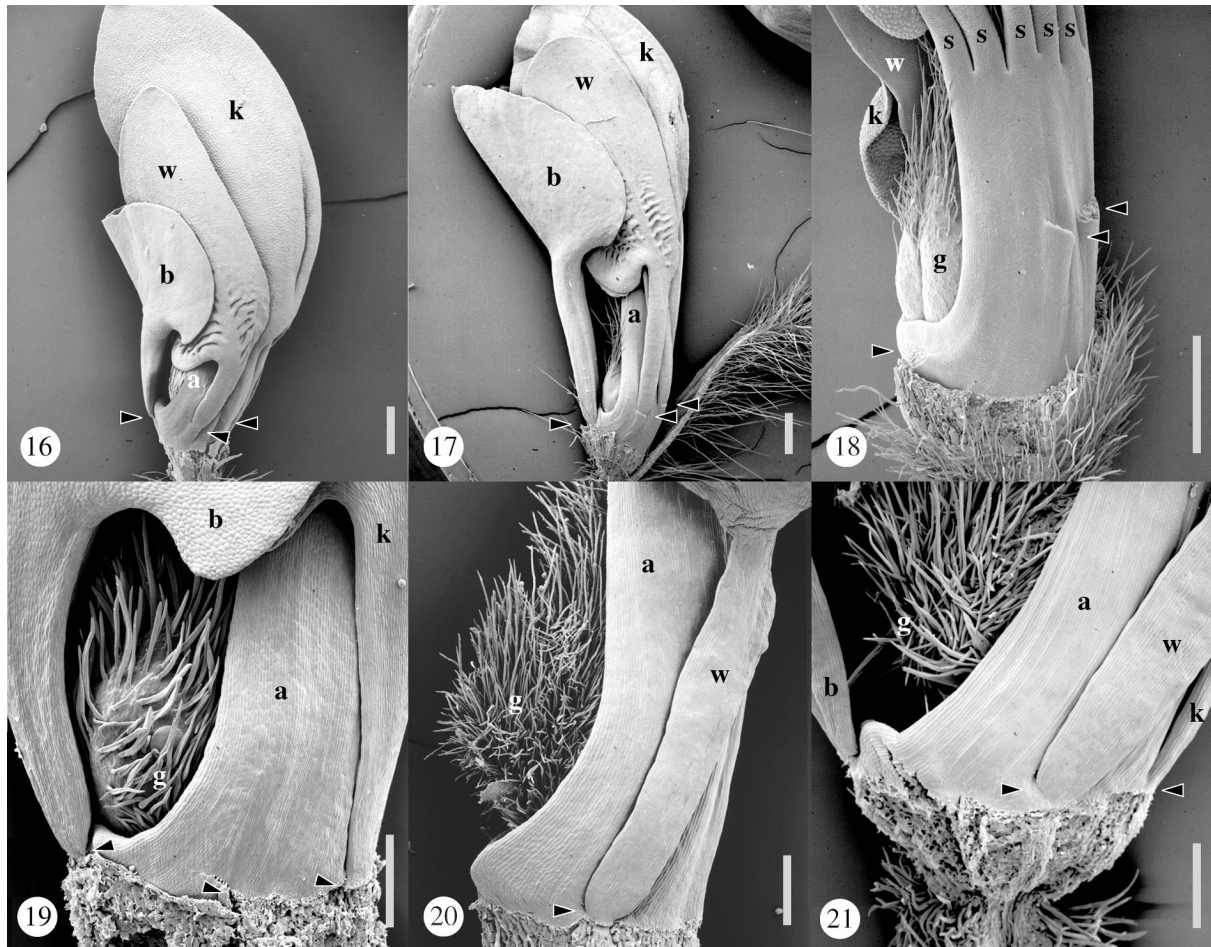
Figs. 16–21. Lateral views of anthetic flowers of various daleoid Amorpheae (calyces removed in all, some petals removed in Figs. 18–20). Arrowheads indicate petal attachments; torn tissue at bottom of flowers indicates calyx insertion. **16.** *Marina calycosa*. Petals are inserted relatively close to the calyx insertion, so the stemonozone is proportionally short. **17.** *Dalea pulchra*. Petals are inserted more distally than in *M. calycosa* but are still low relative to the top of the staminal sheath, where the stamen filaments are free (not visible). **18.** *Dalea capitata*. Wing and keel petal sockets (left-facing arrowheads) are higher, i.e., the stemonozone is more extensive than in the previous two figures. **19.** *Psorothamnus polydenius* var. *polydenius*. The petals attach directly to the top of the hypanthium, at the point of calyx insertion. **20.** *Psorothamnus emoryi*. The wing and keel petals (keels not visible) attach very close to the calyx insertion. The outside of the petal is at the level of calyx insertion, but the inside of the petal (arrowhead) is slightly above this point. **21.** *Psorothamnus scoparius*. Wing and keel petals attach (arrowheads) entirely above the calyx insertion, although much closer to the calyx insertion than in *Marina* and *Dalea*. Scale bars = 0.5 mm in Figs. 16–18; = 0.25 mm in Figs. 19–21.

though the homology of this region will be discussed later. Other than the corolla and androecium, the flower of *Dalea candida* is similar to the other two in having a synsepalous calyx, a single carpel, and a hypanthium, although the hypanthium is relatively short (Fig. 11).

Other Amorpheae—All species of *Marina* investigated (http://ajbsupp.botany.org/v89/) are similar to *M. maritima* in having relatively short hypanthia and stemonozones (e.g., *M. calycosa* in Fig. 16). As described by Barneby (1977), all but one *Marina* (*M. vetula*) have a region below the petal insertion points that is much shorter than the stamen sheath (i.e., the petals are attached low in the flower); our results confirm this condition for the taxa studied.

The daleas that we investigated demonstrate more variability in the level of the petal attachments than that seen among the marinas. Relative lengths of regions vary from *D. pulchra*, which has a short petal-stamen tube and a longer stamen sheath (Fig. 17), to *D. capitata*, in which these two regions

are approximately equal (Fig. 18). Daleas with even higher petal attachment points are reported (Barneby, 1977).

We studied all species of the genus *Psorothamnus* and found that two species have forms similar to *P. kingii*, *P. arborescens*, and *P. polydenius* (Fig. 19), in which petals attach directly to the rim of the hypanthium. However, we also found that a very short petal-stamen tube occurs in some members of the genus. *Psorothamnus spinosus*, *P. thompsonae*, and *P. emoryi* (Fig. 20) have petals that attach in such a way that the outside of the petal touches the rim of the hypanthium (where the calyx attaches), but the inside of the petal claw attachment is above the rim. *Psorothamnus thompsonae* and *P. scoparius* (Fig. 21) have petal attachments entirely above the rim. Additionally, in *P. fremontii*, though the lateral and abaxial petals attach on the rim of the floral cup, the banner attaches just above the rim, as in *Dalea* and *Marina*.

Floral development—*Psorothamnus kingii*—Flowers are initiated singly in the axils of bracts (Fig. 22), situated along
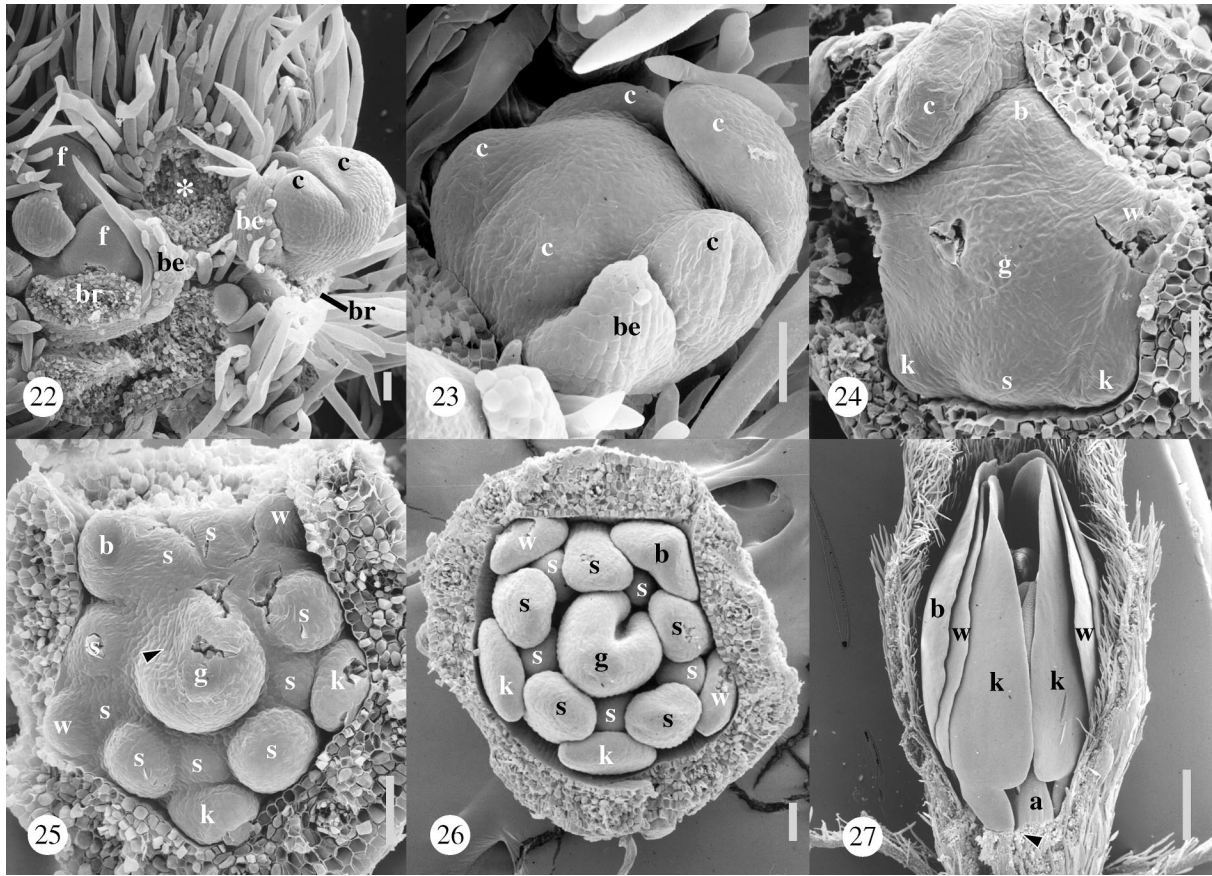
Figs. 22–27.   Floral ontogeny of *Psorothamnus kingii*. Abaxial side is towards right in Figs. 22–23 and towards base in Figs. 24–26. **22.** Young inflorescence, showing floral buds initiating in the axils of bracts (removed), clustered around a terminal spine (removed, at star). **23.** Bud after the five calyx lobes initiated. **24.** Bud at beginning of stamen initiation, after the calyx, corolla, and carpel primordia established (four calyx lobes have been removed). **25.** Bud after calyx, corolla, stamens, and gynoecium have initiated. Calyx tube surrounds the corolla and the androecial primordia. The adaxial stamen is to the right of the banner primordium and the gynoecial cleft (arrow) is established. **26.** Bud in which antesepalous stamens have become larger than the petals. **27.** Abaxial view of preanthetic bud showing petals enclosing the androecium. One keel petal insertion is visible (arrowhead) at the level of calyx insertion where the calyx has been partially removed. Scale bars = 50 μm in Figs. 22–26; = 0.5 mm in Fig. 27.

a short shoot, the apex of which becomes spine-tipped. A pair of bracteoles forms at the apex of each pedicel (Figs. 22 and 23). Sepals initiate unidirectionally (sensu Tucker, 1984), starting abaxially (Fig. 23). The sepals grow relatively quickly and cover the meristem. Petals and the carpel initiate on the convex meristem (Fig. 24). Last to initiate are the stamens (Fig. 25), beginning with the abaxial antesepalous stamen (Fig. 24). Based on the relative sizes of the stamen primordia shortly after initiation, it appears that the antesepalous stamens initiate unidirectionally (Fig. 25); this may be the case for the antepetalous stamens as well. The adaxial antepetalous stamen lies to one side of the adaxial petal (Fig. 25). As the carpel cleft deepens, the petals elongate and broaden laterally (Fig. 26). At this stage, the antesepalous stamens overtop the antepetalous stamens and the lateral petals (Fig. 26). Later in development, as all organs continue to develop, the petals elongate more extensively and enclose the androecium and gynoecium (Fig. 27).

In the flowers of *P. kingii*, zonal growth occurs in three regions (Fig. 58). The first region to begin zonal growth is below the sepals. As this zone elongates, the sepals are raised, and a congenitally fused calyx tube is formed, eventually surrounding the base of the flower (Figs. 25 and 26). This process

begins as organogenesis ends. The second region to initiate zonal growth is the region below all organs except the carpel, producing the hypanthium. This process begins after organogenesis is complete, while organ differentiation is occurring (Figs. 28–30). Finally, the region below the stamens undergoes zonal growth, producing the stamen tube. As zonal growth occurs, the ten stamens are elevated on a congenitally fused staminal column, open almost entirely on one side (Fig. 2). This growth begins shortly after the initiation of the growth that leads to the hypanthium; only buds that are about a millimeter or less have a hypanthium without a stamen tube (Figs. 28–30). As the flower matures, elongation occurs in all three of these regions. At anthesis, the *P. kingii* hypanthium is extensive (about one-half the length of the ovary) (Fig. 3).

Marina maritima—Flowers of *Marina maritima* initiate in acropetal succession, in the axils of bracts. No bracteoles are initiated at the apex of the pedicel. Floral organogenesis proceeds on a convex apical meristem. The abaxial sepal is the first to initiate (Fig. 31), followed by the two lateral sepals, then by the adaxial pair (Figs. 32 and 33). The whorl of five petals initiates with the abaxial pair becoming largest first (Fig. 32), and then the single carpel forms in the center (Fig. 33),
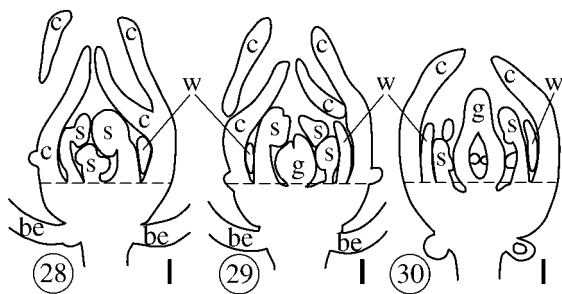
Figs. 28–30. Line drawings of serial longitudinal sections through a floral bud of *Psorothamnus kingii* showing presence of hypanthium but no stamen tube. Dashed line indicates level of calyx insertion, i.e., top of the hypanthium. Trichomes are not drawn. **28.** Section through adaxial side of bud showing stamens separately inserted at the same level as the calyx. **29.** Section 60 μm closer to median than previous figure, showing the adaxial side of the gynoecium. **30.** Near-median section 130 μm more abaxial than previous figure, showing the gynoecium inserted below the level of the calyx insertion. One wing petal and two stamens are inserted at the level of calyx insertion, i.e., on the rim of a hypanthium. Scale bars = 0.1 mm.

followed by the stamens (Figs. 33 and 34). Last to initiate are the antepetalous stamens, arising between and approximately on the same circumference as the antesepalous stamens (Fig. 35). In general, the adaxial stamen, i.e., the antepetalous stamen nearest the banner, lies to one side of the banner (Fig. 36); occasionally it is absent.

The elongating sepals enclose the meristem as the remaining organs are initiating. The carpel also elongates relatively quickly, developing a groove as the latest stamen primordia are formed. The antesepalous stamens elongate, becoming longer than the petals by the time the antepetalous stamens are initiated (Fig. 35). The antesepalous stamens remain taller than the petals until much later in development and taller than the antepetalous stamens through anthesis.

In the flowers of *M. maritima*, zonal growth occurs in four regions (Fig. 58). The first region to initiate zonal growth is that below the sepals. As this zone elongates, the sepals are raised, and a congenitally fused calyx tube is formed, eventually surrounding the base of the flower (Figs. 34–36). The second region to initiate zonal growth is that below the stamens (Figs. 40–42). This occurs after anther differentiation, while the thecae are forming. Zonal growth below the filaments occurs nonuniformly, with less growth near the banner petal. This results in a stamen tube that is continuous just above the hypanthium, but distally discontinuous with the interrupted portion on the adaxial side of the flower. As zonal growth occurs, the ten stamens are elevated on a staminal column (Figs. 37 and 38), almost entirely open on one side (Fig. 39). The third region to initiate zonal growth is below the petals and the staminal sheath, forming the stemonozone (Figs. 43–45). Again, this growth is nonuniform; the keel petals are elevated more than the wing petals, and the banner is elevated the least (Figs. 38 and 39). In this way, the petals become attached to what appears to be fused filaments. The fourth region of zonal growth is below all organs except the carpel. As this region elongates, the stamens, petals, and sepals are elevated on a common tube of tissue that forms a cup, the hypanthium, around the ovary (Fig. 7). We infer from relative bud size that these processes of zonal growth occur in quick succession. For example, the buds that have a calyx tube, a stamen tube, and a stemonozone (Figs. 43–45) are generally only slightly larger than the buds with a calyx tube, a stamen tube, and no stemonozone (Figs. 40–42). As the flower matures, further elongation occurs in all four of these regions. At anthesis, the *M. maritima* hypanthium is very short, and the stemonozone is shorter than the stamen sheath, i.e., the petals appear to attach low on the staminal column (Fig. 6).

Dalea candida—Flowers are initiated singly in the axils of bracts in acropetal order (Fig. 46) without bracteoles at the apex of the pedicels. Sepals are initiated first (Fig. 47). The floral meristem is pentagonal in cross section; the banner and the petaloid structures initiate on the corners of the pentagon (Fig. 48), in the same positions as petals in the other two species (Figs. 24 and 33). Five stamens initiate in positions alternate with the petaloid structures (Figs. 48 and 49). The ten organs that initiate between the carpel and the calyx occur in two whorls that soon become distinct as the inner five develop anthers and the outer five develop laminar, enclosing blades (Figs. 50–52).

In the flowers of *D. candida*, zonal growth occurs in three regions (Fig. 58). The first to initiate is the region below the sepals, producing a calyx tube. The second region to initiate is below the stamens and petaloid structures (Figs. 53–57). For ease of description, we will call this region a stemonozone, although the identity of the structure depends on the homology of the petaloid structures (if they are petals, it is a stemonozone; if they are stamens, it is a stamen tube). Finally, zonal growth begins below all organs but the carpel, forming the hypanthium (Fig. 11). As in the previous two species, the initiation of these three regions of zonal growth occur in relatively quick succession. For example, the buds that have only a calyx tube and a stemonozone, without a hypanthium, are approximately one-half of a millimeter across (Figs. 55–57). Slightly larger buds have all three structures. As the flower matures, growth occurs in all three of these regions. At anthesis, the *D. candida* hypanthium is very short, and the stemonozone is extensive (Fig. 10).

Developmental summary—Comparing these developmental data, we find that the taxa differ little in early ontogeny. All organs develop from individual primordia on a convex meristem. The petals, antesepalous stamens, and carpel initiate close to one another in time. In the taxa that have antepetalous stamens, *M. maritima* and *P. kingii*, they are the last whorl to initiate, and the adaxial stamen is not directly in front of the banner. Later in ontogeny, we find differences among taxa in the order of zonal growth (Fig. 58). In *M. maritima*, the stamen tube begins developing prior to the onset of growth that produces the hypanthium. In *P. kingii*, the hypanthium begins before the stamen tube. In *D. candida*, the hypanthium begins developing after the stemonozone begins (Fig. 58).

DISCUSSION

Epistemonous petals, the unusual condition of having free petals synorganized with fused stamens, is an important aspect of floral evolution in Amorpheae. Petal-stamen synorganization occurs in all species of *Dalea* and *Marina*, as well as in some (but not all) *Psorothamnus* (about 200 of the about 240 species in Amorpheae). Species vary tremendously in the height of the stemonozone (the region of petal-stamen synorganization), just as they vary in other floral proportions. The
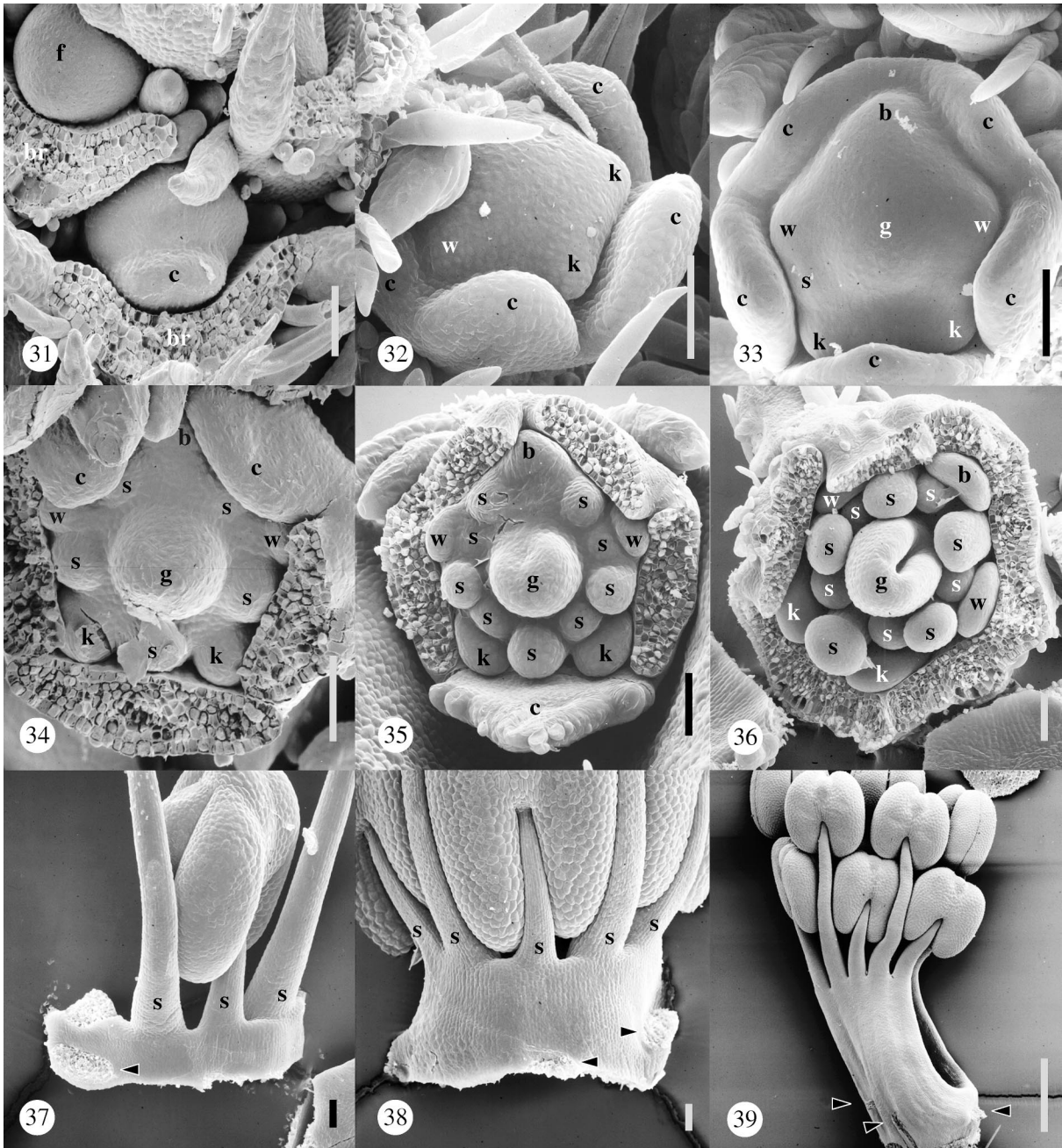
Figs. 31–39.   Floral ontogeny of *Marina maritima*. Abaxial side is at base in Figs. 31, 33–36. **31.** Two floral primordia in the axils of bracts (removed) on an inflorescence. At upper left, floral primordium before sepal initiation; in center, flower at abaxial sepal initiation. **32.** Bud after calyx lobes and three petal primordia established. **33.** Bud at beginning of stamen initiation, after calyx, corolla, and gynoecium primordia established. **34.** Bud after the five antesepalous stamens initiated (three calyx lobes removed). **35.** Bud after all but the adaxial antepetalous stamen initiated (four calyx lobes removed). **36.** Bud in which all calyx, corolla, androecium, and gynoecium appendages have been established; adaxial antepetalous stamen is left of center of the banner petal. **37.** Part of the early stamen sheath and very early stemonozone, showing petal attachment (arrowhead). **38.** Part of the stamen sheath and stemonozone with two petal attachments visible (arrowheads). **39.** Androecium and stemonozone of flower from which the calyx, petals, and gynoecium have been removed; three petal attachments are visible. Scale bars = 50 μm in Figs. 31–38; = 0.5 mm in Fig. 39.

three exemplar species studied for development are consistent in some features, such as the presence of a calyx tube and its primacy in development. Stamen fusion is common, and hypanthia are ubiquitous. Before we address specific questions of homology in Amorpheae, we would first like to establish a context for these morphological observations by discussing relevant morphology in other papilionoids.

Forms of stamen connation—Traditional classifications of papilionoid androecia focus on the patterns of stamen connation among the (usually) ten stamens (Polhill, 1981b). In diadelphous flowers, nine stamens are fused in a sheath and the adaxial stamen remains free. In pseudomonadelphous flowers (Gillett, 1961), the adaxial stamen is fused only to its neighbors above the base, leaving a pair of gaps between the adaxial
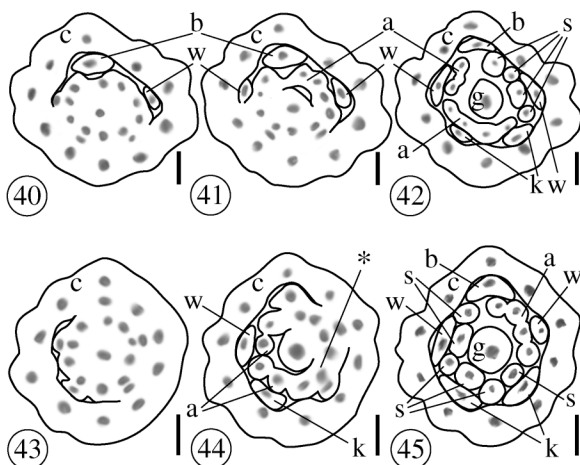
Figs. 40–45. Line drawings of serial cross sections through two floral buds of *Marina maritima*. Vasculature is indicated by shading, trichomes are not drawn. Figs. 40–42. Bud showing presence of calyx tube and stamen tube but no stemonozone nor hypanthium. **40.** Section showing calyx tube partially separate and the banner and one wing petal entirely separate. **41.** Section 6 μm more distal than previous figure, showing additional wing petal entirely separate and stamen tube partially separate from the gynoecium. **42.** Section 36 μm above the previous figure showing calyx tube, all five petals, and gynoecium separate. Portions of the stamen tube ("a") are present (upper and lower left) but four stamens ("s") are separate (upper right). A portion of one theca is visible in the section but is removed from drawing for clarity. Figs. 43–45. Bud showing presence of the calyx tube, the stamen tube, and the stemonozone, but no hypanthium. **43.** Section showing partial separation of the calyx tube. Petals are not separate at the point of calyx separation, as was seen in Fig. 40. **44.** Section 24 μm more distal than in previous figure showing calyx tube and gynoecium partially separate, one wing and one keel petal separate, but androecium and other petals not separate. In the region indicated by the asterisk, the keel petal and the androecium are not separate whereas the ovary is separate. The keel petal is thus attached above the separation point of the ovary, as well as above the separation point of the calyx; therefore, this bud has a stemonozone. **45.** Section 30 μm above the previous figure, showing separate calyx tube, corolla, gynoecium, and six stamens; a portion of the stamen tube is present (upper right). Scale bars = 0.1 mm.

stamen and its neighbors at the base of the androecium. In monadelphous flowers, all stamens are fused. However, monadelphy can take two forms: the stamens can be fused into a complete tube, or, as in the Amorpheae flowers studied here, they can be fused into a sheath, open (usually) on the adaxial side. Distinctions among the traditional classifications (monadelphy, diadelphy, and pseudomonadelphy) lie in the number of stamens fused together. An alternative view would be to focus on symmetry. In one form of monadelphy, the complete tube, androecial symmetry is radial, unlike any other androecial form in papilionoid legumes. In the other form, the sheath, androecial symmetry is bilateral, or approximately so. Therefore, the appropriate comparisons for Amorpheae androecia may be not with other androecia designated monadelphous, but with other bilaterally symmetric androecia.

We have shown for *M. maritima* and *Psorothamnus kingii*, and infer for the remaining sheathed taxa, that the sheath develops by zonal growth in an incomplete band of tissue below the stamens, with a gap between the adaxial stamen and one of its neighbors. This zonal growth occurs after initial organ elongation and differentiation, so the anthers are formed and the filaments are distinct atop the elongating sheath. This developmental pattern is similar to that seen in other sheathed taxa (e.g., *Machaerium villosum* [Klitgaard, 1999]). It is also

similar to that which produces the sheath portion of the androecium in diadelphous taxa (e.g., *Glycine max* (L.) Merrill [Crozier and Thomas, 1993]) and pseudomonadelphous taxa (e.g., *Pisum sativum* [Tucker, 1989], *Psoralea pinnata* L. [Tucker and Stirton, 1991]).

Petal-stamen synorganization—Petal-stamen synorganization occurs in a variety of forms, most commonly as epipetalous stamens. Epipetalous stamens are commonly initiated on a floral apical meristem as primordia separate from petals, and the epipetaly develops through zonal growth below the corolla and stamens (e.g., *Vinca rosea* [Boke, 1949], *Synthyris*, and *Besseya* [Hufford, 1995]). This is similar in a very general way to the pattern of petal-stamen synorganization seen in the daleoid Amorpheae; the major difference appears to lie in the fact that in the asterids mentioned, the corolla is sympetalous and the androecium consists of free stamens, whereas in the daleoids, the androecium is synandrous and the corolla consists of free petals.

A very few papilionoid taxa outside the Amorpheae are known to have petal-stamen synorganization. A member of the Dalbergieae, *Inocarpus fagifer* (Parkinson) Fosberg, has a highly unusual sympetalous corolla (with strap-shaped petal lobes) on which ten epipetalous stamens are inserted, similar in general appearance to an asterid flower (Polhill, 1981a). In a single species from the tribe Psoraleeae, *Psoralea leucantha* F. Muell. of Australia, the "corolla and staminal tube are fused for a short distance at the base" (Grimes, 1990, p. 16). This description does not clarify whether the corolla forms a tube that is fused to the staminal tube, or the petals are free and inserted on the staminal tube (as in Amorpheae), nor can we say whether the fusion is postgenital or congenital. The clearest example of a similar situation in papilionoids is seen in *Trifolium pratense* L. (Picklum, 1954; Retallack and Willison, 1990). Picklum's cross sections show petal-stamen synorganization similar to that seen in the daleoids. Retallack and Willison also found a "staminal-corollary tube" but did not describe its morphology or development in sufficient detail to allow comparison with the daleoid stemonozone. We have found in another clover with a corolla-stamen tube, *Trifolium macrocephalum* (Pursh) Poir., that the petals peel away from the fused region and are not set in sockets, as in the daleoid flowers. This structural difference may be significant; however, further study is required to know if there are developmental differences as well. Though these cases of petal-stamen synorganization in papilionoids are interesting, they are clearly isolated by phylogenetic distance from Amorpheae (Kajita et al., 2001; Pennington et al., 2001) and are therefore unlikely to be homologous (i.e., similar by descent) to the daleoid synorganization.

Assessing homology in Amorpheae—Armed with a morphological description of the petal-stamen synorganization of daleoid flowers, the ontogeny of three flowers in Amorpheae, and an idea of the context in which these occur, we now turn our attention to three specific questions of structural homology. First and most important, (1) What is the stemonozone? Is it homologous to receptacle, to androecium, or are there other possibilities? Because the identity of the stemonozone is not immediately obvious, its presence has led to interpretations of floral structures that we wish to redress via the remaining two questions. (2) Do the prairie clovers have staminodes? That is, are the four lateral petaloid structures in these taxa modified
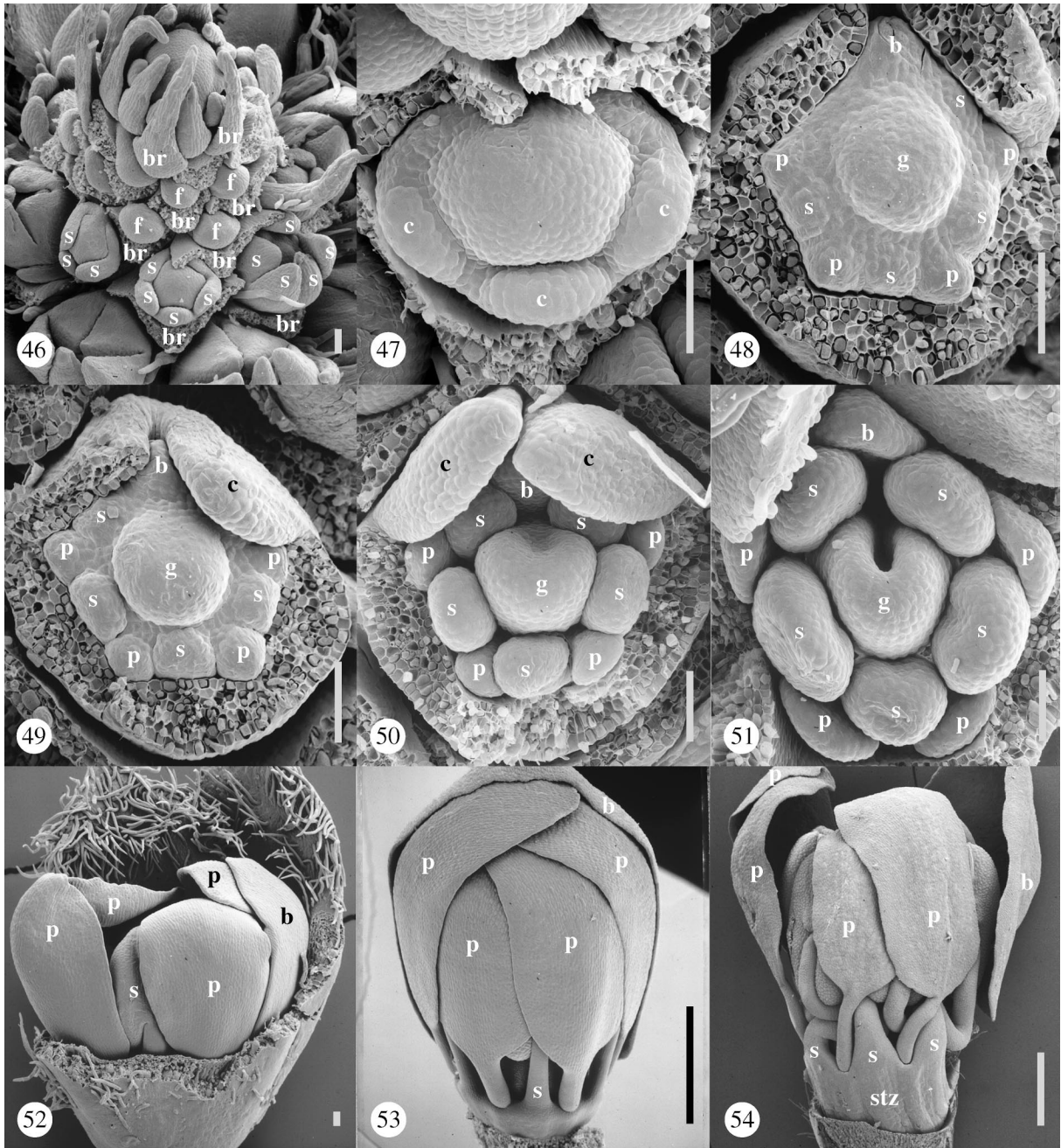
Figs. 46–54.   Floral ontogeny of *Dalea candida*. Abaxial side at base in Figs. 47–51. **46.** Young inflorescence showing flowers initiating singly in acropetal order in the axils of bracts. **47.** Flower primordium during calyx initiation; the remaining floral meristem is slightly pentagonal in polar view. **48.** Bud on which petaloid structures initiated in alternisepalous positions (visible at corners of pentagonal floral meristem) and four stamens forming in antesepalous positions. **49.** Bud in which stamens have been formed in all antesepalous positions. Inner margins of stamen primordia are slightly centripetal to the petal primordia. **50.** Bud in which the stamens have overgrown the petaloid structures. **51.** Bud showing arrangement of petaloid structures in whorl centrifugal to stamens. The petaloid structures have become slightly laminar. Stamens are at stage of thecal differentiation. **52.** Bud showing marginal expansion of petaloid structures becoming vernate and enclosing the androecium. **53.** Vernate petaloid structures completely enclose the androecium; a short stemonozone has extended below their insertion points and those of the free stamens. **54.** Nearly anthetic bud showing almost completely extended stemonozone. Scale bars = 50 μm in Figs. 46–52; = 0.5 mm in Figs. 53–54.

stamens (Moore, 1936; Faegri and van der Pijl, 1979) or are they modified petals (Wemple and Lersten, 1966; Barneby, 1977)? (3) Does the presence of the stemonozone indicate that the daleoid taxa reinvented a papilionaceous flower (Barneby, 1977)? Conversely, are the papilionaceous daleoid flowers structurally homologous to other papilionoid flowers?

Two approaches help us answer our questions of homology. By comparing across morphologies, we can describe similarities in special attributes and in relative position and evaluate possible intermediates (Remane's [1952] principal criteria of homology [Riedl, 1978]). By comparing morphologies through development, we can additionally describe similarities
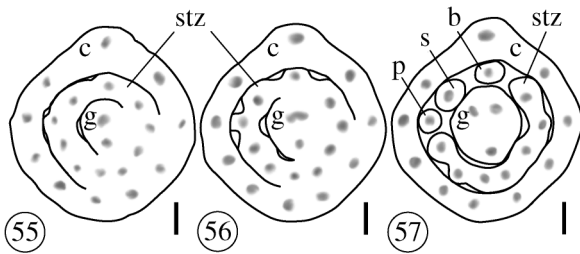
Figs. 55–57. Line drawings of serial cross sections through a floral bud of *Dalea candida* showing the presence of a calyx tube and stemonozone but no hypanthium. Trichomes are not drawn. **55.** Section showing calyx, stemonozone, and gynoecium partially separate. **56.** Section 24 μm more distal than previous figure, showing further separation of calyx tube, gynoecium, and stemonozone. **57.** Section 24 μm more distal than previous figure, showing fully separate calyx tube and gynoecium. One stamen, the banner petal, and one petaloid structure are separate. Scale bars = 0.1 mm.

in timing, as well as positions at initiation and throughout development. None of these are absolute arbiters of structural homology. Rather, they are similarities that we would expect to observe if the genetic programs that underlie the structures were, indeed, inherited in common.

(1) What is the stemonozone?—Structures that are the products of zonal growth below multiple whorls of organs have long presented difficult homology problems. The stemonozone, above the hypanthium and below the corolla and the androecium, is just such a structure, similar to hypanthia (below corolla, androecium, and calyx), gynostegia (below androecium and gynoecium), or the walls of inferior ovaries (be-

low corolla, androecium, calyx, as well as involving gynoecium). Of these, homology of the walls of inferior ovaries has received the most attention (Kaplan, 1967; Kuzoff, Hufford, and Soltis, 2001), concentrating on the fundamental question of whether they are homologous to shoots (receptacular) or to appendages (appendicular), a question relevant to our case as well.

Barneby (1977) tentatively suggested that the stemonozone was an upgrowth of the receptacle. Positionally, it is below corolla and androecium, where we find receptacle tissue in other papilionoids. However, it is above (distal to) the insertion point of the calyx and distant from the base of the gynoecium, inconsistent with it being receptacular tissue. Special attributes of the stemonozone favor an appendage interpretation: the form and the histology of the structure are indistinguishable from androecium, as indicated in the common description of the flowers as having "epistemonous petals" (Barneby, 1977). This is not to say that it is androecial tissue, but the form of the structure lends weight to an appendicular interpretation rather than receptacular. Remane's third criterion, the presence of intermediates, is more difficult to apply in this case because the question has not been asked for any other legumes with petal-stamen synorganization.

Kaplan (1967) described two sets of criteria for interpreting an appendicular origin of the inferior ovary in *Downingia bacigalupii* Weiler and the receptacular origin for that in *Pereskia aculeata* Mill.: (1) the pattern of vasculature and (2) relationships between developmental events and processes. In *Downingia*, vascular bundles branch below the ovary; the wall of the inferior ovary therefore contains distinct bundles that lead to stamens and perianth parts. In *Pereskia*, vascular bundles
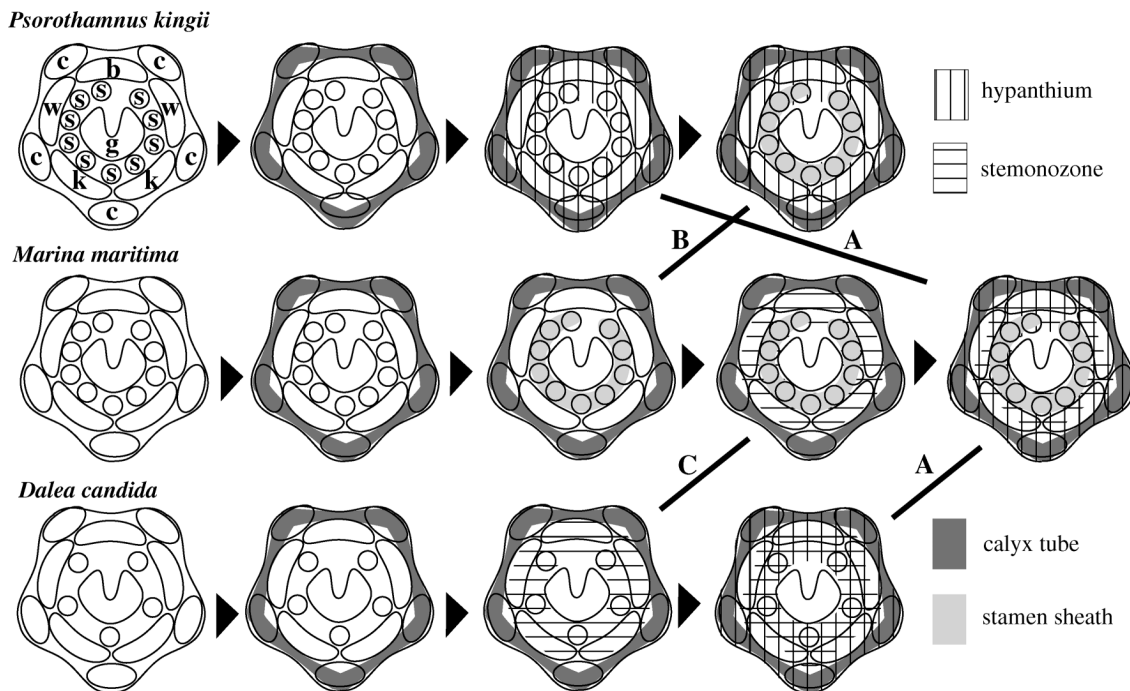

Fig. 58. Regions of zonal growth in the flowers of *Psorothamnus kingii*, *Marina maritima*, and *Dalea candida*. Arrows indicate developmental progression within taxa. Shading and bars indicate areas of zonal growth. Heavy lines indicate correspondence of events between taxa: lines A indicate corresponding onset of zonal growth that will produce the hypanthium. Line B indicates corresponding onset of zonal growth that will produce the stamen sheath. Line C indicates the corresponding onset of zonal growth that will produce the stemonozone. Note that the calyx tube is the first to develop in all taxa, but subsequent development differs between taxa. In *P. kingii*, the hypanthium begins to develop before the stamen sheath, whereas in *M. maritima* and *D. candida*, the hypanthium begins to develop last; thus, lines A and B cross in the upper portion of the figure.

branch above the ovary; some of these branches lead to peri-anth, some to stamens, and some loop down the inside of the ovary wall (recurrent vascular bundles) to the placentae. The positional difference in vascular branching is used to infer an important difference. The recurrent vasculature in *Pereskia* supports the idea that the receptacle has spread out and up, forming a concavity on which floral organs form. Nonrecurrent vasculature in *Downingia* supports the idea that the border between appendage and receptacle is below the ovary, so the ovary wall is appendicular.

Using the inferior ovary wall example as a model, we can develop expectations for the daleoid stemonozone. If the stemonozone is receptacular, then the plesiomorphic receptacle would have spread out and up, as in *Pereskia*. Moreover, if the vasculature reflected this change, then we would expect to see vascular patterns that include complexities such as recurrent bundles. Instead, we see vascular bundles that are separate, leading to the stamens and to the petals, branching below the stemonozone (Fig. 14). This configuration is similar to that in legumes without stemonozones and shows nothing that indicates upgrowth of the receptacle. Therefore, evidence from daleoid vasculature is more consistent with an appendicular interpretation, as in the case of *Downingia*. Thus, the special attribute of vasculature, in addition to general form as described above, supports an appendicular interpretation for the stemonozone.

If we are correct that the stemonozone is appendicular, then what sort of appendage is it? Key alternatives are androecium, corolla, both, or neither (i.e., a new appendage altogether). Position of the stemonozone argues against it being solely androecium or solely corolla, because it is below both corolla and androecium. If homology of the stemonozone is with both whorls, we might be able to observe histological differences among regions as seen in *Eucnide aurea* (A. Gray) H. J. Thomps. & W. R. Ernst (Hufford, 1988). This may be the case for some *Trifolium* flowers that have petal-stamen synorganization, in which the petals easily peel away. However, in the daleoid stemonozone, there are no regional differences in tissue histology (data not shown), nor is there tissue that peels (Fig. 8); therefore, we have no evidence for a compound structure. Mature morphology of the stemonozone provides evidence for appendicular homology but no evidence to homologize the stemonozone with particular appendages.

Evidence from development was critical in the inferior ovary example described above: "The differences in the two types of inferior ovaries reflect a difference in the time when the floral bud becomes concave. In *Downingia bacigalupii* formation of the floral cup occurs in conjunction with organ initiation, whereas in *Pereskia aculeata* floral cup formation takes place after *and independent of* initiation of appendages" (Kaplan, 1967, p. 1288; emphasis added). Because the floral cup forms after the organs form in *Pereskia*, Kaplan says that this floral cup is receptacular; coincident initiation of cup and organs results in an inference of appendicular affinity. This implies that we can use the timing of events to infer independence or nonindependence of events, and, further, that independence informs homology inference.

Kaplan was interested in the relationship between organ initiation and the development of synorganization. In the daleoids, however, this relationship tells us little: in all taxa studied, organ initiation occurs prior to any synorganization. Instead, it may be more important to focus on relationships among synorganizations. As discussed above, daleoid flowers
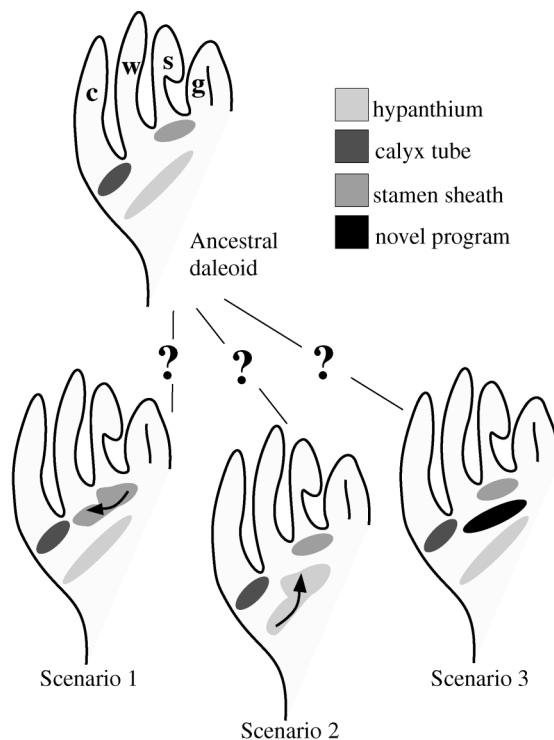

Fig. 59. Scenarios for the evolution of petal-stamen synorganization in daleoid flowers from flowers that have no stemonozone (presumed ancestral; see DISCUSSION). Scenario 1: staminal column zonal growth program extends to include region below the petals. Scenario 2: hypanthial zonal growth program extends to include zonal growth in region below stamens and petals. Scenario 3: petal-stamen zonal growth arises from an entirely novel developmental program.

have some synorganization in common with other papilionoids. Hypanthia are frequent in papilionoids, as are a variety of forms of staminal fusions. Are any of these ontogenetic events related to the daleoid petal-stamen synorganization?

One possibility is that the daleoid flowers have a developmental program homologous to, in modified form, the developmental program underlying the androecium in other taxa (Fig. 59, scenario 1). The fused portion of the androecium (distal to the stemonozone) is similar in development and in mature form to the fused portion of the androecium found in other papilionoids. Perhaps, in the daleoid flowers, the zonal growth involves not only the tenth stamen, but the petals as well.

A second possibility is that the developmental program that produces the hypanthium might be involved in the formation of the petal-stamen synorganization (Fig. 59, scenario 2). The hypanthium is a product of zonal growth and occurs to some extent in many legumes, regardless of the conformation of the androecium. In *Dalea* and *Marina*, below where the petals and stamens are being elevated by an unusual synorganizing zonal growth, all organs are being elevated by zonal growth that will eventually produce the hypanthium. However, we have one line of evidence against this inference: the zonal growth below the petals and stamens in both *D. candida* and *M. maritima* occurs earlier in development than (and therefore potentially independent of) the zonal growth that produces the hypanthium.

A third interpretation is that the developmental program that produces the synorganization is novel (Fig. 59, scenario 3).

This interpretation differs greatly from the previous two by invoking the addition of a developmental program, rather than a modification of a preexisting program (either the program that produces a hypanthium or the program that produces a sheathed androecium). As evidence against this interpretation, the zonal growth below the petals and stamens produces tissue that closely resembles androecium, which might be unexpected if the developmental program was entirely novel.

Therefore, based on the data at hand, we hypothesize that the stemonozone is a product of a modified androecial development program (Fig. 59, scenario 1). Comparison of development across several more taxa will allow us to investigate this hypothesis further. If, for instance, the timing of the zonal growth below the stamens and petals always follows close behind the onset of growth below the stamens (as in *M. maritima*) but is relatively uncorrelated with the growth of the hypanthium, the case for scenario 1 (Fig. 59) would be strengthened. Opposing evidence, i.e., correlation with hypanthial growth but not with staminal sheath growth, would support the model shown in Fig. 59, scenario 2. If the timing of the zonal growth below the stamens and petals is not correlated to any other process of zonal growth, then it may be possible to infer that the underlying developmental program is a novel addition, as in Fig. 59, scenario 3.

We conclude that the stemonozone is appendicular, but beyond that, we cannot say exactly to which organ or whorl of organs it is homologous. Instead, we favor the interpretation that the developmental process producing the stemonozone is a modified form of the process that produces the androecium. For the case of the stemonozone, perhaps for other synorganized structures as well, inferring an evolutionary source for its underlying developmental process allows a clearer idea of its homology than does focusing on the mature structure itself.

(2) Do the prairie clovers have staminodes?—The second homology issue we will address concerns a set of approximately 22 species of *Dalea*, subgenus *Dalea* section *Kuhnistera* (Lamarck) Barneby, previously known as the genus *Petalostemon* Michaux, or "prairie clovers." In this group of species, distributed from southern Canada to northern Mexico but most diverse in the U.S. Great Plains, the total number of organs is reduced relative to most of the genus *Dalea*. Furthermore, the identity of four of the petaloid organs has been questioned.

As described above (see description of *Dalea candida* in RESULTS), only five fertile stamens are present, not the common ten (or more rare nine). The corolla consists of at least one petal, the banner (medial adaxial) petal. In addition to the banner, four sterile laminate structures are present, but whether they are staminodes or petals has been debated (Moore, 1936; Wemple and Lersten, 1966; Faegri and van der Pijl, 1979). The interpretation that these structures are staminodes is due, in part, to their positions between the free filaments of the five antesepalous stamens. These positions would be occupied by four of the five stamens that are present in other synandrous papilionoids but are absent in the prairie clovers. Also, all four of the structures are quite similar to one another, in most cases not distinguishable as "wing" and "keel" petals. However, the structures are petaloid: sterile, laminar, and frequently colored like the banner.

Applying Remane's (1952) criteria, we find that the petaloid structures, at maturity, are positionally most similar to antepetalous stamens; they alternate with the sepals (as do petals) but they are on the same circumference as the stamens. However, early in development, these structures are in positions centrifugal to the antesepalous stamens (Figs. 48–51), which we would expect for petals. Special attributes of the structures include claws and lamina, in common with petals but not with stamens. These laminae form early in development (Fig. 51) and later enclose the stamens (Figs. 52–54), as do petals in other Amorpheae. Another special attribute lies in the attachment of the structures. They attach to the flower in distinct sockets (just as petals of other daleoid flowers), unlike the smooth, jointless attachment of stamen filaments. When calling the structures staminodes, Faegri and van der Pijl (1979) and Moore (1936) were essentially weighing the positional criterion more highly than the criterion of special attributes. Furthermore, they did not have key data on early development, so the positional criterion was applied only to the flower at maturity. Turning to the third criterion, we find that there are no cases that could be interpreted as intermediates for the staminode interpretation of the structures, i.e., there are no other known taxa in Amorpheae with staminodes. However, daleoid taxa have petals attaching at a variety of heights on the "staminal" column, from very close to the hypanthium (e.g., *Psorothamnus emoryi*; Fig. 20), to very close to the filament separation point (e.g., *Dalea grayi* [Barneby, 1977]). This range of attachment heights represents a set of intermediate conditions between the laminar structures in section *Kuhnistera* and petals in other papilionoids.

Wemple and Lersten (1966) examined mature flowers from all species of *Petalostemon* and many species of *Dalea* and interpreted the structures as petals. Their conclusion was based on the presence of the sockets and on the presence, in some species, of subtle differentiation among lateral appendage pairs, as in wing and keel petals. Our results, using developmental information and applying explicit criteria for structural homology, agree with that of Wemple and Lersten (1966), strengthening the case for the presence of petals in the prairie clovers, i.e., that the laminar structures are structurally homologous to petals and not to staminodes.

(3) Are daleoid flowers homologous to those of other papilionoids?—We will now address whether the flowers found in *Dalea* and *Marina* may represent an independent derivation of the papilionoid form, as tentatively suggested by Barneby (1977), or if they are structurally homologous to other papilionoid flowers. The criteria of position and special attributes are key. There are many attributes that *Dalea* and *Marina* share with other papilionoids. For most daleoid flowers, the number of organs in each whorl and their relative positions are the same as found in most papilionoids (five sepals, five petals, ten stamens, single carpel) although there are exceptions, as discussed above. The process of organ initiation demonstrated by the three daleoids studied is similar to that seen in other papilionoids (Picklum, 1954; Sattler, 1973; Tucker, 1984, 1989; Derstine, 1988; Retallack and Willison, 1990; Tucker and Stirton, 1991; Klitgaard, 1999). In most papilionoids studied, organ initiation is generally unidirectional (Tucker, 1984), often with overlapping initiation among the whorls (Tucker, 1989). Also, the adaxial petal of the daleoids is external in bud, producing cochleate vernation, just as in other papilionoids. Moreover, most daleoid flowers are strongly zygomorphic (i.e., the corolla is differentiated into a banner, two wings, and two keel petals), as is typical for papilionoids. These characteristics are powerful similarities because they are not wide-

ly distributed among eudicots; indeed, zygomorphic cochleate flowers distinguish the subfamily Papilionoideae (Polhill, 1981b; but see Herendeen [1995] for exceptions in Swartzieae). Daleoid flowers, therefore, share special attributes with other papilionoid flowers. However, similarity can arise via homoplasy. Indeed, Barneby's question was whether *Dalea* and *Marina* arrived at this general floral appearance via homoplastic evolution. Finding no major structural differences outside of the petal-stamen synorganization is reassuring but negative evidence.

Therefore, we must turn to the final criterion of structural homology: the presence of intermediate forms. For this we consider the flowers of *Psorothamnus*. Some species have a short zone of petal-stamen synorganization (e.g., *P. emoryi*) whereas others have no such zone (e.g., *P. kingii*). The flowers of those *Psorothamnus* species that lack petal-stamen synorganization are similar to those of other papilionoids whereas those with a short stemonozone are intermediate between the daleoids and typical papilionoids. In other respects, however, *Psorothamnus* flowers are similar to other papilionoids: same organ number, strong zygomorphy, and cochleate vernation. This bears substantially on the question of homology between daleoid flowers and other papilionoid flowers: by encompassing a series of intermediate forms, *Psorothamnus* provides evidence for morphological continuity in the zone of petal-stamen synorganization. Therefore, the third criterion is satisfied, and we infer that the flowers of *Dalea* and *Marina* are structurally homologous to other papilionoids and probably do not represent an independent derivation of the papilionoid facies, as tentatively suggested by Barneby. Reconstruction of the Amorpheae phylogeny will allow us to confirm homology, provided we can infer the ancestors of the group to have been papilionoid.

Conclusions—Structural homology is essential for understanding the evolution of form. In our study, evidence from the morphology of structures, at maturity and throughout development, and evidence from the timing of developmental events allow us to infer homology at several levels in the daleoid Amorpheae. We infer the daleoid stemonozone to be appendicular and to be related to the androecium developmentally, and we infer that the prairie clovers have five petals and five stamens, rather than one petal and nine stamens. Finally, we infer the daleoid flower to be structurally homologous to other papilionoid flowers. These inferences provide testable hypotheses for phylogenetic study of the group.

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