Development of the gametophytes, flower, and floral vasculature in Dichorisandra thyrsiflora (Commelinaceae)[1]

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The flowers of *Dichorisandra thyrsiflora* (Commelinaceae) are monosymmetric and composed of three sepals, three petals, six stamens, and three connate carpels. The anthers are poricidal and possess a wall of five cell layers (tapetum included). This type of anther wall, not previously observed in the Commelinaceae, is developmentally derived from the monocotyledonous type via an additional periclinal division and the persistence of the middle layers through anther dehiscence. Secondary endothecial thickenings develop in the cells of the two middle layers only. The tapetum is periplasmodial and contains raphides. Microsporogenesis is successive and yields both decussate and isobilateral tetrads. Pollen is shed as single binucleate grains. The gynoecium is differentiated into a globose ovary, hollow elongate style, and trilobed papillate stigma. Each locule contains six to eight hemianatropous to slightly campylotropous crassinucellar ovules with axile (submarginal) placentation. The ovules are bitegmic with a slightly zig-zag micropyle. Megagametophyte development is of the Polygonum type. The mature megagametophyte consists of an egg apparatus and fusion nucleus; the antipodals having degenerated. The floral vasculature is organized into an outer and inner system of bundles in the pedicel. The outer system becomes ventral carpellary bundles. All other floral vascular traces originate from the inner system.

Key words: buzz pollination; Commelinaceae; *Dichorisandra*; embryology; floral development; floral vasculature; gametophyte development; poricidal anthers.

Previous floral developmental studies in the Commelinaceae have shown a considerable amount of variation in apparently fundamental processes. Variations in stamen development include the overall centrifugal patterns in certain species of *Tradescantia* and *Callisia* (Payer, 1857; Hardy and Stevenson, in press a), the simultaneous to slightly centripetal development in *Gibasis* (Rohweder, 1963; Stevenson and Owens, 1978), and centripetal patterns in *Cochliostema* (Hardy and Stevenson, in press b) and *Geogenanthus* (C.R. Hardy, unpublished data). A surprising amount of variation in megagametophyte (embryo sac) development has also been reported. In addition to the monosporic Polygonum type most frequently encountered in the Commelinaceae (e.g., Maheshwari and Singh, 1934; Murthy, 1938; Maheshwari and Baldev, 1958; Chikkannaiah, 1962, 1963, 1964; Chikkannaiah and Hemaraddi, 1979; Grootjen and Bouman, 1981; Grootjen, 1983), the range in embryo sac variation also encompasses the bisporic Allium type and the tetrasporic Adoxa type (McCollum, 1939; Stevenson and Owens, 1978; Davis, 1966, and references cited therein). Additionally, both tenuinucellar and crassinucellar ovules are known to occur in the family (as reviewed by Johri, Ambegaokar, and Srivastava, 1992).

The following is a description of the structure and development of the flower, gametophytes, and floral vasculature in the Brazilian species *Dichorisandra thyrsiflora* Mikan. *Dichorisandra,* with at least 25 species (Faden, 1998), represents more than one-half of the subtribe Dichorisandrinae (sensu Faden and Hunt, 1991), a taxon encompassing the greatest diversity for the family in South America and for which no detailed embryological studies have been reported. Species of *Dichorisandra* are characterized primarily by their arilloid seeds and, with only a few exceptions, poricidally dehiscent anthers (Faden, 1998). Within the family, poricidal anthers are also known in five species distributed among the genera *Amischotolype, Coleotrype,* and *Porandra*; however, none of them are considered to be especially closely related to *Dichorisandra* (Faden and Hunt, 1991; Evans, 1995). An objective of the current investigation was to provide the first description of anther and microgametophyte development in a porandrous member of the Commelinaceae. An additional objective of this and future studies was the collection of embryological data from *Dichorisandra* and other members of the Dichorisandrinae that will be used in future phylogenetic studies within the subtribe. An adequate description of the general morphology of the flower and vegetative form of *D. thyrsiflora* has already been given by Hunt (1971).

MATERIALS AND METHODS

Material was collected from living plants in collection at the New York Botanical Garden and fixed in FAA (formalin:acetic acid:50% ethanol, 1:1:8 v/v) prior to being transferred into 50% ethanol for storage. Materials taken were from two different accessions of *D. thyrsiflora,* and voucher specimens (Hardy 227 and 228) were deposited in the New York Botanical Garden herbarium (NY). Young inflorescences and flowers in various stages of development were removed and dehydrated to 100% ethanol. Some young inflorescences and flowers were then transferred to acetone via an ethanol-acetone series, critical point dried, and coated in gold-palladium for scanning electron microscopy. Additional flowers of various stages were prepared according to standard methods of paraffin embedding (Johansen, 1940) and sectioned using a rotary microtome. Serial sections of 10–12 μm were stained in safranin and astra blue, dehydrated through an ethanol series to 100% ethanol, transferred to Hemo De, mounted in Kleermount, and examined using conventional

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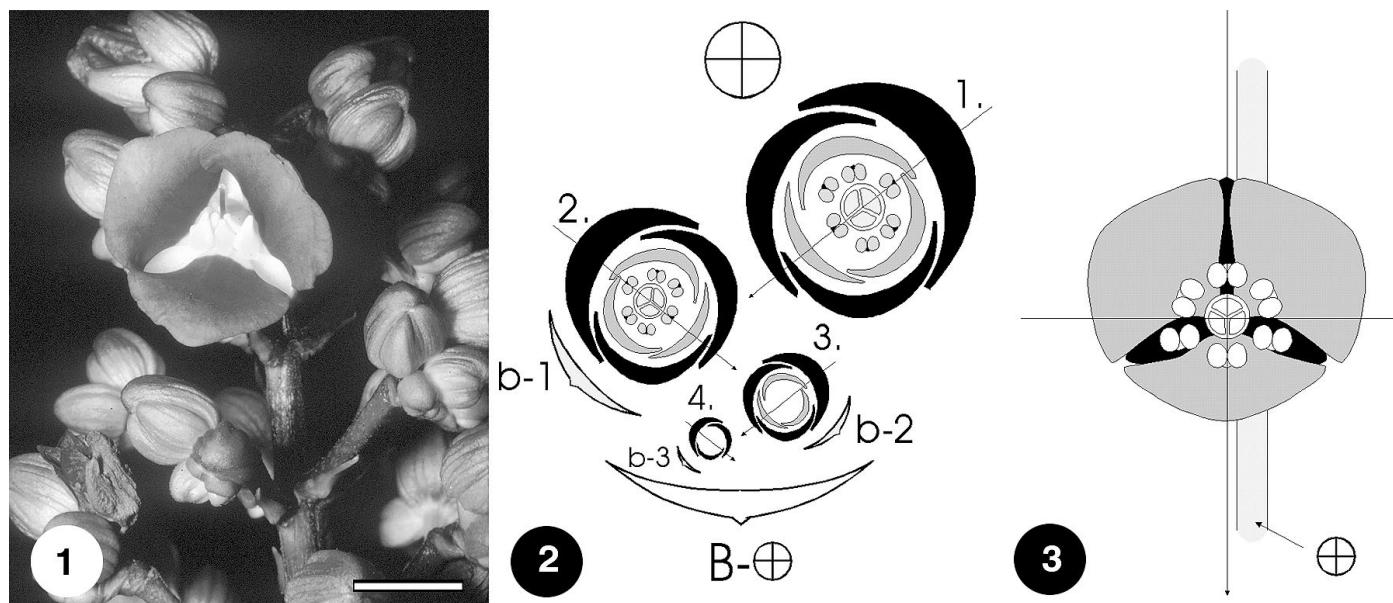
Figs. 1–3.   Inflorescence and flower of *Dichorisandra thyrsiflora*. **1.** Thyrse with open flower; scale bar = 1 cm. **2.** Diagram of individual cincinnus; flowers are numbered according to order of initiation; arrows represent plane of floral symmetry. **3.** Stylized floral diagram portraying the orientation and symmetry properties of an open flower.

Figure Abbreviations: ⊕, thyrse axis; *, non-functional megaspore; AC, archesporial cell; Ad, adaxial side; Ai, inner whorl stamen or stamen vascular trace; Ao, outer whorl stamen or stamen vascular trace; b, bracteole; b-n, bracteole borne on axis of flower "n"; B-⊕, cincinnus bract; C, petal or petal vascular trace; D, dorsal carpellary trace; E, egg; Ep, epidermis; ES, embryo sac or embryo sac cavity; F, filiform apparatus; FMS, functional megaspore; FN, fusion nucleus; G, carpel; ii, inner integument; K, sepal or sepal vascular trace; Kn, nth-initiated sepal; L, connective lacuna; MMC, megaspore mother cell; oi, outer integument; P, procambial stand; PC, parietal cell; PN, polar nuclei; S, synergid; V, ventral carpellary trace; VB, vascular bundle.

brightfield microscopy. Observations of pollen grain nuclei and mature mega-gametophytes were also made by clearing pollen and ovules in a modified Herr's clearing fluid (lactic acid:chloral hydrate:phenol:clove oil:Hemo De, 2:2:2:2:1 by mass; based on Herr, 1971). These cleared preparations were placed on slides in the Herr's fluid and examined using differential interference contrast (DIC) optics.

RESULTS

Overview of inflorescence and floral morphology—The inflorescence of *Dichorisandra thyrsiflora* is a terminal thyrse composed of numerous pedunculate scorpioid cymes (Fig. 1). Each scorpioid cyme (cincinnus) is several flowered and is subtended by a lanceolate to linear bract. Growth of an individual cyme continues from the axil of a bracteole borne on the axis terminated by the previous flower (Fig. 2). Plants of *Dichorisandra* are andromonoecious. In the functionally male flowers a diminutive pistil considerably smaller than its counterpart in the bisexual flowers is present. Ovules are initiated in the male flowers, although it appears they abort sometime just prior to archesporial cell formation and integument initiation. Other than those associated with the gynoecium, there appear to be no other differences in the development of male and bisexual flowers.

The individual flowers are monosymmetric (sensu Endress, 1994), a symmetry achieved early in development and most conspicuous in the androecium and calyx (Figs. 1, 3–7). At anthesis, the flower possesses a single plane of symmetry, which is vertical and parallel to the thyrse axis. Floral asymmetry occurs on either side of the horizontal axis (Fig. 3). The two members of each whorl of three that lie on one side of the horizontal axis are identical to each other and together different in form or orientation from the third that lies on the other half. In the descriptions that follow, members of a whorl are referred to as "upper" or "lower" according to whether they occur above or below this horizontal axis, respectively.

Perianth—The calyx consists of three, subequal, more or less glabrous sepals. The sepals are imbricate in bud, with one sepal completely outside and another completely inside the others (Fig. 2). The upper sepal is always the outermost in bud and the largest of the three. The corolla consists of three subequal petals, the two upper petals being broader than the lower for the duration of development. The aestivation of the corolla, like the calyx, is imbricate; the lower petal is always the outermost of the three in the floral bud (Fig. 2).

Sepal and petal organogenesis—The sepals are sequentially initiated, whereas the petals are initiated in a nearly simultaneous fashion (Figs. 4, 5). The first-initiated (upper) sepal increases in size much more rapidly than the other two and serves as the primary protective structure of the inner whorls in the floral bud (Figs. 4, 13).

Androecium—Each stamen is composed of a short filament and a relatively long basifixed anther. Though not uncommon in the Commelinaceae, the stamens are devoid of any filament hairs for which other members of the family (e.g., *Tradescantia*) are well known (Faden, 1992). The stamens are inconspicuously united at the base of their filaments, which are basally adnate to the corolla (Fig. 16). As a consequence of the adnation of these basally fused filaments to the corolla, the otherwise free petals are indirectly united as in *Dichorisandra hexandra* and certain other Commelinaceae (Rohweder, 1969). At maturity, each anther opens by an apical pore (Figs. 14,
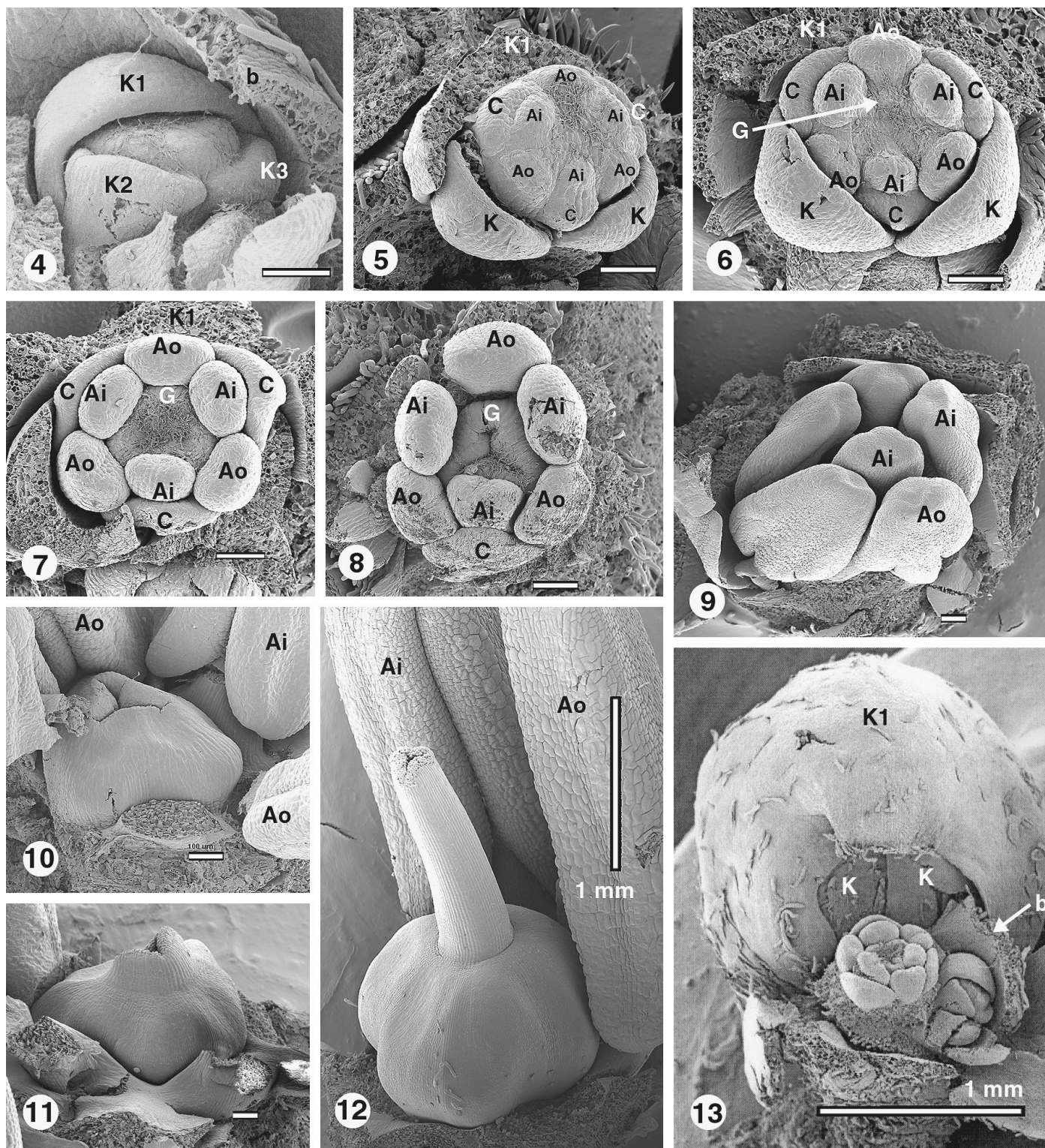
Figs. 4–13.   Floral organogenesis. Scale bars = 100 µm except where indicated otherwise. Sepal 1 on top in all figures except in Figs. 11 and 12. **4.** All sepals initiated; surrounding bracteoles partially removed. **5.** Petal and stamen initiation; first-initiated sepal (K1) partially removed. **6.** Carpel initiation; K1 partially removed. **7, 8.** Early gynoecium development; early anther differentiation in stamen primordia; all sepals partially removed; upper two petals removed in Fig. 8. **9.** Late-stage androecium development, with stamens obscuring gynoecium from view and perianth removed. **10–12.** Mid- to late-stage development of gynoecium; some stamens removed. **13.** Young cincinnus with three young flowers in early to late stages of organogenesis; bracteoles mostly removed.
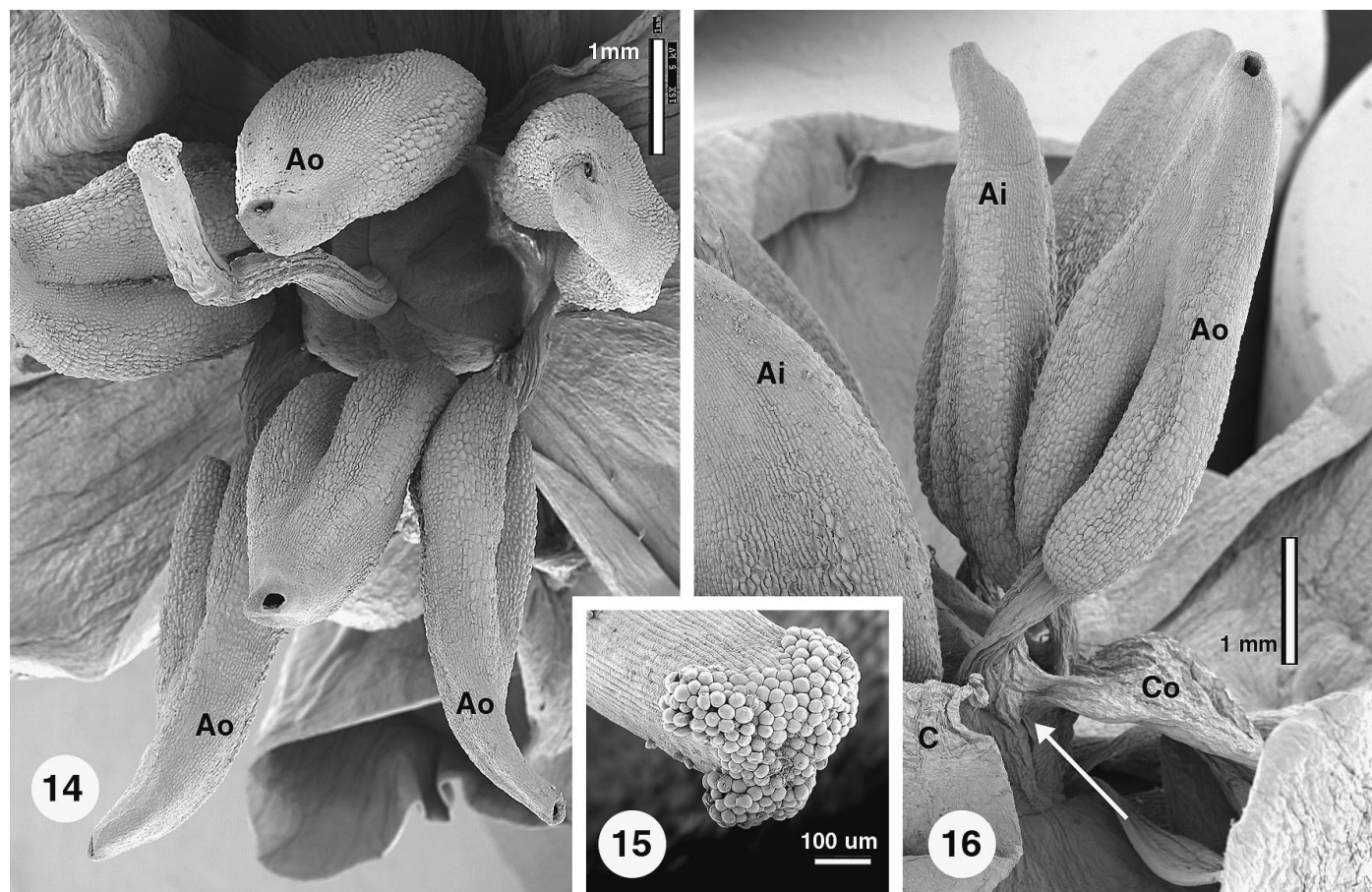
Figs. 14–16.   Flower at anthesis. **14.** Mature flower; perianth not in view. The wide spread of the stamens exaggerated as an artifact of critical point drying; twisting of filaments of the lower outer whorl stamens (Ao) exaggerated slightly as an artifact of critical point drying. **15.** Stigma of flower in Fig. 14. **16.** Different view of flower in Fig. 14 demonstrating adnation (arrow) of filaments to corolla.

16), and pollen is apparently released by the vibration induced by pollen-collecting bees as in many other buzz-pollinated flowers. Vibration-mediated removal of pollen by bees of the genus *Bombus* has been observed for cultivated plants of *D. thyrsiflora* (Boaventura and Matthes, 1987; C.R. Hardy, personal observation). Buzz pollination by euglossine bees has been observed in the field for two additional species of *Dichorisandra* in Brazil (Sigrist and Sazima, 1991).

Stamen organogenesis—The stamen primordia arise on the flanks of the floral shoot apex as small mounds in two alternating whorls of three (Figs. 4, 5). Stamen initiation and early maturation are centripetal. Stamens of the outer whorl arise first and nearly simultaneously. Initiation of the inner whorl follows and is approximately concomitant with the development of dorsiventrality in the petal primordia. Within the inner whorl, growth in size of the third and lower stamen lags slightly behind that of the upper two stamens, which develop synchronously (Figs. 6–8). The reduced growth of the lower stamen of the inner whorl results in a bilateral symmetry of the androecium at an early stage and persists throughout development. At the time of carpel initiation, the anthers of the outer whorl have begun to differentiate and are slightly bilobed (Fig. 6). When the gynoecium is discernible as a three-lobed ring, anthers of the inner whorl have begun to differentiate (Figs. 7, 8). By the start of style formation, the anthers have

elongated considerably and the basally saccate characteristic of mature anthers is present (Figs. 10, 12, 16). At anthesis, the monosymmetry of the androecium is maximal as the two lower stamens of the outer whorl extend and curve towards the outside via a slight twist of their filaments (Figs. 1, 3, 16). The orientation of the apical pores of the anthers also contributes to the monosymmetric nature of the mature androecium as the pored tips of the anthers become upwardly curved (Figs. 1, 14).

Anther development—The anthers are tetrasporangiate (Fig. 17), with the two adaxial sporangia being developmentally confluent distally (Fig. 18).

Formation of the anther wall begins as periclinal divisions of the archesporial cells give rise to the cells of the primary parietal layer externally and primary sporogenous cells internally. With three additional periclinal divisions, the primary parietal layer gives rise to the four layers of the anther wall below the epidermis (Figs. 20–22). The innermost of these layers becomes the tapetum.

During early prophase of meiosis I in the microsporocytes, the tapetal cell walls break down (their inner tangential walls first) and the tapetum becomes periplasmodial. Raphides were observed in the plasmodium, as has been reported for numerous other species of Commelinaceae (e.g., Mascré, 1925; Maheshwari and Singh, 1934; Nanda and Gupta, 1977). The per-
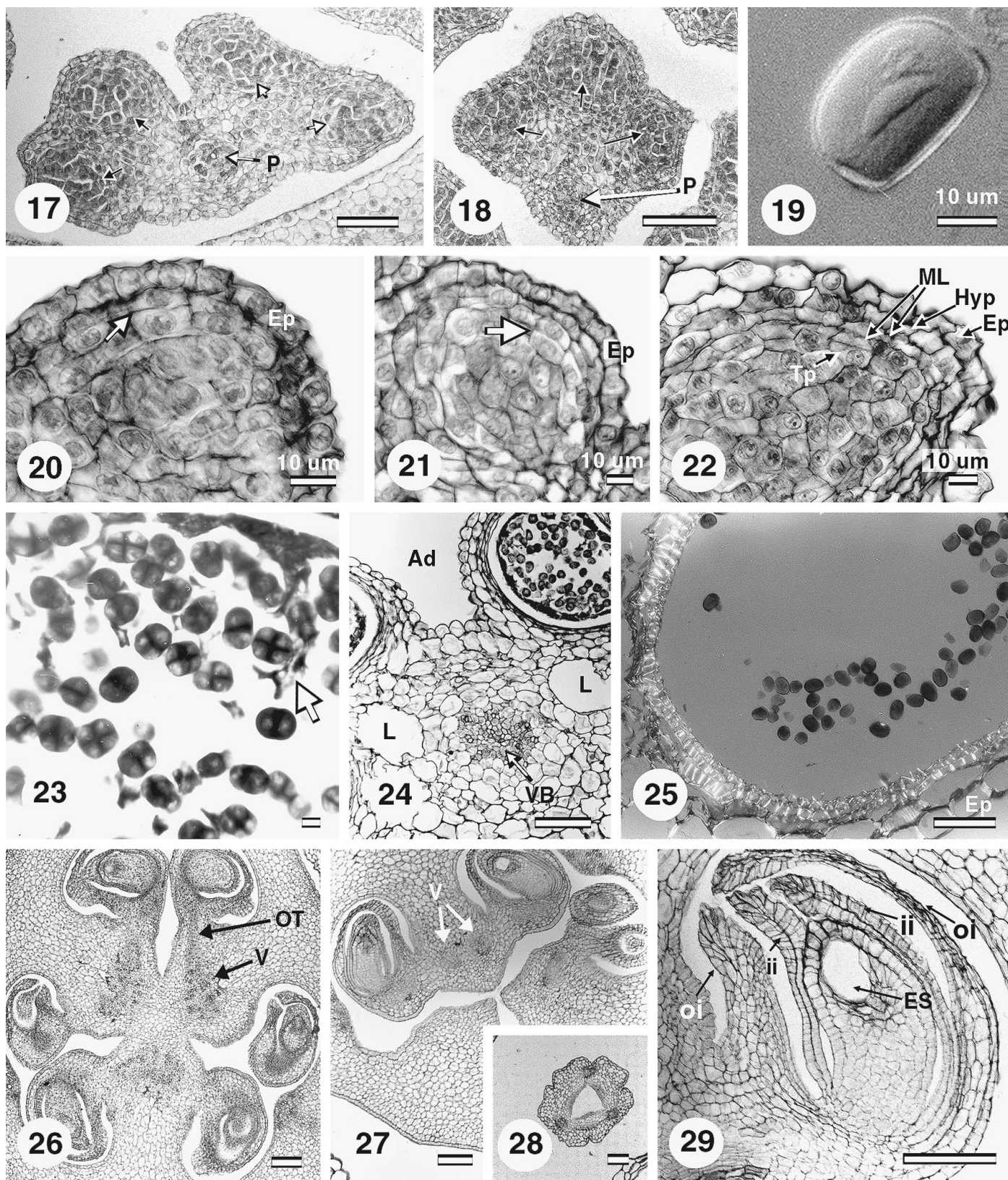
Figs. 17–29. Gynoecium and androecium anatomical and histological development, mid- to late stages. Scale bars = 100 μm, except where indicated otherwise. **17.** Basal portion of young anther with four sporogenous zones (four unlabeled arrows). **18.** Distal portion of same anther in Fig. 17, with three sporogenous zones (three unlabeled arrows). **19.** Two-celled pollen grain at dispersal stage. **20.** Early-stage anther wall formation; formation of the secondary parietal layers. Cell wall formed by recent periclinal division indicated by arrow. **21.** Mid-stage anther wall formation; formation of third wall layer. Cell wall formed by recent periclinal division indicated by arrow. **22.** Late-stage anther wall formation; formation of the tapetal layer of cells. **23.** Isobilateral and decussate

iplasmodium starts to degenerate after microsporogenesis is complete (Figs. 23, 24). The mature anther wall is composed of four (in spots five) layers: two (occasionally three) middle layers, the epidermis, and a hypodermal layer between the epidermis and outer middle layer (Figs. 24, 25). The two middle layers differentiate as a bilayered endothecium, the cells developing secondary thickenings ranging from spiral or annular to occasionally reticulate patterns (Fig. 25). Secondary thickenings do not develop in any cells of the septa separating the two microsporangia of each theca. The middle layers in the region of the incipient apical pore are destroyed prior to the formation of endothecial thickenings in these layers. The septa that once separated the two microsporangia per theca are ruptured just prior to dehiscence. Therefore, the base of the dehiscent anther is bilocular and both of these locules are confluent with the single distal locule. The distal anther locule is confluent with the stomium of apical pore.

Stamen vasculature—Shortly after the stamen primordia arise, a procambial strand differentiates in each primordium. At around the time of sporogenous tissue differentiation, a single series of sieve elements differentiates throughout the length of the procambium and prior to any tracheary elements. Early vascular differentiation proceeds acropetally in the stamen with the differentiation of a second longitudinal series of sieve elements. Concurrent with or shortly after the second series of sieve elements differentiates in the stamen bundle, a single longitudinal series of protoxylem elements with annular thickenings differentiates. At the time the microsporocytes have entered prophase of meiosis I, four to six sieve elements and about three tracheary elements may be distinguished in a transverse section of the connective. At maturity, each stamen possesses a single amphicribral vascular bundle (Fig. 24), which ends blindly in the distal portion of the connective. Spatially, the transition from the collateral arrangement in the receptacle to the amphicribral arrangement of the vascular tissue in the staminal bundle occurs in the base of the filament.

Microspore and microgametophyte development—Microsporogenesis is successive with the formation of both decussate and isobilateral tetrads in the same anther locule (Fig. 23). These microspores separate and begin to take on shape and wall characteristics of mature pollen as the fibrous endothecial thickenings develop. Pollen is shed as single binucleate grains (Figs. 19, 25).

Gynoecium—The superior trilocular ovary is composed of three united carpels. Each loculus contains six to eight hemianatropous to slightly campylotropous ovules (Figs. 26, 27, 29). Within each locule, the ovules are arranged in two longitudinal series on alternating submarginal placentae (Fig. 26). Within the context of the syncarpous ovary, the placentation may be described as axile. The three-lobed style is relatively long and slender with a hollow canal (Fig. 28) and is capped by a three-lobed papillate stigma (Fig. 15).

Carpel organogenesis and development—The gynoecium initiates as a whorl of three mounds alternating with the inner whorl of stamen primordia (Figs. 6, 7). Carpel initiation occurs at about the time that the outer whorl stamen primordia have become slightly bilobed. Carpel fusion is soon evident as a result of zonal growth from the floral apex between carpel margins. The gynoecium is soon represented by a trilobed ring (Figs. 7, 8). The gynoecial septa gradually rise from the gynoecium base (Fig. 8), and the synascidiate nature of the gynoecium base becomes apparent. The apicalmost portion of the mature ovary appears unilocular due the fact that the ovary locules are confluent with the stylar canal (compare Figs. 26 and 27).

Ovule, megaspore, and megagametophyte development—Prior to integument initiation, an archesporial cell differentiates (Fig. 30). Then the inner integument is initiated in the dermal layer. By the time the microspore dyads form, the archesporial cell of the ovule divides to produce a single parietal cell and the megasporocyte (Fig. 31). Initiation of the outer integument follows and is also dermal in origin (Fig. 31). The megasporocyte enlarges and begins meiosis at about the time that meiosis is completed in the anthers. The expanding meiotic megasporocyte and resultant megaspores eventually crush the parietal cell.

A linear tetrad is formed. The leading edges of the inner and outer integuments have grown to roughly the same level near the apex of the nucellus (Fig. 32). The chalazal megaspore is functional and the three micropylar megaspores degenerate (Fig. 33). Embryo sac development is of the Polygonum type (sensu Maheshwari, 1950). The three antipodals degenerate and the two polar nuclei fuse to form a secondary fusion nucleus (Figs. 34–37). The mature embryo sac consists of the egg, two synergids with filiform apparatus, and a central cell with a fusion nucleus (Figs. 35–37). Growth of the outer integument (and, to a lesser degree, the inner integument) is substantially greater on the dorsal side farthest from the placenta. At maturity, the micropylar path is formed by both integuments and jogs slightly between the endostome and exostome (Fig. 29).

Gynoecial vasculature—Each of the three carpels has three vascular bundles, one dorsal and two ventrals. As described below for the floral vasculature as a whole, the dorsal carpellary bundles originate from the inner vascular system of the receptacle and depart radially into the carpels. The six ventral bundles originate in the receptacle from the outer vascular system and migrate to the center of the floral axis prior to entering the carpels. The two neighboring ventral bundles from adjacent carpels partially unite in the base of the ovary (Figs. 39, 40), and the resulting bundles appear as double bundles. As such, the ovary contains three ventral "double" bundles for most of its length. These double bundles yield single traces to each of the six to eight ovules per locule (Figs. 26, 41). Each half of the double ventral bundle supplies the ovules of the

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microspore tetrads; remnants of periplasmodium indicated by arrow. **24.** Basal portion of late-stage anther, just before development of endothecial thickenings. Pre-pollen one-celled, with remnants of periplasmodium. Lacunae (L) in basal half of connective only. **25.** Anther locule at dehiscence, photographed under partially polarized light. Endothecial thickenings birefringent and anther wall four-layered. **26.** Nearly mature ovary sectioned at mid-level; two ovules have been sectioned in each locule. Note double ventral bundles (V) and ovular trace (OT). **27.** Same ovary as in Fig. 17 sectioned in distal portion of ovary. **28.** Style from gynoecium in Figs. 26 and 27 sectioned at mid-level. **29.** Longitudinal section of mature ovule showing integuments and embryo sac cavity.
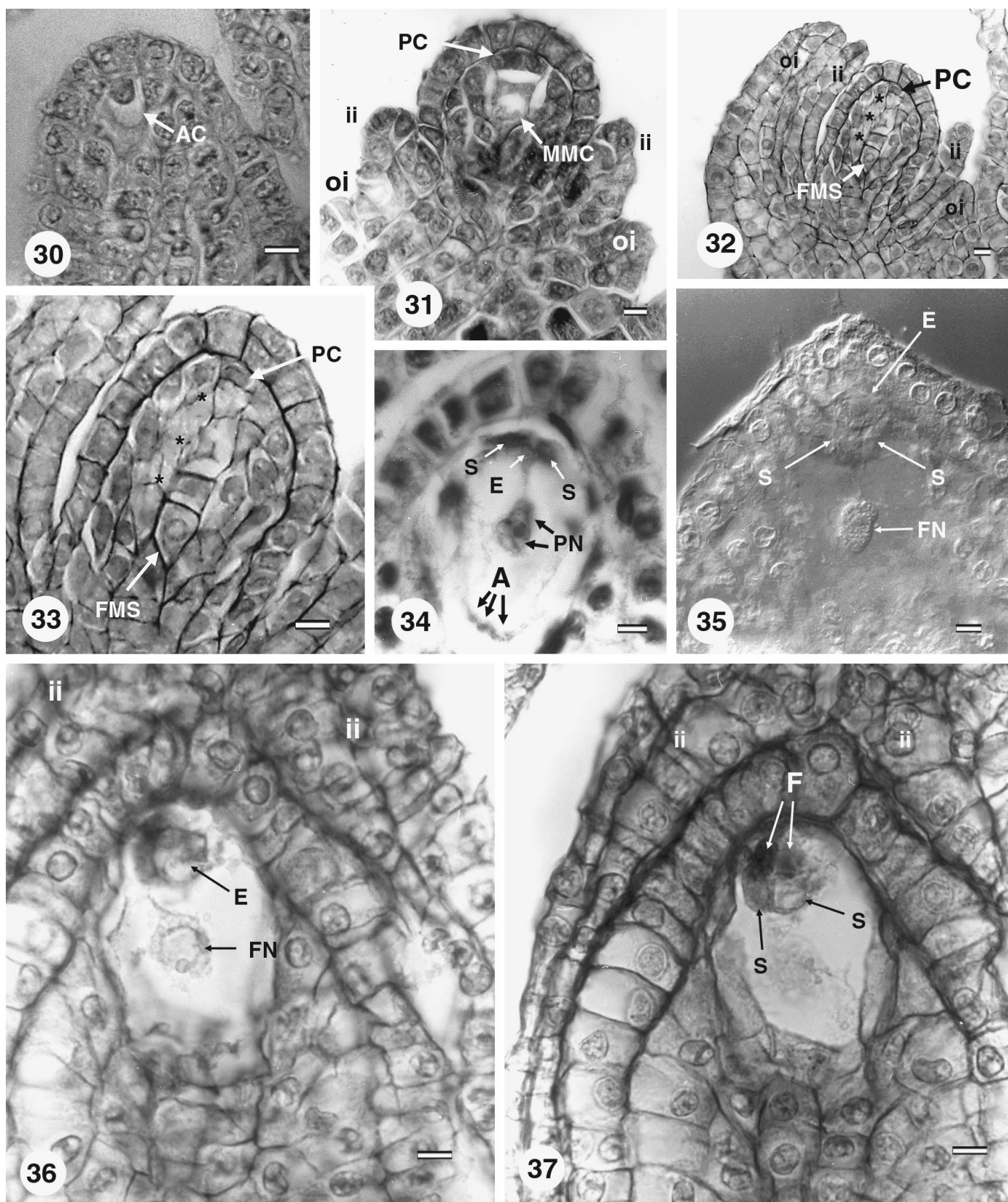
Figs. 30–37. Megagametophyte (embryo sac) development (brightfield micrographs except for Fig. 35, which is a micrograph taken using Differential Interference Contrast—DIC—optics). Micropylar end of nucellus at top in each figure. Scale bars = 10 μm. **30.** Young ovule with archesporial cell. **31.** Ovule with megasporocyte, parietal cell, and both inner and outer integuments initiated. **32.** Linear megaspore tetrad with functional chalazzal megaspore and three degenerating micropylar megapores. **33.** Close-up of Fig. 32. Parietal cell shows signs of being crushed. **34.** Eight-nucleate embryo sac, showing antipodals degenerating and polar nuclei just prior to fusion. **35.** DIC image of mature megagametophyte. **36, 37.** Mature megagametophyte in two different sections to show all nuclei.
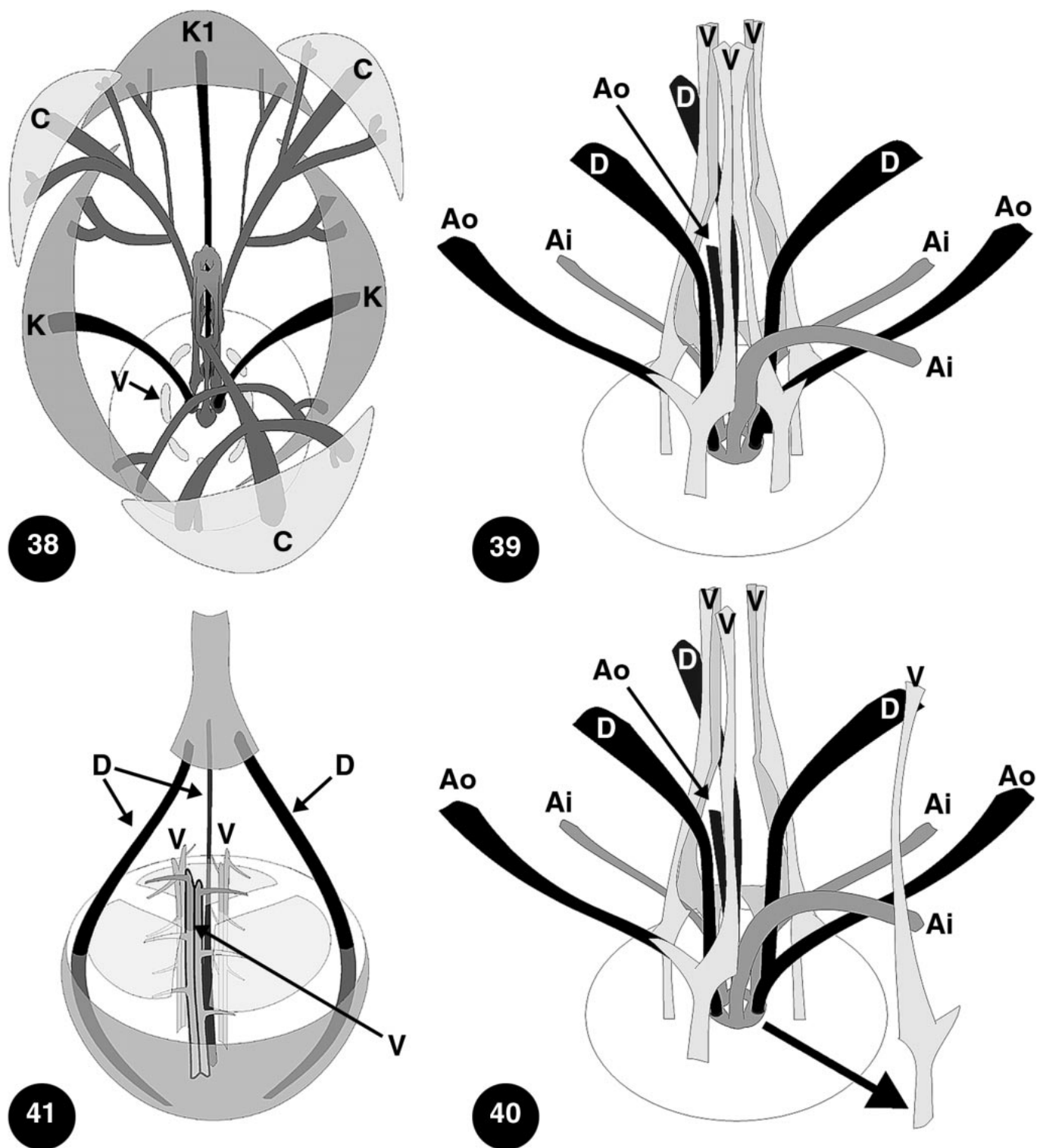
Figs. 38–41.   Floral vascular course. **38.** Course of the vascular traces to the perianth (that to the stamens and gynoecium not shown). Outer ring of bundles (V) shown in gray and indicated in this figure only at the base so as not to obscure the inner system. **39.** Vascular traces to the outer whorl and inner whorl stamens (continued from Fig. 38). Vasculature of outer system shown throughout. **40.** Same diagram as Fig. 39, but with one ventral carpellary trace removed in order to show branching pattern of bundles supplying the stamen and dorsal carpellary traces. **41.** Gynoecial vasculature, with transparent overlay of a portion of the gynoecium to portray spatial relationships of vasculature to carpels and locules (continued from Figs. 39 and 40).

carpel with which that half bundle was associated before it united with its neighbor. These ventral bundles end in the top of the ovary just after the last ovular trace of each loculus departs (Figs. 27, 41). Each ovular trace ends in the funiculus, and the integuments are not vascularized at embryo sac maturity. With the ventral bundles ending in the apex of the ovary, the dorsal carpellary bundles follow the narrowing of the ovary and enter the style where they continue acropetally through the style as three distinct bundles (Fig. 28) before ending blindly in the base of the stigma.

Bundles of the ovary are collateral and mature acropetally. As in all other floral organs of *D. thyrsiflora* examined, protophloem maturation proceeds slightly ahead of protoxylem maturation, and a single longitudinal series of sieve elements in each procambial strand is first to mature. A strand of protoxylem then matures, and this may be concurrent with or precede slightly the maturation of a second strand of sieve elements. By the time the archesporial cell of the ovule is discernible (i.e., during formation of the periplasmodium and prior to the first meiotic division of the microsporocytes in the anthers), the first mature sieve and tracheary elements are evident in the dorsal carpellary bundles. Vascular maturation in the ventral bundles does not occur until embryo sac maturity and does not occur in the funiculus until after fertilization.

Course of the floral vasculature—The longitudinal course of the bundles of the floral vascular system (Figs. 38–41) is described below as an acropetal sequence.

Relatively low in the pedicel, both an inner and an outer system of vasculature is discernible. The inner system exists at this level as a ring or nearly solid cylinder from which will depart the traces to the sepals, petals, stamens, as well as the three dorsal carpellary bundles. The outer ring consists of bundles that variously anastomose and branch during their longitudinal course through the pedicel and receptacle and eventually organize into the six ventral carpellary bundles. Upon entering the receptacle, the inner ring of vasculature is fragmented when the three median sepal traces depart from it. The separate bundles remaining in the inner system continue their acropetal course and anastomose again to form a closed or nearly closed ring. Then the ring is fragmented as the three primarily petal-bound traces depart from it. As these three traces pass through the outer system, minor branches from the outer system may anastomose with them. Also at this point, each trace branches into three bundles, one that maintains a direct radial course to the petals and two laterals that diverge to become the lateral traces of two adjacent sepals. Each of these lateral sepal traces bifurcate at least once upon entering a sepal. At their departure from the receptacle, the two lower sepals (the second and third initiated) are five traced, consisting of the single primary or midvein bundle and two lateral bundles on each side. The upper sepal is five to seven traced, with any additional traces derived from an additional bifurcation of each lateral trace. Each sepal lateral trace continues to bifurcate through its course in the sepal.

Sharing its origin with the lateral sepal traces, the third branch described above maintains a direct course for each petal. Prior to entry into the petal from the receptacle, this bundle branches into three bundles, such that each petal is essentially three traced when it departs from the receptacle. As the lateral traces enter the petal, the first of many bifurcations occurs, such that each petal at maturity contains many veins.

The separate bundles remaining in the inner system after the departure of the sepal and petal traces continue their acropetal course and anastomose to form a closed ring. This ring becomes discontinuous as six discrete bundles organize. Those bundles alternating with the petals quickly bifurcate, giving rise to the traces of the three stamens of the outer whorl and the incipient dorsal carpellary bundles. The three bundles opposite the petal traces then depart as traces to the three inner whorl stamens. At this point, the bundles of the outer vascular system that began their course in the pedicel briefly anastomose with the departing staminal bundles, organize into six discrete bundles, and enter the ovary as the ventral carpellary bundles. Concurrent with the migration of the ventral carpel traces from the outer ring to the center of the floral axis, the dorsal carpellary traces depart from the receptacle and enter the carpels.

DISCUSSION

Gynoecium—Embryo sac development in *Dichorisandra thyrsiflora* is of the monosporic Polygonum type. The Polygonum type is also known in the majority of Commelinaceae for which data are available (Maheshwari and Singh, 1934; Murthy, 1938; Maheshwari and Baldev, 1958; Chikkannaiah, 1962, 1963, 1964; Chikkannaiah and Hemaraddi, 1979; Grootjen and Bouman, 1981; Grootjen, 1983; and others as cited in Johri, Ambegaokar, and Srivastava, 1992). The Allium type (Davis, 1966) and Adoxa type (McCollum, 1939; Stevenson and Owens, 1978) have also been reported in the family. Despite this variation in modes of development, the features shared by most Commelinaceae investigated thus far are early antipodal degeneration (except in *Tinantia fugax* [= *T. erecta*]; Chikkannaiah, 1962, 1964–1965) and fusion of the polar nuclei prior to fertilization. This is indicative of a master control over final megagametophyte structure that is to some degree independent of the number of megaspores contributing to its formation. Attributing taxonomic significance to the variation between monosporic, bisporic, and tetrasporic types known within the family should be cautioned. The findings of Hjelmqvist and Grazi (1965) and Dharamadhaj and Prakash (1978) in certain non-commelinaceous taxa indicate that environmental factors such as temperature may influence modes of development.

Androecium—The majority of features of stamen, anther, and microspore development in *D. thyrsiflora* are generally concordant with previous observations for the Commelinaceae. These features are the periplasmodial tapetum, successive microsporogenesis to yield both isobilateral and decussate tetrads, and the two-celled (three-celled in *Floscopa scandens*; Chikkannaiah, 1962) pollen grains at dispersal (as reviewed by Johri, Ambegaokar, and Srivastava, 1992). However, the current and previous observations on anther structure in *Dichorisandra* have revealed two interesting points of variation within the genus. First, the number of pores per anther varies from one to two. Examples of one-pored anthers include *D. thyrsiflora* (this article), *D. hexandra,* and *D. ulei* (C.R. Hardy, personal observation), whereas examples of two-pored anthers (one per theca) include *D. speciosa* (Endress, 1996, his Fig. 7). Secondly, in a survey of endothecial thickenings among monocots with poricidal anthers, Gerenday and French (1988) found that only half of the six *Dichorisandra* species they surveyed, including *D. thyrsiflora,* had fibrous endothecial

thickenings. These findings have identified potential phylogenetically informative variations within *Dichorisandra.*

The major contribution of our findings on the anther wall in *Dichorisandra thyrsiflora* has been the recognition of an additional type of anther wall development in the Commelinaceae. At anther dehiscence, the anther wall consists of four (in spots five) cell layers: the two middle endothecial layers, a hypodermal layer, and the epidermis (Fig. 25). With the exception of the reduced type in *Gibasis* (Stevenson and Owens, 1978), the monocotyledonous type of anther wall development, with a degenerative middle layer, has been reported in *Tradescantia spathacea* (= *Rhoeo spathacea*; Nanda and Gupta, 1977) and is suspected in many other commelinaceous species for which only the number of wall layers has been reported (e.g., Maheshwari and Singh, 1934; Murthy, 1938; Maheshwari and Baldev, 1958; Chikkannaiah, 1963, 1964). The defining point of the monocotyledonous-type anther wall is that it is the inner secondary parietal layer that divides periclinally once to yield a middle layer and the tapetum. In *Dichorisandra thyrsiflora,* the inner cell layer produced by the division that would otherwise yield the middle and tapetal layers under the monocotyledonous mode of development goes through an additional periclinal division such that, in total, two middle layers are formed (Fig. 22). As such, development of the anther wall in *D. thyrsiflora* should be considered as developmentally derived from the monocotyledonous type. Furthermore, the two middle layers, rather than the hypodermal layer, in *D. thyrsiflora* develop secondary endothecial thickenings. Davis (1966) describes how the middle layers of most taxa are usually crushed or become disorganized under the strain of the multiplying sporogenous tissue and expanding anther locules. In *Dichorisandra thyrsiflora,* the transversely elongated appearance of the cells of these two middle layers at dehiscence indicates that they experienced a considerable degree of stretching and/or compression under the strain induced by an expanding anther locule (Figs. 24, 25). It may be that the development of endothecial thickenings in these layers is a major factor in their persistence through anthesis.

Several modifications in androecia are plausible evolutionary responses to a shift to buzz pollination, a system in which there is an increase in the direct manipulation (in the form of grasping and vibrating) of the anthers by medium to large bees to effect the removal of pollen from the anthers (Michener, 1962; Buchmann and Hurley, 1978; Roubik, 1989). The morphological, anatomical, and histological characteristics common to many buzz-pollinated androecia have been summarized by many authors (e.g., Vogel, 1978; Buchmann, 1983; Endress, 1994, 1996; Bernhardt, 1996). Aspects of the buzz pollination syndrome, as it is found in *Dichorisandra* and many other angiosperm taxa, include stamens with short, stout filaments and long, basifixed, poricidal anthers. The extent to which the relatively thicker anther walls in *D. thyrsiflora* may be correlated with buzz pollination in the Commelinaceae can only be determined by future comparative studies. From a biomechanical perspective, however, such a correlation might be predicted, as the proliferation, persistence, and secondary thickening of the two middle layers in *D. thyrsiflora* may provide structural reinforcement of the thecal walls.

Outside of the Commelinaceae, supernumerary endothecial layers and/or the proliferation and persistence of middle layers in the anthers of buzz-pollinated flowers is not uncommon. In the Gentianaceae, for example, Sankara Rao and Chinnappa (1982) found three persistent middle layers in the porandrous buzz-pollinated genus *Exacum.* Sankara Rao and Chinnappa found only a single ephemeral middle layer in the other gentianaceous genera they investigated, all of which possess longitudinally dehiscent anthers and are not buzz-pollinated. Additional examples are found in Melastomataceae, where two to three middle layers with thickened walls have been described from the dehiscent anthers of certain porandrous, buzz-pollinated taxa (e.g., Subramanyam, 1948; Renner, 1990, her Fig. 2). In contrast, the longitudinally dehiscent anthers of the melastomataceous genus *Memecylon* have considerably thinner walls, forming and possessing just one middle layer, if any (Subramanyam, 1942; Venkatesh, 1955). In the Leguminosae, a variety of the porandrous taxa in the subtribe Cassiinae have been characterized as forming relatively massive anther walls consisting of a nonfibrous hypodermis and up to seven middle layers (e.g., Venkatesh, 1957; Matthews and Maclachlan, 1929). In some (but not all) of the investigated species of Cassiinae, the hypodermis and one to three middle layers persist and become sclerified, thereby adding considerably to the rigidity of the anther wall. In contrast, the anther walls of certain other, longitudinally dehiscent, members of the Leguminosae have been shown to possess just an epidermal and endothecial layer at dehiscence, the middle layer(s) being ephemeral (e.g., Buss, Galen, and Lersten, 1969; Tian and Shen, 1991).

Among monocotyledonous groups, many porandrous and buzz-pollinated Rapateaceae have been described by Tiemann (1985) as possessing anther walls with one to three fibrous endothecial layers and one to four (mostly persistent) middle layers in addition to the epidermis and tapetum. Although, to our knowledge, buzz pollination has never been observed for the porandrous *Mayaca* (Mayacaceae), the wall of the young anthers in at least one species, *M. fluviatilis,* consists of an exothecium, hypodermis, and one or two persistent middle layers (Stevenson, 1983; Venturelli and Bouman, 1986). Among those families with which Rapateaceae and Mayacaceae are traditionally allied (Cronquist, 1981; Takhtajan, 1997; but also see Tiemann, 1985; Stevenson, 1998), Eriocaulaceae and Xyridaceae possess longitudinally dehiscent anthers and anther walls with, at most, a single ephemeral middle layer (e.g., Ramaswamy and Arekal, 1982; Tiemann, 1985; Rudall and Sajo, 1999). Although there has been one report of buzz pollination for a single Brazilian species of *Xyris* (S. Renner in Kral, 1998), the primary system of pollination in Eriocaulaceae and Xyridaceae does not appear to be buzz pollination (Stützel, 1998; Kral, 1998).

Several taxonomic groups in which this correlation does not occur include the porandrous, buzz-pollinated genera *Dillenia* and *Hibbertia* (Dilleniaceae) (Bernhardt, 1996; Endress, 1997), the anthers of which lack any extra wall layers (Sastri, 1958). Although the correlation in certain Melastomataceae was noted above, the buzz-pollinated melastomataceous *Rhexia virginica* (Larson, 1999) possesses poricidal anthers with walls consisting only of an epidermis and a hypodermis without fibrous thickenings (Eyde and Teeri, 1967). The wall of the longitudinally dehiscent anthers of the buzz-pollinated flowers in *Trichodesma* (Boraginaceae) (Ahmed et al., 1995) consists only of an epidermis, fibrous endothecium, and a single ephemeral middle layer in addition to the tapetum (Tasneem, 1967; Khaleel, 1977). In these latter taxa, if any mechanical strengthening in response to buzz pollination has occurred, it has been accomplished through means other than increasing the number of anther wall layers.

The survey presented above, although far from exhaustive, indicates that a correlation between buzz pollination and comparatively thick anther walls, while occurring in certain taxonomic groups, does not hold for a broad array of buzz-pollinated taxa. However, the current understanding of the evolutionary influence of buzz pollination on the developmental anatomy and histology of the anther wall is far from complete. This, in part, is due to the poor degree to which definitive data on pollination and anther anatomy/histology overlap taxonomically. Furthermore, in the embryological/anatomical literature, investigators have not always distinguished between the number of anther wall layers that are formed and the number of those layers that persist at the time of anther dehiscence. For now, the lack of complete data on the pollination biology and the anatomy and histology of the dehiscent anther in many taxonomic groups will continue to confound a thorough consideration into the functional aspects of the anther wall during pollination.

Floral vasculature—Floral vasculature in the Commelinaceae has been studied previously by Murty, Saxena, and Singh (1974), Rohweder (1963, 1969), and Stevenson and Owens (1978). Details as to the entire course of the floral vasculature and the relative receptacular connections of the floral organ traces in Commelinaceae were first provided for *Gibasis geniculata* (Rohweder, 1963) and *G. venustula* (Stevenson and Owens, 1978). The majority of information to be extracted from Murty, Saxena, and Singh (1974) concerns only the number of traces received by each of the floral organs in seven genera (nine including segregate genera) and 14 species.

As with *Gibasis,* the major feature of the floral vasculature in *D. thyrsiflora* is its organization into an outer and inner system (or ring) in the pedicel. The outer ring in *Gibasis* and *D. thyrsiflora* is comprised only of the incipient ventral carpellary bundles. Although, as reported by Stevenson and Owens (1978), there was some ambiguity as to the composition of the outer ring in *Gibasis venustula,* a reinvestigation of the same material has found that the outer ring in this species is, in fact, comprised of only the ventral carpellary traces (C.R. Hardy and D.W. Stevenson, unpublished data). The only other taxon in the family for which two rings of bundles in the pedicel have been reported is *Murdannia spirata* (Murty et al., 1974). However, in *M. spirata* it is reported that the outer ring is comprised only of sepalar traces. If confirmed, this discrepancy between the old world *Murdannia* (tribe Commelineae) and the new world *Dichorisandra* and *Gibasis* (tribe Tradescantieae, sensu Faden and Hunt, 1991) in floral vascular organization warrants an expansion of such investigations to additional taxa in order to evaluate its potential as a taxonomically-informative character. Murty et al. (1974) did not observe a two-system organization in the other species of Commelinaceae they surveyed probably because they did not investigate the vasculature below the receptacle.

The course of the floral vasculature in *Dichorisandra thyrsiflora* is fundamentally the same as that reported for *Gibasis venustula* by Stevenson and Owens (1978) and *Gibasis geniculata* by Rohweder (1963). Two aspects of the vasculature in *D. thyrsiflora* that warrant discussion are the multitraced sepals and the absence of ''lateral'' carpellary bundles.

Firstly, the lateral carpellary bundles (i.e., those supernumerary to the ventral and dorsal bundles) formed in *Gibasis* as branches from the ventral bundles just prior to their entry into the ovary are absent in *D. thyrsiflora.* Supernumerary carpel bundles have also been reported for *Tinantia fugax* (= *T. erecta*), *Commelina attenuata,* and *C. paludosa,* (Murty, Saxena, and Singh, 1974), although their homology with those of *Gibasis* is questionable. In *T. fugax, C. attenuata,* and *C. paludosa,* the extra bundles provide the ovules with vascular traces supplementary to those of the ventral bundles. The increased vasculature provided by the extra bundles in these particular taxa may be correlated with ovary, ovule, and/or seed size, as more massive ovaries, ovules, or seeds may require additional vasculature to supplement or reallocate vascular supply. Alternatively, the presence or absence of lateral carpellary bundles in the family may be determined more by phylogenetic rather than by functional constraints. At present, there is not enough information on the distribution of the character of lateral presence within the family to make such inferences.

With respect to the number of sepal traces, the sepals of *Gibasis* (as with *Cyanotis axillaris, C. cristatus,* and *Tradescantia zebrina*; Murty, Saxena, and Singh, 1974) are one traced and those of *D. thyrsiflora* receive essentially three through the addition of lateral traces. Although lateral sepal traces have been reported to be of common occurrence in the Commelinaceae (Murty, Saxena, and Singh, 1974), the contribution of the current study of *Dichorisandra thyrsiflora* has been in demonstrating the precise origins of the lateral sepal traces, and how they differ from the laterals received by members of the corolla. As diagrammed in Fig. 38, the middle trace and lateral traces of each sepal in *D. thyrsiflora* depart at different levels from the floral vascular stele. The lateral sepal traces originate as lateral branches from those bundles that initially depart from the inner system as petal traces, i.e., the lateral sepal traces have their most recent receptacular connections with bundles other than the median sepal traces that depart earlier. In contrast, the lateral traces of the petals share a most recent connection with the middle trace of the same petal.

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