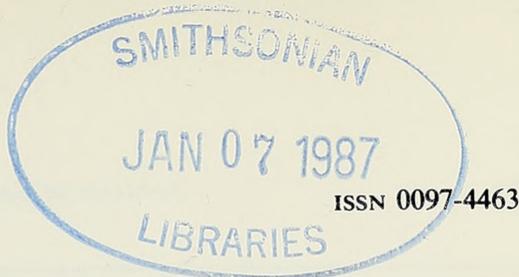


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## FLORAL MORPHOLOGY AND VASCULAR ANATOMY OF *AMIANTHIUM MUSCAETOXICUM* (WALTER) A. GRAY (LILIACEAE-VERATREAE) WITH NOTES ON DISTRIBUTION AND TAXONOMY

FREDERICK H. UTECH

### ABSTRACT

Presentation of pedicel to stigma vasculature of the monotypic *Amianthium muscaetoxicum* as a Veratrean example documents the perigyny, spiral insertion of floral parts and an apocarpous gynoecium which are encountered. Total floral vascularization is derived from three lower pedicel bundles. A spiral series of divisions and fusions in the upper pedicel produces three compound outer tepal and three inner tepal bundles. From the former, outer tepal medians, tepal laterals, stamen and dorsal bundles result, while from the latter, inner tepal medians, tepal laterals and stamen bundles result. Due to perigyny, their formation is above that at which the ventral and ovular supplies are established. The ventral supply is spirally derived from continuing bundles following the formation of the compound inner tepal bundles. Within each septal arm, a compound lateral is associated with a compound ventral and both undergo radial divisions. Opposing lateral and ventral products fuse as the perigynous condition ends and the three carpels are freed. Each carpel has two simple ventrals, two laterals and a dorsal in the upper perigynous zone and two fusion ventrals and a dorsal in the upper freed zone. Neither tepal glands nor nectaries occur in this species. Epidermal cells characterized by homogenous tannins occur in the pedicel, receptacle wall, abaxial tepal surfaces, filaments and freed carpels. Raphides commonly occur in cells along the lower margins of the inner tepals.

### INTRODUCTION

*Amianthium muscaetoxicum* (Walter) A. Gray is a monotypic species of eastern North America with centers of distribution in both the Ozark-

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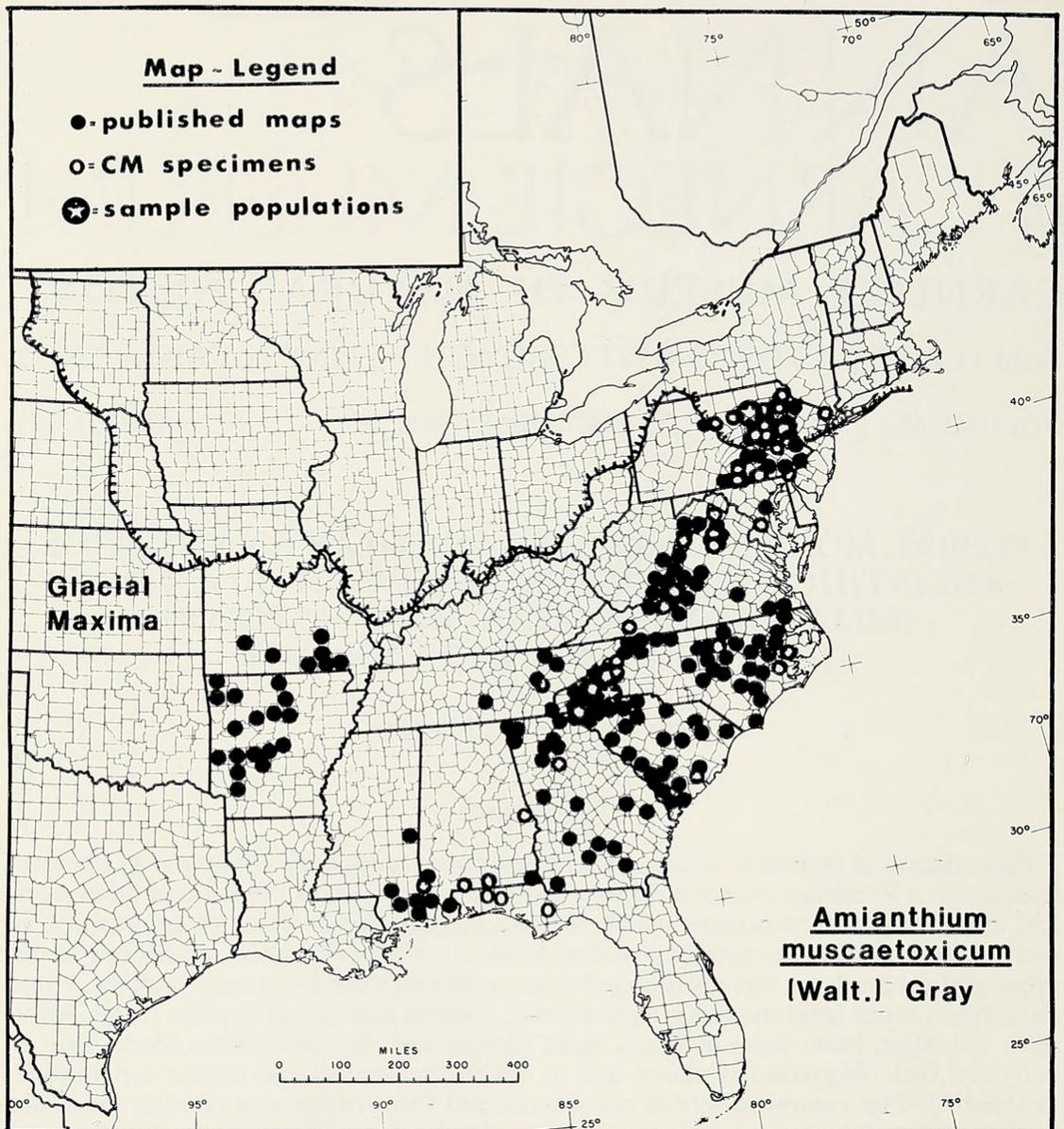


Fig. 1.—Distribution of *Amianthium muscaetoxicum* in eastern United States based on published maps (Steyermark, 1963; Radford et al., 1968; Johnson, 1969; Smith, 1978; Wherry et al., 1979) and collections at Carnegie Museum of Natural History (open circles). Johnson (1969) surveyed 46 herbaria in his southeastern United States treatment of the Liliaceae. Sampled populations are indicated by circled stars.

ian and Appalachian regions (Fig. 1). It occurs in mesic to dry wooded slopes and coastal plain savannas and pinelands. Familial and subfamilial names associated with *A. muscaetoxicum* have changed during the last century, but the tribal association with *Melanthium*, *Schoenocaulon*, *Stenanthium*, *Veratrum* and *Zigadenus* “sensu lato” (including *Toxicoscordion*, *Anticela*, *Tracyanthus* and *Oceanoros*) has remained. Bentham and Hooker (1883) included these six genera in the tribe

Veratreae, as did Engler (1889), Krause (1930), Melchior (1964), Thorne (1968), Takhtajan (1969), and Hutchinson (1934, 1959, 1973). Within this tribal grouping, two lines—the *Veratrum-Melanthium* and the *Zigadenus* lines—are generally recognized (Anderson, 1940; Preece, 1956; Zimmerman, 1958; Kupchan et al., 1961; Ambrose, 1975, 1980; Sterling, 1982). *Amianthium* and *Stenanthium* are generally placed somewhere between these two evolutionary lines. Engler (1889) initiated the association of the Veratreae with the subfamily Melanthioideae. This subfamily has been twice segregated as a separate family, the Melanthiaceae (Gates, 1918; Small, 1933; Dahlgren, 1980; Dahlgren and Clifford, 1982; Dahlgren and Rasmussen, 1983; Dahlgren et al., 1985) and the Colchicaceae (Baker, 1879).

Genera in the other tribes of the Englerian Melanthioideae share separate styles and septicial capsules with the genera in the Veratreae, though the latter possesses unusual extrorse anthers with valvular dehiscence that open into peltate discs (Krause, 1930; Zimmerman, 1958; Kupchan et al., 1961) and usually many bitegmic, basitropic and campylotropous ovules per carpel (Sterling, 1982), except for *Amianthium* which has two, rarely four.

*Amianthium* of Asa Gray (1837) is a conserved generic name (Farr et al., 1979; Voss, 1983) and its monotypic species, *A. muscaetoxicum* (Walter) A. Gray (1837), has gone under various names since it was first described by Walter in 1788 as *Melanthium muscaetoxicum*. Later synonyms include: *Melanthium laetum* Solander in Aiton (1789), *Melanthium myoctonum* J. F. Gmelin (1796), *Helonias erythrosperma* Michaux (1803), *Helonias laeta* (Solander in Aiton) Kew-Gawler (Curtis, 1805), *Amiantanthus muscaetoxicum* (Walter) Kunth (1843), *Zigadenus muscaetoxicus* (Walter) Regel (1883), and *Chrosperma muscaetoxicum* (Walter) Kuntze (1891). Excluded species of *Amianthium* and their current status include: *A. nuttallii* A. Gray var. alpha (1837) (*Zigadenus nuttallii* A. Gray ex S. Watson), *A. nuttallii* A. Gray var. beta (1837) (*Z. paniculatus* (Nutt.) S. Watson), *A. angustifolium* A. Gray (1837) (*Z. densus* (Desr.) Fernald), *A. leimanthoides* A. Gray (1837) (*Z. leimanthoides* A. Gray), and *A. texanum* (Bush) Gates (1918) (*Z. leimanthoides* A. Gray).

Considerable biological information is implied in this species binomial. *Amianthium* is derived from the Greek *amianthos* for “unspotted” and *anthos* for “flower,” an allusion to a major generic character, that is the lack of glands or nectaries on the perianth. The specific name, *muscaetoxicum*, translates literally as “fly poison.” In 1883, a note in *Gardeners' Chronicle* “stated that the root, when bruised and mixed with honey, acts as a poison to flies.” While the species is commonly known as “fly poison,” it has also been known as “crow poison” and “swagger grass” (Muenscher, 1939, 1960). Several poi-

sonous alkaloids are associated with the leaves and underground bulbs of the species and are reported to cause death in cattle and sheep (Pammel, 1911; Marsh et al., 1918; Muenscher, 1939, 1960; Kingsbury, 1964). Amianthine, a steroidal or modified steroidal alkaloid with a  $C_{27}H_{41}O_2N$  formula, has been described from the roots and leaves of *A. muscaetoxicum* as well as jervine and two unidentified ester alkaloids (Neuss, 1953). The latter alkaloids were shown to be responsible for the high toxicity of the species (Neuss, 1953). Although numerous and highly poisonous alkaloids commonly occur throughout the tribe Veratreae, amianthine has only been reported in *Amianthium* (Kupchan et al., 1961; Willaman and Schubert, 1961; Hegnauer, 1963).

Two meiotic chromosome counts of  $n = 16$  have been reported for *A. muscaetoxicum*: Ambrose (1975) from Bear Creek, Pennsylvania and Preece (1956) from Big Laurel Gap, Yancey County, North Carolina. Excluding various polyploid multiples, *Melanthium*, *Veratrum* and *Zigadenus* (= *Zygadenus*; Preece, 1956) all share  $n = 16$  (Fedorov, 1969; Moore, 1973; Goldblatt, 1981). It is quite apparent that  $x = 8$  is the basic number unifying the Veratreae.

In focusing on both the floral morphology and vascular anatomy of *A. muscaetoxicum* a comparative model of a Veratreaean gynoecium will be established in this paper. Similar treatments for the other tribal members of the Veratreae, such as *Melanthium*, *Stenanthium*, *Veratrum* and *Zigadenus*, are in preparation and will continue the studies of Buxbaum (1925, 1927), Anderson (1940), El-Hamidi (1952), Ambrose (1975, 1980) and Sterling (1982) on the vascularization of the Veratreaean carpel.

#### MATERIALS AND METHODS

Flowering and fruiting inflorescences of *Amianthium muscaetoxicum* were collected from two different populations—Pennsylvania: Clinton County, Mt. Tableland, ca. 4.5 mi E of Sinnemahoning, 20 July 1979, *Utech* 79-241 (CM), and North Carolina: Macon County, ca. 3.5 mi N of Highlands, near Whiteside Mt., Nantahala National Forest, 28 July 1982, *Utech and Ohara* 82-270 (CM). The collected materials were fixed in acetic-ethanol (1:3) for 10 h with subsequent storage in 70% ethanol. Standardized paraffin sectioning (14–16 microns) and staining (saffarin-methylene blue) techniques (Johansen, 1940; Sass, 1958) were used on samples (10 flowers and 10 young fruits of varying ages) from both populations. As an additional check on these serial sections, whole flowers and fruits were cleared and stained in a NaOH-1% fuchsin mixture (Fuchs, 1963).

Composite photomicrographs (Figs. 3–5, 7–8, 10) present the vascular floral anatomy and morphology of *A. muscaetoxicum*, whereas Figs. 6 and 9 are summary line diagrams for the species. No teleological implications are intended in the descriptive ascent and departure of the various floral bundles which are letter-coded for ease in comparison. This coding parallels that used in our previous liliaceous studies (*Utech*, 1978a–1978e, 1979a, 1979b, 1982, 1984; *Utech and Kawano*, 1975, 1976, 1980, 1981).

#### OBSERVATIONS

*Amianthium muscaetoxicum* is a glabrous, subscapose, perennial herb from a thick bulb (Fig. 2). At anthesis, the linear basal leaves are

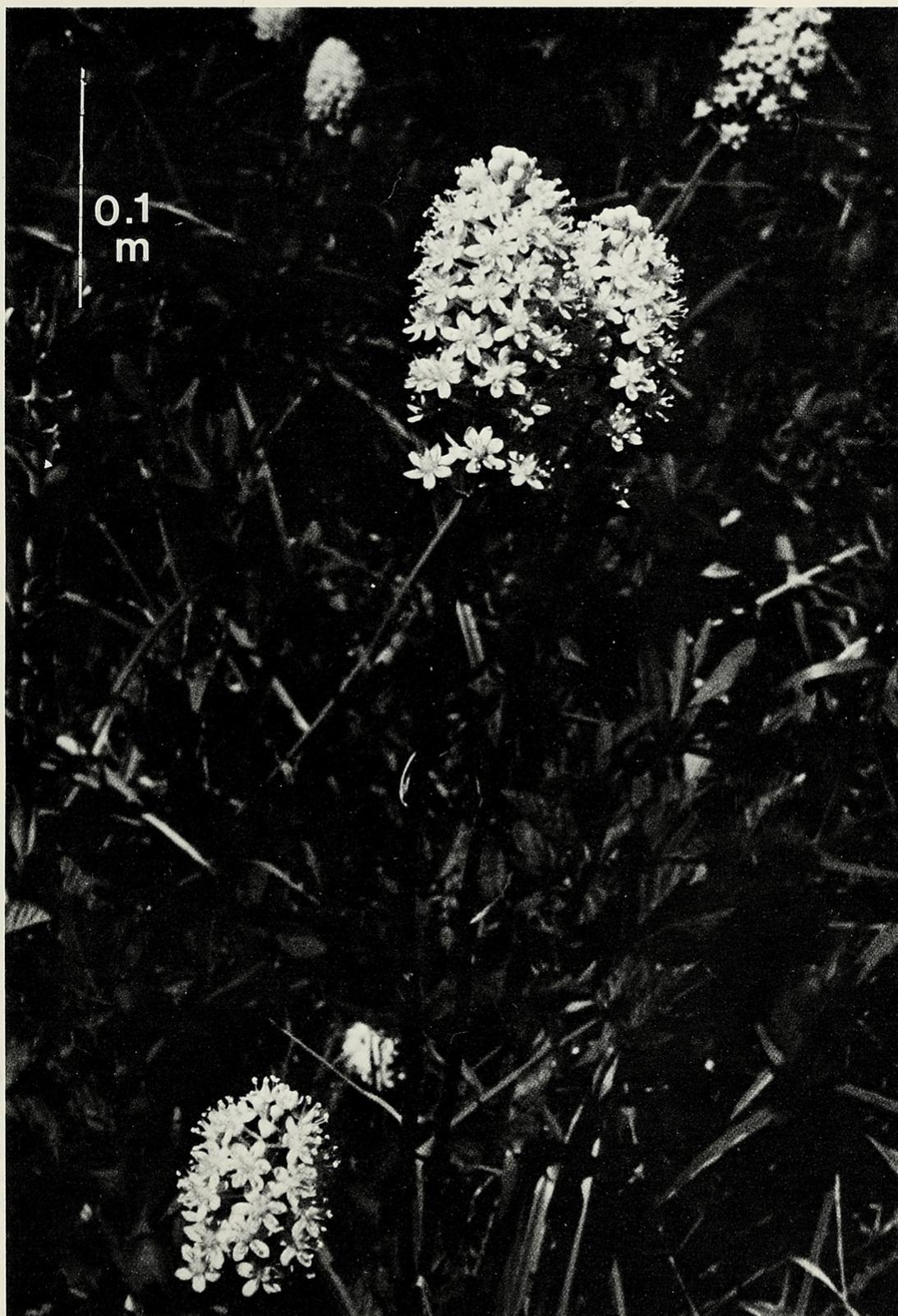


Fig. 2.—Flowering individuals of *A. muscaetoxicum* in Macon County, North Carolina (Utech and Ohara 82-270, CM) (scale indicated).

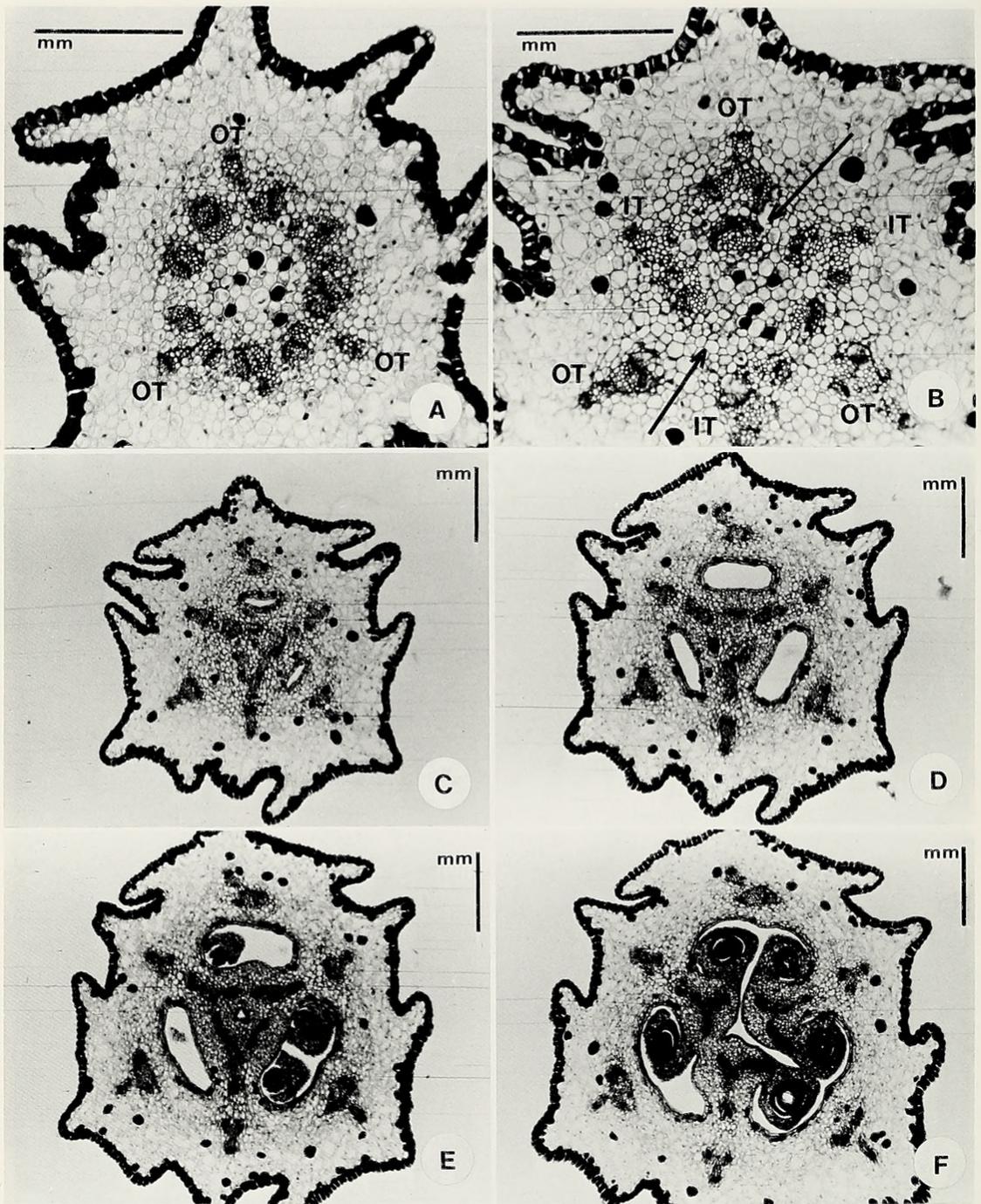


Fig. 3.—Cross-sections from the pedicel and lower receptacular areas of *A. muscaetoxicum* showing the spiral opening of the locules, the degree of perigyny and distribution of epidermal tannin cells. A. Mid-pedicel section showing the formation of three compound outer tepal (OT) bundles. B. Upper pedicel section showing formation of three compound inner tepal (IT) bundles and departure of compound OT bundles. Due to spiral bundle formation, a fusion bundle is opposite the upper OT bundle and a gap opposite the lower left OT bundle (arrows). C. Transition between upper pedicel and lower receptacle areas showing the opening of two locules, the departure of three IT bundles and the remaining central bundles which form the ventral supply. D. Lower receptacle area with perigyny

shorter than the stem. The few cauline leaves are progressively reduced and bract-like. The bracteate raceme is at first ovoid to conic, but at maturity it becomes cylindrical, measuring 4–14 cm long by 2–4 cm wide. Initially the flowers are white, but following anthesis the persistent tepals turn yellowish green or greenish purple and present a most striking color pattern.

The flowering pedicels are normally 7–17 mm long and ascending. In fruit, the pedicels are decidedly horizontal and much elongated. Internally, the fruiting and flowering pedicels have the same bundle number, though the vasculature in fruit is surrounded by a sclerenchymatous sheath. Lower flowering pedicel cross-sections are broadly triangular with three large, centrally arranged bundles. These three bundles establish the complete floral vasculature and are located on the radii which run from the middle of the “flat side” to the section’s center. These three radii are designated the outer tepal (OT) radii. The three radii from the “corners” to the center are designated the inner tepal (IT) radii. Mid-pedicel cross-sections are characterized by broad fluting and ridges (Figs. 3 and 9) which continue through the perigynous zone.

The three lower pedicel bundles along OT radii undergo tri-parted, radial divisions with three resulting bundles from each division. These divisions occur at slightly different levels, that is they are not co-planar, but rather in a spiral pattern. Within each division a gap is created by the outward departure of a central bundle product. Three such central bundles, designated compound outer tepal (OT) bundles (dorsal-compound bundle; Sterling, 1982) depart along OT radii and remain free of other vasculature. Eventually they establish the dorsals (D), the outer tepal medians (OTM), the outer tepal laterals (OTL), and the outer stamen (OS) bundles (Figs. 6, 9A–D).

The two resulting lateral bundles which are opposite a gap following the tri-parted divisions fuse with similar adjacent laterals along the IT radii. These fusion bundles are formed in a spiral pattern and undergo a tri-parted division similar to that observed at a lower level among the three original bundles. The central bundles of this second set of divisions depart along the IT radii and establish the compound inner tepal (IT) bundles (“zwischenbündel”; Sterling, 1982).

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evident and three open locules with formation of the central ventral supply. E. Mid-receptacle area showing the central hole and the ventral supply. F. Upper receptacle area showing the spiral septal arm formation within the perigynous zone, inter-locular connections and placental supply. Dorsal bundles are not established at this level (scale indicated).

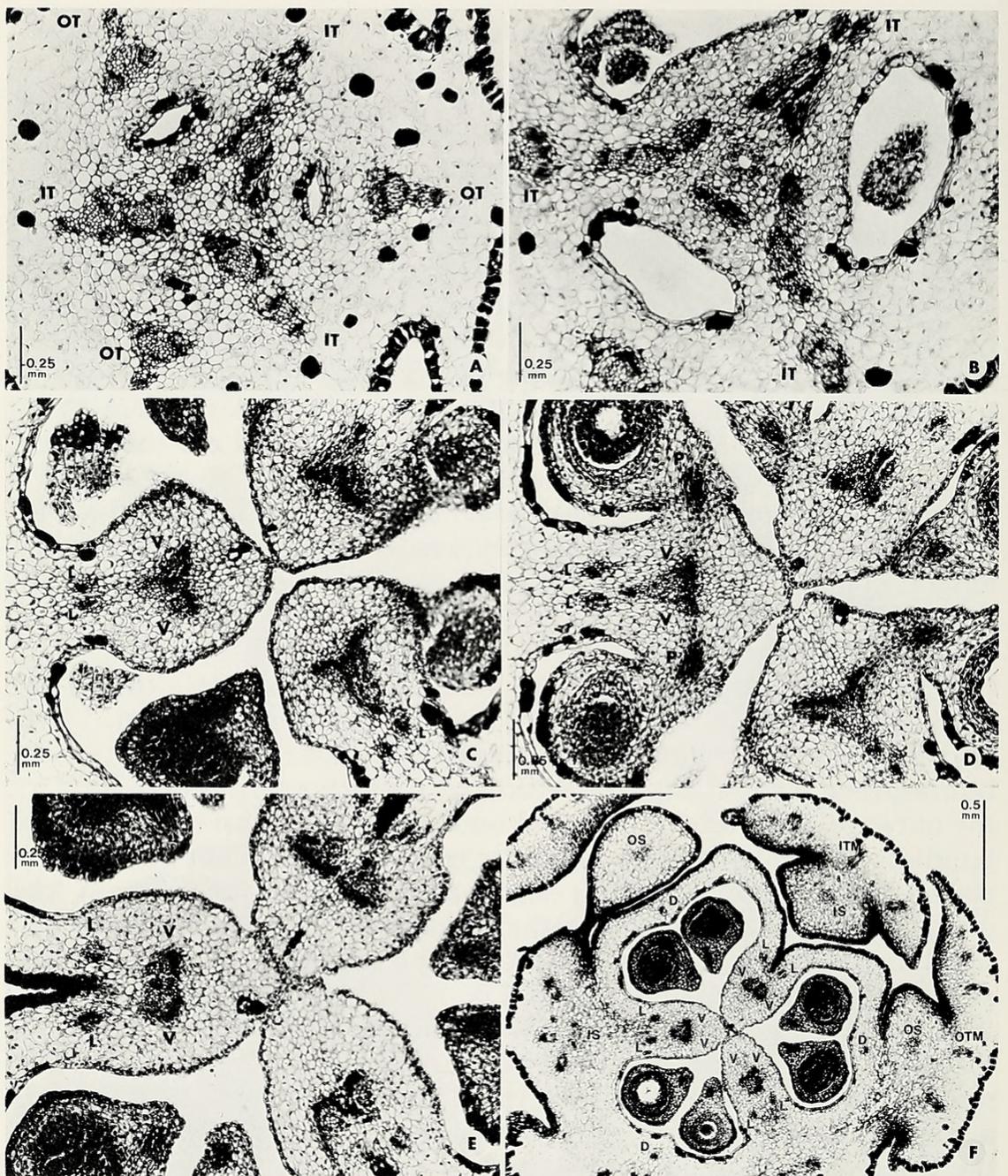


Fig. 4.—Cross-sections from the lower receptacle to upper perigynous areas of *A. muscaetoxicum*. A. Lower receptacle section showing the departure of compound OT and IT bundles, opening of two locules and formation of three bundles opposite IT bundles which establish the ventral supply. B. Section above A showing three open locules and the central hole. While three IT bundles depart, fusion and division occur among the remaining septal arm bundles. C. Section above B showing three freed septal arms between the inter-connected locules. Each septal arm has two laterals (L) and a compound ventral (V) from which placental bundles (P) arise. D. Section above C showing ovule supply via placental (P) bundles and the paired laterals and ventrals within the septal arms. E. Section above D showing the division of the compound ventral bundle (V) and the two laterals (L) within a septal arm. Papilloid nurse cells lining the inner septal arm

From the second set of tri-parted divisions, the two remaining lateral bundles fuse laterally with adjacent laterals, close the OT radii gaps formed when the compound OT bundles departed and eventually establish the total ventral supply (Fig. 6). These three fusion bundles undergo simple radial divisions in a spiral pattern. The two resulting products of this radial division fuse laterally with a similar adjacent lateral and form three fusion bundles along IT radii which close the gaps formed during the departure of the compound inner tepal (IT) bundles. Subsequent divisions among the compound OT and IT bundles will be discussed later. A given pedicel cross-section will usually show one bundle departing, another being formed and a gap in an area where a third will be formed.

The gynoecium and its associated vasculature can best be described in two parts: that in the lower perigynous zone and that in the upper freed zone. Ventral supply formation, locule opening and ovule placentation all occur within the lower perigynous zone (Figs. 3C–F; 4, 6). The dorsal bundles, on the other hand, which are derived from compound outer tepal (OT) bundles are established in the upper limits of the peripheral perigynous zone.

The ridged outline observed in the lower pedicel occurs up through the upper perigynous region where the tepals and stamens are freed (Figs. 3, 4F). Following the formation and departure of both the compound OT and IT bundles, a triangular vascular zone (“stele”) remains in the central area (Figs. 3C–D, 4A–B). The three large bundles along IT radii establish the triangle’s corners. These three complex fusion bundles which closed the gaps formed by the departure of compound IT bundles (Fig. 6) generally have two phloem caps or poles. Once these three corner bundles are established, the three locules which are perpendicular to OT radii open spirally.

With locular opening, each of the three compound bundles along IT radii undergoes a simple tangential division (Figs. 4B–C, 5A, C). Both resulting bundles are along the IT radii. The outermost division product has normally arranged xylem (adaxial) and phloem (abaxial), while the inner product has reversed conducting elements. Phloem strands frequently are observed to lag and may rarely and irregularly anastomose with other bundles (Fig. 5A–B).

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margins are weakly appressed. F. Upper perigynous section showing the spiral arrangement of tepals, stamens and partially, freed carpels. Dorsals (D) are established at this level. Paired lateral (L) and ventral (V) products within septal arms are indicated as are outer tepal medians (otm), inner tepal medians (itm), outer stamen (os) and inner stamen (is) bundles. Epitepaly between an inner tepal and inner stamen is shown in the upper right (scale indicated).

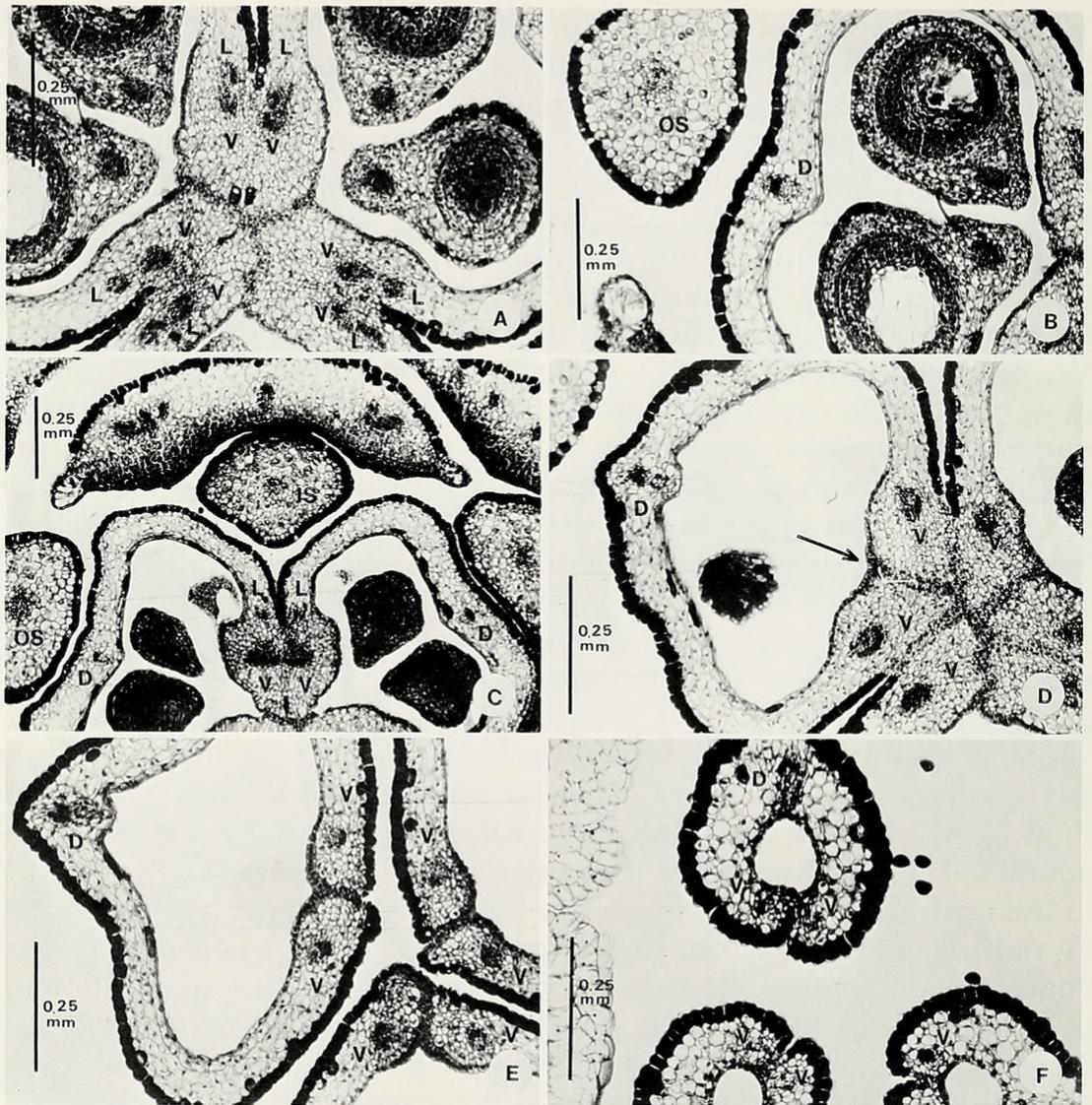


Fig. 5.—Cross-section of the middle to upper gynoecium of *A. muscaetoxicum*. A. Central zone showing three appressed septal arm tips and radial arm separation with paired lateral (L) and ventral (V) bundles. B. Section, same level as A, showing an outer stamen (OS) bundle and dorsal (D). An inner carpillary wall indentation, not a notch, is associated with each dorsal. C. Section above A showing the separated gynoecium and perianth. Within a septal arm, a given ventral and opposing lateral fuse to form a new, compound central in the same position as the lower, simple ventral. D. Section above C showing two compound ventrals (V) and dorsal (D) per carpel. The inner septal arm tips are further divided (arrow) compared with A. E. Section above D showing three free carpels each with a dorsal (D) and two ventrals (V). F. Styler zone with the dorsal (D) and two ventrals (V) still present in each carpel (scale indicated).

The appearance at this level of a central opening or “hole” along the central floral axis (Figs. 3E, 4B) indicates inter-connection of the three locules will follow. Openings develop from this hole along the OT radii to each of the three locules (Fig. 3F). As openings inter-connect the

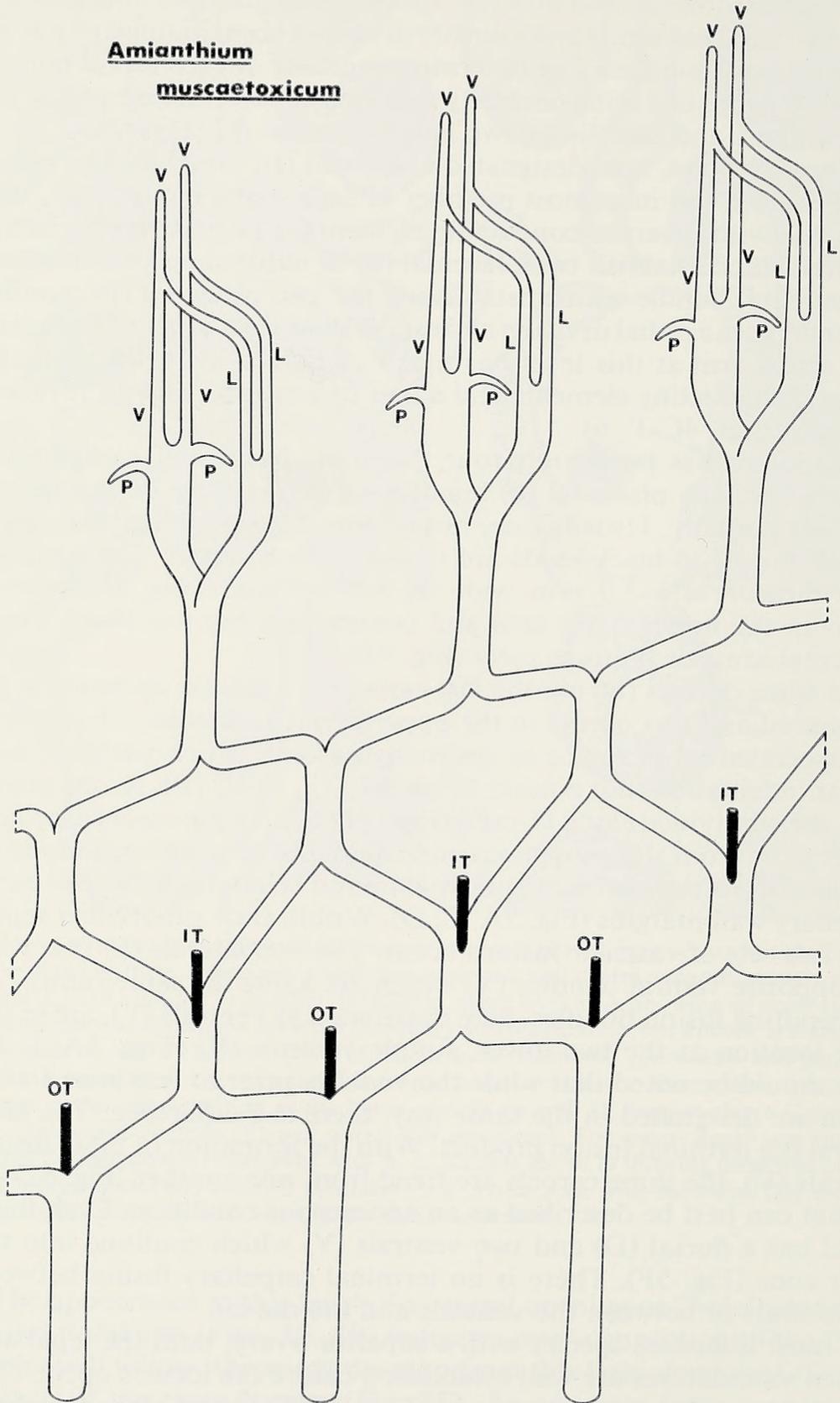
three locules, three septal arms or wings are established along the IT radii. Within these septal arms further divisions occur among the paired ventral supply bundles. The outermost member of each septal bundle pair, that is the one with normally arranged conducting elements, divides radially and establishes two lateral bundles (L) (Figs. 4C–D, 5A, 6). (These bundles, here designated as laterals (L), could also be called septal axials.) The innermost member of each septal bundle pair, that is the one with reversed conducting elements, also undergoes a radial division which establish two placental (P) or ovule supplying bundles. The parental bundle which established the two placental (P) bundles also undergoes a radial division and establishes two ventral (V) bundles. Each septal arm at this level has a pair of laterals (L) with normally arranged conducting elements and a pair of ventrals (V) with reversed elements (Figs. 4C–F, 6).

Each locule has two, rarely four, bitegmic, basitropic, campylotropous ovules. The placental (P) bundles supplying these ovules depart quite horizontally. Usually one, rarely two, ellipsoidal, lustrous, dark reddish brown to black seeds are found in each carpel. The wingless seeds measure 1.5–2.0 mm wide by 4.5–6.0 mm long. Dehiscence begins in the upper styler area and continues along the zones where the septal arms or margins meet (Fig. 5D–F).

The three dorsals (D) are the last carpellary vascular elements to be established and this occurs in the upper perigynous zone. The dorsals are associated with a zone of parenchyma cells which protrude as a locular indentation, not a notch (Figs. 4F, 5B, D–E, 7B). As the septal arms are subdivided along IT radii (Figs. 4E–F, 5A), the outer carpellary wall is freed from the perigynous zone. Septal arm subdivision follows the changing distribution of epidermal tannin cells which line the outer carpellary wall margins (Fig. 5A, C, D). Within each subdivided septal arm, two sets of vascular fusions occur. The two laterals (L) fuse with two opposite ventral bundles (V) which are along the same radii. The two resulting fusion bundles, here designated as ventrals (V), are in the same location as the two lower, simple ventrals (V) (Figs. 5A, C–D, 6). It should be noted that while the ventrals prior to fusion and after fusion are designated in the same way, there is a difference. The later ventral is a terminal fusion product. With the formation of these fusion ventrals (V), the three carpels are freed from one another (Fig. 5D–F) in what can best be described as an apocarpous condition. Each freed carpel has a dorsal (D) and two ventrals (V) which continue into the styler zone (Fig. 5F). There is no terminal carpellary fusion between the ventrals or between the ventrals and the dorsal.

In most liliaceous species with a superior ovary, both the tepal and stamen vasculatures are well established before the locules open. This is not the case in *A. muscaetoxicum* (Figs. 3C–F, 9) and other members

**Amianthium**  
**muscaetoxicum**



of the Veratreae due to the basal perigynous condition. The six freed perianth parts, that is, the three outer and three inner tepals which are spirally inserted (Fig. 4F), are separate to their respective bases and spread widely. The inner tepals which measure 5–7 mm are slightly longer than the outer tepals. There are no glands or claws associated with these perianth parts as is frequently reported in *Melanthium* and *Veratrum*. The abaxial tepal surfaces of all six tepals are characterized by a single epidermal layer containing homogenous tannins (Fig. 8D). This epidermal tannin layer also occurs in the filaments and freed gynoecium. In addition to these tannin cells, there are randomly scattered tannin cells throughout the floral tissue. The adaxial tepal surfaces, on the other hand, lack these tannin cells and instead have papilloid cells (Fig. 8D). These papilloid cells occur from the basal regions of the freed tepals to the apices.

There are other differences between the inner and outer tepals (Figs. 7, 8). The inner tepals are differentiated from the outer in having a short vertical zone of enlarged cells along the basal tepal margins (Figs. 4F, 8B, C). These enlarged cells frequently contain long raphides. Epitely between the inner stamens and tepals is the rule (Figs. 4F, 8A, B). Epitely between the outer stamens and tepals occurs, but it is not as pronounced as the former.

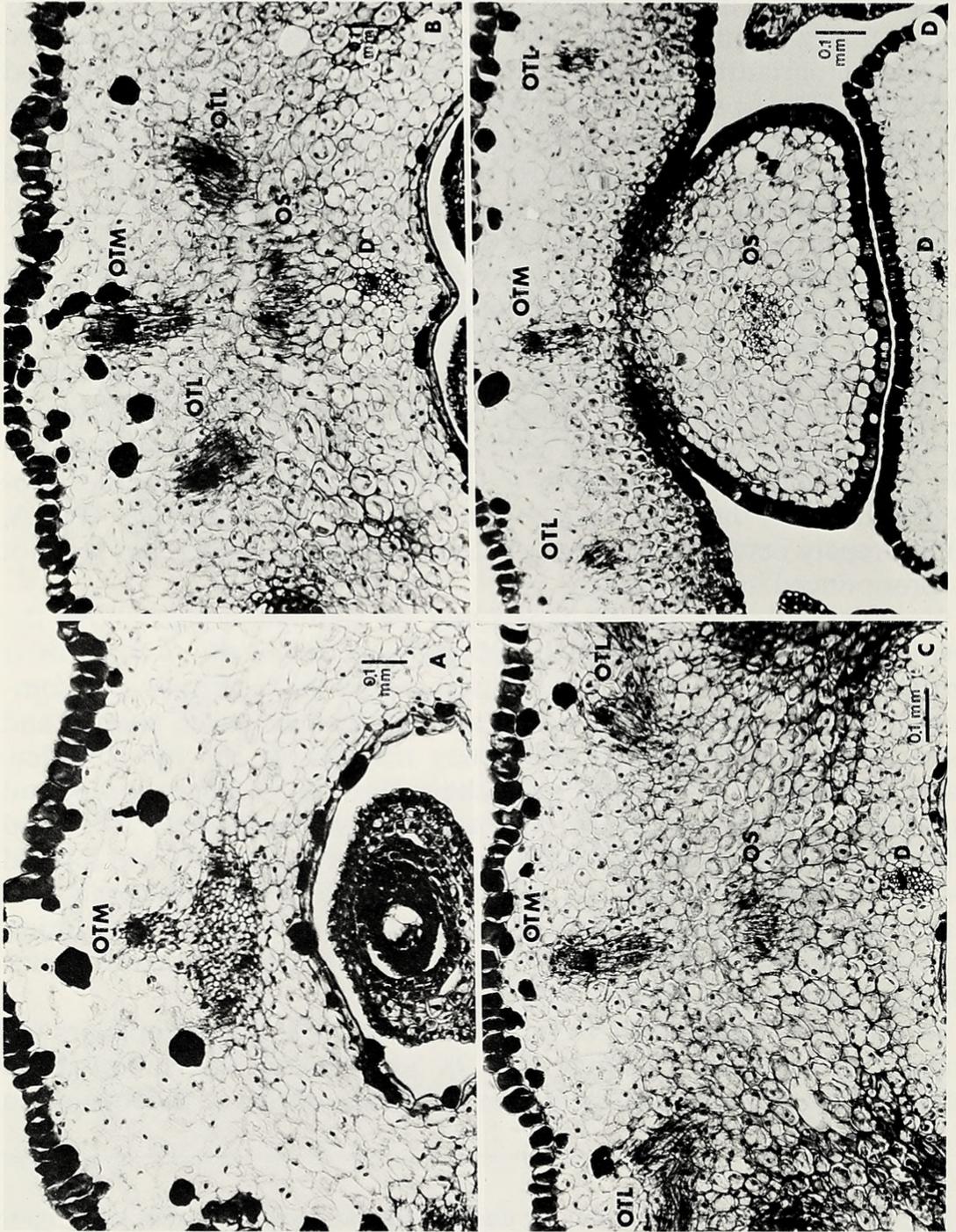
Vascularization of the six tepals and six stamens occurs above the level at which the ovules are supplied (Figs. 3C–F, 4F, 7–9). This is due to the typical perigynous condition within the Veratreae. Six compound bundles, derived via fusion and established in the pedicel and lower receptacle levels, are ultimately responsible for the complete vascularization of the tepals and stamens (Figs. 6, 9). These compound bundles have been designated as the compound outer tepal (OT) and compound inner tepal (IT) bundles, respectively, for they are located along those respective radii. Insertion and departure of tepals and stamens follow a spiral pattern (Figs. 4F, 6, 9). A vascular description for one compound OT and IT bundle will illustrate the patterns for both sets since they are free from each other.

In the upper perigynous zone, a compound OT bundle appears triangular in cross-section (Figs. 7A, 9). Several complex subdivisions occur within the compound OT bundles which results in the formation

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Fig. 6.—Roll-out longitudinal summary diagram for the floral vasculature of *A. muscaetoxicum*. A spiral pattern is indicated, in part, by the shifted levels at which the compound OT and IT bundles depart. Various text discussed bundles have been given the following code: L = lateral, V = ventral (simple and compound) and P = placental. Those bundles derived from the compound OT and IT bundles are not shown, see Figs. 7–9.



of an outer tepal median (OTM), two outer tepal laterals (OTL), an outer stamen bundle (OS) and a dorsal (D). The OTM is established first and has normally arranged xylem (adaxial) and phloem (abaxial) (Figs. 7A, 9B). The remaining product, after the departure of the OTM, undergoes a rapid and complex subdivision in which two OTLs, an OS and a D are established (Figs. 7, 9). The OTM, OS and D bundles all lie along the same radius. It should be noted that the outer tepal laterals are derived from the remaining product bundles, not the OTM. Basally each outer tepal receives three bundles, an OTM and two OTLs. The laterals undergo further radial divisions to establish additional laterals (Fig. 7C). In freed outer tepals, a seven bundled condition is typical, that is three OTLs + OTM + three OTLs.

The origin of the inner tepal median (ITM), the two inner tepal laterals (ITL), and an inner stamen bundle (IS) from a compound inner tepal bundle (IT) is similar to the outer series (Figs. 8, 9). The vascularization of the inner tepals and stamens is in a spiral pattern. The ITM, two ITLs and IS bundles have normally arranged xylem (adaxial) and phloem (abaxial). Basally each inner tepal is supplied with three bundles, an ITM and two ITLs. The laterals undergo further radial divisions, as in the outer series, to establish additional laterals (Fig. 8C). In freed inner tepals, a five bundled condition, rarely seven, is encountered, that is two ITLs + ITM + two ITLs. There is no fusion between the laterals or between laterals and medians in either tepal set. Tepal bundles follow a parallel course and end along tepal margins.

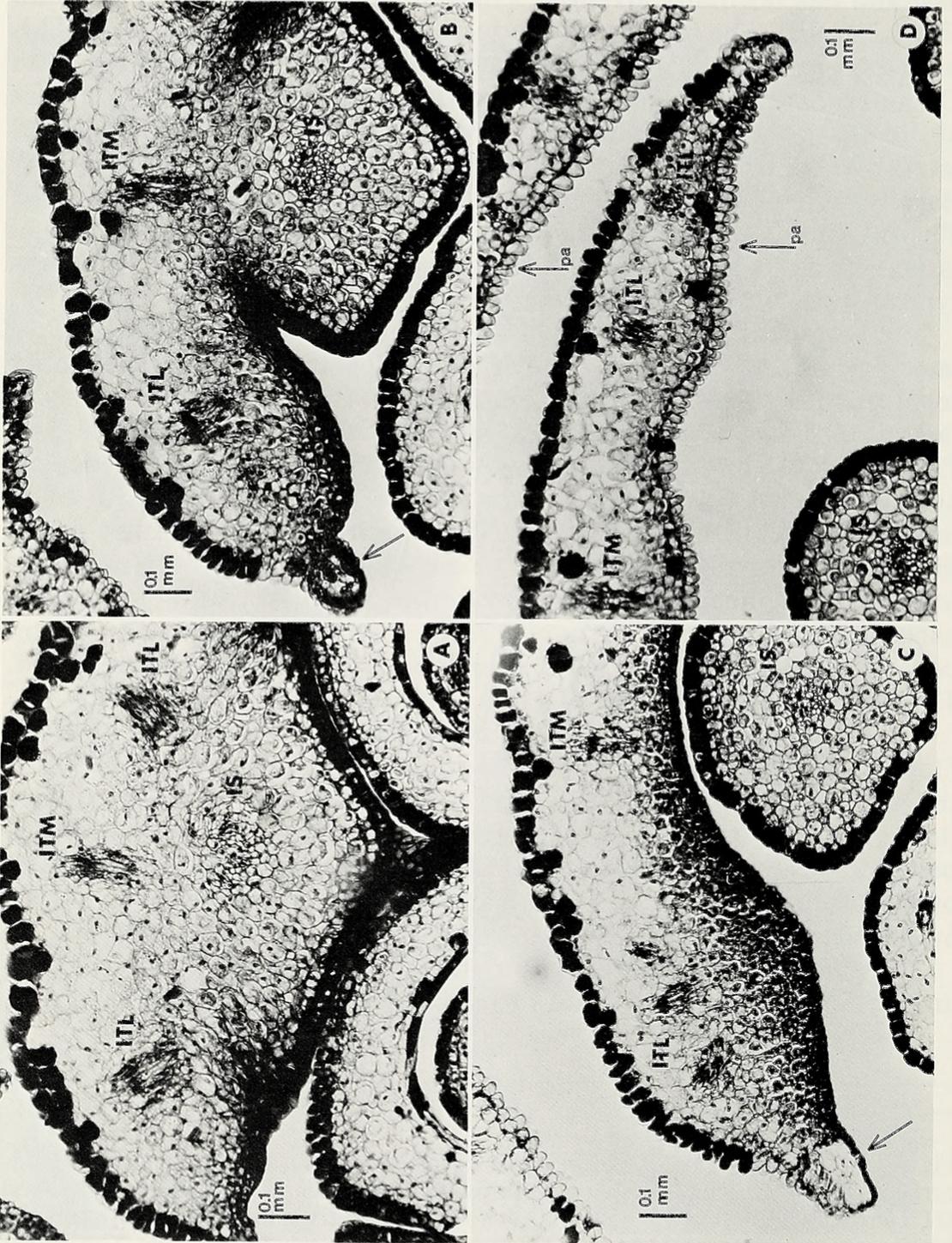
The six equal stamens are nearly as long as the inner tepals. The filament's epidermal layer contains tannins (Figs. 7D, 8C, 10A), while the anther walls do not. The basifixed, extrorse anthers have a valvular (lateral) dehiscence between the confluent thecae which open into a peltate disc (Fig. 10). The endothecium has wall thickenings or bands of the girdle type (Dahlgren and Clifford, 1982). This type of anther and mode of dehiscence is characteristic of the Veratreae.

The difference between outer and inner stamen vascularization which arose from compound OT and IT bundles, respectively, is that a dorsal

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Fig. 7.—Vascularization of the outer tepals and stamens in *A. muscaetoxicum*. A. Mid-perigynous zone showing the departure of an outer tepal median (OTM) from a compound OT complex. B. Section above A showing the further division of the compound OT bundle into two outer tepal laterals (OTL) and an outer stamen (OS) bundle. The locular indentation associated with the dorsal (D) is evident. C. Upper perigynous section above B showing further division among the outer tepal laterals (OTL). D. Section above C showing the freed outer tepal and outer stamen (scale indicated).



is associated with division of the OT parental bundle and there is no counterpart with the IT compound bundle (Figs. 7B–D, 8A–C, 9).

#### DISCUSSION AND CONCLUSIONS

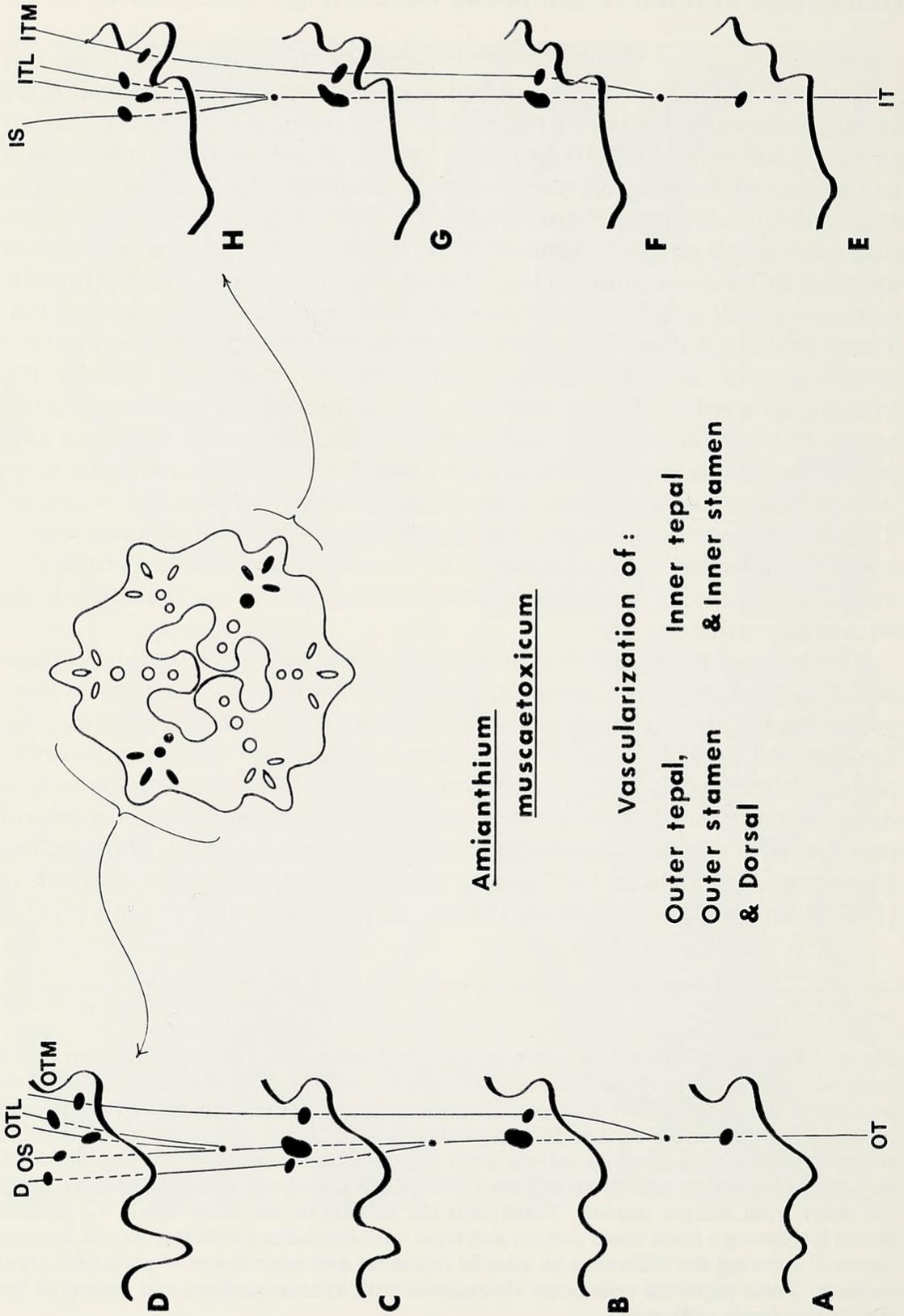
In describing the vascular floral anatomy and carpel morphology within selected members of the liliaceous tribe Veratreae, Anderson (1940), El-Hamidi (1952), Ambrose (1975), Sterling (1982), and Utech in this report have noted characteristic similarities and differences between the flowers and fruits of *Amianthium muscaetoxicum* and the other members of the Veratreae. A common pattern of vascularization appears to be consistently observed within the tribe, while major differences which are frequently used to differentiate genera are reported. These anatomical and morphological characters include the presence or absence of sutural openings and a central carpellary hole at the lowermost level of ovular insertion, the degree of carpellary separation below the locular apex (an apocarpous tendency), the number of carpellary lateral or septal axial bundles and a hypogynous or perigynous versus epigynous condition at the lowermost level of ovular insertion. The floral vascular anatomy and carpel morphology of *A. muscaetoxicum* as reported here will serve as a case study of the continuous vascularization of a Veratrean gynoecium for further comparative work within the tribe.

The pedicel to stigma vasculature of *A. muscaetoxicum* is most unusual in that perigyny, spiral insertion of floral parts and apocarpous gynoecia are encountered. Through a complex series of divisions and fusions the complete floral vasculature is derived from three lower pedicel bundles. In the middle to upper pedicel a series of successive divisions and fusions in a spiral sequence produces three compound outer tepal (OT) bundles and three compound inner tepal (IT) bundles. From each compound OT bundle (dorsal-composite bundle; Sterling (1982)), an outer tepal median (OTM), several outer tepal laterals (OTL),

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Fig. 8.—Vascularization of the inner tepals and stamens in *A. muscaetoxicum* with a tepal surface comparison. A. Epitepaly between an inner tepal and stamen is shown as an inner tepal median (ITM) is derived from a compound IT bundle. Subsequent division of the IT bundle establishes two inner tepal laterals (ITL) and inner stamen (IS) bundle. An epidermal tannin layer surrounds both the tepal and stamen. B. Section above A showing epitepaly as well as specialized cells which frequently contain raphides along the inner tepal margin (arrow). These cells are lacking in the outer tepals. C. Section above B showing a freed inner stamen and tepal with specialized cells (arrow). D. Section above C showing the difference in adaxial (tannins) and adaxial (pa = papilloid) tepal surfaces. These papilloid cells occur throughout both adaxial surfaces and extend to the tepal's tips (scale indicated).



Amianthium

muscaetoxicum

Vascularization of:

- Outer tepal, Inner tepal
- Outer stamen & Inner stamen
- & Dorsal

an outer stamen (OS) and a dorsal (D) result. Similarly, from each compound IT bundle (“zwischenbündel”; Sterling (1982)), an inner tepal median (ITM), and an inner stamen (IS) bundle result. Due to the perigynous condition, the formation of these tepal, stamen and dorsal bundles is at a level above that at which the ventral and ovular supplies are established.

The spiral origin of the ventral supply is via successive divisions and fusions of continuing lateral branches following the formation of the compound IT bundles. Within each of the three undivided septal arms, that is, the perigynous zone where the three locules are not interconnected, a lateral bundle (L) (compound septal axial bundle; Sterling (1982)) is associated with a ventral (V) (compound placental bundle; Sterling (1982)). The lateral bundle has normally arranged xylem and phloem while the ventral bundle has reversed conducting elements. There is a radial subdivision within each septal arm of both the ventral and lateral bundles. Each ventral bundle fuses with an opposite lateral bundle as the perigynous condition ends and the three carpels are freed.

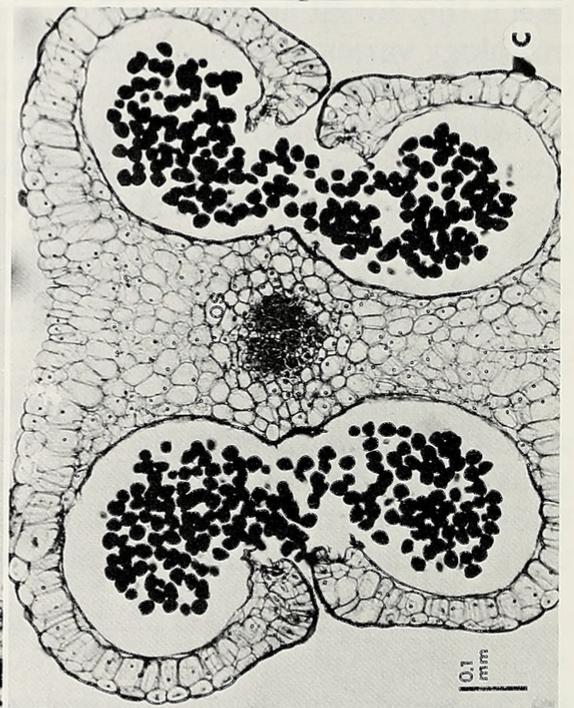
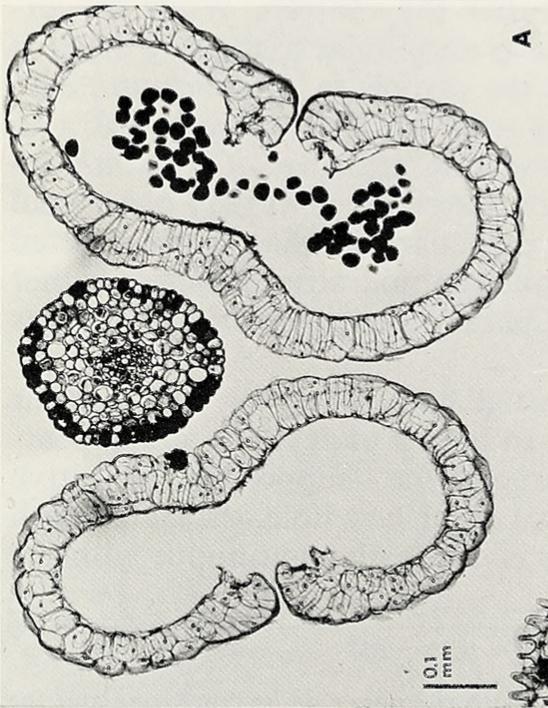
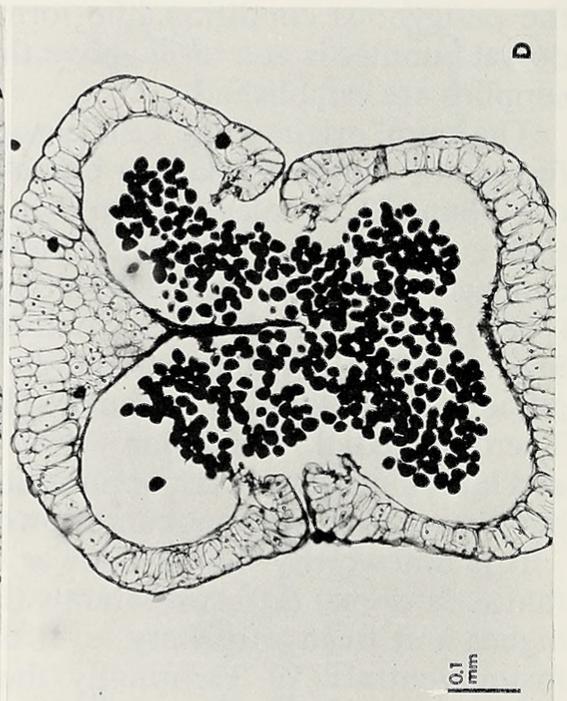
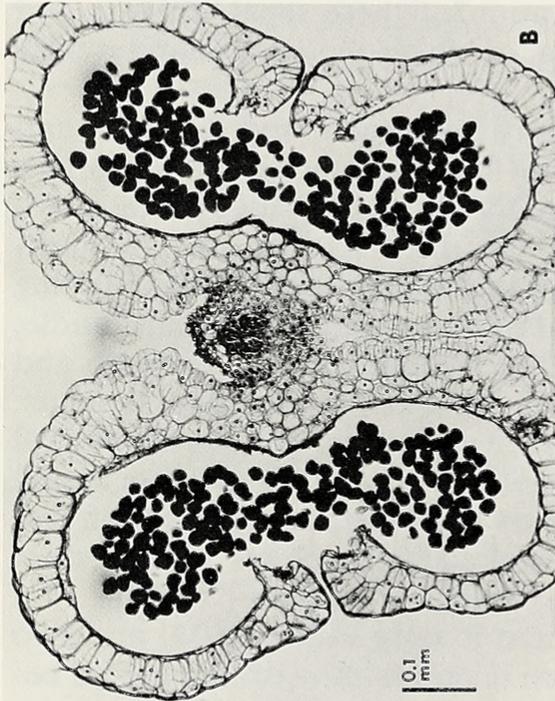
It is noteworthy that at a lower level each carpel has five bundles, that is, a dorsal (D), two laterals (L) and two ventrals (V) while at a higher and freed carpellary level there is only a dorsal (D) and two fusion ventrals (V). Terminally, there is no fusion within a carpel between the dorsal and ventrals or between the ventrals. While the terminology varies, the above observations are similar to those of Sterling (1982). Anderson (1940) noted that the carpels in *Amianthium*, *Melanthium*, *Veratrum*, and *Zigadenus* were supplied by a dorsal, two laterals and two ventrals. The cross-section drawings of *Amianthium* by Ambrose (1975; fig. 32G–K) were described as having one dorsal and four ventrals. Simply counting carpellary bundles from selected cross-sections is not adequate for detailed comparative purposes, rather the continuity of the complete floral pattern including origins, fusions and divisions must be followed.

The combination of spirally inserted floral parts as well as their spirally derived vasculature coupled to both a perigynous and apocarpous gynoecium is most unusual among the “supposedly primitive lilies.” Furthermore, there is a central carpellary hole associated with the gynoecial base. This central hole is internally continuous with the

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Fig. 9.—Line drawing showing cross-sections from the upper perigynous zone and the resulting vascularization from both a compound OT bundle (A–D) and a compound IT bundle (E–H). The outer tepal median (OTM), outer tepal laterals (OTL), outer stamen (OS) and dorsal (D) bundles are all derived from the compound OT bundle, while the inner tepal median (ITM), inner tepal laterals (ITL), and inner stamen (IS) bundles are derived from the compound IT bundle.



three locules and the open stylar canal. Such a central hole according to Sterling (1982) could be taken to represent a partially closed suture or a remnant of an open portion of the stylar canal. The three carpels are essentially free above the perigynous zone. The inner septal wing tips that form the stylar canal are weakly differentiated into papilloid nurse cells. In this inner zone, dehiscence occurs exposing the single, rarely two, wingless seeds of each carpel. Such inner septal margin separation is a variation of the typical septicidal capsule dehiscence where splitting occurs between two adjacent carpels along a common septal radius.

Neither tepal glands nor nectaries occur in *Amianthium* though they are commonly encountered throughout the Veratreae. The epidermal layers of both abaxial tepal surfaces as well as that of the pedicel, the complete perigynous zone, the filaments and the freed carpels are characterized by cells with homogenous tannins. However, the adaxial surfaces of both the inner and outer tepals have a generalized epidermis of small papilloid cells. Furthermore, as a possible defensive adaptation, raphides are observed in cells along the lower, outer margins of the inner tepals. Though there has been limited differentiation between the adaxial and abaxial tepal surfaces, they are not specialized as nectaries or glands. Travis (1984) observed that foraging beetles are the chief pollinators for *A. muscaetoxicum* and experimentally demonstrated that this species is nearly self-incompatible and the fecundity and fruit set levels are at least partly pollinator limited. Furthermore, only a small percentage of seeds from self-pollinated plants are viable.

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Fig. 10.—Cross-sections of an outer stamen in *A. muscaetoxicum*. A. Section through a filament with a tannin epidermal layer and two lower anther thecae which lack tannins. B. Section above A showing the central basifixed position of the filament. C. Section above B showing the central position of the outer stamen (OS) bundle. D. Upper anther zone section above C showing confluent thecae which open into a peltoid disc (scale indicated).

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