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FLORAL VASCULAR ANATOMY OF *MEDEOLA VIRGINIANA* L. (LILIACEAE-PARIDEAE = TRILLIACEAE) AND TRIBAL NOTE

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ABSTRACT

The complete vascular floral anatomy of *Medeola virginiana* L. ("Indian cucumber") from its mid-pedicle to the recurved style-stigmas is presented. The lower pedicle contains a double ring of 12 (that is, six inner plus six outer) bundles. The six outer do not branch or fuse and directly establish the six tepal medians, three in an outer whorl and three in an inner whorl. The six inner bundles, which alternate with the six tepal median establishing bundles, are clearly compound, and following successive radial divisions and planar fusions establish the tepal laterals (both whorls), the stamen traces (both whorls), the three dorsals, the six dorsal laterals, the three ventral laterals, the six ventral placentals, and the three septal axials. The stamen, dorsal, ventral lateral, and septal axial traces are all fusion products. No septal glands or dorsal notches occur in this species, neither do raphides. The three inner, fused septal wings are completely free centrally at the gynoeceal base, hence this tricarpellate gynoeceum is unilocular. Three bundles (that is, continuing dorsal plus two branches from different ventral laterals) occur in each of the three recurved stylar arms. A stigmatoid support system composed of papilloid cells lines the inner notched stylar furrows and is continuous through the short, common, hollow stylar canal to the base of the gynoeceum along the inner septal wing margins.

INTRODUCTION

Medeola virginiana L. is a monotypic species of eastern North America (Fernald, 1950; Johnson, 1969) with a reported chromosome number of $2n = 14$ (Stewart and Bamford, 1942; Woodard, 1948). This report on the vascular floral anatomy of *M. virginiana* supplements the preliminary reports made by Anderson (1940) and Berg (1962a), and is part of a larger study of the baccate species of the Liliaceae Alliance

(Utech and Kawano, 1976a, 1976b, 1978). The manner of vascular presentation for *M. virginiana* will parallel that published for the other liliaceous species.

Historically, the berry fruit has been the major basis of taxonomic association of *Medeola* with *Trillium*, *Scoliopus*, and *Paris*. It is hoped that this investigation of the complete floral vascular anatomy of *Medeola* can be used directly in its tribal (or familial) accessment by establishing the vascular pattern underlying the berry fruit.

MATERIALS AND METHODS

For this vascular anatomical study, a series of floral buds through mature flowers of *M. virginiana* was collected over a month period from Laurel Hill State Park, Somerset Co., Pennsylvania (Utech, 76-201 CM) with fixation in acetic ethanol (1:3) and subsequent storage in 70% ethanol. Twenty-five flowers (buds to maturing fruits) were sectioned between 12–16 μ using standard paraffin techniques and stained in safranin and methylene blue (Sass, 1965; Johansen, 1950; Berlyn and Miksche, 1976). Checks on these serial preparations were made by observing whole flowers which had been cleared in 10% NaOH with the vasculature simultaneously stained in 1% fuchsin (Fuchs, 1963; Utech and Kawano, 1976a). Neither ontogenetic nor teleological implications are intended by the vascular description of the hypothetical ascent of the bundles from the pedicel to the stigma. Figs. 1–3 present photomicrographs of the pedicel to stigma vasculature, whereas Figs. 4–5 summarize the overall floral vasculature patterns. Text introduced coding is presented for the various bundle types.

Although the letters for the various vascular bundles are similar to those used in previous papers, a correspondence is given here between them and those used by Berg (1962a) for *M. virginiana*: D (dorsal) = m.s. (median carpellary strand); D_L (dorsal lateral) = s.s. (small strand); V_L (ventral lateral; compound) = l.s. (lateral strand; composite); vlb (ventral lateral branch) = l'.s (lateral strand; single, simple); Ventral Supply-SA (septal axials) + V_P (placentals) + F (funicular) vs. pl.s. (placental strand).

OBSERVATIONS

Pedicel Vascularization

In both the flowering and fruiting pedicel, the vascular bundle arrangement is exactly the same. Each pedicel in cross-section has a broad ring of 12 separate bundles that are clearly divisible into two groups, that is, six smaller bundles which are somewhat further from the center than the second set of six larger alternating bundles (Fig. 1A–C). The six smaller bundles represent the tepal medians (three outer tepal medians—OTM; three inner tepal medians—ITM). They depart from their outer pedicel position in two whorls to directly supply the three outer and three inner tepals, respectively. No fusion or cross-innervation occurs in their formation (Fig. 5). The six larger bundles (P), on the other hand, are responsible via repeated lateral division for the formation of the tepal laterals (TL) of both tepal whorls, and with additional division and cross-fusion for the total stamen, the dorsal and the ventral supplies (Figs. 4, 5).

Both in bud and early flower, the flowering pedicel is curved down-

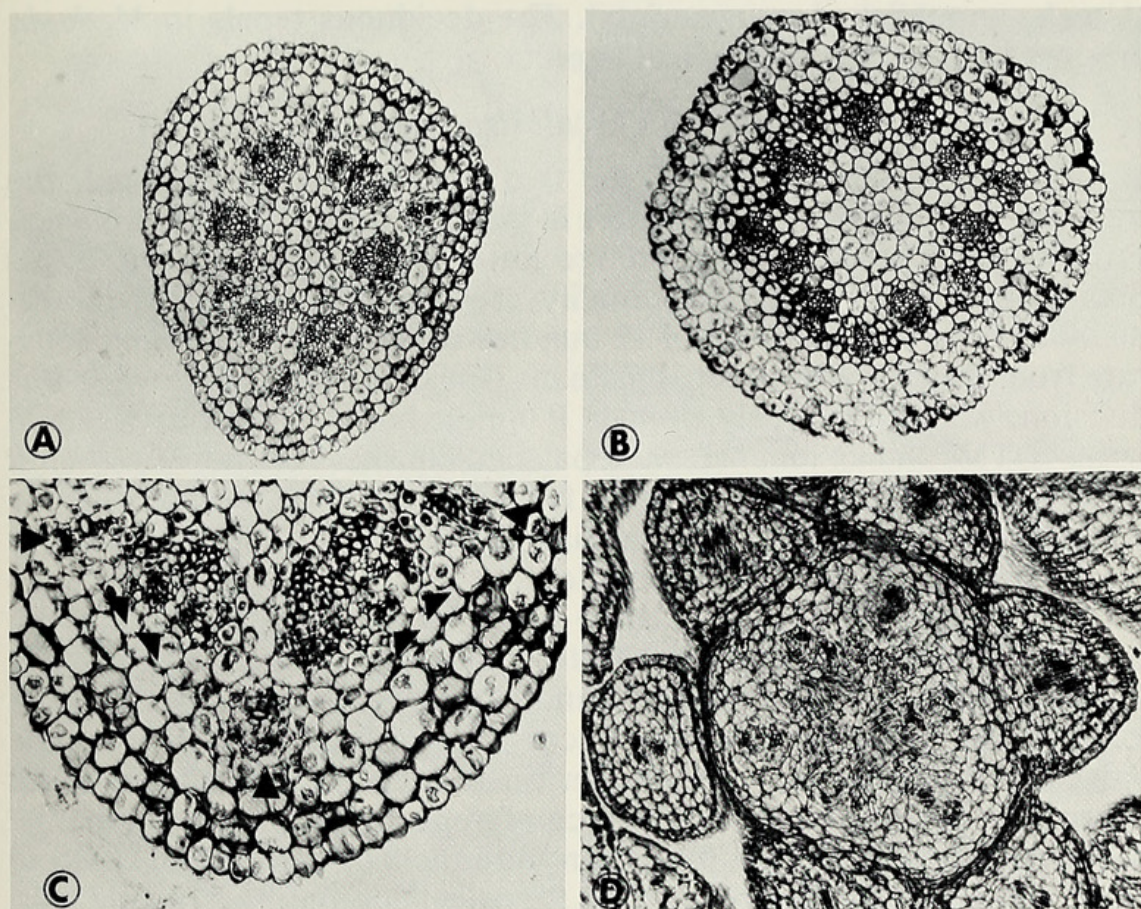


Fig. 1.—Vascularization of *Medeola virginiana*. A. Mid-length cross-section through a flowering pedicel showing the two sets of six bundles. The outer, smaller six depart directly to form the two whorl sets of tepal medians. The inner, larger six are compound and establish via repeated division the remaining floral vasculature (45 $\times$). B. Mid-length cross-section through a fruiting pedicel with a similar bundle arrangement as in A, but with the additional sclerenchymatous sheath around the bundles (45 $\times$). C. Enlargement of A showing three outer pedicel bundles (isosceles triangles) with two alternating inner compound bundles (paired equilateral triangles) (100 $\times$). D. Young bud cross-section showing bundle arrangement at the base of the receptacle. The two whorls of three stamens each are freed and their single fusion bundles lie along similar radii as the three dorsals and the three ventral laterals (40 $\times$).

wards below the upper whorl of leaves, and there is no sclerenchymatous sheath which encloses the 12 pedicel bundles. However, the fruiting pedicel which is erect and has undergone an upwards shift does have a sclerenchymatous sheath (Fig. 1B). It may be that the thickening of certain cell walls in this central zone (Fig. 1A–C) is directly related to the post-anthesis movement of the flowers. A similar time delayed development of a sclerenchymatous sheath coupled to a pedicel rotation has also been observed in *Convallaria* (Utech and Kawano, 1976b) and in *Streptopus*, *Clintonia*, and *Polygonatum*

(Utech, unpublished manuscripts). The deciduous tepals in *Medeola* are lost by the time the pedicel is erect.

Tepal Vascularization

Although vascularization of the two tepal whorls is identical, the traces to the two whorls do depart in two vertically separated planes. Prior to the divergence of the three lower OTM, all six of the larger pedicel bundles (P) become broadly crescent-shaped and divide radially to form an inner ring of 12 bundles which are distinct and separate from the two sets of tepal medians (Figs. 1C, 4, 5). Following this division, where previously a single P bundle had occurred between an outer (OTM) and an inner (ITM) tepal median, there are now two half P bundles. Tepal laterals (TL) arise from these P bundle halves at the same level as their respective medians (OTM or ITM) depart. Clearly the P bundles are compound bundles.

On both sides of an OTM, there is a P bundle half. Within a given outer tepal, the two basal tepal laterals (TL), which depart with the OTM, originated in a different P bundle halves via radial division (Fig. 5). A similar pattern of division occurs among two different P bundle halves in the formation of the inner tepal laterals (TL). At this latter receptacle height, within a 60° circumference of a cross-section, the following bundles can be found: an unbranched, departing OTM; an outer tepal lateral (TL) arising from a vertical continuing P bundle half; the other P bundle half, which branches to give an inner tepal lateral (TL); a soon-to-depart ITM (Fig. 5).

The manner in which the outer and inner tepals are cut off from the receptacle base, as well as their size and shape, are exactly the same. Neither staminal epitepaly nor lateral syntepaly occurs basally (Figs. 1D, 2C-D). Nectiferous tissue and pubescence are absent from both tepal cycles. At its level of attachment, each tepal receives three traces, that is, its median (either OTM or ITM) and two tepal laterals (TL) (Fig. 5). Neither branching nor fusion of the tepal medians occurs within the laminal tepal surface. The tepal laterals, on the other hand, each undergo two radial divisions after the tepal based is freed from the receptacle. Subsequently, each mature tepal has seven veins, that is, three TL plus median plus three TL.

Stamen Vascularization

Following the radial formation of the 12 half bundles and the subsequent one-sided division and departure of the outer tepal laterals from six of the half bundles, another radial division occurs among these same six P bundle halves. These resulting branches are on the same side of their parental bundles as the previously derived outer tepal laterals. Each of the three separate paired sets of such branches fuse

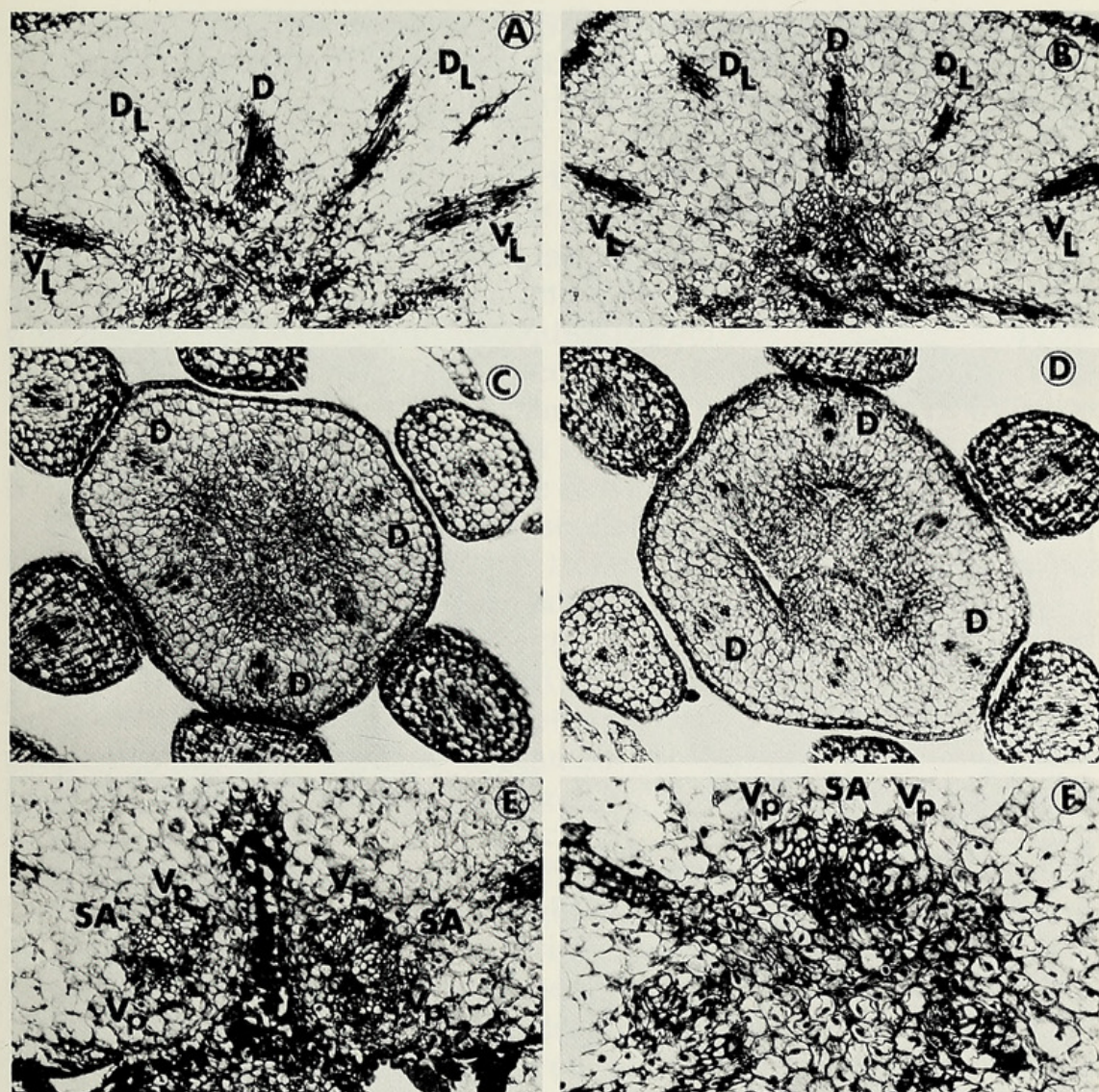


Fig. 2.—Vascularization of *Medeola virginiana*. A. Gynoecial base cross-section showing the departure of a fusion dorsal (D) with two associated dorsal laterals (D_L), as well as two fusion ventral laterals (V_L). Ventral plexus bundles remain (125 $\times$). B. Similar to A, but a higher section (125 $\times$). C. Central opening of the locules. No dorsal grooves evident. Both ventral laterals and ventral plexuses evident along the septal radii. (35 $\times$). D. Closing of the ventral laterals still present, whereas the inner ventral placentals are ending (35 $\times$). E. Enlarged cross-sectional view of a mature flower showing two septa with their two ventral placentals (V_p) and a central septal axial (SA) (150 $\times$). F. Lower cross-section than in E showing the two ventral placentals (V_p) and a median septal axial (SA) (150 $\times$).

along the three OTM radii and form the three outer stamen traces (OS). Each OS is separated by 120° and their formation closes the gap along the OTM radii (Fig. 5).

The six remaining and continuing P bundle halves (three pairs) which had branches to form the OTM and the OS traces, then fuse in pairs to

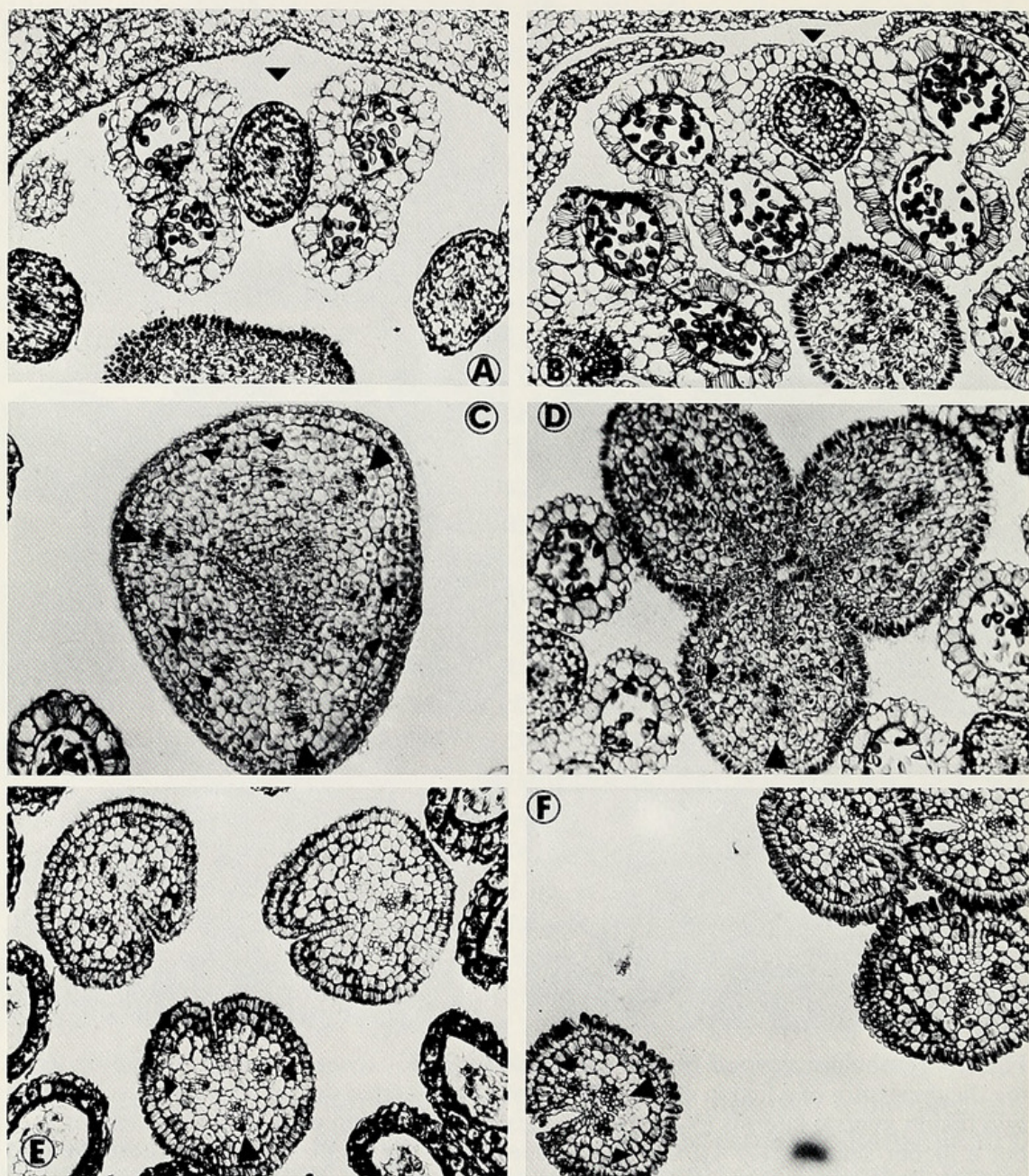


Fig. 3.—Vascularization of *Medeola virginiana*. A. Stamen cross-section, the triangle indicates the shorter, inner filament with its associated anther sacs, in the lower right is a longer, outer filament (35 $\times$). B. Stamen cross-section, higher section than in A, the triangle indicates an outer stamen with its filament still unattached to the anther, whereas the filament and anther of an inner stamen in the lower left are attached. Extrorse condition and the banded epithelial thickenings are evident (35 $\times$). C. Cross-section through the common hollow style, the ventral laterals have divided into pairs of bundles (paired triangles), dorsals indicated (large triangles) (35 $\times$). D. Cross-section showing the formation of the 3 stylar arms, each arm has 3 bundles, the continuing dorsal and two branch bundles from different ventral laterals (small triangles) (35 $\times$). E. Cross-section above D showing the free stylar arms, the stylar furrows are directed away from the surrounding anther zone. (35 $\times$). F. Stylar cross-section above the stamens showing in the lower left one of recurved stylar arms with its outward directed stylar furrow (35 $\times$).

form the three carpel dorsals (D). Both the outer stamen traces and the dorsals (D) are fusion products involving the same six P bundle halves. Again, this repeated division of the P bundles attests to their compound nature.

The origin of the inner stamen traces (IS) is similar to that of the outer stamen (OS) traces (Fig. 5). The previously uninvolved and remaining six bundle halves form lateral branches via radial division. These new branches are on the same side of their parent bundles as the inner tepal laterals. These new lateral branches then fuse along the ITM radii and form the inner stamen traces (IS). Their formation closes the gap along the inner tepal median radii. There are three IS traces so formed, each 60° from an adjacent OS trace.

The remaining six parent bundle halves which branched to give rise to the inner stamen traces fuse subsequently along the common ITM-IS radii (really the septum) to form three independent plexuses, which constitute the lateral and ventral supply system (Fig. 1D).

The six stamens are freed directly in two cycles from the hypogynous gynoecial base (Figs. 1D, 2C–D). Neither raphides, epidermal pubescence, epitepaly nor lateral stamen fusion occurs within the two stamen cycles. The inner three filaments are slightly longer (ca. 1 mm) than the outer three filaments (Fig. 3A–B). All six dorsifixed anthers have identical lengths within both cycles. The adaxial point of filament attachment is the same within both cycles, but due to the differential filament length, the effective height of the presented anther zone is greater than the length of an individual anther (Fig. 3A–B). The morphological variation in cycle filament length increases the pollen dispersal zone, because the anthers dehisce via lateral, vertical slits (extorse condition). The epithelial cell walls lining the stamen sacs have banded thickenings (Fig. 3B). Each stamen receives a single fusion trace. The base of the gynoecium contains essentially six fusion product bundles each separated by 60° —the three dorsals (D) and the three ventral plexuses (Figs. 1D, 2C–D, 4, 5).

Gynoecial Vascularization

The oval-oblong, tricarpellate gynoecium of *M. virginiana* lacks notches or grooves over the dorsals. Septal glands or indentations are also lacking. When present in other liliaceous species such glands frequently function as nectaries. Because septal glands are lacking, the three carpels of the ovary are completely fused along the outer septal margins. The inner septal margins are, however, free on their wing tips from each other throughout the ovary length (Fig. 2C–D). The tricarpellate ovary, therefore, must be considered unilocular. The resulting common hollow ovary cavity is continuous with the common hollow stylar canal. The gynoecium terminates in a very short common style,

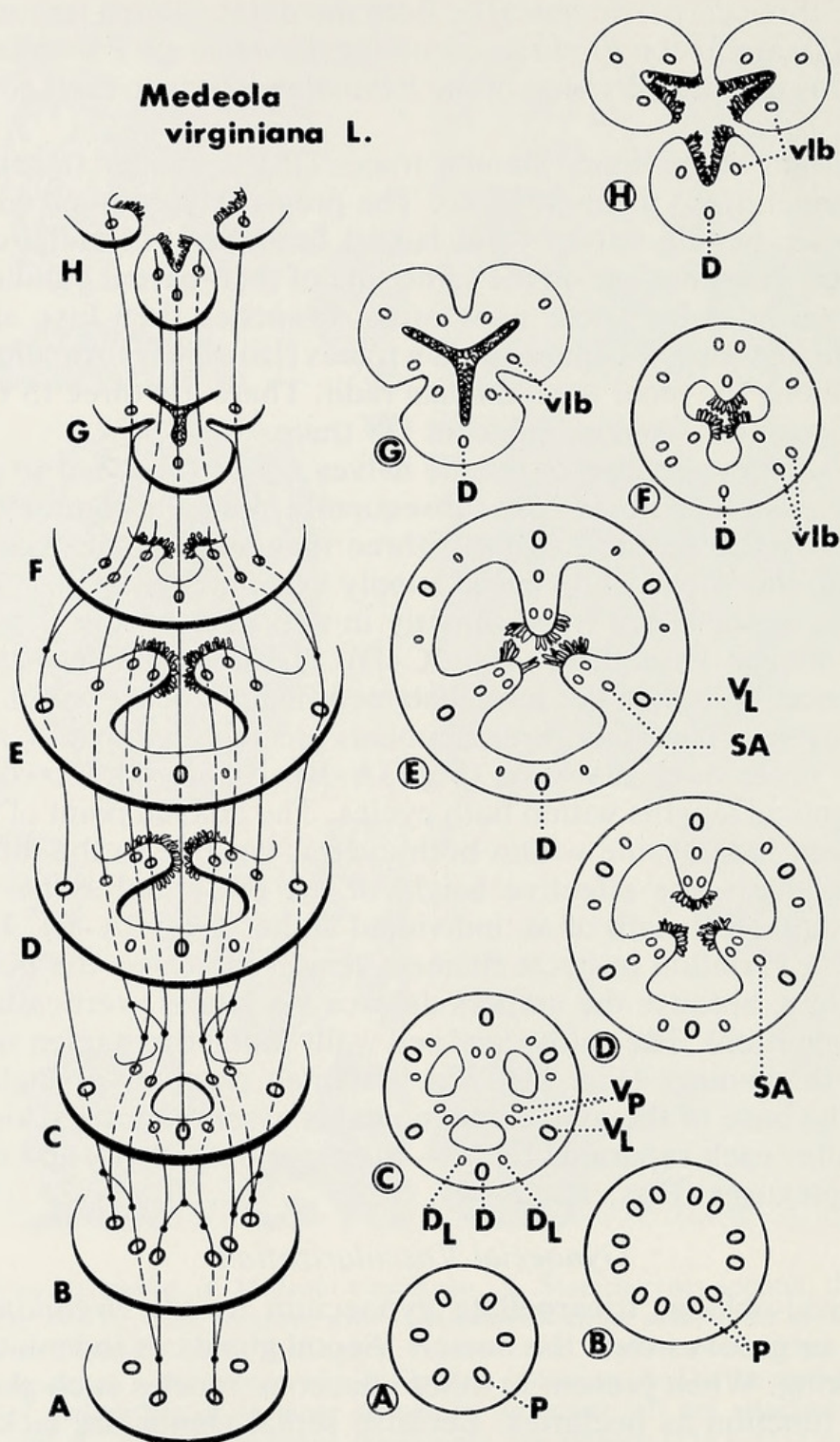


Fig. 4.—Serial cross-sections of *Medeola virginiana* and their associated projections that have had the various bundles connected. The series runs from the mid-pedicel to the region of the three free stilar arms. The formation of the tepal and stamen traces are not indicated.

which is divided into three long style-stigmata branches (Fig. 3C–F). The common style along with the three long stigmata branches is deciduous and leaves a terminal, circular ovary scar.

Dorsal Supply

Basically, the gynoecium has six fused sets of P bundle halves. Fig. 4 does not show the derivation and departure of the tepal and stamen vasculature, only the gynoecial vascularization is presented. The three dorsals (D) are fusion products formed from three paired sets of receptacle P half bundles and lie along the OTM-OS radii.

There is a movement of the newly formed dorsals (D) outward so as to pass under the unopened locules (Fig. 2A–B). As the three locules do open, two minor lateral branches depart on each side of the three fused dorsals (D). These side branches, designated dorsal laterals (D_L) ascend upwards, parallel with their dorsal in a subtending, outer locule position (Figs. 2A–B, 4, 5). The D_L do not fuse terminally with their parent dorsals or branch further, but simply terminate in the upper gynoecial areas. The dorsals (D), on the other hand, continue up into the common style unbranched, and terminate in the recurved stigma tips (Figs. 3D–F, 4, 5).

Ventral and Lateral Supply

The ventral supply which involves both laterals (V_L) and septal axial (SA) in addition to the placental supply (V_P) is far more complex than that reported for the dorsal (D) supply. The three remaining sets of paired bundle halves at the base of the gynoecium constitute the source for the total lateral and ventral supply (Figs. 1D, 2C–D).

At a level above that at which the dorsals (D) are formed, two adjacent bundle halves, which had branches to form the ITM and IS traces, branch again. These two branches then fuse and form a bundle which lies along the septum radius, which is also the ITM and IS traces. This new fusion bundle is the ventral lateral (V_L). There are three of them each 120° apart (Fig. 2A–B, 4, 5). Their formation is analogous to that of the dorsals (Figs. 4, 5). Their position of formation, like that of the dorsals, means that the V_L exhibit a net outward movement.

As two dorsal laterals (D_L) are associated with a given dorsal (D), similarly two traces remain and continue upwards in the septal areas following the formation of the outer ventral laterals (V_L) (Figs. 4, 5). With locule opening these continuing traces (3 paired sets) move inwards along the septal radii and establish the placentals (V_P) and septal axials (SA) within each septum (Figs. 2E–F, 4, 5).

The unilocular condition arises through the freeing of the fused inner septal margins near the gynoecial base (Fig. 2C). At this level, the three pair of continuing ventral bundles have moved to the inner septal wing

margins. Here another fusion product, the septal axial (SA), is formed via branches from each of two placental bundles (V_P) in each septum that fuse (Fig. 2E-F). Three of these bundles (SA_1 - SA_3) are so formed (Figs. 4, 5). They lie along the same radius as the ventral laterals (V_L). One peculiar characteristic of the septal axials (SA) is the reversal of their xylem and phloem in relations to all of the other bundles. The septal axials (SA) and the two associated ascending placental bundles (V_P) per inner septal wing margin show no signs of cross-connection throughout their vertical ascent and all three terminate in the upper gynoecial region. (Figs. 2D, 3C, 4, 5).

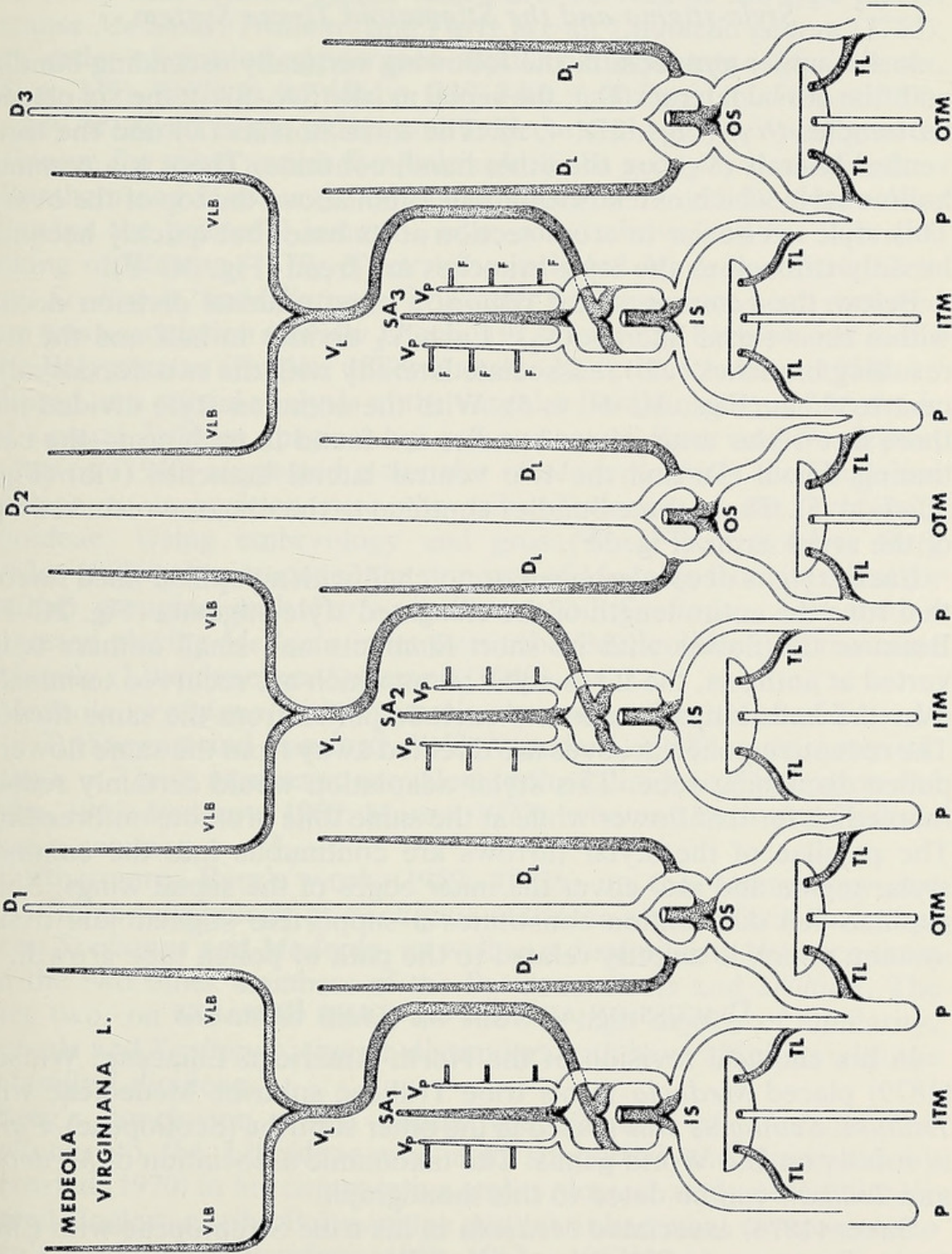
It should be noted that the dorsal laterals (D_L), the septal axials (SA), and the ventral system (placentals— V_P and funicular traces—F) are not observed in sections of buds or early flowering material. They are definite, however, in the more mature flowers and early fruits. The summary diagrams (Figs. 4-5) present these bundles, but it must be remembered that they do not occur in the younger material.

Horizontal funicular (F) branches arise in alternate ranks from the parallel placental bundles (V_P) within each of the three septa (Fig. 5). A maximum number of 18 ovules was observed, that is, six funicular branches (F) per septum or three funicular branches per placental bundle. Because the placental (V_P) and their associated funicular branches (F) are ranked alternately on different sides of the fused margin of two different carpels and the supplied ovules have a vascular supply from two and not one carpel, (Figs. 4, 5), the placentation is parietal (see also Berg, 1962a). Initially, the ovules have a pleurotropic orientation, but following fertilization their orientation changes to a more hypotropic condition. There is a further differential shifting of the developing seeds especially in the upper tier of the mature fruit, such that the resultant seed packing could best be described as heterotropic (terminology after Björnstad, 1970).

The greenish flowering gynoecium is relatively small (diameter, 3-4 mm) compared to that of the globose, purplish-blue berry fruit (diameter, 9-15 mm). The fruit is indehiscent (there were no notches or grooves in the flower to indicate weakness zones) and pulpy. The

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Fig. 5.—Vascularization summary diagram for *Medeola virginiana* showing the following text introduced and discussed bundles and traces: TL = tepal laterals; OTM = outer tepal median (three); ITM = inner tepal median (three); P = large pedicel bundle (six); OS = outer stamen (three; fusion product); IS = inner stamen (three; fusion product); D = dorsal (three; fusion product); D_L = dorsal lateral (three pairs); V_L = ventral lateral (three; fusion product); vlb = ventral lateral branch (three pairs); V_P = ventral placentals (three pairs); SA = septal axial (three; fusion product).



increase in size is chiefly due to the increase in the seed volume and a parenchymatic increase in the number of cells in the pericarp.

Style-stigma and the Stigmatoid Tissue System

In the upper gynoecium, the following vertically ascending bundles end: the dorsal laterals (D_L); the septal axials (SA_1 - SA_3); the six placental bundles (V_P) (Figs. 2D, 4, 5). The three dorsals (D) and the three ventral laterals (V_L), on the other hand, continue. There is a common hollow style which extends for about 1 mm above the top of the ovary. This style is circular in cross-section at its base, but quickly becomes broadly trilobed as the style branches are freed (Fig. 3C-F).

Below the common styler region, a most unusual division occurs within the ventral laterals (V_L). Each V_L divides in half and the two resulting branches (vlb) reassociate laterally with the two dorsals adjacent to them (Figs. 3C-F, 4, 5). With the common style divided into three free styler arms, three bundles are found in each arm—the continuing dorsal (D) and the two ventral lateral branches (vlb) (Figs. 3C-F, 4, 5). These three bundles continue to the extreme recurved tips of the styler arms (Fig. 3F).

Each style is deeply grooved or notched with a papillae-lined furrow that runs the entire length of the elongated style-stigmata (Fig. 2C-F). Because the flower with its short filaments and small anthers is inverted at anthesis, the three styler arms which are recurved terminally over the anther tips function to exclude pollen from the same flower. The receptive pollen grooves are directed away from the same flower's pollen dispersing zone. This styler adaptation would certainly reduce inbreeding for that flower while at the same time promote outbreeding. The papillae of the styler furrows are continuous into the common styler region and also cover the inner edges of the septal wings. Such papillae cell distribution constitutes a supportive stigmatoid tissue system, which is directly related to the path of pollen tube growth.

DISCUSSION AND CONCLUDING REMARKS

In his classical revision of the North American Liliaceae, Watson (1879) placed *Medeola* in his tribe Trillieae subtribe Medeoleae with *Trillium*. *Scoliopus* was placed in the other subtribe (Scoliopeae). *Paris* is strictly an Old World genus. The taxonomic association of *Medeola* and *Trillium* can be dated to this monograph.

Baker (1876) associated *Medeola* in his tribe Streptopeae with *Clin-tonia*, *Prosartes* (= *Disporum* section *Prosartes*), *Disporum* (=section *Eudisporum*), *Streptopus*, and *Kruhsea* (= *Streptopus*). Today all of these genera except *Medeola* are placed in the tribe Polygonatae. In the Englerian system (Engler, 1888; Krause, 1930), *Medeola* is placed in the small, but advanced liliaceous tribe Parideae along with *Paris*,

Trillium, and *Scoliopus*. In recent years, this tribe has been alternatively segregated from the Liliaceae as the family Trilliaceae (Hutchinson, 1934) with *Trillium* rather than *Paris* serving as the type genus. Because *Medeola*, *Trillium*, and *Paris* are all Linnaean genera (1753), their order of printed appearance should be important—*Medeola* (n. 455; p. 339), *Trillium* (n. 456; p. 339–340), and *Paris* (n. 500, p. 367). Clearly *Medeola* is the oldest and indeed should be the valid generic basonym for tribal and/or familial rank, if the group is maintained.

Bentham and Hooker (1883) put *Medeola* in their tribe Medeoleae following the printed Linnaean order noted above and the subtribal ranking of Watson (1879). Their tribe included *Medeola*, *Paris*, *Trillium*, *Scoliopus*, and *Clintonia*. The latter has long since been removed from this association (review Utech, 1973), and has been placed in the tribe Polygonatae (Engler, 1888; Krause, 1930; Hutchinson, 1934).

Based on a partial analysis of the vascular floral anatomy of *Medeola* and several *Trillium* species, but not on that of *Paris* and *Scoliopus*, Anderson (1940) suggested a transfer of *Medeola* from the Englerian Parideae to a position near the tribe Tulipeae of the subfamily Lilioideae. Using embryology and gross floral morphology, Berg (1962a, 1962b) also proposed the removal of *Medeola* from its tribal (or familial) grouping with *Paris*, *Trillium*, and *Scoliopus*, and further suggested placing *Medeola* in its own tribe (Medeolideae) in the same subfamily (Lilioideae) as Anderson (1940).

Medeola virginiana with a somatic chromosome number of $2n = 14$ ($n = 7$) (Stewart and Bamford, 1942; Woodard, 1948) is characteristic of the $x = 7$ base number so prevalent in the Lilioideae (Darlington and Wylie, 1955; Federov, 1969; Moore, 1973), whereas *Paris* and *Trillium* share a common $x = 5$.

Furthermore, Berg's work (1959, 1962b) on the embryology and gross floral morphology of *Scoliopus* indicates a high dissimilarity between *Scoliopus* and *Medeola*, as well as a dissimilarity between them and the two other members of the Parideae, *Paris* and *Trillium*. The latter two, on the other hand, do show a high degree of similarity. *Medeola* and *Scoliopus*, though dissimilar, both have affinities with the subfamily Lilioideae.

Berg's conclusion which relates the affinities of *Medeola* and *Scoliopus* to the Lilioideae was also supported and discussed by Björnstad (1970) in his comparative embryological study of the closely related Englerian tribe Polygonatae and his subsequent comparison to Berg's work on the Parideae (1959, 1962a, 1962b).

The taxonomically important berry fruit so crucial in delineating certain Englerian subfamilies and tribes may well represent a unit of convergent evolution. Though the liliaceous berries are superficially similar and useful (visually) taxonomically, they may not at all reflect a

natural relationship. The bird dispersal of these red, blue, and black berries so common in the forest environments would be a selective pressure for this type of convergent evolution.

It is hoped that the detailed examination of the total vascular floral anatomy which underlies the liliaceous berry can be used in establishing lines of natural relationships. It is from this point of view, that the floral anatomy of *Medeola* is here presented. Similar investigations are currently in progress on *Scoliopus*, *Trillium* and *Paris*, as well as other members of the berry-fruited tribe Polygonatae.

SUMMARY

The total floral vascularization of *Medeola virginiana* results from two different sets of six pedicel bundles. A sclerenchymatous sheath differentiates the flowering from the fruiting pedicel. The lower pedicel contains a double ring of six inner and six outer bundles. The six outer bundles establish the three outer and three inner tepal medians directly in two whorls without fusion or branching. The six inner bundles, on the other hand, are clearly compound and undergo several radial divisions each. These divisions are subsequently followed by various whorl-separated levels of fusion. The lower whorl division results in the formation of six (three sets of two) outer tepal laterals. No fusion is associated with the formation of the tepal laterals, but they do branch further in laminal tepal surface. Each tepal has seven parallel veins, that is, three TL plus median plus three TL.

Further division and fusion of the continuing inner pedicel bundles result in the formation of the six stamen traces (both whorls), the three dorsals, the six dorsal laterals, the three ventral laterals, the six ventral placentals, and the three sepal axials. The stamen, dorsal, ventral lateral, and septal axial traces are all fusion products.

The tricarpellate gynoecium is unilocular, because the septal wing tips are free at the gynoecial base. This species lacks raphides, septal glands, and dorsal notches. Three bundles (that is, continuing dorsal plus two branches from different ventral laterals) occur in each of the three recurved stylar arms. Papilloid cells line the three inner notched stylar arms and are continuous downward through the common hollow stylar canal to the base of the gynoecium.

In flower, the pedicels are directed downwards, whereas in fruit, they are erect. The development in the fruiting pedicel of a sclerenchymatous sheath around the vascular bundles may be related directly to upward shift of the pedicel. The pendulent flower, on the other hand, has a style-stigma system which excludes its own pollen due to the location of the outward directly stylar furrows and the long, recurved stylar tips. The extrorse anthers also promote outbreeding. The flowering gynoecium is relatively small compared to the size of the resulting

fruit. A maximum number of 18 ovules (six/carpel) is not uncommon. The ovule arrangement is variable.

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