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Staminal Vascular Architecture in Five Dicotyledonous Angiosperms

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Staminal Vascular Architecture in Five Dicotyledonous Angiosperms[1]

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Staminal vasculature is usually depicted as a single bundle extending unchanged through the filament and ending at some level in the anther. Because some authors have suggested that this view is oversimplified, stamens of five dicot species were studied in detail. The basifixed anthers of *Asarum canadense, Drimys winteri,* and *Isopyrum biternatum* have a single vascular bundle which becomes dilated in the connective, along with other specializations which vary from species to species. *Pyrus* sp. and *Prunus virginiana* have dorsifixed anthers in which the filament bundle branches after entry into the anther. The extent of branching, and the internal architecture of the bundles, varies with the form of the stamen.

INDEX DESCRIPTORS: Floral anatomy, stamen anatomy, staminal vasculature, stamen filament, anther.

As pollen develops in the anther, relatively large amounts of nutrients flow through the staminal vasculature. Staminal vein endings, therefore, unlike those of other organs such as the leaf or root, are concerned with nutrient release rather than nutrient accumulation or uptake. Since the gross morphology of stamens is quite varied it could also be expected that variations would occur in the staminal vascular architecture. Some investigators (Eames, 1931; Wilson, 1942; Canright, 1952; Heel, 1966; Schmid, 1976; Stevenson and Owens, 1978) have shown that variations do exist, especially in the patterning and branching of the vascular bundle.

Although it has been shown that variation does exist in the vascular morphology of staminal bundles, virtually all textbooks which include floral anatomy and morphology (e.g. Eames, 1961; Esau, 1965, 1977; Foster and Gifford, 1974), and many other works on floral anatomy, continue to depict the "common stamen" as having a single uniform, unbranched bundle which ends abruptly in the connective of the anther.

An often cited source for the generalization that stamens have a simple bundle is Wilson (1942), who stated: "A preliminary and by no means exhaustive survey of the nature and direction of the course of the vascular bundles of stamens makes possible an estimate that in probably 95 percent of angiosperms the stamen is supplied with a single vascular bundle which transverses the filament. This bundle may end at the base of the anther or may ascend the connective for some distance, to end blindly at a greater or lesser distance from the apex." Wilson did not mention the extent of his study or the species used, nor did he cite any other studies to support his statement. Due to this uncertainty in the literature it seemed desirable to sample further. This paper describes the staminal vasculature of 5 selected dicotyledonous species.

MATERIALS AND METHODS

The species studied were *Asarum canadense* L. (Aristolochiaceae), *Drimys winteri* Forst. (Winteraceae), *Isopyrum biternatum* (Raf.) T.&G. (Ranunculaceae), *Prunus virginiana* L. (Rosaceae), and *Pyrus* sp. (a cultivated flowering crab, Rosaceae). Flowers and flower buds were collected from living plants in or around Ames, Iowa, except for *Drimys winteri*, which had been collected previously in San Francisco, California and preserved. All flowers were fixed in formalin-acetic acid- alcohol.

Samples consisting of whole flowers and/or individual stamens were cleared using the method of Shobe and Lersten (1967). Specimens were transferred from NaOH to full-strength household bleach for a few minutes before rinsing in water. All clearings were stained with safranin and chlorazol black E.

Specimens to be sectioned were dehydrated in an ethanol-xylene series and embedded in 56° mp paraplast. Stamens of all species except for *D. winteri* were sectioned 8-12 μm thick in both longitudinal and transverse planes, stained with safranin and chlorazol black E (Berlyn and Miksche, 1976), and mounted in either Permount or Piccolyte.

OBSERVATIONS

Drimys winteri

The stamen of *D. winteri* has laterally protuberant locules (Fig. 1, 2). Bailey and Nast (1943) noted that the vascular bundle of winteraceous stamens may remain unbranched, or it may give off one or more branches that are directed toward the locules. I also found that in most stamens a single vascular bundle passes through centrally and ends just short of the distal end of the anther. The end of the vascular bundle appears frayed in clearings because the terminal tracheary elements are directed outward from the core of the bundle (Fig. 1). Branching of the bundle was seen in only one stamen. Each branch ended at the base of a different anther lobe, and the central bundle ended just short of the distal end of the stamen (Fig. 2). Each bundle in this branched system, however, showed the frayed terminus characteristic of other *D. winteri* stamens.

Isopyrum biternatum

The stamen has a single vascular bundle which ends just short of the distal end of the anther. In transverse view the anther is radially symmetrical with the locules distributed equally about the vascular bundle in the central part of the connective. The vascular bundle is collateral throughout the filament and anther, though in the anther the bundle is somewhat dilated, as has also been observed in *Aquilegia formosa* (Ranunculaceae) by Tepfer (1953). Surrounding the bundle is a ring of enlarged cells which appears to be a bundle sheath (Fig. 13). The filament bundle has a group of about 6 tracheary elements and 2-5 (most commonly 3 or 4) sieve tube members in transectional view. Tracheary elements and sieve tube members are separated by a few layers of vascular parenchyma cells (Fig. 13, 14). In the anther, tracheary elements remain in a tight group but sieve tube members diverge into several smaller groupings of strands. However, the total number of sieve tube members, as seen in transectional view, is the same following divergence. Similarly, the number of tracheary elements remains constant after the bundle passes from the filament to the anther.

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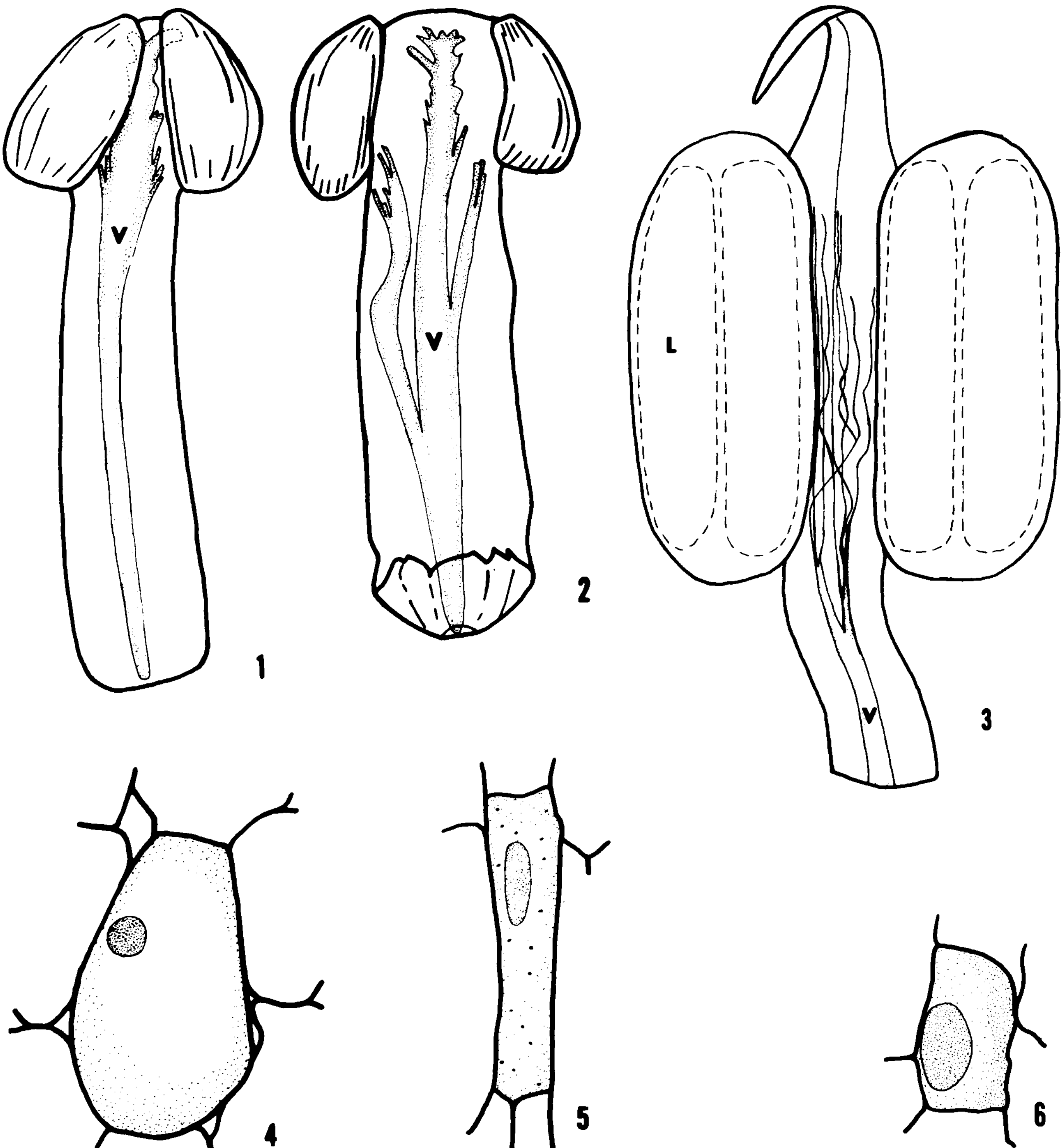


Fig. 1-6. Fig. 1-3. *Diagrammatic representations of stamens from clearings*. Fig. 1. Drimys winteri *with a single vascular bundle (V) showing "frayed" terminus caused by turning outward of the xylem strands*. Fig. 2. Drimys winteri *with branched vascular bundle (V)*. Fig. 3. Asarum canadense *xylem strands within the vascular bundle (V) separate from one another upon entry into the anther. L indicates locule*. Fig. 4-6. *Parenchyma types of the* Asarum canadense *anther*. Fig. 4. *Connective parenchyma. X3300*. Fig. 5. *Phloem parenchyma. X3300*. Fig. 6. *Xylem parenchyma. X3300*.

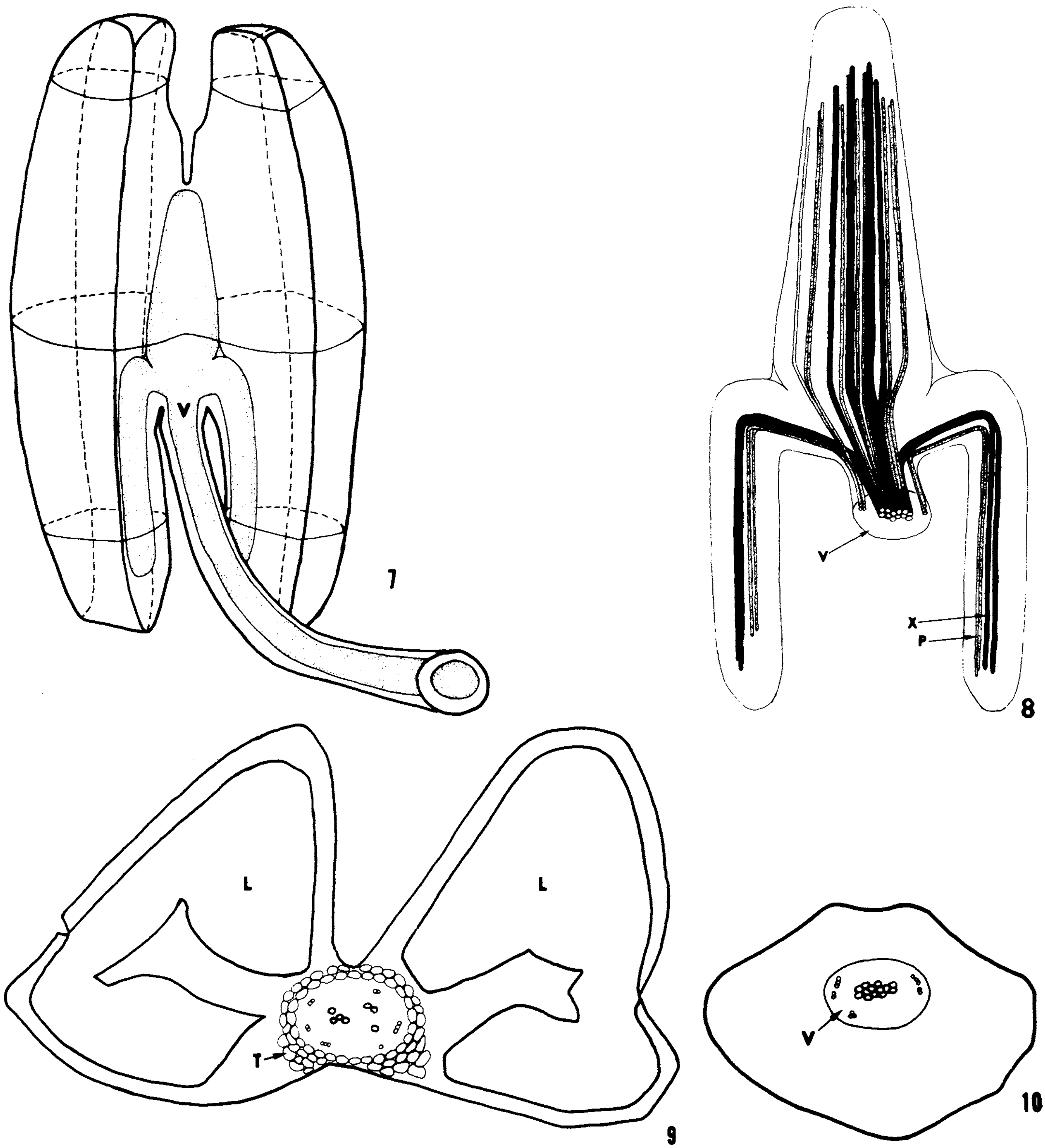
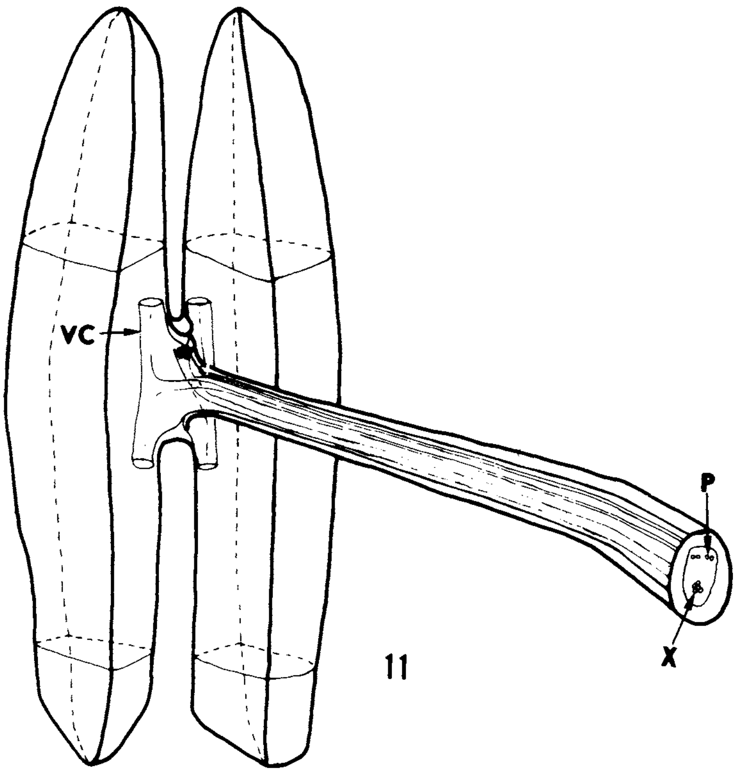


Fig. 7-10. *Diagrammatic representations of the* Pyrus *sp. stamen.* Fig. 7. *Gross morphology showing the outline of the single vascular bundle (V) in the filament and its branching pattern in the dorsifixed anther.* Fig. 8. *Diagrammatic reconstruction of the anther vasculature shown in fig. 7. Stippled strands (P) indicate phloem, solid strands (X) are xylem. Vascular bundle enters anther from filament at V. A single large bundle ascends the central connective (see fig. 9), and two small bundles descend into the lower portions.* Fig. 9. *Transection of the upper portion of the anther, as in fig. 7, near dehiscence. The ascending amphicribral bundle is surrounded by tanniniferous cells (T). L indicates locule.* Fig. 10. *Filament transection showing amphicribral to hemiamphicribral vascular bundle (V).*



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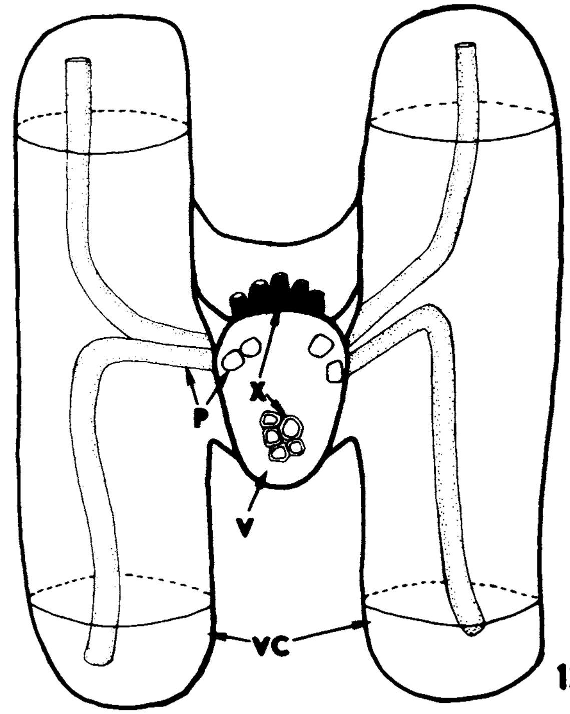

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Fig. 11-12. Fig. 11. *Diagrammatic reconstruction of* Prunus virginiana *stamen showing the single collateral vascular bundle in the filament and its 4 vascular cylinders (VC) in the anther.* Fig. 12. *Enlargement of vascular cylinders of Fig. 11 as viewed from the end of the filament. Collateral bundle (V) of filament enters anther and branches into 4 vascular cylinders (VC). A single strand of phloem (P) enters each vascular cylinder. All xylem strands (X) turn upward and end in the broadened vascular mass between branches.*

Asarum canadense

A single vascular bundle passes through the filament and anther, then extends up into a distal appendage. (Fig. 3). In the filament the bundle is a slender, tight cylinder, but as it enters the anther this cylinder expands to cover an approximately one-third larger area, transectionally. Throughout the stamen the vascular bundle is collateral or hemiamphicribral with the phloem in a semicircular arc around the central core of xylem.

No visible bundle sheath separates the vascular bundle from the connective of the anther. Successive connective parenchyma cells are progressively smaller closer to the bundle.

The vascular bundle of the anther has a large quantity of xylem parenchyma cells which separate strands of tracheary elements (Fig. 16). The cytoplasm of these parenchymatous cells stains more intensively than cytoplasm of parenchymatous cells in the connective. Xylem parenchyma cells are smaller and more box-like in form than the connective cells (Fig. 4, 6), and have large, prominent nuclei approximately 1/3 larger in diameter than the nuclei of the connective cells. Between the phloem and the xylic core of the bundle are other parenchyma cells, more slender than the connective parenchyma (Fig. 5).

A semicircular arc of phloem is located on that side of the bundle nearest to the adaxially aligned locules (Fig. 15). Sieve tubes occur in slender groups of strands separated from one another by parenchymatous cells (Fig. 16). Each phloem group usually contains 3 sieve tube members but some have more or less. These groups extend continuously through the anther, ending at various levels as the vascular bundle narrows distally, near the upper end of the locules. The relative positions of the phloem groups do not vary significantly throughout the anther.

In the filament, and in the proximal portion of the anther, the sieve tube members with their associated companion cells are quite prominent. Each group of sieve tube members is associated with one or two companion cells, which could be identified by their extremely dense cytoplasm in relation to surrounding parenchyma cells.

Tracheary strands in the filament bundle occur as one cylinder or as two adjacent cylinders. As the vascular bundle enters the anther it expands and the xylem separates into several strands, which remain distinct in their meandering paths upward (Fig. 3). Most of these strands end at various levels in the anther. Near the distal end of the anther, where the locules end, the vascular bundle narrows and the remaining tracheary strands converge. One or two strands continue up into the distal appendage (Fig. 3).

Tracheary elements in the filament are slender and elongate with flat end walls. After the xylem strands diverge in the anther, however, many tracheary elements appear twisted or bent, with knobby or otherwise distorted connections between cells, while others have long overlapping end walls (Fig. 17-19). Tracheary elements in the anther appear similar to the terminal tracheids or "storage tracheids" (Foster, 1956) which occur near or at vein endings in many leaves.

Pyrus

A single hemiamphicribral to amphicribral bundle extends through the filament; however, at the junction of the filament and the anther this bundle gives off two smaller bundles, each of which proceeds down-

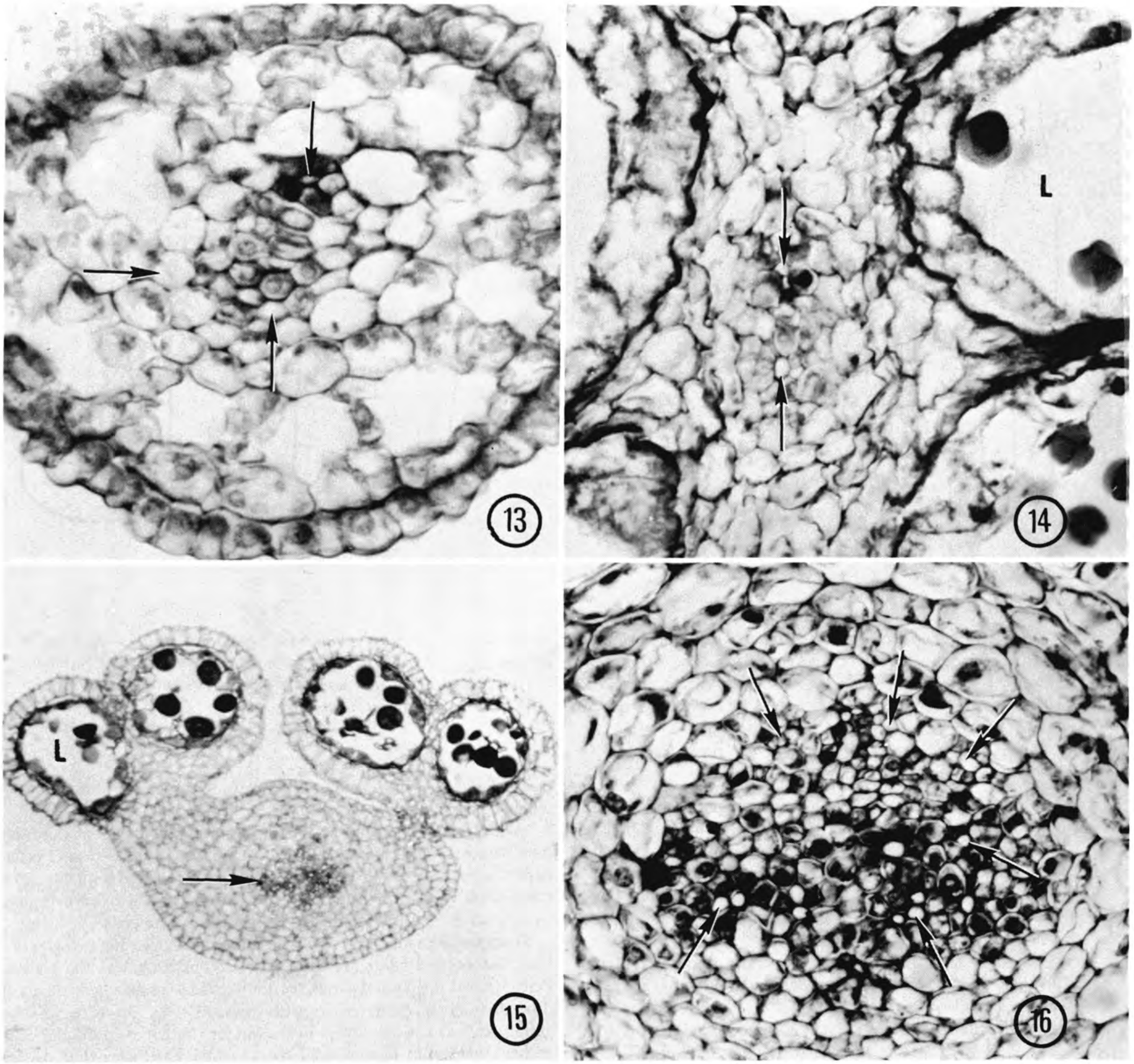

Fig. 13-16. Fig. 13. Isopyrum biternatum *filament transection showing single vascular bundle with surrounding bundle sheath (middle arrow). Xylem (lower arrow) and phloem (upper arrow) are separated by a few layers of vascular parenchyma cells. X1100.* Fig. 14. Isopyrum biternatum. *Transection of connective shows vascular bundle located centrally between the four locules (L). As in the filament, the collateral bundle has phloem (upper arrow) flanked by xylem (lower arrow). X530.* Fig. 15. Asarum canadense *anther transection showing vascular bundle (arrow) location in relation to the locules (L). X100.* Fig. 16. *Enlargement of the anther vascular bundle in Fig. 15. Groups of sieve tube members (3 indicated by upper arrows) are found in a semicircular arc around the centrally located xylem strands (3 indicated by lower arrows). X430.*

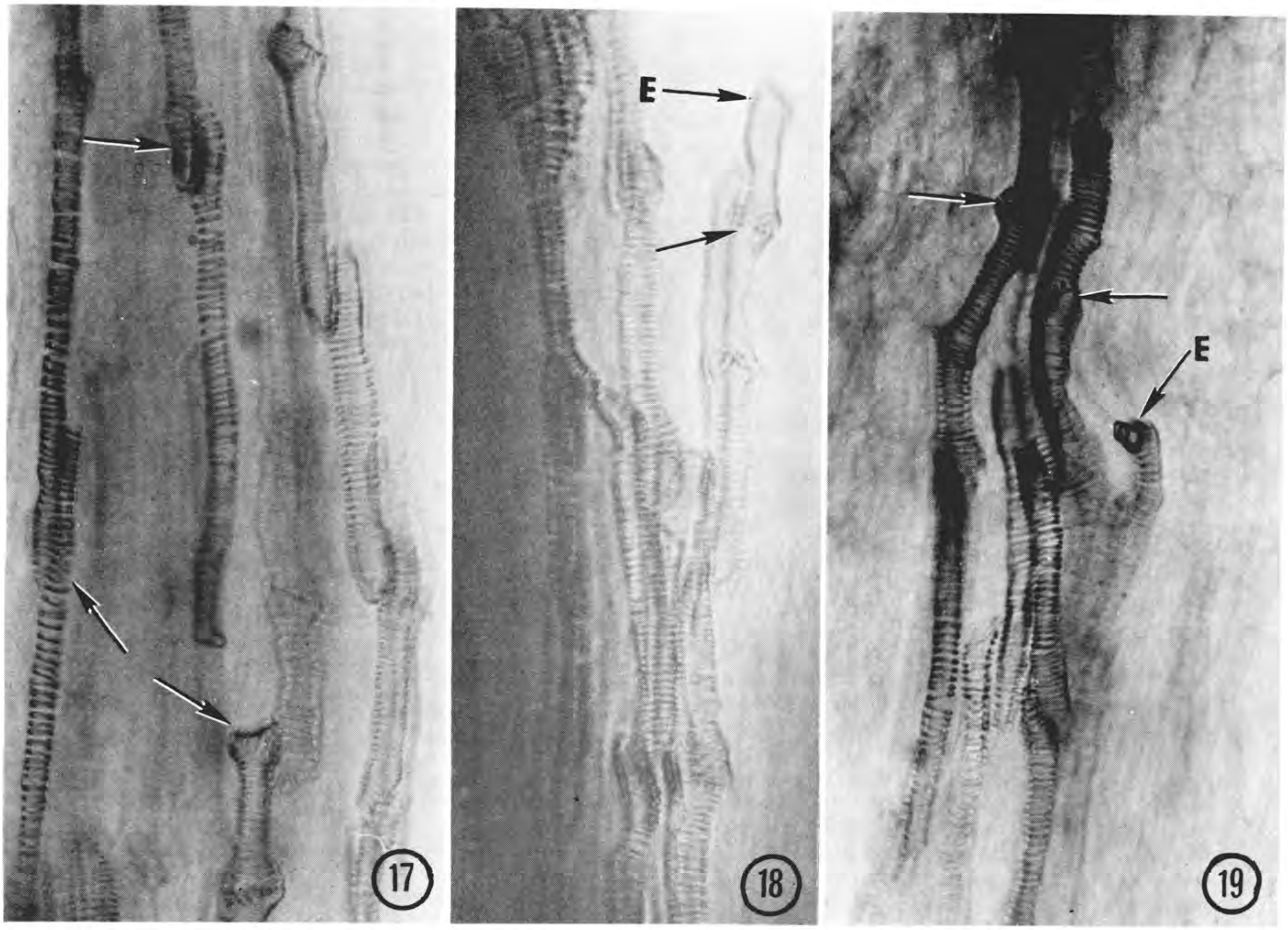

Fig. 17-19. *Tracheary elements of the* Asarum canadense *anther from cleared preparations. Many tracheary elements of the xylem strands have a characteristic form similar to "storage tracheids".* Fig. 17. *Xylem strands near mid-anther. Two upper arrows show cells with long overlap of their ends. Lower arrow shows an example of the knobby joint often seen in these cells. X530.* Fig. 18. *Point in the anther of one strand ending (E). Lower arrow points out another example of the knobby connections found between many of these cells. X530.* Fig. 19. *Illustration of the convergence of the strands near the distal end of the locules. A strand ending is shown at E. The 2 upper arrows point out further variation in the joints between these cells. X530.*

ward into a lobe of the anther (Fig. 7) but ends short of the lobe tip. The major bundle ascends into the central area of the connective tissue that joins the two anther lobes and ends at the level where the lobes of the anther separate from one another.

The ascending bundle is approximately half again as large in diameter as the bundle in the filament, and it retains its hemiamphicribral to amphicribral orientation. The phloem of the ascending bundle occurs as several small groups of strands, each with 2-3 sieve tube members (Fig. 8). Most of the phloem strands are found on the side of the anther toward the filament junction; however, some were also found on the sides of the bundle nearer the locules (Fig. 9).

The two descending bundles have approximately 8 tracheary strands and approximately 6 sieve tubes in each trace (Fig. 8). In these bundles the xylem strands are on the side of the bundle toward the locules and the phloem strands are on the outside. As the bundle descends the lobe the amount of phloem decreases rapidly.

In transectional view, there was no increase of sieve elements in the anther over that seen in the filament. In some stamens, the groups of sieve tube members present in the filament diverged upon passage into the anther but no increase in number of sieve tube members was noted (Fig. 9, 10).

The tracheary elements of the *Pyrus* anther also resembled storage tracheids, but not as much as in *Asarum*. The tracheary elements appeared to change in form upon entry into the anther, as in *A. canadense*.

The vascular bundle of the *Pyrus* anther, like the anther bundle in *A. canadense*, was composed largely of vascular parenchyma. Tanniniferous cells surround all of the bundles in the anther, but such cells were not found around the bundle in the filament (Fig. 9, 10). The tanniniferous cells appear to form a bundle sheath. In the descending bundles they occupy an area as great as, or greater than, the area of the bundles. In many places along the bundles the tanniniferous cells were more than one layer thick.

Prunus virginiana

One vascular bundle extends through the filament and, as in *Pyrus*, it branches at the junction of the filament and anther. The anther is composed of two almost separate lobes, which are joined tenuously only where they connect to the filament (Fig. 11). The bundle broadens greatly at this junction and some vascular branching occurs. Compared with the *Pyrus* anther, however, vascular branching in *P. virginiana* is extremely reduced. The degree of branching varies from anther to anther, as does the direction taken by the branching bundles. In some anthers 4 branch bundles may exist, in others 3 or 2, and in some only 1 may branch from the broadened vascular mass at the junction point; infrequently, the bundle may even remain unbranched. Short vascular branches may extend upward and/or downward into either lobe, or variations on this may occur.

The branches usually contain 1-2 phloem strands and no tracheary elements. The xylem strands turn upward and fray outward in the broadened mass of vascular tissue near the anther/filament joint, but do not progress toward any branch (Fig. 12).

As in *Pyrus*, tanniniferous cells surround the anther bundle and any branch bundles that may occur. A layer of these cells surrounds the anther bundles as a bundle sheath. Tanniniferous cells were not found around the vascular bundle in the filament.

DISCUSSION

The evidence from this study supports the observations of others (Wilson, 1950; Heel, 1966; Schmid, 1976) who have shown that there is great variation in staminal vasculature. The internal architecture of each bundle is also variable from species to species. It appears that the orientation of xylem and phloem within each bundle of each species is adapted for efficiency to the particular form of the stamen. It has been conjectured by Schmid (1978) that these specific xylem and phloem orientations are more efficient in supplying nutrients to the developing pollen grains. In *Pyrus* I noted that the phloem in the ascending trace lies in close proximity to the locules (Fig. 9). Even in the highly reduced anther bundle of *Prunus virginiana*, the phloem strands become directed into or near the anther lobes (depending on the branching pattern of that particular stamen), whereas the xylem strands end in the tenuous connective area (Fig. 11 and 12). In the *Asarum* stamen, all of the locules are in one plane with the vascular bundle along the adaxial (inner) surface (Fig. 15). The collateral or hemiamphicribral bundle, with phloem oriented toward the locules, could be an adaptation for more efficient nutrient delivery in this stamen.

In the radially symmetrical anther of *Isopyrum biternatum* one would have expected an amphicribral bundle similar to that of the ascending bundle of the *Pyrus* anther; instead, the anther bundle in *I. biternatum* is collateral, with relatively little phloem (Fig. 14). However, it does possess a bundle sheath, a feature lacking in stamens of all other species studied. Therefore, the bundle sheath may have a function in directing the flow of nutrients to the radially oriented locules.

Wilson (1942) saw phylogenetic significance in certain variations of staminal bundle patterns. In agreement with Eames (1931), Wilson considered a 3-bundle system in the anther as primitive. Schmid (1972), in contrast, viewed amplification of staminal vascular patterns as a functional response in relationship to form. The branching of the bundles in *Pyrus* and *Prunus* anthers could be interpreted as adaptations to the form of these groups. These rosaceous species with branching anther bundles both had dorsifixed anthers, whereas in the basifixed anthers of *Isopyrum biternatum* and *Asarum canadense* there was only a single, unbranched vascular bundle.

It is evident from even this small sample that vascular structure of stamens is more elaborate than the simple, unbranched, uniform bundle usually depicted in botanical works. Except for pollen development, stamen anatomy has been largely neglected and greatly oversimplified as a result. This study shows that stamen vasculature is unexpectedly varied, and that a broader survey of stamen anatomy is needed.

REFERENCES

BAILEY, I.W., and C.G. NAST. 1943. The comparative morphology of the Winteraceae. I. Pollen and stamens. J. Arnold Arb. 24:340-346.

BERLYN, G.P., and J.P. MIKSCHE. 1976. Botanical microtechnique and cytochemistry. Iowa State Univ. Press, Ames.

CANRIGHT, J.E. 1952. The comparative morphology and relationships of the Magnoliaceae. I. Trends of specialization in the stamens. Amer. J. Bot. 39:484-497.

EAMES, A.J. 1931. The vascular anatomy of the flower with refutation of the theory of carpel polymorphism. Amer. J. Bot. 18:147-188.

EAMES, A.J. 1961. Morphology of the angiosperms. McGraw-Hill, New York.

ESAU, K. 1965. Plant anatomy. John Wiley & Sons, New York.

ESAU, K. 1977. Anatomy of seed plants. John Wiley & Sons, New York.

FOSTER, A.S. 1956. Plant idioblasts: remarkable examples of cell specialization. Protoplasma 46:184-193.

FOSTER, A.S., and E.M. GIFFORD. 1974. Comparative morphology of vascular plants. W.H. Freeman and Co., San Francisco.

HEEL, W.A. VAN. 1966. Morphology of the androecium in Malvales. Blumea 13:177-394.

SCHMID, R. 1972. Floral bundle fusion and vascular conservatism. Taxon 21:429-446.

SCHMID, R. 1976. Filament histology and anther dehiscence. Bot. J. Linn. Soc. 73:303-315.

SCHMID, R. 1978. Reproductive anatomy of *Actinidia chinensis* (Actinidiaceae). Bot. Jahrb. Syst. 100:149-195.

SHOBE, W.R., and N.R. LERSTEN. 1967. A technique for clearing and staining gymnosperm leaves. Bot. Gaz. 128:150-152.

STEVENSON, D.W., and S.J. OWENS. 1978. Some aspects of the reproductive morphology of *Gibasis venustula* (Kunth) D.R. Hunt (Commelinaceae). Bot. J. Linn. Soc. 77:157-175.

TEPFER, S.S. 1953. Floral anatomy and ontogeny in *Aquilegia formosa* var. truncata and *Ranunculus repens*. Univ. Calif. Pub. Bot. 25:513-576.

WILSON, C.L. 1942. The telome theory and the origin of the stamen. Amer. J. Bot. 29: 759-764.

WILSON, C.L. 1950. Vascularization of the stamen in the Melastomaceae, with some phyletic implications. Amer. J. Bot. 37:431-444.