

THE NODAL ANATOMY AND THE PRIMARY VASCULAR CYLINDER OF THE CALYCANTHACEAE

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With two plates

THE VASCULAR ANATOMY of the Calycanthaceae has long been known to be of a peculiar character, owing to the presence in the internodes of most stems of four ¹ inverted "cortical" vascular bundles. These bundles ² which first appear in the epicotyl of the seedling extend throughout the stems of mature plants and have branches which enter the opposite leaves at the nodes.

In the past, investigators in studying the anatomy of the stem have focused their attention largely upon the structure and behavior of the aberrant cortical bundles.³ Less attention has been given to tracing the course of the strands in the normal part of the eustele. There is evidence in some dicotyledons which may be interpreted as indicating the derivation of cortical bundles by modification of the lateral traces of plants having trilacunar or multilacunar nodes. It is important in studying the relationships of the Calycanthaceae to determine whether the cortical bundles of the family have evolved in this way or have developed by the addition of a superimposed system of vasculature in plants having fundamentally unilacunar nodal structure. In this connection we have made a detailed investigation of the primary vascular cylinder of the Calycanthaceae which we report in the following pages.

MATERIAL AND METHODS

Material of both *Calycanthus* and *Chimonanthus* was examined. Branches of *Calycanthus fertilis* Walt. (*C. glaucus* Willd.), Arnold Arboretum 12946, *C. fertilis* Walt. var. *laevigata* (Willd.) Bean (*C. fertilis* var. *ferax* (Michx.) Rehd.) A. A. 13400, *C. floridus* L., A. A. 5255 and *C. floridus* L. var. *ovatus* (Ait.) D.C., A. A. 1542 were obtained from shrubs growing at the Arnold Arboretum. Branches of *Chimonanthus praecox* (L.) Link. (*C. fragrans* Lindl.) were secured from the garden of Dr. H. L. Blomquist, Durham, N. C.

The youngest parts of the growing shoots — the vascular system of which consisted of primary tissue only — were cleared by heating in lactic acid, and were examined, after removal of the hairy epidermis, while

¹ Baillon (3) refers to the occurrence of five such bundles in a specimen of *Chimonanthus fragrans* (= *C. praecox*). This rapidly elongating specimen had a 2/5, instead of the usual decussate, phyllotaxis.

² Van Tieghem (13) claimed that they develop in the pericyclic tissue of *Chimonanthus*.

³ In this connection see Baillon (3), Boureau (4), Lignier (6), Quinlan (10), Tieghem (13), Woronin (14) and Worsdell (15).

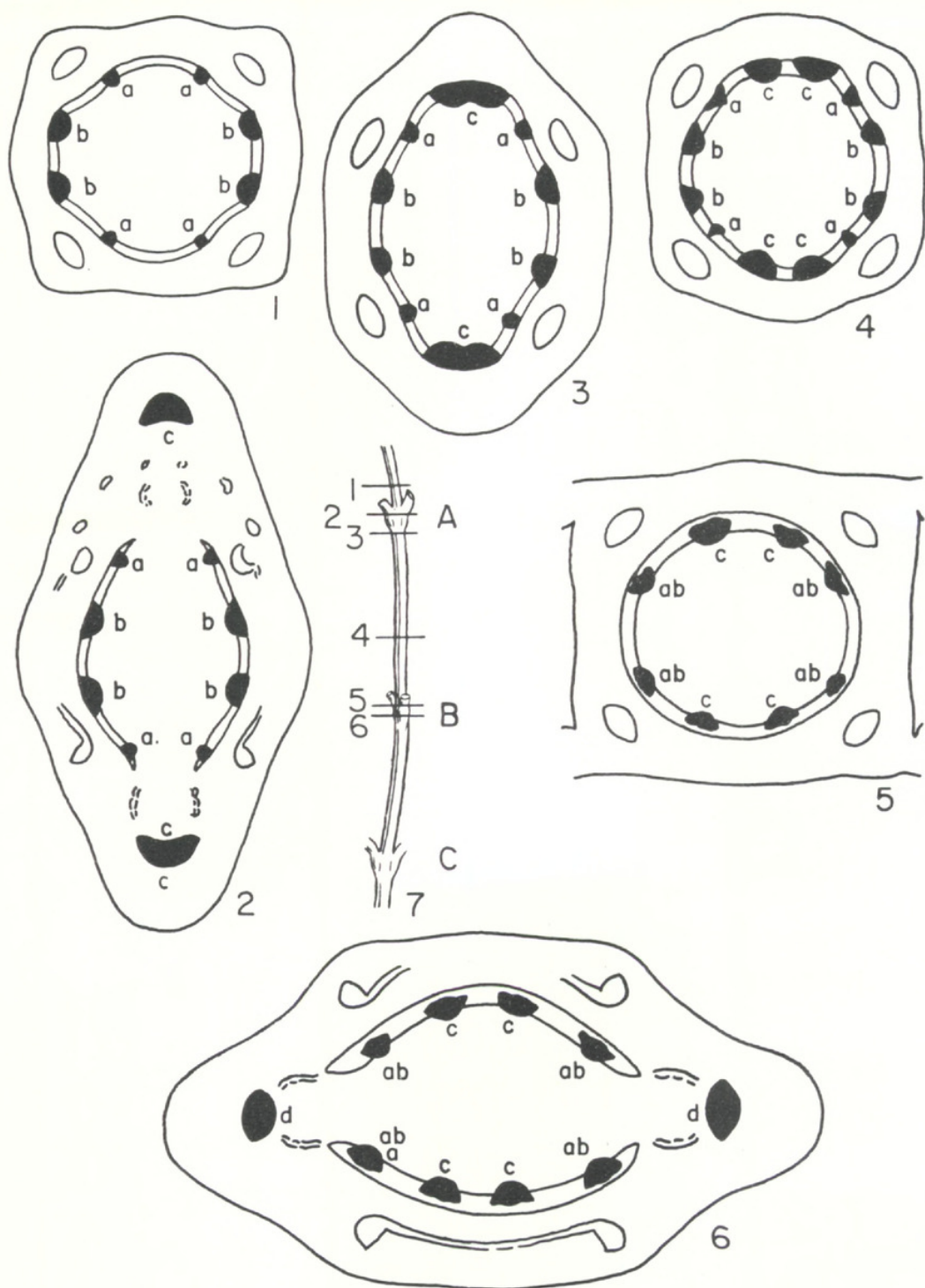
preserved in the acid. In some cases, it was necessary to treat the cleared material for about 20 minutes with a 10% solution of sodium hydroxide in order to remove crystals which appeared after clearing with lactic acid. In addition, the terminal parts of growing stems were embedded in paraffin and serially sectioned through 3–4 nodes from the apex downward. These serial transverse sections were stained with safranin and fast green. Parts of branches having secondary vascular tissues were serially cross-sectioned through three nodes. The sections were made from living stems with a sliding microtome without embedding. They were arranged serially on slides in glycerine mounts.

OBSERVATIONS

The primary vascular pattern in the stems of the species examined was found to be basically the same in both genera of the Calycanthaceae. The chief differences observed were in the levels of “branching” and “fusing” of the vascular bundles of the eustele. In both genera, it was possible to follow successive stages in the “fusing” of pairs of leaf traces during the development of the unilacunar nodes and during the elongation of the internodes.

In the terminal parts of cleared growing shoots, *Plate I, A & B*, the developing leaf traces reveal no appearance of approximation or fusing below the levels of attachment of the leaves. In serial cross sections of such immature parts of the stems, there are two discrete strands of xylem and phloem. No procambial tissue could be detected between them, indicating that two independent strands of procambium develop at an early stage. At lower, more laterally expanded levels of the shoot, *Plate I, B*, approximation of the vascular strands of each foliar pair is attained by the downward extension of additional longitudinal files of tracheary cells. This appearance of ontogenetic fusing is obvious in comparing successively formed pairs of leaf traces in the same orthostichy of the decussate phyllotaxis. Each trace of a foliar pair also fuses with a trace of another leaf, approximately two nodes below the level of the leaf which it vascularizes, *Plate I, B*.

In serial cross sections of older parts of the stem, the existence of a similar pattern of primary vasculature may be traced. For example in cross sections of *Calycanthus fertilis* var. *laevigatus*, *Fig. 7*, there are eight primary bundles in the eustele just above the level of node A, *Fig. 1*; two pairs of traces labeled (a) and two pairs marked (b). At the nodal level of A, there are two additional large vascular strands (c) located opposite two conspicuous gaps in the eustele, *Fig. 2*. Just below the nodal level of A, these strands (c) form integral parts of the eustele, *Fig. 3*, which now consists of 10 traces. Lower in the internode the inherent doubleness of strands (c) becomes increasingly apparent, *Fig. 4*, and there are 12 well separated traces. At the base of the internode, *Fig. 5*, the number of discrete strands is reduced to eight by the approximation or “fusion” of four pairs of the (a) and (b) strands. At node B, *Fig. 6*, the arrangement



FIGURES 1-6. Cross sections of the mature part of a shoot of *Calycanthus fertilis* var. *laevigatus*, cut at the successive levels shown in FIGURE 7. The primary xylem of the eustele and the median vascular strand of the leaf-base are shown in solid black. The cortical bundles, the vascular strands of the buds and the secondary xylem are merely outlined.

described at node A recurs except that the axis of the leaf gaps is now at right angles to that at node A.

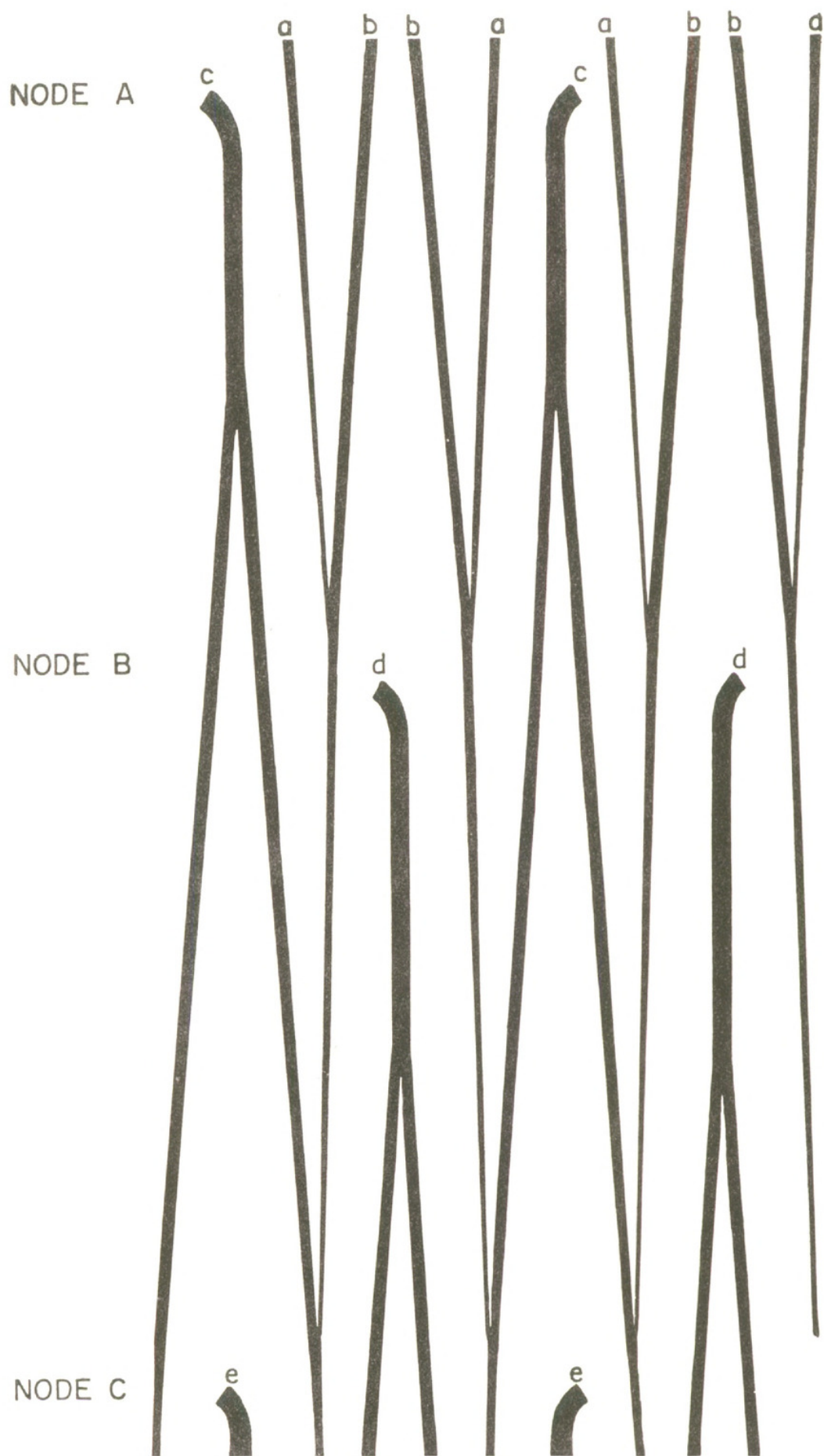


FIGURE 8. Diagrammatic reconstruction of the longitudinal course of the vascular strands of the eustele in *Calycanthus fertilis* var. *laevigatus*.

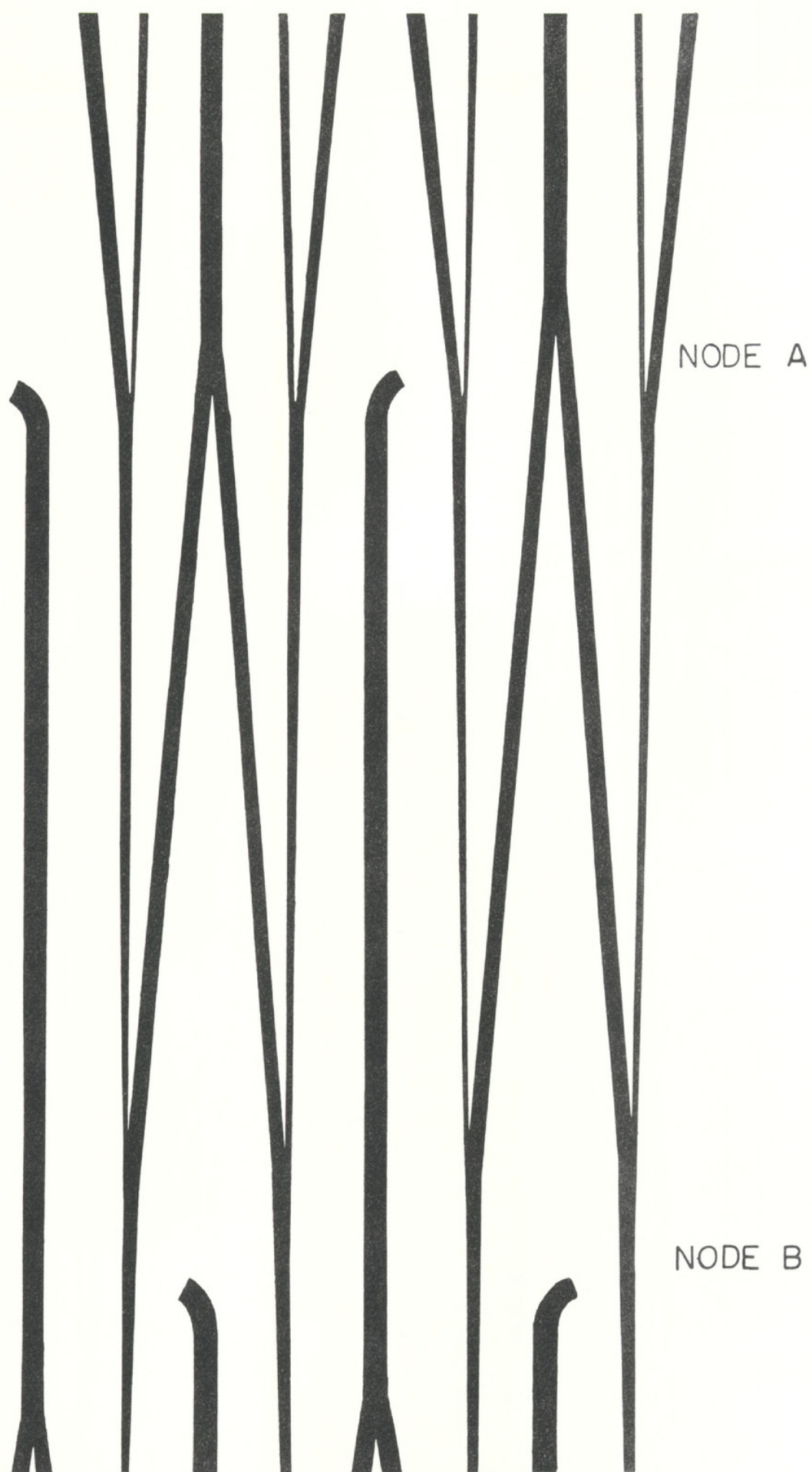


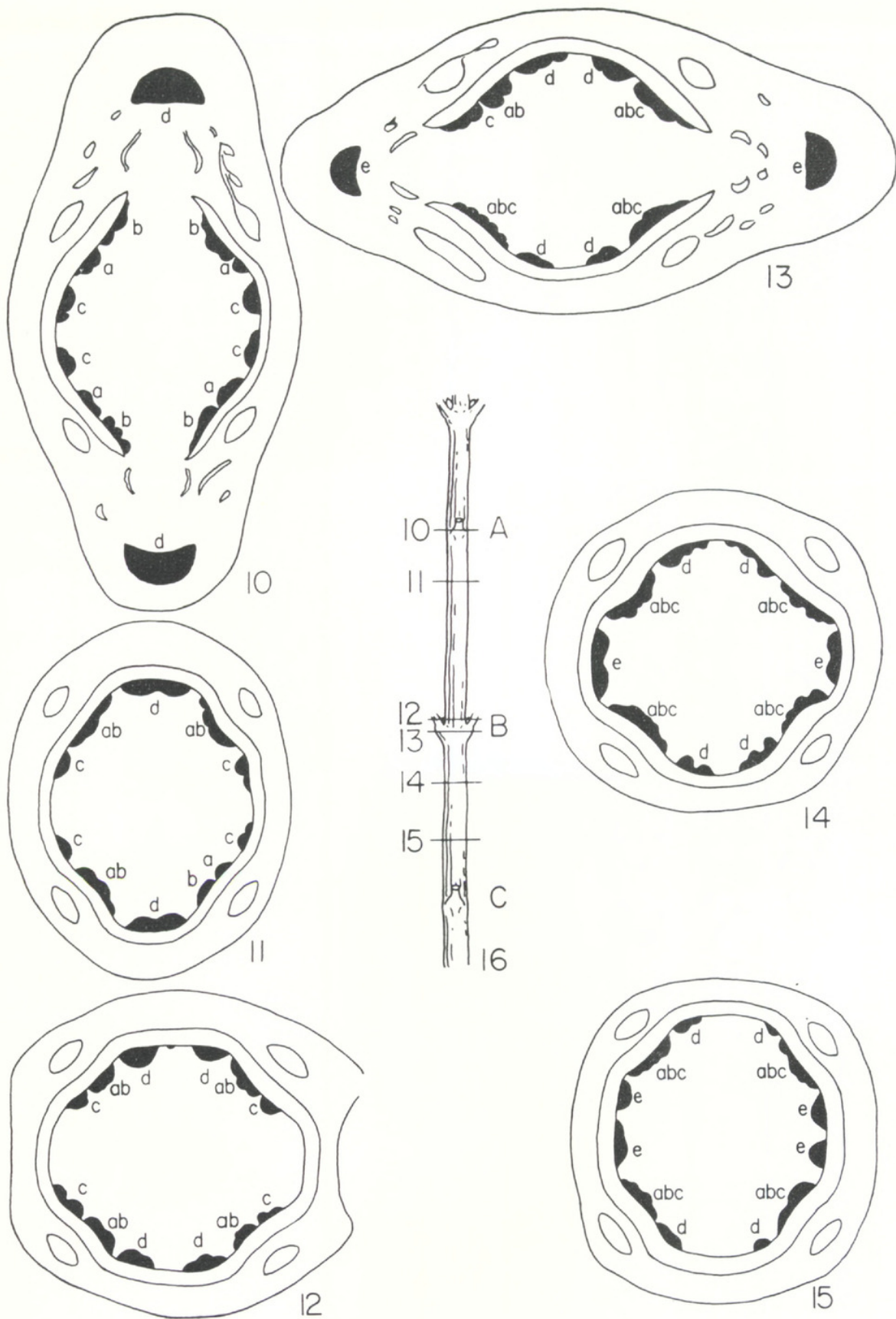
FIGURE 9. Diagrammatic reconstruction of the longitudinal course of the vascular strands of the eustele in *Calycanthus floridus* var. *ovatus*.

The longitudinal course of the leaf traces in the mature stem may be reconstructed from serial cross sections, and is diagrammatically shown in *Fig. 8*. The pattern is in agreement with ontogenetic evidence obtained from the elongating, immature, terminal parts of the axis, *Plate I, B*.

In fully matured stems, the paired leaf traces commonly approximate or apparently "fuse" in the middle part of the first subtending internode below the level of attachment of a leaf. In early ontogenetic stages, the fusing of the two principal foliar strands, as previously mentioned, occurs only within the leaf itself, *Plate I, B*.

As in the case of *Austrobaileya*, *Trimenia*, *Ascarina* and other plants having fundamentally double-trace unilacunar nodes, there is considerable individual and interspecific variation in the levels at which fusing of the two leaf traces occurs and in the levels at which these traces join the traces of other leaves, compare *Figs. 8 and 9*. Thus, the number of discrete strands visible in cross sections of mature stems varies at times even at corresponding levels. For example, as shown in *Fig. 8*, there commonly are in stems of *Calycanthus fertilis* eight bundles in cross sections cut immediately above the node, twelve bundles at a slightly higher level and ten strands in the upper part of the internode. In branches of *Calycanthus floridus* and in some stems of *C. fertilis*, the number of vascular strands differ from this at corresponding levels. For instance, in *Fig. 9*, there are only six bundles immediately above node B and eight strands immediately below it. In some stems there may be as many as fourteen discrete strands at certain levels. In this connection, it is desirable to consider the effects of variations in internodal elongation.

In branches of *Chimonanthus praecox*, obtained through the courtesy of Dr. Blomquist, the primary vascular bundles, as seen in transverse sections, are relatively broad and the interfascicular spaces of the eustele are comparatively very narrow. This feature develops very early in the ontogeny of the axis, *Plate II, B*. It makes it difficult at times to follow the course of individual traces during later stages of the maturation of the stem. However, careful analysis of serial cross sections makes it possible to reconstruct the following pattern. At node A, *Fig. 10*, there are twelve bundles and two large detached strands opposite the two conspicuous gaps in the eustele. Somewhat below the node there are eleven or ten strands, *Fig. 11*, due to the inclusion of the two (d) traces and the fusion of three or four pairs of (a) and (b). In some cases the (a) and (b) strands fuse at a lower level and there are fourteen bundles at this level. At a lower level the number of bundles is commonly twelve due to separation of the (d) strands into their constituent halves and the fusion of all four pairs of (a) and (b) strands, *Fig. 12*. At nodes B and C, the fusing of the bundles (ab) and (c) occurs above the nodal level. The total number of bundles at these levels was therefore eight only, *Figs. 13 & 17*.



FIGURES 10-15. Cross sections of the mature part of a shoot of *Chimonanthus praecox*, cut at the successive levels shown in FIGURE 16. The primary xylem of the eustele and the median vascular strand of the leaf-base are shown in solid black. The cortical bundles, the vascular strands of the buds and the secondary xylem are merely outlined.

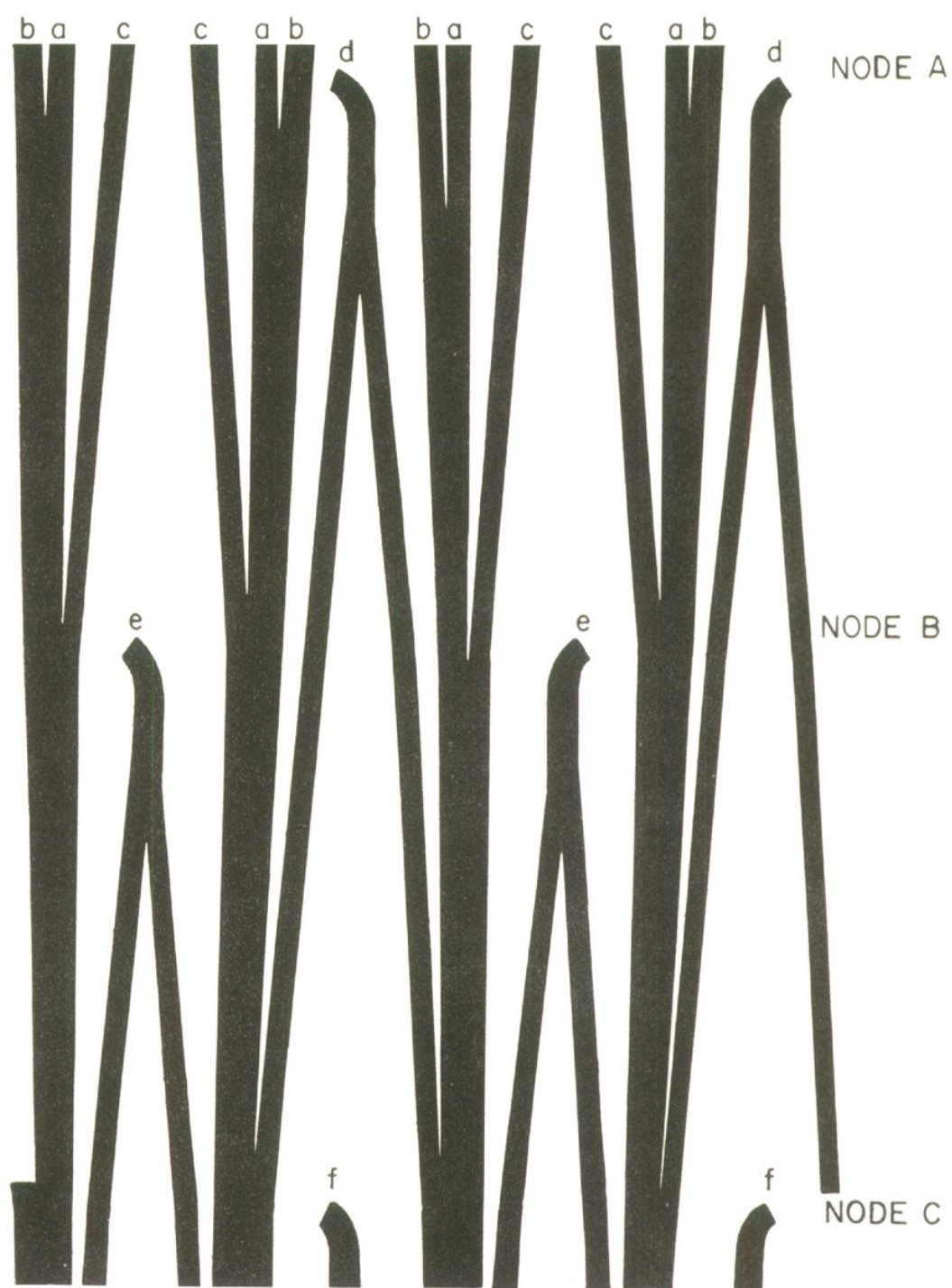


FIGURE 17. Diagrammatic reconstruction of the longitudinal course of the vascular strands of the eustele in *Chimonanthus praecox*.

INDEPENDENCE OF THE CORTICAL SYSTEM
OF VASCULATURE

The course and behavior of the cortical vascular strands in our material — we have not studied the floral axis as yet — is in general agreement with that reported by previous investigators. Each of the four cortical strands has three lateral branches at the nodal level, *Plate II*. One of these runs independently through the petiole and into the marginal basal part of the lamina. The other two unite with the large median strand in the base of the petiole. There are in addition two transverse connections between the cortical strands at the nodal level in stems of *Calycanthus*, *Plate II*, *A*. These connections occur in the two opposite sides of the stem which do not form foliar gaps at the node, *Fig. 6*. However, in our specimens of *Chimonanthus praecox* they are very tenuous in some of the immature nodes. They are absent in others and in all mature stages examined, *Plate II*, *B*. In some cases, there are indications that early tenuous inter-strand connections may possibly have been disrupted during subsequent lateral enlargement of the stems. There are no connections in our material of immature and mature stems between the cortical vascular strands and the central eustele, except in the epicotyl between the cotyledonary node and the first foliar node.

Seedlings grown from seed labeled *Calycanthus floridus* and *C. laevigatus* have the fundamental, double-trace, unilacunar, cotyledonary structure that occurs in so many dicotyledonous families, Bailey (1). The branches of the two discrete traces may extend independently throughout the lamina of a cotyledon or certain of their branches may approximate giving the appearance of a midvein.

DISCUSSION AND CONCLUSIONS

Our investigations of both genera of the Calycanthaceae indicate that these plants belong in the category of unilacunar dicotyledons which have been shown in recent years ⁴ to have leaves and cotyledons that are vascularized by ramifications of two traces that are related to independent parts of the eustele. In certain representatives of this category, e. g. *Ascarina*, *Austrobaileya*, *Trimenia*, the two traces and their branches extend at times independently throughout the stem, petiole and lamina of the leaf. In many others, approximation or apparent fusion of the two vascular strands, or of certain of their branches, occurs at various levels of the stem, petiole or lamina,

The Calycanthaceae are significant in the latter connection exhibiting various stages of approximation and fusion in mature cotyledons and during the ontogenetic development and maturation of the stem and its foliar appendages. In addition, the two genera of the family are of interest in illustrating a special trend of modification of the basic double-trace, uni-

⁴ In this connection see Bailey and Swamy (2), Money, Bailey & Swamy (9), Swamy & Bailey (12), Swamy (11), Marsden & Bailey (7), Bailey (1).

lacunar form of vasculature, viz. the development of a superimposed independent system of cortical strands. In none of our material of seedlings and adult plants is there any evidence indicative of the derivation of the cortical system by modification of trilacunar or multilacunar structure.

The double-trace, unilacunar structure of the primary vascular cylinder of the Calycanthaceae, which so clearly resembles that of representatives of the Austrobaileyaceae, Trimeniaceae, Chloranthaceae and Lactoridaceae, is suggestive of relationship between these families, but taken *by itself* is not conclusive proof of *close* affinity since the structural similarities might be due to parallel or convergent evolution or to the persistence of a primitive form of vasculature — such as occurs in *Ginkgo biloba*, Gunckel & Wetmore (5), certain species of *Ephedra*, Marsden & Steeves (8), and other gymnosperms — in dicotyledons of relatively remote relationship. It should be noted in this connection that a fundamentally similar form of vasculature occurs within the Verbenaceae, Labiatae and Solanaceae. Only when considered in connection with the *totality* of evidence from all organs and parts of the plant do vascularization patterns become reliably significant in studying problems of phylogeny and natural relationships.

As emphasized by Money, Bailey & Swamy (9), there are two distinct categories of woody ranalian families which have ethereal oil cells and monocolpate pollen or pollen which has evolved by phylogenetic modification of such grains. One of these groups of families — the Winteraceae, Degeneriaceae, Magnoliaceae (*sensu stricto*), Himantandraceae, Annonaceae, Eupomatiaceae, Myristicaceae — are characterized by having trilacunar or multilacunar nodes. The other category — the Austrobaileyaceae, Amborellaceae, Trimeniaceae, Monimiaceae, Gomortegaceae, Lauraceae, Hernandiaceae, Chloranthaceae, Lactoridaceae — have double-trace unilacunar nodes or unilacunar modifications of this basic form of vasculature. Our investigations of the eustele of the Calycanthaceae when considered in the light of a summation of collateral evidence indicates that the family belongs in the second category of ranalian families and is more closely related to them than to any of the families in the first category.

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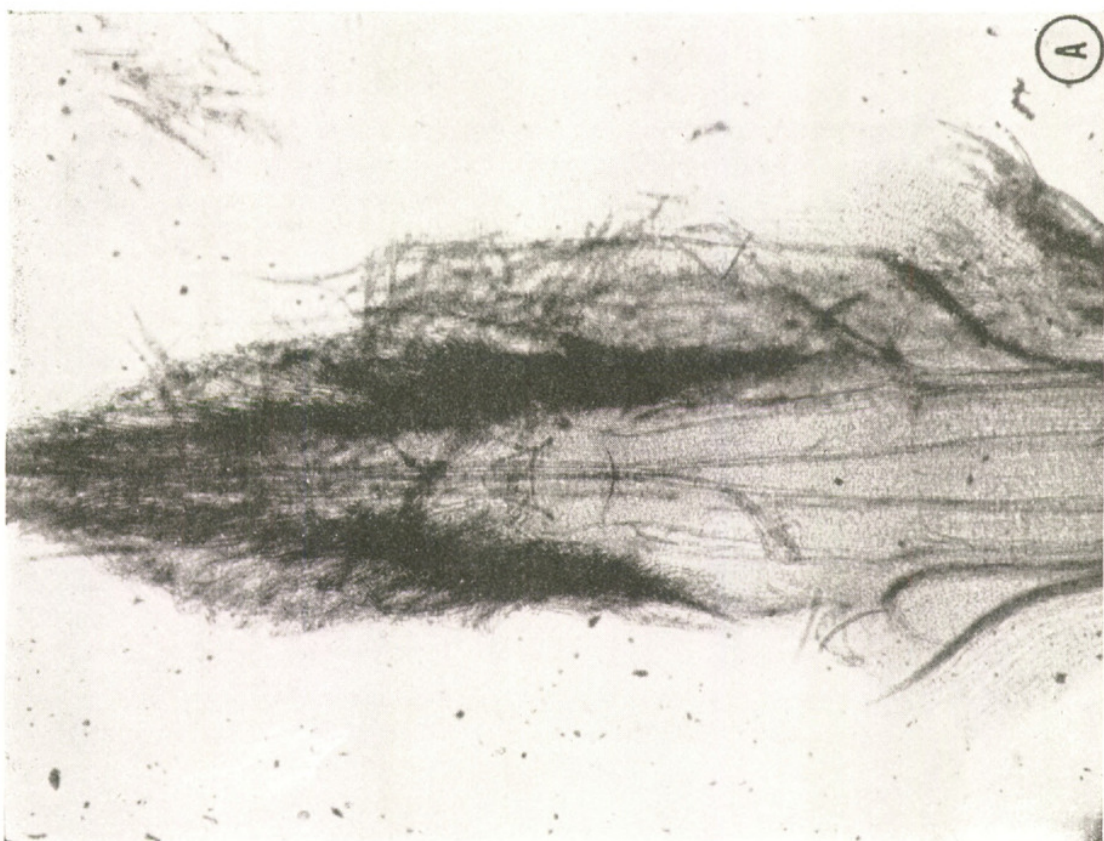
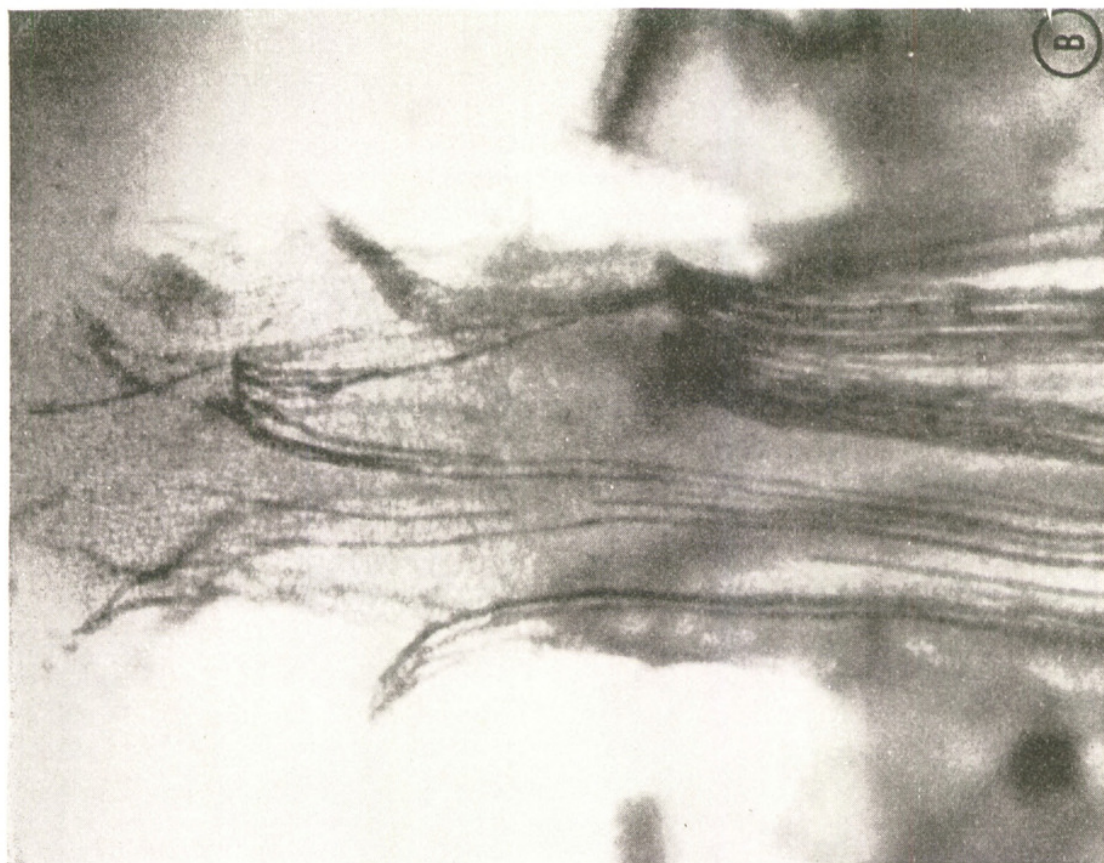
DESCRIPTIONS OF PLATES

PLATE I

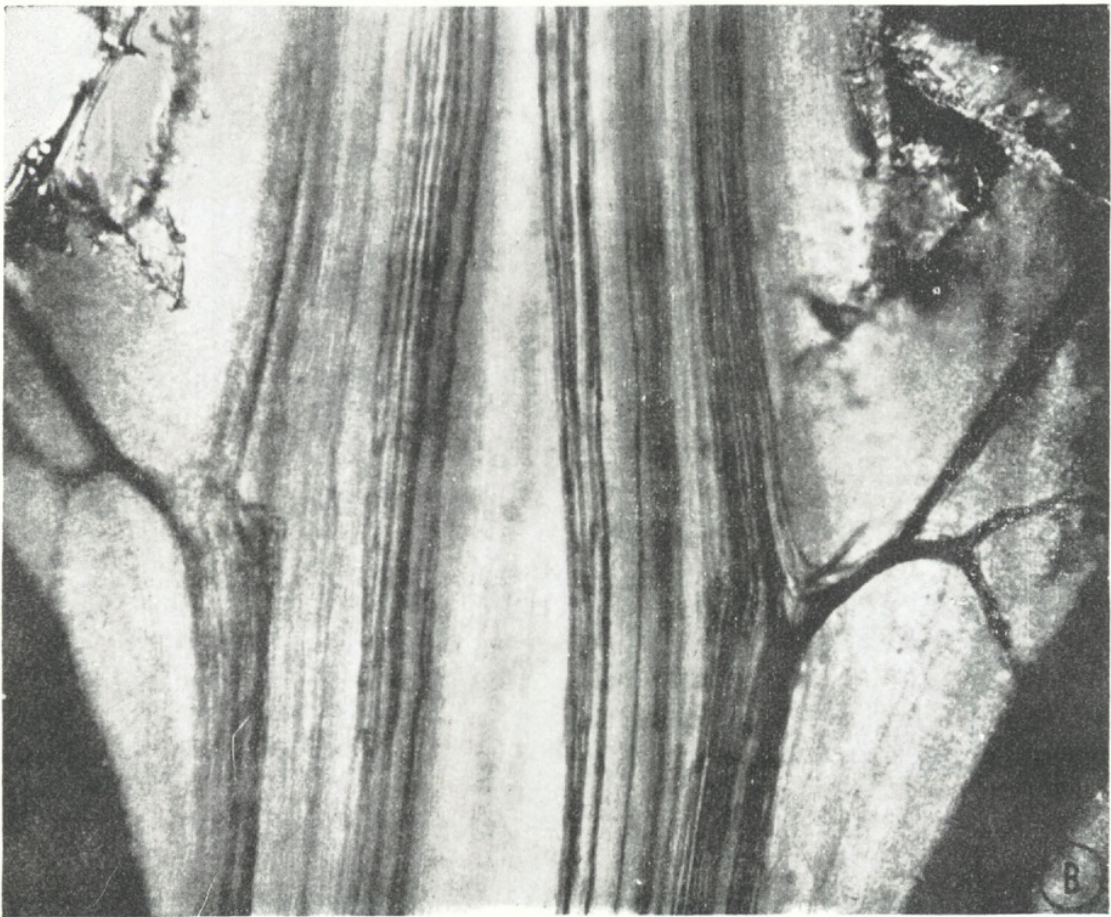
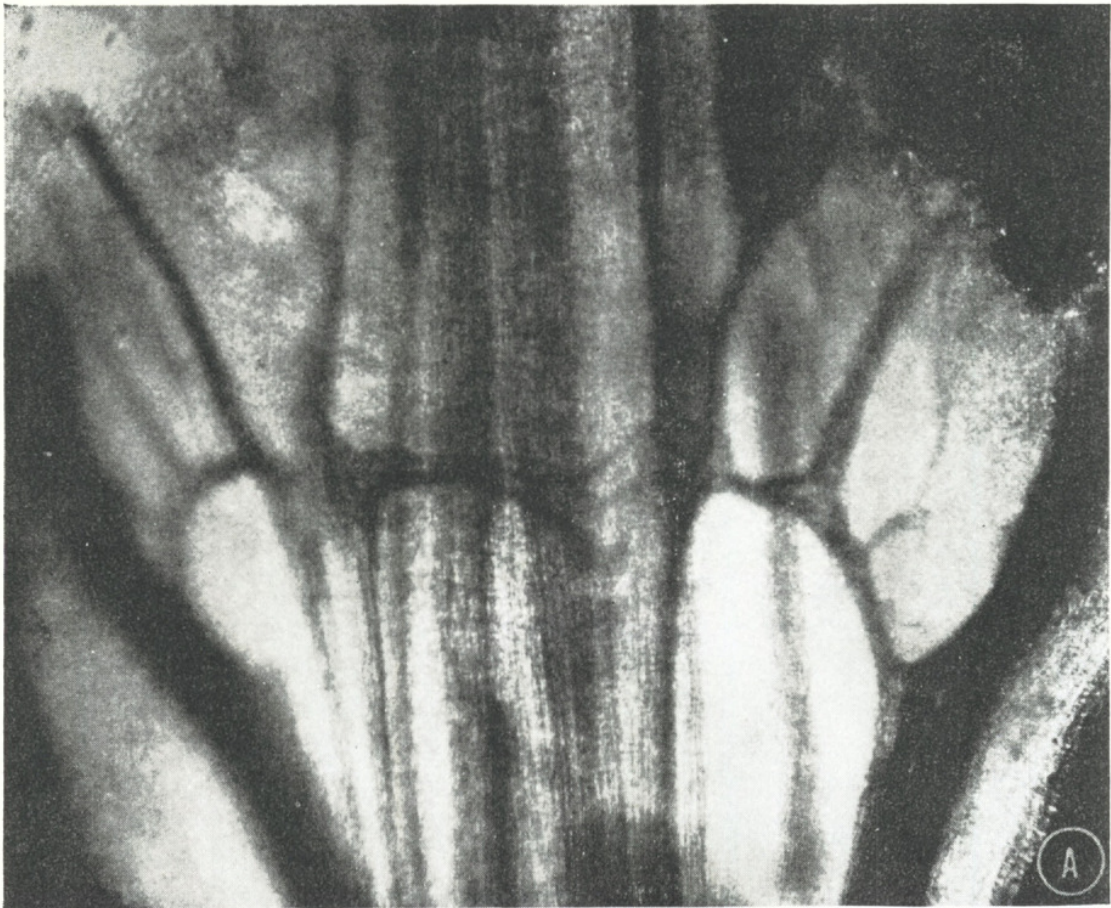
Cleared terminal parts of young shoots. The epidermis and some of the cortical tissue have been removed. A. *Calycanthus fertilis* var. *laevigatus*, showing two separate traces entering a young leaf. B. *Chimonanthus praecox*, showing the vascular strands of the eustele.

PLATE II

Mature nodes after clearing and removing the epidermis. A. *Calycanthus floridus* var. *ovatus*, showing lateral connection between two cortical strands and the branches which enter the leaves. B. *Chimonanthus praecox*, showing the absence of transverse connection between the two cortical strands.



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