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## DEVELOPMENT OF WOODY BRANCH ATTACHMENTS IN *SCHEFFLERA* (ARALIACEAE OR APIACEAE)<sup>1</sup>

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Attachment of branches in *Schefflera* is unusual in that it involves fingerlike woody extensions that originate in the cortex and pass gradually into the woody cylinder of the parent shoot. We tested the hypothesis that these structures could be roots since *Schefflera* is a hemi-epiphyte with aerial roots. These branch traces originate by secondary development in the many leaf traces (LTs) of the multilacunar node together with associated accessory traces. In the primary condition, the LTs may be described as cortical bundles. Leaves are long persistent and can maintain a primary stem connection across a broad cylinder of secondary xylem. Under the stimulus of branch development, the LTs form a template for secondary vascular development. Because the LT system is broad, with many traces, the branch attachment is also broad. The fingerlike extensions are attached to the surface of the woody cylinder of the parent stem but are progressively obscured as a continuous cambium is formed. Bark tissues are included within the branch axil because of the extended cortical origin of the initial attachment. The results are discussed in the context of branch-trunk unions in tropical plants, an important component of canopy development.

**Key words:** Araliaceae; branch insertion; leaf gap; leaf trace; nodal anatomy; *Schefflera*; secondary xylem.

There is little information concerning the structural mechanisms involved in secondary changes while woody branches develop a vascular connection to their parent axis. This omission is largely a consequence of the need to study large structures at a microscopic level. Standard texts may devote only a few paragraphs to the topic (e.g., Fink, 1999; Larson, 1994). In contrast, there are extensive descriptions of nodal vasculature in dicotyledons, in which primary construction may have systematic relevance (Howard, 1979), but they relate largely to leaf traces (LTs) alone, with incidental reference, if at all, to branch traces in the primary condition (Eames and MacDaniels, 1947; Esau, 1965, 1977). The chief emphasis is on herbaceous plants and simple systems where bud traces are attached to the margins of stelar leaf gaps, but without details of how an axillary bud develops a mature stem attachment.

Branch-trunk attachments are known to be important features of structural compartmentalization in tree construction (Shigo, 1985) and are certainly an essential component in the development of a forest canopy because branch persistence demonstrates mechanical and physiological efficiency. Knowledge of branch attachment is also important in correct pruning practices in arboriculture (Shigo, 1989). We draw attention to this topic by describing the distinctive method of branch attachment in the tropical genus *Schefflera* (Araliaceae or Apiaceae, Judd et al., 2002). The leaves are sheathing, with many LTs arising from a multilacunar node (Howard, 1979).

*Schefflera* can develop as a hemi-epiphyte producing aerial roots. Hallé (1991) illustrated unusual fingerlike extensions of wood from lateral branches where they connect with the main

axis. He hypothesized that these branches (or “reiterations”) might represent roots extending from the base of the branch similar to the way aerial roots develop in this and some other woody species (Hallé, 1991). However, no developmental evidence was offered. We show that quite complex processes are involved in the production of these fingerlike extensions of the branch. The primary configuration is itself complex, and the result may be interpreted as a particularly efficient method of branch insertion. To the best of our knowledge, this distinctive developmental process has not been reported previously. Using developmental evidence, we tested an initial hypothesis that leaf traces and branch traces are associated in unusual ways.

### MATERIALS AND METHODS

Two species of *Schefflera* were studied; one tree species, *S. actinophylla* (Endl.) Harms, is widely planted and can be invasive because of its habit; a smaller species, *S. arboricola* (Hayata) Merr., is a commonly cultivated ornamental shrub. We examined *S. arboricola* in greater detail because of its smaller size, with the primary axes of the order of 1 cm diameter, which can be conveniently serially sectioned.

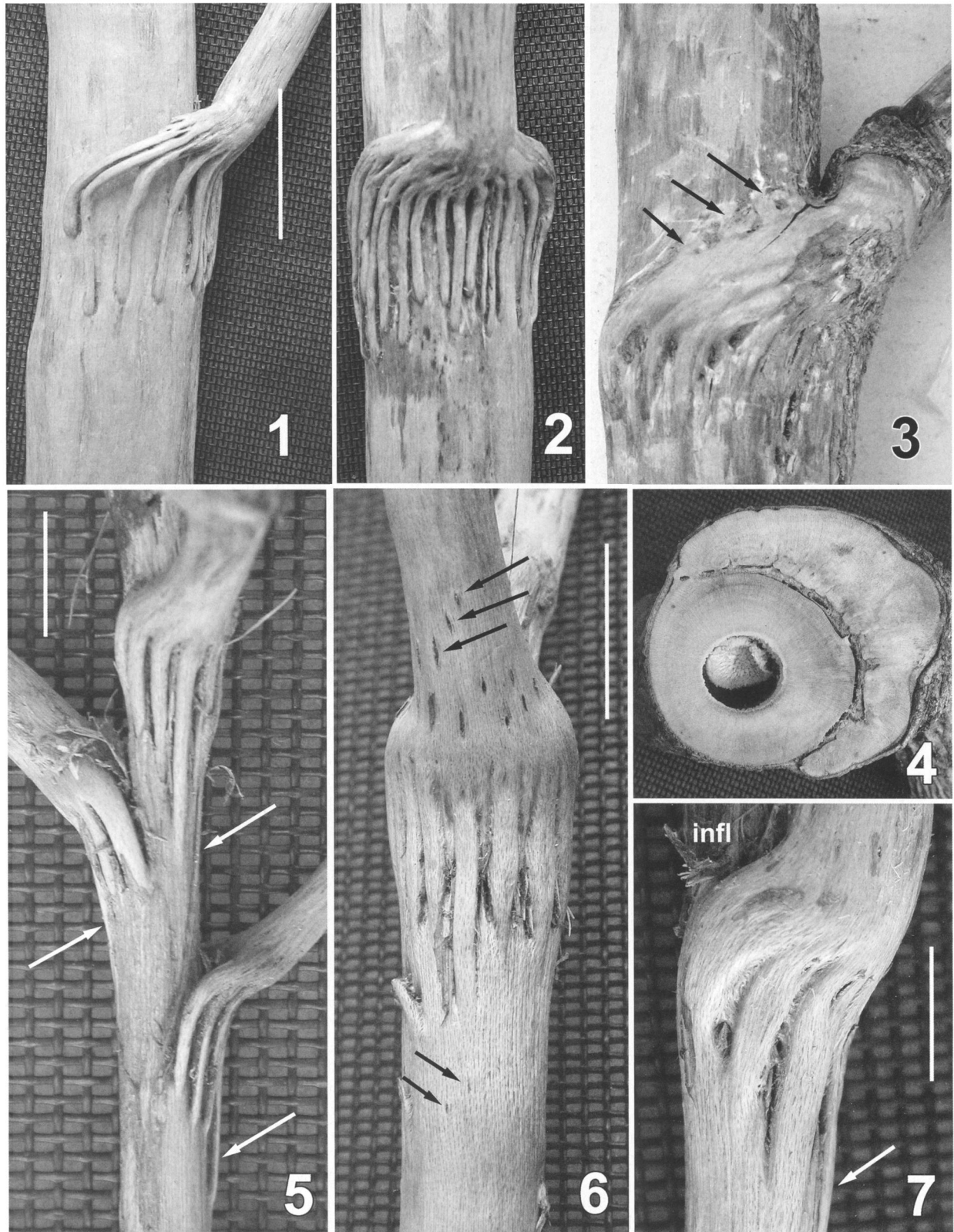
**Surface morphology**—Fresh or partly dried stems can be decorticated by removing all tissues external to the cambium to reveal the branch attachment with reference to the surface morphology of the secondary xylem of the parent axis (Figs. 1–7). Some of these specimens were subsequently sawn transversely (Fig. 4).

**Anatomy**—For anatomical study, material was either unfixed or fixed in formalin-acetic-alcohol (FAA; 85 parts 70% ethanol, 10 parts glacial acetic acid, and 5 parts 40% formaldehyde) and sectioned on a sliding microtome. Fixed material was washed well in tap water before sectioning. Sections were cut transversely and to a lesser extent longitudinally at 60–120  $\mu$ m thickness, serially or sequentially, to ensure whole sections for vascular continuity. Sections were all stained in 0.5% aqueous toluidine blue (Sigma, St. Louis, Missouri, USA) and mounted in glycerine : water (1 : 1) as temporary preparations. To facilitate photographic documentation, selected sections were

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Figs. 1-7. *Schefflera* spp., decorticated dried axes. Figs. 1, 2. *S. cf. actinophylla*. Figs. 3, 4. *S. actinophylla*. Figs. 5-7. *S. arboricola*. **1.** Branch insertion from the side; orientations are changed; the branch was originally vertical and the main axis oblique. **2.** Front view of Fig. 1. **3.** Older axis showing continuous complete fusion of branch base with parent axis, arrows indicate acropetal connections. **4.** Transverse section of an older axis showing inclusions of cortex and secondary phloem between enveloping branch and parent axis with collapsed pith. **5.** Axis with branches attached at three successive nodes below an aborted trunk. Arrows indicate long median branch traces. **6.** Older axis from front with more complete fusion. Arrows indicate scars of leaf traces. **7.** Branch insertion below remains of inflorescence (infl), branch traces almost completely fused; arrow as in Fig. 5. Scale bars = 4 cm for Figs. 1-4; = 1 cm for Figs. 5-7.

bleached for 10–20 min in sodium hypochlorite (commercial bleach) diluted 1 : 2 with tap water to remove cell contents. Such sections were rinsed well in tap water, dehydrated in ethanol, and stained in 1% safranin (Sigma) and 1% alcian green (Sigma Chemical, St. Louis, MO) (5 : 1 mix) both in 70% ethanol and mounted in Permount (Fisher Scientific, Fair Lawn, New Jersey, USA).

To study the primary vasculature, axes with little secondary growth were initially sectioned, followed by axes with developing branch attachments of increasing size, continuing to stages when the branch attachment had become quite woody. Because of the quantitative variation seen in a preliminary study, over 20 shoots were examined in all these ways.

**Photography**—Illustrations from these various preparations were made using a Nikon (Tokyo, Japan) Coolpix 4500 digital camera, with an attached Leitz (Rockleigh, New Jersey, USA) Periplan lens for microscopic images. Images were processed via Photoshop 9 (Adobe, San Jose, California, USA) with the original color mode converted into black and white.

## RESULTS

**Architecture**—In the typological terminology of the system of Hallé et al. (1978) the two species (and many other species in the Araliaceae) may be referred to Leeuwenberg's model, i.e., trees have orthotropic axes, each axis determinate and ending in a terminal inflorescence. Branching by substitution (Hallé et al., 1978) occurs subsequently from axillary buds below the inflorescence. Additional branches may develop below cut shoots or, on undamaged leaning or vigorous vegetative shoots, suggesting a more random process. Branches always develop by prolepsis, i.e., from buds that have undergone a period of dormancy (Hallé et al., 1978).

**Primary shoot morphology**—Shoots have spirally arranged leaves and internodes of varying length. Individual leaves have a sheathing base and an insertion that includes about 60–70% of the stem circumference. Each leaf subtends a single axillary bud that initially remains undeveloped; each bud has a pair of unequal but overlapping scalelike prophylls. Leaves are long-lived and persist as functional organs on axes with appreciable secondary growth, as described later (in Leaf longevity). However, in the absence of growth rings, we do not know their precise age.

**Surface morphology**—A striking example of a younger stage in branch attachment in the larger species shows 17 cylindrical strands of secondary xylem confluent with the secondary xylem of the trunk (Figs. 1, 2). These illustrations, for convenience, have the parent axis placed vertically, although originally the branch was vertical on a leaning shoot. Older branches show that a continuous woody attachment is formed after the independent strands become confluent, their outline represented by surface fluting (Fig. 3). Encircling attachments of this kind can occupy over 180° of the circumference of the parent axis (Fig. 4). In the smaller species, a sequence of branch attachments can occur along a single axis, showing the consistency of the structural arrangement (Fig. 5). As the axis thickens, the strands broaden (Fig. 6) and become progressively confluent (Fig. 7). In positions where a branch occurs below an old inflorescence, all distal tissue is that of the branch (Fig. 7). Because the strands are of cortical origin, bark and intervening cortical tissues are extensively included within the branch crotch (Fig. 4).

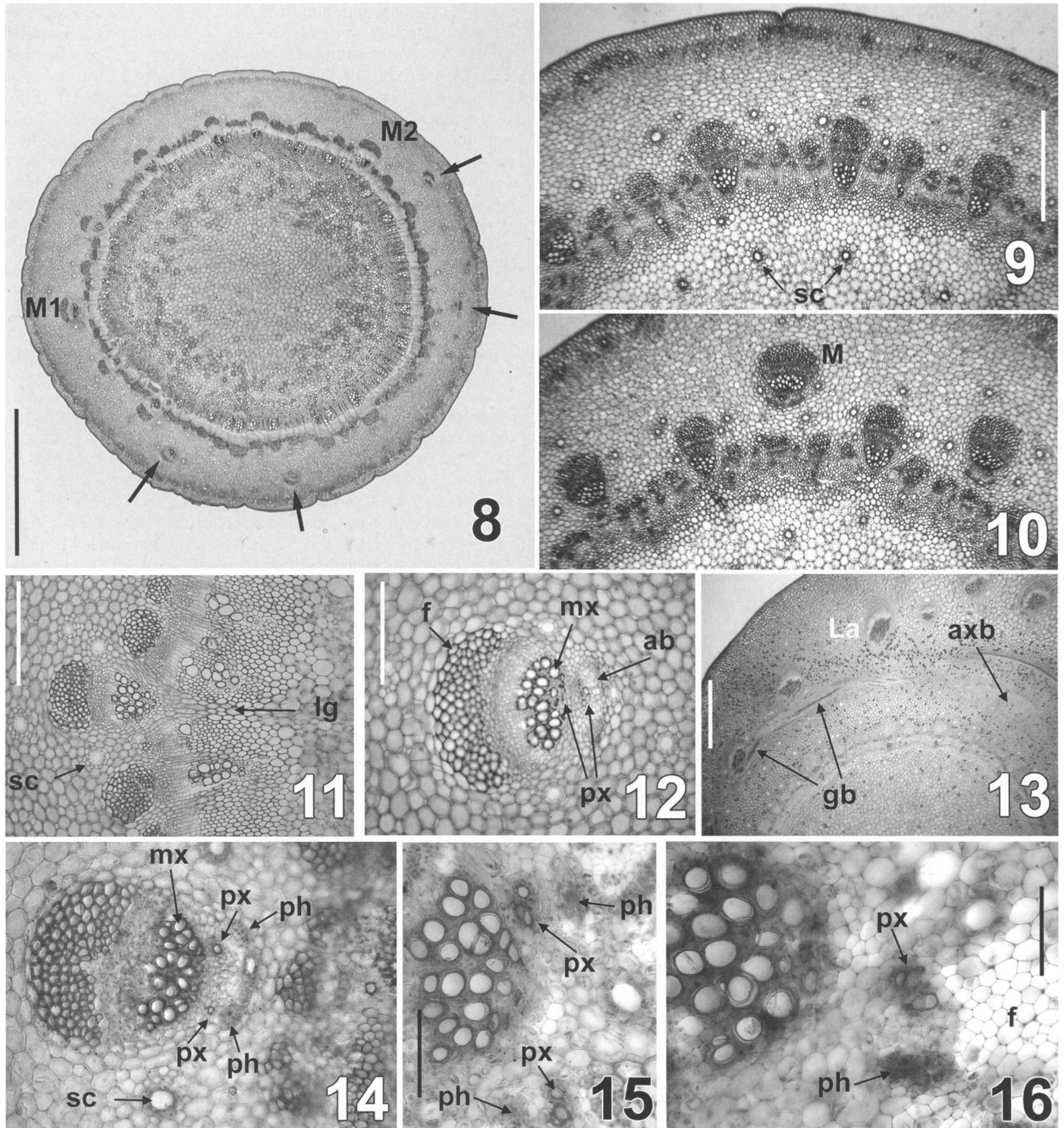
**Primary stem anatomy**—The vascular cylinder has a normal eustelic organization, but with numerous collateral vas-

cular bundles separated by narrow rays (Figs. 8–11). Each vascular bundle is delimited externally by a strand of thick walled fibers seen in transverse section (TS) as a cap (see f in Figs. 11, 12). Internally, LTs close to their departure from the stele are recognized by extensively developed primary xylem (Figs. 9, 10). Such exiting LTs leave a narrow gap in the parent vascular cylinder (lg in Fig. 11), the gap capable of subsequent complex development as described later (in Basal attachment). Cortical features include a well-developed collenchymatous hypodermis, peripheral chlorenchyma, and a colorless inner region (Figs. 9, 10). Secretory canals (sc in Figs. 9, 14) occur in both medulla and cortex, the two systems often being interconnected through the leaf gaps. The periphery of the pith is composed of sclerotic parenchyma, within which the protoxylem is embedded (Fig. 11).

**Cortical traces**—Leaf traces to each leaf in the smaller species number between 16 and 19 and originate shortly above the level of insertion of the leaf below: i.e., they traverse within the cortex almost a whole internode. Because of this extended cortical position, they are seen in transverse section as "cortical bundles," in the terminology of Howard (1979). Individual LTs depart from the stele in a somewhat irregular sequence (Fig. 9), with the median trace usually leading (M in Fig. 10) and lateral traces irregularly following. This irregularity can be seen clearly in decorticated specimens because each trace leaves a small scar on the surface of the wood (black arrows in Fig. 6). Additional bundles can arise irregularly and without reference to the leaf immediately above, but they exit at the next higher node; i.e., they can extend through almost two internodes. These bundles are usually positioned outside the LT system that supplies the leaf immediately above (arrows in Fig. 8).

Individual LTs have a conventional distribution of vascular tissues (Fig. 12), with endarch protoxylem, abundant tracheary metaxylem elements with compact helically sculptured wall thickenings, and a narrow phloem region. The sclerenchymatous bundle cap of the stelar bundle continues into the LT (Fig. 11), but is replaced over a short distance by unlignified cells at the node. In any one LT system, the median bundle (e.g., M in Fig. 10) is largest with a progressive size reduction into the leaf margin (bundles of decreasing size leaving the stele in Fig. 8). At the node, the median bundle and those immediately on either side enter directly and radially into the leaf base, but marginal bundles adopt an almost circumferential and horizontal course, girdling the stem within the cortex (gb in Fig. 13). Consequently, the arc over which LTs depart from the stele is much wider (up to 80% of the stem circumference) than the leaf insertion itself. Some of these girdling traces are connected by accessory bundles to the axillary bud (axb in Fig. 13) and are an important component of the future branch traces. This accounts for part of the characteristic topography of the future branch insertion (Figs. 1, 2) whereby the lateral-most traces become united horizontally. In Fig. 8, median bundles M1 and M2 are those belonging to two successive nodes.

**Accessory bundles**—An easily overlooked feature of most of the wider median bundles of any one leaf insertion is the series of narrow vascular strands on the inner face of the LT bundle, i.e., on the adaxial side, adjacent to the protoxylem (ab in Fig. 12). These accessory bundles arise by the dedifferentiation of the parenchyma cells in this position, and they



Figs. 8–16. *Schefflera arboricola*. Primary stem structure in transverse section (TS). Sections were wet preparations stained in toluidine blue, except Figs. 11–13, which are taken from permanent preparations stained in safranin–alcian green. **8.** Stem with leaf traces (LTs) diverging from stele; arrows indicate LTs originating in previous internode below and with the median LT to leaf at next node above and at two nodes above. **9.** LTs originating in stele at base of an internode. **10.** LTs entering cortex at different levels; the median trace has originated at a lower level than adjacent lateral traces. **11.** LT and associated leaf gap, no accessory bundles. **12.** Details of leaf trace with accessory adaxial vascular bundles. **13.** TS young axis at leaf insertion where incipient vascular system of axillary bud is present; lateral leaf traces are present in leaf base, and girdling cortical traces branch from ventral portion of LT system (cf. Figs. 1 and 2). Figs. 14–16. Details of accessory bundles on adaxial side of cortical LTs. **14.** Accessory bundle with undifferentiated phloem tissue and two protoxylem poles and metaxylem of LT. **15.** LT with two accessory bundles, the upper with inverted orientation, protoxylem to the outside, the lower with normal orientation, protoxylem to the inside, prior to fusion with the stelar bundles. **16.** Accessory bundle with a single protoxylem strand and phloem incompletely differentiated fibers forming an internal cap; Secretory canals are visible in Figs. 9, 11, 14. Scale bars = 2.5 mm for Fig. 8; = 1 mm for Figs. 9, 10, 13; = 500  $\mu$ m for Fig. 11; = 250  $\mu$ m for Figs. 12, 14; = 125  $\mu$ m for Fig. 15; = 100  $\mu$ m for Fig. 16. *Figure abbreviations:* ab, adaxial bundle; axb, axillary bud bundle; bt, branch

may consist either of procambium alone, or include a few sieve tubes and at most both sieve tubes and a few narrow tracheary elements (Figs. 14–16). Vascular tissue in these bundles usually has an inverse orientation to that of the parent LT, with the protoxylem exarch, i.e., opposed to the normal endarch protoxylem (px in Figs. 12, 14). There is great diversity in the frequency and disposition of these bundles. Normally, they are absent from the marginal bundles except as they approach the leaf insertion. Their connections also vary widely. They may end blindly, be connected to the stele (rarely) or, most commonly, connect to the incipient stele of the axillary bud at the node above. Sometimes they connect to the normally oriented vascular tissue of the parent LT by inverting their own vascular organization. Only two further examples are illustrated. In Fig. 15, two accessory bundles are shown, the upper with inverted vasculature, the lower with normal orientation prior to its presumed fusion with the stele. In Fig. 16, the accessory bundle has a transverse orientation, indicating it will fuse at a higher level with the parent LT. We have avoided using the term bud trace for these bundles because they do not necessarily play a consistent role in branch connection. The emphasis is on the variability of structures shown, but always with a position internal to a LT.

**Petiole vasculature**—At the node, the radially and circumferentially departing LTs enter the leaf base and form an anastomosing system whose complexity we have not yet unraveled. The petiolar vascular bundles distally form two concentric circles in transverse view. The inner consists of vascular bundles with an inverse orientation, but these inverted bundles form no specific connection with the similarly inverted accessory bundles of the LTs. The significance of this configuration has not been examined.

**Axillary bud vasculature**—Immediately below the median portion of the leaf insertion and in the outer cortex of the stem, but below an undeveloped axillary bud, the incipient stele of the bud is seen in TS as an elliptical cylinder of procambial tissue with little vascular differentiation; at most including limited protoxylem and protophloem elements (axb in Fig. 13). As we have stated, a connection between this provascular bud tissue and the exiting LTs can be made via some of the accessory bundles, most conspicuously seen as girdling traces (gb in Fig. 13). When a branch grows out, the bud procambial cylinder establishes the basal cambial cylinder of the branch, which develops acropetally, as distinct from the basipetal changes in the cortex. The basal stelar portion of this developing branch cylinder is somewhat elliptical in section, but becomes a regular cylinder distally. It is important to emphasize that there is no direct basal connection between the distally developing branch vasculature and the stele of the parent stem at this early stage. All connections are initiated via cortical traces.

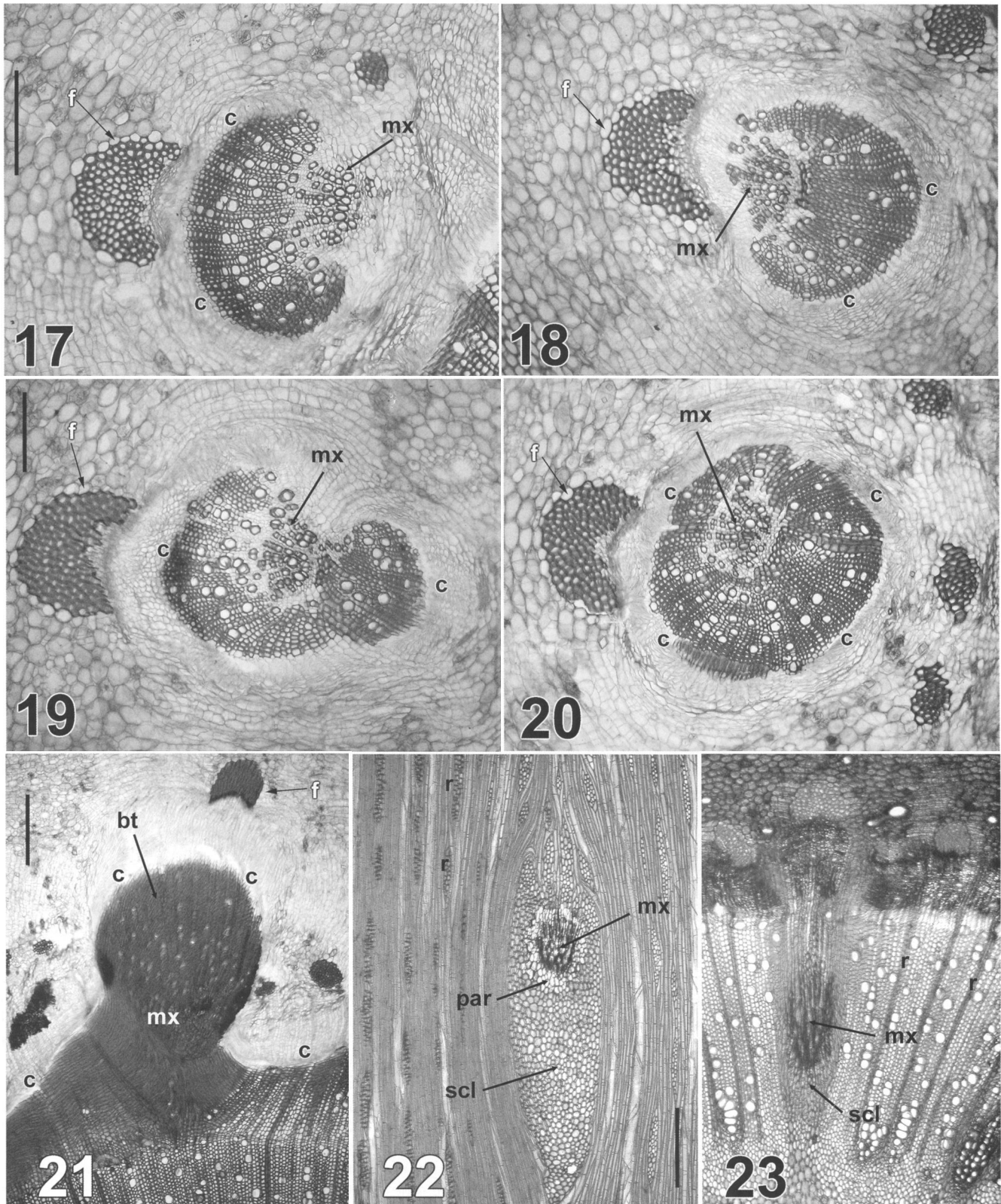
**Leaf longevity**—Functioning leaves remain on the shoot for extended periods (possibly years), as determined by the amount of secondary xylem that can form on the main axis but without growth rings. Leaf traces at their attachment to

the primary vascular bundles of the stele accommodate this secondary growth by adding tissue of cambial origin, leading to a distinctive condition (Figs. 22, 23) in which an extended secondary portion of the LT connects to the central and cortical regions of the original primary LT, without xylem rupture. The secondary portion in radial longitudinal view is a slightly upwardly inclined strand in the secondary xylem between pith and cortex, so that in TS it is sectioned slightly obliquely (Fig. 23). The LT xylem (mx in Fig. 22) is surrounded by unglified parenchyma (par in Fig. 22) and the trace tissue completed by sclerotic cells (scl in Fig. 22). This configuration is best seen in tangential longitudinal view within the secondary xylem of older axes (Fig. 22). The LT xylem consists of tracheary elements with helically sculptured walls that are indistinguishable from the original elements of the primary xylem. All this tissue is of secondary origin because it originates from cambial derivatives much in the manner of normal xylem rays (r in Figs. 22, 23).

**Branch attachment**—When a bud grows out, basipetal differentiation begins within LTs just below its node of insertion. Thus, LTs provide the template for the future branch attachment as structures to which the term “branch trace” can now be applied. Development normally begins with the activation of cells either on the abaxial side of the LT, between xylem and phloem (cf. Figs. 12, 17), or in the procambial tissue of some of the associated accessory bundles (cf. ab in Fig. 12). In a third situation, dedifferentiation of cells on abaxial, adaxial, and lateral sides of the primary xylem can result in the formation of a complete cambial cylinder within the leaf trace (Fig. 20). Activity of the cambium mostly produces somewhat irregular radial files of derivatives that differentiate as normal wood cells. This represents the beginnings of the fingerlike future extensions seen below a maturing branch (Figs. 1, 2). Basipetal development of tissues is indicated by the downward-tapering of the branch trace (Fig. 5), which later becomes more uniform (Fig. 6). The longitudinal extent of each branch trace represents the original total internodal extent of the LT as a cortical bundle.

In the development of this woody structure, several alternatives are possible. Although both accessory and LT tissue can be involved simultaneously, either the LT alone or the accessory bundle alone can initiate the new cambium and resultant secondary vascular tissue. The three possible conditions can be distinguished readily in transverse section by the position of the primary xylem in the LT complex (Figs. 17–19). Where secondary xylem occurs exclusively on the abaxial side, only original LT tissue was involved (Fig. 17). Where secondary xylem occurs on the adaxial side (Fig. 18), only accessory bundle tissue was involved, and the undeveloped original LT is recognizable on the outside of the branch trace. Where the primary xylem is surrounded entirely by secondary xylem, development has occurred on both adaxial and abaxial regions of the LT (Fig. 19), resulting in an eventual concentric structure (Fig. 20). In all conditions, the fiber cap of the LT marks its original position (to the left, f in Figs. 17–18). All differentiation of tissue occurs basipetally; there is no distal extension along a LT should the leaf be still attached, with the

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Figs. 17–23. *Schefflera arboricola*. Secondary vascular development in cortical LTs, all from permanent sections stained in safranin and alcian green showing fiber cap and metaxylem of original LT. **17.** Secondary tissue exclusively abaxial, derived entirely from cambium of the LT itself. **18.** Secondary tissue exclusively adaxial, derived entirely from cambium originating in an accessory bundle. **19.** Secondary tissue derived from cambium of both LT and accessory bundle, and with central metaxylem. **20.** Older branch trace with continuous cambial cylinder and concentric secondary tissue. The central position of the metaxylem indicates both LT and accessory bundle tissue were initially involved. **21.** Fusion of secondary tissue of branch trace with secondary xylem of original stele, the fiber cap of the original LT at f; original metaxylem of LT obscure at mx. Cambium of branch trace and stem are not quite continuous at this level. **22.** Tangential

possible exception described later (in Acropetal development). The different conditions seem to occur at random within a LT system, the consistent feature being the way in which the trace bundles (both LTs and accessory bundle) serve as a template for the future branch traces.

**Girdling traces**—The marginal (lateral) LTs that form the circumferential and girdling cortical strands at the leaf insertion (gb in Fig. 13) undergo the same transformation, but almost exclusively on the adaxial side because of their late-differentiating accessory bundles. The configuration of the branches suggests that secondary tissues differentiate initially along the circumferential course of the primary bundle and then into the descending portion (Figs. 1, 2). Often this tissue exceeds that of the median traces and as independent cambia fuse, a single thick strand results (Fig. 4).

**Cortical expansion**—By virtue of the extensive development of secondary vascular tissue, both of the parent stem and the expanding LTs (as branch traces), either inside or within the original cortex, secondary enlargement occurs within the cortex itself. Initially, this involves tangential expansion and radial division of cortical parenchyma cells (Fig. 17), but may include extensive calluslike proliferation of parenchyma around the branch traces (Fig. 19). In this way, additional cortical tissue comes to surround these structures as well as being included in the angle between branch and parent axis (Fig. 4).

**Basal attachment**—The fingerlike developing branch connections extend and enlarge basipetally to the level of insertion of the original LT on the stelar surface (Fig. 21). This can theoretically be primary or secondary, depending on the age of the axis, but is typically secondary as a result of prolepsis. Insertion is always via the original leaf gap and at the level of the cambium, however, much of the gap may have been augmented by secondary growth (Fig. 23). No significant differentiation of axial secondary xylem occurs within the leaf gap; instead, the cambium of each branch trace becomes confluent with that of the parent stele. Consequently, all subsequent union is applied to the surface of preexisting xylem and a protruding flange of secondary xylem is formed. In TS, this is seen as a bubble-like extension of the surface of the wood (Fig. 21). Progressively, the cambia of the originally separate LTs thus become continuous, and only the flanges are visible externally (Figs. 3, 7). The inner surface forms a crescent-shaped structure, that is distally continuous with the cylindrical branch base. Because active cambial regions of parent stem and branch face each other, there is considerable compression and necrosis of tissue formed outside the cambia, i.e., within the branch axil, a normal condition in woody axes (Fig. 4).

**Acropetal development**—Although we have described the branch attachment onto the parent axis as basipetal in development, dissected specimens show occasional distal connections above the girdling traces (arrows in Fig. 3). These apically directed strands seem to be derived in the same way as the basal strands, but by secondary activity in cortical traces

that diverge early and run through two internodes (arrows in Fig. 8). They have the same capacity to develop a cambium, but this soon becomes continuous with that of the branch trace system below. They thus add branch–trunk continuity in a distal direction, but their significance hydraulically and mechanically may be small. We have not investigated them further.

**Vascular continuity**—The final branch union is eventually secured by the existence of a single cambial plate continuous between branch and parent axis (Fig. 3). In the larger species (*S. actinophylla*), this complete fusion may take several years, although in the absence of clearly defined growth rings, the period cannot be estimated precisely.

## DISCUSSION

The summary of branch development and vascular attachment between branch and parent axis is presented in diagrammatic format (Fig. 24). These observations demonstrate that, despite their rootlike appearance (Hallé, 1991), the young digitate branch attachments of *Schefflera* are derived from LT tissue in the parent stem cortex. As an axillary bud develops, the leaf traces de-differentiate and establish new vascular cambia, which are propagated basipetally, and develop secondary vascular tissue with permanent xylem. Woody basal extensions (“branch traces”) are thus established via the template of the original primary leaf vasculature, which itself is distinctive because of its extended cortical pathway. Referring to the LT system as cortical is in agreement with that part of the classification of cortical bundles used by Howard (1979), in which all cortical bundles function directly as leaf traces. More complex systems exist, as in Myrsinaceae, where lateral traces of a trilacunar system are structurally independent of the leaf supply (Pipoly, 1987). The present article demonstrates that cortical LTs, whatever their primary origin and distribution, can have an important secondary function in facilitating branch attachment.

When growing vegetatively in the rainforest, *Schefflera* sp. (Hallé, 1991) forms orthotropic side shoots (i.e., reiterated branches) from axillary buds on leaning or damaged orthotropic parent axes. Thus, these branches can more accurately be termed “reiterations” (sensu Hallé et al., 1978). We refer to these lateral axes as “branches” in the generic sense to simplify the explanation of their development.

The distinctiveness of *Schefflera* resides in extensive, encircling branch attachments, some of which have a tangential course in the cortex of the parent stem. This is a consequence of the multilacunar node, together with the incipient accessory bundles associated with the inner face of the LTs and the longevity of the LTs themselves. The secondary continuity made by the LTs with an expanding stem xylem cylinder is a complex topic (cf. Fig. 85B in Eames and McDaniels, 1947). Elliott (1937) emphasized that in dicotyledons, connections are made only with the first year’s xylem, which seems to be the rule followed by *Schefflera*. However, Elliott (1937) contrasted conifers in this respect because secondary connections of a LT occur with more than one annual increment of secondary xy-

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section of a secondary LT forming a broad lignified secondary ray; metaxylem-like tissue is surrounded by unlignified parenchyma, the ray tissue completed by lignified sclerenchyma. **23.** Transverse section of a LT to an attached leaf that crosses extensive secondary xylem, labeling as in Fig. 22. Scale bars = 250  $\mu$ m for Fig. 17; = 250  $\mu$ m for Figs. 18–20; = 1.5 mm for Fig. 21; = 500  $\mu$ m for Figs. 22, 23.

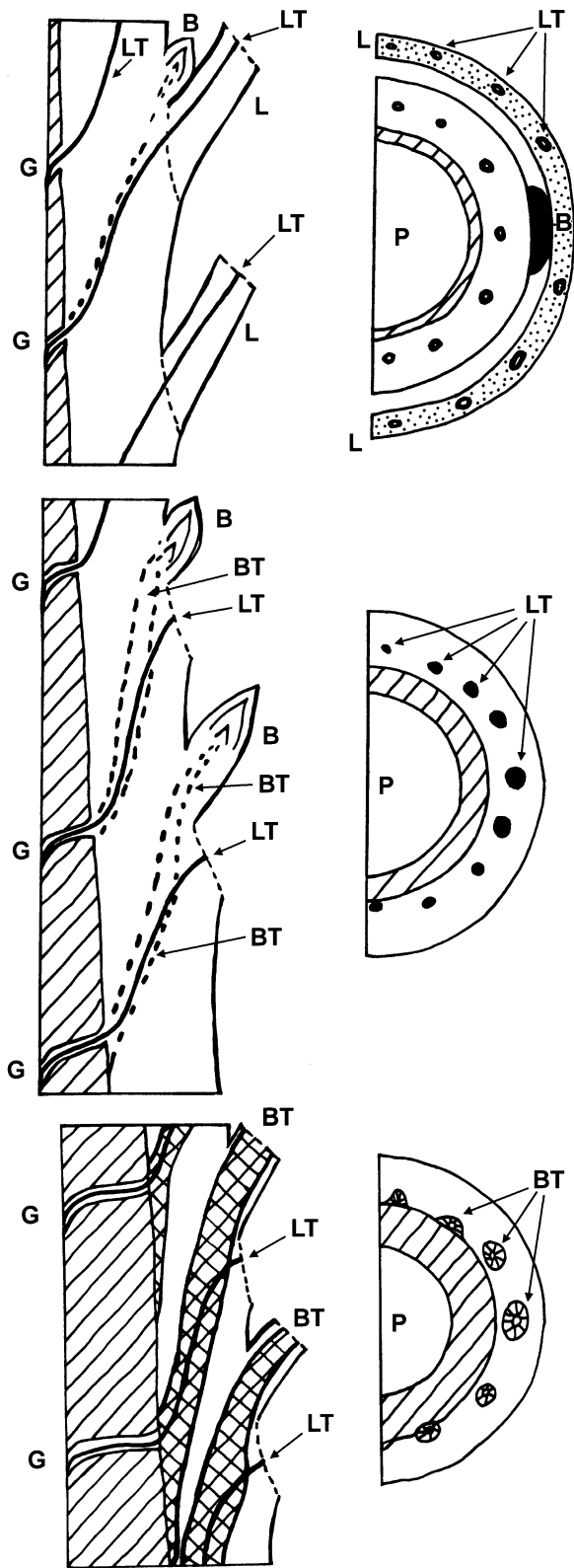


Fig. 24. Diagram of three stages in development of branch traces in *Schefflera* as seen in longitudinal (left) and transverse (right) sections. Top: Young shoot with branch bud and subtending attached leaf (stippled). Leaf traces (longitudinal section) with leaf trace gaps in the primary and beginning of secondary xylem (single hatch). Earliest evidence of accessory bundles (dotted line) near some leaf traces. Middle: Later stage with branch bud beginning to expand, leaves have abscised, and accessory bundles (dotted lines) well

lem. This statement was recently exploited experimentally by Maton and Gartner (2005, see their Fig. 1). The apparent anomaly is that tissues with a primary configuration (e.g., tracheary elements with helical wall sculpturing) develop within the secondary body of the plant, being derived ultimately from the vascular cambium. We have preferred the term "accessory" bundle for the incipient bundles associated with many LTs because they lack the precise position of "bud traces" in normal nodal anatomy, i.e., as traces that connect from the bud to the margin of the leaf gap, as described in standard anatomy texts (e.g., Eames and MacDaniels, 1947; Esau, 1965, 1977). The LT in *Schefflera* is a more complex entity and can be converted directly into a secondary vascular strand, at which time it becomes a branch trace in a novel sense. Mechanical efficiency is suggested by the broad basal insertion, while the extensive surface area occupied by xylem connecting branch to trunk indicates hydraulic efficiency. The morphogenetic implications of this system should be of interest to developmental biologists because they involve interplay between primary and secondary tissues of an unusual kind. Experimental and comparative study is required.

That this connection functions in transport was demonstrated by simple experiments (R. Villalobos, unpublished data). Conductive continuity can be demonstrated by gravity-infiltrating aqueous dyes into the living branch or leaf. We used 0.5% aqueous safranin under the low pressure of a 1-m-tall column that was fed into a lateral branch or attached leaf petiole for 18 h. Even though there is a leaf trace connection via secondarily derived metaxylem-like elements through a "branch gap" to the original stem stele, the dye can be seen to extend basally from a branch only in the late-formed secondary xylem of both branch and parent axis, i.e., only in branch tissue fused to the surface of the secondary xylem of the trunk. This is understandable from a functional viewpoint because a connection between young and old tissues would be unusual. Dye fed into attached leaves (with dormant buds) travels directly through LTs into the primary xylem of the stem and does not enter the secondary xylem of the stem.

The method of leaf attachment and constant proleptic branch development in Araliaceae suggest that similar developmental events involving LTs and branch unions may be common in the family although early literature, while describing cortical bundles, makes no mention of their ultimate role (Viguier, 1906, 1909; Joshi, 1931; Metcalfe and Chalk, 1950). Otherwise, most literature makes reference only to herbs, or deals with relatively simple systems in some tropical families (e.g., Wheat, 1979, 1980, 1981 for Sterculiaceae, Myrsinaceae, and Rhizophoraceae, respectively). Here the added complexity is the contrast between proleptic and sylleptic branch unions. Although LTs in both stems and petioles are normally ephemeral features of plant construction, their significance disappearing with leaf loss, it is of interest that petiolar vascular bundles in some other species can retain further developmental capability under appropriate circumstances. This is demonstrated in the extensive secondary growth of petiolar graft

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developed near leaf traces. Stem has developed secondary xylem (single hatched) and leaf trace gaps have extended radially. Bottom: Later stage with branches growing and producing bundle traces with secondary xylem (double hatched) from the combined accessory bundles and leaf traces. B, branch bud; BT, branch trace; G, leaf trace gap; L, leaf; LT, leaf trace; P, pith of stem.

unions in *Acer* (Weidlich, 1980) and in long-lived petioles of *Guarea* in the Meliaceae (Fisher, 1992).

Our observations on *Schefflera* suggest a mechanically and hydraulically distinctive branch union, which we believe has not been reported before. The formation of branch unions is an essential factor in the formation of tree crowns and forest canopy structure and remains little investigated. Its study could involve collaboration between ecologists, plant anatomists, and structurally focused foresters.

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