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P. Barry Tomlinson

Harvard University; National Tropical Botanical Garden

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STEM ANATOMY OF CLIMBING PALMS IN RELATION TO LONG-DISTANCE WATER TRANSPORT

P. BARRY TOMLINSON

Harvard Forest, Harvard University, Petersham, Massachusetts 01366, USA and National Tropical Botanical Garden,
3530 Papalina Road, Kalaheo, Hawaii 96741, USA
(pbtomlin@fas.harvard.edu)

ABSTRACT

Palms lack secondary growth so their primary vascular system is long-lived and must be minimally vulnerable to dysfunction. For water movement, the axial xylem must be well defended against cavitation. Climbing palms can be very long and represent a maximum solution to transport problems. How is this demonstrated in their anatomy? This article contrasts stem vascular anatomy in a cane-like “tree palm” (*Rhapis excelsa*) with that in the American climbing palm *Desmoncus* and the Old World rattan genus *Calamus*. *Rhapis*, representing the basic classical palm vasculature, has a continuously integrated vascular system determined by branching of the axial (stem) system to produce leaf traces, bridges, and continuing axial bundles. Axial transport is favored over appendicular structures because leaves are irrigated solely by narrower protoxylem tracheids. Maximum stem vessel length is inherently limited by the leaf contact distance (LCD). *Desmoncus* is very similar except that interconnections involve more numerous bridges and axial continuity is less obvious. Both *Rhapis* and *Desmoncus* retain scalariform perforation plates in their stem vessels. However, *Calamus* lacks axial continuity because axial bundles extend distally into leaves as leaf traces but end blindly in a basipetal direction. The only interconnection is via narrow transverse commissures (not bridges). *Calamus* stem metaxylem vessels have simple perforation plates. Resistance to water transport can be calculated, based on axial changes in metaxylem vessel diameter and is very high in the climbing palms. The unique features of *Calamus* may relate to safety of the hydraulic system as much as its efficiency, with *Desmoncus* an intermediate condition more clearly based on the classical model of palm vasculature. *Calamus* may have also evolved to mitigate the limitation of vessel length determined by LCD. Further anatomical solutions to the climbing habit in palms are briefly discussed.

Key words: *Calamus*, climbing palms, *Desmoncus*, *Rhapis*, stem, vascular anatomy.

INTRODUCTION

Monocotyledons for the most part, and almost certainly ancestrally (Tomlinson 1995), lack secondary growth and therefore have little ability to renew, repair, or augment primary vascular tissues. The stem vascular system must be efficient since it functions throughout the life of any axis. Structurally, the stem initially needs to be overbuilt since it must anticipate later increases in length without the addition of either mechanical or conducting tissues. The mechanical principles are well understood (Holttum 1955) and have been discussed in relation to overall habit (Tomlinson 1995). However, hydraulic constraints are not as well known.

Palms, the tallest and most abundant woody monocotyledons, offer the best opportunity to investigate the hydraulics of monocotyledonous stems that lack secondary growth (Tomlinson 1990). A well-established feature, presumably applicable to all monocotyledons, is that axial integrity is maintained at the expense of appendicular supply by the high hydraulic resistance at the leaf insertion. This results from the exclusive protoxylem connection along leaf traces (Zimmermann and Sperry 1983; Sperry 1986). These numerous, but narrow elements cannot compensate for the reduction in tracheary element diameter at the vascular insertion, resulting in an appreciable reduction in conductivity. This structural feature, in turn, is a developmental consequence of the presence of intercalary meristems and basipetal maturation of leaf and stem tissues. Metaxylem, although it is initiated

during tissue extension, does not mature until after elongation ceases. Protoxylem matures during elongation growth, continuously producing elements that are extensible and replaceable. This is not a theoretical conclusion; it is based on direct observation of the developing palm crown (Zimmermann and Tomlinson 1967; Tomlinson and Vincent 1984).

In the present article, the special case of climbing palms is considered because they represent the ultimate in success of woody climbers without secondary growth. Some of the structural features of monocotyledonous climbers have been discussed in the Second International Conference on the Biology of Monocotyledons (Tomlinson and Fisher 2000). The investigation here continues with a more detailed comparison of a palm treelet (*Rhapis* L. f. ex Aiton) with the American rattan analogue, *Desmoncus* Mart., and with *Calamus* L., the largest genus of true rattans. The two climbing palms represent only two of the estimated seven palm lineages in which the scandent habit has evolved (Baker et al. 2000). However, the comparison is intended to be typological rather than phylogenetic because the sample size is small and deals with unrelated palms. Ultimately, a more complete understanding of the structure of all climbing palms will be attempted.

MATERIALS AND METHODS

Information was derived from a series of recent and older papers in which three-dimensional vascular analysis of long

stem pieces (up to 2 m) had been produced. This involved cutting complete transverse sections at regular intervals (up to 1 cm apart), the sections either double-stained and mounted permanently, or stained in toluidine blue and mounted temporarily in 50% glycerine:water, and observed with frame-by-frame ciné or video microphotography. The course of individual vascular bundles was then plotted directly from the resulting films or tapes, which were kept as permanent records. Details of the methods and diagrams of the plotted results are in the published papers cited below.

Terminology of motion was used descriptively and was appropriate in relation to the dynamic presentation of results. In this article, plotted results are represented by simplified diagrams. Original results are: for *Rhapis* summarized in Tomlinson (1990), for *Desmoncus* in Tomlinson and Zimmermann (2003), and for *Calamus* in Tomlinson et al. (2001) and Tomlinson and Spangler (2002). However, all photographic illustrations are original in the present article. Photomicrographs of additional taxa not dealt with in detail are taken from a permanent collection of microscope slides at Harvard Forest.

RESULTS

1. *Rhapis excelsa* (Fig. 1–8)

The construction of the aerial stems of *Rhapis excelsa* (Thunb.) A. Henry ex Rehder is referred to generally as the “*Rhapis* principle” and can be applied universally, not only to palms but also probably to all monocotyledons with extended aerial internodes. Followed from base to apex of the stem any vascular bundle in the central cylinder originates as a branch of an outgoing leaf trace as the trace moves toward the stem periphery (base of Fig. 1A). The continuing axial bundle moves gradually toward the stem center, achieves a maximum penetration, and then diverges abruptly into the leaf base as a leaf trace, whereupon the branching cycle is repeated (apex of Fig. 1A). This is the principle of the “double curve,” first elucidated by Hugo von Mohl (1824), but without the recognition of the branching principle. The distance between each node with which the bundle can be said to make a leaf contact is the “leaf contact distance” (LCD) (Fig. 1A); this becomes significant in later discussion of vessel length. Although all bundles essentially behave in the same qualitative way, there are quantitative differences between major, intermediate, and minor bundles depending on their relative time of differentiation in the palm crown. The later a bundle appears, the shorter the LCD and the more limited is its radial displacement. Interconnection between adjacent vascular bundles is afforded by upwardly diverging bridges that link outgoing leaf traces to nearby axial bundles (Fig. 1B). Bridges integrate the axial system completely and they originate early as procambial strands as part of overall crown development. Inflorescence traces in mature reproductive stems also diverge from outgoing leaf traces but do not contribute to axial vascular integrity. For this reason they are not considered further in this discussion. The current interest is in the effects of the changes in bundle structure at the exit of a leaf trace (Fig. 1C). Outer bundles are crowded, with well-developed fibrous sheaths (Fig. 2), whereas central bundles are diffusely distributed and with limited fiber development (Fig. 3).

Xylem structure.—The vascular system thus outlined provides the template for differentiation of vascular tissues. Only xylem in relation to stem hydraulics is considered in detail here. The pathway for water movement in the xylem is made complex by the difference between protoxylem (PXY), which matures during axial extension, and metaxylem (MXY), which is initiated during axial extension but only matures after extension ceases. Consequently, PXY is continually disrupted by extension growth after it completes differentiation and is continually replaced. The last-formed elements of the PXY are retained in some numbers as the vascular supply to the leaf (Fig. 1C), but the functional connection is lost with leaf senescence. In peripheral stem regions the axial bundles contain little or no PXY (Fig. 4); such bundles represent the basal ends in the leaf contact cycle (Fig. 1A). Tracheary elements of the PXY are always narrow tracheids with annular or spiral wall sculpturing, which permits some passive stretching. Metaxylem is permanent; its elements are wide vessels and in *Rhapis* have scalariform perforation plates. Metaxylem provides the axial pathway for water movement over long distances. In the stem center one can contrast the basal portion of an axial bundle with the distal portion of nearby bundles by the difference in amount of PXY (Fig. 5).

In most of its course, an axial bundle includes a single metaxylem vessel at any one level and a number of protoxylem elements, which can be contiguous with the MXY (e.g., right-hand bundle in Fig. 5). Distally, within a bundle in its outward passage into a leaf, the MXY disappears from the leaf trace but continues via short and narrow vessels into either the axial bundle branch (AB) or the bridges (br) (Fig. 6–8). Protoxylem elements increase in number distally and only they are continuous into the leaf base; i.e., the leaf is irrigated solely by PXY (Fig. 8). However, at a lower level within a stem bundle, PXY and MXY are contiguous (Fig. 5, RH bundle) so that the pathway of water from stem to leaf is direct. Followed basally, the number of PXY elements progressively declines; this is a developmental consequence of the progressively limited time of extension growth to which the bundle has been subjected and the progressively basipetal sequence of PXY maturation within an axial bundle.

In any major bundle, i.e., one that largely occupies the stem center, the number of PXY elements seen in transverse view is thus a measure of that level below the bundle’s distal departure from the stem as a leaf trace. Basal and distal portions of two different axial bundles are thus contrasted in Fig. 5. Intermediate and minor bundles have less PXY. One can use the property of different amounts of PXY to extrapolate LCD in analysis of relatively short stem lengths by adding together incomplete short lengths of different major vascular bundles, e.g., as done in the analysis of *Calamus* (in Tomlinson et al. 2001) and in *Desmoncus* (in Tomlinson and Zimmermann 2003).

Although this “*Rhapis* principle” of vascular construction was demonstrated nearly 40 years ago, it is here applied as background to our understanding of how stem vasculature in climbing palms may be seen as the structural principle variously modified to accommodate the greater distances that water must be transported. In *Calamus*, surprisingly, the modification is considerable, but in *Desmoncus* much less so.

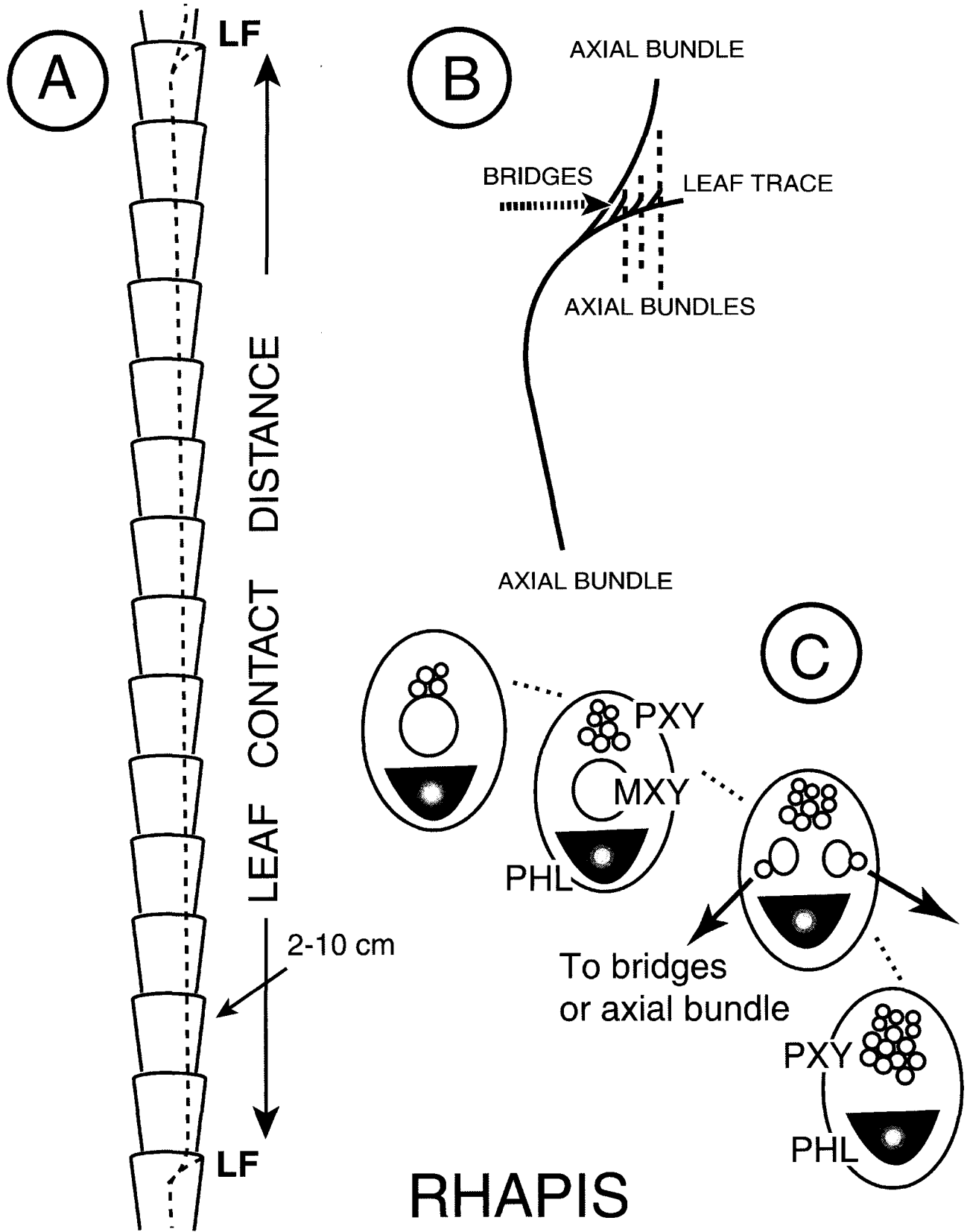


Fig. 1.—A—C. *Rhaps excelsa*. Simplified diagrams of the course of vascular bundles and vascular bundle construction.—A. A single axial bundle represented as making contact via a leaf trace with nodes separated by 14 internodes to illustrate the concept of “leaf contact distance.” Range of internode lengths indicated.—B. Details of the branching of an axial bundle at a node.—C. Diagrams of vascular bundle construction in transverse section at the node to show continuity of the metaxylem into bridges and an axial bundle, but not into the leaf trace, which is irrigated solely by protoxylem. The descending diagrams read from left to right represent in transection (TS) the distal part of an axial bundle as it moves into the leaf.

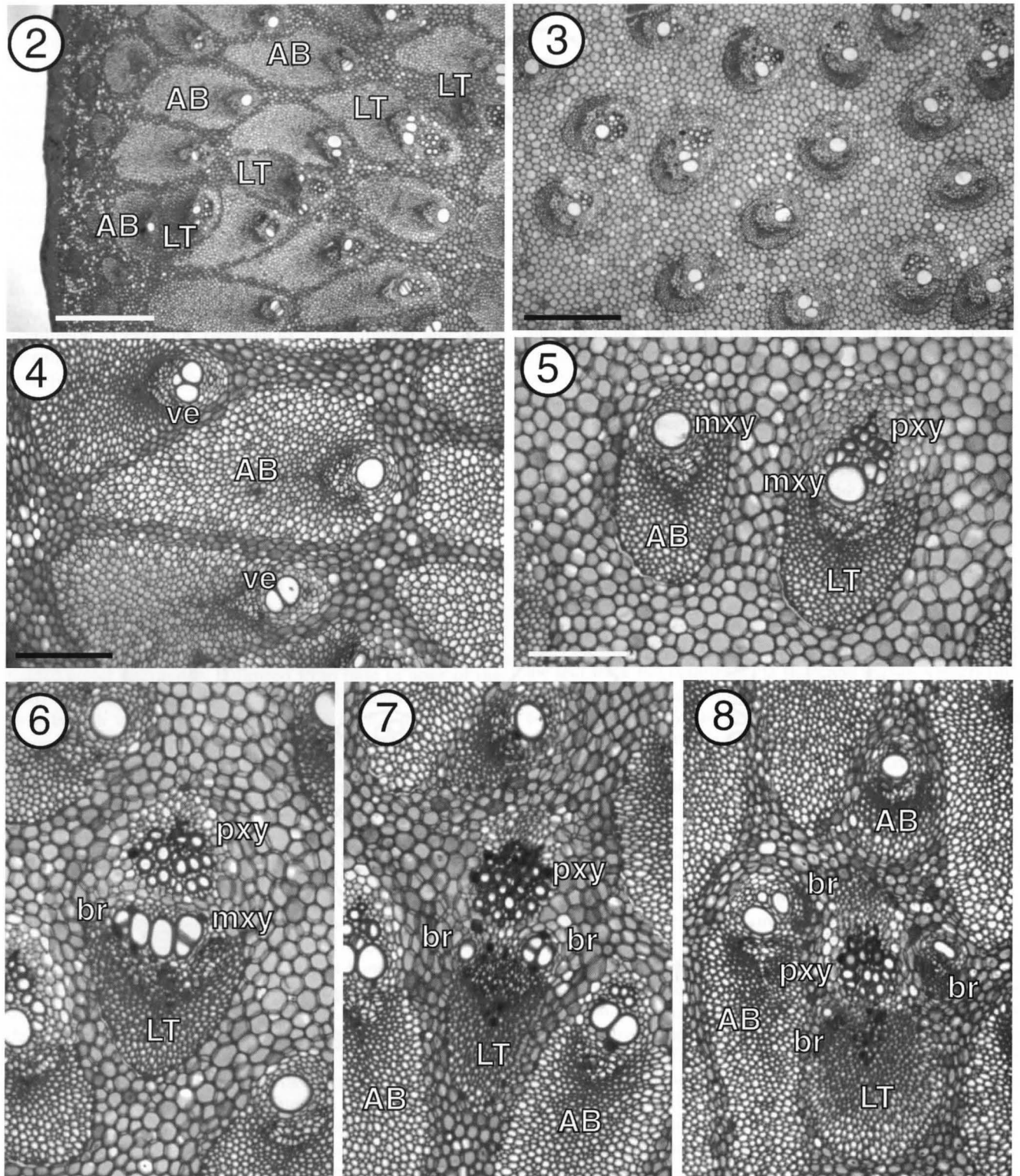


Fig. 2–8.—*Rhapsis excelsa*. Transection of stem to show xylem construction.—2. Stem periphery, with outgoing leaf traces (LT) contrasted with continuing axial bundles (AB).—3. Stem center; axial bundles with relatively narrow MXV vessels and frequent overlapping vessel ends; PXY varying in number of elements.—4. Peripheral axial bundle (AB) with no PXY; MXV with overlapping vessel ends at ve.—5. Two contrasted central axial bundles; left hand with no PXY, representing proximal portion of LCD, right hand with abundant PXY in contact with MXV, representing distal portion of LCD.—6–8. Details of loss of MXV from outgoing leaf trace via bridges (br), the MXV is represented by several overlapping elements in Fig. 6, is converted to bridge xylem in Fig. 7, and makes contact with neighboring axial bundle at left as in Fig. 8; branching axial bundle (AB) at upper right in Fig. 8; scale bar = 500 μ m in Fig. 2–3; = 200 μ m in Fig. 4–5; same for Fig. 6–8.

2. *Calamus* (Fig. 9–15)

Calamus is the largest genus of palms, with about 350 species, demonstrating its ecological and evolutionary success. Some species also have weedy tendencies. It is the champion of all woody climbers because aerial stems can approach 200 m in length (Burkill 1966). Our present understanding of three-dimensional vasculature is based on analysis of very few species (Tomlinson et al. 2001; Tomlinson and Spangler 2002), but descriptions of stem anatomy in a larger number based on single transverse and longitudinal sections suggests the universal applicability of results (Weiner 1992). Unlike *Rhapis*, the bundles are more uniformly distributed throughout the stem, with limited peripheral crowding and absence of well-developed fiber sheaths in outer bundles (Fig. 10, 11). Internode lengths in *Calamus* are at least an order of magnitude greater than in *Rhapis* (cf. Fig. 1A and 9A). Central bundles at any one level include a single large MXY vessel, two phloem strands, and varying amounts of PXY (Fig. 12). Leaf traces are recognized by the abundant development of PXY (Fig. 12–14).

Three-dimensional analysis shows an extreme departure from the *Rhapis* principle because axial continuity is minimal (Fig. 9A). Axial bundles do not interconnect directly and any axial bundle followed basally in the stem ends blindly (see asterisk [*] in Fig. 9A, B). Consequently, the *Rhapis* system of a continuing branch axial bundle and bridge branching has been lost (Fig. 9B). Interconnection among axial bundles is via narrow transverse commissures (Fig. 9B, C); these are rather obscure in transection (Fig. 14). Transverse commissures are not the developmental homologues of bridges because they originate late and by de-differentiation within ground parenchyma cells produce narrow procambial strands (see “tc” in Fig. 15). The transverse commissures at maturity also lack sheathing fibers, unlike bridges. Their narrow metaxylem vessels make a late connection to MXY of axial bundles (Fig. 9C).

Extrapolated values of individual axial bundle length are of the order of 15 internodes. For a stem with internodes 30 cm long, this is an actual distance of 4.5 m. Metaxylem vessels are up to 350 μm in diameter and the volume occupied by these wide elements may be up to 30% of total stem volume, determined in some species by wider vessels and more crowded bundles (cf. Fig. 11). Vessels have simple perforation plates and are very long, with measured values in excess of 3 m (J. B. Fisher pers. comm.). A further departure from the *Rhapis* model is the lack of PXY to MXY contact since the two tissues are always separated by at least one cell layer of conjunctive parenchyma (Fig. 12, 13). This is a feature seemingly characteristic of many climbing monocotyledons (Tomlinson and Fisher 2000). The contrast between outgoing leaf traces and axial bundles, the latter with a very wide MXY vessel at any one level, is shown in Fig. 9C and 12.

In the stem center the basal ends of discontinuous axial bundles can be seen as narrow bundles of varying diameter (see “ba” in Fig. 12, 14). They have short, narrow MXY vessels, as seen in numerous overlapping ends. The contrast between these vessels and both leaf traces and axial bundles is thus extreme, especially their ultimate ends with few cells. The distinctive feature of the leaf traces, as shown in Fig.

12–14, is the abrupt narrowing of MXY and its final complete loss, so that a leaf trace close to its departure into the leaf base (Fig. 13) shows the abundant PXY and absence of MXY. The two phloem strands also become narrow. These details are summarized in Fig. 9C.

All these observations suggest that such stems are highly specialized in their vasculature and represent a considerable departure from the *Rhapis* model of palm vasculature.

3. *Desmoncus* (Fig. 16–24)

This genus, of as many as 60 species, is exclusive to tropical America and represents a distinct lineage within which the climbing habit has evolved, with the large genus *Bactris* Jacq. ex Scop. as a sister group (Uhl and Dransfield 1987). Its climbing grapnels are modified distal leaflets that function as reflexed spines.

The vascular system closely resembles that of *Rhapis* (Tomlinson and Zimmermann 2003) but with important quantitative differences (Fig. 1A and 16A). Internodes are long (to 30 cm in the studied examples) and MXY vessels of the axial bundles are up to 200 μm in diameter (Fig. 17, 19) but with scalariform perforation plates. Outgoing leaf traces branch extensively (Fig. 16B) to produce a series of up to eight bridges, i.e., more numerous than in *Rhapis*. These bridges (br) are shown in Fig. 20 as the MXY progressively disappears from an outgoing leaf trace. Some short bridges may be overlooked in serial analyses if they are shorter than the section spacing. The leaf trace in Fig. 21 also shows three bridges (br) with narrow MXY, completing the loss of this tissue from the original axial bundle. It is clear that there is extensive interconnection between the MXY of outgoing leaf traces and that of adjacent axial bundles at the periphery of the central cylinder (Fig. 16C).

As in *Rhapis*, direct axial continuity is also provided by an axial bundle that can branch from each leaf trace, usually as the last derived branch bundle (Fig. 16B). Thus, a precise LCD can be recognized (Fig. 16A). Because the continuing axial bundle is narrow and appears at the periphery of the central cylinder it is rather obscure in mature stems and is best recognized in the procambial state in the developing crown. It is represented by a dotted line in Fig. 16B in order to emphasize this feature. Despite this somewhat obscure feature the presence of bridges and a branch axial bundle confirms the *Rhapis* principle in this genus (cf. Fig. 1A and 16A). However, unlike *Rhapis*, but as in *Calamus*, there is little or no MXY/PXY connection (Fig. 19).

In all palms the importance of protoxylem in the developing crown is emphasized in this genus by the illustrations from still extending axes that form Fig. 22–24. Outgoing leaf traces at the stem periphery have abundant PXY (Fig. 22), as do central axial bundles (Fig. 23). At this level MXY is established, but elements are still immature. The absence of MXY/PXY contact that will be maintained in a mature bundle is shown in Fig. 24 in which the last-formed PXY and the single-wide MXY vessel is still incompletely differentiated. Clearly the developing crown is irrigated exclusively by PXY, a feature emphasized in climbing palms because of internodal extension.

The section sequences that were analyzed were too short to measure LCD in major axial bundles, but extrapolation

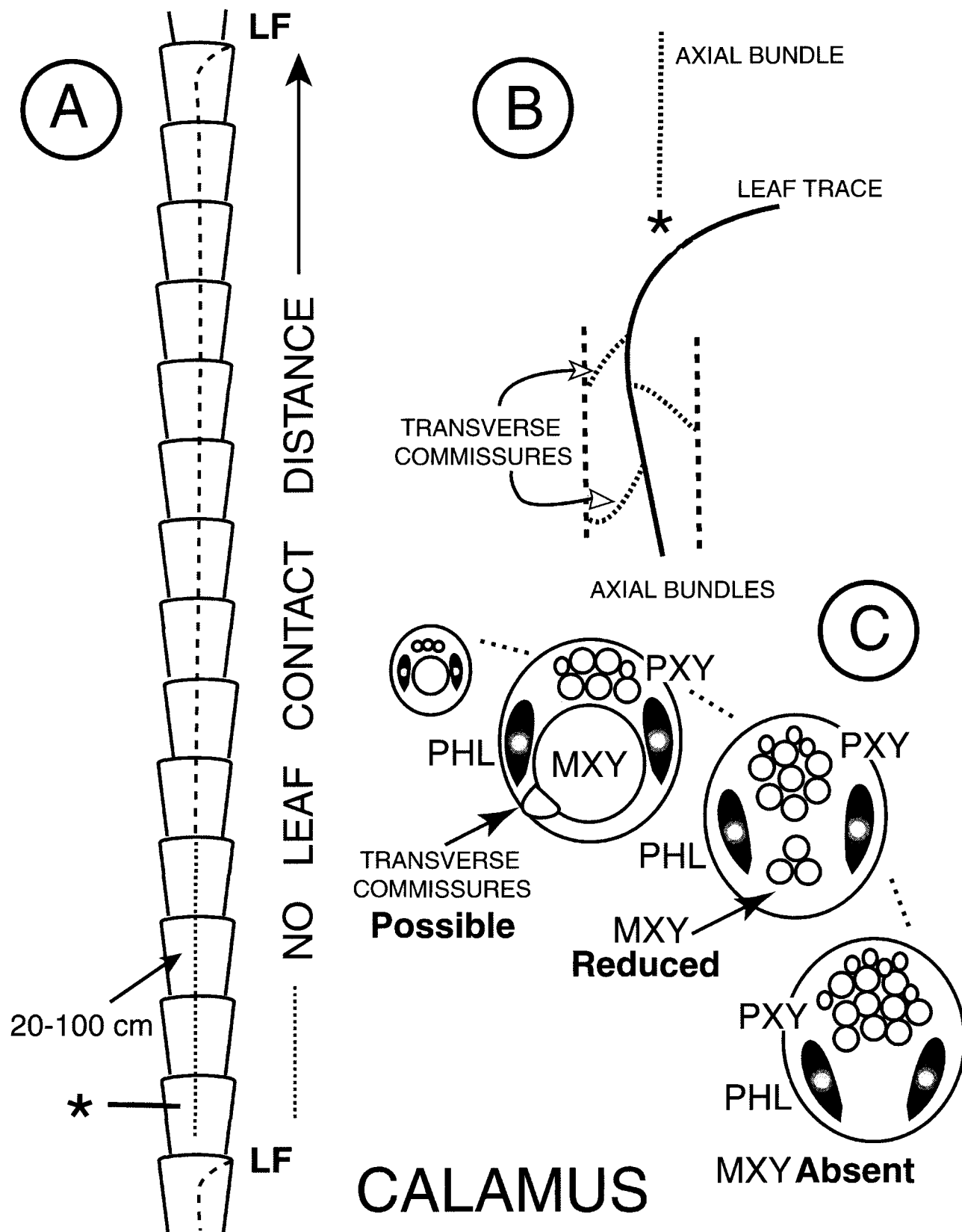


Fig. 9.—A–C. *Calamus* sp., simplified diagram of the course of vascular bundles and vascular bundle construction.—A. A single axial bundle makes contact with a leaf distally, but there is no basal contact, i.e., no leaf contact distance (cf. Fig. 1A). Range of internode lengths indicated.—B. Details of the departing leaf trace, but without continuing axial bundles or bridges; axial bundle connection is represented by irregular transverse commissures.—C. Diagrams of vascular bundle construction in the departing leaf trace with simple reduction and loss of MXY. Transverse commissures may connect to axial MXY. The descending diagrams read from left to right represent in TS the distal departure of an axial bundle (basally a narrow strand) into the leaf base.

Table 1. Comparison of stem internal tracheary element diameter in three palms.

	Metaxylem (= vessels)		Protoxylem (= tracheids)	
	(a) Axial bundle mid-portion	(b) Axial bundle branch	(c) Bridge or transverse commissure	(d) Leaf trace
<i>Rhapis</i>				
Diameter	80 μm	40 μm	25 μm	25 μm
Ratios		a/b 2:1 ^a	a/c 3.2:1	a/d 3.2a:1
<i>Calamus</i>				
Diameter	250 μm	N/A	35 μm	60 μm
Ratios		N/A	a/c 7.1:1	a/d 4.1:1
<i>Desmoncus</i>				
Diameter	180 μm	25 μm	50 μm	35 μm
Ratios		a/b 7.2:1 ^b	a/c 3.6:1	a/d 5.1:1

^a Smallest ratio to the fourth power = 16.

^b Largest ratio to the fourth power \approx 2500.

based on the number of protoxylem elements in axial bundles indicates a value of about 15 internodes, which is in comfortable agreement with the maximum LCD in *Rhapis*. This represents an approximate actual length of 3–4 m. Because MXY elements of major axial bundles are so wide, the contrast between them and PXY is more pronounced than in *Rhapis* and the relatively abrupt narrowing of MXY elements in the leaf trace is also striking, with important hydraulic consequences as discussed in the next section.

DISCUSSION

Hydraulic Constraints

With information about xylem structure it is possible to assess the efficiency of the axial water transport system in the three palms. This can be done through a theoretical consideration of resistances to water flow (i.e., loss of conductivity) based on the internal diameters of the various tracheary components. These include axial MXY, PXY, and the MXY connections between bridges or transverse commissures and axial bundles. Because connections to inflorescence branches have no influence on axial vascular integrity they are discounted.

Tracheary elements (vessels and tracheids) may be treated as ideal capillaries in which water moves by laminar flow. Conductivity is estimated from the Hagen-Poiseuille equation (Zimmermann 1983).

$$L_p = \frac{r^4 \pi}{8\nu}$$

where L_p = conductivity
 r = internal radius of capillary
 ν = viscosity of the moving fluid

Assumptions governing this use, based on measurements of tracheary element diameter, are considerable, as emphasized by Lewis and Boose (1995), but the approach is justifiable in a comparative context. In addition, there is appreciable direct measurement of conductivity values that support some aspects of this model (Sperry 1986). The essential principle extracted from the equation is that conductivity increases directly proportional to the fourth power of the internal radius of a conduit. Doubling the diameter of a cap-

illary increases the conductivity 16-fold. In comparative terms it requires 16 elements of unit diameter to move the same volume of water at a constant rate as a single capillary of twice the unit diameter.

If one treats the xylem interconnections as open capillaries, this neglects the resistance occasioned by the pit membranes through which water moves from one unit to another (either vessel or tracheid). Because PXY tracheids are necessarily shorter than vessels, longer vessels clearly minimize this resistance. Over long distances, axial water movement occurs in the MXY of axial bundles and from bundle to bundle via bridges and along branch axial bundles. This is the condition in *Rhapis* and *Desmoncus*. Decreased conductivity is the result of the gradual or abrupt narrowing of MXY in regions of transition. In *Calamus* the same conditions apply except that direct axial continuity is lost in the absence of branch axial bundles and resistance is considerable in the connection between wide axial MXY vessels and narrow MXY elements of the transverse commissures. Comparative information is summarized in Table 1. This shows the enormous disparity in the ratios of tracheary element diameters in the climbing palms, compared with *Rhapis*, a consequence of larger MXY vessel diameters in the former.

Movement of axial water into appendicular pathways (leaves) involves a movement from MXY to PXY. This is direct in *Rhapis*, but in *Desmoncus* and *Calamus* there is no MXY/PXY connection. In *Rhapis* there is thus resistance to flow as a result of the change from wide to narrow tracheary elements at the "vascular leaf insertion" within the stem, to use the terminology of Zimmermann and Sperry (1983). This is compensated somewhat by the larger number of PXY elements that irrigate the leaf, but this number is never sufficient to eliminate the resistance since the minimum of 16 elements in the lowest ratio (2:1 in Table 1) is never achieved. Other things being equal, the preferred course of the transpiration stream thus is axial. In *Desmoncus* and *Calamus* the vascular leaf insertion does not exist because of the absence of a direct MXY/PXY connection. Under these circumstances water can only move into the PXY of a leaf trace either symplastically (via the vacuole of the separating conjunctive parenchyma) or apoplastically along cell walls (or possibly within intercellular spaces).

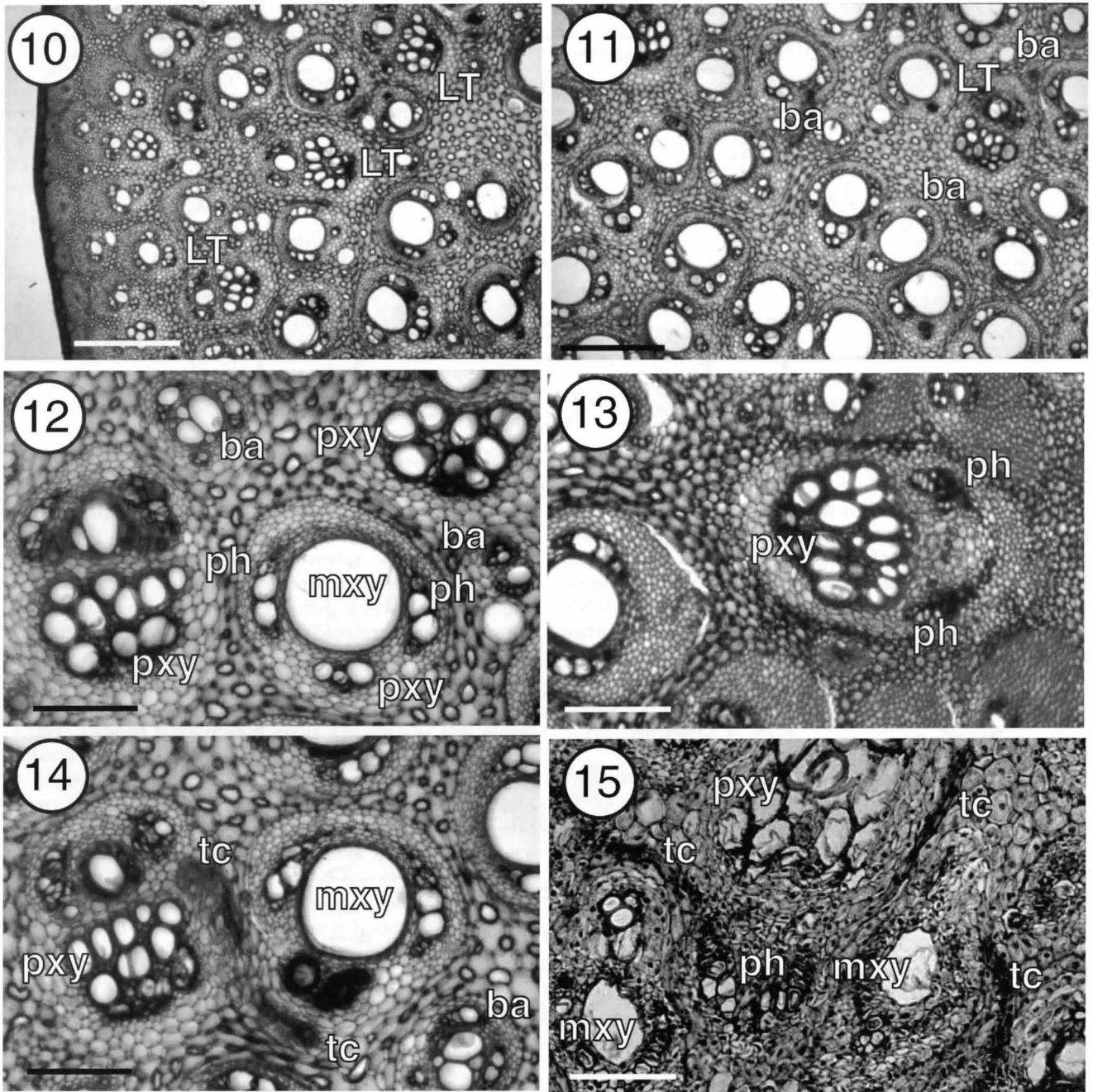


Fig. 10–15.—*Calamus longipinna* K. Schum. & Lauterb. Transection (TS) of stem to show xylem construction.—10. TS of stem periphery with leaf traces (LT) and their abundant PXY contrasted with axial bundles and their single wide MXY vessel.—11. TS of stem center and wide axial bundles; narrow bundles (ba) are axial bundles near their proximal termination.—12. An axial bundle (right) with wide MXY vessel contrasted with a leaf trace (left) with abundant PXY; ba represent basal ends of axial bundles.—13. Leaf trace close to node, without MXY but abundant PXY.—14. Contrast between axial bundle and leaf trace with indications of transverse commissure (tc); ba as in Fig. 11–12.—15. Leaf trace (with abundant PXY) and axial bundles (with developing MXY vessels) in immature internode. Transverse commissures (tc) appear as procambial strands developed by dedifferentiation of ground tissue. Scale bars = 500 μ m in Fig. 10–11; = 200 μ m in Fig. 12–14; and, = 100 μ m in Fig. 15.

Calculated values for the drop in conductivity from elements of large to small diameter are such that the increase in number of PXY elements does not compensate for this high resistance. Even though the number of PXY elements can be considerable (e.g., Fig. 12–13), it is far short of the estimated ca. 2500 needed (Table 1).

In summary, palm stems show two major resistances to

axial water flow. First, there is axial resistance because of the limited extent of any one vascular bundle and interconnection between narrowed MXY elements. Second, there is appendicular resistance resulting from interconnection between axial bundles and leaf traces also along narrow PXY elements. Similar considerations are likely to apply generally to larger woody monocotyledons that are based on the

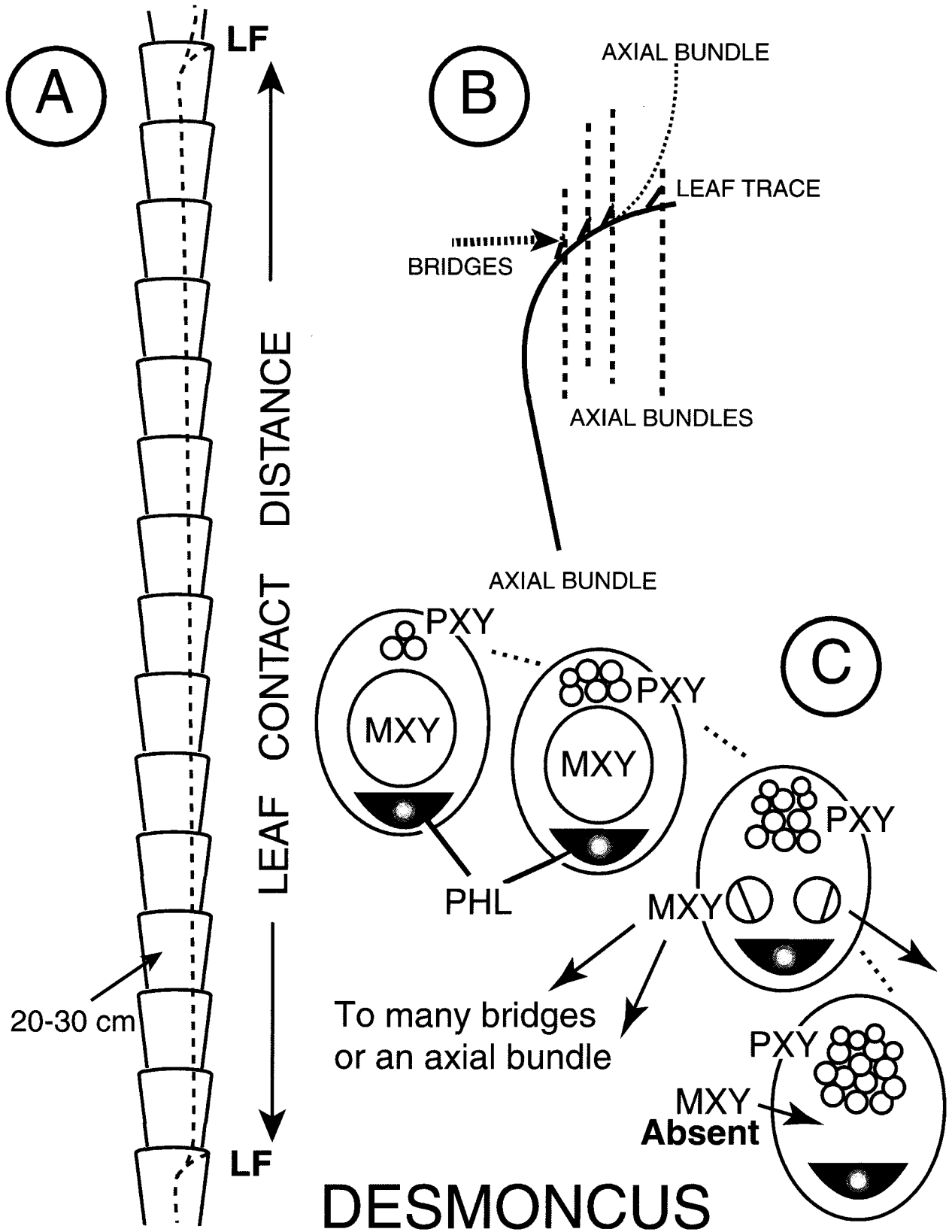


Fig. 16.—A–C. *Desmoncus* sp., simplified diagram of vascular bundles and vascular bundle construction.—A. A single axial bundle with a leaf contact distance over 14 internodes (cf. Fig. 1A). Range of internode lengths indicated.—B. Details of the branching of an axial bundle via bridges and a continuing axial bundle at a node. As in *Rhapis* (Fig. 1B) but with more numerous bridges and an inconspicuous axial bundle (dotted).—C. Diagram of vascular bundle construction at the node to show continuity of MXY into bridges and an axial bundle, as in *Rhapis* (Fig. 1C) but with bigger difference between tracheary element diameters of PXY and MXY. The descending diagrams when read from left to right represent in TS the distal departure of an axial bundle into the leaf base.

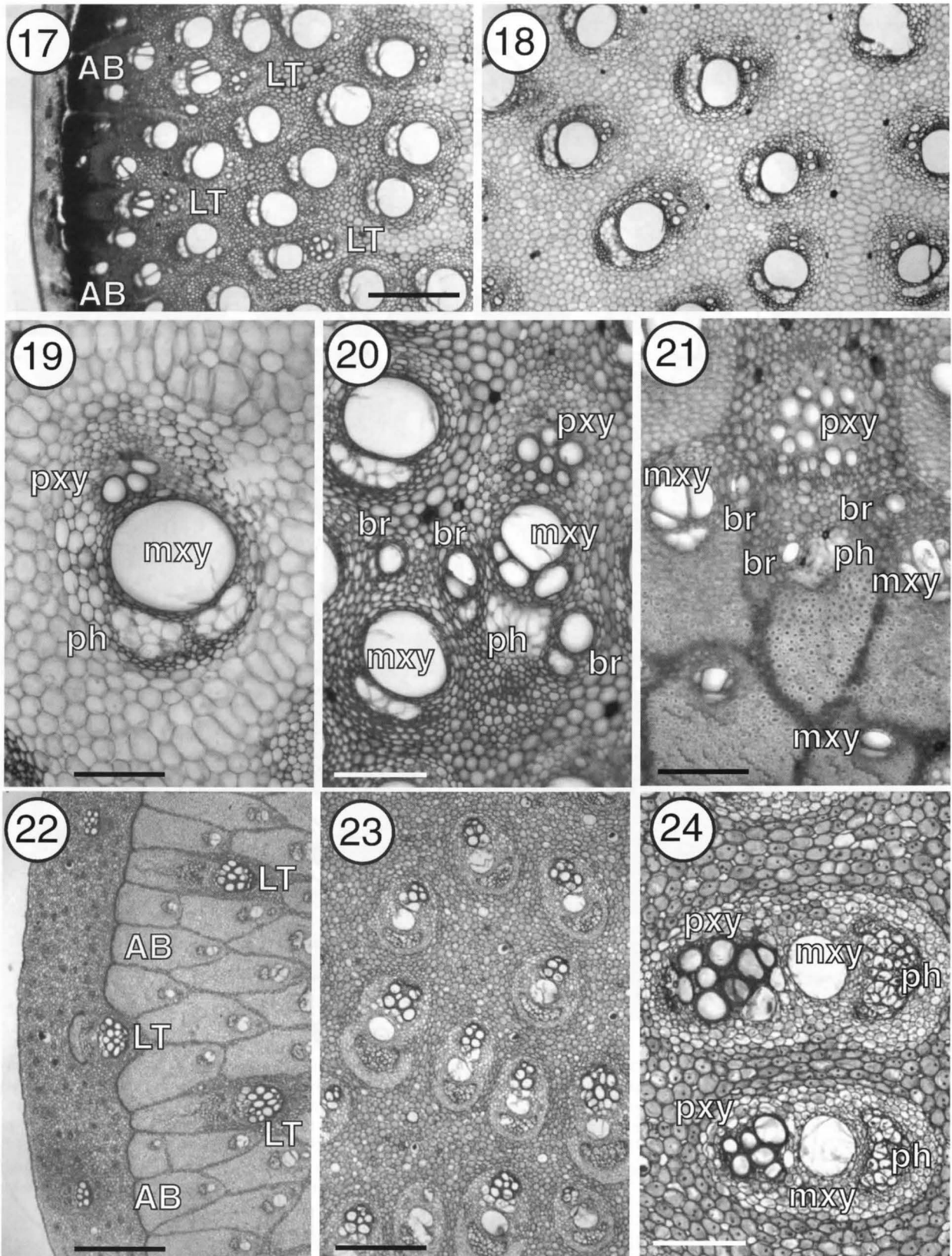


Fig. 17–24.—*Desmoncus* spp. Transection of stem to show xylem construction and development.—17–20. *D. chinantlensis* Liebm., mature stem.—21–24. *D. orthacanthos* Mart., mature and immature stem.—17. Stem periphery with contrast between axial bundles (without overlapping MXY vessel ends) and outgoing leaf traces with abundant PXY and narrow MXY elements with numerous overlapping vessels. Peripheral axial bundles (AB) with narrow MXY vessels.—18. Stem center, axial bundles with varying amounts of PXY.—19. Detail of single axial bundle, PXY and MXY not in contact.—20. Outgoing leaf trace with narrowing MXY and branching bridge bundles with narrow MXY elements.—21. Mature outgoing leaf trace without MXY, the adjacent axial bundles with which the bridges make contact,

Rhapis principle. In climbing palms, because of their distinctive construction, most clearly shown in *Calamus*, the calculated resistances become enormous.

Safety and Efficiency

In his book on the ascent of sap in the xylem, Zimmermann (1983) emphasizes the contrast between the *safety* of the transport system and its *efficiency*, two factors that are essentially opposed. Conifers and flowering plants provide examples of contrasting strategies. The wood of conifers, being vesselless and largely made up of short, narrow tracheids is inefficient in conduction, but safe because the volume of conducting units is small and loss of single units by cavitation less detrimental. Dicotyledonous wood, with fewer but longer and wider units (vessels), is more efficient in conduction, but less safe because cavitation in a single vessel will eliminate a larger proportion of conductive capacity. In both types of unit, extension of an embolism is contained by the structure of the pit-membrane and is particularly notable in conifers, where the torus of the pit-membrane serves as an apoplastic seal.

In climbing palms, as *Calamus* and *Desmoncus* illustrate, efficiency of water transport is presumably promoted by the development of wide MXY vessels in axial bundles. Furthermore, that these vessels are also long is evident from direct measurement but also by the paucity of overlapping vessel ends, as can be seen in single sections (e.g., Fig. 11, 18). Long vessels are also a direct consequence of the long internodes that characterize climbing palms. Nevertheless, the *Rhapis*-model shows that LCD puts an upper limit on vessel length (Fig. 1A). Any axial MXY vessel is interrupted at the departure of a leaf trace, with continuity provided via the narrow and short MXY vessels along bridges and into branch axial bundles. This constraint also exists in *Desmoncus* (Fig. 19).

The uniquely discontinuous vascular system of *Calamus*, without a continuing axial bundle as a branch of a leaf trace, apparently eliminates this constraint because a LCD does not exist (Fig. 9A). Theoretically any axial bundle could have unlimited extent and MXY vessels of indefinite length could be produced. It is, therefore, not surprising that MXY vessels are long and could be longer than in *Desmoncus*. Only extensive measurements of vessel length in climbing palms can answer such questions.

There are no current means for quantifying safety. Safety, in principle, can involve two processes: first, one that minimizes the risk of cavitation and, second, one that promotes the refilling of embolized vessels. One feature in which *Calamus* and *Desmoncus* are apparently contrasted with other palms is the absence of PXY to MXY direct contact. Can this in some way "protect" the axial system on the assumption that it prevents an embolism extending from PXY to MXY? The xylem vascular system to a leaf is entirely made

up of numerous but narrow protoxylem elements. It is not permanent and is dispensed with after leaf fall, whereas the axial system is permanent and irreplaceable. Refilling of embolized vessels remains uninvestigated except that positive root pressures have never been recorded for *Calamus* (J. B. Fisher pers. comm.). In view of the great lengths achieved by rattan stems, it seems unlikely that root pressure is a mechanism for solving the safety problem.

The paradox of the *Calamus* stem still remains because it has a xylem structure seemingly highly favorable to rapid movement of water over long distances via numerous long and wide vessels but with extensive resistances to flow from one axial bundle to another and from axial bundles into leaves.

Other Climbing Palms (Fig. 25–32)

The comparison of the vascular systems in *Calamus*, *Desmoncus*, and *Rhapis* provides a typology that is informative of the structural features that might be looked for in other climbing palms. In the remaining five lineages of palms in which the scandent habit has evolved (Uhl and Dransfield 1987; Tomlinson and Fisher 2000) we still lack three-dimensional analysis that would further elucidate the situation. However, study of the single sections can indicate some significant features, especially in a comparative context. The publications of Weiner (1992) and Weiner and Liese (1993) are rich in information that needs to be understood in a developmental and three-dimensional context.

Figures 25–32 give some indication of this diversity. *Korthalsia* Blume superficially resembles *Calamus* in bundle construction, but I have seen no evidence for blind-ending basal bundles (Fig. 25, 26). In *Myrialepis paradoxa* (Kurz) J. Dransf. there is a marked contrast between peripheral bundles, each with a single MXY vessel (Fig. 27) and central bundles, each with two very wide vessels (Fig. 28). The center also includes scattered narrow vascular and fibrous bundles (Fig. 28) of unknown significance. The phloem is represented by a single-phloem strand, albeit with a tendency to form a median sclerenchymatous strand, as is common in palms. Scattered central fibrous strands occur in the related *Plectocomiopsis geminiflora* Becc. (Fig. 29). *Daemonorops oxycarpa* Becc. (Fig. 30), in the same tribe as *Calamus*, has very similar vascular bundles (cf. Fig. 32) but with little evidence for blind-ending bundles (Fig. 30). The West African rattans form a separate clade to the Asian species, except for *Calamus deerratus* G. Mann & H. Wendl. The three other genera lack the complexity of *Calamus* (e.g., Fig. 31) but need detailed analysis. *Calamus deerratus* itself shows features typical for Asian species, with good evidence for blind-ending bundles (see "ba" in Fig. 32). It should be emphasized that climbing palms include 20% of all palm species. Further study will require extensive comparison.

Observations of three-dimensional features of palm vas-

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show numerous overlapping narrow vessels.—22. Periphery of immature stem, leaf traces (LT) with abundant PXY, axial bundles (AB) with differentiated but immature MXY.—23. Stem center; axial bundles with varying amounts of mature PXY; MXY represented by immature vessels.—24. Two immature central axial bundles, the last-formed and immature PXY elements do not make contact with the maturing MXY elements. Scale bar = 500 μm in Fig. 17 and Fig. 22–23, same for Fig. 18; = 100 μm for Fig. 19, 20, 24; = 200 μm for Fig. 21.

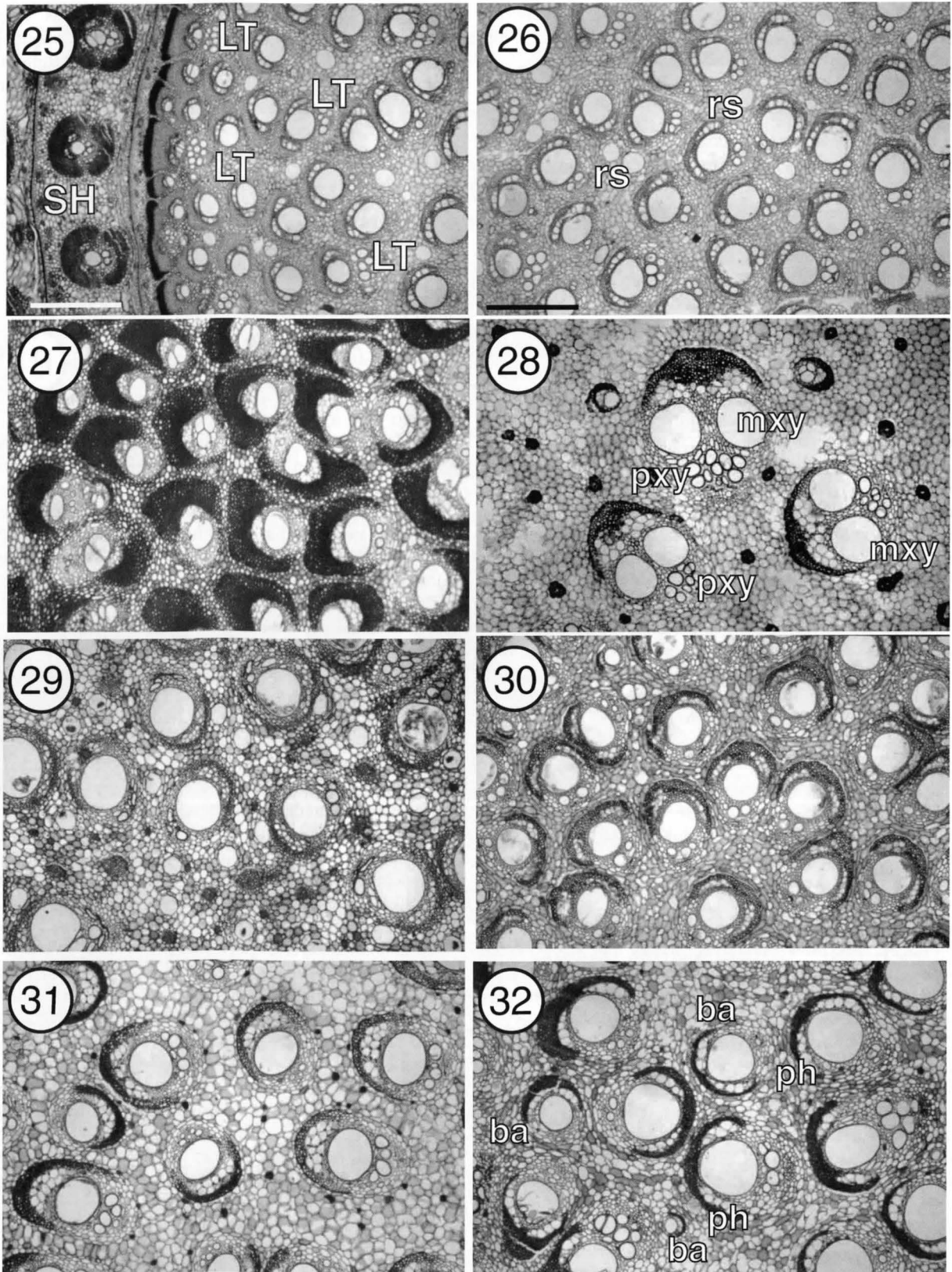


Fig. 25–32.—Transverse sections of stems of additional climbing palms; all at same magnification.—25. *Korthalsia rostrata* Blume, stem periphery including part of leaf sheath (SH), leaf traces (LT) with abundant PXY shortly below entry into leaves at next two higher nodes.—26. *Korthalsia rostrata*, stem center with conspicuous raphide canals (rs).—27. *Myrialepis paradoxa*, stem periphery with relatively well-developed bundle sheaths, axial bundles with a single MXY vessel.—28. *M. paradoxa*, stem center, axial bundles each with two very wide MXY vessels.—29. *Plectocomia elongata* Mart. & Blume, stem center with raphide canals and isolated fibrous bundles.—30. *Daemonorops oxycarpa*, stem center, resembling *Calamus* but without obvious blind-ending basal bundles.—31. *Laccosperma* (G. Mann. & H. Wendl.) Drude sp., stem center.—32. *Calamus deerratus*, stem center with evidence of basal ends of axial bundles (ba). Scale bar in Fig. 25, 26 = 500 μ m, same for Fig. 27–32.

culature would have wider significance in several fields. The physical movement of water over long distances in palms is determined by the structure of the same kinds of tracheary elements as are found in all vascular plants. Any theory of xylem sap flow developed by physiologists must be universally applicable to all plants; evident structural anomalies, as in those of the *Calamus* stems must be accommodated by the theory. Putting these functional objectives in the context of the systematics and evolution of monocotyledons adds to our interest in the group.

Note added in proof.—A more recent examination of an unidentified species of *Daemonorops* Blume ex Schult. f. shows that there is vascular discontinuity as in *Calamus*. However, the basal blind-ends of axial bundles originate consistently where each leaf trace departs, maintaining the one-to-one relation between axial bundle and leaf trace that is a feature of the *Rhapis* model. In the structural typology described here *Daemonorops* would fit conveniently between *Desmoncus* and *Calamus*.

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