

ANATOMY OF THE PALM RHAPIS EXCELSA II. RHIZOME¹

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THE PALM *Rhapis excelsa* develops horizontal, subterranean rhizomes which bear only non-assimilating scales. This kind of axis may be contrasted with that of some other palms like *Nypa* or *Sabal minor* in which the foliage leaves are borne directly by the underground stem. Scale-leaf bearing rhizomes of the *Rhapis* type are relatively rare in the Palmae (Tomlinson, 1961) although common in other monocotyledonous orders (e.g., Scitamineae, Liliiflorae).

Anatomical comparison of the scale-leaf bearing rhizome with the aërial axis which bears the assimilating foliage is of considerable interest because the two types are morphologically equivalent but their development must be quite different from a nutritional point of view. The present paper is an account of the vascular structure of the mature rhizome. The development of the two types of axes will be described in a later paper in this series.

Palms show two major growth forms. In one kind the vegetative axis is unbranched, producing solitary columnar stems, as in the coconut, in the other it is caespitose by the production of axillary vegetative axes, as in the date. Branching of the second type is always restricted to the base of the parent axis for simple adaptive reasons which are well known (Tomlinson, 1964). Normally these basal suckers rapidly turn erect. The first leaves produced by lateral branches are reduced to scales, but there is a rapid transition to normal assimilating foliage leaves as the branch assumes a vertical position. Thus the construction of the parent axis is repeated and by further branching of all axes a tufted and congested sympodial system results. *Rhapis* represents a growth form in which mutual competition of successive segments of the sympodium is eliminated by long-continued horizontal growth of the branch before it turns erect (FIG. 1A). The rhizome in *Rhapis* is essentially the early stage of sucker development which has become much protracted. In some ways it is a "persistently juvenile" stage of axis development.

MORPHOLOGY OF THE RHAPIS RHIZOME

Axillary shoots which grow out as rhizomes appear in the seedling² of *Rhapis*. After a variable period of horizontal growth the rhizome apex turns

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² Seedling morphology and anatomy will be described in a subsequent paper.

erect and there is a rapid period of transitional growth leading to the establishment of an erect leafy shoot. Features of the construction and growth of rhizome segments are shown in FIGS. 1 and 2. In the transitional period of growth the axis is somewhat swollen (FIGS. 2B, C, D, 1B) and successive leaves are elaborated so that a transition between the scale leaves of the rhizome (FIG. 1C) and the foliage leaves of the aërial stem occurs (FIGS. 1D-F). Transitional leaves show a gradual development of the blade which may be initially either compound or simple depending on the vigor of the shoot. Only compound leaves are illustrated in FIG. 1D-F. This transitional sequence clearly illustrates that the scale leaf is morphologically equivalent to the base of the adult foliage leaf.

The sympodium is continued by new rhizomes originating as buds in the axils of scale or transitional leaves at the base of the newly-erect shoot



FIGURE 1. Relation of aërial to underground axes in *Rhaps excelsa*. A. One segment of sympodium, foliage leaves removed from aërial shoot at left, $\times 1/8$. B. Base of right-hand aërial shoot of FIG. 1A, all but distal leaves removed, $\times 1/4$. Numbers 1-5 refer to renewal shoots of successive age, youngest distal, oldest proximal, number 4 is on the remote side of the axis. C. Scale leaf from rhizome, $\times 1/2$. D-F. Successive leaves from transitional sequence at base of erect shoot, $\times 1/4$, showing gradual development of blade. Adult foliage leaves have blades 4-5 times wider than that of leaf illustrated in FIG. 1F.

(FIG. 2D). Several buds may grow out, in the order of their age (FIG. 1B) and in this way the sympodium multiplies. With frequent production of laterals sympodia may become very complex (FIG. 2E). Clonal spread of *Rhapis* under favorable conditions is therefore rapid. Erection of rhizome

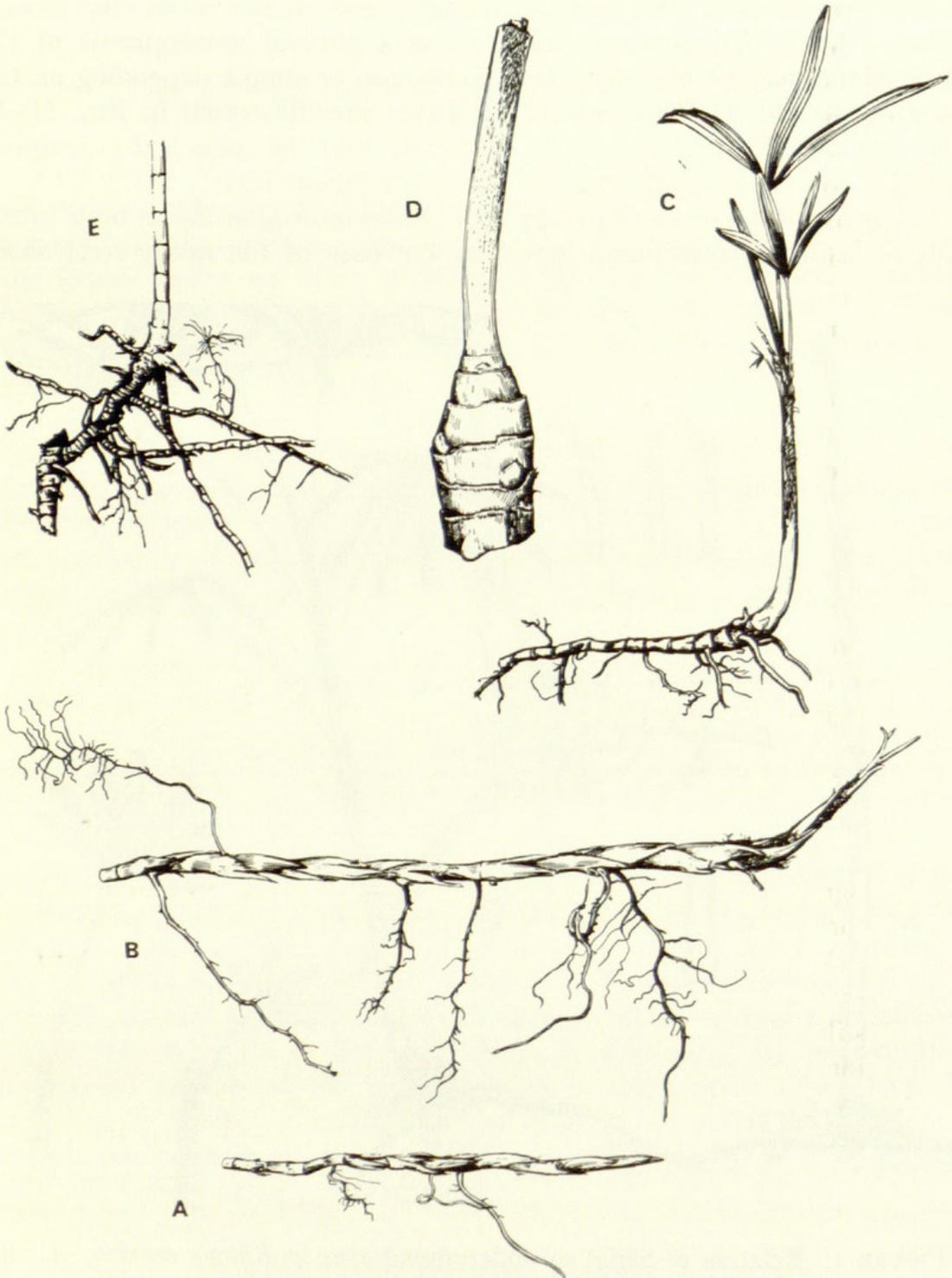


FIGURE 2. Development of rhizome system in *Rhapis excelsa*. A. Apex of underground creeping rhizome, $\times 1/4$. B. Apex of rhizome becoming erect; transitional type of foliage initiated, $\times 1/4$. C. Later stage, transitional leaves with well-developed blades, $\times 1/6$. D. Base of erect shoot at a stage of development corresponding to FIG. 2C; leaves removed to show buds of renewal shoots, $\times 1/2$. E. Old, much-branched rhizome complex, $\times 1/8$.

apices and the morphological responses it induces seem independent of the season in South Florida since all stages of development can be found at any time of year.

Horizontal, underground parts of the rhizome, with which this article is concerned, may be up to 1 meter long and 1 to 1.5 cm. in diameter; the apex is protected by the rigid overlapping scales (FIG. 2A). Scales, like the foliage leaves of the aerial stem, are arranged in a $2/5$ phyllotactic spiral. Each originates as a closed tube with a narrow distal opening which is widened by enlargement of enclosed organs (FIG. 1C). Internodes are 1.5 to 2 cm. long in older parts of the rhizome. The covering of scale leaves is retained for a long time (FIG. 2B). Very old rhizomes still bear the fibrous remains of decayed scales. Neither buds nor their vestiges are associated with scale leaves; they are restricted to the transition region where the rhizome turns erect (FIG. 2D). Roots are borne all around the rhizome at irregular intervals. We have not recorded this quantitatively but it seems to us that root insertions are associated (a) with each other and (b) less obviously, with the nodes. Root production is also vigorous on the swollen regions at the junction of successive sympodium segments. Rhizomes are always colorless and non-assimilating.

MATERIALS AND METHODS

Rhizome segments used in this investigation are all from specimens cultivated at Fairchild Tropical Garden. Sequential sections 30–50 μ thick were cut at 0.5 mm. intervals, stained and mounted by procedures previously described (Zimmermann & Tomlinson, 1965). In order to clarify the vascular system, starch was eliminated from the tissue by immersing sections for 5 to 10 minutes in 50 per cent hydrochloric acid prior to washing and bleaching. For details of nodal anatomy a continuous series of sections from a short length of rhizome was prepared.

Cinematographic analysis was carried out with the drawing method described before (Zimmermann & Tomlinson, 1965) as well as with the optical shuttle (Zimmermann & Tomlinson, 1966). The optical shuttle was also very useful in making quantitative plots of single vascular bundles of the types illustrated in FIG. 4.

In addition to microscopic analysis we have studied the rhizome structure extensively by macro-cinematography of cut surfaces on the microtome. A special clamp for the 'Reichert' sliding microtome was designed and constructed which allows continuous advance of long specimens. Such motion picture sequences give an excellent over-all view of the vascular system.

GENERAL RHIZOME ANATOMY OF RHAPIS

An over-all view of a transverse section of the rhizome is given in FIG. 3.

Rhizome 1–1.5 cm. in diameter, divided into cortex 1–1.5 mm., central

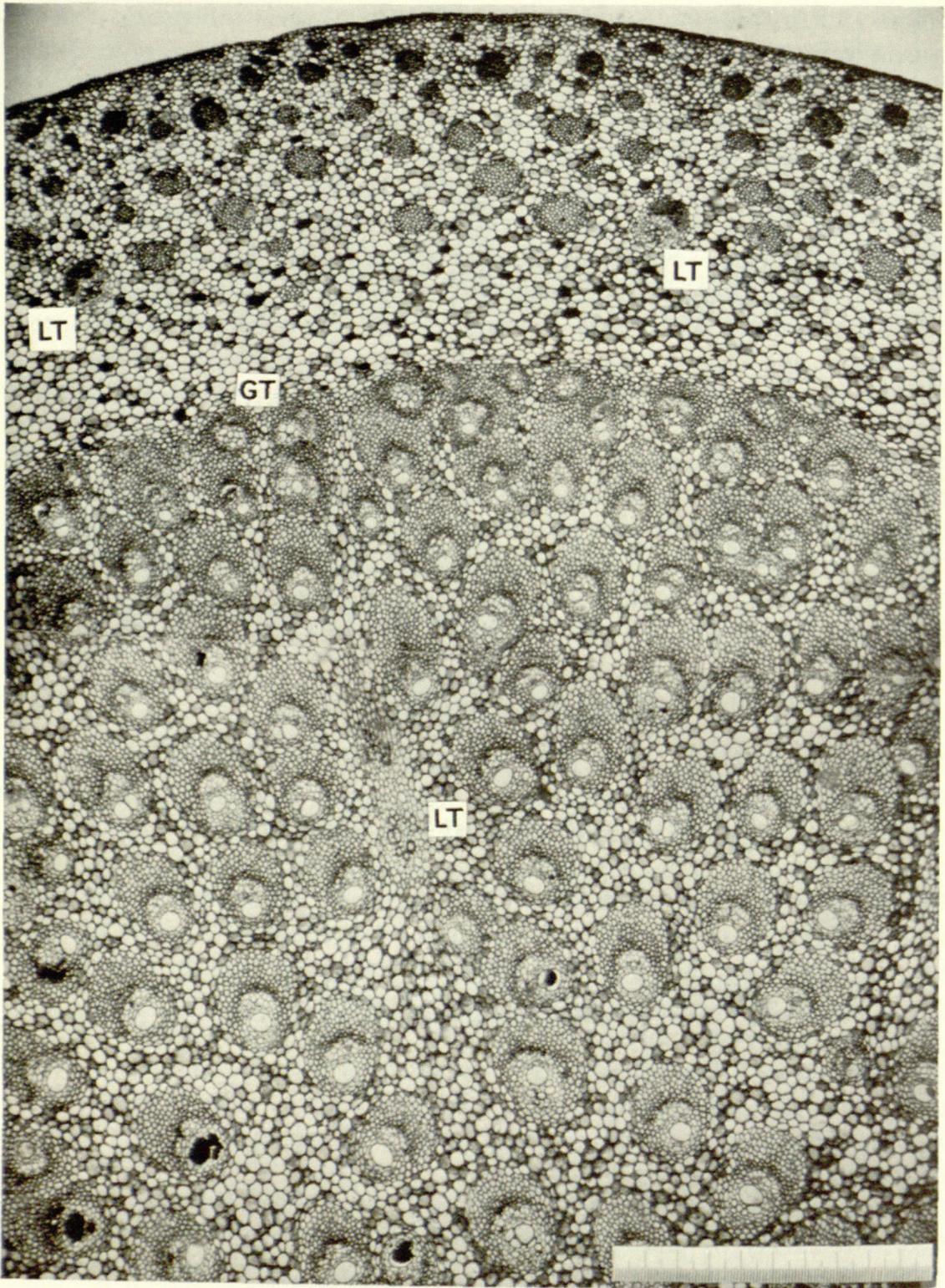


FIGURE 3. *Rhaps excelsa*, transverse section of rhizome. Major leaf trace (LT) to next node above level of section shown in center of figure; two minor leaf traces (LT) to same node shown in cortex. Peripheral girdling traces (GT) are ultimate endings of root traces. Black deposits in lower left-hand corner are tannins. Scale equals 1 mm.

cylinder 8-14 mm. wide. Epidermis uniform, cells elongated, rectangular in surface view with transverse end walls or frequently somewhat spindle-shaped with oblique end walls. Outer epidermal wall thickened, uniformly cutinized.

occasional cells with pronounced pitted thick secondary walls becoming lignified. Stomata not infrequent, resembling those of aërial stem but without chloroplasts and presumably non-functional. Periderm not developed except locally around wounds and leaf scars by ligno-suberisation of ground parenchyma accompanied by divisions of "etagen" type.

Cortex with 3-4 outermost layers of narrow cells with truncate end walls; walls thickened and becoming ligno-suberized to form a narrow hypodermal sclerotic layer interrupted below stomata by loose, wide unligified cells continuous with middle cortex. Middle and inner cortical ground parenchyma with a well-developed intercellular space system, cells frequently becoming slightly thickened and prominently pitted with age. Cortex (FIG. 6), apart from inconspicuous transient leaf traces, including a series of purely fibrous strands, peripheral strands usually narrower than central; largest fibrous strands (up to 120 μ wide) including a narrow central strand of vascular tissue, often only phloem. Innermost cortical layers usually free of fibrous bundles.

Central cylinder not delimited from cortex by endodermis or other specialized layer, but by abrupt transition to narrow compact ground parenchyma with slightly thickened walls and zone of narrow, somewhat congested peripheral vascular bundles. Compact peripheral zone only interrupted by parenchyma at exit of leaf traces to form distinct "leaftrace gaps" (FIG. 6). Central vascular bundles wider, more diffuse. Central ground parenchyma very uniform, cells somewhat wider and looser than those at periphery. Individual vascular bundles of central cylinder more or less completely sheathed by fibrous tissue, but fibers least well developed around xylem. Fibers narrowest and most heavily lignified next to phloem. Peripheral vascular bundles somewhat more fibrous than central, but difference much less pronounced than in aërial stem. Vascular tissues including usually one wide metaxylem vessel and often protoxylem in varying amounts (see below). Phloem strand narrow, uniform, never with a distinct median sclerotic isthmus as is common in bundles of aërial stem. Metaxylem vessel elements average 60 μ wide, 1-1.5 mm. long with oblique or slightly oblique scalariformly perforated end walls with 6-10 thickening bars. Sieve-tubes average 15 μ wide with compound sieve-plates on slightly oblique end walls. Starch abundant in ground parenchyma except for narrow starch-free zone in outer cortex; grains either solitary, more or less spherical or more usually compound, angular. Tannin abundant as dark-brown deposits in otherwise unmodified parenchyma cells in all parts. Vascular tissues commonly occluded by tanniferous deposits giving a strong positive lignin reaction with phloroglucinol and concentrated HCl; tannin occlusions not especially restricted to traces to old leaves. Stegmata (silica cells) only observed next to cortical fibrous bundles. Raphide sacs not observed.

In summary, the general anatomy of the rhizome, as seen in a single transverse section, differs from the aërial stem as follows: relatively greater development of cortex and cortical fibrous system; central and peripheral vascular bundles of central cylinder less conspicuously different; less obvious variation in the numbers of metaxylem elements.

COURSE OF VASCULAR BUNDLES IN THE RHIZOME

Central system. In spite of frequent root insertions the over-all course of vascular bundles in the *Rhapis* rhizome remains quite clear. It resembles

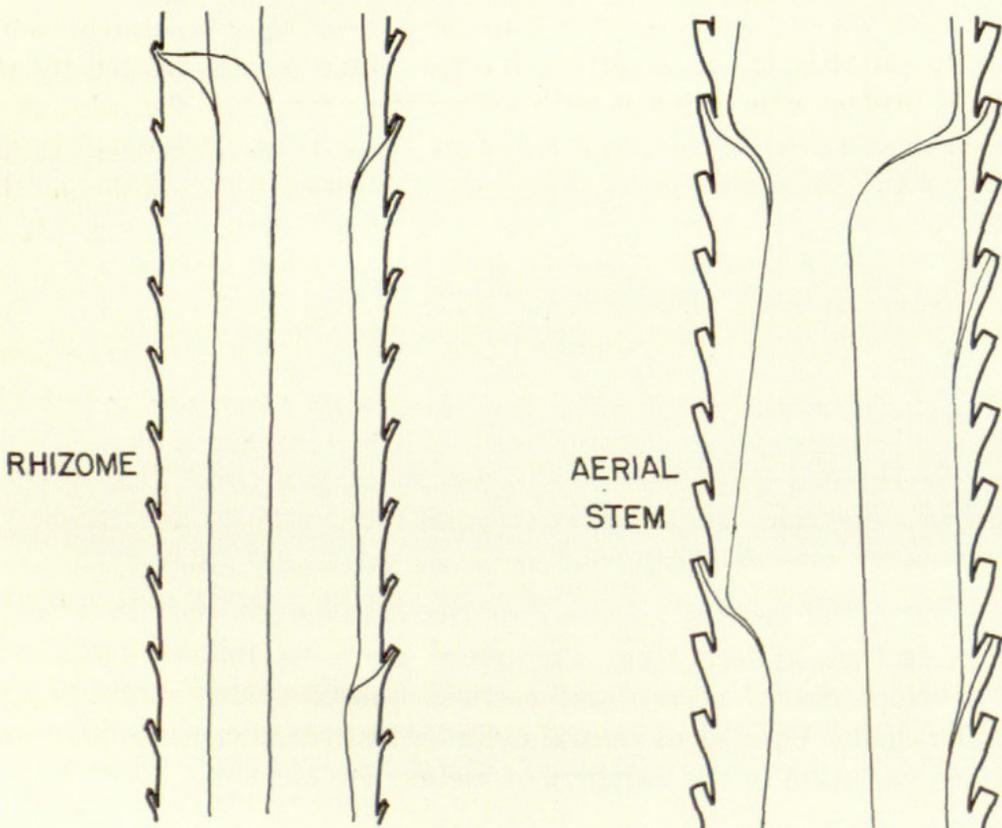
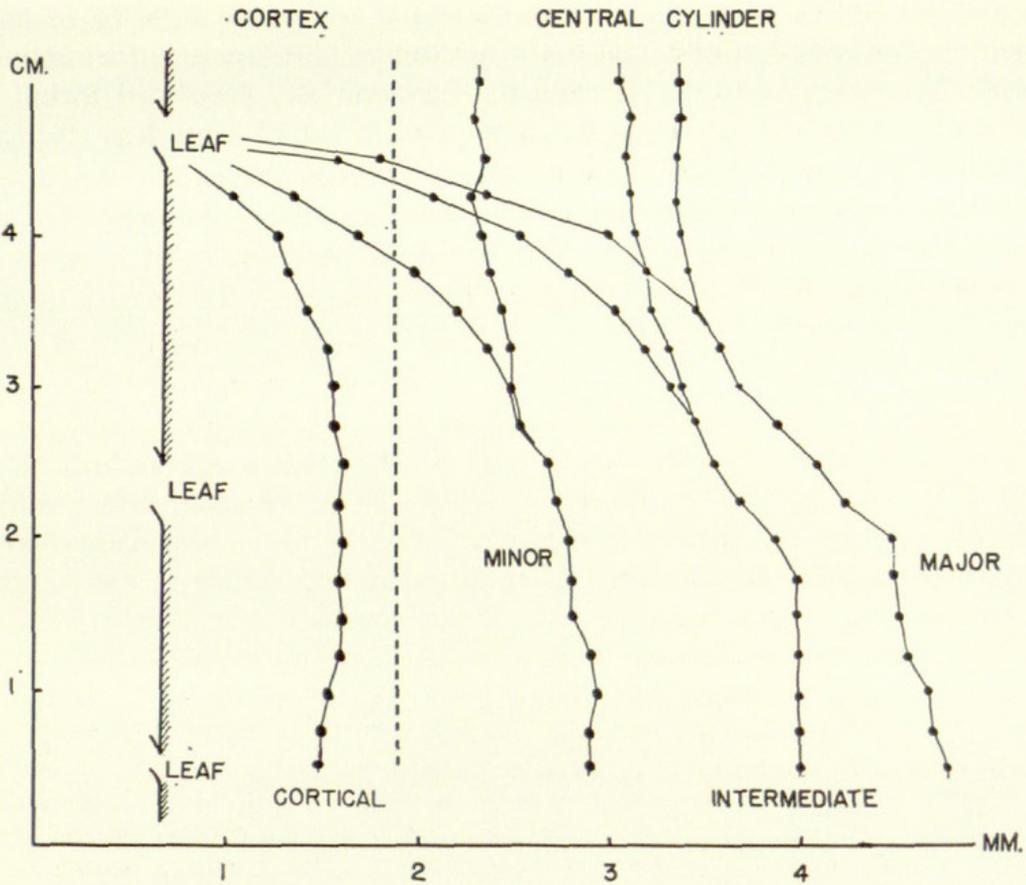


FIGURE 4. ABOVE: plots of vascular bundles supplying scale leaf of rhizome. Measurements taken from microtome sections. Course of major, intermediate, and minor bundles from central cylinder, with continuing vertical bundles, and a cortical bundle without a continuing vertical bundle. The figure is diagram-

the aërial stem and may be described in the same terms. Vascular bundles behave essentially alike, maintaining their individuality throughout the stem. At irregular intervals each of these *vertical bundles*³ forks to give off a *leaf trace* which passes sharply outward into a scale leaf, the vertical bundle continuing distally, eventually to repeat the cycle. Each leaf receives a few branches from the central bundles (*major bundles*) which pass primarily to the dorsal side of the leaf, a larger number of branches from sub-peripheral bundles (*intermediate bundles*), and the largest number of branches from peripheral bundles (*minor bundles*) which pass to all parts of the leaf. There is a continuous series from major (dorsal) to minor (ventral) leaf traces around the stem circumference at each node. Major bundles pass into the leaf much more abruptly than minor bundles (FIG. 4); they may sometimes be horizontal or even pass below the horizontal and are commonly sinuous so that different parts of the same leaf trace occur in a single section. Part of this unevenness is due to the oblique insertion of most scale leaves.

The most significant way in which rhizome bundles differ from those of the aërial stem in over-all distribution is that rhizome bundles deviate from the vertical at points of leaf contact much less than in the aërial stem. Von Mohl's classic "double curve" which is so characteristic of the vascular bundles of aërial stems of palms is therefore not so obvious in the rhizome (FIG. 4 below). Likewise the central bundles of the rhizome do not describe a regular helical path as is common in the aërial stem.⁴ A slight movement does, however, tend to occur in one direction, suggesting an incipient helix.

As in the aërial stem, departure of the leaf trace is complicated by the presence of *bridges* which link it with adjacent vertical bundles, always in an upward direction (FIG. 5D). One to four (usually two) bridges are developed by each leaf trace. Narrow bridges may contain only phloem; the narrowest are sometimes fibrous strands without vascular tissue. Most bridges are short, 2 to 6 millimeters long, but occasionally there are much longer ones resembling vertical bundles until they fuse distally. The significance of this is discussed below. Satellites, which in the aërial stem irrigate inflorescences (or their aborted vestiges), are absent from the rhizome which wholly lacks this lateral type of appendage.

Brief mention may be made of irregular *girdling traces* (FIG. 6 GT)

³ Vertical bundles of the rhizome run horizontally, of course, but the term is used because they are homologous with the vertical bundles of the aërial axis.

⁴ More recent observation of the aërial stem of *Rhapis* has revealed that this internal helix is correlated with phyllotaxis; stems with a right-handed phyllotactic spiral have a right-handed internal helix and vice versa.

matic in that the bundles are all represented in one plane, in fact they enter the leaf along different, widely divergent radii. Dotted vertical line represents limit between cortex and central cylinder, arbitrarily chosen as a base line in making measurements. Horizontal exaggeration 12.5 times.

BELOW: diagrammatic comparison of course of vascular bundles in rhizome and aërial stem (latter figure taken from Zimmermann & Tomlinson, 1965). For comparative purposes the horizontal rhizome is represented in an erect position.

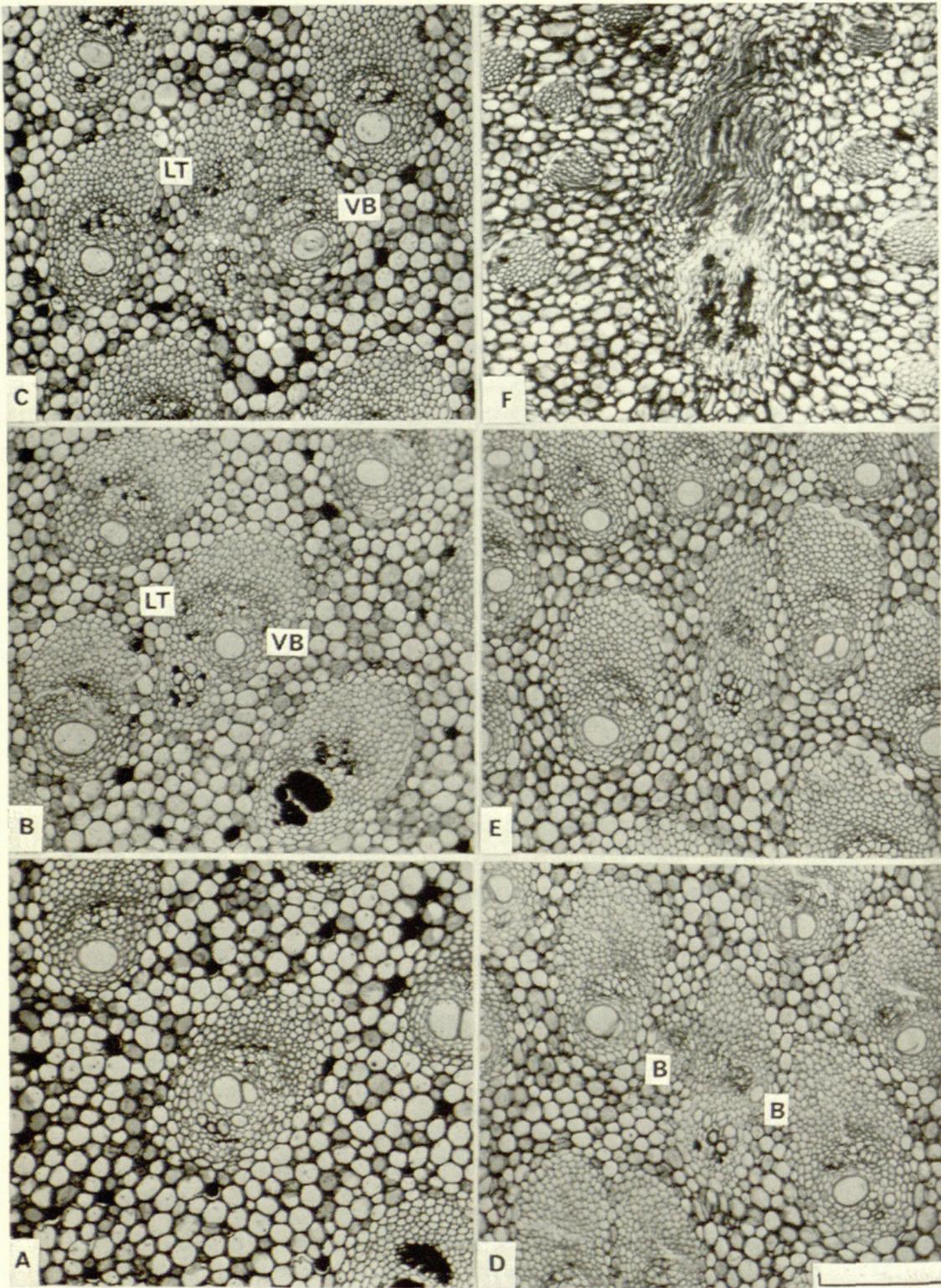


FIGURE 5. Successive transverse sections of the same leaf trace complex from rhizome of *Rhaps excelsa*. In all figures the cortex is towards the upper, the central cylinder towards the lower margin of the plate. Scale is 250μ . A. Vascular bundle in uncrowded central part of stem, below level of forking and with well-developed protoxylem. B. Vertical bundle (VB) to right splitting from leaf trace (LT) at left; 1.85 cm. above A. C. Vertical bundle (VB) at right including one wide metaxylem vessel, no protoxylem, free of leaf trace (LT) at left with no wide metaxylem elements; 2.25 cm. above A. D. Leaf trace further towards cortex splitting off bridges (B) to left and right; vertical bundle is now left behind and is no longer associated with leaf trace; 2.9 cm. above A.

among the peripheral bundles of the central cylinder. These appear to be the ultimate extensions of the root trace system which will be described in a subsequent article.

Cortical system. Fibrous (less commonly narrow vascular) bundles of the cortex are continuous with the same system in the leaf. Traced downwards from the leaf insertion they are seen to form an irregularly anastomosing system which remains quite independent of the central vascular system. Cortical bundles all ultimately seem to end blindly below; occasional cortical strands which end blindly in each direction have been observed. Endings are, however, always near other fibrous bundles and suggest branching during early stages of development. Larger bundles with distinct vascular tissue connect the leaf with the inner part of the cortex (e.g., FIG. 6 CBL and cortical bundle plotted in FIG. 4). Smaller bundles (FIG. 6 CBS), usually without vascular tissue, remain in the peripheral part of the cortex.

DETAILS OF VASCULAR BUNDLE ANATOMY

Variation in the anatomy of a single bundle throughout its length resembles that described for the aërial stem (FIG. 5). A vertical bundle at its point of divergence from a leaf trace includes one wide metaxylem vessel, no protoxylem (VB in FIG. 5C). At some higher level narrow protoxylem elements appear and increase to reach a maximum number of elements just below the next higher leaf contact (FIG. 5A). At the forking of the vascular bundle the leaf trace loses its metaxylem to the vertical bundle (FIG. 5B, C), so retaining only protoxylem. Scale leaves are thus irrigated solely by protoxylem (FIG. 5E, F). Unlike the aërial stem, however, there is little or no proliferation of metaxylem elements just below a leaf contact because there are fewer branches (no satellites). Proliferation of metaxylem represents vessel overlap. Overlapping vessels occur regularly where vascular bundles branch, for example in the leaf-trace complex and where bridges unite with vertical bundles (in the vertical bundle immediately to the right of the leaf trace in FIG. 5E), and at the periphery of the central cylinder under the influence of root insertions (GT in FIGS. 5 and 6).

COMPARISON OF THE RHIZOME WITH THE AERIAL STEM

Described in qualitative terms, the vascular anatomy of the *Rhapis* rhizome seems to differ little from that of its aërial stem. Important differences become obvious, however, when quantitative aspects are considered. These show that the over-all plan is less regular than in the aërial stem. We are content at the moment merely to draw attention to this plasticity, an explanation of which must be deferred until development of the vascular

E. Leaf trace passing through crowded periphery of central cylinder; 3.15 cm. above A. (Configuration of metaxylem of adjacent vertical bundle to right suggests a recent bridge linkage to another leaf trace.) F. Leaf trace in cortex passing almost horizontally into leaf; 3.65 cm. above A.

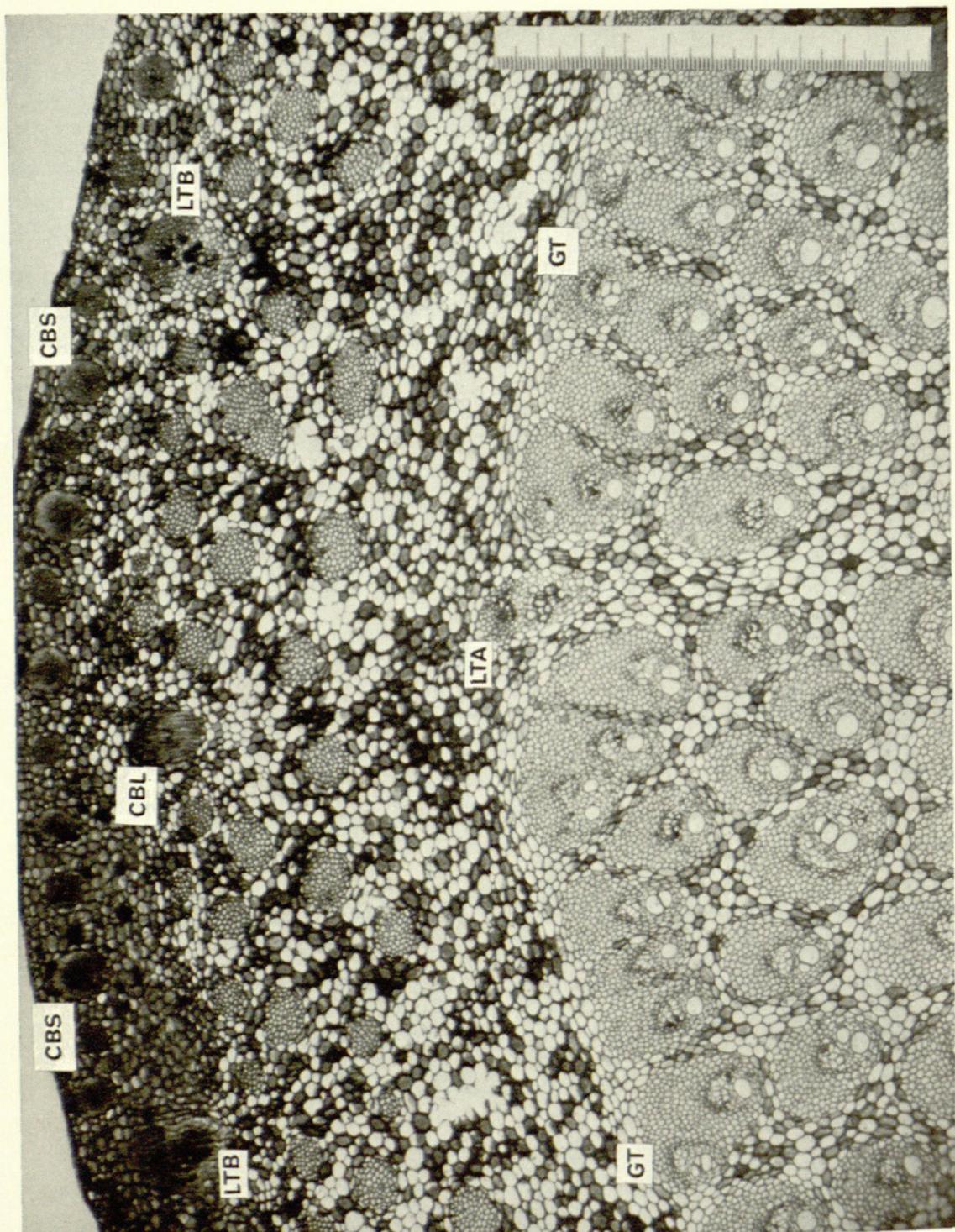


FIGURE 6. *Rhaps excelsa*, transverse section of rhizome including cortex and periphery of central cylinder immediately below a node. Sclerotic base of leaf, inserted obliquely on rhizome, included in upper left-hand part of figure. Trace system to this leaf includes a major leaf trace (LTA) at periphery of central cylinder, two minor leaf traces (LTB) close to their insertion in the leaf, a large cortical bundle (CBL) passing into the leaf from the inner cortex and the system of many small cortical bundles (CBS) diverging from the outer cortex. Girdling traces (GT) are ultimate ends of root traces. Scale equals 1 mm.

system in the rhizome apex is considered. Because relatively few leaf traces enter the scale leaves in proportion to the total number of central cylinder bundles, it is clear that on average any bundle must make a leaf contact

TABLE I. Essential Differences Between Rhizomes and Aërial Stems

RHIZOME	AËRIAL STEM
MORPHOLOGY	
Horizontal	Vertical
Subterranean	Aërial
Roots present	Roots absent
Scale leaves, protective, non-assimilating	Foliage leaves, assimilating
Axillary buds absent	Axillary buds developed distally as lateral inflorescences
Vegetative buds abundant in the transition region between rhizome and aërial stem.	
ANATOMY	
Cortex wide, with conspicuous system of fibrous bundles	Cortex narrow, with few fibrous bundles
Peripheral congested bundles of central cylinder mechanically insignificant	Peripheral congested bundles of central cylinder mechanically significant
Leaf contacts irregular, peripheral bundles often of "indefinite length"	Leaf contacts relatively uniform
Internal helix not obvious	Internal helix obvious
Vascular bundles deviate relatively little at leaf contact	Vascular bundles deviate considerably at leaf contact
Branching at leaf contact: Leaf trace Vertical bundle Bridges	Branching at leaf contact: Leaf trace Vertical bundle Bridges Satellites
Metaxylem vessel overlap not pronounced in leaf trace complex (few branches)	Metaxylem vessel overlap pronounced in leaf trace complex (many branches)

much less frequently than in the aërial stem. Measurements confirm this. Peripheral bundles without protoxylem have been traced up to distances of 20 cm. without change. This implies vascular bundles of "indefinite length." However, once protoxylem appears in such a bundle, the bundle will make a leaf contact by splitting off a leaf trace. Protoxylem-bearing lengths of vascular bundles from 3 to 14 cm. were measured in the rhizome. A measured leaf contact distance of 25 cm. (10 cm. bearing protoxylem, 15 cm. protoxylem-free) over 15 internodes compares favorably with central bundles in the aërial stem; values of 12 cm. (6 protoxylem-free, 6 protoxylem-bearing) over 6 internodes for a peripheral bundle may be cited

to show that these may make frequent leaf contacts. However, we do not wish to emphasize these few isolated figures in the absence of developmental information.

Plasticity of the vascular system of the rhizome is also demonstrated by certain qualitative variations from the basic patterns which have been noted. Apart from the very long bridges already mentioned which resemble irregular anastomoses between vertical bundles, we have seen occasional vertical bundles split. As in the aërial axis, leaf traces occasionally give off either two or no vertical bundles. Once we recorded a single vertical bundle, originating as two separate strands one from each side of a leaf trace, which fused distally. Vertical bundles of the central cylinder never end blindly.

Essential differences between rhizomes and aërial stems are summarized in TABLE I. Structural differences between rhizome and aërial stem are based on the difference in the physiology of their respective development. In the aërial stem, leaf contacts are established in the apex; we assume therefore that mature leaves supply developing leaf primordia and young leaves. The rhizome, on the other hand, is never an assimilating organ; movement of nutrients must, therefore, be along the axis toward the apex. In this light, the presence of bundles of "indefinite length" seems explicable. However, differences between the aërial stem and the rhizome can only be fully understood when the anatomy and development of their respective apices are known. Such studies are under way; a report about them will be published in a later paper of this series.

SUMMARY

Analysis of the vascular system of the subterranean, scale-bearing rhizome of *Rhapis excelsa* by cinematographic methods demonstrates a system with the essential features of the aërial stem. Satellite bundles are absent since the rhizome bears no lateral inflorescences. The vascular system is less regular than that of the aërial stem and deviation of vertical bundles at points of leaf contact are less pronounced. Leaf contact intervals in peripheral bundles may be very long. These differences must be related to the non-assimilating nature of the rhizome.

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Miss Lesley Jackson carried out the routine serial sectioning on which this study is based. Her reliable help is very much appreciated. We are indebted to Miss Priscilla Fawcett, Botanical Illustrator at Fairchild Tropical Garden, for FIGURES 1 and 2.

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