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Author(s): Martin H. Zimmermann and P. B. Tomlinson

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## VASCULAR CONSTRUCTION AND DEVELOPMENT IN THE AERIAL STEM OF PRONIUM (JUNCACEAE)<sup>1</sup>

MARTIN H. ZIMMERMANN AND P. B. TOMLINSON

Harvard University, Cabot Foundation, Petersham, Massachusetts  
and  
Fairchild Tropical Garden, Miami, Florida

### A B S T R A C T

The aerial stem of *Pronium* has been studied by motion-picture analysis which permits the reliable tracing of one among hundreds of vascular strands throughout long series of transverse sections. By plotting the path of many bundles in the mature stem, a quantitative, 3-dimensional analysis of their distribution has been made, and by repeating this in the apical region an understanding of vascular development has been achieved. In the mature stem axial continuity is maintained by a vertical bundle which branches from each leaf trace just before this enters the leaf base. Lateral continuity results from bridges which link leaf traces with nearby vertical bundles. Development of the provascular system involves a meristematic cap into which the blind ends of vertical bundles can be followed. Leaf traces are produced continuously in association with developing leaf primordia for a period of over 30 plastochrones; they connect with the vertical bundles in the meristematic cap and so establish the essential vascular configuration which is later reorientated through about 90° by overall growth of the crown. The last bundles to differentiate from the leaf do so outside the meristematic cap and thus fail to make contact with the axial system; they appear in the mature axis as blind-ending cortical bundles. *Pronium* is only distantly related to palms and its vascular histology is quite different. Nevertheless, the course of vascular bundles and the origin of this pattern in the stem resembles that of a palm. It is suggested that we are examining the fundamental pattern of vascular development in large monocotyledons.

RECENT reexamination of the vascular system in the stems of larger monocotyledons, particularly the palms, shows that earlier anatomists had incompletely observed the fundamental principle underlying construction of these axes and could therefore arrive at no true understanding of developmental processes (Zimmermann and Tomlinson, 1965, 1967). Using the small palm *Rhapis excelsa* as a model it has been shown that the classical researches of Hugo von Mohl (1824, 1849) and de Mirbel (1843-44) on the palm stem were correct but incomplete. They did not reveal the axial continuity of vascular strands although this is essential to an appreciation of the pathway for long-distance transport. It has also been shown that any understanding of this pathway which modern textbooks may claim to illustrate has arisen by a process of "paper evolution" with no

relevance to the situation as it exists in nature (Tomlinson and Zimmermann, 1966). Nevertheless, since the time of von Mohl, the "palm-type" of vascular arrangement has been regarded as the one basic for the stem in most groups of monocotyledons. Continuing reexamination of monocotyledonous anatomy, far from demolishing this concept, is likely to strengthen it by putting it on a firm factual foundation which was originally lacking. The only literature to which modern work has any direct relevance is that of about 100 years ago because in subsequent years anatomists have virtually neglected a topic which, like many others in the classical botanical tradition, has been regarded as "fully worked out" and therefore dismissed by later generations of investigators.

Investigation of the palm *Rhapis* revealed a well-defined organization of the mature vascular system, as well as a clearly recognizable pattern of development. The question naturally arose whether this vascular pattern is fundamental for the palms and perhaps even for the monocotyledons as a whole. The answer to this question will require a great deal of work. A number of plants in various families have been observed but any vascular pattern fundamentally different from that of *Rhapis* has not been found. The present article provides further evidence in this direction

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by demonstrating that the vascular pattern, which seems characteristic of the palm stem, also occurs in a plant having no obvious systematic affinity with the palms. The present study of the "tree-rush," *Pronium serratum* (Juncaceae), amply confirms our prediction. This species was selected because it was a suitably large monocotyledon and yet proved amenable to investigation by the methods we have employed. The anatomy of *Pronium* has been described in considerable detail by Buchenau (1893) but without attention to the arrangement and development of the vascular bundles.

**MATERIAL AND METHODS—Material—***Pronium serratum* (L.f.) Drège is a gregarious plant of wet places in the Cape and elsewhere in South Africa where it is known as "Palmiet." Living specimens have not been seen but Hooker (1868) illustrated cultivated specimens and from his figures subsequent habit drawings are largely derived (e.g., Buchenau, 1893, 1906; Vierhapper, 1930). It is described by Buchenau as a plant with perennial erect shoots arising from creeping, scale-bearing rhizomes. The aerial stems considered in this study are erect shoots up to 2 m tall with a terminal cluster of lanceolate leaves up to 1 m long, each shoot eventually producing a terminal, paniculate inflorescence. Stems are clothed with the fibrous remains of persistent leaf bases, the axis proper being of the order of 5 cm in diam. Internodes are close set and only 2–3 mm long. Branching of the erect axis is infrequent, but according to Buchenau (1893) it may sometimes be sympodial and associated with flowering, as in *Yucca* and many other arborescent monocotyledons. Otherwise branching is irregular and determined by no obvious morphological rule. Axillary buds, protected by a conspicuous prophyll, are distributed without obvious order and are strongly suppressed.

A portion of the aerial stem together with a number of shoot apices fixed in FAA were provided by Dr. R. G. Strey of the Natal Herbarium, Durban, South Africa. The axis which we studied was mature but only slightly hardened and therefore easy to cut, making it a subject suitable for our purpose. This is in contrast to the experience of Buchenau (1893) who evidently had much older and more lignified stems from which he could get useful sections only by means of a circular saw.

**Sectioning**—For analysis of the mature vascular system a series of sections 60  $\mu$  thick were cut from the unembedded material using a Reichert sliding microtome. Central and peripheral regions were analyzed separately because single sections of the whole stem would not fit on a standard 25  $\times$  75-mm microslide. In each region the first 100 sections were retained as a continuous series;

subsequently only every third section was kept to give a total of 200 slides.

Sections were bleached briefly in Clorox, washed well in running water and stained in safranin and Delafield's haematoxylin. They were then mounted one per slide to permit vascular analysis by means of our optical shuttle (Zimmermann and Tomlinson, 1966). For a study of histological details thinner sections were cut from small blocks which had been embedded in celloidin. These sections were stained either in safranin and Delafield's haematoxylin or in the tannic acid-ferrie chloride-resorcin blue combination of Cheadle, Gifford, and Esau (1953).

Shoot apices were dehydrated and embedded in Paraplast by normal procedures. Continuous series of sections 10  $\mu$  thick, in transverse and longitudinal planes, were cut on a rotary microtome, stained in safranin and Delafield's haematoxylin and mounted in the usual way. Individual transverse sections were so large that only two could be mounted on each 50  $\times$  75-mm microscope slide. This proved beneficial in the subsequent plotting of the developing vascular system since the optical shuttle could be used in the way described below.

**Serial analysis**—The vascular system of the adult axis was unravelled with the aid of the cinematographic methods, including the optical shuttle, described in detail elsewhere (Zimmermann and Tomlinson, 1965, 1966). This involves the use of a ciné camera to photograph, frame by frame, successive sections observed through the microscope. The optical shuttle is a device which uses two microscopes to superimpose the images from two successive sections in such a way that they are precisely registered in the film plane of the camera and then photographed in turn. A further improvement of the method described in the earlier article is a foot-operated device which switches each microscope on or off in turn, leaving both hands free to adjust the microscope stage. Optical alignment of subsequent sections was then achieved by reduction of the apparent motion between the two images viewed alternately by operating the foot switch, rather than by superimposition of images seen at the same time. In addition a number of ciné sequences were photographed through a Wild M-5 stereomicroscope at a magnification lower than that which could be obtained with the compound microscope, using the drawing method to align the series of sections for the camera.

The vascular system in the developing crown was plotted using the paraffin-embedded series of transverse sections. The method was outlined in detail in a paper describing the analysis of the developing shoot system of *Rhapis excelsa* (Zimmermann and Tomlinson, 1967). This involved carefully mapping the course of the leaf traces on an outline plan of the axis in quantita-

tive detail as shown in Fig. 14. A major trace from each successively younger leaf as well as a number of minor and cortical traces were plotted in a basal direction to the bottom of the series of sections. Vertical bundles were plotted in the reverse direction as far as possible towards the shoot apex proper. Plotting involves following a particular bundle continuously throughout the series of sections and measuring its position at intervals of about 0.2 mm. Measurements were taken from the selected bundle to the center of the stem which was determined by eye in each section. The fact that the stem center is not precisely definable inevitably led to some irregularities in the original plots; their representation in Fig. 14 omits these irregularities and draws the course of bundles as smooth curves. This more nearly represents the actual course of bundles in the stem.

The success of this plotting method depends on the certainty with which an individual vascular strand can be followed from section to section without an inadvertent jump being made from one bundle to another. The optical shuttle method makes this possible. The film which is made during the plotting process is not essential but provides a useful record for later review. The optical shuttle can be used even with two sections on one slide if sections are lined up in the order 1A-2A, 1B-2A, 1B-2B, 2B-3A, etc., whereby the numbers indicate slides, A and B the two sections on each slide, and italics the sequence of photography. The resulting ciné film demonstrates the general construction of the vascular system in the developing crown, but the information of most value is the measurements incorporated in Fig. 14.

**OBSERVATIONS—Mature stem**—The anatomy of the stem of *Prionium* has been described in detail by Buchenau (1893). The following notes briefly summarize his and our own observations. The surface layers include a narrow zone of suberized cells about eight cell layers beneath the thin-walled epidermis. The cortex is 5-8 mm wide and consists of loose, lobed but otherwise undifferentiated parenchyma within which are large conspicuous collateral leaf traces together with a few narrow bundles with reduced vascular

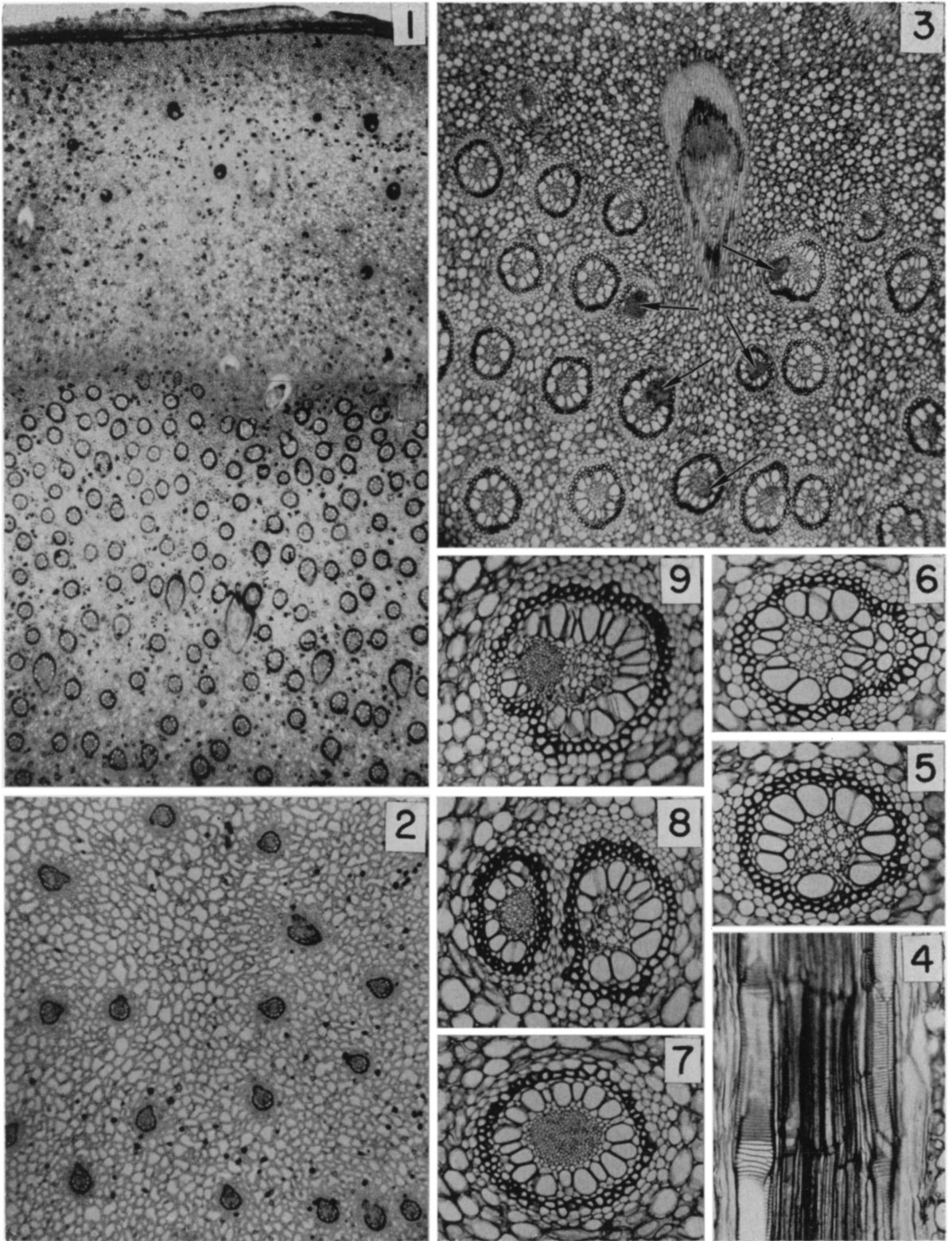
tissues which are described subsequently as cortical bundles (Fig. 1). There is no specialized layer which delimits the wide central cylinder from the cortex. Towards the center of the stem the ground tissue is again somewhat spongy and without special differentiation, except for frequent tannin cells (Fig. 2). The central cylinder is recognized by its crowded peripheral vascular bundles and a fairly abrupt transition to more compact ground parenchyma. Vascular bundles become wider and somewhat more diffuse towards the stem center. Outgoing leaf traces together with the derivative bundles described below are conspicuous in the periphery of the central cylinder.

Individual bundles are amphivasal. Each includes a central phloem strand surrounded by a complete cylinder of angular vessels, the vessels in turn surrounded by short fairly narrow and slightly thick-walled fibers. The outer limit of the bundle is represented by thin-walled cells which are sharply delimited from the ground parenchyma (Fig. 5-9). These sheathing layers become much thicker walled in older stems, as is evident from Buchenau's description. Conducting elements of metaxylem and metaphloem are short (rarely more than 150  $\mu$  long), with coincident end walls (Fig. 4). The phloem includes conspicuous sieve tubes up to 25  $\mu$  wide, with more or less transverse, simple sieve plates, together with narrow phloem parenchyma and densely stained companion cells. Vessel elements up to 70  $\mu$  wide slightly oblique, scalariformly or reticulate perforated end walls and scalariform pitting on the lateral walls. The tracheary elements are incompletely sheathed by conspicuously pitted parenchyma cells, the vessels otherwise often abutting directly on sheathing fibers. Narrow protoxylem elements with spiral wall thickenings are distributed on the inner side of leaf traces at certain levels in the manner indicated below. The specialized phloem of bridge bundles in the leaf trace complex is also described below.

The peripheral layers of the central cylinder are complicated by the insertion of traces to dormant root initials which do not, however, disrupt the overall picture. No axillary buds were present in the piece of stem which was analyzed.

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Fig. 1-9. *Prionium serratum*, vascular anatomy of mature stem.—Fig. 1. Transverse section through peripheral region of mature stem,  $\times 10$ . The upper half illustrates the cortex with few leaf traces and cortical bundles. The lower half with the numerous vascular bundles illustrates the peripheral portion of the central cylinder. Outgoing leaf traces, cut at an angle, appear oval in shape.—Fig. 2. Transverse section through the central region of the mature stem at the same low magnification,  $\times 10$ . Vascular bundles are less crowded, ground parenchyma lacunose.—Fig. 3. Transverse section through peripheral region of central cylinder at higher magnification,  $\times 37$ . A leaf trace is shown entering the cortex (upper third of illustration). Bridges and vertical bundle, which are branches from this leaf trace, appear below and can be recognized by their densely stained phloem (arrows). Compare this transverse section with the plotted diagram, Fig. 13.—Fig. 4. Longitudinal section through an individual vascular bundle, showing coincident end walls of sieve-tube elements and vessel elements,  $\times 104$ .—Fig. 5. Vertical bundle without protoxylem,  $\times 104$ .—Fig. 6. Vertical bundle with protoxylem,  $\times 104$ .—Fig. 7. Vertical bundle or bridge, immediately above the point of branching from parent leaf



trace,  $\times 104$ . Note the peculiar phloem.—Fig. 8. Bridge (left) above the point of branching from parent leaf trace, immediately below the point of fusion with a neighboring vascular bundle (right),  $\times 104$ .—Fig. 9. Similar bundles as shown in Fig. 8, but a little higher, at point of fusion,  $\times 104$ .

*Course of the vascular bundles*—The vascular system of *Prionium* corresponds exactly to that described for the palm *Rhapis excelsa* (Zimmermann and Tomlinson, 1965) except for quantitative differences. Each leaf is supplied by a series of vascular bundles (leaf traces). Major leaf traces diverge from the center of the stem into the leaf. Bundles which diverge at a shallower angle from progressively more peripheral regions may be arbitrarily designated intermediate and minor bundles. The relative disposition of each type of bundle going to a single leaf is shown in the plotted diagram used to make Fig. 13. Towards the periphery of the central cylinder each outgoing leaf trace gives off one (sometimes two) continuing vertical bundles which proceed up the stem to repeat the process of branching in association with some higher leaf (Fig. 3, 13). The series analyzed have all been too short to measure leaf-contact distances directly, but by extrapolation (adding the distal part of one bundle to the proximal part of another) it can be estimated that this distance is about 30 internodes for a major bundle. The course of vertical bundles in the stem is not uniformly axial but shows the so-called "double-curve" principle of von Mohl. Traced in an upward direction bundles can be followed gradually towards the stem center before they bend out sharply at the next leaf contact. Major bundles extend inwards all the way to the stem center during this upward course and describe the longest path between leaf contacts. Intermediate and minor bundles are progressively restricted to the stem periphery, accounting for the vascular congestion at the periphery of the central cylinder. Their leaf-contact distances are correspondingly shorter.

Apart from the large leaf traces which cross the cortex in their outward course there are narrow bundles restricted to the cortex. Traced downwards from the leaf insertion these cortical bundles end blindly below, never extending more than two or three internodes. Although insignificant in terms of vasculature, these bundles are very meaningful when development of the vascular system is considered.

The anatomy of each vascular bundle changes in its course up the stem in exactly the same way as in *Rhapis*. On diverging from the leaf trace the bundle is as shown in Fig. 5 and includes no protoxylem.<sup>2</sup> At the higher level, protoxylem is developed on the inner face of the bundle (Fig. 6), and the number of elements progressively in-

creases to reach a maximum at the level where the sharp outward curve of the bundle begins. There is little change in the number of sheathing fibers throughout the bundle, as in *Rhapis*.

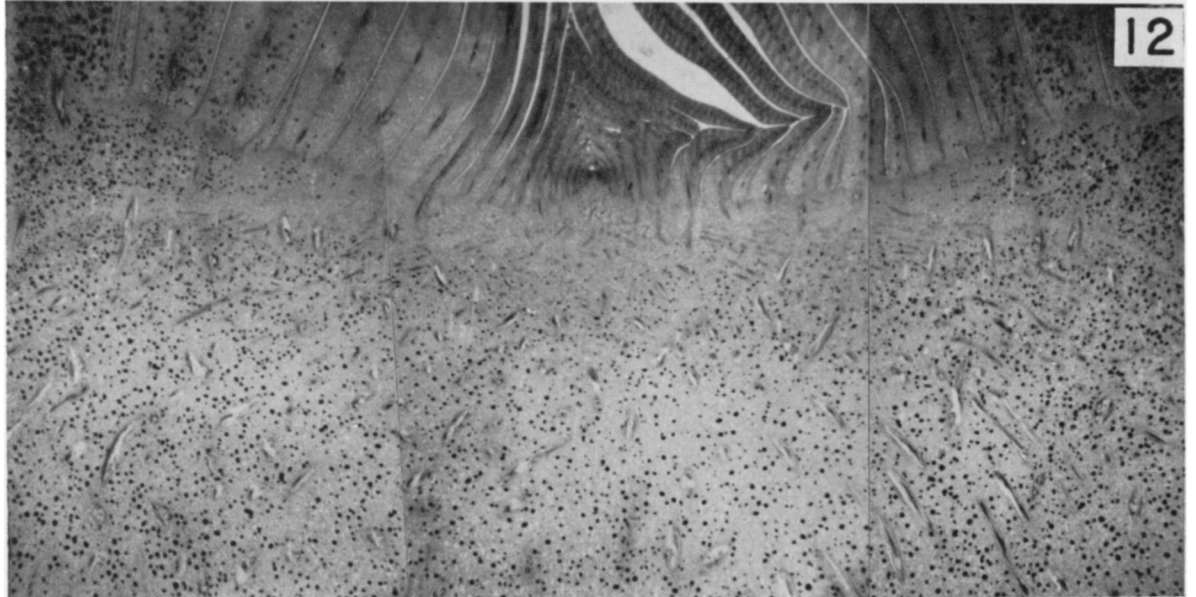
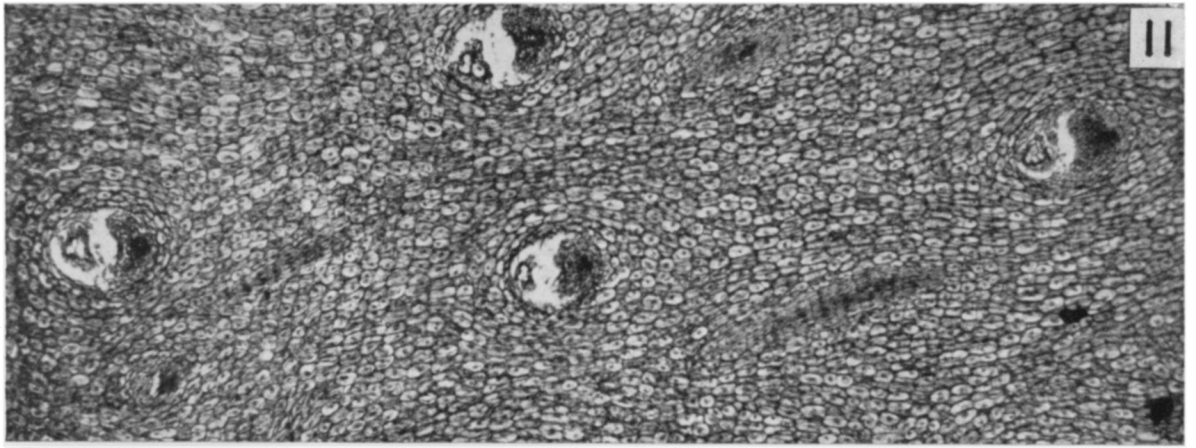
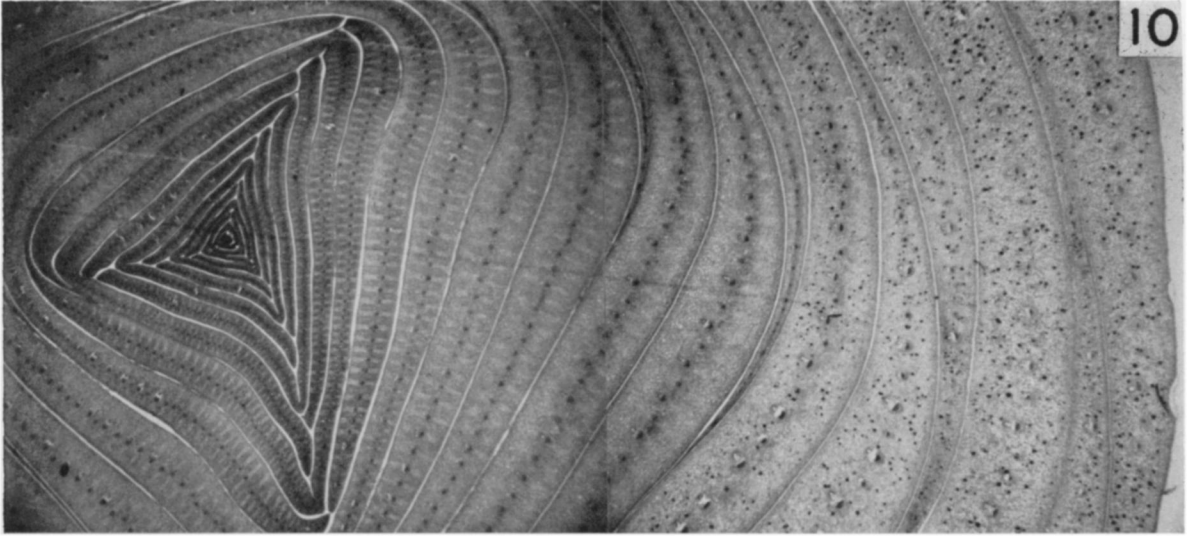
*Bridges*—The above system describes longitudinal continuity in the vascular system. Lateral continuity, as in *Rhapis*, involves bridge bundles which branch from the outgoing leaf trace, always in an upward direction, and link with adjacent vertical bundles in the stem periphery (Fig. 3, 13). Bridges are amphivasal, often quite long and somewhat narrower than their parental leaf trace. They occasionally split so that they make distal contact with two vertical bundles. A peculiarity of derivative bundles (both bridges and the lowest part of the continuing vertical bundle) which distinguishes them readily in single sections is their modified phloem (Fig. 7). The familiar phloem tissue of the normal bundles is replaced by a small-celled tissue without clearly circumscribed sieve tubes. This tissue has not been examined in detail, but it appears to consist of horizontal bands of narrow, nucleate cells alternating irregularly with bands of somewhat wider cells with callose deposits on indistinct pit-like areas but not aggregated into definite sieve plates. Similar phloem has been encountered in the bridge bundles of those members of the Pandanaceae whose vascular anatomy we have investigated (results unpublished). These modified phloem cells also recall those in the glomeruli of the node in members of the Dioscoreaceae (Braun, 1957). In *Prionium* the modified phloem of the bridge continues into the vertical bundle above the point of union for some distance so that a recent fusion is easily recognized. It is equally persistent in vertical bundles (Fig. 3, 7-9).

Major leaf traces give off up to six bridges, intermediate and minor traces progressively fewer. The outgoing leaf trace loses almost all of its metaxylem to the derivative bundle and passes into the leaf base as a collateral bundle, which construction is retained throughout the leaf (Buchenau, 1893). Unlike *Rhapis* there is no elaboration of the leaf-trace complex in association with lateral inflorescences (Tomlinson and Zimmermann, 1968) since *Prionium* has a terminal inflorescence.

<sup>2</sup>Protoxylem is distinguished structurally from metaxylem by its narrow elements with annular or helical wall thickenings and by its situation on the inner side of the bundle.

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Fig. 10-12. *Prionium serratum*, vascular anatomy of the meristematic crown.—Fig. 10. Transverse section through the meristematic crown of the aerial stem at the level of the apical meristem,  $\times 11$ .—Fig. 11. Transverse section through meristematic crown 0.5 mm below leaf insertions 22-24,  $\times 98$ . Four leaf traces are shown. The procambial strands are cortical traces. Below the leaf insertion they turn out radially towards the stem periphery. They do not enter the central cylinder but end blindly below in the cortex (see also Fig. 14).—Fig. 12. Median longitudinal section through the meristematic crown. The overall shape, given by the leaf insertions, is a shallow bowl. The shape of the meristematic central cylinder is that of a very shallow cone. It can be recognized by the whitish line of tissue lacking tannin-filled cells.



*Topography of the crown*—The general configuration of the developing crown is shown in longitudinal section in Fig. 12. The overall outline is a shallow bowl, and that of the meristematic central cylinder is a shallow cone. It is crowned by the shoot apex proper. Developing vascular strands are represented by series of procambial initials which are progressively less easily recognized as one approaches the apex. Leaves are arranged in a one-third spiral phyllotaxis, each leaf having a short, closed tubular base (Fig. 10). Since there is no regular internal helix and because the phyllotaxis is simpler, the plotted diagram (Fig. 14) represents more realistically a radial section of the apex than did the corresponding diagram which resulted from our analysis of *Rhapis* (Zimmermann and Tomlinson, 1967; Fig. 2). In *Rhapis* the leaves have a two-fifths spiral and individual bundles describe a helix in the direction of the phyllotactic spiral. In *Prionium* major bundles merely describe a sharp 360° turn in the stem center (Fig. 15).

Figure 14 represents the major dorsal leaf trace from each leaf along one orthostichy.

Comparing the arrangement of mature vascular bundles with that in the crown (Fig. 13 with 14) it is evident that primary growth reorientates the vascular system through about 90° so that leaf traces which run more or less parallel to the axis in the crown become obliquely radial, whereas vertical bundles change from an obliquely radial direction to one more or less parallel to the axis.

In the crown vertical bundles, of which an inner (IVB) and an outer (OVB) are shown in Fig. 14, can be traced upwards until their identity is lost in a histologically well-defined region here called the "meristematic cap." That bundles end blindly in this region is a matter of observation which can be further verified by calculation. On this basis many traces which end blindly in the cap will make connection only with a leaf primordium which will not be visible before some 10 others have appeared.

Leaf traces (with the exception of cortical bundles) are always continuous below with vertical bundles and this connection must take place within the meristematic cap as is discussed below. Therefore leaf traces which have established continuity extend through the cap. The number of traces in successively older leaves follows approximately a sigmoid curve (Fig. 16). There is of course some variation in the number of bundles in individual leaves and some guesswork is involved in counting the number of recognizable procambial strands. For each mature leaf there are about 95 traces continuous into the central cylinder and 45 cortical traces. Leaf-trace differentiation continues for about 30 plastochrons.

DISCUSSION—*Vascular differentiation*—The in-

formation provided in Fig. 14 and 16 permits a reasonable assessment of the process of vascular differentiation which is summarized in Fig. 17. Procambial strands initiated by the leaf base link with a vertical bundle differentiating on the lower (inner) face of the cap. The first strands are major traces and the linkage is in the center of the stem. Linkage is effected with a bundle which has grown blindly in association with the meristematic cap for the maximum length of time. This makes a maximum leaf-contact distance. Subsequently differentiated bundles (on the steeply rising part of the curve in Fig. 16) link progressively within the meristematic cap with progressively more peripheral and shorter vertical bundles. These are the intermediate and minor bundles of which one of each is shown in Fig. 14 continuous into leaf 16. At a level when the primordium is about the 16th youngest, differentiation of the vascular bundles within the leaf slows down (Fig. 16). Differentiation of these last formed bundles occurs outside the cap and after all possible leaf trace connections have been completed. Consequently these bundles fail to unite with the axial system and they are seen as bundles which end blindly in the cortex after traversing two or three internodes. Three such cortical bundles belonging to P23, P24, and P25 are shown in Fig. 14. Figure 11 shows some of them as procambial strands in a transverse section 1.1 mm below the apical meristem, and ca. 100  $\mu$  below leaf insertions 23–25. They are not numerous enough (about 50 per leaf) to make contact with each other as occurs in *Rhapis*, where there are about 1,000 per leaf. There is thus a complete developmental explanation for the disposition of leaf traces between cortex and central cylinder. Both bundles are developmentally homologous, but the last to differentiate do so outside the meristematic cap and fail to establish axial continuity.

In serial sections the periphery of the meristematic cap cannot be determined very precisely because of the way in which procambial strands gradually differentiate out of it. The information in Fig. 14 and 16, however, provides two methods of estimating its extent. From Fig. 14 its outer limit must be about the upper end of OVB and below the base of leaf 21, since OVB was one of the outermost vertical bundles which could be plotted. Furthermore the extent of the cap is given by the distance from the apical meristem proper to the first leaf base having the full complement of vascular bundles. Allowing generously for the subjective error resulting from the need to distinguish between vascular and cortical bundles, it is seen in Fig. 16 that the edge of the cap is where a leaf has produced between 80 and 100 bundles. This lies on a steep part of the curve so the limit is fairly sharply defined as somewhere below leaves 14 to 16, even allowing for error in counting. Returning to Fig. 14 in which an outer vertical

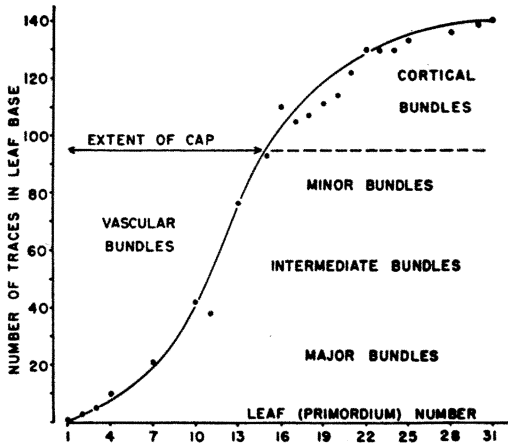


FIG. 16

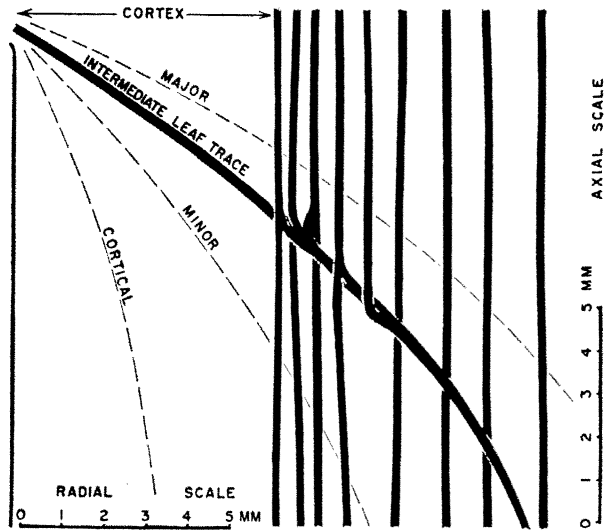


FIG. 13

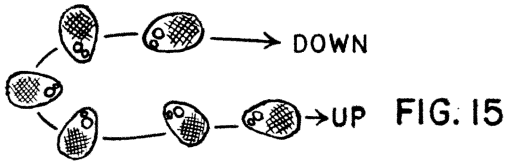


FIG. 15

FIG. 14

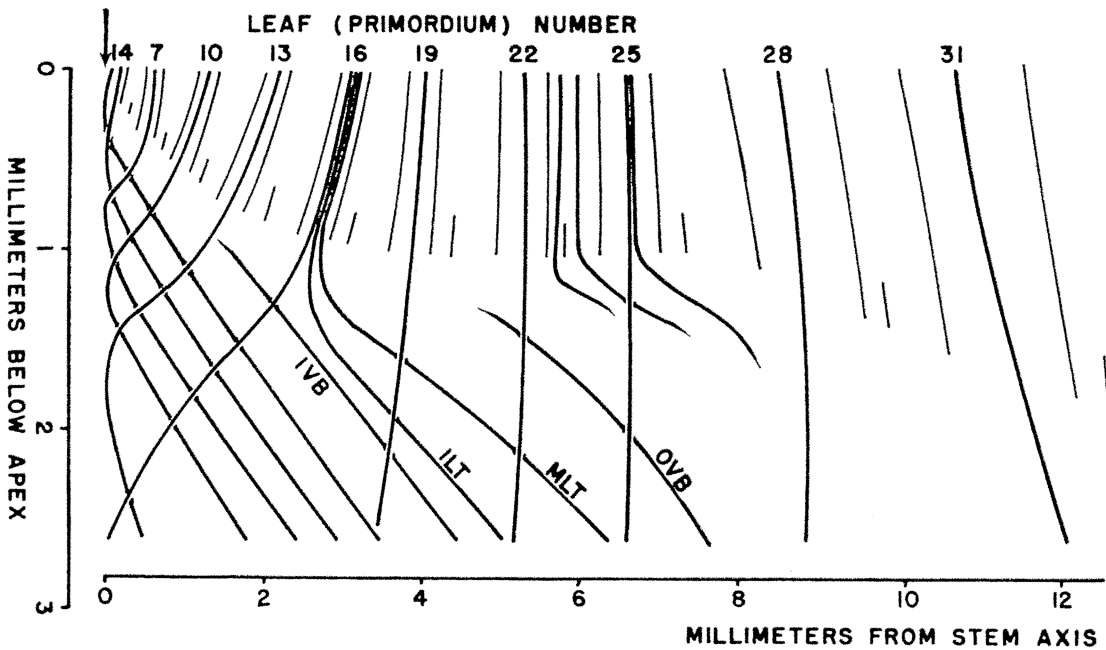


Fig. 13-16.—Fig. 13. Plotted diagram of leaf-trace departure in the mature stem.—Fig. 14. Plotted diagram of vascular traces in the meristematic crown. Note that the axial scale is stretched about two times for the sake of clarity. One major leaf trace is shown for all leaf primordia in one orthostichy. In addition, the following traces are shown: one intermediate (ILT) and one minor leaf trace (MLT) from P16, one cortical trace each from P23, P24, and P25. An inner (IVB) and an outer vertical bundle (OVB) are shown ending blindly in the cap. The arrow points to the location of the apical meristem.—Fig. 15. Diagram showing the 360° turn of a major leaf trace in the stem center.—Fig. 16. Number of traces in leaves and leaf primordia at the point of their insertion. The extent of the meristematic cap is given by the position of the youngest leaf which has the complete set of vascular traces, but no cortical traces.

bundle (OVB) is shown to fuse with the cap directly below leaf 21, it is evident that this would have to establish leaf contact, within the cap, with a bundle continuous with leaf 15 to make the last minor bundle. Beyond the meristematic cap in leaf positions later than about P15, vascular bundles continue to differentiate in the leaf (for about 15 more plastochrons), but they can make no vascular connection with the central cylinder and end blindly in the area distinguished as cortex in the mature stem.

Because cortical traces are directed downwards we infer that their predecessors, the leaf traces which enter the central cylinder, are "sent down" from the leaf primordium into the cap, rather than in the reverse direction. However, the "direction" of bundle differentiation between leaf primordium and cap remains unknown; the present paper is not specifically concerned with this question.

*Renewal of vertical bundles*—Although the longest piece of crown which could be accommodated on the microtome was sectioned, the series was still not sufficiently complete to show a leaf contact between two major leaf traces. The trace to the oldest leaves in Fig. 14 do not show the youngest continuing vertical bundles along the radius illustrated. However, the sections were slightly oblique and on another radius they were just evident in the lowest slides. The reader is also referred to Fig. 2 and 3 in Zimmermann and Tomlinson (1967) where several such vertical bundle branches are shown. It is evident that as vertical bundles, initially ending blindly in the cap, become connected to newly differentiating leaf traces they must be replaced. This must occur on the outer (upper) side of the cap and newly differentiated bundles must be continuous with leaf traces in the downward direction (Fig. 17). The origin of new vertical bundles is also closely associated with the origin of bridges which resemble vertical bundles in their anatomy and the direction in which they diverge from the leaf trace. Bridges and vertical bundles are developmental homologues. One of these derivative bundles makes contact with the margin of the meristematic cap. This contact is maintained as the bundle continues to differentiate until it links with a leaf trace. This is the vertical bundle. Other bundles make contact only with existing vertical bundles and so become bridges.

*"Primary thickening meristem"*—Previous investigations of the apical development of large monocotyledons (Helm, 1936; Ball, 1941; Eckhardt, 1941) have apparently relied on serial longitudinal and transverse sections which had been studied singly. No attempt had been made to reconstruct the vascular system in the crown three-dimensionally. Only careful plotting of individual strands throughout entire section

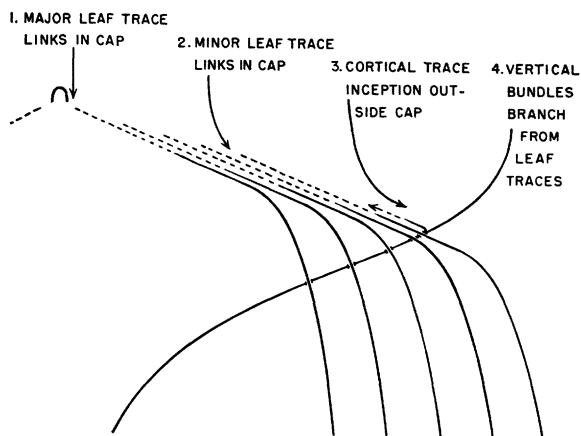


Fig. 17. Diagrammatic representation of vascular differentiation in the crown of the monocotyledonous stem. The meristematic cap is indicated by dashed lines. Three positions of leaf trace inception are shown by arrows which, however, are not intended to imply the unknown direction of differentiation. 1. Major leaf trace links with a potential vertical bundle in the cap near stem center. 2. Minor leaf trace links later with a potential vertical bundle near the cap periphery. 3. Leaf traces appearing still later, when the leaf is situated outside the cap, fail to make contact with the vascular system of the central cylinder and thus become cortical traces, ending blindly below in the cortex. Cap renewal is from leaf traces at the point where they begin to branch (4).

series permits this. For these reasons previous investigators have described development in terms of cytohistological zonation and cell seriation. In many species the meristematic cap can be recognized in single longitudinal or transverse sections. As a result, it acquired the name "primary thickening meristem." As shown in this and in the previous paper on the vascular development of *Rhapis*, the meristematic cap has nothing to do with primary thickening. Primary thickening involves both elongation and expansion of the stem, and most important, a reorientation of all tissue through about 90°. It is suggested that the term "primary thickening meristem" be discarded, because the tissue which really merits the name is diffusely located *below* the tissue for which the term was originally coined. The alternate possibility of maintaining that name for what has been called in this study meristematic cap would be incorrect and therefore misleading.

In conclusion the foregoing remarks might be strengthened by saying that the vascular topography of further monocotyledonous crowns which fully confirms previous findings has been analyzed. We are progressing toward an understanding of the monocotyledonous vascular system and its development.

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