

M. H. Zimmermann

INTERNATIONAL ASSOCIATION OF WOOD ANATOMISTS

Bulletin

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by P. B. Tomlinson and M. H. Zimmermann

ZÜRICH 1967/2

Editor: A. Frey-Wyssling, ETH Zürich

EDITORIAL

On September 2nd, 1967, the International Academy of Wood Science (IAWS), founded by Prof.F.Kollmann (Munich), held its first Scientific Session on Basic Wood Research at the Mozarteum in Salzburg (Austria). Members from Austria, Czechoslovakia, Finland, France, Germany, India, Japan, Poland, Sweden, Switzerland and USA, as well as representatives of the local authorities, of FAA, of IUFRO, of the Association of the Friends of IAWS, and of Universities and Research Institutes from Overseas and Africa were present.

After the official address by President F.Kollmann, three scientific papers were presented. Prof.K.Kratzl (Vienna) from the chemical class related on the problem of "The Biogenesis and the Decomposition of Wood", Prof. E.Fukada (Tokio) from the physical-technological class spoke on the "Piezoelectricity of Wood" and your Secretary-Treasurer from the biological class lectured on the "Ultrastructure of Wood".

In the meeting of domestic affairs the election of a new member was validated. The membership of the Academy is now specified as follows:

Regional Working Group	Scientific Classes		
	A.Biological	B.Chemical	C.Physical-Technol.
European-African	7	3	8
Pan American	-	2	1
Asia-Pacific	1	1	2

Toward the evening a reception by the Provincial Government and the Mayor of Salzburg in the Marble Hall of the renowned Mirabell Palace closed the memorable session in Salzburg which place has not only a famous episcopal and musical tradition, but also a most interesting history of wood production, floating transport and wood consumption in connection with its salt mining.

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Secretary-Treasurer

IRVING WIDMER BAILEY
1884 - 1967

The death of Professor Irving Widmer Bailey on May 16, 1967, ended a long and remarkably productive career and in a real sense concluded a chapter in the history and development of plant anatomy and morphology.

Irving Bailey was born in Tilton, New Hampshire, August 15, 1884. Several years after his birth, his father, a distinguished astronomer was appointed Director of Harvard University's southern hemisphere astronomical station near Arequipa, Peru. Bailey's boyhood was spent in the high Andes, with interludes in the rainforests of the eastern slopes and on the arid coastal plains of Peru. Few parts of the world are featured by such extreme variety of both climate and vegetation as the central Andes of South America and their eastern and western slopes. These boyhood experiences were deeply engrained in Irving Bailey's later scientific interests in natural phenomena and especially his growing absorption, while a student at Harvard College, in the form and structure of plants, in particular forest trees.

Although Professor Bailey's affiliation throughout his lifetime was primarily with Harvard University, he was involved in various governmental activities from time to time which drew upon his special knowledge in forestry, forest trees, wood structure and the physical properties of wood. Among these were his assignment in World War I to the Bureau of Aircraft Production, at Wright Field, Dayton, Ohio, where he was in charge of the Wood Section of the Materials Engineering Division. In 1926, Professor Bailey was appointed to the Committee on Forestry Research of the National Academy of Sciences in whose functions he took a leading part for several years. This work involved extensive travel in the United States, Canada, and Europe in surveying laboratories, tree plantations and forest experiment stations. The results of these field studies were published jointly with Dr. Herman Spoehr of the Carnegie Institution of Washington in a book entitled "The Role of Research in the Development of Forestry in North America" (1929).

In the unusually favorable scientific environment of Harvard's former Bussey Institution for Applied Biology, Irving Bailey was associated for many years with distinguished colleagues in various areas of biology. During this period, in the 1920's, he became involved in collaborative studies with Professor William Morton Wheeler, one of the great figures

in American entomology. An outcome of their joint studies on the relation of ants and their "symbiotic" relations with plants in tropical America was a unique series of papers on myrmecophily, that curious and complex relationship between plant structure, adaptation and their insect co-inhabitants in certain tropical trees.

Professor Bailey's versatility and wide ranging interests in the biology of trees and woody plants in general was based on an extraordinary knowledge of plant structure and structural variation. This resulted from years of intensive study of the optical microscopy of wood and its optically resolvable microstructure. His interest in, and now classic contributions to, the structure of the plant cell wall were an effort to penetrate, insofar as possible by white-light microscopy, the ultimate structure of the plant cell wall. In this he succeeded uniquely, and his skilled photomicrographic and histochemical techniques were a needed prelude to the subsequent application of electron microscopy to the yet developing area of biological "ultra-structure", as applied to study of the plant cell wall.

Irving Bailey's interests in the anatomy of woody plants was featured even from his earliest work in 1909 to extend far from the confines of description and characterization of structure per se. As one of my senior colleagues (Professor Paul C. Mangelsdorf) recently wrote concerning Professor Bailey's career, "His research was motivated less by curiosity than by a desire to construct an integrated body of knowledge about the tissues of woody plants that would be valid and useful not only to this generation but through the generations". In this statement, I would concur heartily. Having known Professor Bailey for nearly exactly 30 years I well learned his pragmatism and analytical approach to scientific problems, as well as the foibles of selective judgment in attempting to solve the intricacies of comparative morphology and evolutionary processes which have proceeded through geologic time.

In concluding this minute on the life of Irving Widmer Bailey I should perhaps add a few comments which relate both to his personal and scientific attributes. Although Professor Bailey was formally retired from the Faculty of Harvard University, in the capacity of Professor of Plant Anatomy and Director of the Institute of General Plant Morphology in June 1955, he continued daily in his research and contributed actively in seminars with

colleagues and students until within a few days of his death, and indeed left an unfinished manuscript and micro-slides of his uncompleted work. His incisive and purposeful approach to scientific problems, his breadth of knowledge and his intellectual vigor, will remain in the memory of those of us who knew him.

*

THE "WOOD" OF MONOCOTYLEDONS

by P.B. Tomlinson and M.H. Zimmermann

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Elementary courses in botany and many botanical textbooks describe monocotyledons as non-woody plants with little emphasis on those with long-lived parts. This is inevitable because botanical science has developed in regions where monocotyledons are herbaceous and contrast strikingly with woody dicotyledons in size and growth habit. Lilies, grasses, rushes, sedges and orchids are the characteristic representatives of the Monocotyledons in temperate floras. Where perennial parts are developed they are usually underground parenchymatous storage organs. Under these circumstances it might be thought that monocotyledons have no significance for the wood anatomist. A transposition to the tropics completely changes the picture. Here there are many conspicuous, tree-like monocotyledons with massive long-lived trunks. Their stems are obviously "woody" and indeed may be so hard as to dull the sharpest axe. This article analyzes in general ways the nature of this wood and the plants which produce it, so serving to draw attention to a very much neglected chapter of botany (see also TOMLINSON, 1964).

A feature of the taxonomic distribution of arborescent monocotyledons is the diversity of groups which includes them. The Palmae and Pandanaceae are large and natural families, predominantly tree-like. Otherwise trees occur as rather scattered representatives, mostly within the Liliales. Hutchinson's family Agavaceae is largely established on the basis of growth form (HUTCHINSON, 1959) but whether the group is natural remains uncertain. His Xanthorrhoeaceae, to which the grass-trees of Australia belong, is a much more natural assemblage. Otherwise tree-like monocotyledons occur as isolated representatives within otherwise wholly herbaceous groups. The bamboos within the grasses are a special case. Others include Aloe in the

Liliaceae, Strelitziaceae in the Scitamineae, Puya in the Bromeliaceae. Further examples could be produced although this may require us to stretch our definition of tree rather unnecessarily.

The evolutionary relationship between arborescent and herbaceous forms in the monocotyledons is not understood. It is common, however, to find the two contrasted habits represented in different species within one genus suggesting that the step from one growth form to another does not involve major genetic changes. There is good argument for regarding the arborescent habit in at least some groups as primitive, as with the Strelitziaceae in the Scitamineae (TOMLINSON, 1962). It has been suggested, from time to time, that all herbaceous monocotyledons are essentially the juvenile forms of palm-like plants modified in many diverse ways. This idea has been most recently promoted by CORNER (1966) in his book on the natural history of palms. We may contrast this idea (based on vegetative habit) with the more generally accepted and classical notion of monocotyledonous phylogeny (based on floral morphology) which argues that monocotyledons have diverged from a Ranalean ancestor via the Alismatales. This idea is completely oblivious to the difficulties involved in deriving large woody forms, like palms, from essentially aquatic or swamp-dwelling herbs often with specialized growth forms. Perhaps these classical concepts reflect the ideas of botanists only with first-hand acquaintance of temperate floras.

Familiarity with woody monocotyledons in the tropics does show that although they grow tall in a competitive search for light they only have adaptive advantages over dicotyledonous trees in specialized environments. In tropical rain forests palms may be a characteristic feature of the understories but never contribute significantly to the canopy. On the other hand in swamps and river margins (e.g. Raphia in West Africa and Mauritia in South America), in mangroves (Nypa in the Far East), sea-shores (Pandanus in the Pacific), in savannahs (Copernicia in Brazil), in deserts (Yucca in Central America) and on mountains (Ceroxylon and Puya in the Andes) palms or palm-like plants are conspicuous or even dominant forms. From this we may conclude that whereas large monocotyledons are relatively unsuccessful in mesophytic habitats they are often better adapted to certain special habitats.

The absence of arborescent monocotyledons from temperate floras needs explanation. Most probably, although they can endure extremes of heat and drought, they cannot endure cold because they have no mechanism for making a dormant terminal bud capable of overwintering. Growth is continuous.

This may account for the fact that monocotyledons in temperate latitudes are largely represented by herbs with underground overwintering buds. Bud scales, reflecting a periodic change in the apical meristem, are virtually unknown in monocotyledons. Lateral buds in woody forms are mostly protected by an enveloping prophyll, as in Yucca. The prophyll is large and woody in the inflorescence buds of the caryotoid palms. In Dracaena and Pandanus, on the other hand, lateral buds are small, inconspicuous and largely enveloped by stem tissues. In palms and to a certain extent in Aloe dormant vegetative buds are absent.

The most remarkable feature of woody monocotyledons is that most of them achieve their stature without secondary thickening. Their "wood" is primary tissue and in developmental terms is not comparable to the wood of coniferous and gymnospermous trees. Nevertheless, because they reach a stature * comparable to that of other trees, these woody monocotyledons are subjected to the same mechanical and physiological stresses as are all tall plants. How, in the absence of secondary wood, is this stature achieved and is mechanical strength provided? These questions concern growth and construction and have been very much neglected.

Arborescent monocotyledons are either unbranched with uniformly cylindrical trunks (most palms) or sparingly branched with tapering trunks (pandans). They have large leafy crowns usually with congested internodes. A massive primary axis requires a massive bud. Branches, if present, must develop early (i.e. close to the apex) since vascular union of branch and main axis can only be effected by the development of primary vascular bundles. A feature of Pandanus and the Agavaceae is the sympodial growth of the axis, branching being closely associated with the development of terminal inflorescences. The growth-limiting characteristic was appreciated and discussed by earlier botanists, in particular Schoute, who made many careful observations on branching in the arborescent monocotyledons (e.g. SCHOUTE, 1903, 1918). It is regrettable that his ideas and observations have found no place in modern botanical textbooks.

We must continually bear in mind growth-habit in discussing woody monocotyledons. In this way we can divide them into three fairly natural groups; 1) the palms, most of which have unbranched stems (in the vegetative state) and no secondary thickening; 2) the pandans with branched stems and no secondary thickening; 3) the somewhat miscellaneous assemblage of plants, characterized by the tree-lilies, with branched stems and a very peculiar type of secondary thickening.

*Footnote: The palm Ceroxylon often exceeds 50 meters. Early travellers in the Andes considered it the tallest of trees, apparently without making actual measurements. The unbranched habit undoubtedly exaggerates its stature.

Palms

Anyone who concerns himself with the microscopic anatomy of palm stems sails in uncharted seas. Our ignorance of the histology of palm wood has various causes. Palms are relatively inaccessible (at least to the botanist in temperate regions), and their tissues are notoriously difficult to section on the microscope. Investigations are not stimulated by wide commercial use of palm wood, and finally, we are dealing here with a microscopic problem on a truly macroscopic scale.

To even the most casual observer the tissue of the palm stem (Figs. 1-6) is evidently very different from the wood which constitutes the familiar constructional timbers of commerce. Under the microscope a small sample of palm wood reveals all the tissues associated with different functions but one needs to appreciate the overall distribution of tissues in order to grasp the functional efficiency of the trunk. In a palm stem numerous small strands, never more than 2-3 millimeters in diameter, run through a matrix of ground tissue. Within each strand there is a clear distinction between xylem (water-conducting tissue), phloem (sugar-conducting tissue), and an incompletely enveloping sheath of fibers (mechanical tissue). Although it is clear that the individual vascular bundles represent the pathway for long-distance transport, it is much more difficult to demonstrate vascular continuity. The ground tissue is usually full of starch so it is easy to appreciate that the matrix serves as a food-storage reservoir. The starch is extractable and may be of considerable food value, for example, commercial sago is obtained from the palm Metroxylon.

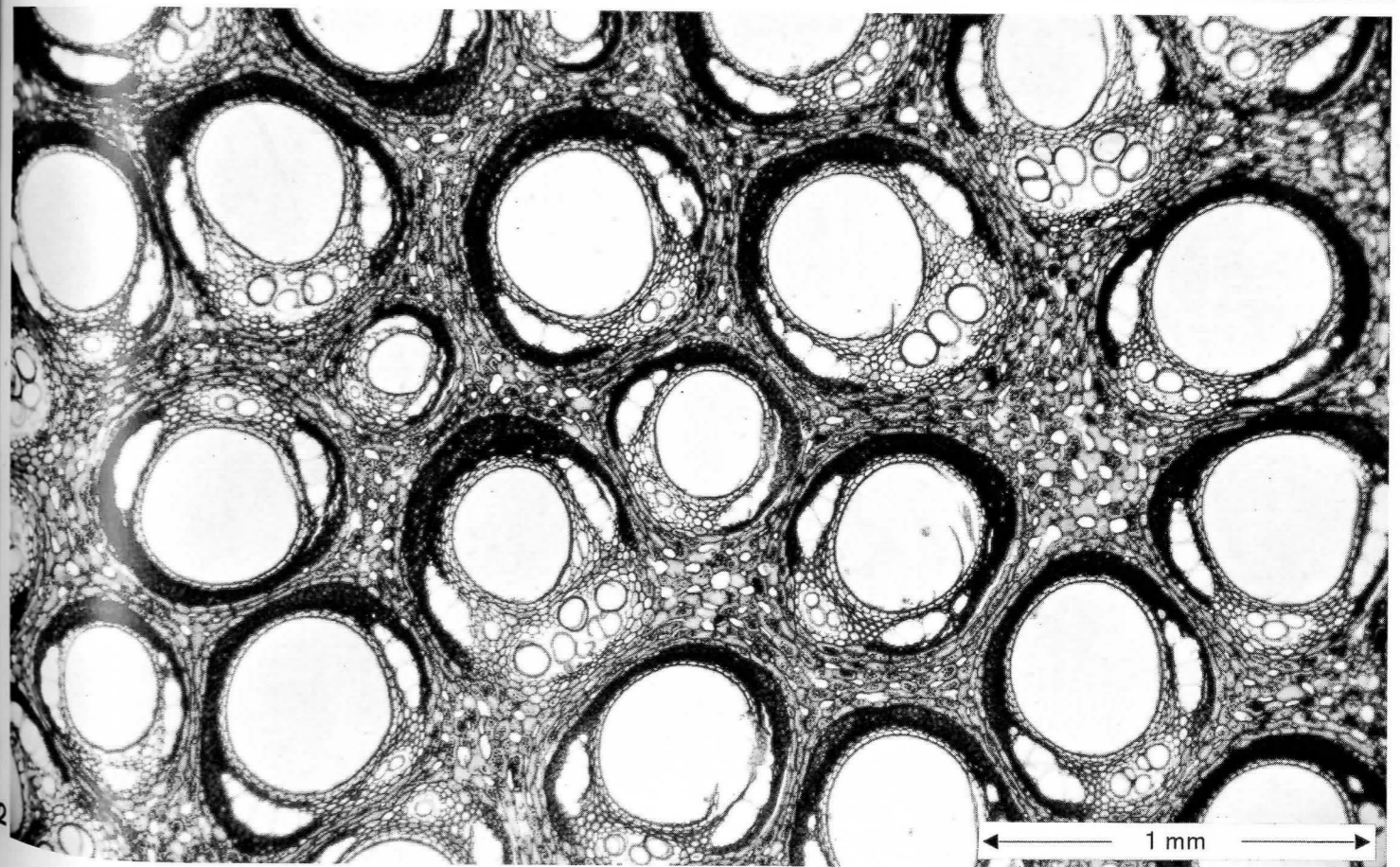
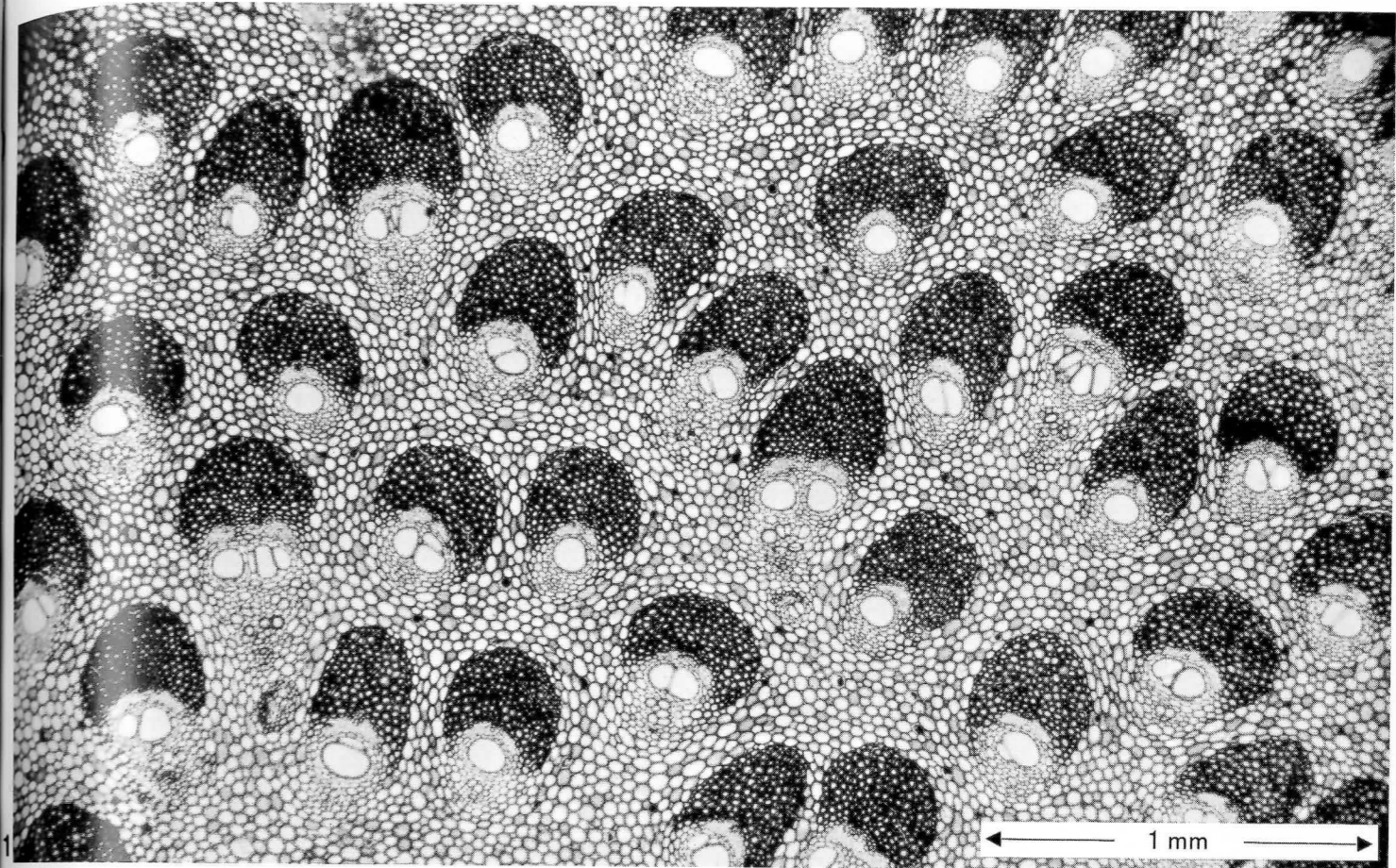
The overall distribution of the fibers associated with the conducting bundles gives us an appreciation of the mechanical efficiency of the palm stem. The strands are usually crowded towards the stem periphery (Fig. 3), this being associated with a considerable increase in the number of fibers around each peripheral strand. The overall effect is that of a column with the strongest tissues around the periphery, mechanically a very effective arrangement. It is interesting to compare the stem of palms with that of bamboos. The bamboo stem has a hollow center, it lacks the softer, central storage tissue. This is of course correlated to the differing growth habits of the two types of plants. The central vascular bundles of the palm stem are helically arranged. We do not know if this is of structural significance, but we do know that it is of physiological importance in respect to lateral translocation. The mechanical strength of palm stems is shown by the way in which these plants can endure a hurricane. They bow before the wind and are more easily uprooted than broken.

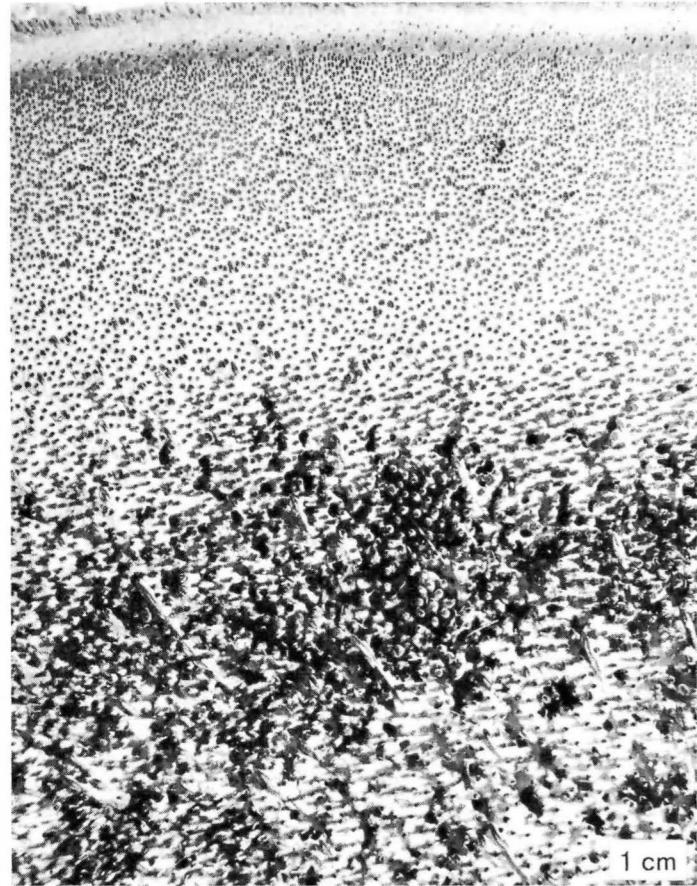
In spite of all the features which make the palm stem mechanically efficient

as a whole, its value in the timber trade is minute. Palm stems cannot be sawn into planks like dicotyledonous and coniferous logs. Palm wood therefore finds its way into commerce only as a curiosity called "porcupine" wood because of the protruding, needle-like ends of vascular bundles (Figs.3 and 5). It may be met with in the form of carved curios (usually the wood of Cocos, Borassus or some other common palm) but seldom as constructional timber. It must be realized that the texture of palm stems varies enormously and different woods have different properties. Coconut wood (Fig.6) is relatively homogeneous because the vascular bundles are uniformly distributed and the ground parenchyma is lignified. However, the wood splits when dried and is of little value. In most other species there is a sharp distinction between the soft, pithy central tissues and the sclerotic peripheral layers. Such stems are easily split and hollowed out.

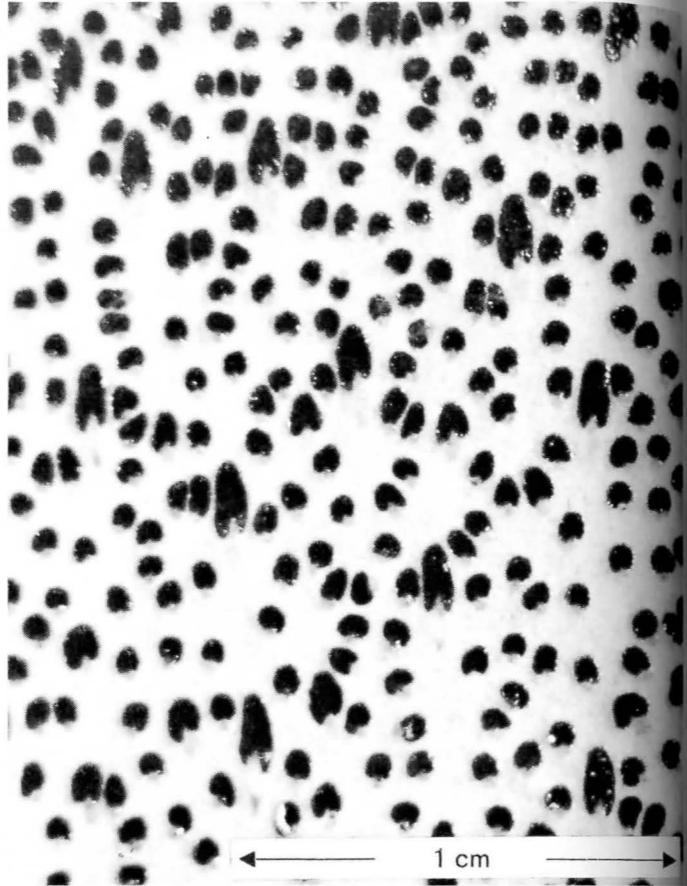
Although palm woods are of little significance to the international timber trade, they are of great local importance in some tropical countries and the literature on their economic botany is voluminous (CORNER,1966 and TOMLINSON, 1961,p59-63). Palm trunks are a ubiquitous building material. This is largely because those properties unique to the palm stem are put to good use. The more homogeneous stems are most often employed in their entirety as stakes, beams or rafters. They may be valuable because of special properties. Borassus wood is said to be termite resistant. Oncosperma survives well in salt water and is used in fish traps. Of species in which the centre of the stem is soft the logs may be allowed to rot and the peripheral woody cylinder split into narrow planks, as with Roystonea in Cuba (Fig.7). The Cubans also make boats out of entire trunks of Colpotherinax in the same way. The soft centre does not have to be wasted. It can be fed to stock. As mentioned before, in Metroxylon it is the source of commercial sago. Palm starch mobilized as sugars may be tapped from living trunks via the inflorescence and becomes a valuable source of sugar and alcohol ("toddy"). Hollowed stems may serve as pipes and gutters. The narrow stems of Iriartea are made into blow-pipes by American Indians. The tip of the dart may be a spine from a palm. We cannot dismiss these facts as trivial. Peasant economy in large parts of the tropics is subsistence economy. Food and raw materials are those which are available most cheaply and most abundantly.

Rattans constitute an exception to the generalization that palm stems are of no significance in world trade. These are mostly Malaysian species of the genus Calamus. The climbing stems of these species have long narrow internodes - sometimes the internodes are 2 meters long. The stems' overall length commonly

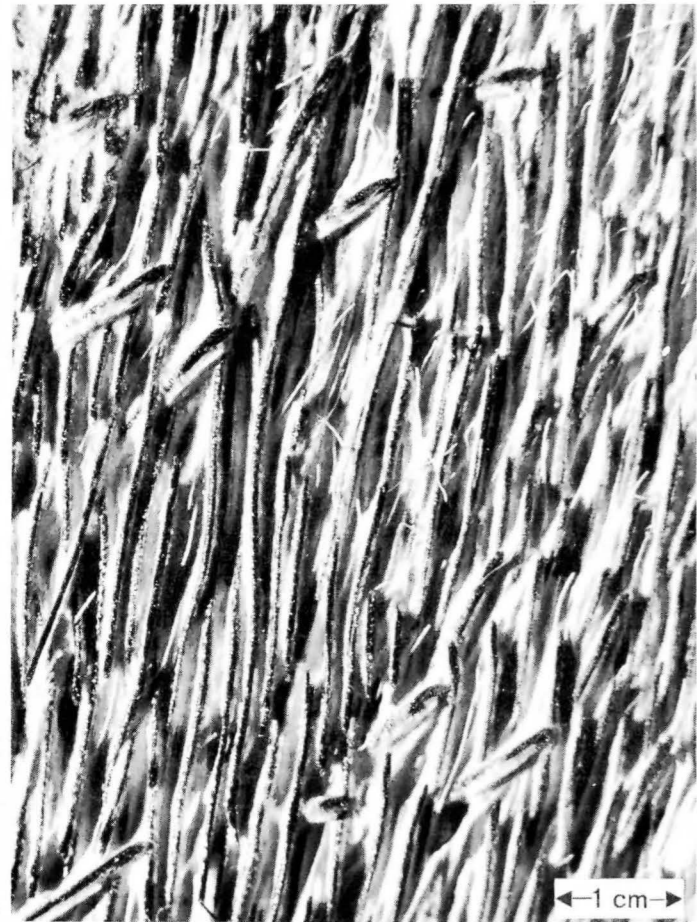




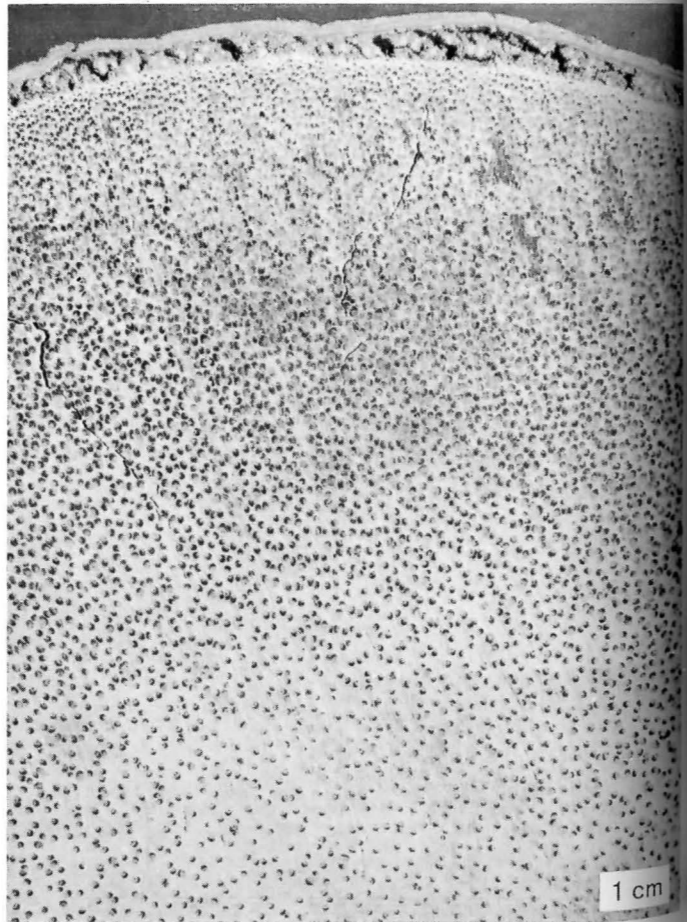
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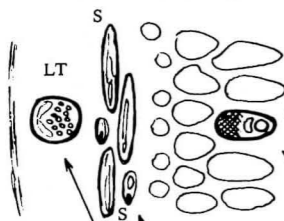


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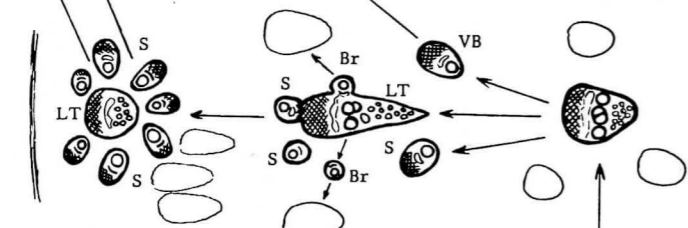


6 B

7. LEAF TRACE ENTERS
LEAF BASE
SATELLITE BUNDLES
ENTER INFLORESCENCE



1. VERTICAL BUNDLE NEAR STEM PERIPHERY ON ITS WAY UP

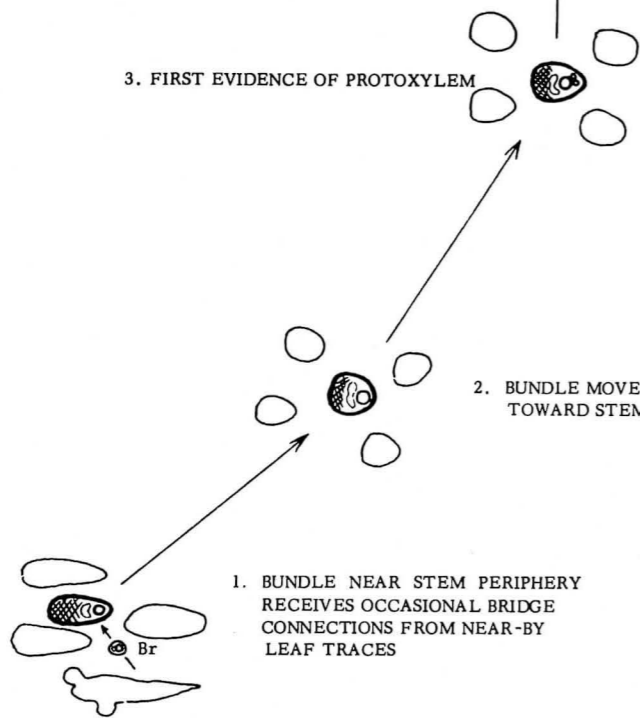


5. BUNDLE MOVES TOWARD
STEM PERIPHERY AND
BREAKS UP INTO LEAF TRACE
(LT), VERTICAL BUNDLE (VB),
SATELLITE BUNDLES (S) AND
BRIDGES (Br)

6. LEAF TRACE AT
BASE OF INFLORESCENCE
SURROUNDED
BY SATELLITE BUNDLES.

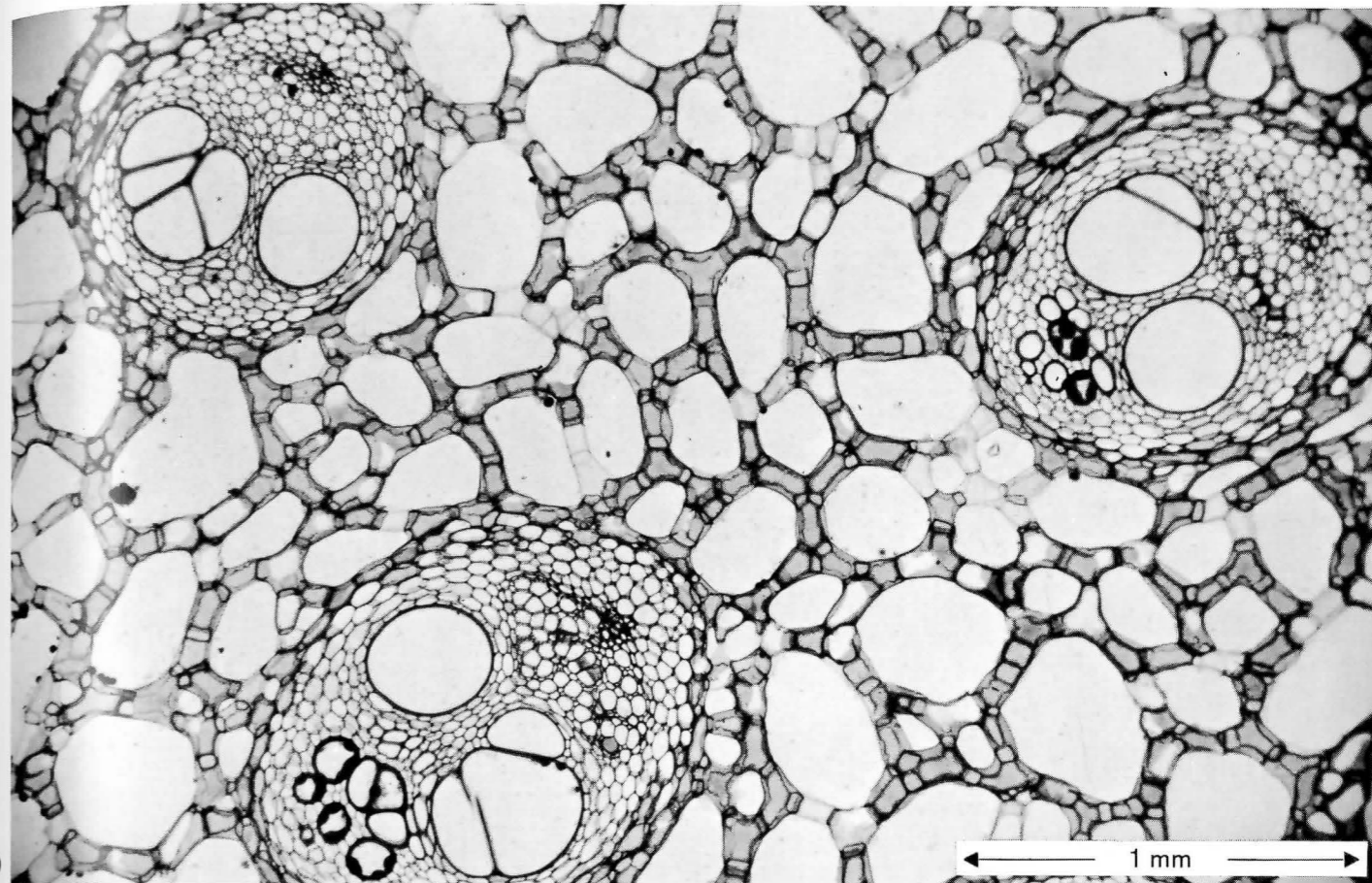
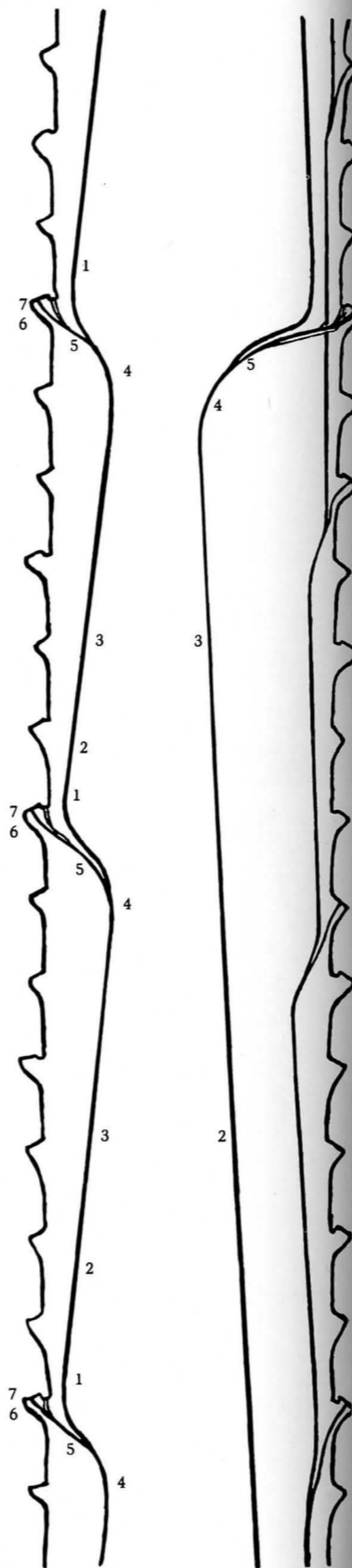
4. BUNDLE INCREASES
IN SIZE

3. FIRST EVIDENCE OF PROTOXYLEM

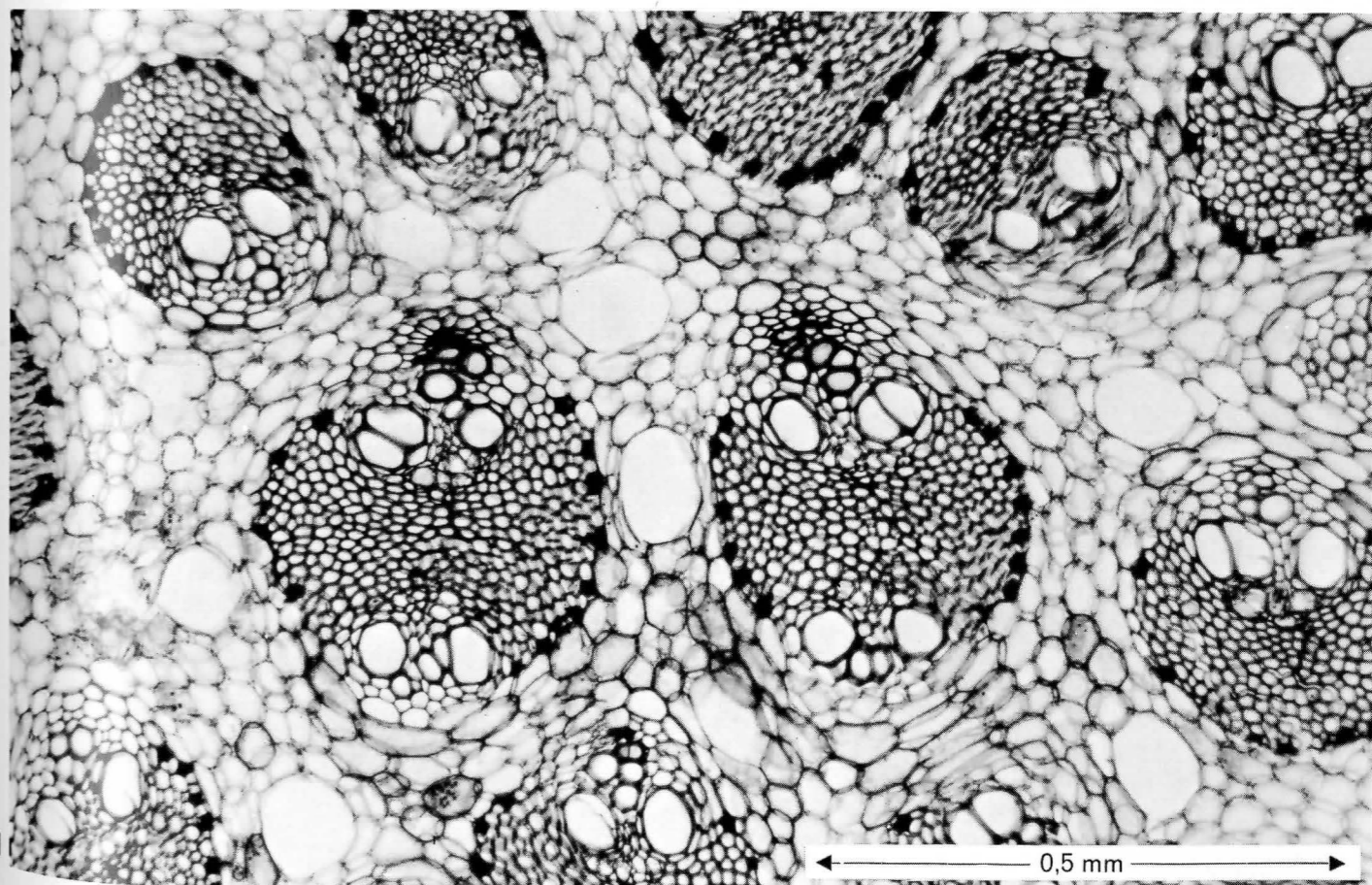


1. BUNDLE NEAR STEM PERIPHERY
RECEIVES OCCASIONAL BRIDGE
CONNECTIONS FROM NEAR-BY
LEAF TRACES

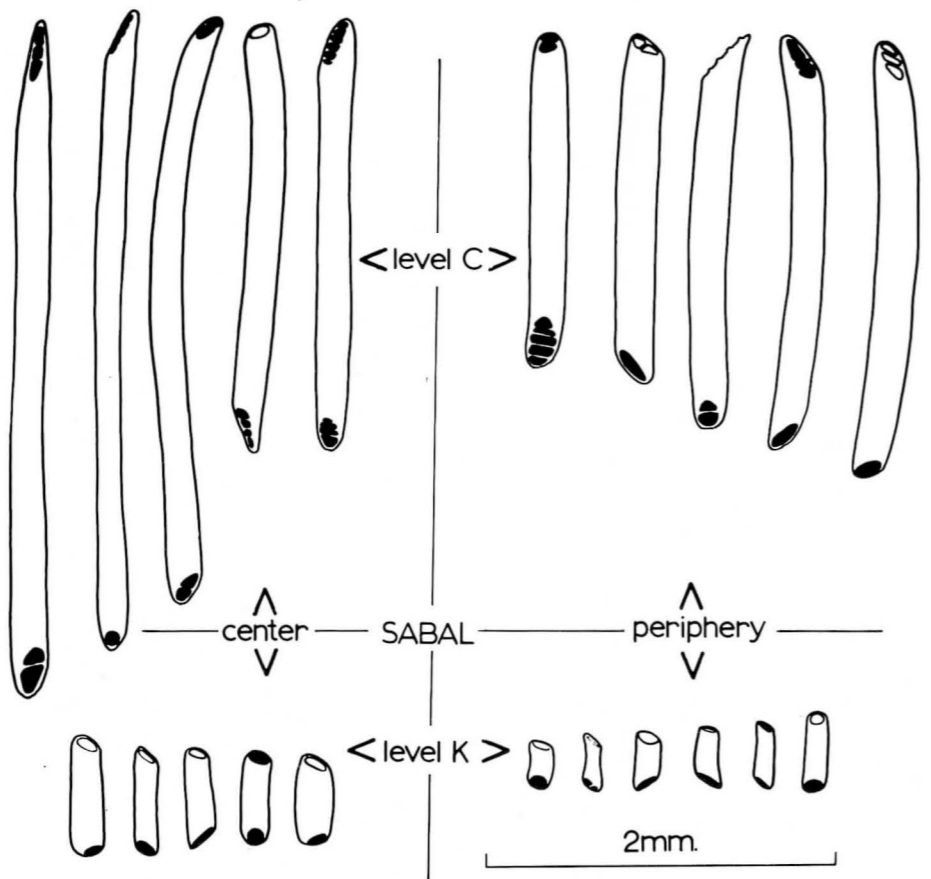
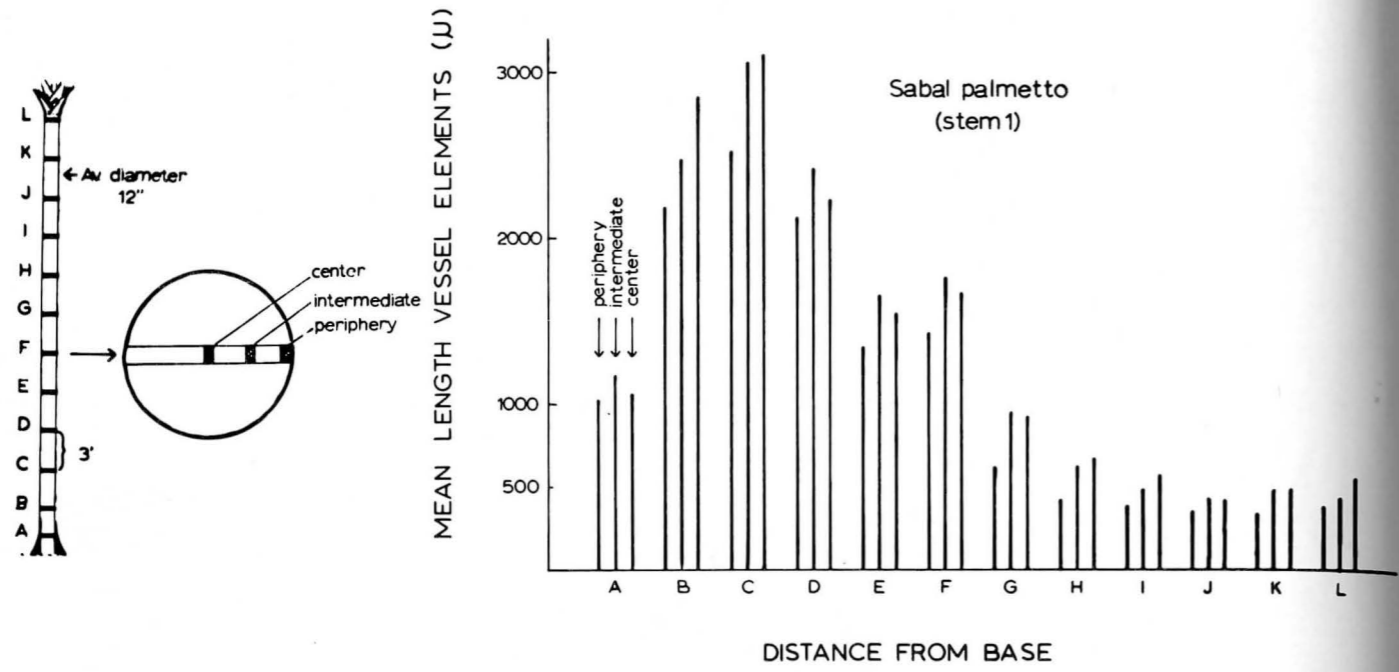
2. BUNDLE MOVES
TOWARD STEM CENTER



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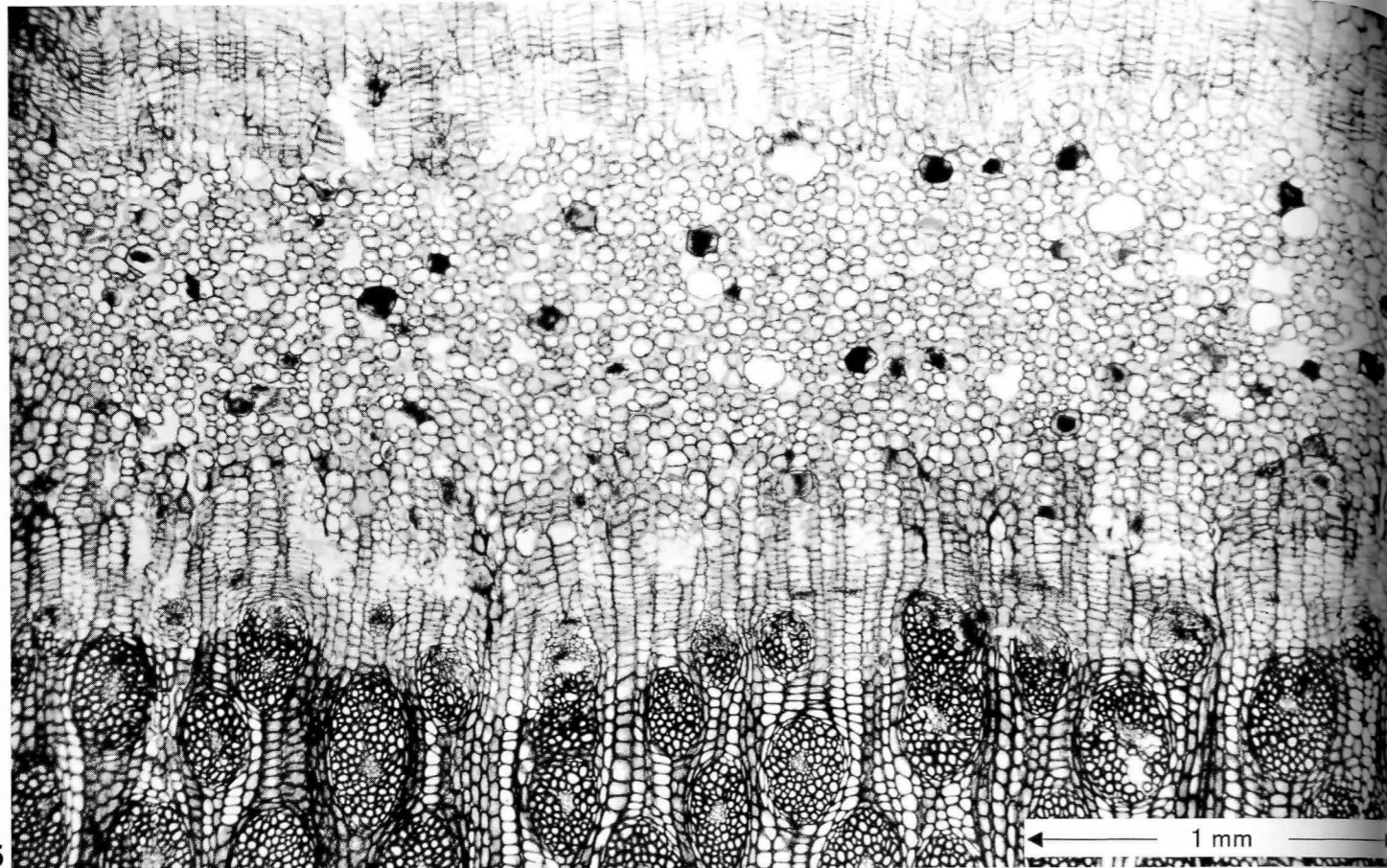
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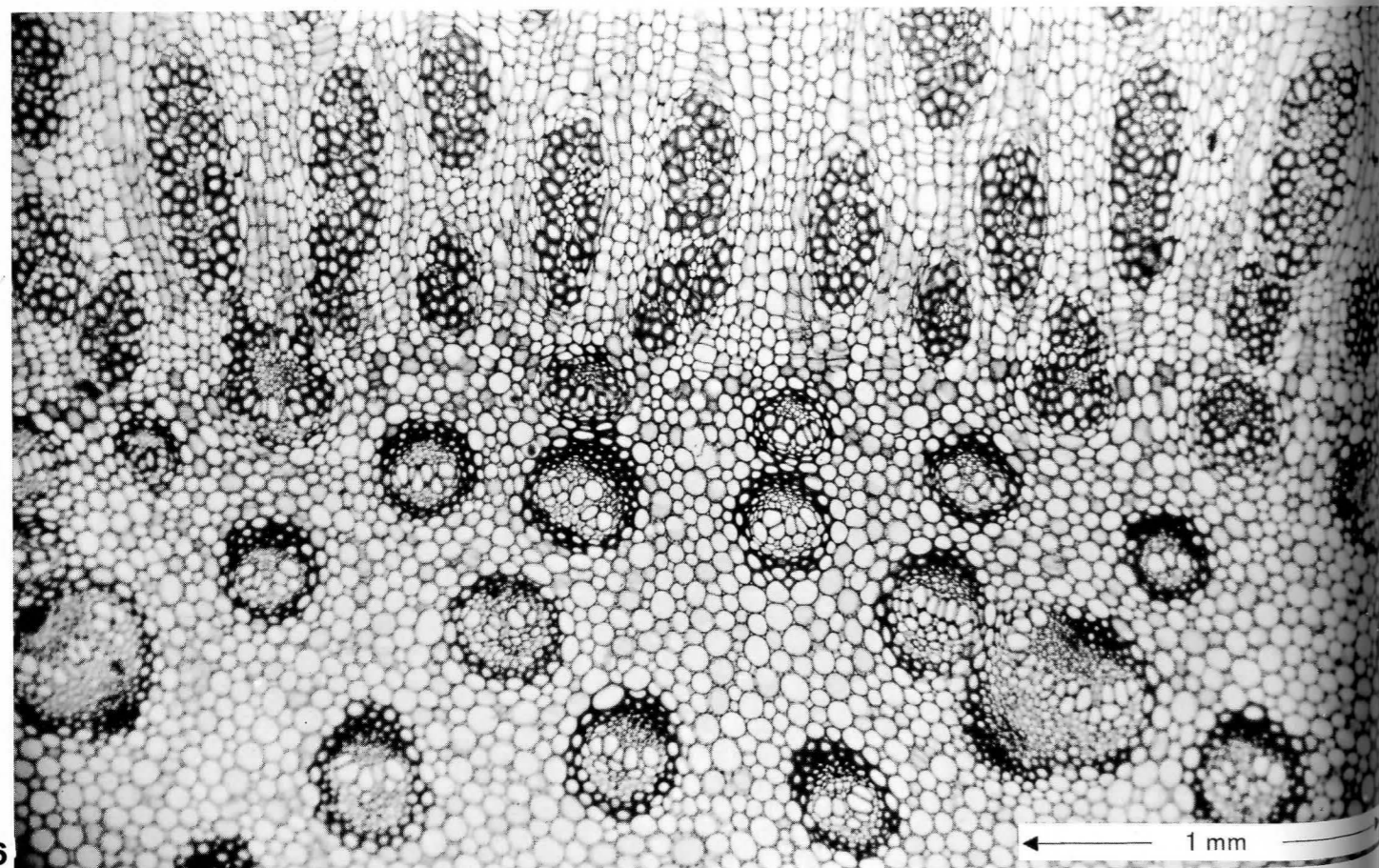
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exceeds 30 meters; figures of 200 meters have even been claimed. The wood is light because it is very porous (wide vessels) as befits a scandent plant (Fig.2). It is homogeneous because it is not self-supporting and the stems are very pliant, especially when steamed. Rattan stems, split or unsplit, are valued for furniture. This exception serves to emphasize the great variability in palm stems which in turn reflects a great variation in growth habit. One of the chief values of CORNER's recent book (1966) is the way in which it dispels any notion that the palms are a uniform, easily understood group.

The neglect of palms is a modern phenomenon. Earlier botanists accorded palms a central place in their understanding of plant development because they represent one of the main kinds of tree-habit. In view of this long history of investigation, statements about our current ignorance of palm stems might be received with some skepticism had we not demonstrated this ignorance ourselves. Vascular continuity within the axis, so important in an understanding of long-distance transport, has only recently been demonstrated (Fig.9; ZIMMERMANN and TOMLINSON, 1965). Despite the considerable efforts of 19th century botanists this aspect of vascular continuity in palm stems was left in an incompletely understood state and diagrams in modern textbooks have gradually evolved by "improvement" (TOMLINSON and ZIMMERMANN, 1966). If the vascular anatomy of the mature palm stem was poorly known until recently, its development was entirely unknown. We are only beginning to understand vascular development in the apical region. This is an important step in understanding monocotyledons as a whole, because possible patterns of vascular distribution in monocotyledonous stems may be limited in developmental terms. We suspect that some of the patterns described by FALKENBERG (1876) may have been analyzed incorrectly. In raising these doubts we are not belittling the remarkable efforts of earlier workers but emphasize that this aspect of plant anatomy represents virgin territory.

Palms differ from most other trees in the longevity of their tissues. They have no secondary vascular tissues and their primary tissues function throughout the entire life-time of the plant. There are conspicuous differences between old, basal and young, terminal parts. Ground tissues may expand perceptibly producing measurable increases in stem diameter (SCHOUTE, 1912). This diffuse secondary thickening often results in a very lacunose ground parenchyma (Fig.10). Rigid peripheral layers may be ruptured, leading to dilatation of cortical layers. In addition the walls of living cells continue to thicken and lignify so that the oldest, basal tissues become very hard. Indeed, since in addition they are always associated with silica deposits, basal parts of some palms are amongst the hardest tissues found in the vegetable kingdom.

A number of palms have pronounced, often localized swellings of the trunk. It is not known to what extent in these "bottle-palms" this enlargement is due to diffuse secondary growth. In other palms, like Borassus and Roystonea, variation in crown size seems to be a factor in changes in stem diameter (Fig.8).

Phloem is not short-lived as in most dicotyledonous and coniferous trees but functions throughout the life of the palm (PARTHASARATHY and TOMLINSON, 1967). The contrast between thin-walled, functional sieve-tubes and the surrounding, iron-hard sclerenchyma is remarkable.

Differences between base and apex of a palm stem do not entirely result from secondary changes with age. The tissues laid down by the crown at successive stages also seem to differ. A regular pattern of change along the palm trunk can be demonstrated most easily by the range in size of vessel elements throughout the stem (Fig.12).

The apical part of a palm stem is always softer than the basal part. Consequently a dead, fallen palm trunk always rots from the apex to the base. Even this elementary observation is not without significance to the anatomist since it must have been an important factor in the fossilization of palm stems. The base of the palm stem must have fossilized more readily than the apex. Fossil palm woods are abundant in recent deposits. Their identification often involves matching fossil with existing forms. This is a dubious procedure when one considers our ignorance of the anatomy of living palms. Further doubt may be cast on these identifications since they are often based on a comparison of the distal part of a living palm, which is easy to section, with the basal part of a fossil palm, which is most likely to fossilize. Indeed the first question the palaeobotanist might well ask, especially with regard to the earliest fossils, is: "Are these palm-like stems really those of palms?" - bearing in mind the possible evolutionary relation between monocotyledons and palm-like plants.

From these considerations we can see that the study of palm stems has many interesting implications. First, the taxonomy of palms as well as the evolution of monocotyledons cannot possibly be understood without a more thorough study of anatomy and development. Second, anatomical differences within a single stem must be understood before botanists can even attempt to assemble a microscopic key to monocotyledonous woods as they exist for dicotyledonous and coniferous trees. Third, the physiology of palms can only be understood if it has a sound anatomical basis. Fourth, the study of development of palm stems (and indeed of all monocotyledons) can only be begun with an understanding of the complex course of procambial strands in the apical region. We were entirely ignorant about this until very recently (ZIMMERMANN and TOMLINSON, 1967)

Pandanus

The second largest group of arborescent monocotyledons is characterized by the large tropical genus Pandanus. This genus is little understood taxonomically but seems to include upwards of 500 species. These plants, like palms, lack secondary vascular tissues, but unlike most palms, are branched, often copiously so. There is a mechanical limitation to the branching of axes without secondary growth (SCHOUTE, 1904). Firstly, the main axis does not thicken as the crown develops so that plants easily become top heavy. Secondly, branches must attach early to the main axis since no secondary vascular tissue is available to supplement branch-axis union. Similar physiological limitations are also obvious. The main axis must anticipate future demands on its ability to supply water to the crown.

Mechanical and physiological limitations are overcome in a number of ways. The main axis is usually massive but successive orders of branches are progressively reduced in diameter (Fig.14) so that the aspect of a dicotyledonous tree with narrow distal branches and a wide main trunk is produced. However, this simulation of secondary growth is entirely misleading. Lower branches tend to be supported by massive stilt roots which provide a direct pathway to soil water. Pandanus trees are usually of low stature and diffuse growth habit. Tall species (some may exceed 30 meters) are little-branched.

The problem of branch-attachment is overcome in a distinctive way and involves sympodial growth. Lateral shoot growth is largely stimulated by the development of a terminal inflorescence. The peculiar process of eviction of this inflorescence was clearly described by SCHOUTE (1905). It is alarming to see modern "evolutionary" interpretations of monocotyledonous habit which describe Pandanus as branching by a "primitive dichotomy". The axis in Pandanus forks when two, instead of one, axillary buds grow out. Nothing is known of the method whereby vascular connections are made between branch and main axis.

Pandanus wood is much softer than that of palms and has no commercial value. Our own preliminary investigation shows essentially the palm-type course of vascular bundles. In individual transverse sections Pandanus wood can easily be distinguished from that of palms. A characteristic feature is an abundance of compound (bipolar or tripolar) vascular bundles (Fig.1). These are the result of temporary union of two or more vascular strands without vascular contact. These bundle "fusions" are therefore not physiologically significant. Pandanus wood has no silica but large and conspicuous crystals (calcium oxalate?).

Monocotyledons with secondary growth

Palms and pandans have solved the problem of how to achieve massive proportions in the absence of secondary thickening. But there are arborescent monocotyledons which show appreciable secondary growth in thickness from a vascular cambium, they are represented by genera like Beaucarnea (Fig.13), Cordyline, Dasyllirion, Dracaena, and Yucca in the Agavaceae and Aloe in the Liliaceae. These are neither particularly abundant nor dominant and it seems as if secondary tissues confer no marked adaptive advantages. Few of them approach a stature which is common in palms, although many produce very wide stems at the base. The aspect of a dicotyledonous tree, with many narrow branches is found in only a few species of Dracaena (WRIGHT, 1901), otherwise the massive trunk seems out of proportion to the small, little-branched crown (Fig.13). It appears that these plants are a derived and not a primitive group. Their construction involves sympodial branching with eviction of a terminal inflorescence just as in Pandanus.

Our own study of the vascular anatomy of monocotyledons with secondary growth has only just begun. So far we have been able to show that the primary structure is in principle the same as that of palms (shown for Rhapis in Fig.9). Earlier authorities had largely assumed the equivalence of the primary structure of these plants with that of the palm even though they were ignorant of the fact that the palm itself had not been analyzed correctly.

The secondary vascular tissue in these plants is of considerable interest to the wood anatomist. The microscopic anatomy of this wood has been much studied but, as with the primary tissue, there are still many unknown 3-dimensional aspects. The wood itself is distinctive because it consists of vascular bundles embedded in secondary parenchyma (Figs.15 and 16). Usually the secondary vascular bundles are very different from the primary bundles (Fig.16; CHEADLE, 1937).

The cambium itself is unlike that of the gymnosperms and dicotyledons. Instead of a single layer of initials there is continuous replacement of initials which produce derivatives for only a short time (Fig.15). In older plants initials function for longer periods. SCHOUTE (1902) described this type of cambium as an "etagen" (tiered) cambium (from the French 'étage'; tier) in contrast to the "initial" cambium of other trees. He found some similarity between the monocotyledonous cambium and the early stages in development of interfascicular cambium in dicotyledons.

The method of production of vascular bundles from such a cambium seems well understood although the early investigation of this problem was not without its vicissitudes (see SCOTT and BREBNER, 1893). A vertical series of cambial

derivatives divides longitudinally in various planes. From this prodesmogen strand tracheids, sieve-tubes and parenchyma differentiate. Differentiation of tracheids is remarkable because each tracheid initial may extend to more than 30 times its original length by sliding growth. A number of observers have commented that the secondary vascular bundles include no vessels, only tracheids, regardless of the type of tracheary elements in the primary tissues. We can appreciate that this is simply a result of the way in which the tracheary elements develop. Sliding growth implies pointed ends which are unlikely to become perforated. The amount of secondary tissue produced by the cambium varies. Indistinct growth rings have been recorded, but whether this is related to seasonal periodicity in cambial activity is not known.

The relation between apical growth and secondary activity has not yet been investigated in the light of modern concepts of hormonal induction simply because few observers have been able to study living plants. Nor were hormonal concepts current at a time when there was major interest in woody monocotyledons. Nevertheless, analogies between Dracaena and dicotyledonous trees are not hard to find. Lateral buds are suppressed and subjected to strong apical dominance. Leaning or horizontal stems produce an asymmetrical distribution of secondary tissue and a release of dormant buds on the upper side. Another example of the release of apical dominance is the outgrowth of a lateral bud immediately below the aging (terminal) inflorescence.

Outgrowing buds stimulate cambial activity immediately below. One finds therefore secondary tissue below each sympodial branching. The stimulus does not seem to move far, for secondary tissue diminishes in the basal direction and usually tapers out completely a few centimeters below the branch. There is considerable cambial activity further down in the stem, but we have at present no idea of how it is stimulated there.

Suppressed lateral buds maintain contact with the primary vascular tissue of the central cylinder in a way which recalls the attachment of suppressed buds in dicotyledonous trees (e.g. KORMANIK and BROWN, 1964). When such buds are released by environmental changes, they make vascular connection with the main stem via secondary tissue. Details of this, however, are still unknown.

A peculiar feature of these monocotyledonous trees is the persistence of functional leaf traces through cambium and secondary tissue. In a stem of Yucca aloifolia, for example, leaves remain functional several decimeters below the level of cambial activity of secondary initiation. This is not so unusual in monocotyledons; the basal part of mature, functioning palm leaves also remains meristematic for a long period.

There are many developmental and functional analogies between dicotyledonous and monocotyledonous trees but at the same time there are striking differences. The monocotyledons are an important group and their "trees" have been neglected far too long.

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Legends to Figures

Fig. 1 (Top) Transverse section of stem of Geonoma umbraculifera, a small palm from South America. The ground parenchyma is here very uniform.

Fig. 2 (Bottom) Transverse section of stem of a Calamus sp. This wood was taken from an umbrella handle. The greater diameter of the metaxylem vessels contrasts with that of the more normal vascular bundles of Figure 1.

Fig. 3 (Top left) Sawn surface of stem of Corypha elata, a common Indian species. There is an abrupt transition from the hard outer to the softer inner part.

Fig. 4 (Top right) Part of outer surface of Figure 3 enlarged. The vascular bundles with larger fibrous sheaths are outgoing leaf traces cut at an angle.

Fig. 5 (Bottom left) Longitudinal surface of Figure 3. Leaf traces cross at an angle to overall course of other bundles.

Fig. 6 (Bottom right) Sawn surface of a stem of coconut (Cocos nucifera), much more homogeneous than wood in Figure 3.

Fig. 7 (Top) Hollowed stem of a Cuban Royal palm (Roystonea sp.) ready for splitting into narrow boards, as at right.

Fig. 8 (Bottom) Avenue of Royal palms in Fairchild Tropical Garden, Miami. The diameter of the stem is not uniform in these specimens. In a few other species of palm a much greater localized swelling of the trunk is habitual.

Fig. 9 Diagram of course of vascular bundles in the palm Rhaps excelsa (from ZIMMERMANN and TOMLINSON, 1965). The course of a major, an intermediate and a minor vascular bundle is shown to scale on the right, but without representing the internal helix. To the left overall changes in the anatomy of a single bundle at levels corresponding to the figures in the right-hand diagram.

Fig. 10 (Top) Mauritia sp. Transverse section of stem to show markedly lacunose ground parenchyma resulting from enlargement of intercellular spaces.

Fig. 11 (Bottom) Pandanus sp. Transverse section of stem including two bipolar vascular bundles. Crystal-bearing cells are conspicuous next to bundle fibres. The enlarged cells of the ground tissue are raphide-sacs.

Fig. 12 Diagrams illustrating the range in size of metaxylem vessel elements in Sabal palmetto. To the left of the graph the method of sampling a tall trunk (average diameter 12 inches = ca. 30 cm) by sawing out discs at intervals of 3 feet (= ca. 90 cm) is shown. The mean length of metaxylem vessels from three samples from each disc representing its central, intermediate and peripheral tissues is shown graphically to the right. Elements were isolated for measurement by maceration. - The bottom half of the figure shows representative vessel elements from levels C and K to illustrate extremes of cell size. These quantitative studies on palm stems were made possible by a grant from the American Philosophical Society.

Fig. 13 (Top) Beaucarnea recurvata, a specimen cultivated at Fairchild Tropical Garden.

Fig. 14 (Bottom) Pandanus utilis in cultivation in Miami, Florida. This species has aerial roots only at the base of the trunk. (Photography by Nixon Smiley).

Fig. 15 (Top) Coryline indivisa, the mountain cabbage tree of New Zealand; transverse section of stem at the periphery of the wood to show etagen cambium and stages in development of vascular bundles. A periderm originating from an etagen cambium is shown in the outer cortex at the top of the picture.

Fig. 16 (Bottom) Dracaena hawaiiensis, transverse section of stem to show abrupt boundary between primary wood (collateral bundles at bottom of picture) and secondary wood (amphivasal bundles amidst radially-seriated parenchyma at top of picture).