who may be able to furnish information on the genetical, morphological and anatomical variations in palms." Prof. Davis has been doing research on the coconut for the past fifteen years.

Palms in England

From East Grinstead, Sussex, England, Mr. Michael A. F. Carter writes: "You may be interested to know that I have photographed a 'Canary Island Date' (*Phoenix canariensis*) at Torquay, which was twenty-five feet high — quite something, being over 50° north of the equator! Palms are not a regular feature of the English garden; only *Trachycarpus Fortunei* and *Chamaerops humilis* being offered by a few specialist nurserymen, but some form very handsome trees. They have been severely tested in recent years, the winters of 1961/62 and 1962/63 giving them a difficult time. The winter of 1961/62 gave us six weeks of continuous north winds, except for two days, which according to the weather office was unprecedented. In 1962/63 the winter was even more severe, the worst for one hundred and thirty years, according to official sources, with snow on the ground for ten weeks.

"The majority of palms sustained leaf damage, but survived, and again look healthy. The Chusan palms are now flowering."

LUCITA H. WAIT

Unravelling the Palm Stem

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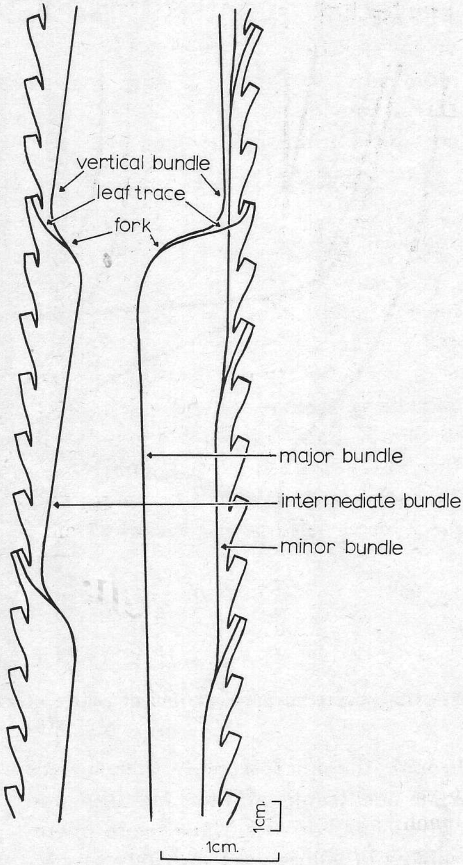
One cannot understand the workings of an automobile engine (or any other machine) without a very detailed knowledge of how it is put together. With this knowledge of how a machine works and is constructed, it then becomes possible to repair it if it breaks. As with a machine, so with plants. Unfortunately plants have not been built by human engineers, and the reason we often know so little about their physiology is simply because their anatomy is not known. From a structural point of view, palms are the least understood of large plants. This ignorance of fundamental structures means that our understanding of palm physiology is deficient so that in turn we have little hope of solving practical problems of disease and nutrition.

The problem of the palm stem had been tackled but not solved by nineteenth century scientists. More recently, investigators have not shown sufficient interest in the subject to make any helpful contribution. In fact, the original and often essentially correct observations of earlier scientists have been largely misinterpreted on their way to the pages of modern botanical textbooks. The problem has hitherto remained unsolved because it is so complex. Essentially it is a microscopic problem, but nobody has found a convenient way of getting a whole palm stem on the stage of a microscope.

Within the last year, however, we have jointly developed a new approach which suggests that this problem has been overcome and that at last the palm stem has been "unravelled." Like many complex problems in science, the governing principle is found to be very simple. A more detailed and scientific account of these discoveries has been given elsewhere in a more appropriate journal (Zimmermann and Tomlinson,

1965) but we feel that readers of PRINCIPES have reason for being especially aware of these findings.

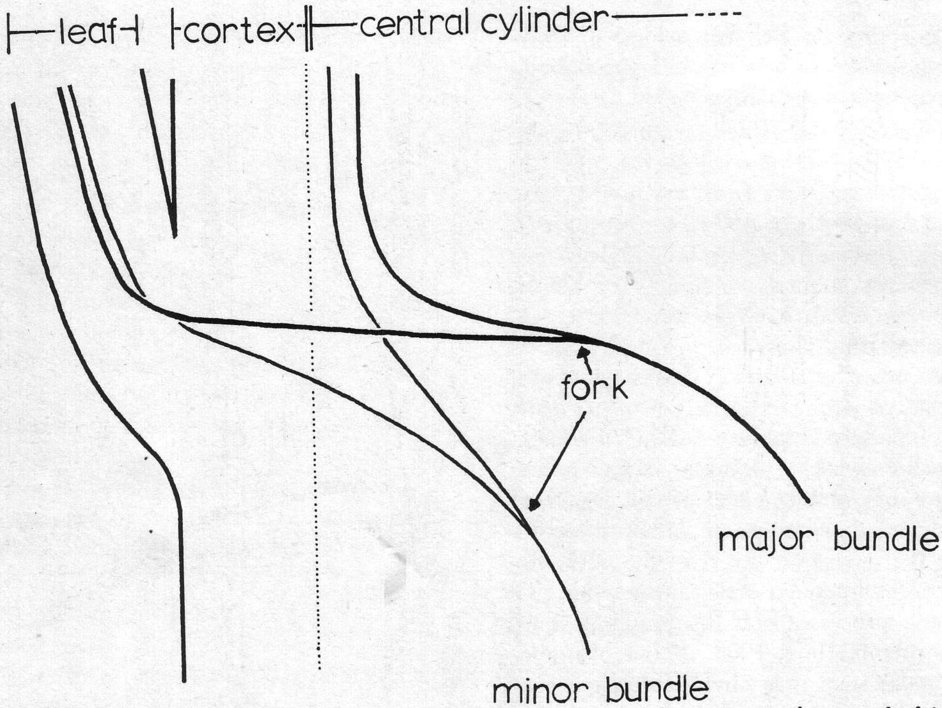
Some of the general features of palm stems, and in particular the ways in which they differ from hardwood trees, are outlined elsewhere in this journal (Tomlinson, 1961). In a dicotyledonous tree, represented by an oak or maple, tissues which conduct water are separated from those which conduct sugars and other nutrients. A tree has a central massive core of wood (xylem) surround by a thin layer of soft tissue in the inner bark (phloem). Water moves upwards in the outer, newest layers of the wood, nutrients in either direction in the innermost layers of the bark. Recent semi-popular articles which describe these processes may be found in Zimmermann, 1961, 1963. If one examines a palm stem it is obvious that the conducting tissues are different. A rotting palm stem, for example, splits into a very large number of narrow strands never more than a few millimeters in diameter. Under the microscope it can be seen that each strand contains fibrous tissue which makes the strand rigid, together with a fine strand of each type of connecting tissue, xylem and phloem. From this construction it is not difficult to see how these strands got their name "fibro-vascular bundle," nowadays abbreviated to vascular bundle. The two types of conducting tissue in a palm are therefore always closely associated, unlike in a hardwood tree. Dissection of a partly decomposed palm stem demonstrates that these bundles are very large and very numerous. It is rather like a telephone cable consisting of a whole cluster of fine wires but differing in that the palm stem must stand erect, supporting its own weight and the leafy crown.



67. Representation to scale of course of vascular bundles in *Rhapis excelsa.* Horizontal dimension expanded 4x.

Quite obviously the first step in understanding long distance transport in a palm stem would be to unravel the innumerable strands and find out how they are interconnected. This is, however, just what the botanist has so far been unable to do.

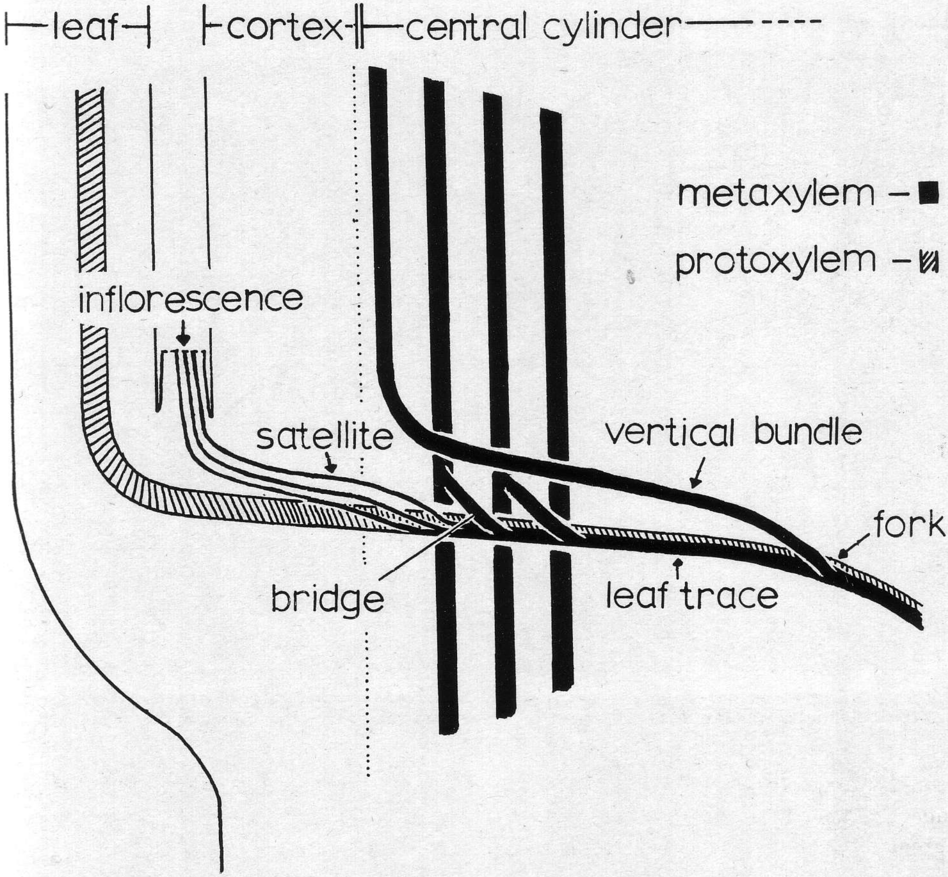
In tackling the problem at first hand, we simplified it in two ways. First we used a small palm, *Rhapis excelsa,* with narrow, cane-like stems 3-4 centimeters in diameter. Even in this small palm one can see about a thousand vascular bundles in a cross-section of the stem. Second we devised a method of using a ciné camera to photograph cut surfaces, either directly or as thin sections seen



68. Diagrammatic representation of course of major and minor bundles going to the same leaf in *Rhapis excelsa.*

through the microscope. Each surface made one frame of the ciné film and a great number of surfaces were photographed in sequence. Ultimately we produced a movie which when projected gave the impression of traveling up or down the palm stem, depending on whether the film was run forwards or backwards. Essentially it was the movie which we analyzed in great detail and which finally gave us the clue to the construction of the *Rhapis* stem. This small palm could have been atypical for palms as a whole, but we have considerable evidence which disproves this and also we are sure that we can ultimately adapt the ciné technique to analyze large stems.

Figure 67 shows the actual path of three of the many bundles we have traced. All bundles behave alike but differ in small quantitative ways. One can follow each bundle more or less indefinitely through the stem. It does not make a straight line. We can only show its outline in one plane in this figure. Actually all bundles describe a uniform, shallow helix, twisting up the stem like a spiral staircase. They are inclined towards the center of the stem as can be shown in Fig. 67, but at regular intervals bend out sharply towards a leaf. As they bend they split, one fork going into the leaf as a "leaf trace." The other fork follows the leaf trace to the periphery of the stem, whereupon it turns erect and once again leans towards the stem center. It is most convenient to refer to this strand as the "vertical bundle" and in terms of growth the vertical bundles continue indefinitely from base to apex of the stem giving off leaf traces at intervals. The basic pattern varies somewhat. One may distinguish, as in Fig. 67, "major" bundles which fork least frequently and reach the cen-

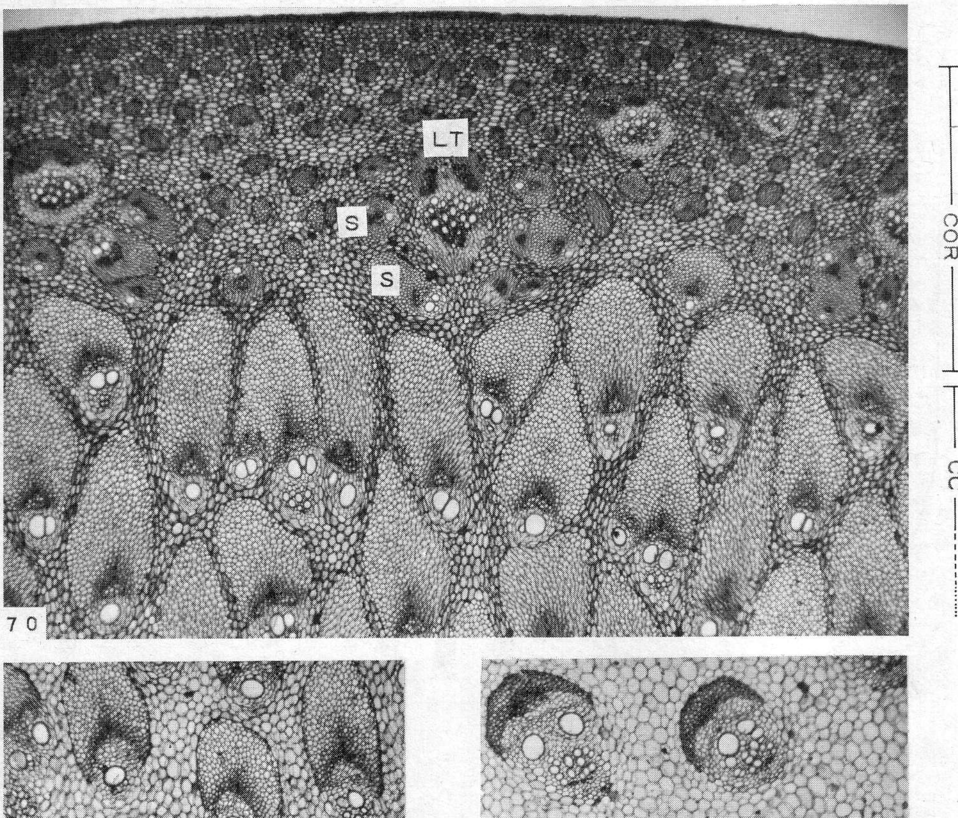


69. Diagrammatic detailed representation of leaf trace complex in *Rhapis excelsa.* Metaxylem (solid black) is that part of xylem which develops later than protoxylem (cross-hatched).

ter of the stem before bending towards a leaf, from "minor" bundles which fork most frequently and move only a little way towards the stem center between each fork. "Intermediate" bundles are common. Each leaf has an encircling insertion and receives several major but more minor and intermediate bundles from around the entire circumference of the stem. This leaf supply bends outwards from the stem at varying heights (Fig. 68) so that there is no plate of leaf-supplying tissue as is so obvious in a vertical section of a corn stem.

The whole arrangement satisfactorally accounts for the crowding of peripheral strands (Fig. 70) since only relatively few major bundles reach the stem center (Fig. 72), although all bundles in turn bend towards the periphery. This crowding is further accentuated because peripheral bundles have well developed fibrous tissue and are wider than central strands (Figs. 70 and 72). Because a palm stem has this peripheral concentration of mechanical tissue, it stands firmly erect. Such an arrangement of strands also explains how fluids are transported long distances through the stem, the leaves supplied by bundles from the main pathway.

Are these strands linked in any way? Experiments suggest that cross-connec-



70-72. *Rhapis excelsa* transverse section of stem (x 40). 70. Peripheral region. 71. Intermediate region. 72. Central region. LT-leaf trace; VB-vertical bundle; S-satellite; B-bridge; F-fibers; PH-phloem; MX-metaxylem; PX-protoxylem; C-cortex; CC-central cylinder.

tions are frequent. Dyes injected via a bore hole spread rapidly above the level of injection. The path of the dye is not a narrow helical band as it would be if there were no cross-connections. Ciné analysis has demonstrated cross-connections and also hitherto unsuspected complexities in the leaf trace (Fig. 69). Beyond the fork which splits off the leaf trace from the vertical bundle, the leaf trace itself gives rise to a number of additional strands, many from major bundles, few from minor bundles. Of the first of these, 1-3 form short "bridge bundles" which link with neighboring vertical bundles. They are the cross-connections suggested by the dye experiments. There are also several (up to 10) narrow branches which we call "satellite bundles" because they cluster around the leaf trace. These satellites do not enter the leaf but pass into the inflorescence. This inflorescence is only developed fully in the upper parts of the stem, but surprisingly in the lower parts, even though there is no external evidence of an inflorescence, satellites are still developed as an anatomical precursor.

From this kind of three-dimensional analysis we now understand the *Rhapis* stem in great detail. We only have to look through the microscope at single sections of other palms, large and small, to see the same sort of features visible in the photographs Figs. 70-72. We can see similar "leaf trace complexes" but are not always sure about the difference between bridges and satellites. These have to be followed in serial sections to be identified with certainty. Nevertheless we are reasonably sure that *Rhapis* is an accurate, small-scale model of all palm stems. Future work with the ciné camera should establish this beyond all doubt.

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The Inflorescence of Nigerian Lepidocaryoid Palms

P. Tuley

The inflorescence of the *Raphia* palm has been described as a terminal raceme with several branches (Tomlinson, 1962; Russell, 1965). In the course of an investigation into the production of *Raphia* wine (Tuley, 1965), the emergence and size of the terminal leaves was found to be of importance when assessing the readiness of the palms for tapping. The number of reduced leaves is always equal to the number of emerging spadices and as there appeared to be a clear relationship between the two, a mature specimen of *R. Hookeri* was felled and the stem apex dissected. On dissection, the inflorescence primordia were found to be separate structures, arising in the axils of the reduced terminal leaves (Figs. 73-76). The development of a typical group of spadices from just