VASCULAR PATTERNS IN PALM STEMS: VARIATIONS OF THE RHAPIS PRINCIPLE

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SOME YEARS AGO, we published our first joint paper on the vascular pattern in the stem of *Rhapis excelsa*, a small ornamental palm of South Florida, native of eastern Asia (Zimmermann & Tomlinson, 1965). *Rhapis* was chosen for our first analyses for quite practical reasons. The plant is not too big and is available in quantity. Its stem contains only about 1000 vascular bundles in a transverse section, and it is relatively easily sectioned. Anyone who has ever attempted to section palm stem tissues knows that most species are notoriously difficult to handle, because their hard resistant fibrous vascular bundles are surrounded by soft, yielding parenchyma.

The choice of *Rhapis* proved very fortunate because the vascular pattern of its stem is relatively simple. Ever since its discovery this pattern has served us as a model for the understanding of the more complicated vascular patterns of other monocotyledonous species.

As soon as the study of *Rhapis excelsa* was well on its way we began to look both at other species of palms and at other families of monocotyledons. So far we have studied, in greater or lesser detail, about 30 species of palms in addition to plants of other families (e.g., *Prionium* (Juncaceae), Zimmermann & Tomlinson, 1968; *Dracaena* (Agavaceae), Zimmermann & Tomlinson, 1969; Pandanaceae, Zimmermann *et al.*, 1974; and others as yet unpublished, members of the Araceae, Bromeliaceae, Cyperaceae, Dioscoreaceae, Flagellariaceae, Smilacaceae, Strelitziaceae, Xanthorrhoeaceae). From a taxonomic point of view this is indeed a small number, but from an anatomical point of view it is an amount of information which could not, with conventional anatomical methods, have been gathered by us within our whole lifetimes. We have so far analyzed, and can at any time review again, over 300,000 transverse images.

During the course of our study a number of basic anatomical principles have emerged, the discussion of which is the purpose of this paper. Some of these principles may have physiological, others developmental significance. At the moment we have too little information to comment at length on the taxonomic significance, although in at least one instance it is clear (Pandanaceae; Zimmermann *et al.*, 1974). For the time being, we merely want to describe the variability of the three-dimensional vascular anatomy of the palm family which we have found so far.

METHODS

A motion-picture technique has been used throughout this study. An overall view is obtained by surface methods, whereby transversely cut sur-

faces of the stem or parts of stem are photographed while held in the micro-tome, usually at axial intervals of 0.1–1 mm. (depending upon the species) over a length of up to 100 cm. (Zimmermann & Tomlinson, 1967b). One m. is the distance from the laboratory floor to the top of the microtome on the bench. Our instrumentation is steadily improving. Specially con-structed microtome clamps permit the continuous advance of the specimen itself rather than the clamp, in contrast to most commercially available sliding microtomes. Focusing of the camera is rather difficult and critical because of the very shallow depth of field in close-up photography. Pre-viously two microscope lamps were used, but this does not give sufficiently bright illumination to allow the camera lens to be stopped down appreci-ably. A brighter light source was found in an electronic flash, constructed for us by the Electronics Design Center of Harvard University. It is used in conjunction with a synchronized Bolex H 16 REX camera and has several special features. A recycling time of 0.5 sec. enables us to work at a normal rate. A long-life flash lamp is necessary because a single film requires the firing of 4,000 flashes. Ordinary electrolyte condensers failed after several thousand flashes; therefore, large storage condensers were necessary. When the light and depth-of-field problems were finally solved, we found ourselves with too much light! As the camera lens is stopped down, theoretical resolution deteriorates. Resolution limits have been calculated for a number of typical settings and we are now careful to balance the light in such a way that we can stop down far enough for maximum depth of field but still make use of the full resolving power of the 16 mm. film, which is of the order of 20–60 lines per millimeter (50–15 μm.), depending on contrast.

In order to analyze large palms (such as *Cocos*) a piece of stem was quarter cut into a (radial) board with a circular saw. This was further sub-divided into two to six "sticks" (or positions) (Figure 1). Each of these positions was analyzed separately. The resulting films were studied by pro-jection onto a white sheet of paper on a table via a mirror, where plots could be made by taking positional measurements of individual vascular strands. Radial and longitudinal magnifications were determined in each case by the appearance, on the screen, of a ruler photographed on the first frame of each sequence, and by the number of frames of each sequence and the sectioned length of stem.

Microscopic details were obtained from sequential photography through the microscope of section series cut on a sliding microtome. Most micro-photography was done with our shuttle microscope (Zimmermann & Tomlinson, 1966). Since the lowest magnification of the M20 shuttle is limited to a width of ca. 5 mm. on the microslide, and we often needed lower magnification for the larger plants, analyses have also been made with the older drawing method (cf. Zimmermann & Tomlinson, 1965) and a specially adapted M5 Wild stereomicroscope. Since the drawing method is a much slower procedure than the shuttle method, we therefore developed, in collaboration with the Brookfield Machine Company, West Brookfield, Massachusetts, a low-magnification shuttle which now enables us to photo-
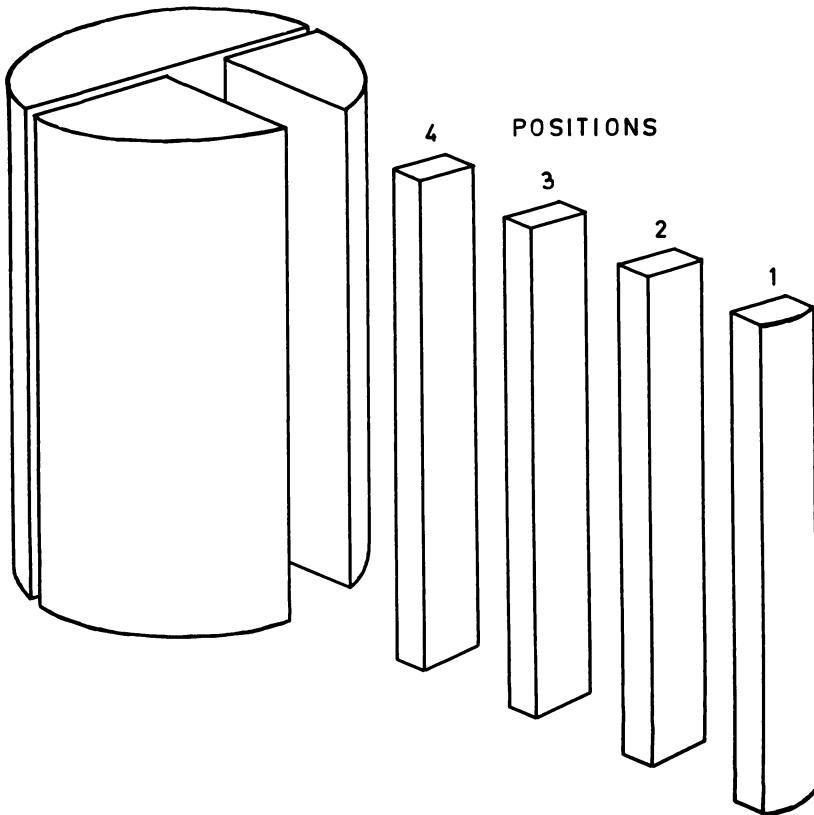
FIGURE 1. Method of dividing a large palm stem into "positions" which are analyzed separately by surface photography.

graph sections up to 24 mm. wide. (This instrument is illustrated on p. 12 in Zimmermann, 1971).

TERMINOLOGY OF THE VASCULAR SYSTEM

It is perhaps useful if we start out with a brief summary of our terminology as we have used it in our earlier papers. Longitudinally running stem bundles are now called *axial bundles* (a term we have substituted for "vertical bundles," which was used in our earliest papers, because axial bundles are horizontally oriented in rhizomes). As we follow an axial bundle distally, it approaches the center of the stem and then reaches a point where it turns out toward the stem periphery and finally enters a leaf. This point of deepest penetration into the stem is regarded as the most distal point of the bundle. Arbitrarily from this point to the level of entry into the leaf, the bundle is referred to as a *leaf trace*. *Major, intermediate*, and *minor* leaf traces (bundles) are distinguished which differ

not only in diameter (major ones being the widest), but also in degree of penetration from surface towards the stem center. Axial-bundle length is measured by number of internodes from one leaf trace to the next, the *leaf-contact distance*, and is usually longest in major bundles.

Structurally the most important feature of monocotyledonous vascular anatomy is the upward-branching of each leaf trace. Normally, one axial bundle is among these branches, though there may be none or more than one. Thus the stem maintains a more or less constant number of vascular bundles as it grows taller. Other types of bundle branch upward from the leaf trace. *Bridges*, up to as many as six, connect the leaf trace with neighboring axial bundles. In the presence of an axillary bud or branch, either vegetative or reproductive, and even if the branch is aborted early during development, there are additional branches of the leaf trace, called *satellite bundles*, or simply *satellites*, connecting the leaf trace with the axillary axis (Zimmermann & Tomlinson, 1972; Tomlinson, 1973).

In addition to the vascular system of the central cylinder which we refer to as the *inner system*, there is a system of fibrous cortical traces which we refer to as the *outer system*. The developmental significance of the two has been discussed recently (Zimmermann & Tomlinson, 1972). Additional fibrous strands are present in certain species among the regular vascular bundles of the central cylinder; these are described under the heading "Fibrous bridges."

We would like to emphasize again at this point that in our descriptions we use a terminology which is descriptive of what one can see in analytical films. We speak of "leaf-trace departure," of bundles that "move," "give off branches," are "borrowed," etc. It does not imply developmental events, or movement, but merely describes what one can see in the projected films.

THE THREE-DIMENSIONAL BUNDLE ARRANGEMENTS

From the outset we were faced with the problem of representing for publication three-dimensional bundle paths in two dimensions. We usually do this by showing all bundles in a single radial plane, regardless of their relative compass orientations within the stem. Description in the text or a complementary plot on a transverse plane was used to help the reader to reconstruct the three-dimensional image in his mind. FIGURE 2 shows the plots of two bundles of *Geonoma* in the conventional radial and transverse views.

In stems of many palms, as one watches surface motion-picture sequences, one can see the central bundles all following a helical path, i.e., they describe a rotating motion clockwise or counterclockwise on the projection screen. This helical path of axial bundles is established early during development (*cf. Figure 1* in Zimmermann & Tomlinson, 1967a) and goes in the same direction as the phyllotactic spiral of the stem. The helical path may be more or less distinct, and in some cases there may be two helices rotating in opposite directions in the central and subperipheral areas of the
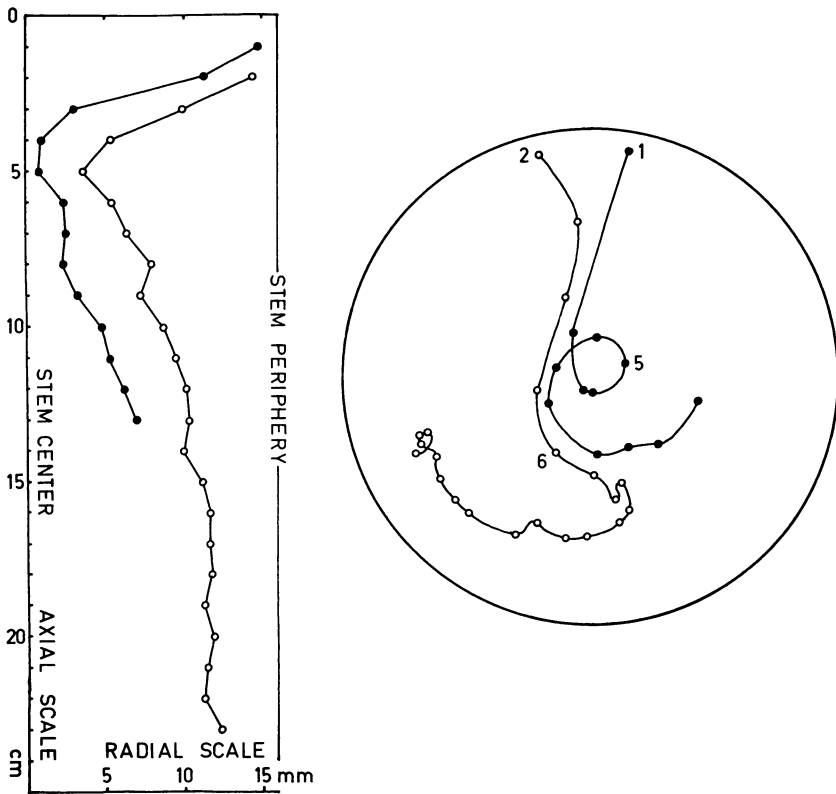
FIGURE 2. The three-dimensional course of two bundles of *Geonoma*. On the left Von Mohl's "double curve" of two vascular bundles along the stem is shown in a radial plane. The plot on the right shows the same bundles and the same points of measurement in axial view, i.e. projected onto a transverse plane. The numbers indicate centimeters on the axial scale. The bundle indicated with dots described two full turns along the inner helix before it left the field of view. The bundle indicated by the circles described a half turn along the inner helix, then a fourth of a turn along the outer (counter-running) helix before nearing the periphery of the central cylinder. Note that the axial scale in the left-hand figure is about 5 times foreshortened.

stem respectively, with only one of them corresponding to the phyllotactic spiral. This is so in *Geonoma* and can be recognized in FIGURE 2.

For reasons of clarity we ordinarily ignore the helical-bundle path and use our conventional two dimensional illustrations in which all bundle positions within the stem are rotated into a single radial plane. In other words positions are given as distances from stem center (or periphery) regardless of compass orientation.

AXIAL BUNDLE CONTINUITY

Perhaps the most important single aspect of monocotyledonous stem anatomy is the pattern that provides the continuity of vascular bundles along the stem. When we started our work with *Rhapis* the question we asked ourselves was why is the stem not depleted of vascular bundles, if of the 1,000 axial bundles in a single transverse section 100 "depart" as leaf traces into each leaf? The answer for *Rhapis* and many other plants, as is now well known, is the fact that each departing leaf trace branches upwardly and thus gives rise to a continuing axial bundle. However, we have subsequently found that this is not the only answer. Furthermore, bundle continuity must be looked at from a functional as well as developmental point of view.

One could regard the continuing axial bundle of the *Rhapis* stem as a single structure from which, at certain intervals, leaf traces branch off, as has been done for dicotyledons (cf. Devadas & Beck, 1972). This makes sense functionally because the continuing bundle consists of metaphloem and metaxylem whereas the leaf trace portion contains only protophloem and protoxylem. Functionally even more important than the axial-bundle branch, at least in a quantitative respect, are the bridges which provide, from each leaf trace, half a dozen or so alternate translocation pathways (Zimmermann, 1973). During later maturation of the stem the axial-bundle branch is often obliterated by weathering of the stem surface if it is located near the stem periphery, and bridges thus provide the only axial continuity because they are more centrally located (cf. FIGURE 3, Type C).

However, from a developmental point of view, the continuing axial bundle cannot be regarded as a continuous unit with leaf traces attached at intervals, because vascular strands differentiate in distinct stages. The leaf trace branches at the periphery of the cap, and as the stem apex grows distally away from the leaf trace, the axial bundle elongates with its proximal end attached to the leaf trace and its distal, growing end in the cap. This elongation continues until the distal end of the axial bundle in the cap is connected with a newly arising leaf trace into a growing leaf primordium. Thus the developing unit is a vascular bundle consisting of an axial bundle and its upper leaf-trace end (Z-Y-X in *Figure 3* in Zimmermann & Tomlinson, 1972). This unit remains discrete for a number of plastrochrones until its distal leaf-trace end branches as it reaches the cap periphery.

SMALL-PALM TYPES

The vascular patterns of small palms so far examined (with stems up to a diameter of about 3 cm.) are all similar to the *Rhapis* type; they differ merely in the position of the axial bundle branch, which can be located anywhere between the stem center and the periphery (FIGURE 3).
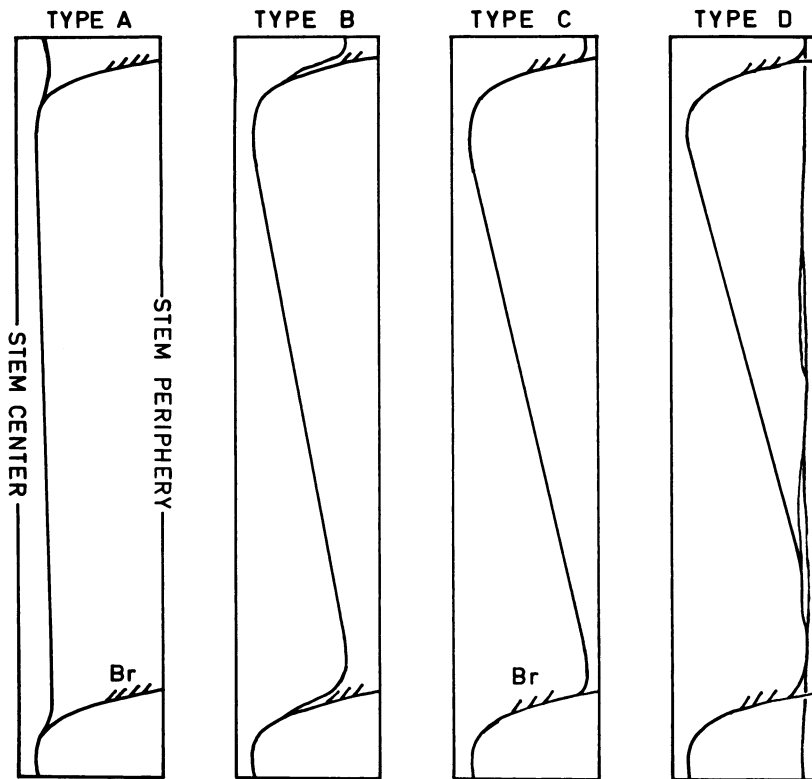
FIGURE 3. Diagrammatic representation of the path of vascular bundles in some small palms. The helical path is ignored, bundle positions are all shown in a single radial plane.

The Rhapis-Rhizome Type (FIGURE 3, Type A). This pattern was first found in the *Rhapis* rhizome and has been illustrated before (*Figure 4* in Tomlinson & Zimmermann, 1966a). The illusion that the leaf trace is merely a branch of the axial bundle is most pronounced in this example because the axial bundle maintains an almost perfectly axial path even in the region of leaf-trace departure. However, even here the developmental sequence indicates that the axial bundle with its distal leaf-trace end develops six plastochrones before the axial-bundle branch (the continuing axial bundle) is initiated (*Figure 3* in Zimmermann & Tomlinson, 1967a). The seeming redundancy of a vascular system in an organ like the scale leaf, which neither assimilates nor has any storage function, underscores the importance of the developmental events which lead to the establishment of the vascular system of the axis.

The Rhapis-Aërial-Stem Type (FIGURE 3, Type B). This pattern has received sufficient attention in numerous publications that we need not describe it further. As in the previous type, the axial bundle is usually developmentally the first, and in the mature stem the most proximal, leaf-trace branch. In a motion picture of transverse sections it can be seen to follow the leaf trace on its way toward the periphery, while numerous additional branches are given off from the leaf trace. These branches are mostly bridges, but at the level where the stem has become reproductive many are also satellites. The axial bundle is left behind near the periphery of the central cylinder; from there it resumes its course up the stem and repeats the cycle. *Bactris major, Chrysalidocarpus lutescens,* and *Hyospathe elegans* are of this type, although they are somewhat different from *Rhapis* in other respects.

The Geonoma Type (FIGURE 3, Type C) differs from the previous one in that the axial-bundle branch is one of the most distal (peripheral) to come from the leaf trace, very near the periphery of the central cylinder. The distinction between Types B and C is somewhat arbitrary; the patterns of *Rhapis* and *Geonoma* are quite similar. The juvenile axis of *Iriartea exorrhiza* is of this type. *Iriartea* is a stilt palm; the diameter of its stem increases from less than one to some 20 cm. over a height of 1–2 meters (see *Figure 6* in Tomlinson, 1961). We have not yet looked at a large-diameter stem.

The Chamaedorea Type (FIGURE 3, Type D). *Chamaedorea* was one of the first genera that we investigated after we had studied *Rhapis*, because the genus contains a number of small, easily obtainable species. It resembles *Geonoma* in that each leaf trace often gives off one, or occasionally two axial bundles near the periphery of the central cylinder. On the other hand, many outgoing leaf traces can be observed in motion-picture sequences, which give off only bridges and no discrete axial bundle. *Chamaedorea* has practically no cortical (fibrous) bundle system. However, the periphery of the central cylinder consists of numerous crowded, small vascular bundles which are quite freely anastomosing (FIGURE 4). As one follows a transverse section series upwards, one can observe that departing leaf traces contribute bridges to this peripheral small "bundle-pool" and that larger, discrete (i.e. nonanastomosing) vascular bundles emerge from this "pool" and continue to repeat the cycle at a higher level. This behavior has also been found in *Desmoncus* and *Ptychosperma*. It has been described before for *Dracaena fragrans* (*Figure 10* in Zimmermann & Tomlinson, 1969).

It should be stressed that there is no sharp distinction between the four types shown in FIGURE 3 and described above. There is a continuous range of patterns from A to D, and any one palm may either resemble a given type closely or be intermediate between two of them. Furthermore, it is possible that the pattern gradually changes with increasing height within a single stem, as is described below in a special section. So far at least, this
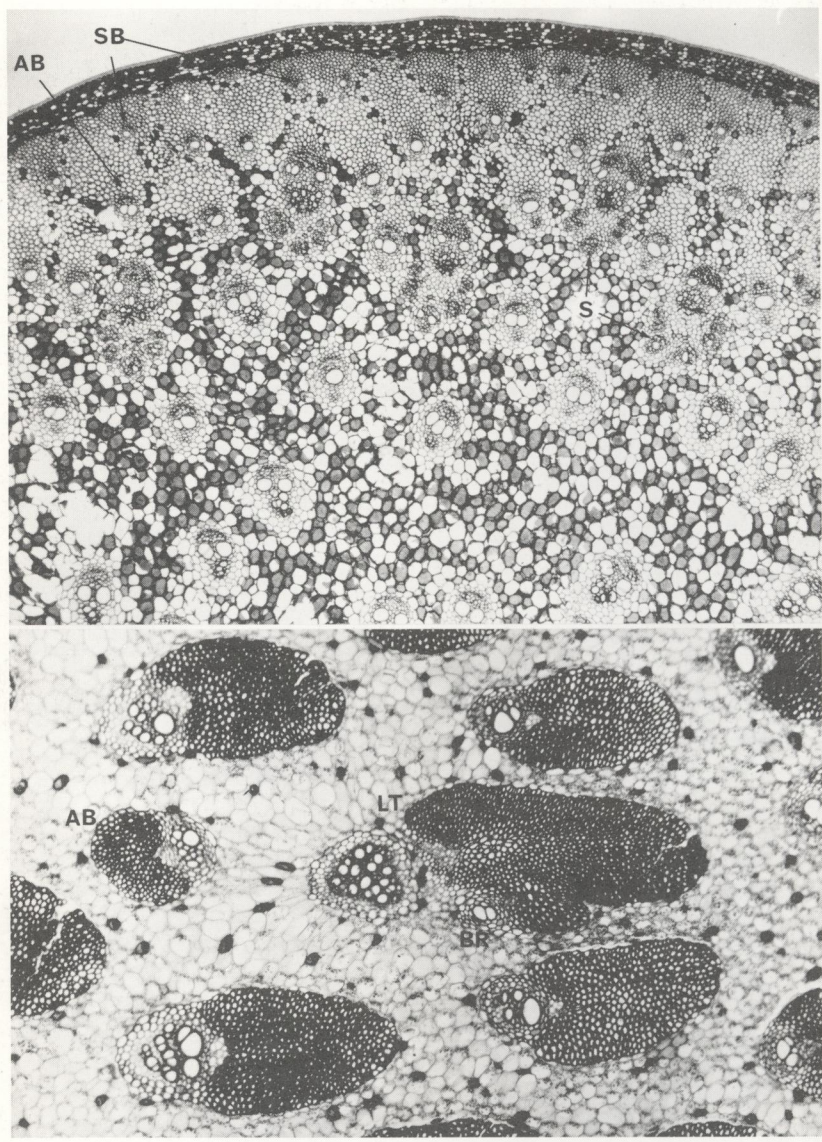
FIGURE 4 (above). Stem transverse section of *Chamaedorea* sp., showing axial bundles (AB) and peripheral, small, anastomosing bundles (SB). Deeply-inserted satellites (S) are seen associated with leaf traces.

FIGURE 5 (below). Detail from stem transverse section of *Nannorrhops ritchiana*. From a single section it is impossible to know whether an axial bundle (AB) associated with a leaf trace (LT) is either a branch of this leaf trace or merely "borrowed." A presumed bridge (BR) can be seen splitting off the leaf trace (LT).

classification of patterns serves the purpose of allowing us to describe the vascular pattern in each new species we investigate.

<div style="text-align:center">LARGE-PALM TYPES</div>

While the patterns in small palm species resemble each other, larger palms (with stems well above a diameter of 3 cm.) do not merely show the *Rhapis* principle in bigger dimensions; their patterns are considerably more complicated. The reason for this is probably functional: the apical region of a large palm could not receive nutrients in as straightforward a way as in small palms simply because the direct distance from mature photosynthesizing leaves to meristem is too great across the immature tissues of the crown region. Although we have not as yet analyzed the developmental pattern of a palm as large as a coconut, we believe that from our knowledge of the structure of a small apex we can make certain extrapolations to the larger ones. It remains to be seen whether this assumption will prove to be correct.

Large palms cannot be analyzed as completely as small ones. Sheer size makes it impossible to follow a bundle, particularly a major one, along its entire leaf-contact distance. With the surface method we can follow bundles over a maximum axial distance of 100 cm. (provided they are not lost to the field of view) as described in the METHODS section. We then have to piece together and intrapolate what we have seen. Even in a relatively small palm like *Chrysalidocarpus lutescens* where we have followed entire leaf-contact distances of minor bundles over distances of about 40 cm., plots of individual parts of major bundles indicate that leaf-contact distances of major bundles may be as long as 2 meters or more (FIGURE 7). Nevertheless, the necessarily incomplete analyses which we have so far carried out have provided a wealth of information for comparative purposes.

The Phoenix Type. The central part of aërial stems of a number of species show a vascular pattern of the Type A as illustrated in FIGURE 3. This was first found in the two *Phoenix* species we analyzed (*P. roebelenii* and *P. dactylifera*) and involved major as well as intermediate bundles (FIGURE 6). It was further found in a number of other palms, namely *Acoelorrhaphe* (*Paurotis*) *wrightii, Sabal palmetto, Washingtonia filifera,* and others, but here only in major bundles, i.e., only in the very center of the stem. The plotted course of some central (major) bundles of *Phoenix roebelenii* is shown in FIGURE 6. As a consequence of this branching pattern axial bundles run much more nearly axis-parallel than in the other types. A comparison of Type A with Types B–D (FIGURE 3) makes this clear.

It is interesting to note that Hilgeman (1951) had recognized this phenomenon in *Phoenix dactylifera* and therefore concluded that Von Mohl was incorrect in his classic description of a "double curve" for monocotyledonous stem bundles (i.e. the bundle path as shown in FIGURE 2). We know now that Von Mohl (1824) was not wrong. The double curve is

practically always present as FIGURE 6 shows; it is merely less pronounced in the one species investigated by Hilgeman.

Although all leaf traces show numerous bridges, intermediate and minor bundles (in *Washingtonia* and *Sabal*) and minor bundles (in *Phoenix*) do not show any leaf-trace-axial-bundle branch. This observation leads to a consideration of the next type.
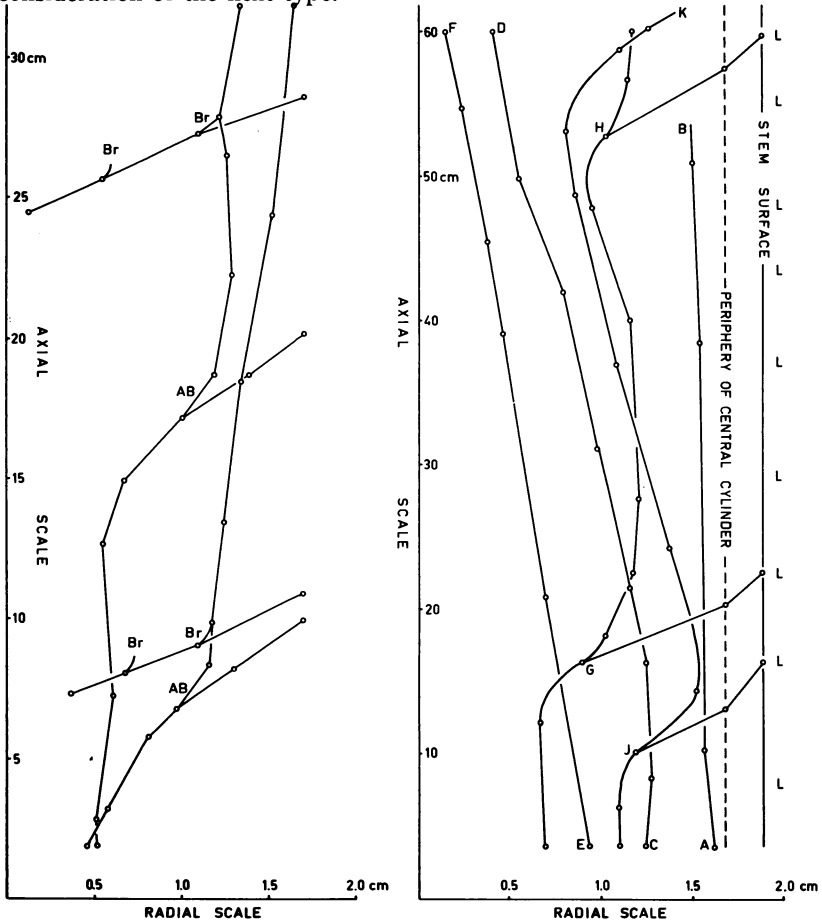
FIGURE 6 (left). Intermediate position in the stem of *Phoenix roebelenii* showing plots of two different leaf-trace-axial-bundle branches (at AB), and bridges to these axial bundles from other leaf traces (Br). Note that the position of the radial scale is arbitrary, neither periphery nor center of the stem are in the field of view. The axial scale is foreshortened about six times.

FIGURE 7 (right). The peripheral stem region of *Chrysalidocarpus lutescens*. Leaf insertions are indicated by (L) along the stem periphery. One complete leaf contact is shown for a minor bundle (G–H); it is six internodes long. Another minor leaf contact (J–K), eight internodes long, is almost complete. Axial-bundle portions A–B, C–D, and E–F indicate that the leaf-contact distance of major bundles must be very long (two or three meters). The stem center is outside the field of view. The axial scale is foreshortened about 12 times.

The Regeneration Type. Palms like *Phoenix* and *Sabal* puzzled us because we could not see any axial bundle branch off the intermediate and minor leaf traces. As one follows a transverse-sectional series up the stem, leaf traces continuously depart and bundles are thus lost from the stem. In careful study of the peripheral area in which, we were certain, must lie the answer to this puzzle, it was discovered that, going up, the axial bundles are continuously "replenished" by fibrous cortical bundles "drifting" from cortex to central cylinder and becoming vascular (axial) bundles. When followed on their way up, these replenishing bundles appear initially very small as they enter the central cylinder, but quickly enlarge into fully fledged vascular bundles as they receive bridges from departing leaf traces. We may define these cortical bundles as inner-system bundles (Zimmermann & Tomlinson, 1972). It took some time (and thousands of sections!) before the proximal ends of these fibrous bundles were found. The inner system seems to be regenerated from the outer one, in a manner comparable to the establishment-growth phase of *Dracaena fragrans* which we have already described (Zimmermann & Tomlinson, 1970). There is a regular network of outer fibrous (and phloem-containing) bundles (i.e. outer leaf traces) in the outer cortex with which axial bundles are in contact via inner fibrous cortical bundles (FIGURE 9). The Regeneration Type is very common in large palms such as *Cocos, Elaeis, Phoenix, Roystonea, Sabal, Washingtonia*, etc., but we have also observed it in the basal part of the stem of *Chrysalidocarpus lutescens*. In *Bismarckia* we found it in spite of the fact that almost all leaf traces (even minor ones) have an axial bundle branch. However, many of the peripheral axial bundles are lost to the inflorescence (see the section on BORROWED AXIAL BUNDLES).

In *Chamaerops humilis, Elaeis guineensis*, and other palms, we have seen fibrous axial bundles branching from minor leaf traces in the inner cortical region, just outside the central cylinder. Followed in an upward direction these fibrous bundles enter the central cylinder where they become regular vascular axial bundles by receiving bridges from outgoing leaf traces (FIGURE 9, at C).

It must be emphasized that these axial-bundle origins which we have described are not very distinctly different from each other. In fact, there is a rather continuous range of ways in which the axial bundle can be derived from lower traces. The structural interrelationship may be expressed as follows, for descriptive, comparative purposes (Types A–D as illustrated in FIGURE 3, Regeneration Type in FIGURE 9):

Type A $\longleftrightarrow$ Type B $\longleftrightarrow$ Type C $\begin{array}{l}\longrightarrow \text{Type D}\\ \longrightarrow \text{Regeneration Type}\end{array}$

This is intended to suggest that any one type can be regarded as a modification of another.

Any one palm can be assigned a region along this continuous range of possibilities. Thus *Chamaedorea* species, for example, are actually most often intermediate between the *Chamaedorea* (D) and the *Geonoma* Type
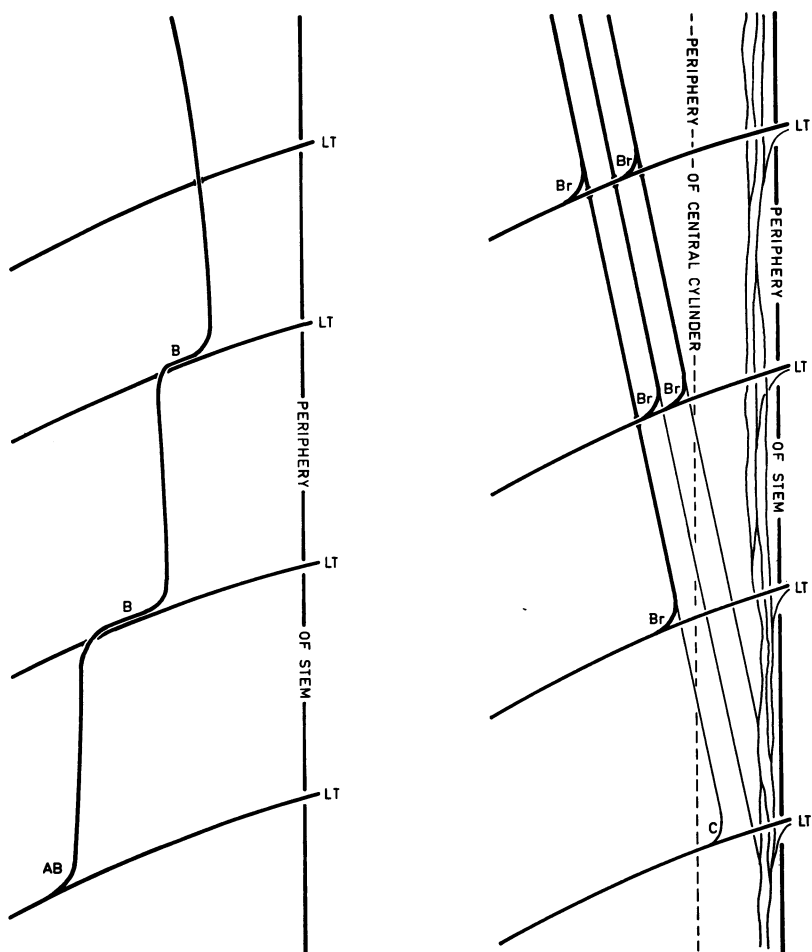
FIGURE 8 (left). The principle of a "borrowed" axial bundle shown in a radial plane. An axial bundle branches off a leaf trace (at AB). Higher up in the stem it closely follows other leaf traces on their path toward the stem periphery (at B). LT = leaf trace.

FIGURE 9 (right). The principle of regeneration of the inner from the outer system shown in a radial plane. From the network of fibrous bundles and fibrous leaf traces near the stem periphery (thin lines, the outer system), fibrous bundles enter the central cylinder in a distal direction. By receiving bridges from outgoing leaf traces (at Br), they become regular, xylem-containing axial bundles. In some cases fibrous axial bundles are given off the leaf trace in the cortical region (as indicated at C). These also enter the central cylinder and become axial bundles by receiving bridges from outgoing leaf traces. Each leaf insertion is shown with one inner and one outer leaf trace at LT.

(C). *Phoenix, Sabal,* and *Washingtonia* occupy two regions along this continuous scale. The stem center is of the *Rhapis* Rhizome Type (A), whereas the periphery is of the Regeneration Type.

Borrowed Axial Bundles. A further complication of the pattern of leaf-trace-axial-bundle branching is shown diagrammatically in FIGURE 8, a very common type in large palms. As one follows a leaf trace acropetally one can see the axial bundle branching off at the point where it begins to turn toward the periphery (FIGURE 8, AB). On its way up, the axial bundle can be seen to follow closely another, unrelated leaf trace for a short distance, but it is left behind again. It may do this repeatedly. Thus it may eventually reach a point nearer the periphery of the central cylinder whence it gradually regains the stem center again (upper part in FIGURE 8). In our working jargon, we call this a "borrowed" axial bundle. Axial bundles which are borrowed, i.e., follow unrelated leaf traces, have no vascular contact with them. In a single transverse section such grouping of a leaf trace and an axial bundle looks conspicuous (FIGURE 5) and only three-dimensional analysis shows whether the axial bundle is actually a branch of the leaf trace or is merely "borrowed." As an example, a plot of the paths of two "borrowed" axial bundles is shown in FIGURE 10. The possible developmental significance of borrowed bundles is discussed further below.

It may be added that the "borrowing" of axial bundles can take place to a variable degree. It is very pronounced in many palms such as *Cocos nucifera, Chamaerops humilis,* etc., or there may be only a slight tendency for it in smaller palms such as *Chrysalidocarpus lutescens* where it is easily overlooked.

BRIDGES

The presence of bridges, i.e. upwardly-directed branches of the leaf trace connecting with neighboring axial bundles, is one of the most constant features of monocotyledonous vasculature as we have observed it in representatives from a wide range of families (information largely unpublished). About 2 to 6 bridges usually come off each leaf trace. These are often very short, such as in *Dracaena fragrans* (Zimmermann & Tomlinson, 1969) or the peripheral region of *Geonoma.* A departing leaf trace in that case almost touches the neighboring axial bundle at the point where vascular contact is made via a bridge. Bridges are often longer, i.e. one to several millimeters, and then link bundles more remote from each other.

From a functional point of view, bridges are of considerable importance, because they provide alternate axial as well as lateral pathways of translocation (Zimmermann, 1973). In palms of the type described under the heading "Regeneration Type," where direct axial branches from leaf traces are missing, they are indeed the only means of providing axially continuous pathways. This is also true, as we have mentioned, in palms with very peripherally located axial bundle branches when the old stem periphery, as often happens, weathers away.

ANASTOMOSING BRIDGE SYSTEMS

In certain cases, bridges are quite long. As one watches such a bridge in a transverse-sectional series in acropetal direction, one gets the initial impression that one is following an axial bundle which has branched from the
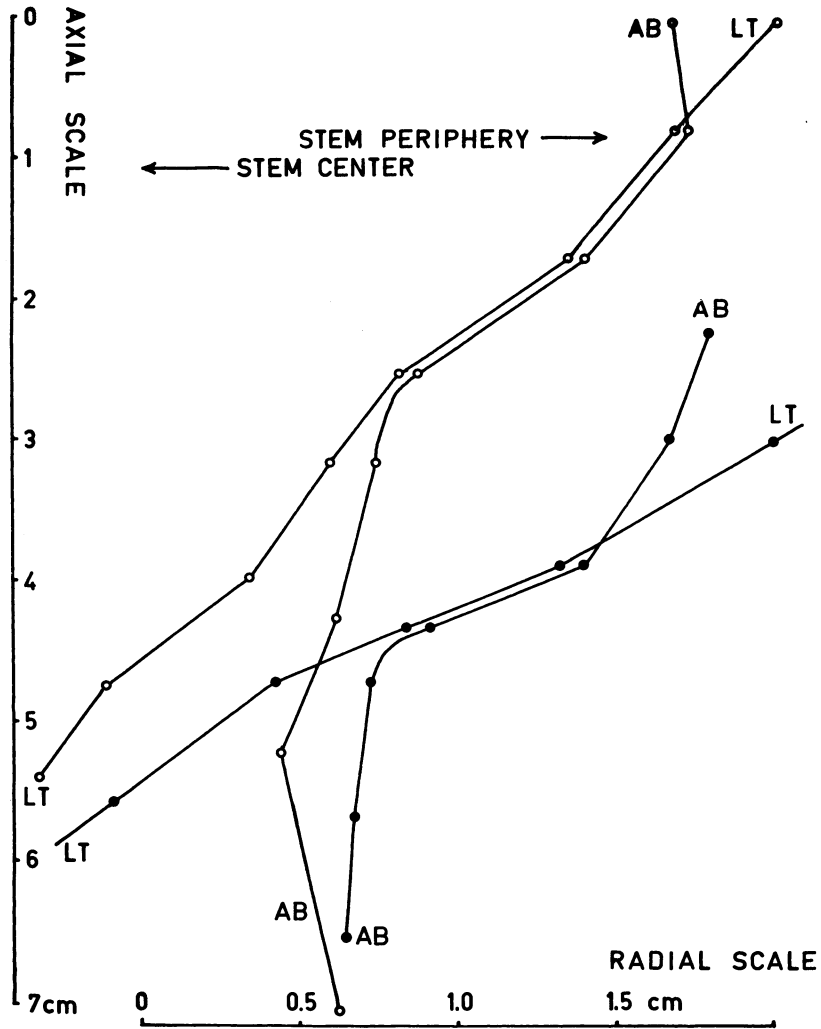
FIGURE 10. Parts of the paths of two leaf traces in an intermediate position of the stem of *Arecastrum romanzoffianum* plotted on a radial plane. Neither the stem periphery nor the stem center are in the field of view. The radial scale is in an arbitrary position. Along each leaf-trace path (LT) an unrelated axial bundle (AB) is shown to run closely parallel. This is referred to in the text as "borrowing." Note that the axial scale is foreshortened about two times.

leaf trace. As one continues to follow the course of this bundle further, it may then finally fuse with a neighboring axial bundle and thus manifest itself as a bridge. This has been found in the *Rhapis* rhizome (Tomlinson & Zimmermann, 1966a, p. 310). In other cases numerous long bridges come off the leaf trace and anastomose freely among each other; some of the branches fuse with neighboring axial bundles, others may become independent axial bundles. This was first found in the juvenile axis of *Rhapis* (Tomlinson & Zimmermann, 1966b). Anastomosing bridge systems are quite common in larger palms such as *Cocos* and *Nannorrhops*.

FIBROUS BRIDGES

Vascular tissues of bridges are usually similar in their appearance to those of vascular bundles, thus indicating that they are regular pathways of transport. The chief difference is mechanical, since axial bundles have a much greater development of fibrous sheathing tissue. Indeed the functional significance of bridges, i.e. their full transport capacity, has recently been confirmed in an experiment in which ^{14}C sugar has been found to move freely from bundle to bundle via bridges (Zimmermann, 1973).

In other cases, bridges are very small and consist only of a fibrous strand, sometimes with a phloem center. We interpret these fibrous bridges tentatively as vascular strands which are functional only during earlier stages of stem development and cease to function as transport channels as the stem matures. Such bridges are found occasionally in some species, but in others they are a regular feature. In the central part of the *Geonoma* stem, for example, there is a regular anastomosing fibrous bridge system. Some of these bridges have a central phloem core and it is not known whether these are still functional in sugar transport in the mature stem.

If, in a single stem transverse section, small fibrous strands are seen among the regular vascular bundles, these may be fibrous bridges as in the center of the stem of *Geonoma* and the basal part of *Cocos*. In other cases small fibrous strands, although continuous, do not seem to be connected with the vascular system of the stem. In *Bactris major*, for example, single stem transverse sections show numerous fibrous strands among the vascular bundles. In spite of considerable effort to elucidate their significance in analyses of the mature stem as well as the apical region, it has not yet been possible to find their relation to the vascular system of the stem.

VASCULAR CONNECTIONS BETWEEN STEM AND AXILLARY INFLORESCENCES

SATELLITES

Most palm species begin to produce axillary inflorescences only after they have reached a certain height (the "reproductive phase" of growth, Tomlinson, 1964). If one studies the vascular system of the stem in prior phases, one can see anatomical evidence of inflorescence vestiges at a height below

the point where flowering actually begins. This evidence within the stem consists of many leaf-trace branches which are additional to the regular axial-bundle continuity and the bridges. These additional branches can be seen to follow the leaf trace to the stem periphery and then enter the axillary shoot (e.g., *Figure 6* in Zimmermann & Tomlinson, 1965). These are present even if the inflorescence does not continue to develop into an externally visible organ. Because these branches surround the leaf trace in the manner of a halo in section, we have called them satellite bundles (cf. *Figure 9* in Zimmermann & Tomlinson, 1965).

BORROWED SATELLITES, AND DEVIATION OF AXIAL BUNDLES

In many species, such as *Chamaerops humilis* in which borrowing of axial bundles is common, satellites are also borrowed. In ascending motion pictures of the stem one can see in the peripheral region satellites diverging from the leaf trace. Some of these may be left behind as the leaf trace enters the leaf, i.e., they do not irrigate the inflorescence in the axil of the supplied leaf, but they subsequently follow another leaf trace to the stem periphery, i.e., they enter a more distal inflorescence. This is a phenomenon very similar to the borrowing of axial bundles which has been described before in this paper.

In many cases, one can see a large number of peripheral axial bundles leaving the central cylinder to enter the axillary inflorescence, following a leaf trace in a satellitelike manner. This is well seen in *Serenoa repens*. These redirected axial bundles (minor bundles in all cases) must have been rerouted very early during development as a small portion of the meristematic cap of the main axis forming the cap of the axillary shoot. The developmental timing of these events has been explained and illustrated in one of our recent papers (*Figure 5*, region B, in Zimmermann & Tomlinson, 1972; illustrated also in Tomlinson, 1973).

DEEPLY INSERTED SATELLITES

As one follows leaf traces down into the stem in *Chamaedorea, Arecastrum romanzoffianum*, etc., one frequently sees that they are followed (on the inside) by a number of small satellites which do not fuse with the leaf trace until several internodes below the leaf insertion. In some cases, such as in *Bactris major*, and *Caryota mitis*, these are in part real satellites (i.e., attached to the leaf trace at their lowest extremity), and in part "demand-type" bundles which finally fuse with neighboring axial bundles (such as develop in region D, *Figure 5*, Zimmermann & Tomlinson, 1972). In *Geonoma* they are borrowed satellites, originating from the fibrous anastomosing bridge system of the stem center. In *Cocos* the borrowed satellites are regular bundles. These facts serve to illustrate the diversity of methods by which lateral inflorescences are irrigated in palms.

VARIATIONS OF STRUCTURE WITH HEIGHT IN STEM

To anyone familiar at all with the internal structure of the stems of palms, quantitative variation in gross anatomy at different heights in a single stem is obvious and considerable. Differences in vascular-bundle density, the average diameter of individual bundles, the extent of the fibrous sheath associated with each bundle, and the amount of cell wall lignification are evident when single transverse surfaces at different heights are compared. In *Chrysalidocarpus lutescens*, for example, the vascular-bundle diameter was found to be of the order of 0.8 mm. and the bundle density 50 per cm.^{2} at 20 cm. above ground, while near the top of the stem, at 120 cm. above ground level, bundle diameters were 0.4 mm. and the density 300 per cm.^{2}. The difference in bundle diameter appeared to be primarily due to a more fully developed fibrous sheath at the base, and the lesser bundle density at the base partly to a thickening of the stem by expansion of the ground parenchyma during stem maturation. Measurements of cell sizes also show differences at different heights. Vessel-element length shows distinct trends in *Sabal palmetto* (Tomlinson & Zimmermann, 1967) which are to a large extent paralleled by sieve-tube-element length (Parthasarathy & Tomlinson, 1967). This published work is supported by additional unpublished records for several species and other cell types (e.g., fiber length). In *Washingtonia*, for example, average vessel-element length at the base of the stem may be five times that in mature tissue close to the top of the tree. The question has already been asked — is it possible to find more than one vascular pattern in a single axis?

Some effort to provide an answer to this question has been made with *Cocos* by means of surface analyses of the stem of an eleven-meter-tall trunk at one and ten meters in height respectively. Considerable uniformity was found to be imposed on the more obvious dimensional trends. Thus, regeneration of the inner from the outer system, as well as anastomosing bridge systems were found at both heights. Satellites, expectedly absent at the base in view of the lack of inflorescences at the lower nodes, were numerous at ten meters in height, with bundle borrowing very common. One of the differences in stem transverse sections at different heights is the presence of numerous fibrous bundles among the vascular strands in the central cylinder at the base of the stem. These have been found to come off distally from every departing leaf trace and thus represent a fibrous bridge system. Their distal ends disappear from view on the surface film and will have to be followed in serial section in the shuttle microscope. We intend to publish these findings in detail elsewhere.

A difference in three dimensional structure at the two heights in *Chrysalidocarpus* has been mentioned before: 20 cm. above ground, the stem shows a distinct regeneration type (i.e. no axial-bundle branches), while in the distal part of the stem (50 cm. above ground and higher) a very distinct *Rhapis*-type structure is observed.

A systematic investigation of structural differences of different heights

was not intended to be the topic for this paper; this may be done in greater detail in the future. However, at the present, we know enough to make us very cautious in attaching taxonomic significance to differences found in various species. It should also be a warning to paleobotanists dealing with palm stems. It is easy to assign fossil stem fragments to different species even if these fragments originated from a single individual stem!

DISCUSSION
DEVELOPMENTAL INFERENCES

In an earlier paper we introduced the concept of an inner and an outer vascular system in monocotyledons (Zimmermann & Tomlinson, 1970). This concept is based upon the pattern of development in the meristematic crown; it has been described in general terms in a more recent paper (Zimmermann & Tomlinson, 1972). According to this concept, all vascular bundles of the central cylinder in *Rhapis* are inner bundles, all fibrous cortical strands are outer bundles. This distinction can be made because the former develop from the meristematic cap, the latter outside the cap; the situation in *Rhapis* is relatively simple.

Results discussed in the present paper add a complication. When, as in *Chamaerops*, axial bundles branch off the leaf trace as fibrous bundles in the inner cortical region, we could consider this cortical fibrous-bundle region as belonging to the inner system. The same would have to be said for the Regeneiation Type. In other words, only the very outermost cortical fibrous-bundle region would then be part of the outer system.

On the other hand, we could say that only vascular bundles, i.e. the xylem-containing bundles of the central cylinder, are derived from the cap. Since the question is one of defining the cap region in the meristematic crown, it is, therefore, really only a semantic one. Therefore we would like to leave it open until we know more about developmental patterns in larger palm crowns.

We have not yet investigated the Regeneration Type during its course of development. From the mature structure we infer that the inner, fibrous cortical bundles, originally procambial and then protophloem strands, regenerate the cap (the future central cylinder) from the outer system. Evidently their functional life terminates early during development, but not before their developmental and functional role has been taken over by bridges from developing leaf traces. It is hoped that the developmental pattern of this type can be studied in the future. It will not be an easy task because very large apical regions will have to be analyzed microscopically.

We do not yet know the developmental significance of "borrowing." However, there is some similarity of this structure with the arrangement of the inverted bundles in the Pandanaceae (Zimmermann *et al.*, 1974). In Pandanaceae it is the proximal parts of axial bundles which run closely parallel (and inverted) along more distal parts of other axial bundles. The overall pattern appears similar in "borrowed" bundles where proximal axial-bundle ends run parallel to other leaf traces. The "borrowed" bundle

is often also inverted, but in a different way, depending on the species, the xylem of the borrowed bundle in some cases facing the xylem of the leaf trace (cf. FIGURE 5). The developmental pattern of bundle formation of the Pandanaceae has been worked out (Zimmermann et al., 1974) and it remains to be seen whether the "bundle borrowing" in palms is due to a similar developmental sequence of events.

FUNCTIONAL INFERENCES

There may be a functional difference between the vascular patterns of the Type A and B–D respectively (FIGURE 3). The apical region of the aërial stem of *Rhapis* is almost certainly fed directly from the mature leaves, i.e., from the stem periphery near the apical region, whereas the rhizome apex must be fed axially from behind because the rhizome bears only non-photosynthesizing scale leaves. It is possible that vascular differentiation is influenced by the origin of nutrient supply. This would mean that the central apical region of larger stems (such as *Phoenix, Sabal,* and *Washingtonia*) is fed in an axial direction from below, while the peripheral regions are fed from current photosynthate of mature leaves in a more radial direction. This would make sense because in large stems the apical region of enclosed (i.e., unilluminated and therefore assimilate-importing) leaf primordia is separated from the green, photosynthesizing leaves by very large areas of meristematic tissue. Even though the path of movement across this meristematic tissue is the shortest, it may be useless because long-distance phloem transport can go only through mature vascular tissue. The central part of the apical region might, therefore, be fed not via the shortest, but rather via an indirect route from old leaves deeply down into the stem, and from there axially up via *Phoenix*-type major axial bundles.

TAXONOMIC SIGNIFICANCE

In view of the small number of species examined so far, it is appreciated that any comment about the taxonomic significance of our findings is likely to be premature. In addition, we have suggested that some of the patterns we have described relate to the size of the trunk; this is implied in the distinction we make between bundle types in large- and small-stemmed palms. In other cases (e.g., *Chrysalidocarpus*) we have found significant differences in a single stem at different heights.

However, we have shown elsewhere (Zimmermann et al., 1974) that members of the family Pandanaceae do have diagnostically useful features of stem anatomy which are related directly to the 3-dimensional course of vascular bundles. We already have some indication that a similar construction may occur in certain Araceae and can suggest that the features which categorize the *Pandanus* type of vasculature may represent variants of developmental principles which operate in other large woody monocotyledons. Furthermore, we know that in Strelitziaceae and Zingiberaceae outer bundles contain xylem (cf. *Figure 6* in Zimmermann & Tomlinson, 1972). Within the Strelitziaceae, a very natural group, the same pattern of inner-

bundle grouping is suggested by our preliminary examination of its three constituent genera, *Phenakospermum*, *Ravenala*, and *Strelitzia*. Thus the possibility exists that interfamily relationships may be revealed by this type of analysis.

In the Palmae itself we have suggested that the *Phoenix* Type (which occurs in several genera) may be related to the method of irrigation of the meristematic crown. Even so, within the genus *Phoenix*, in stems as divergent in size as those of *P. dactylifera* and *P. roebelenii*, the constructional pattern is identical. Furthermore, where we have examined several species of a genus, the range of variation seems small, e.g., several species of *Chamaedorea* show the *Chamaedorea* principle and several of *Geonoma*, the *Geonoma* principle.

Our present position can be summarized by saying that it is unlikely that this method of analysis will provide much evidence for taxonomic interrelationships, except where taxa of high rank are concerned. But information at this level may be very significant and the possibility of establishing interfamily relationships is continually borne in mind as further analyses are made.

SUMMARY

The variety of vascular patterns in stems of different palm species is described as a series of types. In the *Rhapis*-Rhizome Type the axial bundle branches off the leaf trace at the point of leaf-trace departure, in the *Geonoma* Type at the very periphery of the central cylinder. In the *Chamaedorea* Type only a few of the leaf traces give off a discrete axial bundle. At the same time all leaf traces contribute, via bridges, to a peripheral "pool" of small, anastomosing vascular bundles from which axial bundles come off distally toward the inside. Large palm stems are more complicated. In some cases (e.g., *Cocos*) axial bundles branch off the leaf trace at the point of leaf-trace departure. These axial bundles then follow other, unrelated leaf traces towards the periphery of the central cylinder ("borrowing") whence they resume their distal course, regaining the center. In *Phoenix*, *Sabal*, and *Washingtonia*, major bundles (i.e. those of the stem center) are *Rhapis*-rhizomelike, while minor bundles originate from the cortical fibrous strands. In many large palms the lower ends of most vascular bundles are continuous with fibrous cortical strands (Regeneration Type).

Bridges, i.e. upwardly-directed branches of the leaf trace, distally fusing with neighboring axial bundles, are the most constant feature of monocotyledonous vascular anatomy. Variations of the pattern of bridges, and the patterns of vascularization of the axillary inflorescence are described.

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