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Observations on Diameters of Vessels in Stems of Palms

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Abstract

Diameters of the wide vessels of metaxylem were measured in axial bundles in the central part of the stem of 166 species of palms. Relative to the diameter of the stem and the diameter of the petiolar vessels, the vessels in the stem tend to be widest in the lianoid species, narrowest in the rhizomatous species, and intermediate in the erect-stemmed species. Among the erect-stemmed palms within the various taxonomic groups, the most slender species have the narrowest vessels. Diameter of vessels is not generally related to form of perforation plates except that the small, slender species with erect stems tend to have the narrowest vessels and the most primitive perforation plates within their respective major groups.

Introduction

Vessels are the principal conduits of water in palms.[2] The physical dimensions of vessels are significant regarding the physiological characteristics of water conduction (Zimmermann, 1978). This paper presents observations on the diameters of the wide[3] vessels of metaxylem in the stems of palms (Fig. 1). The data originally composed part of a larger study on the form of vessel elements in palms (Klotz, 1977). Tomlinson (1961, unpublished data) and Mahabalé (1959) have also produced data on diameters of vessels in stems of palms, but they did not sample as many species or examine the data in the same way as does the present study.

Materials and Methods

Diameters of vessels were measured in stems of 166 species of palms representing all but one of the major taxonomic groups (Moore, 1973).[4] A piece from one stem constituted the sample in most of the species. The measurements were obtained from transverse sections made with razor blades or a sliding microtome. The sample was taken within the central one-third of the diameter of the stem except in a few species in which only the peripheral two-thirds of the stem were available for study. These specimens were sampled as near to the interior of the stem as possible, for the diameter of the vessels decreases toward the periphery of the stem (P. B. Tomlinson, unpublished data). The position of the sample along the length of the stem was usually not known, but the middle of the length

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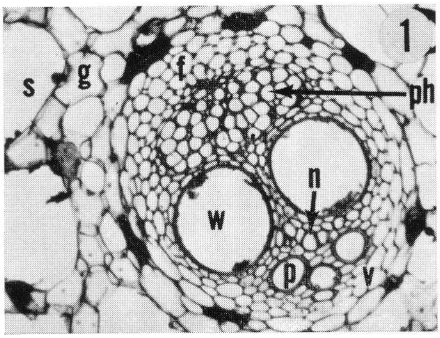
[2] One species (*Ammandra decasperma*) possibly has only tracheids in its rhizomatous stem but is nevertheless included in the present tabulations.

[3] In the vascular bundles of palm stems, one or more vessels of the metaxylem are markedly wider than the other tracheary elements (Fig. 1). The former are here termed "wide" and the latter, "narrow."

[4] A list of the species examined is available with author citations and collection data (Klotz, 1977). Stems of the borassoid major group were not available at the time of the study.



1. Vascular bundle from central part of stem of *Mauritiella pacifica.* Two wide vessels in metaxylem. Debris adhering to their walls possibly remnants of their protoplasts. × 52. Explanation of details: *f*, fibers; *g*, ground parenchyma; *n*, narrow tracheary elements of metaxylem; *p*, tracheary element of protoxylem; *ph*, phloem; *s*, intercellular space; *v*, parenchyma of vascular bundle; *w*, wide vessel of metaxylem.

was selected where possible.[5] The range of the diameters of the vessels in each species was based on 10 or more wide vessels from the sample of the stem. The choice of the vessels to be included in these ranges was necessarily somewhat subjective. Only vascular bundles of comparable form and size were considered—i.e., the large axial bundles (Zimmermann and Tomlinson, 1974). The measurements include the thickness of the cell wall and were made to the nearest 0.01 mm across the maximum diameter of the wide vessels, which usually are approximately circular in transverse section. The ranges of the samples varied from 0.02 to 0.16 mm. The mean of the ranges was 0.06 mm, with a standard deviation of 0.03 mm. The midpoints of the ranges constitute the data in this paper and are intended to indicate collectively the general trends of diameters of vessels in palms rather than to represent valid estimates of the characteristic diameters of vessels for individual species.[6, 7]

Results and Discussion

Diameters of the wide vessels of metaxylem in stems of palms show relationships with the habit of the species. Scatter diagrams of diameter of vessels plotted against diameter of stems show that most of the lianas have wider vessels relative to the diameter of the stem than are found in the other habit categories

[5] The diameter of vessels can vary along the length of the stem, but no consistent pattern of variation has been observed (L. H. Klotz, unpublished data; P. B. Tomlinson, unpublished data). However, in the larger palms examined, the vessels tend to be wider toward the middle of the stem than toward the basal or apical ends.

[6] The midpoint differed from the mean on the average of 0.005 mm in samples of wide vessels from various organs where a mean of 10 or more measurements was obtained (Klotz, 1977).

[7] Klotz (1977) examined different collections of two of the same species investigated by Mahabalé (1959) and 10 of those investigated by Tomlinson (1961, unpublished data). The data of Klotz (1977) agree to the nearest 0.1 mm with those of the other authors.

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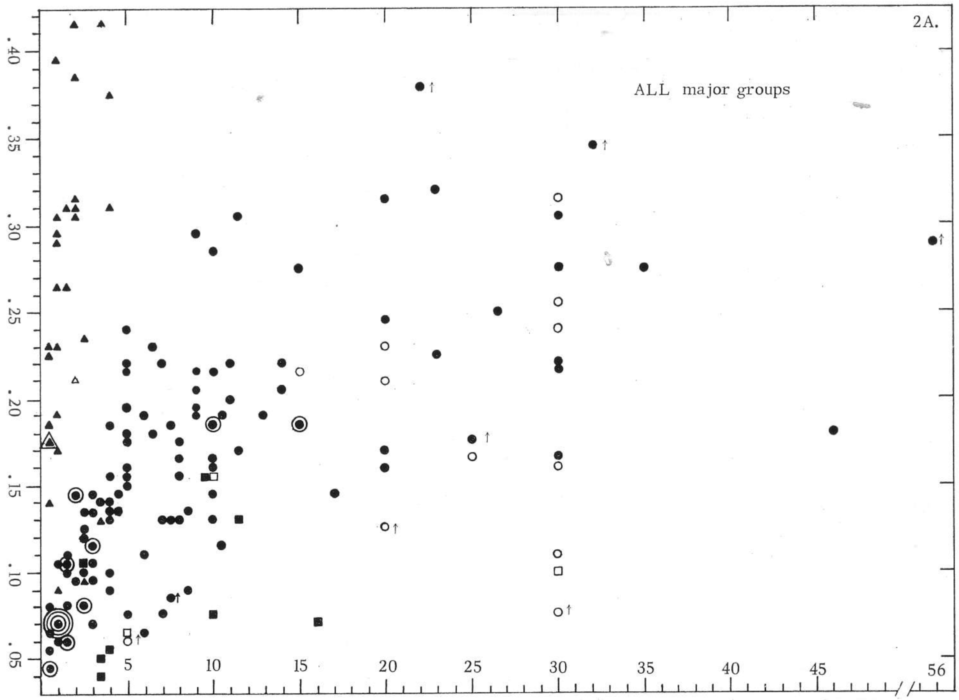
2A–2H. Diameters of wide vessels of metaxylem: Midpoints of ranges (in millimeters) on vertical axis plotted against respective diameters of stems (in centimeters) on horizontal axis. Circles = erect stems. Triangles = scandent stems (lianas). Squares = rhizomatous stems. Concentric circles and triangles = two (in one case, four) coincident points on the chart. Solid markers (and open markers which are concentric with solid markers) = specimens for which the diameter of the stem could be measured. Single, open markers = specimens for which the diameter of the stem had to be estimated. Small arrows to right of circles = specimens taken within the peripheral two-thirds of the diameter of the stem (rather than within the central one-third of the diameter); the midpoints might have been slightly higher if the central part of the stem had been used.


2A.
ALL major groups
.40
.35
.30
.25
.20
.15
.10
.05
5
10
15
20
25
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35
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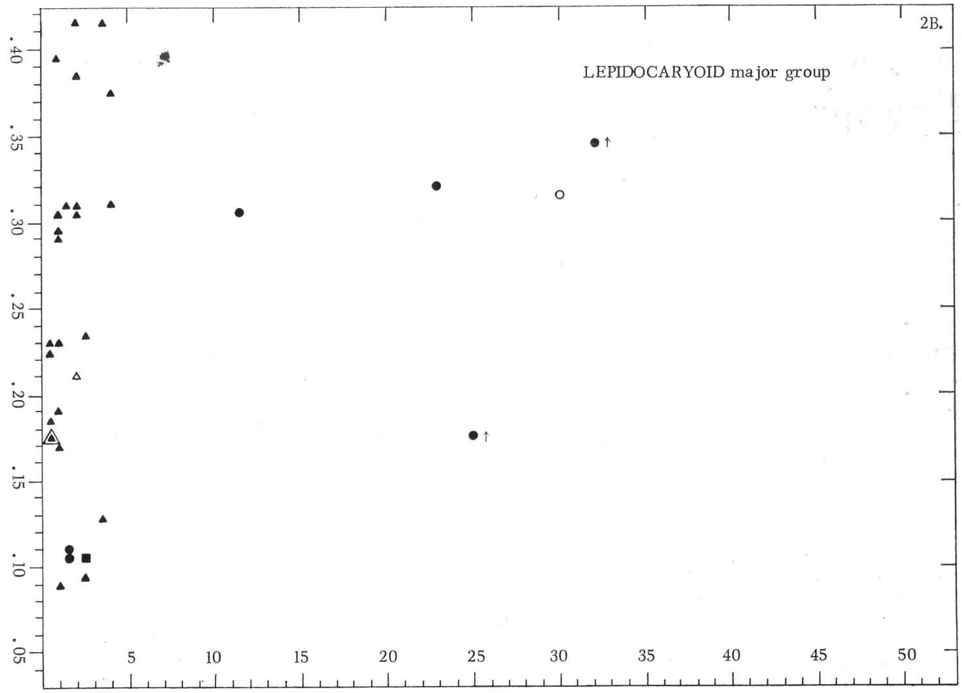
45
56


2B.
LEPIDOCARYOID major group
.40
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.05
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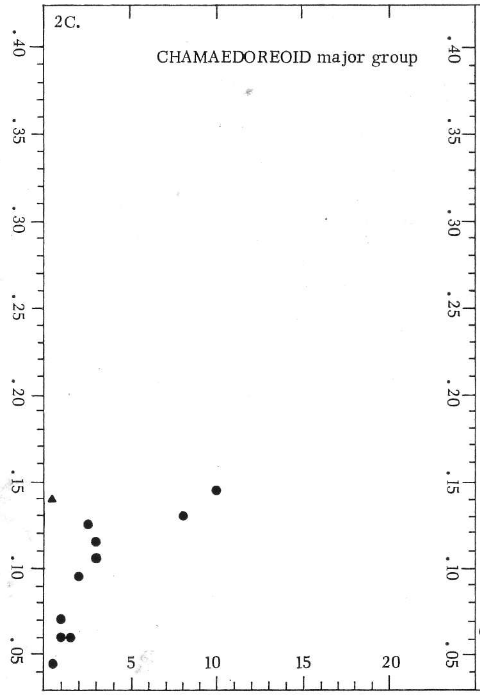
2C.
CHAMAEDOREOID major group
.40
.35
.30
.25
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.10
.05
5
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15
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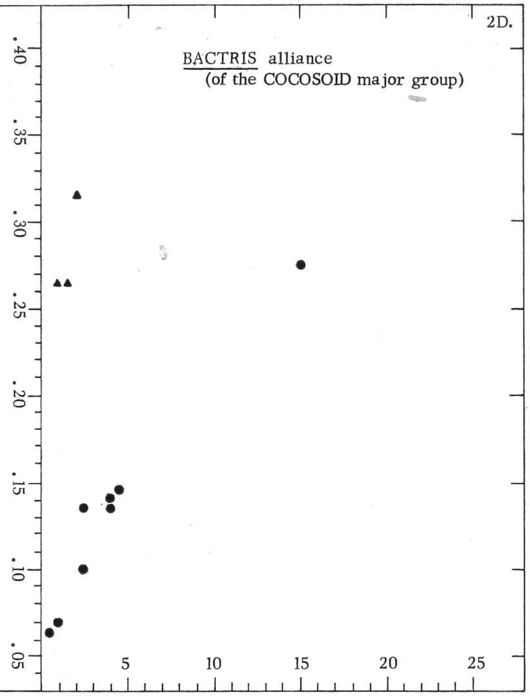
2D.
BACTRIS alliance
(of the COCOSOID major group)
.40
.35
.30
.25
.20
.15
.10
.05
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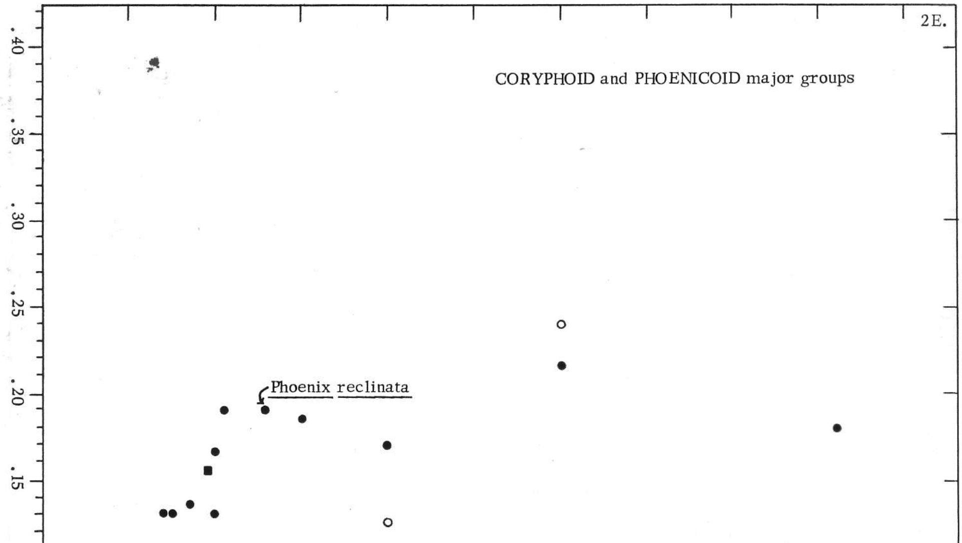
25


2E.
CORYPHOID and PHOENICOID major groups
Phoenix reclinata
.40
.35
.30
.25
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.05
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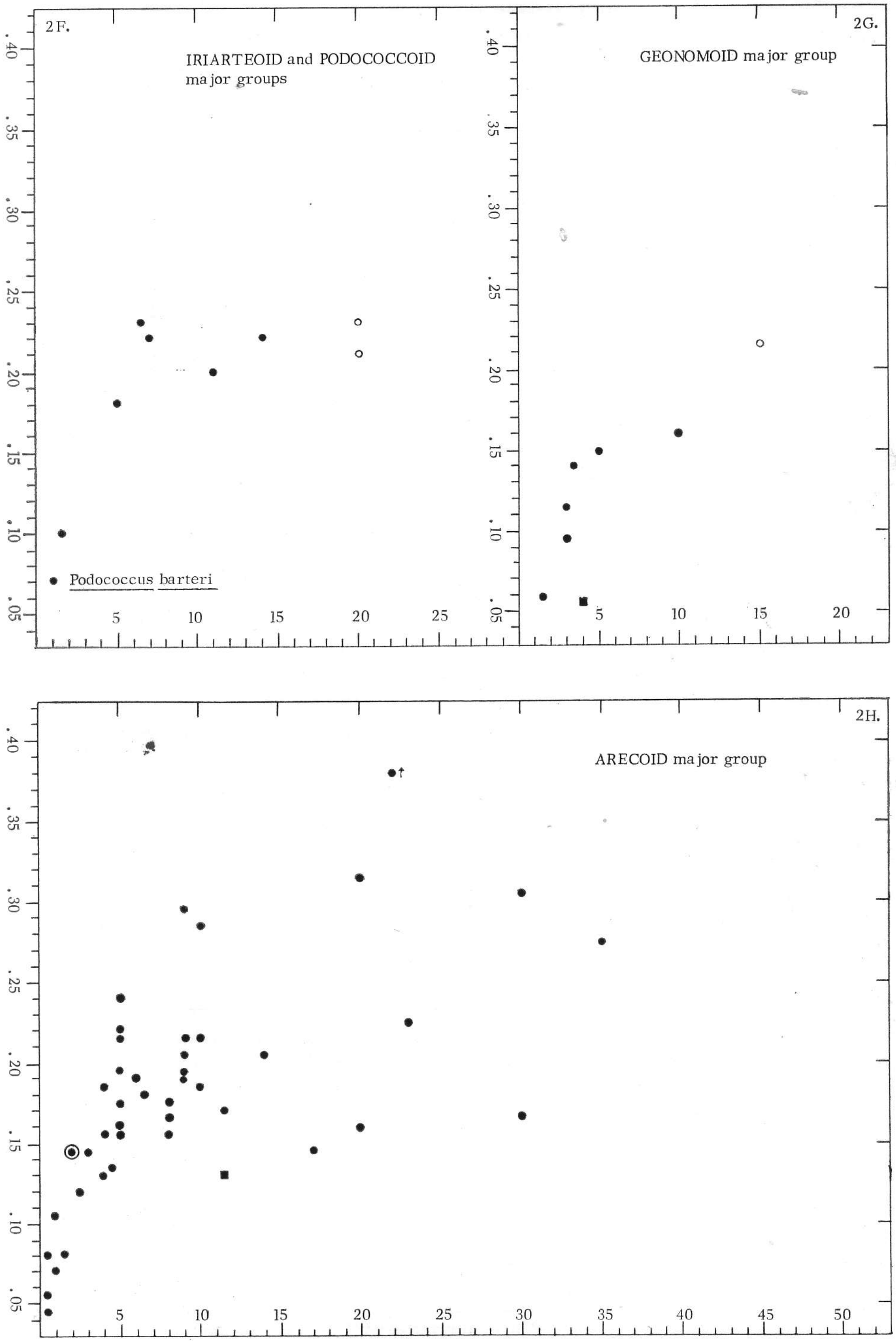
2F.
IRIARTEOID and PODOCOCCOID major groups
Podococcus barteri
.40
.35
.30
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.05
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2G.
GEONOMOID major group
.40
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.05
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2H.
ARECOID major group
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Table 1. Diameters of wide vessels of metaxylem in stems: Total ranges of measurements and means of sample range midpoints for the three categories of habit

Habit	Number of species	Total range of vessel diameters (mm)	Mean of range midpoints (mm)
Erect	127	.04–.45	.16
Scandent	28	.07–.46	.25
Rhizomatous	11	.03–.18	.09

(Fig. 2A–2D). The diameters of the vessels in stems of the erect-stemmed and lianoid species are similar in range, but the lianas have a higher average value (Table 1). Dicotyledonous lianas also have relatively wide vessels (Carlquist, 1975). The rhizomatous species of palms have relatively narrow vessels for the diameter of the stem, although there is overlap with some of the erect-stemmed species in this regard (Fig. 2A, B, E, G, H). Diameters of the vessels in the stems of the rhizomatous palms are lower in both range and average than in the other two categories (Table 1). The above trends of diameters of vessels in stems of palms relative to habit of the species agree with Tomlinson's (1961) observations in palms and Carlquist's (1975) predictions for monocotyledons in general.

The trends in diameters of vessels among the three habit categories are also reflected in the comparison of diameters of vessels between petiole and stem (Table 2). In species with both organs from the same collection, the petiolar vessels are more uniform in average diameter than are those of the stem among the three habit categories. Vessels from stems of the erect-stemmed and lianoid species are generally wider than the corresponding petiolar vessels, but the converse relationship occurs in the rhizomatous species. The average difference in diameter of vessels between

Table 2. Diameters of wide vessels of metaxylem: Comparisons of midpoints of the ranges for petiole (p) and central part of stem (s). In the species considered, both organs are from the same collection. All measurements are in millimeters

Habit	Number of species	Range of p	Range of s	Mean of p	Mean of s
Erect	81	.04–.34	.05–.32	.12	.16
Scandent	16	.08–.22	.13–.42	.15	.28
Rhizomatous	8	.05–.18	.04–.16	.12	.09

Habit	Range of (p–s)	Mean of (p–s)	Species with $p < s$	Species with $p = s$	Species with $p > s$
Erect	–.15–+.03	–.04	72 (89%)	2 (3%)	7 (9%)
Scandent	–.25–+.05*	–.14	15 (94%)		1* (6%)
Rhizomatous	+.01–+.07	+.03			8 (100%)

* This specimen (*Ancistrophyllum secundiflorum*) is unusual within this sample of lianas. For the other 15 lianas, the high end point of the range of (p–s) is –.03 mm.

stem and petiole is greater in lianas than in the erect-stemmed palms.

Figures 2B to 2H suggest that for the erect-stemmed species, the diameter of the vessels may be positively correlated with the diameter of the stems (up to a certain diameter of stem) within some of the taxonomic groups of palms. At least, the narrower vessels in the groups tend to occur in the most slender species. For example, most of the chamaedoreoid palms are very slender, and all of them have narrow vessels in the stem; but the stout *Hyophorbe* species (the two widest stems in Fig. 2C) have some of the wider vessels in this major group. When all of the species are plotted together (Fig. 2A), the points appear more widely scattered and this relationship is less clear. This situation indicates that the relationship between diameter of stems and diameter of vessels is not simple, for the sample of stems is heterogeneous in various factors that were not considered —for example, number of vascular bundles per unit cross-sectional area of stem, number of wide vessels per vascular bundle, form of the perforation plates, and perhaps other anatomical or physiological aspects of the water-conducting system of the plant.

The lepidocaryoid major group (Fig. 2B) contains the widest vessels in the stems among all the groups of palms. Maximum diameters of over 0.4 mm were observed in four species of the lianas. (In stems of the other major groups of palms, maximum diameters of over 0.4 mm were observed only in *Roystonea oleracea* of the arecoid major group.) Vessels in the stems of the lepidocaryoid lianas have a higher average and range of diameters than in the other habit categories, but some of the lepidocaryoid trees also contain remarkably wide vessels.

The diameter of vessels in stems of palms does not show a consistent relationship to the form of the perforation plates except that the small, slender species with erect stems tend to have the narrowest vessels and the most primitive perforation plates within their respective major groups (Klotz, 1977, 1978). This trend for palms compares with Carlquist's (1975) observation in the secondary xylem of dicotyledons that the primitive vessel elements (i.e., those with scalariform perforation plates) tend to be narrower than vessel elements in dicotyledons as a whole. In contrast, the general lack of correspondence of diameter of vessels with form of perforation plates in palms agrees with Cheadle's (1943) conclusion that in monocotyledons there is "no readily available evidence . . . to indicate that the diameter of vessels increases (or decreases) during specialization as measured by other characteristics." For example, the cocosoid lianas (*Desmoncus* spp.) and the lepidocaryoid lianas (e.g., *Calamus* spp.) tend to have wide vessels (Fig. 2B, D), but the two groups differ markedly in the form of their perforation plates, which are scalariform in *Desmoncus* but simple in the lepidocaryoid lianas (Klotz, 1977, 1978).

Carlquist (1975) noted in the secondary xylem of dicotyledons that "relatively few vessels with scalariform perforation plates are exceptionally wide." This generalization may also apply to the primary xylem of palms. The frequency distribution of diameters of vessels in stems of palms is skewed toward the narrower diameters (Klotz, 1977); and, as mentioned above, the slender species of erect-stemmed palms tend to have the narrowest vessels and most primitive perforation plates within their respective major groups. However, the converse of this generalization is not true in palms, for many of the wider vessels in the stems of palms have scalariform perforation plates—for example, in some of the arborescent species of the lepidocaryoid and arecoid major groups and in the scandent genus *Desmoncus* of the cocosoid major group.

Further investigation of the significance of vessel diameters in palm stems should consider the characteristic maximum height of the species. The height to which water can be transported adequately in a palm depends on the conductive efficiency of the vessels, a property that is determined largely by their diameter—i.e., wide vessels are much more efficient than narrow vessels (Zimmermann, 1978). Although data on height of stems were not obtained for this study, the author's impression is that the very slender palms with erect stems (mostly species of forest understory) are generally shorter than the species with wider stems. This study has shown that the most slender species have the narrowest vessels. Thus, the narrowest vessels in stems of palms occur among the shorter species. On the other hand, the widest vessels in stems of palms occur in the group containing the species with the longest stems—i.e., the lepidocaryoid lianas, of which some species reach a length of over 100 meters (Moore, 1973, personal communication). Stems of many lianoid palms attain much greater lengths and have markedly wider vessels than stems of the erect-stemmed species of comparable diameter. The relatively narrow vessels of the stems of rhizomatous palms are adequately efficient in conduction because the vertical distance of water transport is slight and because the horizontal (or axial) distance is reduced by the presence of adventitious roots near the leafy crown.

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