# A systematic histological analysis of palm fruits VII. The Cyrtostachydinae (Arecaceae)

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Essig, F. B. & L. Litten (Institute for Systematic Botany, Department of Biology, SCA 110, University of South Florida, 4202 E. Fowler Ave., Tampa, FL 33620-5200, U.S.A.; email: essig@chumal.cas.usf.edu). A systematic histological analysis of palm fruits VII. The Cyrtostachydinae (Arecaceae). Brittonia 56: 375-379. 2004.—Fruit specimens representing five taxa of the genus Cyrtostachys were examined histologically in order to characterize the pericarp anatomy of the monogeneric subtribe Cyrtostachydinae (tribe Areceae, subfamily Arecoideae), as part of an ongoing survey of the family. The pericarp in this genus can be characterized by a combination of papillate epidermis, heavy layer of tanniniferous/ pigmented cells below the epidermis, a system of vascular bundles with thick fibrous sheaths with purely fibrous bundles frequently above and below, absence of brachysclereids, and a very thin sclerified locular epidermis. On the basis of pericarp structure alone, the genus might be most closely related to the Gronophyllum alliance of the subtribe Arecinae. This diverges somewhat from the hypothesis of relationship with the Areca group of the Arecinae resulting from two DNA-based phylogenetic studies, and even further from the hypothesis of relationship with Iguanura suggested by another DNA-based phylogenetic study.

Key words: Arecaceae, Cyrtostachys, palm, fruit, pericarp, histology, Palmae.

The subtribe Cyrtostachydinae (tribe Areceae) consists of a single genus, Cyrtostachys, with eight species ranging from Southeast Asia to the Solomon Islands, with the greatest concentration in New Guinea. These species have solitary or clustering, unarmed trunks, pinnate leaves with welldeveloped crownshafts, infrafoliar inflorescences with short peduncles, flowers arranged in triads along long, unbranched rachillae, and pseudomonomerous drupaceous fruits with apical stigmatic remains. They thus appear to be morphologically a part of the large close-knit group of pseudomonomerous Arecoid palms centered in the islands of the southwestern Pacific (tribe Areceae: subtribes Arecinae, Ptychospermatinae, Archontophoenicinae, Linospadicinae, and parts of the Iguanurinae). The genus is distinctive by its strongly divaricate inflorescence branches, flowers partially sunken into pits on the rachillae, and connate petals and filaments of the staminate flower (Uhl & Dransfield, 1987). Uhl and Dransfield considered the genus to be isolated with no clear relatives. Recent phylogenetic studies have suggested an affinity with *Iguanura* (Lewis & Doyle, 2002), *Nenga*, and *Areca* (Asmussen & Chase, 2001), or *Areca* (Hahn, 2002).

As part of ongoing studies of fruit histology in the subtribes of the tribe Areceae (subfam. Arecoideae) (Essig, 1977, 1999, 2002; Essig & Young, 1979; Essig & Hernandez, 2002; Essig et. al., 1999, 2001), five taxa of *Cyrtostachys* were examined in order to characterize the fruit of the subtribe and genus, to shed light on their relationship with the other subtribes, and to assess variation within the genus.

## Materials and Methods

Dried and preserved fruits were obtained from herbaria and colleagues in the field.

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available specimens for most taxa consisted of just a few fruits from a single collection, while in two cases there were a few fruits from additional collections. One fruit representing each species was sectioned, photographed, and illustrated, while additional fruits were examined when available to confirm the observations and measurements made with the primary specimen. These data are intended only to provide a sampling of the variation found within the monogeneric subtribe Cyrtostachydinae and to characterize it sufficiently for comparison with other subtribes of the tribe Areceae. A detailed analysis of the species of the genus is beyond the scope of this paper and not feasible with the available material.

As documented in the Results section.

Specimens representing three named species, including *Cyrtostachys renda* Blume from Southeast Asia, *C. glauca* H. E. Moore from New Guinea, and *C. kisu* Becc. from the Solomon Islands, were included in the study, along with two that are presently unidentified. The two unidentified specimens consist of one from Indonesian Papua (formerly Irian Jaya) and one from southern Papua New Guinea. Thus a good representation of the geographic range of the genus was obtained.

Preserved fruits were dehydrated in an ethanol/tertiary butynol series and embedded in a standard paraffin/plastic medium, sectioned, and stained with safranin and fast green. Drawings were derived from digital photographs of transverse equatorial sections.

#### Results

Variation among the five species described and illustrated below is relatively minor. The genus and subtribe can be characterized as having a papillate epidermis with a prominent cuticle, a thick band of tanniniferous cells below the epidermis, a mixture of large fibrous bundles and fibrous vascular bundles throughout the middle and inner pericarp, and a thin, sclerified, locular epidermis. Brachysclereids appear to be lacking entirely. Raphide-bearing cells were seen in only one specimen. There is some degree of specialization of both the outer-

most and innermost bundles as purely fibrous bundles, with most of the central bundles containing vascular strands. The descriptions below illustrate the range of variation found in the genus, but should not be interpreted as definitive characterizations of the species.

1. Cyrtostachys renda Blume (Thailand: Barford & Ueachirakan 41772, K), fruit 8 mm long, 4 mm diam., pericarp ca. 0.5 mm thick; tanniniferous cells small, nearly the same size as the epidermal cells; conspicuous raphide-bearing cells in the outer pericarp just below the tanniniferous zone; most of the bundles containing vascular tissues within thick fibrous sheaths, with smaller fibrous bundles to the exterior and occasionally to the interior of the main bundles (Fig. 1A).

Two additional specimens identified as Cyrtostachys renda [Niyomdham 852 (K) from Thailand and Salleh 1214 (K) from Sarawak] are similar to the above, notably for the thin layer of tanniniferous cells in the outer pericarp and the several tiers of rounded fibrous vascular bundles.

- 2. Cyrtostachys sp. (Indonesia, Papua, Fak-Fak: Heatubun 194, K), fruit 12 mm long, 5 mm diam., pericarp ca. 0.4–0.5 mm thick; tanniniferous cells similar to those of C. renda; bundles generally larger and fewer, in roughly two series, the innermost and some of the outer bundles purely fibrous and the remainder containing vascular tissues within the thick fibrous sheaths; the epidermis apparently lacking pigmentation (Fig. 1B).
- 3. Cyrtostachys sp. (Papua New Guinea, Gulf Province: Baker 1110, K), fruit 10.5 mm long, 5 mm diam., pericarp ca. 0.6–0.7 mm thick; tanniniferous cells becoming substantially larger toward the center of the pericarp; a series of purely fibrous bundles on either side of a central series of fibrous vascular bundles; large flattened cavities, filled with an amorphous material, occasional just below the epidermis (Fig. 1C).
- 4. Cyrtostachys glauca H. E. Moore (Papua New Guinea, Morobe Province: Moore 9272, holotype, BH), fruit 10 mm long, 5 mm diam., pericarp ca. 0.4 mm thick; tanniniferous tissue similar to that in Baker 1110; parenchyma tissue external to

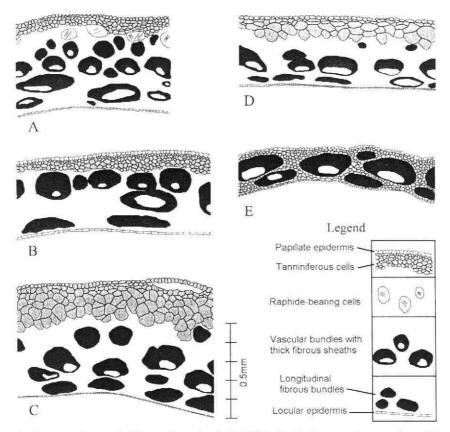


Fig. 1. A. Cyrtostachys renda Blume (from Barford 41772, K). B. Cyrtostachys sp. (from Heatubun 194. K). C. Cyrtostachys sp. (from Baker 1110, K). D. Cyrtostachys glauca H. E. Moore (from Moore 9272, holotype, BH). E. Cyrtostachys kisu Becc. (from Guppy 235, holotype, K).

the primary vascular bundles somewhat radially extended; bundles confined mostly to the inner half, with large fibrous vascular bundles mostly in the middle, a series of flattened fibrous bundles on the inside close to the locular epidermis, and a somewhat separated series of small, rounded fibrous bundles toward the exterior (Fig. 1D).

Another specimen identified as *Cyrtostachys glauca* [Papua New Guinea, Morobe Province: *Essig LAE 55009* (BH)] is consistent with the above, agreeing in particular with the flattened inner fibrous vascular bundles and the thick layer of tanniniferous cells in the outer pericarp.

5. Cyrtostachys kisu Becc. [Solomon Islands: Guppy 235 (holotype), K], fruit 4.5 mm diam., pericarp ca. 0.2–0.3 mm thick; with tanniniferous cells throughout; a series of very large vascular bundles with thick

fibrous sheaths in mid-pericarp, with a series of mostly fibrous bundles to the interior and an occasional fibrous bundle exterior to the main series; the epidermis apparently lacking pigmentation (Fig. 1E).

#### Discussion

Examination of five taxa, representing at least three of the eight recognized species and including those of westernmost and easternmost distribution, provides a good characterization of the general pericarp structure of the monogeneric subtribe Cyrtostachydinae, and of the range of variation within it. The number of samples is insufficient, however, to definitively characterize individual species. Fruits of the five taxa examined differ subtly, primarily in the size and number of vascular and fibrous bun-

dles, and in the extent of tanniniferous tissue and the size of individual tanniniferous cells. Cyrtostachys kisu appears to be the most distinctive, with relatively few, large bundles and tanniniferous tissue throughout the pericarp.

The relationship of vascular bundles to fibrous bundles is of interest, as there is a variety of distinctive patterns within the Arecoid palms. Within the pseudomonomerous arecoid palms at least, an oft-repeated trend is from a single system of fibrous vascular bundles to a dual system consisting of vascular and fibrous bundles in the inner pericarp and a series of purely fibrous bundles in the outer pericarp (Essig, 1977, 1999, 2002; Essig & Young, 1979; Essig & Hernandez, 2002; Essig et al., 1999, 2001). In some subtribes, the best example being the Arecinae (Essig & Young, 1979), one can see a range of intermediate conditions. suggesting that dual systems do in fact evolve through disruptive specialization of a single system.

In Cyrtostachys, vascular bundles with thick fibrous sheaths and bundles consisting solely of fibers intermingle within a single system, but with a tendency for the innermost and/or outermost bundles to differentiate as purely fibrous bundles. In C. glauca, it appears that a series of small, rounded, fibrous bundles have in fact become more or less separated from the main bundle system. This may represent an early stage in the formation of a distinct outer series of fibrous bundles, but this trend has not proceeded very far in this genus.

The complete absence of brachysclereids in the pericarp of *Cyrtostachys* is also notable, considering their widespread occurrence in other subtribes. The presumed protective role of brachysclereids appears to be taken over by tanniniferous tissues in this genus. To some degree the two types of tissues show an inverse relationship in their distribution among the Arecoid palms.

In both the emphasis on tannin over sclereids, and in overall structure, the fruits of *Cyrtostachys* resemble most closely those of the *Gulubia/Gronophyllum/Hydriastele/Siphokentia* complex of the subtribe Arecinae (Essig & Young, 1979). This complex features heavy tanniniferous layers

and mixed systems of fibrous and vascular bundles with some separation of an outer fibrous system in some species.

The Gronophyllum complex has traditionally been included in the subtribe Arecinae, with a somewhat different complex that includes Areca, Nenga, Gigliola, Loxococcus, and Pinanga. In the molecular studies of both Asmussen and Chase (2001) and Hahn (2002), these two complexes are on separate clades that each include genera from other subtribes, suggesting that the Arecinae is polyphyletic. The same two studies suggest affinity of Cyrtostachys with the Arecinae, but with the Areca complex rather than with the Gronophyllum complex. Fruits of the Areca complex differ sharply from those of the Gronophyllum complex, having prominent layers of brachysclereids and relatively few tanniniferous cells. Thus the hypothesis of relationship for Cyrtostachys suggested by fruit structure differs somewhat from that suggested by molecular data.

The results of a third DNA-based phylogenetic study by Lewis and Doyle (2002) suggest a relationship with Iguanura, although this study did not include any members of the Arecinae, so a direct comparison of the studies cannot be made. With a simple system of fibrous vascular bundles. abundant tanniniferous cells in the outer pericarp, and few to no brachysclereids, the pericarp histology of Iguanura is in fact similar to that of Cyrtostachys. However, fruits in that genus have basal stigmatic residues, inflorescences are long-pedunculate, and usually interfoliar, and leafsheaths do not usually form a distinct crownshaft, in contrast to the apical stigmatic residues, short-pedunculate, infrafoliar inflorescences, and well-developed crownshafts of both Cyrtostachys and the Arecinae. Overall, therefore, Cyrtostachys seems to have more natural affinity with the Arecinae than with Iguanura.

These phylogenetic analyses of the Arecoid palms provide conflicting hypotheses about the affinities of specific genera, as much from the differing set of taxa included in the studies as from the different DNA regions used in the analyses. Data from pericarp structure provides still other hypotheses, and will be of great value in future studies that incorporate a wider variety of data.

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