

A systematic histological study of palm fruits. IV. Subtribe Oncospermatinae (Arecaceae)

FREDERICK B. ESSIG,¹ LISA BUSSARD, AND NICOLE HERNANDEZ

Essig, F., L. Bussard & N. Hernandez (Institute for Systematic Botany, Department of Biology—SCA 110, University of South Florida, Tampa, FL 33620-5200, U.S.A.). A systematic histological study of palm fruits. IV. Subtribe Oncospermatinae (Arecaceae). *Brittonia* 53: 466–471. 2001.—Pericarp histology in the Oncospermatinae reveals distinctive characters at the generic level but no unique characters at the subtribal level. Pericarp structure is diverse but parallels the diversity found in other subtribes of the Arecaceae. The subtribe appears to be divisible into two distinct groups: one in which sclereids alone provide the primary protective barrier in the outer fruit and one in which fibrous bundles, sometimes in combination with brachysclereids, form the outer barrier. This division of the subtribe supports similar conclusions derived from morphological data.

Key words: Oncospermatinae, palms, Arecaceae, pericarp histology, anatomy.

Introduction

The subtribe Oncospermatinae (Arecaceae, subfamily Arecoideae, tribe Arecaceae) consists of eight, mostly monotypic, genera distributed primarily on islands in the Indian Ocean. Five monotypic genera are confined to the Seychelles and two to the Mascarene Islands. Only *Oncosperma* departs from this pattern, with five species distributed from Sri Lanka, across continental southeast Asia, to the Philippines and the Moluccas. The group is traditionally united on the basis of two characters: the presence of emergent spines on various parts of the plant and the presence of an operculum on the endocarp of the fruit. The latter character suggests an affinity with the Iguanurinae (Uhl & Dransfield, 1987).

This small group of isolated genera is, however, diverse in floral and vegetative characters, with both inter- and infrapolar inflorescences, with and without the leaf sheaths forming distinct crownshafts, with the staminate flowers symmetrical or asymmetrical, and the fruit with apical, lateral or basal stigmatic remains (Uhl & Dransfield,

1987). Morphologically, it appears to be divisible into two subgroups, with *Verschaffeltia*, *Phoenicophorium*, *Roscheria*, and *Nephrosperma* in one group; and *Acanthophoenix*, *Tectiphiala*, *Deckenia*, and *Oncosperma* in the other group.

The first group is characterized by several features, including inflorescences that are erect, long-pedunculate, interfoliar, and possessing persistent prophylls, leaf sheaths that are not formed into distinct crownshafts (except in *Roscheria*), leaf blades that are irregularly divided or multi-ribbed, and staminate flowers with rounded sepals. These genera are confined to the granitic Seychelles.

The second group is characterized by the possession of distinct crownshafts, leaves regularly divided into single-ribbed pinnae, short-pedunculate infrapolar inflorescences with caducous prophylls, and staminate flowers with acute sepals. These genera collectively are widespread, occurring from the Mascarenes and Seychelles to Indonesia and the Philippines.

Previous investigations of palm fruit histology have revealed striking differences in the distribution of protective tissues, which include a radially thickened locular epider-

¹ Author to whom all correspondence should be addressed. E-mail: essig@chumal.cas.usf.edu

mis, sclerified ground tissue, fibrous sheaths around vascular bundles, separate fibrous bundles, brachysclereids, tanniniferous cells, and raphide-bearing cells (Essig, 1977, 1982, 1999; Essig & Young, 1979, 1985; Essig et al., 1999). These differences in pericarp structure generally can be used to distinguish genera and even species, but distinctions are more ambiguous at higher levels, due to apparent extensive parallelism. More thorough reviews of palm pericarp histology can be found in Essig (1999) and Essig et al. (1999).

This paper continues the survey of fruit structure in the palm family, with a preliminary analysis of the eight genera of the subtribe Oncospermatinae.

Materials and Methods

Preserved specimens of fruit representing all eight genera were obtained from the L. H. Bailey Hortorium (BH), and include specimens recently collected by Carl Lewis for a morphological study. Fruits were prepared for paraffin embedding using standard methods, and stained with safranin and fast green. Sections were taken from the middle region of the fruit, away from stigmatic residues when these were positioned laterally. Sections were photographed digitally; simplified, semi-diagrammatic line drawings were made from them. These are intended to show accurately the size, distribution, and composition of the different tissue regions, but not cellular detail. In some cases, specimens were difficult to section due either to the juxtaposition of hard and soft tissues or to the climacteric deterioration of soft tissues in fully ripened fruit samples, and thus the drawings represent reconstructions based on fragmentary microtomed sections supplemented with hand sections.

In a few cases, only a single fruit or several fruits from the same tree were available for study. Where more than one specimen was available, quantitative variation (relating to variation in fruit size), but no significant qualitative variation, has been seen. Fruit sizes and pericarp thicknesses given in the descriptions or represented in the drawings should be recognized as single

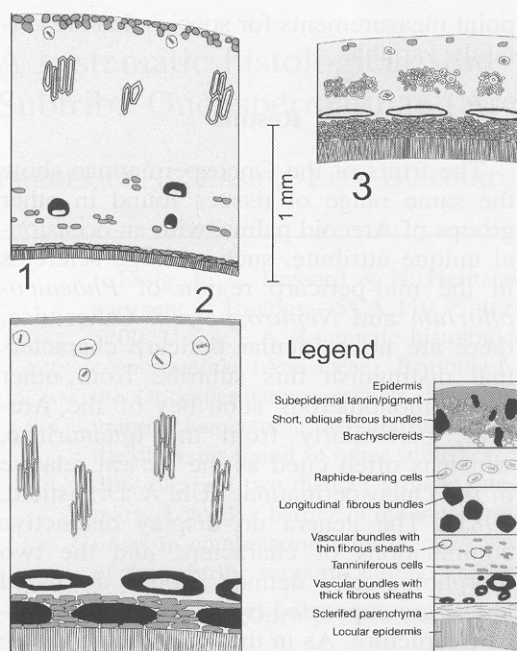
point measurements for species that are certainly variable.

Results

The fruits of the Oncospermatinae show the same range of tissues found in other groups of Arecoid palms, with an occasional unique attribute, such as large sclereids in the mid-pericarp region of *Phoenicophorium* and *Nephrosperma*. Otherwise, there are no particular pericarp characters that distinguish this subtribe from other pseudomonomerous subtribes of the Arecaceae, particularly from the Iguanurinae, which is often cited as the closest relative of the Oncospermatinae (Uhl & Dransfield, 1987). The genera do display distinctive combinations of characters, and the two morphologically defined groups discussed above are supported by differences in pericarp structure. As in the Iguanurinae (Essig et al., 1999), the terms 'endocarp' and 'exocarp' have no consistent histological definition in the Oncospermatinae, so the distribution of the tissues will first be discussed in terms such as the 'outer,' 'middle,' or 'inner' pericarp. In the discussion, comparison will be made with the endocarps and exocarps described in other groups of palms.

Phoenicophorium, *Nephrosperma*, *Verschaffeltia*, and *Roscheria* (Figs. 1–4) all feature prominent mantles of sclereids, without fibrous bundles, in the middle to outer pericarp. Within that group, *Phoenicophorium* and *Nephrosperma* are similar in that the sclereids are quite large, elongate, and oriented obliquely to radially relative to the surface. *Verschaffeltia* and *Roscheria* are quite similar, with thick mantles of small brachysclereids and with vascular bundles that lack fibrous sheaths.

Tectiphiala, *Deckenia*, *Acanthophoenix*, and *Oncosperma* (Figs. 5–8) all possess nonvascular, fibrous bundles in the middle to outer pericarp, sometimes associated with a thick mantle of small brachysclereids. In *Tectiphiala* the fibrous bundle system is interconnected with the vascular system, whereas in *Deckenia* the fibrous bundles form a distinct subepidermal series. *Acanthophoenix* and *Oncosperma* are quite



FIGS. 1–3. 1. *Phoenicophorium borsigianum* (from Moore 10093, BH). 2. *Nephrosperma vanhoutteanum* (from Lewis 98-006, BH, and Read 1551, BH). 3. *Roscheria melanochaetes* (from Moore 10091, BH).

similar overall, with the fibrous bundles short, radially to obliquely oriented, and embedded within a mantle of brachysclereids, and with the vascular bundles lacking thick fibrous sheaths.

The genera are discussed individually below. Distributional data for the Seychelles is from Robertson (1989), and for other regions from Uhl and Dransfield (1987).

1. *PHOENICOPHORUM BORSIGIANUM* (K. Koch) Stuntz. (Seychelles: Moore 10093, BH). A monotypic genus. (Fig. 1)

Fruit ovoid, 7.5 mm diam., 8 mm long, with pericarp 1.5 mm thick, stigmatic remains subbasal—unusual among the pseudomonomerous Arecoideae palms (but similar to *Nephrosperma*) in the very distinctive, large, somewhat elongate and sometimes obliquely oriented sclereids in the outer pericarp; further characterized by the thick layer of tanniniferous cells and occasional raphide cells below the epidermis, the very thick fibrous sheaths around the nearly te-

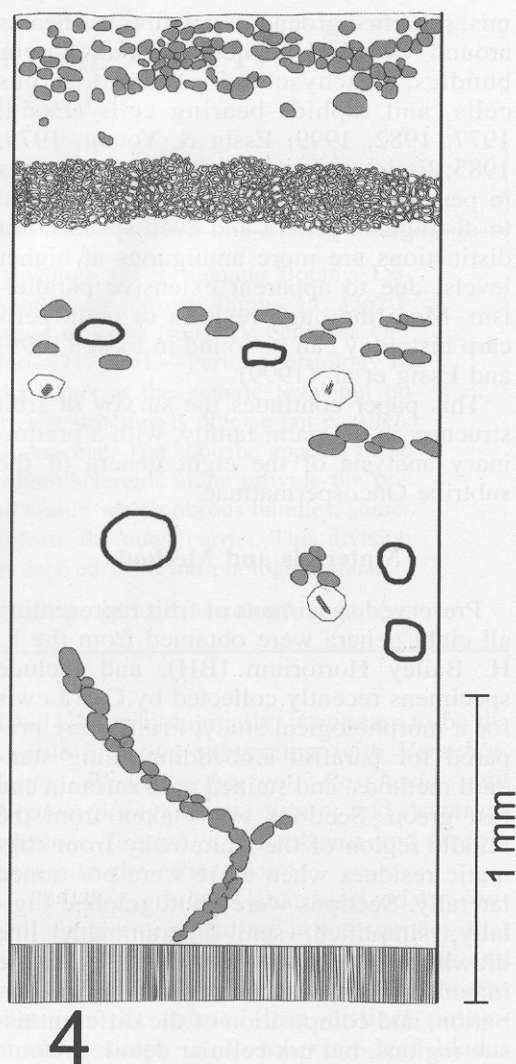
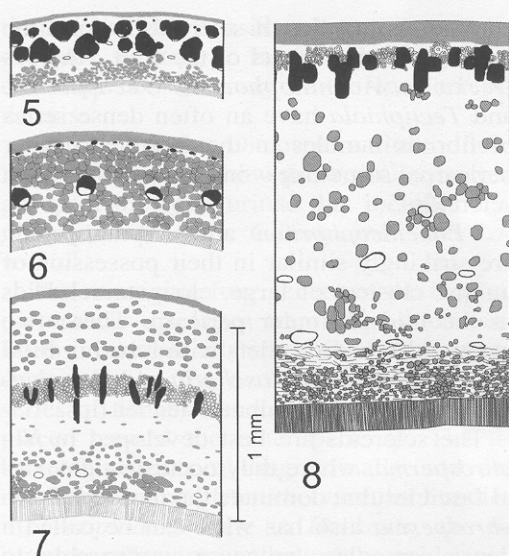


FIG. 4. *Versaffeltia splendida* (from Lewis 98-044, BH).

rete vascular bundles, and the thin layer of tanniniferous cells in the inner pericarp.

2. *NEPHROSPERMA VANHOUTTEANUM* (H. Wendl. ex van Houtte) I. B. Balfour. (Seychelles: Lewis 98-006, BH, Read 1551, BH). A monotypic genus. (Fig. 2)

Fruit subglobose, 14 mm diam., 12 mm long, with pericarp 2 mm thick, stigmatic remains lateral—resembling *Phoenicophorium* in the presence of large sclereids in the middle pericarp, but these larger, more



FIGS. 5–8. 5. *Tectiphiala ferox* (from Moore 9925, BH). 6. *Deckenia nobilis* (from Moore s.n., BH). 7. *Acanthophoenix rubra* (from Vaughn 851(a), BH). 8. *Oncosperma horridum* (from Lewis 98-052, BH).

elongate, and forming distinct fascicles in the middle pericarp; further characterized by a thin subepidermal pigmented zone, a layer of loosely distributed raphide cells in the outer pericarp, a layer of flattened vascular bundles with thick fibrous sheaths adjacent to a layer of flattened fibrous bundles surrounded by densely packed tanniferous cells in the inner pericarp, and a very thick locular epidermis.

3. *ROSCHERIA MELANOCHAETES* (H. Wendl.) H. Wendl. ex I. B. Balfour. (Seychelles: Mahe, Silhouette and Praslin Islands, Moore 10091, BH). A monotypic genus. (Fig. 3)

Fruit globose, 6 mm diam., with pericarp 0.8 mm thick, stigmatic remains subbasal—similar to *Verschaffeltia*, but the pericarp much thinner and with the mantle of brachysclereids thinner and less continuous; further characterized by tanniferous cells that are sparse in the outer pericarp, but forming a massive mantle in the inner pericarp, with the vascular bundles flattened against that mantle, and by a very thick locular epidermis.

4. *VERSCHAFFELTIA SPLENDIDA* H. Wendl. (Seychelles, Mahe, Silhouette and Praslin Islands: Lewis 98-044, BH). A monotypic genus. (Fig. 4)

Fruit globose, 2.5 cm diam., with pericarp 3 mm thick, stigmatic remains basal, seed and endocarp sculpted—distinctive within the group for its large size, and for a thick zone of tanniferous cells below the epidermis, followed by a dense zone of brachysclereids; further characterized by a broad zone of parenchyma with occasional tanniferous cells, raphide cells and large, nearly terete vascular bundles with little or no fibrous sheaths, and by a very thick locular epidermis.

5. *TECTIPHIALA FEROX* H. E. Moore (Mauritius: Moore 9925, BH). A monotypic genus. (Fig. 5)

Fruit ovoid, 7 mm diam., 8 mm long, with pericarp 0.45 mm thick, stigmatic remains apical—unique within the subtribe for the mixed mantle of fibrous bundles and heavily sheathed vascular bundles filling the outer half of the pericarp, and for the total lack of sclereids; further characterized by a thick zone of tanniferous cells in the inner half to third of the pericarp, and a moderately thick locular epidermis.

6. *DECKENIA NOBILIS* H. Wendl. ex Seemann. (Seychelles: Moore s.n., BH). A monotypic genus. (Fig. 6)

Fruit narrowly ovoid, 4 mm diam., 12 mm long, with pericarp 0.5 mm thick and stigmatic remains basal—distinctive within the subtribe for the single series of small, widely spaced fibrous bundles with occasional brachysclereids just below the epidermis, and for the single series of heavily sheathed, nearly terete vascular bundles in mid-pericarp; further characterized by a thick pigmented zone below the epidermis, by the tanniferous cells packed densely throughout the pericarp, and by the moderately thick locular epidermis.

7. *ACANTHOPHOENIX RUBRA* (Bory) H.

Wendl. (Mauritius and Reunion Islands: *Vaughan 851(a)*, BH). A monotypic genus. (Fig. 7)

Fruit globose, 10 mm diam., with pericarp 1.5 mm thick, and stigmatic remains lateral to subapical—most distinctive for its dense zone of brachysclereids with embedded short, obliquely to radially oriented fibrous bundles in the middle pericarp; further characterized by a thick pigmented zone below the epidermis, abundant tanniferous cells in the outer third of the pericarp, followed by scattered and sometimes densely clustered tanniferous cells in the inner half of the pericarp, by the vascular bundles few, small and with thin or no fibrous sheaths, and by the very thick locular epidermis.

8. *ONCOSPERMA HORRIDUM* Scheff. (Malaysia: *Lewis 98-052*, BH). One of five species in a genus distributed from Sri Lanka to the Philippines and Indonesia. (Fig. 8)

Fruit globose, 20 mm diam., with pericarp 1.9 mm thick and stigmatic remains lateral or subapical—similar to *Acanthophoenix* but with the mantle of brachysclereids and short oblique fibrous bundles close to the epidermis, and with the subepidermal pigmented zone much thicker; further characterized by the vascular bundles scattered throughout the inner to middle pericarp, and a very thick zone of sclerified parenchyma and small tanniferous cells adjacent to the very thick locular epidermis.

Discussion

Data from pericarp histology supports the separation of the eight genera of this subtribe into two main groups, in agreement with the morphological division discussed earlier. The genera within the two groups show some similarities with one another, but often show equal or stronger similarity to genera in other subtribes, particularly the *Iguanurinae*.

Phoenicophorium, *Nephrosperma*, *Verschaffeltia*, and *Roscheria*, all confined to the Seychelles, rely primarily on clusters or

continuous mantles of sclereids to form the outer protective layers of the fruit, whereas *Deckenia*, *Acanthophoenix*, *Oncosperma*, and *Tectiphiala* have an often dense series of fibrous bundles in the middle to outer pericarp, sometimes in association with sclereids.

Phoenicophorium and *Nephrosperma* are strikingly similar in their possession of unique clusters of large, elongate sclereids in the mid- to outer pericarp. These two genera also have leaflets with lobed or bifid tips, as opposed to *Roscheria* and *Verschaffeltia*, which have truncate leaflet tips.

The sclereids are best developed in *Nephrosperma*, where they occur in tight, rigid fascicles that dominate the mesocarp. *Nephrosperma* also has what can be called a dense, complex endocarp comparable to that in the subtribe Ptychospermatinae, consisting of the thick, flattened fibrous sheaths of the vascular bundles, flattened fibrous bundles, a thick zone of tanniferous cells and a thick locular epidermis.

The pericarp of *Phoenicophorium*, however, is conspicuously less endowed with protective tissues, with fewer sclereids, thinner fibrous sheaths around the vascular bundles, and only thin layers of tanniferous cells in the outermost and innermost zones. Neither *Phoenicophorium* or *Nephrosperma* has what could be called an exocarp (other than a layer of tanniferous cells just below the epidermis).

Outside of the *Oncospermatinae*, the nearest parallel to these first two genera is *Bentinckia* (subtribe *Iguanurinae*), which also has large sclereids in the outer pericarp. In the latter, however, the sclereids are nearly isodiametric, not in distinct clusters, and grade into smaller brachysclereids near the epidermis.

Verschaffeltia and *Roscheria* have very thick and very thin manifestations of a similar pericarp histology, in which there is a thick zone of brachysclereids in the mid- to outer pericarp (but not close enough to the epidermis to be called an exocarp), and scanty fibrous sheaths around the vascular bundles. *Roscheria* shows some similarity with *Nephrosperma* in its flattened vascular bundles and thick zone of tanniferous cells next to the locular epidermis. These

tissues can be considered to comprise a complex endocarp. In *Verschaffeltia*, the endocarp consists only of the locular epidermis.

Outside of the Oncospermatinae, these latter two genera show great similarity to a group of the Iguanurinae that includes *Cyphokentia*, *Moratia*, *Clinosperma*, and *La-voixia*.

The remaining four genera of the Oncospermatinae display a trend that finds parallels in several other subtribes of the Areceae, namely, the evolution of a separate series of fibrous bundles progressively displaced toward the outer pericarp. The fibrous bundles run longitudinally and are not fully separate from the vascular bundles in *Tectiphiala*, while in *Deckenia*, the fibrous bundles are just below the epidermis, but still more or less longitudinal.

In *Acanthophoenix*, the fibrous bundles have become short, nearly perpendicular to the axis of the fruit and embedded in a mass of brachysclereids in mid-pericarp. In *Oncosperma* they are also short and oblique but displaced to the subepidermal zone and there form a complex exocarp in combination with brachysclereids. This kind of exocarp is similar to that of *Ptychosperma* and related genera of the Ptychospermatinae, as well as in some members of the Iguanurinae such as *Physokentia*. In *Oncosperma* there is also a complex endocarp consisting of compressed, sclerified parenchyma in conjunction with a thick locular epidermis. This is similar also to the endocarp of the Ptychospermatinae, but without the thick fibrous bundle sheaths found in that group, and is perhaps even more similar to the structure found in *Neoveitchia* in the Iguanurinae.

Conclusions

Although one can see evidence of affinity within the two subgroups of the subtribe Oncospermatinae, there is little in pericarp structure that could be used to define the subtribe or distinguish it from other subtribes, particularly the Iguanurinae. Similar-

ities of these genera with genera in other subtribes of the tribe Areceae may simply be due to parallel evolution of highly adaptive combinations of protective tissues or may in some cases indicate actual affinity. Little is known about the dispersal ecology of these fruits, although it is presumed that most of the brightly colored arecoid palm fruits are dispersed by birds. Field studies on this subject may shed some light on the meaning of both the striking diversity of palm fruit structures, as well as of the apparent parallelism in their evolution. Combination of this pericarp data with morphological and DNA data, should soon elucidate the evolutionary history of this most diverse tribe of palms.

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