

# A systematic histological study of palm fruits. VI. Subtribe Linospadicinae (Arecaceae)

FREDERICK B. ESSIG

---

Essig, F. (Institute for Systematic Botany, Department of Biology—SCA 110, University of South Florida, Tampa, FL 33620, U.S.A.; email: [essig@chuma1.cas.usf.edu](mailto:essig@chuma1.cas.usf.edu)). A systematic histological study of palm fruits. VI. Subtribe Linospadicinae (Arecaceae). *Brittonia* 54: 196–201. 2002.—The pericarp structure of representative species of the four genera of the subtribe Linospadicinae is described and compared. Tissues found in the pericarp of this group are similar to those found in other subtribes of the Arecaceae, with no characters unique to the subtribe and nothing to suggest its closest affinities. The four genera, as well as each species examined, do show distinctive pericarp features, however. *Laccospadix* and *Linospadix* are similar, both with a single series of fibrous bundles and an outer series of prominent raphide-bearing cells dominating the pericarp. In both *Howea* and *Calyptrocalyx*, a complex exocarp forms from a series of fibrous bundles and brachysclereids, but each genus has other distinctive characters. *Howea* has vascular bundles in the exocarp zone, an outer series of raphide-bearing cells, and a conspicuously thickened locular epidermis. Based on a limited sample of four species, raphide-bearing cells appear to be always interior to the exocarp in *Calyptrocalyx*, and the locular epidermis is thin.

**Key words:** Linospadicinae, palms, Arecaceae, pericarp, histology, anatomy.

---

## Introduction

This paper continues a series on the anatomy of the pericarp in palm fruits (Essig, 1977; Essig & Young, 1979; Essig et al., 1999, 2001; Essig & Hernandez, 2002). The subtribe Linospadicinae (Arecaceae, subfamily Arecoideae, tribe Areceae) consists of four genera distributed from the eastern Moluccas, across New Guinea to Australia and Lord Howe Island. *Laccospadix* is a monotypic genus from northeastern Queensland, and *Howea* has two species, both from Lord Howe Island. *Linospadix* comprises five species from eastern Australia and two from New Guinea (Dowe & Irvine, 1997; Dowe & Ferrero, 2001), while the largest genus, *Calyptrocalyx*, comprises 26 species from eastern Indonesia and New Guinea (Dowe & Ferrero, 2001).

## Materials and Methods

Preserved specimens of fruit representing the four genera were obtained from the L.

H. Bailey Hortorium (BH) and from A. K. Irvine (CSIRO, Atherton, Queensland, Australia). Fruits were embedded in a commercial paraffin-based embedding medium, and sectioned on a rotary microtome. Sections were floated onto gelatin-coated slides, dried, and stained with Safranin-O and Fast Green. Transverse sections were taken from the middle region of each fruit. Sections were photographed digitally, and simplified, semi-diagrammatic line drawings were derived from them. These are intended to show accurately the size, distribution and composition of the different tissue regions but not cellular detail. A very limited amount of material was available for each species, so the specimens described here should be recognized as single-point samples for species that are certainly variable.

## Results

As a whole, the Linospadicinae displays the same types of pericarp tissues and the

same trends of specialization as other groups of pseudomonomerous arecoid palms from the Pacific area. The occurrence of fibrous bundles and fibrous vascular bundle sheaths is common and quite variable in this group, ranging from long, axially oriented bundles in the middle to inner pericarp in all genera to short, radially oriented bundles in the subepidermal region in some species of *Calyptrocalyx*. Vascular bundles are also variable, with naked vascular bundles in some species and bundles with rounded to flattened fibrous sheaths in others.

Brachysclereids have been found only in *Calyptrocalyx* and *Howea*, in the latter forming a thick protective mantle in the outer pericarp. Tanniniferous and raphide-bearing cells are widespread but quite variable in their occurrence, distribution and abundance. The locular epidermis is thin and inconspicuous in this subtribe, except in *Howea*, where it forms a thick palisade layer of closely packed macrosclereids. Sclerified parenchyma, common in the inner fruit region of some other subtribes (e.g., Ptychospermatinae: Essig, 1977), is unknown in this group.

The representative specimens are discussed in more detail below. Unless otherwise noted, information on numbers and distribution of species is from Uhl and Dransfield (1987).

1. *LACCOSPADIX AUSTRALASICA* H. Wendl. & Drude (Australia: Queensland, *Irvine s.n. SFR 194*, BRI). A monotypic genus from northeastern Australia. (Fig. 1)

Fruit ovoid, 8 mm diam., 12 mm long, with pericarp 0.6 mm thick, stigmatic remains apical. Pericarp is distinctive for the very large raphide-bearing cells that fill the outer half of the pericarp and for the lack of brachysclereids and tanniniferous cells in the outer pericarp; fibrous bundles large, tereete to slightly radially distended, in a single series just below mid-pericarp, vascular bundles somewhat flattened, with moderately thick fibrous sheaths, in a single series along with small, flattened, tanniniferous cells in the inner pericarp; locular epidermis sclerified but thin.

2. *LINOSPADIX MONOSTACHYA* H. Wendl. (Australia: New South Wales, *Irvine 1820*, BRI). One of seven species (five in Australia, two in New Guinea; Dowe & Fererro, 2001. (Fig. 2)

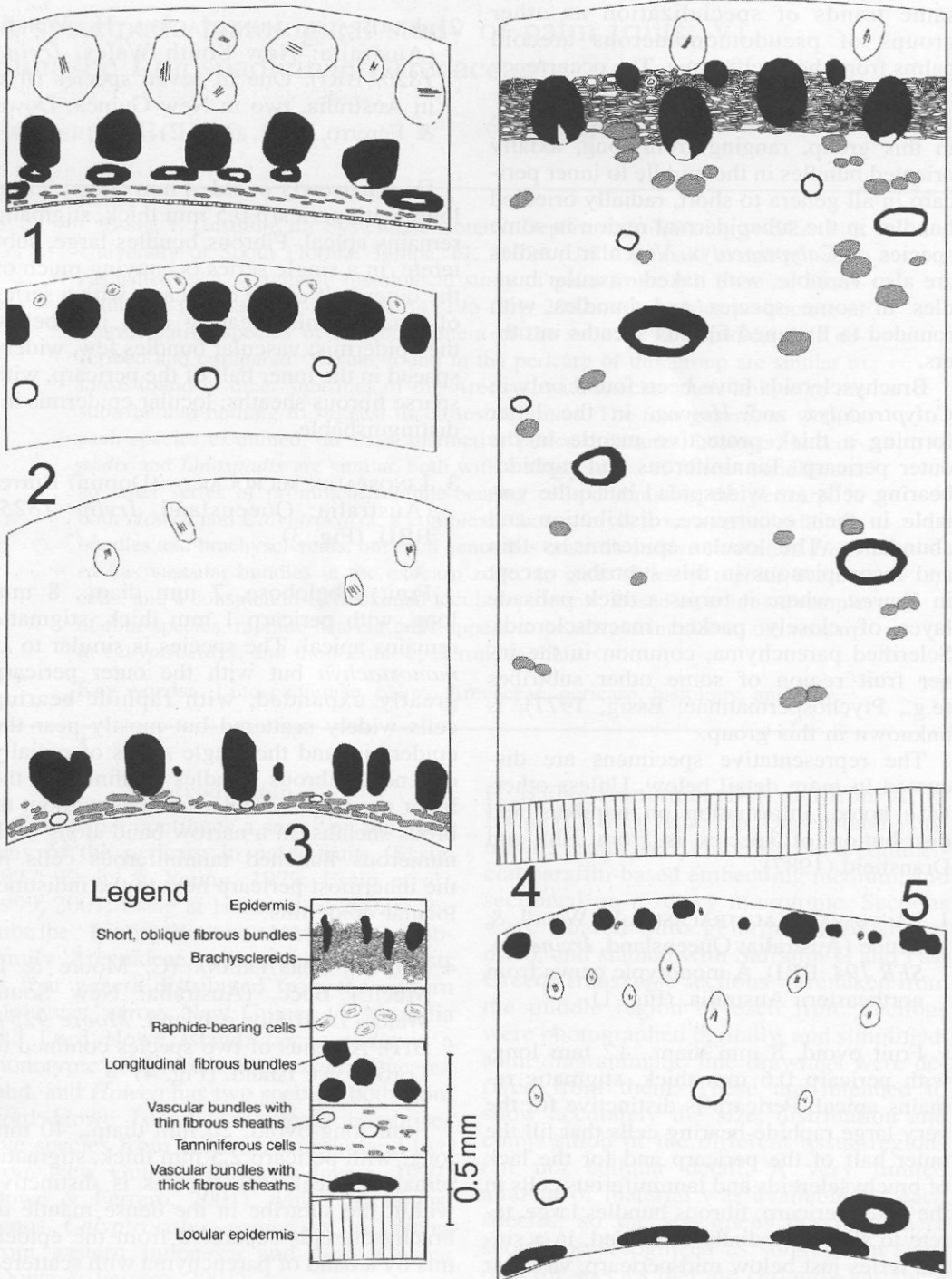
Fruit narrowly ovoid, 4 mm diam., 9 mm long, with pericarp 0.5 mm thick, stigmatic remains apical. Fibrous bundles large, subterete, in a single series occupying much of the outer half of the endocarp, with a series of small raphide-bearing cells just below the epidermis; vascular bundles few, widely spaced in the inner half of the pericarp, with sparse fibrous sheaths; locular epidermis indistinguishable.

3. *LINOSPADIX MICROCARYA* (Domin) Burret (Australia: Queensland, *Irvine 1825*, BRI). (Fig. 3)

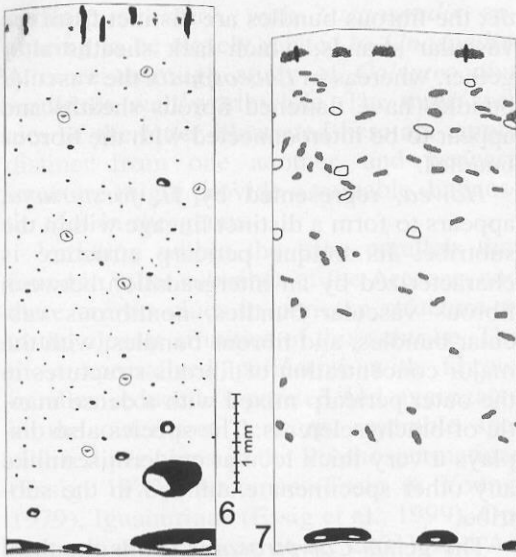
Fruit subglobose, 7 mm diam., 8 mm long, with pericarp 1 mm thick, stigmatic remains apical. The species is similar to *L. monostachya* but with the outer pericarp greatly expanded, with raphide-bearing cells widely scattered but mostly near the epidermis, and the single series of radially distended fibrous bundles confined to the inner pericarp; vascular bundles without fibrous sheaths, in a narrow band along with numerous flattened tanniniferous cells in the innermost pericarp next to the indistinct locular epidermis.

4. *HOWEA FORSTERIANA* (C. Moore & F. Muell.) Becc. (Australia: New South Wales, Lord Howe Island, *Moore 9254*, BH). A genus of two species confined to Lord Howe Island. (Fig. 4)

Fruit long-ovoid, 20 mm diam., 40 mm long, with pericarp 2.5 mm thick, stigmatic remains apical. The species is distinctive within the subtribe in the dense mantle of brachysclereids separated from the epidermis by a band of parenchyma with scattered raphide-bearing cells; vascular bundles with thick fibrous sheaths intermixed with fibrous bundles and embedded within the mantle of brachysclereids; vascular bundles with thinner fibrous sheaths scattered



FIGS. 1-5. 1. *Laccospadix australasica* H. Wendl. & Drude (from Irvine s.n. SFR 194, BRI). 2. *Linospadix monostachya* H. Wendl. (from Irvine 1820, BRI). 3. *Linospadix microcarya* (Domin) Burret (from Irvine 1825, BRI). 4. *Howea forsteriana* Becc. (from Moore 9254, BH). 5. *Calyptrocalyx lepidotus* (Burret) Dowe & M. D. Ferrero (from Essig & Young LAE 74033, BH, USF).



FIGS. 6-7. 6. *Calyptrocalyx albertisianus* Becc. (from Essig LAE 55171, BH). 7. *Calyptrocalyx lauterbachianus* Warb. ex Becc. (from Moore 9261, BH).

throughout the middle and inner pericarp, along with scattered tanniferous cells; distinctive also within the subtribe in the very thick palisade-like locular epidermis.

5. CALYPTROCALYX LEPIDOTUS (Burret) Dowe & M. D. Ferrero (Papua New Guinea: Western Province, Nomad, Essig & Young LAE 74033, BH, USF). One of 26 species distributed in eastern Indonesia and New Guinea (Dowe & Ferrero, 2001). (Fig. 5)

Fruit long-ovoid, 3.5 mm diam., 7 mm long, with pericarp 1 mm thick, stigmatic residue apical. Fibrous bundles subterete, varied in diameter, and in a single series just below the epidermis with sparsely scattered brachysclereids; raphide-bearing cells large and scattered throughout the mid to outer pericarp, along with a few vascular bundles with thin fibrous sheaths; vascular bundles with thick, strongly flattened fibrous sheaths in one to two series pressed against the indistinct locular epidermis.

6. CALYPTROCALYX ALBERTISIANUS Becc. (Papua New Guinea: Central Province, Essig LAE 55171, BH). (Fig. 6)

Fruit ovoid, 28 mm diam., 55 mm long, with pericarp 5 mm thick, stigmatic residue apical. This species is quite different from the preceding species, with a series of short, radially oriented fibrous bundles and widely scattered brachysclereids just below the epidermis, a lack of tanniferous cells, and numerous very narrow longitudinal fibrous bundles and scattered raphide-bearing cells throughout the middle pericarp; vascular bundles with thick fibrous sheaths, mostly flattened against the thin sclerified locular epidermis, but with a few large, rounded bundles scattered outward in the inner 1/4 of the pericarp, and occasional very small bundles through the outer and middle pericarp.

Note: The pericarp of *Calyptrocalyx hollrungii* H. E. Moore (based on Moore & Henty 9274, BH) is similar to that of *C. albertisianus*, but not as thick (2-3 mm), with many large tanniferous cells, and no longitudinal fibrous bundles in the middle pericarp.

7. CALYPTROCALYX LAUTERBACHIANUS Warb. ex Becc. (Papua New Guinea: Morobe Province. Moore & Millar 9261, BH). (Fig. 7)

Fruit ovoid, 20 mm diam., 30 mm long, with pericarp 4.5 mm thick, stigmatic residue apical. This species differs from the preceding in the lack of fibrous bundles in the pericarp, except for the series of short, radial bundles just below the epidermis, the more abundant brachysclereids in the sub-epidermal region, and the presence of numerous tanniferous cells throughout, and the presence of two kinds of vascular bundles, a multiseriate system in the outer 2/5 of the pericarp that lack fibrous sheaths, and another series of with extensive flattened fibrous sheaths pressed against an indistinct locular epidermis.

### Discussion

On morphological grounds, the genera of the Linospadicinae appear to form a fairly close-knit and most likely monophyletic group. They share a distinctive set of characters including long-pedunculate, spicate

inflorescences with the flowers sunken into pits in the thick rachis, a lack of crownshafts, and a similar flower structure (Uhl & Dransfield, 1987). Phylogenetic studies based on DNA (Asmussen & Chase, 2001; Hahn, 2002; Lewis & Doyle, in press; Savolainen et al., unpubl. data) are shedding light on the relationships among palms, but are somewhat inconclusive with respect to affinities of the *Linospadiaceae*. None of the studies included all four genera of the subtribe, but collectively (except for Hahn, 2002) they appear to support the monophyly of the group. Each genus has been represented in at least one analysis, and has consistently fallen into the major clade of pseudomonomerous arecoid palms, among genera of the southwest Pacific and Australian area.

Precise relationships are less clear, with *Heterospatha* indicated as the sister group of *Linospadiaceae* in Lewis and Doyle (in press), *Gronophyllum* as sister group of *Linospadiaceae* and *Laccospadiaceae* in Asmussen and Chase (2001), and with *Howea* and *Calypstrocalyx* non-monophyletic within a clade that includes Iguanurinae, Archontophoenicinae and Ptychospermatinae in one analysis (18S nuclear DNA region) presented by Hahn (2002), although widely separated in another analysis (atpB+rbcl chloroplast DNA regions) in the same paper.

Pericarp structure varies significantly within the *Linospadiaceae*, helping to elucidate relationships within the group, but with no clear clues as to relationships outside of the group. Tissues and trends of specialization are similar to those in other subtribes of the *Areceae*, providing another example of the remarkable parallelism to be found within this tribe, and the rarity of apomorphic characters at the subtribal level.

Within the *Linospadiaceae*, the genera can be placed into three groups on the basis of pericarp structure. One group includes *Laccospadiaceae* and *Linospadiaceae*, characterized by a series of large subterete fibrous bundles found variably from the inner to the outer pericarp, and by a distinctive series of raphide-bearing cells in the outermost pericarp. There are, however, some key differences between the two genera. In *Linospa-*

*dix* the fibrous bundles are distinct from the vascular strands, which lack sheaths altogether, whereas in *Laccospadiaceae* the vascular bundles have flattened fibrous sheaths and appear to be interconnected with the fibrous bundles.

*Howea*, represented by *H. forsteriana*, appears to form a distinct lineage within the subtribe. Its unique pericarp structure is characterized by an intergradation between fibrous vascular bundles, nonfibrous vascular bundles, and fibrous bundles, with the major concentration of fibrous structures in the outer pericarp mixed with a dense mantle of brachysclereids. The species also displays a very thick locular epidermis, unlike any other specimens examined in the subtribe.

The genus *Calypstrocalyx* forms the third group within the subtribe. This is a large genus, and further study may reveal considerable variation, but the three species illustrated here have several features in common: The fibrous bundles are mostly confined to the subepidermal zone and can be considered to form an exocarp, while the vascular bundles are primarily located in the innermost pericarp, have flattened fibrous sheaths, and can be considered part of the endocarp. In all three species, however, there are also vascular bundles, mostly without fibrous sheaths, scattered throughout the mesocarp. Raphide-bearing cells are interior to the outer fibrous bundles, unlike in *Linospadiaceae* and *Laccospadiaceae*. Brachysclereids are present around the fibrous bundles below the epidermis, but not as thick as in *Howea*. In *C. lepidotus*, the fibrous bundles appear to be essentially parallel with the surface, subterete, and elongate, similar to the fibrous bundles in *Linospadiaceae*. In *C. albertisianus* and *C. lauterbachianus*, the outer fibrous bundles are short and oblique or perpendicular to the surface, a specialized condition also seen in some genera in nearly every other subtribe of the *Areceae*. Additionally, in *C. albertisianus* there are numerous very narrow fibrous bundles running axially throughout the mesocarp.

In short, based on this limited sampling, it appears that the genera of this subtribe can be readily distinguished on the basis of

pericarp structure, with *Laccospadix* appearing to be closely related to *Linospadix*. A more thorough study of *Calyptrocalyx* would be well worthwhile. The three species of the latter illustrated here are amply distinct from one another, and pericarp structure might provide a valuable diagnostic tool in the genus.

Variation within the tribe parallels that found in other subtribes of the Areceae, and there are no clues in pericarp structure as to the closest affinities of this subtribe. The most specialized pericarps, with fibrous bundles reduced, separated and aggregated in the outermost pericarp, resemble specialized pericarps in the Ptychospermatinae (Essig, 1977), Arecinae (Essig & Young, 1979), Iguanurinae (Essig et al., 1999), Oncospermatinae (Essig et al., 2001), and Archontophoenicinae (Essig & Hernandez, in press), but in each of these subtribes there are also pericarps with elongate, interconnected fibrous bundles, sometimes associated directly with the vascular system, ranging from the middle to outer pericarp. The significance of this remarkable parallelism remains a mystery.

### Acknowledgments

I thank Nicole Hernandez for technical help with the early stages of this project, John Dowe for commenting on an early draft of the paper and for his help with identifying some of the specimens. I thank also Bill Baker and Carl Lewis for suggestions concerning the phylogenetic relation-

ships of the group. I thank also the L. H. Bailey Hortorium at Cornell University, and Tony Irvine of the CSIRO at Atherton, Queensland, Australia, for providing many of the specimens examined.

### Literature Cited

- Amussen, C. B. & M. W. Chase. 2001. Coding and noncoding plastid DNA in palm systematics. *Amer. J. Bot.* 88: 1103–1117.
- Dowe, J. L. & M. D. Ferrero. 2001. Revision of *Calyptrocalyx* and the New Guinea species of *Linospadix* (Linospadiaceae: Arecoideae: Arecaceae). *Blumea* 46: 207–251.
- & A. K. Irvine. 1997. A revision of *Linospadix* in Australia, with the description of a new species. *Principes* 41: 192–197, 211–217.
- Essig, F. 1977. A systematic histological study of palm fruits. I. The *Ptychosperma* alliance. *Syst. Bot.* 2: 151–168.
- & N. Hernandez. 2002. A systematic histological study of palm fruits. V. Subtribe Archontophoenicinae (Arecaceae). *Brittonia* 54: 65–71.
- & B. Young. 1979. A systematic histological study of palm fruits. II. The *Areca* alliance. *Syst. Bot.* 4: 16–28.
- , T. Manka & L. Bussard. 1999. A systematic histological study of palm fruits. III. Subtribe Iguanurinae (Arecaceae). *Brittonia* 51: 307–325.
- , L. Bussard & N. Hernandez. 2001. A systematic histological study of palm fruits. IV. Subtribe Oncospermatinae (Arecaceae). *Brittonia* 53: 466–471.
- Hahn, W. J. 2002. A molecular phylogenetic study of the Palmae (Arecaceae) based on atpB, rbcL and 18S nr DNA sequences. *Syst. Biol.* 51: 92–112.
- Lewis, C. E. & J. J. Doyle. In press. A phylogenetic analysis of tribe Arecaceae (Arecaceae) isomg twp pw-copy nuclear genes. *Pl. Syst. Evol.*
- Uhl, N. & J. Dransfield. 1987. *Genera Palmarum: a classification of palms based on the work of Harold E. Moore, Jr. L. H. Bailey Hortorium and the International Palm Society, Ithaca, New York; Allen Press, Lawrence, Kansas.*