

A systematic histological study of palm fruits. V. Subtribe Archontophoenicinae (Arecaceae)

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Essig, F. & N. Hernandez (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). A systematic histological study of palm fruits. V. Subtribe Archontophoenicinae (Arecaceae). *Brittonia* 54: 65–71. 2002.—Pericarp histology in the Archontophoenicinae provides little to characterize the subtribe as a whole, revealing instead two separate trends with parallels in other subtribes of the Areceae. The data support a close relationship among the three genera occurring in New Caledonia: *Chambeyronia*, *Actinokentia*, and *Kentiopsis*, in which there is a complex endocarp consisting of short, oblique fibrous bundles embedded in a thick mantle of brachysclereids, and a loose endocarp of heavily fibrous, flattened vascular bundles adjacent to a relatively thin locular epidermis. The data also support a close relationship between the two genera of the New Zealand/Tasman Sea region: *Hedyscepe* and *Rhopalostylis*, in which the pericarp is more or less fibrous throughout, with purely fibrous bundles in the outer pericarp and heavily fibrous vascular bundles in the inner pericarp. These results confirm relationships revealed by other morphological data. *Archontophoenix* appears to be most like the New Caledonian genera in its pericarp structure, with a similar mantle of short fibrous bundles embedded in a mantle of brachysclereids in the outer pericarp, although it differs significantly in other aspects of morphology and anatomy.

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

Introduction

The subtribe Archontophoenicinae (Arecaceae, subfamily Arecoideae, tribe Areceae) consists of six genera distributed from Australia to New Zealand and New Caledonia. The subtribe is considered a rather homogeneous group morphologically. All have well-developed crownshafts; acute pinnae; prophyll and peduncular bracts that are similar in shape and size; infrafoliar inflorescences with short, stout peduncles; and pseudomonomerous fruit with apical stigmatic residue (Pintaud, 1999). Three of the genera (*Chambeyronia*, *Actinokentia*, and *Kentiopsis*) are confined to New Caledonia, and these appear to form a natural group, based on distinctive leaf anatomy

(Uhl & Dransfield, 1987) and the cladistic analysis based on morphology and anatomy conducted by Pintaud (1999). A fourth genus, *Mackeeia* has recently been included in *Kentiopsis* (Pintaud & Hodel, 1998). In that same cladistic analysis, *Rhopalostylis* and *Hedyscepe*, from the New Zealand/Tasman Sea area, are also found to form a well-defined clade. The affinities of the Australian genus *Archontophoenix* are less certain. It forms a distinct lineage that may be basal to the rest of the subtribe (Pintaud, 1999) or, in a revised analysis (Pintaud, unpubl. data), basal to the New Caledonian clade.

This investigation of the pericarp anatomy of the Archontophoenicinae continues a survey of the subtribes of the tribe Areceae, with the aim of helping to clarify relationships among these groups. Previous inves-

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tigations have found that pericarp tissues, including various forms of sclerenchyma, tanniferous cells, and raphide-bearing cells, form in patterns that are distinctive primarily at the species and generic levels (Essig, 1977, 1982, 1999; Essig & Young, 1979, 1985; Essig et al., 1999, 2001), with much apparent parallelism at higher levels.

Materials and Methods

Preserved specimens of fruit representing all six genera were obtained from the L. H. Bailey Hortorium (BH) and from Jean-Christophe Pintaud (Centre IRD, Montpellier, France). Fruits were prepared for paraffin embedding using standard methods, and stained with safranin 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. In some cases, specimens were difficult to section due to the juxtaposition of hard and soft tissues or to the climacteric deterioration of soft tissues in fully ripened fruit samples, and the drawings represent reconstructions based on fragmentary microtomed sections supplemented with hand sections.

In some cases, only a single fruit specimen, or several fruits from the same tree, have been available for study. Where more than one specimen was available, quantitative variation (relating to variation in fruit size) was observed, but no significant qualitative variation was seen. Fruit size and pericarp thickness given in the descriptions or represented in the drawings should be recognized as single-point samples for species that are certainly variable.

Results

The fruits of the Archontophoenicinae show the same range of tissues found in other subtribes of the Areceae. In general, the locular epidermis is thinner in this group than in most others, and the fibrous sheaths of the vascular bundles are generally thicker than in most.

Aside from those few generalizations, there appears to be a sharp division within the subtribe. The New Caledonian genera (*Actinokentia*, *Chambeyronia*, and *Kentiopsis*) and the Australian *Archontophoenix* possess a series of short, oblique to radial fibrous bundles embedded in a thick mantle of brachysclereids. In the three New Caledonian genera this mantle is clearly positioned as a complex exocarp (a layer of protective tissues adjacent and closely adherent to the epidermis). The short fibrous bundles press against the epidermis of the fruit, giving it a "pebbled" appearance when dry.

In *Archontophoenix*, the mantle varies in position from mid-pericarp to the subepidermal zone in the one fruit examined, and typically has much parenchyma and some large raphide-bearing cells between it and the epidermis. It is less clearly an exocarp but does adhere to the outer pericarp as the fruit dries, sometimes giving it a pebbled appearance.

The system of fibrous vascular bundles and/or purely fibrous bundles in the inner pericarp of the latter four genera tend to form a complex endocarp (a region of protective tissues adjacent to, and generally adhering to, the seed). The vascular bundles, and in particular their very thick fibrous sheaths, tend to be flattened, or greatly distended tangentially, and in *Chambeyronia* the parenchyma between the bundles is compressed and sclerified when mature.

Rhopalostylis and *Hedyscepe*, on the other hand, have pericarps that are fibrous throughout, with long, terete, bundles of fibers running longitudinally through the outer pericarp, and a mixture of possibly interconnected fibrous bundles and fibrous vascular bundles in the inner pericarp. The two genera lack brachysclereids altogether. Neither endocarp nor exocarp can therefore be recognized.

The genera are discussed individually below. Unless otherwise noted, information on numbers and distribution of species is from Uhl and Dransfield (1987).

1. *Rhopalostylis sapida* H. Wendl. & Drude (New Zealand: Pintaud 402, K, NY). One of two or three species from New

Zealand, Chatham, Norfolk, and Raoul Islands (Fig. 1).

Fruit ovoid, 9 mm diam., 13 mm long, with pericarp 0.8–1.1 mm thick, stigmatic remains apical—remarkable for the continuous system of fibrous vascular bundles and longitudinal fibrous bundles, the two types of bundles intermixed and moderately flattened in the inner pericarp, becoming totally fibrous and nearly terete in the outer pericarp; further characterized by raphide-bearing cells scattered throughout the outer 2/3 of the pericarp, the lack of any brachysclereids or tanniferous cells in the pericarp, and a very thin locular epidermis.

A specimen of *Rhopalostylis baueri* H. Wendl. & Drude (*Pintaud* 384, NY) exhibits very similar structure but has a thicker pericarp with many more fibrous bundles.

2. *Hedyscepe canterburyana* (C. Moore & F. Muell.) H. Wendl. & Drude (Lord Howe Island: *Moore & Schick* 9252, BH). A monotypic genus (Fig. 2).

Fruit ovoid, 28 mm diam., 43 mm long, with pericarp 1.65–1.75 mm thick, stigmatic remains apical—very similar to *Rhopalostylis sapida*, with a few small, terete fibrous bundles intermixed with flattened, heavily sheathed vascular bundles in the inner pericarp, and numerous totally fibrous bundles in the outer 1/3 of the pericarp, and a series of vascular bundles with very thin fibrous sheaths in mid-pericarp, and a lack of brachysclereids throughout; further characterized by the numerous small tanniferous cells clustered around the bundles in the middle pericarp and scattered through the inner pericarp, raphide-bearing cells primarily in a band below the outer epidermis, and a moderately thin locular epidermis.

3. *Archontophoenix cunninghamiana* (H. Wendl.) H. Wendl. & Drude (cult., California: *Pintaud* 449, TL). One of six species, all from eastern Australia (cf. Dowe & Hodel, 1994) (Fig. 3).

Fruit globose, 11 mm diam., with pericarp 1–1.2 mm thick, stigmatic remains apical—differing sharply from the preceding

two genera by the presence of only a single series of short fibrous bundles embedded in a dense mantle of brachysclereids variably positioned in the subepidermal to mid-pericarp regions; further characterized by a series of raphide-bearing cells between the mantle and the outer epidermis, by flattened vascular bundles with extensive fibrous sheaths occupying the inner 1/3 of the pericarp, by tanniferous cells forming continuous sheets over the large vascular bundles and scattered between the bundles, and by a very thin locular epidermis.

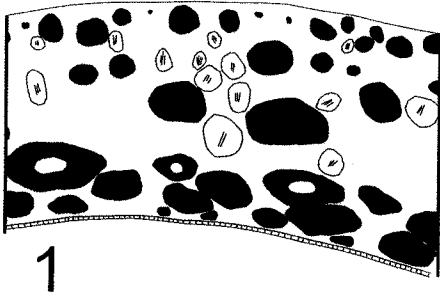
4. *Chambeyronia macrocarpa* (Brongn.) Vieill. ex Becc. (New Caledonia: *Pintaud* 308, K, NY, P). One of two species, both from New Caledonia (Fig. 4).

Fruit ovoid, 30 mm diam., 55 mm long, with pericarp 2.4 mm thick, stigmatic remains apical—as in the following genera, fibrous bundles are short, oblique, embedded in a mass of brachysclereids, and located just below the outer epidermis; further characterized by the presence of additional, larger brachysclereids scattered just below the outer mantle, scattered clusters of tanniferous cells in the inner pericarp, by a thick zone of sclerified parenchyma surrounding the inner vascular bundles, which are moderately flattened and have thick fibrous sheaths, and by a moderately thick locular epidermis.

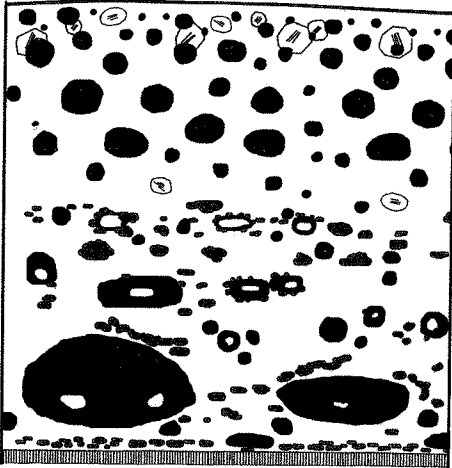
An additional specimen (*Moore* 9975, BH) has essentially the same structure, as does a slightly immature specimen of *Chambeyronia lepidota* H. E. Moore (*Moore & Schick* s.n., BH).

5. *Actinokentia divaricata* (Brongn.) Damer. (New Caledonia: *Pintaud* s.n., USF—pickled fruits only). One of two species, both from New Caledonia (Fig. 5).

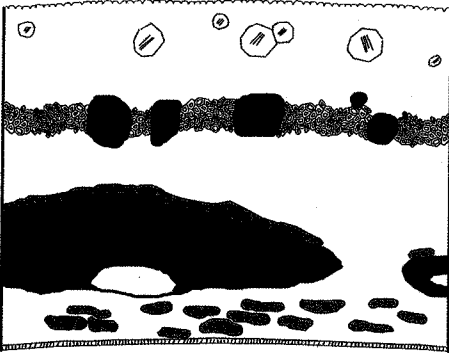
Fruit ovoid, 9 mm diam., 26 mm long, with pericarp 1.6 mm thick, stigmatic remains apical—resembling *Chambeyronia*, except that the vascular bundles are nearly terete, with very slender strands of vascular tissue surrounded by very thick sheaths, and occupying the inner half of the pericarp, lacking the larger sclereids below the



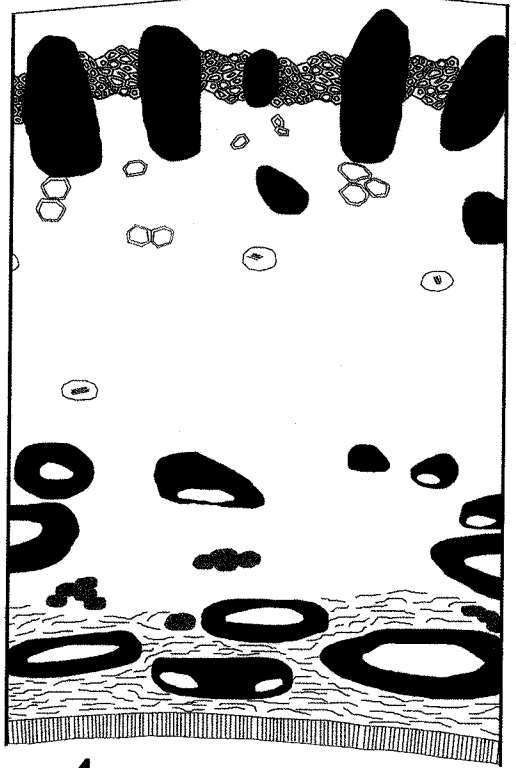
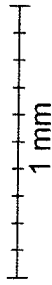
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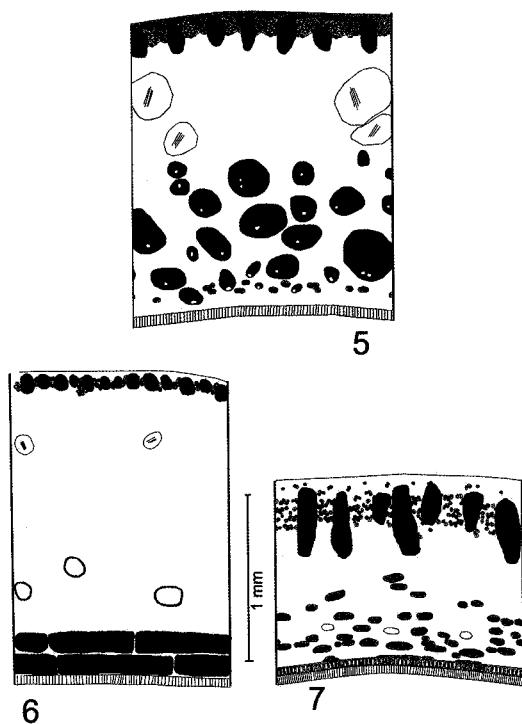


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Legend

- Epidermis
- Subepidermal tannin/pigment
- Short, oblique fibrous bundles
- Brachysclereids
- Raphide-bearing cells
- Longitudinal fibrous bundles
- Flattened fibrous bundles
- Vascular bundles with thin fibrous sheaths
- Tanniniferous cells
- Vascular bundles with thick fibrous sheaths
- Sclerified parenchyma
- Special endocarp sclereids
- Locular epidermis

FIGS. 1-4. 1. *Rhopalostylis sapida* (from Pintaud 402, K, NY). 2. *Hedysepe canterburyana* (from Moore & Schick 9252, BH). 3. *Archontophoenix cunninghamiana* (from Pintaud 449, TL). 4. *Chambeyronia macrocarpa* (from Pintaud 308, K, NY, P).



FIGS. 5-7. 5. *Actinokentia divaricata* (from *Pintaud s.n.*, USF). 6. *Kentiopsis oliviformis* (from *Pintaud 324*, BH, BRI, K, NY, P). 7. *Kentiopsis magnifica* (from *Moore 10054*, BH).

mantle and lacking the sclerified parenchyma in the inner pericarp; further characterized by rather large raphide-bearing cells and a thin series of tanniferous cells between the vascular bundles and the moderately thick locular epidermis.

6. *Kentiopsis oliviformis* (Brongn. & Gris) Brongn. (New Caledonia: *Pintaud 324*, BH, BRI, K, NY, P). One of four species, all from New Caledonia (Fig. 6). (See also *K. magnifica*, below.)

Fruit ovoid, 9 mm diam., 20 mm long, with pericarp 1.6 mm thick, stigmatic remains apical—remarkable for the two concentric rings of very flat fibrous bundles adjacent to the locular epidermis, with vascular bundles lacking fibrous sheaths in the inner 1/3 of the pericarp; further characterized by a thin subepidermal mantle of brachysclereids with embedded narrow, short fibrous bundles, a lack of tanniferous

cells, and a moderately thick locular epidermis.

7. *Kentiopsis magnifica* (H. E. Moore) Pintaud & Hodel (New Caledonia: *Moore 10054*, BH) (Fig. 7). (Until recently, recognized as a distinct genus, *Mackeea*; cf. Pintaud & Hodel, 1998.)

Fruit ovoid, 10 mm diam., 22 mm long, with pericarp 1 mm thick, stigmatic remains apical—similar to the preceding only in its vascular bundles, which lack sheaths and constitute a single series in the inner 1/3 of the pericarp, otherwise remarkably different: characterized by a unique continuous layer of short columnar sclereids pressed against the locular epidermis, and resembling it, giving the appearance of a double locular epidermis, the outer short fibrous bundles much larger and the mantle of brachysclereids more diffuse, and with numerous tanniferous cells in the inner 1/2 of the pericarp.

A specimen representing a third species, *Kentiopsis piersoniorum* Pintaud & Hodel (*Pintaud 309*, BH, P), has a structure intermediate between the two preceding species, with the outer fibrous bundles much larger and reaching to the middle pericarp (more like *K. magnifica*), and the vascular bundles with broad, flat, fibrous sheaths encircling the seed, as in *K. oliviformis*, but these not dissociated from the vascular bundles as in the latter species. It also lacks the peculiar layer of sclereids found next to the locular epidermis in *K. magnifica*. A specimen of *K. pyriformis* Pintaud & Hodel (*Pintaud 348*, BH, BRI, K, NOU, NY, P) has a structure most similar to *K. piersoniorum*, but with the fibrous vascular bundles more varied in size and not as flattened.

Discussion

Pericarp data support the monophyly of a New Caledonian clade including the genera *Actinokentia*, *Chambeyronia*, and *Kentiopsis*. These genera have similar complex exocarps of brachysclereids and short oblique fibrous bundles, as well as endocarps consisting primarily of the heavy sheaths of the vascular bundles and a mod-

est locular epidermis. Similar exocarps are found in *Ptychosperma* and related genera in the Ptychospermatinae (Essig, 1977), as well as in *Lepidorrhachis*, *Veillonina*, *Cyphosperma*, and *Physokentia* of the Iguanurinae (Essig et al., 1999), and in *Oncosperma* of the Oncospermatinae (Essig et al., 2001). The endocarp of *Chambeyronia*, which incorporates fibrous bundle sheaths and sclerified parenchyma, is also like that found in the Ptychospermatinae (Essig, 1977) and in *Neoveitchia* in the Iguanurinae.

The dramatic variation seen in the genus *Kentiopsis*—where an endocarp is formed of two concentric rings of flattened fibrous bundles in *K. oliviformis*, of flattened fibrous vascular bundles in *K. piersoniorum*, and of a unique “double” locular epidermis in *K. magnifica* (locular epidermis plus a layer of short macrosclereids)—indicates that variation within genera can be considerable and worthy of study. It also poses a challenge to us to discover the adaptive meaning of these tissue configurations.

The data also support the close relationship of *Rhopalostylis* and *Hedyscepe*, in which the dominant feature of the pericarp is the numerous longitudinal fibrous and fibrous vascular bundles, that form more or less a continuum from the outer epidermis to the locular epidermis. Notable also is the lack of brachysclereids in the pericarp of either genus. Similar systems of longitudinal fibrous bundles can be found in all of the subtribes studied so far, including *Veitchia* and *Normanbya* in the Ptychospermatinae (Essig, 1977), *Areca* in the Arecinae (Essig & Young, 1979), *Burretiokentia*, *Campecarpus*, *Cyphophoenix*, *Heterospatha*, *Neoveitchia*, and *Alsmithia* in the Iguanurinae (Essig et al., 1999), and *Tectiphiala* in the Oncospermatinae (Essig et al., 2001). Specific differences between the two genera are the lack of tannin cells in *Rhopalostylis*, contrasted with their abundance in the inner 1/2 of the pericarp in *Hedyscepe*, the much thicker locular epidermis in *Hedyscepe*, and the more numerous and thicker fibrous bundles in *Rhopalostylis*.

Archontophoenix appears to show greater similarity to the New Caledonian genera than to the two genera from the New Zea-

land/Tasman Sea area. It has short fibrous bundles embedded in a mantle of brachysclereids, as in the New Caledonian genera, but the fibrous bundles are more vertically oriented and not pressed against the epidermis as in those genera. However, the same combination of short fibrous bundles and brachysclereids occurs in a number of subtribes, so this pericarp data could equally well argue for affinities of *Archontophoenix* outside of the Archontophoenicinae.

Archontophoenix, in fact, remains isolated from the New Caledonian genera by other characters brought out by Pintaud's (1999) phylogenetic analysis. Particularly interesting is the pattern of inflorescence development, which differs starkly between the New Caledonian genera and the New Zealand/Tasman Sea/Australian genera. In *Archontophoenix*, *Hedyscepe*, and *Rhopalostylis*, the prophyll and peduncular bract that enclose the inflorescence in bud fall immediately before anthesis, and the flowers consequently are soft and minimally protected with sclerenchyma. In the New Caledonian genera, on the other hand, the bracts fall relatively early during the development of the inflorescence, leaving the flower buds exposed for much of their maturation. Consequently, the perianths of the latter flowers are much thicker, more tightly closed, and more heavily sclerified than those of the first group.

Elsewhere in the tribe, such differences in inflorescence development and floral structure separate entire subtribes. The Ptychospermatinae, for example, follows the pattern of the New Caledonian genera, while the Arecinae follows the pattern of *Archontophoenix*, *Hedyscepe*, and *Rhopalostylis*. The two contrasting development patterns have been related to profound differences in pollination mechanisms (Essig, 1973) and point to a potentially deeper division within the subtribe than is presently realized.

Archontophoenix therefore differs starkly from *Hedyscepe* and *Rhopalostylis* on the basis of fruit anatomy, and from *Chambeyronia*, *Actinokentia*, and *Kentiopsis* on the basis of other morphological characters. Its real affinities within the subtribe are thus not clear, and the data do not preclude the

possibility that *Archontophoenix* could have affinities outside of the subtribe.

There is no conclusive evidence from fruit anatomy either for the monophyly of the Archontophoenicinae in particular or for relationships among the subtribes of the Areceae in general. Study of fruit anatomy does, however, corroborate the monophyly of small groups of genera, while at the same time providing a basis for provocative alternate hypotheses of relationship amongst these palms. Anatomical data from the fruit, in combination with other types of data, clearly will be of value in ongoing phylogenetic studies of palms and, in particular, in the elucidation of relationships among the subtribes of Areceae.

Acknowledgments

We gratefully acknowledge the assistance of Jean-Christophe Pintaud for providing fruit specimens, along with other advice and assistance, and the L. H. Bailey Hortorium, Cornell University, for some additional specimens.

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