A systematic histological study of palm fruits. III. Subtribe Iguanurinae (Arecaceae)

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Essig, F., T. Manka & L. Bussard (Institute for Systematic Botany, Department of Biology—SCA 110, University of South Florida, Tampa, FL 33620, U.S.A.). A systematic histological study of palm fruits. III. Subtribe Iguanurinae (Arecaceae). Brittonia 51: 307–325. 1999.—This study represents a preliminary sampling of the pericarp histology of the subtribe Iguanurinae (tribe Areceae, subfamily Arecoideae) of the family Arecaceae. At least one sample from each of the 27 recognized genera was examined and illustrated with a line drawing. This sampling serves to characterize fruit structure in the subtribe as a whole, to illustrate the diversity of pericarp adaptations found in the subtribe, to characterize the monotypic genera, to provide hypotheses about the characterization of the larger genera, and to test existing phylogenetic hypotheses about the Iguanurinae. There are no unique tissues present in the pericarp in this subtribe, but genera can be readily characterized by unique combinations and distributional patterns in common tissues. These patterns, and some prominent evolutionary trends, parallel those in related subtribes of Areceae, such as the Ptychospermatinae and Arecinae. Significant in this subtribe is variation in the distribution of tanniniferous cells, raphide-bearing cells and brachysclereids, in the sculpturing of the seed and the locular epidermis, in the thickness of the locular epidermis, in the thickness of the fibrous vascular bundle sheaths, and especially in the number, orientation and distribution of nonvascular fibrous bundles. One major trend is the formation of systems of separate fibrous bundles and their progressive displacement toward the outer layer of the fruit, where a complex exocarp may form. The diversity of pericarp structure in the Iguanurinae is far greater than in the two subtribes previously studied.

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

Introduction

This study represents a continuation of a survey of the pericarp histology in the palm family. Following the pioneering survey of Guerin (1949), and important contributions from Murray (1971, 1973), more detailed surveys of the subtribes Ptychospermatinae (as the *Ptychosperma* alliance; Essig, 1977) and Arecinae (as the *Areca* alliance; Essig & Young, 1979, 1985; Essig, 1982) were conducted, which revealed great diversity in the histological structure of the palm pericarp. A broad summary for the family has recently been presented by Essig

(1999). Genera, and sometimes species, have been shown to possess distinctive, recognizable combinations of histological characters, suggesting a high degree of taxonomic resolution for pericarp structure, although resolution at higher levels has been complicated by evident extensive parallelism.

Palm fruits most often consist of a fleshy pericarp surrounding a single large seed. The pericarp may be dry and fibrous in some taxa (e.g., *Cocos nucifera* L.), and more than one seed per fruit can be found in a number of taxa (e.g., *Orania, Attalea, Phytelephas*). Frequently a hard endocarp of varied histological composition is pres-

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ent, as well as a distinctive exocarp. The mesocarp may be soft and succulent or fibrous. Variation in pericarp histological characters includes the thickness of the pericarp; presence or absence of a sclerified, thickened locular epidermis (consisting of radially elongate epidermal cells); varying degrees of sclerification and radial compression of the inner pericarp parenchyma; the number, size, shape, and distribution of vascular bundles in the pericarp; the thickness and shape of fibrous bundle sheaths around the vascular bundles; the number, shape, orientation, and distribution of nonvascular fibrous bundles (sometimes called "sclerosomes" when very short, e.g., Uhl & Dransfield, 1987: 146); and the size, number, and distribution of brachysclereids, raphide-bearing cells, and tanniniferous cells. The "tannins" in palm fruits have not been chemically analyzed and may consist of more than one compound. The term is used here for any dark reddish brown, amorphous material stored in the cell's vacuole, following Uhl & Moore (1973). Dark layers of pigmented tissue just below the epidermis may consist of both tannin and other pigments that are difficult to distinguish in ordinary slide preparations.

The variability and distinctiveness of palm pericarps are due mainly to different combinations of characters, rather than to the presence of unique or unusual characters in particular taxa (Essig, 1999). As such, parallelism in the evolution of various tissue patterns is quite probable.

Two particular trends that appear to have happened many times in the palms are the development of dense, histologically complex endocarps and the not necessarily coordinated development of complex exocarps, both primarily from several types of sclerenchyma. The terms endocarp and exocarp have both been used in varying ways (see Essig, 1977, for discussion).

As most commonly employed, the term endocarp refers to any fibrous, woody or bone-like covering around the seed, that generally persists after the soft parts of the fruit have been removed. Histologically, the endocarp is a distinct, generally sclerenchymatous mantle of tissue closely appressed to the seed. In the Ptychospermatinae (Es-

sig, 1977) this almost always means a complex structure consisting of locular epidermis, fibrous vascular bundle sheaths, and compressed and sclerified ground tissue. In the Arecinae (Essig & Young, 1979) complex endocarps are found in only a few genera, and these are not as well-developed as those in the Ptychospermatinae.

An exocarp is generally defined as a distinct zone of tissue just below the epidermis (Murray, 1971; Essig, 1977). The similar term, epicarp (as in Uhl & Dransfield, 1987), has been defined variously (Essig, 1977), and has often been confused with the exocarp. An epicarp is usually defined as including the epidermis along with underlying tissues, or may refer only to a specialized epidermal layer.

Where distinct exocarps are present, they tend to form early during the development of the fruit, and consist of idioblastic sclereids, tanniniferous cells, or crystal-bearing cells, along with short, disconnected fibrous bundles that can separate during the final, sometimes dramatic, expansion associated with ripening. In contrast, endocarp tissues tend to form in continuous masses that only mature after the seed has reached its full size.

Endocarp, mesocarp, and exocarp are not always clearly defined, and care must be taken not to confuse these zones with particular tissue. The same tissues that commonly make up endocarps and exocarps may be variously dispersed through the pericarp, or may form distinct bands in varying positions. Dense bands of brachysclereids, for example, are an important component of the complex exocarps found in the tribe Ptychospermatinae (Essig, 1977), but commonly form mantles in the middle of the mesocarp in fruits of the Corypheae (Essig, 1999). It is appropriate to first describe the actual distribution of tissues, and then to determine whether these tissues can be meaningfully interpreted as parts of distinct zones. That will be the practice in this paper.

The Iguanurinae, of the tribe Areceae, subfamily Arecoideae (Uhl & Dransfield, 1987), contains 27 genera and ca. 125 species. The greatest diversity is found in New Caledonia, but representatives are distrib-

uted throughout the western Pacific, New Guinea, Indonesia, and as far west as southern India and the Mascarene Islands. The Iguanurinae has the largest number of genera, the widest geographic range, and the greatest range of vegetative, floral, and fruit characters of any of the subtribes of the Areceae. Its position relative to other subtribes is of great interest.

As in other members of the tribe, the gynoecium in the Iguanurinae is pseudomonomerous (having one fertile carpel, but with parts of two other carpels present). A number of morphological characters that are stable in the Ptychospermatinae and Arecinae are variable in this subtribe. For example, the position of the stigmatic remains on the mature fruit varies from basal to apical, and the leaf sheath varies from fibrous and open to fully tubular (forming a crownshaft). The inflorescences tend to be long-pedunculate and interfoliar where the leaf sheaths are open, and short-pedunculate and infrafoliar when a crownshaft is present. The Iguanurinae is also more variable with respect to arrangement of the flowers on the rachillae and in details of floral structure than most other subtribes. The Oncospermatinae shows a variation in these characters similar to that in the Iguanurinae, and the two subtribes also apparently share a conspicuous synapomorphy, the possession of an operculum on the endocarp. For this reason, the Oncospermatinae are considered the closest relative of the Iguanurinae (Uhl & Dransfield, 1987).

A preliminary phylogenetic analysis of the Iguanurinae, using 37 morphological characters, has been recently completed (Pintaud, 1999). Pintaud chose as outgroups three unspecialized and unrelated genera: *Orania* and *Leopoldinia*, each with three fertile locules, and *Dypsis*, with one fertile and two sterile locules. Such gynoecia are logical predecessors to pseudomonomerous gynoecia, and according to Pintaud (1999), the three genera share many of the plesiomorphic morphological characters of the tribe Areceae. The objective of the analysis was to shed light on the biogeography and monophyly of the New Caledonian genera of the Iguanurinae, rather than to generate detailed phylogenetic conclusions, and further analysis is planned.

Pintaud (1999) concluded that the New Caledonian genera do fall within one major clade, which in turn splits into two well-defined lesser clades. *Lavoixia, Clinosperma, Brongniartikentia, Cyphokentia,* and *Moratia* form one close-knit clade; and *Cyphosperma, Basselinia, Burretiokentia, Cyphophoenix, Campecarpus,* and *Veillonia* form another well-supported clade. A small, more problematic, clade at the base of the main New Caledonian clade contains *Alloschmidia* and the non-New Caledonian genera *Bentinckia* and *Lepidorrhachis.*

Positions of the non-New Caledonian genera are not well-supported, according to Pintaud (1999), but all branch off variously below the main New Caledonian clade. *Pelagodoxa, Sommieria,* and *Iguanura,* all with open leaf sheaths and fruit with basal stigmatic remains, branch off near the bottom of the cladogram, while genera with well-developed crownshafts and fruit with apical stigmatic remains occupy the higher clades. A high level of homoplasy amongst the morphological characters indicates the need for the addition of new types of data, including pericarp histology. Pintaud's (1999) analysis does, however, provide a general framework within which to discuss histological data, and also provides a general "arrow" for the major trends of specialization within the group.

Materials and Methods

Fruit specimens, preserved in alcohol, were obtained primarily from the collection of the L. H. Bailey Hortorium (BH), at Cornell University. As materials were limited, a single fruit per collection was sectioned. All 27 of the recognized genera of the Iguanurinae were represented in the study, and in a few cases additional species were examined. *Goniocladus,* listed under this subtribe in Uhl & Dransfield, 1987, has recently been conclusively shown to be synonymous with *Physokentia* (Fuller, 1997). *Carpoxylon* was listed by Uhl and Dransfield (1987) without placement into a subtribe. It has subsequently been recognized

as belonging to the Iguanurinae (Dowe & Uhl, 1989), and is included here.

Identification of the specimens is according to the label data as received from the lending institution, primarily as annotated by the late H. E. Moore Jr., or occasionally by later authorities, including the senior author. Generic determinations are assumed to be accurate, but specific identifications are subject to change, as many of these genera are in need of revision.

Most specimens appear to have been collected when fruits were ripe or nearly ripe, but this is not always easy to discern. The inner sclerenchymatous tissues, including the locular epidermis and fibrous bundle sheaths, generally do not mature until the seed has reached its full size. Some of the variation in these tissues may therefore be related to maturity of the fruit and should be interpreted with caution. In addition, subepidermal pigments may not have formed in fruits that are not quite mature. The absence of such a layer must also be interpreted with caution.

Blocks of pericarp were cut from the equatorial region of each fruit, away from any stigmatic remains, in order to provide standardized, directly comparable sections. After dehydration in an ethanol/tertiary butanol series, the blocks were embedded in a paraffin/plastic medium (Paraplast) and sectioned with a rotary microtome. Sections were stained with a safranin/fast green combination, or with toluidine blue, and mounted on glass slides.

Images of the prepared slides were captured digitally, and the different tissue regions and important cell types were traced, using Adobe Photodeluxe software, to form the basis of the computer-generated line drawings in this article. The drawings are semi-diagrammatic, accurate with respect to the size, shape, and distribution of major tissues and cell types but not detailed to the cellular level. Unspecialized parenchyma tissue, for example, is left blank, fibrous bundles and bundle sheaths are represented as black silhouettes, and the vascular tissues are left as clear areas within fibrous sheaths or as a simple outline where sheaths are thin or lacking. Raphide crystals are represented diagrammatically as a set of subparallel

lines within the outline of the containing cell, and tanniniferous cells are gray. Subepidermal regions of small pigmented or tanniniferous cells are represented as a gray region without the cell boundaries indicated. The drawings are presented at the same scale throughout in order to represent relative size differences.

Results

The results of this investigation are presented primarily in the form of line drawings, along with a brief commentary, for each of the genera. The drawings and the commentaries are in a sequence arranged roughly from least to most specialized, based on correlation of histological characters with the trends in morphological variation presented in Pintaud (1999). This also correlates loosely with the sequence in Uhl & Dransfield (1987).

All samples examined from this subtribe have a well-developed locular epidermis, which varies considerably in thickness from genus to genus and from species to species, and constitutes the entire endocarp in many genera. In Uhl & Dransfield (1987), the endocarp of the various genera of the Iguanurinae is generally described as "thin, vitreous, fragile, bony, shining," or sometimes "thickish or woody," and evidently refers to the locular epidermis alone in most instances. There is a modest development of complex endocarps in some of the genera, such as *Neoveitchia* (see Fig. 12), *Rhopaloblaste* (see Fig. 14), and *Actinorhytis* (see Fig. 17), involving fibrous bundle sheaths and sclerified parenchyma along with the locular epidermis.

Protective tissues in the outer pericarp in the Iguanurinae consist variously of brachysclereids, fibrous bundles, tanniniferous cells, and raphide-bearing cells. These may be aggregated into a distinct subepidermal zone that can be called an exocarp (or "epicarp" in Uhl & Dransfield, 1987). Distinct exocarps can be seen in *Actinorhytis* (see Fig. 17), *Veillonia* (see Fig. 26), and *Physokentia* (see Fig. 27), but the same tissues are more often found dispersed through a large part of the outer and middle pericarp, as in *Heterospathe* (see Fig. 9) or *Neoveit-*

chia (see Fig. 12), or concentrated in mantles well-removed from the epidermis, as in *Cyphokentia* (see Fig. 5), *Moratia* (see Fig. 6), *Clinosperma* (see Fig. 7), or *Lavoixia* (see Fig. 8).

The most conspicuous histological differences among the genera of this alliance concern the distribution of fibers. In the less specialized genera, which are diverse and geographically widespread, fibers are found only in sheaths around vascular bundles, if present at all, or in occasional nonvascular fibrous bundles intermixed with the vascular system, as in *Iguanura* (see Fig. 1), *Pelagodoxa* (see Fig. 2), or *Rhopaloblaste* (see Fig. 14). In such a system there is frequent evidence of branching and/or anastomosis, such as irregularity of size and spacing of bundles, bundles pressed close together, or two or more vascular strands sharing a large fibrous sheaths. Such histologically visible patterns correlate with anastomosing bundle systems seen in macroscopic dissection. Fibrous vascular bundles may be aggregated in the innermost pericarp in such a way as to become part of a distinct endocarp (*Iguanura, Rhopaloblaste*), or dispersed widely through the pericarp (*Pelagodoxa*).

In other genera, a separate system of nonvascular fibrous bundles is present. These tend to be terete in cross section, parallel with the axis of the fruit, evenly spaced, and without evidence of branching or anastomosis. Macroscopic examination (Uhl & Dransfield, 1987) indicates that they are relatively short and disconnected from one another, particularly as they approach the epidermis. In most instances, the fibrous bundles are numerous and in several tiers in a broad region of the outer pericarp, but in a few, such as *Satakentia* (see Fig. 15), *Clinostigma* (see Fig. 18), and *Alloschmidia* (see Fig. 20), they are confined to a single tier in the middle or outer pericarp, not quite forming an exocarp. These systems of fibrous bundles should not be confused with the numerous, heavily sheathed, vascular bundles found throughout the pericarp in such genera as *Pelagodoxa* (see Fig. 2) or *Actinorhytis* (see Fig. 17).

The most specialized nonvascular fibrous bundles are short, oblique or nearly perpendicular to the epidermis, and aggregated, along with a dense layer of brachysclereids, into a distinct exocarp. This type of fibrous bundle is found throughout the *Cyphosperma–Veillonia* clade, but also in *Actinorhytis* (see Fig. 17) and *Lepidorrhachis* (see Fig. 24) that do not appear to be closely related, according to Pintaud (1999).

Mantles of tanniniferous cells, brachysclereids, and/or raphide-bearing cells in the mid- to outer pericarp are common and frequently strongly developed in this subtribe. The heavy mantles of brachysclereids in most genera of the *Brongniartikentia–Lavoixia* (see Figs. 5–8) clade are remarkably like those found in the unrelated Corypheae (Essig, 1999).
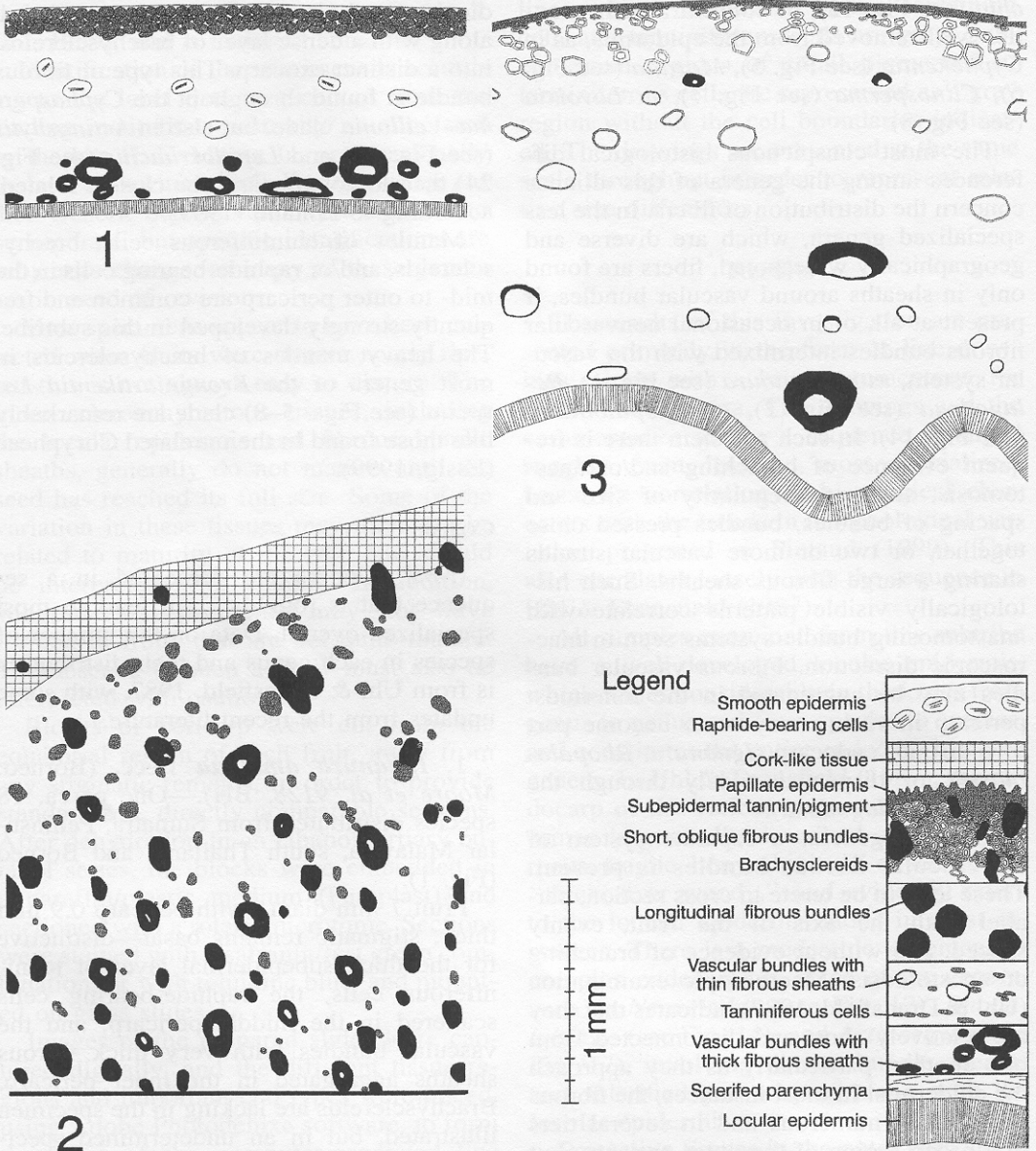
COMMENTARY

(*Note:* Genera are presented in a sequence that is roughly from least to most specialized overall. Data on the number of species in each genus and their distribution is from Uhl & Dransfield, 1987, with some updates from the recent literature.)

1. ***Iguanura ambigua*** **Becc.** (Borneo: *Moore et al. 9128,* BH).—One of ca. 18 species distributed from Sumatra, Peninsular Malaysia, south Thailand, and Borneo (Fig. 1).

Fruit 7 mm diam., with pericarp 0.9 mm thick, stigmatic remains basal—distinctive for the thick subepidermal layer of tanniniferous cells, the raphide-bearing cells scattered in the middle pericarp, and the vascular bundles with very thick fibrous sheaths aggregated in the inner pericarp. Brachysclereids are lacking in the specimen illustrated, but in an undetermined specimen (*Moore 9072,* BH) there is a thin layer of brachysclereids in mid-pericarp.

2. ***Pelagodoxa henryana*** **Becc.** (Marquesas Islands: *Moore 9400,* BH).—A monotypic genus (Fig. 2).

Fruit 45–53 mm diam., pericarp very thick (specimen examined was immature and incomplete), stigmatic remains basal—distinctive for the corky outer region, the numerous vascular bundles with thick fibrous sheaths intermixed with numerous tanniniferous cells throughout much of the

Legend

Smooth epidermis	
Raphide-bearing cells	
Cork-like tissue	
Papillate epidermis	
Subepidermal tannin/pigment	
Short, oblique fibrous bundles	
Brachysclereids	
Longitudinal fibrous bundles	
Vascular bundles with thin fibrous sheaths	
Tanniniferous cells	
Vascular bundles with thick fibrous sheaths	
Sclerified parenchyma	
Locular epidermis	

1 mm

FIGS. 1–3. **1.** *Iguanura ambigua* (from *Moore et al. 9128*, BH). **2.** *Pelagodoxa henryana* (from *Moore 9400*, BH). **3.** *Bentinckia nicobarica* (from *Moore 6034*, BH).

pericarp, and a lack of raphide-bearing cells and brachysclereids. From the immature specimen it appears that there are many large vascular bundles with thicker fibrous sheaths in the inner pericarp and a thickened locular epidermis. This is a specialized fruit with respect to its corky outer region and its numerous vascular bundles, but his-

tologically unspecialized. According to Pintaud (1999) the gynoecium displays a relictual trimerous (trilocular) condition.

3. *Bentinckia nicobarica* Becc. (Nicobar Islands: *Moore 6034*, BH).—One of two species, the other in Travancore, India (Fig. 3). Fruit 11 mm diam., with the pericarp 2–
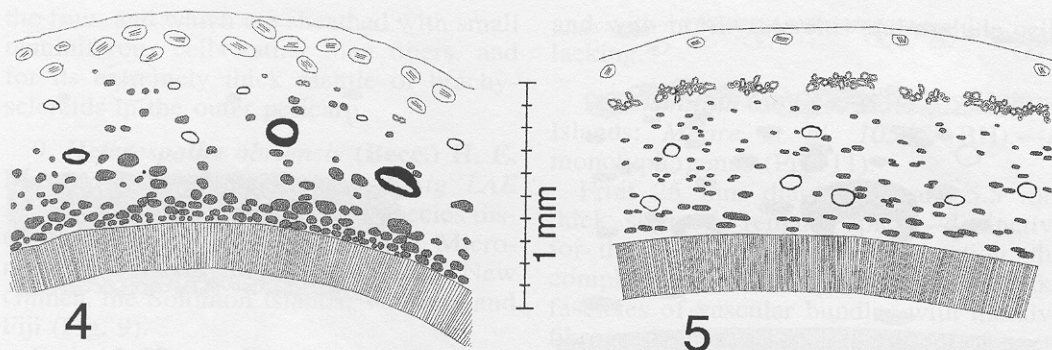
FIGS. 4, 5. **4.** *Brongniartikentia vaginata* (from *Moore 10010*, BH). **5.** *Cyphokentia macrostachya* (from *Moore et al. 9342*, BH).

2.5 mm thick, stigmatic remains basal, seed and locular epidermis grooved—showing no clear affinity with other genera; distinctive for the apparent total lack of tanniniferous or raphide-bearing cells, the concentration of brachysclereids just below the epidermis, and the occurrence of much larger sclereids scattered into the middle pericarp. Some of the larger vascular bundles have thick fibrous sheaths, but most have little or no fibers around them, resembling *Brongniartikentia* in this respect.

4. *Brongniartikentia vaginata* (Brongn.) Becc. (New Caledonia: *Moore et al. 10100*, BH).—One of two species, both in New Caledonia (Fig. 4).

Fruit ca. 7.5 mm diam., with pericarp 1.1 mm thick, stigmatic remains subbasal—differing from *Iguanura* in having fewer vascular bundles with mostly thinner fibrous sheaths, and these located in the middle pericarp; distinctive also for its very thick (0.2 mm) locular epidermis, tanniniferous cells aggregated in the inner pericarp, numerous raphide-bearing cells in the outer pericarp, and brachysclereids widely scattered in the middle pericarp.

5. *Cyphokentia macrostachya* Brongn. (New Caledonia: *Moore et al. 9342*, BH).— A monotypic genus (Fig. 5).

Fruit ca. 9 mm diam., pericarp 1.2 mm thick, stigmatic remains lateral—similar to *Brongniartikentia,* but with very thin fibrous bundle sheaths around all vascular bundles, the brachysclereids concentrated into a distinct mantle in the outer pericarp

but somewhat removed from the epidermis, and with tanniniferous cells confined to the inside of the mantle of brachysclereids.

6. *Moratia cerifera* H. E. Moore (New Caledonia: *Moore et al. 9966, 10035,* BH).—A monotypic genus (Fig. 6).

Fruit 10–11 mm diam., pericarp 1.75 mm thick, stigmatic remains lateral—similar to the preceding two genera, but distinctive for its papillate epidermis, the thicker mantle of brachysclereids, and for the larger tanniniferous cells; some of the vascular bundles have very thick fibrous sheaths, and the locular epidermis is extremely thick (to 0.45 mm).

7. *Clinosperma bracteale* (Brongn.) Becc. (New Caledonia: *MacKee 29191,* BH).—A monotypic genus (Fig. 7).

Fruit 10–11 mm diam., pericarp ca. 3 mm thick, stigmatic remains lateral—very similar to the preceding, but with a more massive (to 0.45 mm thick) mantle of brachysclereids, with larger and more numerous raphide-bearing cells in the outer pericarp, and with the locular epidermis somewhat thinner.

8. *Lavoixia macrocarpa* H. E. Moore (New Caledonia: *Pintaud 364,* P).—A monotypic genus (Fig. 8).
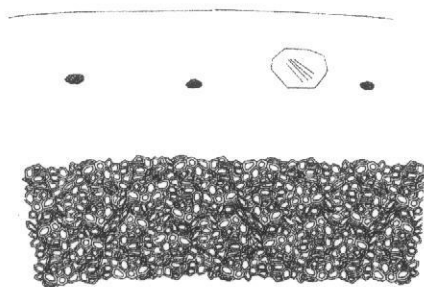
Fruit 3.2 cm diam., with pericarp extremely thick (to nearly 6 mm), seed laterally compressed and irregularly indented—resembling the preceding 4 genera, but distinctive for its unusual branching and twisting vascular bundles that permeate much of
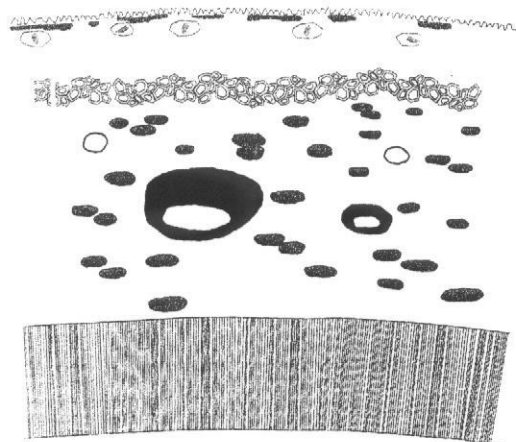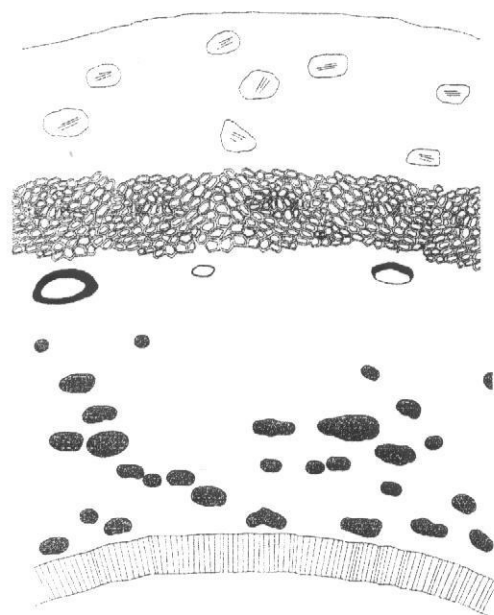
FIGS. 6–8. **6.** *Moratia cerifera* (from *Moore et al. 9966*, BH). **7.** *Clinosperma bracteale* (from *MacKee 29191*, BH). **8.** *Lavoixia macrocarpa* (from *Pintaud 364*, P).

the fruit, and which are sheathed with small tanniniferous cells rather than fibers, and for its extremely thick mantle of brachysclereids in the outer pericarp.

9. *Heterospathe obriensis* (Becc.) H. E. Moore (Papua New Guinea, *Essig LAE 55139*, BH).—One of about 32 species distributed from the Philippines and Micronesia to eastern Indonesia, Papua New Guinea, the Solomon Islands, Vanuatu, and Fiji (Fig. 9).

Fruit 15–20 mm diam., pericarp 3.5 mm thick, stigmatic remains lateral—distinctive for the numerous fibrous bundles distributed throughout the middle and outer pericarp, for the scanty fibrous sheaths of the vascular bundles, which are located in the inner pericarp, with the tanniniferous cells confined to the inner pericarp, with brachysclereids few and scattered in the outer pericarp, not forming a distinct mantle, and with raphide cells common just below the epidermis.

Other species of *Heterospathe* examined show some diversity in pericarp structure. *Heterospathe delicatula* H. E. Moore (Papua New Guinea: *Essig LAE 55226*, BH) and *H. humilis* Becc. (Papua New Guinea: *Moore et al. 9262*, BH) are small-fruited species that differ from the preceding in having thinner pericarps, fewer fibrous bundles, and thicker sheaths around the vascular bundles. *Heterospathe woodfordiana* from the Solomon Islands (*Moore 9306*, BH), has numerous round bundles of rather thin-walled fibers, and is reminiscent of *Campecarpus* and *Cyphophoenix* (see below). This widespread and variable genus is of high priority for more detailed study.

10. *Sommieria affinis* Becc. (Papua New Guinea, *White P/1*, BH).—One of three species in New Guinea (Fig. 10).

Fruit 8.3–9 mm diam., pericarp 1.6 mm thick, stigmatic remains basal—like *Heterospathe,* but distinctive for the large, corky, pyramidal warts that form through cracking of the outer pericarp as it matures, fibrous bundles mostly in the corky regions, these short and irregularly oriented, tanniniferous cells in a thick band adjacent to the locular epidermis and scattered elsewhere, with the vascular bundles with scant fibrous sheaths,

and with brachysclereids and raphide cells lacking.

11. *Alsmithia longipes* H. E. Moore (Fiji Islands: *Moore et al. 10545*, BH).—A monotypic genus (Fig. 11).

Fruit 25 mm diam., pericarp 5.5 mm thick, stigmatic remains apical—distinctive for the seed angled in cross section, the complex inner mantle made up of cable-like fascicles of vascular bundles with massive fibrous sheaths, a separate system of terete fibrous bundles in the outer pericarp, vascular bundles with scant fibrous sheaths scattered throughout the middle pericarp, numerous small tanniniferous cells embedded within the peripheral regions of the fibrous bundles and sheaths, larger tanniniferous cells abundant in the region between the two fibrous zones, brachysclereids lacking, raphide-bearing cells scarce, and the locular epidermis unusually narrow. This is a unique, highly specialized pericarp, with some similarity to *Heterospathe* and *Neoveitchia* in the possession of an expanded series of nonvascular fibrous bundles, and to *Carpoxylon* in the tendency to form large compound vascular bundles with heavy sheaths.

12. *Neoveitchia storckii* (H. Wendl.) Becc. (Fiji Islands: *Moore et al. 9360*, BH).—One of two species, the other in Vanuatu (Fig. 12).

Fruit 26 mm diam., pericarp 3–4 mm thick, stigmatic remains apical—similar to the preceding several genera, particularly with respect to the numerous fibrous bundles in the outer pericarp, but distinctive for its papillate epidermis, vascular bundles with very thick fibrous sheaths, mantle of compressed and sclerified ground tissue in the innermost pericarp, and very thick (0.2 mm) locular epidermis.

13. *Carpoxylon macrospermum* H. A. Wendl. & Drude (Vanuatu: *J. F. Gage s.n.*, BH).—A monotypic genus (Fig. 13).
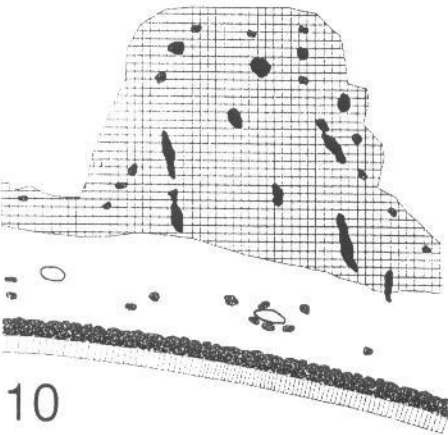
Fruit 26–29 mm diam., pericarp ca 3.2 mm thick, stigmatic remains apical—most resembling *Neoveitchia,* but with a smooth epidermis, fibrous bundles more concentrated into a distinct exocarp, vascular bundles all with heavy fibrous sheaths and dis-
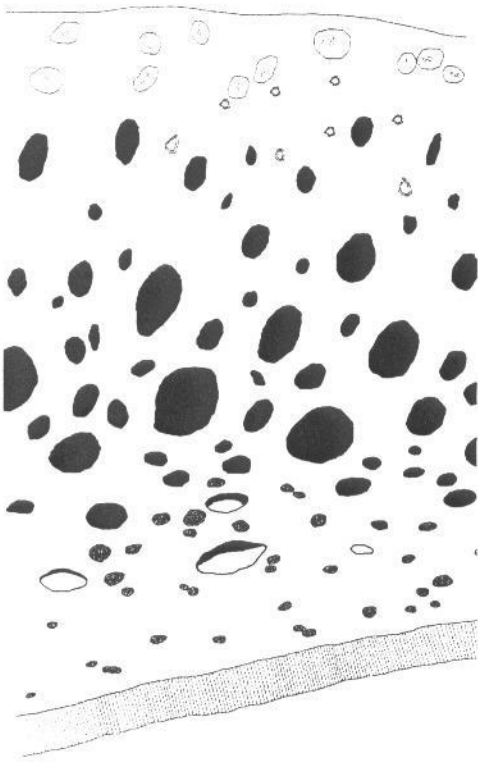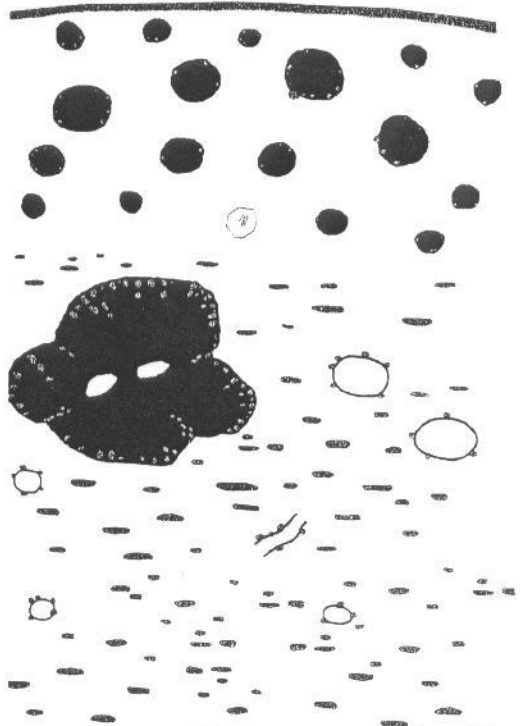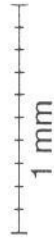
Figs. 9–11.   9. *Heterospathe obriensis* (from *Essig LAE 55139*, BH). 10. *Sommieria affinis* (from *White P/ 1*, BH). 11. *Alsmithia longipes* (from *Moore et al. 10545*, BH).

tributed throughout much of the pericarp (resembling *Actinorhytis* in this respect), lacking sclerified parenchyma in the endocarp region; distinctive also for an occasional very large compound vascular bun-

dle in a heavy sheath (resembling *Alsmithia*).

14. *Rhopaloblaste ledermanniana* Becc. (Papua New Guinea: *Essig & Young LAE*
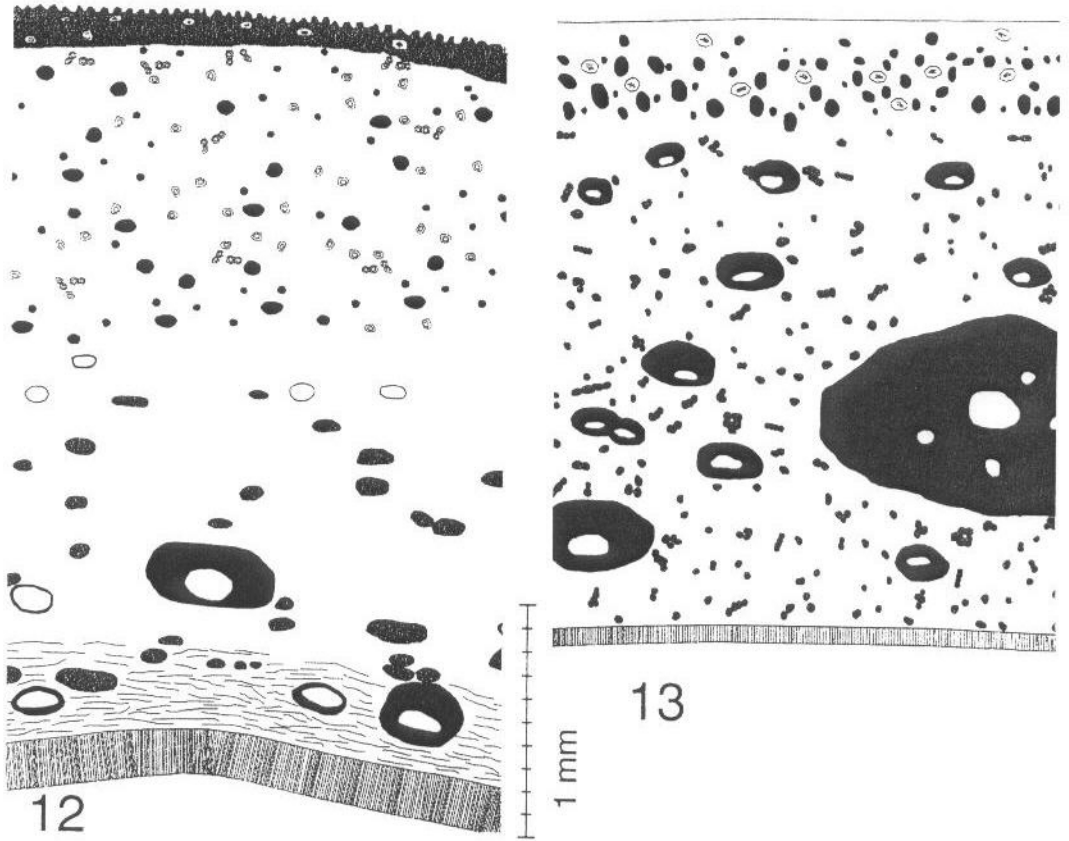
FIGS. 12, 13. **12.** *Neoveitchia storckii* (from *Moore et al. 9360,* BH). **13.** *Carpoxylon macrospermum* (from *J. F. Gage s.n.,* BH).

74044, BH, USF).—One of six or more species distributed from the Nicobar Islands to the Solomon Islands (Fig. 14).

Fruit 8 mm diam., with pericarp 0.5 mm thick, stigmatic remains apical—a very thin pericarp showing little specialization, resembling *Iguanura,* but linked with *Actinorhytis* and *Dictyosperma* on morphological grounds (Pintaud, in press); distinctive for the thicker band of fibrous vascular bundles, the apparent total lack of tanniniferous and raphide-bearing cells, the conspicuous but discontinuous band of brachysclereids in the outer pericarp, the papillate epidermis, and the compressed and sclerified parenchyma between the bundles and the locular epidermis. The latter feature has otherwise been found only in *Neoveitchia* in this alliance, and is reminiscent of the Ptychospermatinae.

Another species examined, *R. elegans* H.

E. Moore (*Moore 9310,* BH) has larger fruit (20 mm diam., with pericarp 1.3–2.4 mm thick), but the arrangement of the tissues is essentially the same.

15. ***Satakentia liukiuensis* (Hatus.) H. E. Moore** (Ryukyu Islands, Japan: *Moore et al. 9382,* BH).—A monotypic genus (Fig. 15).

Fruit 7–7.3 mm diam., pericarp 1.5 mm thick, stigmatic remains apical—similar to *Dictyosperma* and *Clinostigma,* but with a distinctive series of large vascular bundles with very thick fibrous sheaths in mid-pericarp, a papillate epidermis, many large brachysclereids loosely distributed in the outer third of the pericarp, raphide-bearing cells frequent in the outer pericarp, and tanniniferous cells confined to the inner pericarp and rather few in number.
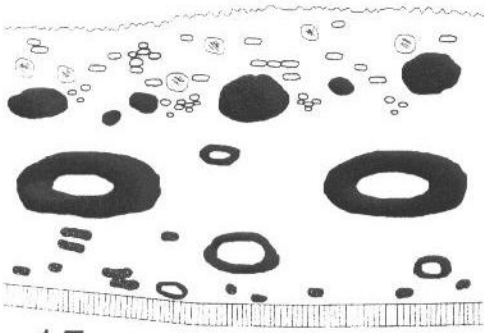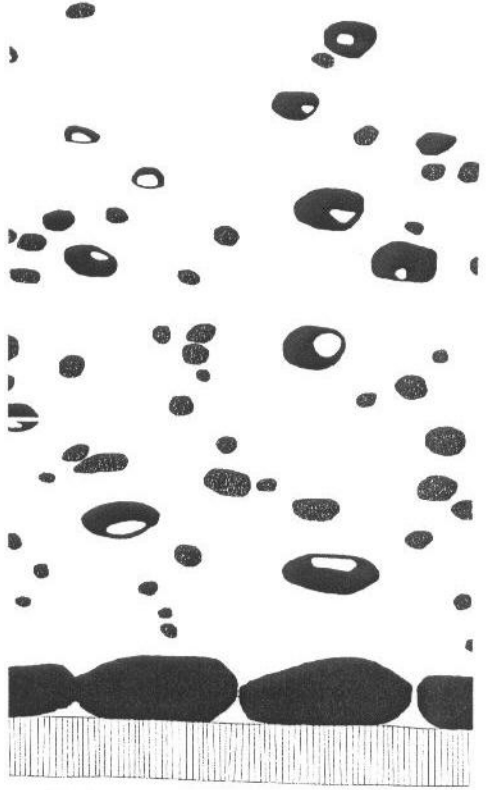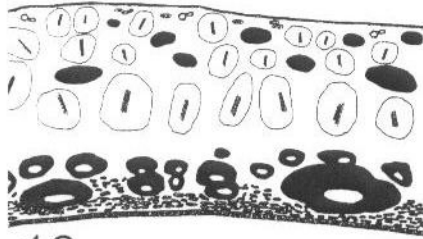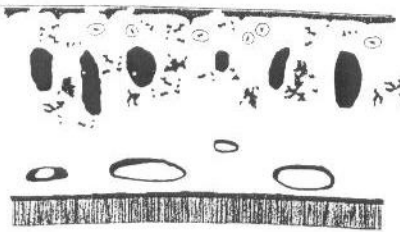
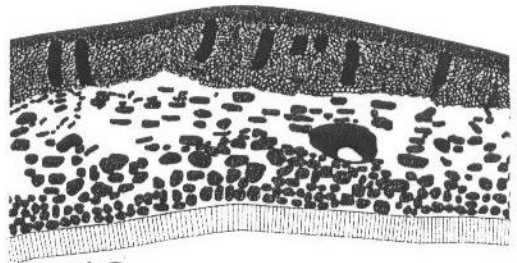16. ***Dictyosperma album* (Bory) H.**

FIGS. 14–19. **14.** *Rhopaloblaste ledermanniana* (from *Essig & Young LAE 74044*, BH). **15.** *Satakentia liukiuensis* (from *Moore et al. 9382*, BH). **16.** *Dictyosperma album* (from *Read 831*, BH). **17.** *Actinorhytis calapparia* (from *Essig LAE 55087*, BH). **18.** *Clinostigma gronophyllum* (from *Corner RSS 108*, BH). **19.** *Basselinia velutina* (from *Moore et al. 9972*, BH).

Wendl. & Drude ex Scheff. (Mascarene Islands: *Read 831,* BH).—A monotypic genus (Fig. 16).

Fruit 10–11 mm diam., with pericarp 0.9 mm thick, stigmatic remains apical—resembling *Iguanura* and *Rhopaloblaste* in the numerous vascular bundles with thick fibrous sheaths that form a mantle in the inner pericarp, but differing in possessing a loose mantle of large fibrous bundles in the outer pericarp. This is one of the few genera (along with *Neoveitchia* and *Alsmithia*) in the Iguanurinae that form such a dual system of protective fibers. It also resembles *Clinostigma,* but the fibrous bundles are more oblique in the latter and the fibrous vascular bundle sheaths not as well developed. Also distinctive are the extremely large and numerous raphide-bearing cells, the thin, intermittent layer of brachysclereids just below the epidermis, and the confinement of tanniniferous cells to the innermost pericarp.

17. *Actinorhytis calapparia* **(Blume) H. Wendl. & Drude ex Scheff.** (Papua New Guinea: *Essig LAE 55087,* BH).—A widespread species in New Guinea and the Solomon Islands, with an additional species restricted to the Solomons (Fig. 17).

Fruit 45 mm diam., pericarp 4–5 mm thick, stigmatic remains apical—not clearly similar to any other genus of the Iguanurinae. Distinctive for its large size, the numerous vascular bundles with thick fibrous sheaths scattered throughout the pericarp, a confluent band of large, flattened fibrous bundles appressed to the thick (0.25 mm) locular epidermis, tanniniferous cells scattered throughout the pericarp, and for a lack of raphide-bearing cells.

18. *Clinostigma gronophyllum* **H. E. Moore** (Solomon Islands: *Corner RSS 108,* BH).—One of ca. 13 species distributed from the Bonin and Caroline Islands to Samoa, Fiji Islands, New Hebrides, Solomon Islands, and New Ireland (Fig. 18).

Fruit 7.5–8 mm diam., pericarp 1 mm thick, stigmatic remains lateral—similar to *Satakentia* and *Dictyosperma,* but with a single series of oblique fibrous bundles in mid-pericarp and a lack of fibrous

sheaths around the vascular bundles; tanniniferous cells confined to brief layers adjacent to both the epidermis and the locular epidermis, brachyscleroids scattered in the outer half of the pericarp, and raphide-bearing cells common just below the epidermis.

19. *Basselinia velutina* **Becc.** (New Caledonia: *Moore et al. 9972,* BH).—One of 11 species in New Caledonia (Fig. 19).

Fruit 10–11 mm diam., pericarp 1 mm thick, stigmatic remains lateral—similar to the preceding three genera, but with a more massive mantle of brachysclereids encasing the oblique fibrous bundles, massive numbers of tanniniferous cells filling the inner pericarp, vascular bundles with thick fibrous sheaths in mid-pericarp, and raphide-bearing cells lacking.
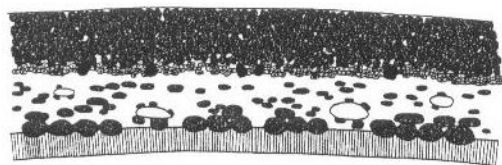
20. *Alloschmidia glabrata* **(Becc.) H. E. Moore** (New Caledonia: *Moore et al. 9957,* BH).—A monotypic genus (Fig. 20).

Fruit 6 mm diam., with pericarp 0.7 mm thick, stigmatic remains apical—a very distinctive pericarp, for the single, mid-pericarp series of fibrous bundles, the lack of fibrous sheaths around the vascular bundle, the extremely thick mantle of tanniniferous cells occupying the outer half of the fruit, the lack of raphide-bearing cells, and for the large tanniniferous cells resting in pits on the locular epidermis.

21. *Campecarpus fulcitus* **(Brongn.) H. Wendl. ex Becc.** (New Caledonia: *Moore 10009,* BH).—A monotypic genus (Fig. 21).

Fruit 14–14.5 mm diam., pericarp 2–2.5 mm thick, stigmatic remains apical—similar to *Cyphophoenix* and *Burretiokentia,* but also to *Heterospathe,* especially *H. woodfordiana,* with numerous, terete bundles of rather thin-walled fibers occupying the outer half of the pericarp. Distinctive for the large and abundant tanniniferous cells occupying the inner half of the pericarp, vascular bundles with scant fibrous sheaths, a thick (0.25 mm) locular epidermis, rather few brachysclereids, no raphide-bearing cells, and a very thick layer of tannin/pigment below the epidermis.
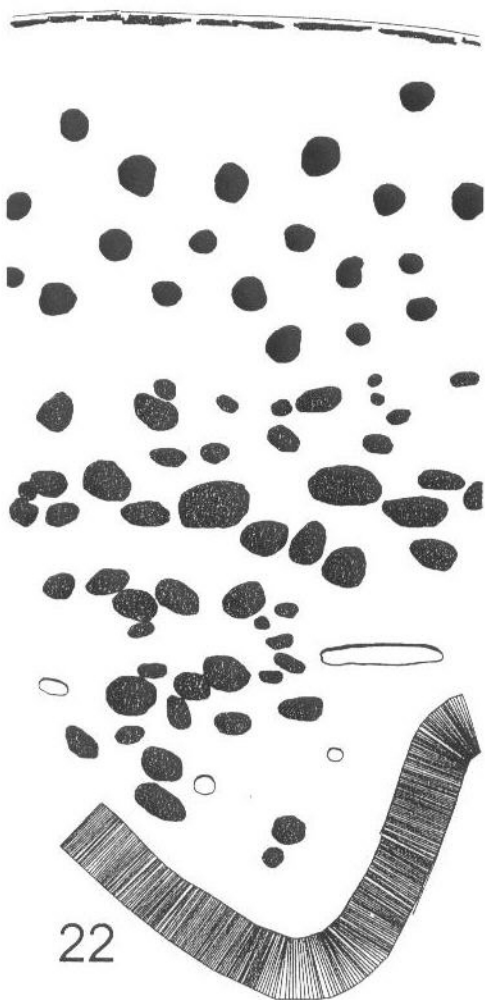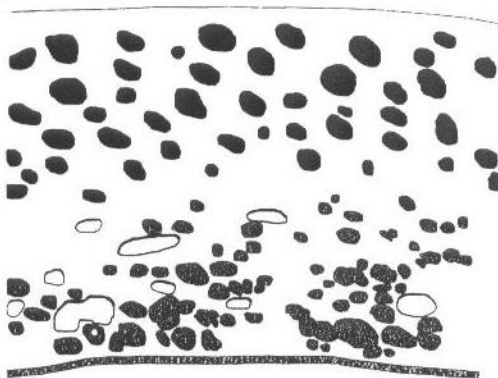
22. *Burretiokentia viellardii* **(Brongn. &**
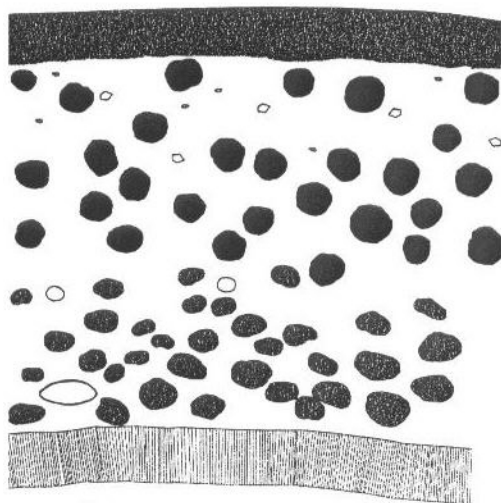
FIGS. 20–23. **20.** *Alloschmidia glabrata* (from *Moore et al. 9957*, BH). **21.** *Campecarpus fulcitus* (from *Moore 10009*, BH). **22.** *Burretiokentia viellardii* (from *Moore et al. 9956*, BH). **23.** *Cyphophoenix nucele* (from *Ingwerson s.n.*, BH).

Gris) Pic. Serm. (New Caledonia: *Moore et al. 9956*, BH).—One of five species in New Caledonia (Fig. 22).

Fruit 14–15 mm diam., pericarp 3–4 mm thick, stigmatic remains apical—similar to the preceding two genera, but with seed and locular epidermis irregularly sculptured, and lacking brachysclereids.
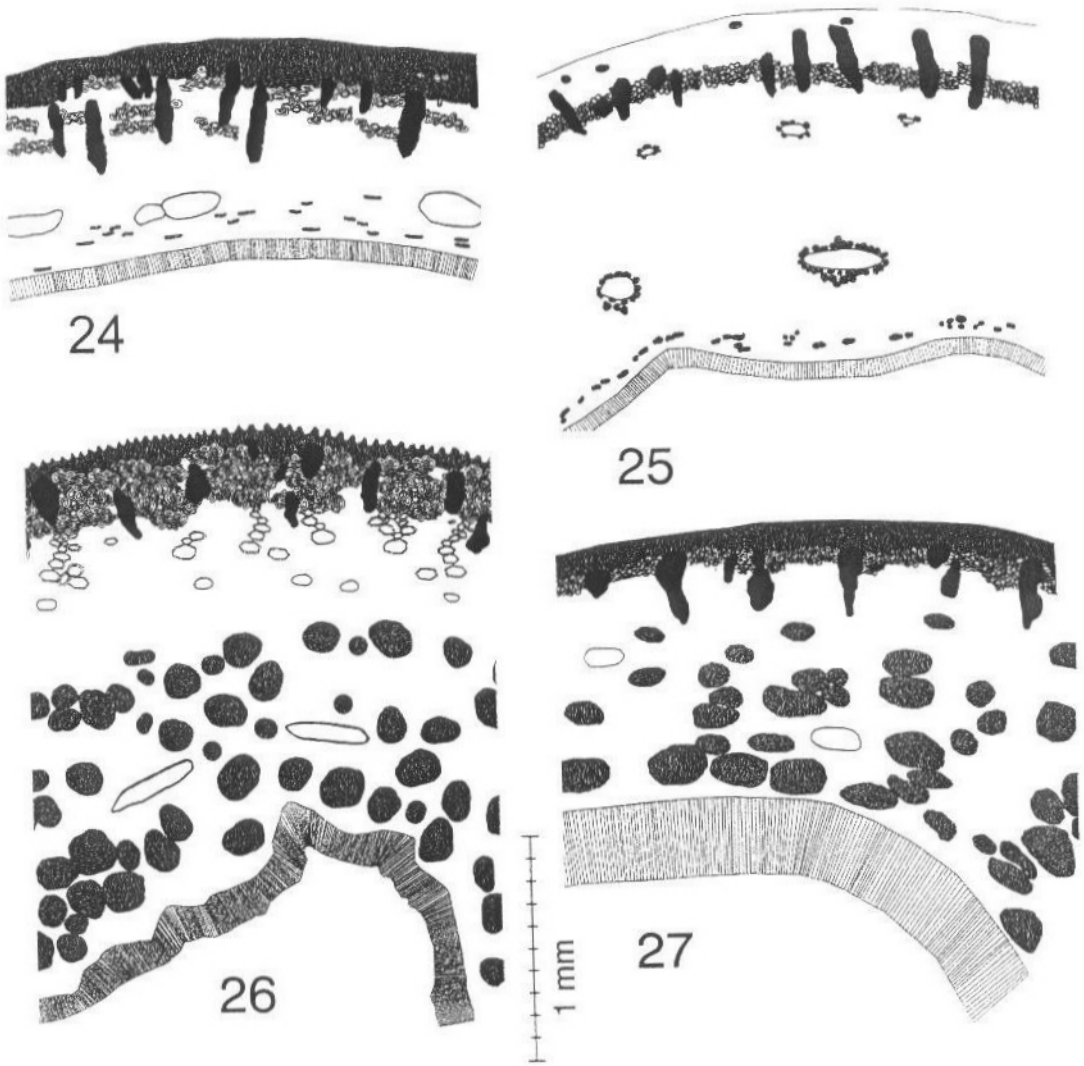
FIGS. 24–27.   **24.** *Lepidorrhachis mooreanum* (from *Moore & Shick 9250*, BH). **25.** *Cyphosperma trichospadix* (from *Moore et al. 9345*, BH). **26.** *Veillonia alba* (from *Schmid 1615*, BH). **27.** *Physokentia rosea* (from *Moore & Koreiveibau 9363*, BH).

23. *Cyphophoenix nucele* **H. E. Moore** (Loyalty Islands, *Ingwerson s.n,* BH).— One of two species, the other from New Caledonia (Fig. 23).

Fruit 8 mm diam., pericarp 1.6 mm thick, stigmatic remains apical—very similar to *Campecarpus,* but with a much thinner locular epidermis, no evident subepidermal pigment layer or brachysclereids, and smaller and more irregular tanniniferous cells.

Cyphophoenix elegans (Brongn. & Gris) H. Wendl. ex Salomon (New Caledonia: *Moore et al. 9323,* BH) has a larger fruit, nearly 13 mm diam., with a pericarp 3.3 mm thick, but histologically similar to *C. nucele.*

24. *Lepidorrhachis mooreanum* (**F. Muell.**) **O. F.Cook** (Lord Howe Island: *Moore & Shick 9250,* BH, *Pintaud 405,* TLS).—A monotypic genus (Fig. 24).

Fruit 14 mm diam., pericarp 1.3–2.2 mm thick, stigmatic remains lateral—similar to

Cyphophoenix, but with the seed and locular epidermis round and smooth, a very thick layer of tannin/pigment tissue adjacent to the epidermis, small tanniniferous cells scattered in the inner pericarp, brachyscereids in scattered patches amongst the oblique fibrous bundles, and raphide-bearing cells lacking.

25. *Cyphosperma trichospadix* (**Burret**) **H. E. Moore** (Fiji: *Moore et al. 9345,* BH).—A genus of four species from New Caledonia, Vanuatu and Fiji (Fig. 25).

Fruit 11 mm diam., pericarp 1.5 mm thick, stigmatic remains lateral, with seed and locular epidermis irregularly sculptured—resembling *Clinostigma,* but with the fibrous bundles nearly perpendicular to the epidermis and embedded in a dense mantle of brachysclereids close to the epidermis. Distinctive for the small tanniniferous cells surrounding the vascular bundles, additional tanniniferous cells forming a thin layer adjacent to the locular epidermis, and scattered widely near the epidermis, and for the lack of raphide-bearing cells.

26. *Veillonia alba* **H. E. Moore** (New Caledonia: *Schmid 1615,* BH).—A monotypic genus (Fig. 26).

Fruit 15 mm diam., pericarp 2.5 mm thick, stigmatic remains subapical, with seed and locular epidermis irregularly sculptured—similar to to *Campecarpus* and *Cyphophoenix,* but with the fibrous bundles shorter, more oblique and confined to the subepidermal region. Also distinctive is the papillate epidermis, the thick subepidermal zone of tanniniferous/pigment tissue, the dense mantle of brachysclereids around the fibrous bundles, the larger brachysclereids scattered toward the middle pericarp, a ring of small vascular bundles without sheaths just above mid-pericarp, large tanniniferous cells in the inner half of the fruit, lack of raphide-bearing cells, and the unevenly thickened locular epidermis (in other irregularly sculptured endocarps the locular epidermis is still evenly thickened).

27. *Physokentia rosea* **H. E. Moore** (Fiji: *Moore & Koreiveibau 9363,* BH).— One of 7 species distributed from Fiji to the

New Hebrides, Solomon Islands, and New Britain (Fig. 27).

Fruit 13–15 mm diam., pericarp 1.5–2 mm thick, stigmatic remains apical—similar to *Veillonia* but with seed and locular epidermis smoothly angled, the epidermis smooth, the zone of brachysclereids narrower, the vascular bundles fewer, and the locular epidermis extremely thick (ca 0.3 mm).

Discussion

The present survey is necessarily limited in depth, given the paucity of available preserved fruit material. Since only one or a few species in each genus have been examined, it would be inappropriate to interpret the differences presented here as diagnostic generic characters, except perhaps in the case of the many monotypic genera in this subtribe. For larger genera, however, the range of variation in pericarp structure remains to be determined. In earlier studies of genera where multiple species have been examined (Essig, 1977; Essig, 1982; Essig & Young, 1985), subgenera, sections, and species have been shown to display unique, recognizable combinations of pericarp characters. The generic characterizations presented here should therefore be considered working hypotheses.

At a broader level, examination of at least one representative from each of the 27 genera of the Iguanurinae provides a valuable opportunity to look at the range of variation within the subtribe, to identify major trends of specialization, and to review existing efforts at phylogenetic analysis in the light of histological data from the pericarp.

Cell types and tissues found in the pericarp of members of the Iguanurinae are essentially the same as those found in the Ptychospermatinae and Arecinae. In the Iguanurinae, however, they exhibit a much greater variety of arrangements and combinations. In this subtribe, for example, one can see the full range of specialization of nonvascular fibrous bundles, from incidental parts of the vascular system, as in *Iguanura* (Fig. 1) or *Pelagodoxa* (Fig. 2), to a system of separate fibrous bundles in the mesocarp, as in *Heterospathe* (Fig. 9) or

Campecarpus (Fig. 21), and finally to an independent system of short, oblique fibrous bundles integrated into a complex exocarp, as in *Veillonia* (Fig. 26) or *Physokentia* (Fig. 27). Similar, but less complete, progressions can be seen in both the Ptychospermatinae (Essig, 1977) and the Arecinae (Essig & Young, 1979), as well as in several other subtribes (Essig, 1999, and unpubl. data).

The logical polarity of this progression, from fibers associated with the vascular system toward separate and shorter fibrous bundles and their displacement toward the epidermis, is consistent with the cladistic analysis of Pintaud (1999), as well as with earlier, informal assessments of evolutionary trends (Uhl & Dransfield, 1987). The least specialized arrangements of fibers is found in genera branching off near the base of the Pintaud tree, with more specialized fibrous bundles found progressively in the upper parts of several major clades. The rise of these more specialized and complex histological structures parallels the modification of open leaf sheaths into crownshafts, the displacement of stigmatic remains from the base to the apex of the fruit, and other morphological trends. These trends in the pericarp have occurred at different rates, in parallel, and possibly with some reversals, along several of the major clades.

In contrast there are no strong or consistent trends toward the development of a complex endocarp in this subtribe. The locular epidermis is quite thick and constitutes the entire endocarp in many genera. In some, such as *Rhopaloblaste* (Fig. 14), *Dictyosperma* (Fig. 16), and *Actinorhytis* (Fig. 17), vascular bundles with thick fibrous sheaths are pressed against the locular epidermis, contributing to the endocarp. *Alsmithia* (Fig. 11) has unusually massive compound fibrous bundle sheaths that make an effective endocarp adjacent to a thin locular epidermis. *Rhopaloblaste* (Fig. 14) and *Neoveitchia* (Fig. 12) have compressed and sclerified parenchyma between the locular epidermis and vascular bundles, a condition reminiscent of the subtribe Ptychospermatinae.

The data from pericarp histology alone are insufficient for drawing specific phylogenetic conclusions, but they do provide support for some of the conclusions reached by Pintaud (1999), and shed light on some of the problematic parts of his analysis. Each of the two major clades of New Caledonian genera, for example, is well-supported by the pericarp data, although the two seem to be quite distinct from one another.

In the first clade, *Brongniartikentia, Moratia, Cyphokentia,* and *Clinosperma* (Figs. 4–7) have pericarp structures that are very similar, whereas *Lavoixia* (Fig. 8) is distinguished primarily by its larger fruits and conspicuously twisting and branching vascular bundles. In this clade there is a remarkable, but not total, lack of fibrous bundle sheaths and nonvascular fibrous bundles, and this is apparently compensated for by the development of a thick mantle of brachysclereids and an exceptionally thick locular epidermis. *Brongniartikentia* (Fig. 4), with open leaf sheath, basal stigmatic remains, and other unspecialized morphological characters, appears to be the histologically least specialized member of this clade as well. Some of its vascular bundles have relatively thick fibrous sheaths and the brachysclereids are not aggregated into a distinct mantle.

The second clade of New Caledonian genera is also well-supported by pericarp data. *Campecarpus* (Fig. 21) and *Cyphophoenix* (Fig. 23) are very similar, and *Burretiokentia* (Fig. 22) differs primarily in having a sculptured seed and endocarp. These genera have an extensive series of separate fibrous bundles in the outer half of the pericarp and an extensive series of large tanniniferous cells occupying the inner half of the pericarp. Brachysclereids are lacking or few in number, while vascular bundles lack fibrous sheaths. *Veillonia* (Fig. 26) is significantly more specialized than the other genera in that the fibrous bundles are short, oblique, and confined to the exocarp region, where there is also a thick aggregation of brachysclereids, and the epidermis is distinctly papillate. The sculpturing of the seed resembles that in *Burretiokentia* but seems to be more irregular.

Basselinia (Fig. 19) is also part of this clade, but the one species examined differs

significantly in that its vascular bundles have heavy fibrous sheaths. The genus is also more variable with respect to the position of the stigmatic remains, and the leaf sheaths, while forming a crownshaft, are partially split open. Since it is a large genus, more species must be sampled before drawing any conclusions about its position.

Cyphosperma (Fig. 25), which is basal to this clade in Pintaud's (1999) analysis, has specialized fibrous bundles as part of the exocarp, like *Veillonia* (Fig. 26), but differs markedly in the size and distribution of tanniniferous cells. They are much smaller and aggregated both around vascular bundles, as in *Lavoixia* (Fig. 8), and in a band close to the locular epidermis. In this genus also the leaf sheath is open, but the stigmatic remains are apical.

The *Cyphosperma–Veillonia* clade is specialized in many other traits as well, including the apparent synapomorphy of the incomplete prophyll (the first inflorescence bract, which in this instance does not completely encircle the peduncle).

Because of very similar pericarp histology, as well as the possession of an incomplete prophyll, *Physokentia* (Fig. 27) seems to belong in this clade as well. It comes out on a rather distant clade in Pintaud's (1999) analysis, however, due to differences in bracteole and staminate flower shape. This conflict remains to be resolved.

The small clade branching off just below the two New Caledonian clades comprises the New Caledonian *Alloschmidia* (Fig. 20), *Lepidorrhachis* (Fig. 24) from Lord Howe Island, and *Bentinckia* (Fig. 3) from India and the Nicobar Islands. This clade receives no support from pericarp histology. *Alloschmidia* (Fig. 20) seems similar to *Campecarpus* (Fig. 21) and *Cyphophoenix* (Fig. 23), but with a much thinner pericarp and only one series of fibrous bundles in midpericarp. Its locular epidermis is unusually pitted due to large tanniniferous cells that appear as if pressed into it. *Lepidorrhachis* (Fig. 24) is unspecialized with respect to its round seeds, complete prophyll, lateral stigmatic remains, and open leaf sheath, but has rather specialized pericarp histology, with short fibrous bundles aggregated into an exocarp, strongly resembling the New Ca-

ledonian *Cyphosperma* (Fig. 25). *Bentinckia* (Fig. 3) seems to be unspecialized histologically, lacking nonvascular fibrous bundles, and has well-developed and unusually large brachysclereids.

Another clade in Pintaud's (1999) tree branches off below the New Caledonian clades and consists of *Carpoxylon* (Fig. 13), *Actinorhytis* (Fig. 17), *Rhopaloblaste* (Fig. 14), *Dictyosperma* (Fig. 16), *Clinostigma* (Fig. 18), and *Physokentia* (Fig. 27). This clade has some support from pericarp structure only if the last genus is removed. Stigmatic remains are apical and, except for *Physokentia*, vascular bundle sheaths are heavy. The latter character is most certainly plesiomorphic, however, as it is found in many genera in the lower part of the tree.

The remaining genera, *Iguanura* (Fig. 1), *Pelagodoxa* (Fig. 2), *Sommieria* (Fig. 10), *Heterospathe* (Fig. 9), *Alsmithia* (Fig. 11), *Neoveitchia* (Fig. 12), and *Satakentia* (Fig. 15) are widespread geographically and branch off individually from the lower part of the tree (Pintaud, 1999). This part of the tree is weakly resolved and there is no clear pattern in the pericarp structure among these genera. Each genus shows a mix of unspecialized and specialized characters, and their phylogenetic relationships require further study.

Conclusions

Once again histological pericarp structures have been shown to be of considerable variety and interest at the subtribal, generic, and specific level. It is recommended that the incorporation of anatomical pericarp data into formal phylogenetic analyses of the palms will be very productive. Such an analysis of the Iguanurinae and related subtribes of the Arecinae is planned. Data from the pericarp should be included wherever possible in monographic studies of individual palm genera as well.

Acknowledgments

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