

A Systematic Histological Study of Palm Fruits. II. The *Areca* Alliance

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Abstract. Pericarp structure in the ten genera of the *Areca* alliance is more heterogeneous than in the *Ptychosperma* alliance, but with some species closely approaching the ptychospermate condition. The endocarp is generally less well-defined, although composed of the same tissue types. Fibrovascular bundles functioning as part of the endocarp tend to be more dispersed among mesocarp tissues, sclerified ground tissue is less prominent, but the locular epidermis shows about the same range of variation. Four different types of exocarp are found in the group: 1) a layer of brachysclereids; 2) a layer of brachysclereids plus fibrous bundles; 3) a series of fibrous bundles alone; 4) a dense layer of specialized tanniferous cells. Fibrous bundles can occur among the vascular bundles, or as separate series in the middle or outer pericarp. The alliance appears to be taxonomically divisible into two groups, on the basis of presence or absence of brachysclereids in the exocarp. Other minor taxonomic suggestions are made.

In this paper, the pericarp histology of representatives from the ten genera of the *Areca* alliance (sensu Moore, 1973) is described. This is the second in a series of papers, of which the first dealt with the *Ptychosperma* alliance (Essig, 1977). The aim of these investigations is to provide a broad survey of the family, in a taxonomic framework, including, where possible, at least one representative from each genus in the family. Such a survey is necessarily shallow, especially where a large genus is represented by only one or a few species. This survey will, however, provide the "first look" at fruit structure in many genera, will provide a uniform terminology for describing fruit structures in the palm family, will characterize the general fruit structure of the alliances and of some small genera, and will suggest characters of potential diagnostic value to be investigated in more detailed studies of larger genera.

The *Areca* alliance is one of the more advanced in the family by the criteria of Moore (1973), and is broadly distributed in the Old World tropics, from India to Micronesia and the New Hebrides. The ten genera together contain about 270 species. The largest is *Pinanga*, with 120 species, but several genera contain only one or a few species (*Loxococcus*, *Gigliolia*, *Nenga*, and *Siphokentia*). Fruits are generally similar to those of the *Ptychosperma* alliance, with usually pseudomonomerous gynoecia resulting in single-seeded drupes with apical stigmatic residues.

MATERIALS AND METHODS

Preserved fruits were obtained from the collection of the L. H. Bailey Hortorium at Cornell University, from the authors' own field collections,

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and from correspondents (Appendix). Materials of most genera were quite limited. In some instances only a single fruit of a genus was available, but usually several fruits per sample were examined to check against intra-sample variability. All fruits were preserved in FAA at the time of collection, and all were essentially mature.

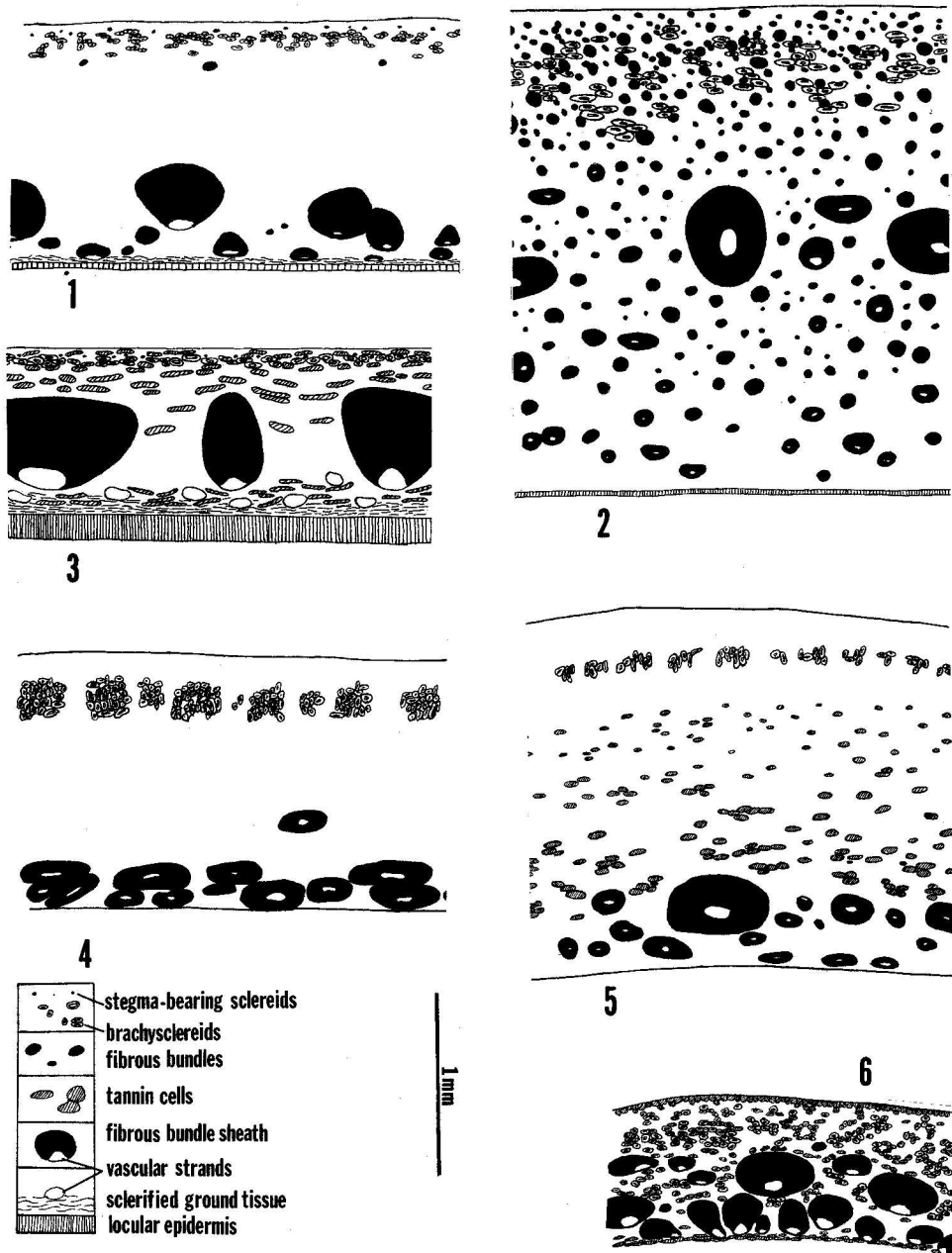
Transverse sections of the fruits were cut 15 μ m thick after conventional paraffin embedding techniques (Essig, 1977). Materials for 3-dimensional analysis were cleared in 5% sodium hydroxide, followed by bleaching in 5% sodium hypochlorite (household bleach), staining with safranin in 50% ethanol, dehydration through an ethanol series, and final clearing in xylene.

GENERAL DESCRIPTION OF THE PERICARP

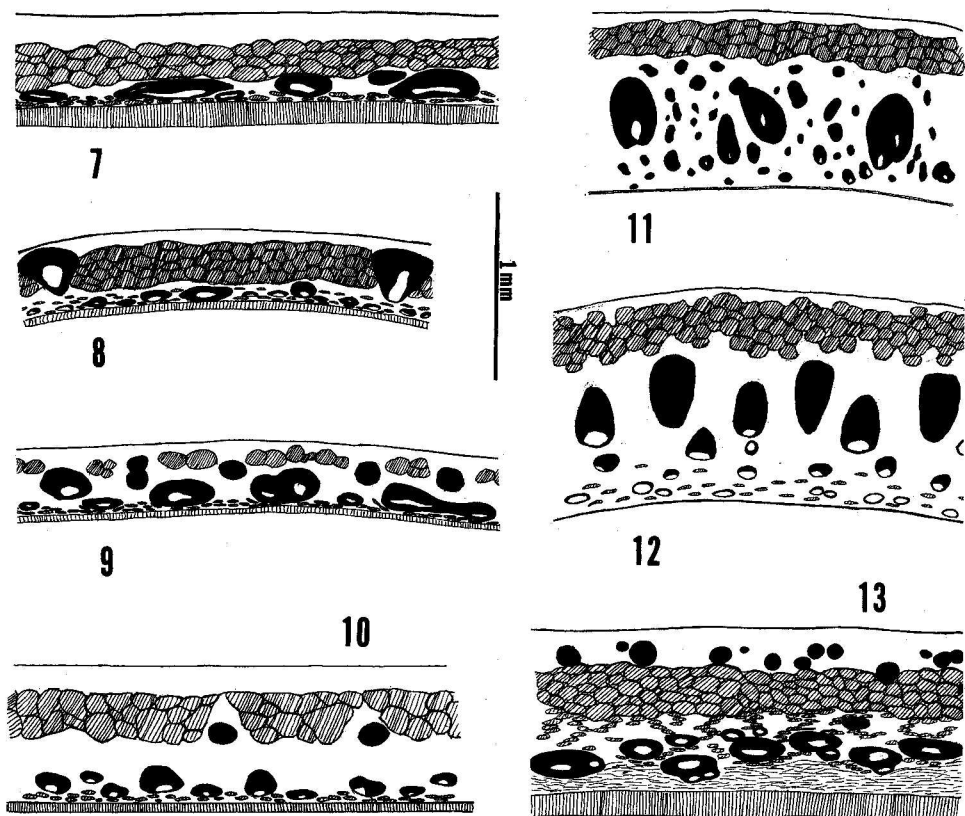
Endocarp, mesocarp, and exocarp are not always histologically well-defined in this group. Vascular and fibrous bundles, which may be dispersed among mesocarp parenchyma in fresh fruits, often persist as a functional endocarp, protecting the seed as the fruit dries, and after a thin fleshy outer region has been sloughed off (or eaten). An exocarp may or may not be present, and may consist of a layer of brachysclereids, a region of dense tanniniferous cells, or rarely as a tier of fibrous bundles. Zonation is lacking in some species of *Areca*, where fibrous bundles occur throughout the pericarp. The whole pericarp then functions as a fibrous husk upon drying. Terms such as inner, middle, and outer pericarp are used here solely to indicate position.

The locular epidermis is modified into a thick palisade layer in some species (Figs. 3, 7, 13), but in others is inconspicuous or lacking altogether in mature fruit. Ground tissue often appears compressed close to the locule as the cells are closely packed, radially very narrow, and tangentially distended (illustrated in Essig, 1977). In developmental studies, Murray (1971, 1973) noted evidence of stretching and crushing of these cells as the seed enlarged within. This inner ground tissue may also be sclerified, but not to the extent seen in many genera of the *Ptychosperma* alliance.

Vascular bundles generally have very thick fibrous sheaths, but in *Nen-gella* (Fig. 12), and *Gigliolia* (Fig. 3), the inner bundles lack sheaths. Vascular bundles may be closely appressed to the locule, as in *Loxococcus* (Fig. 4), *Gulubia* (Figs. 7-9), and *Hydriastele* (Fig. 10), while in others, they are displaced more toward the center of the pericarp. In *Areca catechu* (Fig. 2) vascular bundles are largest in the center of the pericarp, grading smaller toward the locule, and intermixed with smaller fibrous bundles that also occur outward to the epidermis. Fibrous bundles appear to be lacking in several of the species examined, or occur only infrequently among the vascular bundles (Figs. 4, 7). In others, fibrous bundles occur more regularly, usually in the outer portion of the vascularized region (Figs. 9, 11), but sometimes well removed from the



Figs. 1-6. Diagrams of portions of the pericarp in cross section. 1. *Areca* cf. *guppyana*. 2. *Areca catechu*. 3. *Gigliolia insignis*. 4. *Loxococcus rupicola*. 5. *Nenga* sp. 6. *Pinanga punicea*.



FIGS. 7-13. Diagrams of portions of the pericarp in cross section. 7. *Gulubia hombronii*. 8. *Gulubia costata*. 9. *Gulubia macrospadix*. 10. *Hydriastele microspadix*. 11. *Siphokentia beguinii*. 12. *Nengella* sp. 13. *Gronophyllum chaunostachys*.

vascular system, forming an exocarp (Figs. 13, 15). In *Areca* cf. *guppyana* (Fig. 1) there is a series of very small and widely spaced fibrous bundles in the outer pericarp, while in *Areca catechu*, there are hundreds of small fibrous bundles scattered throughout the pericarp.

Brachysclereids occur in five of the genera (*Areca*, *Pinanga*, *Nenga*, *Gigliolia*, and *Loxococcus*), informally designated here as the *Areca* group. These are cells with thick, secondary walls, but differing little in size or shape (in this alliance) from the surrounding parenchyma cells. They are idioblastic, occurring singly or in loose clusters. In the two species of *Pinanga* examined, the brachysclereids are scattered nearly throughout the pericarp, while in the other four genera, they are aggregated into a distinct subepidermal exocarp. Brachysclereids are lacking from the five genera designated here as the *Gronophyllum* group (*Gronophyllum*, *Gulubia*, *Nengella*, *Hydriastele* and *Siphokentia*).

Specialized tannin cells are lacking in *Areca* and *Loxococcus*, and scat-

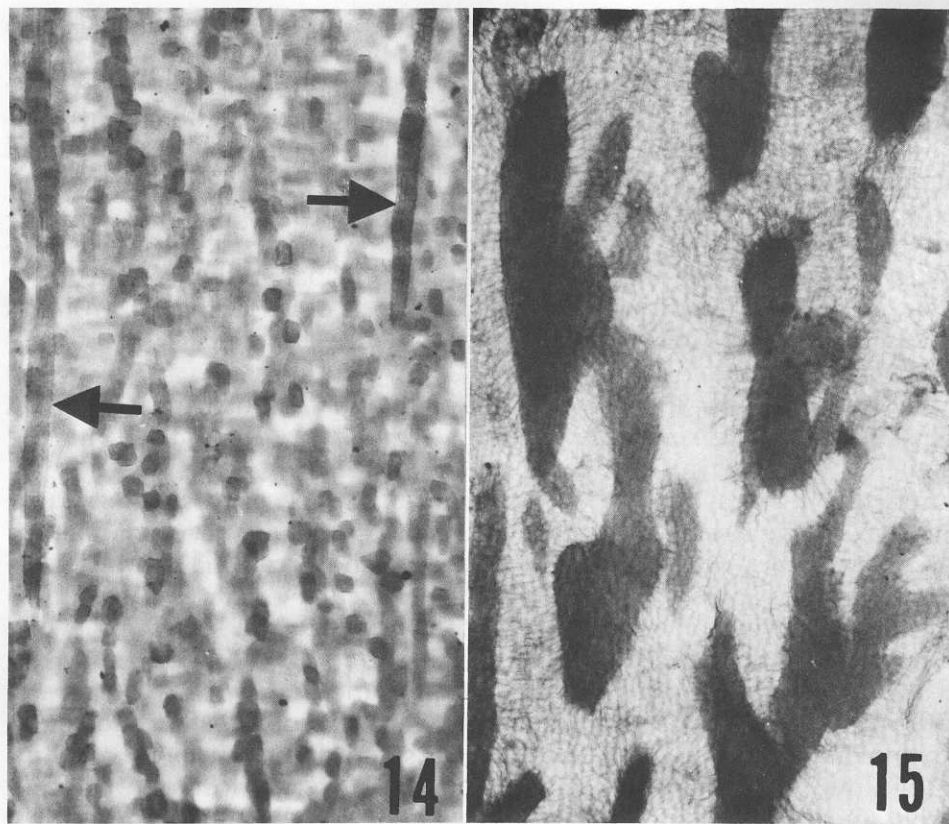
tered throughout much of the pericarp in *Pinanga* and *Nenga*. In the *Gronophyllum* group, tannin cells are conspicuously larger than surrounding parenchyma cells, and usually form a dense layer in the middle to outer pericarp. In *Nengella* and *Siphokentia*, the tanniniferous layer is just below the outer epidermis, and might be interpreted as an exocarp. Enlarged cells containing raphide crystals are sometimes found scattered in the outer pericarp, generally where no tannin is present. Only in *Pinanga* have tannins and raphides been observed together.

Unusual stegma-bearing sclereids have been observed in two species (*Areca* cf. *guppyana* and *Gigliolia insignis*), occurring sporadically just below the epidermis. The term stegma (plural, stegmata), as used by Tomlinson (1961) and Murray (1971, 1973), refers to spherical, spiny silica bodies that are normally closely associated with fibrous bundles and bundle sheaths. These have been illustrated in Essig (1977). Their occurrence on isolated sclereids needs to be explained.

ARECA.—48 species; India and Ceylon to the Philippines, Solomon Islands and Australia. Two species examined in detail: *A. catechu* (fruit 30 mm in diameter) and *A.* cf. *guppyana* (fruit 15 mm in diameter), both with ruminant endosperm. These two species display radically different histological organization and are described separately below.

Areca catechu (Fig. 2): Pericarp 2.7–3.4 mm thick. Locular epidermis sclerified, 13–18 μ m thick, inconspicuous. Fascicular system extensive, consisting of numerous vascular bundles with fibrous sheaths and numerous purely fibrous bundles, the two types of bundles intergrading and interconnected, with mostly small vascular bundles in the innermost pericarp, these then intermixed with fibrous bundles until mid-pericarp where the largest vascular bundles (to 500 μ m thick) occur, then mostly fibrous bundles in the outer half of the pericarp; all bundles subterete to mildly tangentially distended. Ground tissue strongly compressed close to the locule and very weakly sclerified, cells larger and tangentially elongate through the remainder of the pericarp; brachysclereids numerous in a broad band somewhat removed from the epidermis; enlarged cells with raphides frequent; tanniniferous cells absent. Epidermal cells tabloid but somewhat rounded externally, lightly pigmented.

Areca cf. *guppyana* (Figs. 1, 14): Pericarp 1.4 mm thick. Locular epidermis sclerified, 40 μ m thick, weakly developed as a palisade layer. Fascicular system in two disparate parts: the inner close to the locule, consisting of vascular bundles, with thick fibrous sheaths, and occasional small fibrous bundles, largest bundles ca. 600 μ m broad, somewhat tangentially distended; outer system somewhat removed from the epidermis, consisting of widely spaced, disconnected fibrous bundles 300–1400 μ m long. Ground tissue compressed and sclerified close to the locule, cells larger external to the vascular bundles and irregularly shaped and oriented, often radially elongate and radiating outward from the distal sides of the bundles; brachysclereids abundant in a layer between the outer fibrous bundles and the epidermis, smaller stegma-bearing scler-



Figs. 14–15. Cleared portions of the exocarp, viewed from the inside of the fruit toward the outside (both $\times 50$). 14. *Areca* cf. *guppyana*. 15. *Gronophyllum chaunostachys*. Arrows on Fig. 14 indicate fibrous bundles. Remaining structures are brachysclereids.

eids just external to brachysclereids; raphides common in enlarged cells in middle to outer pericarp, tanniniferous cells absent. Epidermal cells broadly tabloid, gently rounded externally, not noticeably pigmented.

Areca macrocalyx and several undetermined specimens closely related to it from New Guinea were examined briefly and appear to have essentially the same structure as *A. catechu*. An undetermined specimen from Sarawak (Moore 9109) is more similar in general organization to *A.* cf. *guppyana* from New Britain. It differs primarily in its possession of a wider, better developed palisade layer (locular epidermis), and conspicuous tannin cells in the outer pericarp. The small stegma-bearing sclereids appear to be lacking also.

GIGLIOLIA.—2 species; Borneo (Fig. 3). One species examined: *G. insignis*; fruit 12 mm in diameter, endosperm ruminant.

Pericarp 1.0–1.1 mm thick. Locular epidermis a sclerified palisade layer 155 μ m thick. Fascicular system of vascular bundles lacking sheaths

near the locular epidermis, but with massive fibrous sheaths in mid-pericarp, the latter to 500 μm thick; no purely fibrous bundles observed. Ground tissue strongly compressed and sclerified internal to the large bundles, cells between the large bundles compressed and greatly distended tangentially, cells of the outer pericarp much shorter, but still somewhat tangentially elongate; brachysclereids abundant in a narrow zone somewhat removed from the epidermis; small stegma-bearing sclereids frequent between brachysclereids and epidermis; tannin cells tangentially elongate and the same size as adjacent parenchyma cells, abundant but scattered in the outer and inner thirds of the pericarp; raphides lacking. Epidermal cells tabloid, slightly rounded externally, not noticeably pigmented.

GRONOPHYLLUM.—14 species; Malaya to New Guinea and Australia (Figs. 13, 15). One species examined: *G. chaunostachys*; fruit 10 mm in diameter, endosperm homogeneous.

Pericarp 1.2 mm thick. Locular epidermis a sclerified palisade layer 150 μm thick. Fascicular system in two disparate parts: the inner of vascular bundles with thick fibrous sheaths and occasional fibrous bundles in a series somewhat distant from the locular epidermis; the outer of short, disconnected, branched fibrous bundles in a series somewhat removed from the outer epidermis; vascular bundles 100–240 μm broad, strongly tangentially distended, the fibrous bundles essentially terete, 40–150 μm in diameter. Ground tissue moderately compressed and sclerified internal to the vascular bundles, cells somewhat larger and frequently tanniniferous around the bundles, much larger and densely tanniniferous in a mid-pericarp zone, smaller and moderately compressed in the outermost zone; brachysclereids and raphides absent. Epidermal cells tabloid, not noticeably pigmented, with a thick cuticle.

GULUBIA.—11 species; Malaya to the Solomons, New Hebrides, Palau and Australia (Figs. 7–9). Four species examined: *P. costata*, *P. hombronii*, *P. macrospadix* and one undetermined; fruit 6–8 mm in diameter, endosperm homogeneous or (in *G. macrospadix*) ruminant.

Pericarp 0.3–1.2 mm thick. Locular epidermis a sclerified palisade layer 25–125 μm thick. Fascicular system of vascular bundles with fibrous sheaths and occasional fibrous bundles aggregated close to the locule, sometimes with a well-defined outer series of fibrous bundles (Fig. 9), or with regularly occurring, greatly enlarged vascular bundles forming ribs around the fruit (Fig. 8); bundles quite variable in size, mostly tangentially distended, but outer fibrous bundles subterete. Ground tissue of small, but uncompressed and unsclerified, frequently tanniniferous cells near the locule, cells becoming somewhat larger and sometimes radially distended toward mid-pericarp; a specialized zone of greatly enlarged tanniniferous cells occupying the middle or outer pericarp; subepidermal zone of parenchyma strongly compressed; raphides and brachysclereids lacking. Epidermal cells tabloid to semi-papillate, with light to moderate pigmentation.

The unidentified species (*Essig LAE 55099*) is not illustrated, but closely resembles *G. hombronii*. It differs from this species primarily in having a larger zone of non-tanniniferous parenchyma, in which the cells are radially distended, between the vascular bundles and the tanniniferous zone. This difference may possibly be due to a difference in maturity of the specimens.

HYDRIASTELE.—8 species; New Guinea, the Bismarck Archipelago and Australia (Fig. 10). One species examined: *H. microspadix*; fruit 6–7 mm in diameter, endosperm ruminant (other species have homogeneous endosperm).

Pericarp 0.6–0.9 mm thick. Locular epidermis a sclerified palisade layer 50 μ m thick. Fascicular system of vascular bundles with thick fibrous sheaths in a single series close to the locule and fibrous bundles well spaced from one another in the middle pericarp; vascular bundles somewhat tangentially distended, 100–180 μ m broad, fibrous bundles subterete, 80–100 μ m in diameter. Ground tissue of compressed, weakly sclerified, and frequently tanniniferous cells internal to the vascular bundles, cells much larger and densely tanniniferous in the middle to outer pericarp, strongly compressed and non-tanniniferous in a brief subepidermal zone; brachysclereids and raphides lacking. Epidermal cells tabloid, moderately pigmented, with a thick cuticle.

Two specimens of this species from northeastern New Guinea were examined and are essentially the same in structure.

Loxococcus.—One species (*L. rupicola*); Ceylon (Fig. 4); fruit 18 mm in diameter, endosperm ruminant.

Pericarp 1.4–1.9 mm thick. Locular epidermis inconspicuous, unsclerified, 1 μ m thick. Fascicular system of vascular bundles with thick fibrous sheaths and occasional fibrous bundles, densely aggregated, one to two bundles deep, close to the locule; bundles all strongly tangentially distended, 150–400 μ m broad, 90–200 μ m thick. Ground tissue moderately compressed around the bundles, weakly sclerified adjacent to the locule, cells abruptly becoming somewhat larger external to the vascular bundles, becoming smaller again near the epidermis, raphides and tanniniferous cells lacking; brachysclereids densely packed in an interrupted layer somewhat removed from the epidermis. Epidermal cells tabloid, not noticeably pigmented.

NINGA.—2 species; Indonesia (Fig. 5). Specimen examined unidentified; fruit 14 mm in diameter, endosperm ruminant.

Pericarp 2 mm thick. Locular epidermis lacking at maturity. Fascicular system of vascular bundles with thick fibrous sheaths and occasional small fibrous bundles aggregated close to the locule, bundles all somewhat tangentially distended, largest bundles 450 μ m broad, smallest about one-tenth the size. Ground tissue strongly compressed but not sclerified close to the locule; cells larger, somewhat tangentially elongate, frequently tanniniferous throughout the middle pericarp; brachysclereids present in a thin, interrupted layer somewhat removed from the epidermis; ra-

phides lacking. Epidermal cells tabloid, tangentially elongate, not strongly pigmented.

NENGELLA.—19 species; New Guinea (Fig. 12). One species examined, unidentified; fruit 9 mm in diameter, endosperm ruminant (other species with homogeneous endosperm).

Pericarp 1.2 mm thick. Locular epidermis sclerified, but thin and inconspicuous. Fascicular system consisting of three types of bundles: vascular strands with little or no fibrous sheath in the inner pericarp, vascular bundles with very thick radially distended fibrous sheaths in the inner middle pericarp, and purely fibrous bundles, the same size and shape as the large vascular bundles and alternating with them in the middle pericarp; largest bundles 300–400 μm wide along the radial axis and 160–200 μm broad; smaller, unsheathed bundles 80–130 μm broad and tangentially distended. Ground tissue moderately compressed near the locule, not sclerified, with frequent tanniniferous cells; cells larger, less compressed in middle pericarp greatly, enlarged and tanniniferous in a thick band somewhat removed from the epidermis; raphides and brachysclereids lacking. Epidermal cells papillate, not densely pigmented.

The taxonomy of this genus is presently being revised. The specimen examined was cultivated at Lae, Papua New Guinea, but representative of a species common and widespread in northeastern New Guinea.

PINANGA.—120 species; India, southeast Asia, the Philippines, Indonesia and New Guinea (Fig. 6). Two species examined, only one in detail: *P. punicea* var. *papuana*; fruit 6 mm in diameter, endosperm ruminant.

Pericarp 0.8 mm thick. Locular epidermis lacking at maturity. Fascicular system of vascular bundles with thick fibrous sheaths, closely packed through the inner half of the pericarp with purely fibrous bundles rare and very small; largest vascular bundles 450 μm broad, somewhat tangentially distended, smallest about $\frac{1}{8}$ the size, irregular in shape. Ground tissue of relatively uniform cell size, slightly compressed but not sclerified near the locule; tanniniferous cells forming a thin, tight layer adjacent to the locule, also scattered throughout the pericarp and forming another thin, tight layer adjacent to the epidermis; brachysclereids numerous, scattered through most of the pericarp, lacking only in the inner 200 μm of the pericarp; raphide-bearing cells common, scattered throughout the pericarp. Epidermal cells papillate, densely pigmented.

Pinanga insignis from the Philippines was briefly examined and appears to have essentially the same structure as the species illustrated. This is a large genus, however, and it is likely that significant variation would be found in a more extensive sampling.

SIPHOKENTIA.—2 species from the Moluccas (Fig. 11). One species examined: *S. beguinii*; fruit 6 mm in diameter, endosperm ruminant.

Pericarp 0.7–0.9 mm thick. Locular epidermis sclerified, 12 μm thick. Fascicular system of vascular bundles with thick fibrous sheaths and purely fibrous bundles distributed throughout the inner two-thirds of

the pericarp. Ground tissue moderately compressed, unsclerified, and fairly uniform through the inner two-thirds of the pericarp, cells much larger, not compressed, and densely tanniniferous in a zone occupying most of the outer third of the pericarp, cells highly compressed in a brief subepidermal zone; brachysclereids and raphides absent. Epidermal cells tabloid, not noticeably pigmented, and with a thick cuticle.

DISCUSSION AND CONCLUSIONS

The only other alliance for which comparable pericarp data are available is the *Ptychosperma* alliance (Essig, 1977). Though the tissue types found in the two alliances are similar (illustrated in Essig, 1977), there are important differences in the organization of these tissues. With respect to this organization, the *Areca* alliance shows considerably more diversity than the *Ptychosperma* alliance, with only a few members approaching the ptychospermate type of organization (e.g., *Areca* cf. *guppyana*). In the *Ptychosperma* alliance, vascular bundles with thick, fibrous sheaths are generally aggregated close to the locule to form the bulk of a well-defined endocarp, while a separate outer series of fibrous bundles reduced to short "sclerosomes" (see Essig, 1977) in most species contributes to a well-defined exocarp, of which the other component is a dense layer of brachysclereids.

The heterogeneity of the *Areca* alliance results primarily from two factors: 1) variation in the distribution of fibrous and vascular bundles, from unitary systems containing only vascular bundles, to double systems with inner vascular and outer fibrous bundles, with many intermediate forms also present; and 2) the absence of a layer of brachysclereids and its replacement by a specialized zone of tanniniferous cells in the five genera designated here as the *Gronophyllum* group.

For these reasons it is impossible to define in any consistent histological manner the boundaries of the endocarp, mesocarp and exocarp zones in this alliance. As was argued earlier, however (Essig, 1977), these are functional-morphological terms, and it is not necessary to define them histologically. Functionally, the endocarp of the *Areca* alliance is generally the same as that of the *Ptychosperma* alliance, conforming to the Type III category of Murray (1971, 1973), in which the vascular bundles, and other sclerenchyma, persist as a protective sheath around the seed after the softer outer pericarp tissues have worn off. This endocarp is however less well developed, i.e., less condensed around the locule, and less prone to be cemented together by the sclerification of the surrounding ground tissue than in the *Ptychosperma* alliance. Thus, vascular bundles functioning as part of the endocarp are interspersed within softer mesocarp tissue that has other functions.

An exocarp may be present in four different forms in the *Areca* alliance as: 1) a layer of brachysclereids (in most of the *Areca* group); 2) as a layer of brachysclereids plus fibrous bundles (the ptychospermate type,

TABLE 1. Taxonomic chart of the species examined, arranged according to important diagnostic characters.

<i>Areca</i> group: Brachysclereids present in pericarp; tanniniferous cells, when present, scattered and not much larger than surrounding cells.		
Tannin cells present		Tannin cells absent
Palisade layer present	Palisade layer absent	Fibrous bundles few, among vascular bundles: <i>Loxococcus rupicola</i>
	<i>Nenga</i> sp.	
Brachysclereids in a subepidermal layer: <i>Gigliolia insignis</i> <i>Areca</i> sp. (Sarawak)		Fibrous bundles many, scattered: <i>Areca catechu</i> <i>Areca macrocalyx</i>
Brachysclereids scattered: <i>Pinanga punicea</i> <i>Pinanga insignis</i>		Fibrous bundles confined to a subepidermal layer: <i>Areca</i> cf. <i>guppyana</i>
<i>Gronophyllum</i> group: Brachysclereids absent; tanniniferous cells enlarged and forming a continuous layer in the middle to outer pericarp.		
Palisade layer present		Palisade layer absent
Fibrous bundles in a separate outer series, external to tanniniferous layer: <i>Gronophyllum chaunostachys</i>		Fibrous bundles small, numerous, scattered: <i>Siphokentia beguinii</i>
Fibrous bundles associated with vascular bundles, internal to tanniniferous layer: <i>Gulubia costata</i> <i>Gulubia hombronii</i> <i>Gulubia macrospadix</i> <i>Gulubia</i> sp. <i>Hydriastele microspadix</i>		Fibrous bundles large, alternating with a series of large vascular bundles: <i>Nengella</i> sp.

found in *Areca* cf. *guppyana*); 3) a layer of tanniniferous cells (*Nengella*, *Siphokentia*); or 4) a series of fibrous bundles external to a tanniniferous mesocarp (*Gronophyllum*). In some genera (*Gulubia* spp.) a tanniniferous zone is present in mid-pericarp, making it difficult to call it an exocarp, but probably serving the same function. These various types of exocarp are generally assumed to be defensive barriers against predation (Uhl & Moore, 1977). Unfortunately, there is no data on the functioning or relative effectiveness of these tissues in palm fruits.

The diversity of pericarp structure in the *Areca* alliance contrasts with the relatively uniform structure in the *Ptychosperma* alliance. The ancestral stock of the latter group had apparently attained its basic pericarp organization before diversifying into the extant genera, while the *Areca*

alliance, if truly monophyletic, appears to have arisen from a less specialized stock and given rise to a greater array of specialized types.

The attainment of a separate, outer series of fibrous bundles, which is the critical feature of the *ptychospermate* exocarp, has occurred at least twice among the members of the *Areca* alliance, in *Areca* and in *Gronophyllum*. While the outer bundles in *Areca* (Fig. 14) are essentially like those in the *Ptychosperma* alliance, the bundles in *Gronophyllum* (Fig. 15) have a unique structure and organization, and certainly arose independently. Preliminary results from other alliances indicate that similar systems have developed a number of times, suggesting a strong selective pressure for the stockade-like exocarp that results. The further specialization of such outer bundles into the "sclerosomes" of the *Ptychosperma* alliance has been documented by Essig (1977).

Hard taxonomic conclusions cannot be drawn from the narrow data base presented here, but some suggestions can be made for consideration in more comprehensive studies of the taxa in question. Table 1 has been presented as a device for displaying characters of potential diagnostic value in a taxonomic framework. The major suggestions are as follows: 1) the alliance can be divided into two groups, the *Areca* group and the *Gronophyllum* group, based on the presence or absence of brachysclereids and correlated characters; 2) the unusual stegma-bearing sclereids found in *Areca* cf. *guppyana* and *Gigliolia insignis* indicate a possible close relationship between these two species; 3) the genus *Areca* appears to be divisible into two groups, one, represented by *A. catechu* and *A. macrocalyx*, with vascular and fibrous bundles dispersed through the entire pericarp, and the other by *A. cf. guppyana* (and *Gigliolia*?), with fibrous bundles only in the exocarp or lacking; 4) *Gulubia* and *Hydriastele* are scarcely distinguishable from one another on the basis of present histological data, suggesting a very close relationship between them.

Comments on the affinities of this alliance among the Arecoid palms will be deferred until data is available from the other alliances.

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APPENDIX: SPECIMENS EXAMINED

- Areca catechu* Linnaeus: *Hirano s.n.*, cult. H. L. Lyon Arboretum, Honolulu (USF).
Areca cf. *guppyana* Beccari: *Essig LAE 55210* (BH).
Areca macrocalyx Zippelius: *Moore & Whitmore 9303* (BH).
Areca sp.: *Moore & Chai 9109* (BH).
Gigliolia insignis Beccari: *Moore et al. 9153* (BH).
Gulubia costata Beccari: *Essig LAE 55178* (BH).
Gulubia hombronii Beccari: *Moore & Whitmore 9296* (BH).
Gulubia macrospadix (Burret) H.E. Moore: *Moore & Whitmore 9305* (BH).
Gulubia sp.: *Essig LAE 55099* (BH).
Gronophyllum chaunostachys (Burret) Burret: *Essig LAE 55137* (BH).
Hydriastele microspadix (Beccari) Burret: *Essig & Katik LAE 55001* (BH); *Moore 9271* (BH).
Loxococcus rupicola (Thwaites) H. Wendland & Drude: *Moore 9031* (BH).
Nenga sp.: *Moore & Pennington 9056* (BH).
Nengella sp.: *Essig s.n.*, cult. National Botanic Garden, Lae, Papua New Guinea (USF).
Pinanga punicea (Blume) Merrill: *Essig LAE 55085* (BH).
Pinanga insignis Beccari: *Moore & Pancho 9389* (BH).
Siphokentia beguinii Burret: *Moore & Pancho 9386* (BH).