A Systematic Histological Study of Palm Fruits.
I. The *Ptychosperma* Alliance[1]

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Abstract. *The fruit of the eight genera of the* Ptychosperma *alliance have complex sclerenchymatous endocarps that typically consist of a palisade layer derived from the locular epidermis, some sclerified ground tissue, and vascular bundles with thick fibrous sheaths. Highly integrated endocarps appear to have evolved in at least six different lines in the alliance, and unspecialized forms can be found in several genera. The exocarp consists of fibrous bundles and brachysclereids, and also shows varying degrees of integration. Although it is difficult to separate the large genera from one another upon pericarp characters alone, small genera, subgenera, and groups of species often separate readily, suggesting that the major taxonomic application of data from the pericarp will be at the infrageneric level in this alliance.*

In this paper, the first in a series presenting histological investigations into the structure of the pericarp in the palm family (Palmae or Arecaceae), the informal groups of Moore's (1973) classification will be followed, beginning with the *Ptychosperma* alliance of the arecoid group. The present research grew out of a taxonomic study of *Ptychosperma* (Essig, 1975) in which certain histological features of the pericarp were found to be of taxonomic significance. Earlier studies (Guérin, 1949; Murray, 1971, 1973) indicated that pericarp histology might provide important systematic information in many groups of palms.

Guérin (1949) made a broad, descriptive survey of palm fruits with representatives from most of the major groups in the family. Though he provided much useful information, he did not analyze his data in a taxonomic framework and did not discuss the phylogenetic or ontogenetic implications of the data. Murray (1971) covered in depth the ontogeny and structure of a relatively few examples from six of the major groups of palms—the coryphoid, chamaedoreoid, pseudophoenicoid, caryotoid, arecoid, and cocosoid groups. Later she published a special analysis of the formation of the endocarp (Murray, 1973), a work providing valuable information on the origin and ontogeny of the various tissues in palm fruits, adding another dimension to Guérin's data. In the work of both authors it is evident that there is great structural diversity in palm fruits that might be exploited in taxonomic and evolutionary studies, as has long been recognized by taxonomists such as Moore (1957). The purpose of the present series of investigations is to augment the base of data established by Guérin, Murray, and others, to synthesize

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fibrous bundle
brachysclereids
tannin cell
vascular strands
fibrous bundle sheath
sclerified ground tissue
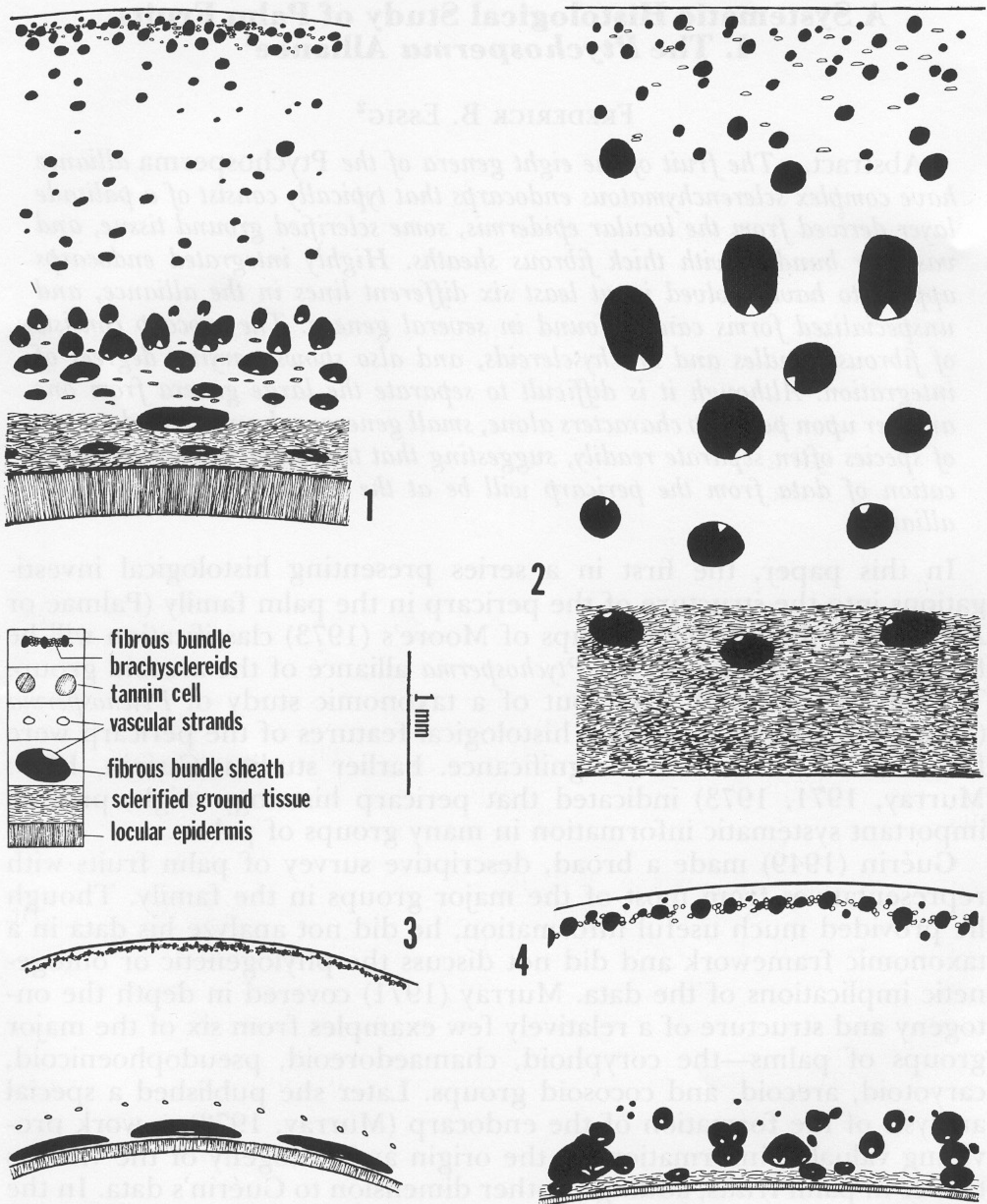locular epidermis

1 mm

1
2
3
4

FIG. 1–4. Diagrams of portions of the pericarp in cross section. 1. *Veitchia joannis*. 2. *Normanbya normanbyi*. 3. *Carpentaria acuminata*. Note ring of naked vascular strands in inner mesocarp. 4. *Drymophloeus subdistichus*.

the information systematically, and to discuss the taxonomic and phylogenetic implictions. An effort will be made to study at least one representative of every genus in the family.

The *Ptychosperma* alliance consists of eight genera native to the southwestern Pacific region. *Ptychosperma* and *Veitchia* are large, diverse genera,

the former centered in New Guinea and the latter in Fiji, the New Hebrides, and the Philippines. *Brassiophoenix* and *Ptychococcus* are small genera related to *Ptychosperma* and also centered in New Guinea. *Normanbya* and *Carpentaria* are monotypic genera from northern Australia, and *Balaka* is a small genus from Fiji and Samoa. *Drymophloeus* is a highly disjunct genus with species in eastern Indonesia, western New Guinea, the Solomon Islands, and Samoa. All genera have pseudomonomerous gynoecia resulting in single-seeded drupaceous fruits. Rarely, two- or three-seeded fruits are produced teratologically in some species (e.g., *Ptychosperma lineare* (Murray, 1971)). Moore (1957) noted that the characters separating genera in this alliance are primarily in the fruit and seed.

Interpretation of Pericarp Zones.—Endocarp, mesocarp, and exocarp are morphological terms convenient for designating inner, middle, and outer regions of the pericarp, particularly in drupaceous fruits, where these regions show specializations of structure and function. The endocarp is typically sclerenchymatous and presumably protects the enclosed seeds from hazards such as predation, desiccation, or crushing. The mesocarp is generally parenchymatous, fleshy and nutritious, serving to attract animal dispersers. It may show other specializations such as being fibrous and buoyant as in the Coconut or the Nypa Palm. The exocarp, when developed, may also be sclerenchymatous or contain secondary substances such as tannins or raphides. It presumably protects the entire fruit, or perhaps mainly the mesocarp, from nondispersive predators or premature dispersers while the fruit is developing. A fourth part of the pericarp, the epicarp, is sometimes recognized for the epidermal layer when it shows some special modification.

These zone concepts have been used quite differently by different authors. Guérin (1949) and Wessels-Boer (1968) used endocarp to refer only to the locular epidermis, even though there were often other adjacent sclerenchymatous tissues in the fruits that they were describing that presumably would contribute to the protection of the seeds. Murray (1971, 1973) and Robertson (1977) have taken the more morphological-functional approach and described endocarps consisting of several types of sclerenchymatous tissues.

Concerning the exocarp there is more confusion. Guérin (1949) did not recognize the exocarp at all, but described an epicarp derived from the epidermis for a number of species. For Wessels-Boer (1968) the exocarp consisted only of the epidermis, even though there was a prominent subepidermal zone of stone cells in some of his examples. Robertson (1977) indicated that the exocarp in *Jubaeopsis* (*Cocos* alliance) had been reduced to only the epidermis, implying that the exocarp might more generally consist of epidermis plus some subepidermal tissues. Murray (1971, 1973) restricted the use of exocarp to a distinctive subepidermal layer and used epicarp for the epidermis and its elaborations. The concepts of Murray are followed here because they are consistent with the traditional morphological-functional use of the terms. The term epicarp
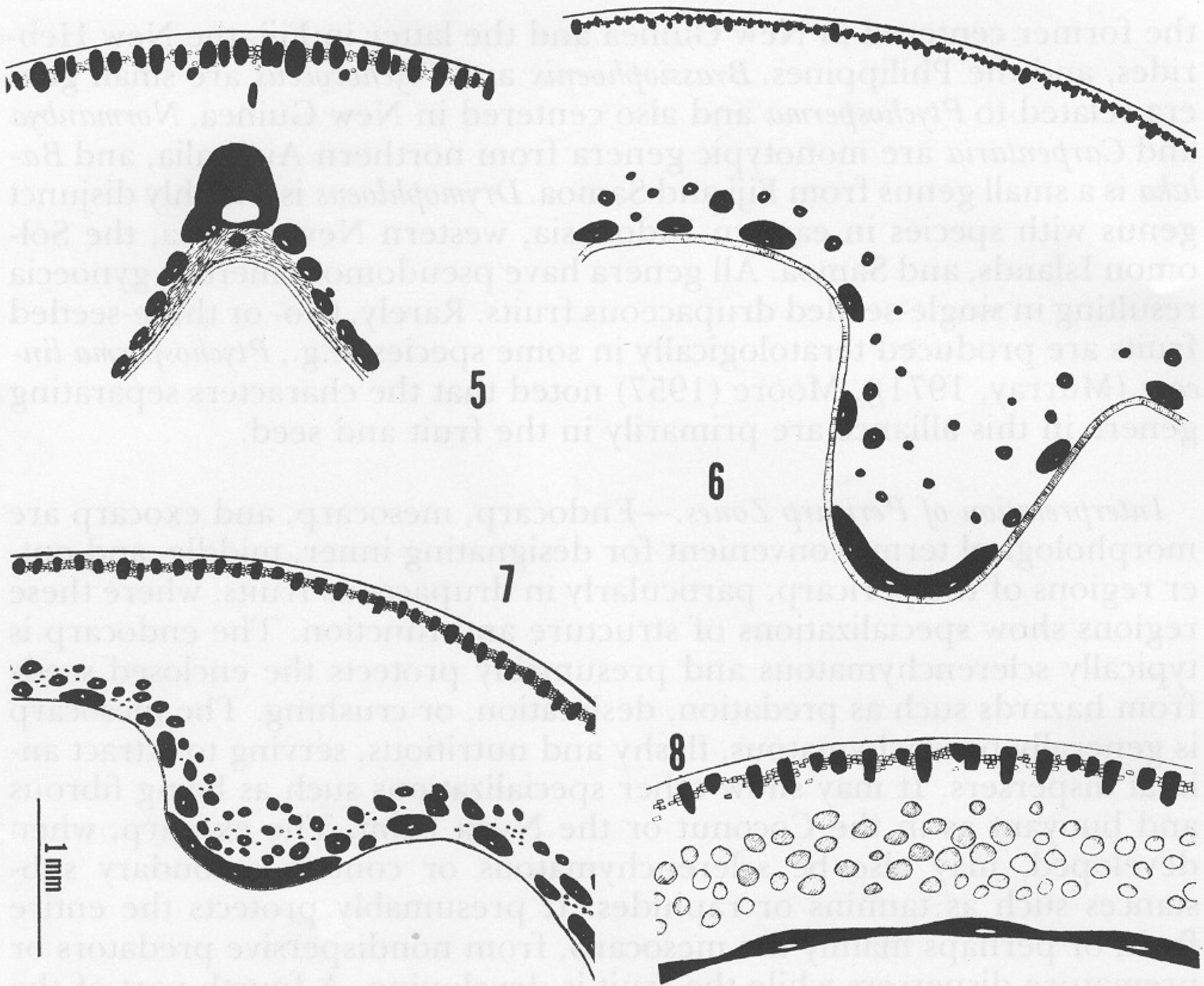
FIG. 5–8. Diagrams of portions of the pericarp in cross section. 5. *Balaka burretiana*. 6. *Ptychosperma schefferi*. 7. *Ptychosperma lauterbachii*. 8. *Ptychosperma salomonense*.

has not been used, largely because the epidermis in the *Ptychosperma* alliance is quite unspecialized.

MATERIALS AND METHODS

Specimens were obtained primarily from the preserved fruit collection at the L. H. Bailey Hortorium, Cornell University, and from my own collections in New Guinea. Some materials were obtained from correspondents and a few were taken from herbarium specimens. Materials were limited, and often only a single fruit could be examined for each species.

Hand sections, rotary microtome sections, and cleared material were used to elucidate structures. Specimens for rotary microtome sectioning were prepared in the conventional manner, though very protracted dehydration and infiltration times were necessary for this material (one to four weeks for each step). Some fruits with very hard tissues (e.g., *Ptychococcus*) have not yet been satisfactorily sectioned despite application of a variety of softening techniques. Sections were secured to slides that
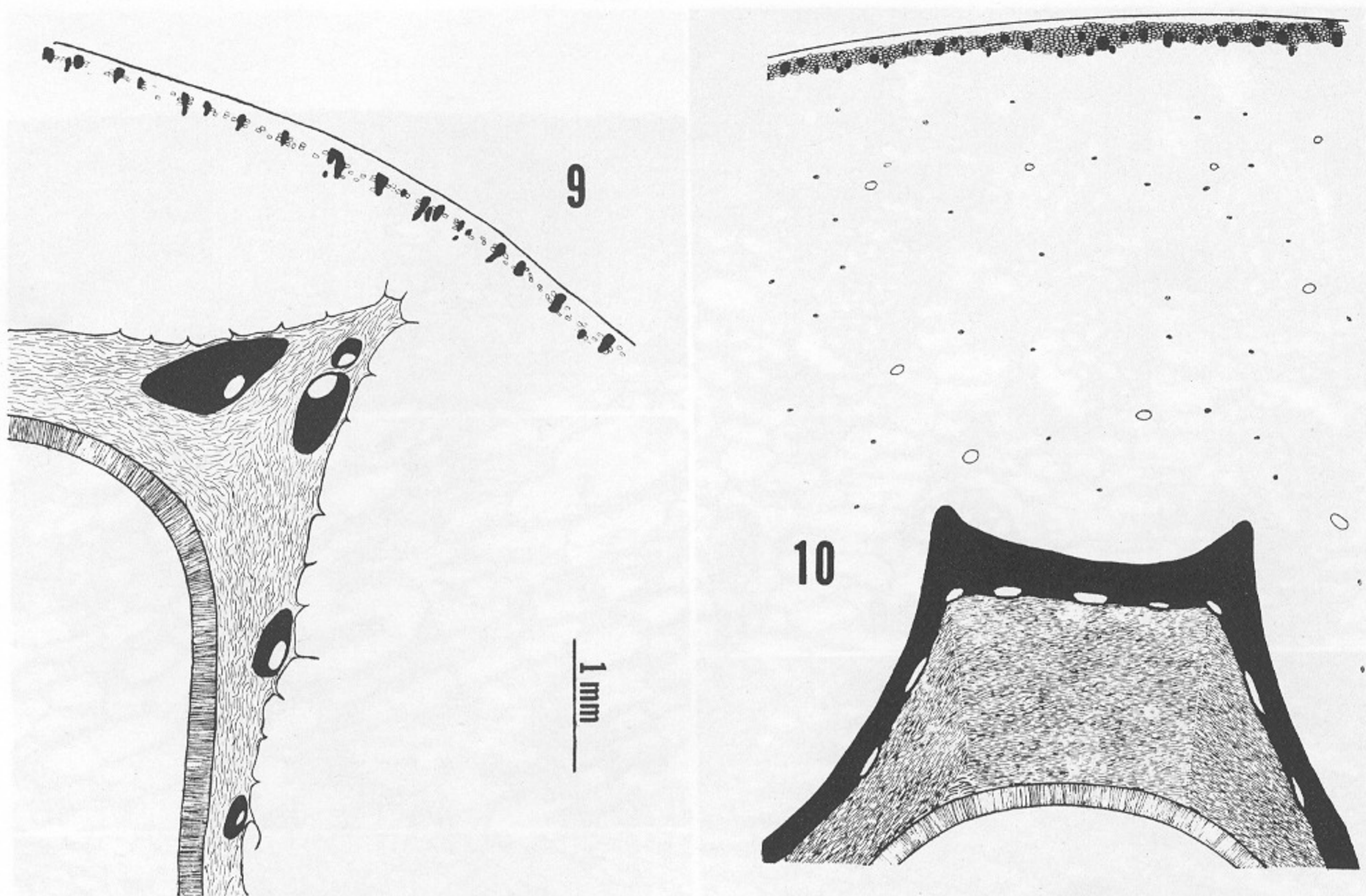
FIG. 9–10. Diagrams of portions of the pericarp in cross section. 9. *Brassiophoenix schumannii*. 10. *Ptychococcus* aff. *elatus*. Note naked vascular strands scattered through mesocarp among small tannin cells.

had been earlier coated with a solution of gelatin and chrome alum, according to the method of Pappas (1971), then stained with safranin, haematoxylin, and fast green.

GENERAL DESCRIPTION OF THE PERICARP

In most genera of the *Ptychosperma* alliance a clear endocarp, mesocarp, and exocarp can be recognized. In some instances the histological boundary between adjacent zones is sharply defined whereas in others the zones merge gradually. In this alliance the endocarp and exocarp are composed of sclerenchymatous tissues but the mesocarp is primarily parenchymatous.

The endocarp may consist of sclerenchyma from all three primary tissue systems (epidermal, vascular, and ground). The locular epidermis typically forms into a palisade layer ["endocarp palissadique" (Guérin, 1949)] through the radial elongation and sclerification of the individual cells (Fig. 13, 17). The thickness of this layer varies considerably, reaching a maximum of 330 μm in *Veitchia joannis*. It is hardly developed at all or is even lacking in some species of *Ptychosperma* subg. *Ptychosperma*. It is also lacking in *Normanbya* and some species of *Drymophloeus*.

The vascular system of the mature fruit is greatly expanded over the simple vasculature of the carpel (Uhl, 1976). Most bundles in the system
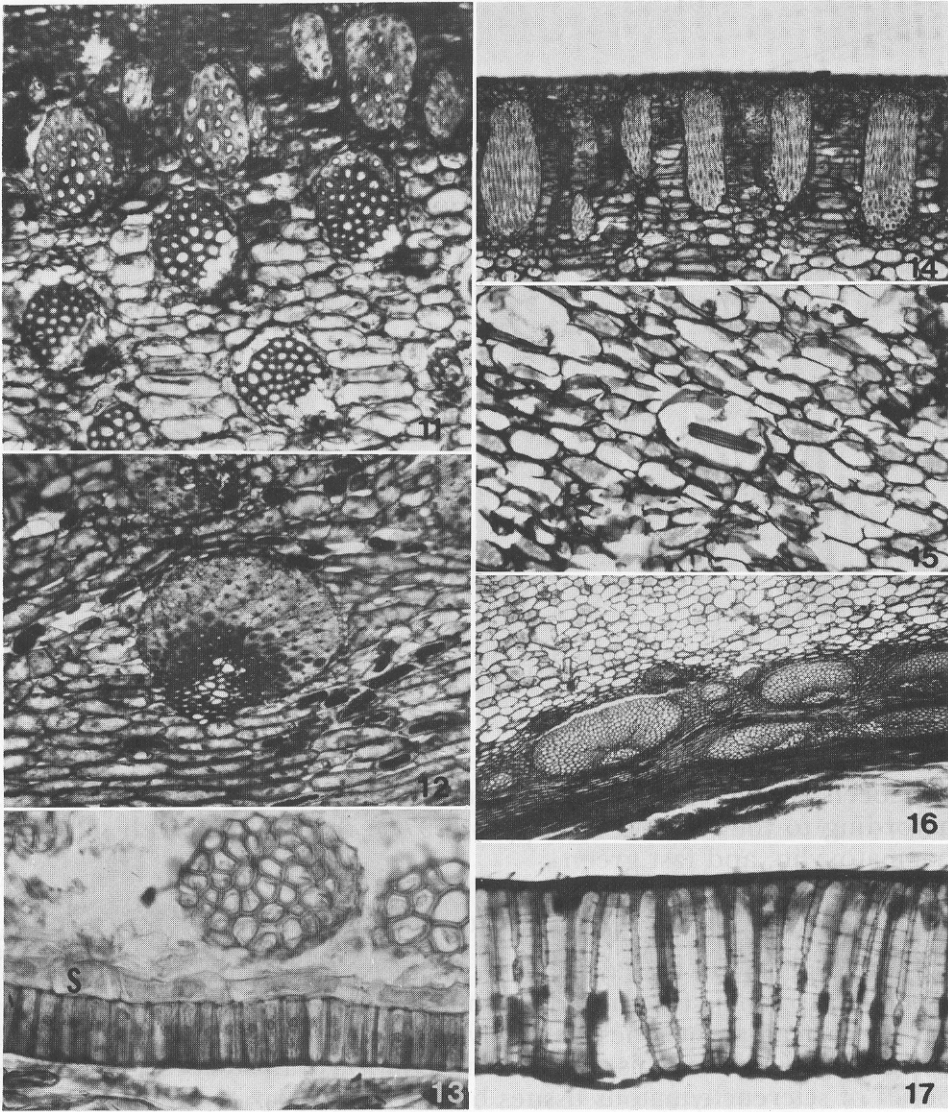
FIG. 11–17. Photomicrographs of portions of the pericarp in cross section. 11. *Veitchia joannis*, part of outer pericarp, with fibrous bundles. The exocarp is the region of darker ground tissue and bundles with thicker cell walls. The epidermis is just out of the picture at the top, ×125. 12. *Veitchia joannis*, vascular bundle. Note thick walls of fibers and stegmata around outside of bundle, ×125. 13. *Ptychosperma schefferi*, endocarp region with locular epidermis, one row of sclerified cells (*S*) and two fibrous bundles, ×315. 14. *Ptychosperma hosinoi*, exocarp region with prominant fibrous bundles, ×125. 15. *Ptychosperma hosinoi*, mesocarp parenchyma with one fascicle of raphides, ×125. 16. *Ptychosperma hosinoi*, endocarp region minus the locular epidermis. Note dorsiventrally compressed vascular bundles and thick zone of compressed and sclerified ground tissue, ×50. 17. *Carpentaria acuminata*, locular epidermis, ×315).
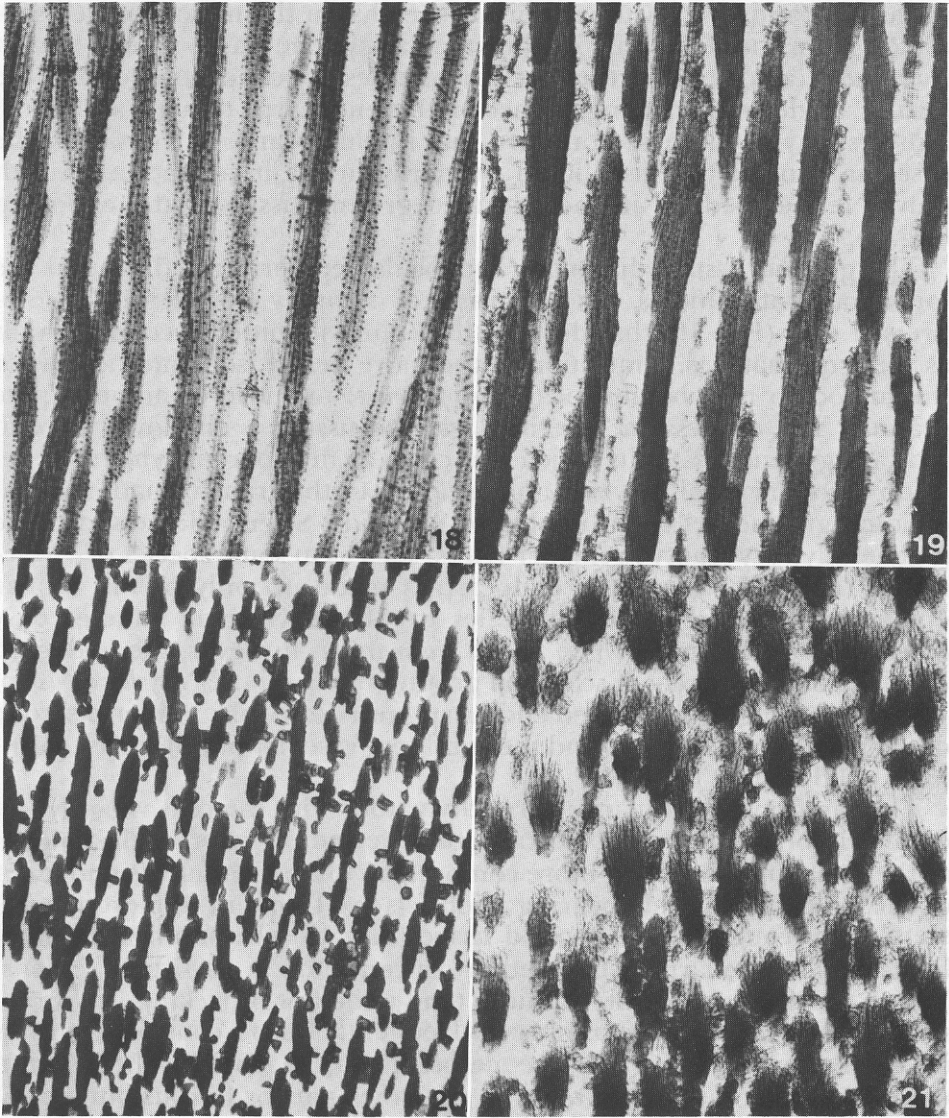
FIG. 18–21. Cleared portions of exocarp viewed from the inside of the fruit toward the outside. Note extreme variation in bundle length in each figure (all ×50). 18. *Drymophloeus beguinii*. Small round structures on bundles are stegmata. 19. *Ptychosperma palauense*. 20. *Drymophloeus subdistichus*. Note shape and distribution of brachysclereids. 21. *Ptychosperma salomonense*.

consist of a strand of vascular conducting tissue incompletely surrounded by a very thick fibrous sheath (Fig. 12, 16). The relative proportions of vascular to fibrous tissues in the bundles is quite variable, however, and there are occasionally wholly fibrous bundles. In some species (*Carpentaria acuminata*, *Ptychosperma hosinoi*, and *Ptychococcus* sp.) there are naked

vascular strands (i.e., without fibrous sheaths) in the mesocarp well sep-
arated from the main part of the vascular system. In all genera except
Normanbya, all or part of the vascular bundles are concentrated near the
locular epidermis, forming a part of the endocarp, though additional
bundles may be dispersed outward into the mesocarp. In *Normanbya* the
vascular bundles are distributed primarily in the inner mesocarp with
only a few embedded in the sclerified ground tissue of the endocarp
(Fig. 2).

The ground tissue adjacent to the locular epidermis and around the
inner vascular bundles often consists of strongly dorsiventrally com-
pressed cells (Fig. 16) that develop thick, heavily pitted secondary walls
as the fruit matures. Transition to the more nearly isodiametric cells of
the mesocarp may be abrupt (*Brassiophoenix*) or more commonly quite
gradual. The expression "sclerified ground tissue" is employed here to
indicate ground tissue in which the cells, at first parenchymatous, de-
velop secondary walls *en masse* as opposed to the transformation of in-
dividual ground cells into idioblastic sclereids. Sclerified ground tissue
is generally very scanty in smaller fruits, such as in some species of *Ptycho-
sperma* (Fig. 13), where the endocarp is made up only of the locular
epidermis and the vascular bundles or of the vascular bundles only
(*Ptychosperma salomonense*, Fig. 8). In *Normanbya*, however, the endocarp
consists almost entirely of sclerified ground tissue (Fig. 2). *Ptychococcus* sp.
has the most highly developed endocarp, with the locular epidermis, zone
of sclerified ground tissue, and the confluent vascular bundles each form-
ing a solid mantle (Fig. 10).

The mesocarp is primarily parenchymatous with the cells roughly iso-
diametric or slightly dorsiventrally compressed, at least in the middle
of the fruit, and becoming more compressed toward either the endocarp
or the exocarp. Raphide-bearing idioblasts are frequent in most genera,
scattered throughout the ground tissue (Fig. 15). Tannin-bearing idio-
blasts may be similarly distributed or concentrated in particular regions.
Where tannin is abundant, raphides tend to be few or lacking. In *Ptycho-
sperma* subg. *Ptychosperma* tannin cells frequently form a conspicuous mass
in the midmesocarp (Fig. 8). The mesocarp may be partially fibrous from
the presence of vascular bundles in the inner part or fibrous bundles in
the outer part (*Normanbya, Veitchia joannis*, Fig. 1, 2).

The exocarp consists of a subepidermal zone of fibrous bundles and
brachysclereids or stone cells. The fibrous bundles may intergrade with
similar bundles in the mesocarp when present (*Veitchia joannis*) and are
quite variable in size both within individual fruits and between different
species and genera (Fig. 18–21). The longest bundles appear to run much
of the length of the fruit, while the smallest resemble patches of sclereids
(see the Discussion for a more detailed interpretation of the exocarp
bundles). Brachysclereids are of the same general size and shape as the
surrounding parenchyma cells and may be solitary, in loose clusters, in
continuous masses, or absent (*Drymophloeus beguinii*).

The epidermis shows little specialization in this group. Cells generally appear tabloid in cross section or slightly rounded on the exterior face. In *Carpentaria*, however, the cells are strongly papillate.

DESCRIPTION OF THE GENERA

The taxonomic treatment that follows must be considered tentative, particularly with respect to the characterization of *Veitchia, Drymophloeus, Balaka,* and *Ptychococcus,* for each of which there are a number of species that have not been examined. In the key based on fruit characteristics note that small-fruited species of *Veitchia* cannot be distinguished as a group from *Drymophloeus* at this point. In *Pytchosperma*, however, a large number of species have been examined and the subgenera can be distinguished upon such characteristics.

KEY, BASED ON FRUIT CHARACTERISTICS, TO THE GENERA OF
THE *PTYCHOSPERMA* ALLIANCE

1. Seed terete in cross section
    2. Fruit greater than 15 mm in diameter; fibrous bundles in the outer part of the pericarp not confined to a subepidermal exocarp
        3. Locular epidermis forming a conspicuous palisade layer; brachysclereids confined to a brief subepidermal region .... VEITCHIA spp.
        3. Locular epidermis lacking at maturity; brachysclereids dispersed through the outer part of the fruit .... NORMANBYA
    2. Fruit less than 15 mm in diameter; fibrous bundles in the outer part of the pericarp confined to a subepidermal exocarp
        4. Vascular bundles in several series, all with thick fibrous sheaths and not strongly dorsiventrally compressed .... VEITCHIA spp., DRYMOPHLOEUS
        4. Vascular bundles in one or two series, the inner bundles with thick fibrous sheaths and strongly dorsiventrally compressed, the outer bundles, when present, lacking sheaths
            5. Outer series of unsheathed bundles lacking; epidermal cells tabloid .... PTYCHOSPERMA spp.
            5. Outer series of unsheathed bundles present; epidermal cells papillate .... CARPENTARIA

1. Seed angled or grooved in cross section
    6. Fruit more than 15 mm in diameter; sclerified ground tissue in endocarp very thick
        7. Unsheathed vascular strands present in mesocarp
            8. Inner vascular bundles with sheaths confluent into a continuous mantle .... PTYCHOCOCCUS
            8. Inner vascular bundles separate .... PTYCHOSPERMA subg. PONAPEA
        7. Unsheathed vascular strands absent, bundles separate but embedded in the osseous sclerified ground tissue .... BRASSIOPHOENIX
    6. Fruit less than 15 mm in diameter; sclerified ground tissue in endocarp sparse
        9. Vascular bundles in a single series, nearly terete in cross section ..... BALAKA
        9. Vascular bundles in several series or, if in a single series, strongly dorsiventrally compressed
            10. Fibrous bundles of the exocarp to 1600 μm long, parallel with the epidermis; locular epidermis sclerified but not forming a palisade layer; endosperm homogeneous .... PTYCHOSPERMA SUBG.NOV.

    10. Fibrous bundles of the exocarp at most 580 μm long, obliquely oriented
        to the epidermis; locular epidermis and endosperm various
           11. Locular epidermis forming a distinct palisade layer; endosperm ho-
                mogeneous or weakly ruminate; raphides common in mesocarp;
                tannin confined to the inner mesocarp ....
            .... Ptychosperma subg. Actinophloeus
           11. Locular epidermis absent or sclerified but not forming a palisade
                layer; raphides uncommon in mesocarp but tannin often abundant
            .... Ptychosperma subg. Ptychosperma

NORMANBYA.—One species; Australia (Fig. 2). Fruit ca. 25 mm in di-
ameter, seed terete in cross section, endosperm ruminate.

Endocarp: Locular epidermis lacking at maturity; ground tissue dor-
siventrally compressed and sclerified in a very thick band from the inner
margin of the pericarp to and including the first series of vascular bun-
dles; vascular bundles in several series (the innermost distant from the
locule, mildly dorsiventrally compressed, and with the vascular tissue on
the outer side of the bundle; the middle bundles nearly terete and var-
iously oriented; the outer bundles somewhat radially distended, with
vascular tissue on the inner side of the bundle).

Mesocarp: Ground tissue parenchymatous, no tannin- or raphide-
bearing idioblasts observed; includes vascular bundles in the inner part
and fibrous bundles in the outer part (described below).

Exocarp: Fibrous bundles distributed through the outer part of the
fruit, not concentrated into a distinct exocarp, inner bundles very long,
apparently running the length of the fruit, gradually becoming shorter
toward the epidermis, some bundles just below the epidermis very short;
brachysclereids sparsely distributed between the fibrous bundles.

VEITCHIA.—18 species; Fiji, New Hebrides, Philippines (Fig. 1, 11, 12).
Fruit examined 7 mm (*V. vitiensis*) to 30 mm (*V. joannis*) in diameter, seed
terete in cross section, endosperm mostly homogeneous, ruminate only
in *V. merrillii*.

Endocarp: Locular epidermis forming a sclerified palisade layer 40
μm (*V. sessilifolia*) and 330 μm (*V. joannis*) thick; in large-fruited species
the vascular bundles numerous, in several series (inner bundles dorsi-
ventrally compressed, middle bundles nearly terete, outer bundles some-
what radially distended), fibrous sheaths very thick, some bundles wholly
fibrous, fibers very thick-walled, ground tissue dorsiventrally compressed
and sclerified around inner bundles; in smaller fruits vascular bundles
roundish, in two or three series, ground tissue compressed and sclerified
briefly next to locular epidermis; in *V. simulans* the bundles in two series,
the inner bundles strongly dorsiventrally compressed, the outer bundles
square in cross-section, appressed laterally to one another but apparently
not fused.

Mesocarp: Ground tissue parenchymatous with frequent raphide-
bearing idioblasts (*V. arecina, V. joannis*), partly fibrous in larger fruits by
the inclusion of vascular or fibrous bundles.

Exocarp: Fibrous bundles scattered through the outer pericarp or confined to a relatively thin subepidermal layer, bundles very long to very short, fibers very thick-walled in bundles just below the epidermis but relatively thin-walled in those away from the epidermis (Fig. 11); brachysclereids frequent, confined to a thin subepidermal zone even if the fibrous bundles are more widely distributed; epidermis of tabloid cells.

DRYMOPHLOEUS.—15 species; eastern Indonesia to Samoa (Fig. 3, 18). Fruit to ca. 15 mm in diameter, seed terete in cross section, endosperm homogeneous in specimens examined.

Endocarp: Locular epidermis indistinguishable at maturity (*D. beguinii*), sclerified but unmodified (*D. pachycladus*), or forming a sclerified palisade layer to ca. 40 µm thick (*D. subdistichus*), ground tissue dorsiventrally compressed, sclerified between the locular epidermis and the inner vascular bundles (*D. beguinii, D. subdistichus*), or farther out around bundles (*D. pachycladus*); vascular bundles with thick fibrous sheaths, nearly terete in cross section (but inner bundles dorsiventrally compressed in *D. beguinii*), main bundles two or three deep all around, sometimes with smaller fibrous bundles at the periphery of the vascular system (*D. subdistichus*).

Mesocarp: Ground tissue parenchymatous, with frequent raphide-bearing idioblasts (*D. beguinii*).

Exocarp: Fibrous bundles in a single subepidermal layer, very elongate (to 2500 µm in *D. beguinii*, shorter in *D. subdistichus* (to 330 µm), not measured in *D. pachycladus*; brachysclereids absent in *D. beguinii*, few in *P. subdistichus*, numerous in *P. pachycladus*; epidermis of tabloid cells.

CARPENTARIA.—One species; Australia (Fig. 4, 17). Fruit 12 mm in diameter, seed terete in cross section, endosperm homogeneous.

Endocarp: Locular epidermis forming a sclerified palisade layer, ca. 85 µm thick; ground tissue scant, cells dorsiventrally compressed and sclerified in the narrow space between the locular epidermis and the vascular bundles; vascular bundles in a single series close to the locular epidermis, with thick fibrous sheaths, strongly dorsiventrally compressed.

Mesocarp: Ground tissue parenchymatous, with occasional raphide-bearing idioblasts, including also some vascular strands without fibrous sheaths near the endocarp.

Exocarp: Fibrous bundles very narrow, to 580 µm long, oblique to the epidermis, in a single subepidermal layer; brachysclereids numerous between bundles; epidermis of strongly papillate cells.

BALAKA.—20 species; Fiji and Samoa (Fig. 5). Fruits examined 9–11 mm in diameter, seeds 4–5-angled, endosperm homogeneous.

Endocarp: Locular epidermis sclerified, unmodified or forming a relatively thin palisade layer (13 µm in *B. seemannii*, 20 µm in *B. microcarpa*, 33 µm in *B. burretiana*); ground tissue sclerified up to five cells thick

between locular epidermis and vascular bundles; vascular bundles with thick fibrous sheaths, terete to somewhat dorsiventrally compressed, in a single series aroung the fruit.

Mesocarp: Ground tissue parenchymatous, *B. burretiana* with occasional raphide-bearing cells, *B. microcarpa* with many tannin-bearing cells scattered throughout the mesocarp.

Exocarp: Fibrous bundles short (to 166 μm long), oblique to the epidermis, closely spaced in a single subepidermal layer; brachysclereids abundant between the fibrous bundles; epidermis with cells irregular in shape, somewhat radially elongate and distally rounded.

PTYCHOSPERMA.—28 species; New Guinea, eastern Indonesia, Australia, Micronesia, Solomon Islands (Fig. 6–8, 13, 19, 21).

Subgenus *Ptychosperma*: Fruit 5–13 mm in diameter, seeds 5-angled or -lobed, endosperm ruminate.

Endocarp: Locular epidermis sclerified but unmodified (6–8 μm thick) or indistinguishable at maturity (e.g., *P. salomonense*); ground tissue scant, cells dorsiventrally compressed, one or two rows adjacent to the locular epidermis, sclerified; vascular bundles with thick fibrous sheaths, distinct, somewhat dorsiventrally compressed, distributed at several levels in the endocarp and inner mesocarp or in a single layer with lateral margins fused (*P. salomonense*).

Mesocarp: Ground tissue with many tannin-bearing idioblasts concentrated in the midregion.

Exocarp: Fibrous bundles very short, to ca. 300 μm long, appressed against the epidermis, irregular; brachysclereids sparse to abundant between bundles; epidermis of tabloid cells.

Subgenus *Actinophloeus*: Fruit 5–11 mm in diameter, seeds 5-lobed, endosperm homogeneous or weakly ruminate.

Endocarp: Locular epidermis forming a sclerified palisade layer, 30–40 μm thick, or sometimes this layer poorly developed (*P. lauterbachii* and *P. mambare*, 13–19 μm); vascular bundles with thick fibrous sheaths, roundish to somewhat dorsiventrally compressed, in several layers close to the locular epidermis on the tips of the lobes, dispersed into the mesocarp between lobes, outer bundles with little vascular tissue.

Mesocarp: Ground tissue parenchymatous, with raphide-bearing idioblasts frequent throughout, sometimes with tannin-bearing idioblasts frequent in the inner region near the vascular bundles.

Exocarp: Fibrous bundles short (to 580 μm long), oblique in a single subepidermal layer; brachysclereids abundant between bundles; epidermis of tabloid cells.

Subgenus *Ponapea*[3]: Fruit examined 17–19 mm in diameter, seed 5-lobed, endosperm homogeneous.

Endocarp: Locular epidermis forming a sclerified, palisade layer 270

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[3] **Ptychosperma subg. Ponapea** (Beccari) Essig, comb. et stat. nov. Basionym: *Ponapea* Beccari, Bot. Jahrb. Syst. 59: 13. 1924.

μm thick; ground tissue of strongly dorsiventrally compressed and sclerified, in a thick but variable zone between the locular epidermis and the vascular bundles; vascular bundles with thick fibrous sheaths, somewhat dorsiventrally compressed, one to two deep all around.

Mesocarp: Ground tissue parenchymatous with frequent raphide-bearing idioblasts and occasional vascular strands without fibrous sheaths in the inner mesocarp.

Exocarp: Fibrous bundles short (to 540 μm long), oblique, in a single subepidermal layer; brachysclereids abundant between bundles; epidermis of tabloid cells, slightly rounded distally.

Subgenus nov. ined. (*Ptychosperma palauense*): Fruit 11–12 mm in diameter, seed 5-lobed, endosperm homogeneous.

Endocarp: Locular epidermis sclerified, only weakly developed into a palisade layer, 20 μm thick; ground tissue irregularly compressed around the bundles, only innermost cells sclerified; vascular bundles with thick fibrous sheaths, large dorsiventrally compressed bundles to the inside, smaller, rounder bundles with little vascular tissue dispersed toward the mesocarp.

Mesocarp: Ground tissue parenchymatous with frequent raphide-bearing idioblasts.

Exocarp: Fibrous bundles elongate (to 1660 μm) in a single subepidermal layer; brachysclereids common between bundles; epidermis of tabloid cells.

BRASSIOPHOENIX.—2 species; New Guinea (Fig. 9). Fruit 17–19 mm in diameter, seed 5-lobed, endosperm homogeneous.

Endocarp: Locular epidermis forming a sclerified palisade layer 125–180 μm thick; ground tissue of dorsiventrally compressed and sclerified cells in a thick band adjacent to the locular epidermis, 165–190 μm thick between lobes, much thicker and forming ridgelike projections on the tips of the lobes; vascular bundles with thick fibrous sheaths, dorsiventrally compressed, embedded within the sclerified ground tissue, in a single series and mostly congregated at the tips of the lobes, vascular tissue chiefly on the abaxial side of the bundles.

Mesocarp: Ground tissue parenchymatous with cells greatly enlarged and weakly tanniniferous in the central mesocarp; raphide-bearing idioblasts infrequent in the outer part of the mesocarp.

Exocarp: Fibrous bundles short (to 250 μm), very oblique to the surface, in a single subepidermal layer; brachysclereids numerous between fibrous bundles; epidermis of tabloid cells.

PTYCHOCOCCUS.—7 species; New Guinea and the Solomon Islands (Fig. 10). Fruit examined ca. 35 mm in diameter, seed 5-lobed, endosperm homogeneous.

Endocarp: Locular epidermis forming a sclerified palisade layer 165–190 μm thick; ground tissue strongly dorsiventrally compressed, sclerified, in a solid band to 1 mm thick around the fruit; vascular bundles

with fibrous sheaths completely connate into an additional sclerified band with the vascular strands at intervals along the inside of this band.

Mesocarp: Ground tissue parenchymatous, with frequent, scattered tanniniferous idioblasts and small, scattered vascular strands without fibrous sheaths.

Exocarp: Fibrous bundles short, oblique, to 750 μm long; brachysclereids extremely abundant, forming a nearly continuous tissue between the fibrous bundles; epidermis of tabloid cells.

DISCUSSION

The endocarp in fruits of the *Ptychosperma* alliance falls into Type III of the three types described by Murray (1973). In this, the most complex type of endocarp, sclerenchyma derived from (locular) epidermal, ground, and fascicular systems forms a thick mantle around the seed. The number of vascular bundles in mature fruits of this type is greatly increased relative to the simple vasculature of the carpel at anthesis (Uhl, 1976). Most of the bundles, moreover, have exceptionally thick, fibrous sheaths and relatively small amounts of vascular tissue. In some genera (*Veitchia, Drymophloeus*, and *Ptychosperma*), entirely fibrous bundles can be found within the vascular system. The primary function of fibrous sheaths around vascular strands is presumably the protection of the strands themselves, but it is evident that the large production of fibrous tissue in the vascular-bundle system in this alliance has also a broader function of protecting the inner tissues of the fruit and the seed. This critical adaptation in ancestors of the *Ptychosperma* alliance set the stage for a varied development of complex endocarps and probably contributed greatly to the success of the group. In the other two of Murray's types, the endocarp is simple, consisting only of the locular epidermis or of sclerenchyma derived from the ground tissue.

The endocarps of *Drymophloeus* and most species of *Veitchia* and *Ptychosperma* are rather similar histologically and rather poorly integrated. The vascular bundles are separate from one another, distributed three-dimensionally around the locule with only the innermost bundles closely associated with the other endocarp tissues (Fig. 1, 4, 6, 7). Sclerified ground tissue around the locule gradually merges with the parenchymatous tissue of the mesocarp and there is no sharp boundary between endocarp and mesocarp. *Normanbya* stands somewhat apart from this group, for its vascular bundles show even less tendency to concentrate near the locule (Fig. 2). The endocarp consists of a thick band of well differentiated sclerenchyma and includes, almost incidentally, a few of the innermost vascular bundles.

The development of more integrated endocarps in this alliance involves the restriction of the vascular bundles to one or two series, the flattening of these bundles against the locule and sometimes the lateral fusion of the sheaths of these bundles into a continuous mantle, and the

sharper delineation of sclerified ground tissue from the mesocarp par-
enchyma. The prominence of the locular epidermal palisade layer in the
endocarp is so variable throughout the alliance that it does not correlate
clearly with any particular trend.

The evolution of more highly integrated endocarps has apparently
occurred independently in six of the eight genera of the alliance. In
Veitchia simulans there are two series of bundles around the locule. The
inner bundles are flattened and separate from one another whereas the
outer ones are crowded together so that each appears roughly square or
rectangular in cross section. The bundles do not appear to be confluent,
however. In *Carpentaria* there are also two series of bundles—the outer
consists of vascular strands without sheaths (and not involved in the
endocarp) and the inner series consists of bundles strongly flattened
against the palisade layer but not confluent with one another (Fig. 3). In
Balaka burretiana the vascular bundles are confined to a single series
abutting a moderate band of sclerified ground tissue but are not flattened
(Fig. 5). In *Ptychosperma salomonense* the single series of vascular bundles
is flattened and confluent into a continuous mantle around the locule
(Fig. 8). Sclerified ground tissue and locular epidermis are lacking. In
Brassiophoenix schumannii a single series of unspecialized bundles is
embedded in a well defined mantle of sclerified ground tissue (Fig. 9).
Finally, in *Ptychococcus* the fibrous vascular bundles are completely fused
into a thick mantle that overlies additional mantles of sclerified ground
tissue and the palisade layer (Fig. 10).

There has been no analysis of exocarp structure in palms comparable
to that done for the endocarp by Murray (1973). The data from the
present investigation show the exocarp to be a complex type somewhat
similar to that of the endocarp. Nonvascular bundles of fibers and
brachysclereids (stone cells) combine in varying degrees of integration to
form a heterogeneous mantle of sclerenchyma just below the epidermis.

Brachysclereids are simply sclerified cells, occurring singly or in loose
clusters, and differing little in size or shape from the surrounding par-
enchyma cells. They occur throughout the angiosperms. Except in *Nor-
manbya*, they are confined in this alliance to a thin subepidermal zone
where they fill in the gaps between the fibrous bundles. They show little
variation in form or distribution.

The fibrous bundles vary considerably in length and in position. Elon-
gate fibrous bundles, running indefinite distances through the mesocarp,
are found in *Normanbya* and some species of *Veitchia*. Such nonvascular
bundles ("cordons fibreux") in the mesocarp were reported by Guérin
(1949) also for some species in the *Areca*, *Clinostigma*, and *Cocos* alliances.
In *Normanbya* and *Veitchia* the long bundles grade into shorter and earlier
differentiating ones (Murray 1971) near the epidermis. Some of these
bundles are scarcely longer than wide. In *Veitchia* there is a distinctly
denser aggregation of bundles in a subepidermal zone where brachy-
sclereids also occur (Fig. 1), but in *Normanbya* neither bundles nor brachy-

scelereids are noticeably more concentrated near the epidermis. Technically then there is no true exocarp in *Normanbya* but rather a fibrous mesocarp (Fig. 2).

In other species of *Veitchia* and in the other genera of the alliance, fibrous bundles and brachysclereids are confined to a distinct subepidermal exocarp. Bundles vary, however, from relatively elongate to relatively short. *Drymophloeus beguinii* (Fig. 18) and *Ptychosperma palauense* (Fig. 19) have bundles intermediate in length between the very long ones of *Veitchia* species and the short ones of *Drymophloeus subdistichus* (Fig. 20) and *Ptychosperma salomonense* (Fig. 21). Also, according to Moore (1957), the exocarp bundles of *V. pedionoma*, *V. sessilifolia*, and *V. petiolata* are all very short compared to those of other species in the genus. Where the bundles are all fairly short, they tend to be oriented obliquely or at right angles to the surface and give the surface a granular appearance, especially when dry. These small bundles have long been known in the taxonomic literature as "sclerosomes" (Moore, 1957) and appear to be similar to the "piliers fibreux" described by Guérin (1949) in other alliances. Murray (1971) interpreted them as "patches of sclereids," apparently not having observed any intergradation between long and short bundles. Such intergradation is clearly demonstrated in the present investigation. The individual cells making up these short bundles are often very short and irregular, but whether these cells should be called fibers or sclereids is of secondary importance to the point that long and short bundles in the exocarp of the *Ptychosperma* alliance are homologous, intergrading structures and quite distinct from the neighboring brachysclereids.

Taxonomic Conclusions.—The data clearly indicate a great diversity in pericarp structure in the *Ptychosperma* alliance. The present application of these data to taxonomy is limited by the relatively small number of species examined in large genera such as *Drymophloeus* and *Veitchia*. The characterizations of these genera, and the somewhat better known *Ptychosperma*, are complex and much qualified. Overlap of character states and parallelism in certain variational patterns make it difficult to separate these genera in simple taxonomic keys. Individual species, small groups of species, and the monotypic genera however are readily characterized and appear to be quite distinct. *Carpentaria, Normanbya* and *Brassiophoenix* each have unique structural features and are readily recognized. *Ptychococcus* appears also to be highly unique and recognizable, but only one out of about eight species has been examined. The large-fruited species of *Veitchia* (*V. arecina* and *V. joannis*) appear to form a natural unit distinct from the smaller-fruited spicies, and *V. simulans* is isolated in the genus by its more highly integrated endocarp. *Drymophloeus beguinii* is much like the small-fruited *Veitchias* except that its locular epidermis is undeveloped. The two other species of *Drymophloeus* examined are distinctive for the small size of their exocarp fibrous bundles.

Ptychosperma has been somewhat more thoroughly sampled than the

other genera in the alliance and it appears that the subgenera can be readily characterized. Variation at the specific level is, however, also significant with *Ptychosperma salomonense* standing out from subgenus *Ptychosperma* by its highly integrated endocarp. Subgenus *Ponapea* is distinguished primarily by the thick layer of sclerified ground tissue that partially surrounds the vascular bundles, and by the presence of unsheathed vascular strands in the mesocarp. A new but unpublished subgenus erected for *Ptychosperma palauense* is based partially on the presence of very elongate fibrous bundles of the exocarp that contrast strongly with the very short bundles of the remaining subgenera. Subgenus *Ptychosperma* is characterized by the lack of development of its locular epidermis and by the tanniniferous mesocarp. Subgenus *Actinophloeus* has the locular epidermis developing into a distinct palisade layer (though it is rather weakly developed in some species) and a nontanniniferous mesocarp in which raphides are frequent.

In short the resolving power of pericarp characters in this alliance appears to be primarily at the subgeneric or lower level. The considerable variation above this level tends to obscure generic distinctions, at least among the larger, more complex genera. In the taxonomic key *Drymophloeus* and *Veitchia* cannot be separated from one another. *Ptychosperma* is easily separated from these two genera only because of the grooved character of its seed, not because of histological characters. Histological studies of the pericarp will clearly be very useful in systematic analyses of the genera in this alliance.

APPENDIX: SPECIMENS EXAMINED

Normanbya normanbyi (W. Hill) L. H. Bailey: *Furtado s.n.*, cult. Singapore (BH).

Veitchia arecina Beccari: *Moore et al. 9329* (BH).

Veitchia joannis Wendland: *Moore et al. 9351* (BH).

Veitchia aff. *montgomeryana* H.E. Moore: *Moore 9318* (BH).

Veitchia sessilifolia (Burret) H.E. Moore: *Moore et al. 9348* (BH).

Veitchia simulans H.E. Moore: *Moore et al. 9352* (BH).

Veitchia vitiensis (Wendland) H.E. Moore: *Moore et al. 9358* (BH).

Drymophloeus beguinii (Burret) H.E. Moore: *W.D. Bell s.n.*, cult. Fairchild Tropical Garden (USF).

Drymophloeus pachycladus (Burret) H.E. Moore: *Corner RSS7* (BH).

Drymophloeus subdistichus (H.E. Moore) H.E. Moore: *Moore et al. 9300* (BH).

Carpentaria acuminata (Beccari) H.E. Moore: *Moore 9228* (BH).

Balaka burretiana Christopherson: *Moore et al. 9981* (BH).

Balaka microcarpa Burret: *Moore et al. 9359* (BH).

Balaka seemannii (H. Wendland) Beccari: *Moore et al. 9356* (BH).

Ptychosperma (subg. Ptychosperma) caryotoides Ridley: *Essig LAE 55133* (BH).

Ptychosperma (P.) elegans (R. Brown) Blume: *D. Hull s.n.*, West Palm Beach, (USF).

Ptychosperma (P.) gracile Labillardière: *Essig LAE 55045* (BH).

Ptychosperma (P.) mooreanum Essig: *Essig LAE 55066* (BH).

Ptychosperma (P.) salomonense Burret: *Moore 9309 bis* (BH).

Ptychosperma (P.) sp. nov. ined.: *Brass 28474* (BH).

Ptychosperma (subg. Actinophloeus) cuneatum (Burret) Burret: *Essig LAE 55097* (BH).

Ptychosperma (A.) lauterbachii Beccari: *Essig. LAE 55060, 55065* (BH).

Ptychosperma (A). mambare (F.M. Bailey) Beccari: *Essig LAE 55152* (BH).

Ptychosperma (A). microcarpum (Burret) Burret: *Essig LAE 55170* (BH).

Ptychosperma (A.) schefferi Beccari: *Essig LAE 55077* (BH).

Ptychosperma (A.) sp. nov. ined. *Essig LAE 55175* (BH).

Ptychosperma (subg. *Ponapea*) *hosinoi* (Kanehira) H.E. Moore & F.R. Fosberg: *Hiyane s.n.*, Ponape (USF).

Ptychosperma (subg. nov. ined.) *palauense* (Kanehira) H.E. Moore & F.R. Fosberg: *Carnwath s.n.*, Palau (USF).

Brassiophoenix schumannii (Beccari) Essig: *D. Hull* s.n., cult. Fairchild Tropical Garden (USF).

Ptychococcus aff. *elatus* Beccari: *Essig LAE 55054* (BH).

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