The Formation of Endocarp in Palm Fruits *

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Abstract

Three types of endocarps are distinguished among palm fruits on the bases of time of differentiation, cell layers involved, and mode of development. The simplest consists solely of the modified locular epidermis; another involves a region of variable thickness separated from the locular epidermis by several cell layers of parenchyma; the most complex includes the inner fibrovascular bundles, the locular epidermis, and the intervening parenchyma. The taxonomic distribution of the types of endocarps and their possible significance are discussed.

Palm fruits are known and used by many peoples throughout the tropics, but anatomy and development have been studied in only two fruits, the coconut (Winton, 1901) and the date (Lloyd, 1910; Long, 1943). Factors contributing to this lack of information include the usually long developmental period between pollination and ripening, the geographical inaccessibility of most palms, and the frequently intractable nature of the fruits themselves.

Mature palm fruits characteristically have a specialized, usually sclerotic, layer known as the endocarp in the inner portion of the fruit wall near the locule. Its formation may involve the locular epidermis only or, more commonly, several to many layers of cells in the inner portion of the gynoecial wall. When the fruit is mentioned in specific descriptions, the endocarp usually receives passing reference as being "stony" or "fibrous" or "papery" with no mention as to its histological nature or its developmental history. As part of a larger study, the development of the endocarp has been followed in the fruits of a number of species of palms.

Materials and Methods

Periodic collections were made of developing fruits of 12 species and mature fruits of six additional species were added resulting in a total of 13 genera examined. Six of the approximately 15 (depending upon author) groups into which palms have been classified (Table 1) were represented. Collections were made from plants growing at the Fairchild Tropical Garden, Miami, Florida, or in the greenhouse at Cornell University, Ithaca, New York. Voucher specimens are located in the L. H. Bailey Hortorium at Cornell University.

The developmental stages and the mature fruits were fixed in FAA, dehydrated, embedded in "Paraplast" and sectioned serially. The sections were stained with Heidenhain's hematoxylin, 1% safranin, and 0.5% aniline blue, modified from Johansen (1940). To insure penetration of the dehydrating and embedding fluids, the younger fruits were slashed through the fruit wall nearly to the locule and the larger fruits

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Table 1. Palms described with documentation and with position in two systems of classification indicated.

Moore, 1973 without rank[a]	Potztal, 1964 as subfamilies
Coryphoid palms	Coryphoideae
Coccothrinax sp. (*FTG:P-2209*)	
Livistona chinensis (*Read 712*)	
Pritchardia pacifica (*Read 9581*)	
Rhapidophyllum hystrix (*BH-60-858*)	
Thrinax sp. (*FTG:101A*)	
Caryotoid palms	Caryotoideae
Caryota mitis (*Read 1429*)	
Chamaedoreoid palms	Arecoideae tribe Chamaedoreeae
Chamaedorea sp. (*Moore & Bunting 8913*)	
C. alternans (*BH-61-1177*)	
C. microspadix (*FTG:P-4083*)	
C. pochutlensis (*BH-60-819*)	
Mascarena lagenicaulis (*Read 770*)	
Arecoid palms	Arecoideae
Ptychosperma macarthurii (*FTG:RM872A*)	
P. lineare (*Essig 710122-1*)	
Veitchia arecina (*Read 9583*)	
V. merrillii (*Read 1235*)	
Cocosoid palms	Cocosoideae
Arecastrum romanzoffianum (*Read 911*)	
Arikuryroba schizophylla (*Read 812*)	

[a] Categories are informal and used in an interim classification of palms.

were cut into small pieces. Dehydration and embedding times also had to be greatly extended. Sections of mature endocarps of the cocosoid fruits were cut on a diamond-edged rock saw, ground by hand on carborundum paper until translucent, and mounted in HSR without staining.

Results

CORYPHOID PALMS. Approximately half of the 31–32 genera have flowers with apocarpous gynoecia and five of these, here represented by *Thrinax*, have only a single carpel. Flowers of the remaining genera are tricarpellate with carpels connate by their styles, here

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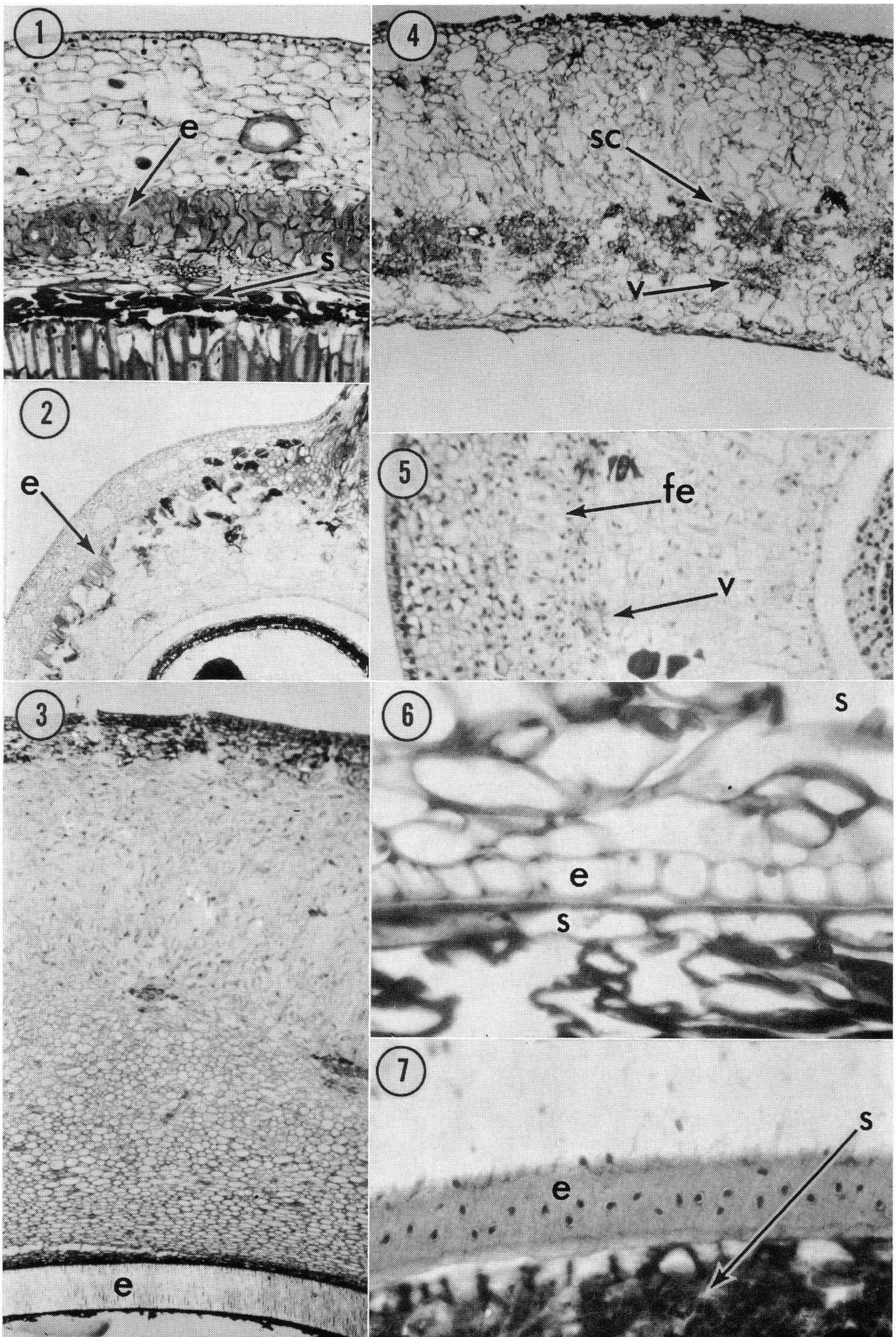
1–7. Structure of carpel and fruit wall. a. *Thrinax* sp., mature fruit wall × 76: e = endocarp; s = seed coat. 2. *Thrinax* sp., developing fruit wall × 31: arrow indicates endocarp (e). 3. *Pseudophoenix sargentii*, mature fruit wall × 31: e = endocarp. 4. *Coccothrinax* sp., mature fruit wall × 31: v = vascular bundle; sc = group of sclereids. 5. *Thrinax* sp., carpel wall × 95: v = developing vascular bundle; fe = radially elongate cells of future endocarp. 6. *Chamaedorea alternans*, mature fruit wall × 300: s = outermost layer of cells of seed coat; e = cell of endocarp. 7. *Caryota mitis*, mature fruit wall × 200: dark area at bottom (s) is seed coat; e = endocarp.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represented by *Pritchardia*, or syncarpous to varying degrees.

Thrinax sp. The one-seeded fruit develops from the single uniovulate carpel. At anthesis, the carpel wall consists of an outer zone of small, isodiametric cells separated by a single ring of procambial strands from an inner zone of larger cells, many of which contain raphides. The endocarp is partially differentiated as a layer of radially elongate cells outside the ring of procambial strands (Fig. 5) in the distal portion of the carpel. The tissues are less well differentiated toward the base but as the fruit ages, this difference in degree of maturation disappears. The endocarp is well differentiated and the cell walls are sclerified (Fig. 2) within seven days of pollination. The sclereids tend to separate as the fruit continues to enlarge and the resulting spaces are filled by the enlargement of adjacent parenchyma cells. These intrude among the existing sclereids, assuming highly irregular shapes, and subsequently become sclerified. In this manner the endocarp is maintained as a continuous layer throughout the development of the fruit. No mitotic figures have been observed in the parenchyma cells mixed with or adjacent to the endocarp and no silica is deposited in the endocarp sclereids. The growing seed eventually crushes the inner zone of large cells and presses the vascular bundles against the endocarp so that the endocarp appears to lie next to the locule in the mature fruit (Fig. 1). The intervening vascular bundles, however, indicate that the endocarp has a more superficial origin.

Related taxa. Thrinax excelsa Loddiges ex Grisebach, as described by Uhl and Moore (1971), is very similar in the structure of the gynoecium, but fruits of the age examined showed no evidence of the endocarp. The closely allied genus, *Coccothrinax*, is similar in the structure of the gynoecium (Uhl and Moore, 1971). Unlike *Thrinax*, the endocarp is not complete but is represented by patches of sclereids separated by groups of parenchyma cells (Fig. 4). The sclereids occur mostly in association with the vascular bundles. No silica occurs in the endocarp sclereids.

Pritchardia pacifica Seemann & H. Wendland. A one-seeded fruit develops from one of three uniovulate carpels that are initially connate by their styles. The aborted carpels are distal on the mature fruit. The endocarp is not differentiated in the carpel wall at anthesis, but within nine days of pollination it differentiates from a region of large parenchyma cells three to four cells away from the locule and interior to the developing vascular system. During fruit enlargement, the sclereids tend to separate from one another, and parenchyma cells immediately outside the endocarp, as well as those mixed among the sclereids, enlarge and intrude among the previously differentiated cells, often assuming highly irregular shapes (Fig. 10). Occasional divisions in the adjacent parenchyma cells add to the endocarp until 25 days after pollination, when all divisions have ceased and silica is deposited. Starting at about 46 days, the silica-containing cells become sclerified, thus increasing the radial extent of the

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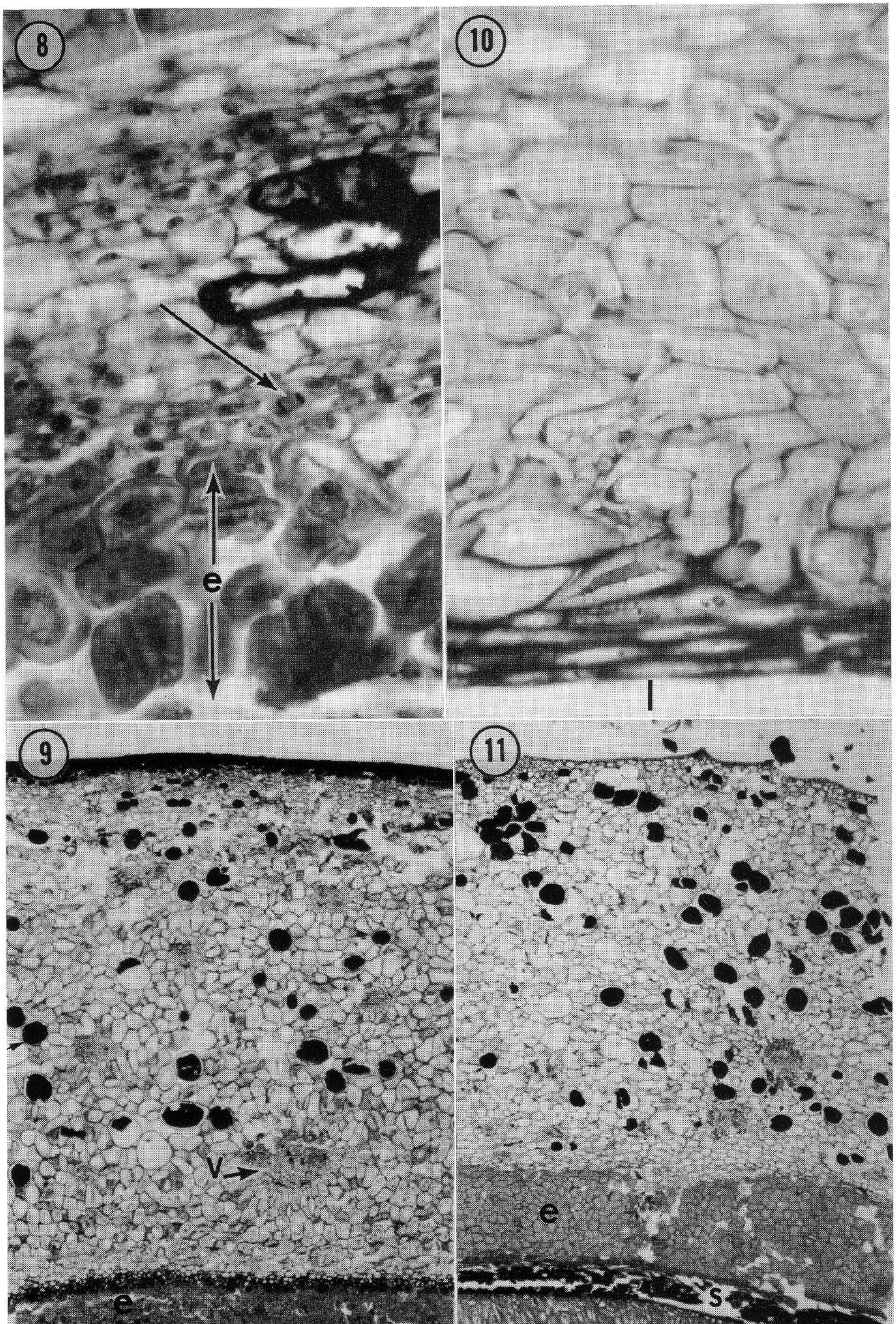
8–11. Structure of fruit wall and endocarp. 8. *Livistona chinensis*, developing fruit wall × 600: endocarp (e) at bottom; plain arrow indicates mitotic figure in meristematic zone. 9. *Livistona chinensis*, mature fruit wall × 31: e = endocarp; v = vascular bundle. 10. *Pritchardia pacifica*, cells of mature endocarp × 600: note thick cell walls and irregular shapes of some of the cells; l = locule. 11. *Rhapidophyllum hystrix*, mature fruit wall × 31: e = endocarp; s = seed coat.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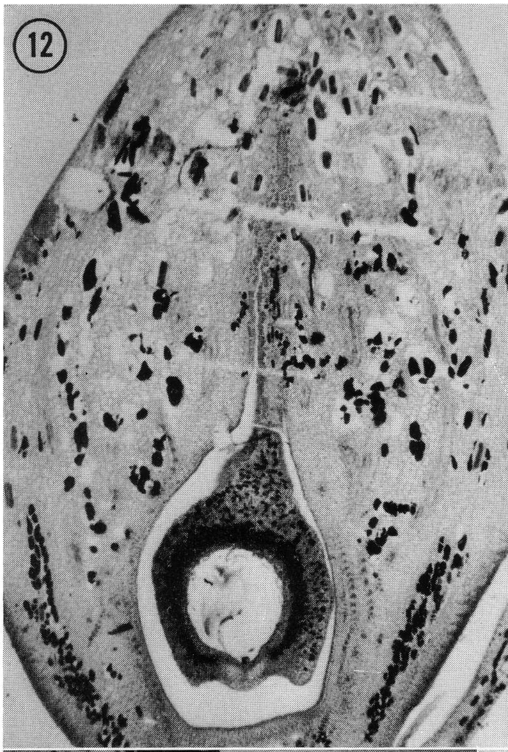
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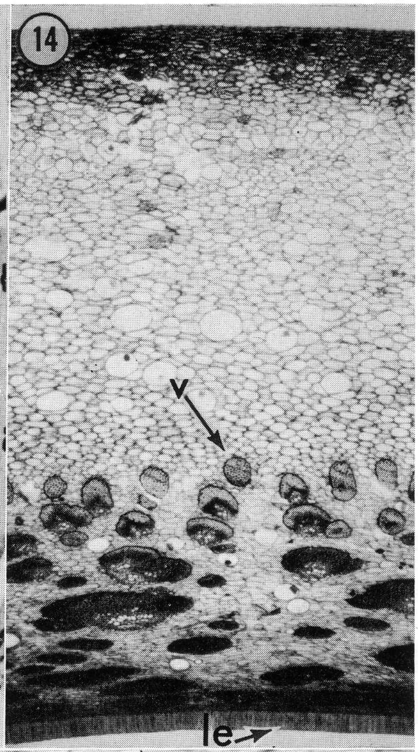
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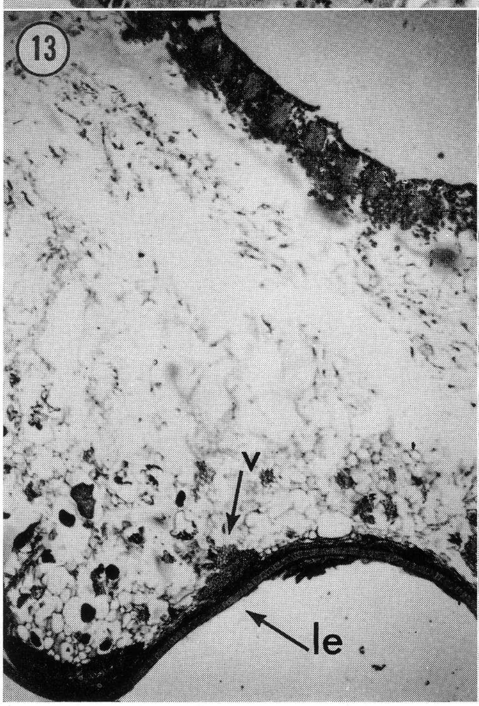
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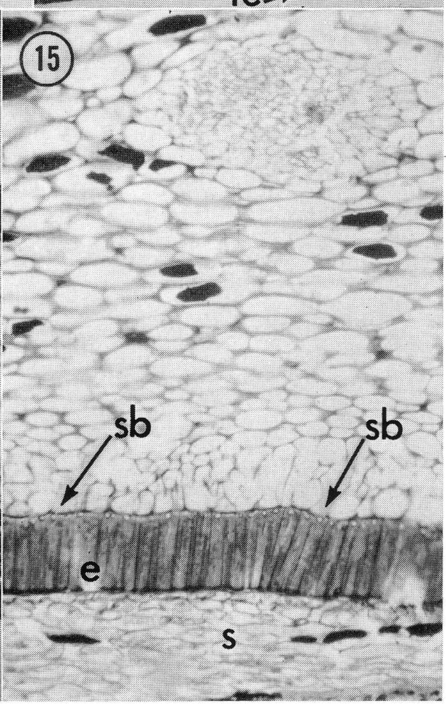
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endocarp without an increase in either cell size or cell number. The endocarp is approximately 240μ thick and lies almost immediately adjacent to the locule (Fig. 10) in the mature fruit.

Livistona chinensis (N. J. Jacquin) R. Brown ex Martius. The one-seeded fruit develops from one of three uniovulate carpels connate by their styles. The aborted carpels abscise. The endocarp, not apparent in the carpel at anthesis, is differentiated shortly after pollination as a tough layer of sclereids mixed with parenchyma, three cells removed from the locule. The endocarp is maintained as a continuous layer throughout fruit enlargement by the activity of a distinct meristematic layer immediately outside it (Fig. 8). The individual sclereids are separated from one another as the fruit enlarges. Cells produced to the inside of the meristematic zone intrude into the sclerotic layer and fill the gaps between the preexisting cells, often assuming highly irregular shapes. Most of these later-formed sclereids contain silica bodies, which the earliest ones lack. Cells are also added to the endocarp by division of the associated parenchyma and of the cells between the endocarp and the locule. With the ripening of the fruit, the endocarp thickens rapidly, due entirely to the sclerification of the cells on both sides of it. The endocarp is approximately 300μ thick in the mature fruit and lies to the interior of the vascular system almost immediately adjacent to the locule (Fig. 9).

Rhapidophyllum hystrix (Pursh) H. Wendland & Drude. The one-seeded fruit develops from one of three uniovulate carpels. The endocarp and, in fact, the entire fruit structure resemble closely the fruits of *Livistona* and *Pritchardia.* No data are currently available on the development of the endocarp in *Rhapidophyllum*, but the endocarp lies between the vascular system and the locule (Fig. 11) in the mature fruit. Cells of the thick (approximately 450μ wide) endocarp are more or less isodiametric and contain silica.

CARYOTOID PALMS. The three genera of this group have flowers with tricarpellate, syncarpous gynoecia. All three carpels enter into the formation of a one- to three-seeded fruit.

Caryota mitis Loureiro. The one-seeded fruit develops from the one- to three-locular syncarpous gynoecium. The endocarp is not formed until the fruit is nearly ripe. At that time the previously isodiametric cells of the locular epidermis elongate radially to a maximum diameter of 50μ, become sclerotic, and form the thin endocarp which tends to adhere to the seed (Fig. 7). Minute grains of silica occur, embedded in the walls of the endocarp cells. In the mature fruit, the "papery" endocarp (Moore, 1960), consists solely of the sclerotic cells of the locular epidermis.

Related taxa. The structure of the fruit wall of *Caryota urens* Linnaeus as described by Rao (1959) is similar to that of *C. mitis.* The histology of the gynoecium of *C. mitis* at anthesis is like that of *Arenga* (Uhl and Moore, 1971).

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12–15. Structure of gynoecium and fruit wall. 12. *Ptychosperma macarthurii*, longitudinal section through gynoecium × 31. 13. *Ptychosperma lineare*, mature fruit wall × 31; le = locular epidermis; v = vascular bundle. 14. *Veitchia arecina*, mature fruit wall × 31; le = locular epidermis; v = vascular bundle at outer limit of endocarp zone. 15. *Mascarena lagenicaulis*, mature fruit wall × 150: e = endocarp; s = seed coat; small white bodies indicated by arrow, sb, are silica bodies in the endocarp cells.

PSEUDOPHOENICOID PALMS. The single genus has flowers with a tricarpellate, syncarpous gynoecium.

Pseudophoenix sargentii H. Wendland ex Sargent. Each lobe of the one- to three-lobed fruit develops from one of the three uniovulate carpels. The endocarp is derived from the locular epidermal cells which begin to elongate radially at 29 days after pollination and which reach a maximum length of 240μ in the next 60 days. The cell walls then become sclerified and the layer forms a hard endocarp which is appressed, but not adherent, to the seed (Fig. 3). No silica occurs in the cells of the endocarp.

CHAMAEDOREOID PALMS. The six genera in this group all have flowers with a tricarpellate, syncarpous gynoecium.

Mascarena lagenicaulis L. H. Bailey. The one-seeded fruit develops from one of the three uniovulate carpels; seeds do not develop in the other two carpels which remain small in the fruit. At about 16 days after pollination, the previously isodiametric cells of the locular epidermis begin to elongate radially. A single silica body is deposited in the outer end of each cell at about 44 days and the cells continue to elongate, reaching a final length of approximately 70μ. Sclerification of the cells does not occur until the fruit is essentially full size and the endocarp consists solely of the sclerified locular epidermal cells (Fig. 15) in the mature fruit.

Chamaedorea sp. (BH-61-1178). The one-seeded fruit develops in the same manner as that of *Mascarena lagenicaulis.* Approximately 25 days after pollination, a single silica body is deposited in each cell of the locular epidermis. There is no further differentiation of these cells which remain unsclerified in the mature fruit. The final structure in this species is similar to that illustrated in Figure 6 for *C. alternans* except that the cell walls are thinner.

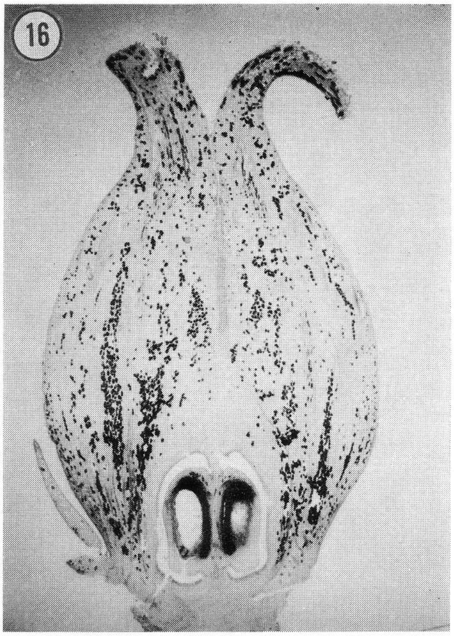
Related taxa. The locular epidermal cells of *C. microspadix* Burret, *C. alternans* H. Wendland, and *C. pochutlensis* Liebmann ex Martius are similar to those of the *Chamaedorea* species described above in that they are isodiametric and contain a silica body (sometimes more than one in *C. microspadix*). However, at least some of the cell walls are sclerified in these species and the endocarp thus formed is more definite than that in *Chamaedorea* sp. The structure of the carpel wall of *C. metallica* O. F. Cook ex H. E. Moore and *C. ernesti-augusti* H. Wendland at anthesis as described by Uhl and Moore (1971) is similar to that in *Chamaedorea* sp. (BH-61-1178). The only significant difference in gynoecial histology between *Mascarena* and *Chamaedorea* is the presence of a large number of tannin-containing cells in the former.

ARECOID PALMS (*Ptychosperma* alliance). All eight genera of this alliance have flowers with tricarpellate, syncarpous gynoecia which are pseudomonomerous and contain solitary ovules.

Veitchia arecina Beccari. The limits of the sterile carpels are not evident in the one-seeded fruit. In the inner portion of the ovary wall at anthesis, longitudinally oriented procambial strands encircle the locule, separated from it by several cell layers of parenchyma. Extensive fibrous sheaths are differentiated around the bundles but are not sclerified. Silica is present in cells surrounding the bundles only in the more mature distal part of the ovary. Maturation is basipetal and centripetal. Fourteen days after pollination, silica has been deposited in cells of the bundle sheaths as far as mid-locule and after 24 days, when sclerification of the fibrous sheaths of the outer bundles has begun in the region of the locule, silica is present in the bundle sheath cells at the base of the locule. The basipetal maturation of the tissues from a diffuse basal meristematic zone occurs at a rate equal to the growth of the fruit during most of the developmental period, thus the only part of the fruit devoid of sclerotic tissue is the area encased in the persistent perianth. Cell divisions in the basal zone occur in all planes, and early in development may occur as high as mid-locule, but later are restricted to the approximate level of the locule floor. When the fruit has reached nearly full size, the parenchyma layer between the locular epidermis and the fibrous zone shows considerable tangential stretching and crushing of the cells. Subsequently, in the ripe fruit, the parenchymatous zone, the locular epidermis, and the fibrous zone are all sclerified, forming a tough endocarp (Fig. 14).

Related taxa. The structure of the gynoecium and the development of the endocarp in *Veitchia merrillii* (Beccari) H. E. Moore are essentially identical to those of *V. arecina* described above. The more extensive fibrous sheaths on the outermost bundles form a more evident outer boundary of the endocarp in *V. arecina,* but otherwise the fruits of the two species are very similar.

The same basipetal and centripetal pattern of maturation is evident in the fruits of *Ptychosperma macarthurii* (H. Wendland) Nicholson (Fig. 12). The locular epidermis is sclerified, as are a few cell layers of parenchyma and the fibrous sheaths of the vascular bundles which lie near the locule. However, the entire zone is far less developed than in the *Veitchia* species. The structure of the mature fruit of *P. lineare* (Burret) Burret (Fig. 13) is similar to that of *P. macarthurii.*

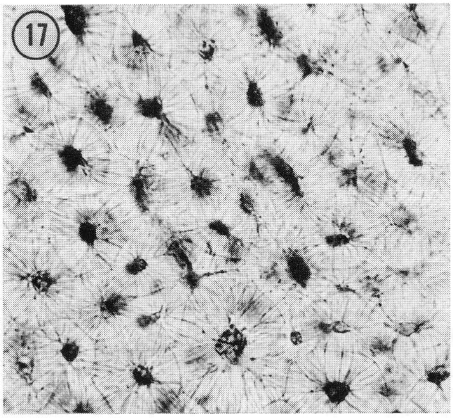


16. *Arikuryroba schizophylla,* longitudinal section through gynoecium × 14.

As described by Uhl and Moore (1971), *Paralinospadix,* of the *Linospadix* alliance, and *Areca,* of the *Areca* alliance, of the arecoid palms show a similar arrangement of longitudinally oriented vascular bundles in the ovary wall and exhibit basipetal and centripetal maturation of the tissues.

Cocosoid palms (*Cocos* alliance). The genera of this alliance have flowers with tricarpellate, syncarpous gynoecia always containing three (or rarely more) ovules at anthesis.

Arecastrum romanzoffianum (Chamisso) Beccari. A one-seeded fruit is formed from all three carpels; the two aborted ovules are crushed against the inside of the endocarp. At anthesis, the endocarp is differentiated as a region of isodiametric, thin-walled parenchyma cells between the locular epidermis and the longitudinally oriented procambial strands of the fibrous zone. The distal



17. *Arecastrum romanzoffianum*, sclerified endocarp cells × 320.

portion of the gynoecium contains fully mature tissues and some sclerified cells in the fibrous bundle sheaths, whereas the basal portion remains meristematic (Fig. 16). Maturation of the tissues is basipetal and centripetal and keeps pace with the enlargement of the fruit from the base, so that only the portion enclosed within the persistent perianth remains without sclerotic tissue. When the fruit has reached about two-thirds of full size, sclerification begins in the distal portion of the parenchyma zone. Sclerification proceeds basipetally and the cell walls become increasingly thick and hard (Fig. 17). In the mature fruit, the sclerification has extended slightly into the parenchyma surrounding the bundles of the fibrous zone and thus the endocarp includes the innermost fibrous bundles.

Related taxa. The gynoecial structure and development of the fruit of the closely related *Arikuryroba schizophylla* (Martius) L. H. Bailey are essentially identical to that described for *Arecastrum*. Uhl and Moore (1971) note the similar maturation of the distal tissues in gynoecia of *Bactris*, *Butia*, and *Elaeis*.

Discussion

The number of genera and species included in this study is so small that only tentative conclusions can be drawn, but the results obtained suggest that the structure and development of the endocarp correlate sufficiently well with other morphological characteristics that they may be useful in indicating relationships and may also be of diagnostic value in some groups.

Among the fruits studied, three endocarp types are distinguishable on the bases of time of differentiation, cell layers involved, and mode of development.

Type I. The Type I endocarp is the simplest and is derived solely from the cells of the locular epidermis which may be isodiametric or radially elongate and are usually sclerotic and contain silica. Differentiation and sclerification of the endocarp do not occur until the fruit has reached essentially full size. The Type I endocarp has been observed in the chamaedoreoid, pseudophoenicoid, and caryotoid groups of palms.

Type II. The Type II endocarp differentiates from the inner portion of the fruit wall early in development. The locular epidermis is not involved in the formation of the endocarp, which is several layers removed from it. After sclerification of the earliest differentiated cells, the endocarp is maintained as an intact layer throughout the growing period by the enlargement and intrusion of adjacent parenchyma cells into the spaces left as the sclereids separate. The Type II endocarp has been observed only in the coryphoid palms.

Type III. The Type III endocarp is the most complex and variable. The endocarp consists of three tissues: the sclerified locular epidermis, the sclerified and sometimes confluent sheaths of the inner vascular bundles, and the intervening parenchyma, also sclerified.

In the cocosoid palms, the parenchymatous zone is greatly exaggerated and may be almost as thick as the rest of the fruit wall. When the endocarp of a cocosoid fruit becomes sclerified, so do the parenchyma cells surrounding the innermost vascular bundles which thus become included in the endocarp. Fruits of the *Ptychosperma* alliance of arecoid palms have a far thinner zone of parenchyma between the locular epidermis and the fibrous zone. In gynoecia having a Type III endocarp, the parenchymatous and fibrous zones are differentiated at the time of flowering. Sclerification of the fibrous bundle sheaths first occurs distally and proceeds basipetally, as does sclerification of the parenchymatous zone. The Type III endocarp has been observed in fruits of cocosoid and arecoid palms.

Comparisons and Relationships

The intrusion of parenchyma cells into an adjacent sclerotic zone and their subsequent sclerification in a manner similar to that which occurs in the Type II endocarp of the coryphoid palms was noted by Lloyd (1910) and Long (1943) in fruits of the date (*Phoenix dactylifera* Linnaeus). The sclerotic zone in the date is located near the outer surface and has been termed an "exocarp" (Lloyd, 1910; Long, 1943). The phoenicoid and coryphoid palms are considered to be closely related (Drude, 1887; Potztal, 1964; Moore, 1973) and a similar mode of growth of a sclerotic zone is not unexpected.

Within the coryphoid group, *Rhapidophyllum* has been placed in the *Trithrinax* alliance of the apocarpous genera along with *Thrinax* and *Coccothrinax* (Moore, 1973) but the position of the endocarp to the interior of the vascular system is more similar to that of *Livistona* and *Pritchardia* of the *Livistona* alliance of syncarpous genera. The location of the endocarp relative to the vascular system needs to be determined for more coryphoid fruits before its significance can be determined. The enlargement of a sclerotic endocarp by a meristematic zone, such as occurs in *Livistona chinensis*, has not been reported elsewhere.

The pseudophoenicoid and chamaedoreoid palms are generally considered to be closely allied (Drude, 1887; Potztal, 1964; Moore, 1973) and their fruits are very similar, especially with regard to the development and mature form of the endocarp. Among the chamaedoreoid palms studied, the five species can be arranged in a series based on the degree of differentiation of the locular epidermal cells: those cells are isodiametric with unmodified walls in *Chamaedorea* sp., isodiametric with the locular tangential and radial walls slightly sclerified in *C. microspadix*, isodiametric with the same walls thicker and more heavily sclerified in *C. alternans*, isodiametric with all walls very thick and heavily sclerified in *C. pochutlensis*, radially elongate and with all walls very thick and heavily sclerified in *Mascarena lagenicaulis*. Although the *Mascarena* endocarp appears distinctive, it is only a further expression of a trend evident among the species of *Chamaedorea*. The endocarp of *Pseudophoenix sargentii* could be added to the series in that it differs from the others only in its cells being more elongate.

Among the cocosoid and arecoid palms, the progressively basipetal maturation of the sclerotic tissues is apparently related to the presence of a basal meristematic zone from which the fruit grows. Uhl and Moore (1971) noted in the material they studied that the basal and central ovarian regions were immature relative to the hard and variously protected stylar regions. In the arecoid and cocosoid species examined, cell divisions were observed to occur in the basal portions of the ovary until the fruit had reached about half its final length. Thereafter, enlargement was due to increase in cell size. The similarities in the development and growth of the endocarp in the arecoid and cocosoid fruits are striking, but it is not wise to draw any conclusions as to the significance of these similarities from the limited data currently available.

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CLASSIFIED SECTION