

The Protection of Pollen and Ovules in Palms

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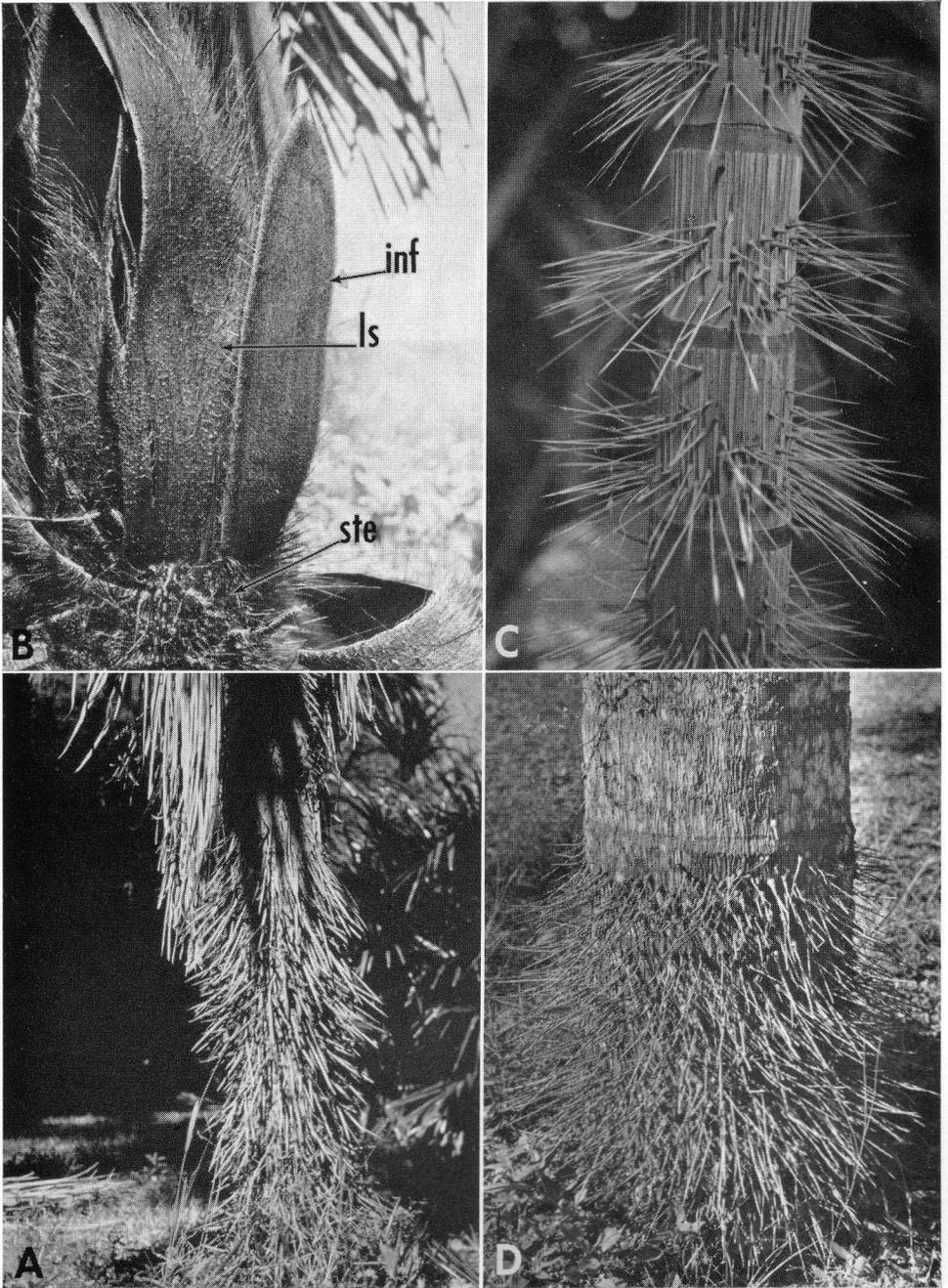
Abstract

An impressive number of structural features in palms appear related to protection of pollen and ovules. These include physical attributes and less evident cellular and intracellular specializations. Leaf sheaths, inflorescence bracts, and many protective mechanisms in floral organs are identified, characterized, and related to general levels of specialization among groups of palms. It is suggested that protection has involved selection for and coordination of characters at different structural levels. Observations suggest long coevolution with chewing insects, but attention is called to the critical need for careful field observations on phenology, floral biology, and general animal-palm interrelationships.

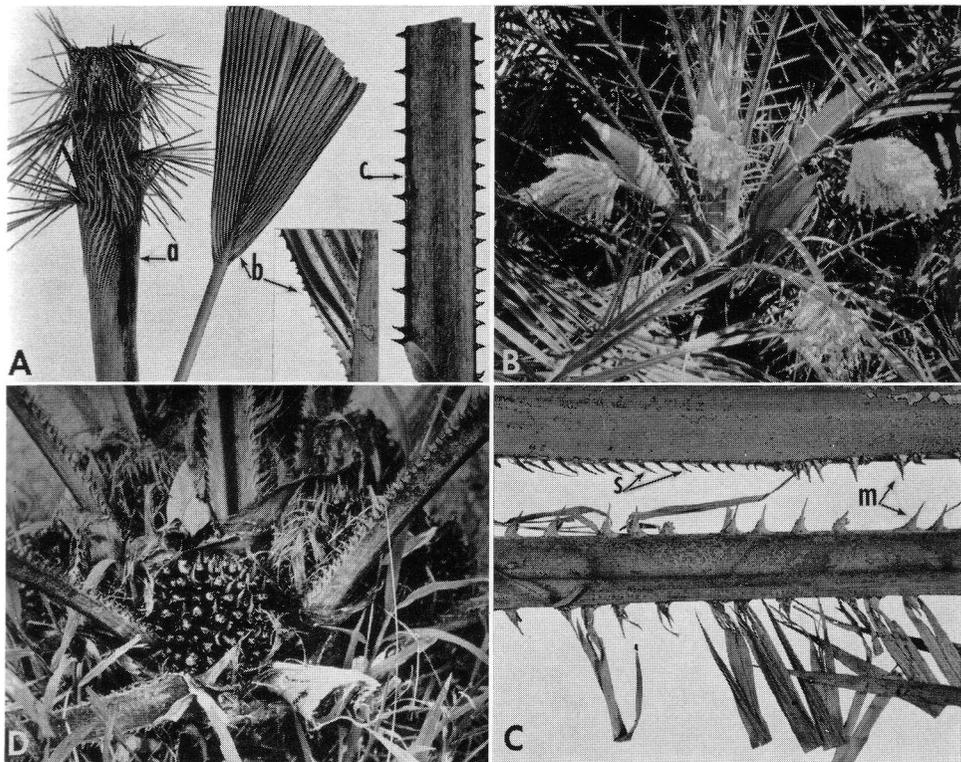
An impressive array of structures protect pollen and ovules in palms; indeed, the diversity of protective mechanisms associated with flowers is probably greater in palms than in any other family of seed plants. Protection may be by physical or chemical means, or by a combination of physical and chemical features. Many of the physical defenses of palms have long been recognized. The literature abounds with references to the size, hardness, and the fierce armature of some. Other protective mechanisms, however, such as specialized sepals and petals, and appropriately located fibers, sclereids, crystals, and tannin layers, become evident only after detailed study. When all aspects of protection are considered, it is apparent that pollen and ovules in some palms are protected by one or two structural mechanisms only, while protection in other palms is achieved by a sequence of mechanisms at different structural levels. How the specific protective fea-

tures of each palm relate to pollinators, predators, or disseminators can be determined only by careful field observations.

An understanding of these structural adaptations is essential to studies of floral biology, ecology, and evolution. That plants have coevolved with insects and animals seems evident, but many of the complex chemical relationships between plants and insects, and plants and other animals have not yet been worked out. Plants have been considered to provide food and shelter for insects or other animals, and to receive transport of pollen or of fruits in return (Southwood, 1973). The structure of flowers is correlated with pollination, the structure of fruits with methods of dispersal. Indeed, the few modern studies of pollination and fruit dispersal that we have for palms reveal a very exact and intricate relationship between the structure of the flower or fruit and the insects or mammals involved (Essig, 1971; Janzen, 1971; Schmid, 1970a,b). As we shall demonstrate, some structures present in the flower continue to protect the developing fruits and seeds, at least for a time. Our major purpose in this paper is to identify the structures that protect pollen and ovules at flowering time. It must be emphasized, however, that more than just protection of pollen and ovules is actually accomplished by the structures to be considered. For example, if pollen is to be transferred, potential vectors must be attracted, and predators satisfied, thwarted, or re-



1. Spines. **A**, Root spines on base of stem in *Cryosophila warscewiczii* (Moore 6017). **B**, Spines on stem (ste), leaf sheaths (ls), and inflorescence (inf) in an undescribed genus of the *Oncosperma* alliance (Moore, Guého & Vaughan 9925). **C**, Spines on a young stem of *Deckenia nobilis*, botanical garden, Victoria, Mahe, Seychelles Islands. **D**, An older trunk of *Deckenia nobilis* with large basal spines in the same botanical garden.



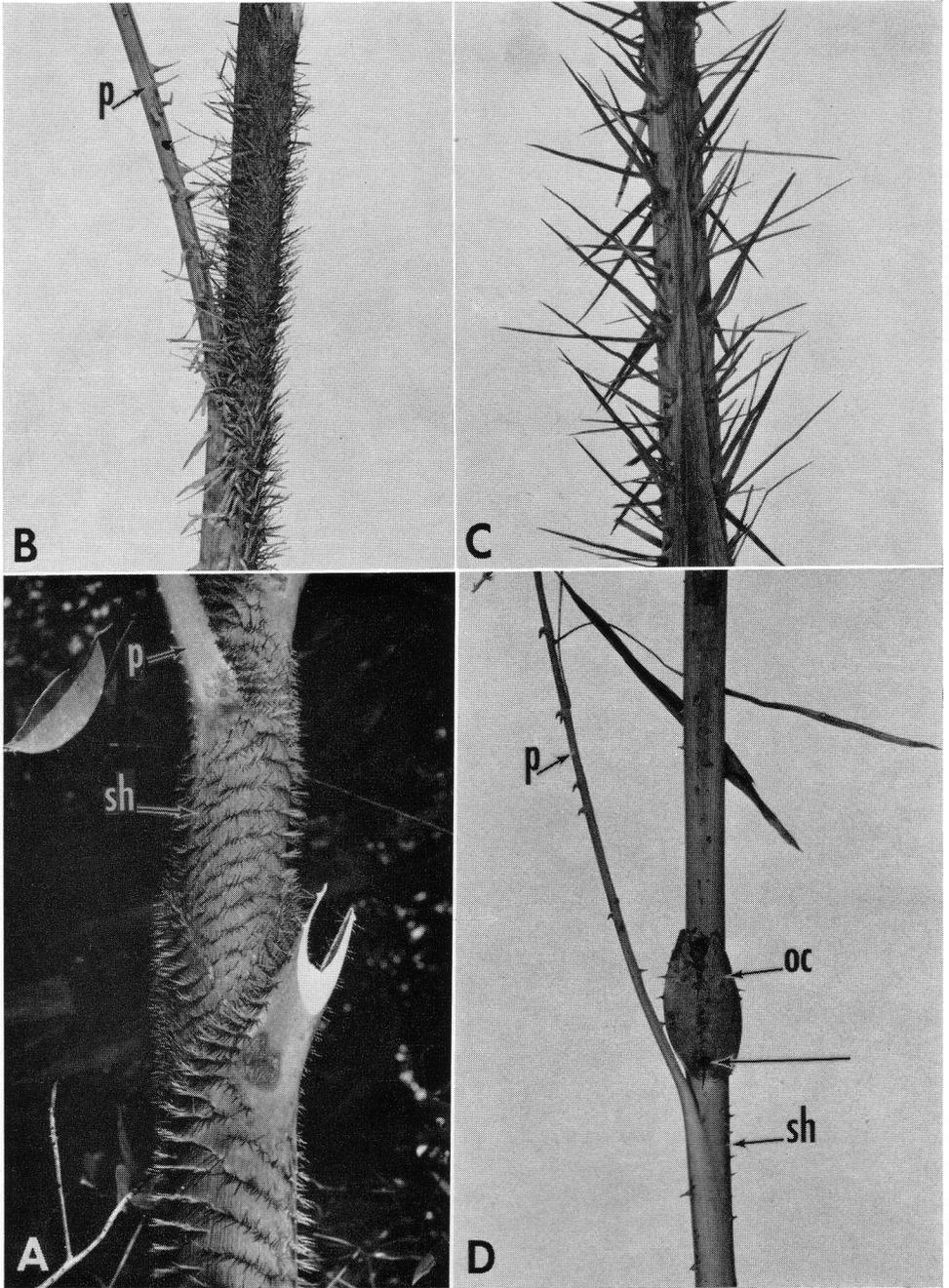
2. Spines. **A**, Coryphoid palms: **Aa**, spines formed from fibrous tips of leaf sheaths in *Zombia antillarum* (Bailey 301); **Ab**, teeth on the petiole and leaf margin of *Johannesteijsmannia altifrons* (Dransfield s.n., a. 1967); **Ac**, petiolar teeth of *Corypha elata* (Bailey 522). **B**, Spines formed by modified pinnae in *Phoenix reclinata*. **C**, Petiolar segments of *Elaeis guineensis* (Read 904) showing spines (s) formed by partial disintegration of the leaf sheaths and spines higher on the petioles (m) formed by the hard, basally swollen midribs of pinnae. **D**, Crown of *Elaeis guineensis* cultivated in Ecuador; note spines formed by pointed tips of rachillae in the center of the fruit bud and two other types, enlarged in C, on petioles.

pulsed. A second objective of this paper is to emphasize the need for information on how insects and other animals function in the natural history of each palm.

Some of the structures to be described occur mainly in certain groups of palms as delimited by Moore (1973); others, such as pits and spines, are structurally different in different groups of palms and obviously represent parallel developments. Maturation sequences are variable in palm reproductive systems and are intricately correlated with structure at all levels. Where flowers are enclosed in bracts or in pits in an axis until

nearly at anthesis, generally few physical protective features are seen in their sepals and petals. The reverse is also true—if bracts are shed or are exceeded by an elongating inflorescence axis when flowers are in early bud, sepals and petals may, in turn, take over the defense of developing pollen and ovules, and may then be tough and fibrous. Even when other organs appear to provide major protection, pistillate flowers are usually more heavily protected than staminate.

In addition to pollen and ovules, the stem apex, the immature leaf bases, and



3. Spines of lepidocaryoid palms. **A**, Spines on trunk and leaf bases of *Plectocomia muelleri* (Moore & Meijer 9158): sheath (sh); petiole (p). **B**, Spines on petiole (p) and stem of *Korthalsia ferox* (Moore & Meijer 9194). **C**, The fiercely armed petiole of *Salacca edulis* (Moore 6804). **D**, A portion of the stem of *Korthalsia scaphigera* (Moore, Chai & Smythies 9084) showing a petiole (p) with recurved spines and the ocrea (oc) formed by the upper part of the leaf sheath (sh), an ant hole marked by unlabeled arrow.



4. Spines formed from lateral roots. **A**, An enlargement of the stilt roots of *Socratea exorrhiza* (Moore, Salazar & Smith 8458) bearing short spines formed by lateral roots. **B**, Base of same plant showing the several large stilt roots of one tree.

the embryo are tender and vulnerable parts of palms. The first structures to be considered—leaf sheaths, and various kinds of spines—usually shield one or more of these vulnerable areas as well as young inflorescences. As will be evident, however, all aspects of protection must be considered if one is to understand the mechanisms operating in a specific palm.

Leaf Sheaths

The young palm inflorescence is at first tightly surrounded by a number of stiff leaf sheaths. The variety of sheath or leaf base structure in palms is sufficient to have merited a separate paper (Tomlinson, 1962b) which does not purport to have exhausted the subject. Two modifications of leaf bases may be mentioned in particular. The tubular leaf sheaths of the royal palm (*Roystonia*), or genera of the *Ptychosperma* and *Clinostigma* alliances, and of other alliances of the arecoid group, as well

as in the iriarteoid group and *Hypophorbe*, sometimes form a spectacular crownshaft which may function in part to protect inflorescences. The sheath is produced above the petiole as an ant-inhabited ocrea in *Ancistrophyllum* (Moore, personal observation) and *Korthalsia* (Beccari, 1884–1886; Dransfield, 1973). The ocrea of a few species of *Calamus* in New Guinea may be supposed to be similarly inhabited and the basal pinnae of *C. amplexans* Becc. in Borneo were described as forming an ant gallery. Ants also inhabit galleries formed by interlocking prickles or spines on the sheaths of several species of *Daemonorops*. The association of ants with these lianes suggests the possibility of a relationship similar, at least in part, to that of ants and species of *Acacia* in Mexico and Central America (see references to papers by Janzen in Southwood, 1973), but the detailed natural history of this relationship has yet to be learned for palms.

Spines

Two aspects of palm spines are particularly interesting because they suggest that spininess has originated several times within the family: (1) spines include three different structural forms; and (2) they occur in several different palm groups. The dual function of some spines which also function as grappnels has been pointed out by Tomlinson (1962a). Spines may be modified organs, modified parts of organs, or autonomous structures unrelated to other organs (Tomlinson, 1962a). The familiar spines on leaves of *Phoenix* (Fig. 2B) are modified pinnae which belong to the first category. These spines have been described as a major and unique protective mechanism for the stem apex in *Phoenix* (Tomlinson, 1962a). That they also defend inflorescences seems evident in Figure 2B. It is noteworthy that only one bract, a prophyll, encloses each inflorescence in *Phoenix*, and that protective mechanisms in floral organs are relatively few. Other spines which are modified organs are the root spines of *Cryosophila*, shown covering the lower part of the trunk in Figure 1A, and short spines formed from branch roots in *Socratea* (Fig. 4). Two examples of spines which are modified parts of organs can be seen side by side in the oil palm, *Elaeis guineensis* Jacq. (Figs. 2C,D). Spines at the base of each petiole are formed by hard fibers from partly disintegrated leaf sheaths, but higher on the petiole, special spines with bulbous bases represent the basal parts of the midribs of disintegrated pinnae.

Emergences formed by epidermal and

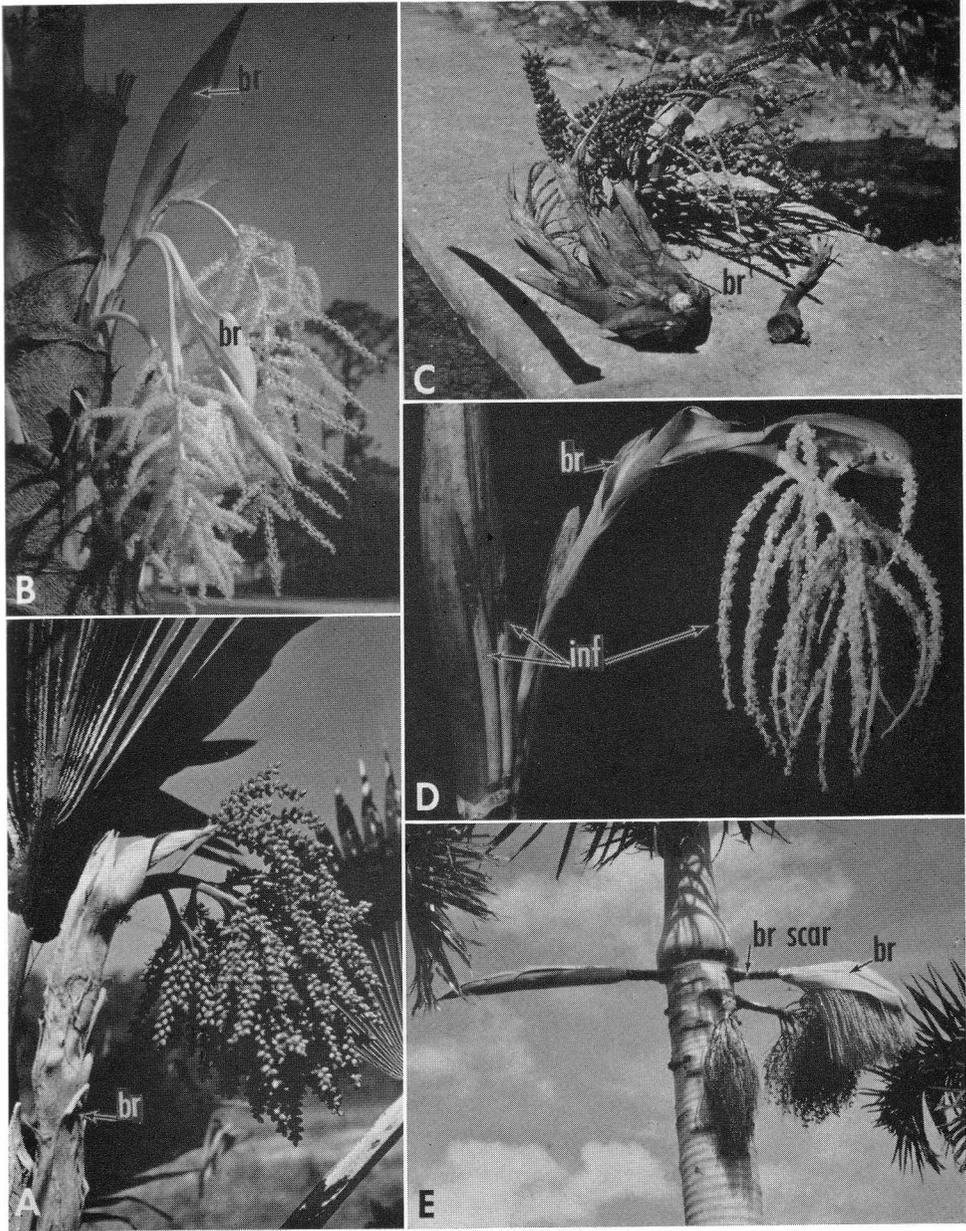
peripheral layers of various organs are the fiercest spines produced and are found most abundantly on stems, leaves, and bracts in three groups of palms—the *Bactris* alliance of cocosoid palms, the *Oncosperma* alliance in the arecoid group, and on various genera among the lepidocaryoid palms. As for other protective mechanisms, how spines function must be determined for each taxon. The large spiny bract appears to shield an inflorescence in fruit as well as in bud and flower in *Bactris* (Fig. 7A). Cocosoid and lepidocaryoid palms occur in regions where possible avian or mammalian predators are or have been present. The selective advantage of spines in genera of the *Oncosperma* alliance on islands (Mascarenes and Seychelles) devoid of obvious predators, however, is not evident.

For those interested in the evolution of palms, it may be noted that all three morphological types of spines occur in the presumably primitive coryphoid group. Emergences, perhaps not fully comparable to those noted above, occur on petioles and occasionally on leaf margins as teeth (Figs. 2Ab,Ac); fibers of long-persistent leaf sheaths form spines in *Zombia* (Fig. 2Aa); and spines representing modified organs are found in the root spines of *Cryosophila* (Fig. 1A). Generally, however, protection is light in the coryphoid palms—the more highly advanced palms have more spines and other protective mechanisms (Table 1).

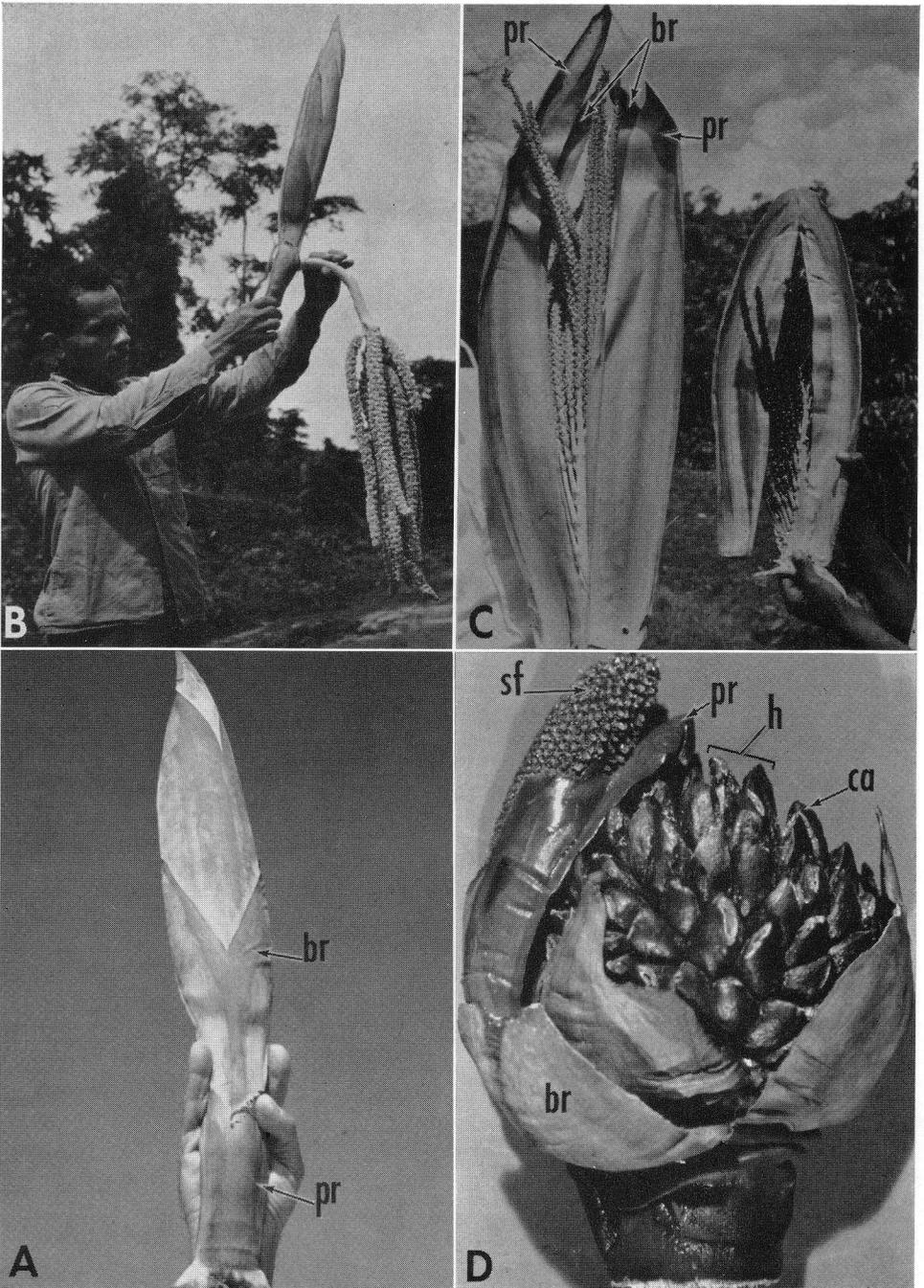
Bracts

The first protective mechanisms to be considered on the reproductive system are bracts—organs which have been

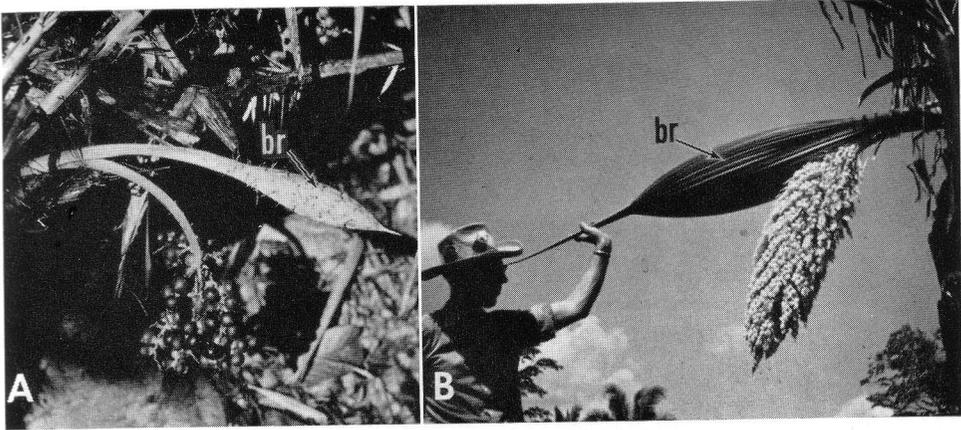
5. Bracts. **A**, Several fibrous overlapping bracts (br) on an inflorescence branch of *Pritchardia pacifica* at Fairchild Tropical Garden, Miami, Florida. **B**, Thinner bracts (br) which open rapidly



on an inflorescence of *Coccothrinax* sp. at Fairchild Tropical Garden; the arrow from the upper br indicates a peduncular bract which enclosed the whole inflorescence; the lower br indicates a bract that enclosed a lateral branch. **C**, A multiple inflorescence of *Arenga undulatifolia* (Moore 6094) with several fibrous overlapping bracts (br) on each axis. **D**, In *Morenia linearis* (Moore, Salazar & Smith 8354), two inflorescences (inf) are enclosed in bracts and a third is exerted showing a number of bracts (br) on the peduncle. **E**, Bracts on *Hyophorbe verschaffeltii* at the University of Mauritius, Reduit, Mauritius are shed in succession, each leaving a circular scar (br scar) on the peduncle; the last bract on inflorescence at upper right has opened to release flowering axes.



6. Bracts. A, The inflorescence of *Socratea exorrhiza* (Moore 9550) is enclosed in about seven tubular bracts; prophyll (pr); first peduncular bract (br). B, Bracts in A split abaxially to release the pendulous flowering axes. C, Only two relatively thin bracts, a prophyll (pr) and a sterile peduncular bract (br), enclose the rachillae in two inflorescences of *Dictyosperma album*



7. Bracts in cocosoid palms. **A**, A spiny bract appears to shield the infructescence in *Bactris brongniartii* (Moore, Salazar & Smith 8404). **B**, The large bract of *Scheelea rostrata* (Moore 6540) is woody and plicate.

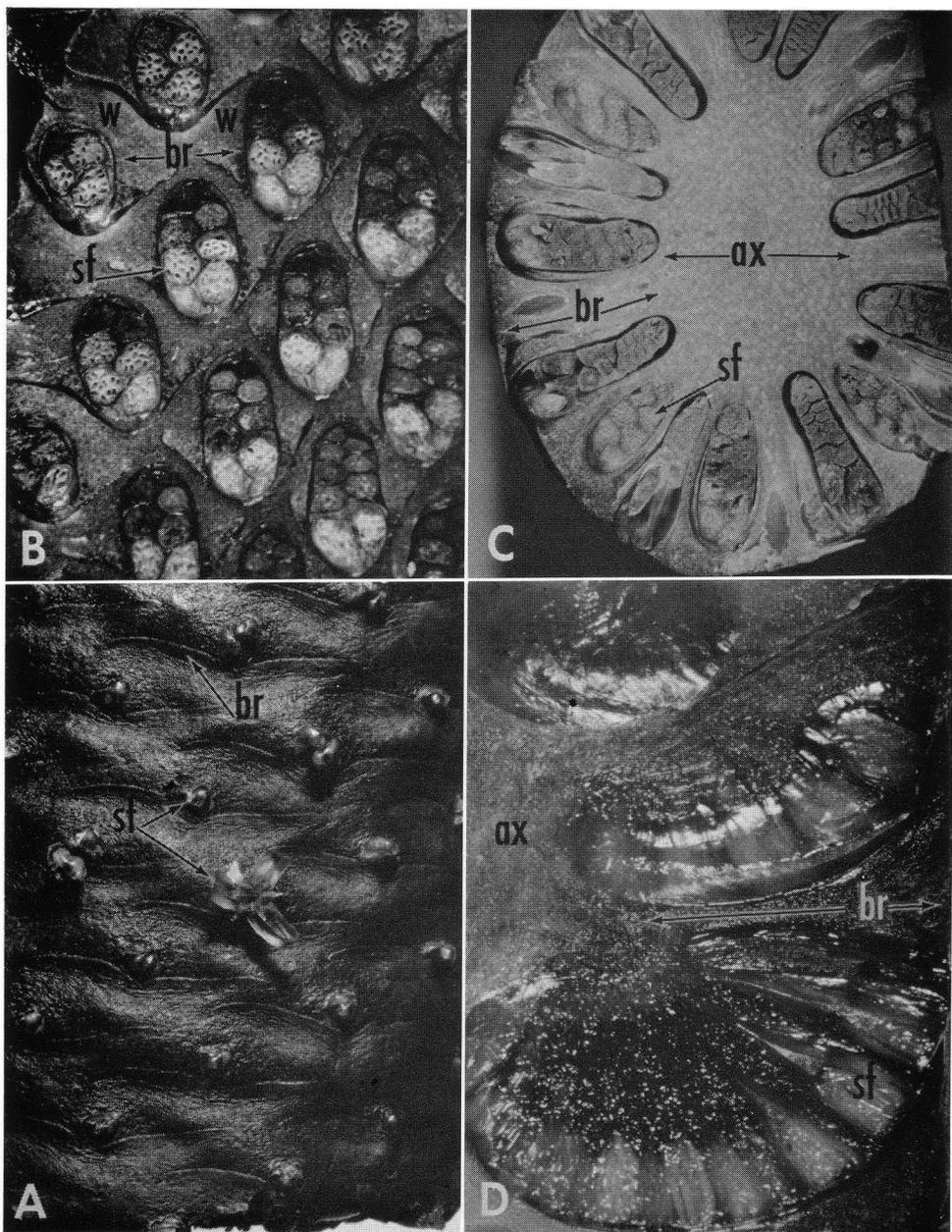
demonstrated in two groups of palms to be structurally reduced and modified leaves (Tomlinson, 1971; Tomlinson and Moore, 1968). The large bracts of many palm inflorescences were too unwieldy for early collectors and only recently has information been amassed on characters and distribution of bracts within the family (Moore, 1973). In the majority of palm groups, several bracts, one borne above the other, are present on the main axis or peduncle of each inflorescence and form a multi-layered sheath around the flower-bearing branches. The several spirally inserted bracts which envelop an inflorescence branch in *Pritchardia pacifica* Seem. & H. Wendl. can be seen in Figure 5A. The bracts may persist on the inflorescence as in *Morenia* (Fig. 5D), or may be shed in succession as in *Hyophorbe* (Fig. 5E), where the last bract remains on the recently expanded inflorescence

to the right of the stem illustrated, and scars of preceding bracts can be seen on the peduncle.

A seemingly more complex situation, both with respect to number and position of bracts and to their opening, occurs in the mangrove palm, *Nypa fruticans* Wurmb (Fig. 6D; Uhl, 1972). Each branch of the inflorescence is enclosed in a prophyll and subtended by a bract which also completely encloses the main axis and all subsequent branches. In many other palm inflorescences, the bracts subtending lateral branches and the prophylls of lateral branches are small or lacking (Figs. 5A,D,E; 6B,C). The terminal pistillate head and the ultimate lateral branch, partially exerted from its prophyll, are shown in a *Nypa* inflorescence in Figure 6D. *Nypa* is protogynous—the pistillate head is exposed before the lateral branches are released from their bracts.

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(Moore & Guého 10101, 10102) from Mauritius. **D**, Three sterile bracts are shown near the base of the terminal pistillate head (h), and the ultimate lateral axis ending in a staminate flower cluster is partially exerted from its keeled prophyll (pr) in *Nypa fruticans* (Moore 5846): carpel (ca); staminate flower (sf).



8. Pits in the staminate inflorescence of *Borassus flabellifer* (Read 716). **A**, The surface of the axis with single buds or flowers (st) exposed, each subtended by a broadly V-shaped ridge (br) representing the outer edge of the subtending bract. **B**, A tangential section of the axis exposing the flower clusters situated in elongate pits formed by partly united bracts: a bract (br) subtending one cluster (indicated by arrows) is shaped, in tangential section, like a butterfly; each lateral wing (w) of the bract forms the lateral side of a lower pit; a staminate flower (sf) is seen in transection. **C**, A transection of the axis shows the radial extent of the many flower-containing pits: arrows indicate the extent of bract tissue (br) and of axis tissue (ax); staminate

In the arecoid and cocosoid palms, there are usually only two principal bracts, a prophyll and one sterile peduncular bract, and bracts which subtend lateral axes within the inflorescence are small or absent (Fig. 6C). A major part of floral protection in the arecoid group appears to be provided by sepals and petals: in many arecoid alliances (e.g., *Ptychosperma*), floral organs are extremely tough and sclerenchymatic. The most bizarre bracts in palms are those of the cocosoid group, where again only two major bracts are present. The large woody bract characteristic of many cocosoid genera, however, is not the first but the second peduncular bract—the prophyll remains obscured by the leaf sheath. In some cocosoid alliances, as illustrated in *Scheelea rostrata* (Oerst.) Burret (Fig. 7B), the large bracts are also plicate. In sum, there may be one, two, or several major bracts enclosing each inflorescence in palms. The bracts may be thin or thick, and papery, fleshy, fibrous, or woody in texture. Number and texture and the time and method of opening are related to the maturity of the flowers within, and certainly also to the climate, insects, and other animals of the palm's particular habitat. Information on details of bract opening is still needed for many palm genera.

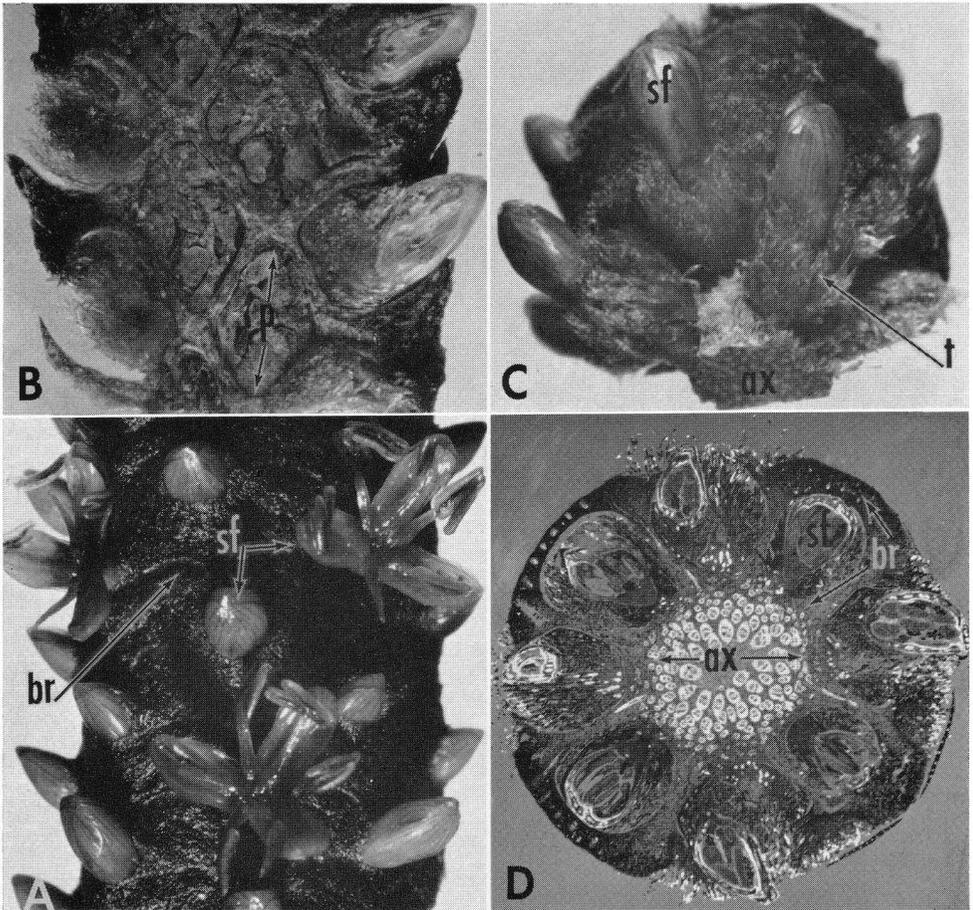
Pits

Borassoid inflorescences exhibit an unusual protective feature—a special cavity or pit in an inflorescence branch in which single flowers or whole flower clusters are partially or completely enclosed. Whole flower clusters in bud are completely concealed in such cavities in

borassoid and geonomoid palms. In other groups, pits are bowl-like, surrounding only the lower parts of the flowers. Structurally, the cavities are formed in three ways: (1) by bracts which may be free (Fig. 10C) or united (Fig. 10D); (2) by a depression in the branch in which the flowers are partially submerged (Figs. 11B,C,D); and (3) by a combination of a depression in a branch and a covering bract (Fig. 12B). The largest pits containing the most flowers are found in the staminate inflorescences of the *Borassus* alliance—specifically in *Lodoicea*. Structurally similar but somewhat smaller pits can be seen in the staminate rachilla of *Borassus* (Fig. 8). One would not suspect from a casual look at the surface of the inflorescence (Fig. 8A) that each single flower protruding from an apparently shallow bract is only one of a cluster of ca. 30 flowers (Figs. 8B,C,D). Each enclosed flower cluster is a reflexed branch (a cincinnus) appearing cocoon-like (Fig. 8D), with the youngest flowers nearest the center of the axis. The bract which subtends each flower cluster can be seen as a shallow curved ridge below each flower or bud in Figure 8A. The unusual “butterfly” shape of each bract is apparent in the tangential section (Fig. 8B). The upper curved surface of each bract forms the floor of one pit; the upper extremity of each “wing” of the bract is fused to the center of the lower side of an upper bract; and the outer margins of each “wing” form the lateral walls of two slightly lower pits. A transection of the branch (Fig. 8C) shows a number of pits cut at different levels and a central group of bundles in the axis. The pits are largely

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flower (sf). **D**, In radial section, flower clusters appear cocoon-like with the youngest flowers of the reflexed branch toward the center of the axis (ax): br indicates extent of bracts, sf, a staminate bud in longitudinal view.

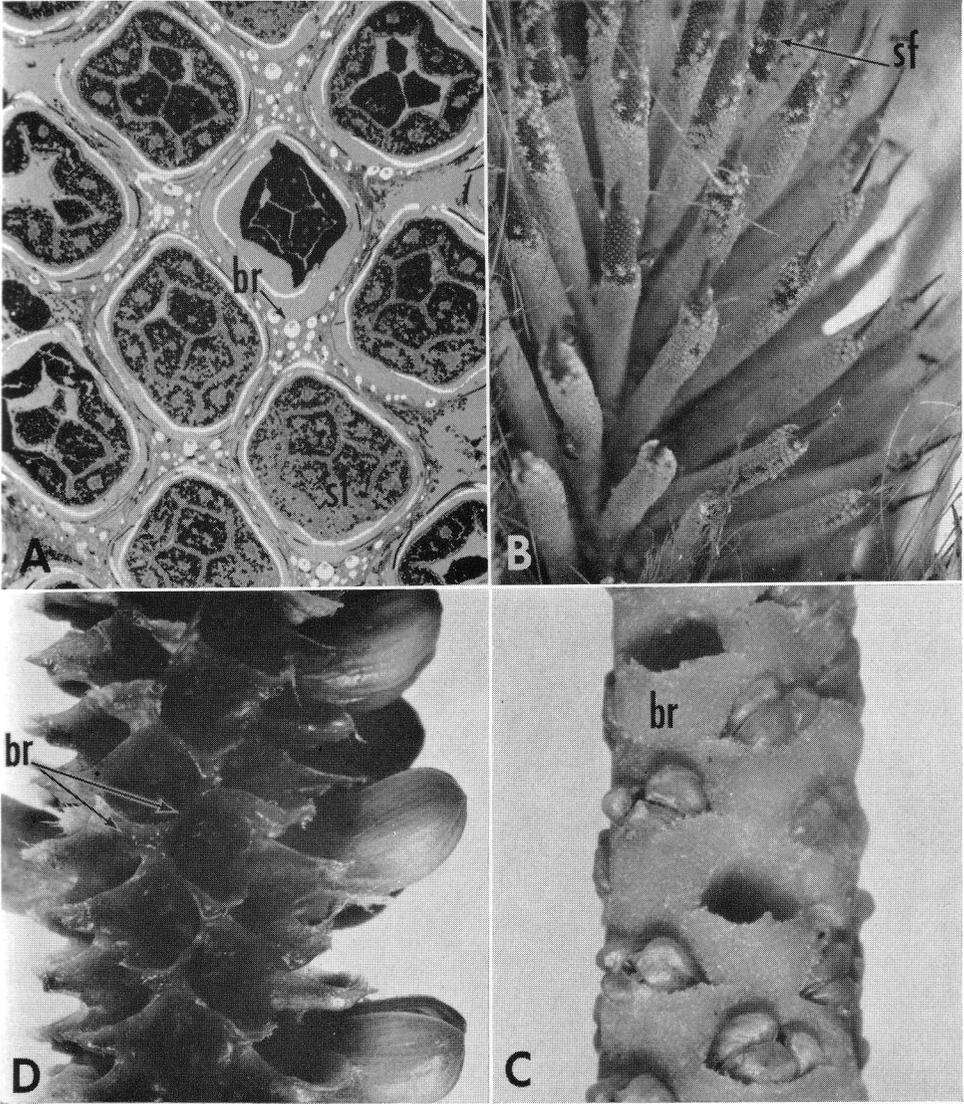


9. Pits in the staminate rachilla of *Hyphaene schattan* (Read 720). **A**, A surface view of the rachilla with a bud or flower (sf) exerted from each pit. **B**, In tangential section, pits (p) are crowded with flower bases and bracts. **C**, When outer bracts are dissected away, a collar of trichomes (t) can be seen surrounding each flower: axis (ax); staminate bud (sf). **D**, Pits formed by united bracts (br) make up about two-thirds the diameter of the inflorescence in transsections: ax, extent of the axis; sf, a staminate bud in longisection.

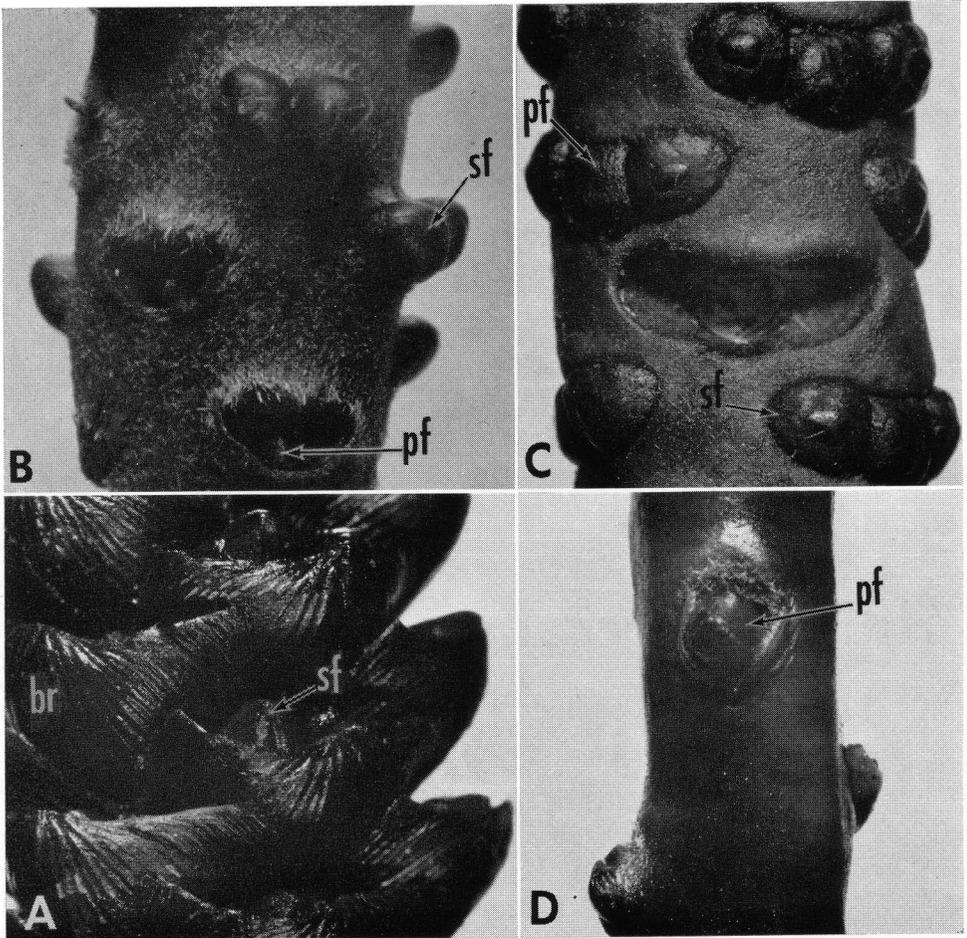
formed from fused bracts—the inner edge of each pit extends only slightly into the central bundle-containing axis (Fig. 8C). One advantage in exposing a single male flower at a time may be the production of pollen over a long period—undoubtedly important in a dioecious genus. Pits are also formed from bracts in the related genus *Hyphaene* (Fig. 9) where bracts are thinner but similar to those of *Borassus* in shape. In *Hyphaene*, only three flowers occur

in each pit, and a collar of large trichomes surrounds the base of each flower (Fig. 9C).

Open pits formed by free or fused bracts occur in some lepidocaryoid and cocosoid palms. Those of *Eleiodoxa* (Fig. 11A) consist of heavily fibrous bracts with straight sides. Staminate flowers of *Acrocomia* are borne in cup-like pits (Fig. 10D) with ragged edges consisting of united bracts. Pits in *Astrocaryum* (Fig. 10C) are of essen-



10. Pits of coccosoid palms. **A**, Pits formed from fused bracts enclose the base of each staminate flower in an oil palm, *Elaeis oleifera* (Read 1388): in this tangential section, bract traces are cut transversely and a large midvein (br) is evident directly below each pit. **B**, Staminate rachillae of *Elaeis guineensis* cultivated at Antalaha, Madagascar, end in spines and the pits formed by united bracts appear "honeycomb"-like distally: sf, a staminate flower protruding from a pit. **C**, Pits are of fleshy but essentially free bracts (br) in *Astrocaryum sciophilum* (Wessels Boer 1429). **D**, Pits with fimbriate edges, also formed by fused bracts, shield the bases of staminate flowers in *Acrocomia* sp. (Cook s. n., a. 1904).

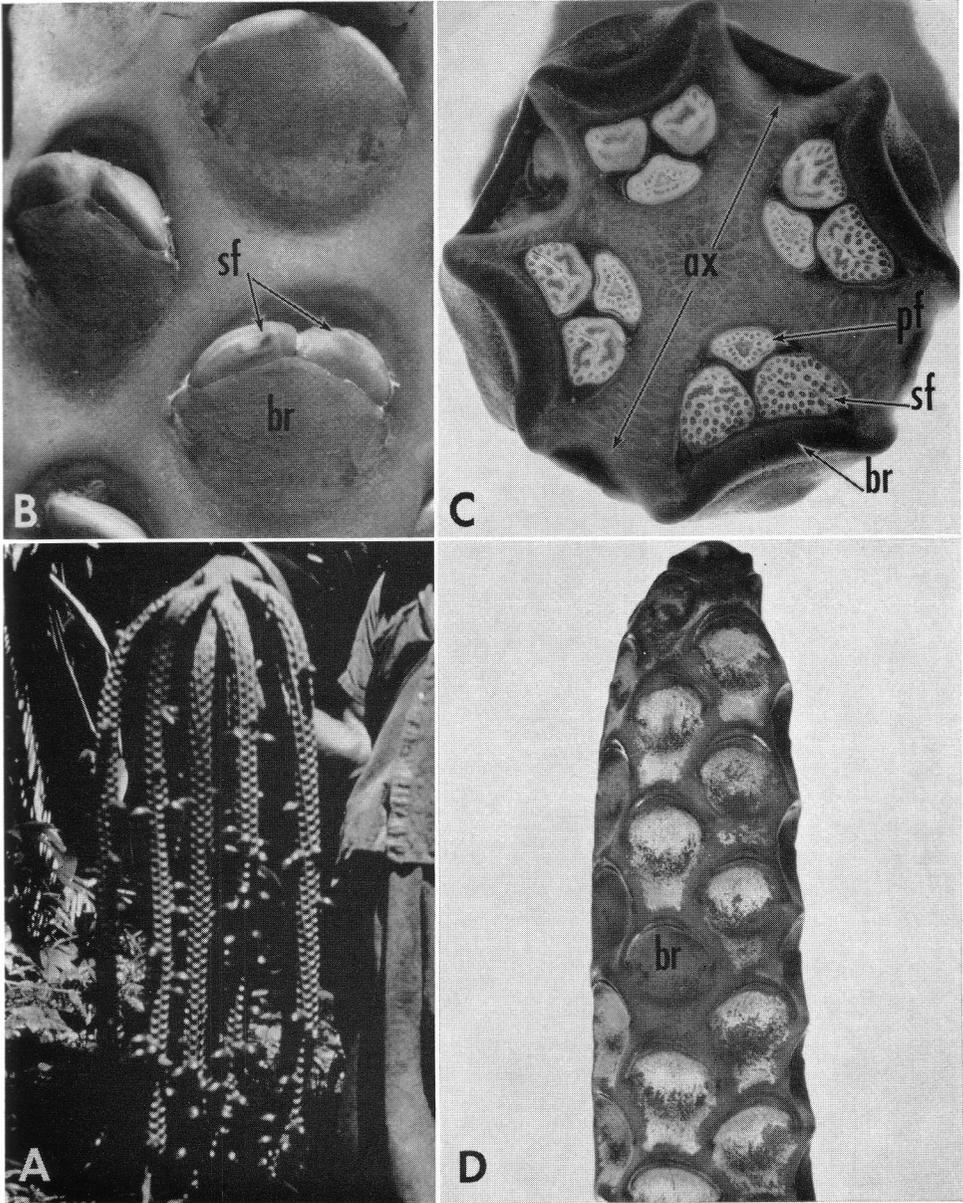


11. Pits. **A**, Pits formed by fibrous bracts (br) in a staminate rachilla of *Eleiodoxa conjerta* (Dransfield 757): sf, a staminate bud. **B**, Pits of the strange African palm *Podococcus barteri* (Moore & Enti 9900) are overhung by large trichomes: pf, pistillate bud, staminate buds (sf) removed. **C**, Pits in an undescribed genus from New Caledonia (Moore, Brinon, Schmid & Veillon 9957) are mouthlike depressions with no evidence of associated bracts: pf, pistillate bud; sf, staminate bud. **D**, A pistillate bud (pf) protrudes from a pit of *Bentinckia nicobarica* (Moore 6097): the pit is an opening in the axis with no apparent associated bract.

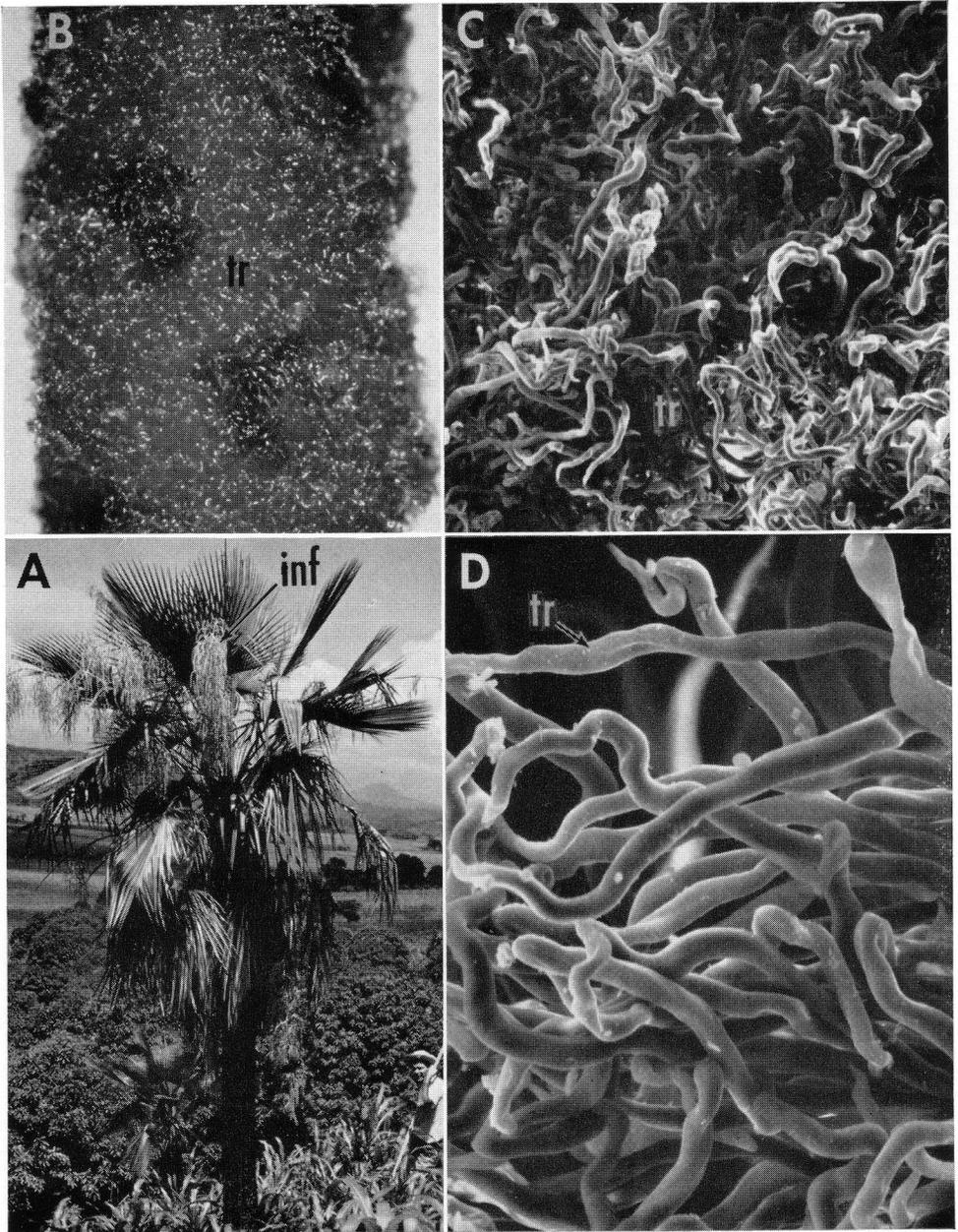
tially free but fleshy bracts. The staminate flowers of the oil palm, *Elaeis guineensis* (Fig. 10B), are situated in pockets in a "honeycomb"-like axis. That cavities are constructed of completely fused bracts can be seen in the tangential section (Fig. 10A), which shows the row of bract traces below each flower.

In certain palms (*Podococcus* and

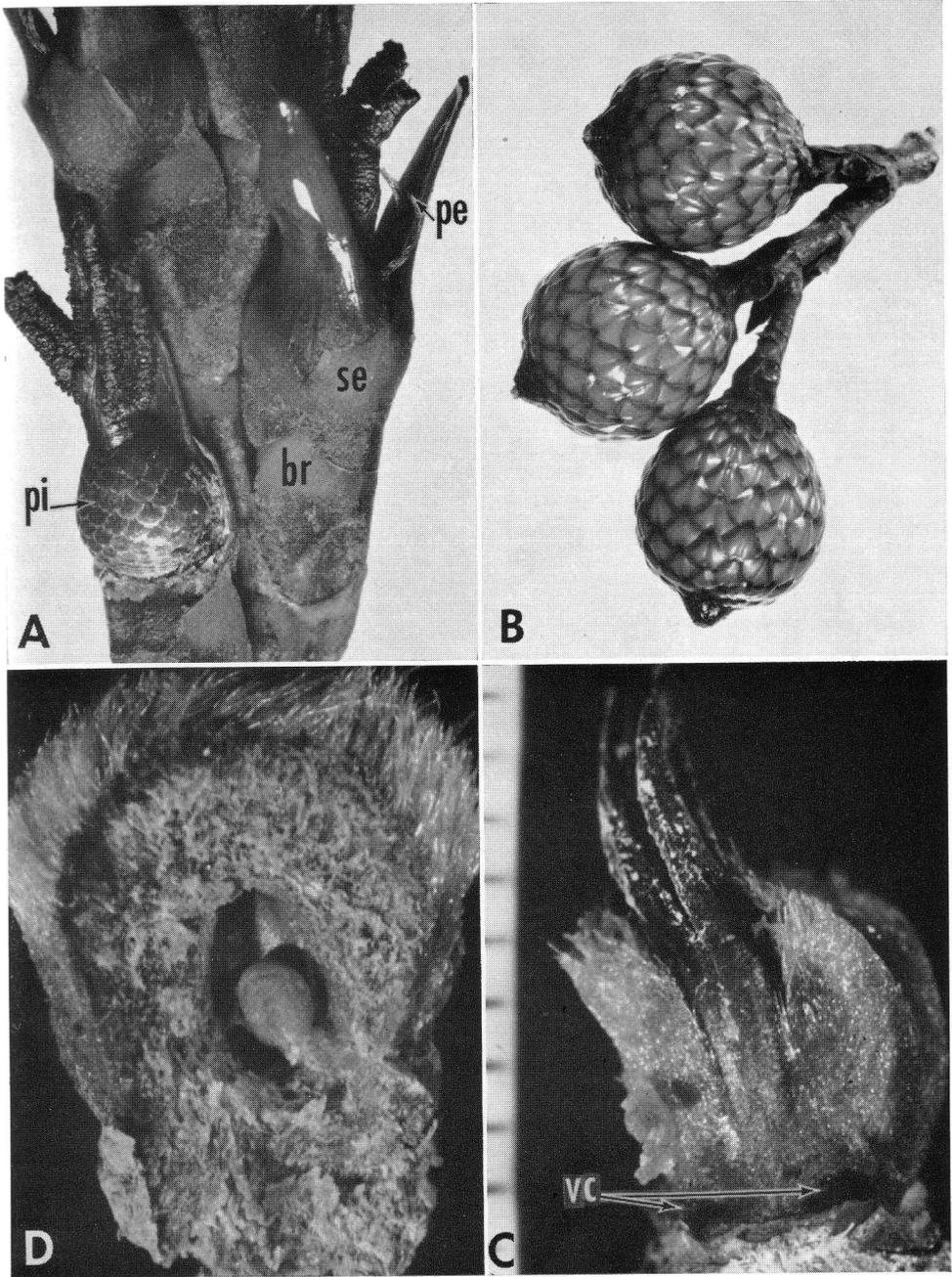
many arecoid genera), pits are cavities in inflorescence axes with any associated bracts reduced or apparently absent. Pits of *Podococcus* (Fig. 11B) are overhung by large trichomes and show little external evidence of any bracts. Anatomy, however, reveals a row of large fibrous bundles representing bract traces along the lower edge of each pit. The staminate flowers in *Podococcus* mature



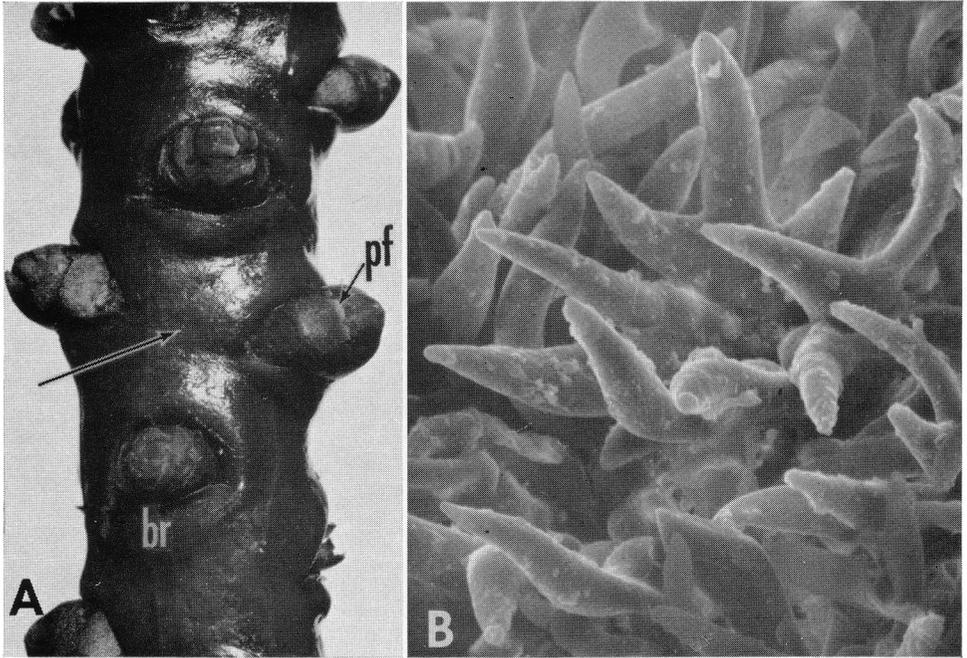
12. The geonomoid pit in *Welfia georgii*. **A**, An inflorescence in fruit from Moore 6557. **B**, A close-up of a rachilla (Moore & Parthasarathy 9412) with staminate buds (sf) protruding from each pit: staminate flowers will open before the pistillate. **C**, A transection of the axis in B exposing the triads of flowers in four pits: the axis (ax) extends between pits; bracts (br) are different histologically from tissues of the axis and appear darker; pf, pistillate flower; sf, staminate flower; dark circles and splotches in flower sections are tannin sheaths surrounding the single bundles in each stamen and staminode. **D**, Part of an inflorescence branch in bud with bracts closing pits (Moore & Parthasarathy 9412).



13. Trichomes of *Brahea calycarea* (Uhl 109). **A**, This palm grows in a valley near Jalcomulco, Veracruz, Mexico: white inflorescences, apparently in flower, protrude from the crown. **B**, A close-up of the rachilla shows that the flowers (dark spots) are actually in bud and are covered by a mass of woolly trichomes (tr), \times ca. 25. **C**, The trichomes, when viewed with the scanning electron microscope, are long and have thick, fibrous walls, \times ca. 120. **D**, A higher magnification of the trichomes, \times ca. 420.



14. Trichomes and scales. **A**, *Daemonorops rubra* (Moore 9947 A), part of a rachilla with perianth removed from a flower at left to expose the pistil (pi)—note that scales decrease in size and maturity toward the base of the pistil: br, bract; pe, petal; se, sepal. **B**, Fruits of *Daemonorops calicarpa* (Dransfield s.n.) show shiny reflexed scales. **C**, Trichomes clothe the fertile carpel of *Wettinia* sp. (Moore & Parthasarathy 9485): vc, arrows, indicate the ovarian parts of the two sterile carpels. **D**, A longitudinal section of the fertile carpel in *Wettinia* shows the ovule shielded by a thick, fibrous wall and by long trichomes.

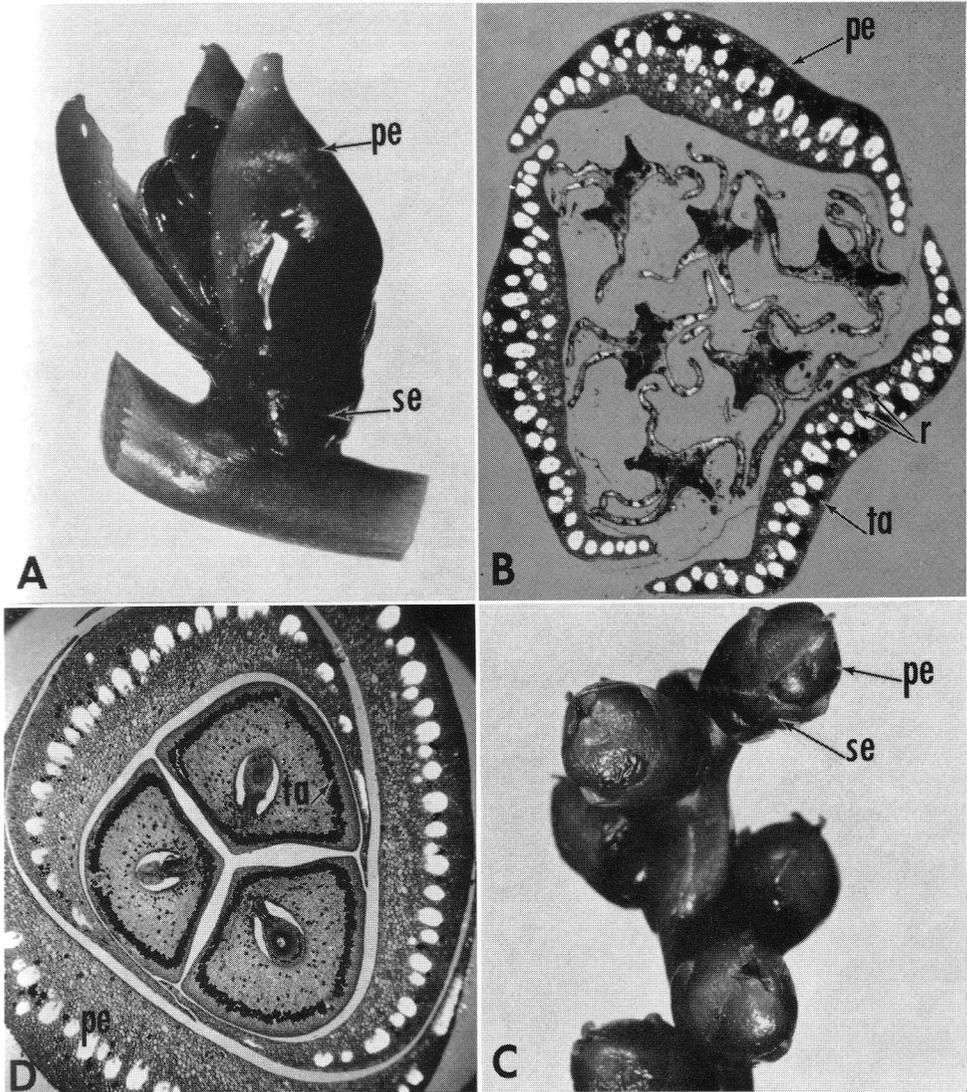


15. "Invisible" trichomes. **A**, The axis of *Burretiokentia vieillardii* (Moore, Schmid & Veillon 9955) appears smooth to slightly grainy. **B**, The scanning electron microscope reveals a thick cover of stellate trichomes in the region indicated by the unlabeled arrow in **A**, \times ca. 600.

first and are shown in late bud in Figure 11B. Staminate buds have been removed from two lower pits in Figure 11B to show the small central pistillate buds which at this stage are shielded by the enlarging male buds and by the walls of the pits. No evidence of pit-associated bracts has been found in *Bentinckia nicobarica* (S. Kurz) Becc. (Fig. 11D), nor in an undescribed genus from New Caledonia distinguished by mouth-shaped pits, enclosing horizontally elongate triads of flowers (Fig. 11C).

The most intricate pits found in palms are those of the geomoid group illustrated by *Welfia* (Fig. 12). Our work on this group has shown that the cortex of the inflorescence axis expands differentially so that arms of the axis extend between triads of flowers partly enclos-

ing the triads and the lower parts of the bracts that subtend them (Fig. 12C). The transection of a branch (Fig. 12C) shows four pits, each with two outer staminate and the inner pistillate flower. Extensions of the axis are evident between the pits (Fig. 12C). The pits are covered by bracts, which are different histologically and appear darker than the tissues of the axis (Fig. 12C). In early bud, the flowers are completely covered by the partly submerged bracts (Fig. 12D). Staminate flowers mature first (Fig. 12B), while the pistillate bud remains deep in the pit. Studies by Schmid (1970a,b) on *Asterogyne* have shown that syrphid flies are the chief pollinators in that genus, although 26 different insects visited the palm, suggesting that this superb protection may be directed against insect predators.

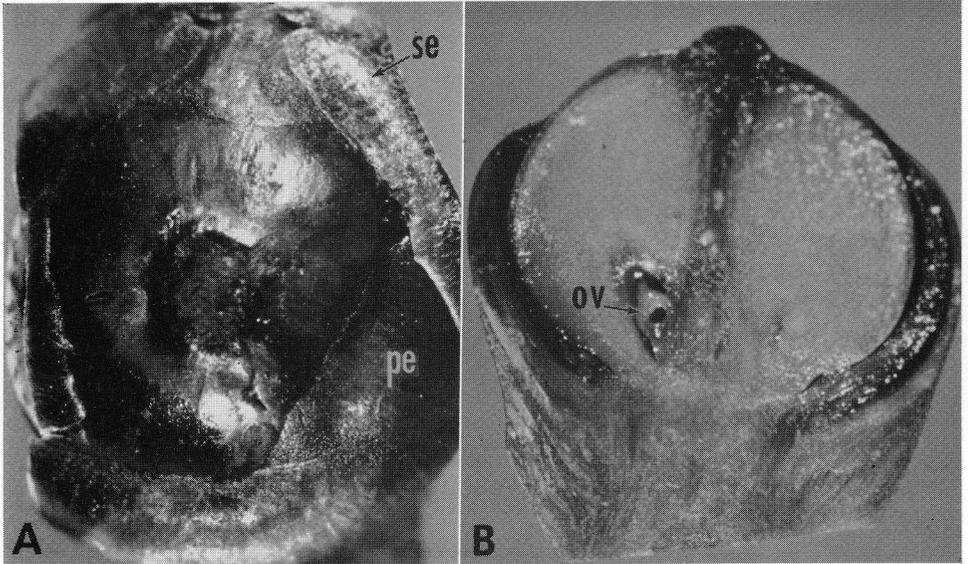


16. Floral mechanisms in *Phoenix caespitosa* (Moore, Germeaux & Martin 9897). **A**, Staminate flower—sepals (se) form a low cup enclosing the bases of the fleshy petals (pe). **B**, A transverse section of A shows petals are fibrous with groups of tannin cells (ta) blocking the spaces between fibers, and raphides (r) present along the inner surfaces: note tannin in the connectives and walls of the open anthers in the center of the section. **C**, Pistillate flowers have fleshy sepals (se) and tightly imbricate petals (pe) slightly open distally to expose the stigmas. **D**, A transection of the pistillate flower (C) shows a row of traces with large fibrous caps in the thick, imbricate petals (pe) and a layer of tannin (ta) in the wall of each carpel.

Trichomes and Scales

Trichomes and scales occur in seemingly endless variety on many organs of palms. A survey of these structures

under a scanning electron microscope is certain to be most profitable. Their possible role in plant defense has been discussed recently by Levin (1973) who



17. Floral mechanisms in the pistillate flower of *Latania verschaffeltii* (Read 1386). **A**, Sepals (se) and petals (pe) are imbricate, leathery in texture, and extremely fibrous, forming a double sheath around the base of the globular pistil. **B**, In longitudinal section, the pistil is largely parenchymatic but has a peripheral layer (not apparent in this section) of sclereids: these and the thick wall also protect the basal ovules (ov).

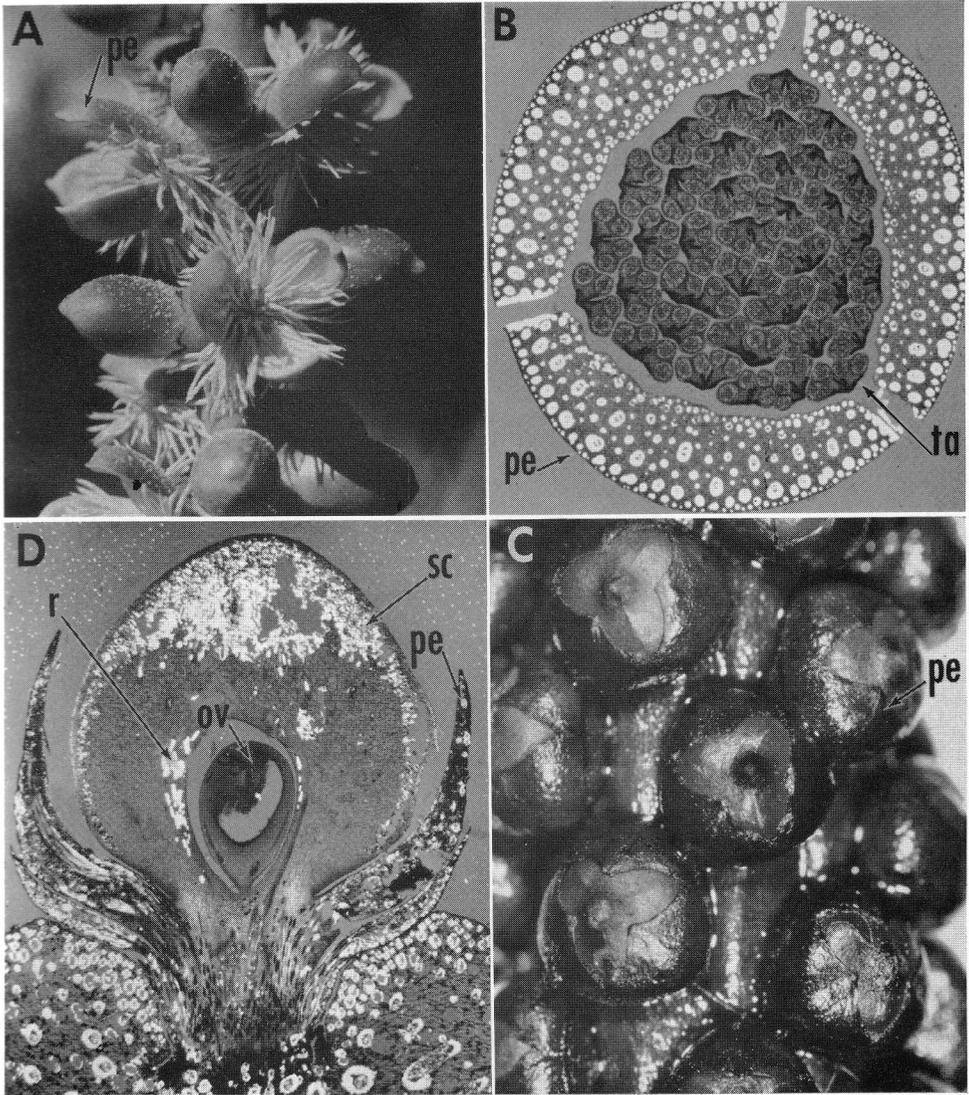
considers that they function mainly against phytophagous insects. Their location on many reproductive organs in palms suggests that they provide protection: for developing buds in the pits of *Hyphaene schattan* Bojer ex Damm. (Fig. 9C), and on the rachillae of *Brahea calcarea* Liebm. (Fig. 13); for the gynoeceium and later fruit in *Wetinia quinaria* (Cook & Doyle) Burret (Figs. 14C,D); and perhaps for the inflorescence axis in *Burretiokentia* (Fig. 15). In *Brahea calcarea*, the large white inflorescences appear to be in flower when seen from a distance (Fig. 13A), but when collected were found to have young buds densely covered with thick whitish trichomes (Fig. 13B). These trichomes, when viewed with the scanning electron microscope (Figs. 13C,D), somewhat resemble spaghetti but are actually fibrous in texture.

Trichomes and scales vary in shape and size. The rachilla of *Burretiokentia*

vieillardii (Brongn. & Gris) Pichi-Sermolli appears only slightly grainy to the naked eye, but is actually covered with stellate trichomes as evident with the scanning electron microscope (Fig. 15B). The scales on the surface of the gynoeceium in *Orbignya speciosa* (Mart.) Barb. Rodr. are irregular (Figs. 27C,D). The scales on lepidocaryoid fruits (Fig. 14B) mature first on the upper surface of the pistil (Fig. 14A) and shield the young ovules in the flower from an early stage. These scales have been considered to represent reduced inflorescences (Eames, 1961) but appear to be homologous to the trichomes of *Wetinia* and, like some prickles, are emergences formed from an epidermal and some underlying cell layers.

Floral Organs

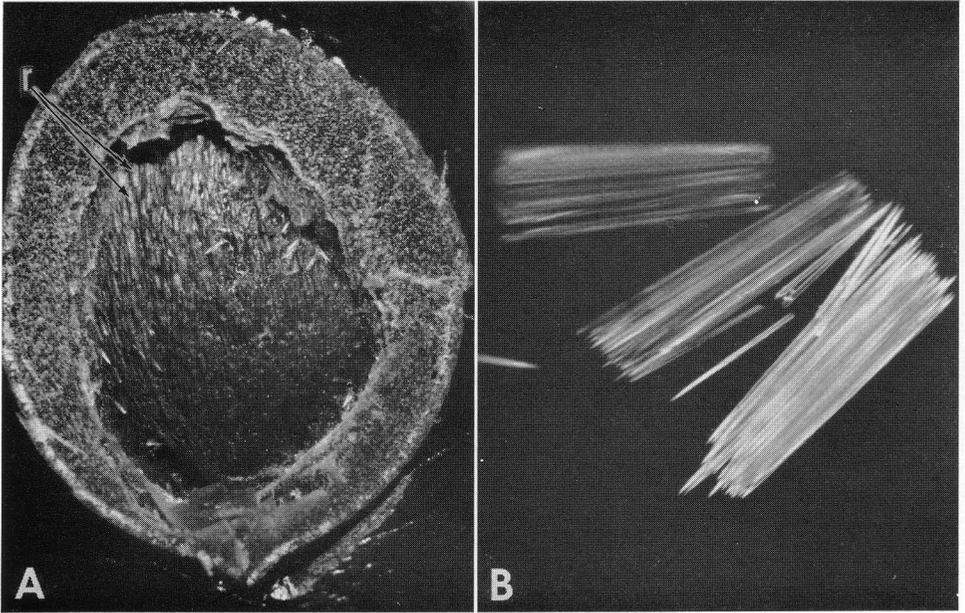
Any floral organ may be specialized for protection. The organs which are so specialized vary in different palms and



18. Floral mechanisms of caryotoid palms. **A**, Staminate flowers of *Arenga undulatifolia* (Moore 6094) have thick, valvate petals (pe) tightly closed in bud. **B**, A transection shows that the petals (pe) are extremely fibrous and that tannin (ta) is present in the connectives of the anthers. **C**, In *Wallichia densiflora* (Moore 9949), pistillate flowers have a tight sheath of petals (pe) around the base of each gynoecium. **D**, A longisection of a pistillate flower of C shows a distal cap of sclereids (sc) in the exposed upper part of the pistil, and raphides (r) forming a sheath around the locule: pe, petal; ov, ovule.

are related to the degree and kind of protection provided for pollen and ovules by other organs or tissues. Protection by floral organs is a function of their shape, size, texture, and/or cellular

and chemical specialization. At the cellular level, strength and support in plants is provided by a special tissue known as sclerenchyma, composed of two cell types with thick cellulose walls



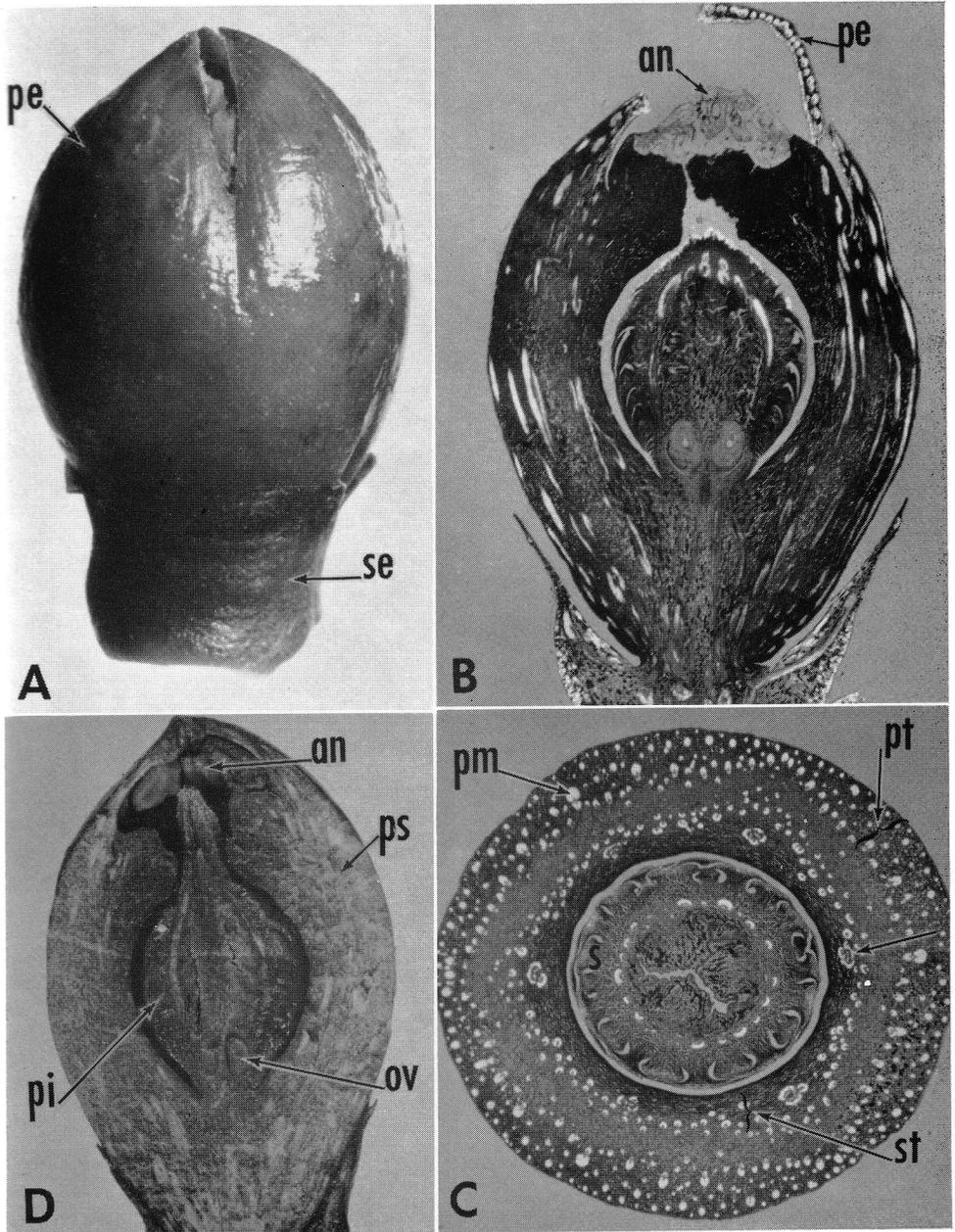
19. Floral mechanisms may also function in fruits. **A**, Removal of the outer layers of the fruit wall in *Arenga engleri* from Fairchild Tropical Garden, Miami, Florida exposes a sheath of raphides (r) on the seed. **B**, A single, rod-shaped bundle of raphides from A, photographed in polarized light, shows many needlelike crystals.

—fibers and sclereids. Fibers are abundant in many palms and commercially important in some. They are long, narrow, thick-walled cells with pointed ends, and groups of them may form sheaths over or around vascular bundles. They may also occur singly or together in various numbers as fibrous bundles. Sclereids also are thick-walled, polyhedral to elongate, sometimes branched cells which may be extremely hard, as in the bony endocarps of cocosoid and other palms. Sclerenchyma has long been recognized as a strengthening tissue in plants and some authors have also pointed out its protective role. Strength in sepals and petals certainly provides protection to organs within, and it seems reasonable to suggest that extremely fibrous tissues do not provide good eating. Many examples, such as the staminate petals of *Phoenix* (Fig. 16B) can be seen where sclerenchyma alternates

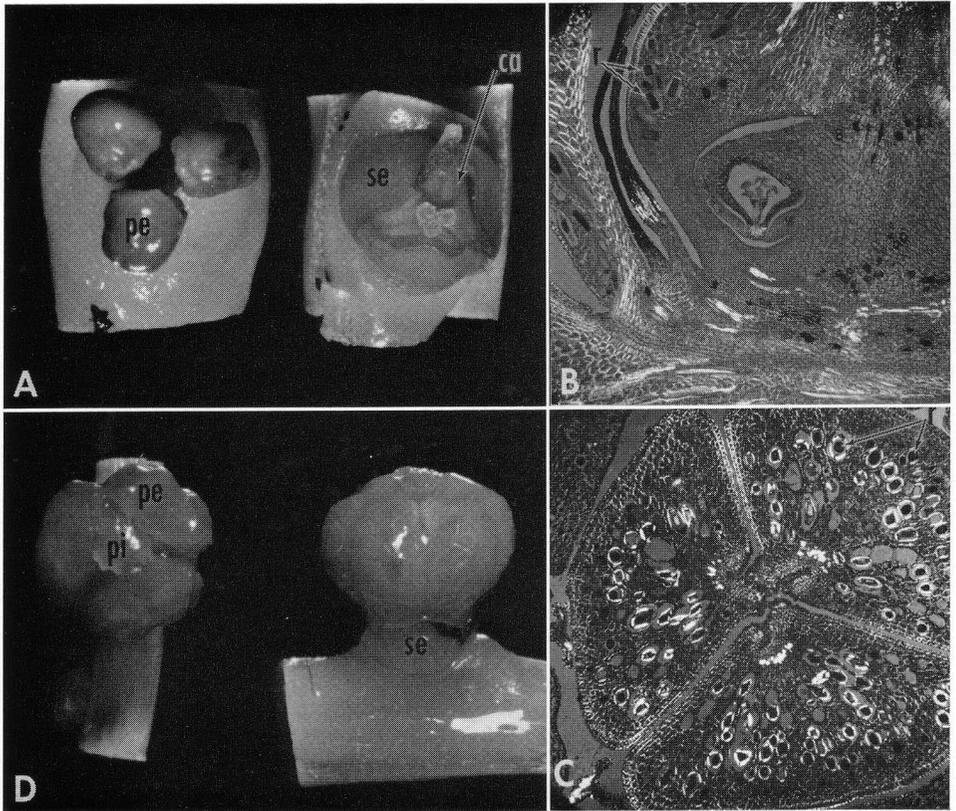
with or reinforces other mechanisms apparently completing a barrier, perhaps against chewing insects.

Chemical Protection

We are just beginning to investigate the complex chemical relationships between plants and other inhabitants of their biospheres. In a recent book on phytochemical phylogeny, McClure (1970, p. 236) has written: "If the secondary compounds are to be understood as they relate to the life of the plant in which they are produced, a bridge needs to be constructed between the patterns of distribution and their possible *in vivo* functions." Two intercellular substances whose distribution indicates that they function in floral protection in palms are crystals of calcium oxalate and tannins. To these should probably be added silica. There seems no question as to the defensive



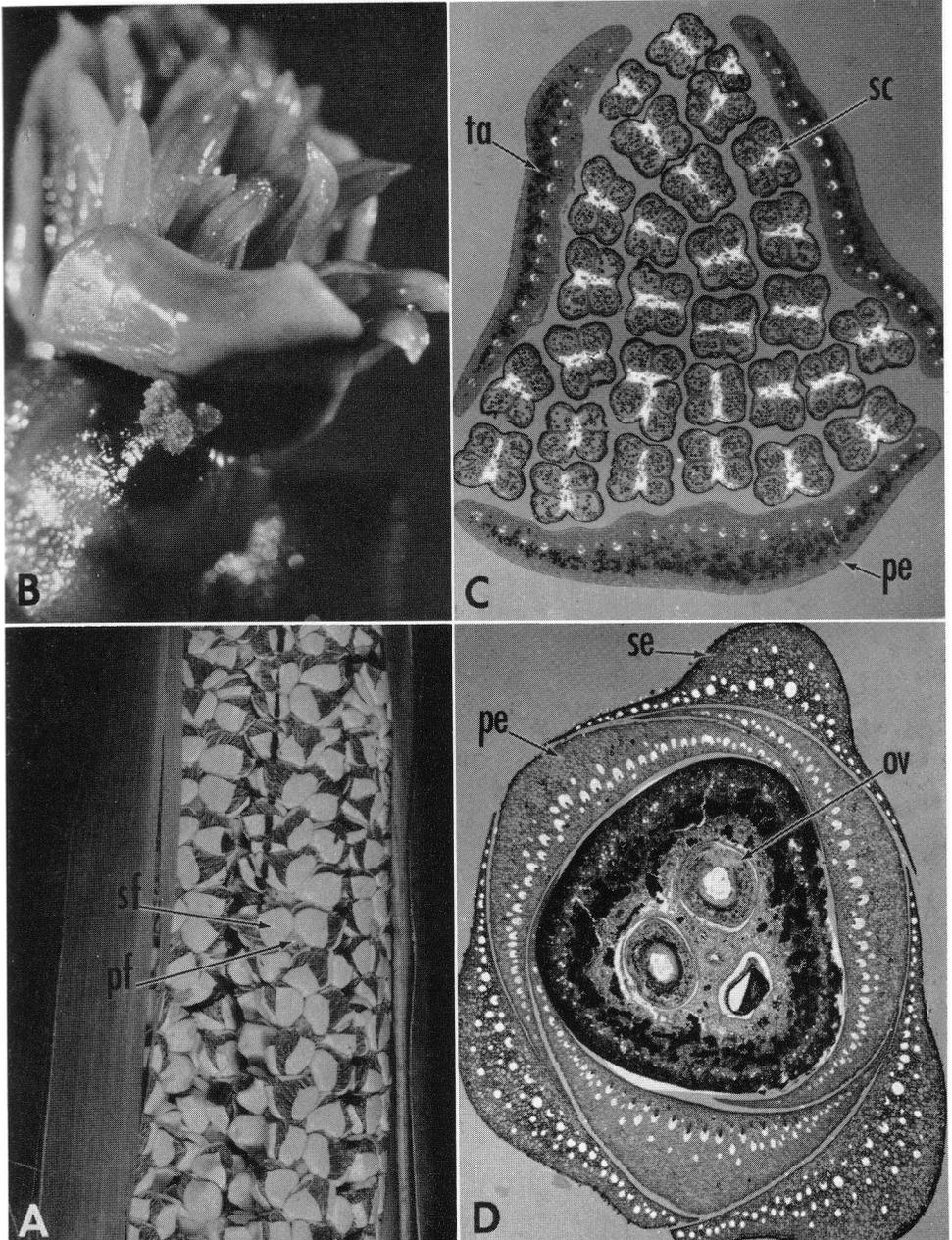
20. Floral mechanisms in *Eremospatha* sp. (Moore & Enti 9893), a lepidocaryoid palm. **A**, Sepals (se) form a low tube around the base of the partly united petals (pe). **B**, In longisection, a thick wall of fused petals and stamens surrounds the gynoecium: anthers (an) are small and situated in a distal cavity; the pistil shows reflexed scales and bright sclerotic cells and fibers distally. **C**, A transection through the center of the flower shows scales on the pistil (pt) and separate vascular systems as bracketed for the stamen tube (st), and for the petal tube (pt); pm, petal midvein; unlabeled arrow indicates one of the six multiple stamen traces. **D**, The pistil (pi) with basal ovule (ov) and the distal anthers (an) are sheathed by the petal-stamen tube (ps).



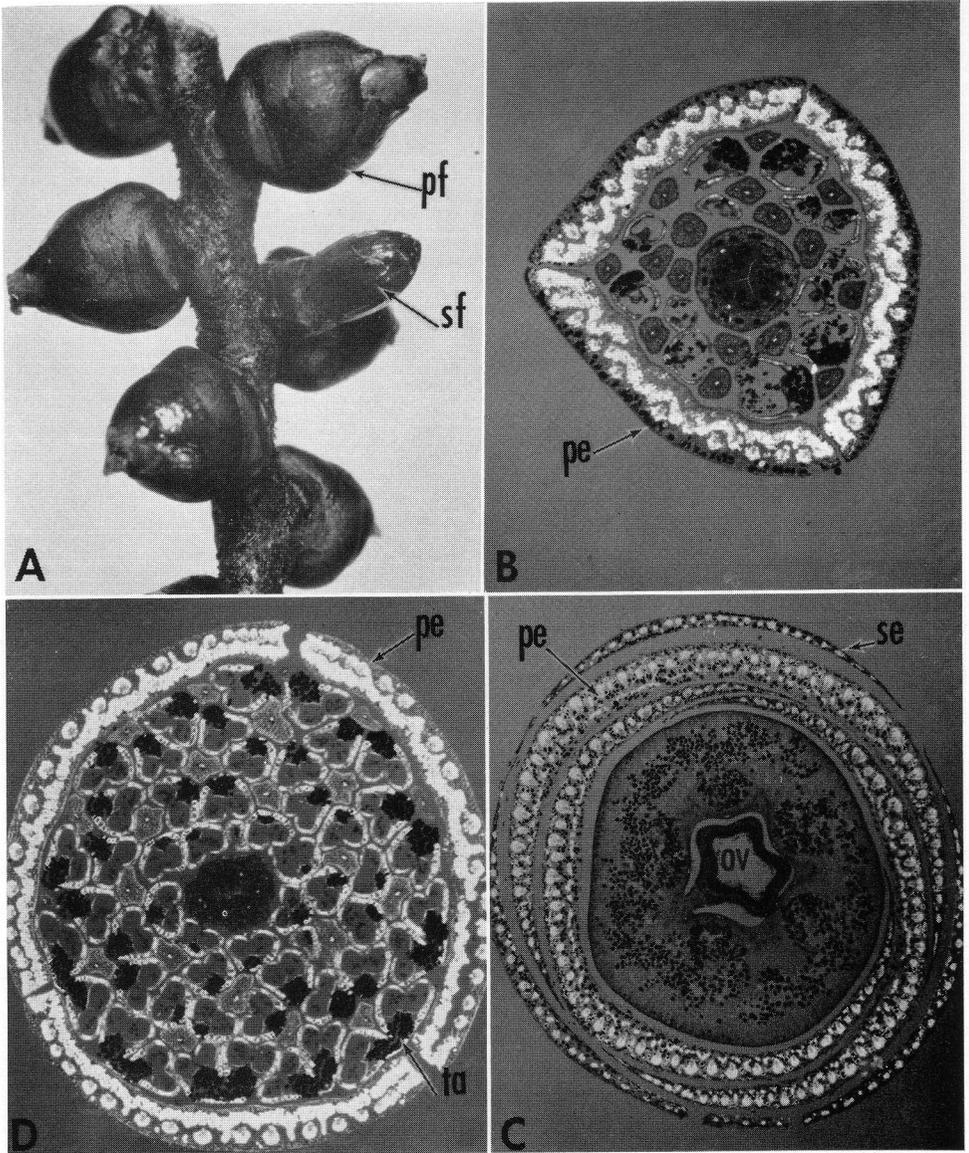
21. Floral mechanisms in *Chamaedorea metallica* (Moore 9373, 9374). **A**, The pistillate flower, left, with hooded petals, and right, with petals removed to reveal the three carpels (ca); se, sepal. **B**, A longitudinal section shows raphides (r) around the locule. **C**, A transection of the styles shows abundant raphides (r). **D**, Staminate flowers are also succulent in appearance, here seen in surface view (left) and side view (right): pe, petal; pi, pistillode; se, sepal.

nature of the needle-shaped raphides of calcium oxalate. The best known example in palms is probably the irritating layer in caryotoid fruits. In *Arenga engleri* Becc., removal of the outer fruit wall (Fig. 19A) reveals a sheath of raphide bundles which covers the seed. Such bundles are also evident surrounding the locules in the flowers of another species at anthesis (Fig. 18D), and, like the scales of lepidocaryoid palms, appear to protect the young ovule as well as the seed. Raphides occur in appropriate locations in sepals, petals, and gynoecea in ceroxylid palms (Uhl, 1969), and surround the locule in the otherwise un-

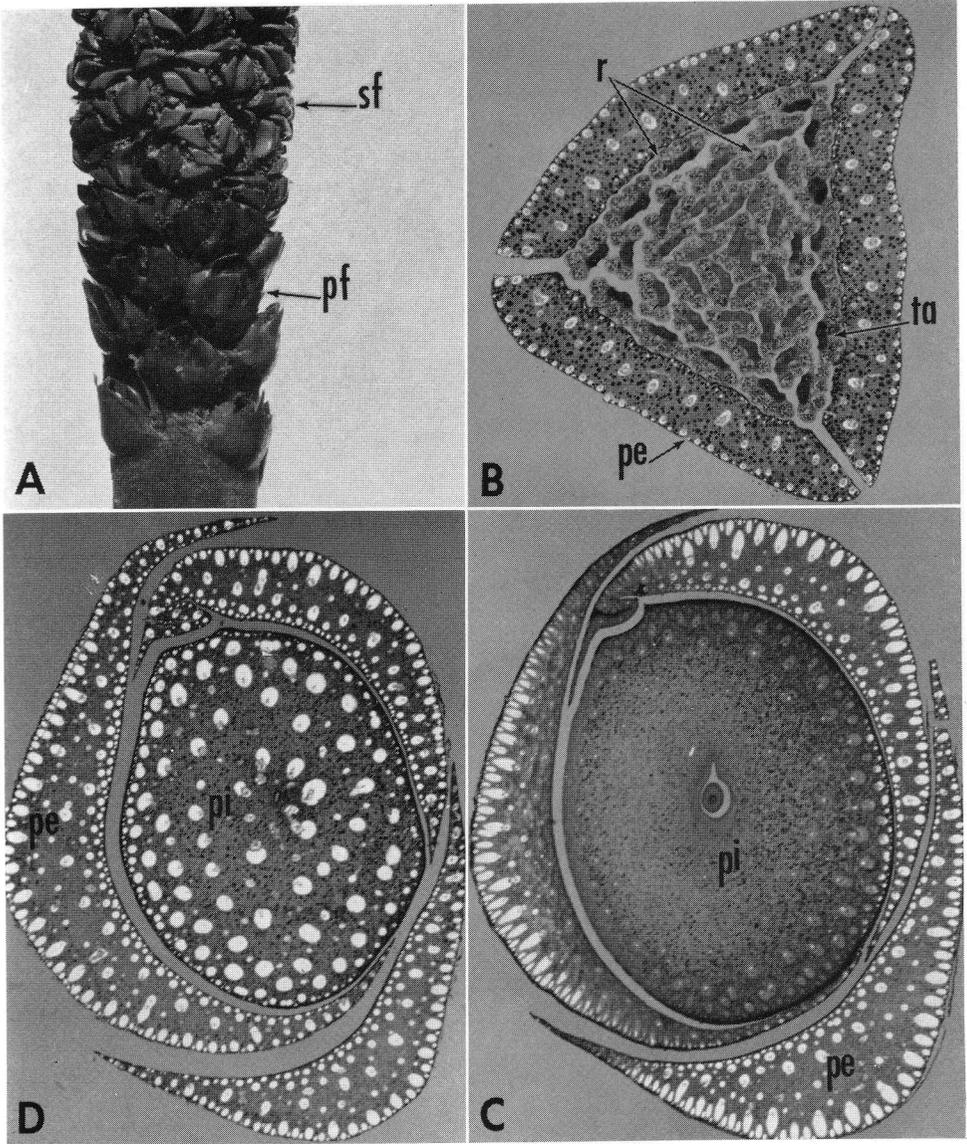
protected flowers in *Zombia*. One of the most striking examples of protection by raphides can be seen in the genus *Chamaedorea* where, in some species, such crystals appear to be the main protective mechanisms. Flowers of *Chamaedorea metallica* H. E. Moore are succulent in appearance (Figs. 21A,D). Sections, however, reveal a large number of raphides in sepals and petals of both staminate and pistillate flowers (Figs. 21B,C). Such crystals are especially numerous around the locules in the pistillate flower (Fig. 21B) and, although not illustrated, are abundant in the lobed pistillode (Fig. 21D) which forms an



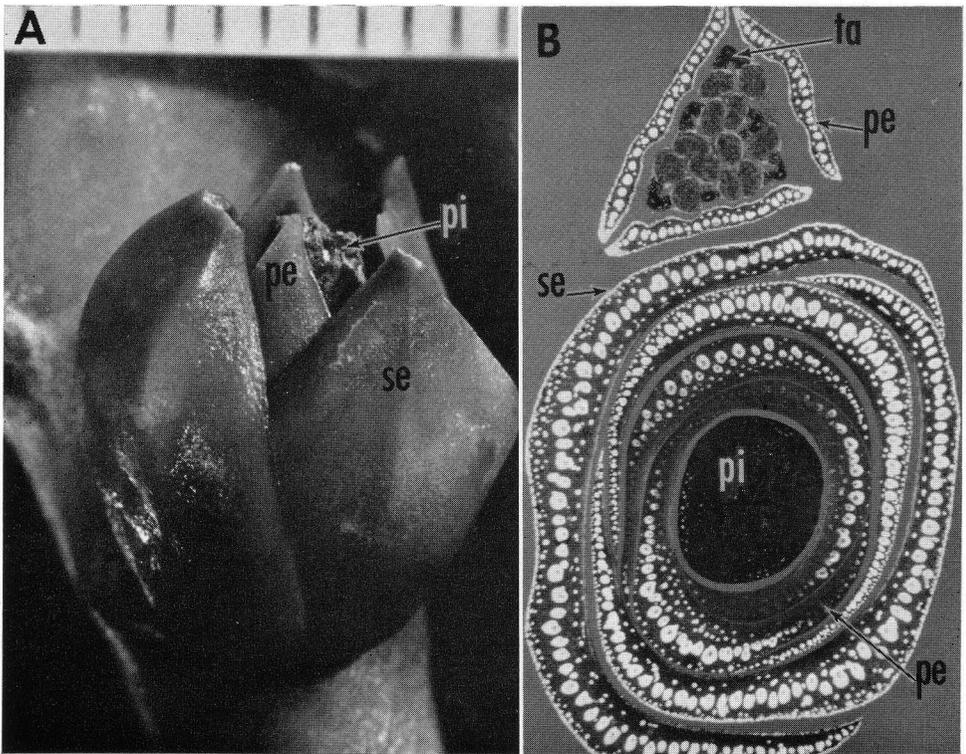
22. Floral mechanisms in *Socratea exorrhiza* (Moore 9950). **A**, An inflorescence with bracts opened to show the flowers which are borne in triads and not closed in bud: pf, pistillate flower; sf, staminate flower. **B**, A pistillate (lower) and a staminate flower, both near anthesis. **C**, Transsection of a staminate flower shows the petals (pe) with only a few fibers in bundle sheaths, but with an abaxial layer of tannin in each petal: ta, tannin; sc, sclerotic parenchyma cells in connectives; note tannin in epidermal layers of anthers. **D**, Transsection of a pistillate flower reveals more fibers in sepals (se) and in the imbricate petals (pe) and both tannins and raphides (large empty cells) in the pistil: ov, ovule.



23. Floral mechanisms in the *Ptychosperma* alliance. **A**, Part of a rachilla of *Ptychosperma caryotoides* (Moore & Womersley 9279) with one remaining staminate (sf) and several pistillate flowers (pf): staminate flowers in this genus are usually shed before the pistillate flowers are receptive. **B**, A transection of the staminate flower shows abaxial tannin in the petals (pe) and a distinctive "scalloped" adaxial band of sclerenchyma: also note tannin in connectives and in the pistillode. **C**, The pistillate flower has tannin interspersed with fibers in sepals (se) and petals (pe) and lightly sclerotic cells (with thin bright walls) between: petals are extremely imbricate; note also large tanniferous cells in the pistil and a ring of tannin around the embryo sac in the ovule (ov). **D**, A transection of a staminate flower of *Veitchia vitiense* var. *parhamiorum* (Moore, Koroiveibau & Parham 9358) has the same pattern of sclerenchyma in the petals (pe): petals, however, lack tannin (ta) which is present in connectives.



24. Floral mechanisms in *Sclerosperma mannii* (Moore & Enti 9883). **A**, Pistillate flowers (pf) are present below the staminate flowers (sf) in the spicate inflorescence. **B**, In transection, fibers and evenly distributed tannin can be seen in the thick, valvate petals of the staminate flowers, and a smooth-appearing tannin (ta) and small dark bundles of raphides (r) are present in the connectives. **C**, In a transection through the ovarian level of the pistillate flower, many fibers can be seen in the thick, imbricate petals (pe): fibers in the pistil (pi) are immature. **D**, At a higher level, the large fibrous bundle sheaths in the pistil (pi) are mature and petals (pe) also have more mature fibers.



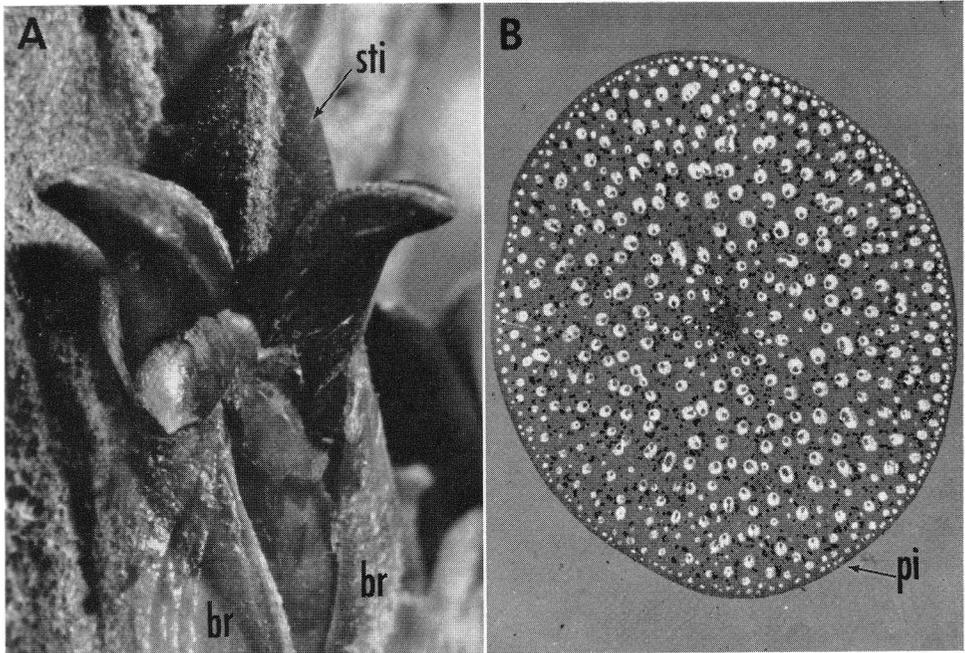
25. Floral mechanisms in cocosoid palms. **A**, Pistillate flower of *Syagrus coronata* (Read 910) with both sepals (se) and petals (pe) thick and imbricate: pi, pistil; scale units equal 1 mm. **B**, In transection, the thin but fibrous, valvate petals (pe) of a staminate flower (upper section) enclose the six anthers with tannin (ta) evident in connectives. The extreme imbrication of both sepals (se) and petals (pe) and the abundant sclerenchyma in both are evident in the pistillate flower (lower section): pi, pistil.

umbrella-like shield over the anthers. Raphides are also present in the anther walls in this species. The possibility of protection of pollen from pollen-eating insects by raphides in anther walls and connectives has been suggested as a factor in plant evolution by van der Pijl (1960). Exactly how protection is provided by raphides is not clear. Puncture by the acicular crystals has been considered mechanical protection and preparation for the entrance of irritating substances (Haberlandt, 1909).

The possible roles of tannins in plants have been discussed by Feeny (1970) who states that there seems little doubt that tannins can defend plants from at-

tack by other organisms. They appear to be broad general protectors against herbivores and pathogens and act in three different ways: as repellents affecting palatability, as growth inhibitors affecting protein availability, and as direct toxic agents.

In palm flowers, intracellular substances which appear to be tannins are present in positions that strongly suggest that tannins have a defensive function. Polyphenols, especially leucoanthocyanins, caffeic acid and flavonols, are reported as widespread in palms and the tannin content in some palms is high enough that they have been tried for tanning leather (Hegnauer, 1963). Chem-



26. Floral mechanisms in cocosoid palms. **A**, The large stigmas (sti) of *Elaeis oleifera* (Read 1366) contain fibers and tannin; the perianth is also fibrous and the lower part of the flower is enclosed in bracts (br) which are split in the figure. **B**, In transection, the style shows many bundles with fibrous sheaths and smaller, entirely fibrous strands around the periphery.

ical analyses of the tanninlike substances in flowers, however, seem not to have been done and are critically needed. Histochemical tests (Jensen, 1962) give positive results for catechol tannin in fresh material of inflorescences and flowers in *Geonoma acaulis* Mart. and *Reinhardtia simplex* (H. Wendl.) Burret (Uhl, unpublished), and tannin in these tests corresponds in position with that identified in our prepared slides.

For purposes of this paper, we are using "tannin" in a loose sense to refer to intracellular substances, usually granular to globular but occasionally smooth in appearance under the light microscope, which stain bright to dark red (dark bluish-red in some) with safranin (see Uhl, 1972, for references to general techniques followed). Both the chemis-

try and the functions of these substances appear complex. Previous reports (Hegnauer, 1963) and our observations on differences in appearance and staining indicate that tannins in palms are chemically variable. The presence or abundance of tannin may vary during flower or fruit development. In view of the complexity of allelochemical reactions, some of the tanninlike substances in palms may serve as attractants or have other functions. As with other aspects, the biology of these substances must be worked out for individual species. However, as we will show, tannins often appear to complement or substitute for other protective mechanisms. The complete absence of tannins in petals of *Bactris* which are chewed by beetles (Essig, 1971) suggests that the tannins do indeed repel certain insects.

Table 1. Summary of protection by major groups*

Group	Degree	Mechanisms
I Coryphoid	Light	Spines; numerous, relatively thin bracts; some fibers in bundle sheaths but not numerous in perianth; tannin sheaths on carpels; some raphides
II Phoenicoid	Moderate	Large spines at leaf base; single bract on inflorescences; tannin, fibrous sheaths, raphides in perianth; tannin sheaths, distal sclereids in carpels
III Borassoid	Heavy	Several fibrous inflorescence bracts; <i>pits formed from thick fibrous bracts enclosing flowers and/or perianth thick and fibrous</i> ; gynoeceium large with distal sheath of sclereids; trichomes (<i>Hyphaene</i>)
IV Lepidocaryoid	Heavy, diverse	<i>Spines</i> ; bracts and perianth fibrous; <i>filaments and staminodes often thick and fibrous</i> ; <i>gynoecea with distinctive scales</i> ; tannins throughout
V Nypoid	Moderate	Numerous bracts; tannin sheaths abaxially in perianth parts of both sexes; <i>distal parts of carpels large, hard, and closely appressed</i>
VI Caryotoid	Moderate to heavy	Several fibrous bracts; perianth parts thick and extremely fibrous in both sexes; fleshy gynoecea with peripheral sclereid sheaths and <i>raphides around locules</i>
VII Pseudophoenicoid	Light	Two tough bracts; <i>raphides</i> and some tannin in floral organs
VIII Ceroxyloid	Light	Numerous bracts; <i>raphides</i> and some tannin in floral organs
IX Chamaedoreoid	Light	Several thin bracts; <i>raphides</i> especially abundant in all floral organs, small amounts of tannin in some

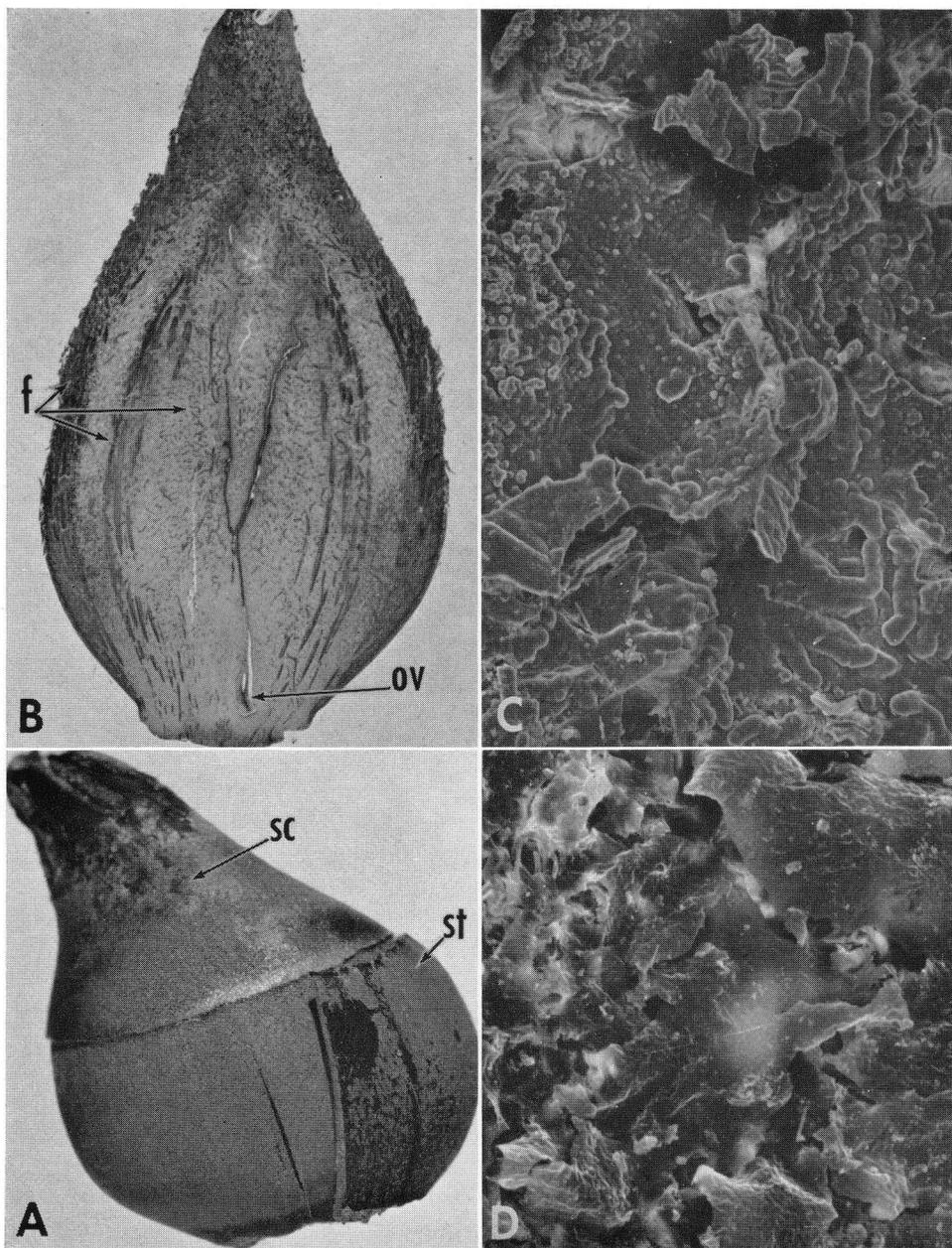
* Mechanisms which predominate in some groups are italicized.

Table 1 Continued

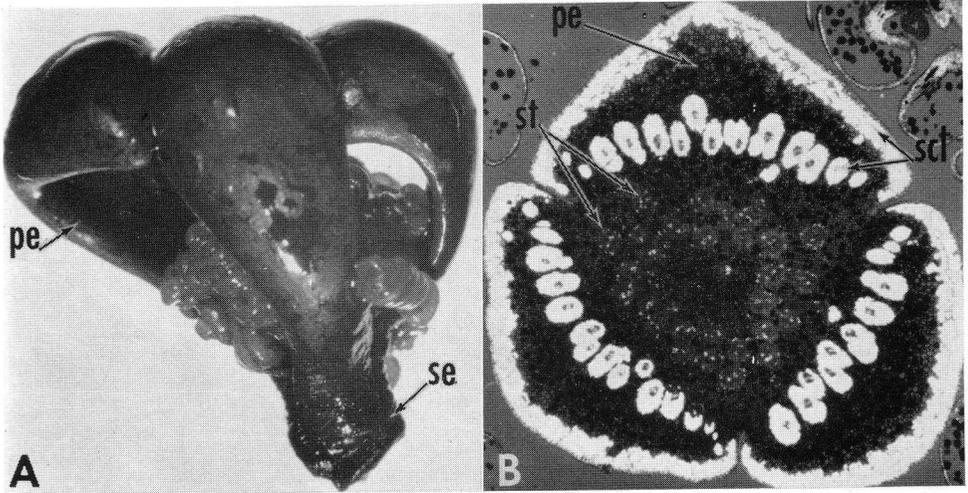
Group	Degree	Mechanisms
X Iriarteoid	Moderate to heavy, diverse	Spines on roots; bracts numerous, sometimes thick; large amounts of tannin and fibers in floral organs; gynoecea with large amounts of tannin, raphides, and a distal sheath of bundles of fiber-sclereids; trichomes (<i>Wettinia</i>)
XI Podococcoid	Light	Pits; trichomes on rachillae; perianth lightly fibrous, a few raphides
XII Arecoid	Moderate to heavy, diverse	Mechanisms varied; spines in one alliance, bracts 1 or 2, not markedly thick; <i>perianth parts extremely fibrous in some; tannins raphides and sclereids in others and in gynoecea</i>
XIII Cocosoid	Heavy, diverse	<i>Spines; hard, woody or fibrous bracts; thick, heavily fibrous perianth; staminodia sometimes thick and fibrous; abundant tannin and raphides in some gynoecea, different systems of fibers in others</i>
XIV Geonomoid	Moderate	One or mostly two fibrous bracts; <i>flowers in pits</i> and floral organs only lightly fibrous, tannin and raphides in some
XV Phytelephantoid	Light to moderate	Staminate flowers lightly protected by single inflorescence bract; pistillate flowers scarcely exerted from leaf sheaths at anthesis; sepals and petals numerous and tanniferous; gynoecea with specialized fiber-sclereid layer

Silica has been designated as a barrier to feeding on plants (Southwood, 1973). Its distribution in palm flowers is so widespread that we routinely treat all floral material with hydrofluoric acid

before attempting to section. Silica is often abundant in flowers that appear soft, as in the staminate flowers of *Welfia*, which contain large amounts of silica but few fibers. Some data on the



27. Floral mechanisms in cocosoid palms. **A**, The multicarpellate gynoecium of *Orbignya speciosa* (Read 912) is enclosed by a staminodial cup (st) which is extensively vascularized and fibrous. **B**, In longitudinal section, several systems of fibers (f) occur in the large styler region of the gynoecium: ovules (ov) are extremely small. **C**, **D**, Two views of the scales (sc) on the upper surface of the gynoecium in A, with the scanning electron microscope, \times ca. 110.



28. Floral mechanisms in cocosoid palms. **A**, Petals of the staminate flower of *Orbignya cuatrecasana* (Moore, Parthasarathy & Orjuela 9450) are thick: pe, petal; se, sepal. **B**, A transection through the lower part of the flower shows the petal bases (pe) which have a wide outer layer of fibers, large fibrous bundle sheaths, and large tannin cells in the ground tissue: scl, sclerenchyma of bundle sheaths and peripheral layer; st, stamen traces.

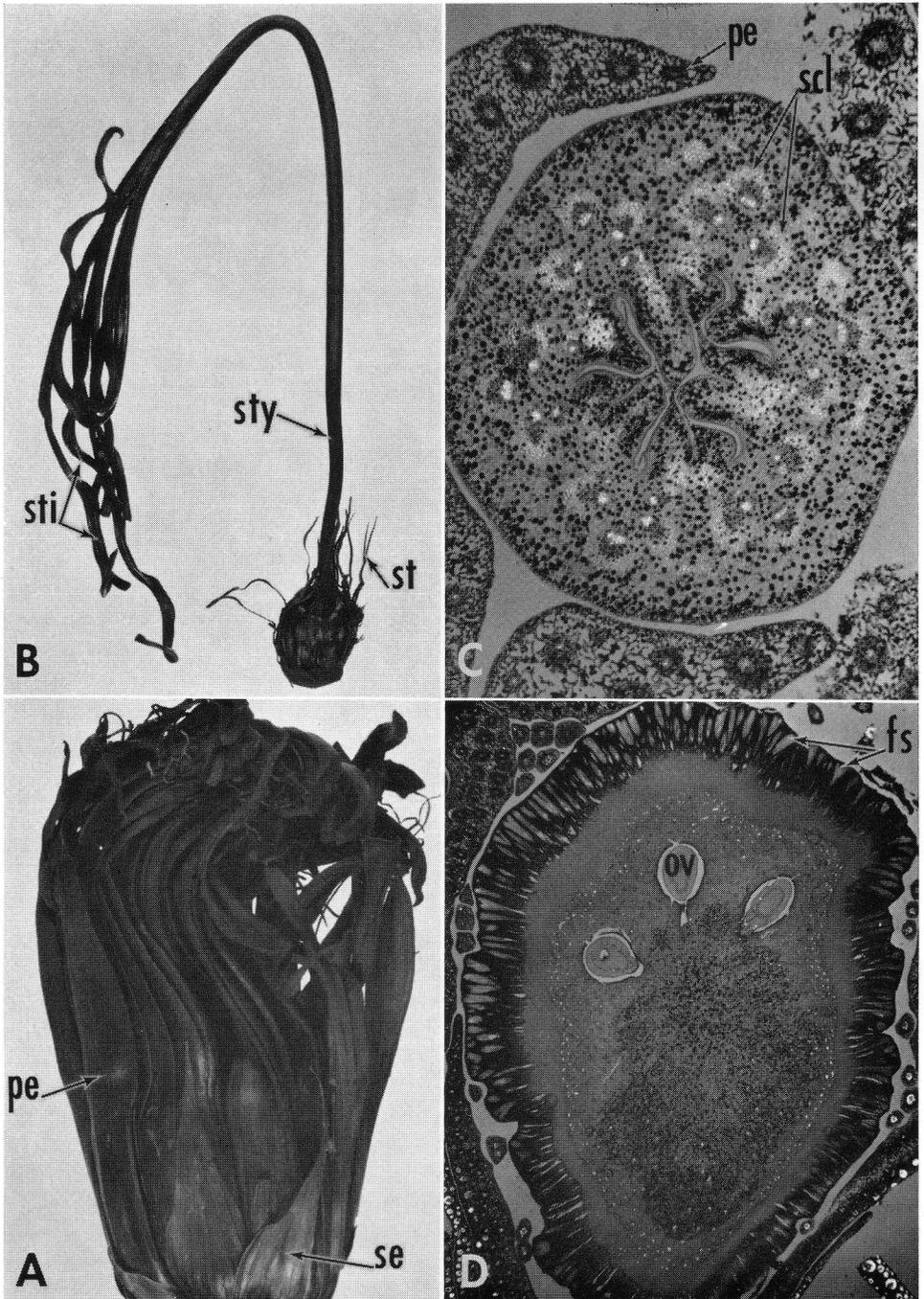
occurrence of silica has been given in studies of fruit development by Murray (1971).

Distribution of Protective Mechanisms

We have assembled a number of figures to illustrate how protective mechanisms are distributed in palm flowers. As previously stated, inflorescences in *Phoenix* are surrounded by unique spines and only a single bract encloses the floral axes (Fig. 2B). Protective devices are also present in the floral organs of both sexes. The connate sepals form a low basal sheath in staminate flowers. Petals are slightly imbricate and moderately thick and fibrous (Figs. 16A,B), with abaxial groups of tanniferous cells more or less blocking the spaces between fibrous bundle caps and raphides present adaxially. Tanninlike material also occurs in the anthers (Fig. 16B). Staminate flowers thus appear to be well fortified against chewing insects. In pistillate flowers (Fig. 16C), the sepal sheath is relatively

higher and the petals are thicker and more imbricate with large fibrous bundle sheaths. A layer of tanniferous cells is present peripherally around the locular part of each carpel (Fig. 16D). The immature ovule-containing lower parts of the carpels are thus sheathed in triplicate: by a sepal tube, by thick, fibrous, imbricate petals, and by a carpellary tanniferous sheath. In addition, the upper parts of the carpels contain sclereids (not illustrated), which provide a hard region that appears to block the opening between the tips of petals through which the stigmas protrude (Fig. 16C).

Phoenix could serve as a model of pollen and ovule protection in many palms. The ovule-bearing region of the palm gynoeceum is enclosed, often by several fibrous or otherwise defensive layers, and the distal opening of the petals, needed to expose a receptive stigmatic surface, is "plugged" by a hard or otherwise defensive upper (stylar) part of the carpel or pistil. In



29. Floral mechanisms in phytelephantoid palms. **A**, Numerous long petals (pe) cover the gynoecium in the pistillate flower of *Phytelephas macrocarpa* (Moore 9951): se, sepal. **B**, With the perianth removed, the multicarpellate gynoecium has a long compound style (sty) and

staminate flowers, sepals are relatively small compared to the petals just before anthesis. Petals usually are valvate, perhaps an adaptation that permits rapid and complete opening, but are often thick and extremely fibrous and may contain tannins and raphides. Protection of anthers seems also provided by tanniniferous material and raphides in connectives.

In borassoid palms, genera of the *Borassus* alliance have thick, leathery, imbricate sepals and petals in pistillate flowers as shown for *Latania* (Fig. 17A). Several genera of borassoid palms have flowers enclosed in pits. Perianth parts of the flowers borne in pits are thin and have relatively few fibers. The exposed surface of the gynoeceum is hard and smooth with a peripheral layer of sclereids just beneath the surface. The ovule is also shielded by the thick wall of the fleshy gynoeceum (Fig. 17B).

Staminate flowers of *Arenga undulatifolia* Becc., a caryotoid palm, have thick, valvate petals (Figs. 18A,B) which are tightly closed in bud. The numerous fibers in the complete bundle sheaths and in small fibrous bundles can be seen in transections of the petals (Fig. 18B). Tannin in the connectives of the anthers may also be protective. Pistillate flowers in *Wallichia densiflora* (Mart.) Mart. (Figs. 18C,D), also of the caryotoid group, show a tight sheath of basally united, fibrous petals open distally to expose the upper surface of the globular pistil in each flower. The protection of the exposed surface of the pistil is by a distal group of sclereids and by elongate bundles of raphides around the locule, evident in the longi-

tudinal section (Fig. 18D). This section, only 15 microns thick, shows a surprisingly large number of raphides which form a complete layer around the locule and later around the seed as in *Arenga* (Fig. 19A). The irritating nature of these crystals, shown enlarged in Figure 19B, is well known.

A unique kind of ovule protection is exhibited by *Nypa fruticans* where the separate carpels of many flowers are closely appressed, forming a hard head (Fig. 6D). The surface of the head bars access to the ovules far below in the soft base of each carpel. The three carpels of each pistillate flower elongate rapidly, surpassing and obscuring the perianth parts by the time the carpels are receptive (Uhl, 1972). The pistils of many palms much surpass perianth members as the fruit develops, but *Nypa* is unusual in the early timing of carpel enlargement. Abaxial tanniniferous sheaths also occur in perianth members of both staminate and pistillate flowers.

The distinctive scales which cover the pistils (Figs. 14A; 20B) are only one of several protective mechanisms exhibited by flowers of lepidocaryoid palms. In an African genus, *Eremospatha*, a tube of connate, fibrous sepals surrounds the base of the fleshy petals (Fig. 20A) in the perfect flower. The thick wall enclosing the pistil (Figs. 20B,D) is made up of three connate petals united with a tube formed by the filaments of the six stamens. A transection of the upper part of the flower (Fig. 20C) reveals the midveins of other bundles of each petal, a bundle-free intermediate area, and an extensively vascularized stamen tube. Note that each stamen has a cen-

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separate stigmas (sti); staminodes (st) surround the ovarian region. C, Large tannin bodies are present in a section of the style and in petals (pe); sclerenchyma cells (scl) around bundles are thin-walled. D, The ovarian part of the gynoeceum is encased by a thick sheath of horizontally oriented bundles of fiber-sclereids (fs) in a tanniniferous outer layer.

tral, "multiple" bundle, and that other bundles in the androecium are reversed in orientation with respect to petal traces. Scales and bundles at the top of the pistil are mature and somewhat birefringent, forming a hard cap over the delicate ovarian part of the pistil. The anthers are borne in a cavity about the styles (Fig. 20D) and are protected in bud by the fibrous distal parts of the petals (Fig. 20B). Tanniniferous cells are widely distributed in the flower and are especially abundant in the upper parts of the filaments. A heavily vascularized androecium, which may be adnate to the petals and which appears to provide an extra protective layer for the ovary, is characteristic of many lepidocaryoid genera. Other protection is achieved by extreme fibrousness of sepals and petals, and by scales and tannins.

A possible relationship between the opening of bracts and flower structure can be observed in *Socratea exorrhiza* (Mart.) H. Wendl. (Fig. 22). The flower-bearing axes are enclosed in about seven tubular bracts (Figs. 6A,B). Inside the bracts, the flowers are open (Fig. 22A) and immature but fully developed. Petals of staminate flowers have opened slightly in Figure 22B, where both flowers are near anthesis. Staminate petals have very little sclerenchyma, but the abaxial tanniniferous area may discourage chewing insects (Fig. 22C). The bright areas between the anthers are sclerotic parenchyma cells which appear to provide protection and support for the long anthers. There is no tannin in the connectives of this species but the epidermal layers of each anther are tanniniferous. The pistil is sheathed by thicker perianth parts with imbricate petals, and more fibers are present in both sepals and petals in pistillate flowers. Abundant tannins and raphides and distal bundles of fiber-

scleireids (not shown) in the gynoecium also protect the ovules.

In contrast to the staminate petals in *Socratea*, petals of staminate flowers in *Ptychosperma* and the related genus *Veitchia* (Figs. 23B,D) have many fibers and distinctive tanniniferous cells between connectives. Staminate flowers of *Ptychosperma* are known to be in early bud with floral organs only partially developed when bracts open (Essig, 1973). The developing floral organs are protected in turn by each heavily fibrous sepal and petal. Patterns of sclerenchyma are similar in the related genus *Veitchia*, but petals in *Ptychosperma* (Fig. 23B) have tannin peripherally which is absent from those of *Veitchia* (Fig. 23D). Pistillate flowers of *Ptychosperma* (Figs. 23A,C) have thin but fibrous sepals, and thicker, imbricate petals with the fibers in bundle sheaths interspersed with sclerotic parenchyma and large tanniniferous cells. Note the large concentrations of tannin in the walls of the pistil and surrounding the embryo sac in the lobed ovule. It is tempting to guess that the lack of fibers in petals of staminate flowers in *Socratea* (Fig. 22C) reflects the complete development of the flowers before the several bracts open to expose them and that the many fibers in staminate petals of *Ptychosperma* and *Veitchia* protect the developing anthers when the bracts open before the flowers are fully developed.

Fibers and tannins occur in many different patterns in palm flowers. A different combination than that in *Ptychosperma* can be seen in the unusual African genus *Sclerosperma* (Fig. 24). The inflorescence is a single spicate axis with a few pistillate flowers at the base and staminate flowers above (Fig. 24A). This axis remains enclosed in two fibrous bracts until fruits are nearly mature. Pollination may be effected by

insects which crawl into the bracts but no observations have been made. Both staminate and pistillate flowers have extremely fibrous sepals and petals. Petals of staminate flowers (Fig. 24B) show large, rather evenly scattered tanniferous cells, and tannin and large raphides are present in the connectives. Petals of pistillate flowers (Figs. 24C,D) are thick and imbricate. Bundles in the lower part of the gynoeceium are immature at anthesis (Fig. 24C), but more distally the bundles have large mature fibrous caps (Fig. 24D). Tannin is also scattered in the upper part of the gynoeceium.

Sclerenchyma, in many patterns, characterizes flowers of cocosoid palms. In the pistillate flowers of *Syagrus* (Figs. 25A,B), both sepals and petals are imbricate and have many fibers. The valvate petals of the staminate flower (Fig. 25B, upper) are also fibrous and the connectives of the stamens are tanniferous. The fleshy stigmas of the oil palm, *Elaeis*, contain both tannins and fibers, and the upper gynoeceium (Fig. 26B) shows numerous bundles with fibrous sheaths and small, completely fibrous strands around the periphery. The gynoeceium of *Orbignya speciosa* is encased by a heavily fibrous staminodial cup (Fig. 27A). The pistil contains several systems of fibrous bundles which provide an extremely tough block above the relatively small ovules (Fig. 27B). Staminate flowers of *Orbignya cuatrecasana* Dug. have hard thick petals (Fig. 28B) that show thick peripheral layers of fibers, large tannin cells in ground tissue, and large fibrous caps on the row of closely aligned bundles. Conceivably, the hard petals of many closely appressed flowers shield the anthers which previously have been protected within a woody, plicate bract, for the petals of individual flowers are not closed (Fig. 28A).

Pistillate flowers of phytelephantoid palms exhibit a different combination of protective structures. Pistillate inflorescences are largely enclosed in leaf sheaths at anthesis and the many long petals of the flowers shield the ovaries. There are some sclerotic parenchyma cells in the long style (Fig. 29B), but large tanniferous cells appear to provide protection in styles and petals. The gynoeceium also has a peripheral layer containing horizontally aligned bundles of fiber-sclereids and abundant tannin (Fig. 29D).

Discussion

Protection of pollen and ovules in palms has involved selection for and coordination of characters at different structural levels. Protection at the morphological level is by different forms of leaf bases, bracts, emergences such as trichomes and spines, floral organs, and by other mechanisms—pits and other spines—which are formed from modified organs or combinations of organs. Fibers and sclereids in appropriate locations provide cellular protection and intracellular substances, identified as tannins, raphides, and silica, provide chemical defenses. Selection at each level appears to have operated to coordinate these protective aspects within each kind of palm, and an intricate correlation of structure with phenology is also evident.

Some groups of palms are characterized to a degree by the presence of certain of these protective mechanisms (Table 1). One or two mechanisms are strikingly exploited by some groups, e.g., the fibrous carpels of *Nypa*, the raphides, or raphides and tannins in pseudophoenicoid, ceroxyloid, and chamaedoreoid palms, and the elaborate pits of geomomoid palms. Several complementary mechanisms may predominate in other groups. For example, in coco-

soid palms thick bracts may be associated with a heavily fibrous perianth and frequently with the presence of tannin, raphides, or fibers in the gynoecea of larger pistillate flowers. Large flowers tend to have more protective mechanisms.

Size of flowers may, in fact, be one of the factors that has evoked the evolution of protective mechanisms. Other factors may be the often slow development and long exposure of buds on inflorescences such as those of *Ptychosperma*, in which months are required before flowers reach anthesis (Essig, 1973), as well as the need for continuing protection of the ovule during development of fruit and seed. A major factor appears to have been the tremendous number of insects to which palms are hosts—752 insects have been identified on the coconut (*Cocos nucifera* L.), 336 on the oil palm (*Elaeis guineensis* Jacq.), and 136 associated with the date palm (*Phoenix dactylifera* L.) according to Lepesme (1947). About one-third of these insects are beetles which, as an order, are known to feed on pollen and to chew ovules and other floral parts. This insect association may be due in part to the nutrient content of the sap of many palms which appears to be high, witness man's tapping of inflorescences in *Arenga*, *Borassus*, *Caryota*, and *Cocos* for sap from which sugar and alcohol are prepared.

Southwood (1973) has stated that plants and insects are two coevolving, competing, often mutually dependent, biochemical systems. It seems reasonable to infer coevolution with insects as a major factor in the evolution of the many protective mechanisms of palm flowers, just as mammals and birds appear to have figured in the evolution of palm fruits. The work of Essig (1971) on the elegant system of pollination in *Bactris*, for example, now enables us to

understand the lack of protection in the staminate flowers, which serve as food for beetles, and the development of fibers in the pistillate gynoeceum, which must resist feeding. Further extensive and intensive studies of phenology, floral biology, and general animal-palm interrelationships are required before our increasing knowledge of the morphology and anatomy of palms can be interpreted biologically.

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LITERATURE CITED

- BECCARI, O. 1884–1886. Piante ospitatrici. Malesia 2: 5–284.
- DRANSFIELD, J. 1973. *Korthalsia hispida* Becc. in Malaya. Gardens' Bulletin, Singapore 26: 239–244.
- EAMES, A. J. 1961. Morphology of the Angiosperms. McGraw-Hill, N. Y.
- ESSIG, F. B. 1971. Observations on pollination in *Bactris*. Principes 15: 20–24.
- . 1973. Pollination in some New Guinea palms. Principes 17: 75–83.
- FEENY, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51: 565–581.

- HABERLANDT, G. 1909. *Physiological Plant Anatomy*. Translated from the 4th German edition by Montague Drummond. Macmillan Co., London [1914].
- HEGNAUER, R. 1963. *Chemotaxonomie der Pflanzen*, Band 2, Monocotyledonae. Birkhäuser Verlag, Basel & Stuttgart.
- JANZEN, D. H. 1971. The fate of *Scheelea rostrata* fruits beneath the parent tree: predispersal attack by bruchids. *Principes* 15: 89-101.
- JENSEN, W. A. 1962. *Botanical Histochemistry*. W. H. Freeman & Co., San Francisco.
- LEPESME, P. 1947. *Les Insectes des Palmiers*. Paul Lechevalier Éditeur, Paris.
- LEVIN, D. A. 1973. The role of trichomes in plant defense. *Quarterly Review of Biology* 48: 3-15.
- MCCLURE, J. W. 1970. Secondary constituents of aquatic angiosperms. In J. B. Harborne (Ed.). *Phytochemical Phylogeny*, pp. 233-268. Academic Press, London.
- MOORE, H. E., JR. 1973. The major groups of palms and their distribution. *Gentes Herbarum* 11: 27-141.
- MURRAY, S. G. 1971. The developmental anatomy of certain palm fruits. Ph.D. Thesis. Cornell University, Ithaca, N. Y.
- PIJL, L. VAN DER. 1960. Ecological aspects of flower evolution. I. Phyletic evolution. *Evolution* 14: 403-416.
- SCHMID, R. 1970a. Notes on the reproductive biology of *Asterogyne martiana* (Palmae). I Inflorescence and floral morphology; phenology. *Principes* 14: 3-9.
- . 1970b. *Ibid.* II Pollination by syrphid flies. *op. cit.* 14: 39-49.
- SOUTHWOOD, T. R. E. 1973. The insect/plant relationship—an evolutionary perspective. In H. F. van Emden (Ed.). *Insect/Plant Relationships*. Symposia of the Royal Entomological Society of London 6: 3-30.
- TOMLINSON, P. B. 1962a. Essays on the morphology of palms VII. A digression about spines. *Principes* 6: 44-52.
- . 1962b. The leaf base in palms, its morphology and mechanical biology. *Journal of the Arnold Arboretum* 43: 23-50.
- . 1971. Flowering in *Metroxylon* (the sago palm). *Principes* 15: 49-62.
- TOMLINSON, P. B. AND H. E. MOORE, JR. 1968. Inflorescence in *Nannorrhops ritchiana* (Palmae). *Journal of the Arnold Arboretum* 49: 16-34.
- UHL, N. W. 1969. Floral anatomy of *Juania, Ravenea*, and *Ceroxylon* (Palmae-Arecoidae). *Gentes Herbarum* 10: 394-411.
- . 1972. Inflorescence and flower structure in *Nypa fruticans* (Palmae). *American Journal of Botany* 59: 729-743.

PALM LITERATURE

- DRANSFIELD, J. 1973. *Korthalsia hispida* Becc. in Malaya. *Gardens' Bulletin*, Singapore 26: 239-244.
- GLASSMAN, S. F. 1972. A Revision of B. E. Dahlgren's Index of American Palms. *Phanerogamarum Monographiae Tomus VI*, 294 pp., Verlag von J. Cramer, 3301 Lehre.
- MOORE, H. E., JR. 1973. The major groups of palms and their distribution. *Gentes Herbarum* 11:27-141; repaged and published as a reprint by the L. H. Bailey Hortorium, 467 Mann Library, Ithaca, N. Y. 14850, \$4.50.
- WILLIAMS, C. A., J. B. HARBORNE, AND H. T. CLIFFORD. 1973. Negatively charged flavones and tricin as chemosystematic markers in the Palmae. *Phytochemistry* 12: 2417-2430.

NOTES ON CULTURE

Member Barry R. McElmurry writes:

"On Page 64, Vol. 17 no. 2 of PRINCIPES, I read of the high mortality encountered in transplanting seedlings. I recently had 100% success on 14 seedlings of *Chrysalidocarpus lutescens* and *Archontophoenix Alexandrae* using the following method: I immerse the entire plant mass, dirt, plants and all in water so that all is covered. Separate plants gently, under water. Prepare pots and plant palms one at a time, gently, with loose sandy mix, and water immediately and heavily. The seedlings were 2-3" tall with one or two leaves each. Hope this helps someone. At least it's something to try.