

Septal Nectaries of *Asterogyne martiana* and Other Palmae

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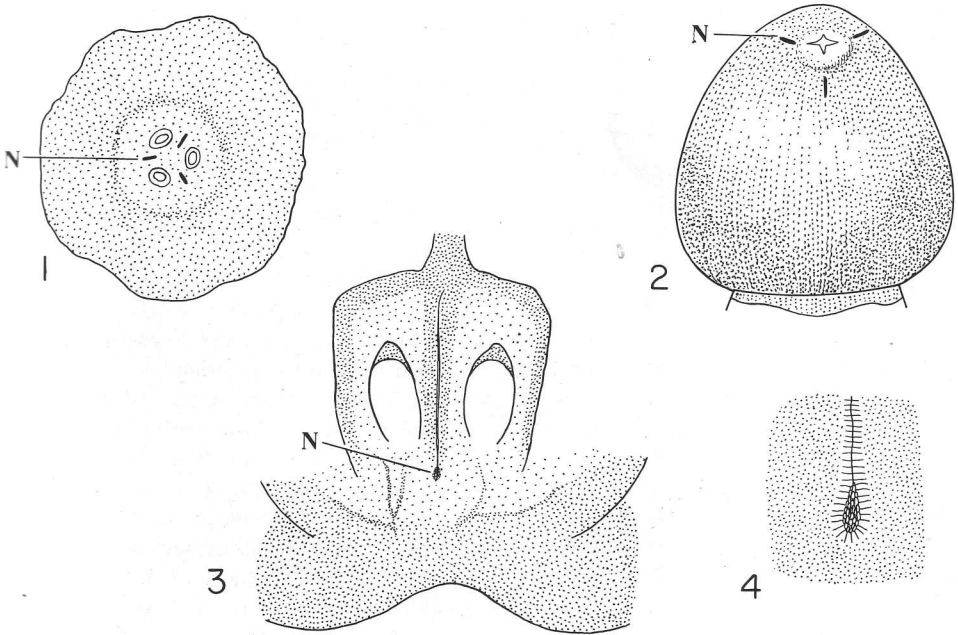
In angiosperms nectaries occur in or on a diversity of reproductive structures, including inflorescence axes, peduncles and pedicels, bracts and bracteoles, fruits, and, most commonly, flowers, where they occur variously on the receptacle, floral tube, perianth, androecium (both filament and anther, and also staminodia), and gynoecium (ovary, style, and even stigma) (Daumann 1970, Fahn 1979, Schmid 1982). Gynoecial nectaries, the most common type of floral nectary, comprise (1) superficially located nectaries of various types, and (2) generally internally located septal nectaries that occur in the septal radii of ovaries (Fig. 1) and that represent intercarpellary cavities resulting from the lack of fusion of the adjacent walls of carpels. Septal nectaries are absent from dicotyledons but are the most common nectarial type in monocotyledons (Daumann 1970, 1974; Schmid 1982).

Although septal nectaries of monocotyledons have received considerable morphological and anatomical attention (for reviews see Daumann 1970, Fahn 1979, and Schmid 1982), for some reason the structure and function of septal nectaries of palms have been particularly enigmatic. For example, Drude (1877: 623, 1887: Fig. 29) clearly described and figured inner septal nectaries in *Borassus flabelliformis* but was totally mystified as to their nature and function. Later Bauch (1911) in a "physiological anatomical" study of palm flowers described (but did not figure) inner septal nectaries in *Cocos nucifera* (see Figs. 1,2) and *Latania loddigesii* but,

incredibly for a student whose dissertation was reviewed by Haberlandt (1914, 1924), the main advocate of physiological plant anatomy, interpreted the nectaries as air canals. Bauch's and Drude's inability to recognize the septal nectaries of Palmae as such was then perpetuated in the surveys by Al-Rawi (1945) and Bosch (1947), both of whom cited Bauch and Drude. Bosch (1947) interpreted the septal nectaries of *Hypphaene coriacea* as evidence for a modified apocarpous gynoecium in the context of the peltate carpel theory (see Guédès & Schmid 1978). Fortunately, other workers on Palmae (see Table 1) have correctly interpreted the structure and function of their septal nectaries.

Many palms apparently are wind-pollinated (see literature review in Schmid, 1970b) and so, not surprisingly, lack nectaries. Very little, however, is known about the anatomy and morphology of the septal and non-septal nectaries of palms. The main detailed study is that of Daumann (1970), who examined anatomically the flowers of 12 species in 11 genera* and found *Rhapis excelsa* (*R. flabelliformis*), *Caryota mitis*, *Chamaedorea oblongata*, *Chrysalidocarpus lutescens*, *Ptychosperma macarthurii*, and "*Pinanga lepida*" (name never published) to lack nectaries, *Chamaerops elegans* (*C. humilis*) and "*C. macrocarpa*" to have androecial nectaries, *Trachycarpus fortunei* (*T. excelsus*) to have superficial gynoecial,

* Daumann's nomenclature given in parentheses has been updated.



1-4. Figures 1, 2. Morphology of inner septal nectaries (labelled N) in ovary of pistillate flower of *Cocos nucifera* in transection (Fig. 1) and surface view (Fig. 2), the latter showing openings of nectaries to exterior. Figures 3, 4. Morphology of outer septal nectaries (labelled N) in ovary of bisexual flower of *Livistona* sp. in non-median (see Daumann 1970: 576) longisections, Figure 4 showing an enlargement through region of nectar-secreting cells at bases of carpels. (Redrawn from Brown 1938, with permission of the American Philosophical Society.)

non-septal nectaries, *Livistona humilis* (see Figs. 3,4) and *Sabal minor* (*S. adansonii*) to have outer septal nectaries, and *Cocos nucifera* (Figs. 1,2) to have inner septal nectaries. Daumann (1970: 575-578) described in some detail for Palmae not only the morphology of their nectaries, but also anatomy, including mode of nectar secretion. The works of Uhl & Moore (1971, 1977) on various palm genera (see Table 1) and Narayana (1937) on *C. nucifera* are also noteworthy, but these works concentrate more on morphological than on anatomical features of septal nectaries.

Septal nectaries seem to be the most common nectarial type in Palmae (Schmid, unpublished literature survey). Table 1 summarizes the occurrence of septal nectaries in palms, as determined from espe-

cially the anatomical literature. This table should be consulted for the variety of morphological types already known for Palmae.

In 1970 I described the reproductive morphology and pollination biology of *Asterogyne martiana* from two sites in Costa Rica, La Selva and Osa (see Schmid 1970*a, b*). Uhl and Moore (1977) provided additional, mainly anatomical information on the same species, including some details on nectarial anatomy. Their anatomical studies and those now reported are based on collections that I made in Costa Rica in 1968 (Schmid 1970*a*). I provide here additional data on the morphology and histology of the inner septal nectaries of *A. martiana* since they seem representative of those of many other palms (see Table 1).

Table 1. Literature Reports of Septal Nectaries in Palmae.^a

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- I. Outer septal nectaries only (inner septal nectaries lacking); nectar secretion in several outer grooves (furrows)^b lying in septal radii of ovary: *Livistona* ♂ (Brown 1938—see Figs. 3,4; Daumann 1970), *Sabal* ♂ (see also Part IIA2 below) (Daumann 1970).
- II. Inner septal nectaries only; outer septal grooves,^b if present, not nectar-secreting; nectar secretion only in the cavities lying internally in septal radii of ovary.^c
- A. Outer septal grooves (furrows)^b absent from compound ovary or lower style.
1. Openings of nectaries in or near base of ovary; *Corypha* ♂ (Moore 1973: 54, Uhl & Moore 1971).
 2. Openings of nectaries near middle of ovary: *Geonoma* ♀ (Uhl & Moore 1971), *Hyophorbe vauhanii* ♀ (see also Part IIA4 below) (Uhl 1978), *Sabal* ♂ (see also Part I above) (Moore 1973: 54, Uhl & Moore 1971).
 3. Openings of nectaries in or near top of ovary or in base of style: *Arenga* ♀ (Moore 1973: 67, Uhl & Moore 1971), *Asterogyne* ♂♀ (Schmid 1970a, and this study—Figs. 5,6; Uhl & Moore 1977), *Borassus* ♀ (Drude 1877, 1887: Fig. 29), *Cocos* ♂♀ (Bauch 1911; Brown 1938—see Figs. 1,2; Daumann 1970; Narayana 1937), *Hyophorbe* ♂ (Uhl 1978), *Hyphaene* ♀ (Bosch 1947), *Latania* ♀ (Bauch 1911, Moore 1973: 54, Uhl & Moore 1971).
 4. Openings of nectaries in middle or top of style: *Butia* ♂♀ (Silberbauer-Gottsberger 1973, Uhl & Moore 1971), *Hyophorbe* ♀ (excl. *H. vauhanii* ♀—see Part IIA2 above) (Uhl 1978), *Paralinospadix* ♀ (Uhl & Moore 1971), *Ptychosperma* ♂♀ (Al-Rawi 1945, Uhl 1976, Uhl & Moore 1977).
- B. Outer septal grooves (furrows)^b present on compound ovary or lower style, but not nectar-secreting, with subcategories (1) through (4) as above—no literature reports for Palmae.
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^a This morphological classification of septal nectaries is modified from the systems of Daumann (1970) and especially Schmid (1982). Palmae have only superior ovaries, and thus the classification given here excludes possibilities for half-inferior and inferior ovaries (for which see Schmid 1982). Studies of Palmae have generally concentrated on the pistils of pistillate flowers rather than on the pistillodia of

Standard anatomical techniques were used to prepare flowers of *Asterogyne martiana* for study (Schmid 1972, 1978). Although its flowers are rather tanniferous (Figs. 5,6), bleaching of sections on slides with Stockwell's solution (Schmid 1977) proved unnecessary. My anatomical observations are based on sections of 5 staminate and 5 pistillate flower buds or open flowers.

Floral morphology and anatomy of the unisexual flowers of *Asterogyne martiana* are detailed in Schmid (1970a, b) and Uhl and Moore (1977). Staminate flowers each have 3 separate sepals, 3 basally connate petals, 6 stamens with the filaments basally united into a short tube that is weakly adnate to the petals, and a small, tripartite rudimentary pistil (or pistillode) about 2 mm long. Pistillate flowers each have 3 separate sepals, 3 basally united petals, 6 very prominent staminodia that are basally connate and strongly adnate to the petals, and a short, trilocular, triovulate ovary surmounted by 3 fused, elongate styles with 3 papillate stigmas that are recurved at anthesis.

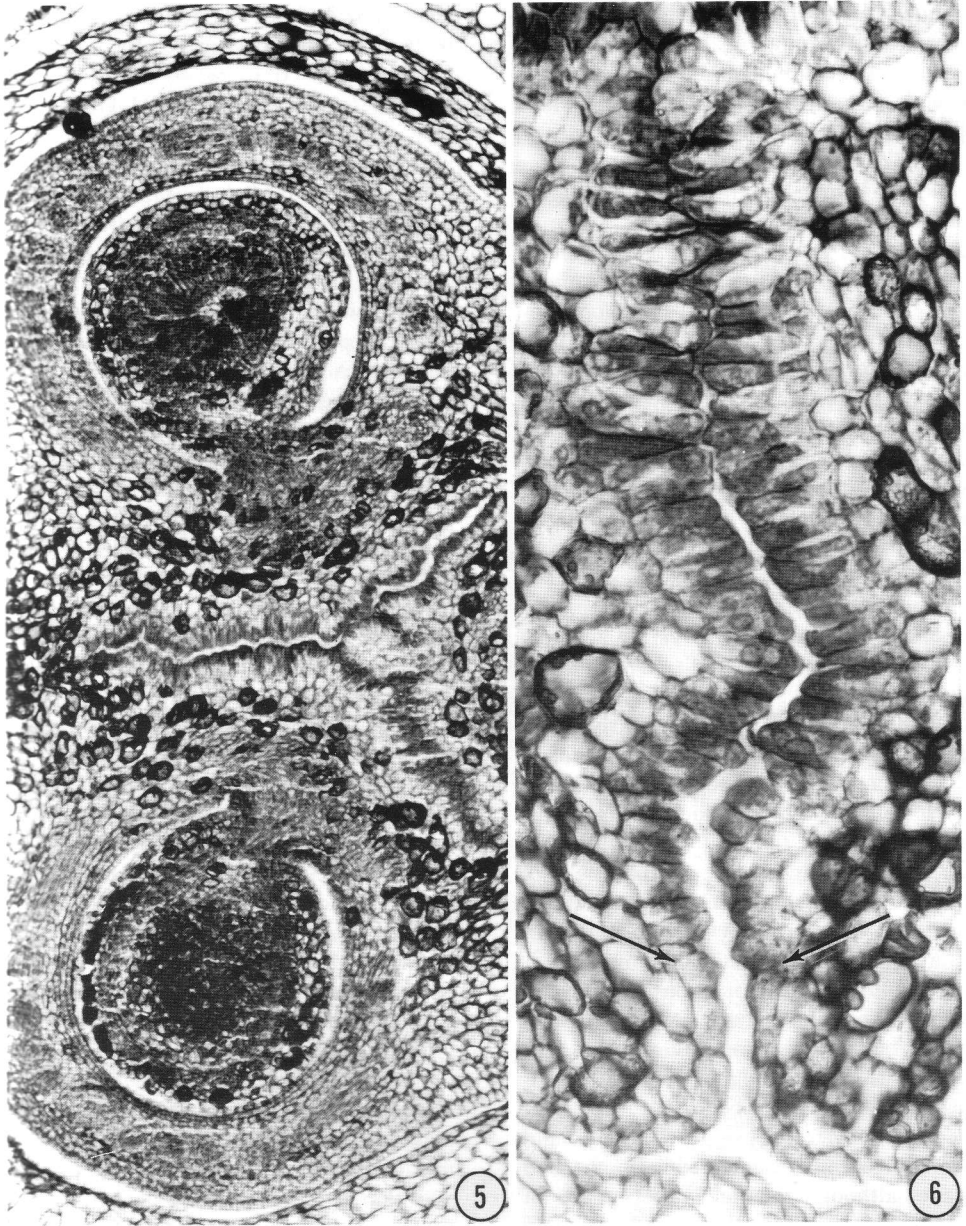
Both staminate and pistillate flowers of *Asterogyne martiana* produce copious amounts of nectar (Schmid 1970a, b). Since the inner septal nectaries in the

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staminate flowers, in those taxa possessing unisexual flowers.

^b As defined in Schmid (1982), septal grooves (furrows) occur in the main nectar-secreting parts of compound ovaries and have an appreciable depth; shallow septal depressions (indentations) as in *Sabal mexicana* or *Latania verschaffeltii* (Uhl & Moore 1971: Figs. 4,6) are not regarded as grooves for classificatory purposes. In addition, only septal grooves below (proximal to) the insertion of openings of the septal nectaries are of significance since more distally located grooves would not be effective in channelling nectar to the base of the flower.

^c *Socratea exorrhiza* ♂ has a "small septal nectary," but the mode of nectarial opening was not indicated by Uhl & Moore (1980). *Ravenea madagascariensis* ♀ and *Ceroxylon* sp. ♀ have septal cavities that apparently are not secretory (Uhl 1969) and thus are not septal nectaries.



5, 6. Transections (somewhat oblique) of inner septal nectary in a pistillate flower bud (near anthesis) of *Asterogyne martiana* showing a triradiate common nectarial cavity in mid-region of ovary (Fig. 5) and, about 100 μ m distally near top of ovary, one of the three nectarial openings to exterior (Fig. 6), the undulate slit in Figure 6 being the distal part of the nectarial arm at the 9:00 position in Figure 5. A petal-staminodial tube is external to the ovary in each figure. The nectary consists of only epidermal tissue lining each side of the nectarial cavity. The arrows in Figure 6 separate the nectar-secreting, columnar cells of the nectary proper (above arrows) from the non-nectar-secreting, rather isodiametric cells of the nectarial canal that leads to the opening. Note the tannin cells in vicinity of nectary (Fig. 5) and nectarial opening (Fig. 6) and the transfer-cell nature of the nectar-secreting cells (see text). $\times 131$, $\times 426$.

gynoecia of the flowers of both sexes are morphologically and anatomically very similar, only the nectaries of the pistillate flowers are described and figured here (Figs. 5,6).

Unlike the ovary of *Cocos nucifera*, which has three separate septal nectaries in its mid-region (Fig. 1), the superior ovary of *Asterogyne martiana* has in its mid-region a triradiate, moderately undulate (but non-labyrinthine) common nectarial cavity (Fig. 5). Such diverse nectarial patterns result from different degrees (more versus less, respectively) of ontogenetic fusion of adjacent carpellary walls during the development of the gynoecium. Distally in the gynoecium of *Asterogyne* the common nectarial cavity separates into three canals that open to the exterior in the top of the ovary (Fig. 6). The nectarial openings are slitlike, with a vertical extent of about 250 μm on the ovarian surface. Uhl & Moore (1977: 183) reported the nectarial openings as occurring "near the base of the ovary," but they clearly occur in the top of the ovary in my material.

Anatomically, the nectary of *Asterogyne* consists of only epidermal tissue lining each side of the nectarial cavity (Fig. 5). In some places the epidermal cells of the nectary are apposed, so that an actual nectarial cavity is not evident (Fig. 5). The significance of this is unknown, but it may simply be a factor of observations on slightly "immature" nectaries since mainly flower buds just before anthesis were sectioned. However, judging from the histological features described below, the septal nectaries of *Asterogyne* are "mature" and already secreting nectar while in the bud stage, although my field observations of nectar secretion were made only on open flowers (Schmid 1970a, b). Generally in both septal and non-septal nectaries nectar secretion begins in the bud just prior to anthesis and then lasts for the life of the flower (Daumann 1970, 1974; Fahn 1979, Schmid 1982).

The nectar-secreting epidermal cells of

Asterogyne are of the columnar type, all the nectarial cells in Figure 5 being secretory. In Figure 6 arrows separate the nectar-secreting, columnar cells of the nectary proper (above the arrows) from the non-nectar-secreting, rather isodiametric cells of the nectarial canal that leads to the opening (at the bottom of the figure). It might be noted that some definitions of "nectary," for example, that of Daumann (1970), would not consider the nectarial canal as part of the septal nectary, but for reasons elaborated in Schmid (1982) I prefer to do so.

The cells of the nectary of *Asterogyne* have thin walls and a very thin cuticle (Figs. 5,6). The dark staining of the outer parts (i.e., by the cavities) of the nectar-secreting, columnar cells in both Figures 5 and 6 is suggestive of wall ingrowths of transfer cells, that is, cells with wall ingrowths specialized for the short distance transport of materials (Cutter 1978). The dark staining, apparently transfer-cell wall regions in Figures 5 and 6 are very similar to ones depicted in light micrographs in Cutter (1978: 230) and Schnepf (1964). Transfer cells, it might be noted, have been demonstrated at the ultrastructural level in both septal and non-septal nectaries of a number of plants (Cutter 1978, Fahn 1979, Schmid 1982, Schnepf 1964). In *Asterogyne* the transfer-cell nature of the cells becomes more apparent proximally in the nectary (compare Figs. 5 and 6).

As noted above, the septal nectaries of *Asterogyne* are strictly epidermal and so lack vascular tissue and other subepidermal components (Figs. 5,6). Placental vascular tissue, however, occurs in the proximity of the nectary on the non-septal radii (Fig. 5). In addition, dark-staining, apparently tanniferous cells surround, but do not occur in the nectaries (Figs. 5,6). Presumably the tannin cells in the vicinity of the nectary in Figure 5 and the nectarial opening in Figure 6 are protective against insect predators, as suggested by

Uhl & Moore (1973, 1977) for *Asterogyne* and other palms. I did not observe any crystals or silica in my floral material. Uhl (1976, 1978, pers. comm. 1978; Uhl and Moore 1971, 1977, 1980), who has examined flowers of many *Palmae*, has never seen tannins, silica, or crystals in their septal nectaries, although these materials often occur close to the nectaries.

Light and electron microscopic studies have revealed that septal and non-septal nectaries secrete nectar by several diverse modes (Cutter 1978; Daumann 1970, 1974; Fahn 1979; Schmid 1982; Schnepf 1964). Daumann (1970) found that of the 106 genera of monocotyledons with septal nectaries that he studied, 94.3% of the genera had nectar secretion through the cell wall and cuticle (if present), the latter either remaining intact and in place or else variously separating from the cell wall and sometimes becoming torn. Daumann (1970) found that all four genera and six species of palms for which he had data (he had none for *Cocos nucifera*) secreted nectar through the cell wall and an undisturbed cuticle. This also seems to be the mode of nectar secretion in *Asterogyne* since the thin cuticle of its septal nectaries appears intact not only in sections of buds near anthesis, but also in sections of open flowers. Unfortunately, there is no other information on mode of nectar secretion in palms, and absolutely no ultrastructural studies of palm nectaries.

Judging from the limited published information available, the septal nectaries of *Asterogyne martiana* and other palms (references in Table 1) conform to the morphological and anatomical stereotypes of septal nectaries of monocotyledons in general as elaborated in Daumann (1970), Fahn (1979), Schmid (1982), and Schnepf (1964). Clearly, however, the number of published studies on septal nectaries of *Palmae* is very small (Table 1). A detailed comparative survey of the morphology and anatomy of the septal and non-septal nec-

taries of many representatives of *Palmae* would thus be highly desirable and no doubt would be invaluable in providing correlations of structure and function (sensu Carlquist 1969, Schmid 1978, Uhl and Moore 1973, 1977).

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