

Foliar, nonstructural nectaries in the Marantaceae

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Nonstructural, foliar nectaries have been found in two genera of the Marantaceae (Zingiberales). Two nectaries are located on each leaf, at the junction of the leaf sheath and petiole. Externally, they may be readily distinguished from the surrounding tissue by their lighter color and absence of hairs. Internally, they show no specifically differentiated nectariferous tissue. In most species, the location of the nectaries is correlated with the distribution of fiber bundles. In nonnectariferous regions these bundles lie directly beneath the epidermis, while in the region of the nectary they occur several cell layers beneath the epidermis. Nectar secretion takes place through stomates. The cells surrounding the substomatal cavity may play an important role in the process of secretion. The distribution of structural nectaries in the family is also discussed.

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Nous avons observé des nectaires foliaires non-structuraux dans deux genres des Marantacées (Zingiberales). Deux nectaires sont présents sur chaque feuille, à la jonction de la gaine foliaire et du pétiole. Extérieurement, on les distingue facilement du tissu environnant par leur couleur plus claire et l'absence de poils. Intérieurement, ils ne montrent pas de tissus nectarifères spécifiquement différenciés. Dans la plupart des espèces, une corrélation existe entre l'emplacement des nectaires et la distribution des faisceaux de fibres. Dans les régions non-nectarifères, ces faisceaux sont situés immédiatement sous l'épiderme, tandis que là où un nectaire est présent, plusieurs assises de cellules les séparent de l'épiderme. La sécrétion du nectar se fait à travers les stomates. Les cellules qui entourent la cavité sous-stomatique jouent peut-être un rôle important dans le processus de sécrétion. Les auteurs discutent aussi de la distribution intra-familiale des nectaires structuraux.

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Introduction

Nonstructural nectaries are nectaries that do not usually show a modified secretory tissue and whose nectar is exuded through stomates (Fahn 1979). Structural and nonstructural nectaries were first clearly distinguished by Zimmermann (1932). Wettstein 1889 recorded the presence of nectar secretions from tissues without a specifically differentiated internal structure. His attention was drawn to these tissues by the presence of ants on specific plant parts. It seems clear that these nectaries would now be classified as nonstructural.

Elias (1983) has recently reviewed the literature on extrafloral nectaries in angiosperms, including some nonstructural nectaries. The present work supplements this knowledge of the distribution and structure of nonstructural nectaries. Previous to this contribution the only nonstructural nectaries reported in the Zingiberales were those on the floral bracts of *Costus* (Costaceae) (Maas 1972; Elias 1983).

Materials and methods

Living material was collected from plants in cultivation at Duke University (Durham, NC, U.S.A.), Fairchild Tropical Garden (Miami, FL, U.S.A.), Royal Botanic Gardens (Kew, England), and Harold L. Lyon Arboretum (Honolulu, HI, U.S.A.). Whenever possible, collections were made at the stage of active nectar secretion. Nectaries of *Stromanthe hjalmarssonii* (Koern.) Petersen, *Ctenanthe dasycarpa* (Donn. Smith) Schumann, *C. aff. dasycarpa* (sp. nov.), *C. glabra* (Koern.) Eichl., and *C. amabilis* (Morren) Kennedy were examined to provide data for the anatomical descriptions.

The nectaries were either fixed in Formalin – acetic acid – alcohol (FAA: 50 mL 95% ethanol, 5 mL glacial acetic acid, 10 mL 40% Formalin, 35 mL H₂O) or examined fresh. Sections were cut by hand and at 50–100 μm on a Reichert sliding microtome. Sections were stained in toluidine blue (Berlyn and Miksche 1976) and mounted in 50% glycerin. Photographs were taken with a Leitz Orthomat photo-

microscope. Several attempts were made to cut sections from paraffin-embedded material. However, complete paraffin infiltration was never achieved. The technique was not successful.

Nectar secretion was observed in the laboratory by floating a fresh piece of tissue containing a nectary in an active state of secretion on a concentrated sugar solution. The nectary was observed under high power (320×) with a Leitz Ortholux 2 microscope equipped with an Ultropak illuminator. After several seconds nectar secretion through individual stomates could be seen.

Stomatal structure was observed with both scanning electron microscopy (SEM) and in cleared paradermal hand sections. Material for SEM was fixed in FAA, dehydrated, and critical point dried in a Denton DCP-1 apparatus. The specimens were mounted on stubs with Tubekote, coated with gold–palladium in a Hummer II sputter coater, and viewed with a Hitachi S-500 scanning electron microscope. Paradermal hand sections were cleared and mounted in lactic acid.

Results

Nonstructural nectaries have been found in two genera of the Marantaceae (Table 1). In addition to the species listed in Table 1, a number of other species in the same genera were checked for the presence of nectaries. This revealed that the nectaries are not a consistent feature of *Stromanthe* or *Ctenanthe*. *Stromanthe sanguinea* Sonder, *S. portiana* A. Gris, *Ctenanthe kummeriana* (Morren) Eichl., *C. oppenheimiana* (Morren) Schumann, and *Ctenanthe* sp. cv. 'Rubra' all lack the nectaries.

The nectaries are located on the leaves in all of the species listed in Table 1. In the Marantaceae each leaf consists of a blade, pulvinus, petiole, and leaf sheath. Two nectaries are located on each leaf at the junction of the petiole and the sheath. One nectary occurs on each side of the wings of the sheath (Fig. 1). In some species (e.g., *C. aff. dasycarpa* (sp. nov.)) the nectary lies predominantly on the sheath side of the junc-

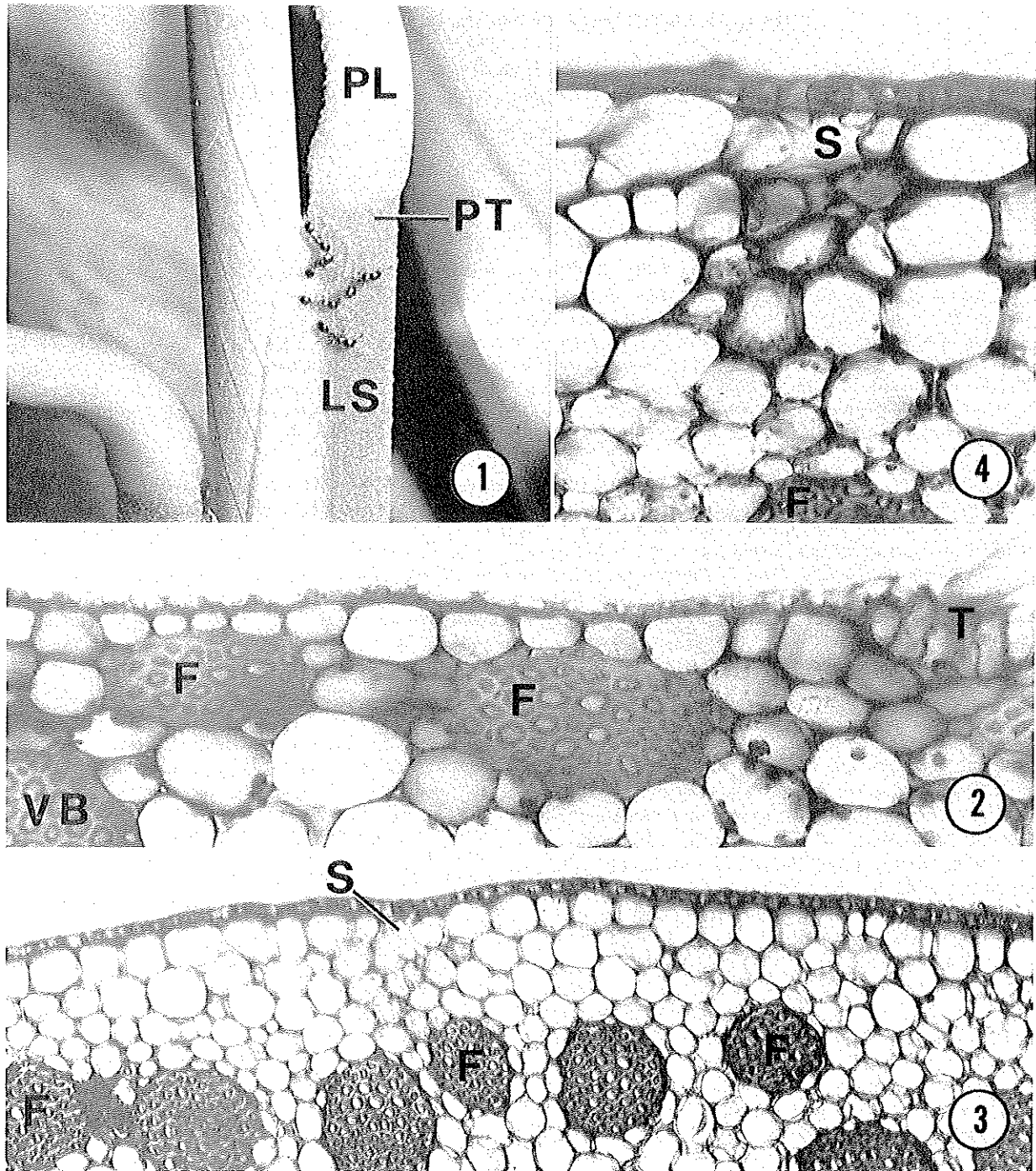


FIG. 1. *Ctenanthe amabilis* growing at Lyon Arboretum, Honolulu, HI, U.S.A. Ants are shown feeding at a nectary located at the junction of the leaf sheath (LS) and petiole (PT). The petiole is very short in this specimen. PL, pulvinus. $\times 4$. FIG. 2. Cross section through a region of the leaf sheath of *Ctenanthe* aff. *dasycarpa* (sp. nov.) showing the relation of the fiber bundles (F) to the epidermis. VB, fiber sheath of a vascular bundle; T, trichome. $\times 420$. FIG. 3. Cross section through the nectary of *Ctenanthe* aff. *dasycarpa* (sp. nov.). The fiber bundles (F) are separated from the epidermis by several layers of cells. S, substomatal cavity. $\times 140$. FIG. 4. Cross section through the nectary of *Stromanthe hjalmarssonii*. Numerous chloroplasts can be seen in the cells surrounding the substomatal cavity (S) and in the region of the fiber bundles (F). $\times 400$.

tion, while in others (e.g., *C. dasycarpa*) it is mainly on the petiole. However, there is a good deal of variability in its precise location within a species.

Externally, the nectary may be distinguished from the surrounding tissues by color and the absence of hairs (Fig. 1). The nectariferous region is usually yellowish green as compared

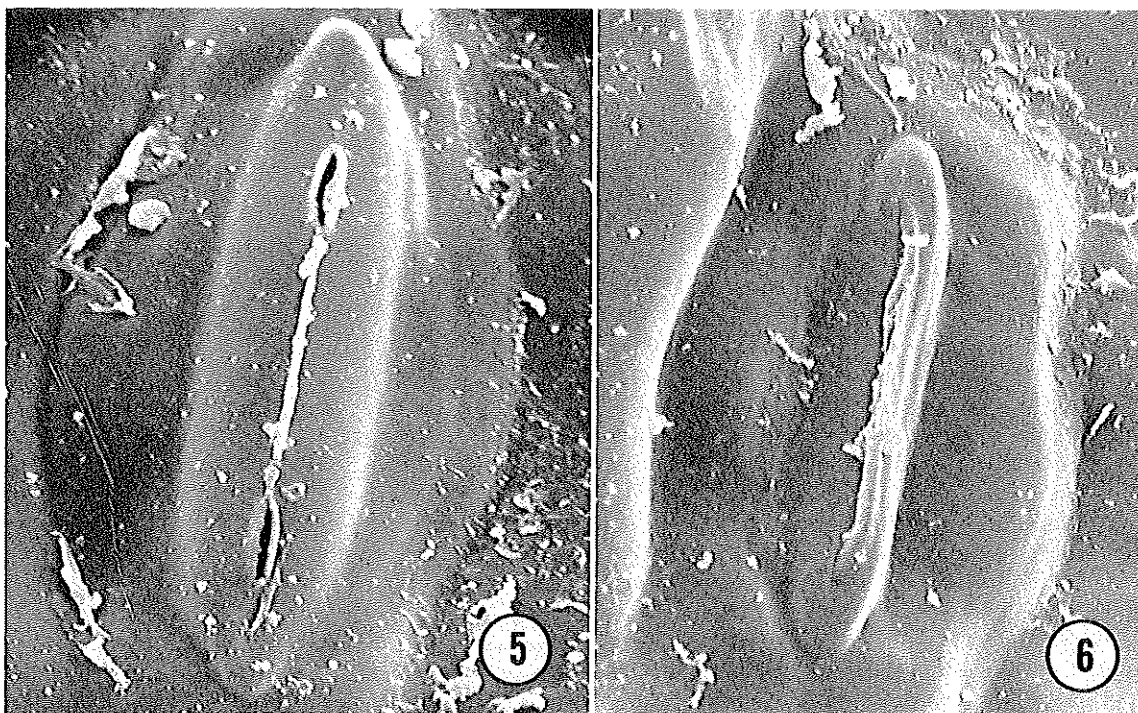
with the darker green of the surrounding regions. In some species (*Ctenanthe amabilis*) the nectary is also slightly raised.

From observation of greenhouse-grown specimens, it appears that nectar secretion occurs only over a short period of time. Production begins approximately when expansion of the leaf sheath and petiole have ceased. In *Stromanthe hjalmarssonii*

TABLE 1. Species with foliar, nonstructural nectaries

Species	Source institution ^a	Accession number	Voucher number	Voucher deposited
<i>Stromanthe hjalmarssonii</i>	FTG	82-371	Kirchoff 85-37	FTG
<i>S. jacquinii</i>	HLA	L.68.354	Nagata 637	HLA
<i>S. macrochlamys</i>	HLA	L.78.792	Kennedy 4475	HLA
<i>S. cf. confusa</i>	HLA	L.82.1315	Kennedy 4322	UBC
<i>Ctenanthe dasycarpa</i>	FTG	84-38	Kress 76-609	DUKE
<i>C. aff. dasycarpa</i> (sp. nov.)	FTG	28-373	Kress 78-898	DUKE
<i>C. lubbersii</i>	HLA	L.76.397	Ishikawa 475	HLA
<i>C. amabilis</i>	HLA	L.76.099	Kennedy 4474	HLA
<i>C. pilosa</i>	HLA	L.79.220	Nagata 3100	HLA
<i>C. setosa</i>	HLA	L.77.310	Nagata 3098	HLA
<i>C. glabra</i>	HLA	L.76.1231	Nagata 3095	HLA
<i>C. compressa</i>	HLA	L.79.210	Kennedy 4467	UBC, HLA

^aFTG, Fairchild Tropical Garden, Miami, FL, U.S.A.; HLC, Harold L. Lyon Arboretum, Honolulu, HI, U.S.A.



FIGS. 5 and 6. *Ctenanthe amabilis*, SEM. Fig. 5. Stomate occurring outside the region of a nectary. $\times 4240$. Fig. 6. Stomate occurring on a nectary. $\times 4240$.

sonii this corresponds roughly to the time when the leaf sheath is forced open by the expansion of the next leaf. In this species, secretion decreases before the next leaf unrolls. The period of secretion in *Ctenanthe dasycarpa*, *C. aff. dasycarpa* (sp. nov.), and *C. amabilis* is longer. In these species, secretion persists after the next older leaf has unrolled.

Anatomically, the nectaries fall into the class known as nonstructural nectaries. These nectaries lack a specifically differentiated nectariferous tissue. They are often difficult to distinguish from the surrounding nonnectariferous tissue. The nectaries of *Stromanthe hjalmarssonii*, *Ctenanthe dasycarpa*, and *C. aff. dasycarpa* (sp. nov.) can be located by the distribution of fiber bundles that lie below the epidermis. In nonnectariferous regions these bundles are set one or two cell layers under the epidermis (Fig. 2). In the region of the nectary the bundles occur at least three cell layers interior to the epider-

mis (Fig. 3). In the nectary of *C. amabilis* and *C. glabra* the fiber bundles are located between one and three cell layers interior to the epidermis. The nectaries in these species are not as readily distinguished from the surrounding tissues as are those of the former species.

In all species the cells that constitute the nectary appear to be ordinary, vacuolate parenchyma cells. There are few intercellular spaces other than the substomatal cavities. The largest concentration of chloroplasts occurs in the cells surrounding these cavities and in the cells surrounding the fiber bundles (Fig. 4). The cells surrounding the substomatal cavities appear to be smaller than the other cells that constitute the nectary.

Nectar secretion takes place through stomates. This has been verified by direct observation (see Materials and methods). No structural difference could be detected between the stomates on the nectary and those outside of this region. However, those on

the nectary (Fig. 6) appear to be slightly smaller than those outside (Fig. 5).

Discussion

The existence of foliar, nonstructural nectaries has not previously been reported in the Marantaceae. The structure of these nectaries seems to agree with that of other nonstructural nectaries (Wettstein 1889; Frey-Wyssling and Häusermann 1960; Fahn 1979). However, there have been so few studies of nonstructural nectaries that it is difficult to determine if significant differences exist within this class. This problem is exacerbated by their lack of internal structure.

Fahn (1979) mentions that it is common to find well-developed intercellular spaces in the tissue of nectaries that exude nectar through stomates. Apart from the substomatal cavities, few or no intercellular spaces were found in the nectaries studied. The cells surrounding these cavities were found to be smaller and to have more chloroplasts than the adjacent cells. These three features suggest that the cells lining the cavities play an important role in secretion.

Stomates that serve as openings for the exudation of nectar are generally modified and unable to close (Fahn 1979). These stomates have been found to have wide, circular or ellipsoidal apertures (Fahn 1952). While we did not investigate guard cell movement, we found no modifications of the stomates. Closure movements have been observed in some members of the Centrospermae (Fahn 1979).

A number of other nectaries occur in the Marantaceae, in addition to the nonstructural nectaries described here. *Schumannianthus dichotomus* (Roxb.) Gagnepain (reported as *Clinogyne dichotoma* by Elias) is reported to possess nonstructural nectaries on the outer surface of its floral bracts (Elias 1983). However, we have been unable to confirm the presence of nectaries on the floral bracts in this species. This type of nectary is found in at least one species of *Marantochloa*. Nectaries are also found on the modified bracteoles subtending the flowers in some species of *Calathea* (Kennedy 1976), *Ischnosiphon*, *Donax* (Elias 1983; H. Kennedy, personal observation), *Thaumatococcus*, and *Schumannianthus dichotomus* (Üxküll-Güldenbandt 1907; Elias 1983). We have also observed structural nectaries at the tip of the cataphylls in *Thaumatococcus daniellii* (Benth.) Milne-Redh. and *Megaphrynium macrostachyum* (Benth.) Milne-Redh. Interestingly enough, those species (with the exception of *Thaumatococcus daniellii*) that have foliar nectaries lack extrafloral nectaries on

modified bracteoles. All species of Marantaceae possess septal nectaries in their flowers.

The function of the foliar nectaries described here has not been studied experimentally. However, ants are frequently found feeding at the nectaries (Fig. 1). This suggests that the nectaries may serve as an attractant for ants, which in turn may provide protection from predators (Bentley 1977).

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