

## FUNCTIONAL INTERPRETATIONS OF THE MORPHOLOGY AND ANATOMY OF SEPTAL NECTARIES

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This review synthesizes personal observations on the septal nectaries (hereafter “SNs”) of 40 species, 32 genera, and 17 families (families sensu AIRY SHAW 1973) with the extensive old literature (much of it pre-1900) and especially with DAUMANN’s (1970) landmark study of the SNs of 202 species, 107 genera, and 21 families. Daumann examined a total of 427 species, 197 genera, and 34 families of monocotyledons, whereas my sample is, respectively, 112, 84, and 35.

“Septal nectary” is defined as follows: a nectariferous, that is sugar- or nectar-secreting, cavity resulting from lack of intercarpellary postgenital fusion and lying in a septal radius (“septum” here is too restrictive because a few taxa with SNs have parietal placentation, eg, Burmanniaceae). The SN may be strictly external (“outer SN”), internal with a non-nectariferous opening to the exterior (“inner SN”), or a combination (“confluent SN”, eg, DAUMANN’s fig. 7–9).

DAUMANN (1970) found SNs in 21 monocotyledonous families sensu AIRY SHAW (1973): \*Agavaceae, Alismataceae, \*Alliaceae, Alstroemeriaceae, Amaryllidaceae, Aponogetonaceae, \*Bromeliaceae, \*Butomaceae, \*Cannaceae, \*Costaceae, \*Dioscoreaceae, Haemodoraceae, \*Heliconiaceae, Iridaceae, Liliaceae, Limnocharitaceae, \*Marantaceae, \*Musaceae, Palmae, Pontederiaceae, and \*Strelitziaceae. New observations for \*Lowiaceae, new observations and new literature records for \*Aphyllanthaceae, Burmanniaceae, \*Petrosaviaceae, \*Tecophilaeaceae, Velloziaceae, and \*Xanthorrhoeaceae, and an unverified report for Pandanaceae (SAUNDERS 1939) suggest that SNs occur in 29 (34.9%) of the 83 monocotyledonous families recognized by AIRY SHAW (1973). Comparable figures for DAHLGREN & CLIFFORD (1982) and THORNE (1983) are, respectively, 37 (38.1%) of 97 families and 20 (38.5%) of 52 families. The former’s attribution of SNs to their Trilliaceae and Thismiaceae is not supported. As far as is known, SNs occur in all members of the families asterisked above. The “liliad” type of SN shown in *fig. 1A* is the most common type in monocotyledons.

All dicotyledons lack SNs (DAUMANN 1974; my data). Non-nectar-secreting septal cavities do occur in *Cneorum tricoccum* (I found none in *C. pulverulentum*), *Koelreuteria paniculata*, *Ruta bracteosa*, and a few other dicotyledons. However, there is no good reason to interpret these as either former or future SNs, that is, as either “rudiments” or “oriments” sensu ABEL (1914).

A morphological classification of SNs has been derived from (1) ovary position, (2) presence versus absence of external ovarian septal grooves (these are

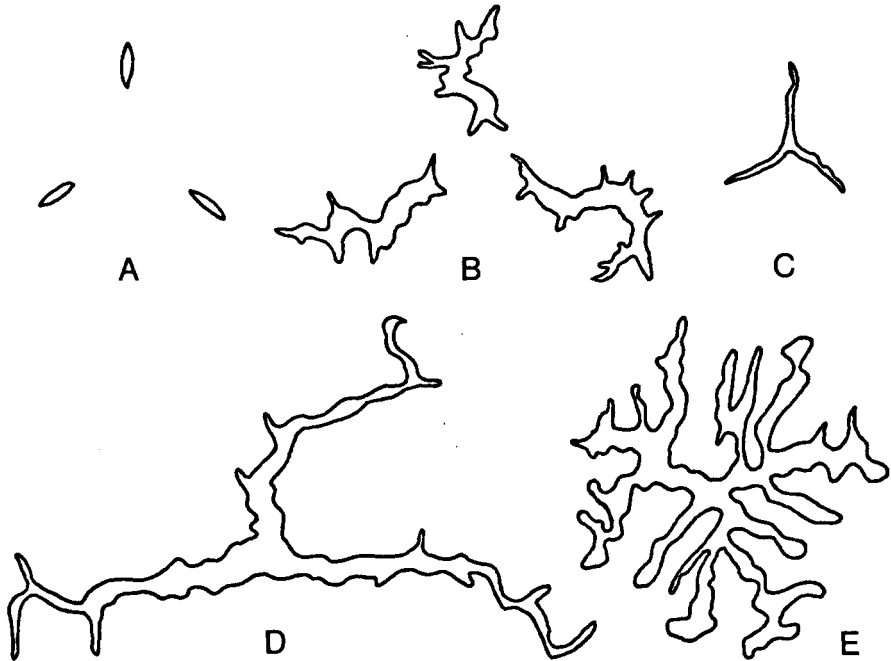


Fig. 1. Basic variational patterns of the septal cavities of inner septal nectaries as seen in transection, with appropriate descriptive terminology. The transections are of the main nectar-secreting parts of tricarpellate ovaries (their loculi and outer limits are not shown). The drawings were based on actual material drawn to the same scale: Fig. A. *Non-labyrinthine distinct septal nectaries* from *Muscari ?armeniicum* (Liliaceae), Fig. B. *Labyrinthine distinct septal nectaries* from *Strelitzia reginae* (Strelitziaceae – distal in flower), Fig. C. *Non-labyrinthine common nectarial cavity* from *Asterogyne martiana* (Palmae – see SCHMID 1983), Fig. D. *Labyrinthine common nectarial cavity* (this triradiate in transection) from *Aechmea fasciata* var. *purpurea* (Bromeliaceae), Fig. E. *Labyrinthine common nectarial cavity* with convoluted proliferations of the carpellary walls, from *Musa acuminata* (Musaceae – from a photograph of a staminate flower in FAHN & KOTLER 1972: Fig. 10C). The outlines of non-labyrinthine septal nectaries may be linear, lenticular (fig. A) or elliptic, or slightly to moderately (fig. C) to considerably undulate or sinuate.

not nectar-secreting, contrary to reports of a “double nectary” by SCHNIEWINDTHIES 1897, and others), and for the SNs themselves (3) their inner or their rare outer or confluent nature, (4) their longitudinal extent, (5) their degree of distinctness, (6) their transectional outline, (7) their distance from the ovarian center, and (8) the position of their openings in the gynoeceum. Basic transectional outlines of SNs are linear, elliptic or lenticular, undulate, and labyrinthine (see fig. 1 and item 3 below). In an ovary SNs may be distinct (typically three per ovary or may be combined (see item 2 below) to form a common nectarial cavity exhibiting the preceding transectional outlines plus (eg, Musaceae and some Bromeliaceae) often a highly proliferated, labyrinthine situation (fig. 1). A classification of the SNs of Palmae (SCHMID 1983) uses many of these criteria.

The nectar-secreting cells of SNs and non-SNs are ultrastructurally and histologically very similar, that is, thin-walled and densely cytoplasmic with a small vacuole and with many organelles, especially Golgi, mitochondria, and endoplasmic reticulum. However, SNs and non-SNs differ in various gross anatomical respects, including, respectively: cuticle usually thin or absent versus usually present (often thick), stomata and trichomes rare versus common (stomata of SNs never secrete nectar), subepidermal tissue more versus less common, vascular tissue *in* the nectaries uncommon versus common, and tannins, crystals, and secretory structures *in* the nectaries uncommon versus common. The last three, however, often occur around SNs, including their openings (eg, tannins in *Asterogyne* – SCHMID 1983) and thus may have protective functions.

Many morphological (items 1–6 below), anatomical (items 7–12), and physiological (item 13) mechanisms probably evolved to increase nectar output of SNs. The “liliad” type of inner SN shown in *fig. 1A* can be regarded as a starting point for many of the following phyletic trends:

- (1) increase in radial and/or longitudinal extent of SNs, often with concomitant increase in floral size;
- (2) increase in nectarial surface area by lack of intercarpellary (postgenital) fusion to give a common nectarial cavity (*fig. 1C–E*);
- (3) increase in nectarial surface area by undulation, and especially by convolution (localized growth) to give labyrinthine SNs (*fig. 1B, D, E*);
- (4) increase in number of SNs per flower by increase in number of carpels and hence number of septal radii;
- (5) increase in number of SNs by doubling of an inner SN in a septum;
- (6) unisexuality, the flowers of one sex (especially male) producing more nectar than those of the other sex (eg, many Musaceae – see also *fig. 1E*);
- (7) increase in surface area of walls of nectar-secreting cells by the transfer cell mechanism of wall ingrowths [Transfer cells were first seen in SNs and in reproductive structures by SAUNDERS (1890:15), who noted for *Kniphofia* a “thickening” of the cell wall that “has the appearance of having undergone corrosion”; also SCHNIEWIND-THIES (1897) on “sekundäre Schicht”];
- (8) changes in and increase in numbers of organelles and/or cellular contents of nectar-secreting cells;
- (9) increase in tangential size of epidermal nectar-secreting cells to give columnar cells forming a palisade (this occurs in 47.7% of DAUMANN’s 1970 generic sample);
- (10) increase in number of layers of nectar-secreting cells by formation of subepidermal secretory tissue (this occurs in 92.5% of DAUMANN’s 1970 generic sample, with up to 30 such layers on each side of the septal cavity of *Strelitzia reginae* – SCHNIEWIND-THIES 1897);
- (11) trend 9, but involving subepidermal tissue;
- (12) increase in amount of vascular tissue in and near the SNs, by (a) formation of vascular tissue (usually just phloem) actually in the SNs, (b) increase in number and/or size of vascular bundles near the SNs, and (c) formation of extra phloem in vascular bundles near the SNs;

(13) increase in intensity and/or duration of nectar secretion.

SCHNIEWIND-THIES (1897) postulated 1, 4, and 5 as general phyletic trends for SNs; the other trends are entirely or substantially novel suggestions. Not all or even many of these mechanisms need occur in a single species. Trends 1, 2, 3, 9, 10, and 12 seem most important; 4, 5 probably of minor importance.

A preponderance of the above trends occurs in Agavaceae, Amaryllidaceae, Bromeliaceae, Iridaceae, and in Zingiberales (all of which have SNs except Zingiberaceae s.s.), most of which have large flowers and are epigynous (or semi-epigynous) and bat- or especially bird-pollinated. Hence adaptations particularly to bird and bat pollination probably necessitated various morphological and anatomical modifications of SNs (see above) to produce the increased amounts of nectar required by these pollinators. A concomitant specialization probably was the evolution of epigyny, with at least two advantages. (1) The phyletic adnation of the perianth parts and stamens to each other and to the gynoecium to result in the inferior ovary (by the tenets of the appendicular concept) would have allowed larger vascular bundles and/or a greater number of bundles to serve the SNs and thus to facilitate their increased nectar output (see trend 12 above). (2) The same phyletic adnation would have a protective/supportive function because, following GRANT's (1950) reasoning, the extra bulk of tissue adnated to the ovary would tend to protect the nectaries against injury and nectar robbing by predators, and, more importantly, to support the flowers during the activities of the relatively large pollinating bats and birds. Concomitantly with the evolution of epigyny additional protective/supportive features were evolved: tannins, crystals, secretory structures, and particularly sclerenchyma.

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