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Nectaries in Some Neotropical Species of *Polypodium* (Polypodiaceae): Preliminary Observations and Analyses

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ABSTRACT

The occurrence of nectaries in ferns is reviewed, and a new report of nectaries in the *Polypodium squamatum* group is made. Nectars of five species of *Polypodium* (*P. myriolepis*, *P. pyrrolepis*, *P. rosei*, *P. sanctae-rosae*, and *P. thysanolepis*), as well as *Drynaria quercifolia*, *D. rigidula*, and *Polybotrya osmundacea*, were analyzed for sugars and amino acids. The majority of the nectars are sucrose-poor, and most have fairly low amino acid concentrations, though a great number of amino acids were detected. The findings are discussed in light of other nectar analyses.

THERE HAS BEEN MUCH INTEREST in the last 100 years in the presence and function of extrafloral nectaries in many kinds of plants, both angiosperms and pteridophytes. A recent review (Bentley 1977) traces the general history of descriptions, observations, and experiments concerning the phenomenon of extrafloral nectar secretion, but mentions the occurrence of nectaries on only one fern, *Pteridium aquilinum* (L.) Kuhn, the common bracken. This species has indeed been the best studied (Darwin 1877, Figdor 1891, Lloyd 1901, Lüttge 1961, Schremmer 1969), but nectaries have also been reported in some other (albeit few) genera. Nectaries (or nectary-like structures) were observed by Bonnier (1879) in *Cyathea arborea* (L.) Sm., *Hemitelia horrida* [\equiv *Cnemidaria horrida* (L.) Presl.], and *Angiopteris*. They have been reported in several genera of Old World Polypodiaceae (*sensu stricto*): *Photinopteris speciosa* (Blume) Presl (Lüttge 1961), *Platynerium* spp. (Dümmer 1911, Lüttge 1961), and in *Drynaria* spp., *Holostachyum*, and *Merinthosorus* (Zamora and Vargas 1974).

We are now able to report the occurrence of nectaries in *Polybotrya* and in five species of Neotropical *Polypodium*. In addition, we confirm their presence and activity in two species of *Drynaria*.

Sota (1966) discussed and illustrated the secretory structures in *Polypodium* and considered them to be a diagnostic character of the *P. squamatum* group. He referred to them as "hidatodos," but was uncertain of their function. Hydathodes are well known in ferns, especially in *Nephrolepis* and in many epiphytic genera such as *Polypodium* and *Grammitis*, and they are generally considered to be structures for exuding water and various salts, particularly calcium carbonate, from tracheary elements (Holtum 1954, Esau 1965). Evaporation of the water from hydathodes leaves a whitish cap or lime-

dot. In contrast, nectaries often have specialized glandular tissue that is served by phloem elements (Esau 1965). Sota's illustrations (1966:94) clearly show that the structures on the auricles of species of the *Polypodium squamatum* group are functioning as nectaries.

Heretofore, analysis of nectars in ferns has consisted primarily of tests for sugars. Bonnier (1879) recorded the presence of sucrose and glucose from *Pteridium aquilinum*. Dümmer (1911) obtained a positive test for glucose from the exudate of *Platynerium*. More recently, Lüttge (1961) recorded the presence of sucrose, fructose, and glucose in nectars of *Photinopteris speciosa*, *Platynerium* spp., and *Pteridium aquilinum*. In addition, he obtained ninhydrin-positive tests on these three genera, indicating the presence of amino acids in the nectar.

In this paper, we describe the location of nectaries in the ferns studied and confirm the presence of various sugars and amino acids in the nectars. In addition, we discuss the functional significance of nectaries in ferns, pointing out a need for field observations and experimental work to test the speculative hypotheses put forth.

MATERIALS AND METHODS

Nectar was collected from the following species growing in the University of California Botanical Garden, Berkeley (UCBG): *Polypodium sanctae-rosae* (Maxon) C. Chr. (UCBG acc. no. 65.893, Mexico, Chiapas, *Alava s.n.*); *P. pyrrolepis* (Fée) Maxon (UCBG 75.057, Mexico, Veracruz, *Ornduff 8127*); *P. rosei* Maxon (UCBG 59.1499, Mexico, Sinaloa, *Kimmach 107*); *P. myriolepis* Christ (UCBG 56.637, Costa Rica, Cartago, *Lankester s.n.*); *P. thysanolepis* A. Br. ex Klotzsch (UCBG 59.1506, Mexico, Sinaloa, *Kimmach 101*); *Drynaria quercifolia* (L.) J. Sm. (UCBG

56.660, Java, Schuurman via Kimnach); *D. rigidula* (Sw.) Bedd. (UCBG 53.385, New Caledonia, *Skottsberg 156*); and *Polybotrya osmundacea* H. & B. ex Willd. (UCBG 58.445, Costa Rica, *Horich s.n.*). Vouchers are deposited at University of California.

Nectar samples were collected using finely drawn micropipettes and spotting the nectar on strips of

Whatman No. 1 chromatography paper. Sugar and amino acid contents were examined using techniques developed by I. and H. G. Baker (Baker and Baker 1976, 1982). Sugar concentrations were measured with a Bellingham and Stanley pocket refractometer (wt./total wt. type). Sugars were separated and identified by descending paper chromatography, and

TABLE 1. Location of nectaries in ferns studied.

| Species | Location | Age of fronds with active nectaries |
|--|---|--|
| <i>Polypodium</i> spp. (listed in table 2 and in Materials and Methods) | on acroscopic lobe at base of individual segments | mainly on young leaves, but often continue to function on some mature fronds |
| <i>Drynaria rigidula</i> | base of pinnae | both young and mature leaves |
| <i>Drynaria quercifolia</i> | many places on abaxial surface of blade | mature leaves |
| <i>Polybotrya osmundacea</i> | on rachis of unfurling fronds | young leaves only |

TABLE 2. Sugars in fern nectars. Replicate runs are parenthetical.

| Species | # of samples | \bar{x} % sugar concentration by wt. (and range) | | | | | | | |
|---------------------------------|--------------|--|---------|---------|----------|--------|--------|--------|--------|
| | | | sucrose | glucose | fructose | melez. | malt. | raff. | S/F+G |
| <i>Polypodium myriolepis</i> | 4 | 24.5 (22-27) | .159 | .490 | .199 | .097 | .020 | .034 | .231 |
| | | | (.125) | (.478) | (.201) | (.134) | (.064) | (—) | (.184) |
| | | | (.176) | (.416) | (.375) | (.027) | (.009) | (—) | (.222) |
| | | | (.142) | (.484) | (.200) | (.116) | (.042) | (.017) | (.208) |
| <i>Polypodium pyrrolepis</i> | 4 | 54 (42-63) | .414 | .348 | .238 | — | — | — | .706 |
| | | | (.113) | (.425) | (.269) | (.113) | (—) | (—) | (.918) |
| | | | (.428) | (.262) | (.311) | (—) | (—) | (—) | (.748) |
| | | | (.361) | (.315) | (.312) | (.012) | (—) | (—) | (.576) |
| <i>Polypodium rosei</i> | 6 | 29.5 (18-47) | .230 | .446 | .324 | — | — | — | .298 |
| | | | (.240) | (.400) | (.359) | (—) | (—) | (—) | (.316) |
| | | | (.221) | (.390) | (.332) | (.061) | (—) | (—) | (.306) |
| | | | (.217) | (.491) | (.288) | (—) | (—) | (—) | (.279) |
| | | | (.350) | (.314) | (.272) | (.065) | (—) | (—) | (.597) |
| (.227) | (.432) | (.326) | (.015) | (—) | (—) | (.300) | | | |
| <i>Polypodium sanctae-rosae</i> | 5 | ±30 (estimated) | .364 | .360 | .275 | — | — | — | .574 |
| | | | (.050) | (.485) | (.364) | (.101) | (—) | (—) | (.059) |
| | | | (.221) | (.456) | (.324) | (—) | (—) | (—) | (.283) |
| | | | (.176) | (.406) | (.304) | (.114) | (—) | (—) | (.248) |
| (.202) | (.427) | (.317) | (.108) | (—) | (—) | (.272) | | | |
| <i>Polypodium thysanolepis</i> | 6 | 30 (21-46) | .103 | .494 | .403 | — | — | — | .115 |
| | | | (.240) | (.370) | (.386) | (—) | (—) | (—) | (.317) |
| | | | (.171) | (.432) | (.394) | (—) | (—) | (—) | (.216) |
| <i>Drynaria quercifolia</i> | 1 | >50 | .070 | .469 | .396 | .040 | .025 | — | .081 |
| <i>Drynaria rigidula</i> | 3 | 63 (54-71) | .204 | .472 | .324 | — | — | — | .256 |
| | | | (.483) | (.256) | (.261) | (—) | (—) | (—) | (.934) |
| | | | (.152) | (.492) | (.273) | (.040) | (.043) | (—) | (.199) |
| <i>Polybotrya osmundacea</i> | 2 | 46 (35-57) | .328 | .445 | .228 | — | — | — | .487 |

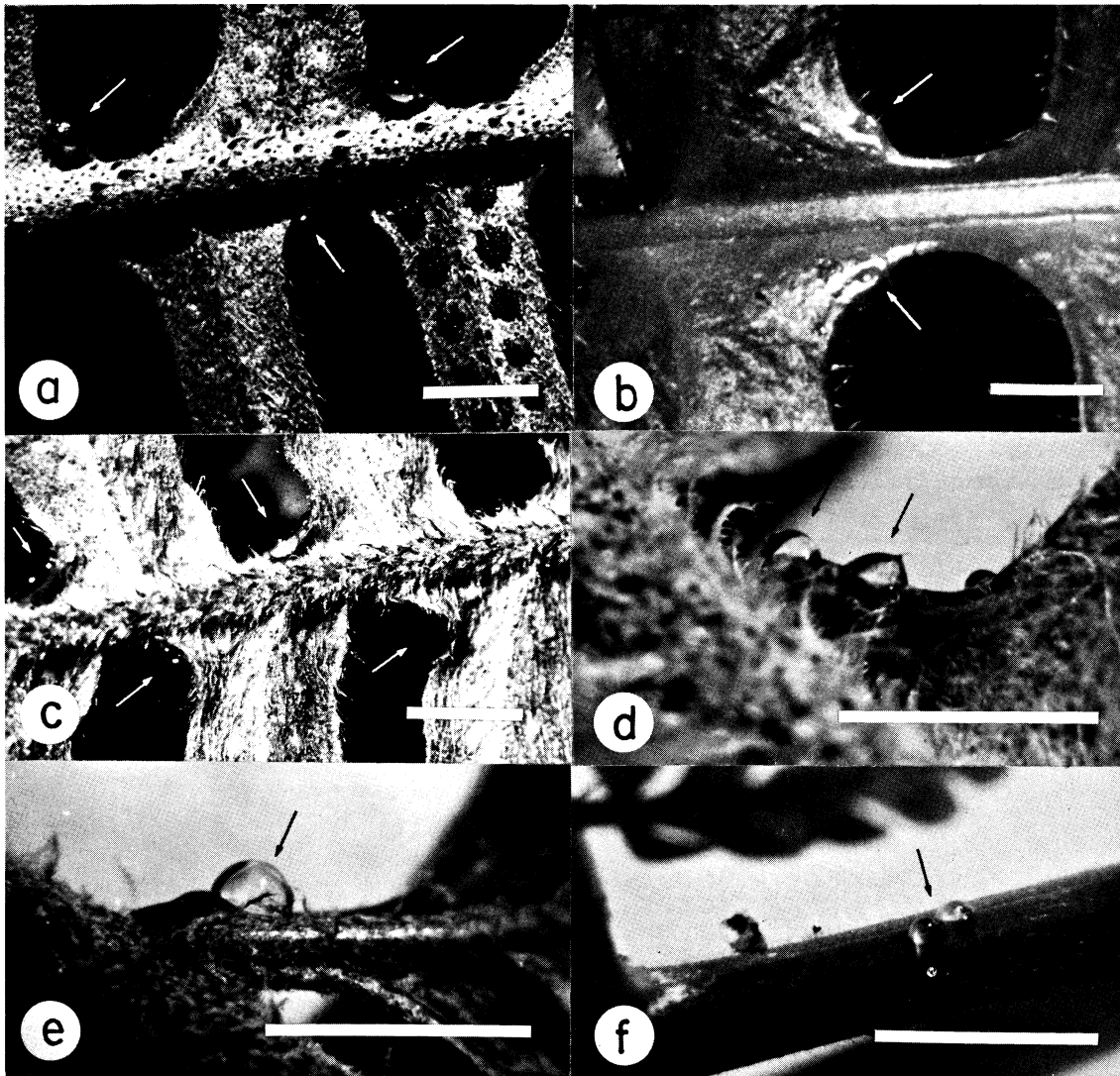


FIGURE 1. Nectaries in ferns. a, *Polypodium myriolepis* (x 3); b, *Polypodium thysanolepis* (x 3); c, *Polypodium rosei* (x 3); d, *Polypodium rosei* (x 7); e, *Drynaria rigidula* (x 7); f, *Polybotrya osmundacea* (x 6). Arrows point to nectaries, whose position is given in table 1. Bar scales represent 0.5 cm.

their relative concentrations determined with fluorometry (Baker and Baker 1982). Overall amino acid concentration was measured by a ninhydrin test, and the histidine scale was employed to translate the intensity of the ninhydrin response into approximate concentration of amino acids. Amino acids were separated and identified using two-dimensional thin-layer chromatography (Baker and Baker 1976). Replicate analyses were performed on some of the species; they are presented as an additional parenthetical entry in the appropriate slot of the tables.

RESULTS

Location of nectaries and age of fronds with actively secreting nectaries is presented in table 1; representative species are illustrated in figure 1. In general, nectar was easiest to collect during morning hours, but under humid greenhouse conditions it remained visible throughout the afternoon and evening. Plants grown in a greenhouse with no ants (or other organisms) to remove the nectar may accumulate nectar sugars in artificially high concentrations.

Sugar composition of the nectars is presented in

table 2. All these nectars contain sucrose, fructose, and glucose; small amounts of other sugars were detected in four *Polypodium* species and in two *Drynaria* species. In their large comparative studies of sugar compositions of nectars, Baker and Baker (1980) found that the sucrose/hexose (fructose and glucose) ratio can often be correlated with visitor-type. We have therefore presented the S/F + G ratios also and will discuss our results in the light of their general findings.

Amino acid composition of the nectars is presented in table 3. The ninhydrin scores have been translated into approximate overall amino acid concentrations, allowing us to compare the amino acid content of these nectars with those reported for many floral and extrafloral nectars by Baker, Opler, and Baker (1978) and Lüttge (1961).

DISCUSSION

The function of nectaries in ferns may be the same as that of foliar extrafloral nectaries as demonstrated on many plants by many investigators (Bentley 1976, Keeler 1977, Janzen 1966, Tilman 1978, Koptur 1979). Darwin (1879) observed ants visiting glands on young fronds of *Pteridium aquilinum*, and it was shown by Cooper-Driver *et al.* (1977) that young fronds of *Pteridium* are not protected by digestibility-reducing substances (tannins) until a late age. These fronds have cyanogenic glycosides, more specific toxins, while young and may use nectaries to attract a more generalized form of defense, i.e., ants. It will be interesting to see if fronds of *Polybotrya osmundacea* (which also has rachis nectaries functioning only on young fronds) have a similar chemical defense strategy. Another well-documented fern/ant interaction is that of *Solanopteris brunei* and *Azteca* ants (Gómez P. 1974, Wagner 1972). This interaction does not appear to involve nectaries but rather morphological adaptations of portions of the rhizomes to house ants. Luis D. Gómez P. (pers. comm.) reports that all clumps of *Drynaria rigidula* in Queensland that he inspected had *Oecophyla smaragdina* ants. He suggests that the ants find the humus collected in rosettes of fronds or in matted tangles of rhizomes a microhabitat useful for foraging or nesting and doubts that the presence of nectar is related to the presence of ants.

In general, nectars of ferns have high sugar concentrations (table 2); the amount of sugar found in these exudates argues against the role of these nectaries as valves for excretion of wastes or excess sap. The majority of the nectars analyzed are sucrose-poor (i.e., the S/F + G ratio is less than 0.5). This agrees

TABLE 3. Amino acids in fern nectars. + = amino acid present in sample, ? = amino acid probably present, — = amino acid not detected.

| Species | approx. amino acid concentration | number of runs | alanine | arginine | asparagine | aspartic acid | cysteine/cystine | glutamine | glutamic acid | glycine | histidine | isoleucine | leucine | lysine | methionine | phenylalanine | proline | serine | threonine | tryptophan | tyrosine | valine | γ -amino butyric |
|---|----------------------------------|----------------|---------|----------|------------|---------------|------------------|-----------|---------------|---------|-----------|------------|---------|--------|------------|---------------|---------|--------|-----------|------------|----------|--------|-------------------------|
| <i>Polypodium myriolepis</i> ^a | 2 | 98 μ M | — | + | — | — | — | + | + | — | — | + | + | + | — | + | + | + | + | + | + | + | — |
| <i>P. pyrrolepis</i> ^b | 3 | 195 μ M | + | + | + | — | — | — | — | — | — | + | + | + | + | + | + | + | + | + | + | + | — |
| <i>P. rosei</i> ^b | 2 | 146 μ M | — | + | + | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>P. sanctae-rosae</i> | 3 | 146 μ M | — | + | + | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>P. thysanolepis</i> ^a | 3 | 391 μ M | + | + | + | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Drynaria quercifolia</i> | 2 | >25mM | + | + | + | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>D. rigidula</i> ^a | 3 | 98 μ M | + | + | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Polybotrya osmundacea</i> | 2 | 98 μ M | — | + | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |

^aMultiple runs of these nectars gave slightly different results (i.e., a couple of amino acids differed between samples or were detected in only one run).

with findings of Baker and Baker (pers. comm.) that extrafloral nectars are usually sucrose-poor. *Polybotrya osmundacea* has a sugar ratio close to 0.5, a "balanced" nectar. The two sucrose-rich exceptions are both polypodiums. Our preliminary results show a greater diversity of sugar ratios within a species than one might expect in a flowering plant. However, all these fern nectaries are totally exposed, and microbial breakdown of sucrose to hexoses may occur easily. The proportions of sugars may vary according to the length of time newly secreted nectar is exposed to the air.

There are many amino acids found in each species, but the overall concentrations are low (in all but *Drynaria*) when compared with other extrafloral and floral nectars. Lüttge (1961) found the amino acid concentration in *Platycerium* to be high and in *Pteridium* to be low (our ninhydrin results with *Pteridium* agree with those of Lüttge). He explained differences in overall amino acid concentrations of nectars from fern nectaries, floral nectaries, and extrafloral nectaries by the degree of complexity in the structure of the nectary. According to Lüttge's generalization, most fern nectars should have high amino acid concentrations because in most cases the nectaries are of rather simple structure. Ferns generally lack secondary tracheary elements, and phloem is the most complex tissue in their circulatory system. Findings of Baker *et al.* (1978) refute Lüttge's hypothesis: the amino acid concentration is not always directly correlated with morphological complexity of the nectary.

Most ants visiting nectaries are in search of sugars for adult nutrition (Bentley 1977); many ants use other nitrogen-containing food sources, but for those

ants restricted to liquid foods as adults, amino acids in nectar may be very important. Studying the ferns in nature and the ants that may have coevolved with them may give some insight into the vastly different amino acid concentrations of different fern nectars.

Nectaries may function on mature fronds as well as on young fronds for attracting and maintaining an ant-guard, but there may be other explanations: e.g., nectaries (especially those in close proximity to sori) may serve to attract ants (or other organisms) that serve as dispersal agents of the spores. Most of these ferns are epiphytes, and could perhaps benefit from a crawling body to transport spores to an area suitable for germination and gametophyte establishment.

Alternatively, fern nectaries may simply be special phloem-associated hydathodes, evolved in adaptation to the environment rather than other organisms. Most of the species of ferns studied here are subxerophytes or xerophytes (*Polybotrya* excepted). Perhaps they are simply exuding surplus metabolic byproducts with a minimal discharge of valuable water, not unlike desert shrews' excreting highly concentrated urine (L. D. Gómez P., pers. comm.). Clearly, more field observations and experiments are needed to test these hypotheses!

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