

Raphides in Palm Embryos and their Systematic Distribution

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- **Background and Aims** Raphides are ubiquitous in the palms (Arecaceae), where they are found in roots, stems, leaves, flowers and fruits. Their occasional presence in embryos, first noticed over 100 years ago, has gone largely unexamined.
- **Methods** Embryos from 148 taxa of palms, the largest survey of palm embryos to date, were examined using light microscopy of squashed preparations under non-polarized and crossed polarized light.
- **Key Results** Raphides were found in embryos of species from the three subfamilies Coryphoideae, Ceroxyloideae and Arecoideae. Raphides were not observed in the embryos of species of Calamoideae or Phytelphantoideae. The remaining subfamily, the monospecific Nypoideae, was not available for study.
- **Conclusions** Within the Coryphoideae and Ceroxyloideae, embryos with raphides were rare, but within the Arecoideae, they were a common feature of the tribes Areceae and Caryoteae.

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Key words: Anatomy, Arecaceae, calcium oxalate, embryology, embryos, Palmae, raphides.

INTRODUCTION

Raphides, bundles of needle-shaped crystals of calcium oxalate monohydrate in specialized cells, are found throughout the Monocotyledonae (Franceschi and Horner, 1980; Prychid and Rudall, 1999) and are ubiquitous in the palms (Arecaceae). They are known from roots, stems, leaves, flowers and fruits (Uhl and Dransfield, 1987; Tomlinson, 1961, 1990) but occasionally turn up in unusual sites, such as anther tissue (Henderson and Rodríguez, 1999), the pseudopedicel epidermis (Barfod and Uhl, 2001) and epidermal trichome ‘sacs’ (Robertson, 1978). They were first noticed in palm embryos by Micheels (1891).

Examining material supplied by M. Treub from the Buitenzorg (now Bogor) Botanic Garden, Micheels (1891) reported the presence of raphides in the embryos of *Caryota* sp. and *Archontophoenix alexandrae* (F. Muell.) H. Wendl. (as *Ptychosperma alexandra*). Osenbrüg (1894) surveyed 35 taxa from throughout the family and found raphides in the embryos of 11 species. More recent embryological accounts pay little attention to raphides. Their absence was not specifically mentioned in accounts on the embryos of coconut (Haccius and Philip, 1979), *Chamaerops humilis* L. (Guignard, 1961), *Elaeis guineensis* Jacq. (Vallade, 1966) and *Livistona chinensis* (Jacq.) R. Br. ex Mart. (Kulkarni and Mahabale, 1974). Rao (1955) made no mention of raphides in the embryo of *Areca catechu* L. Shirke and Mahabale (1972) illustrated raphides in their drawings of *Caryota urens* L. embryos but did not remark on their significance.

Nevertheless, examining Osenbrüg’s work (Osenbrüg, 1894), one finds that the presence or absence of raphides in embryos seems to follow certain presumed evolutionary

lineages within the palm family. The purpose of this survey was to determine if raphides are confined to certain lineages and if they could be used as additional evidence of phylogenetic relationships.

METHODS

Palm seeds were harvested from fruits that were mature and ready to be dispersed. Most material for this study was collected as fresh seeds from Fairchild Tropical Garden (FTG). Some seeds were collected from wild or cultivated plants elsewhere in the Miami area (see Table 1); vouchers for these samples are deposited in the herbarium of FTG. Two samples of African rattans were supplied as living seeds for propagation by Dr T. Sunderland from wild plants in Cameroon (voucher at K, the herbarium of the Royal Botanic Gardens, Kew). Some samples were collected as mature seeds preserved in glycerine–alcohol (in the spirit collection at FTG); the appearance of raphides in pickled and fresh materials was the same.

Seeds were dissected, and the embryos were removed. The embryo usually came away from the endosperm with little effort. It was placed in a drop of toluidine blue, squashed under a coverslip, and examined in polarized and non-polarized light at $\times 100$ and $\times 250$. Raphides, when present, were usually visible in normal light, but became highly visible in polarized light. Images were captured electronically using a Pixera Professional® (Los Gatos, California) digital image capture system, using polarized light. Post-capture processing consisted of converting RGB colour mode to greyscale (half-tone), increasing resolution to 300 dpi, and enhancing contrast.

Raphide presence was further qualified as ‘sparse’ when fewer than ten raphide bundles were seen in the embryo. It was called ‘abundant’ when more than 25 bundles were

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TABLE 1. *Raphides in palm embryos, arranged by tribe (Uhl and Dransfield, 1999)*

Taxon, accession or voucher	Raphides in embryo
Calameae	
<i>Calamus asperrimus</i> Blume, Osenbrüg (1894)	Absent
<i>Calamus paspalanthus</i> Becc., Chee <i>et al.</i> FRIM47366	Absent
<i>Calamus</i> sp., Osenbrüg (1894)	Absent
<i>Daemonorops geniculata</i> Mart., Chee <i>et al.</i> FRIM47312	Absent
<i>Eremospatha wendlandiana</i> Dammer ex Becc., Sunderland 3009 (at K)	Absent
<i>Lacosperma opacum</i> (H. Wendl. & Mann) Drude, <i>Sunderland 3005</i> (at K)	Absent
<i>Raphia farinifera</i> (Gaertner) Hylander, 77222L	Absent
<i>Raphia taedigera</i> (Mrt.) Mart., Osenbrüg (1894)	Absent
Lepidocaryeae	
<i>Lepidocaryum tenue</i> Mart. var. <i>gracile</i> (Mart.) Henderson (as <i>L. gracile</i> Mart.), Osenbrüg (1894)	Absent
<i>Mauritia</i> sp., Osenbrüg (1894)	Absent
Corypheae	
<i>Acoelorrhaphe wrightii</i> (Griseb. & H. Wendl.) H. Wendl. ex Becc., P2313F	Absent
<i>Brahea armata</i> S. Wats., Zona s.n.	Absent
<i>Chamaerops humilis</i> L., Osenbrüg (1894)	Absent
<i>Chuniophoenix nana</i> Burret, 8178E	Absent
<i>Coccothrinax argentea</i> (Lodd. ex Schultes) Sarg. ex Becc. (as <i>Thrinax argentea</i> >Mart.), Osenbrüg (1894)	Absent
<i>Coccothrinax borhidiana</i> Muñiz, 85195B	Absent
<i>Coccothrinax crinita</i> Becc. ssp. <i>brevicrinis</i> Borhidi & Muñiz, 88659A	Absent
<i>Coccothrinax cupularis</i> (León) Muñiz & Borhidi, 87226B	Absent
<i>Copernicia macroglossa</i> H. Wendl., P1894	Absent
<i>Cryosophila stauracantha</i> (Heynhold) R. Evans, 8089A	Absent
<i>Cryosophila warscewiczii</i> (H. Wendl.) Bartlett, RM1338D	Absent
<i>Licuala ferruginea</i> Becc., Chee <i>et al.</i> FRIM47356	Absent
<i>Licuala grandis</i> H. Wendl., 79536B	Absent
<i>Licuala lauterbachii</i> Damm. & K. Schum., 93290E	Absent
<i>Licuala paludosa</i> Griff. (as <i>L. amplifrons</i> Miq.), Osenbrüg (1894)	Absent
<i>Licuala paludosa</i> Griff., 72522A	Absent
<i>Licuala peltata</i> Roxb. ex Buch.-Ham. var. <i>sumawongii</i> L. G. Saw, 70320D	Absent
<i>Licuala rumphii</i> Blume, FG4456A	Absent
<i>Livistona chinensis</i> (Jacq.) R. Br. ex Mart., 94345B	Absent
<i>Livistona endauensis</i> J. Dransf. & K. M. Wong, Chee <i>et al.</i> FRIM47327	Absent
<i>Livistona muelleri</i> F. M. Bailey, FG66762B	Absent
<i>Livistona robinsoniana</i> Becc., 8310A	Absent
<i>Livistona saribus</i> (Lour.) Merr. ex Chev., FG4220A	Present, abundant
<i>Livistona woodfordii</i> Ridl., FG591026A	Absent
<i>Livistona</i> sp., Osenbrüg (1894)	Absent
<i>Pritchardia</i> sp., 93691C	Absent
<i>Rhapis excelsa</i> (Thunb.) Henry, P682A	
<i>Sabal minor</i> (Jacq.) Pers. (as <i>S. adansonii</i> Guers.), Osenbrüg (1894)	Absent
<i>Sabal minor</i> (Jacq.) Pers., RM765C	Absent
<i>Sabal yapa</i> Wright ex Becc., 57690C	Absent
<i>Schippia concolor</i> Burret, 5759A	Absent
<i>Serenoa repens</i> (Bartram) Small, P244A	Absent
<i>Serenoa repens</i> (Bartram) Small, <i>Zona s.n.</i>	Absent
<i>Thrinax excelsa</i> Lodd. ex Mart., 83347E	Absent
<i>Thrinax morrisii</i> H. Wendl., RM2185E	Absent
<i>Thrinax morrisii</i> H. Wendl., 93985C	Absent
<i>Thrinax radiata</i> Lodd. ex J. A. & J. H. Schultes, P2059A	Absent
<i>Trachycarpus fortunei</i> (W. J. Hooker) H. Wendl. (as <i>T. excelsa</i> Wendl.), Osenbrüg (1894)	Absent
<i>Washingtonia robusta</i> H. Wendl., P339B	Absent
<i>Zombia antillarum</i> (Descourt ex Jackson) L. H. Bailey, P2665B	Sparse
Phoeniceae	
<i>Phoenix canariensis</i> hort. ex Chabaud, 672010C	Absent
<i>Phoenix dactylifera</i> L., Osenbrüg (1894)	Absent
<i>Phoenix roebelinii</i> O'Brien, 89800A	Absent
Borasseae	
<i>Bismarckia nobilis</i> Hildebrandt & H. Wendl., 92251D	Absent
<i>Latania lontaroides</i> (Gaertner) H. E. Moore × <i>L. loddigesii</i> Mart., 75611B	Absent
<i>Medemia argun</i> (Mart.) Wuerttemberg ex H. Wendl., Osenbrüg (1894)	Absent
Cyclospatheae	
<i>Pseudopheonix lediniana</i> R. W. Read, 74595A	Absent
<i>Pseudopheonix sargentii</i> H. Wendl. ex Sarg., 5880A	Absent
<i>Pseudopheonix sargentii</i> H. Wendl. ex Sarg., 97608A	Absent
Ceroxyleae	
<i>Ceroxylon alpinum</i> Bonpl. (as <i>C. andicola</i> H.B.K.), Osenbrüg (1894)	Absent
Hyophorbeae	

TABLE 1. Continued

Taxon, accession or voucher	Raphides in embryo
<i>Chamaedorea seifrizii</i> Burret, FG4137	Absent
<i>Chamaedorea seifrizii</i> Burret, RM1556B	Absent
<i>Chamaedorea schiedeana</i> Mart., 931048J	Absent
<i>Chamaedorea tepejilote</i> Liebm. ex Mart., 80709C	Present, abundant
<i>Gaussia attenuata</i> Becc., 79558C	Absent
<i>Gaussia maya</i> (O. F. Cook) R. Read & Quero, 7563A	Absent
<i>Hyophorbe lagenicaulis</i> (L. H. Bailey) H. E. Moore, 80509A	Absent
Caryoteae	
<i>Arenga caudata</i> (Lour.) H. E. Moore, 87536A	Absent
<i>Arenga engleri</i> Becc., 89925A	Absent
<i>Arenga microcarpa</i> Becc., 81598C	Absent
<i>Arenga obtusifolia</i> Mart., 591101C	Absent
<i>Arenga pinnata</i> (Wurmb) Merrill (as <i>A. saccharifera</i> Lab.), Osenbrüg (1894)	Absent
<i>Arenga tremula</i> Becc., DF126A	Sparse
<i>Arenga tremula</i> Becc., P802D	Sparse
<i>Arenga westerhoutii</i> Griff., Chee <i>et al.</i> FRIM47322	Absent
<i>Arenga sp.</i> , 80349D	Present
<i>Caryota cumingii</i> Lodd. ex Mart., 77961C	Present, abundant
<i>Caryota mitis</i> Loureiro, X-9-34	Present, abundant
<i>Caryota mitis</i> Loureiro (as <i>C. sobolifera</i> Mart.), Osenbrüg (1894)	Present
<i>Caryota urens</i> L., Osenbrüg (1894)	Present
<i>Wallichia porpyrocarpa</i> Mart., Osenbrüg (1894)	Present
<i>Wallichia sp.</i> , S-82-97	Present, abundant
Areceae	
<i>Adonidia merrillii</i> (Becc.) Becc., P1163F	Sparse
<i>Archontophoenix alexandrae</i> (F. Muell.) H. Wendl. (as <i>Ptychosperma alexandrae</i> F. Muell.), Osenbrüg (1894)	Present
<i>Areca catechu</i> L., Osenbrüg (1894)	Present
<i>Areca glandiformis</i> Lamarck, Osenbrüg (1894)	Present
<i>Areca guppyana</i> Becc., 93294	Present, abundant
<i>Bentinckia nicobarica</i> (Kurz) Becc., 83150C	Absent
<i>Brassiophoenix drymophloeoides</i> Burret, FG3172J	Sparse
<i>Calyptrocalyx cf. holrungii</i> (Becc.) J. L. Dowe & M. D. Ferrero, 64140	Present
<i>Calyptrocalyx cf. polyphyllus</i> Becc., 86331A	Sparse
<i>Calyptrocalyx spicatus</i> (Lamarck) Blume, Osenbrüg (1894)	Present
<i>Carpentaria acuminata</i> (H. Wendl. & Drude) Becc., 89213B	Absent
<i>Cyrtostachys renda</i> Blume, Chee <i>et al.</i> FRIM 47370	Present, abundant
<i>Clinostigma samoense</i> H. Wendl., 79218G	Absent
<i>Dictyosperma album</i> (Bory) H. Wendl. & Drude ex Scheff. var. <i>aureum</i> Balf. f., 88373A	Absent
<i>Drymophloeus pachycladus</i> (Burret) H. E. Moore, 65982F	Present, abundant
<i>Drymophloeus subdistichus</i> (H. E. Moore) H. E. Moore, 76396A	Present
<i>Dypsis decaryi</i> (Jum.) Beentje & J. Dransf., 92253A	Present
<i>Dypsis leptocheilos</i> (Hodel) Beentje & J. Dransf., 93324B	Present, abundant
<i>Dypsis lutescens</i> (H. Wendl.) Beentje & J. Dransf., FG4016	Present, abundant
<i>Euterpe edulis</i> Mart., Osenbrüg (1894)	Sparse
<i>Euterpe oleracea</i> Mart., Osenbrüg (1894)	Present, abundant
<i>Heterospatha elata</i> Scheffer, 79252B	Absent
<i>Heterospatha phillipsii</i> D. Fuller & J. L. Dowe, Phillips s.n.	Absent
<i>Hydriastele rostrata</i> Burret, FG3175N	Sparse
<i>Iguanura sp.</i> , 87269	Present, abundant
<i>Kentiopsis oliviformis</i> (Brongn. & Gris.) Brongn., 77146C	Absent
<i>Normanbya normanbyi</i> (W. Hill) L.H. Bailey, 66656B	Present, abundant
<i>Oenocarpus bacaba</i> Mart., Osenbrüg (1894)	Present
<i>Oenocarpus bataua</i> Mart., Osenbrüg (1894)	Present
<i>Oncosperma horridum</i> Scheff., Chee <i>et al.</i> FRIM47323	Present, abundant
<i>Oncosperma tigillarum</i> (Jack) Ridl., 6472D	Sparse
<i>Orania sylvicola</i> (Griff.) H. E. Moore (as <i>O. macrocladus</i> Mart.), Osenbrüg (1894)	Absent
<i>Orania sp.</i> , 82434	Absent
<i>Pinanga coronata</i> Blume, 6227G	Present, abundant
<i>Pinanga coronata</i> Blume (as <i>P. kuhlii</i> Blume), Osenbrüg (1894)	Present
<i>Pinanga negrosensis</i> Becc., 92160	Present
<i>Pinanga malaiana</i> Scheff., Chee <i>et al.</i> FRIM47306	Present, abundant
<i>Pinanga malaiana</i> Scheff., Chee <i>et al.</i> FRIM47351	Present, abundant
<i>Pinanga scortechini</i> Becc., Chee <i>et al.</i> FRIM47348	Present, abundant
<i>Prestoea acuminata</i> (Willd.) H. E. Moore var. <i>montana</i> (Graham) Henderson & Galeano (as <i>Euterpe montana</i> Grah.), Osenbrüg (1894)	Sparse
<i>Ptychosperma burretiana</i> Essig, 81592D	Absent
<i>Ptychosperma caryotoides</i> Ridl., 74263D	Sparse
<i>Ptychosperma salomonense</i> Burret, 951015E	Absent

TABLE 1. Continued

Taxon, accession or voucher	Raphides in embryo
<i>Ptychosperma</i> sp., FG4786A	Sparse
<i>Rhopalostylis sapida</i> H. Wendl. & Drude, Boyer s.n.	Absent
<i>Roystonea borinquena</i> O. F. Cook, Zona & Salzman 481	Absent
<i>Roystonea lenis</i> León, Zona <i>et al.</i> 390	Absent
<i>Roystonea oleracea</i> (Jacq.) O. F. Cook (as <i>Oreodoxa oleracea</i> Mart.), Osenbrüg (1894)	Absent
<i>Roystonea oleracea</i> (Jacq.) O. F. Cook, 96538A	Absent
<i>Roystonea princeps</i> Burret, 64563A	Absent
<i>Roystonea regia</i> (Kunth) O. F. Cook, 94-1090A	Absent
<i>Satakentia likiuensis</i> (Hatusima) H. E. Moore, 68317J	Absent
<i>Siphokentia beguinii</i> Burret, 82538C	Absent
<i>Solfia samoensis</i> Reching, Tipama'a 1	Sparse
<i>Veitchia arecina</i> Becc., 74116F	Absent
<i>Veitchia spiralis</i> H. Wendl., 961336G	Sparse
<i>Veitchia winin</i> H. E. Moore, Zona & Lewis 881	Present
<i>Veitchia winin</i> H. E. Moore, 79208A	Sparse
<i>Wodyetia bifurcata</i> A. K. Irvine, 8234E	Absent
<i>Wodyetia bifurcata</i> A. K. Irvine, 93320A	Absent
Cocoeae	
<i>Acrocomia aculeata</i> (Jacq.) Lodd. ex Mart. (as <i>A. sclerocarpa</i> Mart.), Osenbrüg (1894)	Absent
<i>Aiphanes minima</i> (Gaertner) Burret, FG4040	Absent
<i>Allagoptera arenaria</i> (Gomes) Kuntze, 64817R	Absent
<i>Astrocaryum mexicanum</i> Liebm. ex Mart., 931041	Absent
<i>Attalea</i> sp. (as ' <i>Attalea guichire</i> '), Osenbrüg (1894)	Absent
<i>Bactris major</i> Jacq., RM1583A	Absent
<i>Butia capitata</i> (Mart.) Becc. (as <i>Cocos australis</i> hort.), Osenbrüg (1894)	Absent
<i>Cocos nucifera</i> L., 952146A	Absent
<i>Desmoncus orthocanthos</i> Mart., 62153A	Sparse
<i>Elaeis guineensis</i> Jacq., Osenbrüg (1894)	Absent
<i>Elaeis guineensis</i> Jacq., P1959B	Absent
<i>Gastrococos crista</i> (Kunth) H. E. Moore, 661023B	Absent
<i>Syagrus amara</i> (Jacq.) Mart., 80296D	Absent
<i>Syagrus</i> × <i>costae</i> Glassman, 62232D	Absent
<i>Syagrus orinocensis</i> (Spruce) Burret, 61208C	Absent
<i>Syagrus schizophylla</i> (Mart.) Glassman, 961125A	Absent
<i>Syagrus</i> sp., 59894E	Absent
Geonomeae	
<i>Calyptronoma rivalis</i> (O. F. Cook) L. H. Bailey, 81292A	Absent
<i>Geonoma interrupta</i> (Ruiz & Pav.) Mart. var. <i>interrupta</i>, Zona <i>et al.</i> 944	Sparse
Phytelephantoideae	
<i>Phytelephas macrocarpa</i> Ruiz & Pav., Osenbrüg (1894)	Absent

Taxa positive for raphides are in boldface type.

All accession numbers refer to plants growing at Fairchild Tropical Garden. Collector and collection number refer to voucher or spirit collections at FTG, unless otherwise indicated.

Raphide presence was qualified as 'sparse' when fewer than ten raphide bundles were seen in the embryo or 'abundant' when more than 25 bundles were observed.

Material studied by Osenbrüg (1894) is included; nomenclature for his material is updated to follow Moore (1963), Uhl and Dransfield (1987), Henderson (1995) and Henderson *et al.* (1995).

observed in the embryo preparation. No other mineral inclusions, such as silica bodies or styloids, were observed in palm embryos.

RESULTS

The results of this survey of 148 taxa are presented in Table 1, organized by taxonomic tribes (Uhl and Dransfield, 1999), which are more likely to represent monophyletic groups. To present a more complete picture, the 35 observations of Osenbrüg (1894) are also included in Table 1, alongside 127 new observations. The new observations overlap with those of Osenbrüg for only six taxa, but in each case the new results agree with those presented by

Osenbrüg (1894). Eight taxa were sampled from two different accessions, but in each case the results were concordant.

Raphides were observed in the embryos of palms from only six tribes, the Corypheae, Hyophorbeae, Caryoteae, Areceae, Cocoeae and Geonomeae. These tribes are presently classified in three subfamilies: Coryphoideae, Ceroxyloideae and Arecoideae (Uhl and Dransfield, 1999). Raphides were not observed in the following groups: Calameae and Lepidocaryeae (which together comprise the Calamoideae), Phoeniceae, Borasseae, Cyclospatheae, Ceroxyleae and Phytelephantoideae. Embryos of the Nypoideae, Iriarteae and Podococoeae were not available for examination.

Within the Corypheae, *Rhapis excelsa*, one species of *Livistona* and the monotypic genus *Zombia* were observed to have raphides present in their embryos. Many species of *Livistona* remain to be sampled, as do several recognized species of *Rhapis*, but the data show the trait of raphides in embryos to be variable within the genus *Livistona*.

Only one member of the Hyophorbeae, *Chamaedorea tepejilote*, was found to have raphides in its embryos, although two other species were lacking raphides.

The three genera of the Caryoteae, well known for their raphide-rich fruits, were surprisingly diverse in the raphide content of their embryos. Most species of *Arenga* lacked raphides, while *Caryota* and *Wallichia* had raphides in their embryos.

Raphides were present in the embryos of 19 genera from the Areceae, including members of the subtribes Ptychospermatinae (Fig. 1), Dypsidinae, Linospadicinae, Arecinae (Fig. 2), Euterpeinae, Cyrtostachydinae, Oncospermatinae and Archontophoenicinae. One noteworthy sample from among these genera is *Solfia samoensis*, the sole member of its genus. Although the sizes of raphide bundles were not recorded, *Solfia* was unique in having small bundles, less than half the size of bundles in other palms and difficult to see without polarized light.

Only one sample of Cocoeae was observed to have raphides in its embryo: *Desmoncus orthocanthos* (as *D. chinatensis* Leibm. ex Mart) had approximately five raphide bundles in the embryo examined. Likewise, of the two Geonomeae sampled, one, *Geonoma interrupta* var. *interrupta*, was found to have raphides in its embryos.

DISCUSSION

Within the palm family, the systematic value of calcium oxalate crystals was thought to be nil, as raphides are ubiquitous in the vegetative organs of palms (Tomlinson, 1961, 1990); however, Osenbrüg (1894) demonstrated that raphide presence in embryos is a variable trait. The results

presented here give a clearer picture of the systematic distribution of raphides in palm embryos, which are neither randomly nor evenly distributed among the 148 taxa surveyed.

Raphides were observed in three out of 42 Coryphoideae samples, an occurrence rate of 7%. Osenbrüg (1894) did not report raphides among any of the eight genera from the Coryphoideae examined by him. Among the three tribes that comprise the Coryphoideae, only the Corypheae has members with raphides in their embryos. The three samples in which raphides were observed are from three genera – *Livistona*, *Rhapis* and *Zombia* – that are not believed to be closely related (Hahn, 2002).

The subfamily Ceroxyloideae—comprising the Ceroxyleae, Hyophorbeae and Cyclospatheae—is surely not monophyletic; however, its three tribes taken individually show evidence of monophyly (Lewis and Doyle, 2001; Hahn, 2002). No raphides were observed by Osenbrüg in one member of the Ceroxyleae, nor did this study find raphides in the embryos of Cyclospatheae. Raphides were found in one *Chamaedorea* of the Hyophorbeae; however, as the genus *Chamaedorea* is large and diverse additional sampling is needed before one can draw meaningful conclusions about the rate of occurrence of raphides in embryos in this Hyophorbeae.

The subfamily Arecoideae comprises six tribes, four of which were sampled in the present study. In the tribe Caryoteae, which comprises three genera, only *Caryota* and *Wallichia* appear to have abundant raphides in their embryos, and this character may help set these two genera apart from the remaining genus, *Arenga*. The presence of raphides in the embryos of *Arenga tremula*, however, is a caution flag to an otherwise clear distinction between *Arenga* and the other genera.

The tribe Areceae has the most species with raphides in their embryos. Of 55 taxa of Areceae reported in Table 1, 34 were found to have at least some raphides in their embryos, which is an occurrence rate of 62%. Only two genera,

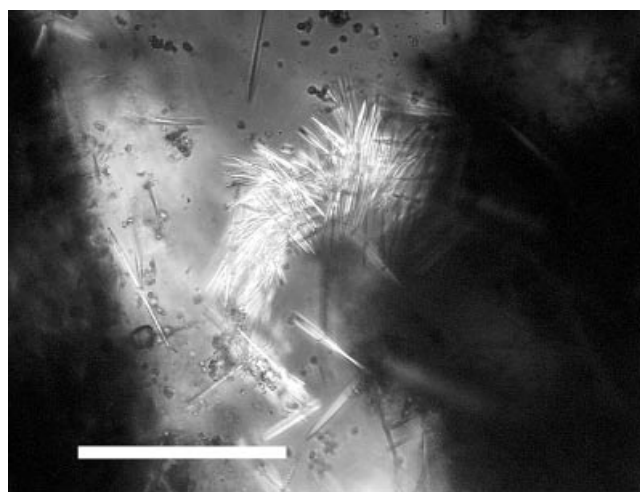


FIG. 1. Embryo squash of *Drymophloeus pachycladus* (65982F) in crossed polarized light, showing abundant raphides of calcium oxalate. Scale bar = 0.1 mm.

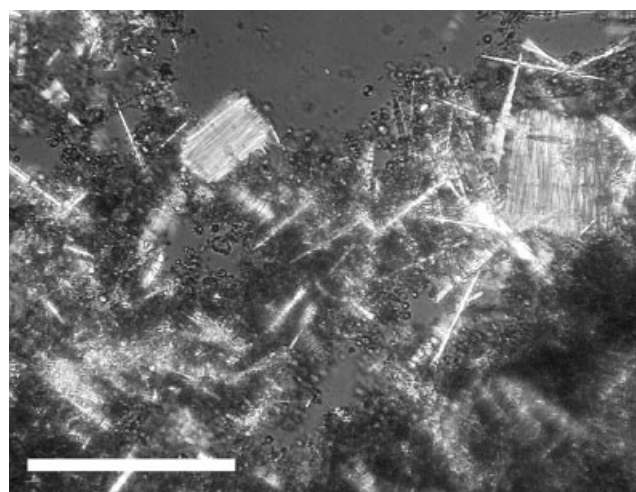


FIG. 2. Embryo squash of *Pinanga negrosensis* (92160) in crossed polarized light, showing abundant raphides of calcium oxalate. Scale bar = 0.1 mm.

Ptychosperma and *Veitchia*, both members of the Ptychospermatinae, had species with and without raphides in their embryos, an observation suggesting that the raphide presence might be taxonomically useful at the species level. The tribe Cocoeae, as reported by Osenbrüg (1894), lacked raphides in the embryos of its species. However, this survey found one member, *Desmoncus orthocanthos*, that has raphides in its embryos, albeit sparsely. One species out of 19 Cocoeae reported in Table 1 is an occurrence rate of 5%. Only two species of Geonomeae were sampled, and one species of *Geonoma* was found to have raphides in its embryos. Additional sampling is desired.

There is no correlation between the presence of raphides in anthers (Henderson and Rodríguez, 1999) and raphides in embryos (this study). Thirty-three taxa were sampled in both studies. The results of a Fisher Exact Probability test show no positive or negative association for the two conditions (P one-tailed = 0.36773; P two-tailed = 0.69422).

The function of raphides in embryos has not been addressed experimentally; however, there are several hypotheses for the function of raphides in plant cells, and these provide a useful framework in which to address the question in regard to palm embryos. Raphides may serve as a calcium storage depot, to be tapped as needed (Franceschi, 1989; Ilarsan *et al.*, 1996; Ilarsan *et al.*, 2001), and certainly, rapid seedling development and growth require an adequate supply of calcium. Raphides may also serve as a source of oxalate, which some plants secrete from their root tips to detoxify aluminium ions in the soil (Ma and Miyasaka, 1998; Ma *et al.*, 2001). Oxalate can be broken down by oxalate oxidase into carbon dioxide and hydrogen peroxide; the latter is critical in cross-linking cell wall polymers during cell wall extension (Lane, 1994), another process that is common in rapidly growing and developing seedlings. Raphides may also play a role in sequestering excess calcium (Franceschi, 1989; Fink, 1991; Webb, 1999), although one imagines that an embryo would be an unlikely sink for excess minerals. Finally, raphides have a known function as an anti-herbivory defence (Ward *et al.*, 1997; Finley, 1999; Molano-Flores, 2001). As herbivores are deterred only after they initiate chewing and as embryos are very small and could be fatally damaged by even minor herbivory, investing embryos with raphides hardly seems like an effective defensive strategy. Palm seeds are, in general, well protected by fibres, tannins, raphides and silica bodies in the tissues of the ovary (Uhl and Moore, 1973). The most likely—but as yet untested—function for raphides in palm embryos is as storage depots for calcium, oxalate and/or hydrogen peroxide.

Regarding those embryos lacking raphides, a question that remains unanswered by this survey is, when do seedlings acquire raphides in their vegetative tissues? At some point, presumably during or immediately after germination, raphides are formed in the seedlings, where they have a presumed defensive function (Tomlinson, 1990).

Given their scattered occurrence in the family, raphides in embryos must have evolved and/or been lost many times. The presence of raphides in palm embryos follows certain phylogenetic trends and most likely has some utility as an

indicator of relationships at the subtribe level or below. In certain genera within which the trait is polymorphic, such as *Livistona* and *Ptychosperma*, the presence of raphides may be a useful taxonomic character as well. The function of raphides in embryos is a topic deserving further study.

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