

Starchy Pollen in Commelinoid Monocots

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The Commelinoid monocots are a monophyletic group comprising the Arecales, Commelinales, Poales and Zingiberales, plus the unplaced family Dasypogonaceae. Pollen from 149 taxa was examined qualitatively for starch as the primary storage product. Starchy pollen was found in 134 taxa (90% of the sample) of Commelinoid monocots. Starchy pollen thus appears to be a characteristic feature of the Commelinoid monocots. Starchy pollen can be easily observed with minimal preparation, making it a demonstrable character useful in the classroom or teaching laboratory. Furthermore, starchy pollen grains were found to be significantly larger in diameter than non-starchy grains, confirming previous hypotheses regarding pollen size and starch. © 2000 Annals of Botany Company

Key words: Arecales, Commelinales, Commelinoid monocots, Monocotyledonae, Poales, pollen, starch, Zingiberales.

INTRODUCTION

In recent years, cladistic analyses of molecular and non-molecular data have identified a well-supported lineage of four orders of Monocotyledonae known as the Commelinoid monocots (Chase *et al.*, 1995, 2000; Stevenson *et al.*, 2000). The clade includes its namesake Commelinales, along with Poales, Arecales, Zingiberales and one unplaced family, the Dasypogonaceae (Chase *et al.*, 2000). The Commelinoid monocots include cosmopolitan families, such as the Poaceae and Cyperaceae, but most of the clade's families are tropical. These tropical families include large and well-known families, such as the Arecaceae, Bromeliaceae and Zingiberaceae, as well as smaller, less-familiar families, such as the Lowiaceae, Hanguanaceae and Centrolepidaceae.

The families of the Commelinoid monocots are given in Table 1, following the classification of the Angiosperm Phylogeny Group (1998) with modifications of Chase *et al.* (2000). The families are ecologically and morphologically diverse, including plants that are arborescent or herbaceous; terrestrial, epiphytic or aquatic; perennial, biennial or annual; polycarpic or monocarpic; and biotically and abiotically pollinated. Nevertheless, they are united by molecular characters, including restriction site mapping (Davis, 1995) and the sequences of the chloroplast-encoded *rbcL* (Chase *et al.*, 1993; Duvall *et al.*, 1993) and *atpB* genes (Chase *et al.*, 2000), the mitochondrion-encoded *atpA* gene (Stevenson *et al.*, 2000), and nuclear 18S ribosomal DNA (Soltis *et al.*, 1997). Moreover, the Commelinoid monocots are also defined by certain anatomical and chemical characters. They share fluorescent ferulic acid in their cell walls (Harris and Hartley, 1980; Harris, 2000), *Strelitzia*-type epicuticular wax (Barthlott and Frölich, 1983), and

starchy endosperm or perisperm, except in the Arecaceae (Dahlgren *et al.*, 1985; Kubitzki, 1998).

Dehiscent pollen of conifers and flowering plants contains as its energy source carbohydrates and lipids. It is likely that all pollen contains at least some lipids, but some pollen appears to use only lipids as a primary source of energy. Conversely, some pollen relies mainly on carbohydrates, although lipids are not completely absent. Among pollen carbohydrate reserves, starch is common, and in practice, pollen can be classified as either 'starchy' (starch-containing) or 'non-starchy' (=lipid rich or starch-free).

Two previous surveys of pollen starch content (Baker and Baker, 1979; Franchi *et al.*, 1996) included some

TABLE 1. *The classification of the Commelinoid monocots (after the Angiosperm Phylogeny Group, 1998), with modifications by Chase et al. (2000). Families sampled for this study appear in bold*

Unplaced	Joinvilleaceae
Dasypogonaceae	Juncaceae
Arecales	Mayacaceae
Arecaceae	Poaceae
Commelinales	Rapateaceae
Commelinaceae	Restionaceae
Haemodoraceae	Sparganiaceae
Hanguanaceae	Thurniaceae (incl. Prioniaceae)
Philydraceae	Typhaceae
Pontederiaceae	Xyridaceae (incl. Abolbodaceae)
Poales	Zingiberales
Anarthriaceae	Cannaceae
Bromeliaceae	Costaceae
Centrolepidaceae	Heliconiaceae
Cyperaceae	Lowiaceae
Ecdiocolaceae	Marantaceae
Eriocaulaceae	Musaceae
Flagellariaceae	Strelitziaceae
Hydatellaceae	Zingiberaceae

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Commelinoid monocots, but neither sampled extensively from throughout the orders that comprise the clade. This survey was undertaken to examine the taxonomic distribution of starchy pollen in the Commelinoid monocots. In addition, I addressed the hypotheses that starchy pollen is associated with large pollen diameter and with pollination by wind or animals that do not feed on pollen.

MATERIALS AND METHODS

The choice of material was opportunistic, governed by flower availability in the living collection of Fairchild Tropical Garden (Miami, USA), which is particularly strong in Arecales, Bromeliaceae and Zingiberales. Material taken from the Garden's living collection is indicated by its accession number in Table 2. For plant groups under-represented in the Garden's living collection, e.g. Poales and Commelinales, herbarium material was used, indicated in Table 2 by collector(s), collection number, and herbarium, either the Royal Botanic Gardens, Kew (K) or Fairchild Tropical Garden (FTG). Grayum (1985) found herbarium material was adequate for starch analysis. Five samples were also taken from unaccessioned plants growing spontaneously in the grounds of Fairchild Tropical Garden. Two samples of Lowiaceae were from the private collection of David Bar-Zvi, Hollywood, Florida.

Fresh material was processed within 1 h of collecting and examined within 30 min of staining. Only mature pollen from dehiscing anthers was surveyed. Pollen mounted in glycerine:water (1 : 1) was examined with a light microscope (200 ×) with polarized light. The presence or absence of birefringence was recorded. Additional pollen was mounted in a drop of IKI stain (Johansen, 1940) and examined for the presence or absence of starch. The staining reaction occurs almost immediately if starch is present. The colour of stained starch was recorded. Herbarium material was stained and examined in the same way.

A positive starch reaction was scored according to the categories proposed by Franchi *et al.* (1996): three colour reactions, brown, blue and black, together with the presence or absence of birefringence. In this study, pollen was scored as brown when the pollen cytoplasm took on a uniform brown colour even though individual starch granules were not apparent. In contrast, pollen that stained black often had visible granules of starch. No blue-staining starch was observed in this study.

Pollen size (longest diameter) was determined from fresh, hydrated pollen measured with an ocular micrometer and is presented as the mean of ten measurements, rounded to the nearest micrometer, and standard deviation. No attempt was made to control for distortions caused by the pressure of the cover slip, but ruptured or squashed pollen was avoided and not included in the size measurement.

RESULTS AND DISCUSSION

Most of the 149 taxa examined had starchy pollen (Table 2). Pollen from 134 taxa (90%) of Commelinoid monocots was classified as starchy. Starch was not found in 15 taxa (10%);

however, seasonal variation may account for the absence of starch in some of these samples (see below).

Only one herbarium specimen of Dasygogonaceae was available for examination. In this survey, *Calectasia cyanea* was found to have non-starchy pollen. Although the family is small, comprising four genera and eight species (Kubitzki, 1998), sampling is not sufficient to suggest general conclusions. Additional samples, preferably from fresh flowers, are needed.

The order Arecales, comprising the family Arecaceae, was well sampled. Most (87%) of the taxa had brown starch in their pollen. Some palms exhibited seasonal variation in their pollen starchiness. Several taxa (*Astrocaryum mexicanum*, *Cocos nucifera*, *Dictyospermum album*, *Dypsis decaryi* and *Phoenix roebelenii*) were sampled during the winter dry season and found to be non-starchy, but the same individuals sampled in the summer were found to have brown starchy pollen. For this reason, only palms sampled in the summer are included in this survey.

Tischler (1910), Todd and Bretherick (1942) and Mameli Calvino (1952) reported that palms have non-starchy pollen. Seasonal variation in starch production may account for their findings, or palms from dry areas may have evolved non-starchy pollen. These workers reported mostly on the genus *Phoenix*, most species of which are denizens of dry, Mediterranean or desertic habitats. Franchi *et al.* (1996) examined two species of *Brahea* (*B. calcarea* Liebm. and *B. edulis* H. Wendl. ex S. Watson) and *Chamaerops humilis* L. and found them to be non-starchy. These palms are also from seasonally dry areas. In grasses, starch synthesis in pollen mother cells is known to be highly sensitive to drought (Dorion *et al.*, 1996; Sheoran and Saini, 1996; Lalonde *et al.*, 1997; Saini, 1997). Pollen of palms from dry areas may have evolved away from starchiness as a way of circumventing the drought sensitivity of starch synthesis in pollen mother cells. Unfortunately, the present survey does not examine the same species of palms found to be non-starchy by previous workers. Nevertheless, the pollen of the palms sampled here was abundantly starchy.

The order Commelinales is under-represented in Table 2, as it includes families not well represented in the living collection of Fairchild Tropical Garden or in herbaria (the deliquescent flowers of Commelinaceae are notoriously difficult to preserve). Most (73%) of the taxa of Commelinales sampled had either brown or black starch. Baker and Baker (1979) listed Commelinaceae, Haemodoraceae and Pontederiaceae as non-starchy, but the results presented here suggest that at least some taxa have starchy pollen.

The order Poales contains some families well known for their starchy pollen, e.g. Poaceae and Typhaceae (Todd and Bretherick, 1942). Sampling was not optimum, as many of the families are not well represented in the living collection of Fairchild Tropical Garden (with the exception of Bromeliaceae). Nevertheless, most (83%) of the taxa of Poales sampled had starchy pollen. Baker and Baker (1979) reported that the Poaceae and Typhaceae are starchy and that the Cyperaceae and Juncaceae contain at least some taxa with starchy pollen. These results also supplement the findings of Franchi *et al.* (1996), who found that all 19 species of Poaceae sampled had starchy pollen of various

TABLE 2. Distribution of starchy pollen in Commelinoid monocots. Starch classification follows Franchi et al. (1996): 1, non-starchy grains; 2, brown not birefringent starch; 3, brown birefringent starch; 4, blue not birefringent starch; 5, blue birefringent starch; 6, black not birefringent starch; 7, black birefringent starch. Asterisk indicates scant presence of starch. Size is the mean of ten measurements

Taxon	Source	Starch	Mean size (µm)	± s.d.
Unplaced Family				
Dasyopogonaceae				
<i>Calectasia cyanea</i> R. Br.	Anway 149 K	1	43	3
Arecales				
Arecaceae				
Arecoideae				
<i>Allagoptera arenaria</i> (Gomes) Kuntze	64817R	2	40	1
<i>Areca vestiaria</i> Giseke	73451B	2	30	2
<i>Astrocaryum mexicanum</i> Leibm. ex Mart.	5880B	2	48	3
<i>Attalea guaranitica</i> Barb. Rodr.	59344A	2	52	3
<i>Carpentaria acuminata</i> (H. Wendl. & Drude) Becc.	89213B	2	48	3
<i>Cocos nucifera</i> L. 'Golden Malay'	952129DD	2	56	4
<i>Dictyosperma album</i> (Bory) Scheffer	88207A	2	45	2
<i>Dyopsis decaryi</i> (Jum.) Beentje & J. Dransfield	92253B	2*	39	4
<i>Gastrococos crispa</i> (Kunth) H.E. Moore	661023B	1	49	8
<i>Pinanga coronata</i> (Bl. ex Mart.) Bl.	6227G	2	42	2
<i>Syagrus</i> sp.	59894F	1	34	2
<i>Syagrus amara</i> (Jacq.) Mart.	80296N	2	40	3
<i>Syagrus sancona</i> H. Karst.	83132F	2	35	2
<i>Veitchia vitiensis</i> (H. Wendl.) H.E. Moore	89204B	2	45	3
Calamoideae				
<i>Calamus</i> sp.	Zona & Hausman 622 FTG	2	29	2
<i>Calamusambojensis</i> Becc.	Zona 617 FTG	2	30	2
<i>Raphia humilis</i> Chev.	Fantz 3462 FTG	1	19	2
Ceroxyloideae				
<i>Chamaedorea metallica</i> O.F. Cook ex H.E. Moore	86173A	2	31	2
<i>Hyophorbe verschaffeltii</i> H. Wendl.	72781A	2*	37	2
Coryphoideae				
<i>Acoelorrhaphe wrightii</i> (Griseb. & H. Wendl.) H. Wendl. ex Becc.	671227B	2	32	2
<i>Chuniophoenix nana</i> Burret	8178C	2	27	2
<i>Hyphaene dichotoma</i> (White) Furtado	64111A	2	35	2
<i>Licuala peltata</i> Roxb. ex Buch.-Ham. var. <i>sumawongii</i> L.G. Saw	70320G	2	37	2
<i>Phoenix reclinata</i> Jacq.	68459	2	20	2
<i>Phoenix roebelinii</i> O'Brien	RM406G	2	18	1
<i>Sabal etonia</i> Swingle ex Nash	87137C	2	41	3
<i>Sabal palmetto</i> (Walt.) Lodd. ex J.A. & J.H. Schultes	s.n.	2	41	3
<i>Serenoa repens</i> (Bartr.) Small	RM2021	2	32	1
<i>Thrinax morrisii</i> H. Wendl.	93985C	2	22	2
Nypoideae				
<i>Nypa fruticans</i> Wurm	FG161A	2	48	2
Phytelephantoideae				
<i>Phytelephas macrocarpa</i> Ruiz & Pavon	70279	1	70	5
Commelinales				
Commelinaceae				
<i>Commelina diffusa</i> Burm. f.	s.n.	6	41	3
<i>Tradescantia pallida</i> (Rose) D. Hunt	93355B	6*	58	2
<i>Tradescantia spathacea</i> Sw.	s.n.	6*	37	4
<i>Tradescantia zebrina</i> Bosse	s.n.	6	70	4
Haemodoraceae				
<i>Anigozanthos flavida</i> DC.	Fisher s.n. FTG	2,6	62	5
<i>Lachnanthes caroliniana</i> (Lam.) Dandy	Penneys & Cherry 1060 FTG	2	33	2
<i>Lophiola aurea</i> Ker Gawl	Wunderlin & Beckner 9300 FTG	1	23	2
<i>Xiphidium caeruleum</i> Aubl.	Sanders 1627 FTG	1	33	3
Hanguanaceae				
<i>Hanguana</i> sp.	Boyce 764 K	1	22	2

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TABLE 2. Continued.

Taxon	Source	Starch	Mean size (μm)	\pm s.d.
Philydraceae				
<i>Philydrum lanuginosum</i> Banks & Sol. ex Gaertn.	Sands 5051 K	2	tetrads	
Pontederiaceae				
<i>Pontederia cordata</i> L.	s.n.	2*	52	4
Poales				
Anarthriaceae				
<i>Anarthria scabra</i> R. Br.	Strid 20445 K	6	45	3
Bromeliaceae				
Bromelioideae				
<i>Aechmea</i> sp.	981267	1	38	5
<i>Aechmea lasserii</i> L.B. Smith	88641	2	72	3
<i>Aechmea luddemanniana</i> (K. Koch) Mez	67406A	2	42	2
<i>Aechmea tesmannii</i> Hamms	ID3172-9952	1	52	2
<i>Aechmea weilbachii</i> F. Didr.	ID324	1	40	3
<i>Androlepis skinneri</i> Brongn.	93376C	1	tetrads	
<i>Billbergia braziliensis</i> L.B. Smith	991530	1,2	66	3
<i>Hohenbergia stellata</i> Schultes f.	981271	2	47	3
<i>Neoregelia ampullacea</i> (E. Morr.) L.B. Smith	88640	2	41	2
<i>Neoregelia odorata</i> Leme	981283	2	43	2
Pitcairnioideae				
<i>Navia arida</i> L.B. Smith & Steyerf.	97503	2	48	7
<i>Pepinia sanguinea</i> H. Luther	961479A	2	46	3
<i>Pitcairnia punicea</i> Scheidw.	FG826	1	41	5
<i>Pitcairnia xanthocalyx</i> Mart.	76582A	1	42	2
Tillandsioideae				
<i>Guzmania sanguinea</i> André ex Mez	82580	2	59	3
<i>Tillandsia hildae</i> Rauh	991521	2	74	2
<i>Vriesia fenestralis</i> Linden & André	82584	2*	82	8
<i>Vriesia imperialis</i> Carriere	95578	2	72	5
<i>Vriesia simplex</i> Beer	84464	2	76	6
Centrolepidaceae				
<i>Centrolepis strigosa</i> (R. Br.) Roem. & Schult.	Coveny & Wilson 11686 K	6	28	3
Cyperaceae				
<i>Carex glaucescens</i> Ell.	Orzell & Bridges 15495 FTG	2	33	2
<i>Eleocharis elegans</i> (HBK) Roem. & Schult.	Kelloff et al. 365 FTG	6	26	2
<i>Eleocharis geniculata</i> (L.) Roem. & Schult.	Bradley 299 FTG	6	32	4
<i>Fuirena squarrosa</i> Michx.	Orzell & Bridges 17961 FTG	2	27	1
<i>Gahnia schoenoides</i> Forst.f.	Fosberg & Sachet 54686 FTG	1	42	2
Ecdiocolaceae				
<i>Ecdiocola monostachya</i> F. Muell.	Briggs & Johnson 8532 K	6	46	2
Eriocaulaceae				
<i>Eriocaulon decangularis</i> L.	Orzell & Bridges 18584 FTG	6	32	1
<i>Lachnocaulon anceps</i> (Walt.) Morong	Orzell & Bridges 16675 FTG	6	27	1
Flagellariaceae				
<i>Flagellaria indica</i> L.	Corner RSS 2701 K	2	18	1
Joinvilleaceae				
<i>Joinvillea ascendens</i> Gaud. ex Brongn. & Gris ssp. <i>borneensis</i> (Becc.) T.K. Newell	Coode et al. 7575 K	6	29	2
Mayacaceae				
<i>Mayaca fluviatilis</i> Aubl.	Orzell & Bridges 15162 FTG	2	42	3
Poaceae				
<i>Muhlenbergia</i> sp.	951089	6	34	4
<i>Setaria palmifolia</i> Stapf	971613	6	41	5
<i>Thysanolaena maxima</i> Kuntze	X1483B	6	30	4
<i>Tripsacum floridanum</i> Porter ex Vasey	89434A	2	41	3
Restionaceae				
<i>Restio pachystachys</i> Kunth	Esterhuysen 29515 K	6	51	4

Table 2 continued over the page

TABLE 2. *Continued.*

Taxon	Source	Starch	Mean size (μm)	\pm s.d.
Sparganiaceae				
<i>Sparganium americanum</i> Nutt.	Correll & Correll 53907 FTG	6	26	3
Xyridaceae				
<i>Abolboda grandis</i> Griseb. var. <i>rigida</i> Malme	Maguire et al. 43817 K	6	179	11
<i>Xyris jupicai</i> L. Richard	Orzell & Bridges 18588 FTG	2	42	3
Zingiberales				
Cannaceae				
<i>Canna indica</i> L.	90335E	2	68	3
<i>Canna jaegeriana</i> Urban	90355	2	76	3
<i>Canna tuerkheimii</i> Kränzlin	951453A	2	70	3
<i>Canna warszewiczii</i> Dietrich	2000-132	2	70	2
Costaceae				
<i>Costus barbatus</i> Suesseng.	8595B	6	117	8
<i>Costus curvibracteatus</i> Maas 'Green Mountain'	97582A	6	104	4
<i>Costus dubius</i> (Afzel.) Schum.	95827A	6	99	4
<i>Costus lucanusianus</i> J. Braun & K. Schum.	95815A	6	95	4
<i>Costus malortieanus</i> H. Wendl.	65596	6	103	3
<i>Costus pictus</i> D. Don ex Lindl.	95814B	6	110	6
<i>Costus talbotii</i> Ridl.	97494	6	101	17
<i>Costus tappenbeckianus</i> J. Braun & K. Schum.	97579A	6	108	7
<i>Dimerocostus strobilaceus</i> Kuntze ssp. <i>strobilaceus</i>	76334	6	154	9
<i>Monocostus uniflorus</i> (Poepp. ex O.G. Pet.) Maas	76678	6	121	9
<i>Tapeinochilos ananassae</i> Hassk.	83458	6	127	13
Heliconiaceae				
<i>Heliconia angusta</i> Vellozo	70563	2	70	5
<i>Heliconia aurantiaca</i> Ghiesbreght ex Lemaire	591160B	2*	67	2
<i>Heliconia chartacea</i> Lane ex Souza	91637	1,2	68	2
<i>Heliconia collinsiana</i> Griggs	77206	1,2	69	2
<i>Heliconia episcopalis</i> Vellozo	93616A	2	91	4
<i>Heliconia indica</i> Lamark 'Spectabilis'	72112	2	81	7
<i>Heliconia metallica</i> Planchon & Linden ex Hooker	81648	2	75	3
<i>Heliconia mutisiana</i> Cuatrecasas	86568	2	76	5
<i>Heliconia rostrata</i> Ruiz & Pavón	62118C	2	74	4
<i>Heliconia subulata</i> Ruiz & Pavón	87248B	2	63	1
<i>Heliconia wilsonii</i> Daniels & Stiles	952078	2	74	2
Lowiaceae				
<i>Orchidantha fimbriata</i> Holttum	s.n.	6	164	23
<i>Orchidantha maxillarioides</i> (Ridl.) K. Schum.	s.n.	2	134	13
Marantaceae				
<i>Calathea albertii</i> (Pynaert & Van Geert) L.H. Bailey	671243	6	133	6
<i>Calathea</i> \times <i>argyrophylla</i> Hort.	83466	6	139	5
<i>Calathea burle-marxii</i> H. Kennedy 'Ice Blue'	83397	6	185	5
<i>Calathea lancifolia</i> Boom	68486	2	124	7
<i>Calathea marantifolia</i> Standley	67664B	6	164	3
<i>Calathea undulata</i> Lindl. & André	88662	6	140	8
<i>Calathea varians</i> (K. Koch & Mathieu) Körn.	724	6	139	3
<i>Calathea warszewiczii</i> (Mathieu) Körn.	69722	2,6	158	12
<i>Donax canniiformis</i> (Forst.) Schum.	951382A	6	125	10
<i>Stromanthe sanguinea</i> (Hook.) Sonder.	71703	6	124	6
<i>Stromanthe stromanthoides</i> (J. F. Macbr.) L. Andersson	93679	6	154	17
Musaceae				
<i>Musa balbisiana</i> Colla.	6222A	6	99	4
<i>Musa beccarii</i> Simmonds	961199	6	112	4
<i>Musa coccinea</i> Andrews	957143	6	95	3
<i>Musa lasiocarpa</i> Franch.	951432	6	104	7
<i>Musa ornata</i> Roxb.	952142A	6	92	10
Strelitziaceae				
<i>Strelitzia nicolai</i> Reg. & Körn.	77117A	2	57	2
<i>Strelitzia reginae</i> Banks ex Dryand.	74500B	2	116	4
<i>Ravenala madagascariensis</i> Sonn.	92511A	2	51	2

Table 2 continued over the page

TABLE 2. *Continued.*

Taxon	Source	Starch	Mean size (μm)	\pm s.d.
Zingiberaceae				
<i>Alpinia</i> sp.	90101	2	57	4
<i>Alpinia</i> cf. <i>assimilis</i> Ridley	X4368A	6	81	3
<i>Alpinia congchigera</i> Griff.	96975	7	96	6
<i>Alpinia elegans</i> K. Schum.	981186A	2,6	79	3
<i>Alpinia formosana</i> Schum.	952145	7	78	11
<i>Alpinia intermedia</i> Gagnep.	952013	6	79	6
<i>Alpinia latilabris</i> Ridley	86573	6	78	3
<i>Alpinia zerumbet</i> (Pers.) B.L. Burtt & R.M. Smith	86463A	6	77	4
<i>Amomum compactum</i> Roem. & Schult.	95159A	6	94	5
<i>Curcuma aromatica</i> Salisb.	96915A	6	84	17
<i>Curcuma parviflora</i> Wall.	97580A	6	62	3
<i>Etilingera elatior</i> (Jack) R.M. Smith	85378	6	80	4
<i>Hedychium coronatum</i> Koenig	67861B	2	81	4
<i>Kaempferia pulchra</i> Ridley	961046	6	112	6
<i>Kaempferia rotunda</i> L.	97490	6	104	9
<i>Nicolaia fulgens</i> (Ridl.) K. Larsen	981074C	2,6	84	5
<i>Riedelia corallina</i> Valetton	95813A	2	87	4
<i>Stahlianthus involucratus</i> (King ex Baker) R.M. Smith	94966	6	62	5
<i>Zingiber spectabilis</i> Griff.	961037	2,6	94	6

kinds, blue, brown or black, sometimes birefringent. Moreover, all eight species of Cyperaceae in their sample had starchy pollen. Two species of Bromeliaceae had non-starchy pollen (Franchi *et al.*, 1996). Baker and Baker (1979) found that the Bromeliaceae are non-starchy. Given their small sample sizes, their data are not inconsistent with those reported here, in which six out of 19 (32%) bromeliads had non-starchy pollen. Within the Bromeliaceae, there is no apparent systematic value in the distribution of starchy pollen at the level of subfamily. Starchy pollen is found in all three subfamilies.

The order Zingiberales is the most uniformly starchy order within the Commelinoid monocots. In this study, all of the taxa in all of the families in the order had starchy pollen. The Costaceae, Marantaceae and Musaceae had large pollen that stains black in the presence of IKI. The Cannaceae, Heliconiaceae and Strelitziaceae had brown-staining pollen. The Lowiaceae and Zingiberaceae had both brown- and black-staining taxa, and two species of *Alpinia* (Zingiberaceae) had birefringent starch. The results presented here are in partial agreement with those of Baker and Baker (1979), who found that the Marantaceae and Cannaceae had starchy pollen. They reported, however, that the Musaceae are non-starchy. Franchi *et al.* (1996) found starchy pollen in one species of *Hedychium* (Zingiberaceae) and one of *Strelitzia* (Strelitziaceae); however, their sample of *Canna* (Cannaceae) was reported to be non-starchy.

Ecological, physiological and evolutionary significance of starchy pollen

The obvious dichotomy of starchy vs. non-starchy pollen has elicited much speculation as to the function or evolutionary significance of pollen storage products. Baker and Baker (1979) addressed several hypotheses: (1) non-starchy pollen is selected when pollen-feeding insects

(Hymenoptera and Diptera) are the pollinators; (2) starchy pollen, because it is energetically less costly to produce, will be favoured in plants that are wind-pollinated or pollinated by birds and Lepidoptera; and (3) when pollen size is small, the more energy-rich lipids will be accumulated, but if pollen size is large, the less costly but less energy-rich starch will be accumulated. Baker and Baker (1979) found strong support for hypotheses 1 and 3 and for the presence of starch in wind-pollinated or autogamous species. The long, tubular flowers of many bird- and lepidoptera-pollinated species typically have long styles. Pollen tubes growing down long styles will have greater energy demands than tubes growing down short-styled flowers (Brink and MacGillivray, 1924). Hence, in long-styled flowers, there is likely to be selection for either starch-free (lipid-rich) pollen or very large starchy pollen. The Bakers (1979) found that, in bird- and lepidoptera-pollinated taxa with long styles, both starchy and non-starchy pollen can be found. In either case, however, the pollen of long-styled species is larger than that found in short-styled species. The findings of Baker and Baker (1979) were codified as 'Bakers' Starch Laws' by Grayum (1985), which say that starchy pollen is larger than non-starchy pollen, and that starchy pollen will be favoured when it is not used nutritionally by pollinators.

The results of this survey of Commelinoid monocots provide some support for Bakers' Starch Laws, but they also provide enough exceptions to suggest that either Bakers' Starch Laws are not invariant, or they are overridden by genetic constraints related to starchy endosperm production.

Pollination syndromes for the Commelinoid monocots are diverse (Kubitzki, 1998). The Poaceae and Typhaceae, both exemplars of starchy pollen, are anemophilous. The Bromeliaceae, Cannaceae and Strelitziaceae are bird-pollinated (Frost and Frost, 1981; Kress *et al.*, 1994), as are some members of the Heliconiaceae, Zingiberaceae,

Musaceae, Costaceae and Haemodoraceae (Nur, 1976; Stiles, 1979). The Lowiaceae are dung beetle-pollinated (Sakai and Inuoe, 1999); some Heliconiaceae and Musaceae are bat-pollinated (Nur, 1976; Kress, 1985). Many Commelinaceae and Marantaceae are autogamous (Faden, 2000; Kennedy, 2000). These pollination syndromes, according to Bakers' Starch Laws, would be expected to be starchy, as there would be no selection for lipid-rich pollen. Indeed, most of the taxa from the previously-named families are starchy. In contrast, many of the palms are bee- or fly-pollinated, as are some Costaceae, Commelinaceae, Marantaceae, Zingiberaceae and Xyridaceae (Schemske, 1981; Classen-Beckhoff, 1991; Kato, 1996; Faden, 2000). In these cases, non-starchy pollen is expected, but the results in Table 2 show that there are many examples of starchy pollen in these families. These exceptions are numerous enough to suggest that forces other than selection by pollinator constrain pollen carbohydrate reserves in these monocots.

Among the starchy pollen found in this survey, size varied from 18 to 179 μm (mean = 71 ± 38). Non-starchy pollen in this survey ranged from 19 to 70 μm (mean = 39 ± 13). Members of the starchy pollen group had significantly larger pollen than those of the non-starchy group (t -test = 3.11, $P < 0.005$, d.f. = 145). Bakers' Starch Laws are upheld in relation to pollen size and starchiness within the Commelinoid monocots.

An ecophysiological function for starchy pollen was advanced by Franchi *et al.* (1996), who suggested that starch in pollen is hydrolysed to form sucrose, which protects pollen membranes against desiccation. They posited that, for plants in which pollination occurs promptly after anther opening, the pollen grains need little protection against desiccation and hence do not store starch. In contrast, for pollen that may face desiccation before it finds a stigma (wind-pollinated plants or plants relying on unreliable vectors), starch offers a source of protective sucrose and other oligosaccharides. This theory may hold true for some plants, but many of the tropical monocots in this survey (e.g. Costaceae, Heliconiaceae) are pollinated by very efficient hummingbirds or euglossine bees. Moreover, the likelihood of desiccation in the humid tropics is low. For the tropical plants in this survey, the hypothesis of Franchi *et al.* (1996) is unsatisfactory.

A different explanation for starchy pollen is the genetic one, that starchy pollen is controlled by the same gene(s) that governs starch accumulation in endosperm (or perisperm). The gametophytic storage products are under the same genetic control, the *waxy* gene, *wx* (also called *glutinous*) (Brink and MacGillivray, 1924; Okagaki and Wessler, 1988). The *waxy* gene encodes granule-bound starch synthase (GBSSI), which is required for synthesis of amylose in endosperm and pollen (Mason-Gamer *et al.*, 1998). Selection for starchy endosperm may constrain evolutionary change in the pollen. This explanation may account for most, if not all, cases of Commelinoid monocots in which both endosperm (or perisperm) and pollen store starch.

Recent work, however, has shown that the expression of starch is tissue-specific and that its expression in the endosperm can be uncoupled from its expression in pollen

(Bryce and Nelson, 1979; Mikami *et al.*, 1999). This uncoupling may account for the presence of starchy pollen in the Arecaceae, where the endosperm contains lipids, proteins and/or mannans but never starch (Dahlgren *et al.*, 1985; Daud and Jarvis, 1992). It may also account for those taxa of Commelinoid monocots that have non-starchy pollen, despite having starchy endosperms.

Although starchy pollen is found in many Araceae (Alismatales), it is absent from the Acoraceae (Acorales) (Grayum, 1985). It is largely absent from the Agapanthaceae, Agavaceae, Alliaceae, Amaryllidaceae, Asparagaceae, Asphodelaceae, Convallariaceae and Iridaceae (all Asparagales), the Liliaceae, Smilacaceae and Colchicaceae (all Liliales), Dioscoreaceae (Dioscoreales), and Aponogetonaceae (Alismatales) (Franchi *et al.*, 1996). Moreover, starchy pollen is absent from members of the Taccaceae (Dioscoreales), Cyclanthaceae and Pandanaceae (Pandanales), and Hypoxidaceae (Asparagales) (Zona, unpub. res.). The distribution and near exclusivity of starchy pollen in the Commelinoid monocotyledons corresponds in large part with the distribution of fluorescent compounds in the cell wall (Harris and Hartley, 1980), *Strelitzia*-type epicuticular wax (Barthlott and Frölich, 1983), and starchy endosperm (Dahlgren *et al.*, 1985). Starchy pollen, along with these other characters, is a characteristic feature of the Commelinoid monocotyledons.

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LITERATURE CITED

- Angiosperm Phylogeny Group.** 1998. An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanic Garden* **85**: 531–553.
- Baker HG, Baker I.** 1979. Starch in Angiosperm pollen grains and its evolutionary significance. *American Journal of Botany* **66**: 591–600.
- Barthlott W, Frölich D.** 1983. Mikromorphologie und Orientierungsmuster epicuticularer Wachs-Kristalloide: Ein neues systematisches Merkmal bei Monokotylen. *Plant Systematics and Evolution* **142**: 1712–1185.
- Brink RA, MacGillivray JH.** 1924. Segregation for the waxy character in maize pollen and differential development of the male gametophyte. *American Journal of Botany* **11**: 465–469.
- Bryce WH, Nelson OE.** 1979. Starch synthesizing enzymes in the endosperm and pollen of maize. *Plant Physiology* **63**: 312–317.
- Chase MW, Stevenson DW, Wilkin P, Rudall PJ.** 1995. Monocot systematics: A combined analysis. In: Rudall PJ, Cribb PJ, Cutler DF, Humphries CJ, eds. *Monocotyledons: systematics and evolution*. Kew: Royal Botanic Gardens.

- Chase MW, Soltis DE, Soltis PS, Rudall PJ, Fay MF, Hahn WH, Sullivan S, Joseph J, Molvray M, Kores PJ, Givnish TJ, Sytsma KJ, Pires JC. 2000. Higher-level systematics of the Monocotyledons: An assessment of current knowledge and a new classification. In: Wilson KL, Morrison DA, eds. *Monocots: systematics and evolution*. Melbourne, CSIRO.
- Chase MW, Soltis DE, Olmstead RG and 39 others. 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences from the plastid gene *rbcL*. *Annals of the Missouri Botanic Garden* **80**: 528–580.
- Classen-Beckhoff R. 1991. Untersuchungen zur Konstruktion des Bestäubungsapparates von *Thalia geniculata* (Marantaceae). *Botanica Acta* **104**: 183–193.
- Dahlgren RMT, Clifford HT, Yeo PF. 1985. *The families of the monocotyledons*. Berlin: Springer-Verlag.
- Davis JI. 1995. A phylogenetic structure of the monocotyledons, as inferred from chloroplast DNA restriction site variation, and a comparison of measures of clade support. *Systematic Botany* **20**: 503–527.
- Daud MJ, Jarvis MC. 1992. Mannan of oil palm kernel. *Phytochemistry* **31**: 463–464.
- Dorion S, Lalonde S, Saini HS. 1996. Induction of male sterility in wheat by meiotic-stage water deficit is preceded by a decline in invertase activity and changes in carbohydrate metabolism in anthers. *Plant Physiology* **111**: 137–145.
- Duvall MR, Clegg MT, Chase MW, Clark WD, Kress WJ, Hills HG, Eguiarte LE, Smith JF, Gaut BS, Zimmer EA, Learn GH Jr. 1993. Phylogenetic hypotheses for the monocotyledons constructed from *rbcL* sequence data. *Annals of the Missouri Botanic Garden* **80**: 607–619.
- Faden RB. 2000. Floral biology of Commelinaceae. In: Wilson KL, Morrison DA, eds. *Monocots: systematics and evolution*. Melbourne: CSIRO.
- Franchi GG, Bellani L, Nepi M, Pacini E. 1996. Types of carbohydrate reserves in pollen: localization, systematic distribution and ecophysiological significance. *Flora* **191**: 143–159.
- Frost SK, Frost PGH. 1981. Sunbird pollination of *Strelitzia nicolai*. *Oecologia* **49**: 379–384.
- Grayum MH. 1985. Evolutionary and ecological significance of starch storage in pollen of the Araceae. *American Journal of Botany* **72**: 1565–1577.
- Harris PJ. 2000. Compositions of monocotyledon cell walls: Implications for biosystematics. In: Wilson KL, Morrison DA, eds. *Monocots: systematics and evolution*. Melbourne: CSIRO.
- Harris PJ, Hartley RD. 1980. Phenolic constituents of the cell walls of monocotyledons. *Biochemical Systematics and Ecology* **8**: 153–160.
- Johansen DA. 1940. *Plant microtechnique*. New York: McGraw-Hill Book Co.
- Kato M. 1996. Plant-pollinator interaction in the understory of a lowland mixed Dipterocarp forest in Sarawak. *American Journal of Botany* **83**: 732–743.
- Kennedy H. 2000. Diversification in pollination mechanisms in the Marantaceae. In: Wilson KL, Morrison DA, eds. *Monocots: systematics and evolution*. Melbourne: CSIRO.
- Kress WJ. 1985. Bat pollination of an Old World *Heliconia*. *Biotropica* **17**: 302–308.
- Kress WJ, Schatz GE, Andrianifahanana M, Morland HS. 1994. Pollination of *Ravenala madagascariensis* (Strelitziaceae) by lemurs in Madagascar: Evidence for an archaic coevolutionary system? *American Journal of Botany* **81**: 542–551.
- Kubitzki K, ed. 1998. *The families and genera of vascular plants. IV. Flowering plants. Monocotyledons, Alismatanae and Commelinanae (except Gramineae)*. Berlin: Springer-Verlag.
- Lalonde S, Beebe D, Saini HS. 1997. Early signs of disruption of wheat anther development associated with the induction of male sterility by meiotic-stage water deficit. *Sexual Plant Reproduction* **10**: 40–48.
- Mameli Calvino E. 1952. Le sostanze diriserva dei pollini e il loro significato, filogenetico, ecologico, embriologico. *Nuovo Giornale Botanico Italiano n.s.* **59**: 1–26.
- Mason-Gamer RJ, Weil CF, Kellogg EA. 1998. Granule-bound starch synthase: Structure, function, and phylogenetic utility. *Molecular Biology and Evolution* **15**: 1658–1673.
- Mikami I, Aikawa M, Hirano H-Y, Sano Y. 1999. Altered tissue-specific expression of the *Wx* gene of the opaque mutants in rice. *Euphytica* **105**: 91–97.
- Nur N. 1976. Studies on pollination in Musaceae. *Annals of Botany* **40**: 167–177.
- Okagaki RJ, Wessler SR. 1988. Comparison of non-mutant and mutant *waxy* genes in rice and maize. *Genetics* **120**: 1137–1143.
- Saini HS. 1997. Effects of water stress on male gametophyte development in plants. *Sexual Plant Reproduction* **10**: 67–73.
- Sakai S, Inoue T. 1999. A new pollination system: Dung-beetle pollination discovered in *Orchidantha inouei* (Labiaceae, Zingiberales) in Sarawak, Malaysia. *American Journal of Botany* **86**: 56–61.
- Schemske DW. 1981. Floral convergence and pollinator sharing in two bee-pollinated tropical herbs. *Ecology* **62**: 946–956.
- Sheoran IS, Saini HS. 1996. Drought-induced male sterility in rice: Changes in carbohydrate levels and enzyme activities associated with the inhibition of starch accumulation in pollen. *Sexual Plant Reproduction* **9**: 161–169.
- Soltis DE, Soltis PS, Nickrent DL, Johnson LA, Hahn WJ, Hoot SB, Sweere JA, Kuzoff RK, Kron KA, Chase MW, Swenson SM, Zimmer EA, Chaw S-M, Gillespie LJ, Kress WJ, Sytsma KJ. 1997. Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. *Annals of the Missouri Botanic Garden* **84**: 1–49.
- Stevenson DW, Davis JI, Freudenstein JV, Hardy CR, Simmons MP, Specht CD. 2000. A phylogenetic analysis of the monocotyledons based on morphological and molecular character sets, with comments of the placement of *Acorus* and Hydatellaceae. In: Wilson KL, Morrison DA, eds. *Monocots: Systematics and evolution*. Melbourne: CSIRO.
- Stiles FG. 1979. Notes on the natural history of *Heliconia* (Musaceae) in Costa Rica. *Brenesia* **15**(Suppl.): 151–180.
- Tischler G. 1910. Untersuchungen über den Stärkegehalt des Pollens tropischer Gewächse. *Jahrbücher für Wissenschaftliche Botanik* **47**: 219–242.
- Todd FE, Bretherick O. 1942. The composition of pollens. *Journal of Economic Entomology* **35**: 312–317.