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Exine Resistance to Fungal Infestations in Strelitziaceae

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ABSTRACT: Fungal infestation of pollen wall and cytoplasm is common in *Strelitzia* and *Ravenala* (Strelitziaceae) after anther dehiscence. The exine, rarely more than 0.1 μm thick, is not degraded by these infestations. Fungal hyphae enter the pollen grain cytoplasm through ruptures in the exine caused by osmotically shocked protoplasm or mechanical damage. We find no evidence that fungal enzymes or other microbes breach the thin exines of this family.

KEY WORDS: Channeled zone, Exine, Fungal hyphae, Fungal infestation, Intine, *Phenakospermum*, Pollen, *Ravenala*, *Strelitzia*, *Strelitziaceae*.

INTRODUCTION

Two types of thread-associations occur on pollen grains of Strelitziaceae, a family consisting of *Phenakospermum* Endl., *Ravenala* Adans, and *Strelitzia* Dryand. Threads several 100 mm long and approximately 10-15 μm wide, hold pollen grains together after anther dehiscence. They are derived from the anther cell wall; this phenomenon has been extensively documented (Palla, 1891; Kronestedt and Bystedt, 1981; Hesse, 1981 Kronestedt and Walles, 1983; Hesse and Waha, 1983; Waha, 1984). A second thread association, apparently undocumented in palynological studies of Strelitziaceae, is characterized by a profusion of equally long but more slender threads (*ca.* 1.5-6 μm), which completely engulf pollen grains on open anthers, often as a dense matting. Frequently, a putrid odor emanates from the vicinity of the anther-thread-pollen association. These threads are the focus of this investigation.

MATERIALS AND METHODS

Collection data for *Phenakospermum guyannense* (L. C. Rich) Endl. ex Miq., *Ravenala madagascariensis* Gmel., and *Strelitzia reginae* Aiton are given in Table 1.

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Preparation for SEM

Strelitziaceae pollen grains were subjected to a variety of drying solvents, adhesives, and metal coatings (Table 2) in order to obtain high quality SEMs from characteristically thin, fragile, and easily distorted pollen grains. Air drying gave inconsistent results (Figs. 5-7),

Table 1. Strelitziaceae pollen examined

Taxon	Locality	Collector	Herbarium
P. guyannense	Bolivia	Solomon 16913	MO
P. guyannense	Brazil	Plowman *et al.* 8540	U
R. madagascariesis	West Indies	Broadway *s. n.* 11/8/32 (Cultivated)	MO
S. reginae	California	Ciereszko (Cultivated)	----
S. reginae	Connecticut	U. Conn. 4 (Cultivated, U. Conn. greenhouse)	----
S. reginae	Missouri	Mo. Bot. Gard. Climatron	MO

Table 2. SEM and TEM Preparation Methods for Strelitzaceae Pollen

Taxon	Collection	SEM				TEM	
		Drying	Adhesive	Coating	Figures	Preparation	Figures
P. guyannense	Plowman	AD	None	Au/Pd	7	--	--
P. guyannense	Solomon	--	--	--	12*	OTOTO	8, 9
R. madagascariensis	Broadway	AD	TEMP	Au/Pd	5, 6	--	--
S. reginae	Ciezersko	CPD	DST	Au/Pd	1, 2	--	--
S. reginae	U. Conn	--	--	--	11*	GO	13-16
S. reginae	Mo. Bot. Gard.	HMDS	DST	OTOTO	3	--	--
S. reginae	Mo. Bot. Gard.	HMDS	DST	Au/Pd	4	--	--
S. reginae	Mo. Bot. Gard.	HMDS	CP	OTOTO	10	--	--

Drying method: AD = air drying from absolute ethyl alcohol (ETOH); CPD = critical point drying (Garner and Bryant, 1973) with a Tousmis Autosandri-814 critical point dryer; HMDS = hexamethyldisilazane (Chissoe *et al.*, 1994a).

Adhesive: None = directly on SEM specimen holder; TEMP = Tempfix adhesive (Chissoe *et al.*, 1994b); DST = double stick tape; CP = carbon paste.

Coating: Au/Pd = sputter coating with 60% gold and 40% palladium; OTOTO = osmium-thiocarbohydrazide-osmium-thiocarbohydrazide-osmium (Chissoe *et al.*, 1995).

*: = acetolysis (Erdtman, 1960) after section deplasticization (Skvarla *et al.*, 1988) followed by SEM.

Preparation for TEM: OTOTO = Chissoe *et al.*, 1995; GO = glutaraldehyde/osmium (as described in text).

critical point drying (Figs. 1, 2) was satisfactory but time consuming, while hexamethyldisilazane (HMDS; Chissoe *et al.*, 1994a) was swift and highly satisfactory (Figs. 3, 4, 10). All adhesives (as well as direct drying directly onto specimen holders), provided sufficient grounding for the pollen, with Tempfix adhesive (Chissoe *et al.*, 1994b) contributing an exceptionally smooth, glassy, and uniformly opaque background (Figs. 5, 6). The most efficient adhesive was double stick tape with HMDS drying. Electrical conductance was satisfactory with either gold/palladium sputter coating (Figs. 1, 2, 4, 5-7) or osmium-thiocarbohydrazide-osmium-thiocarbohydrazide-osmium staining (OTOTO; Figs. 3, 10). The later has the advantage of serving as an agent for both drying and metallic coating of the pollen (Chissoe *et al.*, 1995). SEM examination was accomplished with ISI- Super II and JEOL-880 scanning electron microscopes.

Preparation for TEM

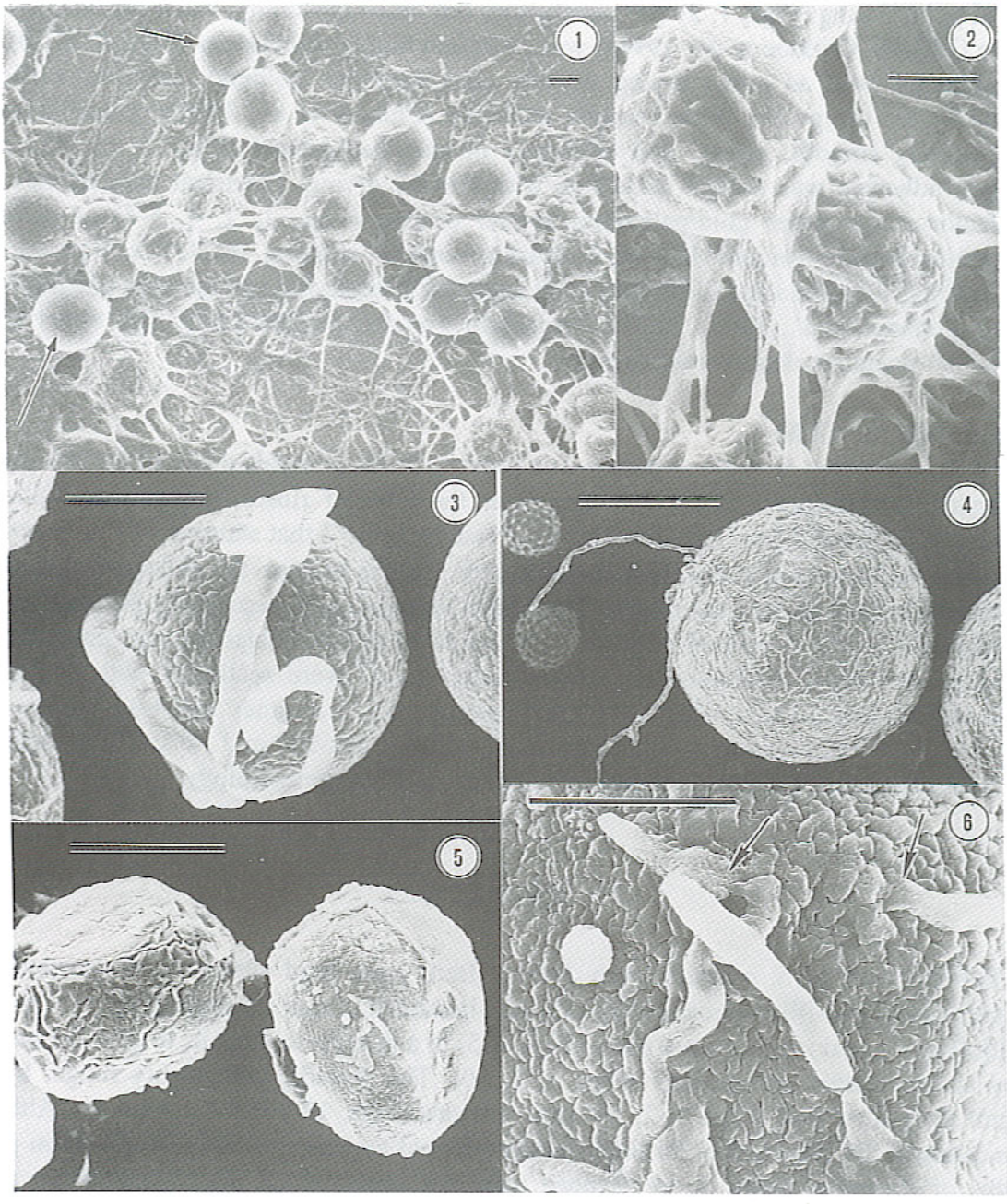
Fresh, cultivated *S. reginae* pollen was fixed in 2.5% glutaraldehyde in 0.15M sodium cacodylate buffer (pH 7.6) for 3 hours. After three buffer rinses, pollen was stained in cacodylate buffered 0.5% OsO_4 for 2 hours. [Note in Table 2 that staining of *P. guyannense* (Solomon collection) includes thiocarbohydrazide. This is because the collection was scarce and the TEM portion was the residue from SEM as previously described.] Pollen was then dehydrated through a graded ethyl alcohol series to absolute alcohol and embedded in Araldite-Epon resin (Mollenhauer, 1964). Pollen grains were sectioned with a diamond knife and section stained with 0.5% uranyl acetate for 5 minutes and lead citrate for 3 minutes. TEM examination was accomplished with Philips-200 and Zeiss-10 transmission electron microscopes. Table 2 includes a summary of TEM methodology.

RESULTS

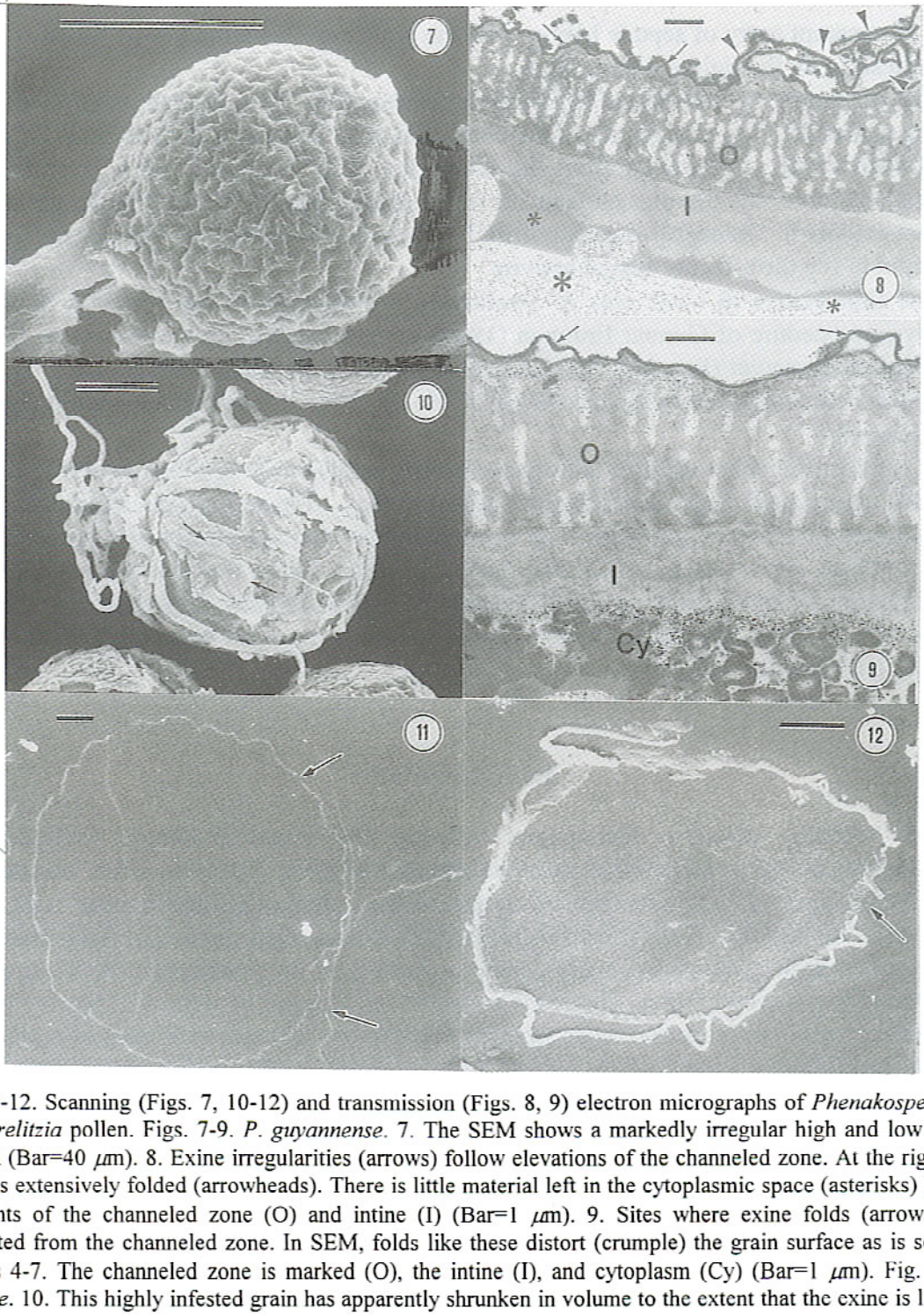
Pollen grains of *S. reginae* taken directly from open fetid anthers were covered with septate, cytoplasm-filled threads (Figs. 13, 16), hundreds of mm in length (Fig. 1), 1.5-6 μm width (Fig. 2), and ranging from a few (Figs. 4-5) to a density so great as to give the pollen a ropy and/or matted morphology (Figs. 1, 2, 10). The threads, presumably fungal hyphae, engulf the pollen wall (Figs. 1, 2, 10) and penetrate (Figs. 13-16) the cytoplasm. Although less dramatically shown than *Strelitzia*, septate fungal hyphae were also observed on pollen grains of *Ravenala* (Figs. 5, 6). Hyphae were not observed on *Phenakospermum* pollen, which is not unexpected since our collections were limited.

There is a direct correlation of the pollen wall in response to fungal activity. The grain of *Strelitzia* in Fig. 10 has been completely infested by fungi. The exine is torn or split and has the aspect of being exfoliated. Under the thin but resistant exine the channeled zone, intine, and cytoplasm are degraded and modified in the vicinity of fungal hyphae (Figs. 13, 14, and 16). In areas subjected to concentrated hyphal action the wall loses definition of channels and appears empty or "glassy" (Figs. 13-16). In Fig. 13 the channeled zone is degraded above hyphae; in Fig. 15 degradation is evident below hyphae. A site where channeled zone material is oozing out from a rupture in the exine is shown in Fig. 14.

Pollen grains of *Ravenala* in Figs. 5 and 6 are infected by fungi. Both grains in Fig. 5 show indications of dehydration, i.e., general collapse, surface texturing and surface folding.



Figs. 1-6. Scanning electron micrographs of *Strelitzia* and *Ravenala* pollen grains showing thread associations. Figs. 1-4. *S. reginae*. 1. Pollen grains are in various stages of infection as seen by the presence of fungal hyphae. Grain marked by arrow is free of hyphae and presumably may not yet be infected (Bar=40 μm). 2. Same area as above but with enlarged view of two pollen grains nearly completely encased by hyphae (Bar=40 μm). 3 The wide threads surrounding the pollen grain are developed from anther wall cells (Bar=40 μm). 4. A few hyphae are in contact with this grain. Note highly folded pollen surface. The two small spinulate pollen grains at the left are march elder, *Iva frutescens*, added to sample during preparation for scale (Bar=40 μm). Figs. 5-6. *R. madagascariensis*. 5. Pollen grains are partly collapsed and their surfaces show folding and areolate-like compression of the exines. There are hyphae associated with the grain at the right. They are shown at higher magnification in Fig. 6 (Bar=40 μm). 6. Hyphae appear to penetrate the exine at sites marked by arrows. TEMs of similar material (i.e., *Phenakospermum* in Figs. 8, 9) indicate that the areolate exine pattern is caused by compression folding and irregularities in the underlying channeled zone (Bar=10 μm).



Figs. 7-12. Scanning (Figs. 7, 10-12) and transmission (Figs. 8, 9) electron micrographs of *Phenakospermum* and *Strelitzia* pollen. Figs. 7-9. *P. guyannense*. 7. The SEM shows a markedly irregular high and low exine pattern (Bar=40 μm). 8. Exine irregularities (arrows) follow elevations of the channeled zone. At the right the exine is extensively folded (arrowheads). There is little material left in the cytoplasmic space (asterisks) below remnants of the channeled zone (O) and intine (I) (Bar=1 μm). 9. Sites where exine folds (arrows) are separated from the channeled zone. In SEM, folds like these distort (crumple) the grain surface as is seen in figures 4-7. The channeled zone is marked (O), the intine (I), and cytoplasm (Cy) (Bar=1 μm). Fig. 10. *S. reginae*. 10. This highly infested grain has apparently shrunken in volume to the extent that the exine is largely separated from the pollen grain contents. The smoothness of the pollen surface is apparent on the flaking exine (Bar=1μm). Figs. 11-12. Acetolyzed sections of *Strelitzia* and *Phenakospermum* pollen. Fig. 11. *S. reginae* The extreme thinness of the exine is evident in this section as is its resistance to hot acid acetolysis. There are several small breaks (arrows) in the exine which may be sites of microbial entry to the pollen contents (Bar=1 μm). Fig. 12. *P. guyannense*. The pollen section was acetolyzed as in Fig. 11 and shows that the exine resisted the hot acid exposure. There is at least one site (arrow) where the exine is broken (Bar=1 μm).

Sites of apparent entry of septate hyphae into the grain are illustrated in Fig. 5 and at higher magnification on the right grain in Fig. 6

The patterning of the surface in *Phenakospermum* (Fig. 7) is a good example of exine folding and underlying irregularity of the channeled zone caused by dehydration (Figs. 8, 9). The folded exine is separated from the channeled zone at several sites, presumably in accommodation to the diminished contents of the grain (Figs. 8, 9). Specific fungal activity was not evident in *Phenakospermum* pollen, but the collections studied were meager and not sufficient to see the effect of fungal activity.

The thin exines (0.1-0.2 μm) of Strelitziaceae pollen grains are resistant to the hot acetolysis procedure of Gunnar Erdtman (1960) as shown in sections of *Strelitzia* (Fig. 11) and *Phenakospermum* (Fig. 12). Several gaps are evident in these exine profiles. They are equivalent to the ruptured exines shown in TEM (e.g., Figs. 14, 16) which are near areas of fungal activity.

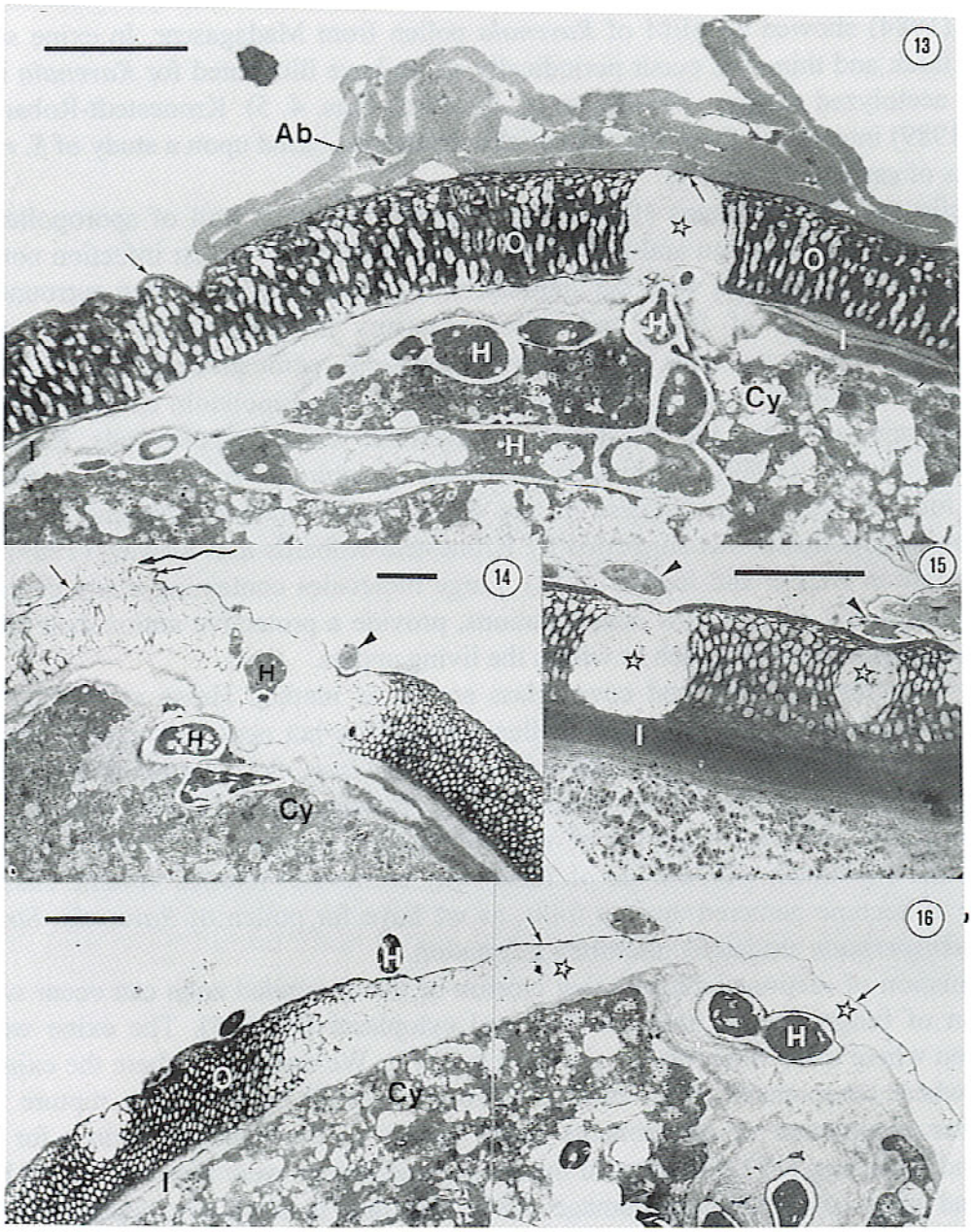
In contrast to hyphal threads, nonseptate threads equally as long but at least 10 μm wide are also associated with Strelitziaceae pollen grains. These threads commonly occur intermingled between pollen masses on opened anthers and are clearly distinguished from fungal hyphae by greater width and lack of septa. Such threads are produced by differentiation of anther wall cells and appear to be a part of anther dehiscence. An example of this type of thread is evident on the textured surface of a pollen grain of *Strelitzia* that is beginning to dehydrate (Fig. 3).

DISCUSSION

Our scanning electron micrographs illustrate the intensive fungal infestation of Strelitziaceae pollen as it occurs on open anthers of *S. reginae*. While no effort was made to identify the class of fungi, the septate nature of the cytoplasm filled hyphae indicates a member of the Ascomycetes. Transmission electron micrographs show that fungi gain entry to the pollen grain protoplasm, with hyphae occurring in the channeled part of the pollen wall, the intine and cytoplasm. The exine appeared undamaged in spite of extensive hyphal positioning near both inner and outer surfaces of the exine. We saw examples of protoplasm erosion inside intact exines where hyphae were adjacent to the outer surface of the exine. There can be no doubt that these apertureless exines are permeable to uptake of nutrients, and apparently they are permeable also to the protoplasm-degrading enzymes of fungi. While there can be no question that there are entry sites through exines we found none in sections. Granted that TEM thin sections are not favorable for hole searching, the absence of entry sites in the hundreds of sections examined indicates the relative infrequency of entry sites.

Fungal hyphae are distinct from other thread-like structures known for pollen. They differ from the ca. 10-15 μm wide threads from anther wall cells in *Strelitzia* (Fig. 3). They are also distinct from nonseptate, sporopollenin viscin threads and exinal bridges found in pollen of Onagraceae, Ericaceae and Leguminosae (Bowers, 1930-31; Skvarla *et al.*, 1978; Cruden and Jensen, 1979; Patel *et al.*, 1985).

Components of the pollen grain wall, i.e., exine, channeled zone and intine, are closely similar in appearance in *S. reginae*, *R. madagascariensis*, and *P. guyannense*. Straka and



Figs. 13-16. Transmission electron micrographs of *Strelitzia* pollen grains with hyphae within them or near the exine surface. 13. A portion of the intine (I) and the channeled zone (O) has been extracted as a consequence of hyphal (H) penetration into the cytoplasm (Cy). The thin exine is marked by arrows on the undulated surface of the channeled zone and within the site of the degraded (star) channeled zone. An exine of a microspore that aborted early in development (as indicated by the approximately. 0.45-0.75 μm thick exine) is on the surface of the *Strelitzia* pollen grain (Bar=5 μm). 14. There are fungal hyphae (H) on the exine surface (arrowhead) and within the channeled zone and the cytoplasm (Cy). The wavy arrow shows a site where material of the channel zone is pushing through a rupture in the exine (arrows) (Bar=5 μm). 15. There are two degraded regions (stars) in this section. Both are under hyphae (arrowheads) adjacent to the intine (I) (Bar=5 μm). 16. The figure illustrates severe degradation of the intine (I), channeled zone (O) and the cytoplasm (Cy) by the presence of hyphae (H) both inside the grain and at the exine surface. The exine (arrows) remains intact within the limits of this section, although one break is suggested to the left of the top arrow. The region of the degraded channel zone is marked by stars (Bar=5 μm).

Friedrich (1984) showed an SEM of *Ravenala* pollen from Madagascar. In exine sections relatively thick and thin sites occur periodically as we have illustrated for *Ravenala* in both fixed and acetolyzed sections (Rowley *et al.*, in press: Figs. 4, 5). Kronestedt-Robards and Rowley (1989) interpreted these sites of variable thickness, based upon a study of *S. reginae*, to be relics of early development.

Staehelin and Pickett-Heaps (1975) proposed that the outer wall of sporopollenin on algal cells prevented infection and resisted enzymes. Protection against infection conferred by the exine is in agreement with our impression that Strelitziaceae pollen surrounded by massive concentrations of fungi and microorganisms in open anthers could remain uninfected for days so long as the thin exine was intact (e.g., some grains in Fig. 1).

Because of the ubiquity of an ultrathin (0.1-0.2 μm) sporopollenin covering for algae, pollen grain apertures, and the extratapetal lamellations around tapetal cells, Kronestedt-Robards and Rowley (1989) reasoned that even an ultrathin covering of sporopollenin is adequate for functional effectiveness of the exine. A free radical trapping antioxidant activity for sporopollenin was suggested by Kronestedt-Robards and Rowley (1989) based upon a review in Burton and Ingold (1984). Large molecules containing many conjugated double bonds would, even at low concentrations, provide a protective antioxidant effect at low oxygen partial pressures, such as within the living anther.

Using a microscope slide and cover glass acetolysis method Hesse and Waha (1983) found that the thin exine of *S. reginae* pollen resisted the hot acid treatment. Hesse and Waha (1983, 1989) illustrated how the exine of *S. reginae* can be smooth after careful drying, as we have illustrated for *Phenakospermum* (Rowley et al., in press: Fig. 1). Hesse and Waha (1983) showed examples of wrinkled (folded) exines of *Strelitzia* following acetolysis and explained, with the aid of TEM, why the loss of internal volume causes the thin exine to become gathered up into folds, as we have for pollen of *Ravenala*, *Strelitzia*, and *Phenakospermum* eroded by microbial infestation.

Examination of sections indicated that erosion of the channeled zone can occur without penetration of fungal hyphae into the wall and cytoplasm (Fig. 15). The exine was not eroded even where there were hyphae above or below it. We saw areas where the exine was torn and where components of the channeled zone extended up through a rupture in the exine. After completion of experiments using pollen as the nutritive source for fungi, Skvarla and Anderegg (1972) concluded that most penetrations were through natural breaks (pores) and sites of mechanical damage. They felt that if fungi are capable of exine degradation, they penetrate the exine to gain access to the protoplasm, not to make use of exines as a nutritional source.

Results of our examination of corroded exines (Rowley *et al.*, 1990; Skvarla *et al.*, 1996) from Havinga' s (1964, 1984) leaf mold experiment complements the conclusions of Skvarla and Anderegg (1972) and ours on exine resistance to fungal infestation in pollen of Strelitziaceae. In our LM, TEM, SEM study of the exines buried by Havinga in a biologically active leaf mold we saw the intricately patterned sites that Havinga (1964) associated with exine corrosion. Such patterned sites have been equated with biologically caused corrosion (e.g., Elsik 1966; 1971). The corrosion sites involved tunneling within exines, but a thin (*ca.* 0.1μm) surface zone remained mostly intact except for small openings having the appearance of mechanical tears and fractures. It is our conclusion that the thin exines of *Ravenala, Phenakospermum* and *Strelitzia* are highly resistant.

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旅人蕉科 (Strelitziaceae) 花粉外壁抗阻真菌的感染

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摘　　要

鶴望蘭屬 (*Strelitzia*) 和旅人蕉屬 (*Ravenala*) 花藥開裂後，常見花粉壁與細胞質受到真菌菌絲的感染。厚度很少超過 0.1 μm 的花粉外壁不因此種感染而瓦解。真菌菌絲是經由花粉外壁受到原生質體滲透壓變異，或是因機械性外力的破壞所形成的裂縫進入花粉粒的細胞質中。我們並沒有找到真菌酵素或其它微生物破壞此科植物之花粉外壁的證據。

關鍵詞：微隙穿孔區，花粉外壁，真菌菌絲，真菌感染，花粉內壁，南美蕉屬，花粉，鶴望蘭屬，旅人蕉屬，旅人蕉科。

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