BLUMEA 38 (1993) 25-38

POLLEN OF HAWAIIAN CYRTANDRA (GESNERIACEAE) INCLUDING NOTES ON SOUTHEAST ASIAN TAXA

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SUMMARY

Pollen of 30 species and 12 hybrids (88 samples in total) of Hawaiian *Cyrtandra*, covering all 6 sections recognized on the Hawaiian archipelago, was examined using light, scanning and transmission electron microscopy. Hawaiian *Cyrtandra* is stenopalynous. The pollen grains are binucleate, isopolar, small-sized and 3-colporoidate (very rarely 4-colporoidate). In equatorial view they are spheroidal, in polar view circular or semiangular. The tectum is mostly microreticulate with brochi of different sizes (heterobrochate), very rarely reticulate or perforate. Supratectal elements are lacking. Some variation can be observed in number and diameter of the lumina. Palynological features of most of the investigated taxa tend to overlap and thus are not very helpful in supporting the infrageneric division of *Cyrtandra* on Hawaii.

Pollen viability of hybrids, which is said to be reduced occasionally, was examined and found to be high with rates of 70 to 99%. Therefore, reduced pollen viability is not a reliable character for designating hybrid status.

Asian *Cyrtandra* is eurypalynous. For this study, 19 species, originating from the Malay Peninsula and Borneo, have been investigated. Two exine types, differing in sculpture and structure, can be distinguished: 1) tectum microreticulate-reticulate, supratectal elements lacking, and 2) tectum microreticulate-perforate with numerous conical supratectal elements. The number, diameter and shape of lumina provide further important diagnostic features.

INTRODUCTION

Cyrtandra, the largest genus of the family Gesneriaceae, comprises about 500-600 species ranging from SE Asia throughout Malesia, NE Australia and the Pacific islands. Centres of diversity include New Guinea, Borneo, each with over 150 species, and the Philippines. The only treatment covering the whole genus dates back to Clarke (1883). However, Clarke's subdivision of the genus into sections is more or less ignored in nearly all subsequent regional treatments because of the confusing delimitation of the sections.

On the Hawaiian archipelago 53 species are recognized currently (Wagner et al., 1990). This means a drastic reduction of species number compared with former treatments, especially that of St. John (1966), who recognized and described 131 species only for the island of Oahu. The considerable discrepancy is due to a different taxonomic philosophy: while St. John delimited species very narrowly, Wagner et al. accepted a number of species to be very polymorphic. Moreover, Wagner et al. interpreted individuals exhibiting intermediate characters between two sympatric species as hybrids. To date, 67 putative hybrid combinations have been recorded (Wagner & Herbst, in prep.).

Table 1. List of investigated taxa of Hawaiian *Cyrtandra*, origins and short characteristics of the exine pattern (number of lumina per 25 µm² of the mesocolpia / diameter of the largest lumina of the mesocolpia in µm).

Taxa	Origin, voucher	Lumina number / size
Sect. ***Crotonocalyces*** Hillebr.		
C. cordifolia Gaud.	Oahu, *Kiehn et al. 900722-5/1* (WU, PTBG)	120 / 0.5
	–, *W.C. Gagne 523* (BISH)	80 / 0.8
C. kealiae Wawra	Kauai, *St. John et al. 23076* (BISH)	90 / 0,5
	–, *Kiehn & Luegmayr 920825-1/1* (WU)	120 / 0.7
C. limahuliensis St. John	Kauai, *Kiehn et al. 900823-2/12* (WU, US)	
C. platyphylla A. Gray	Hawaii, *Kiehn & Cuddihy 900812-2/1* (WU)	120 / 0.8
	s.l., *Warshauer 1933* (BISH)	
	Hawaii, *Warshauer 1275* (BISH)	100 / 0.6
	s.l., *Warshauer 1585* (BISH)	50 / 0.4
	Hawaii, *Kiehn & Luegmayr 920818-2/1* (WU)	70 / 0.6
C. propinqua C. Forbes	Oahu, *Takeuchi 2955* (BISH)	
	–, *Takeuchi 3045* (BISH)	110 / 0.4
	–, *Kiehn et al. 920909-3/2* (WU, US, BISH)	120 / 0.5
C. wawrae C.B. Clarke	Kauai, *Wagner et al. 6064* (BISH)	50 / 0.9
Sect. ***Apertae*** C.B. Clarke		
C. garnotiana Gaud.	Oahu, *Takeuchi 2142* (BISH)	90 / 0.7
	s.l., *Obata 86-650* (BISH)	110 / 0.4
C. laxiflora H. Mann	Oahu, *Kiehn & Obata 890809-1/6* (WU, BISH)	180 / 0,2
	–, *Takeuchi 1779* (BISH)	100 / 0.3
	–, *Takeuchi 1868* (BISH)	60 / 0.7
	–, *Kiehn et al. 920909-3/1* (WU, US)	200 / 0.2
	s.l., *Takeuchi 2532* (BISH)	140 / 0.6
C. sandwicensis (H. Lév.) St. John & Storey	Oahu, *Kiehn et al. 900722-2/1* (WU, PTBG, BISH)	120 / 0.4
	–, Kiehn et al. 900722-2/3 (WU, PTBG, BISH)	80 / 0.4
	–, *Kiehn 920907-1/9* (WU, US)	70 / 0.8
Sect. ***Macrosepalae*** C.B. Clarke		
C. grayana Hillebr.	Maui, Kiehn et al. 890723-2/2 (WU)	90 / 0.3
	Lanai, *Hobdy s.n.* (BISH)	60 / 0.8
	Maui, *Nagata 3558* (BISH)	60 / 0.5
	–, *Warshauer 3044* (BISH)	60 / 0.6
C. grayi C.B. Clarke	Molokai, *Nagata 1141* (BISH)	50 / 0.7
	Maui, *Warshauer 3068* (BISH)	100 / 0.4
	–, *Warshauer 3106* (BISH)	110 / 0.4
C. hashimotoi Rock	Maui, *Kiehn et al. 900803-3/3* (WU, US)	50 / 0.6
	–, *Higashino 9319* (BISH)	40 / 0.3
	–, *Hobdy 1894* (BISH)	80 / 0.7
C. kauaiensis Wawra	Kauai, *Kiehn & Luegmayr 920825-3/3* (WU)	
	–, *Kiehn & Luegmayr 920830-4/1* (WU)	140 / 0.2
	s.l., *Christensen 209* (BISH)	80 / 0.6
C. lysiosepala (A. Gray) C.B. Clarke	Hawaii, *Kiehn & Cuddihy 900812-2/3* (WU, US)	80 / 0.7
	s.l., *Cuddihy 216* (BISH)	150 / 0.3
	Hawaii, *Warshauer 1653* (BISH)	
	–, *Warshauer 1668* (BISH)	120 / 0.6
	–, *Warshauer 1656* (BISH)	

(Table 1 continued)

Taxa	Origin, voucher	Lumina number / size
(Sect. *Cylindrocalyces*)		
C. macrocalyx Hillebr.	Molokai, *Kiehn & Luegmayr 920817-2/2* (WU)	80 / 0.6
C. procera Hillebr.	Molokai, *Kiehn & Cuddihy 900812-2/3* (WU)	90 / 0.8
	s.l., *Warshauer 2385* (BISH)	70 / 0.6
C. cf. *procera*	Molokai, *Kiehn et al. 900806-3/2* (WU)	110 / 0.5
	–, *Kiehn et al. 900806-2/1* (US)	90 / 0.4
C. spathulata St. John	Maui, *Wagner et al. 5847* (BISH)	70 / 0.4
	–, *Kiehn & Luegmayr 920821-2/1* (WU)	
C. wainihaensis H. Lév.	Kauai, *Christensen 270* (BISH)	60 / 0.8
Sect. ***Chaetocalyces*** Hillebr.		
C. giffardii Rock	Hawaii, *Warshauer 1647* (BISH)	40 / 0.2
C. lydgatei Hillebr.	Molokai, *Nagata 1144* (BISH)	60 / 0.3
C. macraei A. Gray	Oahu, *Nagata 3281* (BISH)	
C. menziesii Hook. & Arnott	Hawaii, *Davis s.n.* (BISH)	80 / 0.3
	–, *Kiehn & Luegmayr 920821-1/1* (WU, PTBG)	40 / 0.6
Sect. ***Verticillatae*** St. John		
C. calpidicarpa (Rock) St. John & Storey	Oahu, *Takeuchi 2404* (BISH)	60 / 0.8
	–, *Kiehn et al. 920909-3/3* (WU, PTBG, BISH)	80 / 0.9
C. confertiflora (Wawra) C.B. Clarke	Kauai, *Christensen 251* (BISH)	50 / 1.0
	–, *Perlman 474* (BISH)	70 / 0.5
C. grandiflora Gaud.	Oahu, *Kiehn et al. 900722-1/1* (WU, PTBG, BISH)	40 / 0.7
	–, *Funk 141* (BISH)	50 / 1.3
	–, *Kiehn 920907-1/2* (WU, US)	80 / 0.8
C. hawaiensis C.B. Clarke	Oahu, *Kiehn & Obata 890809-1/3* (WU)	70 / 0.9
	Maui, *Wagner et al. 5855* (BISH)	60 / 0.9
	Hawaii, *Kiehn & Luegmayr 920819-1/1* (WU)	80 / 0.8
	s.l., *St. John 21360* (BISH)	40 / 1.1
C. cf. *hawaiensis*	Oahu, *Kiehn & Obata 890809-1/5* (WU)	80 / 0.8
C. kaulantha St. John & Storey	Oahu, *Kiehn & Obata 890809-2/1* (WU)	50 / 0.7
C. oenobarba H. Mann	Kauai, *Kiehn et al. 900823-1/3* (PTBG)	70 / 0.6
Sect. ***Cylindrocalyces*** Hillebr.		
C. longifolia (Wawra) Hillebr. ex C.B. Clarke	Kauai, *Kiehn & Flynn 900907-1/13* (US)	70 / 0.5
C. paludosa Gaud.	Hawaii, *St. John 23927* (BISH)	
	Maui, *Kiehn et al. 900803-7/1* (WU, US)	60 / 1.0
	Oahu, *Takeuchi & Imada 1835* (BISH)	80 / 0.7
var. *paludosa*	s.l., *Higashino 8015* (BISH)	60 / 0.9

Table 2. List of investigated hybrids of Hawaiian *Cyrtandra*, origins, short characteristics of the exine pattern (number of lumina per 25 μm^2 of the mesocolpia / diameter of the largest lumina of the mesocolpia in µm) and percentages of viable pollen grains. — Symbols for the sections: ● = *Crotonocalyces*, ○ = *Apertae*, ■ = *Macrosepalae*, □ = *Chaetocalyces*, ▼ = *Verticillatae*, ▽ = *Cylindrocalyces*.

Hybrid combinations	Origin, voucher	Lumina Number / Size	Pollen viability (%)
▼ *C. confertiflora* × *C. wainihaensis* ■	s.l., *Perlman 475* (BISH)	50 / 0.7	89
● *C. cordifolia* × *C. sandwicensis* ○	Oahu, *Kiehn 920907-1/8* (WU)	110 / 0.6	
□ *C. giffardii* × *C. platyphylla* ●	Hawaii, *Nagata 2930* (BISH)	60 / 0.4	94
	–, *St. John 22309* (BISH)	50 / 0.6	82
▼ *C. grandiflora* × *C. cordifolia* ●	Oahu, *Kiehn 920907-1/2a* (WU)	90 / 0.6	99
▼ *C. grandiflora* × *C. paludosa* ▽	Oahu, *Takeuchi 3044* (BISH)	50 / 1.4	96
■ *C. grayi* × *C. platyphylla* ●	s.l., *St. John et al. 25741* (BISH)	110 / 0.3	70
▼ *C. hawaiensis* × *C. menziesii* □	Hawaii, *Kiehn & Luegmayr 920819-1/2* (WU)	70 / 0.5	97
	s.l., *Warshauer 1932* (BISH)	40 / 0.3	98
○ *C. laxiflora* × *C. paludosa* ▽	Oahu, *Takeuchi 3049* (BISH)	90 / 0.4	92
▽ *C. paludosa* × *C. hashimotoi* ■	Maui, *Kiehn et al. 900803-7/2* (WU)		
▽ *C. paludosa* × *C. platyphylla* ●	s.l., *Davis 689* (BISH)		82
● *C. propinqua* × *C. calpidicarpa* ▼	Oahu, *Kiehn et al. 920909-3/4* (WU)	60 / 0.7	2
	–, *Kiehn et al. 920909-3/4b* (WU)	60 / 0.7	96
	–, *Takeuchi 2399* (BISH)	80 / 0.7	98
● *C. propinqua* × *C. garnotiana* ○	Oahu, *Kiehn et al. 920909-4/1* (WU)	180 / 0.3	94

Apart from a single taxon (*C. grandiflora*, Roelofs, 1980) palynological information is lacking for Hawaiian *Cyrtandra*. The present study includes 30 species and 12 hybrids, using light, scanning and transmission electron microscopy. The investigation covers representatives of all six sections recognized on the Hawaiian archipelago (see Tables 1 & 2).

In order to evaluate the taxonomic significance of the data obtained and to provide additional palynological information on the genus, Hawaiian *Cyrtandra* is compared with SE Asian taxa. So far 19 species, originating from Borneo and the Malay Peninsula, have been studied (see Table 3); preliminary results of this investigation are provided.

MATERIAL AND METHODS

Pollen samples of Hawaiian taxa were taken either from alcohol- or glutaraldehyde-preserved flowers obtained from BISH and WU, or from plants grown in the greenhouses at the Botanical Garden of the University of Vienna (HBV). For the investigation of Asian taxa only herbarium material was available, except of *Cyrtandra pendula*, which is cultivated at HBV. Because of the marked protandry, flowers shortly

Table 3. List of investigated taxa of SE Asian *Cyrtandra*, origins and short characteristics of the exine pattern (supratectal elements present (+) or absent (–); number of lumina for 25 μm^2 of the mesocolpia / diameter of the largest lumina of the mesocolpia in µm and the presence (+) or absence (–) of rod-like luminal elements. Abbreviations: Sculpt.= supratectal elements; * = lumina at the apocolpia markedly larger and fewer in number.
Sectional allocation according to Clarke (1883) / suggested allocation to sections by Burtt (pers. comm.). Burtt replaced sectional names by ? wherever the species had been wrongly assigned.

Origin, Taxa	Sectional allocation according to Clarke	Sectional allocation according to Burtt	Sculpt.	Lumina No./Size	Luminal Elements	Voucher
Malay Peninsula						
C. cupulata Ridley	?	?	–	50/1.3	+	*W. & A.*[1] *870519-1/3* (WU)
C. dispar DC.	*Dispares* C.B. Clarke	*Dispares* C.B. Clarke	–	40/1.6	+	*Weber 860818-2/2* (WU)
C. pendula Blume	*Jackianae* C.B. Clarke	prob. *Decurrentes* C.B. Clarke	+	130/0.8	–	*Weber 870501-1/17* (WU)
C. wallichii (C.B. Clarke) B.L. Burtt	*Decurrentes* C.B. Clarke	*Decurrentes* C.B. Clarke	+	140/1.1	–	*W. & A. 860828-1/4* (WU)
Borneo						
C. farinosa C.B. Clarke	*Decurrentes* C.B. Clarke	?	–	100/0.7	–	*Weber 790905-1/8* (WU)
C. radiciflora C.B. Clarke	*Decurrentes* C.B. Clarke	?	–	70/0.8	–	*Burtt & Woods B1948* (E)
C. basiflora C.B. Clarke	*Dissimiles* C.B. Clarke	?	–	*110/0.8	+	*Argent et al. 753* (E)
C. multibracteata C.B. Clarke	*Dissimiles* C.B. Clarke	*Dissimiles* C.B. Clarke	–		–	*Burtt & Martin B4801* (E)
C. cretacea Kraenzl.	*Jackianae* C.B. Clarke	?	–	110/0.9	–	*Burtt & Woods B1991* (E)
C. chrysea C.B. Clarke	*Stellatae* C.B. Clarke	?	–		–	*Weber 790922* (WU)
C. eximia C.B. Clarke	*Whitia* (Blume) C.B. Clarke	?	–	80/0.8	–	*Burtt & Woods B1941* (E)
C. oblongifolia (Blume) C.B. Clarke	*Whitia* (Blume) C.B. Clarke	*Whitia* (Blume) C.B. Clarke	+	280/0.3	–	*Argent et al. 742* (E)
C. sarawakensis C.B. Clarke	*Whitia* (Blume) C.B. Clarke	?	–	50/0.6	–	*Burtt & Martin B4712* (E)
C. splendens C.B. Clarke	*Whitia* (Blume) C.B. Clarke	?	–	*130/0.5	+	*Burtt & Martin B4815* (E)
C. clarkei Stapf	?	?	–	70/0.8	–	*Sinclair 9104* (E)
			–	60/0.7	–	*Weber 790924* (WU)
C. gibbsiae S. Moore	?	?	–	60/0.9	–	*Burtt B8268* (E)
C. gillettiana B.L. Burtt	?	?	–	70/1.1	–	*Burtt & Martin B4945* (E)
C. horizontalis B.L. Burtt	?	*Whitia* (Blume) C.B. Clarke	+	190/0.5	–	*Burtt & Martin B5169* (E)
C. woodsii B.L. Burtt	?	*Decurrentes* C.B. Clarke	+	180/0.6	–	*Burtt & Woods B2579* (E)

[1]) Abbreviation for Weber & Anthonysamy.

before or immediately after anthesis are in the best stage for pollen examination. Taxa and collections used for detailed investigations are listed in Table 1 (Hawaiian species), Table 2 (Hawaiian hybrids) and Table 3 (Asian species). The nomenclature follows Clarke (1883), Burtt (pers. comm.) and Wagner et al. (1990).

For LM investigations fresh (living) pollen was mounted in glycerine jelly according to Wodehouse (1935). Pollen of hybrids was stained in acetocarmine for determining the nuclear condition and viability. Ratio of pollen viability is based on respective counts of 100 pollen grains of each sample.

For SEM investigations anthers of dried flowers were soaked in a 10% aqueous mixture of dioctyl sodium sulfosuccinate and 95% acetone for 24 hours (Peterson et al., 1978). Soaked and/or fixed anthers were first dehydrated in an alcohol series, subsequently chemically dehydrated in FDA (formaldehyde-dimethyl-acetal; Gerstenberger & Leins, 1978) and then critical-point-dried. A few samples were acetolyzed following the method of Erdtman (1960). The dried pollen grains were placed on aluminium specimen stubs and sputter-coated with gold.

For TEM investigations fixed anthers were dehydrated in an ethanol series and embedded in Spurr's mixture (Spurr, 1969). The ultrathin sections were stained with uranyl acetate and lead citrate. For detecting neutral polysaccharides ultrathin sections were treated with periodic acid-thiocarbohydrazide-silver protein (PA-TCH-SP) according to Thiéry (1967).

Width and amount of lumina per 25 μm^2 were measured on SEM graphs. Pollen terminology follows Erdtman (1969), Faegri & Iversen (1975), and Praglowski & Punt (1973).

RESULTS

Pollen description of Hawaiian taxa

The pollen grains, binucleate at maturity (Fig. 4A), are isopolar, 3-colporoidate (very rarely 4-colporoidate) and spheroidal (rarely suboblate) in equatorial view (Figs. 1B, 2D, 3C). In polar view the grains are circular or semiangular (Fig. 1D). Average equatorial diameters range from 14 to 23 μm.

The colpi are long and ± tapering; the endexinous colpus membrane is covered with ectexinous granular elements (Figs. 2E, 4A). The colpus membrane is splitting up into lamellae at the equatorial part (Fig. 1E) and, after acetolysis, most colpi show an irregular os in this region (cf. Fritze & Williams, 1988; Luegmayr, 1993). However, endoapertures are not visible in the LM and there is no distinct endosculpturing at the aperture region. Thus, the aperture system is designated as colporoidate in the sense of Erdtman (1952).

The exine patterns at the mesocolpia are mostly microreticulate with minute muri and lumina less than 1 μm in width (Figs. 1C, 2C, 3B, 3D), very rarely reticulate or perforate (see Table 1). Lumina width varies considerably within the mesocolpia of a single grain (e.g. between 0.6 and 0.05 μm in *C. platyphylla*; Fig. 1C). Thus the microreticula are heterobrochate sensu Erdtman (1952). Moreover, the width of the lumina generally decreases towards the polar region and the colpus border (Figs. 1A and 3A show pollen grains with perforate apocolpia). Lumina irregular or circular, without free standing elements.

Supratectal elements are lacking. A fine granular ornamentation, delicate cracks and shallow grooves radiating from the lumina are visible in Figures 1C, 3D and 3C. Except of the latter, these features are probably of artifical nature.

The exine consists of an ectexine (tectum, columellae and foot layer) and an endexine (Fig. 2A). The tectum is thicker than the foot layer; the columellate layer is at least as thick as the tectum thickness. The endexine is thin at the mesocolpia, but increases in thickness at the aperture region, forming a colpus membrane. The intine is 2-layered; the exintine is thickened at the aperture region with radially oriented and transverse channel-like structures (Fig. 1E).

Noteworthy is the occurrence of numerous pollenkitt droplets (Figs. 2B, 3E, 3F). Occasionally crystals cover the pollen grain surface and the inner wall of the anthers (Fig. 4C, E).

Hawaiian hybrids

No significant palynological differences have been found between 'good' species and hybrids, thus the former pollen description is valid for the examined hybrids also. Apart from a single individual of *C. propinqua* × *C. calpidicarpa,* pollen viability is high in hybrids with rates of 70 to 99% (see Table 2 & Fig. 4B, D). Abnormal, infertile pollen grains do not seem to occur more often in supposed hybrids.

One has to note that hybridisation primarily takes place between species of different sections, intrasectional hybrids are rare (see Table 2, cf. Wagner et al., 1990).

Brief palynological description of SE Asian taxa

Pollen grains 3-colporoidate (very rarely 4-colporoidate); spheroidal, outline in polar view circular to semiangular (Fig. 5A, C). Average equatorial diameters: 14–20 µm.

Colpi long and ± tapering; endexinous colpus membrane covered with ectexinous granular elements (Fig. 5B).

Exine pattern: reticulate (Fig. 5G), microreticulate (Fig. 5D, F) or almost perforate (Fig. 5E); supratectal elements present (Fig. 5A, B, D) or absent (Fig. 5C, E–G). Lumina occasionally with rod-shaped elements (Fig. 5G).

Exine consisting of an ectexine (tectum, columellae and footlayer) and an endexine. In *C. pendula* (cf. Luegmayr, 1993) the tectum is three times thicker than the footlayer. Columellate layer thinner than the tectum; supratectal elements conical, 0.2 µm high. Lamellated endexine thin at the mesocolpia, but increasing in thickness at the aperture region, forming a colpus membrane. Intine 2-layered.

DISCUSSION

Hawaiian taxa of *Cyrtandra* are stenopalynous. The pollen grains resemble one another strongly in size (14–23 µm), shape (spheroidal), apertures (3-colporoidate, very rarely 4-colporoidate) and exine ornamentation (microreticulate, very rarely reticulate or perforate; supratectal elements are lacking). Lumina width varies considerably within the mesocolpia of a single grain (e.g. between 0.8–0.08 µm in *C. procera,* Fig. 2C), thus the microreticula (or reticula) are heterobrochate sensu

Erdtman (1952). Moreover, the width of lumina generally decreases towards the polar region and the colpus border. Some variation also occurs in the number of tectal lumina (see Table 1 & 2). The number of lumina per 25 μm^2 ranges from 40 (*C. giffardii, C. grandiflora, C. hashimotoi, C. menziesii*) to 200 (*C. laxiflora*). It is noticed that lumina number is not a constant character within a given species; intraspecific variation is up to 100% (cf. Table 1). Nevertheless, a slight trend can be noticed: pollen grains of taxa of the sections *Crotonocalyces, Apertae* and *Macrosepalae* tend to have more lumina (70–200 per 25 μm^2 at average, rarely 40–60) than taxa of the sections *Chaetocalyces, Verticillatae* and *Cylindrocalyces* (40–80 per 25 μm^2). In general, the palynological data obtained are not helpful in supporting the infrageneric delimitation of Hawaiian *Cyrtandra.*

In contrast to the uniform pollen grains of Hawaiian *Cyrtandra,* SE Asian *Cyrtandra* is eurypalynous. Pollen grains of 19 taxa, originating from the Malay Peninsula and Borneo show two different exine patterns, differing in sculpture and structure: 1) tectum microreticulate-reticulate, supratectal elements lacking, and 2) tectum microreticulate-perforate with numerous conical supratectal elements. The number, diameter and shape of lumina provide further important diagnostic features (see Table 3). The taxonomic value of the present data is not yet assessable since the infrageneric classification of the large variable genus is still in a poor state. A very first, interesting result is, that the few species that Burtt allocated to the sections *Whitia* and *Decurrentes* are palynologically homogeneous by having supratectal elements and a large number of lumina per 25 μm^2 (cf. Table 3). Pollen morphology might be a helpful additional character to find out links with Hawaiian taxa but more data on Asian and Pacific taxa are needed to make more precise statements.

According to Wagner et al. (1990) hybridization is a widespread phenomenon in Hawaiian *Cyrtandra.* One criterion for designating hybrids is the occasionally reduced pollen fertility (actually the authors observed pollen viability by staining the pollen with Alexander's stain; cf. Alexander, 1969). Reduced pollen fertility, however, has not been constantly met, e.g. the hybrid between *Cyrtandra sandwicensis* and *C. grandiflora* occurring on the island Oahu had about 70% fertile pollen grains (Wagner & Herbst, in prep.). In the present investigation hybrids showed high rates of pollen viability, namely between 70 and 99% (see Table 2, Fig. 4D). Even germinated pollen grains with long pollen tubes were found frequently (Fig. 4B). Only one individual of *C. propinqua* × *C. calpidicarpa* had a highly reduced pollen viability. As abnormal pollen grains generally did not occur more frequently in putative hybrids, reduced pollen viability does not seem to be a reliable criterion for establishing hybrid status.

Especially in late anthesis crystals covering the pollen grain surface and inner wall of the anthers occur occasionally (Fig. 4C, E). Crystals (probably calciumoxalate) have been found in the cells of the connective of the anthers too. No satisfactory answer can be offered for the occurrence of crystals in the pollen sac. Some of them might be sluiced away from the connective cells into the pollen sac by the fixative. An artificial origin of the crystals caused by a reaction between the fixative and some components of the pollen sac content, such as pollenkitt, etc. cannot be excluded (cf. Freytag, 1967).

ACKNOWLEDGEMENTS

The herbaria at BISH, WU and E kindly provided dried and fixed material for investigation. Dr. M. Kiehn, the National Tropical Botanical Garden (Kauai/Hawaii) and the Bishop Museum (Oahu/Hawaii) are thanked for their support during my field trip on Hawaii. I am greatful to Prof. Dr. M. Hesse and Prof. Dr. A. Weber for critical comments and reading of the manuscript. This study was supported by the Österreichische Nationalbank (Jubiläumsfondsprojekt 3834).

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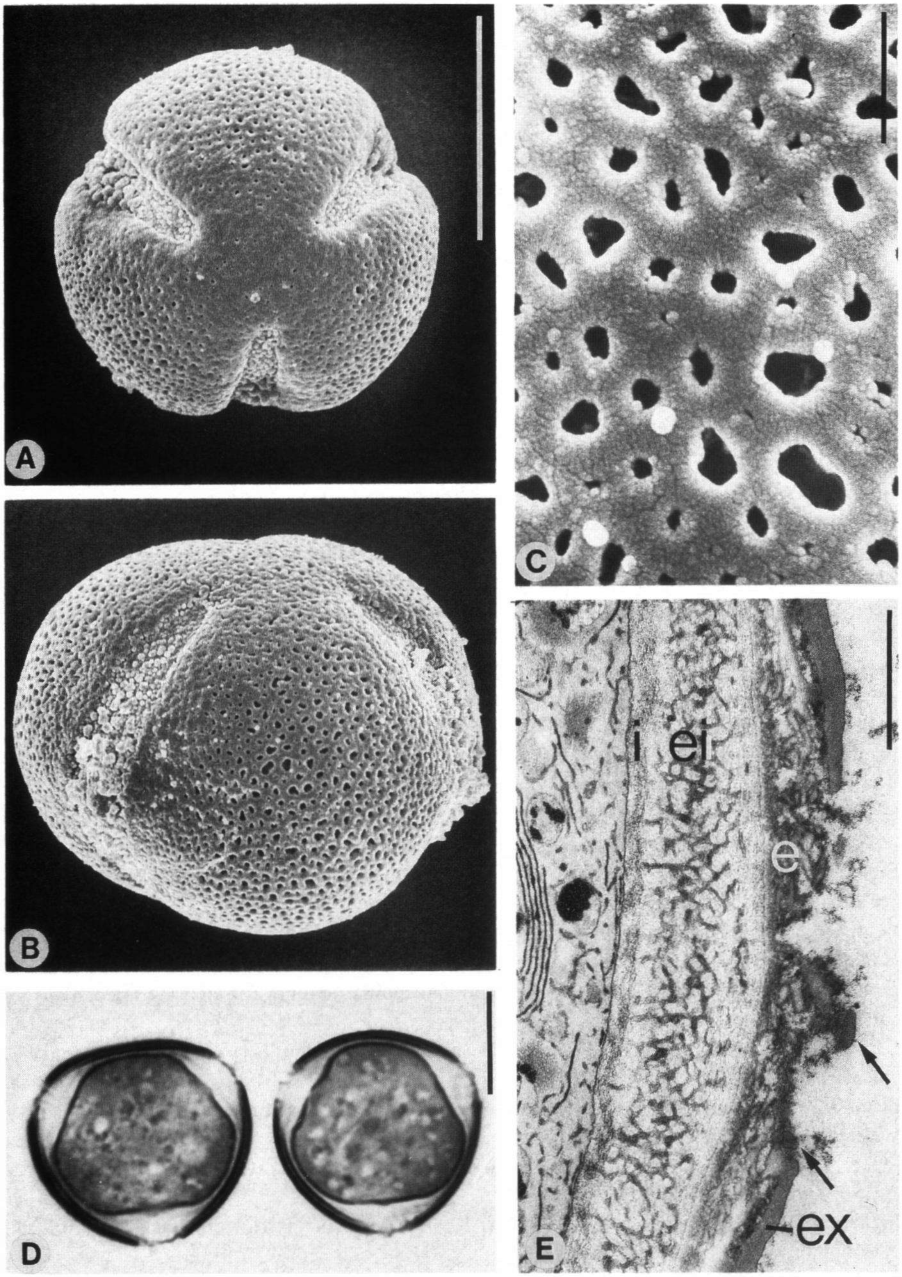

Fig. 1. *Cyrtandra cordifolia*. A: polar view, note perforate apocolpium; SEM. — *C. platyphylla*. B: equatorial view; SEM; C: detail of mesocolpium; SEM. — *C. sandwicensis*. D: pollen grains in polar view, optical cross section; LM; E: ultrathin section of aperture, showing endintine (i), thick exintine with channel-like structures (ei), lamellated endexine (e) and ectexine (ex) being resolved in granular elements (arrows) at the aperture region; TEM. — Scale bars: A = B, D: 10 μm; C, E: 1 μm.

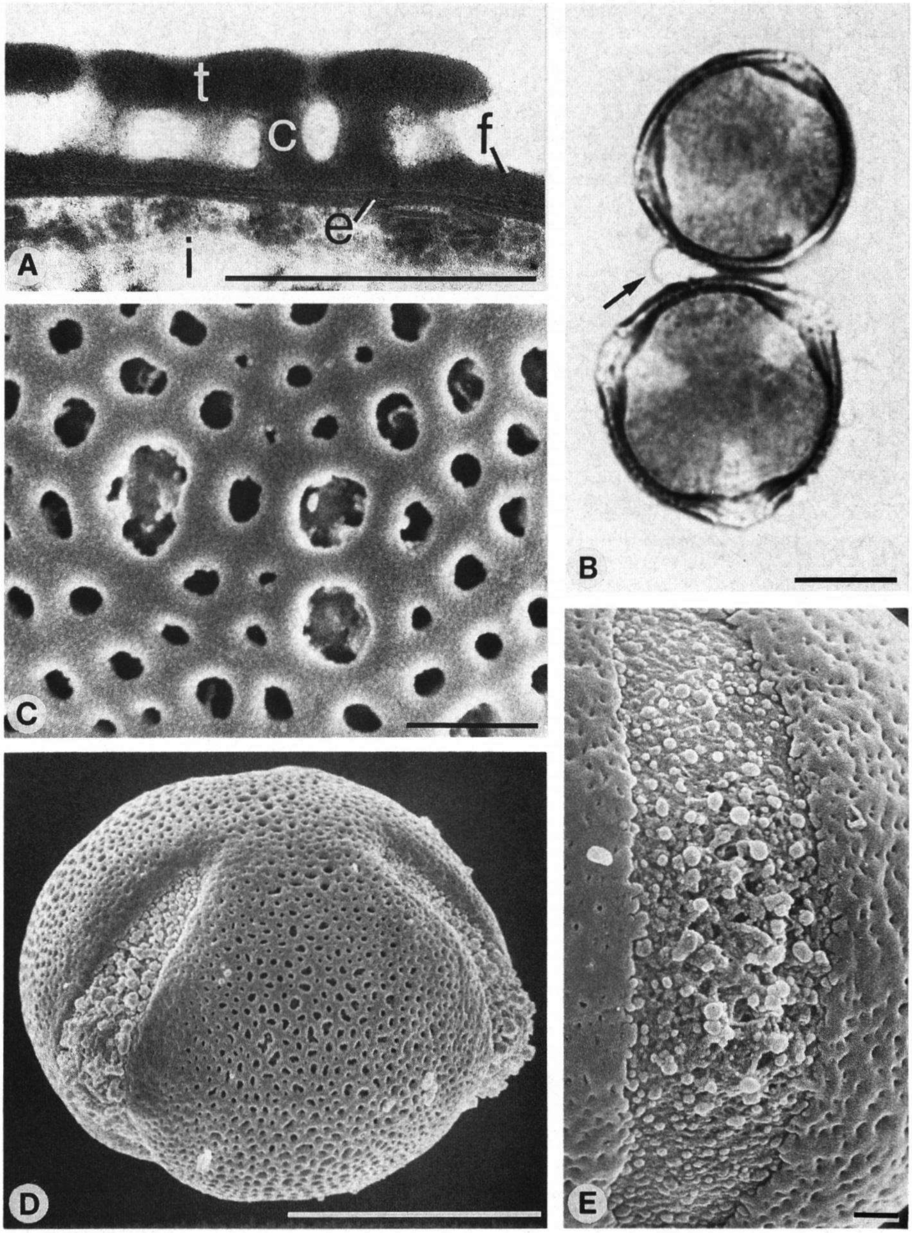

Fig. 2. *Cyrtandra sandwicensis*. A: ultrathin section of the exine, showing ectexine with tectum (t), columellae (c), foot layer (f), endexine (e) and intine (i); TEM; B: pollen grains in ± polar view, showing pollenkitt (arrow) and apertures; LM. — *C. procera*. C: detail of mesocolpium; SEM; D: equatorial view; SEM; E: detail of an aperture; note endexinous colpus membrane and ectexinous granular elements; SEM. — Scale bars: B, D: 10 µm; A, C, E: 1 µm.

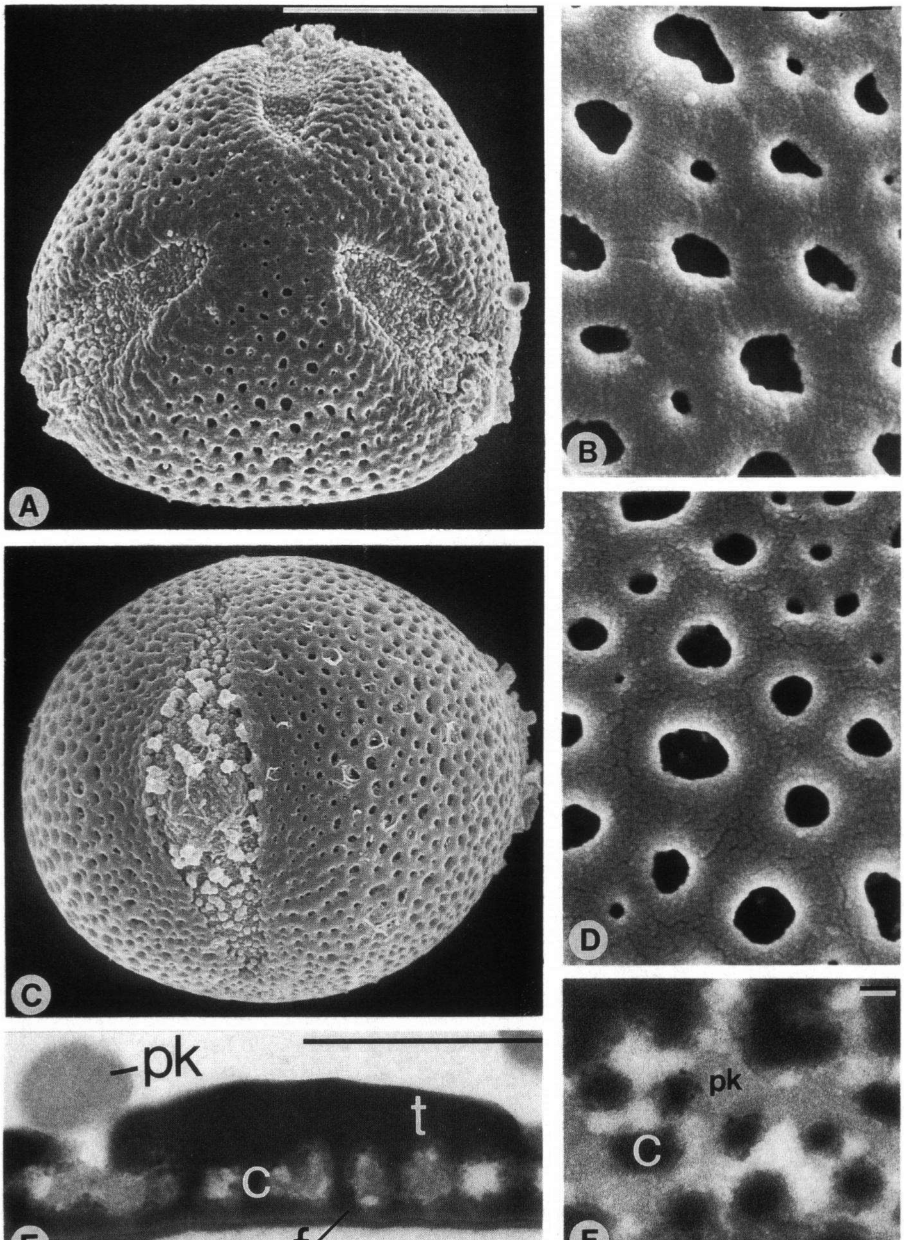

Fig. 3. *Cyrtandra kaulantha*. A: polar view; SEM; B: detail of mesocolpium; SEM. — *C. paludosa* var. *paludosa*. C: equatorial view; SEM. — *C. longifolia*. D: detail of mesocolpium; SEM. — *C. hawaiensis*. E: ultrathin section of exine, showing pollenkitt (pk), tectum (t), columellae (c) and foot layer (f); TEM; F: tangential section of exine; note pollenkitt (pk) in between the exine cavities and columellae (c); TEM. — Scale bars: A = C: 10 µm; B = D, E: 1 µm; F: 0.1 µm.

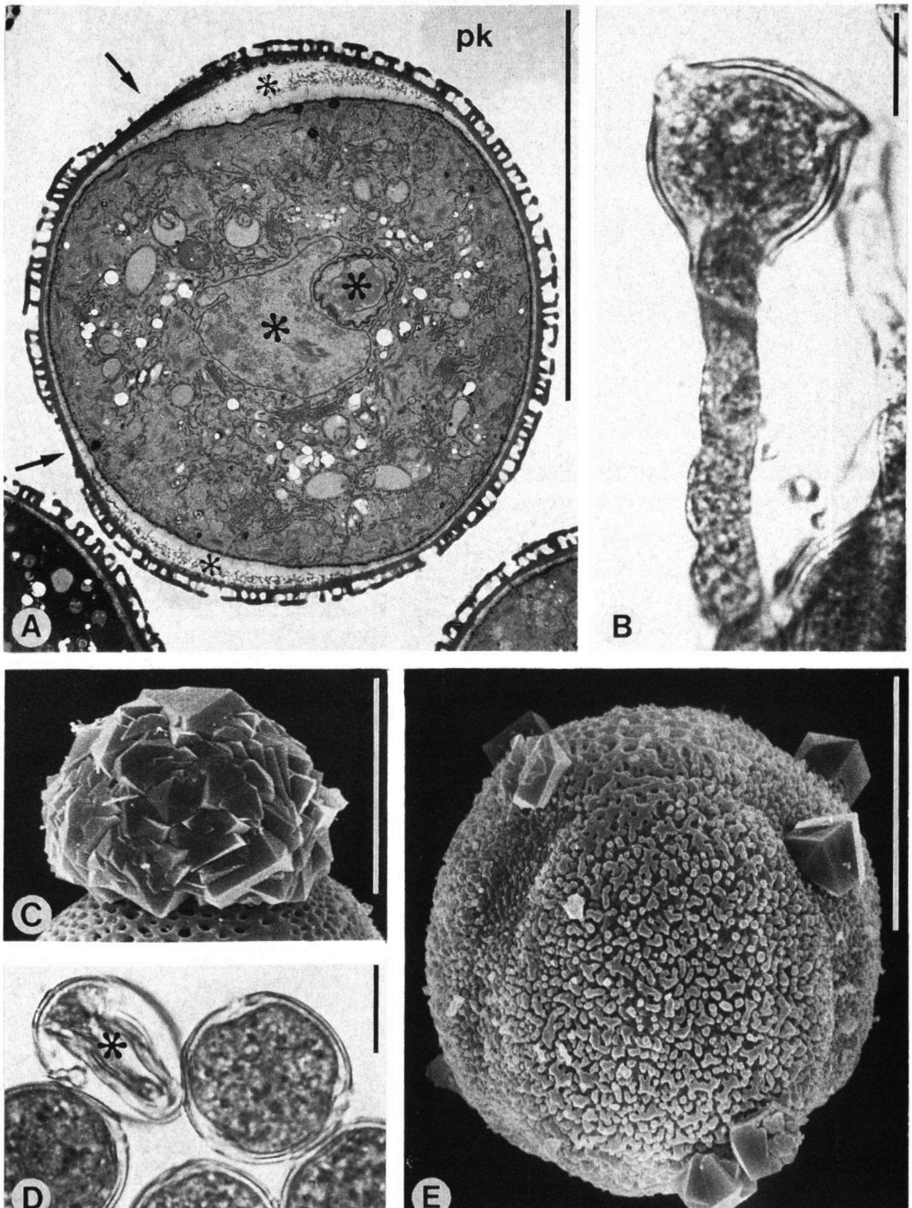

Fig. 4. *Cyrtandra sandwicensis.* A: ultrathin section of a mature pollen grain; note the two nuclei (large ✻), thickened endexine (colpus membranes: arrows) and the thickened exintine (small ✻), pk = pollenkitt; TEM. — *C. paludosa* × *C. platyphylla.* B: germinated pollen grain with long pollen tube; LM. — *C. wawrae.* C: large crystal on surface of a pollen grain; SEM. — *C. laxiflora* × *C. paludosa.* D: one aborted (✻) and some viable pollen grains; LM. — *C. grandiflora.* E: pollen grain with abnormal, rugulate exine pattern; note number of small crystals; SEM. — All scale bars: 10 µm.

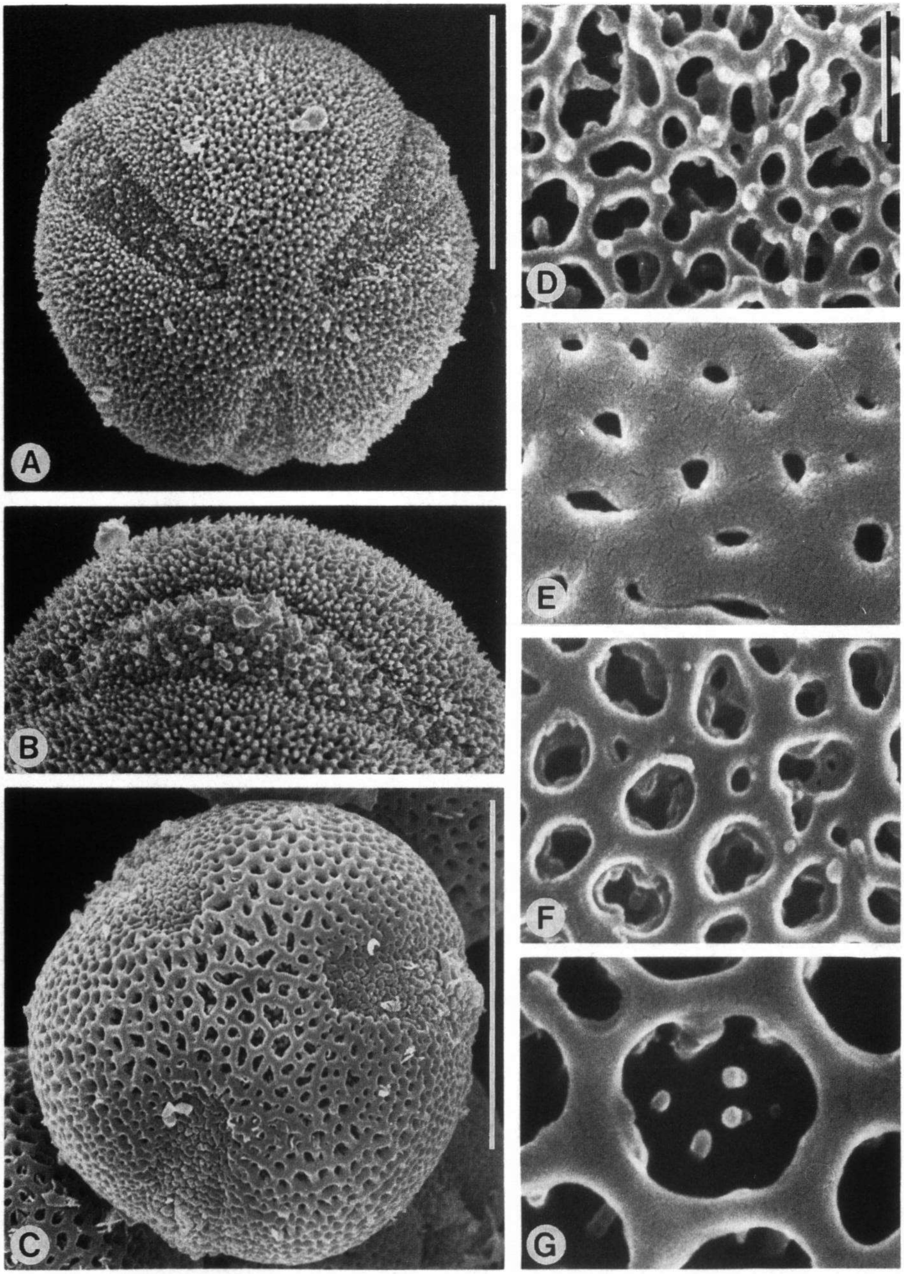

Fig. 5. Pollen of SE Asian taxa; SEM. — *Cyrtandra pendula*. A: polar view; B: aperture and adjacent parts of sexine, note conical supratectal elements. — *C. splendens*. C: polar view. — D–G: Details of the mesocolpia; note the presence or absence of supratectal elements, of luminal elements and the differences in size, shape and number of the lumina; D: *C. wallichii*; E: *C. sarawakensis*; F: *C. farinosa*; G: *C. dispar*.— Scale bars: A, B = C: 10 μm; D = F, G & H: 1 μm.