POLLEN CHARACTERISTICS OF THE GENERA OF THE BEGONIACEAE

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SUMMARY

The three genera of the *Begoniaceae* are characterized by distinct pollen types. The pollen of *Hillebrandia* Oliv. is very similar to certain types of *Begonia* L. pollen, which in itself is very variable. Both genera show 3-colporate, often prolate grains with striate ornamentation. The pollen of the third genus, *Symbegonia* Warb., is strikingly different, being a small, spherical grain with irregular echinate ornamentation. The possible relationships between the genera are discussed.

1. INTRODUCTION

The Begoniaceae are a pantropical family with representatives in America, Africa and Asia, but absent in Australia. Currently only three genera are generally recognized: the large and widely distributed genus Begonia L. comprising about 800 species, the genus Symbegonia Warb. comprising 12 species all restricted to New Guinea and the monotypic genus Hillebrandia Oliv. whose only species Hillebrandia sandwicensis Oliv. occurs on the Hawaiian islands.

At Wageningen Dr. J. J. F. E. DE WILDE is studying the continental African *Begonias* and in order to provide additional information on taxonomically important problems which appeared difficult to solve with macromorphological methods, it was decided to investigate the micromorphology of the pollen of these African representatives of the genus *Begonia* (BERG, R. G. van den (in prep.): Pollen morphology of African *Begonias*). As in the course of this study material of the other two genera also became available and as data on the pollen morphology of the *Begoniaceae* are virtually non-existent (cf. ERDTMAN 1952), it seemed worthwhile to provide a preliminary account of the pollen characteristics of the three genera in the family as a precursor of the detailed study of the pollen morphology of the African species of the genus *Begonia*.

2. MATERIAL AND METHODS

In the greenhouse of the Department of Horticulture of the Agricultural University at Wageningen pollen of two species of *Symbegonia* (S. c.f. strigosa Warb. and S. sanguinea Warb.) could be sampled. Vouchers of these are present in the Wageningen Herbarium (WAG). Herbarium sheets of *Hillebrandia* and of further material of *Symbegonia* were available in Leiden (L).

Specimens examined:

Symbegonia papuana Merr. & Perry – Brass 12161 (L); Symbegonia sanguinea Warb. – Van Veldhuizen 886 (WAG); Symbegonia c.f. strigosa Warb. – Van Veldhuizen 689 (WAG); Symbegonia spec. – Jacobs 8618 (L), Kalkman 5307 (L), Robbins 190 (L), Van den Berg, Katik & Cairo NGF 39909 (L), Van Royen & Sleumer 8033 (L), Vink BW 11478 (L); Hillebrandia sandwicensis Oliv. – Carlquist 1930

(L), Degener 27325 (L), Degener s.n. (L), Hochreutiner 3551 (L).

Pollen of numerous *Begonia* species was studied from living material and from herbarium specimens.

The samples were treated according to the standard acetolysis method and were studied with a Zeiss light microscope (Planapo 63/1.4 Oel) and with a Jeol 35-c scanning electron microscope. Sections of one sample of *Symbegonia* (and several of *Begonia*) were studied with transmission electron microscopy (Philips EM 400 T).

3. DESCRIPTION OF THE POLLEN TYPES

2	1	Symbogonia	tuno
2.	1.	Symbegoma	Lypc.

Plate 1

Pollen class:	3-zono-colporate, occasionally 4-colporate.
P/E ratio:	Spheroidal.
Apertures:	Ectoaperture – colpus, narrow with straight margins, long but never anastomosing at the poles, endings acute, colpus
	membrane granular, no costae.
	Endoaperture – porus, small, lalongate, elliptical, outline distinct, no costae.
Exine:	Thin, stratification hardly visible with LM, TEM observa-
	tions (Plate 4) show a more or less homogeneous inner
	layer (nexine) on which the variably shaped tooth-like ex-
	crescenses (sexine) are placed; sexine as thick as or thicker
	than nexine, columellae not present, wall thickness uni-
	form.
Ornamentation:	The sculptural elements, which are variously shaped but
	often sharply pointed, are arranged in an irregular pattern.
Outline:	Equatorial view – circular to elliptical.
	Polar view – circular/rounded triangular.
Measurements:	P 12-15 μ m, E 12-14 μ m, P/E 1.0-1.1, exine 0,6-1 μ m, porus 1,5 \times 3 μ m.
Species:	This description is valid for the examined species Symbe- gonia papuana Merr. & Perry, S. sanguinea Warb, and S.
	c.f. strigosa Warb. and a number of samples designated
	as S. spec. Some other samples, determined as S. spec.,
	showed both in their pollen and flower morphology the characteristics of <i>Begonia</i> . Pending further investigation
	it cannot be ruled out beforehand that other pollen types
	can be established within the present circumscription of the genus.
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PLATE 1 SEM: 1. Symbegonia c.f. strigosa Warb. (Van Veldhuizen 689) polar view; 2–4. Symbegonia spec. (Van den Berg, Katik & Cairo NGF 39909) equatorial view; all magnifications ca 2650 ×.

Comments: The lack of columellae, as well as the extraordinary ornamentation give this type an isolated position compared to the other types within the family (see: DISCUSSION).

Pollen class:	3-zono-colporate.
P/E ratio:	Prolate.
Apertures:	Ectoaperture – colpus, rather narrow, constricted at equa- tor, long but never anastomosing at the poles, endings acute, colpus membrane granular, no costae. Endoaperture – porus, very small, usually somewhat lalon- gate, irregularly shaped or elliptical, outline indistinct, no costae; in cross section protruding endoapertures (raised sexine).
Exine:	Thin, stratification not visible with LM, wall thickness uni- form or slightly thicker at the poles.
Ornamentation:	Finely striate, the lirae running very close together, orien- tation parallel to the colpi or rather variable, often irregu- lar ornamentation at the poles.
Outline:	Equatorial view – elliptical. Polar view – rounded triangular, with invacinated colpi
Measurements:	P 20-22 μ m, E 12-14 μ m, P/E 1.6-1.7, exine 0,5-0.7 μ m, porus $\pm 1 \times 2 \mu$ m.
Species:	Hillebrandia sandwicensis Oliver.
Comments:	This type resembles certain types of <i>Begonia</i> pollen, especially in apertures, overall shape and ornamentation.



PLATE 2 SEM: 1. Hillebrandia sandwicensis Oliv. (Degener 27325) polar view; 2. id. equatorial view; 3-4 Hillebrandia sandwicensis Oliv. (Carlquist 1930) equatorial view; all magnifications ca 2650 ×.



PLATE 3 SEM: 1. Begonia oxyloba Welw. (Letouzey 15010); 2. Begonia johnstonii Oliv. ex Hook. f. (Schlieben 2920); 3. Begonia quadrialata Warb. (Callens 3567); 4. Begonia ampla Hook. f. (Wrigley & Melville 29); all magnifications ca 2650 ×.

3.3. Begonia type

Pollen class:	3-zono-colporate, occasionally 4-colporate, loxotreme.
P/E ratio:	Subprolate to perprolate.
Apertures:	the poles resulting in syncolpate grains, endings (when pre- sent) acute, colpus membrane granular, granulae coarser at endoaperture, no costae.
	Endoaperture – porus or colpus, small to large, always somewhat (and sometimes very) lalongate, elliptical to ob- long, outline more or less distinct, costae may be present especially along the long sides, the outer endings often dif- fue
Exine:	Thin, stratification hardly visible with LM, TEM observa- tions of several species show a layered structure of the ex- ine: an outer continuous, homogeneous tectum, an infra- tectal layer of more or less regular columellae, and a basal
	footlayer (Plate 4); wall thickness uniform.
Ornamentation:	Finely to coarsely striate, the lirae can vary in width and shape (cross section), lie close together or further apart,
	run parallel to the colpi or show an irregular orientation
	pattern; a special type of deviating non-striate ornamenta-
	tion may occur in a band along the colpi (margo) and also
	at the poles; cross connections between the lirae occur in
	certain species, especially towards the poles.
Outline:	Equatorial view – often elliptical with rounded poles and convex sides, but in certain species con-
	Bolar view – nearly always 3 labate due to the invaginat
	rolat view – hearly always 5-lobate due to the invaginat-
Manauramanta:	D from 16 um to 25 um E from 8 um to 14 um D/E from
measurements.	1 2 to 2.0 aving 0.5 µm, E from 8 µm to 14 µm, F/E from
	1.2 to 2.9, extre 0.5 μm, dimension of endoaper ture in po-
Species	This general description includes all ± 120 even includes all ± 120
species.	This general description includes an \pm 120 examined Am-
Commonto	Due to the veriation in shane, size, details of ornamente
Comments:	tion time and shape of andoaperture ate of the poller
	tion, type and shape of endoaperture etc. of the ponen
	description is given shows for the gamua. Within the gamua
	it is possible to distinguish a large number of nollen tange
	head on these characters, which will be described in a fu
	ture publication
	Ear the present nurness a description of a constal Present
	'ture' is used in order to compare the pollon mornhology
	of the three genera under discussion
	or me mice genera ander ascassion.

4. **DISCUSSION**

Pollenmorphological observations lead to the establishment of distinct, rather uniform pollen types within the genera *Hillebrandia* and *Symbegonia* and of a much more variable 'type' (in fact a number of types) within the genus *Begonia*, in compliance with the number of taxonomically recognizable species within these genera, viz. 1, 12 and 800 respectively.

In order to understand the pollenmorphological interrelations of the genera of the *Begoniaceae* this variation within *Begonia* must be borne in mind. Not only is it possible to find *Begonia* pollen types which show resemblance with the *Hillebrandia* type, even the position of the very different *Symbegonia* type may be understood, notwithstanding its deviating shape, size and, especially, ornamentation, by taking into account a pollenmorphological evolutionary trend (hypothetical line of evolution based on the comparison of morphological features which can be arranged in a sequence from primitive to advanced – PUNT 1976) which can be discerned within *Begonia*.

The fact that it is impossible to observe any stratification of the exine with the light microscope is caused by an apparent reduction of the infratectal layer, viz. the columellae. TEM observations show that different (groups of) species of *Begonia* are characterized by different stages of reduction, from more or less regularly shaped (though very short) columellae to an almost 'alveolar' stage. Accepting this tendency of the columellar layer to become reduced (in a family like the *Begoniaceae*, which can be considered a relatively advanced family, reduction of the columellae is certain to be a derived character), this would point to an extremely derived position of *Symbegonia* where columellae are even absent. The small, spherical grain and the remarkable ornamentation place this type even further apart from the rest of the *Begoniaceae*.

Hillebrandia, on the contrary, shows a pollen type which is much more comparable to that of (at least certain species of) Begonia. Especially the apertures and the striate ornamentation – although the type of closely packed striae is unique - point to a rather close relationship with *Begonia*, especially with those pollen types of Begonia which share the rather small size, prolate P/E ratio and small, elliptical endoaperture without costae. As could be concluded from the examination of the pollen morphology of the African species of Begonia, these are probably primitive character states. Among the evolutionary trends (see above) within *Begonia* pollen can be mentioned a tendency from small to large size, the development of a margo (a band of deviating non-striate ornamentation along the colpi) and of costae (thickenings of the nexine around, in this case, the endoaperture), an increase in size of the endoaperture while its shape changes from elliptical to more or less oblong. In these characters Hillebrandia, which lacks a margo and costae, shows the primitive state and can be compared with types of the pollenmorphologically most primitive African section of the genus Begonia, viz. Mezierea. Hillebrandia is primitive also in possessing parietal placentation. Within Begoniaceae this type of placentation must be considered primitive (GAUTHIER 1950, 1959; REITSMA, this issue). It is of interest that the section



PLATE 4 TEM: 1–2. Symbegonia c.f. strigosa Warb. (Van Veldhuizen 689) 26000 \times ; 3–4. Begonia seychellensis Hemsley (Van Veldhuizen 539) 3: ca 20700 \times , 4: 26000 \times ; 5. Begonia dregei Otto & Dietr. (Van Veldhuizen 477) 34000 \times ; 6. Begonia cavallyensis Chevalier (Van Veldhuizen 502) 34000 \times .

Mezierea also shows parietal placentation. Thus both pollenmorphology and placentation indicate a relationship between the genus *Hillebrandia* and the more primitive representatives of the genus *Begonia*.

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