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
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

#### 3.1. *Symbegonia* type

**Plate 1**

<table>
<thead>
<tr>
<th>Pollen class:</th>
<th>3-zono-colporate, occasionally 4-colporate.</th>
</tr>
</thead>
<tbody>
<tr>
<td>P/E ratio:</td>
<td>Spheroidal</td>
</tr>
<tr>
<td>Apertures:</td>
<td>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.</td>
</tr>
<tr>
<td>Exine:</td>
<td>Thin, stratification hardly visible with LM, TEM observations (Plate 4) show a more or less homogeneous inner layer (nexine) on which the variably shaped tooth-like excrescenses (sexine) are placed; sexine as thick as or thicker than nexine, columellae not present, wall thickness uniform.</td>
</tr>
<tr>
<td>Ornamentation:</td>
<td>The sculptural elements, which are variously shaped but often sharply pointed, are arranged in an irregular pattern.</td>
</tr>
<tr>
<td>Outline:</td>
<td>Equatorial view – circular to elliptical.</td>
</tr>
<tr>
<td>Polar view:</td>
<td>Circular/rounded triangular.</td>
</tr>
<tr>
<td>Measurements:</td>
<td>P 12–15 μm, E 12–14 μm, P/E 1.0–1.1, exine 0.6–1 μm, porus 1.5 × 3 μm.</td>
</tr>
<tr>
<td>Species:</td>
<td>This description is valid for the examined species <em>Symbegonia papuana</em> Merr. &amp; Perry, <em>S. sanguinea</em> Warb. and <em>S. c.f. strigosa</em> Warb. and a number of samples designated as <em>S. spec.</em> Some other samples, determined as <em>S. spec.</em>, showed both in their pollen and flower morphology the characteristics of <em>Begonia</em>. Pending further investigation it cannot be ruled out beforehand that other pollen types can be established within the present circumscription of the genus.</td>
</tr>
</tbody>
</table>
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).

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3.2. *Hillebrandia* type

**Pollen class:** 3-zono-colporate.

**P/E ratio:** Prolate.

**Apertures:**
- Ectoaperture – colpus, rather narrow, constricted at equator, long but never anastomosing at the poles, endings acute, colpus membrane granular, no costae.
- Endoaperture – porus, very small, usually somewhat lalongate, irregularly shaped or elliptical, outline indistinct, no costae; in cross section protruding endoapertures (raised sexine).

**Exine:**
- Thin, stratification not visible with LM, wall thickness uniform or slightly thicker at the poles.

**Ornamentation:**
- Finely striate, the lirae running very close together, orientation parallel to the colpi or rather variable, often irregular ornamentation at the poles.

**Outline:**
- Equatorial view – elliptical.
- Polar view – rounded triangular, with invaginated colpi.

**Measurements:**
- P 20–22 μm, E 12–14 μm, P/E 1.6–1.7, exine 0.5–0.7 μm, porus ± 1 × 2 μm.

**Species:** *Hillebrandia sandwicensis* Oliver.

**Comments:** This type resembles certain types of *Begonia* pollen, especially in apertures, overall shape and ornamentation.
Plate 2 SEM: 1. Hillebrandia sandwicensis Oliv. (Degener 27323) polar view; 2. id. equatorial view; 3–4 Hillebrandia sandwicensis Oliv. (Carlquist 1930) equatorial view; all magnifications ca 2650 x.
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 x.
3.3. **Begonia type**

<table>
<thead>
<tr>
<th>Pollen class:</th>
<th>3-zono-colporate, occasionally 4-colporate, loxotreme.</th>
</tr>
</thead>
<tbody>
<tr>
<td>P/E ratio:</td>
<td>Subprolate to perprolate.</td>
</tr>
<tr>
<td>Apertures:</td>
<td>Ectoaperture – colpus, long, often even anastomosing at the poles resulting in syncolpate grains, endings (when present) 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 oblong, outline more or less distinct, costae may be present especially along the long sides, the outer endings often diffuse.</td>
</tr>
<tr>
<td>Exine:</td>
<td>Thin, stratification hardly visible with LM, TEM observations of several species show a layered structure of the exine: an outer continuous, homogeneous tectum, an infratectal layer of more or less regular columellae, and a basal footlayer (Plate 4); wall thickness uniform.</td>
</tr>
<tr>
<td>Ornamentation:</td>
<td>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 ornamentation 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.</td>
</tr>
<tr>
<td>Outline:</td>
<td>Equatorial view – often elliptical with rounded poles and convex sides, but in certain species concave sides and pointed poles. Polar view – nearly always 3-lobate due to the invaginating colpi.</td>
</tr>
<tr>
<td>Measurements:</td>
<td>P from 16 μm to 35 μm, E from 8 μm to 14 μm, P/E from 1.2 to 2.9, exine 0.5 μm, dimension of endoaperture in polar direction 1.5–5 μm, in equatorial direction 3–8 μm.</td>
</tr>
<tr>
<td>Species:</td>
<td>This general description includes all ± 120 examined African species names.</td>
</tr>
<tr>
<td>Comments:</td>
<td>Due to the variation in shape, size, details of ornamentation, type and shape of endoaperture etc. of the pollen types of the African species of <strong>Begonia</strong>, only a generalized description is given above for the genus. Within the genus it is possible to distinguish a large number of pollen types based on these characters, which will be described in a future publication. For the present purpose a description of a general <strong>Begonia</strong> 'type' is used in order to compare the pollen morphology of the three genera under discussion.</td>
</tr>
</tbody>
</table>

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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. *Mediarea*. *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
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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5. REFERENCES