STUDIES IN BEGONIACEAE II

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POLLEN MORPHOLOGY OF THE GENUS Begonia IN AFRICA

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1. INTRODUCTION

... car la chose la plus importante en histoire naturelle n'est pas de nommer un groupe, genre ou sous-genre, tribu ou famille, c'est d'avoir rapproché ce qui mérite d'être rapproché.

A. DE CANDOLLE (1859, p. 107)

1.1. TAXONOMY OF BEGONIACEAE

The purpose of this study is to describe the pollen morphology of the representatives of the genus *Begonia* in Africa, interpret these data phylogenetically and apply the findings to the existing taxonomical problems. The grouping of taxa resulting from the recognition of pollen types may lead to a better understanding of the interrelations of the taxa within the genus, and even of the genera of the family *Begoniaceae* (VAN DEN BERG, 1984). A brief survey of the taxonomy of the family, with emphasis on the African representatives, will be presented below.

The pantropical family *Begoniaceae* contains only three genera: *Symbegonia* Warb., comprising 12 species restricted to New Guinea, *Hillebrandia* Oliv., monotypic, occurring on the Hawaiian Islands and the widely distributed genus *Begonia* L. with about 900 species. Formerly two more genera were recognized: *Begoniella* A.DC. (Colombia) and *Semibegoniella* C.DC. (Ecuador) with a small number of species which are now considered to belong to *Begonia*. This large genus is divided in 60 sections, a number of which were at one time or another given generic rank. Thirteen of these sections are accepted to occur in Africa and the Madagascan region: *Mezierea* (Gaud.) Warb., *Squamibegonia* Warb., *Tetraphila* A.DC., *Augustia* (Klotzsch) A.DC., *Rostrobegonia* Warb., *Sexalaria* A.DC., *Filicibegonia* A.DC., *Scutobegonia* Warb., *Loasibegonia* A.DC., *Erminea* A.DC., *Nerviplacentaria* A.DC., *Quadrilobaria* A.DC. and *Muscibegonia* A.DC. The circumscription of at least a number of the African sections is in need of critical revaluation.

The study of the *Begonias* of Madagascar, started by H. HUMBERT and M. KERAUDREN-AYMONIN and completed by G. G. AYMONIN & J. BOSSIER, indicated that it is not possible to assign the species to sections, leaving the status of the Madagascan sections (*Erminea, Nerviplacentaria, Quadrilobaria* and *Muscibegonia*) in some doubt (KERAUDREN-AYMONIN, 1983).

The last full treatment of the family was by IRMSCHER (1925). Since then, IRMSCHER published a detailed survey of the sections *Augustia* and *Rostrobegonia* (IRMSCHER, 1961). More recently, accounts have been published of section *Squamibegonia* (DE WILDE & ARENDS, 1980) and on several species of section *Tetraphila* (DE WILDE & ARENDS, 1979, HAGMAN & DE WILDE, 1984).
A synopsis of the taxonomy of African Begonias used as the systematic background of this pollen-morphological study is given below, based on information of Dr. J. J. F. E. De Wilde who is studying the continental Begonias and on Wilczek (1969), Barkley (1972) and Hilliard (1976). The most recent views deviate in a number of instances from the system as accepted up till now. Some of the proposed changes have not yet been validly published. A few recently studied species will be accommodated in new sections, some sections should be combined since they cannot be clearly segregated. The species B. baccata Hook. f. and B. crateris Exell are accommodated in a new section Baccabegonia Reitsma (Reitsma, 1985b). The sections Sexalaria A.DC., Augustia (Klotzsch) A.DC. and Rostrobegonia Warb. may be considered as a single section. The same holds for the sections Scutobegonia Warb. and Loasibegonia A.DC. These sections have still been kept separate in the synopsis pending further research. A number of species should be transferred from section Scutobegonia to section Filicibegonia A.DC., enlarging the latter section from one to twelve species. This decision, based on macromorphological evidence is corroborated by seed morphology and, for most species, also by pollen morphology. For this reason section Filicibegonia is presented in the synopsis in its new circumscription. B. thomaeana C.DC. forms a separate section Cristasemen J. J. De Wilde (De Wilde, 1985b).

1.2. SYNOPSIS OF TAXONOMY OF AFRICAN BEGONIAS

(including the representatives of section Mezierea from Madagascar, the Comores and the Seychelles)

The synopsis represents the recent views on the classification of the African sections and species. Synonyms have only been included when pollen was available.

Mezierea (Gaud.) Warb.
B. cladocarpa Baker
B. comorensis A.DC. ex Warb.
B. seychellensis Hemsley
B. meyeri-johannis Engl.
B. oxyloba Welw. ex Hook. f.
B. pycnocaulis Irmsch.

Only B. meyeri-johannis, B. oxyloba and B. pycnocaulis are found on the African continent. The other species are from Madagascar, the Comores and the Seychelles. B. seychellensis is placed in synonymy to B. comorensis by Keraudren-Aymonin (1983).

Baccabegonia Reitsma sect.nov.
B. baccata Hook.f.
B. crateris Exell

Agric. Univ. Wageningen Papers 84-3 (1984)
These species are removed from section *Squamibegonia* (cf. DE WILDE & ARENDS, 1980 and REITSLMA, 1985b). They are endemics of the island São Tomé.

**Squamibegonia Warb.**
- *B. ampla* Hook.f.
- *B. bonus-henricus* J. J. de Wilde
- *B. poculifera* Hook.f.
- *B. adolfi-friderici* Gilg

This section has been extensively treated by DE WILDE & ARENDS (1980).

**Tetraphila A.DC.**
- *B. alepensis* Chev.
- *B. buchholzii* Gilg
- *B. cavallyensis* Chev.
- *B. cultrata* Irmsch.
- *B. ebolowensis* Gilg
- *B. elaeagnifolia* Hook.f.
- *B. eminii* Warb.
  - *B. ealensis* Irmsch.
  - *B. poggei* Warb.
- *B. epiphytica* Hook.f.
- *B. furfuracea* Hook.f.
- *B. fusicalata* Warb.
- *B. fusicarpa* Irmsch.
- *B. gracilipetiolata* De Wild.
- *B. horticola* Irmsch.
- *B. jussiaeicarpa* Warb.
- *B. kisuhana* Büttin.
  - *B. zobiensis* De Wild.
- *B. komoensis* Irmsch.
- *B. lethomasiae* Wilcz.
- *B. loranthoides* Hook.f.
- *B. macrostyla* Warb.
- *B. mannii* Hook.
  - *B. excelsa* Hook.f.
  - *B. ndongensis* Engl.
  - *B. nicolai-hallei* Wilcz.
  - *B. oxyantha* Warb.
  - *B. polygonoides* Hook.f.
  - *B. capillipes* Gilg.
  - *B. rhipsaloides* Chev.
  - *B. preussii* Warb.
  - *B. rubromarginata* Gilg
  - *B. rubronervata* De Wild.
  - *B. sanjeensis* Wilcz.
  - *B. schultzei* Engl.
  - *B. sessilanthera* Warb.
  - *B. squamulosa* Hook.f.
  - *B. bipindensis* Gilg ex Engl.
  - *B. crassipes* Gilg ex Engl.
  - *B. gladiifolia* Engl.
  - *B. subalpestris* Chev.
  - *B. macambrarenisis* Exell
  - *B. subscutata* De Wild.
  - *B. tatoniana* Wilcz.
  - *B. wilczekiana* Hallé
  - *B. zimmermannii* Peter ex Irmsch.

A number of species is associated in the so-called *B. squamulosa*-aggregate: *B. squamulosa, B. elaeagnifolia, B. gracilipetiolata, B. schultzei* and *B. wilczekiana*. A second aggregate may exist around *B. polygonoides*. The species *B. cultrata* and *B. rubronervata* belong to it.

HAGMAN & DE WILDE (1984) discussed the status of *B. eminii, B. macrostyla, B. poggei, B. preussii, B. warburgii, B. rubromarginata, B. alepensis, B. ealensis* and *B. fusicarpa* in relation to *B. cavallyensis*. Pollen was not available of *B. cultrata, B. elaeagnifolia, B. rubronervata* and *B. zimmermannii*.
Sexalaria A.DC.
*B. annobonensis* A.DC.

A monotypic section, restricted to the islands of Annobon, São Tomé, Principe, and coastal Cameroun.

**Augustia (Klotzsch) A.DC.**

*B. brevibracteata* Kup.  
*B. dregei* Otto et Dietr.  
*B. partita* Irmsch.  
*B. geranioides* Hook.f.  
*B. homonyma* Steud.  
*B. caffra* Meissn.  
*B. rudatisii* Irmsch.

*B. princeae* Gilg  
*B. homblei* De Wild.  
*B. subacuto-alata* De Wild.  
*B. verdickii* De Wild.  
*B. pygmaea* Irmsch.  
*B. riparia* Irmsch.  
*B. socotrana* Hook.f.  
*B. tayloriana* Irmsch.  
*B. wakefieldii* Gilg ex Engl.

The synonymy is according to HILLIARD (1976). *B. socotrana* has been assigned to a special section *Peltaugustia* (cf. BARKLEY, 1972) but is considered here to belong to section *Augustia*. IRMSCHER (1961, p. 117) notes: ‘Besondere Beachtung verdient, daß zu *B. princeae* noch *B. wellmannii* gezogen werden muß. Da diese in Westafrika (Angola) beheimatet ist, *B. princeae* jedoch in Ostafrika, gesellt sich jetzt auch *B. princeae* zu den Arten, die sowohl im westlichen wie im östlichen Afrika vorkommen. Sie reiht sich damit in einen ähnlichen Arealtyp ein, wie ihn *B. oxyloba* und *B. haullevilleana* (= *B. poculifera* var. *poculifera*) vertreten.’

Pollen was not available of *B. pygmaea*, *B. rumpiensis* and *B. tayloriana*.

**Rostrobegonia Warb.**

*B. angolensis* Irmsch.  
*B. bequaertii* Rob. & Law.  
*B. engleri* Gilg  
*B. flava* Marais  
*B. johnstonii* Oliv. ex Hook.f.  
*B. keniensis* Gilg ex Engl.  
*B. nyassensis* Irmsch.  
*B. rostrata* Welw. ex Hook.f.

*B. schliebenii* Irmsch.  
*B. sonderana* Irmsch.  
*B. sutherlandii* Hook.f.  
*B. buttonii* Irmsch.  
*B. dissecta* Irmsch.  
*B. guineziana* (A.DC.) Irmsch.  
*B. wollastoni* Baker

The synonymy is according to HILLIARD (1976).  
About *B. angolensis*, IRMSCHER (1961, p. 176/7) states that ‘sie die westliche vikariierende Form zur östlichen *B. sutherlandii* darstellt (...). Es besteht also hier eine ähnliche Beziehung zwischen ost- und westafrikanischen Vertretern, wie sich auch innerhalb der Arten *B. oxyloba*, *B. haullevilleana* (= *B. poculifera* var. *poculifera*) und *B. princeae* festgestellt wurde.’
Pollen was not available of *B. buttonii*, *B. flava* and *B. nyassensis*.

**Cristasemen J. J. de Wilde sect. nov.**

*B. thomeana* C.DC.

This species is removed from the section *Loasibegonia* (cf. De Wilde, 1985b).

**Felicibegonia A.DC.**

- *B. asplenifolia* Hook.f.
- *B. auriculata* Hook.f.
- *B. elatostemmoides* Hook.f.
- *B. flicifolia* Hallé
- *B. gossweideri* Irmsch.
- *B. graciliaulis* Irmsch.
- *B. iucunda* Irmsch.

Originally, this section contained only one species: *B. asplenifolia*. A number of species of the section *Scutobegonia* shows characters that indicate relationships with section *Felicibegonia* (De Wilde, pers. comm.). This is confirmed by seed morphology, and for the greater part by pollen morphology, too. Pollen was not available of *B. auriculata*.

**Scutobegonia Warb.**

- *B. aggeloptera* Hallé
- *B. anisosepala* Hook.f.
- *B. calophylla* Gilg ex Engl.
- *B. ciliobracteata* Warb.
- *B. clypeifolia* Hook.f.
- *B. comperei* Wilcz.
- *B. dielsiana* Gilg
- *B. ferramica* Hallé
- *B. ficicola* Irmsch.
- *B. gentilii* De Wild.
- *B. hirsutula* Hook.f.
- *B. hookeriana* Gilg ex Engl.
- *B. hydropogae* Winkler
- *B. klainei* Pierre ex Pellegr.
- *B. lacunosa* Warb.
- *B. laporteirolia* Warb.
- *B. macropoda* Gilg
- *B. mayombensis* Irmsch.
- *B. microsperma* Warb.
  - *B. batesii* C.DC.

This section has not been studied in detail, recently. A number of species-Agric. Univ. Wageningen Papers 84-3 (1984)
aggregates may be present (B. lacunosa/staudtii-, B. quadrialata-aggregate). The group strongly suggests to be of recent origin, its taxa are still in the process of 'cristallization'. Consequently, some taxa are extremely variable and difficult to circumscribe. Polyploid taxa have been observed (ARENS, 1985). Furthermore, many species show a restricted distribution. This high degree of endemism also could denote recent speciation. Within the combined group of sections Scuto-
begonia and Loasibegonia it may still be possible to distinguish subgroups based on the length/breadth-ratio and the wings of the fruits.

Pollen was not available of B. anisosepala, B. comperei, B. klainei, B. mayomb-
bensis and B. microsperma.

**Loasibegonia A.DC.**  
*B. dusenii* Warb.  
*B. prismaticarca* Hook.

**Table 1. Number of sections and species of African and Madagascan Begonias**  
1 according to IRMSCHER (1925), 2 according to BARKLEY (1972), 3 according to REITSMA (1983), 4 present synopsis, 5 according to BARKLEY (1972), 6 according to KERAUDREN-AYMONIN (1983).

<table>
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<th>Africa sections</th>
<th>OLD SITUATION</th>
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<th>2 species</th>
<th>RECENT VIEWS</th>
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*Agric. Univ. Wageningen Papers 84-3 (1984)*
Formerly this section also accommodated *B. thomeana* C.D.C. In its present circumscription section *Loasibegonia* does not seem a natural group. Material identified as *B. schäferi* may consist of several taxa.

### 1.3. Pollen Morphology, Taxonomy and Phylogeny

The taxonomy of the genus *Begonia* in Africa is in the process of being revised. Progress has been made in the classification in sections (cf. the synopsis in 1.2. and Reitsma, 1985b, and De Wilde, 1985b). The delimitation of numerous species still presents difficulties, however. A number of species-aggregates may be recognized and polyploid taxa are present. Finally, there are many more specific epithets than species. The synonymy is not yet clear in all cases. This as yet incomplete state of knowledge of the taxonomy presents a problem to the pollen morphologist. A recent and reliable monograph of the family would greatly facilitate pollen studies. There would be no doubt about the identification, classification and nomenclature of all specimens concerned and it would be clear which species (names) belong to which pollen type. On the other hand, pollen-morphological data can be used by a monographer, like any other source of information (macromorphology, karyology, geography, ecology etc.) to arrive at his eventual conclusions. It would be preferential for the taxonomist to possess all this information when embarking on his task, and the influence which the findings of pollen morphology may have on taxonomy should not be underestimated.

A pollen morphologist may collect samples from all available specimens irrespective of their alleged taxonomical status. In this way he will not be biased by existing systematic opinions and avoid circular reasoning. However, he will not be warned against the possibility of parallel evolutionary developments leading to seemingly comparable situations in quite separate taxa. More will be said on this subject in the chapter on phylogeny (chapter 5).

Collecting material from the nomenclatural types of the taxa whenever this is possible is of utmost importance. The descriptions of the pollen can always be linked with the type specimens (to which the name of a taxon is permanently attached) which means that the results of the pollen-morphological investigation remain valid even when future taxonomical research leads to changes in the taxonomy of the group.

Pollen morphology and taxonomy are undoubtedly interrelated. The question remains: what kind of taxonomy? Without wishing to enter into the debate between phylogenetics, evolutionary taxonomy and numerical taxonomy it seems desirable that a classification results which reflects the system of relationships which is hidden in the pluriformity of nature. In the opinion of the present author the goal of taxonomy and related disciplines like pollen morphology should be to unearth this phylogeny.

Pollen morphology is by its method a descriptive discipline. The assembled pollen-morphological data may be used for further interpretation, however.

*Agric. Univ. Wageningen Papers 84-3 (1984)*
this study the pollen-morphological data are interpreted phylogenetically, viz. an attempt to reconstruct the phylogeny of the family Begoniaceae, in particular on the African continent.
2. MATERIAL AND METHODS

2.1. MATERIAL

Herbarium vouchers of nearly all known African species of *Begonia* are present in the herbarium at Wageningen (WAG). Many specimens were received on loan from other herbaria (B, BM, BR, COI, FHI, G, HBG, K, LMA, MO, P, STU, UPS, W). Whenever possible stamens were collected from these sheets. As the male flower in *Begonia* nearly always possesses numerous stamens, sampling proved to be easy. The sheets from which pollen was collected have been marked:

"Pollen specimen taken WAG 19.."

Besides this extensive collection of herbarium material there was the obvious advantage of having a living collection of (a.o.) African *Begonias* at hand, in the greenhouse of the Department of Horticulture of the Agricultural University at Wageningen. Prof. dr. J. Doorenbos and Mr. J. J. Karper are gratefully acknowledged for putting this collection at our disposal.

Furthermore a number of field trips undertaken by the taxonomists of the Department of Plant Taxonomy of the Agricultural University at Wageningen provided new material, often of species which where up till then poorly represented. Although *Begonias* of Madagascar belong to the province of the taxonomists of the Laboratoire de Phanérogame, Muséum National d'Histoire Naturelle in Paris, it was considered of great interest to compare the pollen-morphological data of the continental African *Begonias* with those of Madagascar. Material of Madagascar *Begonias* and also the results of the pollen-morphological (SEM) studies, as far as they were conducted by the late M. Keraudren-Aymonin, were readily made available by G. G. Aymonin. About half of the 52 species recognized at present as published in the Flore de Madagascar et des Comores, famille 144 Bégoniacées, (M. Keraudren-Aymonin, G. G. Aymonin & J. Bosser, 1983) could be sampled (appendix 1). Material of Hillebrandia and Symbegonia (Van Den Berg, 1984) and of Datiscaceae (appendix 2) were provided by the Rijksherbarium at Leiden (L) and through courtesy of Dr. F. Bouman (Hugo de Vries Laboratory, Amsterdam) respectively.

2.2. METHODS

The samples were treated according to a standard acetolysis method (Reitsma, 1969). The samples were boiled for 8 minutes to acquire sufficient colouring. It was found that after acetolysis the grains were best stored in acetic acid (in stead of in aceton or ethylalcohol). If sufficient, the material was divided in two parts, for light microscopic (LM) and electron microscopic observations respectively. For LM observations the pollen grains were mounted in glycerine-
jelly and studied with a Zeiss light microscope (Planapo 63/1.4 Oel). LM photographs were made on Kodak Technical Pan film (18 DIN), developed in HC110 for 8 minutes (dil.F.) and printed on various grades of paper.

For scanning electron microscopic observation (SEM) it proved imperative to use the Critical Point Drying technique (ADAMS & MORTON, 1972; cf. also NILSSON c.s., 1974) to prevent the collapse of the extremely thin-walled grains. The grains were then coated with gold in a Balzers sputtering system, and studied with a Jeol 35-c scanning electron microscope.

For transmission electron microscopic observation (TEM) sections were cut with glass knives. These sections were first fixed in 3% glutaraldehyde in cacodylate buffer (0.1 M, pH = 7.2) for 5 hours at room temperature, then in 1% OsO4 in cacodylate-buffer for 2 hours in darkness, dehydrated in an alcohol-series (50–100%), embedded in Epon and post-stained with 3% uranylacetate and lead-citrate. Observations were made with a Philips EM 400 T transmission electron microscope.

Both electron microscopes were available at the TFDL (Technical and Physical Service for Agriculture) at Wageningen.
3. GENERAL DESCRIPTION OF BEGONIA POLLEN

3.1. INTRODUCTION

Data on the pollen morphology of Begoniaceae in literature are virtually non-existent. IRMSCHER (1925), the last monographer of the family, described the pollen grains as follows:

'Die staubförmigen Pollenkörner sind von ellipsoider Gestalt und fast bei allen Arten gleich groß. Sie sind im Mittel etwa 26 μm lang und 13 μm breit. Das Korn besitzt 3 Meridionalfalten in der sonst glatten Exine, in deren Mitte je eine kreisrunde Durchlaßöffnung für den Pollenschlauch liegt.'

ERDTMAN (1952) noted the small size, the prolate to perprolate shape and the very thin exine which did not show much stratification. He considered the pollen grains of Begoniaceae as ± similar to those in Datiscaceae, also in the occurrence of tetrads. In the present study, however, tetrads were only encountered in obviously immature samples, while comparison with the grains of the Datiscaceae shows the latter to possess a quite different ornamentation and wall structure (see appendix 2 and plate 15). Unfortunately, there is no fossil record of the Begonia type of pollen.

3.2. GENERAL DESCRIPTION (cf. fig. 3.1.)

The pollen grains in Begonia are single, isopolar and generally 3-zono-colporate. Their shape ranges from prolate spheroidal to perprolate while the polar axis measures from 16 to 35 μm and the equatorial diameter from 8 to 14 μm. The outline in equatorial view is mostly somewhat elliptic. The long sides, though usually convex, can be straight or even concave (plate 1, fig. 2), the poles can be rounded, somewhat pointed or, in syncolpate grains, emarginate.

The outline in polar view is circular or rounded triangular with interaxillary apertures, but the invaginating colpi often give a lobate impression (plate 1, fig. 4 and 5). The ectoapertures are very long, ± 2 μm wide colpi with straight margins and closed by a granular colpus membrane. The granulae tend to become coarser in the endoapertural area. The striate ornamentation continues up to the margin of the colpus (plate 1, fig. 2) or a margo of deviating non-striate ornamentation is present along the colpus (plate 1, fig. 3). The endings of the colpi are acute and approach each other closely or even anastomose in symcolpate grains (plate 1, fig. 4).

The endoapertures are always lalongate, wider than the ectoaperture, with a more or less elliptic outline. Especially the long (polar) sides can be distinct through the presence of often rather faint costae (plate 5 and 6). The outer endings, usually rounded, are often diffuse and difficult to observe.

The exine is rather thin (usually less than 0.5 μm) and no stratification is
FIG. 3.1. General morphology of *Begonia* pollen
A. Equatorial view; B. Detail endoaperture; C and D. Details wall structure; E. Polar view.
1. striate ornamentation; 2. margo; 3. colpus membrane; 4. endoaperture; 5. costa(e); 6. endexine; 7. ectexine; 8. tectum; 9. infratectal layer; 10. foot-layer; 11. mesocolpium; 12. apocolpium; P polar axis; E equatorial diameter.

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visible in LM. A layered structure is present, however: a sexine consisting of an outer continuous tectum and an infratectal layer of more or less regular columnellae; and a nexine, a homogeneous basal layer (plate 3 and 4). Wall thickness is uniform except for the slight thickenings of the nexine bordering the endoaperture (costae, plate 4, fig. 3 and 4).

3.3. TERMINOLOGY

The morphology of *Begonia* pollen can be covered by the usual terminology for angiospermous pollen grains (a.o. WODEHOUSE, 1935, ERDTMAN, 1952, FAEGRI & IVERSEN, 1964 and REITSMA, 1970), the latter being a survey of the various terms in use with suggestions towards unification with which the present author does not agree in all details. To prevent any possibility of misunderstanding the most important pollen-morphological terms are defined here as they are used in this study (and therefore with special reference to *Begonia* pollen).

**Pollen class**: Normal grains are 3-*zono-colporate*: provided with three compound apertures of which the ectoapertures are colpi and the endoapertures may be lalongate pori or colpi; the three colpi run meridionally (from pole to pole) and the endoapertures are situated at the equator, equally distributed around the grain (in the more or less triangular polar view the apertures are situated interaxillary, viz. in between the angles).

**P/E ratio**: The ratio between the polar axis (P) and the equatorial diameter (E) can be used to assign the pollen grains to shape classes as follows (ERDTMAN, 1952);

- \( \frac{P}{E} \leq 1 \) spheroidal
- \( 1 < \frac{P}{E} \leq 1.14 \) prolate spheroidal
- \( 1.14 < \frac{P}{E} \leq 1.33 \) subprolate
- \( 1.33 < \frac{P}{E} \leq 2.00 \) prolate
- \( \frac{P}{E} > 2.00 \) perprolate

**Apertures**: The apertures are **compound**: they consist of an ectoaperture (aperture in the sexine) and an endoaperture (aperture in the nexine).

The ectoaperture is a **colpus**: an elongated aperture with a length/breadth ratio higher than 2. The endoaperture is also a colpus or a **porus**: a circular or more or less elliptic aperture, with a length/breadth ratio smaller than 2. The endoaperture is nearly always lalongate: the longest axis is perpendicular to the longest axis of the colpus.

In relatively rare, abnormal grains the colpi converge in pairs: **loxocolpate** (plate 2, fig. 1). If the colpi anastomose at the poles the pollen grains are **syncolpate**. Some authors feel that if the grains are colporate (viz. with compound apertures) the terms should be coined 'loxocolporate' and 'syncolporate'. However, since it are the ectoapertures which converge in pairs and anastomose,
with no consequences for the endoapertures, the full characterization of these grains should be ‘3-colporate, loxocolpate’ and ‘3-colporate, syncolpate’. The endoapertures may be provided with costae: thickenings of the nexine around the endoaperture.

The parts of the grain inbetween the colpi are called mesocolpia. The (very small) area at the poles beyond the endings of ectoapertures is called the apocolpium.

Exine: The pollen wall consists of intine and exine. The latter, outer part is acetolysis-resistant and generally divided in two layers: the sexine and the nexine.

The sexine is the outer, structured layer.

The nexine is the inner, homogeneous layer.

The sexine consists of an outer more or less closed layer, the tectum, which carries the striate surface ornamentation, and an infratectal layer consisting of numerous columellae: pillar-like elements which support the tectum and are themselves implanted on the inner basal layer (‘a term which includes everything found below the infratectal layer’ - A. LE THOMAS, 1981) which corresponds with the nexine. In electron-microscopical investigations a difference in contrast between the outer and inner layers is evident (plate 3 and 4). As is well known from literature (a.o. FAEGRI & IVERSEN, 1964) the boundaries of these layers do not necessarily coincide with the division in sexine and nexine as defined above. For this reason the terms ectexine and endexine will be used in discussing the TEM observations, respectively the outer and inner layer of the exine each comprising all the material of the exine characterized by a particular composition and structure resulting in continuity with respect to electron density. It may be noted here that whether the ectexine or the endexine is more transparent to the electron beam can apparently depend on the pre-treatment and staining methods (cf. plate 3, fig. 3 and 5).

As will be described in more detail in the section on wall structure as observed in TEM a tendency of the columellae to lose their regular pillar-like shape can be observed, while the material at the base of the columellae tends to form a thin, irregular, continuous layer which could be considered as a foot-layer. Since this material is continuous with the columellae it is ectexineous in nature.

The two layers of the exine can separate from each other in the area of the endoaperture, forming a cavity which can be called a fastigium. When this occurs a raised sexine is visible around the endoaperture (plate 2, fig. 2 and plate 11, fig. 5). The term structure is maintained (cf. REITSMA, 1970, p. 45/46 and WALKER & DOYLE, 1975, p. 679) for the arrangement of the exine elements within the wall. Surface ornamentation will be designated as sculpture.

Ornamentation: The sculpture on the surface of the grains is formed by a pattern of exine elements separated by spaces. The exine elements are called muri. The striate pattern shown by all Begonia pollen can be defined as a regular pattern of approximately parallel muri. More in particular in striate grains the
muri, the ridges of exineous material, will be termed lirae, and the grooves in between the ridges striae. Depending on the width of the lirae and striae, the striate pattern can be designated as finely or coarsely striate. This can (approximately) be measured by counting the number of striae/lirae which are visible on the mesocolpia. A number of minute perforations is always present (plate 2, fig. 4). A striking feature of many Begonia pollen types is the presence of a margo: a zone along the ectocolpus showing a deviating non-striate ornamentation (plate 1, fig. 3). The poles do not differ in ornamentation or other features.

3.4. Variability

Pollen morphology studies the morphology of the pollen wall, generally called exine. In order to be able to study only the exine and not be hampered by the other components of the pollen grain the method of acetolysis is used. Through the appliance of aggressive chemicals all traces of the contents (protoplasm and intine) and surface adhering material (pollen kit) are destroyed. This treatment influences the characteristics of the exine, and can cause changes in the size of the grains (see Reitsma, 1969 for a detailed study of the effects of different treatments). Pollen morphology thus applies to the acetolyzed pollen grains, the characters of which can be different from those of the fresh grains as present within stamens or on pistils. It is hard to decide on the 'true' shape or size of the pollen grain. Only by treating all samples in exactly the same way following a standardized procedure it is possible to compare the grains of different taxa and draw conclusions from the comparison.

Even so, within taxa and even within samples a certain amount of variability is still encountered, especially in size, shape, number of apertures and nature of ornamentation.

The mean size as calculated from 10 measurements always shows a variance of ± 2-3 \( \mu m \). This means that a difference in size between two taxa with, for instance, a polar axis of 25 \( \mu m \) and 28 \( \mu m \) respectively, is not interesting, but there is no doubt of the importance of the fact that the polar axis of certain taxa measures ± 15 \( \mu m \), while others always exceed 30 \( \mu m \).

The shape of the grains is strongly influenced by the applied treatment. Generally there is a tendency of the grains to collapse. This is due to the extremely thin exine (often less than 0,5 \( \mu m \)), while in a dehydrated state of the grain the colpi tend to invaginate until they are closed off by the borders of the mesocolpia touching each other. In fact, it proved imperative to use the Critical Point Drying technique for SEM observations in order to study the colpus membrane (see also Adams & Morton, 1972, and Nilsson, Nybom & Praglowski, 1974).

The number of apertures is nearly always three, except for a usually very small percentage of the grains which may be 4-colporate. In these abnormal grains (plate 2, fig. 1) the colpi tend to a loxocolpate arrangement, with the colpi converging in pairs. Some samples contain much greater percentages of these grains and for some of them a connection could be established between this phenome-

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non and polyploidy. However, this connection between polyploidy and deviating aperture-number and -configuration is far from strict: some samples from plants which according to their chromosome numbers were tetraploids did not show any deviation in their pollen. This applies also to size: it could not be established that tetraploids always possess larger pollen than diploids. Often no difference in size was found, or even the reverse appeared to be true.

The ornamentation is always striate. The orientation of the lirae and striae is in principle parallel to the colpi but there is a lot of variation which does not seem to be of taxonomic importance. The 'clean' striate pattern is sometimes replaced by irregular ornamentation, especially towards the poles. Often the lirae are interconnected, resulting in a somewhat reticulate appearance. As far as could be determined these irregularities and deviations are hardly specific. A further variable character is the occurrence of syncolpate grains. The colpi are always very long, leaving only a small apocolpium at the poles. In numerous taxa at least a number of grains is syncolpate, in some cases all of the grains. On the other hand, certain taxa never show this character which points to a, be it restricted, importance.

3.5. WALL STRUCTURE AS OBSERVED IN TEM

The exine of Begonia pollen is extremely thin (0.4–0.6 μm) and stratification can only be observed with the transmission electron microscope (TEM, plate 3 and 4). Both ectexine and endexine layers are present and usually well contrasted. The endexine takes up about 25% of the total wall thickness. It consists of homogeneous material and is uniform in thickness except in the endoapertural area. Here it may form prominent costae bordering the longer sides of the endoaperture (plate 4, fig. 3 and 4) while it also forms the apertural membrane. The granulae which cover this membrane are ectexineous in nature.

The ectexine consists of a tectum, the infratectal layer and, if present, a foot-layer. The tectum is a rather thick, massive layer with only very small perforations (< 0.05 μm) scattered at random over the grain. The striate ornamentation shows up in cross-section as an undulating surface with summits (the lirae) and valleys (the striae). The lirae are usually rounded triangular in outline but sometimes more or less sharply pointed and may be 0.3–0.8 μm or even more than 1 μm apart. This tectum rests on a layer of always rather irregular columellae which only seldom resemble real columns and show no pattern in their configuration. In fact, it is only in a number of pollen types that an infratectal layer consisting in this way of more or less well defined columellae and the spaces in between them can be distinguished at all. In most types the spaces within the infratectal layer are extremely irregular, reduced to a narrow strand between the tectum and the foot-layer. In types where columellae are discernable a foot-layer is not present: the columellae are implanted directly on the endexine.

This observation and the occurrence of situations intermediate between these extremes lead to the following hypothesis: the reduction of the columellae is

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accompanied by the origin of an irregular, more or less continuous, inner layer of the ectexine, covering the endexine, which can be considered as a foot-layer.

Investigating the relation between the occurrence of these types of wall structure and other characteristics of the grains can lead to phylogenetic conclusions as to which conditions are primitive and which advanced, as will be discussed in chapter 5.
4. POLLEN TYPES

... we should not be disappointed if we can impose only a less than perfect order on the endless diversity of nature.

A. CRONQUIST (1968, p. 119)

4.1. KEY TO THE POLLEN TYPES

<table>
<thead>
<tr>
<th>Step</th>
<th>Description</th>
<th>Pollen Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a</td>
<td>Grains spheroidal-subprolate (P/E &lt; 1.33)</td>
<td>B. thomeana-type</td>
</tr>
<tr>
<td>1b</td>
<td>Grains prolate-perprolate (P/E &gt; 1.33)</td>
<td></td>
</tr>
<tr>
<td>2a</td>
<td>Margo present</td>
<td>B. baccata-type</td>
</tr>
<tr>
<td>2b</td>
<td>Margo absent</td>
<td></td>
</tr>
<tr>
<td>3a</td>
<td>Endoaperture small, elliptical</td>
<td>B. comorensis-type</td>
</tr>
<tr>
<td>3b</td>
<td>Endoaperture irregular oblong, lirae sharp</td>
<td>B. baccata-type</td>
</tr>
<tr>
<td>4a</td>
<td>Sides concave</td>
<td></td>
</tr>
<tr>
<td>4b</td>
<td>Sides convex or straight</td>
<td></td>
</tr>
<tr>
<td>5a</td>
<td>Margo present</td>
<td>B. squamulosa-type</td>
</tr>
<tr>
<td>5b</td>
<td>Margo absent</td>
<td>B. quadrialata-type</td>
</tr>
<tr>
<td>6a</td>
<td>Margo present</td>
<td></td>
</tr>
<tr>
<td>6b</td>
<td>Margo absent</td>
<td></td>
</tr>
<tr>
<td>7a</td>
<td>Size &lt; 25 µm</td>
<td></td>
</tr>
<tr>
<td>7b</td>
<td>Size &gt; 25 µm</td>
<td></td>
</tr>
<tr>
<td>8a</td>
<td>Sides straight</td>
<td>B. filicifolia-type</td>
</tr>
<tr>
<td>8b</td>
<td>Sides convex</td>
<td></td>
</tr>
<tr>
<td>9a</td>
<td>Endoaperture large (m 4–5 µ), elliptical, sides very convex</td>
<td>B. annobonensis-type</td>
</tr>
<tr>
<td>9b</td>
<td>Endoaperture medium sized (m 2–3 µ), oblong, sides slightly convex</td>
<td>B. bonus-henricus-type</td>
</tr>
<tr>
<td>10a</td>
<td>Outline in equatorial view ± rhomboidal, very convex sides, raised sexine</td>
<td>B. ampla-type</td>
</tr>
<tr>
<td>10b</td>
<td>Outline in equatorial view elliptical, endoaperture elliptical or oblong</td>
<td></td>
</tr>
<tr>
<td>11a</td>
<td>Endoaperture large (m 4–6 µ), elliptical, outline ± distinct</td>
<td></td>
</tr>
<tr>
<td>11b</td>
<td>Endoaperture medium sized (m 3–4 µ), oblong, outer endings usually</td>
<td></td>
</tr>
<tr>
<td></td>
<td>indistinct</td>
<td></td>
</tr>
<tr>
<td>12a</td>
<td>Poles emarginate, grains syncolpate</td>
<td>B. cavallyensis-type</td>
</tr>
<tr>
<td>12b</td>
<td>Poles smooth, rounded, grains 3-colporate</td>
<td>B. dregei-type</td>
</tr>
<tr>
<td>13a</td>
<td>Margo very narrow, grains perprolate</td>
<td>B. poculifera-type</td>
</tr>
<tr>
<td>13b</td>
<td>Margo broad, grains prolate</td>
<td>B. komoensis-type</td>
</tr>
<tr>
<td>14a</td>
<td>Endoaperture circular/elliptical endoporus, grains mostly 3-colporate</td>
<td>B. oxyloba-type</td>
</tr>
<tr>
<td>14b</td>
<td>Endoaperture narrow endocolpus, grains mostly syncolpate</td>
<td>B. eminii-type</td>
</tr>
</tbody>
</table>
4.2. Description of the Pollen Types

4.2.1. Introduction

The definition of the term ‘pollen type’ will be discussed in detail in the chapter on phylogeny and the methodology of pollen morphology (chapter 5). In this chapter for each pollen type the species (names) are given of the taxa which show this type of pollen, after which the specimens which were used for the observations are cited with their identifications which reflect the present state of taxonomical knowledge of the African representatives of the genus, large parts of which have not yet been extensively studied. In this way mis-identified specimens will be noted and nomenclatural errors will not interfere with pollen-morphological practice.

The descriptions give the differential characters of the pollen type and in the comments the relationship with other pollen types and with taxonomical classification is discussed.

4.2.2. Measurements

Polar axis (P) and equatorial diameter (E) will need no further explanation. The length of the colpus is not given because the colpi are so long that their endings are only visible in polar view. The width of the colpi is obviously related to the state of expansion of the grain.

The dimensions of the endoaperture are measured in meridional and equatorial direction (m and e). Especially the latter is often difficult to observe due to the indistinct outline of the endoaperture.

As with LM stratification of the exine is not visible, no measurements of the thickness of the sexine and nexine and their ratio is given (see however: chapter 3.5. Wall structure as observed in TEM).

4.2.3. Descriptions

1) B. comorensis-type

Small, (sub)prolate or prolate spheroidal pollen grains, characterized by a very small elliptical endoaperture without costae. The colpus can be slightly constricted at the equator. The ornamentation is regular, also at the poles. Margo absent, syncolpate grains do not occur.

Measurements: P 15–17 \( \mu \text{m} \), E 10–11 \( \mu \text{m} \), P/E 1.40–1.50, m 1–2 \( \mu \text{m} \), e 2–3 \( \mu \text{m} \).


Specimens: Forsyth Major 11 (BM) (B. cladocarpa); Hildebrandt 1606 (W) syntype (B. comorensis); Jard. Bot. Tan. 73 (P) (B. comorensis); Schlieben 11196 and 11672 (HBG) (B. seychellensis); Van Veldhuizen 539 (WAG) (B. seychellens
Comments: This type contains the smallest pollen grains found in the present study. It is characteristic for a number of species of section *Mezierea*. Only *B. meyeri-johannis* occurs on the African continent. The other representatives of this type are distributed over the Madagascan region (Madagascar, Seychelles, Comores). *B. seychellensis* Hemsley is considered synonymous to *B. comorensis* by KERAUDREN-AYMONIN (1983).

2) *B. baccata*-type

Small, prolate spheroidal pollen grains with relatively broad colpi and irregularly shaped endoapertures without costae. The grains may be syncolpate, the ornamentation is regular with rather sharp lirae. No margo. Granular colpus membrane well visible.

**Measurements:** P 15–18 μm, E 12–13 μm, P/E 1.20–1.40, m 2–2.5 μm, e 4–5 μm.

**Species:** *B. baccata* Hook.f., *B. crateris* Exell.

**Specimens:** Espirito Santo 155 (COI) (*B. baccata*); Groenendijk 7, 107 (WAG) (*B. crateris*); Mann 1087 (P) isotype (*B. baccata*); Roseira 2931 (COI) (*B. baccata*); Tuinb. Plant. 1247 (WAG) (*B. baccata*); Van Veldhuizen 673 (WAG) (*B. crateris*); De Wilde, Arends & Groenendijk 105 (WAG) (*B. baccata*).

Comments: The size, P/E ratio and lack of costae and margo point to resemblance with the *B. comorensis*-type. The *B. baccata*-type differs in its P/E ratio, which is even more spheroidal due to the larger E, its type of endoaperture which is rather irregularly oblong instead of distinctly elliptical, and the characteristic lirae. The two species in this type are accommodated in a new section *Baccabegonia* (REITSMA, 1985b), which is related to the sections *Mezierea*, *Squamibegonia* and *Tetraphila*.

3) *B. thomeana*-type

Small, prolate spheroidal to subprolate pollen grains with very convex sides. Small elliptical endoaperture. Regular ornamentation except for the narrow margo along the colpi. Some syncolpate grains occur.

**Measurements:** P 15–18 μm, E 11–13 μm, P/E 1.40–1.50, m 2–3 μm, e 4–5 μm.

**Species:** *B. thomeana* C.DC.

**Specimens:** Exell 419 (COI); Groenendijk 138 (WAG); Karper, De Wilde, Arends & Bouman 521 (WAG); Van Veldhuizen 882 (WAG) (*B. thomeana*).
Comments: This type also resembles the *B. comorensis*-type, especially in P/E ratio, size and endoaperture. The main difference is the presence of the narrow margo. The species *B. thomeana* is accommodated in a new section *Cristasemen* (De Wilde, 1985b) characterized by, amongst other features, a unique seed morphology.

4) *B. oxyloba*-type  

Plate 8

Rather small, perprolate pollen grains with slightly convex sides and rounded poles. The grains are not syncolpate, the endoapertures are circular or elliptical endopori with only faint costae. No margo.

Measurements: P 18–22 μm, E 9–12 μm, P/E 1.70–2.10, m 2–3 μm, e 3–4 μm.


Specimens: Karper, De Wilde, Arends & Bouman 744 (WAG), Leeuwenberg & Voorhoeve 4665 (WAG), Letouzey 15010 (P) (*B. oxyloba*); Schlieben 3006 (B) (*B. pycnocaulis*); Schlieben 3451 (MO), Van Veldhuizen 666, 735, 815 (WAG) (*B. oxyloba*).

Comments: A type characteristic for the remaining species of section *Mezierea* (all other species of this section belong to the *B. comorensis*-type). It shows resemblance to types in other sections, especially the *B. eminii*-type of section *Tetraphila*. *B. oxyloba* is the species with the largest distribution in Africa. It occurs from east to west throughout the continent.

5) *B. eminii*-type  

Plate 9

Rather small, prolate or perprolate pollen grains, often syncolpate. No margo along the colpi, endoaperture lalongate, ± oblong endocolpus with rather distinct costae along the longer sides, outer endings mostly indistinct.


Specimens: Bequaert 6120 (BR) (B. horticola); Bokdam 4435 (WAG) (B. eminii); Breterel & De Wilde s.n. (Tuinb. Plant. 1196) (WAG) (B. loranthoides); Brown 85 (B) paratype (B. rhopalocarpa); Chevalier 13752 (P) syntype (B. subalpestris); Chevalier 28046 (P) (*B. ealensis*); Devred 2772 (BR) holotype (B. taton-
iana); Dusén 71 (B) holotype (B. fusialata); Felix 854 (P) (B. mannii); Jans 1141 (BR) (B. tatoniana); Karper, De Wilde, Arends & Bouman 100 (Tuinb. Plant. 1594) (WAG) (B. loranthoides); Karper, De Wilde, Arends & Bouman 382 (WAG) (B. alepensis); Karper, De Wilde, Arends & Bouman 851, 905 (WAG) (B. mannii); Ledermann 1210 (B) holotype (B. ndongensis); Leeuwenberg 8649 (WAG) (B. mannii); Leeuwenberg & Voorhoeve 4792 (WAG) (B. alepensis); Léonard 1880 (BR) (B. fusialata); Le Testu 5043 (P) (B. loranthoides); Letouzey 14448 (P) (B. furfuracea); Letouzey 14444 (P) (B. fusialata); Mildbread 6831 (B) (epiphytica); Mildbread 6985 (HBG) (B. excelsa); A. Moller 3 (G) holotype, A. Moller 3 = 177 (B) isotype (B. molleri); Pogge 962 (B) syntype (B. poggei); Preuss 960 (B) holotype (B. macrostyla); Quintas 6 (G) (B. molleri); Rosen 497 (P) (B. loranthoides); Sanford 4440, 4442 (IFE) (B. spec.); Stuhlmann 1454 (B) syntype, 3828 (B) syntype (B. eminii); Van Veldhuizen 443 (WAG) (B. loranthoides); Van Veldhuizen 540 (WAG) (B. molleri); Van Veldhuizen 1035 (WAG) (B. epiphytica); J. J. de Wilde 7499 (WAG) (B. alepensis); J. J. de Wilde 8119 (WAG) (B. mannii); De Wilde, Arends & Groenendijk 144 (WAG) (B. macambrarensis).

Comments: This type is very similar to the B. oxyloba-type. It differs in its generally somewhat larger size, in being often syncolpate and in the more clearly lalongate endoaperture with distinct costae. It is characteristic for a large number of species of section Tetraphila. The synonymy of B. ealensis and B. poggei to B. eminii, of B. excelsa and B. ndongensis to B. mannii, and of B. macambrarensis to B. subalpestris is confirmed by pollen morphology. A few specimens identified as B. squamulosa (Letouzey 14448 (P), Sanford 4440 and 4442 (IFE) are cited in this pollen type as B. spec, pending further research (see Comments B. squamulosa-type).

6) B. komoensis-type

Medium sized, often prolate pollen grains with rather convex sides, sometimes syncolpate. Margo present. Endoaperture relatively small lalongate pori with only faint costae.

Measurements: P23–27μm, E10–14μm, P/E 1.80–2.00, m3–3.5μm, e5–6μm.


Specimens: Beentje s.n. (Tuinb. Plant. 1384) (WAG) (B. subscutata); Bequaert 6595 (BR) (B. subscutata); Breteler 7610 (WAG) (B. komoensis); Breteler 7641 (WAG) (B. kisuluana); Breteler & De Wilde 702 (WAG) (B. kisuluana); Bos 7165 (WAG) (B. komoensis); Chevalier 2691 (P) holotype (B. komoensis); Hallé 3016 (P) (B. kisuluana); Hallé 3097 (P) (B. komoensis); Hallé & Villiers 5356, 5357 (P) (B. komoensis); Hallé & Villiers 5381 (P) holotype (B. nicolai-
halle); Hallé & Villiers 5525 (P) (B. subscutata); Louis 12242 (BR) (B. subscutata); Overlaet 717 (BR) (B. kisuluana); Preuss 1261 (B) holotype (B. sessilanthera); Van Roeckhoudt 12 (BR) (B. spec.); Seret 499 bis (BR) paratype (B. subscutata); Seret 882 (BR) holotype, 1068 (BR) (B. zobiensis); Trochain 8570 (P) (B. kisuluana); Van Veldhuizen 472 (WAG) (B. komoensis); J. J. de Wilde 7551 (WAG) (B. subscutata).

Comments: This is a rather difficult type to circumscribe, accommodating species which show rather variable pollen more or less intermediate between the B. eminii- and B. cavallyensis-type, differing from the first in the presence of a margo and from the second by the generally smaller size, a more prolate P/E ratio, and the smaller endoaperture with only faint costae. One specimen, Van Roeckhoudt 12 (BR), identified as B. schultzei, differed in its pollen type from the species of the B. squamulosa-aggregate and is accommodated here (cited as B. spec.). It may concern a new species (DE WILDE, pers. comm.).

7) B. cavallyensis-type

Large elliptical, perprolate pollen grains, often syncolpate, with broad margines along the colpi and large, elliptical endopori with distinct costae. The poles are emarginate due to the anastomosing colpi (syncolpate grains).

Measurements: P 28–33 μm, E 14–15 μm, P/E 2.00–2.20, m 5–6 μm, e 6–8 μm.


Specimens: Adam 20851 (UPS) (B. cavallyensis); Aylmer 49 (K) (B. cavallyensis); Baldwin 11417 (K) holotype (B. fusicarpa); Bates 573 (P) holotype (B. sanjeensis); Beentje 1554 (WAG) (B. polygonoides); Buchholz s.n. (March 1874) (BR) (B. buchholzii); Chevalier 21183 (P) holotype (B. rhipsaloides); Conrau 80 (B) holotype (B. rubromarginata); Daramola 40454 (FHI) (B. oxyanthera); Deighton 709 (K) (B. cavallyensis); Dinklage 1232 (B) (B. capillipes); Dusen 427 (B) holotype (B. jussiaeicarpa); Hallé & Le Thomas 283 (P) holotype (B. lethomasiae); Hladik 2721 (P) (B. polygonoides); Johnson 129 (K) (B. cavallyensis); Karper, De Wilde, Arends & Bouman 538 (WAG) (B. polygonoides); Leeuwenberg 3775 (WAG) (B. polygonoides); Leeuwenberg 3870 (WAG) (B. cavallyensis); Leeuwenberg 8650 A (WAG) (B. polygonoides); Leeuwenberg 9956 (WAG) (B. oxyanthera); Letouzey 8800 (BR) (B. oxyanthera); Letouzey 15157 (P) (B. polygonoides); Mildbraed 6186 (B) syntype (B. ebolowensis); Pobeguin 1651 (P) (B. cavallyensis); Preuss 111 (B) lectotype (B. preussii); Preuss 867 (B) syntype (B. oxyanthera); Van Veldhuizen 502 (WAG) (B. cavallyensis); J. J. de Wilde 7486 (WAG) (B. ebolowensis); J. J. de Wilde 8267 A, 8364, 8365 (WAG) (B. lethomasiae).
Comments: This is the largest type found in the African Begonias. The pollen grains of *B. cavallyensis* are almost twice the size of those of *B. comorensis*. There is a rather close resemblance with the *B. dregei*-type (elliptical outline, large endoaperture, presence of a margo), but the members of this latter type are generally somewhat smaller and differ especially at the poles which are mostly rounded and not emarginate, and in the less distinct costae. Hagman & De Wilde (1984) in studying the circumscription of *B. cavallyensis* and *B. fusicarpa* were able to deny the alleged synonymy of *B. cavallyensis* to *B. eminii*. The present author contributed palynological observations which support this: the *B. eminii*-type can be easily distinguished from the *B. cavallyensis*-type. The resemblance of the pollen of *B. ebolowensis* to that of *B. cavallyensis* is in accordance with the findings of Reitsma (1984) who concluded that these two species stand apart in section *Tetraphila* on account of the placentation characters. The synonymy of *B. polygonoides* with *B. rhipsaloides* and *B. capillipes* is corroborated by pollen morphology, while *B. lethomasiae* may very well be related to *B. ebolowensis*, and *B. jussiaeicarpa* can be synonymous to *B. oxyanthera*, since all these species can be accommodated in the same pollen type. One specimen, Letouzey 12808 (P) was apparently misidentified (as *B. polygonoides*) and is referred to the *B. squamulosa*-type.

8) **B. squamulosa-type** Plate 10

Large, perprolate pollen grains with often concave sides and pointed poles. Margo present. Endoapertures lalongate, endocolpi with rather heavy costae. Syncolpate grains do not occur.

Measurements: P 26–28 μm, E 10–13 μm, P/E 2.50–2.80, m 2–3 μm, e 6–7 μm.


Comments: The characteristic concave sides of this type occur also in the B. quadrialata-type which accommodates most of the species of section Scutogeonia. The B. squamulosa-type differs from the B. quadrialata-type in the possession of a margo and the somewhat larger size. Karyological investigations have shown the occurrence of tetraploid taxa in the B. squamulosa-aggregate, 'a group of morphologically similar taxa (2 × and 4 ×) with strong genetic barriers' (ARENDS, 1985). No relation between the pollen size and polyploidy was found.

The species of the B. squamulosa-aggregate could not be segregated on the basis of pollen morphology. Pollen of B. elaeagnifolia was not investigated, the synonymy of B. bipindensis, B. crassipes and B. gladiifolia to B. squamulosa is corroborated by pollen morphology. A number of specimens, identified as B. squamulosa, definitely did not show the B. squamulosa-pollen type as described above. They are referred to other pollen types and should be studied closely macromorphologically to ascertain their taxonomical status (spec.nov.?). These specimens are: Van Roeckhoudt 12 (BR), referred to the B. komoensis-type, and Letouzey 14448 (P), Sanford 4440 and 4442 (IFE), referred to the B. eminii-type.

9) B. bonus-henricus-type

Plate 11

Rather small, perprolate pollen grains, with narrow margo. Small lalongate oblong endoaperture.

Measurements: P 18–23 μm, E 8–10 μm, P/E 2.00–2.30, m 2–3 μm, e 4–5 μm.

Species: B. bonus-henricus J. J. de Wilde.

Specimen: /. / de Wilde 8404 (WAG).

Comments: Very little material was available and this was partly immature. This type is closely related to the B. poculifera-type and might only constitute a small subgroup of that type. Pending further investigation on more specimens it is tentatively kept separate here.

10) B. poculifera-type

Plate 11

Large, perprolate syncolpate pollen grains with very narrow margo and straight to slightly convex sides. Oblong, rather narrow, endoapertures (endo-colpi) with distinct costae.


Specimens: Braun 85 (B) (*B. poculifera*); Breteler & De Wilde 314 (WAG) (*B. poculifera*); Gutzwiller 10002 (WAG) (*B. poculifera*); Leeuwenberg 10002 (WAG) (*B. poculifera*); Letouzey 14685 (P) (*B. poculifera*); Mann 314 (K) lectotype (*B. ampla*); Mann 1276 (K) lectotype (*B. poculifera*); Mildbraed 3242 (B) (*B. poculifera*, holotype of *B. adolfi-friderici*); Sebald 5002 (STU) (*B. poculifera*); Swarbrick 2454 (FHI) (*B. ampla*).

Comments: This type, characterized by its large size, narrow margo and narrow endocolpi accommodates all specimens identified as *B. poculifera* Hook.f. and part of those identified as *B. ampla* Hook.f. (see comments on the *B. ampla*-type). The synonymy of *B. adolfi-friderici* Gilg to *B. poculifera* is confirmed by pollen morphology. It proved impossible to distinguish the varieties within *B. poculifera*.

11) *B. ampla*-type

Large, prolate pollen grains, often somewhat rhomboidal due to the large E and very convex sides. A rather narrow margo is present. This type is characterized especially by the raised sexine in the endoapertural area (fastigium). The endoaperture is rather narrow and appears constricted. The grains may be syncolpate.

Measurements: P 26–28 µm, E 14–15 µm, P/E 1.70–1.90, m 2–3 µm, e 5–6 µm.

Species: *B. ampla* Hook.f. (pro parte).

Specimens: Groenendijk 126 (WAG) (*B. ampla*); Quintas 149 (999) (K) (*B. ampla*); Wrightley & Melville 29 (BR) (*B. ampla*).

Comments: This type can be clearly distinguished from the pollen type shown by a number of specimens identified as *B. ampla* but here accommodated in the *B. poculifera*-type. All specimens of *B. ampla* showing the *B. ampla*-type were collected on the islands of São Tomé and Annobon, while the specimens showing the *B. poculifera*-type come from the continent (Cameroon and Zaire) and from Fernando Po. These results would point to a special position of the *B. ampla* populations on the (oceanic) islands. However, although DE WILDE & ARENDS (1980, p. 389) noted that ....'The character combination (type of indu­mentum and shape of leaf-base) which is diagnostic on the continent and also holds for the majority of the specimens collected on the islands, seems to become fallible for a part of the islands populations', the examined specimens showing the *B. ampla*-type proved to be intermediates linking the aberrant with the typical individuals. Unfortunately, neither the aberrant nor the typical individuals...
could be sampled. It is thus not possible to determine the meaning of the occurrence of this deviating pollen type in part of the specimens of *B. ampla*.

12) **B. annobonensis-type**

Rather small, (per)prolate pollen grains with very convex sides, rounded poles with rather irregular ornamentation, very narrow margo and equatorial constrictions of the colpi (due to raised sexine in the endoapertural area). Endoaperture a relatively large porus.

**Measurements:** P 18–22 μm, E 9–10 μm, P/E 2.00–2.10, m 4–5 μm, e 5–6 μm.

**Species:** *B. annobonensis* A.DC.

**Specimens:** Beentje 1443 (WAG), Mildbraed 6627 (HBG), Rose 570 (P), Van Veldhuizen 621 (WAG) (*B. annobonensis*).

**Comments:** The special features of the endoapertural area (especially the relatively large endoaperture) make this type easily recognizable and distinguishable from the representatives of the sections *Augustia* and *Rostrobegonia*. While the latter sections might be combined (see comments on the *B. dregei-type*) the monotypic section *Sexalaria* is pollen-morphologically distinct.

13) **B. dregei-type**

Perprolate, elliptical pollen grains with convex sides and smooth, rounded poles (only seldom syncolpate). A prominent margo bordering the colpi. Rather large, elliptical endoporus with distinct costae.

**Measurements:** group I: P 26–28 μm, E 12–13 μm, P/E 2.00–2.20, m 3–4 μm, e 6–7 μm. group II: P 20–22 μm, E 10–11 μm, P/E 2.00–2.20, m 2.5–3.5 μm, e 4–5 μm.


**Specimens:** Bachman 890 (B), Beyrich 1887/89 (B) (*B. partita*); Bequaert

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4267 (BR) holotype (B. bequaertii); Brummit & Banck 9195 (BR) isotype (B. brevibracteata); Buuk s.n. (HBG) (B. dregei); Bullock 2135 (BR) (B. princeae); Chevalier 34192 (P) (B. rostrata); Deru 332 (BR) (B. bequaertii); Drège 4704 (B) holotype (B. caffra); Dutton 68 (LMA) (B. sonderana); Engler 640 (B) syntype (B. engleri); Gilbert & Thulin 781 (WAG) (B. wollastonii); Gueinzius 248 (W) holotype (B. gueinziana); Holst 3381 (B) (B. johnstonii); Homblé 239 (BR) holotype (B. homblei); Homblé 956 (BR) holotype (B. subacuto-alata); Lebrun 4434 (BR) (B. lebrunii); Milne-Redhead 3670 (BR) (B. princeae); Milne-Redhead & Taylor 8471 (BR) (B. sutherlandii); Morton A 4038 (WAG) (B. rostrata); Münzer 101 (B) (B. princeae); Nolde 176 (B) holotype (B. angolensis); Polhill 2772 (BR) (B. sutherlandii); Prince s.n. (B) (B. princeae); Reichenbach f. (W) 204812 herb. (B. dregei); Richards 3699 (B), Richards 7767 (BR) (B. sutherlandii); Rudatis (128) 347 (B) (B. geranioides); Rudatis 602 (B) holotype (B. rudatisii); Rudatis 811 (B) (B. sutherlandii); Rudats 1876 (W) isotype (B. partita); Schlechter 6781 (B) (B. geranioides); Schlieben 1806 (B) holotype (B. riparia); Schlieben 1941 (WAG) (B. sutherlandii); Schlieben 2807 (B) (B. johnstonii); Schlieben 2920 (B) (B. johnstonii); Schlieben 3584 (WAG) isotype (B. schliebenii); Schlieben 4378 (B) (B. johnstonii); Schlieben 6453 (B) (B. wakefieldii); Schweinfurth 608 (B) (B. socotrana); Stolz 160 (B) (B. sutherlandii); Stolz 166 (B) (B. princeae); Stolz 1042 (B) (B. sutherlandii); Strey 6070 (STU) (B. dissecta); Strey 6311 (BR) (B. sonderana); Van Veldhuizen 444 (WAG) (B. johnstonii); Van Veldhuizen 476 (WAG) (B. homonyma); Van Veldhuizen 477 (WAG) (B. dregei); Van Veldhuizen 507 (WAG) (B. suffruticoso); Van Veldhuizen 543 (WAG) (B. sutherlandii); Van Veldhuizen 642 (WAG) (B. engleri); Van Veldhuizen 874 (WAG) (B. partita); Verdick 250 (MO) (B. engleri); Verdick 306 (MO) (B. wakefieldii); Verdick 274 (BR) holotype (B. verdickii); Welwitsch 874 (BR) isotype (B. rostrata); J. de Wilde 113 (BR) (B. wollastonii); Wilms 1269 (B) (B. sonderana); Wood 759 (MO) (B. keniensis); Wylie & Wood 6762 (B) (B. geranioides).

Comments: This type is characteristic for all species of the sections *Augustia* and *Rostrobegonia*. A small subgroup may be distinguished based on a significant difference in size: while most of the species possess pollen measuring 26–28 μm (P), a number of species (from section *Rostrobegonia*) shows much smaller grains (P ± 22 μm). This group (group II) consists of *B. johnstonii*, *B. engleri*, *B. bequaertii*, *B. dissecta* and *B. keniensis*. The other members of section *Rostrobegonia* (e.g. *B. sutherlandii*) are largely identical with representatives of section *Augustia* (*B. dregei*, *B. princeae* etc.) and pollen-morphologically there can be no objection to combining the species of these two sections into one section. *B. socotrana* has been placed in a separate section *Peltaugustia* (BARLEY (1972)). The pollen of a specimen of this species collected on the island Socotra (Schweinfurth 608 (B)) conforms to the description of the *B. dregei*-type. A plant grown in the greenhouse of the Department of Horticulture of the Agriculture University of Wageningen, proved to possess aberrant pollen (*Van Veldhuizen 449 (WAG)*). In view of the uncertain identity of this latter specimen (perhaps the result of hybridization?) the species *B. socotrana* is recorded here to possess pol-
len belonging to the *B. dregei*-type.

The *B. dregei*-type shows resemblance to the *B. cavallyensis*-type but differs in size and polar outline.

14) **B. filicifolia-type**

Rather small (per)prolate pollen grains, with straight sides and rounded poles. Elliptical endoporus with only faint costae. Margo present. Syncolpate grains may occur.

**Measurements:** P 16–22 μm, E 8–10 μm, P/E 2.00–2.20, m 2–3 μm, e 4–5 μm.


**Specimens:** Bos 3635 (WAG) (*B. elatostemmoides*); Bos 10357 (WAG) (*B. macrocarpa*); Breteler & De Wilde 261 (WAG) (*B. sciaphila*); Breteler & De Wilde 263 (WAG) (*B. minutifolia*); Callens 2435 (BR) (*B. iucunda*); Chevalier 21400 (P) (*B. macrocarpa*); Enti SP 254 (WAG) (*B. macrocarpa*); Farron 5016 (P) (*B. gossweileri*); Gossweiler 7636 (COI) (*B. macrocarpa*); Guineo 2294 (K) (*B. sessilifolia*); Hallé 871 (P) (*B. asplenifolia*); Hallé 1708 (P) (*B. elatostemmoides*); Hallé 2256 (P), 2421 (P) holotype (*B. filicifolia*); Hallé 3878 (P) (*B. macrocarpa*); Hallé & Villiers 4824, 4870 (P) (*B. sciaphila*); Hallé & Villiers 5223 (P) isotype (*B. minutifolia*); Karper, De Wilde, Arends & Bouman 330 (WAG) (*B. asplenifolia*); De Koning 6921 (WAG) (*B. macrocarpa*); Lecomte C-74 (P) (*B. gossweileri*); Letouzey 12424 (P) (*B. sciaphila*); Preuss 200 (B) (*B. macrocarpa*); Sita 1274 (P) (*B. gossweileri*); Sita 3067 (P) (*B. iucunda*); Staudt 193 (HBG) isosyntype (*B. latistipula*); Van Veldhuizen 626 (WAG) (*B. sessilifolia*); Van Veldhuizen 875 (WAG) (*B. elatostemmoides*); J. J. de Wilde 8722 (WAG) (*B. macrocarpa*); W. J. de Wilde c.s. 1615 (WAG) (*B. macrocarpa*); Zenker 307 (MO) isotype (*B. sciaphila*).

**Comments:** This type is characteristic for most of the species which, according to Dr. J. J. E. E. DE WILDE, should be removed from section *Scutobegonia* (series *Longicaules* Engl.) and accommodated in section *Filicibegonia*. The small pollen grains with straight sides and rounded poles, with margo, are easily distinguishable from the pollen of the rest of the species of section *Scutobegonia*, which are generally larger, more perprolate and possess concave sides. *B. gracilicaulis*, which according to macromorphology should also be accommodated in section *Filicibegonia*, shows pollen which must be referred to the *B. quadrialata*-type of section *Scutobegonia*. The circumscription of the sections *Filicibegonia*, *Scutobegonia* and *Loasibegonia* should be thoroughly studied. The pollen-morphological observations should be checked when more material is available.

Perprolate pollen grains with high P/E ratios due to the very small E. The long sides of the grains are concave, the endoaperture is a rather narrow endocolpus. The grains are often syncolpate. A margo is not present.

**Measurements:** group I: $P$ 18-22 μm, $E$ 8-9 μm, $P/E$ 2.20-2.70, $m$ 1.5-2.5 μm, $e$ 5-6 μm. group II: $P$ 24-28 μm, $E$ 8-10 μm, $P/E$ 2.30-2.80, $m$ 2-3 μm, $e$ 5-6 μm.


**Specimens:** Babet s.n. (P) (B. quadrialata); Bates 475 (BR) isotype (B. batesii); Bos 3367 (WAG) (B. dielsiana); Bos 3425 (WAG) (B. zenkeri); Bos 4746 (WAG) (B. dielsiana); Breman 8432 (P) isosyntype (B. salisburyana); Breteler 2125 (WAG) (B. quadrialata); Breteler & De Wilde 25, 188 (WAG) (B. lacunosa); Breteler & De Wilde 263 (WAG) (B. clypeifolia); Breteler & De Wilde 273 (WAG) (B. staudtii); Breteler & De Wilde 274 (WAG) (B. lacunosa); Breteler & De Wilde 334 (WAG) (B. staudtii); Breteler & De Wilde 369 (WAG) (B. peperomioides); Callens 3367 (BR) (B. quadrialata); Christiaensen 1511 (BR) (B. schäferi); Conrau 10 (B) holotype (B. pseudoviola); Coombe 202 (K) (B. pseudoviola); Cult. Kew s.n. (P) ‘from type-plant’ (B. modica); Dinklage 257 (HBG) holotype (B. dielsiana); Dinklage 1029 (HBG) (B. ciliobracteata); Dusen 18 (B) holotype (B. hookeriiana); Dusen 90 (B) holotype (B. dusenii); Gentil s.n. (BR) holotype (B. gentiliii); Gossweiler 7989 (B) holotype (B. quadrialata); Gossweiler 8225 (COI) (B. scutifolia); Hallé 2292, 2841 (P) (B. triflora); Hallé 3034 (P) (B. quadrialata); Hallé & Villiers 1828 (P) (B. hirsutula); Hallé & Villiers 4407 (P) (B. scutulum); Hallé & Villiers 4501, 4565 (P) (B. hirsutula); Hallé & Villiers 4712, 4786 (P) (B. scutulum); Hallé & Villiers 4817 (P) holotype (B. aggeloptera); Hallé & Villiers 5095 (P) holotype (B. vittariifolia); Hallé & Villiers 5177 (P) (B. scutulum); Hallé & Villiers 5277 (P) (B. hirsutula); Hallé & Villiers 5330 (P) (B. scutulum); Irvine 3344 (BR) (B. quadrialata); Karper, De Wilde, Arends & Bouman 64, 127, 128 (WAG) (B. ciliobracteata); Karper, De Wilde, Arends & Bouman 324, 325 (WAG) (B. triflora); Karper, De Wilde, Arends & Bouman 441 (WAG) (B. quadrialata); Karper, De Wilde, Arends & Bouman 925 (WAG) (B. scutulum); Van Kerckhoven 12 (BR) holotype (B. vankerckhovenii); Léonard 6400 A (B) holotype (B. subtilis); Leeuwenberg 11076, 12021 (WAG) (B. quadrialata); Léonard...
2935 B (BR) (B. scutulum); Leroy 12 (P) (B. triflora); Le Testu 551 (P) (B. clypeifolia); Letouzey 10993 (P) (B. scapigera); Louis 3633 (BR) (B. quadrialata); Mann 1946 (P) isotype (B. scapigera); Mildbraed 3124 (B) holotype (B. mildbraedii); Mildbraed 5624 (HBG) (B. staudtii); Mildbraed 7046 (B) (B. prismatocarpa); Preuss 119 (B) syntype (B. quadrialata); Preuss 183 (B) holotype (B. lacunosa); Preuss 952 (B) (B. scapigera); J. & A. Raynal 10412 (P) holotype (B. raynaliorum); Sanford 4415 (IFE) (B. prismatocarpa); Satabié & Letouzey 338 (WAG) (B. staudtii); Staudt 51 (B) holotype (B. staudtii); Van Veldhuizen 445 (WAG) (B. staudtii); Van Veldhuizen 447 (WAG) (B. prismatocarpa); Van Veldhuizen 609 (WAG) (B. potamophila); Van Veldhuizen 884 (WAG) (B. triflora); Van Veldhuizen 1050 (WAG) (B. clypeifolia); Wellens 410 (BR) (B. calabarica); Whyte s.n. (K) holotype (B. whytei); J. J. de Wilde 7471 (WAG) (B. cilio-bracteata); J. J. de Wilde 7909 A (WAG) (B. staudtii); J. J. de Wilde 8662 (WAG) (B. pseudoviola); W. J. de Wilde c.s. 2325 (WAG) (B. schäferii); Zenker 596 (MO) (B. prismatocarpa); Zenker 2831 (B) (B. macropoda); Zenker 3005 A (B) holotype (B. zenkeri); Zenker 3141 (B) (B. calophylla); Zenker 4651 (B) holotype (B. gracilicaulis).

Comments: The slender pollen grains with concave sides and narrow endocolus of this type are characteristic for a large number of species of the section(s) Scutobegonia/Loasibegonia. Variability is high, however. Size is an especially variable character in this type and a subdivision in two size classes is possible (see Measurements). Group I consists of B. aggeloptera, B. batesii, B. calophylla, B. cilio-bracteata, B. clypeifolia, B. dielsiana, B. dusenii, B. gracilicaulis, B. hirsutula, B. hookeriana, B. macropoda, B. peperomioides, B. potamophila, B. prismatocarpa, B. pseudoviola, B. schäferii (p.p.), B. vittariifolia and B. zenkeri. Group II consists of: B. calabarica, B. lacunosa, B. mildbraedii, B. modica, B. quadrialata, B. raynaliorum, B. salisburyana, B. scapigera, B. scutifolia, B. scutulum, B. staudtii, B. triflora, B. vankerckhovenii and B. whytei. Some species (B. hirsutula, B. mildbraedii, B. vittariifolia) showed deviating pollen in certain specimens. Resampling could ascertain the membership of these species to the B. quadrialata-type in most cases. Two specimens of B. schäferii could be accommodated in the B. quadrialata-type (group I) but a third specimen (Satabié 163 (WAG)) showed aberrant, irregular pollen and could not be classified. Of those species, which, according to the taxonomist Dr. J. J. F. E. DE WILDE should be placed in section Filicibegonia, (series Longicaules Engl.) only B. gracilicaulis failed to show this in its pollen which fits in the B. quadrialata-type. The four species of section Loasibegonia are referred to two pollen types: B. prismatocarpa, B. dusenii, and (part or the specimens of) B. schäferi are accommodated in the B. quadrialata-type, B. thomeana in the B. thomeana-type characteristic for the monotypic section Cristasemen. The pollen grains of a few species (B. ferramica Hallé, B. ficicola Irmsch. and B. laporteifolia Warb.) deviate from the B. quadrialata-type, especially in possessing convex sides. They are also not similar among themselves which precludes the establishment of a distinct pollen type to accommodate these species. Furthermore, these deviations are mostly found in one specimen only, while further material was not available. For these reasons they
will not be placed in a pollen type but they are grouped here as exceptions, deserving further investigation, when more material is available. The specimens concerned are:

*Breteler & De Wilde* 650 (WAG) (*B. ferramica*); *Bos* 5110 (WAG) ‘from type-locality’ (*B. ficicola*); *Preuss* 563 (B) syntype (*B. laportefolia*); *Van Veldhuizen* 446 (WAG) (*B. ficicola*).

The high variability of the pollen characteristics within the *B. quadrialata*-type, the fact that many species are only represented by one specimen, the occurrence of deviating characters in different samples of the same species, the possibility of the occurrence of polyploid taxa, and the incomplete state of taxonomical knowledge, all these factors make it difficult to assess the importance of the pollen-morphological observations. However, it may be concluded that:

- the sections *Loasibegonia* and *Scutobegonia* can be combined;
- section *Scutobegonia* s.l. (but series *Longicaules* excluded) is characterized by one rather variable pollen type.
Plate I SEM: 1. B. comorensis A.DC. ex Warb. (Hildebrandt 1696), equatorial view; 2. B. scutatum Hook.f. (Hallé & Villiers 4786), equatorial view; 3. B. princeae Gilg (Münzer 101), equatorial view; 4. B. subsutata De Wilde (J. J. de Wilde 7551), polar view; 5. B. spec. (Sanford 4442) polar view; all magnifications ca 2670x.

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PLATE 2 SEM: 1. B. baronii Baker (Perrier de la Bathie 12365), loxocolpate grain; 2. B. ampla Hook.f. (Wrigley & Melville 29), raised sexine; 3. B. goudotii A.DC. (Perrier de la Bathie 6664), sectioned grain; 4. B. subscutata De Wild. (Beentje s.n., Tuinb. Plant. 1384), detail striate ornamentation; 5. B. princeae Gilg (Münzer 101), detail endoaperture; all magnifications ca 2670x except 4.: ca 13335x.
PLATE 3 TEM: 1. B. seychellensis Hemsley (Van Veldhuizen 539); 2. B. baccata Hook.f. (Tuinb. Plant. 1247); 3. B. pociulifera Hook.f. (Letouzey 14685); 4. B. mannii Hook. (Leeuwenberg 8649); 5. B. subscutata De Wild. (J. J. de Wilde 7557); 6. B. squamulosa Hook.f. (Breiteler & De Wilde s.n., Tuinb. Plant. 1210 C); 7. B. polygonoides Hook.f. (Leeuwenberg 8650 A); 8. B. dregei Otto & Dietr. (Van Veldhuizen 477); 9. B. stauntdii Gilg (Van Veldhuizen 445); 10. B. asplenifolia Hook.f. (Karper, De Wilde, Arends & Bouman 330); all magnifications 34000x.

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PLATE 5 LM: 1–2. B. seychellensis Hemsley (Van Veldhuizen 539); 3–4. B. baccata Hook.f. (Mann 1087); 5–6. B. ihomeana C. DC. (Exell 419); 7–8. B. pycnocaulis Irmsch. (Schlieben 2006); 9–10. B. alepensis Chevalier (Leeuwenberg & Voorhoeve 4792); 11–12. B. subscutata De Wild. (Bequaert 6593); 13–14. B. cavallyensis Chevalier (Leeuwenberg 3870); 15–16. B. squamulosa Hook.f. (Letouzey 12765); all magnifications 1440x.

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PLATE 6 LM: 1–2. B. annobonensis A. D.C. (Beentje 1443); 3–4. B. dregei Otto & Dietr. (Reichenbach f. 2048/12); 5–6. B. bonus-henricus J. J. de Wilde (J. J. de Wilde 8404); 7–8. B. poculifera Hook.f. (Leeuwenberg 10002); 9–10. B. ampla Hook.f. (Wrigley & Melville 29); 11–12. B. sessilifolia Hook.f. (Van Veldhuizen 626); 13–14. B. quadrialata Warb. (Leeuwenberg 11076); all magnifications 1440x.

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PLATE 7 SEM: 1–2. B. seychellensis Hemsley (Schlieben 11672), equatorial and polar view, 4000x; 3. B. baccata Hook.f. (De Wilde, Arends & Groenendijk 105), equatorial view, 3600x; 4. B. comorensis (A.D.C.) Warb. (Hildebrandt 1606), equatorial view, ca. 2670x; 5. B. meyeri-johannis Engl. (J. v.d. Walle 3845), equatorial view, ca 2670x.
Plate 10 SEM: 1. *B. rubromarginata* Gilg (Conrau 80), equatorial view; 2. *B. lethomasiae* Wilcz. (J. J. de Wilde 8365), equatorial view; 3. *B. wilczekiana* Hallé (Breteler & De Wilde 385), equatorial view; all magnifications ca 2670x.
Plate II SEM: 1–2. B. bonus-henicus J. J. de Wilde (J. J. de Wilde 8404), equatorial views; 3. B. poculifera Hook.f. (Leeuwenberg 10002), equatorial view; 4. B. ampla Hook.f. (Wrigley & Melville 29), equatorial view; 5. id. detail raised sexine; all magnifications ca 2670x except 5: ca 6670x.

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5. PHYLOGENETIC CONSIDERATIONS

Constructing phylogenies is a stimulating mental exercise.

G. L. Stebbins (1974, p. 122)

The main question to be answered in this chapter is: how can pollen-morphological data contribute to the reconstruction of phylogeny? The most direct evidence would obviously be a complete fossil record of the studied group. In the case of Begoniaceae there is no such record. All speculations on phylogeny must be inferred from the features of recent representatives.

5.1. METHOD OF POLLEN MORPHOLOGY

The method of pollen morphology will now be examined in order to indicate the possibilities of reconstructing phylogeny with the help of pollen-morphological data.

Pollen of all studied taxa is sampled and treated according to a standard method to produce comparable results (chapter 2). The pollen grains are examined and described in detail, recording all observed morphological features. In most cases the pollen grains of one taxon will be uniform, all grains resembling each other, while a certain variability is admitted. The pollen grains of different taxa can resemble each other, too. A generalized description can be made to include all taxa with similar pollen. These taxa belong to one pollen type. The members of a pollen type possess pollen which differs in at least one character from that of all other pollen types (Punt, 1971). Within a pollen type subtypes may be distinguished. The pollen types as such may be arranged in clusters (Punt, 1975), resulting in a hierarchical system in analogy to taxonomical practice.

Members of a pollen type are morphologically similar in their pollen and therefore ‘related’. Although this relationship rests methodologically on the same basis as taxonomical affinity, it remains to be ascertained whether pollen-morphological affinity coincides with taxonomical affinity. A pollen subtype, type or cluster may coincide with a taxon (species, section, genus etc.) but may ignore such taxonomical demarcations.

Pollen types are characterized by certain differential characters. It is often possible to establish a morphological series comprising the different manifestations of a character (character states, see 5.4.) within the studied group. By postulating the direction within a series from ‘primitive’ to ‘advanced’ the morphological series is converted into an evolutionary trend: ‘a hypothetical line of evolution, established by comparison of features of recent taxa which can be arranged in a sequence from primitive to advanced’ (Punt, 1978). Or, in the words

Through these evolutionary trends the relative degree of derivation (evolutionary level) of a pollen type can be estimated, and the types can be arranged in a scheme of pollen-morphological relationships with, for instance, the more primitive types at the base and the centre of the scheme and the more advanced types towards the sides and the top (PUNT, 1978). Such a scheme can be considered to reflect the evolutionary pathways within the studied group. In this way insight is acquired into the way a taxonomical group is structured and the results may be used in classification. If the pollen types comprise several taxa, new configurations of taxa may have arisen and can be compared with the data of classical macromorphological taxonomy. Finally, by comparing the data on the geographical distribution of the taxa and the pollen types the place of origin of the studied group may be deduced (see chapter 6).

5.2. AUTONOMY OF POLLEN MORPHOLOGY

Characteristically, the described method demands complete autonomy of pollen morphology with respect to taxonomy. Only in the final stage, when the construction of the phylogenetic scheme based on pollen data has been completed, the relation between pollen morphology and taxonomy may be considered. The main advantage of this procedure is the avoidance of circular reasoning (see below), while nomenclatural errors and misidentifications of specimens will not influence pollen morphological research.

However, the separation between the two disciplines is hardly this strict. By insisting on correctly identified material (PUNT, 1976) the pollen morphologist allows the taxonomist’s view on the classification and, consequently, on the evolutionary background of the group, to influence his work, already at the outset of his investigations. His pollen types will contain only taxa as established by the taxonomist. The arrangement of the taxa according to pollen morphology may differ from the grouping according to taxonomy. Species from quite separate taxa (sections, genera) may be placed into one pollen type without taking into account the probable relationships of these taxa as established by macro-morphological taxonomy. In this way the delimitations of all taxonomical categories would be ignored by pollen morphology whenever discrepancies between the two disciplines would arise. In practice, the delimitations of families and other higher categories are usually taken for granted. It might be argued that this should also hold for sections, genera, tribes and subfamilies.

The work of GUINET (1969) on the pollen of the Mimosaceae illustrates this approach. In this study, each of the three tribes Piptadenieae, Adenanthereae, and Eumimoseae, were found to possess two basic types of pollen: ‘simple’ (monads) and ‘composite’ (polyads). The question which arises is: ‘... si les groupes
Table:

<table>
<thead>
<tr>
<th>Tribe</th>
<th>Pollen Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Piptadenieae</td>
<td>POLLEN SIMPLE</td>
</tr>
<tr>
<td>Adenanthereae</td>
<td>POLLEN COMPOSÉ</td>
</tr>
<tr>
<td>Eumimoseae</td>
<td></td>
</tr>
</tbody>
</table>

A et B sont plus naturels, que les groupes I, II, III’ (see fig. 5.1.).

The first possibility results in two artificial groups (A and B) characterized by their pollen types (all monads in one group, all polyads in the other). The alternative conforms to the classification based on macromorphological taxonomy and admits the derivation of one type from the other. Within the three tribes parallel developments have taken place leading (according to Guinet) from polyads towards monads. The merit of the second viewpoint is that it seems to provide a plausible explanation of the evolutionary history of this group of taxa.

Clearly, the manner in which the pollen-morphological results are presented and interpreted, determines the impact of the contributions of pollen morphology to taxonomy. And, although a regrouping of taxa on the basis of pollen morphological evidence alone may in some cases be justified – the taxonomist might be able to substantiate this regrouping with macromorphological evidence which he had so far ignored – in order to integrate the results of several disciplines (in the ideal multi-disciplinary approach to a taxonomically difficult group) it is preferable for all disciplines to use the same classification, provided by taxonomy, as a base. With this approach to the relation between pollen morphology and taxonomy more may be accomplished than in maintaining the autonomy of pollen morphology and concluding (Punt, 1976): ‘... the two systems are often remarkably in agreement but in detail many questions are left open.’

If the systems are in fact kept separate, on comparing them one may find that taxa which are closely related according to taxonomy, are referred to very different pollen types, which are far removed from each other in the phylogenetic scheme based on pollen morphology. Conversely, taxa belonging in widely separate taxonomical units, could find themselves in one and the same pollen type due to the similarity of their pollen. These discrepancies may be explained by assuming that current taxonomical classification is incorrect. Seemingly closely related taxa are in fact not all that close, higher taxonomical units prove to be artificial, etc. Alternatively, accepting the taxonomical classification based on observations of the entire plant, the explanation for the discrepancies must be found in parallel development, convergence, and different rates of evolution in pollen morphology with respect to macromorphology.

Stebbins (1974, p. 45) states that convergence is characteristic of all kinds of adaptation, while Mayr (p. 294) observes: ‘The same parallel specializations
are frequently acquired in independent lines. This is sometimes due to a basic relationship (...). In other cases such parallelism is due to convergence, based on the fact that some of the fundamental structures can change only in very few directions'. The occurrence of similar pollen types in quite different taxa can be explained by this phenomenon of convergence: the acquiring of a certain degree of specialization is expressed in a similar manner in different taxa. The evolutionary level reached by the taxa showing convergence is comparable. Other taxa may express their specialization in quite another way. Evolutionary level refers only to the relative distance from a 'basic' situation, the direction of the developments is not specified. The evolution of different organs or even different parts of one organ at unequal and strongly variable rates results in 'a veritable mosaic of evolutionary levels' (cf. LE THOMAS, 1981, p. 334). The evolutionary level of a pollen type is the resultant of the degrees of derivation in all the various characters of that type.

5.3. THE POLLEN TYPE

The crucial problem in this discussion is the status of the pollen type. In the hierarchically arranged system of pollen morphology, the pollen type may be seen as the fundamental unit, in analogy with the position of the species in the taxonomical system. A main difference which must be faced is in the extent to which the two concepts can claim to be 'real' entities. In this context HENNIG (1966, p. 80/81) may be quoted: '... there can be no doubt that all the suprainsividual categories, from species to the highest category rank, have individuality and reality. They are all segments of the temporal stream of successive 'interbreeding populations'. As such they have a beginning and an end in time and there is a constant causal connection between the phases in which they are found at different times. All this is missing in the categories of the morphological or typological system which, consequently, are timeless abstractions and therefore have neither individuality nor reality'. A clear distinction should thus be made between typological constructions and bio-systems (DE WIT, 1959, p. 19). Only the latter refer to living taxa as present in nature and are subject to the process of evolution. A pollen type does not possess reproductive patterns similar to those of species, unless it coincides with a species. The question whether phylogenies can be erected based on the concept of pollen type as established so far should be critically evaluated. As HENNIG (1966, p. 29) stated: '... by definition phylogenetic relationships exist only between species; they arise through the process of species cleavage'.

A pollen type as defined above contains all taxa with pollen answering to the type description. These taxa may come from different (higher) taxonomical units, or from different parts of the distribution area of the studied group. In the author's opinion this leads to pollen types which cannot be considered as natural units. In order to use the pollenmorphological units in phylogenetic reconstruction an amended definition of the term pollen type will be presented later in this chapter.
The concept of the pollen type can thus be used as an indicator of (pollen-morphological) affinity or only as indicative for parallel course of evolution and of comparable evolutionary level. Punt (1975) in his study of the pollen of Dichapetalaceae makes use of a strictly formalized pollen type as outlined above, determined by the steps in evolutionary trends that have apparently been taken. The pollen types are arranged in a scheme of pollen-morphological relationships, primitive types at the base and middle of the scheme, more advanced types towards the sides and the top. The types are connected by presumed lines of evolution. All information about the trends is incorporated in the scheme. The result is a kind of evolutionary tree showing possible evolutionary relationships. Muller & Leenhouts (1976) give a scheme of pollen types in the Sapindaceae. They distinguish a basic type (A). Different trends in apertural type lead from this basic type in several directions to relatively specialized types (B-H). The sculpture of type A is variable and includes virtually the whole range found in Sapindaceae. Thus it is clear that Muller uses a different pollen type concept: a close morphological similarity is not necessary for taxa to be a member of type A. Furthermore, the types are arranged according to trends in, essentially, one feature: type of aperture. Also, in a study of the pollen of Lepisanthes (Muller, 1970) the types are arranged to 'the two most significant morphological features.' (p. 549). This is a different procedure from using all trends. Finally, Muller & Leenhouts (op cit.) accepted existing taxonomy (the system of Radlkofer, revised by Leenhouts) with the 'generic and specific delimitations as determined on macromorphological evidence' (p. 412). In this way a 'diverging evolutionary radiation pattern' is postulated, showing in what way the family is composed out of groups and which were the evolutionary pathways of development.

All this shows that different authors can apply different approaches to pollen morphology even when using the same terms 'pollen type', 'evolutionary trend', 'phylogenetic scheme'. It is essential that each author should make his concepts explicitly clear.

5.4. POLLEN MORPHOLOGY AND THE RECONSTRUCTION OF PHYLOGENY

Before embarking on the application of these theoretical considerations we shall return to the original question: how can pollen-morphological data be used in reconstructing phylogeny? 'Die meist optimistisch interpretierten aber doch unterschiedlichen Ergebnisse pollenmorphologisch-systematischer Untersuchungen lassen Fragen nach den theoretischen Grundlagen dieses Wissensweiegener auftauchen. Ist es grundsätzlich möglich, von der Pollenmerkmalen her phylogenetische Schluβe zu ziehen?' (Leuenberger, 1976, p. 15). In fact, two questions must be asked:

(1) can phylogenetic conclusions be reached based on pollen-morphological data? and, if so, (2) how may these conclusions be reached? (1) Obviously, pollen morphology is a rather restricted discipline: only the morphology of the pollen
grains is studied. Physiological, ontogenetical, pollination ecological data etc. are ignored. Furthermore, since only the male haploid generation is studied, the greater part of the life-cycle of the plant is not considered. It must be noted, however, that the morphology of the pollen wall is not under genetic control of the haploid nuclei: ‘Exine structure is determined sporophytically, notwithstanding the early period of growth within the tetrad’ (HESLOP-HARRISON, 1976, p. 29). Nevertheless, pollen morphology seems a rather narrow basis for the speculative undertaking of reconstructing the phylogeny of a complex taxon. A case can be made, however, for assigning a restricted importance to pollen-morphological data, following an argument of STEBBINS (1974, p. 38), who distinguishes between functions associated with survival and functions associated with reproduction. In animals the former functions need a high degree of integration, and selection usually produces variations or modifications in the character complexes associated with these functions of survival (diet, habitat, locomotion).

In plants the mechanisms for survival are relatively similar in all groups while it is especially the functions for reproduction which require a high degree of integration, and may be expected to show the variation produced by selection. The assumption that character complexes associated with reproduction (amongst which the morphology of the pollen wall) will reflect the course of evolution may well be warranted.

(2) The second question involves especially the problem of circular reasoning. This occurs when external evidence (from without pollen morphology) is used in the interpretation of pollen-morphological results. If taxonomy indicates a close affinity between two taxa, the pollen types which can be established in these taxa will automatically be considered as allied. This will affect the interpretation of all further to-be-discovered pollen types of the group to which the two taxa belong. A pollen-morphological classification of the group will be biased by the knowledge of the taxonomical system. Another pitfall is establishing the direction of an evolutionary trend on the notions about primitiveness derived from macromorphological evidence. The use of external evidence should be avoided, but this will hardly be possible.

Within pollen morphology, circular reasoning is also possible. A well known example (VAN CAMPO, 1966) investigates the status of oblate and prolate shape. Starting from the assumption that the possession of apertures not placed on the equator of the pollen grain must be a primitive character (making use of external evidence: such non-equatorial apertures occur in primitive families) the observation that most pollen grains with such apertures are oblate leads to the conclusion that oblate shape is primitive, prolate advanced. Further observations, establishing the relation oblate/colpate and prolate/corporate ‘prove’ the primitiveness of colpate apertures.

This line of reasoning seems inadmissible. The conclusions that are reached may only be applied to the investigated taxa. Generalization will be very uncertain. Even when the general trend in shape of pollen grains runs from oblate to prolate, at each stage along the series a new line of development can be initiat-
ed following a pattern of its own. Only the most primitive representatives of taxa of higher order can be compared with each other in this way, and moreover, only tentatively.

This is not to say that a number of general trends cannot be established, if only with caution and realizing the possibility of reversal and other exceptions. PUNT (1976) arranged a large number of trends in categories according to the amount of general consensus among authors. A number of trends, for instance the increase in size, is accepted by all authors. Other trends are less certain, accepted by some but not all authors. Controversial trends are the subject of dispute between two or more authors, debating the direction of the trends. Some trends are restricted to only a few taxa ('special trends') but e.g. MULLER & LEENHOUTS (1976, p. 411) mention trends not restricted to Sapindaceae but occurring in several other dicotyledonous families.

To avoid any chance of circular reasoning all considerations should be based on pollen-morphological evidence from the studied taxon. This demand makes it hard to propose the direction in a morphological series. It is necessary to be able to use arguments for judging certain character states as more derived than others. MULLER (1970) mentioned a number of arguments which can be used to arrive at a decision as to the direction of the trends. Some of these arguments are based on external evidence.

The arguments are (p. 551):
1. fossil record
2. functional interpretation
3. comparison with trends established in other taxa
4. geographical distribution of the taxa
5. taxonomy.

Arguments 1-3 are based on internal, pollen-morphological evidence, but argument 3 is not restricted to the studied group. Arguments 4 and 5 are clearly external evidence. These arguments will now be discussed:

1. Unfortunately, a fossil record is often not available. Still, data on fossil pollen, in particular on the first Early Cretaceous angiosperm pollen grains, can be used in deciding the direction of trends. MEEUWIS & PUNT (1983) note that these Cretaceous pollen grains must be considered primitive. They are characterized, amongst other things, by small size, long colpi, finely reticulate ornamentation and slightly prolate P/E ratio. The authors conclude that pollen grains showing characters other than those mentioned, must be regarded advanced (op. cit. p. 140). The sequence in which the various morphological types appear in the sediments also might provide data on the probable course of evolutionary trends (cf. LAING, 1976).

This approach seems to oversimplify the problem. Fossil palynological evidence suggests that the angiosperms diversified greatly and rapidly after their origin. Various features of pollen could evolve with very different evolutionary rates producing combinations of primitive and advanced conditions which defy interpretation. Reduction might lead to seemingly primitive conditions and reversals of trends might also occur. Each stage in the general trend from the
primitive Early Cretaceous type towards more advanced types might function as a starting point for a unique trend deviating from this general trend and only the most primitive members of (higher) taxa might be expected to conform to it. In short, data on Early Cretaceous angiosperm pollen grains may be used profitably in reconstructing the evolutionary pathways in certain higher taxa but will not be helpful in many other, especially highly derived, taxa.

2. A functional interpretation, placing emphasis on the adaptive significance of the structure and sculpture of the exine, can be used to assign a direction to morphological series. However, this approach also meets serious difficulties, since the evolutionary advantage of many morphological features is not at all clear. Generally speaking, the morphology of the pollen grain will be a compromise resulting from the (conflicting) demands posed by the various functions of the exine: protection, adaptation to volume changes (harmomegathy), transportation during pollination and, finally, germination on the pistil. The resulting morphology will reflect answers to all of these demands and, consequently, will be hard to interpret. Also, the demands of, for instance, harmomegathy can be answered in very different ways. In order to be able to withstand the tensions in the wall caused by loss of water, the exine might develop heavy thickenings, or become as thin and flexible as possible. No direction is indicated. As Eldredge & Cracraft (1980, p. 13) state: '... theories tend to be invented which can explain all patterns (a frequent and often justified complaint about the use of the concept of adaptation by natural selection, for example)'.

This is not to say that in some cases a functional approach cannot be exceedingly useful, as was shown by Muller (1981) for some Lythraceae and Sonneratiaeae.

3. Comparison with other taxa, strictly speaking being external evidence, is a highly suspect source of support. Trends, even well known ones, in other taxa, might be misleading. The important and difficult question remains which taxa to select for comparison. The only other genera of the Begoniaceae, Hillebrandia and Symbegonia, will be the obvious choice in the case of Begonia. The comparison is indeed fruitful (cf. Van den Berg, 1984).

4. The geographical distribution of the taxa in relation with their pollen type can provide interesting information but much more insight must be acquired in the history of the distribution areas to use this as a criterion in establishing the direction of evolutionary trends.

5. Finally, as has been argued, arguments based on the taxonomy of the studied group must be used with the greatest caution. The danger of circular reasoning is evident. Ideally, the pollen-morphological evolution pattern should be deduced 'from the evidence provided by the pollen grains alone' (Muller and Leenhouts, 1976, p. 412, who, however, add: 'except taking for granted generic and specific delimitations as determined on macromorphological evidence'). It seems that a close connection between pollen morphology and taxonomy cannot be avoided.

In view of these considerations it may be stated that pollen-morphological data can indeed be used for phylogenetic reconstruction but that one should
be very careful in their interpretation. Circular reasoning should be avoided as far as possible (cf. KALKMAN, 1982, p. 13), but the disciplines taxonomy and pollen morphology should cooperate closely to insure that the taxa and the pollen types may be considered as 'natural' units, subject to the evolutionary process. As a consequence, the term pollen type as defined in 5.1. (used both in the sense of the morphological category and the group of taxa characterized by a certain type of pollen) will be formulated as follows: a pollen type is an informal grouping of taxa based on pollen-morphological similarity which should be restricted to a taxon or a group of closely related taxa. All specimens showing this type of pollen and belonging to this group of taxa, may be included in the pollen type. Specimens showing similar pollen but belonging to a different taxonomical unit (section, genus etc.) must be considered evidence for parallel developments or convergence. These phenomena may be rather frequent.

The resulting pollen types can be used in phylogenetic considerations because they may be considered as natural units. After the recognition and delimitation of these pollen types their evolutionary level should be appraised. This must be based on an analysis of the degree of derivation of the various characters shown by the pollen type. The procedure of pollen morphology as outlined in 5.1. (recognition of morphological series and establishing evolutionary trends by determining the direction of the series) seems an adequate way to arrive at such a 'Merkalsphylogenie' (cf. DE WIT, 1959, p. 14). For this purpose the used terminology can be re-defined in terms of 'character state' as follows:

- a character is a (pollen-)morphological feature;
- a character state is the condition of a character in relation to the most primitive and most derived condition of that character;
- a morphological series is an enumeration of the character states of a character;
- an evolutionary trend is a sequence of character states from primitive to advanced;
- a pollen type is characterized by a specific combination of character states;
- the evolutionary level of a pollen type is the resultant of the degree of derivation in all characters.

It will be necessary to distinguish the different character states (and to recognize them as the different states of one character!). Different characters may have developed with different evolutionary rates: certain characters reached a derived state, while other characters, displayed by the same pollen type, remained relatively primitive. Each pollen type thus presents a mosaic of character states, derived in different degrees. A general assessment of the degree of derivation in the characters of a pollen type compared with that of other types, determines its evolutionary level. A phylogenetic scheme can be used to illustrate the evolutionary levels of pollen types in relation to each other. The resulting scheme of more and less advanced pollen types and the distribution of the different character states over the studied taxon, should be logical and internally consistent. The directions of the several trends on which the scheme is based should coincide, thus reinforcing each other. Furthermore, a few general assumptions
about the evolutionary process to be considered in determining the direction of trends, are:
- evolution is a development from simple to more complex forms;
- the absence of a feature is generally more primitive than the presence;
- apparent reduction indicates a derived stage;
- reversals of trends may occur but are generally rare.

After the establishment of a number of morphological series, the following procedure may be followed:
- the direction of one particular series is postulated;
- the pollen types are arranged according to this trend;
- this arrangement will dictate the direction of other recognized series;
- the resulting system should be tested for its consistency: the distribution of character states over the taxa and pollen types should be logical (cf. HENNIG's 'criterion of the correlation of series of transformation' (HENNIG, 1966, p. 96): individual stages of several series of transformations (which) usually or always appear together. 'Such correlations are of significance to phylogenetic systematics only if the direction of one of two or more transformation series is known').
- any series can be used as starting point;
- the most plausible pollen-morphological system can be compared with macro-morphological and distributional evidence.

If, for instance, there is a variation in size, the pollen types can be arranged from small to large (a generally accepted evolutionary trend). The trend in shape of the grains is then established, too: if spheroidal or slightly prolate grains are always small in size and (per)prolate grains are large, the two trends reinforce each other. If, however, also large spheroidal grains and small perprolate grains occur, the resulting system is not consistent and the postulated trend from small to large grains is not acceptable as the general line of evolution characterizing the studied group. The trend may still occur, however, in certain sub-groups. By trying out the various series as hypothetical evolutionary trends, in addition to the general evolutionary considerations as outlined above (including taking into account the possibilities of reduction and reversibility) a pollen-morphological scheme is reached which may be compared with the findings of taxonomy. The established trends hold only for the studied group, although a number of them may occur in other taxa.

5.5. PHYLOGENY OF AFRICAN BEGONIAS

As will be apparent from the descriptions (chapter 4), a number of morphological series can be discerned, and interpreted as evolutionary trends by postulating the direction of the trends from primitive towards derived as discussed above.

The characters and the postulated trends are:
<table>
<thead>
<tr>
<th></th>
<th><strong>Size</strong></th>
<th><strong>P/E ratio</strong></th>
<th><strong>Costae</strong></th>
<th><strong>Margo</strong></th>
<th><strong>Ornamentation</strong></th>
<th><strong>Sides</strong></th>
<th><strong>Poles</strong></th>
<th><strong>Pollen class</strong></th>
<th><strong>Size endoaperture</strong></th>
<th><strong>Outline endoaperture</strong></th>
<th><strong>Infratectal layer</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>small (15 μm) - large (30 μm)</td>
<td>spheroidal - prolate - perprolate (P/E ± 1 - ± 3)</td>
<td>absent - present</td>
<td>absent - present</td>
<td>regular - irregular</td>
<td>convex - straight - concave</td>
<td>rounded - pointed</td>
<td>3-colporate - syncolpate</td>
<td>small (2 μm) - large (5 μm) (meridional diameter)</td>
<td>elliptical endoporus - oblong endocolpus</td>
<td>distinct columellae - columellae reduced</td>
</tr>
</tbody>
</table>

Differences in size are difficult to assess due to the variability of this character. WALKER & DOYLE (1975, p. 702) note: ‘Pollen size is undoubtedly an easily reversible character and determination of the primitive size class for pollen of any particular taxon (order, family, etc.) must be based on correlation of pollen size with other characters of the taxon’. Still, the extremes are easily recognizable: the smallest grains, found in the *B. comorensis-* , *B. baccata-* , and *B. thomeana-* type, measure ± 15–18 μm (polar axis), while at the other extreme several types from different sections measure ± 27–30 μm or more: *B. cavalleyensis-* and *B. squamulosa-* type (*Tetraphila*), *B. dregei-* type (*Augustia*) and *B. ampla-* type (*Squamibegonia*). Generally speaking, three size-classes can be distinguished:

- **< 20 μm**
- **> 20 μm, < 25 μm**
- **> 25 μm**, but the demarcations are non too clear. It seems safer not to rely too heavily on size in distinguishing types.

The trend in P/E ratio is towards an elongation of the polar axis, leading to a pronounced (per)prolate P/E ratio (up to 3.0). Only in the smallest grains the P/E ratio may be more or less spheroidal. The larger grains are without exception prolate or even perprolate. Since no large spheroidal grains nor small perprolate grains occur, the two trends, in size and P/E, tend to reinforce each other.

Larger, more prolate grains acquire thickenings around the endoaperture. These costae, which are never very pronounced, are absent only in the smallest and ± spheroidal types. They only occur along the long sides of the lalongate endoaperture, the short sides are often rather diffuse.

The presence of a margo also seems an derived character, acquired in the course of evolution. Here the picture is more complex, however. While it is true that small spheroidal grains usually lack a margo (*B. comorensis-* and *B. baccata-* type), the *B. thomeana-* type presents an exception. Also, among the larger perprolate grains margines are present except in the representatives of the section *Scutobegonia/Loasibegonia*. Ornamentation is usually regular: the striae run parallel to each other and to the colpi. Deviation from this pattern is random although this seems to occur more often in relatively advanced types.
The outline of the grains being always more or less elliptical, the sides are usually convex. In the *B. filicifolia*-type (*Filicibegonia*) the rather small grains are characterized by straight sides. The *B. squamulosa*-type and most representatives of *Scutobegonia/Loasibegonia* show distinctly concave sides. The sequence convex-straight-concave can hardly be called a hypothetical line of evolution. Rather, the concave types represent specializations in certain lines, while the most common outline in equatorial view remains (convex) elliptical. The outline of the poles is correlated to that of the sides: convex and straight sides imply rounded poles, while concave grains tend to possess more or less pointed poles.

The very long colpi sometimes anastomose at the poles. These syncolpate grains can be either the exception, as in the smaller types, or the rule, as in certain more derived types. The distribution of this character is, like irregularities in ornamentation, too random to be of use as a clear evolutionary trend, but can still indicate relative advancement.

The size and outline of the endoaperture, although obviously related to the size and shape of the total grain show a distinct development from a small elliptical endoaperture without costae towards a large, more or less oblong endoaperture bordered by costae. Minor variations on this theme occur: extremely lalongate endocolpus in *Scutobegonia*, raised sexine around the endoaperture in *Squamibegonia* and *Sexalaria*.

Finally, in the structure of the wall a tendency towards reduction of the infratectal layer leading to less distinct columellae (which are completely absent in *Symbegonia*) can be observed (see chapter 3). The occurrence of rather distinct columellae in the small spheroidal/prolate types, while the reduction of the infratectal layer is most explicit in the large, perprolate types of *Tetraphila, Augustia* and *Scutobegonia*, again strengthens the direction of the various trends as described above.

The phylogenetic conclusions which may be reached by taking into account the established trends can be illustrated in a phylogenetic scheme (fig. 5.2.). Relatively primitive types are placed at the bottom of the scheme, more derived types towards the top, according to the appraisal of their evolutionary level. The circumscriptions of the presently recognized sections has been superimposed. In some cases a pollen type coincides with a section (*Baccabegonia, B. baccata*-type, *Cristasemen, B. thomeana*-type, *Filicibegonia, B. filicifolia*-type, *Scutobegonia, B. quadrialata*-type). Other sections contain more than one pollen type, differing in evolutionary level.

The sections *Mezierea, Baccabegonia, Cristasemen* and *Filicibegonia* possess relatively primitive pollen types with regard to size, outline and endoaperture. The presence of a margo in the pollen of section *Cristasemen* and *Filicibegonia* is remarkable, and both the *B. thomeana*-type and the characteristic small grains with straight sides of section *Filicibegonia* may have to be interpreted as more derived than is obvious on first glance. This is also indicated by the presence of a reduced infratectal layer in representatives of *Filicibegonia*.

The most derived type of section *Mezierea* resembles the most primitive type of section *Tetraphila*, which may point to a phylogenetic connection between

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these sections. Section *Tetraphila* seems most heterogenous in its pollen morphology. An interesting case of convergence may be noticed in the resemblance of two highly derived types: the *B. cavallyensis*-type in *Tetraphila* and the *B. dregei*-type in *Augustia*. The absence of a margo in the pollen of section *Scutobegonia* is a striking exception of the general occurrence of this character in derived types.

Summarizing, a number of evolutionary levels is discernible in the pollen types. The basic type is a small, spheroidal or only slightly prolate grain without costae and margines. This type occurs in sections *Mezierea* and *Baccabegonia*. The types of sections *Cristasemen* and *Filicibegonia* might be modifications of this basic type but probably constitute different lines of development, showing a reduction in size. The second level is represented by a prolate grain, still without margo and with only faint costae, as occurs in the *B. oxyloba*-type (most advanced within section *Mezierea*) and the *B. eminii*-type (primitive within *Tetraphila*). Higher evolutionary levels are represented by a variety of types: large, perprolate grains with margo such as in *Tetraphila* and *Augustia*, large grains with concave equatorial outline, extremely lalongate endoaperture without margo as in *Scutobegonia*, large concave grains with margo as in the *B. squamulosa*-type (*Tetraphila*) and large, rather convex grains with specializations in the endoapertural area (raised sexine) as in *Squamibegonia*. The evolutionary level of all these types is high but the developments have taken place in a number of directions, sometimes, diverging, sometimes converging.

5.6. THE MULTIDISCIPLINARY APPROACH

In order to unravel the evolutionary history of a group, as many aspects as possible should be investigated. It is fortunate that the African *Begoniaceae* are currently studied in a number of ways, and it is of interest to compare the results of pollen morphology with those of other disciplines.

The morphology of the seed coats is being studied by Dr. A. De Lange and Dr. F. Bouman (Hugo de Vries Laboratory, University of Amsterdam), Ir. J. M. Reitsma (Dept. of Plant Taxonomy, Agricultural University Wageningen) investigated the placentation and Ir. J. C. Arends (Dept. of Plant Taxonomy, Agricultural University Wageningen) is studying the karyology of the family.

Finally, a comparison with the most recent concepts of the taxonomy of the genus, as developed by Dr. J. J. F. E. De Wilde (Dept. of Plant Taxonomy, Agricultural University Wageningen), allows an assessment of the contribution which pollen morphology can make to the solution of taxonomical problems.

*Begonia* seeds show a great diversity in structure, shape and size (Bouman & De Lange, 1983). Within the African representatives it is possible to distinguish three groups, each comprising a number of sections (De Lange & Bouman, 1985):

1. *Augustia, Sexalaria, Rostrobegonia*: the seeds are of medium size and show a distinct sculpture pattern in the cuticle. The seeds of the three sections cannot
be distinguished from each other.

2. **Mezierea, Squamibegonia, Tetraphila**: this group is characterized by reduction or absence of the cuticular pattern, a feature which combined with the occurrence of fleshy fruits may be related to a zoochorous way of dispersal. The seeds within this group are rather large. Section **Mezierea** seems most original. The seeds of the three sections can be distinguished from each other.

3. **Filiticbegonia, Scutobegonia, Loasibegonia**: the seeds are small and, especially within **Scutobegonia** the cuticular sculpture is very well developed. **Filiticbegonia** seeds can be distinguished from those of **Scutobegonia**, but the distinction of **Loasibegonia** and **Scutobegonia** seeds is not possible.

The results of seed and pollen morphology are in agreement in a number of instances. The similarity of the sections **Augustia** and **Rostrobegonia** is also apparent in pollen morphology. The transfer of a number of species from **Scutobegonia** to **Filiticbegonia** is supported by both disciplines, as is the impossibility to distinguish between **Scutobegonia** and **Loasibegonia**. A phylogenetic interpretation of the seed-morphological data may be based on the relation between seed structure and means of dispersal: smooth seeds are rare and occur in the sections **Mezierea, Baccabegonia, Squamibegonia** and **Tetraphila** which possess fleshy fruits. This can be interpreted as a development towards zoochorous dispersal. The sections, showing this reduction in cuticular sculpture, might then be considered as relatively derived, compared to the more common anemochorous **Begonias** with dry, winged fruits and seeds with pronounced surface sculpture. These conclusions, interestingly, would be opposed to those reached on pollen-morphological grounds, designating section **Mezierea** as most primitive and indicating several lines of development leading to the more advanced sections, among which certainly also all **Begonias** with winged fruits must be counted.

The study of the type of placentation, undertaken by **REITSMA** (1984, 1985a) yielded many interesting results. Parietal placentation proved to occur more often than was assumed. This type of placentation is characteristic for the sections **Mezierea, Tetraphila, Squamibegonia** and **Baccabegonia**, the other sections show axile placentation. In **Begoniaceae** the parietal condition is primitive, as is clear among other things from the placentation of the primitive genus **Hillebrandia** (cf. **GAUTHIER**, 1959). **REITSMA** was able to demonstrate a development from parietal (**Mezierea**), via septal (**Baccabegonia, Tetraphila**) to pseudo-axile (**Squamibegonia**). Real axile placentation occurs in the more advanced sections **Scutobegonia, Loasibegonia, Filiticbegonia, Cristasemen, Sexalaria, Augustia** and **Rostrobegonia**. These phylogenetic interpretations conform remarkably with those based on pollen morphology. In the first place the pollen morphology of **Hillebrandia** (**VAN DEN BERG**, 1984) indicates a relationship between this genus and the most primitive pollen types within **Begonia** as found in section **Mezierea**. Furthermore the proposed lines of development towards **Tetraphila** and **Squamibegonia** and the derived condition of the sections showing axile placentation fit in well with the phylogenetic scheme of pollen types.

The karyology of **Begoniaceae** is studied by **ARENDS** who provided the follow-
ing preliminary results (ARENDS, 1985). The chromosomes of Begonia are small (ca 1–2 μm). A limited variation in the number of somatic chromosomes, probably due to accessory chromosomes, has been found between species and sometimes even in one plant. The basic number for the different sections ranges from \( x = 11 \) to \( x = 19 \). It is possible to distinguish a number of groups according to karyotype similarity:

1. **Sexalaria** \((x = 11)\), **Augustia** \((x = 13/14)\), **Rostrobegonia** \((x = 13/19)\). In this group **Sexalaria** seems most advanced.

2. **Mezierea** \((x = 12/13)\), distinct by its symmetrical (primitive?) karyotype.

3. **Baccabegonia, Squamibegonia, Tetraphila** (all with \( x = 18 \)), characterized by karyotypes which are the most asymmetric of African Begonias.

4. **Filikibegonia** \((x = 18)\), **Cristasemen** \((x = 19)\), **Scutobegonia** \((x = 17/19)\), **Loasibegonia** \((x = 16)\), with less asymmetric karyotypes and smaller chromosomes than those of group 3.

The groups recall those based on seed morphology and placentation type but it appears difficult to give a phylogenetic interpretation. The designation of Mezierea as primitive fits in, as has been seen, with pollen-morphological conclusions. A further link between karyology and pollen morphology is to be found in the occurrence of polyploid taxa. The polyploid condition can but need not be expressed in pollen morphology (irregular shape, large size, greater number of apertures). The \( B. \) *squamulosa* -aggregate in *Tetraphila* with \( 2 \times \) and \( 4 \times \) species and cytotypes, showed no deviating type of pollen in the polyploids, contrary to \( B. \) *macrocarpa* (Filikibegonia) where there is a clear distinction between normally developed and aberrant polyploid grains.

The main taxonomical conclusion that can be reached from this comparison of the results of pollen morphology, seed morphology, placentation and karyology is that for the Begonias of the African continent the sections can be considered as natural taxa and useful working-units. They can often be distinguished or at least be grouped together and related to each other in a general phylogenetic scheme.

In the macromorphological characters a number of trends in specialization can be established, leading, for instance, from hygrophytic terrestrials towards mesophytic epiphytes and other growth forms, from woody plants towards herbs, from actinomorphic towards zygomorphic flowers, from 4 or 5 perianth segments towards 2, from fleshy unwinged towards dry, winged fruits, etc. (DE WILLE, 1985a). Most of these trends agree with those noted in, especially, placentation and pollen type and lead to a similar grouping in more and less advanced sections. In the following the main results of pollen morphology with their bearing on taxonomy are summarized.

**Mezierea**: Pollen morphology establishes a link between the African continent and the Madagascan region. The most primitive pollen type within African Begonias (the \( B. \) comorensis-type) also occurs on Madagascar (\( B. \) *cladocarpa*), the Seychelles (\( B. \) *seychellensis*) and the Comores (\( B. \) *comorensis*). On the continent \( B. \) *meyeri-johannis* shows the same pollen type. Pollen-morphologically \( B. \) *
oxyloba is a more derived taxon, not to be equated with either B. seychellensis or B. cladocarpa.

Baccabegonia: B. baccata and B. crateris were removed from section Squamibegonia by De Wilde & Arends (1980) and tentatively referred to section Mezierea. Their pollen type is certainly closely related to the B. comorensis-type of section Mezierea but since it can be distinguished from it, the establishment of a new section Baccabegonia for these two species (Reitsma, 1985b) seems warranted.

Squamibegonia: De Wilde & Arends (1980) admitted only three species to this section. Bouman & De Lange (1982) agreed with this concept on the basis of seed morphology which is similar for the three species and different from all other African sections. The pollen-morphological situation is somewhat more complex. B. bonus-henricus possesses pollen which is much smaller than that of the other two species but is probably closely related to B. poculifera. All three species have pollen with a mostly rather narrow margo and there is a general resemblance to the more derived types of section Tetraphila. Within B. ampla two types occur: one which resembles that of B. poculifera and a second characterized by protruding endoapertures. This latter type occurs on the islands São Tomé and Annobon. Intriguingly, De Wilde & Arends (1980, p. 389) noted the occurrence of aberrant specimens of B. ampla on these islands, ‘missing the diagnostic stellate of indumentum’. Unfortunately, pollen of these specimens was not available. The B. ampla-type occurs in specimens which De Wilde & Arends designate as intermediates between aberrant and typical individuals and thus does not seem to coincide with the aberrant island populations.

Tetraphila: This large section, containing more than 30 species, is the most heterogeneous section in its pollen morphology. At least three evolutionary levels can be distinguished in the pollen types:

1) an only slightly advanced type, the B. eminii-type, which closely resembles the B. oxyloba-type, rather small grains without margo and with only faint costae. It is characteristic for a large number of species (names): B. alepensis, B. ealensis, B. eminii, B. epiphytica, B. excelsa, B. furfuracea, B. fusialata, B. horticolata, B. loranthoides, B. macambrarensis, B. macrostyla, B. mannii, B. molleri, B. ndongensis, B. poggei, B. subalpestris and B. tatoniana. These results corroborate a number of established and assumed synonymies;

2) an intermediate type, the B. komoensis-type, more advanced, prolate, somewhat larger, and in possession of a margo, but with a relatively small endoaperture and only faint costae. B. kisuluana, B. komoensis, B. nicolai-hallet, B. sessilanthera, B. subscutata and B. zobiensis can be placed in this type;

3) two advanced pollen types, one characteristic for the members of the B. squamulosa-aggregate, the other for a large number of species (names): B. buchholzii, B. capillipes, B. cavallyensis, B. ebolowensis, B. fusicarpa, B. jussiaeicarpa, B. lethomasiae, B. oxyanthera, B. polygonoides, B. preussii, B. sanjeensis, B. rhip-
It should be noted that as regards pollen morphology these four sections *Mezierea, Baccabegonia, Squamibegonia* and *Tetraphila*, which are often placed together by the other disciplines, do not constitute a homogeneous unity. There is a large pollen-morphological variation. Sections *Mezierea* and *Baccabegonia* are clearly closely related. *Mezierea* is linked to *Tetraphila* through the similar *B. oxyloba*- and *B. eminii*-types. The position of section *Squamibegonia* is less clear.

*Augustia/Rostrobegonia/Sexalaria*: In their pollen morphology these three sections do show some variation but this falls within the variability of one pollen type with the exception of the monotypic section *Sexalaria*, whose species *B. annobonensis* possesses a pollen type of its own. The pollen grains of some representatives of *Rostrobegonia* are somewhat smaller than those of *Augustia*. Macromorphological taxonomy tends to consider these sections as one group. Pollen morphology agrees with this as far as the sections *Augustia* and *Rostrobegonia* are concerned. Both pollen morphology and macromorphological taxonomy designate these sections as derived.

*Scutobegonia*: A large section, the taxonomy of which presents many problems. Most species can be accommodated in the *B. quadrialata*-type which shows the characteristic concave sides and narrow, extremely lateral endoaperture. All pollen of the species of the section *Scutobegonia* lack a margo. Variability is high, even within specimens, a feature which may be associated with recent speciation, which also led to a high degree of endemism.

*Loasibegonia*: The few taxa of this section cannot on pollen-morphological grounds be separated from *Scutobegonia*. It seems appropriate to treat *Loasibegonia* and *Scutobegonia* as one group. *B. thomeana* is removed from this section (De Wilde, 1985b) and accommodated in a new section: *Cristasemen* (see below).

*Filicibegonia*: A number of species which were formerly accommodated in section *Scutobegonia* (series *Longicaules*) should probably be assigned to section *Filicibegonia*, which so far consisted only of *B. asplenifolia*. This supposition of Dr. J. J. F. E. De Wilde is corroborated by seed morphology (Bouman & De Lange, pers. comm.). Pollen morphology also points to a relationship of most of the species mentioned by De Wilde to *B. asplenifolia*: *B. elatostemoides*, *B. filicifolia*, *B. gossweileri*, *B. latistipula*, *B. macrocarpa*, *B. minutifolia*, *B. sciaphila* and *B. sessilifolia*. This group of species is characterized by rather small pollen with straight sides and rounded poles, and a relatively large endoaperture.

*Cristasemen*: Formerly assigned to section *Loasibegonia*, the species *B. tho-
meana deviates in a number of characters from this, and also from all other sections (cf. DE WILDE, 1985b). Its isolated position is supported by pollen morphology (unique combination of small size and + spheroidal P/E ratio with the presence of a margo).

Finally, the pollen types of the other genera of the Begoniaceae may be mentioned. As stated above (cf. the remarks on placentation) the pollen morphology of *Hillebrandia sandwicensis* points to an affinity with the most primitive type of the African *Begonias* as found in *Mezierea*. *Symbegonia*, on the other hand, shows a remarkable pollen type, quite different from all other *Begoniaceae* (VAN DEN BERG, 1984). This type is certainly derived. In the taxonomist's view (DE WILDE, 1985a) there is also no doubt about the derived status of *Symbegonia* but it is deemed preferable to assign the taxon the rank of section. The difference in pollen morphology is so profound, however, that the generic rank of *Symbegonia* seems well warranted.
6. PHYTOGEOGRAPHY AND ECOLOGY

When morphological, phylogenetic, and geographical data are used to support one another, the validity of the conclusions regarding direction of migration depends upon the validity of the morphological criteria employed.

S. A. Cain (1944, p. 206)

6.1. INTRODUCTION

Data on plant distribution can contribute to the understanding of the history of a group. The present-day distribution reflects the phylogeny of the taxa. The main aspects of interest are the centre of origin of a group and the pathways of migration followed by the taxa. In order to use phytogeographical data for phylogenetic considerations, apart from the relevant distributional data, a theory about the relationships among the taxa which is not itself based on the distributional data, should be available. As was discussed in chapter 5 such a theory may be deduced from pollen-morphological data. The relation between geographical distribution and the occurrence of pollen types can be used to deduce the course of evolution of a group.

Several authors have commented on the use of distributional data in relation to pollen morphology, a.o.: Muller (1970, p. 55), Punt (1975, p. 62), Hideux & Ferguson (1976, p. 346), Le Thomas (1981, p. 21). Furthermore, there is an abundance of literature about the principles of plant geography, and especially the concept 'centre of origin' has been the subject of much thought and hypothesis, often leading to conflicting statements. The very concept of centre of origin has been criticized (cf. Cain, 1944, p. 186). From the phylogeneticist's point of view two assumptions must be made, at least if one wants to concur Hennig's 'Progression Rule' (cf. Wiley, 1981, p. 152, 288):

1) a centre of origin existed from which migration took place,
2) this migration was accompanied by speciation.

The criteria which should be used to indicate an area as a centre of origin have been much debated. For instance, about the problem where the primitive forms of a group might be expected to be located, two diametrically opposed views have been put forward (Cain, 1944, p. 196):

a) the most primitive members of a group are still to be found at or near the centre of origin of a group, or:
b) they are to be found at the periphery of the area because they have been crowded from the centre by younger members of the group.

Other criteria include the location of the largest diversity and of the greatest number of individuals, species or higher categories. All these rules of thumb
have their exceptions and especially the possibility of the occurrence of secondary centres of speciation and migration complicates these matters. Still, the following general statements about the relation between degree of derivation and geographical distribution seem reasonable:
- primitive types are expected to occur in the original area, derived types will occur outside the original range, especially in the peripheral ranges of the area (WILEY, 1981, p. 152)
- primitive types are relatively widely distributed, derived types are often restricted to particular geographic regions, isolated at the periphery of the total geographic area or endemic in some other way (MULLER, 1970, p. 551)
- assumed centres of origin may instead be locations which ‘have suffered the least disturbance during the past 50 to 100 million years, and so have preserved the highest proportion of archaic forms in an essentially unchanged condition’: the museum-hypothesis (STEBBINS, 1974, p. 166)
- ‘... a genus may show a center of development (where there are many species) that is far removed from the center of origin of the genus. A young genus in expanding its area may encounter a region of varied habitats in which the process of speciation (adaptive radiation) may occur extensively’ (CAIN, 1944, p. 176).

The several predictions made by these theoretical considerations must be tested by the actual distribution patterns of the pollen types in relation to their evolutionary level. As will be shown, the phylogenetic interpretation of pollen morphology combined with distributional data can in fact give rise to a hypothesis of the history of the genus on the African continent. This history is an element of a larger course of events: the origin and evolution of the family Begoniaceae, which will be discussed first.

6.2. HISTORY OF THE FAMILY

As fossil evidence is lacking, the time of origin of the Begoniaceae cannot be pin-pointed. The distribution of the family (South America, Africa, Madagascar, India, South-east Asia) suggests an origin before the Gondwana continent split up (ca 100 m.y. B.P., cf. RAVEN & AXELROD, 1974, whose outline of geological events is followed here) or at least before contact between these continents became impossible. Angiosperms had, at that time, only been in existence for the relatively short period of 25–30 million years and an advanced family like the Begoniaceae will not have been among the first to arise. Still, short of trying to explain the present day distribution mainly by long distance transport, a stock of ‘pre-Begonias’ which originated in presumably, west-Gondwana land (South America + Africa) and was able to provide all continents-to-be (except Australia) with representatives, must be hypothesized. After the separation of South America from Africa these continents remained in near contact until at least 90 m.y. B.P., while by the late Cretaceous (ca 65 m.y. B.P.), when the distance had grown to 160 km, they were still linked by numerous islands (RAVEN &
AXELROD, 1974, GREY-WILSON, 1980). It seems thus probable that the family existed at the time that it was still possible to migrate between continents. The position of Antarctica between Africa and Australia seems to have precluded migration towards this latter continent.

Within the Gondwana continent Africa is the most likely place of origin. Although the African continent is relatively poor in Begonia species, the variation, especially in evolutionary level, seems largest. The most primitive forms of, for instance, placentation and pollen type, are found here. In their placentation – a character of which the parietal condition may be interpreted as primitive compared to the derived axial type (REITSMA, 1984, 1985a) – almost all Begonias occurring outside Africa show this derived axial condition (only one Asiatic section, Coelocentrum Irmsch., shows parietal placentation). On the African continent both types occur. The pollen-morphologically most primitive African section, Mezierea, is the only one with representatives both on the continent and on Madagascar, the Seychelles and the Comores. In fact, the B. comorensis pollen type is considered in this study as the most primitive type within Begonia. Pollen morphology would thus indicate a centre of origin comprising the land mass which later formed the islands of the Seychelles and Comores, Madagascar and East Africa.

![FIG. 6.1. A reconstruction of Laurasia and Gondwanaland, ca 100 million years B.P. (after Smith, Briden & Drewry, 1973) with the approximate present-day distribution of the Begoniaceae (after Heywood, 1978)](image-url)
South America will have been colonized from the east while direct migration was still possible. From there the genus managed to reach Central America and even the southwesternmost region of North America, probably in Eocene time or subsequently (RAVEN & AXELROD, 1974, p. 627). Other representatives invaded India and, travelling along with the northward motion of this continent, reached Asia (45 m.y. B.P.). Even more recent will have been the migration of Asian plants into Australasia and it is significant that Begonias do occur in New Guinea but have not reached Australia, while pollen morphology indicates that the genus Symbegonia, which occurs on New Guinea, possesses an extremely derived pollen type (VAN DEN BERG, 1984).

Within each continent local developments took place in ecological requirements coupled with the invasion of new habitats and the emergence of a wide spectrum of morphological diversity.

This view of the history of the family, a diverging development with Africa as the most probable centre, seems to provide a reasonable explanation for the recent distribution pattern, with one notable exception: Hillebrandia. This monotypic genus constitutes a very primitive Begoniaceae. Both macromorphological evidence (GAUTHIER, 1959, REITSMA, 1984) and pollen morphology (VAN DEN BERG, 1984) corroborate this. The occurrence of this genus on islands of the Hawaii archipelago is an enigma. Although opinions about the age of these islands differ, they are probably very recent and in view of their distance to the closest continental land mass were colonized through long-distance dispersal. For Begoniaceae the most probable source area would be South America where, however, no Begonia species have been found so far, that could one way or another be related to the primitive Hillebrandia. Hillebrandia is the only representative of the Begoniaceae occurring on these islands and it is hard to understand how and when it arrived there.

6.3. DISTRIBUTION PATTERNS

A pollen type may be characteristic for one species, more often for a group of species which may or may not coincide with the recognized sections. In investigating to what extent the phylogenetic interpretation of the pollen-morphological data is in accordance with the geographical data, a survey of the distribution patterns of, in first instance, the sections is most usable. The geographical data on which this paragraph is based were provided by J. M. REITSMA who prepared provisional maps of the distributions of all African species and sections.

Except for the small sections with restricted areas (Baccabegonia, Cristasemen, Sexalaria), there exists a large overlap in distribution area for most of the sections. Only the species of the sections Augustia and Rostrobegonia display a preference for drier and more open regions and thus avoid the main distribution areas occupied by species of the sections Tetraphila, Squamibegonia, Scutobegonia (including Loasibegonia) and Filicibegonia. For convenience sake Africa and Madagascar may be divided in a number of geographic regions (see Fig. 6.2.).
TABLE 2. Distribution of the sections of the genus *Begonia* in Africa and Madagascar.

1. Upper Guinea: from Guinea-Bissau to Dahomey
2. Gulf of Guinea: Principe, São Tomé, Annobon
3. Lower Guinea: Nigeria, Fernando Po, Cameroun, Gabon, Congo (Brazzaville) plus Cabinda
4. Central Africa: Zaire, Rwanda, Burundi, Uganda
5. East Africa: Kenya, Tanzania, N. Mozambique
6. Angola: Angola minus Cabinda
7. South-east Africa: Natal, S. Mozambique
8. Madagascan region: Madagascar, Seychelles, Comores

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Fig. 6.2. Geographic regions.

The distribution of the sections over these regions is given in Table 2. (X = main distribution, x = peripheral occurrence).

It should be noted that these regions are not to be compared with phytochoria as circumscribed by White (1979). They are only used here to show the differences in area between the sections in a convenient way. Furthermore, region no. 8 is much richer in Begonia but the non-African species and sections have not been treated in detail in this study.

As shown in Table 2 there is only one section, Mezierea, which is found both on the African continent and in the Madagascan region. This section contains the most primitive pollen type encountered in this study: the B. comorensis-type, which is also characteristic for B. meyeri-johannis which grows in East Africa. Furthermore, B. oxyloba, which possesses a slightly more derived pollen type, is one of the few species with an east to west distribution. These data suggest a centre of origin in the area formerly made up out of Madagascar, the Comores and the Seychelles, and a westward migration leading to the widespread distribution as shown by B. oxyloba.

The Lower Guinea region, especially Cameroun and Gabon, shows a high density in the number of species and a high percentage of endemics. This area can be interpreted as a secondary centre from which a diverging development took place leading to several relatively derived sections. The increasing drought which occurred at the close of the Oligocene and caused a substantial impoverishment of the African flora (Raven & Axelrod, 1974, p. 607 ff.) will have led to a shrinking of the areas of distribution, which was followed by a renewed dispersion from any secondary centre where the taxa had managed to survive, when conditions improved again. The distribution of the sections Tetraphila, Squamibegonia, Scotobegonia (including Loasibegonia) and Filicibegonia, all reflect this diverging development from the secondary centre(s) towards the adjacent areas of dense tropical forest. Pollen-morphologically these sections are rather uniform except section Tetraphila, where a relation between derived pollen type and a more peripheral distribution can be noted: the less advanced type, pollen-morphologically closely related to the B. oxyloba-type, shows a large overlap with the area occupied by B. oxyloba, while representatives of a more derived pollen type of section Tetraphila such as the B. cavallyensis-type show a distribution extending into or even confined to Upper Guinea, which can be considered as a more peripheral distribution. There is a striking agreement in the distributional history of Begonia and that of Impatiens in Africa (cf. Grey-Wilson, 1980). This genus also shows many endemics in the area of Cameroun and Gabon where it probably survived the period of aridity in the moister areas of the montane forest regions. ‘Most species are typical of the hygrophytic flora of the continent, frequently associated with plants like Begonias, Dorstenias and Streptocarpus’, (Grey-Wilson, 1980, p. 43).

The areas occupied by the sections Augustia (mainly eastern and southern regions) and Rostrobegonia (as Augustia, but with B. rostrata as a western representative in Angola and up into Upper Guinea) point to the different character
of these sections. They constitute no doubt derived taxa (as is clear from pollen morphology) but their relation with the here hypothesized primary and secondary centres of origin, is not clear.

A number of sections shows a very restricted area of distribution (Baccabegonia, Cristasemen, Sexalaria). The members of such geographically restricted sections may represent either derived endemics or taxa which have retained primitive conditions due to their isolation in a relatively stable environment (museum-hypothesis, STEBBINS, 1974). Especially the species of section Baccabegonia suggest this latter alternative in their pollen type which is undoubtedly primitive and rather closely related to that of the primitive representatives of section Mezierea. Still, the occurrence of B. baccata and B. crateris on the island of São Tomé, which probably has not been in existence very long, presents another problem similar to that of Hillebrandia on the Hawaiian archipelago.

In the other, more widespread sections, often a high percentage of endemics is present. Especially in Scutobegonia numerous species occupy only small areas. 'The degree of endemism suggests active recent evolution' (GREY-WILSON, 1980, p. 37) and this may well be the case in this and other sections where species are difficult to circumscribe and may be members of species-aggregates. This is reflected in pollen morphology by a large but inconstant variability.

In summary, the migration pathways of Begonia on the African continent can be hypothesized as follows:

After the origin of primitive, Mezierea-like Begonias in the East African/Madagascan region, the continent was colonized from east to west. Following the establishment in the Cameroun/Gabon area and the colonization of the West-african islands, new evolutionary developments occurred radiating out of this secondary centre, resulting in several more derived sections. A number of taxa extended their area towards Upper Guinea. About the phytogeographical history of sections Augustia and Rostrobegonia nothing definite can be said.

6.4. Ecology

A relation between ecology and pollen type is hardly present or, if it is, it can hardly be discerned. Although African Begonias can occupy rather diverse habitats, this difference in environmental requirements is not expressed clearly in pollen morphology. Generally, Begonias prefer moist (semi-)shaded places, be it dense tropical forest or high rainfall montane areas. On the other hand, the representatives of the sections Augustia, Sexalaria and Rostrobegonia prefer drier and more open habitats. There is a large variety in growth forms: epiphytes (sections Tetraphila and Squamibegonia), therophytes (section Sexalaria), creepers with stolons (members of the B. squamulosa-aggregate), subxerophytes with underground tubers (sections Augustia and Rostrobegonia), rootclimbers (section Cristasemen) and even a liana (B. meyeri-johannis). In fact two groups of African Begonias can be recognized (DE WILDE, 1985a):

1) a group showing a strong specialization towards an epiphytic habit of growth,
with fleshy fruits without wings and probably zoochorous, and
2) a group of terrestrials with dry, winged fruits specialized for anemochory
(with the exception of section Scutobegonia which has small seeds, probably
dispersed by animals (epizoochory).

It is significant that through convergence the pollen types of such widely dif-
ferent sections as Tetraphila and Augustia are closely alike. This might reflect
the more exposed conditions shared by, on the one hand, epiphytes in trees which
would be more subject to dry periods compared with Begonias growing on the
protected forest floor (cf. Haussler, 1983) and, on the other hand, the plants
preferring drier and more open habitats. The possession of a rather broad margo
by both of these types might be considered as a functional adaptation if the
margo could be interpreted as an extension of the colpus membrane, thus facili-
tating the invaginating of the colpi by which loss of water may be minimized
(as was suggested to the author by Dr. J. Muller, pers. comm.). In this connec-
tion the lack of a margo in section Scutobegonia may be understood, since the
representatives of this section grow in humid conditions, preferably along
streams.

However, in other cases the relation between pollen-morphological characters
and environment is non too clear and further conclusions about lines of develop-
ment and ecology can hardly be drawn.

APPENDICES

Appendix 1: Pollen of Madagascan Begonias Plate 14

Attention to the Begonias of Madagascar was drawn by the presence in the
herbarium at Wageningen of specimens of B. cladocarpa Baker, B. comorensis
A.DC. ex Warb. and B. seychellensis Hemsley, species which occur on Madagas-
car and the Comores and Seychelles respectively, and belong to section Mezier-
ea. Among these, B. seychellensis was recently reduced to a synonym of B. comor-
ensis by Keraudren-Aymonin (1983). Mezierea is the only section found on
both Madagascar and the African continent. Four other sections, all endemic
to Madagascar, are recognized: Erminea A.DC., Nerviplacentaria A.DC., Quad-
rilobaria A.DC. and Muscibegonia A.DC. The relation between these sections
and those on the African continent is not clear and M. Keraudren-Aymonin,
having studied the 52 Begonia species of Madagascar (Keraudren-Aymonin,
1983), decided not to consider a classification in sections.

Keraudren-Aymonin also investigated the pollen of a number of species with
the scanning electron microscope. She concluded that taxonomically significant
characters were lacking (op. cit. p. 11: 'Quelques espèces ont été analysées; l'or-
nementation de l'exine a semblé très homogène.'). The present author could
examine both the results of the SEM study of Keraudren-Aymonin and pollen
material sampled from 16 specimens in the Laboratoire de Phanérogame, Muse-

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um National d’Histoire Naturelle in Paris. Dr. G. G. Aymonin is gratefully acknowledged for his help in providing the micrographs and the samples.

Pollen of about half of the 52 species recognized in the Flore de Madagascar et des Comores (Keraudren-Aymonin, 1983) has been examined.

Specimens examined by the author: B. androrangensis Humbert – P. Morat 2830 (P); B. ankaranensis Humbert – Cours 5456 (P); B. antisiranensis Aymonin & Bosser – Bosser 20165 (P) isotype; B. baronii Baker – Perrier de la Bathie 12365 (P); B. bogneri Ziesenh. – Van Veldhuizen 475 (WAG); B. boiviniana A.DC. – Boivin 37 (P); B. comorensis A.DC. ex Warb. – Jard. Bot. Tan. 73 (P); B. coursii Humbert ex Keraudren – Humbert & Cours 23890 (P) isotype; B. goudotii A.DC. – Perrier de la Bathie 6664 (P); B. heteropoda Baker – Perrier de la Bathie 6677 (P); B. humbertii Humbert – Humbert 23126 (P); B. isalensis Humbert – Humbert 28741 (P); B. lyallii A.DC. – Humbert 23272 (P); Bégué 22 (P); B. marojejyensis Humbert – Jard. Bot. Tan. 9, 10 (P); B. nossibea A.DC. – Hildebrandt 2995 (G), Bosser 20129 (P); B. tsaratananensis Aymonin & Bosser – Humbert & Capuron 24886 (P).

The following species have been studied with SEM (cf. plate 14): B. baronii, B. bogneri, B. comorensis, B. goudotii, B. heteropoda, B. nossibea.


The pollen grains of the investigated Madagascan Begonias are generally rather small, with a P ranging from 18 to 22 µm, rarely exceeding 24 µm, and a E of 10–12 µm. An exception is B. bogneri which shows rather large grains (P 25–27 µm). The shape is mostly prolate/perprolate (P/E ratio 2.0), sometimes more spheroidal (B. comorensis, B. coursii). The outline in equatorial view is more or less elliptical with convex sides except in B. bogneri which shows concave grains. In polar view the outline is always more or less circular. All grains belong to the 3-zono-colporate pollen class, the colpi never anastomose at the poles. The margins of the colpi can be either straight or show a distinct equatorial constriction (B. antisiranensis, B. boiviniana, B. goudotii, B. heteropoda, B. isalensis, B. tsaratanensis). The lalongate endoapertures are elliptical in outline and mostly rather distinct. Costae are present in most cases. The striate ornamentation is similar in all species and fully comparable with that of the pollen grains of African Begonias. It is striking, however, that in the pollen of Madagascan Begonias a margo is never encountered.

The rather small size, the absence of a margo and of syncolpate grains, point
to a relatively low evolutionary level, comparable with that reached on the African continent by the *B. oxyloba*- and *B. eminii*-types. Derived types like the large perprolate grains with margo along the colpi as encountered in the more derived species of sections *Tetraphila, Augusta, Squamibegonia* etc. have not been found among the Madagascan *Begonias*.

The classification in, apart from *Mezierea*, four Madagascan sections, is not supported by pollen morphology. There are no distinct groups conforming to the recognized sections *Erminea, Quadrilobaria, Nerviplacentaria* and *Muscibegonia*. Despite the existence of a certain variability among the pollen of the examined species, it seems prematurely to establish pollen types. This should await further research. Here it is only noted that the relative primitiveness in pollen morphology of the Madagascan *Begonias* fits rather well into the pollen-morphological evolutionary hypotheses as expounded in chapter 5 and 6.

Appendix 2: Pollen characteristics of the Datisaceae

Many authors consider the families *Begoniaceae* and *Datisaceae* as rather closely related. They belong to the order *Violales* in the system of Cronquist (1968) or even constitute an order *Begionales* (*Datiscales*) according to Takhtajan (1969). The recent ‘Compendium van de Spermatophyta’ (Stoffers (ed.), 1982) points to the similarity in ovule, embryo, fruit and pollen grains. The information on pollen morphology will probably have been derived from Erdtman (1952) who states (p. 70):

‘The pollen grains in *Begoniaceae* are ± similar to those in *Datisaceae* (cf. apertures, size, etc.; also in the occurrence of tetrads in *Datisca* (....))’.

In the course of the study of the pollen of the *Begonias* of Africa, material of a few specimens of the *Datisaceae* - which is a small family consisting of three genera with a total of four species - became available. A comparison between the pollen grains of both families was suggested by Dr. F. Bouman (Hugo de Vries Laboratory, University of Amsterdam) who in his work on seed morphology had also noted a resemblance in this character (Bouman & De Lange, 1983, p. 78; cf. also Boeseewinkel & De Lange, 1983, p. 424). Dr. Bouman is also acknowledged here for providing part of the material used for the analysis.

The following specimens were examined: *Datisca cannabina* L. – culta Hortus Botanicus (Univ. of Amsterdam), *Hohenack 776* (WAG); *Datisca glomerata* (Presl.) B. & H. – *Heller 1902* (L); *Octomeles sumatrana* Miq. – *Schram 2930* (L); *Tetrameles nudiflora* R.Br. – *Koorders 14047 β* (WAG).

Both species of *Datisca* possess the same pollen type, distinct from that of the other genera. The following provisional description of the pollen of the *Datisaceae* is based mainly on light microscopic observations.

The grains are rather small, with \( P \) ranging from 12 to 20 \( \mu m \) and \( E \) from 10 to 17 \( \mu m \). Their \( P/E \) ratio is mostly prolate spheroidal or subprolate in *Datisca* and *Tetrameles*. In *Octomeles* distinctly oblate grains also occur. In polar view
Datisca and Tetrameles show rounded triangular grains with convex sides, those of Octomeles are triangular with straight sides. All three genera possess 3-colporate grains with long colpi, which never anastomose. The margins of the colpi are straight, the colpus is distinctly sunken in Datisca and only slightly sunken in Tetrameles and Octomeles. The outline of the endoaperture is always very indistinct and, when discernable, irregular. In Datisca a rather large endoaperture area with multiple endoapertures as defined by Verbeek-Reuvers (1978) is present. Costae do not occur.

The sculpture of the exine is verrucate in Datisca, psilate in Tetrameles and Octomeles (plate 15, fig. 2 and 3). Numerous perforations occur in all grains. The pollen wall is ca 1 μm thick and shows in Datisca and Tetrameles a well developed columellae-layer (plate 15, fig. 1), which is less clear in Octomeles.

As can be gathered from the descriptions and plate 15, the similarity between the pollen grains of Datiscaeae and Begoniaceae is not all that evident. They all belong to the same 3-zono-colporate pollen class but differ in P/E, ornamentation and wall structure. The verrucate exine sculpture of the Datisca species and the psilate surface of Tetrameles and Octomeles pollen grains do not occur in Begonia and, especially the wall structure of Datisca, with its clearly defined columellae-layer differs widely from the much thinner exine with reduced infratectal layer of Begonia. The endoapertures are indistinct and irregular in Datiscaeae and show no costae as in most species of Begonia. Finally, the oblate P/E ratio of Octomeles pollen grains is never encountered in Begonia.

It must be concluded that the close relationship between the families is not corroborated by pollen morphology.
PLATE 15 TEM: 1. Datisca cannabina L. (cultu Hort. Bot. Amsterdam), cross-section, 8000x; SEM:
2. Datisca cannabina L. (Hohenack 776), polar view, ca 2670x; 3. Octomeles sumatrana Miq. (Schram 2930), polar view, ca 2670x.

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SUMMARY

The morphology of the pollen grains of African *Begonias* is described, leading to the recognition of 15 pollen types. These pollen types are assumed to constitute natural units produced by evolution and the main purpose of this study has been to reconstruct the course of evolution and to apply the resulting insights to the various taxonomical problems. It has been attempted to formulate a critical approach to the problem of applying pollen-morphological data to phylogenetic reconstruction. The evidence from pollen morphology is compared with that from other disciplines, viz. seed morphology, the study of placentation types, karyology and, especially, macromorphological taxonomy. The relation between pollen morphology and geographical distribution is discussed, while the pollen morphology of Madagascan *Begonias* as well as of the allegedly related family of the *Datiscaceae* is also investigated.

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J. v. d Walle 2845 (1)
Wellens 410 (15)
Welwitsch 874 (13)
Whyte s.n. (15)
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J. J. de Wilde 7471 (15); 7486 (7); 7499 (5); 7551 (6); 7909 A (15); 8119 (5); 8267 A, 8364, 8365 (7); 8404 (9); 8662 (9); 8722 (14); 8765 (8)
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BEGONIA SECTION BACCABEGONIA
REITSMA, SECT. NOV.

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1. INTRODUCTION

Warburg (1894) arranged the continental African Begoniaceae into 9 sections. Ever since, students in Begoniaceae disputed this classification, among whom IRMSCHER (1961) and HALLÉ (1967). However, apart from minor corrections and suggestions Warburg's arrangement has not been changed fundamentally, and stands up till now. In the course of the study of B. baccata and B. crateris we found that it is not warranted to accommodate these two species in any of the sections known at present. Accordingly, the creation of a new section was found necessary (see 2.2). Thus, the new section Cristasemen De Wilde (this issue) included, the number of African sections is raised to 11.

2. CIRCUMSCRIPTION OF BEGONIA
SECTION BACCABEGONIA REITSMA

2.1. LATIN DESCRIPTION OF THE NEW SECTION

Type species: B. baccata Hook.f.

Plantae paulo ramosae monoecae fruticosae usque 4 m altae. Indumentum quoad densitatem variabile, pilis sessilibus squamiformibus vel dentatis vel stellatis formatum. Stipulae deciduae naviformes, exteriores cuiusque paris in parte superiori carinatae. Folia longe petiolata, basi profunde cordata usque peltata, apice acute acuminata, margine fere integra, saepe maxima.


2.2. TAXONOMIC POSITION AND RELATION TO THE OTHER AFRICAN SECTIONS

Warburg (1894: 140) accommodated B. baccata in section Squamibegonia Warb. This was followed by Engler (1921: 614) where, unfortunately, the name
B. baccata was omitted from the text, although the short description: 'Spreiten von 2-3 dm Durchmesser, mit kurzer Spitze, auf San Thomé', leaves no doubt about the identity of the species meant. From Fig. 262 E in IRMSchER (1925: 565) it might be concluded that this author placed B. baccata in section Squamibegonia as well. DE WILDE and ARENDS (1980) presented arguments to exclude B. baccata and B. crateris from section Squamibegonia and, hesitatingly, referred both species to section Mezierea (Gaud.) Warb. This opinion was already expressed by BARKLEY (1972) without any further discussion.

Considering the characters of the ovaries and fruits of both species it is clear that they show affinities to the sections Mezierea, Squamibegonia and Tetraphila A. DC., all characterized by exalate ovaries and fundamentally parietal placentation, as was demonstrated by REITSMA (1984); the remaining continental sections show axile placentation and, as a rule, alate ovaries. Confronted with the question where to accommodate the two present species within the three sections mentioned, it became clear that none of them justified such an attribution. This led to the concept of a new section Baccabegonia. In Table 1 some major characters are listed allowing differentiation among the four sections.

Regarding pollen morphology the section Baccabegonia has a rather isolated position. Its pollen may be readily distinguished from that of the other African sections. Major affinities are with the primitive pollen type found within section Mezierea (VAN DEN BERG, 1985).

Micromorphology of the seed-coat was studied by DE LANGE (see 4.).

The somatic chromosome number for B. baccata and B. crateris varies from

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**Table 1. Important characters to discriminate the sections Baccabegonia, Mezierea, Squamibegonia and Tetraphila.**

<table>
<thead>
<tr>
<th></th>
<th>Baccabegonia</th>
<th>Mezierea</th>
<th>Squamibegonia</th>
<th>Tetraphila</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of perianth</td>
<td>♀ flowers: 2</td>
<td>♀ flowers: 2</td>
<td>♀ flowers: 2</td>
<td>♀ flowers: 4</td>
</tr>
<tr>
<td>segments</td>
<td>♂ flowers: 2</td>
<td>♂ flowers: 2, 4</td>
<td>♂ flowers: 2</td>
<td>♂ flowers: 4</td>
</tr>
<tr>
<td>Shape of ovary</td>
<td>globose</td>
<td>ellipsoid</td>
<td>obovoid</td>
<td>fusiform</td>
</tr>
<tr>
<td>Placentation*</td>
<td>septal; 4 placenta per locule</td>
<td>parietal</td>
<td>(pseudo-)axile</td>
<td>usually septal: 2 placenta per locule</td>
</tr>
<tr>
<td>Number of ovules*</td>
<td>250–300</td>
<td>80–100</td>
<td>110–115</td>
<td>4–56</td>
</tr>
<tr>
<td>per cross-section</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fruits</td>
<td>dehiscent</td>
<td>indehiscent</td>
<td>indehiscent</td>
<td>dehiscent</td>
</tr>
<tr>
<td>Somatic chromosome</td>
<td>36 (+ 1 or 2)</td>
<td>24, 48</td>
<td>36 (+ 1 or 2)</td>
<td>36 (+ 1 or 2)</td>
</tr>
<tr>
<td>numbers**</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* See REITSMA, 1984.
** See DE WILDE & ARENDS, 1980: p. 416–420 (Squamibegonia); ARENDS, unpublished (Baccabegonia, Mezierea, Tetraphila).
2n = 37 to 38. This variation in the number may be attributed to the presence of 1 or 2 accessory chromosomes. The somatic karyotypes of the two species are very similar. Hence they cannot be distinguished by their chromosomes. The total somatic chromosome length varies from 29 to 35 μm for the cells of which the chromosomes could be measured. When the karyotypes of the species of the section Baccabegonia are compared with those found in other African Begonia species, they are most similar to those observed for the species of the section Squamibegonia (ARENDS, pers. comm.).

In our judgment the macromorphological characters of section Baccabegonia point to a strong affinity with section Squamibegonia. Other differential characters besides the fruit and placentation characters listed in Table 1, are the considerable lengthening of the inflorescence-axes, the absence of a perianth-tube in the female flowers of section Baccabegonia and, moreover, the absence of bracts which envelop the inflorescence and are persistent in the infructescence of section Squamibegonia. In combination these characters, in our opinion, delimitate the section Baccabegonia proposed here and justify its status among the other African sections.

3. THE SPECIES B. BACCATA HOOK. F. AND B. CRATERIS EXELL.

3.1. HISTORY AND TAXONOMY

B. baccata was validly published by J. D. Hooker in 1866. The description is accompanied by a coloured plate, which erroneously shows unisexual inflorescences. In a description of this species by the same author in the Flora of Tropical Africa (1871, vol. 2: 573) it is stated that the peduncles (actually the inflorescences!) are unisexual; a comprehensible error as the female flowers do not show when the male flowers are at anthesis, whereas the male flowers are already shed when the female flowers reach anthesis (see also DE WILDE & ARENDS, 1980: 381).

As far as could be traced the first specimen of B. crateris ever collected was discovered by Aug. Chevalier in 1905 (no. 13748). However, it was not until 1944 that it was recognized as a separate taxon and validly published by Exell who based his description on a single collection, viz. Exell no. 224. In the protologue he erroneously used the occurrence of bisexual inflorescences in B. crateris as a character to keep it apart from B. baccata; actually both taxa show this type of inflorescence. As this character appears to be fallacious, the differentiation of both taxa becomes more complicated and, only after considerable consideration, it was decided to maintain their status. Exell, in his protologue to B. crateris, already stated that in the field both species are very similar in appearance. This also holds for plants of both taxa at present in cultivation at the
Department of Horticulture of this University at Wageningen. Here, plants of
_B. crateris_ look duller in general appearance, probably due to the heavier indu-
mentum, as compared to the more shining plants of _B. baccata_. As spatial sepa-
ration in the natural habitat was not obvious (pers. comm. De Wilde and Ar-
ends), mutual gene-flow should not be ruled out. Additional field-work is needed
to clarify pollination biology and to search for possible ecological breeding bar-
rriers and for the occurrence of hybrid populations.

Although Monod (1960: 54) and Ferreira (1965: 533) followed by Barkley
(1972) expressed the opinion that _B. crateris_ is a later synonym of _B. baccata_,
this is not followed here. Use of the combined differential characters (see also
3.2.) simple leads to one of both species, certainly when complete material is
available.

### 3.2. KEY TO THE SPECIES AND SPECIES DESCRIPTIONS

- Plants ferruginously tomentose in almost all parts. Full-grown leaves usually
  peltate. Filaments at least as long as the anthers, usually longer and up to
  $3\frac{1}{2}$ times the anther-length. Pedicels not elongated in fruit . . . . . . . _B. crateris_

- Plants glabrescent, more rarely tomentose. Full-grown leaves deeply cordate.
  Filaments at best as long as the anthers (rarely a few longer), usually shorter.
  Pedicels as a rule considerably elongated in fruit . . . . . . . . . . . _B. baccata_

**Description of _B. baccata_ Hook.f.**

_B. baccata_ Hook.f. in Curt. Bot. Mag. 92, t. 5554. 1866; Hook.f. in Oliver,
O. Warburg in Engl., Nat. Pflanzenfam. 1st ed. 3 (6a): 140, fig. 49E. 1894;
E. Irmscher in Engl., Nat. Pflanzenfam. 2nd ed. 21: fig. 262 E. 1925; A. W.

Holotype: _Mann no. 1087_; K (5 sheets); isotypes in B and P.

Description: Stout, poorly branched shrubby plants, up to 4 m tall, often
rupestral. Stems erect, rarely pendent, woody in the lower part, up to 5 cm diam.;
pale-brown to red, usually squamulose, glabrescent, the herbaceous parts often
loosely covered with a ferruginous indumentum of sitting, scaly, denticulate to
stellate hairs (representing the only type of indumentum occurring on the plant);
the nodes sometimes with adventitious aerial roots. Leaf-scars conspicuous,
about 1–1½ cm diam. Stipules caducous, boat-shaped, in folded position up to
6.5 × 2.5 cm, glabrous or nearly so, the bigger outer one conspicuously keeled
in the upper part. Leaves herbaceous; petioles red to brown, 12–30(–41) cm long,
glabrescent to tomentose; the blade asymmetric, obliquely orbicular to ovate,
especially in the young leaves sometimes (sub-)peltate, 22–40(–50) × 20–40(–50) cm; the upper surface glabrous to glabrescent, the lower surface covered with scattered hairs, more intensely on the nerves; deeply cordate at base, cuspidate to acuminate at apex, acumen up to 3 cm long; margin entire; palmately 7–9-nerved, mostly with 4 prominent nerves, the nerves branching dichotomously. Inflorescences conspicuous, axillary, representing androgynous, dichasial cymes with branches up to the eighth order and counting up to 46 male and 30 female flowers in a single inflorescence; at complete development reaching up to 27 × 34 cm, flowering strictly proterandrous; peduncles 5–13 cm long; the axes elongating in the course of flowering. Bracts of successive order early caducous, arranged in pairs; the two bracts of each pair boat-shaped and unequally sized, the outer one the broadest and overlapping the inner one largely, glabrous. Peduncle and axes of the inflorescence glabrescent to tomentose. Male flower: tepals two, white, broadly ovate, cordate at base, 24–43 × 25–47 mm; androecium fasciculate, stamens (19–)40–100(–116); filaments free, white, (0,2–)0,8–3,0 (–4,2) mm long; anthers yellow, 2,5–3,5 (–3,8) mm long and 0,6–0,8 mm diam., tapering towards the base, opening laterally with two longitudinal slits. Female flower: tepals two, white, orbicular to broadly ovate, slightly cordate at base, 18–37 × 21–43 mm. Styles (4–)5–6(–7), yellow, at their base fused over 1–2 mm, the free parts including the stigmas 5.0–8.5 mm long, horseshoe shaped forked, each arm covered with a continuous, 1,5–2 times spirally twisted, papillose stigmatic band. Ovary (sub-)globose, somewhat urceolate, 7–11 × 8–13 mm, longitudinally shallowly (4–)5–6(–7)-grooved, (4–)5–6 (–7)-locular, covered with scattered hairs or even tomentose; placentation septal, the septiform placentas branching once or often twice resulting in 2–4 ovula-bearing placenta branches per locule. Pedicels (4–)5–13(–21) mm long. Infructescence up to 30 cm long and containing up to 21 fruits; the fruit-bearing stipes (5–)9–30(–34) mm long. Mature fruit glossy, orange-red with white lenticels in vivo, almost glabrous, subglobose, 12–17 × 16–25 mm, baccate, with many seeds, dehiscent; the fleshy pericarp rupturing from the apex towards the base, forming irregular shaped valves, in number more or less corresponding with the number of locules. Seeds yellow-brown, ca 0,5 × 0,25 mm.

Distribution: Endemic on the island of São Tomé (see Map 1). The fact that *B. baccata* has been collected mainly along the coast and above 800 m alt. is probably explained by the very intensive cultivation of the intervening area.

Ecological notes: *B. baccata* is frequently observed growing on rocks, both near the ocean shore and inland along watercourses. It even occurs on walls. The preference for moist conditions is obvious. Its altitudinal range is 0–1500 m, which implies that *B. baccata* is lacking in the highest parts of the real mist forest region extending from 1400–2024 m alt. (Exell, 1944: 16–23). Monod (1960: 50) indicated that it is growing between 800–1750 m, overlooking the lower part of its altitudinal range. Neither Ferreira (1965: 533) nor we found evidence of the occurrence of *B. baccata* above an altitude of 1500 m. As appears
from collectors’ notes this species is often found at forest-edges and in open places in wooded surroundings, for instance secondary forests and old deserted plantations.

**Vernacular name:** fia boba d’obo.

**Specimens examined:** Monte Rosa, Chevalier 14193 (P); Porto Alegre, Chevalier 14208 (P); S. Pedro, Chevalier 13656-bis (P); Monte Café and Pic de São Tomé, Chevalier 14545; 14546 (P); between Nova Moka and Lagôa Amelia, De Wilde, Arends & Groenendijk 105 (WAG); Nova Moka, Espirito Santo 155 (BM, COI, LISJC); Ribeira Peixe, Espirito Santo 3881 (COI, LISC); ibid., Espírito Santo 3898 (LISJC); Juliana de Sousa, Espirito Santo 3965 (LISJC); sin. loc., Espirito Santo 4254 (LISC); Binda, Espirito Santo 4344 (LISC); S. Nicolaou, Espirito Santo 4463 (LISC); Santa Catarina, Espirito Santo 5005 (LISC); Lagôa

**FIG. 1.** Begonia baccata Hook.f. - 1: branch with leaf (upper side) and terminal bud (× 4); 2: part of inflorescence in $\varphi$ flowering stage (× 4); 3: 2 schematically (a: terminal flowers (3) of the dichasium); 4: part of the inflorescence in the $\varphi$ flowering stage (× 4); 5: style, abaxial side (× 5); 6: ovary and pedicel (× 1); 7: peltate hairs, frontal view (× 15); 8: cross section of ovary, ca in the middle (× 3); 9: detail of placenta tissue bearing ovules (× 20); 10: mature fruit with elongated pedicel (× 1); 11: dehisced fruit (× 1); 12: mature seed (× 30); 13: longitudinal section of $\varphi$ flower, schematically (a: dorsal side; ca × 3); 14: stamen with relatively long filament, side view and frontal view (a: dorsal side; × 10); 15: stamen with relatively short filament, side view and frontal view (a: dorsal side; × 10). Material used: 1: Espirito Santo 4463 and Groenendijk 115; 2-3 and 13-15: Groenendijk 131 (spirit mat.); 4-9: Groenendijk 132 (spirit mat.); 10: Groenendijk 71 (spirit mat.); 11-12: De Wilde, Arends and Groenendijk 105 (spirit mat.).

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Amelia, Espírito Santo 5034, 5149, 5150 (LISC); between Bassalar (not localized) and Quija, Espírito Santo 5138 (LISC); between Lagôa Amelia and Esperança, Espírito Santo 5155 (LISC); Vanhulst (Macambrarâ), Exell 184 (BM, BR, COI); Traz-os-Montes, Gama & Pénétra s.n. (COI); ocean shore rocks between Diogo Vaz and Santa Catarina, Groenendijk 7, 65, 115 (WAG); S. Nicolau, 6 km from Monte Café, Groenendijk 9 (WAG); Praia Grande, 5 km S.W. of Ribeira Peixe, Groenendijk 38 (WAG); along a track from St. Adelaide to Zampalma, Groenendijk 66, 67 (WAG); Lagôa Amelia, Groenendijk 71 (WAG); between Binda and Juliana da Sousa, Groenendijk 131, 132 (WAG); sin. loc., Mann 1087 (K: holotype; B, P: isotypes); sin. loc., Mildbraed 3473 (B); sin. loc., Moller 146 (B); Bom Sucesso, Moller 219 (COI); Lagôa Amelia, Monod 11736 (BM, COI); along the Rio Paga Fogo, Rozeira 2151 (COI); between Ermelinda and Cacumbé, Rozeira 2843 (COI); near the border of the Mussacavu, Rozeira 2931 (COI); between the rivers Quija and Chufe Chufe, Rozeira 2971 (COI); S. Manuel, Rozeira 2992 (COI); Monte Palissota (not localized), Rozeira 3136 (COI); Formoso, Rozeira 3246 (COI); Lagôa Amelia, Rozeira 3319 (COI); between Binda and Juliana da Sousa, Rozeira 3346 (COI).

Culta: Department of Horticulture, Agricultural University, Wageningen, The Netherlands, from material sent by Bredero (s.n.), 1977.

**Description of B. crateris Exell**


Type: _Exell no. 224_ (S. Tomé, Lagôa Amelia, on the crater rim, 1480 m; holotype in BM, isotype in COI).

**Description:** _B. baccata_ and _B. crateris_ are very similar in appearance; therefore, in the following description the differential characters are stressed.

Poorly branched shrubby plants, up to 3 m tall, often rupestral. Stems densely ferruginously tomentose as are the petioles, peduncles, axes of the inflorescence, ovaries and fruits. Stipules glabrous. Full-grown leaves usually peltate, more rarely (sub-)cordate; the lower surface especially on the prominent nerves covered with a more or less dense ferruginous indumentum, the upper surface scattered with hairs; in sicco the leaves often greyish-brown and firm (as compared to greenish and more tender in _B. baccata_).

Male flowers containing 32-44 (58) stamens; filaments 3-5 mm long, anthers 1.5—2.5(—3.0) mm long; the length of the filaments and anthers shows within the same flower less variability as compared to _B. baccata_. Female flowers: styles 4-6; ovary 4-6-locular. Pedicels (3—)4—9(—10) mm long, scarcely lengthening and in the fruit 5—11 mm long.

**Distribution:** São Tomé (see Map 1). It is obvious that _B. crateris_ is lacking in the lowest regions of the island; it has never been collected on coastal rocks. All specimens were collected between 900 and 1500 m alt. with one exception.
PHOT. 1. Huge specimen of *B. crateris* Exell (upper half of the phot.) in its natural habitat, in the foreground Miss Liza Groenendijk; surroundings of Lagôa Amelia, São Tomé
(Phot. J. C. Arends).
only, viz. Chevalier 13748 (ca 300 m alt., surroundings of Boa Entrada).

Ecological notes: The absence of B. crateris from the coastal region supports the idea that this species has a clear preference for a constant high humidity of the air as is found in the higher mountainous regions. There, similar to B. baccata, it favours rocky mossy places near watercourses. The mature fruits expose after dehiscence the yellow placenta-tissue (similar to B. baccata), which suggests a zoochorous dispersal.

Specimens examined: Boa Entrada and surroundings, Chevalier 13748 (P); Calvario, Espírito Santo 5060, 5064, 5066, 5067, 5069 (IISC); Lagōa Amelia, crater rim, Exell 224 (BM: holotype; COI: isotype); ibid., Groenendijk 72 (WAG); along track from Lagōa Amelia to Pico Calvario, Groenendijk 107 (WAG); Lagōa Amelia, Monod 11786 (BM); Calvario, Monod 11819 (BM, COI); sin. loc., Monod 11820 (BM, COI); Traz-os-Montes, Calvario, Rozeira 573 (COI); Lagōa Amelia, Rozeira 3276 (COI).

Culta: Department of Horticulture, Agricultural University, Wageningen, The Netherlands, from material of Groenendijk s.n.: Van Veldhuizen 673, 817 (WAG) and from Groenendijk 107: Van Veldhuizen 597 (WAG).

4. SEED STRUCTURE IN BEGONIA SECTION BACCABEGONIA REITSMA

by A. de Lange, Hugo de Vries-Laboratory, University of Amsterdam

The seeds of Begoniaceae are characteristic at the family level by having so-called collar cells furthering germination. On the other hand there is a great diversity in size, shape and micromorphology (BOUMAN & DE LANGE, 1983), which provides an additional character set conceivably of importance for establishing intrageneric relationships.

Seed structure of Begonia baccata Hook.f. (Fig. 3a)
Seeds ellipsoid, but not always fully symmetrical. Variation in length from 5.5 to 6.3 \( \times 10^{-4} \) m, in width from 3.0 to 3.3 \( \times 10^{-4} \) m; mean 5.9 \( \times 3.1 \times 10^{-4} \) m. Length: width ratio 1.9. Collar cells varying in length from 1.3 to 3.0 \( \times 10^{-4} \) m; mean 2.0 \( \times 10^{-4} \) m. Collar: seed length ratio 1: 2.9. Seeds of the different samples show marked differences in size, e.g. the seeds of Groenendijk 115...
FIGS. 3a-f SEM photomicrographs. a: Begonia baccata Hook.f., mature seed; b-c: B. crateris Exell, mature seed and detail of collar cells; d: B. oxyloba Welwitsch ex Hook.f., mature seed; e: B. ampla Hook.f., mature seed; f: B. fusicarpa Irmsch., mature seed.
Form of the collar cells rather irregular; anticlinal cell walls between the collar cells but rarely straight, mostly slightly curved. At their chalazal side these cells often dovetail into the adjacent testa cells. Also the borderline with the operculum is relatively irregular.

Arrangement of the testa cells irregular, only those adjacent to the collar cells sometimes in line. The basal form of the testa cells isodiametrical. Anticlinal walls mostly curved, sometimes straighter.

Operculum obtusate, sometimes slanting, built up of many irregular small cells, the lowermost more prominent. Anticlinal walls of the operculum cells more pronounced than those of the testa cells.

Micromorphology: No distinct anticlinal boundaries. Due to the strongly thickened inner periclinal walls, the testa cells have a shallow appearance. The outer periclinal walls are very thin and collapse in mature seeds, thus reflecting the structure of the inner periclinal walls (c.f. Fig. 3c). The surface of the outer cell walls smooth, the cuticle almost without clear micro-ornamentation. Remnants of cuticular striiae are present on the anticlinal walls of the operculum cells and occasionally also on those of other cells. In seeds of Groenendijk 115 (WAG) the surface of operculum and collar cells shows a faint pattern of parallel-running striae.

Seed structure of *Begonia crateris* Exell (Fig. 3b, c).
The seeds of *B. crateris* very closely resemble those of *B. baccata* in shape and size. The mean size of the seeds is $6.1 \times 3.2 \times 10^{-4}$ m, with a length: width ratio of 1.9. Also in the micromorphology no distinguishing characters could be observed.

Sectional relationships
The seeds of these two species clearly belong to the *Mezierea-Squamibegonia-Tetraphila* section complex. However, they do not fit well into one of the three described sections (De Lange & Bouman, 1985). The complex is characterized by the presence of fleshy fruits and a presumably zoochorous way of dispersal, concomitant with a reduction or absence of a cuticular ornamentation. Section *Mezierea* seems to be the most original. The seeds are medium-sized (about 0.4 mm) and still show some cuticular structure. The collar cells are relatively large and straight and form a distinct transverse ring (Fig. 3d). Section *Squamibegonia* has relatively large seeds (0.7-0.8 mm), characterized by the absence of any cuticular sculpturing and by a cleavage of the anticlinal walls (Bouman & De Lange, 1982). The collar: seed length ratio varies from about 1: 5 to 1: 7 (Fig. 3e). Section *Tetraphila* forms a larger section comprising a few groups of species that show a striking variation in length from about 0.6 mm to more than 2 mm. All species lack a cuticular structure. On the other hand they are provided with an aril-like funicular outgrowth. In contrast to the two other sections, the fruits of this sec-
tion are dehiscent and expose their seeds. Also the collar: seed length ratio varies considerably from 1:2 to 1:6.5 (Fig. 3f).

Although the seeds of *B. baccata* and *B. crateris* show the greatest resemblance with those of *Mezierea*, their characters do not correspond with any of the species so far investigated.

Their seed micromorphology supports the inclusion of these two species into a separate section *Baccabegonia*.

**SUMMARY**

The present publication deals with a new small section in *Begonia*, section *Baccabegonia* Reitsma. It comprises two closely related species viz. *B. baccata* Hook.f. and *B. crateris* Exell, both endemics from the island of São Tomé in the Gulf of Guinea, Africa. Its position among other African sections is discussed. All taxa are typified and circumscribed, their distribution and ecology are given. The somatic chromosome number of both species is 2n = 36.

**ACKNOWLEDGEMENTS**

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**REFERENCES**


Berg see Van den Berg


*Agric. Univ. Wageningen Papers 84-3 (1984)*


LANGE see DE LANGE


WILDE see DE WILDE.
BEGONIA SECTION CRISTASEMEN
J. J. DE WILDE, SECT. NOV.

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1. INTRODUCTION

In February 1983, during a botanical exploration in Gabon, *Begonia thomeana* C.DC., a species hitherto exclusively known from the island of São Tomé, was discovered and collected on the African continent for the very first time. In order to verify the identity of the newly collected material it was analysed, described and compared with the type. In the course of this work it became evident that *B. thomeana* shows a combination of characters which does not fit into any of the African sections hitherto known. A number of extra-African sections was screened as well, among others, *Begonia* section *Haagea* (Klotzsch) A.DC. from Asia. None of these, however, proved suitable to accommodate *B. thomeana*.

Unlike KERAUDREN-AYMONN, AYMONN AND BOSSER (1983) who found it most difficult and undesirable to follow a sectional treatment for the 52 species which they recognized on Madagascar and the Comores, we are of the opinion that a clear-cut classification into sections for the continental African *Begonia* species is well within reach. The existing classification into sections, lastly emended by IRMSCHER (1925), already provides a workable basis. This framework shows indeed some lapses but apart from comparatively few really essential modifications, it leads to a more or less natural key to the sections (in prep.). In this context we think it justified to erect the here described new monotypic section.

2. DESCRIPTION OF BEGONIA SECT. CRISTASEMEN

J. J. DE WILDE, SECT. NOV.

Type species: *B. thomeana* C.DC.

duobus brevioribus abaxialibus duobus longioribus adaxialibus, apice bracchiorum planato hippocrepiforme margine stigmatosi. Pistillum ellipticum, triangulare, tripterum, ala una ceteris multo maje, triloculare, placentis indivisis, axillaribus. Infructescencia usque 15 cm longa, pendula, plerumque fructum unicium ferens. Fructus maturus capsulam alatam formans apice stylis desiccatis coronatus et rimis dehiscentes. Semina basi et apice comosa coma cellis testae elongatis formatas.

In São Tomé et Gabon supra 900 m crescent.

3. BEGONIA THOMEANA C.DC.  Fig. 1; Map 1

3.1. TAXONOMY


Type material and typification: Quintas no. 5 (São Tomé, alt. 950-1450 m, May-July 1888, lectotype and two paratypes in G; isoparatypes: 3 sheets numbered Quintas 178 at B, 1 sheet numbered Quintas 1273 in both COI and BM); Quintas no. 1339 (São Tomé: Rio Contador, alt. 1450 m, isoparatype, COI).

Note: QUINTAS made two collections of B. thomeana on São Tomé viz. Quintas no. 1273 collected at Traz-os-Montes at 950 m altitude in May 1888 and Quintas no. 1339 collected at Rio Contador at 1450 m altitude in July 1888. Both gatherings are at COI and are provided with the original tickets of the QUINTAS collection. There is no doubt about the identity of the material which is very homogeneous. In the protologue DE CANDOLLE only stated: 'In altitudine 950-1450 m (F. QUINTAS)'.

According to EXELL (i.e., 1944, page 383) HENRIQUES distributed duplicates of the QUINTAS collection under numbers different from the original numbers to various herbaria for identification by specialists. In this process he often added an indication to the original labels to show under what number the duplicates had been sent and to what place. The information on the labels going with these duplicates distributed by HENRIQUES was often a summary of the information given on the original tickets. The duplicates, moreover, were selected at random from the material available, often from several gatherings.

The Geneva herbarium contains three sheets of B. thomeana which belong
to the Quintas collection; all three bear a number 5. Among these one sheet has a label on which it is stated: 'Ins. St. Thomé (950–1450 m) and legit F. Quintas, 5–7, 1888'. On this particular sheet a hand-written diagnosis of the plant signed by Casimir de Candolle is added. Moreover, Quintas no. 1273 in COI, bears a label on which it is annotated: 'DC. no. 5, B. 178, Kew 147'.

From this it is concluded that Henriques sent duplicates of Quintas no. 1273 (probably mixed with material of Quintas no. 1339) to de Candolle in Geneva under no. 5 and to Berlin under no. 178 (I have not seen this material at Kew). The eclectic label added to the Geneva duplicates gives a compilation of the information supplied by Quintas on the original labels of both his gatherings nos 1273 and 1339. It is not possible to decide whether the Geneva material is part of Quintas no. 1273 or that it consists of a mixture of both Quintas' gatherings.

Under these circumstances the sheet bearing the annotations by de Candolle present in Geneva is selected as the lectotype. The other two sheets in G, beyond doubt also seen by de Candolle, are paratypes as it is not clear to which of the two Quintas gatherings they belong. All the relevant Quintas material present in other herbaria is indicated as isoparatypes.

**Description:** Monoecious creeper covering rocks on ground level but finally always climbing up trunks of trees; flowers only found three or more meters above the ground. The thin fleshy stems repeatedly branched, pale brown or reddish in vivo, terete, 1–3(–4) mm diam., up to 10 m long, profusely covered with short, adventitious roots on the side directed towards the substrata (like ivy, *Hedera helix* L.), otherwise loosely puberulous or rarely glabrescent; the indumentum composed of whitish simple hairs and minute pale brown trichomes. Internodes up to 5 cm long, usually shorter.

Stipules persistent, patent, in vivo pale green and with diaphanous often revolute edges, 6–11 mm long by 2–6 mm wide, triangular to broadly triangular, asymmetric and often somewhat sickle-shaped, outside and on the edge with a few white hairs especially near the base and loosely scattered with in vivo short brownish trichomes, inside glabrous but for a few trichomes.

Leaves long persistent, in vivo herbaceous, somewhat glossy bright green above, conspicuously glossy and paler green beneath; petioles flattened or slightly furrowed above, otherwise terete, 2–9(–10) cm long, in vivo often pale brownish-red, puberulous to glabrescent, the blade forming an almost right angle with the petiole. Blades almost symmetric to asymmetric, ovate to broadly ovate, (1,5)3–7,5(–8,5) cm, deeply cordate and with the leaf-edges slightly overlapping at the very base or the base truncate, acuminate at the apex; the margin coarsely dentate and in vivo somewhat undulating; both surfaces covered with an open sparse indumentum of short erect whitish hairs and loosely scattered with very minute brownish trichomes, the indumentum more pronounced on the upper surface; the leaves rarely almost glabrous; palmately 5–8-nerved, the nerves arising from the base, or the central ones from somewhat above the base, all nerves 1–3 times dichotomously branched, the branches reaching the margin and the tips ending in a tooth, prominent beneath, not or slightly prominent above;
veins rather indistinct.

Inflorescence an axillary dichasial cyme, protandrous-androgynous, comparatively few-flowered, containing up to 4 male and 3 female flowers, exceeding the leaves at the time of flowering; one or both lateral branches (1st order) usually branched again, rarely a branch 2nd order also branched and in that case the branching monochasial. Axes first order up to 15 mm long, axes second order (if present) ca 5 mm long, glabrescent, loosely scattered with very minute brownish trichomes. Within the inflorescence each dichasial branching terminated by a male flower, the female flowers found on laterals from the ultimate dichasial cymelets; a cymelet usually consisting of a terminal male flower (see above) and a single lateral female flower, the axis opposite the female flower not developed or abortive, sometimes however both laterals developed, both bearing a female flower. Peduncle 3–6.5 cm long, at the apex with the two opposite bracts (subtending the axes 1st order); bracts 3–9 × 2–6 mm, ovate to obovate, more or less transparent, crenate and with a few minute brownish trichomes on the edge; bracts of subsequent dichasial branchings becoming

Fig. 1. *Begonia thomeana* C.D.C. – 1: branch climbing with adventitious roots (x 4); 2: margin of developing leaf, upper side (x 4); 3: idem, underside (x 4); 4: section of young stem (x 2); 5: section of full-grown stem (x 1); 6: protandrous-androgynous inflorescence (x 4); 7: ♀ fl. (x 4); 8: androecium (x 4); 9 and 10: different stamenshapes, frontal view (x 4); 11: ♂ fl. (x 4); 12: styles and stigmata (x 4); 13: idem, schematic; 14 and 15: different shapes of stigmata (x 6); 16: transverse section of ovary, ca in the middle (x 4); 17: part of ovuliferous placenta (x 20); 18: infructescence (x 4); 19: mature seed (x 26). – 1: living material introduced from São Tomé by De Wilde. Arends and Groenendijk (herb. no. 141) and Van Veldhiuizen 882, spirit material from the same introduction; 2–4 and 7–17: De Wilde c.s. 141; 5, 18, 19: De Wilde, Arends, Bouman, Karper and Louis 521 from Gabon; 6: Groenendijk 138.
smaller, otherwise similar. Male flowers readily caducous and then the inflorescence seemingly female.

Male flower supported by a 3.5–13 mm long ‘pedicel’, the length dependent on the place in the cyme. The ‘pedicel’ (the support of a single male flower) distinctly articulated near the base; the part above the articulation (the perianth-cylinder) 3–12 mm long, loosely scattered with minute brownish trichomes; the part below the articulation (the true pedicel) 0.5–1.0 mm long, with slightly denser indumentum and darker in colour, otherwise similar. Perianth-segments (tepals) two, opposite, in vivo orange-yellow, 12–20 mm in diameter, very broadly ovate, cordate at the base, glabrescent, the basal part on the outside scattered with minute trichomes.风格cale fasciculate, asymmetric; stamens 10–16, arranged in the way of a raceme of bananas. Filaments fused at the base over 0.5–1.5 mm, otherwise free; 1.5–3.5 mm long. Anthers all facing the same direction, 2.0–3.5 × 1 mm, narrowly oblong to obovate, truncate to obtuse at apex, opening more or less laterally, lengthwise; the actual slits widest near the apex.

Female flower long pedicellate; the pedicel (in fact an ultimate axis of the inflorescence) variable in length, 5–25 mm long but largely elongating in fruit, puberulous by minute trichomes. Perianth-segments (tepals) two, similar to the segments found in male flowers; the margins of both segments fused at the extreme base and the segments directly implanted on the top of the ovary. Styles 3, long persistent, fused at the base over ca 1 mm; each style forked twice, the first forking ca 1.5–2 mm above the fused part, a second forking into branches of uneven length (up to 4 mm and 2 mm long respectively) ca 1.5 mm higher, the forking in two perpendicular planes, resulting in a 4-armed style, the two shorter arms abaxial. Apical part of each arm thickened, flattened and curved in the shape of a horseshoe, the rim densely papillose, the papillae glanduliferous (stigmatic tissue). Ovary 3-winged, in vivo green, trigonous, ellipsoid, up to ca 15 × 7 mm (wings excluded), scattered with minute brownish trichomes all over. The wings unequal in size, one wing much more developed as compared to the others; each wing starting as a sharp keel at the base of the ovary; the larger wing gradually expanding and reaching a width of 5–7 mm (ca 4 mm underneath the apex of the ovary) from where it narrows and from where the outline continues along a rather straight line towards the apex; the other wings widest in the basal part, reaching a width of up to 1.5 mm and gradually narrowing towards the apex. The ovary 3-locular with axile placentation. Placentas entire, flat, stretching deep into the locules, densely packed with ovules on both sides; the ovules side by side, perpendicular to the surface of the placenta (see also Reitsma, 1984).

Inflorescences drooping, up to 15 cm long, usually containing one fruit, rarely more; the peduncle reaching a length of 6.5 cm, firm, brown, longitudinally finely furrowed; the axis first order up to 2.5 cm long, somewhat thinner and flattened; the fruiting pedicel up to 4.5 cm long, flattened and furrowed as well; the fruit hanging by the long pedicel. Mature fruit a dry, brown, trigonous, winged capsule, up to 3.5 cm long, still crowned by the persistent styles; the larger wing thick pergamenous, strongly veined, reaching a width of 2.2 cm;
the other two wings much narrower, up to 0.5 cm, otherwise similar. Dehiscence by slits formed by the pericarp breaking away from the wings but leaving the latter intact and, moreover, by longitudinal splitting of the septa; the process progressing from the base of the capsule towards above, not reaching the apical zone, however.

Mature seed glossy light brown, very characteristic as a result of the much enlarged testa cells found at the base and apex which give the seed a tufted appearance, 0.9–1.3 × 0.2–0.3 mm (the tufts included). For details, see 3.2.

**Distribution**: São Tomé, Gabon.

**Distributional, ecological and biological notes**: Until recently *B. thomeana* was only known as a narrow endemic species from the island of São Tomé. A reference to its occurrence in Cameroon by Barkley (1972, 1974) could not be substantiated. On São Tomé it is found in the mountain rain-forest that stretches from Lagôa Amelia to the Pico de São Tomé and in the corresponding range of what is called the mist-forest region by Exell (I.c.: 21. 1944) at altitudes between 950 m and 1700 m. In February 1983, during a botanical expedition to Gabon the species was discovered for the very first time on the continent. It was collected in southern Gabon in the Massif du Chaillu, ca 15 km along the road Mimongo-Mbigou on the top of Mount Naguila in (sub-)montane forest at 880 m altitude (teste J. J. de Wilde, Arends, Bouman, Karper and Louis no. 521, WAG). In November 1983 a second expedition to the same area found *B. thomeana* in primary forest on neighbouring Mt Songou (1°37'S. × 11°46'E.) at ca 1020 m altitude (teste A. M. Louis, Breteler and De Bruijn nos 982 and 983, WAG). The physiognomy of this habitat of *B. thomeana* in Gabon, although somewhat lower in altitude, strikingly resembles that of where the species was found on São Tomé, where it was collected among others by De Wilde, Arends and Groenendijk (no. 141, WAG). The trees do not reach such large dimensions as at lower altitudes and almost all are profusely covered with epiphytes, predominantly mosses and ferns. The rainfall is high and mist is a common feature.

From a taxonomic (and phylogenetic) point of view close relatives of *B. thomeana* do not occur on São Tomé. However, on the continent and in particular in the Lower Guinea subdivision of the Guineo-Congolian Region, *Begonia* clearly shows a centre of variation as testified by the occurrence of about 50 species in Gabon only (out of ca 125 species on the continent). None the less in Gabon *B. thomeana* seems to occupy an isolated taxonomic position as well. The fact that populations of the species on São Tomé and in Gabon resemble each other so closely and in the course of evolution remained unchanged, combined with the observation that variability and species segregation among African *Begonia* taxa is a common and wide-spread feature, once again points into the direction of the here adopted status of *B. thomeana* as a section by itself.

At maturity the dry winged fruits are pendulous and dehisce with slits. This in combination with the special structure of the seed which is equipped with a
pair of ‘flying tufts’, indicates dispersal by wind (see also Bouman and De Lange (1983), and the following paragraph).

In cultivation B. thomeana is difficult to grow owing to its high requirements as regards shade and humidity of the air.

Specimens examined:
São Tomé: between Monte Café and the Pico, Chevalier 14539 (P); between Lagôa Amelia and Calvario, J. J. de Wilde, Arends and Groenendijk 141 (WAG); near Vanhulst (Macambrârâ), Exell 419 (BM, BR, COI, MO); between Lagôa Amelia and Calvario, Groenendijk 138 (WAG); Lagôa Amelia, Monod 11782 (BM, COI); Calvario, Monod 11844 (BM, COI); slopes N.W. of the Pico, Monod 12253 (BM, COI); Ins. St. Thomé (950–1450 m), legit F. Quintas, 5–7, 1888, Quintas 5 (G, 3 sheets, lectotype and two paratypes); sin. loc., Quintas 178 (B, 3 sheets, isoparatypes); Tráz-os-Montes, Quintas 1273 (BM, COI, isoparatypes); Rio Contador, Quintas 1339 (COI, isoparatype).

Gabon: Massif du Chaillu, Mt. Naguila, ca 15 km on the road Mimongo-Mbigou, ca 4 km S.E. of Mouyana, J. J. de Wilde c.s. 521, 1983 (WAG, Libreville-LIBRV–); Massif du Chaillu, Mt. Songou between Dibandi and Mouyana, ca 20 km E. of Mimongo, A. M. Louis, Breteler and De Bruijn 982 (WAG, LIBRV); ibid., 1°37’S. x 11°46’E., A.M. Louis c.s. 983 (WAG, LIBRV).

Culta: Agricultural University Wageningen, The Netherlands; from living material originally introduced by De Wilde, Arends and Groenendijk from São Tomé, Van Veldhuizen 882 (WAG).

3.2. SEED STRUCTURE OF B. THOMEANA C.DC.
(by F. Bouman, Hugo de Vries Laboratory, University of Amsterdam)

Shape and size:
Seeds narrowly elliptic to narrowly oblong in outline, one or both of its sides sometimes curved and rendering the seeds J-, or slightly S-shaped (Figs. 2a and b). Micropylar and chalazal ends of the seeds composed of blown-up, air-filled cells (Figs. 2c and d). The central part, covered by the collar cells, contains the embryo. Micropylar, central and chalazal part each take up about one third of the seed.

Seeds of B. thomeana from Gabon (De Wilde c.s. 521) vary in length from 11.0 to 12.9 x 10^-4 m, in width from 2.1 to 2.6 x 10^-4 m; mean 12.0 x 2.4 x 10^-4 m. Length: width ratio 5. Central part: seed length ratio 3.5.

Seeds of B. thomeana from São Tomé (Quintas 5, lectotype, G) slightly differ in dimensions: variation in length from 9.4 to 11.8 x 10^-4 m; in width from 2.3 to 2.6 x 10^-4 m; mean 10.0 x 2.4 x 10^-4 m. Length: width ratio 4.2. Central part varying in length from 3.4 to 3.9 x 10^-4 m; mean 3.6 x 10^-4 m. Central part: seed length ratio 2.8.
FIGS. 2a–e Begonia thomeana C. DC. SEM photomicrographs. a: mature seed (Quintas 5, São Tomé, lectotype); b: mature seed (De Wilde c.s. 521, Gabon); c: micropylar part; d: detail of blown-up chalazal cells with striate cuticle; e: detail of collar cells with collapsed outer walls, reflecting pits; Fig. 2f Begonia glabra Aublet var. cordifolia (C. DC.) Barkley, seed.

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Primary sculpture:
Collar cells strongly elongated, regular; the anticlinal cell walls between the collar cells straight. Border line with the micropylar part sharp, that with the chalazal part more indented. Outer periclinal walls thin, collapsing in the mature seed and reflecting the pitted structure of the inner periclinal wall (Fig. 2e).
Testa cells of the chalazal part irregularly arranged, elongated, especially those adjacent to the collar cells. Outer periclinal walls bulging towards the chalazal apex. Anticlinal walls straight or slightly curved.
Operculum massive. Exostome rim oblique, the longer side often cristate. Hilum sunken, hidden by the exostomal rim. Appearance of the cells resembling that of the chalazal ones.

Micromorphology:
Collar cells with sunken anticlinal boundaries. Due to the bulging outer walls, this character is not so conspicuous in the other parts of the seed. Surface of the testa cells with a striate cuticular ornamentation. Striae varying in length and density, sometimes locally with slight undulations. Testa cells sometimes with one or more patches lacking any sculpture. Cuticular pattern most prominent on the chalazal part and almost absent on the collar cells, the latter often with (mainly transverse) folds on the collapsed outer wall.

Sectional relationships:
The seed morphology of *Begonia thomeana* is highly aberrant from all African *Begonia* species thus far studied. The micropylar and chalazal ends of the seed consisting of air-filled cells are supposed to function as balloons, thus promoting wind dispersal. Although the majority of the *Begonias* have wind-dispersed seeds, a specialized construction as balloon cells is but rarely encountered. A comparable structure has been found in some American species, by the author in *B. glabra* Aublet var. *cordifolia* (C.DC.) Barkley (Section Pritzelia, Fig. 2f) and had already been described by SEITNER (1972) in *B. odorata* Willd. (Section Begonia) and *B. lobata* Schott (Section Ewaldia).
In IRMSCHER's classification *B. thomeana* is placed in section Loasibegonia, but the seeds of this section are very different from those of *B. thomeana*. They are characterized by their small size (mostly under 0.3 mm), curved anticlinal walls and a thick cuticle with a much pronounced ornamentation (DE LANGE & BOUMAN, 1985). The seeds of section Loasibegonia closely resemble those of section Scutobegonia. Hydro/ombrochory and epizoochory are probably the most important forms of dispersal.
The morphological seed characters support the establishment of a separate section Cristasemen for *B. thomeana*.

3.3. Karyology
Ir. J. C. ARENDS (pers. comm.) informs us that the somatic chromosome
number of the cultivated specimen of *B. thomeana* (greenhouse accession number T1268, voucher herbarium De Wilde, Arends & Groenendijk no. 141, WAG) is 2n = 38. Its karyotype is similar to that of several species of the section *Scutobegonia* such as *B. ciliobracteata* Warb. The total chromosome length of the somatic complement is about 25 μm.

4. DISCUSSION

Originally Warburg (1894) accommodated *B. thomeana* in section *Loasibegonia* A.DC. (1864: 389). This section, in its original circumscription by Alphonse De Candolle, is characterized by two yellow perianth-segments in both male and female flowers and a 4-locular elongated prismatic 4-ribbed ovary crowned by 4 styles which are connate in the lower part and which bear reniform stigmas at their apexes. Furthermore there are 4 entire placentas, one in each locule. At the time De Candolle only knew *B. prismatocarpa* Hook., which thus automatically fixes the type species. Mature fruits were not known to De Candolle.

Warburg (1894: 140) added 4 species to this section and among these mentioned only *B. thomeana* and *B. quadrialata* Warb. specifically. On this occasion the circumscription of section *Loasibegonia* was altered. By now 3 or 4 styles were admitted and these might even be branched manifold (as found in *B. thomeana*). Most remarkably, the placentas were now unequivocally indicated as bifid, a condition not found in any of the species cited by Warburg (see also Reitsma, 1984).

Engler (1921: 618), following Warburg's opinion that the placentas in section *Loasibegonia* are bifid, excluded *B. quadrialata* from the section (this species is transferred to section *Scutobegonia* Warb.). Next to *B. prismatocarpa* and *B. thomeana* he admitted 4 other species into the section, viz. *B. scutifolia* Hook.f., *B. scapigera* Hook.f., *B. dusenii* Warb. and *B. schaeferi* Engl. The main criterion used by Engler to incorporate these 4 species into section *Loasibegonia* is probably found in the condition that the ovaries and fruits of these species are almost devoid of wings.

Irmscher (1925: 574) repeated the description of section *Loasibegonia* supplied by Warburg almost verbatim, stating again: 'Samenleisten 2 spaltig. Frucht prismatisch, manchmal sehr lang, mit 3–4 meist schmalen, zuweilen nur angedeuteten Flügeln'. He admits 6 species, probably following Engler (see above).

Nicolas Hallè (1967: 507), in a discussion on the sections *Loasibegonia* and *Scutobegonia* cited a number of species that at one time were accommodated in section *Loasibegonia* and at another time in *Scutobegonia* and vice versa. From this he concluded that the characters used in separating both sections are inconsistent and that in his opinion both sections should be merged into one taxon.
for which he supplied a circumscription. In Halle's new concept both entire and bifid placentas are admitted and the fruits are dry and winged or not winged. The inflorescence, more in particular, is described as a monoecious, proterandrous, 'pseudo-umbel' terminated by one (rarely two) female flower(s) flanked by usually 2, and more rarely 3–5, male flowers.

Although we do not have detailed information on all the species belonging to both sections, we analysed and studied a number of them and concluded that the fruits remain more or less fleshy and do not dehisce as maturity, as opposed to the dry dehiscing fruits of sect. Cristasemen (see also our opinion about a necessary transfer of section Scutobegonia series Longicaules Engl. to section Flicibegonia A.DC. on page 127). As regards the structure of the inflorescence in the sections Loasibegonia and Scutobegonia we disagree with Halle. In our opinion the female flower represents a lateral of a contracted monochasial cyme. This however, applies also to the situation found in section Cristasemen.

Halle attributed both sections to Warburg as the publishing author, ignoring De Candolle. Using A. De Candolle's original diagnosis of section Loasibegonia as a basis it might, in our opinion, still be possible to keep it apart from section Scutobegonia. Our current knowledge does not allow us to solve the problem. Whatever the outcome may be we feel that B. thomeana does not fit in either section nor in any of the other sections known at present. This view is based on the observation of the following characters which we consider to be of primary importance for a sectional arrangement:

1. the habit of the plants;
2. the number of perianth-segments in both male and female flowers;
3. the placentas;
4. the fruit;
5. the seeds.

These characters are discussed hereafter for section Cristasemen and in relation to the above-mentioned sectional arrangement of the continental African species often placed in a wider context.

1. In section Cristasemen the plants are climbing on trees by means of numerous short adventitious roots. This habit represents a unique growth-form as far as African Begonia species are concerned. It is, however, also found in some extra-African sections but then always associated with very different character combinations.

2. Section Cristasemen shows 2 perianth-segments in both male and female flowers. This is a common feature in a number of African sections viz. in Bacca-begonia, Flicibegonia, Loasibegonia, Mezierea, Scutobegonia and Squamibegonia. This character is very constant and holds for all species belonging to these sections. To our knowledge it only breaks down for section Mezierea, where B. meyeri-johannis Engl. shows 4 tepals in the male flowers and 2 in the female flowers. The stability and value of this flower character on a sectional level is further emphasized by the outcome of Irmscher's (1961: 106) monographic revision of the African sections Augustia (Klotzsch) A.DC. and Rostrobegonia Warb. comprising 29 species in all. Among these he found 7 species characterized
by male flowers showing 2 perianth-segments (the other species have 4) whereas none of these 29 species showed 2 perianth-segments in the female flowers (the number is here 3, 4, 5 or rarely 6). In sect. Tetraphila A.DC. recently defined by DE WILDE & ARENDS (1979: 357) all ca 35 species have 4 perianth-segments in both male and female flowers though there is a tendency towards suppression of the innermost perianth-whorl in flowers of both sexes as demonstrated by HAGMAN & DE WILDE (1984) in B. cavallyensis A. Chev.

3. REITSMA (1984) studied the placentation in African Begonia species and came to a division into two main groups based on the criterion of the nature of the septa which are either true or partly false. He subdivided these main groups into subgroups using exclusively the characters of the placentas and finally arrived at species groups in which the species share a number of placentation characters. According to this findings B. thomeana C.DC. is characterized by completely true septa and by a single axile entire placenta in each of the three locules of the triangular ovary. The ovules are regularly arranged in a single layer around the placenta. A similar character combination he found in six other species at present accommodated in the sections Scutobegonia (1 species), Rostrobegonia (1 species) and Augustia (4 species). With regard to the latter two sections we found that two perianth-segments in the female flower, as in B. thomeana, are inadmissible (see above). The single species (traditionally accommodated in section Scutobegonia viz. B. sciaphila Gilg ex Engl.) analysed and admitted to this species group by REITSMA, belongs, in our opinion, to section Filicibegonia. The same holds for B. sessilifolia Hook.f., B. elatostemmoides Hook.f. and B. macrocarpa Warb., placed by REITSMA in a different but closely related species group and traditionally also placed in section Scutobegonia.

Summarizing it may be stated that the placentation found in B. thomeana excludes it from the sections Baccabegonia, Mezierea, Squamibegonia and Tetraphila and that it shows similarities with the placentation found in the remaining continental African sections. At the same time it is concluded that placentation alone is insufficient to arrive at a sectional arrangement.

4. The characters of the fruit as shown in B. thomeana, viz. a dry winged capsule opening with slits, are similar to those found in the sections Augustia, Rostrobegonia, Sexalaria A.DC. and Filicibegonia. Among these the first three sections never show 2 perianth-segments in the female flowers (see also above). Section Filicibegonia, in our concept comprising besides B. asplentifolia Hook.f. also section Scutobegonia series Longicaules Engler (1921: 616), forms a homogeneous taxon of white or pinkish flowering, rather low terrestrial branched herbs showing 2 perianth-segments in both male and female flowers. Despite of the signalized similarities in the characters of flowers, placentation and fruits we strongly feel that it is not warranted to place B. thomeana in section Filicibegonia, taking into account its climbing growth-form, the unique seed morphology and as additional segregating characters the singular forkings of the styles and the yellow colour of the flowers.

5. BOUMAN and DE LANGE (1982, 1983) demonstrated that micromorphological characters of the seeds are of great taxonomic value in Begonia. Recent re-
search by these authors (De Lange and Bouman, 1985) points, more in particular, to the diagnostic value of these characters with regard to the delimitation of sections, at least as far as the African taxa are concerned. In this context it can be put forward that the seeds of *B. thomeana* show a morphology which stands completely apart from the rest of the *Begonia* species on the African continent. For details, see paragraph 3.2.

Weighing the evidence and data discussed above it is concluded that *B. thomeana* occupies an isolated position within the African species and that it is justified to give this taxon a sectional status.

**SUMMARY**

In 1983 botanical exploration in Gabon revealed the occurrence of *B. thomeana* on the African continent. This species was hitherto considered to be a narrow endemic confined to the island of São Tomé. Subsequent analysis of the collected plants and of all living material and herbarium specimens available leads to the conclusion that the circumscription of none of the known sections in *Begonia* permits the inclusion of a combination of characters as shown by *B. thomeana*. As a consequence of this a new section *Cristasemen* is proposed and circumscribed and its place among the continental African sections is discussed. The type species, *B. thomeana*, is lectotypified and its distribution, ecology and karyology are given. Dr. F. Bouman contributed a description of the micromorphology of the very characteristic seed which shows a specialization functional to wind-dispersal.

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REFERENCES

Lange see De Lange
Wilde see De Wilde.

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