POLLEN MORPHOLOGY OF THE GENUS BEGONIA IN AFRICA

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POLLEN MORPHOLOGY OF THE GENUS BEGONIA IN AFRICA

Proefschrift
ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
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STELLINGEN

I

Polyploidie uit zich lang niet altijd in groter of anderszins afwijkend pollen.

II

De Datiscaceae zijn pollenmorfologisch niet nauw verwant aan de Begoniaceae.

III

De relatie vorm-functie kan de bouw van een stuifmeelkorrel vaak niet afdoende verklaren.

IV

Pollentypen opgevat als zuiver typologische constructies zijn niet bruikbaar voor het reconstrueren van fylogenie.

V

In de fylogenie is de cirkelredenering moeilijk geheel te vermijden.

(C. KALKMAN, De twee vragen van de Plantensystematiek 1982:13)

VI

De scheiding tussen fundamenteel en toegepast onderzoek is noch fundamenteel noch toepasbaar.

VII

De tendens om β-taxonomie te stimuleren ten koste van α-taxonomie zal spoedig leiden tot een situatie waarin de bioloog de computer moet vragen zijn materiaal te determineren.

(H. F. LINSKENS, Vakblad voor Biologen 64(19), 1984:432)

VIII

Een taxonoom dient zich niet te beperken tot het vervaardigen van een catalogus van de door hem/haar onderzochte soorten.

IX

Het meten van de doelmatigheid en de kwaliteit van wetenschappelijk onderzoek door het tellen van het aantal publicaties en citeringen is bij uitstek een voorbeeld van slecht onderzoek.

X

Aangezien het discriminerend moet worden geacht als in een sollicitatieprocedure 'bij gelijke geschiktheid' van een aantal kandidaten de voorkeur wordt gegeven aan een vrouw, lijkt het juister in zo'n geval het lot te laten beslissen.

XI

De educatieve waarde van de blokfluit voor het muziekonderwijs aan beginners wordt verre overtroffen door die van de synthesizer.

XII

Van het concept des levens krijgt niemand een cladogram.

R. G. VAN DEN BERG
Pollen morphology of the genus Begonia in Africa

Wageningen, 19 april 1985

Aan mijn moeder

PREFACE

This thesis is the result of a three year study on the pollen of the *Begoniaceae*, with emphasis on the representatives of the genus *Begonia* in Africa. The purpose of this investigation of the micromorphology of the pollen of *Begonia*, instigated by the taxonomist working on the genus, dr. J. J. F. E. de Wilde, was to provide pollen-morphological data which would be useful to elucidate taxonomical problems. It will be no surprise that not all taxonomical problems could be solved by pollen morphology. Still, it was possible to arrive at a grouping of species, to evaluate the traditional grouping of the species in sections, and to indicate a broad outline of the phylogeny of the family in Africa. An account of the pollen morphology of the other two genera of the *Begoniaceae* (*Hillebrandia* Oliv. and *Symbegonia* Warb., occurring on the Hawaiian islands and New Guinea, respectively) could be published in the course of this study (Van den Berg, 1984) and is included in the present volume.

A number of persons contributed to the final version by their stimulating interest and valuable criticism, often during long, searching, and thoroughly enjoyable discussions. My indebtedness in matters of science and in preparing the manuscript is recognized in the acknowledgements at the end of the text, here I would like to express my gratitude to a few of those who determined my outlook and modus operandi in other, more subtle ways:

Jan Muller, who guided my first steps in palynology, for always being willing to help and stimulate my research. It is cause for great sadness that he should not be able to witness the result.

Hans de Wilde, a fine scholar, for, amongst many other things, his sense of humor...

Coen Arends and Frank van der Laan, inhabitants of the "lab", who shared the morning coffee.

Judith van Medembach de Rooy-Ronkel, Marina Wassink and Cees de Groot, for always being there when needed.

Wil Wessel-Brand, for sharing the room and the laughter.

And, of course, Esther, who did nót efface herself, but was indispensable anyway.

CONTENTS

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. Bosser, 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. thomeana* 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

These species are removed from section *Squamibegonia* (cf. DE WILDE & ARENDS, 1980 and REITSMA, 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. fusialata* Warb.
- *B. fusicarpa* Irmsch.
- *B. gracilipetiolata* De Wild.
- *B. horticola* Irmsch.
- *B. jussiaeicarpa* Warb.
- *B. kisuluana* Büttn.
  - *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. molleri* (C.DC.) Warb.
- *B. nicolai-hallei* Wilcz.
- *B.oxyanthera* 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. macambrarensis* 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. suffruticosa* Meissn.
- *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. rumpiensis* Kup.
- *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. gueinziana* (A.DC.) Irmsch.
- *B. wollastonii* Baker
  - *B. lebrunii* Rob. & Law.

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).

Filicibegonia A.DC.
- *B. asplenifolia* Hook.f.
- *B. auriculata* Hook.f.
- *B. elatostemmoides* Hook.f.
- *B. filicifolia* Hallé
- *B. gossweileri* Irmsch.
- *B. gracilicaulis* Irmsch.
- *B. iucunda* Irmsch.
- *B. latistipula* Engl.
- *B. macrocarpa* Warb.
- *B. minutifolia* Hallé
- *B. sciaphila* Gilg ex Engl.
- *B. sessilifolia* Hook.f.

Originally, this section contained only one species: *B. asplenifolia*. A number of species of the section *Scutobegonia* shows characters that indicate relationships with section *Filicibegonia* (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. hypogaea* Winkler
- *B. klainei* Pierre ex Pellegr.
- *B. lacunosa* Warb.
- *B. laporteifolia* Warb.
- *B. macropoda* Gilg
- *B. mayombensis* Irmsch.
- *B. microsperma* Warb.
  - *B. batesii* C.DC.
- *B. mildbraedii* Gilg
- *B. peperomioides* Hook.f.
- *B. potamophila* Gilg
- *B. pseudoviola* Gilg
- *B. quadrialata* Warb.
  - *B. calabarica* Stapf
  - *B. modica* Stapf
  - *B. whytei* Stapf
- *B. raynaliorum* Wilcz.
- *B. salisburyana* Irmsch.
- *B. scapigera* Hook.f.
- *B. scutifolia* Hook.f.
- *B. scutulum* Hook.f.
- *B. staudtii* Gilg
- *B. subtilis* Irmsch.
- *B. triflora* Irmsch.
- *B. vankerckhovenii* De Wild.
- *B. vittariifolia* Hallé
- *B. zenkeri* Irmsch.

This section has not been studied in detail, recently. A number of species-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 (ARENDS, 1985). Furthermore, many species show a restricted distribution. This high degree of endemism also could denote recent speciation. Within the combined group of sections *Scutobegonia* 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. mayombensis* and *B. microsperma*.

Loasibegonia A.DC.

B. dusenii Warb.
B. prismatocarpa Hook.
B. schäferi Hook.f.

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).

OLD SITUATION			RECENT VIEWS		
Africa	**1**	**2**		**3**	**4**
sections	species		sections	species	
Mezierea	5	9	Mezierea	10	3
			Baccabegonia	–	2
Squamibegonia	7	10	Squamibegonia	3	3
Tetraphila	?	43	Tetraphila	35	36
Sexalaria	1	1	Sexalaria	1	1
Augustia	9	13	Augustia	13	11
Rostrobegonia	7	18	Rostrobegonia	18	12
Scutobegonia	?	38	Scutobegonia	50	35
Loasibegonia	6	9	Loasibegonia	5	3
Filicibegonia	1	1	Filicibegonia	2	11
			Cristasemen	–	1
9 sections	?	142	11 (or 8) sections	137	118
Madagascar		**5**			**6**
Erminea		4	Mezierea		2
Nerviplacentaria		2			
Quadrilobaria		5	?		
Muscibegonia		1			
4 sections		12	? sections		52

Formerly this section also accommodated *B. thomeana* C.DC. 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. In 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 the *Begonias* of Madagascar belong to the province of the taxonomists of the Laboratoire de Phanérogamie, 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 Madagascan *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 glycerinejelly 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 cacodylatebuffer (0,1 M, pH = 7,2) for 5 hours at room temperature, then in 1% 0s 0_4 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 leadcitrate. 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 syncolpate 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

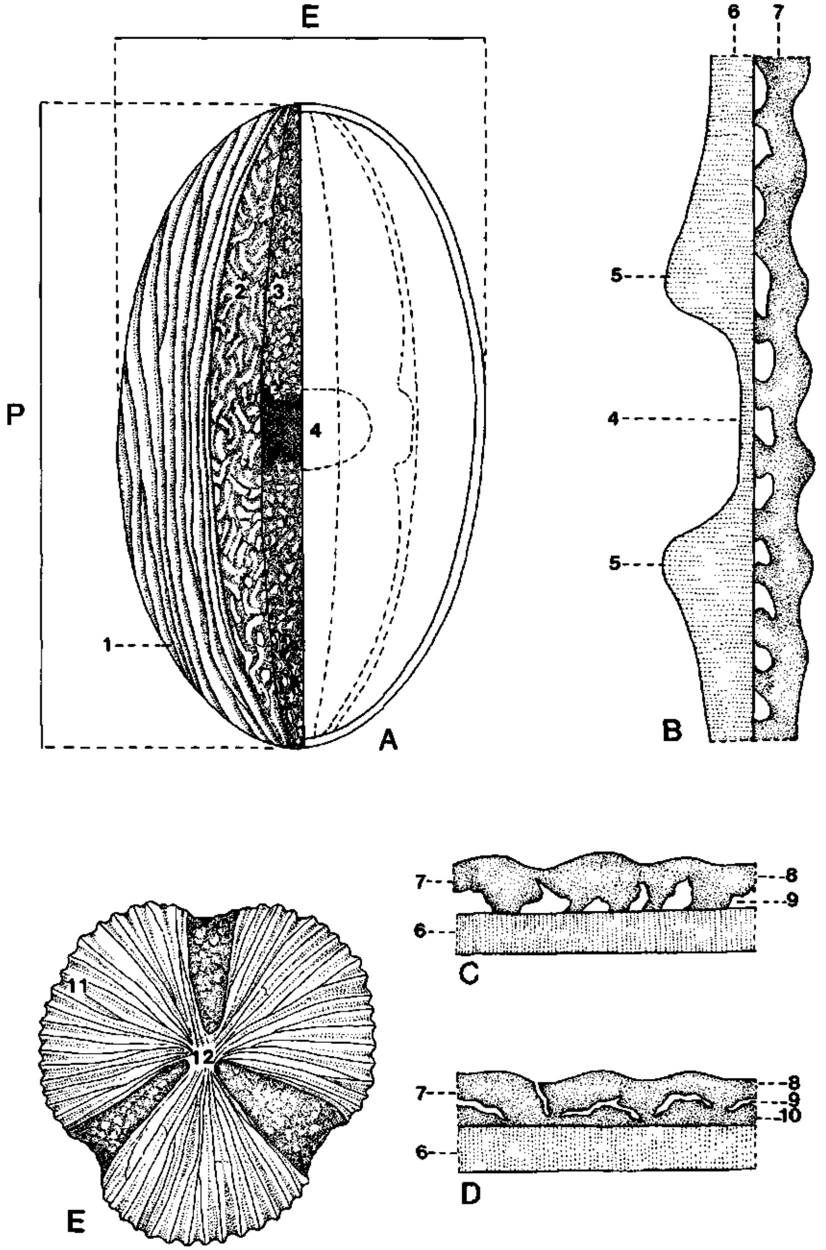

FIG. 3.1. General morphology of *Begonia* pollen
A. Equatorial view; B. Detail endoaperture; C and D. Details wall structure; E. Polar view.
1. striate ornamentation; 2. margo; 3. colpus membrane; 4. endoaperture; 5. costa(e); 6. endexine; 7. ectexine; 8. tectum; 9. infratectal layer; 10. foot-layer; 11. mesocolpium; 12. apocolpium; P polar axis; E equatorial diameter.

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 columellae; 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);

P/E 1	**spheroidal**
P/E 1–1.14	**prolate spheroidal**
P/E 1.14–1.33	**subprolate**
P/E 1.33–2.00	**prolate**
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 outher, 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 inbetween 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 µm. This means that a difference in size between two taxa with, for instance, a polar axis of 25 µm and 28 µm respectively, is not interesting, but there is no doubt of the importance of the fact that the polar axis of certain taxa measures ± 15 µm, while others always exceed 30 µm.

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 µm), 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 phenomenon 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

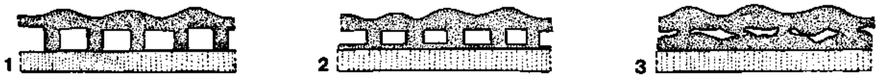

FIG. 3.2. Reduction infratectal layer. 1. distinct columellae; 2. foot-layer present; 3. reduced infratectal layer.

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

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

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** **Plate 7**

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 µm, E 10–11 µm, P/E 1.40–1.50, m 1–2 µm, e 2–3 µm.

Species: *B. cladocarpa* Baker, *B. comorensis* A.DC. ex Warb., *B. meyeri-johannis* Engl., *B. seychellensis* Hemsley.

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. seychellen-*

sis); *J. v. d. Walle 3845* (BR) (*B. meyeri-johannis*).

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** **Plate 7**

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 lirea. No margo. Granular colpus membrane well visible.

Measurements: P15–18 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** **Plate 8**

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.

Species: *B. oxyloba* Welw. ex Hook.f., *B. pycnocaulis* Irmsch.

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.

Measurements: P 20–25 µm, E 11–13 µm, P/E 1.60–2.00, m 2–3 µm, e 5–6 µm.

Species: *B. alepensis* Chev., *B. ealensis* Irmsch., *B. eminii* Warb., *B. epiphytica* Hook.f., *B. excelsa* Hook.f., *B. furfuracea* Hook.f., *B. fusialata* Warb., *B. horticola* Irmsch., *B. loranthoides* Hook.f., *B. macambrarensis* Exell, *B. macrostyla* Warb., *B. mannii* Hook., *B. molleri* (C.DC.) Warb., *B. ndongensis* Engl., *B. poggei* Warb., *B. subalpestris* Chev., *B. tatoniana* Wilcz., *B. spec.*

Specimens: *Bequaert 6120* (BR) (*B. horticola*); *Bokdam 4435* (WAG) (*B. eminii*); *Breteler & 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 14186* (P) (*B. furfuracea*); *Letouzey 14448* (P) (*B. spec.*); *Mildbraed 5580* (B) (*B. fusialata*); *Mildbread 6831* (B) (*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 **Plate 9**

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

Measurements: P 23–27 µm, E 10–14 µm, P/E 1.80–2.00, m 3–3,5 µm, e 5–6 µm.

Species: *B. kisuluana* Büttn., *B. komoensis* Irmsch., *B. nicolai-hallei* Wilcz., *B. sessilanthera* Warb., *B. subscutata* De Wild., *B. zobiensis* De Wild., *B. spec.*

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-*

hallei); *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 **Plate 10**

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.

Species: *B. buchholzii* Gilg, *B. capillipes* Gilg, *B. cavallyensis* Chev., *B. ebolowensis* Gilg, *B. fusicarpa* Irmsch., *B. jussiaeicarpa* Warb., *B. lethomasiae* Wilcz., *B. oxyanthera* Warb., *B. polygonoides* Hook.f., *B. preussii* Warb., *B. rhipsaloides* Chev., *B. rubromarginata* Gilg, *B. sanjeensis* Wilcz.

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.

Species: *B. bipindensis* Gilg ex Engl., *B. crassipes* Gilg ex Engl., *B. gladiifolia* Engl., *B. gracilipetiolata* De Wild., *B. schultzei* Engl., *B. squamulosa* Hook.f., *B. wilczekiana* Hallé.

Specimens: *Annet 223* (P) (*B. bipindensis*); *Bates 300* (G) (*B. squamulosa*); *Bequaert 6474* (BR) (*B. squamulosa*); *Breteler & De Wilde 38, 196, 204* (WAG) (*B. squamulosa*); *Breteler & De Wilde 276* (WAG) (*B. wilczekiana*); *Breteler & De Wilde 323, 335, 355, 356, 600* (WAG) (*B. squamulosa*); *Van Goossens 1579* (BR) (*B. gladiifolia*); *N. Hallé 3372, 4011* (P) (*B. squamulosa*); *Hallé & Villiers 4452* (P) (*B. schultzei*); *Hallé & Villiers 4560* (P) (*B. wilczekiana*); *Hallé & Villiers 5272* (P) (*B. squamulosa*); *Karper, De Wilde, Arends & Bouman 100, 119* (WAG) (*B. squamulosa*); *Karper, De Wilde, Arends & Bouman 158* (WAG) (*B. wilczekiana*); *Karper, De Wilde, Arends & Bouman 179, 180, 181, 326, 483, 931* (WAG) (*B. squamulosa*); *Leeuwenberg 9288, 9294* (WAG) (*B. squamulosa*); *Letouzey 12765* (P) (*B. squamulosa*); *Letouzey 12808* (P) (*B. polygonoides*); *Mildbraed 5925* (B) (*B. squamulosa*); *Onochie 34803* (FHI) (*B. squamulosa*); *Schultze in Mildbraed 6208* (B) (*B. schultzei*) syntype; *Van Veldhuizen 736, 737, 739* (WAG) (*B. squamu-*

losa); *Van Veldhuizen 744* (WAG) (*B. wilczekiana*); *Van Veldhuizen 1051* (WAG) (*B. squamulosa*); *J. J. de Wilde 8765* (WAG) (*B. squamulosa*); *Zenker 3152* (B) (*B. crassipes*).

Comments: The characteristic concave sides of this type occur also in the *B. quadrialata*-type which accommodates most of the species of section *Scutobegonia*. 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: *J. J. 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 (endocolpi) with distinct costae.

Measurements: P 27–30 µm, E 12–13 µm, P/E 2.10–2.30, m 2–3 µm, e 6–7 µm.

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

Specimens: *Braun 85* (B) (*B. poculifera*); *Breteler & De Wilde 314* (WAG) (*B. poculifera*); *Gutzwiller 2196* (BR) (*B. poculifera*); *Karper, De Wilde, Arends & Bouman s.n.* (Tuinb. Plant. 1607) (WAG) (*B. poculifera*); *Lebrun 5102* (BR) (*B. ampla*); *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** **Plate 11**

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*); *Wrighley & 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 (Cameroun 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 (all from São Tomé) 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** **Plate 12**

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** **Plate 12**

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.

Species: *B. angolensis* Irmsch., *B. bequaertii* Rob. & Law., *B. brevibracteata* Kup., *B. caffra* Meissn., *B. dissecta* Irmsch., *B. dregei* Otto & Dietr., *B. engleri* Gilg, *B. geranioides* Hook.f., *B. gueinziana* (A.DC.) Irmsch., *B. homblei* De Wild., *B. homonyma* Steud., *B. johnstonii* Oliv. ex Hook.f., *B. keniensis* Gilg ex Engl., *B. lebrunii* Rob. & Law., *B. partita* Irmsch., *B. princeae* Gilg, *B. riparia* Irmsch., *B. rostrata* Welw. ex Hook.f., *B. rudatisii* Irmsch., *B. schliebenii* Irmsch., *B. socotrana* Hook.f., *B. sonderana* Irmsch., *B. subacuto-alata* De Wild., *B. suffruticosa* Meissn., *B. sutherlandii* Hook.f., *B. verdickii* De Wild., *B. wakefieldii* Gilg ex Engl., *B. wollastonii* Baker.

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

4267 (BR) holotype (*B. bequaertii*); *Brummit & Banck 9195* (BR) isotype (*B. brevibracteata*); *Buek 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*); *Rudatis 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. suffruticosa*); *Van Veldhuizen 543* (WAG) (*B. sutherlandii*); *Van Veldhuizen 642* (WAG) (*B. engleri*); *Van Veldhuizen 874* (WAG) (*B. partita*); *Verdcourt 250* (MO) (*B. engleri*); *Verdcourt 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. socotrona* 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 pollen 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 **Plate 13**

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.

Species: *B. asplenifolia* Hook.f., *B. elatostemmoides* Hook.f., *B. filicifolia* Hallé, *B. gossweileri* Irmsch., *B. iucunda* Irmsch., *B. latistipula* Engl., *B. macrocarpa* Warb., *B. minutifolia* Hallé, *B. sciaphila* Gilg ex Engl., *B. sessilifolia* Hook.f.

Specimens: *Bos 3635* (WAG) (*B. elatostemmoides*); *Bos 10357* (WAG) (*B. macrocarpa*); *Breteler & De Wilde 261* (WAG) (*B. sciaphila*); *Breteler & De Wilde 265* (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.

15) **B. quadrialata-type** **Plate 13**

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.

Species: *B. aggeloptera* Hallé, *B. batesii* C.DC., *B. calabarica* Stapf, *B. calophylla* Gilg ex Engl., *B. ciliobracteata* Warb., *B. clypeifolia* Hook.f., *B. dielsiana* Gilg, *B. dusenii* Warb., *B. gentilii* De Wild., *B. gracilicaulis* Irmsch., *B. hirsutula* Hook.f., *B. hookeriana* Gilg ex Engl., *B. lacunosa* Warb., *B. macropoda* Gilg, *B. mildbraedii* Gilg, *B. modica* Stapf, *B. peperomioides* Hook.f., *B. potamophila* Gilg, *B. prismatocarpa* Hook., *B. pseudoviola* Gilg, *B. quadrialata* Warb., *B. raynaliorum* Wilcz., *B. salisburyana* Irmsch., *B. schäferi* Engl. p.p., *B. scapigera* Hook.f., *B. scutifolia* Hook.f., *B. scutulum* Hook.f., *B. staudtii* Gilg, *B. subtilis* Irmsch., *B. triflora* Irmsch., *B. vankerckhovenii* De Wild., *B. vittariifolia* Hallé, *B. whytei* Stapf, *B. zenkeri* Irmsch.

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 3567* (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. hookeriana*); *Dusen 90* (B) holotype (*B. dusenii*); *Gentil s.n.* (BR) holotype (*B. gentilii*); *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. cilio-bracteata*); *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*); *Ledermann 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 5511* (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. schäferi*); *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 endocolpus of this type are characteristic for a large numer 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. schäferi* (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. schäferi* 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. laporteifolia*); *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.

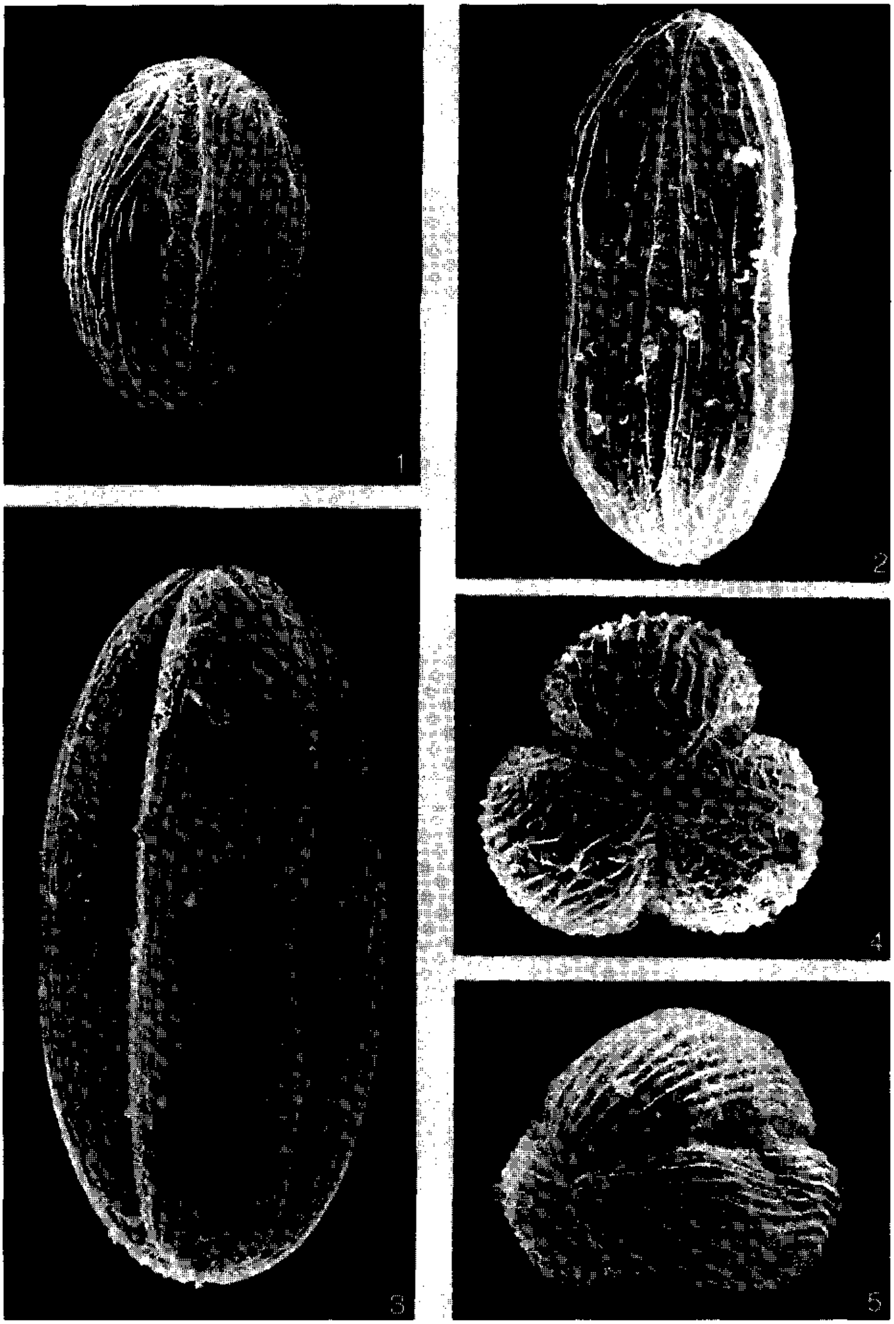

Plate I sem: 1. ***B. comorensis*** A.DC. ex Warb. (*Hildebrandt 1606*), equatorial view; 2. ***B. scutulum*** Hook.f. (*Hallé & Villiers 4786*), equatorial view; 3. ***B. princeae*** Gilg (*Münzer 101*), equatorial view; 4. ***B. subscutata*** De Wild. (*J. J. de Wilde 7551*), polar view; 5. ***B. spec.*** (*Sanford 4442*) polar view; all magnifications ca 2670x.

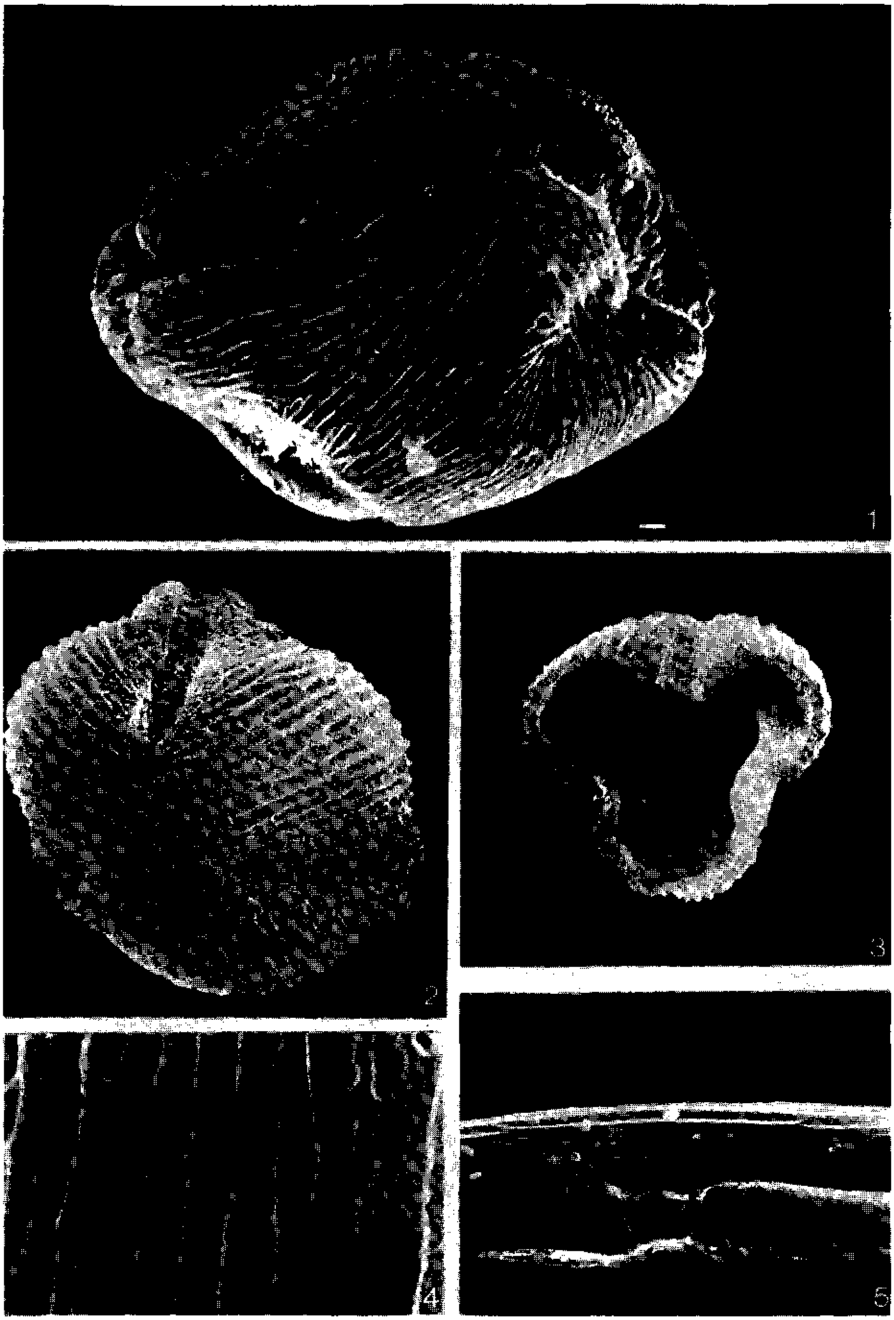

PLATE 2 SEM: 1. *B. baronii* Baker (*Perrier de la Bathie 12365*), loxocolpate grain; 2. *B. ampla* Hook.f. (*Wrigley & Melville 29*), raised sexine: 3. *B. goudotii* A.DC. (*Perrier de la Bathie 6664*), sectioned grain; 4. *B. subscutata* De Wild. (*Beentje s.n.*, Tuinb. Plant. 1384), detail striate ornamentation; 5. *B. princeae* Gilg (*Münzer 101*), detail endoaperture; all magnifications ca 2670x except 4.: ca 13335x.

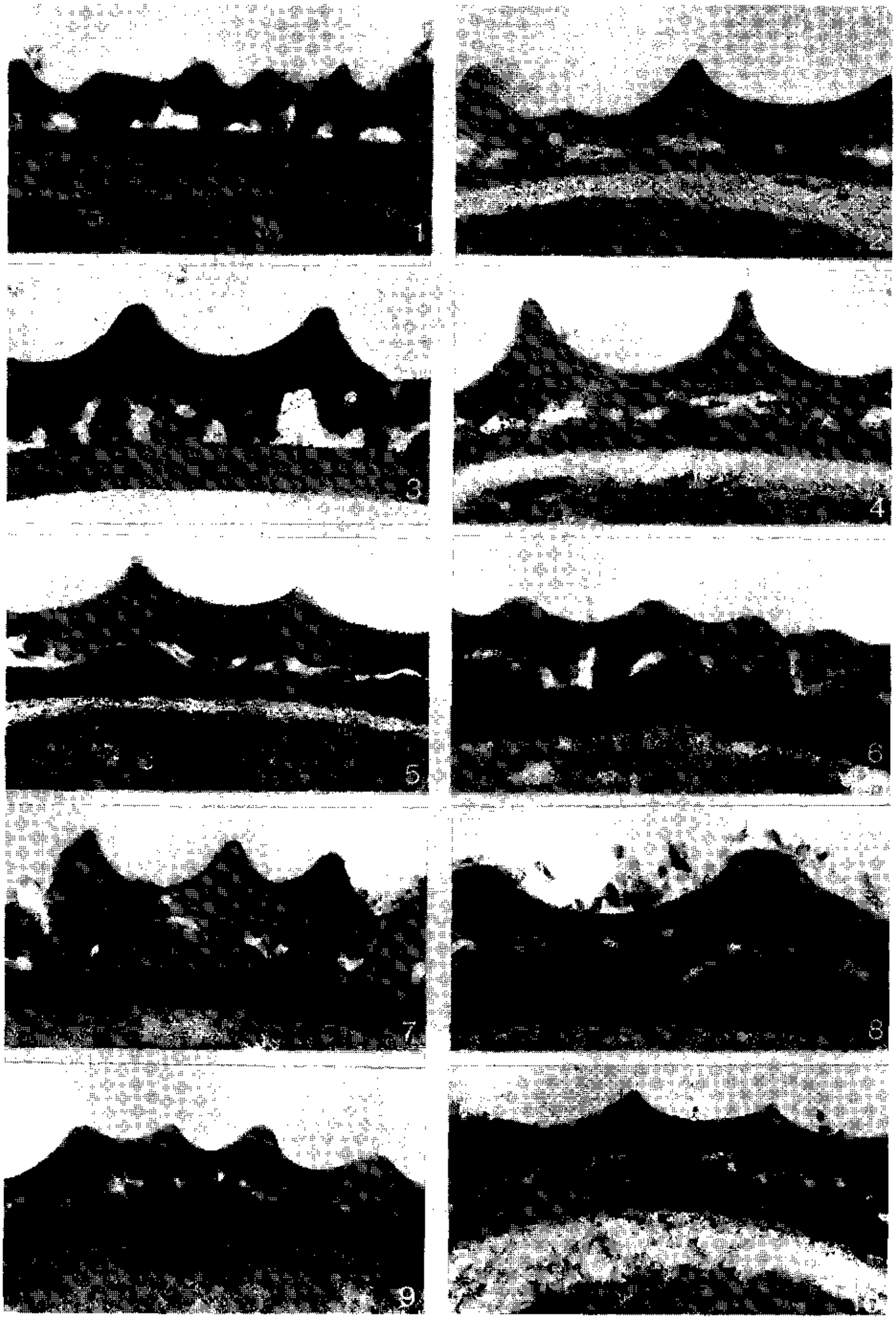

PLATE 3 TEM: 1. *B. seychellensis* Hemsley (*Van Veldhuizen 539*); 2. *B. baccata* Hook.f. (Tuinb. Plant. 1247); 3. *B. poculifera* Hook.f. (*Letouzey 14685*); 4. *B. mannii* Hook. (*Leeuwenberg 8649*); 5. *B. subscutata* De Wild. (*J. J. de Wilde 7551*); 6. *B. squamulosa* Hook.f. (*Breteler & De Wilde s.n.*, Tuinb. Plant. 1210 C); 7. *B. polygonoides* Hook.f. (*Leeuwenberg 8650* A); 8. *B. dregei* Otto & Dietr. (*Van Veldhuizen 477*); 9. *B. staudtii* Gilg (*Van Veldhuizen 445*); 10. *B. asplenifolia* Hook.f. (*Karper, De Wilde, Arends & Bouman 330*); all magnifications 34000x.

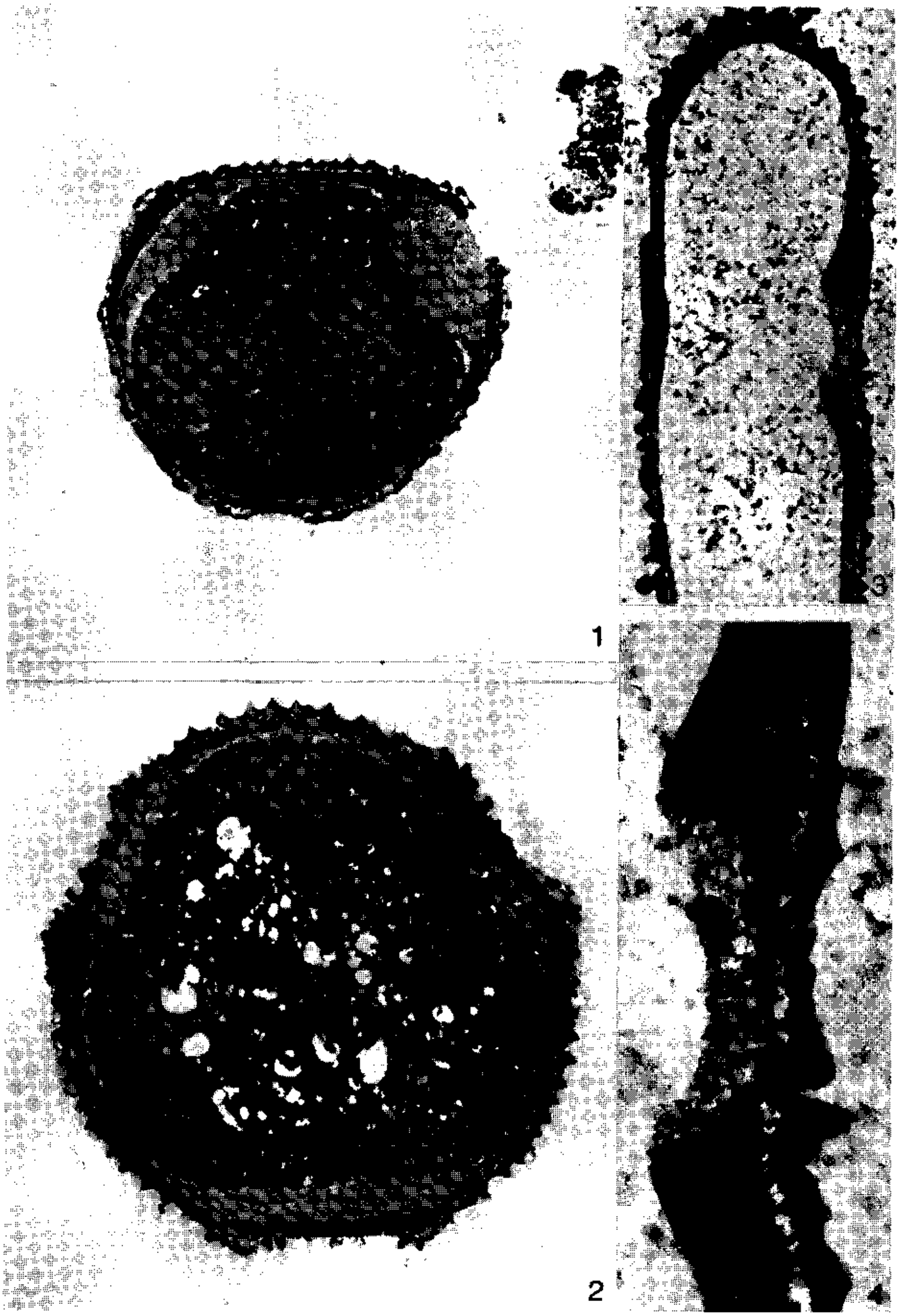

PLATE 4 TEM: 1. *B. seychellensis* Hemsley (*Van Veldhuizen 539*), cross-section, 5600x; 2. *polygonoides* Hook.f. (*Leeuwenberg 8650 A*), cross-section, 5600x; 3. *B. rostrata* Welw. ex Hook.f. (*Chevalier 34192*), cross-section endoaperture, 6400x; 4. *B. rostrata* Welw. ex Hook.f. (*Chevalier 34192*), detail endoaperture, ca 23335x.

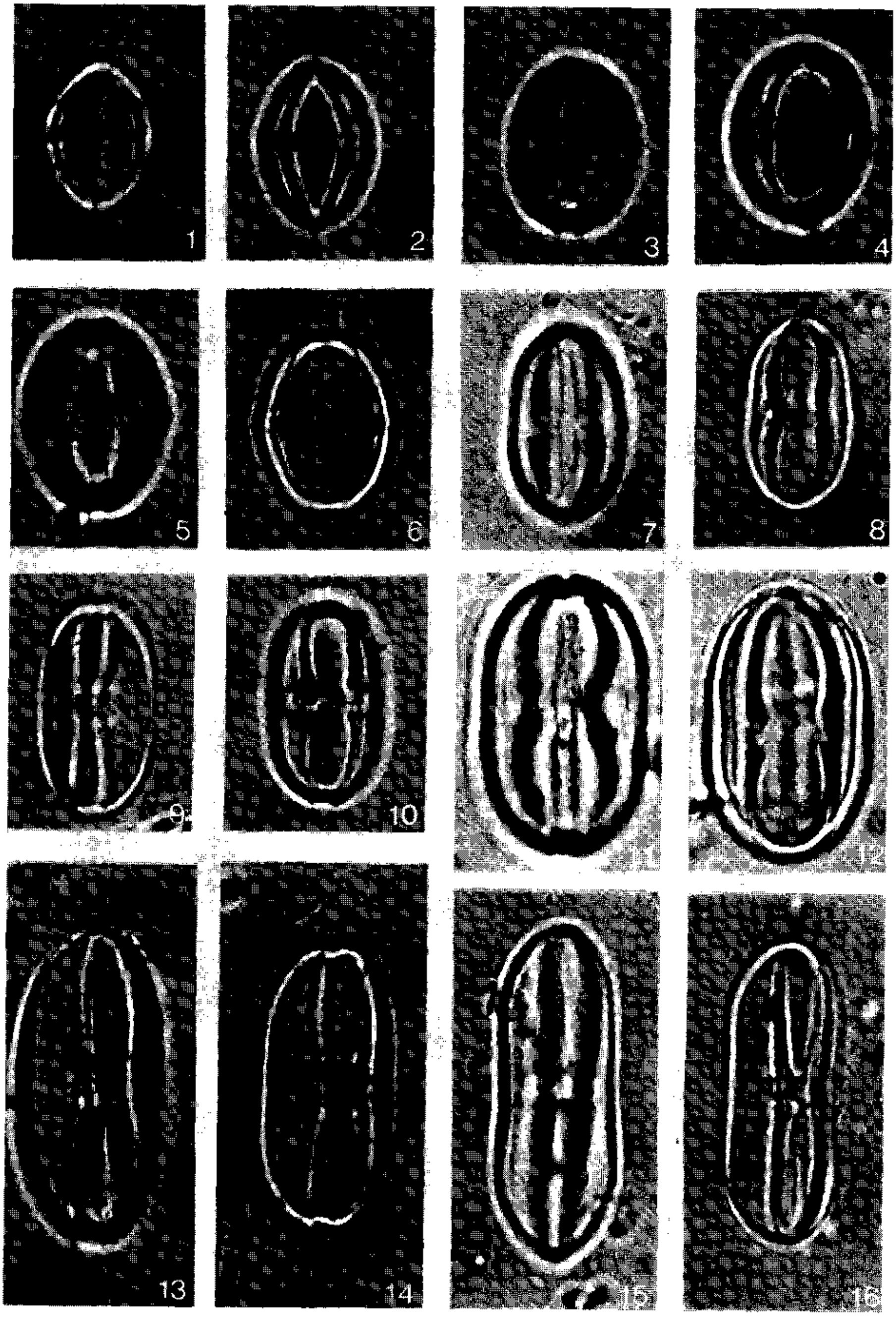

PLATE 5 LM: 1–2. *B. seychellensis* Hemsley (*Van Veldhuizen 539*); 3–4. *B. baccata* Hook.f. (*Mann 1087*); 5–6. *B. thomeana* C.DC. (*Exell 419*); 7–8. *B. pycnocaulis* Irmsch. (*Schlieben 3006*); 9–10. *B. alepensis* Chevalier (*Leeuwenberg & Voorhoeve 4792*); 11–12. *B. subscutata* De Wild. (*Bequaert 6595*); 13–14. *B. cavallyensis* Chevalier (*Leeuwenberg 3870*); 15–16. *B. squamulosa* Hook.f. (*Letouzey 12765*); all magnifications 1440x.

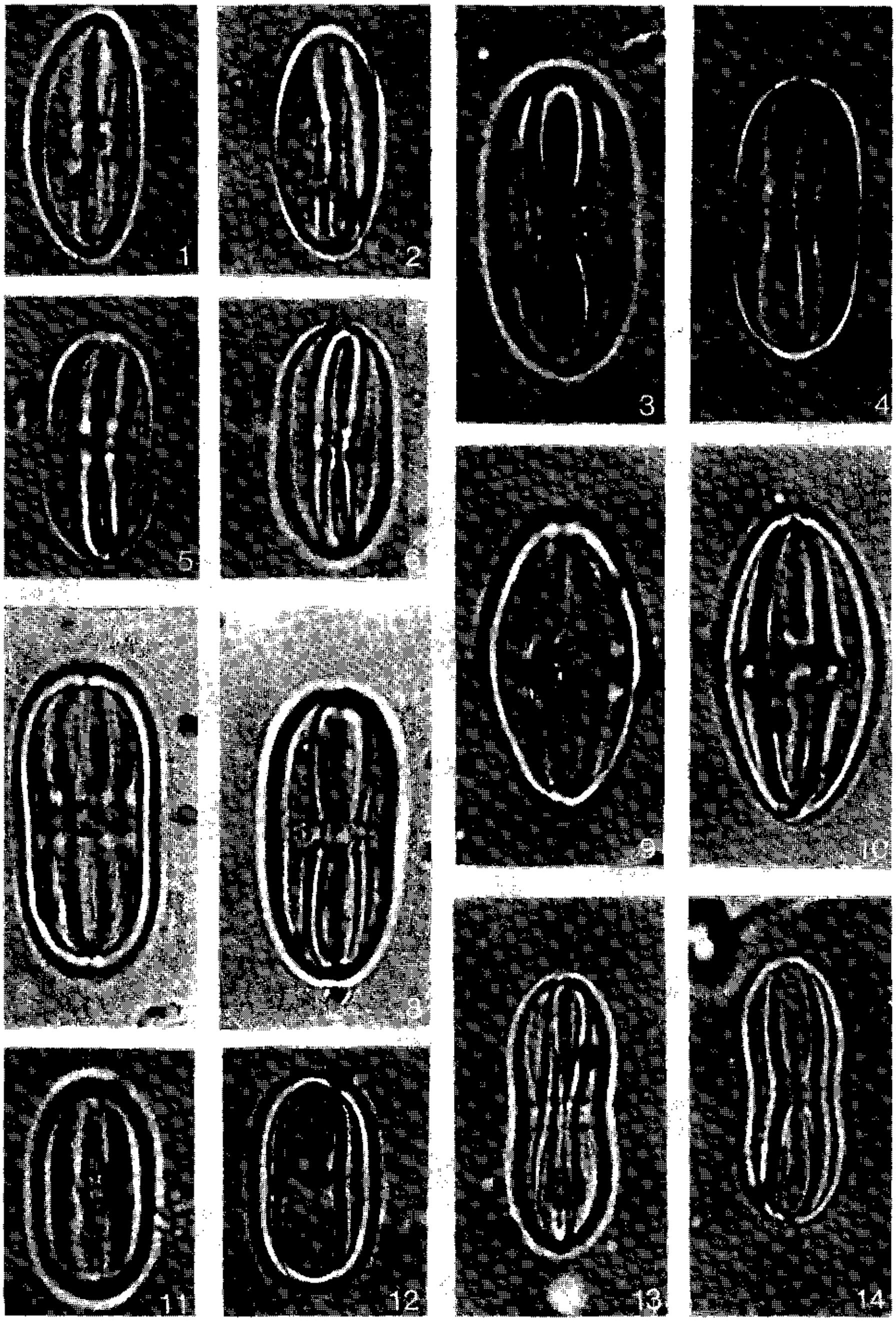

PLATE 6 LM: 1–2. *B. annobonensis* A.DC. (*Beentje 1443*); 3–4. *B. dregei* Otto & Dietr. (*Reichenbach f. 204812*); 5–6. *B. bonus-henricus* J. J. de Wilde (*J. J. de Wilde 8404*); 7–8. *B. poculifera* Hook.f. (*Leeuwenberg 10002*); 9–10. *B. ampla* Hook.f. (*Wrigley & Melville 29*); 11–12. *B. sessilifolia* Hook.f. (*Van Veldhuizen 626*); 13–14. *B. quadrialata* Warb. (*Leeuwenberg 11076*); all magnifications 1440x.

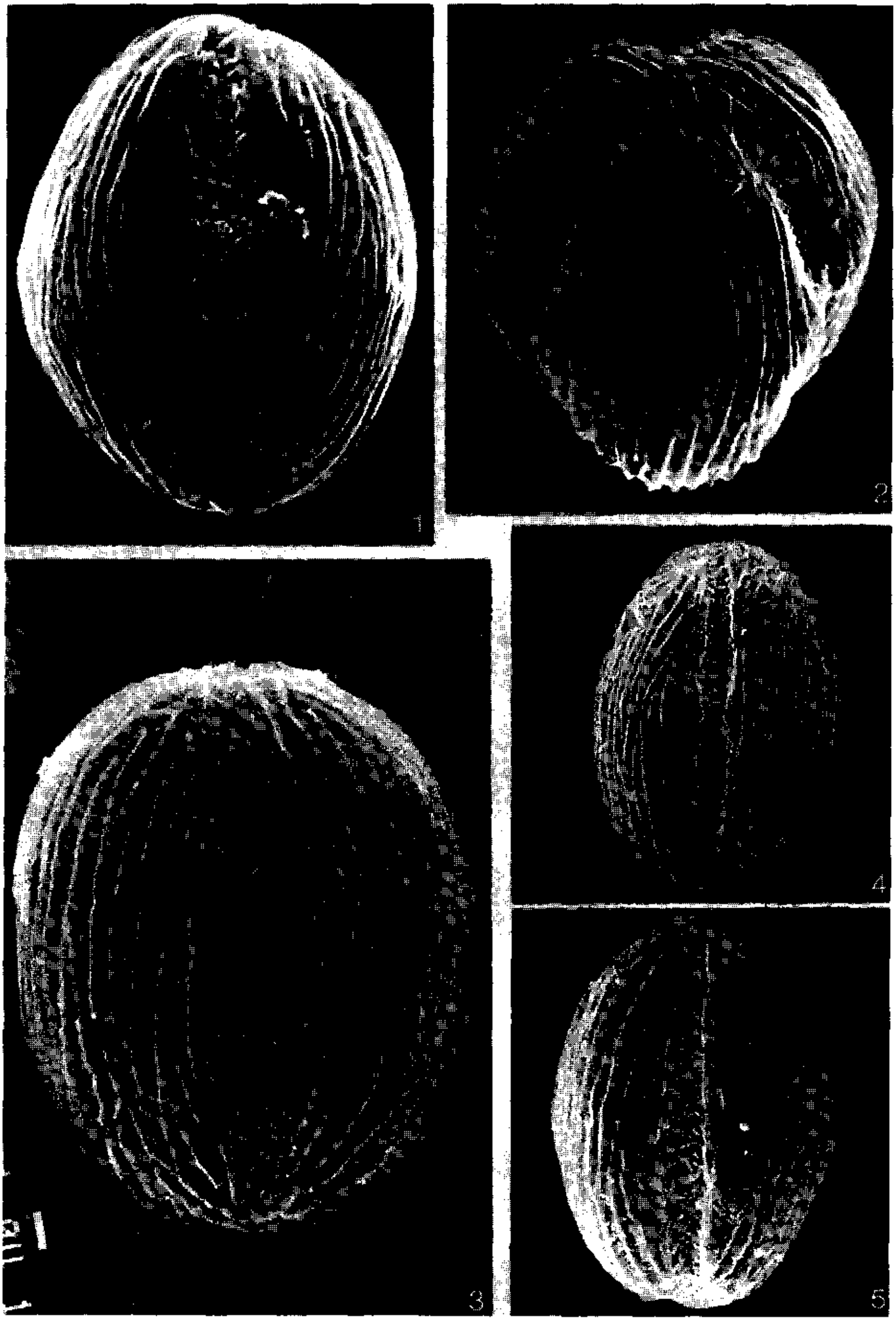

PLATE 7 SEM: 1–2. *B. seychellensis* Hemsley (*Schlieben 11672*), equatorial and polar view, 4000x; 3. *B. baccata* Hook.f. (*De Wilde, Arends & Groenendijk 105*), equatorial view, 3600x; 4. *B. comorensis* (A.DC.) Warb. (*Hildebrandt 1606*), equatorial view, ca. 2670x; 5. *B. meyeri-johannis* Engl. (*J. v.d. Walle 3845*), equatorial view, ca 2670x.

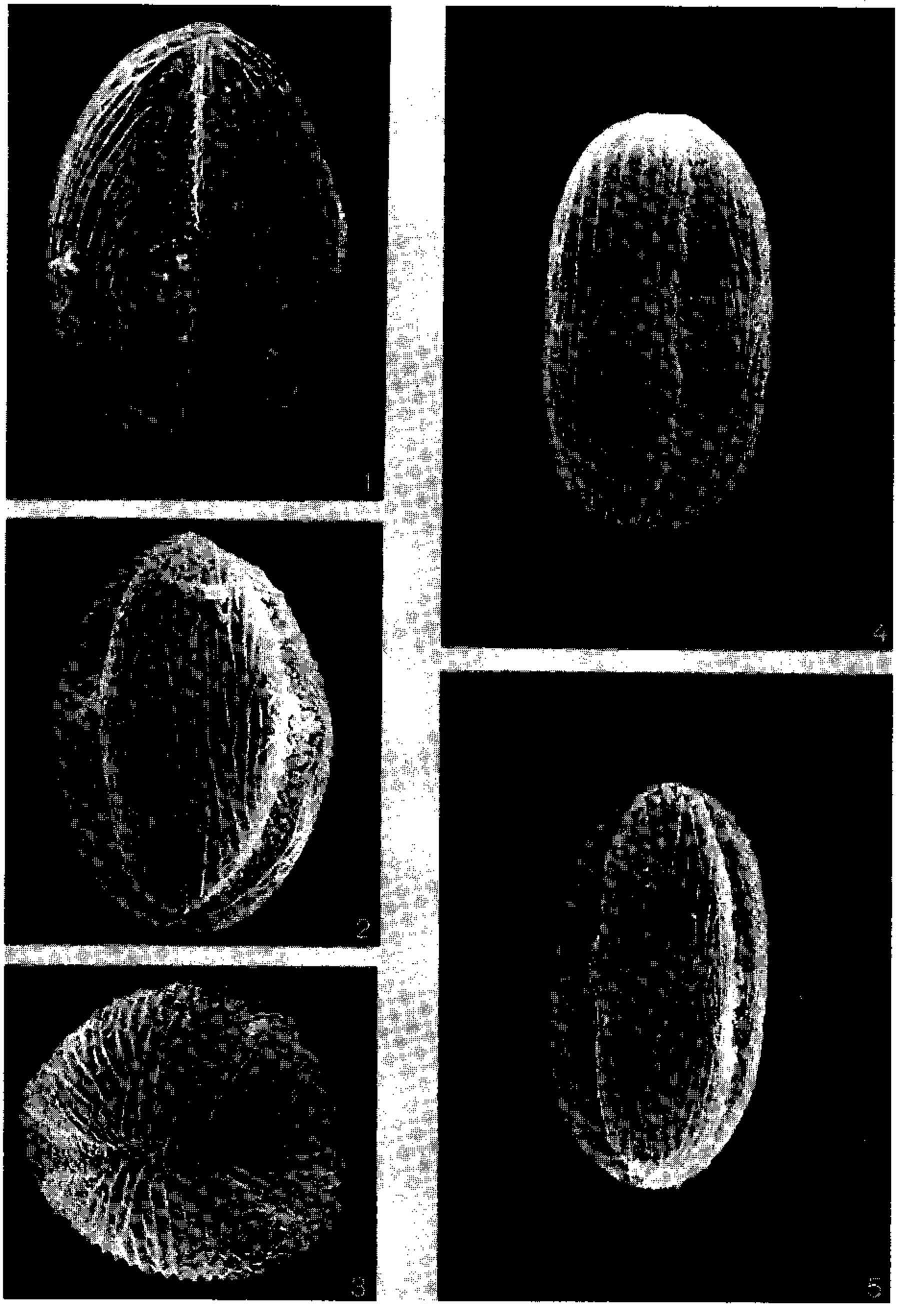

PLATE 8 SEM: 1–3. *B. thomeana* C.DC. (*Exell 419*), equatorial views and polar view; 4–5. *B. oxyloba* Welw. (*Letouzey 15010*), equatorial views; all magnifications ca 2670x.

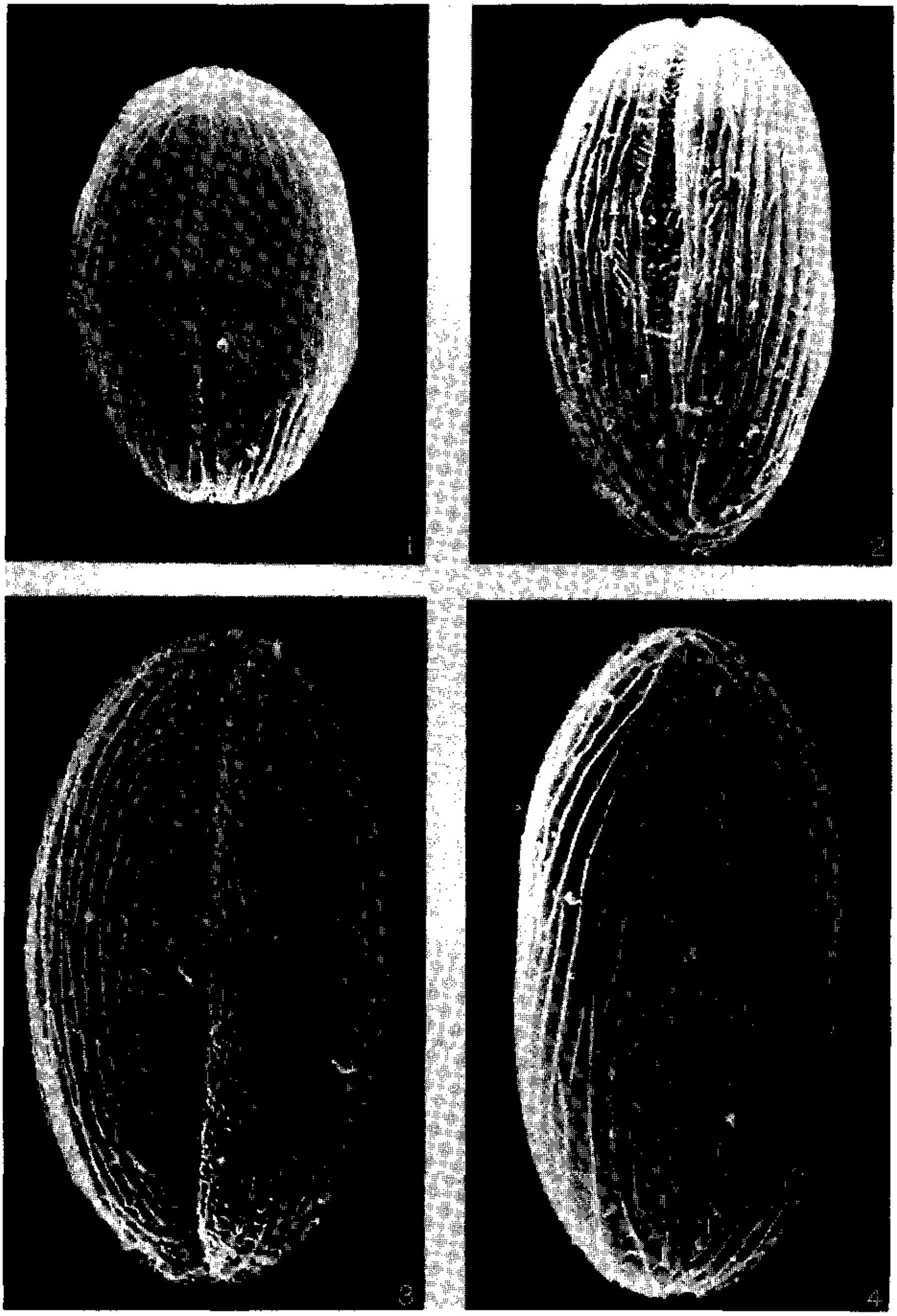

PLATE 9 SEM: 1. *B. spec.* (*Sanford 4442*), equatorial view; 2. *B. molleri* Warb. (*Moller 3*), equatorial view; 3. *B. komoensis* Irmsch. (*Hallé 3097*), equatorial view; 4. *B. kisuluana* Büttn. (*Trochain 8570*), equatorial view; all magnifications ca 2670x.

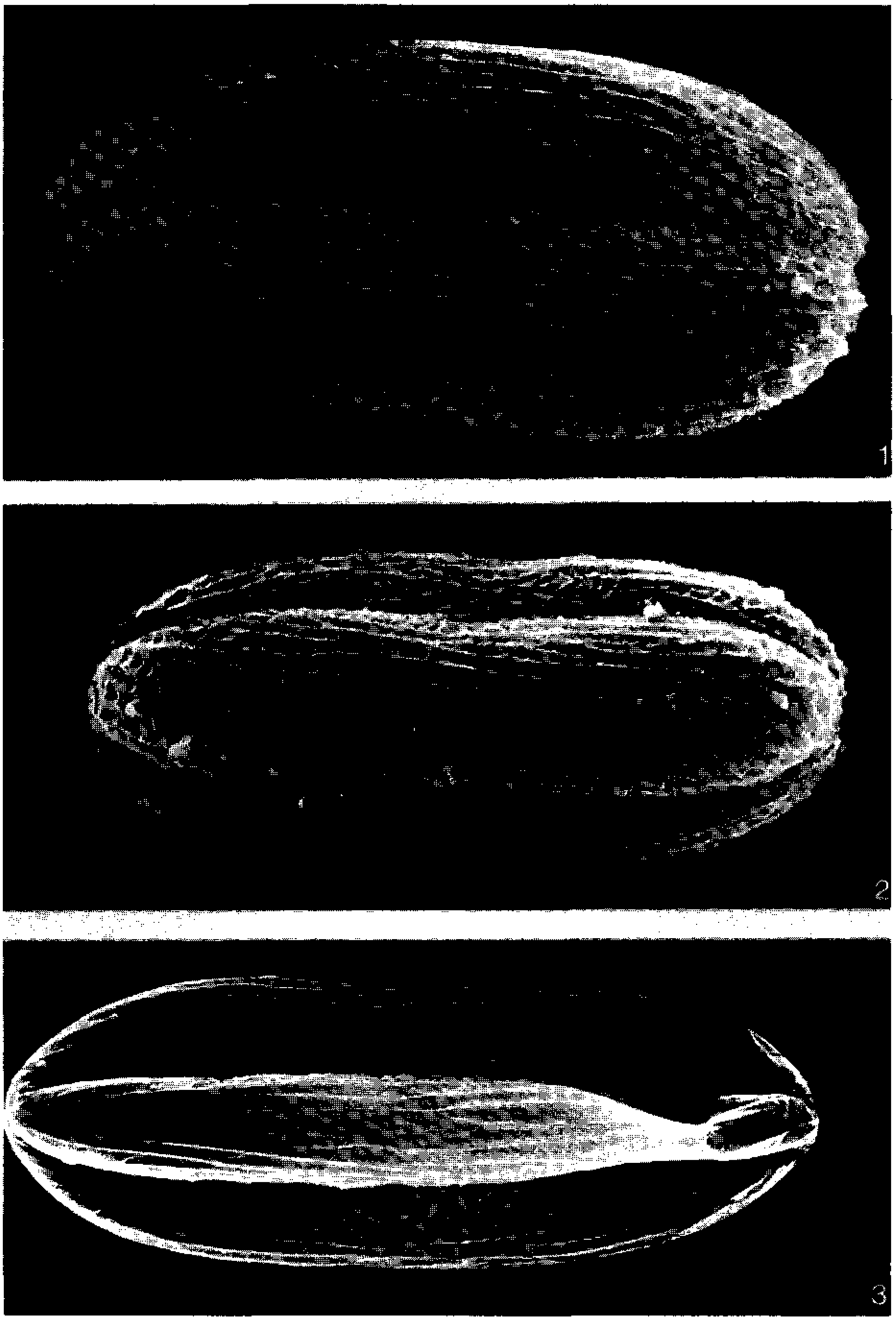

PLATE 10 SEM: 1. *B. rubromarginata* Gilg (*Conrau 80*), equatorial view; 2. *B. lethomasiae* Wilcz. (*J. J. de Wilde 8365*), equatorial view; 3 *B. wilczekiana* Hallé (*Breteler & De Wilde 385*), equatorial view; all magnifications ca 2670x.

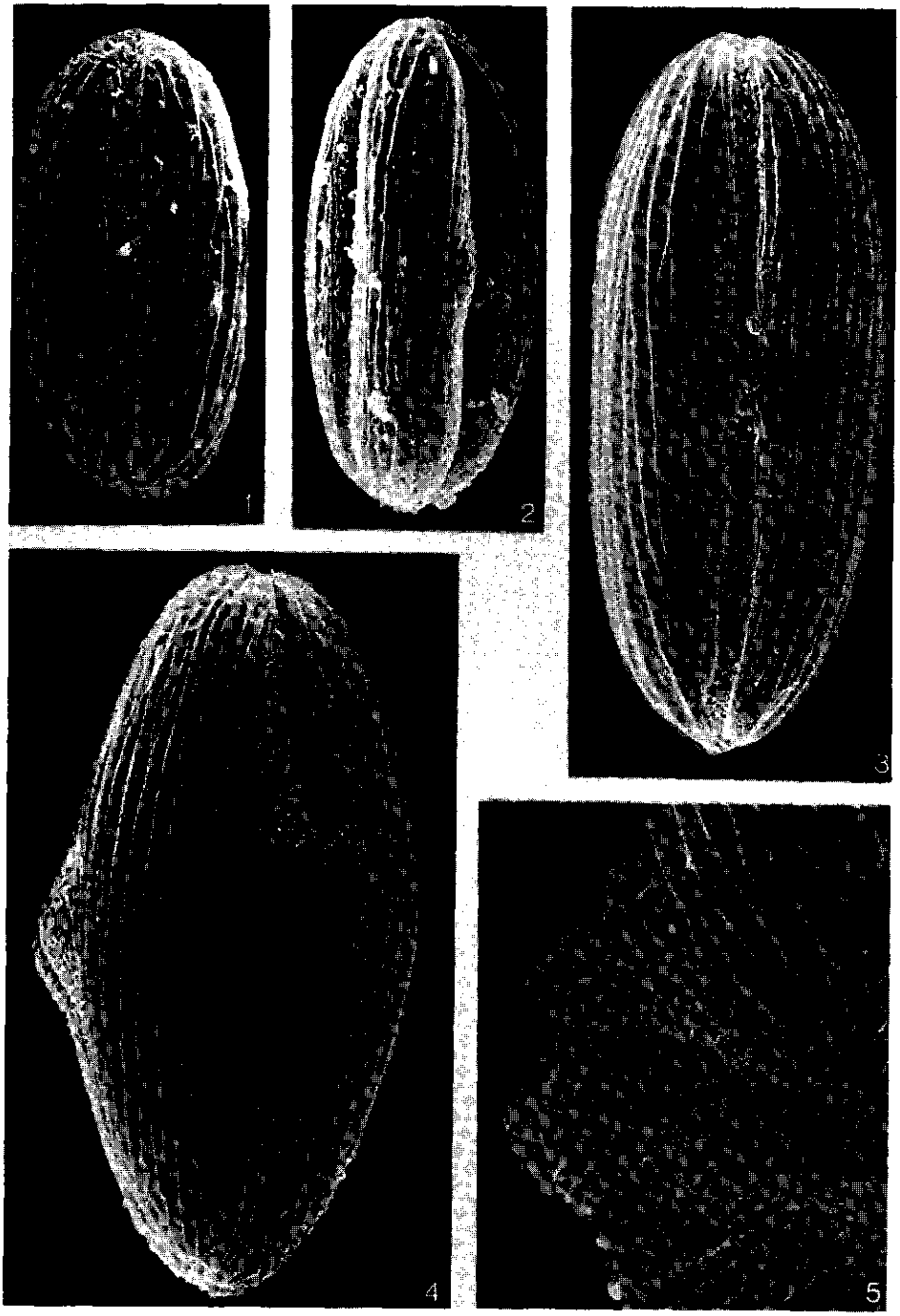

PLATE II SEM: 1–2. *B. bonus-henricus* J. J. de Wilde (*J. J. de Wilde 8404*), equatorial views; 3. *B. poculifera* Hook.f. (*Leeuwenberg 10002*), equatorial view; 4. *B. ampla* Hook.f. (*Wrigley & Melville 29*), equatorial view; 5. id. detail raised sexine; all magnifications ca 2670x except 5.: ca 6670x.

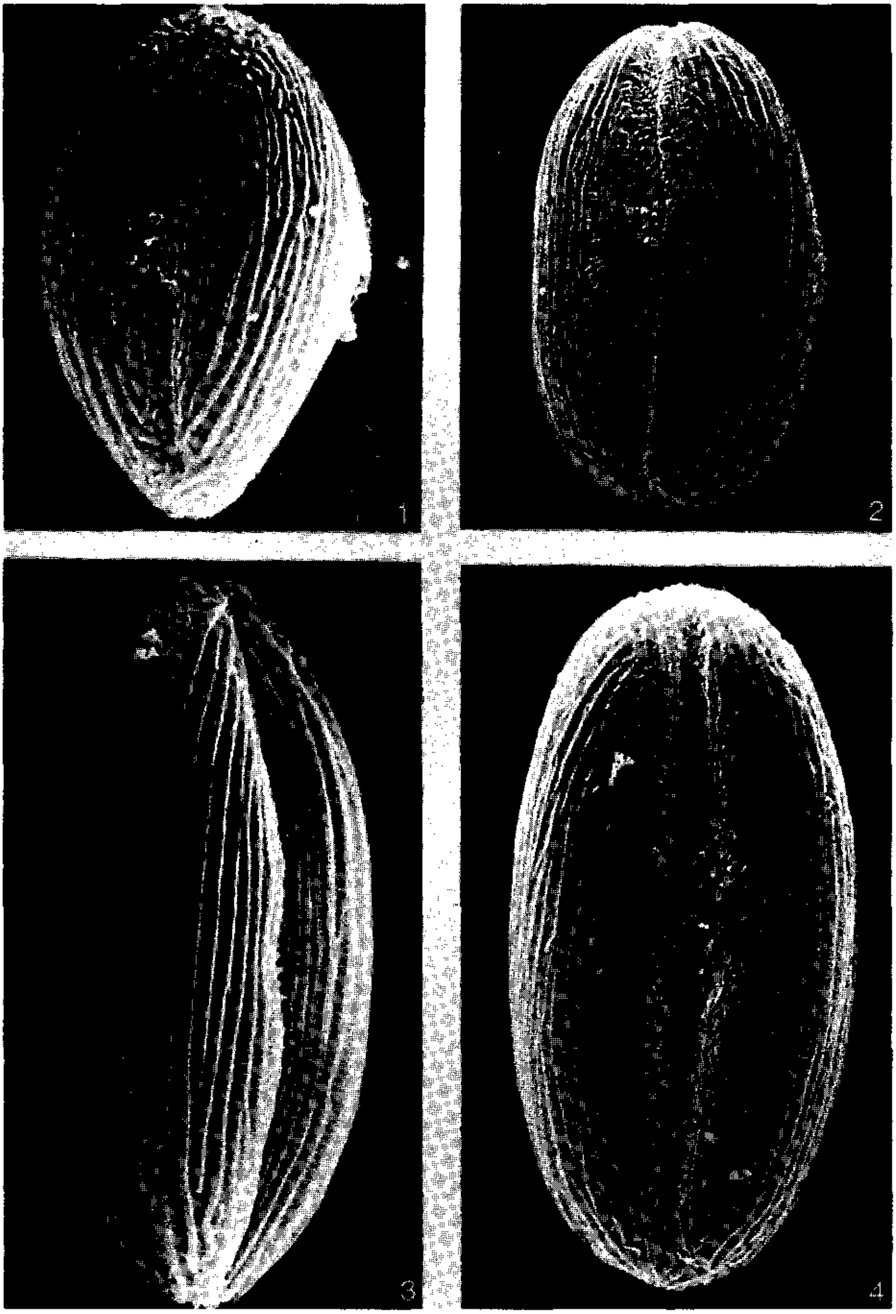

PLATE 12 SEM: 1. *B. annobonensis* A.DC. (*Beentje 1443*), equatorial view; 2. *B. johnstonii* Oliv. ex Hook.f. (*Schlieben 2920*), equatorial view; 3. *B. partita* Irmsch. (*Van Veldhuizen 874*), equatorial view; 4. *B. princeae* Gilg (*Münzer 101*), equatorial view; all magnifications ca 2670x.

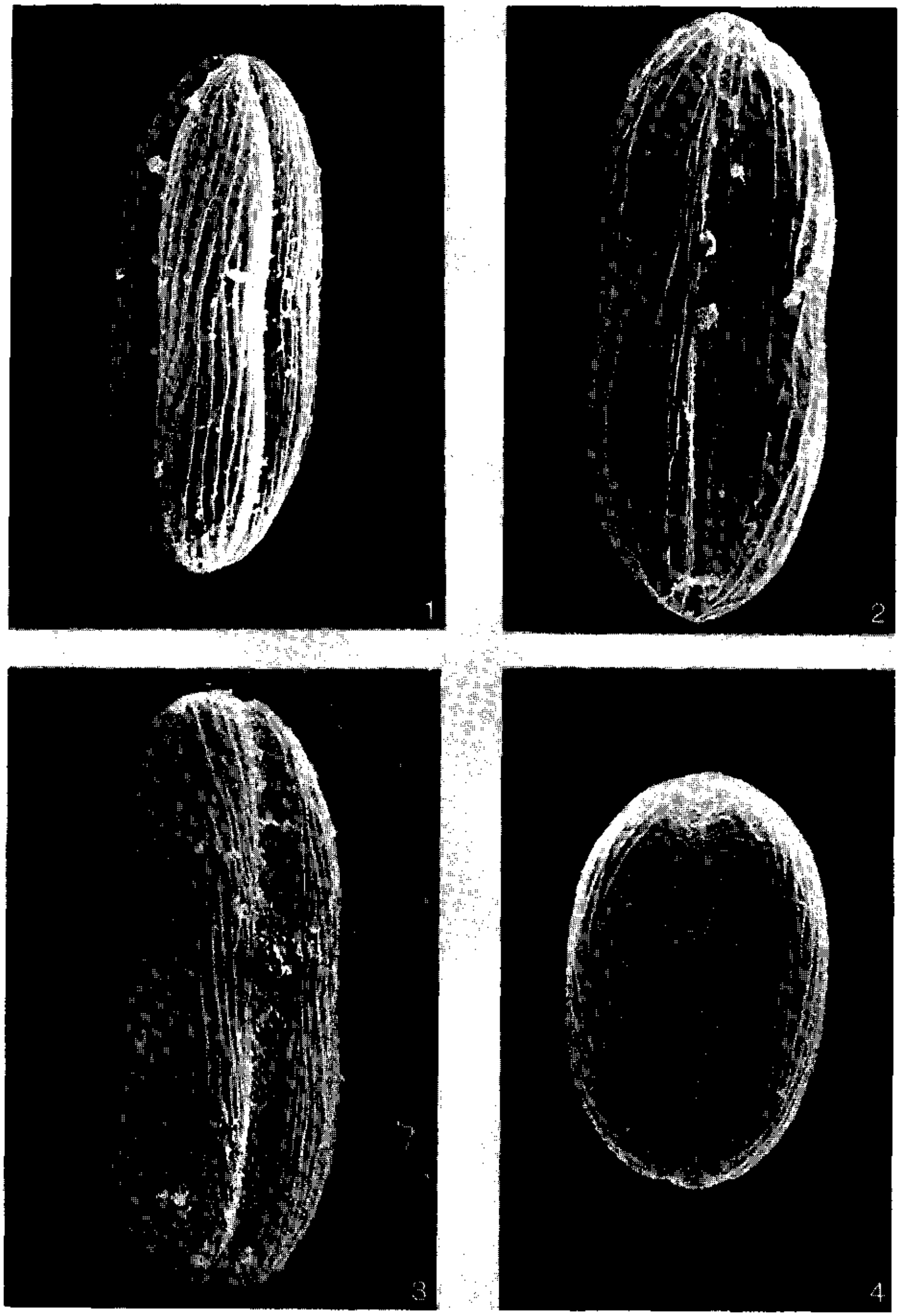

PLATE 13 SEM: 1. *B. dielsiana* Gilg (*Dinklage 257*), equatorial view; 2. *B. scutulum* Hook.f. (*Hallé & Villiers 4786*), equatorial view; 3. *B. lacunosa* Warb. (*Breteler & De Wilde 25*), equatorial view; 4. *B. sessilifolia* Hook.f. (*Van Veldhuizen 626*), equatorial view; all magnifications ca 2670x.

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 of Leuenberger (1976, p. 173): 'Die morphologische Reihen, welche bei der Typisierung der Polleneigenschaften dargestellt worden sind, können unter Umständen gleichzeitig Evolutionsreihen sein, also für phylogenetische Betrachtung Verwendung finden'.

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 macromorphological 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 'composé' (polyads). The question which arises is: '... si les groupes

	Piptadenieae	Adenanthereae	Eumimoseae
A		POLLEN SIMPLE	
B		POLLEN COMPOSÉ	
	I	II	III

FIG. 5.1. After Guinet 1969 p. 73

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 view-point 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 taxomonically 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 supra-individual 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 Wissenzweigens auftauchen. Ist es grundsätzlich möglich, von der Pollenmerkmalen her phylogenetische Schlüße 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/colporate '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 initiated 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 & CRACAFT (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 *Sonneratiaceae.*

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 'Merkmalsphylogenie' (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 macromorphological 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:

1.	Size	small (15 µm) – large (30 µm)
2.	P/E ratio	spheroidal – prolate – perprolate (P/E ± 1 – ± 3)
3.	Costae	absent – present
4.	Margo	absent – present
5.	Ornamentation	regular – irregular
6.	Sides	convex – straight – concave
7.	Poles	rounded – pointed
8.	Pollen class	3-colporate – syncolpate
9.	Size endoaperture	small (2 µm) – large (5 µm) (meridional diameter)
10.	Outline endoaperture	elliptical endoporus – oblong endocolpus
11.	Infratectal layer	distinct columellae – columellae reduced

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. cavallyensis*- 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

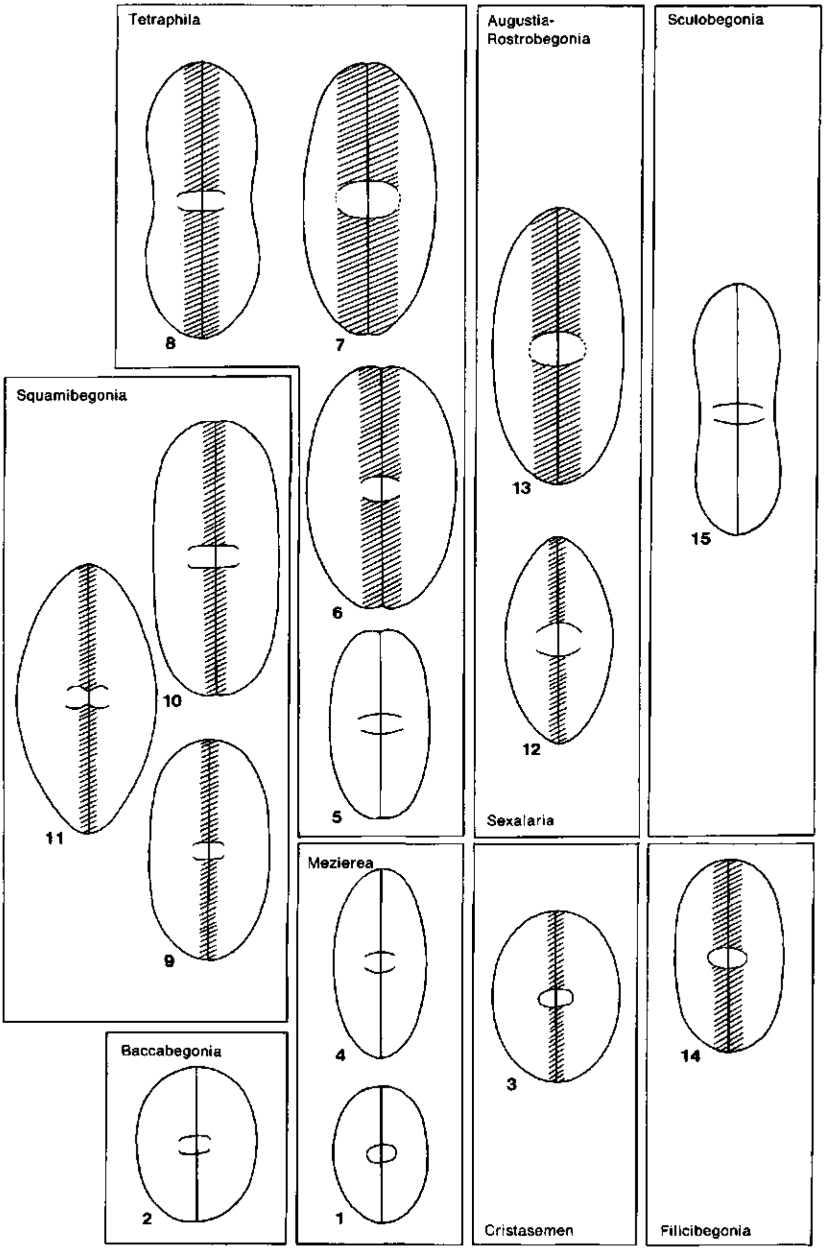

FIG. 5.2. Phylogenetic scheme. 1. *B. comorensis*-type; 2. *B. baccata*-type; 3. *B. thomeana*-type; 4. *B. oxyloba*-type; 5. *B. eminii*-type; 6. *B. komoensis*-type; 7. *B. cavallyensis*-type; 8. *B. squamulosa*-type; 9. *B. bonus-henricus*-type; 10. *B. poculifera*-type; 11. *B. ampla*-type; 12. *B. annobonensis*-type; 13. *B. dregei*-type; 14. *B. filicifolia*-type; 15. *B. quadrialata*-type.

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 groups 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. *Filicibegonia, Scutobegonia, Loasibegonia*: the seeds are small and, especially within *Scutobegonia* the cuticular sculpture is very well developed. *Filicibegonia* 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 *Filicibegonia* 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, Filicibegonia, 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 following 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. *Filicibegonia* ($x = 18$), *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 × and 4 × species and cytotypes, showed no deviating type of pollen in the polyploids, contrary to *B. macrocarpa* (*Filicibegonia*) 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 actinomorphous towards zygomorphous flowers, from 4 or 5 perianth segments towards 2, from fleshy unwinged towards dry, winged fruits, etc. (DE WILDE, 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. horticola, 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-hallei, 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-*

saloides and *B. rubromarginata.*

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 lalongate 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. elatostemmoides, 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 critized (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 raditation) 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 contintents 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.

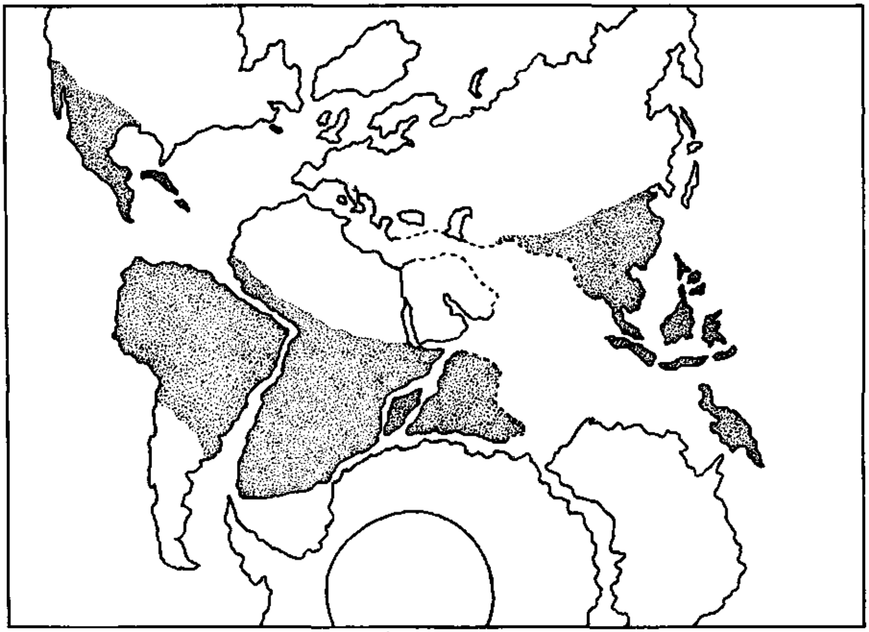

FIG. 6.1. A reconstruction of Laurasia and Gondwanaland, ca 100 million years B.P. (after SMITH, BRIDEN & DREWRY, 1973) with the approximate present-day distribution of the *Begoniaceae* (after HEYWOOD, 1978)

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.).

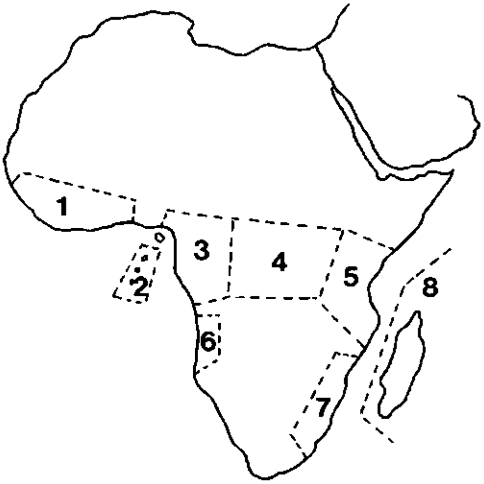

FIG. 6.2. Geographic regions.

	1	2	3	4	5	6	7	8
Mezierea	X		X	X	X	x	X	X
Baccabegonia		X						
Squamibegonia		X	X	X	X	X		
Tetraphila	X	X	X	X	X	x		
Sexalaria		X	x					
Augustia				x	X	X	X	
Rostrobegonia	X			x	X	X	X	
Scutobegonia	X		X	X		x		
Filicibegonia	X		X	X		x		
Cristasemen		X	X					

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

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 *Begonias* 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 occurrred 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, Scutobegonia* (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-morphologicall 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 different 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 facilitating 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 connection 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 development 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 Madagascar and the Comores and Seychelles respectively, and belong to section *Mezierea*. Among these, *B. seychellensis* was recently reduced to a synonym of *B. comorensis* 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., *Quadrilobaria* 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'ornamentation de l'exine a semblé tres 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 Phanérogamie, Museum 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. antsiranensis* 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* Keraudren – *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.*

Specimens examined by Keraudren-Aymonin: *B. betsimisaraka* Humbert – *Randriamahavita, RN 9375* + *Humbert & Capuron 22298* (P); *B. bosseri* Keraudren – *Sajy, RN 5761* (P); *B. françoisii* Guillaumin – *Jard. Bot. Tan. 176* (P) holotype; *B. kalabenonensis* Humbert – *Perrier de la Bathie 15469* (P) isotype; *B. madecassa* Keraudren – *Jard. Bot. Tan. 13* (P) isotype; *B. majungaensis* Guillaumin – *Bosser 19613* (P); *B. mangorensis* Humbert – *Perrier de la Bathie 17176* (P); *B. nana* l'Heritier – *Humbert 22400* (P); *B. tsimihety* Humbert – *Perrier de la Bathie 6678* (P).

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 ouline 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, Augustia, 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 Datiscaceae **Plate 15**

Many authors consider the families *Begoniaceae* and *Datiscaceae* as rather closely related. They belong to the order *Violales* in the system of CRONQUIST (1968) or even constitute an order *Begoniales* (*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 *Datiscaceae* (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 *Datiscaceae* – 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 BOESEWINKEL & 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 µm and E from 10 to 17 µm. 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 *Datiscaceae* 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 *Datiscaceae* 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.

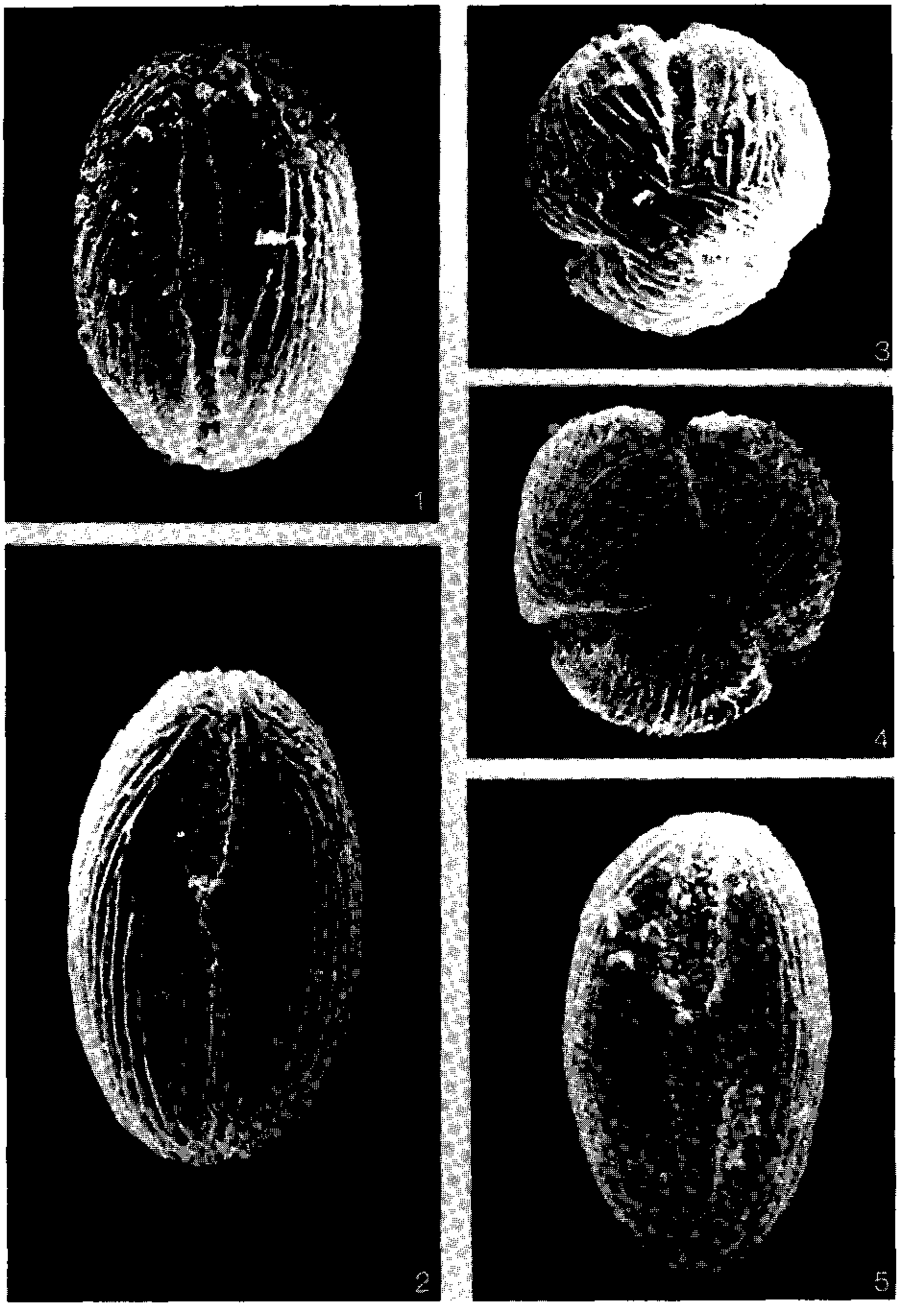

PLATE 14 SEM: 1. *B. nossibea* A.DC. (*Bosser 20219*), equatorial view; 2. *B. goudotii* A.DC. (*Perrier de la Bathie 6664*), equatorial view; 3. *B. nossibea* A. DC. (*Bosser 20129*), polar view; 4. *B. baronii* Baker (*Perrier de la Bathie 12365*), polar view; 5. *B. heteropoda* Baker (*Perrier de la Bathie 6677*), equatorial view; all magnifications ca 2670x.

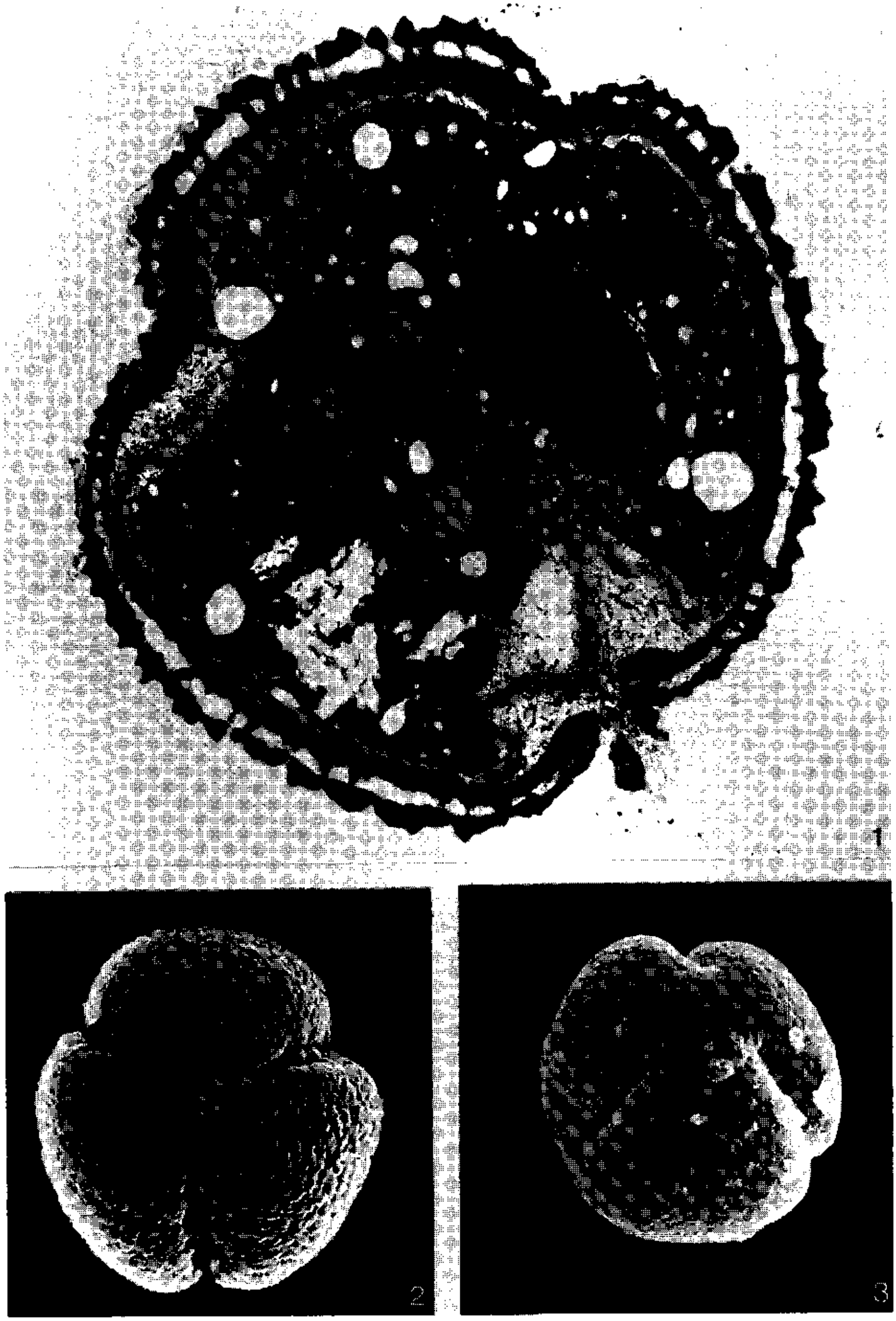

PLATE 15 TEM: 1. *Datisca cannabina* L. (culta Hort. Bot. Amsterdam), cross-section, 8000x; SEM: 2. *Datisca cannabina* L. (*Hohenack 776*), polar view, ca 2670x; 3. *Octomeles sumatrana* Miq. (*Schram 2930*), polar view, ca 2670x.

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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INDEX OF SCIENTIFIC NAMES

INDEX OF EXSICCATAE

Numbers in parentheses refer to the pollen types (chapter 4). Specimens of Madagascan *Begonias* and of *Datiscaceae* are cited in appendix 1 and 2, respectively.

(**15**); *335, 355, 356* (**8**); *369* (**15**); *600* (**8**); *650* (**15**); *702* (**6**); *s.n.* (Tuinb. Plant. 1196) (**5**)
Brown 85 (**5**)
Brummit & Banck 9195 (**13**)
Buchholz s.n. (**7**)
Buck s.n. (**13**)
Bullock 2135 (**13**)
Callens 2435 (**14**); *3567* (**15**)
Chevalier 2691 (**6**); *13752* (**5**); *21183* (**7**); *21400* (**14**); *28046* (**5**); *34192* (**13**)
Christiaensen 1511 (**15**)
Conrau 10 (**15**); *80* (**7**)
Coombe 202 (**15**)
Cours 5456 (Madagascar)
Culta Hort. Bot. Amsterdam (*Datiscaceae*)
Culta Kew s.n. (**15**)
Daramola 40454 (**7**)
Deighton 709 (**7**)
Deru 332 (**15**)
Devred 2772 (**5**)
Dinklage 257, 1029 (**15**); *1232* (**7**)
Drège 4704 (**13**)
Dusen 18 (**15**); *71* (**15**); *90* (**15**); *427* (**7**)
Dutton 68 (**13**)
Engler 640 (**13**)
Enti SP 254 (**14**)
Espirito Santo 155 (**2**)
Exell 419 (**3**)
Farron 5016 (**14**)
Felix 854 (**5**)
Forsyth Major 11 (**1**)
Gentil s.n. (**15**)
Gilbert & Thulin 781 (**13**)
Van Goossens 1579 (**8**)
Gossweiler 7636 (**14**); *7989, 8225* (**15**)
Groenendijk 7, 107 (**2**); *126* (**11**); *138* (**3**)
Gueinzius 248 (**13**)
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Gutzwiller 2196 (**10**)
Hallé 871, 1708, 2256 (**14**); *2292* (**15**); *2421* (**14**); *2841* (**15**); *3016* (**6**); *3034* (**15**); *3097* (**6**); *3372* (**8**); *3878* (**14**); *4011* (**8**)
Hallé & Le Thomas 283 (**7**)
Hallé & Villiers 1828, 4407 (**15**); *4452* (**8**); *4501* (**15**); *4560* (**8**); *4565, 4712, 4786, 4817* (**15**); *4824, 4870* (**14**); *5095, 5177* (**15**); *5223* (**14**); *5272* (**8**); *5277, 5330* (**15**); *5356, 5357, 5381, 5525* (**6**)
Heller 1902 (*Datiscaceae*)
Hildebrandt 1606 (**1**); *2995* (Madagascar)
Hladik 2721 (**7**)
Hohenack 776 (*Datiscaceae*)
Holst 3381 (**13**)
Homblé 239, 956 (**13**)
Humbert 22400, 23126, 23272, 28741 (Madagascar)
Humbert & Capuron 22298, 24886 (Madagascar)
Humbert & Cours 23890 (Madagascar)
Irvine 3344 (**15**)
Jans 1141 (**5**)
Jard. Bot. Tan. 9/10, 13, 73, 176 (Madagascar)
Johnson 129 (**7**)
Karper, De Wilde, Arends & Bouman 64 (**15**); *100* (**8**); *100* (Tuinb. Plant. 1594) (**5**); *119* (**8**); *127, 128* (**15**); *158, 179, 180, 181* (**8**); *324, 325* (**15**); *326* (**8**); *330* (**14**); *382* (**5**); *483* (**8**); 521 (**3**); *538* (**7**); *744* (**4**); *851, 905* (**5**); *925* (**15**); *931* (**8**); *s.n.* (Tuinb. Plant. 1607) (**10**)
Van Kerckhoven 12 (**15**)
De Koning 6921 (**14**)
Koorders 14047 (*Datiscaceae*)
Lebrun 4434 (**13**); *5102* (**10**)
Lecomte C – 74 (**14**)
Ledermann 1210 (**5**); *6400 A* (**15**)
Leeuwenberg 3775, 3870 (**7**); *8649* (**5**); *8650* A (**7**); *9288, 9294* (**8**); *9956* (**7**); *10002* (**10**); *11076, 12021* (**15**)
Leeuwenberg & Voorhoeve 4665 (**4**); *4792* (**5**)
Léonard 1880 (**5**); *2935 B* (**15**)
Leroy 12 (**15**)
Le Testu 5043 (**5**); *5511* (**15**)
Letouzey 8800 (**7**); *10993* (**15**); *12424* (**14**); *12765, 12808* (**8**); *14186, 14448* (**5**); *14685* (**10**); *15010* (**4**); *15157* (**7**)
Louis 3633 (**15**); *12242* (**6**)
Mann 314 (**10**); *1087* (**2**); *1276* (**10**); *1946* (**15**)
Mildbraed 3124 (**15**); *3242* (**10**); *5580* (**5**); *5624* (**15**); *5925* (**8**); *6186* (**7**); *6627* (**12**); *6831, 6985* (**5**); *7046* (**15**)
Milne-Redhead 3670 (**13**)
Milne-Redhead & Taylor 8471 (**13**)
Moller 3, 177 (**5**)
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Münzer 101 (**13**)
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Pogge 962 (**5**)
Polhill (**13**)
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Prince s.n. (**13**)
Quintas 6 (**5**); *149(999)* (**11**)

POLLEN CHARACTERISTICS OF THE GENERA OF THE *BEGONIACEAE*

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CONTENTS

SUMMARY

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

1. INTRODUCTION

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

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

2. MATERIAL AND METHODS

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

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

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

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

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

3. DESCRIPTION OF THE POLLEN TYPES

3.1. **Symbegonia type**

Plate 1

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

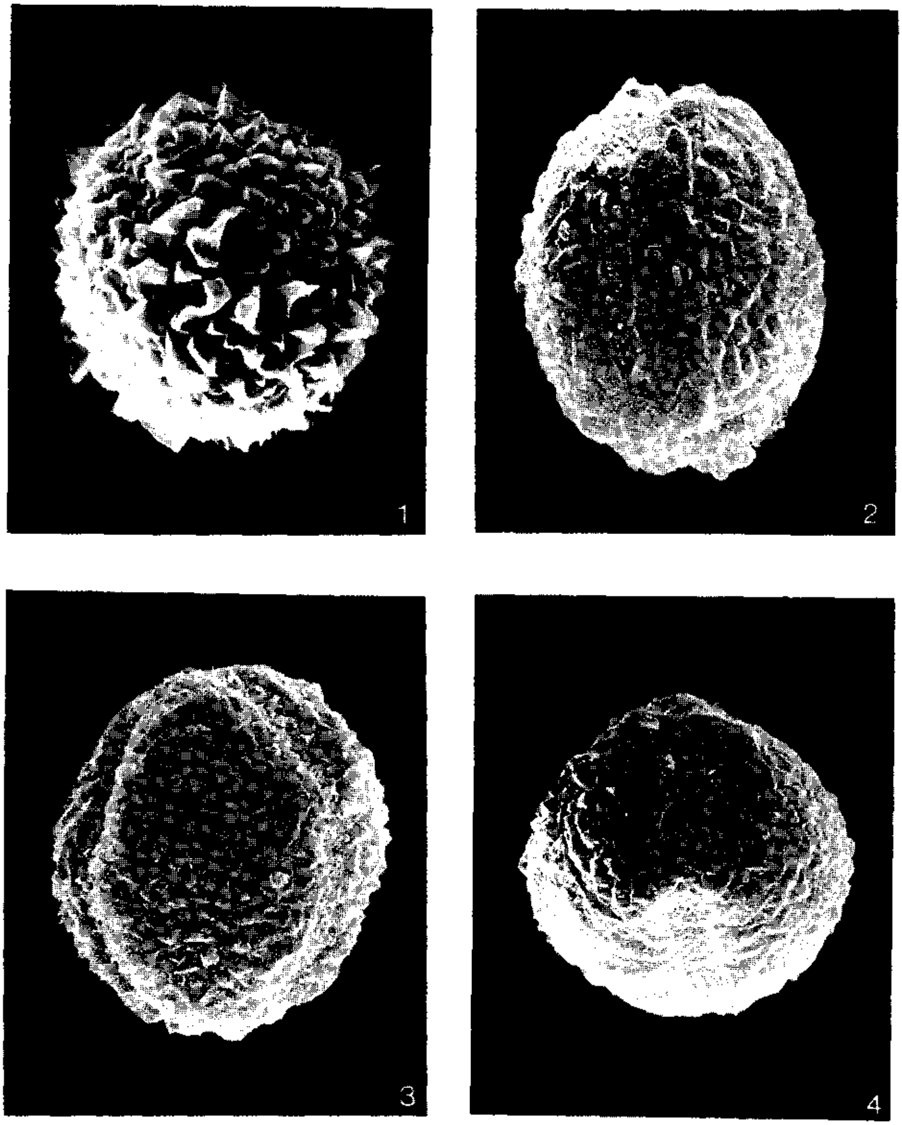

PLATE I SEM: 1. *Symbegonia* c.f. *strigosa* Warb. (*Van Veldhuizen 689*) polar view; 2–4. *Symbegonia* spec. (*Van den Berg, Katik & Cairo NGF 39909*) equatorial view; all magnifications ca 2650 ×.

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

3.2. **Hillebrandia type** **Plate 2**

Pollen class: 3-zono-colporate.

P/E ratio: Prolate.

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

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

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

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

Measurements: P 20–22 μm, E 12–14 μm, P/E 1.6–1.7, exine 0,5–0.7 μm, porus ± 1 × 2 μm.

Species: *Hillebrandia sandwicensis* Oliver.

Comments: This type resembles certain types of *Begonia* pollen, especially in apertures, overall shape and ornamentation.

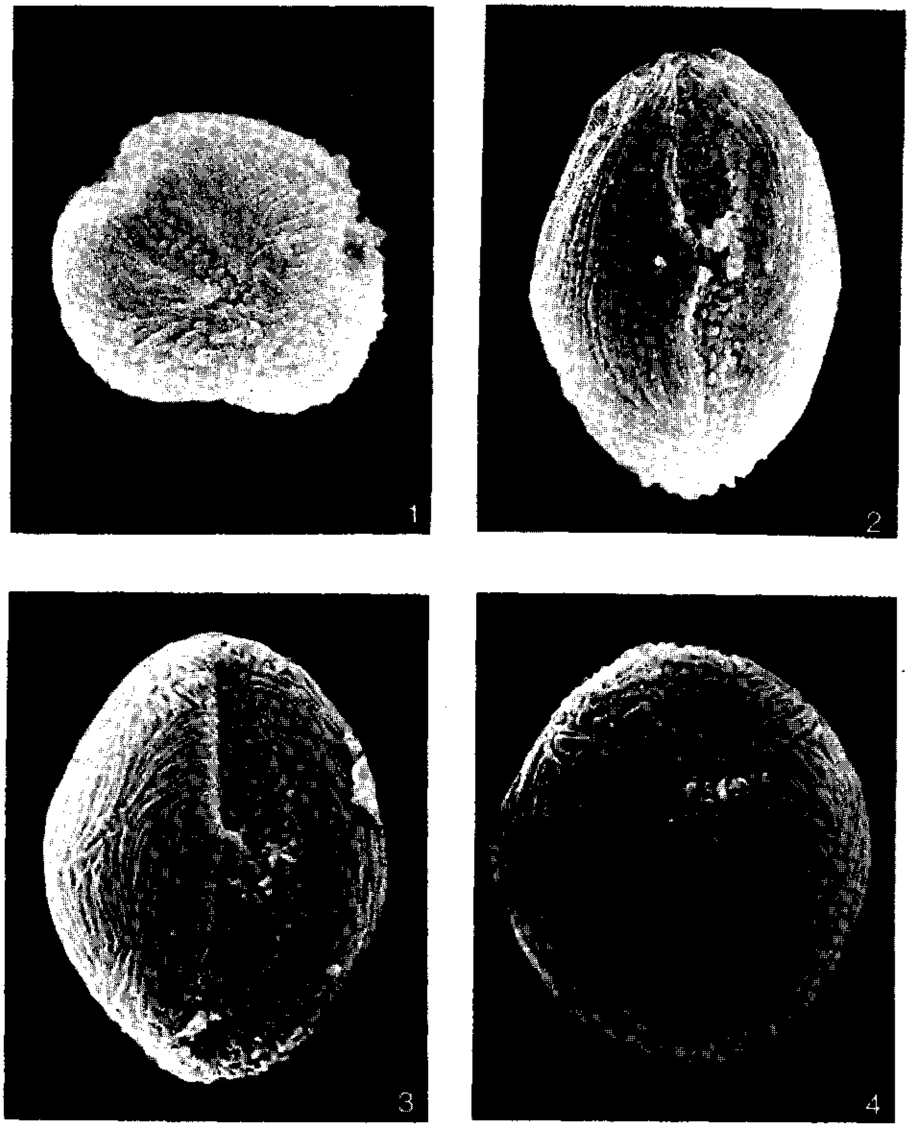

PLATE 2 SEM: 1. *Hillebrandia sandwicensis* Oliv. (*Degener 27325*) polar view; 2. id. equatorial view; 3–4 *Hillebrandia sandwicensis* Oliv. (*Carlquist 1930*) equatorial view; all magnifications ca 2650 ×.

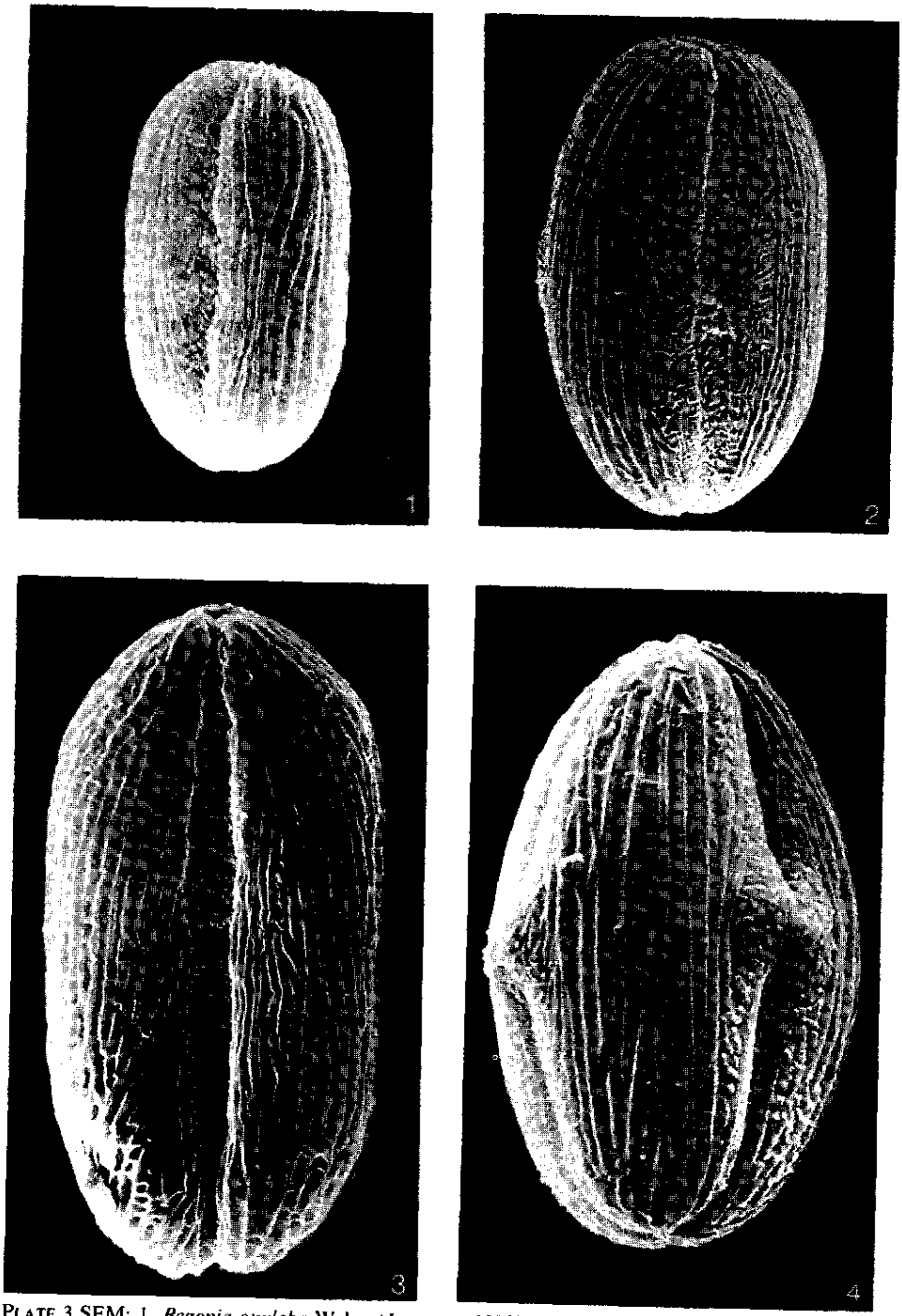

PLATE 3 SEM: 1. *Begonia oxyloba* Welw. (*Letouzey 15010*); 2. *Begonia johnstonii* Oliv. ex Hook. f. (*Schlieben 2920*); 3. *Begonia quadrialata* Warb. (*Callens 3567*); 4. *Begonia ampla* Hook. f. (*Wrigley & Melville 29*); all magnifications ca 2650 ×.

3.3. Begonia type

Plate 3

Pollen class:	3-zono-colporate, occasionally 4-colporate, loxotreme.
P/E ratio:	Subprolate to perprolate.
Apertures:	Ectoaperture – colpus, long, often even anastomosing at the poles resulting in syncolpate grains, endings (when present) acute, colpus membrane granular, granulae coarser at endoaperture, no costae. Endoaperture – porus or colpus, small to large, always somewhat (and sometimes very) lalongate, elliptical to oblong, outline more or less distinct, costae may be present especially along the long sides, the outer endings often diffuse.
Exine:	Thin, stratification hardly visible with LM, TEM observations of several species show a layered structure of the exine: an outer continuous, homogeneous tectum, an infratectal layer of more or less regular columellae, and a basal footlayer (Plate 4); wall thickness uniform.
Ornamentation:	Finely to coarsely striate, the lirae can vary in width and shape (cross section), lie close together or further apart, run parallel to the colpi or show an irregular orientation pattern; a special type of deviating non-striate ornamentation may occur in a band along the colpi (margo) and also at the poles; cross connections between the lirae occur in certain species, especially towards the poles.
Outline:	Equatorial view – often elliptical with rounded poles and convex sides, but in certain species concave sides and pointed poles. Polar view – nearly always 3-lobate due to the invaginating colpi.
Measurements:	P from 16 μm to 35 μm, E from 8 μm to 14 μm, P/E from 1.2 to 2.9, exine 0,5 μm, dimension of endoaperture in polar direction 1,5–5 μm, in equatorial direction 3–8 μm.
Species:	This general description includes all ± 120 examined African species names.
Comments:	Due to the variation in shape, size, details of ornamentation, type and shape of endoaperture etc. of the pollen types of the African species of *Begonia*, only a generalized description is given above for the genus. Within the genus it is possible to distinguish a large number of pollen types based on these characters, which will be described in a future publication. For the present purpose a description of a general *Begonia* 'type' is used in order to compare the pollen morphology of the three genera under discussion.

4. DISCUSSION

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

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

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

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

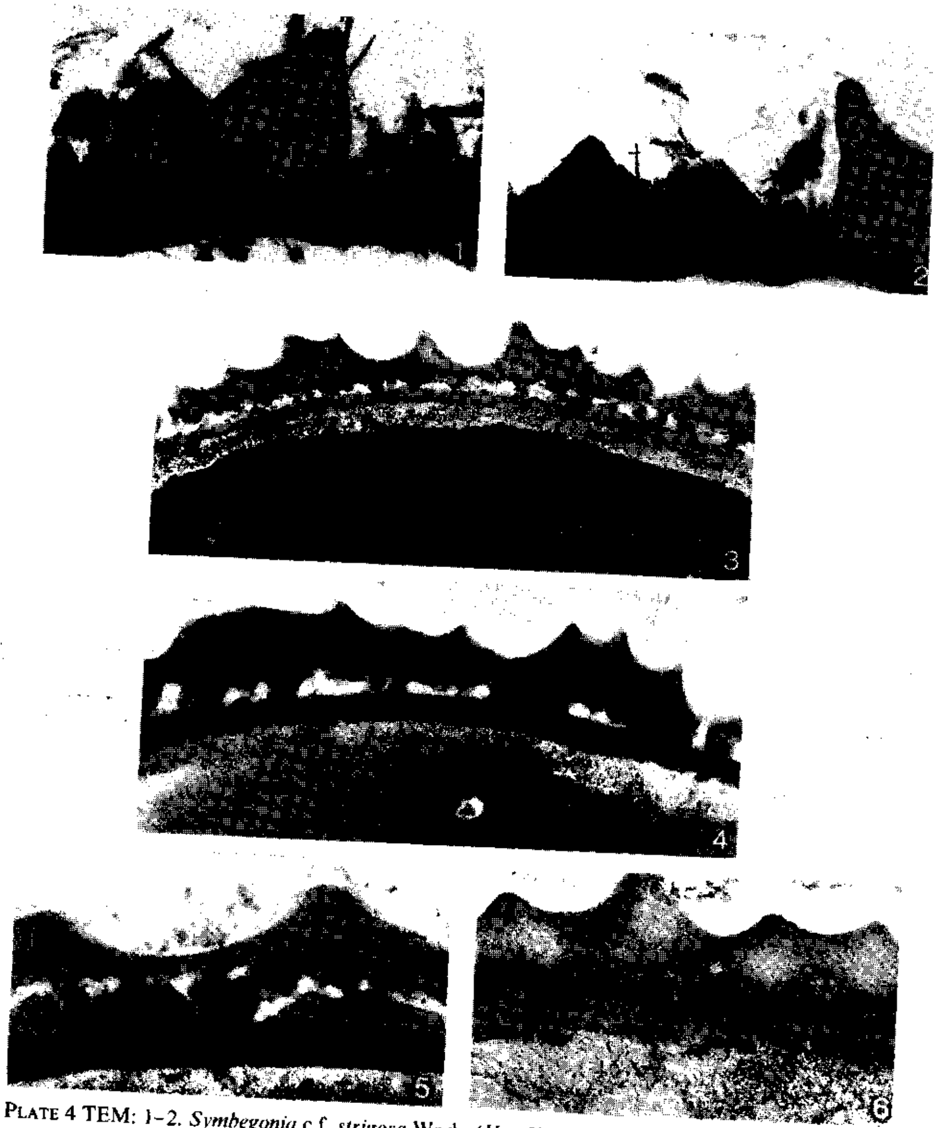

PLATE 4 TEM: 1–2. *Symbegonia* c.f. *strigosa* Warb. (*Van Veldhuizen 689*) 26000 ×; 3–4. *Begonia seychellensis* Hemsley (*Van Veldhuizen 539*) 3: ca 20700 ×, 4: 26000 ×; 5. *Begonia dregei* Otto & Dietr. (*Van Veldhuizen 477*) 34000 ×; 6. *Begonia cavallyensis* Chevalier (*Van Veldhuizen 502*) 34000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

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

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SAMENVATTING

De bouw van de stuifmeelkorrels van Afrikaanse *Begonias* wordt beschreven. Dit leidt tot de opstelling van een aantal pollen typen. De pollen typen worden geacht natuurlijke eenheden te vormen, ontstaan door evolutie en het doel van deze studie is het verloop van deze evolutie te reconstrueren en de opgedane inzichten toe te passen op de taxonomische problemen. De toepassing van pollenmorfologische gegevens bij fylogenetische reconstructie is kritisch bekeken. De uitkomsten van de pollenmorfologie zijn vergeleken met die van andere disciplines zoals de zaadmorfologie, de bestudering van de placentatie, de karyologie en, vooral, de macromorfologische taxonomie. De relatie tussen pollenmorfologie en geografische verspreiding wordt besproken, terwijl ook de pollenmorfologie van de *Begonias* van Madagascar en die van de verwante familie der *Datiscaceae* is onderzocht.

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