Acta Bot. Neerl. 31 (4), August 1982, p. 297–305.

MICROMORPHOLOGY OF THE SEED COATS IN BEGONIA SECTION SQUAMIBEGONIA WARB.

F. BOUMAN and A. DE LANGE

Hugo de Vries-Laboratorium, Universiteit van Amsterdam.
Plantage Middenlaan 2A, 1018 DD Amsterdam

SUMMARY

Begonia seeds can be distinguished from all other angiospermous seeds by the presence of a ring of collar cells under the micropylar-hilar part of the seed, which acts as an operculum during germination. Moreover, the differences in size, epidermal pattern, form of the cells and sculpturing of the testa provide additional characters, which can be of use in the delimitation of species and sections of the genus.

The recent circumscription of *Begonia* Sect. *Squamibegonia* Warb. by DE WILDE is corroborated by the micromorphological characters of the seed coats. The seeds of the section are relatively large and characterized by the absence of clear cuticular sculptures and by a cleavage of the anticlinal walls.

The loss of micromorphological ornamentation seems to be related with the change-over to a different dispersal strategy.

1. INTRODUCTION

The genus *Begonia*, with an ample 800 species arranged in 60 sections, constitutes one of the larger genera of the flowering plants. The two other genera of the Begoniaceae (*Symbegonia* and *Hillebrandia*) contain 12 and 1 species, respectively. The last monograph of the family (IRMSCHER 1925) needs, in the light of the systematic progress, critical readjustment. Next to the traditional gross-morphological characters, additional character sets taken from a.o. anatomy, palynology, cytology and chemotaxonomy may be of considerable use to the taxonomist in the delimitation of species and sections.

DE WILDE & ARENDS (1980) typified and circumscribed *Begonia* sect. *Squamibegonia* Warb. anew. One of the striking characters of this section is the development of a "perianth-cylinder" in the female flowers. After a critical revision they recognized only three species, *viz.*, *Begonia ampla* Hook. f., *B. poculifera* Hook. f., and *B. bonus-henricus* J. J. de Wilde. Several synonyms were eliminated and four species formerly included in this section were transferred to section *Tetraphila* A. DC., *viz.*, *B. loranthoides* Hook. f., *B. cataractarum* J. Br. et K. Schum., *B. rhopalocarpa* Warb. and *B. zimmermannii* Peter ex Irmsch. Also *B. baccata* Hook. f. and *B. crateris* Exell were excluded from *Squamibegonia*. These

species were tentatively referred to the section *Mezierea,* a more final taxonomic position awaiting further research.

In addition to the work of Dr. J. J. F. E. de Wilde on the African Begonias the micromorphological characters of seeds were studied.

Present knowledge of the development and structure of *Begonia* seeds is rather scanty. According to DAVIS (1966) and CORNER (1976) the ovules are bitegmic and crassinucellar. The micropyle is formed by both integuments. The outer and inner integuments are both only two-layered and not or only slightly multiplicative. The nucellar epidermal cells elongate radially and simulate an endothelial layer. During seed development the nucellus is resorbed and the integuments are crushed except for the outer layer of the outer integument, which forms an exotesta with lignified inner an anticlinal walls. The endosperm is nuclear, but becomes cellular in later stages. Mostly, only the outermost layer persists in the mature seed as an aleuron layer.

Begonia seeds are small, and therefore it is difficult to study their exomorphic details by optical microscopy. Photographs or drawings generally lack details necessary for comparative studies. Such details can be obtained with the Scanning Electron Microscope (SEM). Earlier SEM studies on seeds (see for reviews BRISSON & PETERSEN 1976, BARTHLOTT & EHLER 1977) have clearly shown that micromorphological characters of seed coat surfaces can be of taxonomically diagnostic value.

From an explorative study of about 50 species from 20 different sections it appears that *Begonia* seeds show a great diversity in structure (BOUMAN & DE LANGE, in prep.). As far as can be ascertained *Begonia* seeds are discernible from the seeds of all other angiospermous families by the presence of so-called collar cells. These collar cells form a transverse ring around the seed and bound the micropylar-hilar region. During seed germination this micropylar-hilar part functions as a seed lid (operculum) which is lifted after the splitting of middle lamellae of the cell walls between operculum and collar cells. Moreover, also the walls between the collar cells can split, thus clearing the way for the seedling.

Apart from these shared characters *Begonia* seeds show a great diversity in structure. Seed length differs considerably, *e.g.,* from about 0.28 mm in *B. semiovata* Liebmann to more than 2 mm in *B. eboloensis* Engler. The form of the seed varies from narrowly to broadly ellipsoid. The seed coat shows a clear cellular pattern. There are great differences in the arangement of the exotestal cells and in the form of the single cells. The anticlinal walls may be straight or undulated. The testa surface can be smooth or covered by an excessive pattern of cuticular foldings. In some cases the seed is provided with an aril-like structure. Thus, it appears that micromorphological features of *Begonia* seeds are of taxonomic value.

The purpose of this study is to compare the above-mentioned revision of *Begonia* sect. *Squamibognia* with the results of a comparative study of the seed micromorphology.

2. MATERIAL AND METHODS

Specimens examined:
Begonia ampla Hook. f., São Tomé, Groenendijk 126, (WAG), also cultivated,
Begonia poculifera Hook. f. var. *poculifera* Culta, Bot. Gardens, Meise, Belgium, J. J. de Wilde 8771 (WAG), also cultivated,
Begonia poculifera Hook. f. var. *teusziana* (J. Braun et K. Schum.) J. J. de Wilde, Cameroun, Leeuwenberg 10.002 (WAG) and Breteler and J. J. de Wilde 314 (WAG), also cultivated,
Begonia bonus-henricus J. J. de Wilde, Cameroun, J. J. de Wilde 8404 (WAG, YA).

As far as necessary, dust-polluted seeds were treated in an ultrasonic cleaner (freq. 50 kHz). The seeds were sputter-coated with gold-palladium for about 3 min. and observed in a Cambridge Stereoscan Mark 2a.

3. RESULTS

3.1. *Begonia ampla* Hook. f. *Fig. 1* A–F

Seeds elliptic to narrowly elliptic. Variation in length from 6.70 to 7.55 $\times 10^{-4}$m, in width from 2.75 to 3.15 $\times 10^{-4}$m; mean 7.05 $\times$ 2.97 $\times 10^{-4}$m. Ratio length: width is 2.4. Collar cells varying in length from 1.18 to 2.07 $\times 10^{-4}$m; mean 1.56 $\times 10^{-4}$m. Ratio collar: seed length is 1:4.6. Form elongated, irregularly tetragonal. Anticlinal cell walls between the collar cells almost straight, those adjacent to testa cells mostly slightly curved.

Testa cells partly in a longitudinal pattern, those in continuation of the collar cells more or less clearly arranged in short, irregular rows of 4–6 cells. The cells of the chalazal region more disorderly arranged. Form of the testa cells isodiametric-polygonal, mostly hexagonal. Anticlinal cell walls from almost straight to curved.

Operculum obtusate, composed of many irregularly arranged small cells. Cuticle with small parallel foldings on the anticlinal walls.

Micromorphology: Anticlinal boundaries usually smooth, in dried seeds, however, splitting along the middle lamellae. This results in a typical structure. The cuticle ruptures and the outermost part of the anticlinal walls unfolds. This may occur both in testa and in collar cells. Outer periclinal walls concave without significant sculpture. The surface of the outer cell wall smooth, the cuticle without clear micro-ornamentation.

3.2. *Begonia poculifera* Hook. f. var. *poculifera* *Fig. 2* A–F

Seeds elliptic to narrowly elliptic, varying from almost straight to weakly sigmoid or curved. Variation in length from 7.44 to 8.02 $\times 10^{-4}$m, in width from 2.74 to 3.86 $\times 10^{-4}$m; mean 7.79 $\times$ 3.42 $\times 10^{-4}$m. Ratio length: width is 2.3.

Collar cells varying in length from 0.71 to 1.64 $\times 10^{-4}$m; mean 1.17 $\times 10^{-4}$m. Ratio collar: seed length is 1:6.7. Form elongated, irregularly tetragonal. Anticlinal cell walls straight.

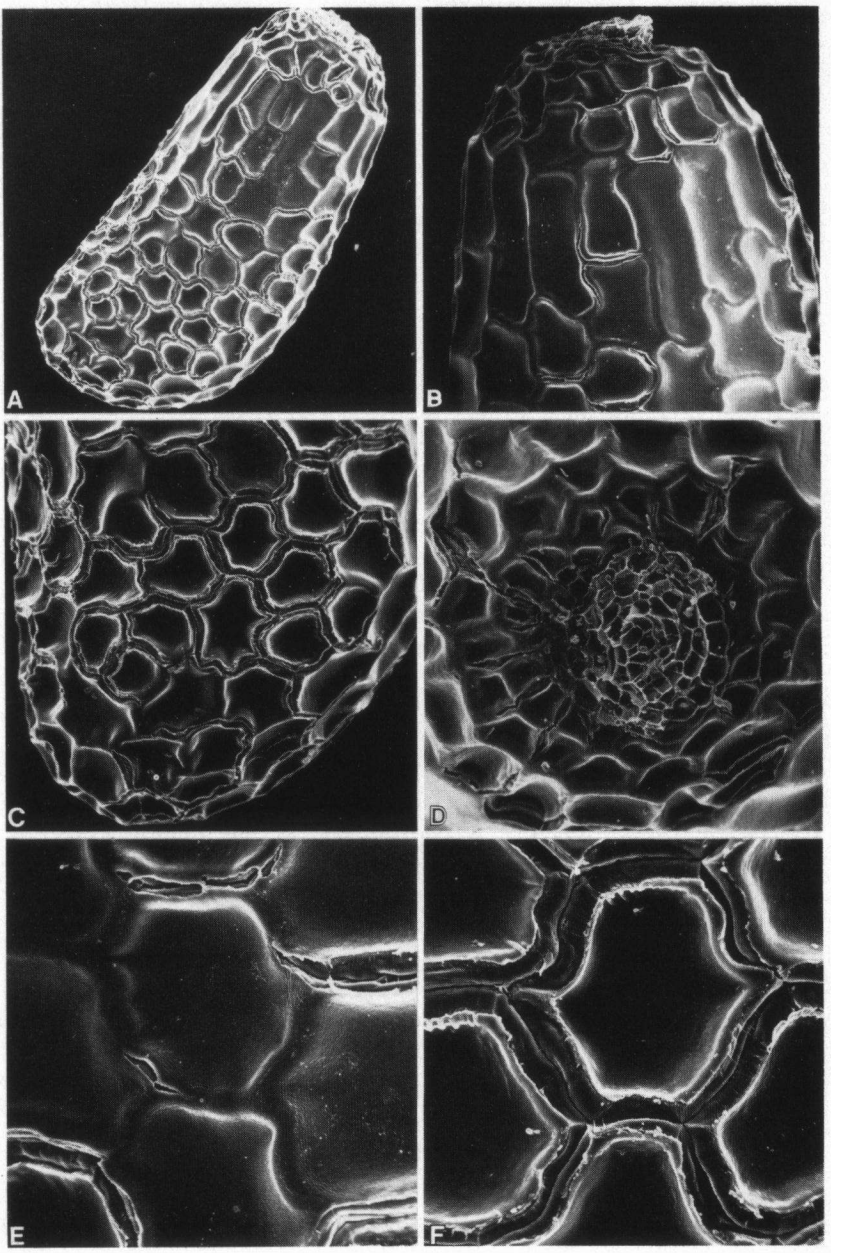

Fig. 1. *Begonia ampla*. A: mature seed (c. × 75); B: micropylar part with collar cells and operculum (c. × 165); chalazal part (c. × 160); D: top view of operculum with micropyle and hilar scar (c. × 260); E, F: testa cells with splitting of the anticlinal boundaries (c. × 525).

Testa cells mostly in rather regular rows. The cells of the chalazal region irregularly arranged. Form of the testa cells isodiametric polygonal, mostly hexagonal. Anticlinal cell walls straight, occasionally slightly curved.

Operculum as in *B. ampla,* but the cuticular foldings on the anticlinal walls are inconspicuous.

Micromorphology: Anticlinal boundaries usually smooth and splitting along the middle lamellae as in *B. ampla.* Outer periclinal walls concave without clear micro-ornamentation.

The seeds of *B. poculifera* Hook. f. var. *teusziana* (J. Braun et K. Schum.) J. J. de Wilde closely resemble those of the var. *poculifera.* The seeds of var. *teusziana* seem to be straighter in form in general and they are smaller, their size varying from 6.67 to 7.48 by 2.63 to 3.36 $\times 10^{-4}$m; mean 7.26 $\times$ 2.90 $\times 10^{-4}$m. Ratio length: width is 2.5.

3.3 *Begonia bonus-henricus* J. J. de Wilde *Fig. 3* A–F

Seeds elliptic to narrowly elliptic. Variation in length from 7.00 to 8.15 $\times 10^{-4}$m, in width from 3.05 to 3.61 $\times 10^{-4}$m; mean 7.68 $\times$ 3.39 $\times 10^{-4}$m. Ratio length: width is 2.3.

Collar cells varying in length from 1.08 to 2.35 $\times 10^{-4}$m; mean 1.57 $\times 10^{-4}$m. Ratio collar: seed length is 1:4.9. Form elongated irregularly tetragonal. Anticlinal cell walls between the collar cells straight.

Testa cells in clear longitudinal rows almost to the chalazal end. The cells are in form isodiametric-polygonal in shape, mostly hexagonal. Most anticlinal walls straight, some slightly curved, especially those bordering the collar.

Operculum as in *B. ampla.*

Micromorphology: Anticlinal boundaries thickened like a string of pearls with a small central groove. In dried seeds splitting along the middle lamellae, but to a much lesser extent than in the other species. Outer periclinal walls slightly concave to almost flat. Central part of these walls in most cells verrucose, sometimes slightly wrinkled.

4. DISCUSSION

The seeds of *Begonia ampla, B. poculifera* and *B. bonus-henricus* are very similar. This type of seed is quite different from seeds of other African sections as far as can be ascertained. (*cf.* BOUMAN & DE LANGE, in prep.) Thus, the micromorphological characters of the seeds clearly support the recent delimination of section *Squamibegonia* Warb. by DE WILDE & ARENDS (1980).

The seed characters of *B. loranthoides* subsp. *rhopalocarpa* differ clearly from those of section *Squamibegonia* and fit into section *Tetraphila,* The seeds of the species of this section are characterized by the presence of an aril-like funicular outgrowth. No seeds of *B. loranthoides* subsp. *loranthoides* and *B. zimmermannii* were available for comparison. Also the seeds of *B. baccata* and *B. crateris* differ

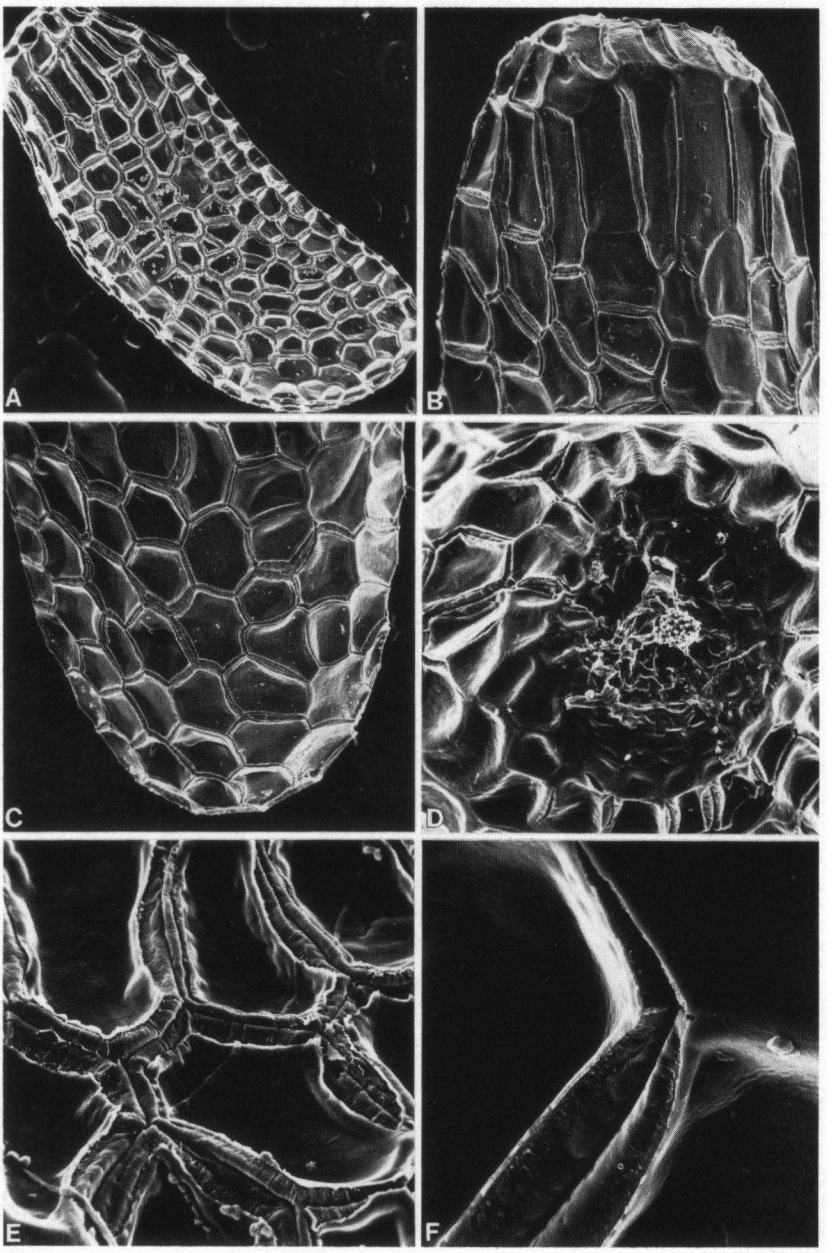

Fig. 2. *Begonia poculifera* var. *poculifera*. A: Mature seed (c. × 70); B, C: micropylar and chalazal part, respectively (c. × 170); D: top view of operculum (c. × 260); E: testa cells (c. × 525); F: detail of splitting and unfolding of the anticlinal boundary (c. × 1000).

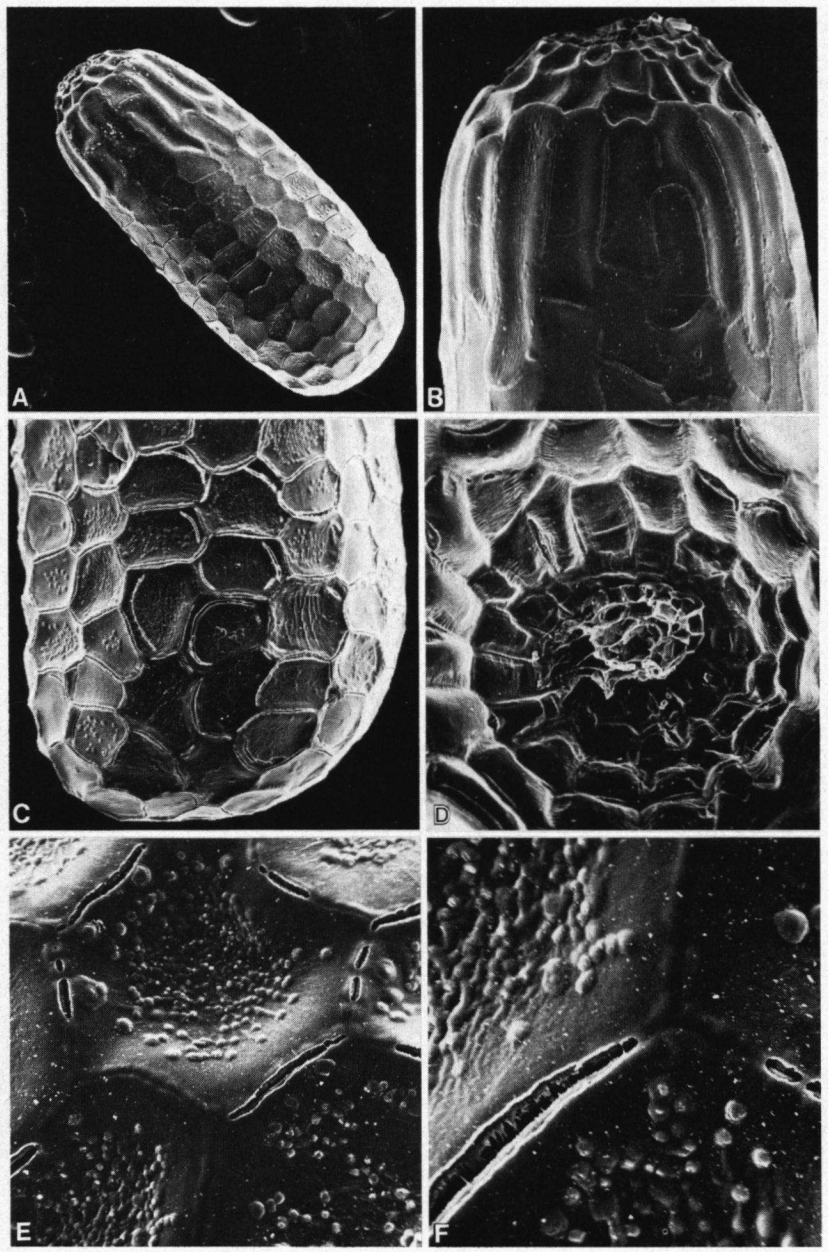

Fig. 3. *Begonia bonus-henricus*. A: mature seed (c. × 70); B, C: micropylar and chalazal part, respectively (c. × 160); D: top view of operculum (c. × 280); E: testa cells with verrucose sculpture (c. × 525); F: detail of splitting of anticlinal boundary (c. × 1000).

from those of section *Squamibegonia*. They are smaller, lack the splitting of anticlinal walls and may show a faint cuticular pattern. Until more complete information on the seed morphology of the sections *Mezierea* and *Tetraphila* is available, no suggestion can be made as regards the relationship of these species.

The section *Squamibegonia* as redefined by DE WILDE & ARENDS (1980) is characterized by relatively large seeds, a splitting of the anticlinal walls along the middle lamellae and the absence of cuticular foldings. The seeds are between 0.67 and 0.82 mm long.

The splitting of the anticlinal walls in dry seeds has till now only been found in the three species described here and seems to be a unique character of the section. The functional aspects of this phenomenon are obscure. The absence of cuticular foldings has till now only been observed in species of the African sections *Meziera, Tetraphila* and *Squamibegonia*.

The sections *Squamibegonia* and *Mezierea* have berry-like fruits with a white or pink fleshy pericarp. On the basis of the epiphytic growth habit and the fruit morphology DE WILDE & ARENDS suggest a zoochorous dispersal. Also the fruits of the section *Tetraphila* are fleshy, but always dehiscent, however. They open by valves exposing the seed-bearing placental tissue (DE WILDE & ARENDS 1979). Their seeds are provided with funicular outgrowths, which sometimes become aril-like. A zoochorous way of dispersal, among which myrmecochory, is likely.

Most Begoniaceae have dry dehiscent fruits and the most common way of seed dispersal is by anemochory. The wings on the fruits of several Begonias may help in shaking the fruit, an activity promoting the liberation of the small anemochorous seed (VAN DER PIJL 1969). Surface "roughness" as caused by cuticular foldings has several advantages for the seed: it may cause turbulency in laminar air flow and therefore increase the thermodynamic exchange (BARTHLOTT 1981) and slow down the rate of fall (RAUH, BARTHLOTT & EHLER 1975). Besides, it increases the floating power of the seed.

The loss of micromorphological ornamentation may be related with a change-over to a different dispersal strategy in the sections *Mezierea, Tetraphila* and *Squamibegonia*.

ACKNOWLEDGEMENTS

The authors are indebted to Professor A. D. J. Meeuse for critical examination of the English text. This study has been done in co-operation with Dr. J. J. F. E. de Wilde and Dr. J. C. Arends (Laboratory of Plant Systematics and -Geography, Wageningen). Their valuable comments and stimulating interest are highly appreciated. Professor J. Doorenbos and Mr. J. J. Karper (Department of Horticulture, Wageningen) are acknowledged for providing seeds of cultivated specimens.

REFERENCES

BARTHLOTT, W. (1981): Epidermal and seed surface characters of plants: systematic applicability and some evolutionary aspects. *Nord. J. Bot.* **1**: 345–355.

— & N. EHLER (1977): Raster-Elektronenmikroskopie der Epidermis-Oberflächen von Spermatophyten. *Trop. Subtrop. Pflanzenwelt* **19**: 1–105.

BOUMAN, F. & A. DE LANGE: Structure and micromorphology of Begonia seeds. *The Begonian* (in preparation).

BRISSON, J. D. & R. L. PETERSON (1976): A critical review of the use of scanning electron microscopy in the study of the seed coat. *Scanning electron microscopy* (IIT Research Inst. Chicago) **2:** 477–495.

CORNER, E. J. H. (1976): *The seeds of dicotyledons.* 2 vols. Cambridge.

DAVIS, G. L. (1966): *Systematic embryology of the angiosperms.* New York, London, Sydney.

IRMSCHER, E. (1925): Begoniaceae in: ENGLER & PRANTL, *Die natürlichen Pflanzenfamilien* **2(21):** 548–588.

PIJL, L. VAN DER (1969): *Principles of dispersal in higher plants.* Berlin.

RAUH, W., W. BARTHLOTT & N. EHLER (1975): Morphologie und Funktion der Testa staubförmiger Flugsamen. *Bot. Jahrb. Syst.* **96:** 353–374.

WILDE, J. J. F. E. DE & J. C. ARENDS (1979): Begonia loranthoides Hook. f. (sect. Tetraphila A. DC.). *Acta Bot. Neerl.* **28:** 357–374.

— & — (1980): Begonia section Squamibegonia Warb. A taxonomic revision. *Misc. Papers.* (Landbouwhogeschool, Wageningen) **19:** 377–421.