Seed Micromorphology of Neotropical Begonias

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SMITHSONIAN CONTRIBUTIONS TO BOTANY • NUMBER 90

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Smithsonian Institution Press
Washington, D.C.
1999

ABSTRACT

Lange, A. de, and F. Bouman. Seed Micromorphology of Neotropical Begonias. *Smithsonian Contributions to Botany,* number 90, 49 pages, 1 figure, 21 plates, 1999.—The seeds of about 235 Neotropical *Begonia* species, representing almost all recognized American *Begonia* sections, were studied using scanning electron microscopy. The seeds show an appreciable diversity in size, shape, and micromorphology, which is helpful in the delimitation of sections and sometimes also of species. Mean seed length varies from 235µm in *Begonia filipes* to 1450 µm in *B. fruticosa;* most seeds have a length between 300 µm and 600 µm. The shape of the seeds varies from almost globular to narrowly elliptic, and the length to width ratio ranges from 1.2 in *B. hexandra* to 8.1 in *B. fruticosa.* Further differences exist in the shape of the testal cells, the undulation of the anticlinal walls, the bulging of the outer periclinal walls, and the pattern and roughness of the cuticle.

Five of the 15 mainly Brazilian, five of the 12 Andean and Guianan, and one of the eight middle American sections have a seed structure that is characteristic at the sectional level. All these sections have a relatively restricted geographical distribution, and they may differ in growth form or habitat. Most species of the other sections, including the larger and more widely distributed sections *Begonia, Gireoudia,* and *Knesebeckia,* have seeds conforming to the ordinary seed type.

In a number of the sections, the structural differences of the seeds are nicely correlated with differences in growth form and/or in means of dispersal. In contrast to the African begonias, the great majority of the Neotropical begonias have anemoballistic dispersal. Seeds may be adapted to wind dispersal by extended micropylar and/or chalazal ends with inflated, air-filled cells, such as in the Brazilian sections *Solananthera, Trendelenburgia,* and *Enita* and in the Andean section *Rossmannia,* or by a more pronounced surface with deep, collapsed testal cells, such as in sections *Gobenia* and *Scheidweileria.* Zooballistic dispersal by passing animals is supposed to be present in section *Casparya.* The seeds of sections *Casparya* and *Trachelocarpus* have very pronounced cuticular patterns and may be secondarily dispersed by rain wash or by adhering to animals.

No distinct indications for an intercontinental relationship between Neotropical, African, and Asiatic sections could be established.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Annals of the Smithsonian Institution.* SERIES COVER DESIGN: Leaf clearing from the katsura tree *Cercidiphyllum japonicum* Siebold and Zuccarini.

Library of Congress Cataloging-in-Publication Data
De Lange, A. (Anton)
Seed micromorphology of neotropical begonias / A. de Lange and F. Bouman.
p. cm. — (Smithsonian contributions to botany ; no. 90)
Includes bibliographical references.
1. Begonias—Seeds—Morphology. 2. Scanning electron microscopy.
I. Bouman, F. II. Title. III. Series.
QK1.S2747 no. 90
[QK495.B4]
580 s—dc21
[583'.6271467] 99-30195
CIP

♾ The paper used in this publication meets the minimum requirements of the American National Standard for Permanence of Paper for Printed Library Materials Z39.48—1984.

Contents

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and F. Bouman

Introduction

The genus *Begonia* L. represents one of the larger genera of flowering plants and has a complicated taxonomic history. Generic concepts in the family Begoniaceae have changed much; about 50 genus names have been put into synonymy with *Begonia*. According to current opinions, the family comprises only the genera *Begonia, Hillebrandia,* and *Symbegonia,* although *Symbegonia* was classed under *Begonia* by Mabberley (1989). *Hillebrandia sandwicensis* Oliver, of the monotypic genus *Hillebrandia,* is endemic to Hawaii.

According to Smith et al. (1986) and Golding (1992), *Begonia* comprises almost 1400 species arranged into 78 sections (Baranov and Barkley, 1974), some of which are dubious or under discussion. Each section is restricted to a single continent except sections *Begonia* and *Knesebeckia,* which have an American-Asian distribution.

The seeds of Begoniaceae are characterized at the family level by the presence of a transverse ring of so-called collar cells. These cells are usually elongated and border the micropylar-hilar part of the seed. During germination, this part separates along preformed rupture lines and is lifted off like a seed lid or operculum (Figure 1), and the walls between the collar cells split to clear the way for the emerging seedling (Bouman and de Lange, 1983). The seeds of begonias show an appreciable diversity in size, shape, and micromorphology. The most common "ordinary" *Begonia* seeds mostly measure between 300 µm and 600 µm long. As far as is known, the extremes are found among the African begonias: the smallest seeds are recorded from *B. iucunda* Irmscher, with a mean seed length of 220 µm, and the largest are from *B. ebolowensis* Engler, with a mean length of 2240 µm (de Lange and Bouman, 1992).

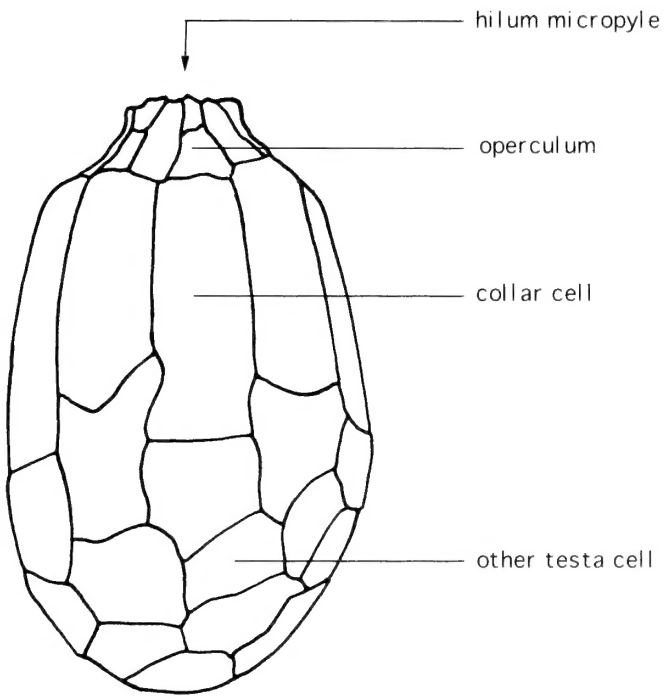

FIGURE. 1.—Diagram of a *Begonia* seed with various parts labelled.

The African begonias have received considerable attention by De Wilde and colleagues during the last 15 years (de Wilde, 1985, 1992). Using a multidisciplinary approach (including karyology, pollen morphology, stigma morphology (Panda and de Wilde, 1995), placentation, seed morphology, and leaf anatomy (Sosef, 1994)), sections have been revised and intersectional relations have become clearer. A comparative scanning-electron-microscopy (SEM) study proved seed micromorphology to be a very useful additional character set, especially at the sectional level (de Lange and Bouman, 1992). The African begonias showed a considerable diversity in seed size and

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structure. Moreover, differences in seed structure appeared to be distinctly related to the means of seed dispersal. In contrast to the general opinion that wind dispersal is the predominant means of dispersal in *Begonia* (van der Pijl, 1972), the seeds of the majority of the African *Begonia* species are dispersed by alternative ways. Animals may eat the fleshy, often colored fruits; seeds also may be dispersed by mud on the legs of passing animals or by rain wash (de Lange and Bouman, 1992).

The taxonomy of the Neotropical begonias is far from settled. During his long botanical career, Lyman B. Smith, in cooperation with Bernice G. Schubert and later Dieter C. Wasshausen, published a series of contributions to regional or national floras. Taxonomic revisions at the sectional level, however, unfortunately are lacking, with the exception of the study by Burt-Utley (1985) on the Central American and Mexican species of section *Gireoudia.* Because of the lack of a recent, updated revision of the Neotropical *Begonia* sections we have mainly followed the publication of Baranov and Barkley (1974) for sectional classifications and for the determination of their type species. It is important, however, to realize that their work was in large part based on published descriptions and did not involve critical examination of many species. A number of new sections described later have been added. For the sectional affiliation of species, we have used the publication of Barkley and Golding (1974) supplemented with data from later publications on newly described species.

In the Neotropics, about 600 *Begonia* species are recognized. According to Baranov and Barkley (1974), these are arranged in 47 sections; however, four of these sections, *Auriformia, Irmscheria, Quadriperigonia,* and *Saueria,* have since been eliminated due to synonymy. The monotypic section *Dasystyles* is of uncertain origin and is based on cultivated specimens. Twenty of the sections dealt with in the present paper have held generic status in the past (e.g., *Casparya, Gireoudia, Huszia, Pritzelia, Scheidweileria*).

For convenience, we have arranged the sections discussed herein according to six areas of geographical distribution. Thirty-five sections have a restricted geographical distribution, with the species of 15 sections confined mainly to Brazil and some adjacent countries, 12 sections confined to the Andean and Guianan regions, and eight sections confined to the Central American, Mexican, and Caribbean regions. The species of seven sections have a wider distribution: two sections occur in both Brazilian and Andean regions, one section occurs in both Andean and Central American regions, and four sections have a more extended Neotropical distribution.

The possibility of a sectional classification within the genus *Begonia* has been questioned repeatedly. Smith and Schubert (1946) discussed the use of placental form as the basis for division into sections but in subsequent publications ignored sections altogether. In her description of the begonias of Madagascar, Keraudren-Aymonin (1983) also renounced classifying species into previously recognized sections. The studies on African begonias, however, clearly demonstrated the sensibleness and usefulness of a sectional division. Sosef (1994:11) made a strong plea to taxonomists always to denote the section to which any given species belongs.

Our study aims at a better insight into the diversity of seed structure of Neotropical begonias and the adaptive characters for dispersal. Moreover, it may provide arguments for sectional delimitation.

ACKNOWLEDGMENTS.—The authors are much indebted to J. Doorenbos (Department of Horticulture, Wageningen, the Netherlands), who sparked our enthusiasm for Neotropical begonias and who supplied us with a number of seed samples from his former collection of cultivated species. Moreover, he critically reviewed the manuscript and especially added valuable data to the descriptions and relationships of the sections. We thank the late Lyman B. Smith (National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C.) for his indications of taxonomic problems on sectional delimitation. Dieter Wasshausen (NMNH) is gratefully acknowledged for his interest and hospitality during the first author's visit to the United States National Herbarium.

We thank J.J.F.E. de Wilde and M.S.M. Sosef of the Department of Plant Taxonomy, Wageningen Agricultural University, for their stimulating discussions on *Begonia* systematics. The directors and curators of herbaria cited in the text are gratefully acknowledged for providing facilities to study their collections or for loan of material.

M.G. Bouman and N. Devente assisted in the typing of the manuscript, F.D. Boesewinkel and J. Dahmen processed several thousands of SEM photographs, and W. Takkenberg provided technical assistance with SEM (Hugo de Vries-Laboratory, Amsterdam). The Netherlands Organization for Scientific Research financed the visit of the first author to the herbaria of Washington, D.C., and St. Louis, Missouri.

MATERIAL AND METHODS.—Most of the seed material was collected by visits to and/or by loan from the following herbaria: AAU, AMD, B, COL, CR, G, GENT, K, L, MO, P, PDA, PRE, RB, SP, U, US, and WAG. Moreover, seeds were received from the American *Begonia* Society Seed Fund (ABS), the former collection of cultivated begonias at the Department of Horticulture, Wageningen (WAG), and from the collections of L. Goldsmith (University of Vermont (VT)) and R. Ziesenhenne (Santa Barbara, California). Of the seeds received from Ziesenhenne, vouchers are present in his personal herbarium. No vouchers are available for the seeds obtained from ABS.

For the smaller sections, seeds of all available species were collected and studied. For the larger sections, seeds of a number of representative species were chosen. Mature seeds were sputter-coated with gold-palladium for 2 to 3 minutes and were observed using either a Cambridge Stereoscan MK 2a or an ISI DS-130. Dirty seeds were cleaned by soaking in water with a detergent and by subsequent ultrasonic vibration.

Seed size was determined from SEM measurements of usually six seeds. The seed width was measured at the widest apparent point. All mentioned mean sizes are arithmetically determined.

Description of Seeds of Neotropical Begonias

In the descriptions of Neotropical *Begonia* seeds, we emphasize those sections with a characteristic seed structure that sometimes can be related to special growth forms or to methods of seed dispersal. Sections with seeds conforming to the ordinary seed type are dealt with more briefly. Although variation in seed micromorphology between sections can provide taxonomic information, in view of the issue of correct identifications and the sometimes complicated nomenclature, detailed comparative studies are most valuable when done in close cooperation with taxonomists.

The results are presented according to the main geographical distributions of the sections for reason of surveyability and are not intended to suggest evolutionary relationships.

1. Sections Mainly Confined to Brazil and Some Adjacent Countries

Of the 15 Brazilian or mainly Brazilian sections, five (*Enita, Scheidweileria, Solananthera, Trachelocarpus, Trendelenburgia*) share a unique seed structure that is characteristic at the sectional level. Seeds of the species within each of these sections can be distinctly discerned from those of all other sections. Of nine remaining sections, the seeds of all or most species have a more ordinary structure. No seeds were available from *B. schlumbergerana* Lemaire of the monotypic section *Plurilobaria.* This section is questionable because it is based on a dubious type species described from a cultivated specimen, probably related to section *Ewaldia* (Warburg, 1894).

1.1. Section ***Trachelocarpus*** A. DC.

Plate 1*a–c,e,f*

This taxon was first described by Klotzsch as the genus *Trachelanthus* in 1855. C. Mueller (1857) changed the name to *Trachelocarpus,* and subsequently A. De Candolle (1859) reduced its status to sectional level. The section now comprises six species, restricted to Brazil. The taxonomically correct section type (Doorenbos et al., 1998) is *Begonia depauperata* Schott (=*B. rhizocarpa* Fischer ex A. DC.). Seeds were not available for *B. angraensis* Brade, *B. fulvo-setulosa* Brade, or *B. velloziana* Walp.

The species of the section are characterized by a rhizomatous habit and almost equal-sided lanceolate leaves. Moreover, the inflorescences are unisexual: the male ones are stalked cymes; the female ones are reduced to a single subsessile flower. The ovary and fruit have three narrow wings joining a beak-like elongation bearing tepals and styles with stigmas. All species are epiphytic, creeping herbs.

Type Species.—*Begonia depauperata* (Plate 1*e*).

Seed Structure: Seeds ellipsoid to narrowly ellipsoid, 750–830 µm in length, 305–330 µm in width, mean 800 µm × 320 µm, length:width ratio 2.5. Collar cells relatively short, 175–280 µm in length, mean 205 µm, number in seed circumference about 14. Ratio of collar-cell length to seed length 1:4.0. Other testa cells polygonal, arranged in rows of about 10 cells. Anticlinal walls straight to slightly curved. Testa cells shallow, with collapsed outer periclinal walls forming ridges parallel to anticlinal boundaries. Operculum obtusate, composed of many irregularly arranged small cells.

Seed Micromorphology: Anticlinal boundaries straight or sometimes sunken. Cuticle with net-like structure of upright or folded-over pleats. Cuticular striae usually occurring only locally, especially on anticlinals or in patches on smaller apical cells of operculum.

Specimen Examined:

B. depauperata, BRAZIL: *Campos Goer 140* (B).

Other Species Observed (Plate 1*a–c,f*).—*Seed Structure and Micromorphology: Begonia herbacea* Vellozo and *B. lanceolata* Vellozo (syn. *B. attenuata* A. DC.) have seed structures that resemble those of *B. depauperata* in general morphology and cuticular structure. Seeds of *B. herbacea* have a mean size of 850 µm × 370 µm. Seeds of *B. herbacea* var. *ellipticifolia* Irmscher are slightly longer, 855–935 µm (mean 910 µm × 370 µm), have a length:width ratio of 2.5, and the anticlinal boundaries of the collar and testa cells are much more distinctly sunken. The seeds of *B. lanceolata* have a mean size of 1030 µm × 410 µm.

Specimens Examined:

B. herbacea var. *ellipticifolia,* BRAZIL: *Ule 4240* (B).

B. herbacea var. *herbacea,* BRAZIL: *Loefgren s.n.* (B); *Lisedeceales s.n.* (B).

B. lanceolata, BRAZIL: *L.B. Smith & Pereira 15343* (US).

1.2. Section ***Solananthera*** A. DC.

Plate 1*d,g,h*

The section *Solananthera* was established by A. De Candolle in 1859. It contains three species restricted to Brazil. The species are epiphytic, climbing subshrubs. The section is characterized by the presence of porate anthers and two-divided placentas, the lobes of which cling to each other. The seeds of the three species have been described in detail (de Lange and Bouman, 1986).

Type Species.—*Begonia solananthera* A. DC. (Plate 1*d*).

Seed Structure: Seeds narrowly elliptic to narrowly obovate, mostly straight, sometimes J- or C-shaped. Mean seed size 755 µm × 145 µm, length:width ratio 5.2. Mean length of collar cells 250 µm, with collar-cell length : seed length ratio of 3.0. Other testa cells elongated, anticlinal walls finely undulated. Outer cell walls convex. Operculum obtuse, funnel-like, with sunken hilum.

Seed Micromorphology: Anticlinal boundaries flat. Cuticular pattern consisting of long linear undulated striae.

Specimen Examined:

B. solananthera, BRAZIL: cult., Dept. Horticulture (WAG).

Other Species Observed (Plate 1*g,h*).—*Seed Structure and Micromorphology: Begonia radicans* Vellozo and *B. in-*

tegerrima Sprengel have seed structures that resemble those of *B. solananthera* in shape, general morphology, and cuticular pattern. Mean seed sizes are 1060 µm × 170 µm and 885 µm × 155 µm, respectively, and the length:width ratios are 1:6.2 and 1:5.7, respectively. The seeds of *B. radicans* also strongly resemble those of *B. fruticosa* of section *Trendelenburgia.* The periclinal walls of the testa cells are collapsed, with the exception of those at the chalaza of *B. radicans.*

Specimens Examined:

B. integerrima var. *integerrima,* BRAZIL: *E. Pereira 606* (RB).

B. radicans, BRAZIL: *H. Luederwaldt s.n.* (SP); *A.P. Duarte 3377* (RB).

1.3. Section ***Trendelenburgia*** (Klotzsch) A. DC.

PLATE 2*a,f*

The taxon *Trendelenburgia* was first described by Klotzsch as a genus in 1855 on the basis of one of the early *Begonia* collections by Ludwig Riedel in 1839. A. De Candolle (1864) changed the status to sectional level. Most probably the section is monotypic, with *B. fruticosa* as the type species.

The section is characterized by three-celled fruits with three equal-sized, very narrow wings and undivided placentas. The plants are slender-stemmed shrubs with a tendency to climb and with simple, pinnately veined leaves. *Begonia fruticosa* occurs in Argentina and southern Brazil.

TYPE SPECIES.—*Begonia fruticosa* A. DC. (Plate 2*a,f*).

Seed Structure: Seeds narrowly ellipsoid, extended micropylar and chalazal ends composed of bulging, air-filled cells. Testa cells covering central, embryo-containing part collapsed. One or both sides of seeds may be curved, rendering seeds J- or slightly S-shaped. Seed length 1310–1540 µm, width 160–200 µm, mean 1450 µm × 180 µm, length:width ratio 8.1 (slenderest seeds ever encountered in *Begonia*). Seeds of above described collection (*Martins 8380*) the biggest. Seeds of collections *Herb. Brasil 1717, Kummrow 1636,* and *Herb. Brasil 850* with mean lengths of 1060 µm, 1005 µm, and 965 µm, respectively, and length:width ratios of 7.3, 5.4, and 6.3, respectively. Ratio of embryo-containing part to seed length 1:2.4. Collar cells strongly elongate, 275–380 µm in length, mean 325 µm, number in seed circumference about 10. Collar-cell length to seed length ratio 1:4.5. Longitudinal anticlinal walls of collar mostly undulated along entire length. Other testa cells of central part of seed also distinctly elongated and with undulated walls. Cells of operculum adjacent to collar elongated. Hilum sunken.

Seed Micromorphology: Anticlinal boundaries of operculum and chalaza sunken, those of central part of seed somewhat less so. Cuticle smooth, locally with faint, striate ornamentation, cuticle of central part of seed reflecting underlying pits. Larger pits present at bases of anticlinal walls.

Specimens Examined:

B. fruticosa, BRAZIL: *R. Kummrow 1636* (MO); *H.F. Martins 8380* (US); *H. Schenck, Herb. Brazil 850, 1717* (B).

1.4. Section ***Scheidweileria*** (Klotzsch) A. DC.

PLATE 2*b–e,g,h*

The section *Scheidweileria* was described by Klotzsch as a genus in 1855. The section comprises six species, one of which, *B. luxurians,* is well known as a collector's plant. They are shrubs or small trees with compound, palmately veined leaves containing cystoliths and with large inflorescences that are dichotomous at the bases. The female flowers are characterized by five tepals, stigmas as helical bands with three turns, and undivided placentas. No seeds were available for *B. semidigitata* Brade.

Most species of the section are limited to Brazil, but *B. parviflora* Poeppig & Endler has a wider distribution, extending to southern Central America.

TYPE SPECIES.—*Begonia pentaphylla* Walpers (Plate 2*b,c*).

Seed Structure: Seeds ellipsoid to narrowly ellipsoid, 600–680 µm in length, 220–300 µm in width, mean 640 µm × 265 µm, length:width ratio 2.4. Collar cells elongate, 180–280 µm in length, mean 225 µm, number in seed circumference about 12. Ratio of collar-cell length to seed length 2.8.

Longitudinal anticlinal walls of collar straight. Other testa cells polygonal, with straight anticlinal walls. Testa cells at chalaza with higher anticlinal walls and becoming deep due to collapse of outer periclinal walls. Chalaza usually flattened on one side, probably from contact with inner surface of fruit wall, resulting in cell crumpling. Border between collar and operculum abrupt. Operculum nipple-shaped, with collapsed cells.

Seed Micromorphology: Anticlinal boundaries flat. Cuticular pattern variable, that of collar cells mainly linear, that of remaining testa cells with shorter linear, undulated, or short zigzag striae. Locally, patches with less pronounced, mainly linear pattern.

Specimen Examined:

B. pentaphylla, BRAZIL: *B. and C. Maguire and J. Murca Pires 44596* (US).

OTHER SPECIES OBSERVED (Plate 2*d,e,g,h*).—The seeds of other species observed are characterized by a flattened chalaza with deep testa cells as described above for *B. pentaphylla,* but they show distinct differences in seed lengths.

Seed Structure and Micromorphology: The seeds of *B. parviflora* are 270–350 µm in length, 155–180 µm in width, with a mean of 315 µm × 170 µm, and have a length:width ratio of 1.9. They most resemble the ordinary type of begonia seed.

The seeds of *B. luxurians* Scheidweiler and *B. digitata* Raddi are longer and closely resemble each other. *Begonia luxurians* seeds (*Hoehne 2370*) are 580–640 µm in length and 180–200 µm in width, with a mean of 610 µm × 185 µm and a length:width ratio of 3.3. The collection *de Barros 1139* has smaller seeds, with a mean of 485 µm × 195 µm. *Begonia digitata* seeds are 595–655 µm in length and 165–210 µm in width, with a mean of 625 µm × 185 µm and a length:width ratio of 2.9. The operculum in *B. digitata* and *B. luxurians* is broadly

nipple-shaped, sometimes obtusate, and has a sunken hilum (*Sellow s.n.* and *Martinelli c.s. 8045,* respectively).

The seeds of *B. incisoserrata* A. DC. vary appreciably in size, being 370–500 µm in length and 170–215 µm in width, with a mean of 425 µm × 185 µm and a length : width ratio of 2.4.

The species of the section have straight or slightly curved anticlinal walls except *B. parviflora,* in which all specimens locally have slightly undulated anticlinal walls in the collar and testa. The species have a cuticular pattern as described for *B. pentaphylla.*

Specimens Examined:

B. digitata var. digitata, BRAZIL: *Martinelli & Maas 3271* (U); *Sellow s.n.* (P); *L.B. Smith cs. 6691* (US).

B. incisoserrata, BRAZIL: *A.C. Brade 20096* (B); *G. Hatschbach & R. Kummran 45532* (US).

B. luxurians var. *luxurians,* BRAZIL: *D. de Barros 1139* (B); *F.C. Hoehne 2370* (B); *G. Martinelli, Kautsky, & Leme 8045* (US).

B. parviflora, COLOMBIA: *Ed. André K 284* (K); *J. Cuatrecasas 11311* (US); *Killip 7837* (US). ECUADOR: *Holguer Lugo S 1808* (MO).

1.5. Section ***Ewaldia*** A. DC.

PLATE 3*a–d*

This taxon was described by Klotzsch (1855) as a genus and was reduced to a section by A. De Candolle in 1864. It was maintained as such by subsequent monographers (Warburg, 1894; Irmscher, 1925). The section comprises about 11 species. They resemble the species of section *Scheidweileria* in a number of characters, but they differ, among other characters, in the pinnate venation and in the shape and hairiness of the leaves. Except for the Venezuelan species *B. boucheana* (Klotzsch) A. DC., the species are limited to Brazil.

TYPE SPECIES.—*Begonia lobata* Schott (Plate 3*a*).

Seed Structure: Seeds ellipsoid to narrowly ellipsoid, 565–650 µm in length, 195–215 µm in width, mean 605–200 µm, length:width ratio 3.0. Seeds of collection *Esteves c.s. CFCR 6028* differ in size and shape, with mean seed size of 515 µm × 265 µm and length:width ratio of 1.9. Collar cells elongate, 115–210 µm in length, mean 165 µm, number in seed circumference about 13. Ratio of collar-cell length to seed length 3.6. Testa cells adjacent to collar somewhat elongated, those at chalazal end more polygonal. Anticlinal walls straight. Chalaza usually flattened, but cells not crumpling. Operculum broadly nipple-shaped.

Seed Micromorphology: Anticlinal boundaries flat. Cuticular pattern coarse, that of chalazal cells with short linear or short undulated striae. Locally, patches with less pronounced, denser pattern.

Specimens Examined:

B. lobata, BRAZIL: *G.L. Esteves c.s. CFCR 6028* (SP); *G. Hatschbach 30073* (US), *36564* (MO).

B. aff. *lobata,* BRAZIL: *P.J.M. Maas c.s. 3318* (U).

OTHER SPECIES OBSERVED (Plate 3*b–d*).—*Seed Structure and Micromorphology:* The seeds of *B. rigida* Linden ex Regel, *B. scharffii* Hook.f., and *B. tomentosa* Schott resemble those of *B. lobata* in the coarse cuticular pattern and the straight anticlinal walls and boundaries. They differ, however, in a nipple-shaped operculum, smaller size, and the presence of a cuticular pattern with both short linear and short undulated to short zigzag striae. Mean seed sizes are 390 µm × 190 µm (*B. rigida*), 485 µm × 220 µm (*B. scharffii*), and 485 × 210 µm (*B. tomentosa*), with length:width ratios of 2.1, 2.2, and 2.3, respectively. The seeds of section *Ewaldia,* especially those of *B. lobata,* resemble the seeds of section *Scheidweileria* in shape, in size, and in having a somewhat massive operculum.

Specimens Examined:

B. rigida, BRAZIL: ABS Seed Fund (1983).

B. scharffii, BRAZIL: *Palacios-Cuezzo 2930* (US).

B. tomentosa var. *tomentosa,* BRAZIL: *A.C. Brade 18572* (US).

1.6. Section ***Enita*** Brade

PLATE 3*e,f–k*

The species now constituting section *Enita* have a rather complicated taxonomic history. Klotzsch (1855) attributed the species then described, together with a number of species now mainly in section *Pritzelia,* to his genus *Wageneria.* A. De Candolle (1861) transferred this genus to *Begonia* section *Wageneria.* Warburg (1894) merged *Wageneria* with the large section *Pritzelia,* and this opinion was shared by Irmscher (1925). Brade (1945) established *Enita* as a subsection and later raised it to sectional level (Brade, 1957). The correct name of the section should be *Wageneria* Klotzsch, with *B. fagifolia* hort. Petrop. ex Otto & Dietrich as type species (Doorenbos et al., 1998). The section comprises probably 10 species. The species of section *Enita* deviate from those of section *Pritzelia* by having stamens with filaments slightly united below and anthers usually much shorter than the filaments, and by having cylindrical seeds crowned with a group of larger cells at the chalaza. Moreover, they are climbing semishrubs with stems that often produce adventitious roots at the nodes and that have symmetrical or subsymmetrical, pinnately or palmately veined leaves.

All species are limited to Brazil except *B. glabra* Aublet, which has a wider distribution, occurring in the West Indies and from Mexico to Colombia and Ecuador.

TYPE SPECIES.—*Begonia convolvulacea* (Klotzsch) A. DC. (Plate 3*e*).

Seed Structure: Seeds narrowly ellipsoid, micropylar and chalazal ends differing, 635–705 µm in length, 180–215 µm in width, mean 675 µm × 195 µm, length:width ratio 3.4. Collar cells elongate, 130–475 µm in length, mean 275 µm, number in seed circumference about 11. Ratio of collar-cell length to seed length 2.4.

Longtitudinal anticlinal walls of collar and other testa cells usually straight, sometimes slightly undulated. Other testa cells

also elongated. Chalazal end of seed flattened and with cells with higher anticlinal walls. These cells may become deep from collapse of outer periclinal walls or somewhat inflated from bulging of outer walls. Operculum obtusate, with sunken hilum.

Seed Micromorphology: Anticlinal boundaries usually flat but sunken at boundary of collar and operculum and at chalaza. Cuticular pattern weakly developed, with linear or short linear striae, more distinct at operculum. Locally, patches without ornamentation.

Specimens Examined:

B. convolvulacea, BRAZIL: *G. Hatschbach 9193* (B, L); *H. Schenck, Herb. Brazil 858* (B).

OTHER SPECIES OBSERVED (Plate 3*f–k*).—*Seed Structure:* The seeds of *B. epibaterium* Martius ex A. DC., *B. fagifolia*, and *B. glabra* are quite similar in general shape to those of *B. convolvulacea,* but they may vary in the condition of the chalazal and micropylar ends, cells of which may be shriveled or inflated.

Unfortunately, only immature seeds of *B. smilacina* A. DC. were available; however, their morphology corresponds to that of other species of section *Enita.* No seeds were available of *B. inconspicua* Brade, but the drawing of Brade (1945, pl. 4.12) shows the seed type particular to section *Enita.*

In all specimens of the species observed, the chalazal side is flattened, probably from contact with the fruit wall, except in *B. epibaterium* (*Scott Mori & Forbes Benton 12856*), which has a more tapering, often somewhat asymmetric chalaza. Seed size in *B. epibaterium* tends to be a little smaller, as in *B. convolvulacea.* The mean seed size varies from 495 µm × 170 µm in *B. epibaterium* (*Dos Santos 3408*) to 660 µm × 150 µm in *B. glabra* (*Laurito 8172*). The length:width ratio in section *Enita* varies between 2.9 and 4.4. In all specimens observed the anticlinal walls may be undulated; however, some variation exists in the presence and extent of the undulations.

Remarks: The seeds of the different collections of the widespread species *B. glabra* vary in respect to the above-mentioned characters. The specimens from Surinam differ by having conspicuous chalaza with inflated cells, which make the chalaza even broader than the central part of the seed. The cuticular structure of the chalazal cells is more pronounced, with a more randomly orientated zigzag ornamentation and distinct patches with a confluent cuticular pattern.

The seeds of the collection from Cuba have few collar cells (mean=eight), with a mean length of 315 µm, and the ratio of collar-cell length to seed length is 2.0. This may be compared with, for instance, the collection from Costa Rica, the seeds of which have about 10 collar cells in the seed circumference. The collar cells have a mean length of 195 µm, and the ratio of collar-cell length to seed length is 3.4.

Our samples of *B. glabra* var. *amplifolia* (A. DC.) L.B. Smith & B.G. Schubert and *B. glabra* var. *cordifolia* (C. DC.) Irmscher do not show specific characters and more resemble *B. convolvulacea* in having less-inflated chalazal cells.

Specimens Examined:

B. epibaterium var. *epibaterium,* BRAZIL: *Dos Santos 3408* (US); *Scott Mori & Forbes Benton 12856* (US).

B. fagifolia, BRAZIL: *Brade 19144* (B); *Gaudichaud 1060* (P).

B. glabra var. *amplifolia,* COLOMBIA: *E.P. Killip 7722* (K).

B. glabra var. *cordifolia,* CULTIVATED: *van Veldhuizen 370* (WAG).

B. glabra var. *glabra,* COLOMBIA: *T.A. Sprague 403* (K). COSTA RICA: *Gomez Laurito 8172* (CR). CUBA: *C. Wright 2627* (P). ECUADOR: *Grubb c.s. 1199* (K). GUYANA: *G. Cremers 81* (P). SURINAM: *Indigen 270* (U); *H.S. Irwin c.s. 54738, 54818* (U).

1.7. Section ***Pritzelia*** (Klotzsch) A. DC.

PLATES 4, 5*a,b*

The section is characterized by male flowers with four tepals, free filaments, and anthers longer than the filaments and by female flowers with five tepals and undivided placentas. The leaves contain cystoliths. The section comprises about 100 species and is the largest section in Brazil. Only a few species of this section have a wider distribution. The section includes the former section *Saueria* A. DC.

SPECIES OBSERVED.—Seeds of 19 species have been observed using SEM. With a few exceptions, the seed structure corresponds with the ordinary begonia seed type. The seeds of the species differ in shape, size, and micromorphology to some extent.

Seed Structure: The seed shape is ellipsoid to slightly narrowly ellipsoid. The mean seed size of the section type, *B. dietrichiana* Irmscher, is 350 µm × 195 µm, with a length:width ratio of 1.8. Within the section the mean seed length varies from 310 µm in *B. acida* Vellozo to 620 µm in *B. angulata* Vellozo var. *serrana* Brade, and the length:width ratio varies from 1.7 to 2.6, respectively.

The anticlinal walls of the testa cells are straight or almost straight but are somewhat curved to slightly undulated in *B. paranaensis* Brade. The operculum is mostly nipple-shaped, sometimes broadly nipple-shaped, or obtusate in *B. coccinea* Hooker.

Seed Micromorphology: The anticlinal boundaries are flat except for those of *B. grisea* A. DC. and *B. itaguassuensis* Brade, which have sunken and locally sunken anticlinals, respectively. The majority of the seeds have a fine, dense cuticular pattern of mainly short linear striae, more zigzag in *B. epipsila* Brade and *B. paranaensis.* In *B. grisea* the cuticle is almost without ornamentation. Five species deviate in cuticular sculpture. *Begonia acida, B. hispida* Schott, and *B. sanguinea* Raddi have a more pronounced and coarse, mainly zigzag pattern. In *B. angulata* and *B. coccinea* the cuticular pattern is very pronounced, consisting of long zigzag, sometimes even pleat-like, striae. The seeds of *B. itaguassuensis* also have a fine, dense cuticular pattern; however, they differ from the seeds of all other observed *Pritzelia* species by having anticlinal walls that are

more thickened and elevated, are straight and form a distinct polygonal pattern at the outside, and are undulated, with pockets at their bases.

Begonia grisea and *B. paranaensis* resemble each other in shape and testal pattern. The seeds of *B. bradei* Irmscher, *B. crispula* Brade, *B. dietrichiana,* and *B. olsoniae* Smith & Schubert also resemble each other in some respects. The seeds of *B. itupavensis* Brade most resemble those of *B. hookerana* Gardner (*Occhioni 4788*) of section *Steineria.*

Remarks: The monotypic section *Saueria* A. DC. was eliminated by the placement of the Colombian type species *B. sulcata* Scheidweiler in Otto & Dietrich into synonymy with the Venezuelan species *B. dichotoma* Jacquin of section *Pritzelia* by L.B. Smith (1973). Although unfortunately no seeds of *B. dichotoma* were at our disposal, the seeds of *B. sulcata* quite closely resemble those of some other species of section *Pritzelia* from Brazil, e.g., *B. angulata.*

Specimens Examined:

B. acida, BRAZIL: cult., *Boone-Hahn 108* (WAG); cult., Hort. bot. Liège.
B. angularis Raddi var. *angularis,* BRAZIL: *D.R. Hunt 6470* (K).
B. angulata var. *angulata,* BRAZIL: *Hatschbach 8831* (L).
B. angulata var. *serrana,* BRAZIL: *Brade 17531* (U).
B. bradei, BRAZIL: cult., Dept. Horticulture (WAG).
B. coccinea, BRAZIL: *Burchell 219A* (P); cult., *Ziesenhenne s.n.*
B. crispula, BRAZIL: cult., *Boone-Hahn 13* (WAG).
B. dichotoma, COLOMBIA: cult., *Boone-Hahn 25* (WAG, as *B. sulcata*).
B. dietrichiana, BRAZIL: *A.P. Duarte 378* (US).
B. epipsila, BRAZIL: cult., *Boone-Hahn 27* (WAG).
B. grisea, BRAZIL: *St. Hilaire B 2027* (P); *H.S. Irwin c.s. 27654* (MO).
B. hispida var. *hispida,* BRAZIL: *Bailey & Bailey 710* (L); *Vauthier 542* (P).
B huegelii (Klotzsch) ex A. DC., BRAZIL: *Altamira & Wolter 11* (U).
B. itaguassuensis, BRAZIL: *A. Lourteig 3236* (P).
B. itupavensis, BRAZIL: *Hatschbach 11713* (U).
B. olsoniae, BRAZIL: cult., *van Veldhuizen 408* (WAG); *E. Pereira 307* (RB, as *B. vellozoana* Brade, paratype).
B. paranaensis, BRAZIL: *Hatschbach 8941* (L).
B. petasitifolia Brade, BRAZIL: cult., *van Veldhuizen 997* (WAG).
B. reniformis Dryander, BRAZIL: *Luederwaldt & Fonseca 18031* (B); *Ynes Mexia 5148* (P).
B. sanguinea, BRAZIL: *Bailey & Bailey 706* (L).

1.8. Section ***Philippomartia*** A. DC.

PLATE 5*c–e*

According to Irmscher (1953), the species of this section closely resemble those of section *Pritzelia* except for some stigmatic characters and for a ring of tentacle-like processes at the top of the petioles. Such a ring also is known in a number of species of *Pritzelia* and in some other sections. The section comprises two or three species, *B. leptophylla* Taubert, *B. membranacea* A. DC., and *B. neglecta* A. DC. The taxonomic position of *B. leptophylla* is questionable (Doorenbos et al., 1998). No seeds of *B. neglecta* were available.

SPECIES OBSERVED.—*Seed Structure:* The seeds of *B. leptophylla* and *B. membranacea* resemble each other and agree in many characters with those of species in section *Pritzelia,* such as *B. dietrichiana.* The mean seed length of both species lies between 300 µm and 360 µm. The testa cells are polygonal, with straight anticlinal boundaries, and the operculum is nipple-shaped.

Seed Micromorphology: The cuticular pattern is fine and dense; the striae are short linear in *B. leptophylla* and are zigzag in *B. membranacea.*

Specimens Examined:

B. leptophylla, BRAZIL: *A. Mo 4331* (MO).
B. membranacea, BRAZIL: *H.M. Curran 170* (US); Ex herb. horti Petropolitani Brasilia Castelnuovo (K).

1.9. Sections ***Steineria*** (Klotzsch) A. DC. and ***Bradea*** Toledo

PLATES 5*f–n,* 6*a,b*

Section *Bradea* was separated from section *Steinera* by Toledo in 1946 on the basis of differences in the staminate flower. The sections *Steineria* and *Bradea* comprise about four species (seeds of *B. caraguata-tubensis* Brade were not available) and 10 species, respectively. The two sections cannot be distinguished from each other on the basis of seed characters.

The species of both sections are restricted to Brazil, with the exception of the questionable species *B. opuliflora* Putzeys from the former New Granada, which is based on a drawing of a horticultural specimen.

TYPE SPECIES, SECTION *Steineria.*—*Begonia hookerana* Gardner (Plate 5*f,j*).

Seed Structure: Seeds narrowly ellipsoid to ellipsoid. Mean seed size 465 µm × 180 µm, length:width ratio 2.6. Collar cells elongated, other testa cells polygonal, with straight or slightly curved anticlinal walls. Operculum nipple-shaped.

Seed Micromorphology: Anticlinal boundaries flat. Cuticular pattern consisting of mainly short linear striae. Seeds of collection *Burchell 2539* somewhat smaller, with locally undulated anticlinal walls and fainter cuticular pattern.

Specimens Examined:

B. hookerana, BRAZIL: *Burchell 2539* (K); *P. Occhioni 4788* (US).

OTHER SPECIES OBSERVED, SECTION *Steineria* (Plate 5*g,l*).—The seeds of *B. arborescens* Raddi var. *arborescens* and *B. oxyphylla* A. DC. resemble those of *B. hookerana,* especially collection *Burchell 2539.* Their mean seed sizes vary between 330 µm and 415 µm. They all show locally undulated anticlinal walls with pockets at their bases and thin outer periclinal walls reflecting many small pits. The cuticular pattern of

both species and of the variety *B. arborescens* var. *confertiflora* A. DC. show some minor differences.

Specimens Examined:

B. arborescens var. *arborescens,* BRAZIL: *M. Clausen 63* (P); *Grisebach s.n.* (K); *J. Miers 3291* (K).

B. arborescens var. *confertiflora,* BRAZIL: *Gardner 602* (K, type).

B. oxyphylla, BRAZIL: *Inh. Vien s.n.* (1828) (K).

TYPE SPECIES, SECTION *Bradea.*—*Begonia rufosericea* Toledo (Plate 5*m*).

Seed Structure and Micromorphology: Seeds closely resembling those of (especially) *B. arborescens* in general aspect and in above-mentioned characters, except for less-pronounced undulation of anticlinal walls.

Specimens Examined:

B. rufosericea, BRAZIL: *Oswaldo Hanro s.n.* (B); cult., *van Veldhuizen 496* (WAG).

OTHER SPECIES OBSERVED, SECTION *Bradea* (Plates 5*h,k,n,* 6*a,b*).—Some other seed collections of section *Bradea* observed, especially those of *B. bidentata* Raddi and *B. polyandra* Irmscher, resemble *B. rufosericea.* They differ by having curved anticlinal walls and a more distinct cuticular pattern of zigzag striae. The seeds of *B. bidentata* collection *Riedel s.n., B. parvifolia* Schott, and *B. dentatiloba* A. DC. show a more reticulate character set.

Specimens Examined:

B. bidentata var. *bidentata,* BRAZIL: *A. Glaziou 11873* (K); *G. Peckolt 75* (B); *E. Pereira 287* (B); *Riedel s.n.* (U).

B. dentatiloba, BRAZIL: *L.B. Smith 1935* (K).

B. parvifolia, BRAZIL: *d'Alleizette s.n.* (L); *A. Glaziou 15388* (K); *Brasilia Schott s.n.* (B).

B. polyandra, BRAZIL: *Herb. Hieronymus s.n.* (B, type).

1.10. Section ***Tetrachia*** Brade

PLATE 6*c,g*

The monotypic section *Tetrachia* was established by Brade in 1945 on the basis of his newly described species *B. quadriloculariis.* This species was put into synonymy with *B. egregia* by Smith and Schubert (1955). The section is characterized by ovaries with four locules and by the presence of four styles and four-winged capsules. The number of tepals of the staminate and pistillate flower is two and six, respectively. The species is restricted to the state of Rio de Janeiro, Brazil.

TYPE SPECIES.—*Begonia egregia* N.E. Brown (Plate 6*c,g*).

Seed Structure: Seeds ellipsoid, 500–550 µm in length, 250–300 µm in width, mean 530 µm × 275 µm, length:width ratio 1.9. Collar cells 155–230 µm in length, mean 190 µm, number in seed circumference about 12. Ratio of collar-cell length to seed length 1:2.8. Testa cells polygonal, anticlinal walls somewhat thickened, straight, slightly curved toward collar. Operculum broadly nipple-shaped.

Seed Micromorphology: Anticlinal boundaries straight. Cuticular pattern consisting of long linear and long zigzag striae, the latter locally more pronounced.

Remarks: Seeds resemble those of *B. itaguassuensis* of section *Pritzelia* in the more thickened, straight, and elevated anticlinal walls.

Specimens Examined:

B. egregia, BRAZIL: *J. Santos Lima s.n.* (US, as *B. quadriloculariis* Brade, isotype); cult., *Boone-Hahn 1* (WAG).

1.11. Section ***Gaerdtia*** (Klotzsch) A. DC.

PLATE 6*d–f,h*

The placenta provides the most obvious character for this section. The placentas are two-parted, and the two lobes in each locule cling together and bear ovules on their outer sides only. The section contains about six species, three of which, *B. maculata* Raddi, *B. corallina* Carriere, and *B. undulata* Schott, were observed.

TYPE SPECIES.—*Begonia maculata* (Plate 6*e,f*), the seeds of which are to some extent characteristic and deviate in size and shape from the two other species observed.

Seed Structure: Seeds elliptic, sometimes narrowly elliptic. Mean seed size 565 µm × 240 µm, length: width ratio 2.4. Collar cells relatively long, mean length 290 µm. Ratio of collar-cell length to seed length 1.9. Testa cells adjacent to collar also elongated. Operculum long nipple-shaped. Anticlinal walls mainly straight.

Seed Micromorphology: Anticlinal boundaries flat, locally sunken. Cuticular pattern short zigzag.

Specimens Examined:

B. maculata var. *maculata,* BRAZIL: *Gentry & Zardini 49513* (MO); *Maas & Carauta 3149* (U).

OTHER SPECIES OBSERVED.—*Seed Structure and Micromorphology:* The seeds of *B. corallina* and *B. undulata* are smaller, with a mean seed length of 495 µm and 460 µm, respectively.

Specimens Examined:

B. corallina, CULTIVATED: *Boone-Hahn 114* (WAG).

B. undulata, BRAZIL: *Gaudichaud 1067* (P); cult., *Hort. Bogoriensis 6071 AB* (L).

1.12. Section ***Latistigma*** A. DC.

PLATE 6*j–l,n*

The species of this section are characterized by the presence of five tepals in the pistillate flowers and by broad, lobed styles. The section contains three species, *B. aconitifolia* A. DC. and *B. platanifolia* Schott from Brazil, and *B. leathermaniae* O'Reilly & Karegeannes from Bolivia.

TYPE SPECIES.—*Begonia aconitifolia* (Plate 6*j*).

Seed Structure: Seeds ellipsoid, mean seed size 440 × 250 µm, length:width ratio 1.8. Testa cells polygonal, with straight or slightly curved anticlinal walls. Anticlinal walls with more or less distinct pockets at bases.

Seed Micromorphology: Cuticular pattern fine and very dense, consisting of mainly short zigzag striae.

Specimens Examined:

B. aconitifolia, BRAZIL: *Glaziou 13389* (B).

OTHER SPECIES OBSERVED.—*Seed Structure and Micromorphology:* The seeds of *B. platanifolia* and *B. leathermaniae* closely resemble those of *B. aconitifolia,* differing mainly by their somewhat smaller size.

Specimens Examined:

B. leathermaniae, BOLIVIA: *O. Kuntze s.n.* (B); *M. Moraes 1056* (US).

B. platanifolia var. *platanifolia,* BRAZIL: *Creagh s.n.* (B); *G. Hatschbach 46298* (US).

1.13. Section ***Pereira*** Brade

PLATE 6*m*

This monotypic section is characterized by two-lobate broad stigmata that are almost kidney-shaped and cymatium-like.

TYPE SPECIES.—*Begonia edmundoi* Brade, limited to Brazil.

Seed Structure and Micromorphology: Seeds conforming to ordinary seed type, not showing distinguishing characters. Mean seed size 460 × 230 µm, length:width ratio 2.0. Anticlinal walls straight and relatively thin. Cuticular pattern consisting of short linear to short zigzag striae.

Specimen Examined:

B. edmundoi, BRAZIL: *E. Pereira 366* (B, cotype).

2. SECTIONS MAINLY CONFINED TO THE ANDEAN AND GUIANAN REGIONS

Of the 12 Andean sections, five (*Casparya, Gobenia, Hydristyles, Rossmannia, Warburgina*) have a characteristic seed structure that distinguishes them from all other Neotropical sections.

2.1. Section ***Casparya*** (Klotzsch) A. DC.

PLATES 7–9

Section *Casparya* has a very complicated taxonomic history. Shortly after its establishment as a genus by Klotzsch (1855), A. De Candolle (1864) extended it by including in it Klotzsch's genera *Isopteryx, Sassea,* and *Stibadotheca* and his newly described sections *Aetheopteryx* and *Andiphila.* Warburg (1894) reduced the genus *Casparya* to sectional level and reduced De Candolle's sections to subsections, actions that were later accepted by Irmscher (1925). Moreover, he inserted *Isopteryx* in *Andiphila.*

Smith and Schubert (1955) expressed the opion that the sympetalous character upon which the genera *Begoniella* Oliver and *Semibegoniella* C. DC. were based no longer was tenable. Consequently, the two species constituting genus *Semibegoniella* were placed into synonymy with *Begonia grewiifolia* (A. DC.) Warburg and so transferred to section *Casparya.* Smith and Schubert (1955) also merged the five species of the former genus *Begoniella* with section *Casparya.*

The section is characterized by bifid, or many-, or irregularly branched styles and by triquetrous fruits that are not winged but have each of the edges terminating in a horn. The capsule dehisces at the edges. The plants are mostly erect semishrubs and usually grow above 2000 m elevation, especially in the Andean region of Colombia and Ecuador and in Venezuela. The section comprises about 40 species.

Begonia urticae Group

Begonia urticae LINNAEUS F. (Plate *7a,b,d*).—Type species of section *Casparya.*

Seed Structure: Seeds narrowly ellipsoid, micropylar ends flattened. Seed shape slightly varying from ellipsoid to more ovoid, with greatest width in middle or more to micropylar or chalazal end. Length 695–780 µm, width 370–390 µm, mean 745 µm × 385 µm. Length:width ratio 1.9.

Collar cells relatively short, 90–155 µm in length, mean 130 µm, number in seed circumference about 15. Ratio of collar-cell length to seed length 1:5.7. Longitudinal walls of collar undulated over entire length. Other testa cells polygonal, mostly not arranged in distinct rows. Anticlinal walls strongly undulated. Operculum nipple-shaped, sometimes almost flat. Ring of cells bordering collar slightly deepened.

Seed Micromorphology: Anticlinal boundaries straight. Cuticular pattern rough, with relatively thick, linear to short linear or slightly undulated striae. No distinct patches.

Remarks: The 10 samples of *B. urticae* studied, the most common and most widely distributed species of section *Casparya,* show some variation in size and micromorphology.

The seeds of the collections *Schultes & Villarreal 7786, Dryander 1694, Bouman s.n., Bonpland s.n.,* and *Irally 192* closely resemble those of the above-described collection *Harling et al. 20465.* The mean seed size varies from 675 µm × 335 µm (*Schultes & Villarreal 7786*) to 785 µm × 430 µm (*Irally 192*). The length:width ratio varies from 1.7 (*Dryander 1694*) to 2.0 (*Schultes & Villarreal 7786*). The collections *Bohlin 975* (originally described as *B. urticae* var. *retusa* Smith & Schubert), *Cuatrecasas 23515, de Escobar c.s. 8521* (originally described as *B. antioquensis* (A. DC.) Warburg), and *Scott Hoover 442* deviate from the above-mentioned ones by having a smaller seed size and a more conspicuous undulation of the anticlinal cell walls. The mean seed size in collections *Cuatrecasas 23515* and *Scott Hoover 442* are 585 µm × 320 µm and 605 µm × 315 µm, respectively. In both collections, however, the cuticle has undulated striae of normal thickness. The collection *Scott Hoover 442* deviates by having larger collar cells with straighter longitudinal anticlinal walls. Mean length of the collar cells is 185 µm, with a collar-cell length to seed-length ratio of 1:3.3.

Specimens Examined:

B. species, ECUADOR: *van der Werff & Palacios 9135* (MO); *Scott Hoover & Wormley 1822* (MO).

B. urticae, COLOMBIA: *M.A. Bonpland s.n.* (P); *F. Bouman s.n.* (AMD); *Cuatrecasas 23515* (US); *E. Dryander 1694* (US); *de Escobar, Velasquez, & Marulanda 8521* (US); *W. Irally 192* (K); *W. Scott Hoover 442* (US); *Schultes & Villarreal 7786* (US). ECUADOR: *J.E. & M. Bohlin 975* (US); *Harling et al. 20465* (US).

OTHER SPECIES OBSERVED (Plate 7*c,e–g*).—*Seed Structure and Micromorphology:* The seeds of *B. fuchsiiflora* (A. DC.) A. Baranov & F.A. Barkley, *B. gamolepis* L.B. Smith & B.G. Schubert, *B. longirostris* Bentham (*Harling & L. Andersson 11608*), and *B.* species (*Scott Hoover & Wormley 1771*) resemble those of *B. urticae* collection *Bohlin 975* in size and in the strongly undulated anticlinal walls of both the testa and collar cells. Mean seed size varies from 545 µm × 310 µm in *B. gamolepis* to 630 µm × 375 µm in *B. fuchsiiflora.* All collections have a cuticle with mainly undulated striae of normal thickness except for collection *Scott Hoover & Wormley 1771,* which has a faint double structure.

Specimens Examined:

B. fuchsiiflora, ECUADOR: *M.T. Madison 6854* (US); *W. Scott Hoover 515* (MO).

B. gamolepis, COLOMBIA: *Barkley & Araque M. 185094* (US); *Killip & A.C. Smith 16037* (B).

B. longirostris, ECUADOR: *Harling & L. Andersson 11608* (US).

B. species, ECUADOR: *Scott Hoover & Wormley 1771* (MO).

Begonia ferruginea Group

Begonia ferruginea LINNAEUS F. (Plate 7*h–k*).—*Seed Structure:* Seeds narrowly obovate to obtriangular, micropylar end flattened, becoming acute at chalazal end. Length 770–960 µm, width 265–325 µm, mean 880 µm × 290 µm. Length:width ratio 3.0. Number of collar cells in seed circumference about 14. Longitudinal walls of collar cells straight, sometimes slightly undulated. Other testa cells often elongated, with undulated anticlinal walls, cells of chalazal part more polygonal. Operculum nipple-shaped.

Seed Micromorphology: Anticlinal boundaries flat. Cuticular ornamentation conspicuous, more or less plicate, composed of long, undulated foldings forming loose structure. Locally, patches with long, parallel striae.

Remarks: The seeds of two other collections are smaller and more variable in shape than the above-described collection (*Langenheim 3387*). Mean seed size is 775 µm × 345 µm in collection *Grubb et al. 534* and is 710 µm × 345 µm in collection *Steyermark & Dunsterville 100784,* with length:width ratios of 2.2 and 2.1, respectively. The seeds are ellipsoid, with rounded or more acute chalazal ends. Seeds of *B. ferruginea* var. *dilatata* Smith & Schubert are narrowly ellipsoid, with a mean seed size of 700 µm × 240 µm and a length:width ratio of 2.9. There are about 16 collar cells in the seed circumference, and the chalazal end is rounded or somewhat acute. The cuticular plicas and foldings are long and are undulated or somewhat zigzag.

Specimens Examined:

B. ferruginea var. *dilatata,* COLOMBIA: *H. Garcia-Barriga 12053* (US).

B. ferruginea var. *ferruginea,* COLOMBIA: *Grubb, Curry, & Fernandez-Perez 534* (US); *J.H. Langenheim 3387* (US); *Steyermark & Dunsterville 100784* (US).

B. species, COLOMBIA: *F.A. Barkley 38c120* (US).

Begonia trispathulata Group

Begonia trispathulata (A. DC.) WARBURG (Plate 8*a,b*).—*Seed Structure:* Seeds ellipsoid, micropylar end flattened, seeds 420–470 µm in length, 280–285 µm in width, mean 445 µm × 280 µm, length:width ratio 1.6. Seeds of collection *L. Goldsmith 169* shorter than those of above-described collection (*S.S. Tillett 739-585*), with mean length of 375 µm. Collar cells relatively short, number in seed circumference about 15. Other testa cells polygonal, with undulated anticlinal walls. Operculum nipple-shaped.

Seed Micromorphology: Anticlinal boundaries flat. Cuticle with so-called double structure: more elevated, short zigzag to star-shaped thick foldings and irregular, short zigzag to short linear underlying ornamentation. Locally, patches of labyrinth-like structure.

Specimens Examined:

B. trispathulata, VENEZUELA: *L. Goldsmith 169* (VT); *N. Ramirez 349* (MO); *S.S. Tillett 739-585* (P).

OTHER SPECIES OBSERVED (Plate 8*c–l*).—*Seed Structure and Micromorphology:* A number of species occurring in and mostly endemic to Venezuela resemble *B. trispathulata* in seed structure. All species are characterized by cuticles with a distinct double structure. *Begonia brevipetala* Warburg, *B. mariae* L.B. Smith, and *B. trujillensis* L.B. Smith agree in seed size and shape. In *B. trujillensis* the more elevated elements of the cuticular double structure are short undulated to short zigzag or star-shaped, in *B. brevipetala* they are short zigzag or star-shaped, whereas in *B. mariae* they are mainly star-shaped. The star-shaped ornaments often show a central depression.

The seeds of *B. lipolepis* L.B. Smith differ in some characters. The seeds are quite variable in shape, with a tendency to a tapering chalazal end. The mean seed size is 575 µm × 300 µm, with a length:width ratio of 1.9. The anticlinal walls are less undulated and are sometimes almost straight to slightly curved. The cuticular double structure consists of short zigzag to star-shaped elements.

The seeds of *B. toledana* L.B. Smith & B.G. Schubert have a mean size of 500 µm × 300 µm. The anticlinal walls are distinctly undulated. The double structure is short undulated to short zigzag.

The seeds of *B. formosissima* Sandwith have a mean size of 635 µm × 395 µm. The anticlinal walls are less distinctly undulated. The double structure is composed of relatively dense,

mainly short zigzag elevations that obscure the underlying granular pattern.

Specimens Examined:

B. brevipetala var. *brevipetala,* VENEZUELA: *F.J. Breteler 3468* (US); *L. Goldsmith 160* (VT); *Steyermark & Mehlin 109955* (U).

B. formosissima, VENEZUELA: *L. Goldsmith 166* (VT); *Ruiz-Teran & Figueiras 9306* (US).

B. lipolepis, VENEZUELA: *L. Goldsmith 167* (VT).

B. mariae, VENEZUELA: *L. Goldsmith 163* (VT).

B. toledana var. *toledana,* COLOMBIA: *Killip & A.C. Smith 20270* (B). VENEZUELA: *Steyermark & Dunsterville 100604* (K).

B. trujillensis, VENEZUELA: *L. Goldsmith 168* (VT); *S.S. Tillett 739-611* (US).

Begonia pectennervia Group

Begonia pectennervia L.B. SMITH & WASSHAUSEN (Plate 8*m,n*).—*Seed Structure:* Seeds ellipsoid, 535–590 µm in length, 350–360 µm in width, mean 565 µm × 350 µm, length:width ratio 1.6. Collar cells relatively short, 85–160 µm in length, mean 125 µm, number in seed circumference about 23. Ratio of collar-cell length to seed length 1:4.5. Anticlinal walls of collar straight to slightly undulated, those of other testa cells strongly undulated. Anticlinals broad, without boundary. Outer periclinal walls rather shallow. Collar slightly tapering, operculum therefore rather small. Opercular ring adjacent to collar sunken.

Seed Micromorphology: Anticlinals crossed by radiating longitudinal striae leaving "central field" of randomly orientated, small zigzag cuticular foldings of irregular thickness and elevation.

Remarks: The seeds of collection *Holm-Nielsen et al. 26762* differ slightly from the above-described collection (*Holm-Nielsen et al. 26438*) by having less-shallow testa cells and by having a cuticular ornamentation of short linear to short zigzag striae, sometimes with a faint double structure.

Specimens Examined:

B. pectennervia, ECUADOR: *L. Holm-Nielsen et al. 26438, 26762* (US).

OTHER SPECIES OBSERVED (Plate 9*a–e,g*).—*Seed Structure and Micromorphology:* The seeds of *B. colombiana* Smith & Schubert, *B. killipiana* Smith & Schubert, *B. longirostris* (*Lugo 4699*), and *B. trispathulata* (*Steyermark 103480*) resemble those of *B. pectennervia* in their broad anticlinal and shallow outer periclinal walls. The mean seed size varies from 440 µm × 275 µm in *B. trispathulata* to 655 µm × 470 µm in *B. killipiana.* The number of collar cells in the seed circumference varies from about 17 in *B. colombiana* to 22 in *B. killipiana.* The seeds of *B. killipiana* are characterized by short collar cells that vary in length from 65 µm to 130 µm, with a mean of 90 µm. The testa cells of *B. killipiana* and *B. longirostris* have a cuticular pattern similar to that of the central field, with short zigzag to star-shaped foldings. *Begonia colombiana* has a very dense pattern of short zigzag and short undulated striae; *B. trispathulata* has a double structure of linear, undulated, or zigzag striae of varying length. The star-shaped cuticular foldings in *B. killipiana* occasionally have a central depression. The seeds of *B. killipiana* collections *Killip 7994* and *W.S. Hoover 463* resemble those of *B. antioquensis* collection *Luteyn 12265,* described below, especially in their micromorphological characters. The collar cells of *B. killipiana* and *B. longirostris* are or tend to be very short; those of *B. trispathulata* are relatively short. Of these four species, the seeds of *B. killipiana* most resemble those of *B. hexandra,* described below.

Specimens Examined:

B. colombiana, COLOMBIA: *Schultes & Villarreal 7758* (US).

B. killipiana, COLOMBIA: *Killip 7994* (US); *W. Scott Hoover 27, 463* (US).

B. longirostris, ECUADOR: *Lugo 4699* (MO).

B. trispathulata, VENEZUELA: *Steyermark 103480* (US).

Begonia antioquensis

Begonia antioquensis (A. DC.) WARBURG (Plate 9*f*).—*Seed Structure:* Seeds ellipsoid, without distinct differentiation between operculum and collar, 510–600 µm in length, 295–360 µm in width, mean 560 µm × 325 µm, length:width ratio 1.8. No characteristic collar cells; all testa cells more or less isodiametric or somewhat irregular, not distinctly longitudinally elongated. Anticlinal walls pronounced, with rather obscure undulation, broader distally than proximally, and resembling rope netting. Micropylar end of seed rounded, without distinct hilum and micropyle.

Seed Micromorphology: Anticlinal boundaries obscured, anticlinals rough cross-hatched. Cuticle distinctly double-structured. Elevated parts, about 12 per cell, irregularly round or star-shaped, with central depression and interconnected by radiating linear cuticular striae.

Specimen Examined:

B. antioquensis, COLOMBIA: *J.L. Luteyn 12265* (US).

Begonia hexandra

Begonia hexandra IRMSCHER (Plate 9*h*).—*Seed Structure:* Seeds broadly ellipsoid, without distinct borderline between operculum and collar, 630–680 µm in length, 505–565 µm in width, mean 660 µm × 540 µm, length:width ratio 1.2. No distinct differentiation between collar cells and other testa cells. Cells surrounding micropylar-hilar region somewhat more elongated, over 30 cells in circumference. Shape of testa cells irregular due to strongly undulated anticlinal walls. Anticlinals relatively broad, without boundary. Cell pattern difficult to recognize due to shallowness of outer periclinal walls. Micropyle a small, irregular bulge without distinct exostome and hilar scar.

Seed Micromorphology: Cuticular pattern, if present, reduced, with longitudinal striae.

Specimen Examined:

B. hexandra, COLOMBIA: *E.L. Core 1500* (US).

Begonia diversistipulata Group

Begonia diversistipulata IRMSCHER (Plate 9*j*).—*Seed Structure:* Seeds ellipsoid, with flat operculum, 345–435 µm in length, 270–315 µm in width, mean 390 µm × 295 µm, length:width ratio 1.3. Collar cells 80–150 µm in length, mean 110 µm, number in seed circumference about 13. Ratio of collar-cell length to seed length 1:3.5. Testa cells polygonal, arranged in rows. Anticlinal walls relatively thin, straight or slightly undulated. Micropyle almost not protruding.

Seed Micromorphology: Anticlinal boundaries flat. Cuticular pattern consisting of rather loose, short, undulated striae to more condensed, short zigzag striae.

Specimen Examined:

B. diversistipulata, COLOMBIA: *Giacometto 11* (B).

OTHER SPECIES OBSERVED (Plate 9*k*).—The seeds of *B. umbellata* H.B.K. resemble those of *B. diversistipulata* in the thin, straight or almost straight anticlinal walls and a simple cuticular pattern of short linear to short undulated striae. The seeds, however, differ in size and in the number of collar cells. Mean seed size is 590 × 350 µm with a length : width ratio of 1.7. The number of collar cells in the seed circumference is about 17.

The collection *Scott Hoover 443* differs from the above-described collection (*Killip & Hazen 9165*) by having a denser cuticular pattern, consisting of a double structure of mainly long zigzag striae.

Specimens Examined:

B. umbellata, COLOMBIA: *Killip & Hazen 9165* (US); *W. Scott Hoover 443* (US).

Ungrouped Species

SPECIES OBSERVED (Plate 9*l–n*).—The seeds of *Begonia montana* Warburg, *B. raimondi* Irmscher, *B. hirta* (Klotzsch) Smith & Schubert, and one collection of *B. formosissima* (*Lopez-Figueiras & Dugarte 29409*) could not be incorporated into one of the groups of section *Casparya* described above.

Seed Structure and Micromorphology: Begonia montana and *B. formosissima* have, respectively, mean seed sizes of 545 µm × 340 µm and 565 µm × 360 µm and mean collar-cell lengths of 130 µm and 115 µm. Both have undulated anticlinal walls; those of the collar are straighter.

The cuticular pattern is granular in *B. montana* and is granular to short zigzag and more uneven in elevation in *B. formosissima.*

The mean seed sizes in *B. raimondi* and *B. hirta* are 790 µm × 395 µm and 725 µm × 385 µm, respectively. Mean collar-cell length in *B. raimondi* is 185 µm. The cuticular ornamentation in *B. raimondi* consists of dense, short undulated striae; in *B. hirta* it is more granular.

Specimens Examined:

B. formosissima, VENEZUELA: *Lopez-Figueiras & Dugarte 29409* (US);

B. hirta var. *hirta,* PERU: *R.J. Seibert 2385* (US).

B. montana, VENEZUELA: *Funck & Schlim 1044* (P, isotype); *H. Humbert 26725* (US).

B. raimondi, PERU: *A. Raimondi 2982* (B).

2.2. Section ***Rossmannia*** (Klotzsch) A. DC.

PLATE 10*a–c*

The taxon *Rossmannia* was first described by Klotzsch as a genus in 1855 and was transferred to sectional level by A. De Candolle in 1864. The monotypic section is characterized by pistillate flowers with two-parted placentas and by fruits with two very small wings and one large, subascending wing up to 40 µm long, covered by two large, persistent bracteoles. *Begonia rossmanniae* is a climbing shrub that occurs in humid forests of Ecuador, Peru, and Colombia.

TYPE SPECIES.—*Begonia rossmanniae* A. DC. (Plate 10*a–c*).

Seed Structure: Seeds narrowly ellipsoid, micropylar and chalazal ends extended, one or both sides often curved, rendering seeds J- or slightly S-shaped. Micropylar end of seed composed of uncollapsed, air-filled cells, chalazal end tapering, with elongated, collapsed cells. Length 645–710 µm, width 135–150 µm, mean 675 µm × 140 µm, length:width ratio 4.8. Ratio of embryo-containing part of seed to total length of seed 1:2.8. Collar cells 105–225 µm in length, mean 160 µm, number in seed circumference about 9. Ratio of collar-cell length to seed length 1:4.2. Longitudinal anticlinal walls of collar and adjacent cells straight or slightly undulated, those of operculum and chalaza always straight. Cells of operculum adjacent to collar elongated. Hilum sunken.

Seed Micromorphology: Anticlinal boundaries straight, those of operculum sunken. Cuticle with linear to short linear pattern. Operculum with long linear striae, often running over entire length of cells. Collapsed outer walls reflecting many small, underlying pits. Locally, patches with less pronounced pattern.

Specimens Examined:

B. rossmanniae, COLOMBIA: *H.W. Vogelmann c.s. 1297* (US). ECUADOR: *E. Asplund 9304* (G); *Holguer Lugo S. 4824* (AAU); *J. Jaramillo & F. Coello 3218* (AAU).

2.3. Section ***Hydristyles*** A. DC.

PLATE 10*d–k*

The section was established by A. De Candolle in 1859 and was retained as such by subsequent monographers (Warburg, 1894; Irmscher, 1925). The three species recognized by Irmscher in 1925 have been increased to about 10 in subsequent years, including the transfer of two species from section *Ruizo-*

pavonia. The section deviates from related Andean sections by the presence of five unequal tepals and multifid styles in the female flower. The species are semishrubs and occur in Bolivia, Colombia, Ecuador, and Peru.

TYPE SPECIES.—*Begonia bridgesii* A. DC. (Plate 10*f*).

Seed Structure: Seeds ellipsoid, 440–480 µm in length, 205–235 µm in width, mean 460 µm × 215 µm, length:width ratio 2.1. Collar cells 120–195 µm in length, mean 150 µm, number in seed circumference about 13. Ratio of collar-cell length to seed length 3.1. Longitudinal anticlinal walls of collar straight, those of other testa cells more irregularly curved, sometimes locally undulated. Testa cells somewhat elongated. Operculum nipple- to flat-nipple-shaped.

Seed Micromorphology: Anticlinal boundaries flat. Cuticular pattern short linear; cuticle locally with patches of thin, somewhat dense linear to undulated striae.

Specimen Examined:

aff. *B. bridgesii,* BOLIVIA: *Dereims s.n.* (P).

OTHER SPECIES OBSERVED (Plate 10*d,e,g–k*).—*Seed Structure and Micromorphology:* The seeds of the other species observed agree with those of *B. bridgesii* in the cellular pattern and in the short linear cuticular striae. They differ in shape, seed size, and the thickness and undulation of the anticlinal walls. The smaller seeds are found in *B. juntasensis* Kuntze and *B. subcaudata* Rusby ex L.B. Smith & B.G. Schubert, with mean seed sizes of 340 µm × 175 µm and 380 µm × 185 µm, respectively. The longest ones are found in *B. santarosensis* Kuntze, with a mean size of 630 µm × 205 µm and a length:width ratio of 3.1. The anticlinal walls vary from weakly undulated in *B. subcaudata;* to undulated in *B. andina* Rusby, *B. juntasensis,* and *B. santarosensis;* to strongly undulated in *B. unduavensis* Rusby.

Thicker anticlinal walls with sunken anticlinals are found locally in *B. juntasensis* and *B. unduavensis* (*G. Mandon 1089*). More distinct pockets are found in *B. juntasensis* and *B. santarosensis.*

Specimens Examined:

B. andina, BOLIVIA: *R.S. Williams 1566* (K).

B. juntasensis, PERU: *H.E. Moore Jr., Salazar, & Smith 8601* (US).

B. santarosensis, BOLIVIA: s.n. (P).

B. subcaudata, BOLIVIA: *St.G. Beck 9253* (US).

B. unduavensis, BOLIVIA: *St.G. Beck 4691* (US); *G. Mandon 1089* (K).

2.4. Section ***Warburgina*** O. Kuntze

PLATE 10*l*

The section was named by O. Kuntze in 1893 on the basis of its then newly described species, *B. comata.* The section is monotypic and is restricted to Bolivia. The characters of the section agree to a large extent with those of section *Hydristyles* and also with those of sections *Huszia* (=*Eupetalum*) and *Ruizopavonia.* Section *Warburgina* differs from these sections by having pauciflorous inflorescences enveloped by numerous bracts.

TYPE SPECIES.—*Begonia comata* Kuntze (Plate 10*l*).

Seed Structure: Seeds ellipsoid to narrowly ellipsoid, 365–435 µm in length, 170–185 µm in width, mean 420 µm × 175 µm, length:width ratio 2.2. Collar cells elongated, sometimes divided, 125–200 µm in length, mean 175 µm, number in seed circumference about 10. Ratio of collar-cell length to seed length 2.4.

Anticlinal walls of collar straight or almost straight, those of other testa cells strongly undulated, with pockets at bases of curves. Testa cells somewhat elongated. Operculum nipple-shaped.

Seed Micromorphology: Anticlinal boundaries sunken, those of collar cells strongly undulated. Cuticular pattern short linear, mostly shortly undulated toward anticlinals. Periclinal walls thin, locally reflecting underlying pits.

Specimen Examined:

B. comata, BOLIVIA: *St.G. Beck 12651* (US).

2.5. Section ***Gobenia*** A. DC.

PLATE 11*a–d,f,g*

The section was established by A. De Candolle in 1859 and was retained as such by subsequent monographers. It includes about 15 species and occurs in the nothern Andes, mainly Ecuador. Some of the distinguishing characteristics of the section are united filaments with sessile anthers and pistillate flowers that have extremely small styles with thick, auriculate stigmata. Fruits have three to four ribs or only one wing and are subtended by persistent bracteoles. The leaves are usually peltate. The species are climbing herbs or semishrubs.

TYPE SPECIES.—*Begonia maurandiae* A. DC. (Plate 11*a,d*).

Seed Structure: Seeds ellipsoid, irregular in shape, often obliquely flattened at chalazal side, 500–610 µm in length, 225–285 µm in width, mean 555 µm × 250 µm, length:width ratio 2.2. Collar cells 125–290 µm in length, mean 185 µm, number in seed circumference about 15. Ratio of collar-cell length to seed length 3.0. Anticlinal walls of testa cells straight, sometimes slightly curved. Testa cells at chalazal end deeper due to elevated anticlinal walls. Operculum broadly nipple-shaped, cells bordering collar elongated, forming distinct ring. Micropylar rim often oblique, hilum sunken.

Seed Micromorphology: Anticlinal boundaries always straight. Cuticular pattern with long linear striae, sometimes slightly undulated. Locally, patches with zigzag striae.

Remarks: Seeds of collection *Ed. André 3315* (originally identified as *B. hederacea* A. DC.) deviate from above-described collection (*W.H. Camp E 4974*) in the following characters: mean seed size 420 µm × 170 µm, length:width ratio 2.5; number of collar cells in seed circumference about 11; testa cells with more pronounced anticlinal walls and locally sunken anticlinal boundaries.

Specimens Examined:

B. maurandiae, ECUADOR: *W.H. Camp E 4974* (K). COLOMBIA: *Ed. André 3315* (K).

OTHER SPECIES OBSERVED (Plate 11*b,c,f,g*).—*Begonia pululahuana* C. DC., *B. secunda* L.B. Smith & D.C. Wasshausen, *B. sodiroi* C. DC., and *B. ynesiae* L.B. Smith & D.C. Wasshausen closely resemble one another and agree with *B. maurandiae* (*Camp E 4974*) in general characters, including the large number of collar cells. The seeds are even more variable in shape, sometimes somewhat J-shaped and/or slightly distorted. Mean seed size is 545 µm × 215 µm in *B. pululahuana,* 450 µm × 200 µm in *B. secunda,* 590 µm × 225 µm in *B. sodiroi,* and 560 µm × 220 µm in *B. ynesiae.* In the last species, the anticlinal walls are locally undulated.

Specimens Examined:

B. pululahuana, ECUADOR: *E.W. Davis 500* (US).

B. secunda, ECUADOR: *A. Gentry & G. Shupp 26638* (MO).

B. sodiroi, ECUADOR: *Holm-Nielsen & Jeppesen 1276* (US).

B. ynesiae, ECUADOR: *Ynes Mexia 7706* (K, isotype).

2.6. Section ***Meionanthera*** A. DC.

PLATE 11*e,h*

The section was established by A. De Candolle in 1859 and has remained monotypic, with its only species *B. holtonis* A. DC. The section is characterized by very small, subglobose anthers on long slender filaments, elongate tepals of the pistillate flowers, ovaries with entire placentas, and three-celled fruits with one large wing and two highly vestigial wings. The species is restricted to Colombia. The seeds are not very characteristic and resemble the ordinary type of begonia seed.

Seed Structure and Micromorphology: The seeds of *B. holtonis* var. *holtonis* are ellipsoid, with a mean size of 360 µm × 195 µm. The testa cells are polygonal, with straight or very slightly undulated anticlinal walls, and the operculum is nipple-shaped. The cuticular ornamentation is a fine, dense pattern of short linear or undulated striae. Locally, there are patches with a labyrinth-like structure.

Specimens Examined:

B. holtonis var. *holtonis,* COLOMBIA: *F.A. Barkley c.s. 66* (US); *Holton 725* (G, isotype); *J.L. Luteyn c.s. 10395* (MO); *Uribe Uribe 3878* (US).

2.7. Sections ***Lepsia*** (Klotzsch) A. DC. and ***Tittelbachia*** (Klotzsch) A. DC.

PLATE 11*j–n*

The species of the small sections *Lepsia* and *Tittelbachia* resemble each other in several floral characters and in outer appearance.

TYPE SPECIES.—*Begonia foliosa* H.B.K. var. *foliosa,* type species of section *Lepsia; B. fuchsioides* Hooker var. *fuchsioides,* type species of section *Tittelbachia.*

Seed Structure and Micromorphology: The seeds of the two type species resemble the ordinary type of begonia seed. They are mostly medium-sized, 355 µm × 180 µm and 490 µm × 240 µm, respectively, with distinctly elongated collar cells, variable undulation of the anticlinal testa cells, flat anticlinal boundaries, and a fine, dense cuticular pattern of mainly short linear or undulated striae.

The seeds of the different varieties of *B. foliosa* are rather polymorphic. The seeds of *B. foliosa* var. *putzeysiana* (A. DC.) Smith & Schubert are relatively long, with a mean size of 585 µm × 230 µm and a length:width ratio of 2.5. The seeds of *B. foliosa* var. *rotundata* Smith & Schubert have a very dense cuticle that somewhat obscures the anticlinal walls. The synonymy of *B. poeppigiana* A. DC. with *B. foliosa* var. *australis* Smith & Schubert is sustained by seed micromorphology.

Specimens Examined:

B. foliosa var. *australis,* ECUADOR: *Jameson s.n.* (B). PERU: *Matthias & Taylor 5905* (MO).

B. foliosa var. *foliosa,* COLOMBIA: *Oscar Haught 6159* (K); PERU: Herb. Splitgerberianum (L).

B. foliosa var. *putzeysiana,* COLOMBIA: *Killip & A.C. Smith 19817, 20090* (US).

B. foliosa var. *rotundata,* COLOMBIA: *McDougal & Roldan 3540* (US).

B. fuchsioides var. *fuchsioides,* COLOMBIA: *H.H. Smith 1269* (G); *Killip & A.C. Smith 20552* (US). VENEZUELA: *Maguire & Maguire 35301* (US).

B. fuchsioides var. *miniata* A. DC., COLOMBIA: *Uribe Uribe 5005* (US).

OTHER SPECIES OBSERVED.—The seeds of *B. microphylla* A. DC. are about 550 µm in length and differ from the species described above by having a more irregular seed shape, a broadly nipple-shaped operculum, and testa cells with more elevated anticlinal walls, causing a more shallow appearance. The seeds resemble those of species of section *Gobenia.* The collection *P.E. Berry 3291* is more or less intermediate between the collection *F.J. Breteler 4643* and *B. foliosa* collections.

Specimens Examined:

B. microphylla var. *microphylla,* VENEZUELA: *P.E. Berry 3291* (MO); *F.J. Breteler 4643* (MO); *L. Ruiz-Teran 393* (US).

2.8. Section ***Eupetalum*** (Lindley ex Klotzsch) A. DC., Including the Former Section ***Huszia*** (Klotzsch) A. DC.

PLATES 12, 13*a–c*

Section *Eupetalum* is mainly Andean, with species known from Ecuador and Peru. The type species, *B. geraniifolia* Hooker, has several synonyms.

Smith and Wasshausen (1979, 1986) included the species of section *Huszia* in section *Eupetalum.* The species of former section *Huszia* occur in Bolivia, Peru, and Colombia, occasionally extending into Venezuela or occurring in Mexico.

The species of the two sections as formerly recognized resemble each other quite closely and differ mainly in stem length.

The seeds of all species examined resemble the ordinary type of begonia seed. Although several species locally show crow's-foot-like cuticular striae, the seeds lack distinct features characteristic at the sectional level. Moreover, the seeds show some variation in size, shape of operculum, thickness of anticlinal walls, and density of the cuticular pattern.

FORMER SECTION *Huszia.—Seed Structure and Micromorphology:* The seeds of the former type species, *B. octopetala* l'Héritier, have a mean size of 340 µm × 180 µm and a length:width ratio of 1.9. The seeds of *B. erythrocarpa* A. DC., *B. pastoensis* A. DC., and *B. pleiopetala* A. DC. resemble those of *B. octopetala* in size, testal pattern, and in the very dense cuticular pattern, which consists of short zigzag and crow's-foot-like striae. The synonymy of *B. macbrideana* Irmscher with *B. erythrocarpa* as stated by Smith and Wasshausen (1984) is not substantiated by the seeds examined in this study. *Begonia macbrideana* has a different cuticular pattern and further differs by having an obtuse operculum, a larger number of collar and testa cells, and straight anticlinals. It has the biggest seeds observed in the former section *Huszia,* with a mean size of 455 µm × 300 µm and a length:width ratio of 1.5.

Remarks: The seeds of the three collections of the Mexican species *B. monophylla* Pavon ex A. DC. studied (all collected as *B. unifolia* Rose ex Trelease) closely resemble each other and differ from the seeds of all other *Eupetalum* species by having a broad, nipple-shaped operculum, broader anticlinal walls, and a coarser cuticular pattern of mainly zigzag striae.

Specimens Examined:

B. cinnabarina, BOLIVIA: *R. de Michel 16* (US).
B. erythrocarpa, PERU: *Wasshausen & Salas 1194* (K).
B. hydrophylloides, COLOMBIA: *M. Idrobo & Evans Schultes 560* (US).
B. macbrideana, PERU: *Weberbauer 2011* (B).
B. macra A. DC. aff., VENEZUELA: *Steyermark & Rabe 97300* (B).
B. monophylla, MEXICO: *C.G. Pringle s.n.* (L, PRE); *J.N. Rose c.s. 9367* (P).
B. octopetala, PERU: *L. Holm-Nielsen c.s. 3404* (MO); *A. Lopez c.s. 2709* (US); *O. Tovar 3600* (US).
B. pastoensis, COLOMBIA: *F.C. Lehman 5404* (B); *J. Triana s.n.* (P).
B. pearcei, CULTIVATED: *van Veldhuizen 580* (WAG).
B. pleiopetala, PERU: *Buchtien 653* (B); *Weberbauer 6026* (B).
B. serotina, BOLIVIA: *W.H. Camp E 3716* (P).
B. tumbezensis, PERU: *Weberbauer 7685A* (B).
B. veitchii J.D. Hooker, PERU: *A. Miguel Bang 1862* (B). CULTIVATED: *van Veldhuizen 1108* (WAG).

SECTION *Eupetalum.—Seed Structure and Micromorphology:* The seeds of the three collections of the type species, *B. geraniifolia,* closely resemble one another. The mean seed size is 340 µm × 195 µm, with a length:width ratio of 1.7. They resemble the seeds of the former section *Huszia* species *B. cinnabarina* Hooker, *B. hydrophylloides* Smith & Schubert, *B. pearcei* Hooker, *B. serotina* A. DC., and *B. tumbezensis* Irmscher in general characters, their length:width ratio, and their more granular cuticular ornamentation.

The seeds of the remaining species studied agree in the dense cuticular pattern but show some variation in other characters.

Specimens Examined:

B. aequatorialis Smith & Schubert, ECUADOR: *W.H. Camp E 3268* (MO).
B. geraniifolia, PERU: *Dowbey s.n.* (P); *A. Lourteig 3117* (K); *Sela 259* (B).
B. novogranatae A. DC., COLOMBIA: *M.T. Dawe 272* (K, as *B. inanis* Irmscher, isotype); *P.J. Grubb, Curry, & Fernandez-Perez 628* (K).

2.9. Section ***Apteron*** C. DC.

PLATE 13*d,e*

This monotypic section differs from the other sections by having globose, wingless fruits; it is endemic to Ecuador.

TYPE SPECIES.—*Begonia exalata* C. DC.

Seed Structure and Micromorphology: The seeds of *B. exalata* conform to the ordinary type of begonia seed. The mean seed size is 335 µm × 210 µm, with a length:width ratio of 1.6. The anticlinal walls are straight, slightly curved, or obscured undulated. The operculum is nipple-shaped. The cuticular pattern is quite characteristic, consisting of very dense, mainly short zigzag striae almost without a distinct delimitation at the anticlinals, resulting in a woolly appearance of the seed surface.

The seeds resemble those of *B. pastoensis* of section *Eupetalum* (*Huszia*).

Specimen Examined:

B. exalata, ECUADOR: *Sódiro 597* (US, isotype).

2.10. Section ***Barya*** (Klotzsch) A. DC.

PLATE 13*f–j*

Striking characters in section *Barya* are the presence of erect, lanceolate tepals in both staminate and pistillate flowers and unequal stamens united into an elongated column. *Begonia monadelpha* Ruiz & Pavon ex A. DC. and *B. soror* Irmscher occur in Peru; *B. boliviensis* A. DC. is known from Bolivia and Argentina.

TYPE SPECIES.—*Begonia monadelpha* (Plate 13*h*).

Seed Structure: Seeds ellipsoid to narrowly ellipsoid, somewhat irregular in shape. Length 450–555 µm, width 210–240 µm, mean 510 µm × 225 µm, length:width ratio 2.7. Collar cells elongated, 145–250 µm in length, mean 200 µm, number in seed circumference about 13. Ratio of collar-cell length to seed length 1:2.6. Longitudinal anticlinal walls of collar straight, those of other testa cells straight, curved, or slightly undulated, with pockets. Operculum obtuse to broadly nipple-shaped.

Seed Micromorphology: Anticlinal boundaries straight or locally sunken. Cuticular pattern with linear or short undulated striae.

Remarks: The seeds of collection *Barbour 3993* differ in several respects from the above-described collection *Weberbauer 6714,* being ellipsoid and somewhat smaller, with a mean seed size of 465 µm × 240 µm, a length:width ratio of 1.9, and having thicker, straighter anticlinals.

Specimens Examined:

B. monadelpha, PERU: *P. Barbour 3993* (MO); *A. Weberbauer 6714* (US).

OTHER SPECIES OBSERVED (Plate 13*f,g,j*).—*Seed Structure and Micromorphology:* The seeds of *B. soror* quite closely resemble those of *B. monadelpha* collected by Weberbauer. They have a sunken micropyle and less undulated anticlinal walls.

The seeds of *B. boliviensis* A. DC. differ from the above-mentioned species and more resemble the ordinary begonia seed type. They have a mean seed size of 355 µm × 230 µm, with a length:width ratio of 1.5. The collar cells vary in length from 85 µm to 165 µm, with a mean of 125 µm. The ratio of collar-cell length to seed length is 1:2.8. The operculum is nipple-shaped. The cuticular pattern is short linear to short undulated striae.

Specimens Examined:

B. boliviensis var. *boliviensis,* ARGENTINA: *J.G. Hawkes c.s. 3620* (MO); *S. Venturi 4950* (MO). BOLIVIA: *S.G. Beck 6355* (US).

B. soror, PERU: *J.J. Wurdack 1627* (US).

3. SECTIONS OCCURRING BOTH IN BRAZILIAN AND IN ANDEAN REGIONS

Only two sections have a distribution both from Brazil or Argentina and from the Andean countries.

3.1. Section ***Pilderia*** A. DC.

PLATE 13*k,n*

Klotzsch's genus *Pilderia* was reduced to sectional level by A. De Candolle (1859). The section is characterized by staminate flowers with two to four tepals and pistillate flowers with five persistent tepals and undivided placentas. The plants are herbs or semishrubs with a yellowish pubescence. The section is probably monotypic. *Begonia buddleiifolia* A. DC. has a distribution from Brazil and Peru to Venezuela.

TYPE SPECIES.—*Begonia buddleiifolia* A. DC. (Plate 13*k,n*).

Seed Structure: Seeds conforming to ordinary seed type. Seeds ellipsoid, mean size 285 µm × 150 µm, length:width ratio 1.9. Seeds of collection *Allart 387* somewhat bigger: 320 µm × 175 µm. Testa cells polygonal; anticlinal walls straight and weakly undulated at bases in collection *Allart 387.* Operculum nipple-shaped.

Seed Micromorphology: Anticlinal boundaries flat, sometimes locally sunken. Cuticular ornamentation consisting of zigzag striae of various length.

Specimens Examined:

B. buddleiifolia, BRAZIL: *E. Ule 6466* (K). ECUADOR: *Holguer Lugo S. 5042* (K). VENEZUELA: *Allart 387* (B). NOUVELLE GRENADE: *Goudot s.n.* (P).

3.2. Section ***Australes*** Smith & Schubert

PLATE 13*l,m,o*

The section was established by Smith and Schubert in 1941 and comprises herbaceous or almost herbaceous species with a small tuber at the stem base. The staminate and pistillate flowers have four and five tepals, respectively. The three styles are deeply two-divided on the back and are more or less wavy on the front. The section contains four species, all occurring in Argentina. *Begonia micranthera,* with several varieties, also extends to Bolivia and Peru.

No seeds were available of *B. parodiana* L.B. Smith & B.G. Schubert and *B. sleumeri* L.B. Smith & B.G. Schubert.

TYPE SPECIES.—*Begonia micranthera* Grisebach (Plate 13*m,o*).

Seed Structure: Seeds elliptic. Mean seed size 405 µm × 240 µm in *B. micranthera* var. *micranthera,* 420 µm × 230 µm in *B. micranthera* var. *foliosa* L.B. Smith & B.G. Schubert, and 340 µm × 210 µm in *B. micranthera* var. *fimbriata* L.B. Smith & B.G. Schubert. Length:width ratios 1.7, 1.8, and 1.6, respectively. Relatively many testa cells, those adjacent to collar somewhat elongated, chalazal ones polygonal. Anticlinal walls straight, slightly curved, or slightly undulated. Operculum cone-shaped.

Seed Micromorphology: Anticlinal boundaries flat, locally sunken in *B. micranthera* var. *fimbriata.* Cuticle with short, undulated striae and with slight double structure in *B. micranthera* var. *fimbriata* and var. *foliosa.*

Specimens Examined:

B. micranthera var. *fimbriata,* ARGENTINA: *J. West 8413* (MO, isotype).

B. micranthera var. *foliosa,* ARGENTINA: *S. Venturi 3457* (US); *J. West 6216* (MO).

B. micranthera var. *micranthera,* ARGENTINA: *Petersen & Hjerting s.n.* (L). BOLIVIA: *V.M. Cardenas 4710* (US).

OTHER SPECIES OBSERVED (Plate 13*l*).—The seeds of *B. tafiensis* Lillo closely resemble those of *B. micranthera* var. *foliosa* in size and morphological characters.

Specimen Examined:

B. tafiensis, ARGENTINA: *S. Venturi 3093* (US).

4. SECTIONS MAINLY CONFINED TO THE CENTRAL AMERICAN, MEXICAN, AND CARIBBEAN REGIONS

Of the eight sections confined to Middle America, six could be studied for their seed structure. Of these only one, *Urniformia,* shows a characteristic seed structure that distinguishes

it from all other Neotropical sections. No seeds for study were available of the monotypic sections *Cylindrobegonia* and *Parietoplacentalia.*

4.1. Section ***Urniformia*** Houghton ex Ziesenhenne

PLATE 14*a,b*

This section was draughted by Houghton in 1924 but wasn't published by Ziesenhenne until 1974. The section is monotypic and is restricted to Costa Rica, Guatemala, and Panama. The section is characterized by a one-celled ovary and a capsule with three long, hollow, fleshy horns.

TYPE SPECIES.—*Begonia heydei* C. DC. (Plate 14*a,b*).

Seed Structure: Seeds ellipsoid, 540–620 µm in length, 255–295 µm in width, mean 585 µm × 280 µm, length:width ratio 2.1. Collar cells 165–244 µm in length, mean 205 µm, number in seed circumference about 11. Ratio of collar-cell length to seed length 1:2.9. Testa cells polygonal, sometimes somewhat elongated toward collar. Anticlinal walls curved or slightly undulated. Operculum broadly nipple-shaped.

Seed Micromorphology: Anticlinal boundaries flat. Cuticle smooth, without ornamentation; locally, striae on anticlinal walls of operculum.

Specimens Examined:

B. heydei, COSTA RICA: *Haber & Bello 7645* (MO); *R.A. Ocampo 1323* (CR); *Stone & Stone 2712* (US).

4.2. Section ***Gireoudia*** (Klotzsch) A. DC.

PLATES 14*c–n,* 15*a–c*

Gireoudia was described by Klotzsch in 1854 as a genus. It was reduced to a section by A. De Candolle in 1859. Later, *Gireoudia* was considered to be a subsection of section *Magnusia* along with subsections *Rachia* and *Psathuron.* On the basis of priority, *Gireoudia* is now treated as a section including *Magnusia* and *Psathuron. Rachia* is now included in section *Knesebeckia.* Section *Gireoudia* includes the monotypic section *Auriformia* Ziesenhenne by the synonymy of *B. bakeri* C. DC. with *B. cardiocarpa* Liebmann (Burt-Utley, 1985). We accept the proposal by Burt-Utley (1985) to select *B. plebeja* Liebmann as lectotype of section *Gireoudia* above the more arbitrarily chosen species *B. involucrata* Liebmann (Baranov & Barkley, 1974).

The Central American and Mexican species of the section have been revised by Burt-Utley (1985, 1990). The section is characterized by staminate and pistillate flowers with two tepals and pistillate flowers with two-parted placentas. The plants are rhizomatous perennials or suffrutescent herbs. The section comprises over 60 species, most of which are endemic and restricted to Mexico and Central America. Four species are reported from Colombia, Venezuela, and Guyana.

TYPE SPECIES.—*Begonia plebeja* (Plate 14*c,f*).

Seed Structure: Seeds ellipsoid. Mean seed size 365 µm × 185 µm, length:width ratio 2.0. Testa cells polygonal or more elongated. Anticlinal walls slightly curved. Operculum nipple- to broadly nipple-shaped.

Seed Micromorphology: Anticlinal boundaries flat. Cuticular pattern mainly consisting of short undulated striae. Locally, patches without distinct ornamentation.

Specimen Examined:

B. plebeja, COSTA RICA: *John Taylor 17305* (US).

OTHER SPECIES OBSERVED (Plates 14*d,e,g–n,* 15*a–c*).—The seeds of all species observed by us conform to the ordinary seed type. Seeds vary to some extent in size, number of testa cells, and in micromorphology.

Seed Structure: Seed length varies from 310 µm in *B. jenmannii* Tutin to 445 µm in *B. crassicaulis* Lindley and *B. urophylla* W.J. Hooker. The anticlinal walls are mostly straight, slightly curved, slightly undulated (*B. barkeri* Knowles & Westcott, *B. multinervia* Liebmann, *B. urophylla*), or undulated (*B. sartorii* Liebmann).

Seed Micromorphology: The anticlinal boundaries are always flat. Cuticular ornamentation in most species is mainly granular to short zigzag, as in *B. sericoneura* Liebmann, or short undulated, as in *B. nelumbiifolia* Schlechtendal & Chamisso. The cuticular pattern is fine and very dense, as in *B. cardiocarpa.*

Specimens Examined:

B. barkeri, MEXICO: *Bourgeau 2968* (L); *Ch.L. Smith 690* (US).

B. cardiocarpa, COSTA RICA: *K. Utley 5917* (US). HONDURAS: *P.C. Standley 11403* (US). NICARAGUA: *Ziessenhenne s.n.* (cult., as *B. bakeri* C. DC.).

B. conchifolia Dietrich var. *conchifolia,* PANAMA: *Wilbur 24349* (CR).

B. crassicaulis, GUATEMALA: *J.A. Steyermark s.n.* (US).

B. fusca Liebmann, MEXICO: *Botteri & Sumichrast 1631* (P).

B. heracleifolia Schlechtendal & Chamisso var. *heracleifolia,* MEXICO: *Bourgeau 1583* (P).

B. involucrata, COSTA RICA: *P.C. Standley 34241* (US); *Stanley & Valerio 48137* (US).

B. jenmannii, BRITISH GUIANA (=Guyana): *B. Maguire & Fanshawe 23081* (U).

B. multinervia, COSTA RICA: cult., *van Veldhuizen 661* (WAG).

B. nelumbiifolia, CULTIVATED: Gent, *B.K. Boom 16850* (L).

B. plantaginea Smith & Schubert, MEXICO: *E. Matuda 117945* (US).

B. sartorii, MEXICO: *Bourgeau 2100* (L).

B. sericoneura, HONDURAS: cult., *van Veldhuizen 392* (WAG).

B. squarrosa Liebmann, MEXICO: cult., *van Veldhuizen 623* (WAG).

B. urophylla, COSTA RICA: cult., *van Veldhuizen 655* (WAG).

4.3. Section ***Hexaptera*** Ziesenhenne

PLATE 15*d,e*

In 1974 Ziesenhenne established this monotypic section to accomodate *B. oaxacana,* formerly belonging to section *Knesebeckia.* The section is characterized by the presence of erect

fruits with six small wings. This character, however, is not always present in this variable species. The species occurs in Panama, Costa Rica, Nicaragua, Guatemala, and southern Mexico.

The seeds of *B. oaxacana* differ to some extent from the ordinary type of begonia seed.

TYPE SPECIES.—*Begonia oaxacana* A. DC. var. *oaxacana* (Plate 15*d,e*).

Seed Structure: Seeds ellipsoid. Mean seed size 480 µm × 255 µm, length:width ratio 1.9. Testa cells more or less polygonal, with straight, curved, or sometimes slightly undulated anticlinal walls; anticlinal walls thickened. Operculum nipple- to broadly nipple-shaped.

Seed Micromorphology: Anticlinal boundaries always flat. Cuticular structure variable, from mostly faint linear, to short linear in collection *McVaugh 10266,* to smooth in collection *Davidse et al. 26139.*

Remarks: The seeds of collection *McWilliams & Molina 42675* are comparable in size and shape; however, they differ in having a greater number of collar and testa cells, mainly straight anticlinal walls, and a more distinct cuticular pattern of short zigzag striae.

The seeds of collection *McVaugh 10266* strongly resemble those of *B. udisylvestris* C. DC., a species placed in section *Ruizopavonia* by Barkley and Golding (1974). The seeds of collection *Davidse et al. 26139* resemble those of *B. heydei* (section *Urniformia*) in shape, the smooth cuticle, and the thicker anticlinal walls.

Specimens Examined:

B. oaxacana, COSTA RICA: *G. Davidse et al. 26139* (CR); *P.C. Standley 38821* (US). MEXICO: *R. McVaugh 10266* (US). NICARAGUA: *Williams & R. Molina 42675* (US). PANAMA: *R.L. Liesner 285* (P).

4.4. Section ***Dissepbegonia*** Ziesenhenne

PLATE 15*f,g*

This section was established by Ziesenhenne in 1948 on the basis of the newly described species *B. cavum* Ziesenhenne, found in a small cave in Oaxaca, Mexico. The section closely resembles section *Knesebeckia* but can be distinguished by the presence of placentas affixed to the inner walls of the locules. Later the section was extended with *B. palmeri* S. Watson (Barkley and Golding, 1974).

SPECIES OBSERVED.—Unfortunately no seeds were available of *B. cavum.* The seeds of *B. palmeri* are not characteristic and resemble the ordinary type of begonia seed.

Seed Structure and Micromorphology: Seeds of *B. palmeri* have a mean seed size of 355 µm × 205 µm, with a length:width ratio of 1.7. The testa cells are polygonal, with straight or curved anticlinal walls. The operculum is nipple- to broadly nipple-shaped. The cuticular structure is faint-granular, with more prominent short linear or short undulated striae.

Specimen Examined:

B. palmeri, MEXICO: *Ynes Mexia 219* (MO).

4.5. Section ***Podandra*** A. DC.

PLATE 15*h,j*

The section is characterized by staminate and pistillate flowers with four and five tepals, respectively, and filaments united into a column. The section comprises the type species *B. decandra* Pavon ex A. DC. from Puerto Rico and Mexico. The inclusion of a second species, *B. trichosepala* C. DC. from Guatemala (Barkley and Golding, 1974), is disputed (Doorenbos et al., 1998). No seeds of the latter species were available.

TYPE SPECIES.—*Begonia decandra.*

Seed Structure: Seeds ellipsoid, mean size 370 µm × 180 µm, length:width ratio 2.1. Collar cells distinctly elongated, other testa cells rectangular. Anticlinal walls of collar and testa cells varying between collections: strongly undulated in *Krug & Urban 1121,* undulated to weakly so in *Hoffmann 876,* and weakly undulated to almost straight in *Sintenis 5341.* Operculum nipple-shaped.

Seed Micromorphology: Anticlinal boundaries varying among collections: mostly sunken in *Krug & Urban 1121,* locally sunken in *Hoffmann 876,* and almost always flat in *Sintenis 5341.* Cuticular pattern consisting of short linear and short undulated striae.

Specimens Examined:

B. decandra, PUERTO RICO: *O. Hoffmann 876* (B); *Krug & Urban 1121* (L); *P. Sintenis 5341* (P).

4.6. Section ***Weilbachia*** (Klotzsch & Oersted) A. DC.

PLATE 15*k–o*

Weilbachia was originally described as a genus but was reduced to a section by A. De Candolle (1859). The section probably includes section *Liebmannia* Ziesenhenne, as it is similar to, if not indistinguishable from, section *Weilbachia* (Burt-Utley, 1985). The section is characterized by staminate flowers with two or four tepals and by pistillate flowers with two or three tepals and two-celled ovaries with two or three styles and two-parted placentas. The section is restricted to Central America and Mexico and comprises about 20 species (Burt-Utley, 1985).

TYPE SPECIES.—*Begonia ludicra* A. DC. (syn. *B. liebmannii* A. DC.). The original type species was described by Klotzsch as *Weilbachia reptans,* which was renamed *Begonia liebmannii* by A. De Candolle in 1864.

SPECIES OBSERVED (Plate 15*k–o*).—*Seed Structure:* Seeds ellipsoid, varying in size from 320 µm × 195 µm in *B. aridicaulis* Ziesenhenne to 415 µm × 215 µm in *B. pustulata* Liebmann, with length:width ratios of 1.6 and 1.9, respectively. Testa cells irregularly polygonal. Anticlinal walls undulated in most species but straight to curved in *B. purpusii* Houghton ex Ziesenhenne. Operculum nipple-shaped.

Seed Micromorphology: Anticlinal boundaries always flat. Cuticular pattern short undulated, short linear, or granular. Outer periclinal cell wall sometimes rather thin, almost without cuticular ornamentation, and reflecting underlying pits, as in *B. imperialis* Lemaire.

Specimens Examined:

B. alice-clarkiae Ziesenhenne, MEXICO: cult., *van Veldhuizen 497* (WAG).
B. aridicaulis, MEXICO: cult., *van Veldhuizen 529* (WAG).
B. imperialis var. *imperialis,* MEXICO: *DTH 5397* (L).
B. ludicra A. DC., MEXICO: cult., *van Veldhuizen 414* (WAG).
B. purpusii, GUATEMALA: *J.D. Dwyer 15321* (MO). MEXICO: *E. Matuda 5406* (MO).
B. pustulata, GUATEMALA: *H. von Türckheim 1181* (US).

5. Section Mainly Occurring in both Andean and Middle American Regions

Only one section has a distribution more distinctly restricted to the Andes and Central America and Mexico.

5.1. Section ***Ruizopavonia*** A. DC.

PLATES 16, 17*a,b*

The section was established by A. De Candolle in 1859. Irmscher (1949) discussed the delimitation of the section. *Begonia corredorana* C. DC. and *B. thiemei* C. DC., affiliated to this section by Barkley and Golding (1974), were included in section *Gireoudia* by Burt-Utley (1985).

Most species of the section have only two tepals in the staminate and pistillate flowers, but in some species there are three tepals in the staminate flowers and up to four tepals in the pistillate flowers. The connective of the stamens is a little extended. The styles are deeply two-parted and are sometimes divided again. The plants are suffrutescent, shrubby, or climbing, predominantly with pinnately veined leaves, and with small deciduous bracteoles. The section comprises about 35 species, mostly from the Andes, but eight species are reported from Central America and/or Mexico.

TYPE SPECIES.—*Begonia alnifolia* A. DC. (Plate 16*a,b*).

Seed Structure: Seeds ellipsoid, resembling ordinary begonia seed type. Mean seed size of collection *Mocquerys 1219* 325 µm × 195 µm, length:width ratio 1.7. Collar cells elongated, other testa cells relatively few in number. Anticlinal walls of testa cells thin and straight to curved. Operculum nipple-shaped.

Seed Micromorphology: Anticlinal boundaries flat. Cuticular pattern linear or undulated. Locally, patches without a smooth or fine structure.

Remarks: Seeds of *B.* aff. *alnifolia* collection *A.C. Smith 3169* deviate by having somewhat larger seeds, undulated anticlinals, and a less dense cuticular pattern with underlying pits.

Specimens Examined:

B. alnifolia, VENEZUELA: *Mocquerys 1219* (P). GUYANA: *A.C. Smith 3169* (P).

SPECIES COMPARABLE TO *B. alnifolia* (Plate 16*c–h,k,l*).—Seeds of most of the species observed of section *Ruizopavonia* resemble one another in their relatively small size, curved undulated anticlinals, and in their fine cuticular structure, consisting of linear or undulated striae.

Seed Structure and Micromorphology: Mean seed length varying from 225 µm in *B. corredorana* C. DC., to 255 µm in *B. cooperi* C. DC., to 415 µm in *B. carpinifolia* Liebmann. Length:width ratios varying from 1.4 in *B. peruviana* A. DC. to 2.1 in *B. convallariodora* C. DC. *Begonia carpinifolia* seeds with relatively many testa cells. Seeds of *B. bracteosa* A. DC. resembling those of several Andean species in section *Begonia,* such as *B. cyatophora* Poeppig & Endlicher. Anticlinal walls varying from almost straight, to curved (*B. peruviana*), to distinctly undulated (*B. seemanniana* A. DC.). Compared with other species resembling *B. alnifolia,* seeds of *B. bracteosa* with thicker, curved to undulated anticlinal walls, locally with sunken anticlinal boundaries and coarser cuticular pattern of short linear or short undulated striae.

Specimens Examined:

B. bracteosa, PERU: *Ellenberg 815* (U).
B. carpinifolia, COSTA RICA: *Kappelle & Monge 3635* (CR).
B. consobrina Irmscher, COLOMBIA: *Schultes & Villarreal 7704* (K).
B. convallariodora, COSTA RICA: *Scott Hoover 582* (MO). PANAMA: *Seibert 207* (K).
B. cooperi, CULTIVATED: *van Veldhuizen 396* (WAG).
B. corredorana, COSTA RICA: *A.F. Skutch 4733* (US).
B. peruviana, PERU: *Sandeman 4378* (K).
B. seemanniana var. *seemanniana,* PANAMA: *Seemann 1661* (K, lectotype).
B. thiemei C. DC., MEXICO: *Martinez Calderon 2258* (US).
B. viridiflora A. DC. var. *parviflora* Smith & Schubert, PERU: *Mexia 04152* (MO, isotype).

SPECIES DIFFERING FROM *B. alnifolia* (Plates 16*j,m–o,* 17*a,b*).—The seeds of four species examined differ distinctly from those described above.

Begonia udisylvestris C. DC.: Mean seed size 545 µm × 295 µm, length:width ratio 1.8. Anticlinal boundaries flat, with or without faint cuticular ornamentation. Outer periclinal walls of testa cells often with central field of short undulated striae and longer linear striae radiating toward anticlinal walls.

Begonia suprafastigiata Irmscher: Mean seed size 435 µm × 190 µm, length:width ratio 2.3. Testa cells elongated, in regular rows in continuation of collar cells. Anticlinal walls of testa cells distinctly undulated.

Begonia cuatrecasiana Smith & Schubert: Seeds ellipsoid to narrowly ellipsoid, somewhat varying in shape and dimensions. Operculum obtuse, chalazal end extended. Mean seed size 385 µm × 150 µm, with length:width ratio of 2.6. Anticlinal walls curved to undulated, locally with pockets. Anticlinal

boundaries flat, crosshatched. Seeds of *B. cuatrecasiana* show tendency to scobiformy, as seen more extremely in section *Rossmannia* (see Smith and Schubert, 1946).

Begonia estrellensis C. DC.: Seeds narrowly ellipsoid, with obtuse operculum and extended chalazal end. Mean seed size 625 µm × 170 µm, length:width ratio 3.7. Testa cells elongated. Anticlinal walls elevated and slightly undulated, with many pockets along walls. Cuticular pattern mainly long linear striae. Seeds of collection *Liesner 1023* somewhat smaller and more tapering toward chalazal end.

Remarks: The seeds of *B. estrellensis* resemble those of *B. santarosensis* of section *Hydristyles.* The seeds of *B. udisylvestris* resemble those of *B. oaxacana* of section *Hexaptera.*

Specimens Examined:

B. cuatrecasiana, COLOMBIA: *Forrero-Jaramillo 2403* (COL).

B. estrellensis, COSTA RICA: *Nelson Zamora c.s. 512* (CR). PANAMA: *Liesner 1023* (L).

B. suprafastigiata, PERU: *Weberbauer 7907* (B, holotype).

B. udisylvestris, COSTA RICA: *Burger & Stolze 5250* (CR).

6. Sections with a Wide Neotropical Distribution

The four sections discussed below comprise species distributed over a wide area, ranging from Brazil to Mexico. Two sections, *Begonia* and *Knesebeckia,* also have species in Asia.

6.1. Section ***Doratometra*** (Klotzsch) A. DC.

PLATE 17*c–m*

The section is characterized in part by three two-parted styles with linear branches, undivided placentas, and palmately veined leaves. The species are self-fertilizing herbs.

The section comprises about 12 species. Most species have a restricted distribution; *B. filipes* Bentham, *B. hirtella* Link, *B. humilis* Dryander, and *B. semiovata* Liebmann have a wider distribution in Central and South America. *Begonia hirtella* has been introduced and naturalized in, among other places, South Africa, Java, and Sri Lanka.

TYPE SPECIES.—*Begonia wallichiana* Lehman (Plate 17*d,g*).

Seed Structure: Seeds elliptic, 315–365 µm in length, 185–205 µm in width, mean 340 µm × 195 µm. Length:width ratio 1.7. Collar cells relatively short, with mean length of 100 µm. Testa cells isodiametric, anticlinal walls rather thick, straight or curved or somewhat undulated. Operculum nipple-shaped.

Seed Micromorphology: Anticlinal boundaries flat. Cuticular pattern dense, consisting of mainly granular ornamentation.

Specimens Examined:

B. wallichiana, MEXICO: *J.A. Duke M 3682* (MO); *L.R. Stanford c.s. 972* (MO).

OTHER SPECIES OBSERVED (Plate 17*c,e,f,h–m*).—The seeds of species of this section show some variation in size and micromorphology; the seeds of *B. prieurii* A. DC. and *B. steyermarkii* Smith & Schubert in particular are quite characteristic.

Seed Structure and Micromorphology: The seeds of *B. filipes, B. humilis,* and *B. semiovata* are relatively small (e.g., 235 µm in *B. filipes*), and the anticlinal walls are thinner than in the type species; however, they agree with *B. wallichiana* in general morphology and in the granular cuticular ornamentation. The seeds of *B. tonduzii* C. DC. also are shorter than 300 µm and resemble the above-mentioned species in most characters; however, they deviate by having a sharp demarcation of the anticlinal walls.

The seeds of *B. hirsuta* Aublet and *B. hirtella* are about the same size as those of *B. wallichiana* and have a similar cuticular pattern, but they have more undulated anticlinals. *Begonia hirsuta* has seeds with thick anticlinal walls with obscured boundaries. Seeds of *B. hirtella* plants introduced to and escaped in Java and Sri Lanka more resemble seeds of *B. hirsuta.*

The seeds of *B. prieurii* and *B. steyermarkii* distinctly deviate from the above-mentioned species. The periclinal walls of both the testa and collar cells reflect the presence of more or less evenly distributed knobbles. The anticlinal walls are rather thick in *B. prieurii* and are very thick and distinctly undulated in *B. steyermarkii.* The cuticular pattern consists of short and long zigzag elevated striae. The seeds of the two Brazilian collections of *B. prieurii* are to some extent intermediate between the Guianan collections and *B. steyermarkii.* The seeds of *B. steyermarkii* resemble seeds of certain species of section *Casparya* in general shape and in testal pattern.

Specimens Examined:

B. filipes, PANAMA: *I.M. Johnston 108* (US). COLOMBIA: *H.H. Smith 1264* (L); *M. Thiébaut 41* (P).

B. hirsuta, COSTA RICA: *R. Liesner 4506* (MO). DUTCH GUIANA (=Surinam): *Herb. Splitgerberianum* (L).

B. hirtella var. *hirtella,* BRAZIL: *Lourteig 2308* (U). JAVA: *Dorgelo 3085* (L). SRI LANKA: *Jayasuriya 838* (PDA).

B. humilis var. *humilis,* ECUADOR: *Egger 1404* (L). TOBAGO: *Krug & Urban 3040* (L). VENEZUELA: *J.A. Steyermark 95138* (US).

B. prieurii, FRENCH GUIANA: *Granville 2519* (US); *C. Sastre 1698* (US), *1733* (U). BRAZIL: *H.S. Irwin c.s. 48113* (US); *T. Plowman c.s. 8243* (US).

B. semiovata, BRITISH GUIANA (=Guyana): *B. Maguire & Fanshawe 32449* (US). COSTA RICA: *Tonduz 9588* (US).

B. steyermarkii, BRITISH GUIANA (=Guyana): *R.S. Cowan & Soderstrom 1841* (US).

B. tonduzii, COLOMBIA: *A. Gentry & E. Forero 7327* (MO). COSTA RICA: *Grayum 8132* (CR).

6.2. Section ***Begonia*** Baranov & Barkley

PLATES 18, 19

Baranov and Barkley (1972) named section *Begonia* on the basis of the rules and recommendations of the International Code of Botanical Nomenclature (ICBN). The section comprises parts of the former section *Begoniastrum* A. DC. The taxonomic delimitation of section *Begoniastrum* changed sev-

eral times. According to Baranov and Barkley (1972), section *Begonia* includes the former subsection *Eubegonia* Warburg and the sections *Moschkowitzia* (Klotzsch) A. DC. and *Cyatocnemis* (Klotzsch) A. DC., but *Knesebeckia,* reduced by Warburg (1894) to a subsection, is again a section in its own right. Section *Begonia* has no unique characters and is circumscribed by a combination of more general character states, such as staminate flowers with four (sometimes two) tepals and oblong to linear anthers that are longer than the filaments and pistillate flowers with usually five (sometimes six) tepals and bipartite placentas. With about 75 species, it is the section with the largest number of species in the Neotropics, but according to Barkley and Golding (1974), it also includes about 12 Asian species.

Some groupings can be made on the basis of seed structure. The most distinct is the *B. cucullata—B. fischeri* group, the species of which mainly are found in Brazil, Argentina, Paraguay, and Uruguay, although *B. fischeri* has a more widespread distribution.

Several species, often endemic, are present in the Caribbean region. The seeds of these species may resemble those of the section type, *B. obliqua,* or they may resemble the seeds of the more widespread *B. guaduensis.*

Begonia obliqua Group

Begonia obliqua LINNAEUS (Plate 18*a,d*).—Type species of section *Begonia.*

Seed Structure: Seeds elliptic, 295–420 µm in length, 180–205 µm in width, mean 360 µm × 195 µm, length:width ratio 1.8. Testa cells polygonal. Anticlinal walls thin, straight, or almost straight, but undulated at bases. Operculum nipple-shaped.

Seed Micromorphology: Anticlinal boundaries flat. Cuticular pattern faint, reflecting underlying pits; if present, pattern consisting of short zigzag striae.

Specimen Examined:

B. obliqua, MARTINIQUE: *Duss 973* (US).

CARIBBEAN SPECIES OBSERVED (Plate 18*b,c,e–h,k*).—The seeds observed of species originating from the Caribbean region all belong to the ordinary begonia seed type and more or less resemble *B. obliqua.*

Seed Structure and Micromorpholology: Begonia rotundifolia Lamarck and *B. glandulifera* Grisebach quite closely resemble *B. obliqua* in size, shape, and the thin anticlinals and outer periclinal walls.

The seeds of *B. odorata* Willdenow and *B. retusa* Schulz resemble each other by the undulated anticlinal walls of testa and operculum cells and are to some extent similar to those of the *B. cucullata—B. fischeri* group. The two species differ from each other somewhat in seed size and cuticular pattern.

The seeds of *B. cubensis* Hasskarl and of *B. plumieri* A. DC. var. *barahonensis* O.E. Schulz differ by having almost straight anticlinals and more zigzag striae.

Specimens Examined:

B. cubensis, CUBA: *J. Linden 1730* (GENT, as *B. lindeniana* A. DC., isotype). CULTIVATED: *Ziesenhenne s.n.*

B. glandulifera, TRINIDAD: *Van Steenis 20304* (L).

B. odorata, ST. VINCENT: *C.V. Morton 5066* (US).

B. aff. *odorata,* DOMINICA: *J. Jérémie 1105* (P).

B. plumieri var. *barahonensis,* SANTO DOMINGO: *Padre Miguel Fuertes 432* (L).

B. retusa, SABA: *A.L. Stoffers 3116* (U).

B. rotundifolia, WEST INDIES: Hortus Bot. Liège (cult.); Hortus Bot. Nancy (cult.).

MAINLY ANDEAN SPECIES OBSERVED (Plate 18*j,l,m*).—*Seed Structure and Micromorphology:* The seeds of *B. guaduensis* H.B.K., *B. cyatophora* (type species of former section *Cyathocnemis*), and *B. portillana* S. Watson strongly resemble those of *B. odorata* in shape, size, undulated anticlinal walls, and in the mainly granular to short linear cuticular pattern. The two samples of *B. cyatophora* studied by us differ somewhat in the extent of undulation.

The seeds of *B. altoperuviana* A. DC. and *B. barrigae* Smith & Schubert also conform to the ordinary seed type and do not show special characters.

Specimens Examined:

B. altoperuviana, BOLIVIA: *Weddell 4556* (P).

B. barrigae, COLOMBIA: cult., *van Veldhuizen 872* (WAG).

B. cyatophora, PERU: *Ellenberg 735 A* (U); *Y. Mexia 8128* (MO).

B. guaduensis, GUYANA: *Maas & Westra 3877* (U). PANAMA: *C.E. Smith Jr. & H. Morgan Smith 3272* (US).

B. portillana, MEXICO: *Dunn, Le Doux, & Torke 21820* (MO).

Begonia cucullata—Begonia fischeri Group

Begonia cucullata WILLDENOW (Plate 19*a–d*).—*Seed Structure and Micromorphology:* Among the specimens assigned to this species, three seed types are encountered: (1) narrowly ellipsoid seeds having an obtuse micropylar end with sunken hilum and an extended chalazal end (often J-shaped), a mean size of 670 µm × 185 µm, and a length:width ratio of 3.6; (2) obovate to narrowly obovate seeds having an obtuse operculum with sunken hilum, a somewhat extended chalazal end, a mean size of 550 µm × 220 µm, and a length:width ratio of 2.5; and (3) elliptic seeds resembling the ordinary begonia seed type, having a nipple-shaped operculum, a mean size of 315 × 200 µm, and a length:width ratio of 1.6.

Most seed collections of *B. cucullata* var. *cucullata* belong to the first seed type, with the exception of collections *Bartlett 21359* and *Jorgensen 3473,* which belong to the second and third types, respectively.

The seeds of *B. cucullata* var. *arenosicola* (C. DC.) Smith & Schubert belong to the third seed type, with the exception of collection *Fiebrig 5125,* which belongs to the first seed type.

Testa cells adjacent to the collar are elongated in the first two seed types and are more polygonal in the third type. In spite of

the above-mentioned differences, all three seed types fully agree in their testal pattern, namely, undulated anticlinal walls and a granular to short linear cuticular structure.

Specimens Examined:

B. cucullata var. *arenosicola,* ARGENTINA: *T.M. Pedersen 10232* (P). PARAGUAY: *E. Hassler 6130* (P, isotype); *E. Hassler 7884* (P, isotype); *K. Fiebrig 5125* (L).

B. cucullata var. *cucullata,* BRAZIL: *d'Alleizette s.n.* (L); *Irwin, Maxwell, & Wasshausen 19961* (P); *Y. Mexia 5190* (U); *Hj. Mosén 1598* (P). PARAGUAY: *Jorgensen 3473* (US). URUGUAY: *H.H. Bartlett 21359* (P).

OTHER SPECIES OBSERVED (Plate 19*e–m*).—The seeds of all collections of the more widespread *B. fischeri* Schrank are narrowly ellipsoid with an obtuse micropylar end and with a sunken hilum and an extended chalazal end. They resemble the similar seed type of *B. cucullata;* however, they are somewhat longer, with a mean seed length of 795 µm. The anticlinal walls are mostly somewhat more strongly undulated, with pockets at their bases. The cuticular pattern is less prominent, and the outer walls sometimes reflect underlying pits. *Begonia fischeri* var. *klugii* Irmscher differs in its relatively longer micropylar end, it being one-third of the seed length, whereas this is about one-fourth the seed length in the other collections.

The seeds of *B. alchemilloides* Meisner ex A. DC., *B. balansae* C. DC., *B. descoleana* Smith & Schubert, *B. meridensis* A. DC., *B. per-dusenii* Brade, *B. schmidtiana* Regel, and *B. subvillosa* Klotzsch, mainly from Brazil and/or Paraguay and Argentina, resemble the elliptic seed type of *B. cucullata* in shape, undulated anticlinals, and in the granular to short linear cuticular pattern. The species vary somewhat in seed length, with a mean from 345 µm in *B. subvillosa* var. *leptotricha* (C. DC.) Smith & Wasshausen to 430 µm in *B. descoleana.* They also may show some differences in testal pattern, e.g., *B. per-dusenii* with broad anticlinals and *B. alchemilloides* with a less-pronounced cuticular pattern.

Specimens Examined:

B. alchemilloides, BRAZIL: *H.S. Irwin c.s. 34478* (K).

B. balansae, PARAGUAY: *B. Balansa 3281* (P).

B. descoleana, BRAZIL: *G. Hatschbach 9944* (U).

B. fischeri var. *fischeri,* BRAZIL: *G. Hatschbach 5338* (L); *Prance & Silva 59701* (U). COSTA RICA: *B. Hammel 8377* (MO). VENEZUELA: *Steyermark & Rabe 96605* (P); *Steyermark c.s. 100258* (P).

B. fischeri var. *klugii,* PERU: *G. Klug 3389* (MO, cotype).

B. fischeri var. *macroptera* (Klotzsch) Irmscher, BRAZIL: *B.B. Pickel 2466* (US).

B. fischeri var. *palustris* (Bentham) Irmscher, COLOMBIA: *Hartweg 1022* (P).

B. meridensis, VENEZUELA: *Holst & Liesner 3159* (MO).

B. per-dusenii, BRAZIL: *L.B. Smith, Klein, & Schnorrenberger 11728* (K).

B. schmidtiana, BRAZIL: *B.K. Boom 15916,* cult., Hort. Gent (L).

B. subvillosa var. *leptotricha,* PARAGUAY: *K. Fiebrig 5354* (P, isotype).

B. subvillosa var. *subvillosa,* BRAZIL: *G. Hatschbach 21525* (L); *L.B. Smith & Reitz 1269* (US).

Ungrouped Species

Begonia organensis BRADE (Plate 18*n*).—*Seed Structure and Micromorphology:* The seeds of this species conform to the ordinary seed type and cannot be linked to either of the above-described groups. The mean seed size is 555 µm × 255 µm, with a length:width ratio of 2.2. The anticlinal walls are straight or slightly curved and sometimes are locally undulated. The distinct cuticular pattern consists of linear to undulated striae of varying length, continuous across the anticlinals.

Specimen Examined:

B. organensis, BRAZIL: *D. Sucre c.s. 3005* (MO).

6.3. Section ***Knesebeckia*** (Klotzsch) A. DC.

PLATES 20, 21*a–g*

Section *Knesebeckia* was formerly considered a subsection of section *Begoniastrum* A. DC. by Warburg (1894). The section now includes the former subsection *Rachia* Klotzsch of the former section *Magnusia* Klotzsch (Irmscher, 1960) and the monotypic section *Quadriperigonia* Ziesenhenne, which was eliminated by the synonymy of the type species, *B. abaculoides* Ziesenhenne, with *B. boissieri* A. DC. (Smith and Wasshausen, 1983).

The species of this section are very diverse. Some show a close resemblance to species of *Begonia,* others are similar to species of *Eupetalum, Ruizopavonia,* and some other sections with bifid placentas. The section is characterized by anthers that are globose or obovoid and are much shorter than the filaments, which often are monodelphous. Some species are tuberous, and several also produce bulbils in the leaf axils. The section comprises about 67 Neotropical species, with a concentration in Mexico (Burt-Utley, 1985), and according to Barkley and Golding (1974), also includes about 10 Asian species.

The seeds of the species observed all conform to the ordinary begonia seed type; however, the section is not homogenous in seed structure and shows variation in micromorphological characters.

TYPE SPECIES.—*Begonia incarnata* Link & Otto (Plate 20*a,d*).

Seed Structure: Seeds elliptic, mean size 360 µm × 180 µm, length:width ratio 2.0. Anticlinal walls of testa cells thin, undulated. Operculum nipple-shaped.

Seed Micromorphology: Anticlinal boundaries flat. Cuticular structure mainly short linear.

Specimen Examined:

B. incarnata var. *incarnata,* MEXICO: *Liebmann 177* (US).

OTHER SPECIES OBSERVED (Plates 20*b,c,e–n,* 21*a–g*).—Seed structures vary between the Central American and the Mexican species.

Seed Structure and Micromorphology: *Begonia kellermannii* C. DC. and *B. peltata* Otto & Dietrich resemble *B. incarnata* in the thin, undulated anticlinal walls. The seeds of *B. boissieri* and *B. ludwigii* Irmscher resemble each other in the straight to curved anticlinal cell walls and in the short zigzag to granular cuticular ornamentation.

The seeds of *B. gracilis* H.B.K. and *B. sandtii* Ziesenhenne strongly resemble those of some species of section *Doratometra,* especially *B. wallichiana,* in the relatively small seed size (mean seed length 300 µm in *B. gracilis;* 340 µm in *B. sandtii*), straight or curved anticlinal walls, and the dense cuticular pattern, consisting of a mainly granular ornamentation. The seeds of *B. angustiloba* A. DC., *B. falciloba* Liebmann, *B. ignea* Warzewicz ex A. DC., and *B. uniflora* S. Watson resemble one another in thicker, straight or curved anticlinal walls and a mainly short zigzag cuticular ornamentation.

The seeds of the South American species studied deviate from the above-mentioned ones. The seeds of *B. maynensis* A. DC. and *B. oellgaardii* L.B. Smith & Wasshausen closely resemble one another in their short lengths, 280 and 295 µm, respectively, and a length:width ratio of 1.5. The seeds have broad anticlinals caused by thickening of the outer periclinal walls bordering the anticlinal walls. Anticlinal boundaries are locally sunken. The cuticular pattern is mainly granular to short undulated. The seeds of *B. wollnyi* Herzog resemble the above-described ones somewhat in their small size and in projecting anticlinals.

The seeds of the Brazilian species *B. dichroa* Sprague and *B. olbia* Kerchove resemble each other in size, with a mean length of 420 µm; thin, straight anticlinal walls; flat anticlinal boundaries; and the mainly granular to short linear cuticular ornamentation.

Specimens Examined:

B. angustiloba, MEXICO: *M.L. Diguet s.n.* (P).
B. boissieri, MEXICO: cult., *van Veldhuizen 747* (WAG).
B. dichroa, BRAZIL: cult., *Ziesenhenne s.n.*
B. falciloba, MEXICO: *M. Bourgeau 649* (P).
B. gracilis var. *gracilis,* MEXICO: *Pringle 11452* (L).
B. ignea, COSTA RICA: *H. Pittier & T. Durand 1299* (P).
B. kellermannii, GUATEMALA: cult., *Ziesenhenne s.n.*
B. ludwigii, ECUADOR: cult., *Ziesenhenne s.n.* CULTIVATED: *van Veldhuizen 618* (WAG).
B. maynensis, BRAZIL: *Prance c.s. 7409* (U).
B. oellgaardii, ECUADOR: *M.A. Baker 6396* (US).
B. olbia, BRAZIL: cult., *van Veldhuizen 434* (WAG).
B. peltata var. *peltata,* MEXICO: cult., Hort. Bot. Gent, *B.K. Boom 14288* (L).
B. sandtii, MEXICO: cult., *Ziesenhenne s.n.*
B. uniflora, MEXICO: *J. Roybal 647* (US).
B. wollnyi, BOLIVIA: cult., *van Veldhuizen 435* (WAG).

6.4. Section ***Donaldia*** (Klotzsch) A. DC.

PLATE 21*h–o*

This section, comprising seven species, is characterized in part by pinnate leaves and by male flowers with two (sometimes four) tepals and ellipsoid anthers that are about as long as the filaments. No seeds were available for *B. burlemarxii* Brade or *B. egleri* Brade.

TYPE SPECIES.—*Begonia ulmifolia* Willdenow was described in 1805. It has a wider distribution than other species in the section, being found in Venezuela, Guyana, and Trinidad, and it has been introduced and is naturalized in Sri Lanka (Jayasuriya, 1983).

Seed Structure: Seeds ellipsoid, mean size 290 µm × 190 µm, length:width ratio 1.5. Testa cells polygonal, with curved anticlinal walls. Sample from Sri Lanka differs by more slender seeds with thinner, straight anticlinal walls. Seeds resembling those of *B. gracilis* (section *Knesebeckia*).

Seed Micromorphology: Cuticular pattern consisting of short linear to almost granular and short zigzag striae.

Specimens Examined:

B. ulmifolia, TRINIDAD: *W.H.A. Hekking 1428* (U). SRI LANKA: *A.H.M. Jayasuriya 998* (PDA).

OTHER SPECIES OBSERVED.—Two of the other species observed are limited to Bolivia, and two are limited to Brazil (see "Specimens Examined," below).

Seed Structure and Micromorphology: The seeds of the other four species studied also are relatively small, not exceeding 400 µm, and conform to the ordinary begonia seed type. They differ in anticlinal walls, from straight in *B. dasycarpa* A. DC. to undulated in *B. chaetocarpa* Kuntze var. *chaetocarpa.* They resemble the seeds of *B. ulmifolia* in cuticular pattern except for *B. dasycarpa,* which has long zigzag striae.

Specimens Examined:

B. bangii Kuntze, BOLIVIA: *A. Miguel Bang 406* (K).
B. chaetocarpa var. *chaetocarpa,* BOLIVIA: *O. Kuntze s.n.* (B, isotype).
B. chaetocarpa var. *glabriflora* Smith & Schubert, BOLIVIA: *H.H. Rusby 690* (US, isotype).
B. dasycarpa, BRAZIL: *A. Glaziou 15388* (P).
B. jairii Brade, BRAZIL: *G. Pedro do Cavalo 752* (US).

Discussion

SEED MORPHOLOGY

The seeds of about 235 Neotropical *Begonia* species, representing 39 sections, were studied using SEM. No seeds were available for study in the monotypic sections *Cylindrobegonia, Parietoplacentaria, Plurilobaria,* and the dubious monotypic section *Dasystyles.*

Almost all seeds studied show differentiation between collar and other testa cells, characteristic for *Begonia.* The only exceptions are found in species *B. antioquensis* and *B. hexandra*

of section *Casparya,* the seeds of which show neither a distinct collar nor a borderline with the operculum.

As is the case in African and Asiatic begonias, the seeds of the Neotropical species exhibit an appreciable diversity in seed size and structure. This diversity is not as wide as in the African begonias (de Lange and Bouman, 1992), in which all sections are distinguishable from one another on the basis of seed characters.

The seeds of Neotropical begonias vary in shape from almost globular to narrowly ellipsoidal. The lowest length:width ratio (1.2) is found in *B. hexandra;* the highest one (8.1) is found in *B. fruticosa* (section *Trendelenburgia*). Seed shape may be determined by flattened, extended, or swollen chalazal ends. A flat chalazal end is caused by contact with the ovary or fruit wall. Most seeds have a mean length between 300 µm and 600 µm; the shortest, with a mean length of 225 µm, are found in *B. corredorana* (section *Ruizopavonia*), and the longest ones, with a mean length of 1450 µm, are found in a collection of *B. fruticosa.*

The mean number of collar cells in the seed circumference is mostly between 10 and 12; however, this may be as low as eight in a collection of *B. glabra* (section *Enita*) and as high as 23 in a collection of *B. pectennervia* (section *Casparya*). The collar cells are mostly distinctly elongated; their mean length varies from 100 µm in *B. wallichiana* (section *Doratometra*), to 290 µm in *B. maculata* (section *Gaerdtia*), and to 325 µm in *B. fruticosa.* The mean collar-cell length:seed length varies from 1.9 in *B. maculata* to 5.7 in *B. urticae* (section *Casparya*). The other testa cells are mostly polygonal, sometimes elongated near collar cells. Their anticlinal walls are straight (as in sections *Pritzelia* or *Ewaldia*) or are curved or undulated (as in sections *Casparya* or *Hydristyles*). The anticlinal boundaries are mostly flat but are sometimes sunken or locally sunken (as in section *Warburgina*).

The cuticular ornamentation varies greatly in pattern, thickness, and roughness. The cuticular pattern may be granular, linear, undulated, or zigzag. The surface of the cuticle may be smooth (section *Urniformia*), faint, pronounced, or even forming a net-like structure of pleats (section *Trachelocarpus*). The roughness varies from fine and dense (section *Latistigma*) to rough, as in many species of section *Casparya.* Sometimes the structure of the underlying periclinal wall is reflected, showing pits or pockets at the bases of undulated anticlinal walls. A cuticle with a double structure, i.e., with more elevated, scattered foldings next to a regular cuticular pattern, is especially found in section *Casparya.*

Delimitation and Interrelationships of Neotropical Sections

Within the Neotropical begonias, a number of sections show a special seed structure characteristic at the sectional level. All these sections have a relatively restricted geographical distribution; one or more of such sections are found in each of the three main areas in which Neotropical begonias are found. The sections with a specialized seed structure have a limited number of species, with the exception of sections *Casparya* and *Gobenia.*

Of the Brazilian or mainly Brazilian sections, the following five sections have a characteristic seed structure.

In section *Trachelocarpus* the seeds are relatively large, with a rather unique cuticular structure consisting of upright or folded-over pleats. The seeds of section *Solananthera* are long because of their extended chalazal end. The long seeds in section *Trendelenburgia* have both extended micropylar and chalazal ends. In section *Enita* (*Wageneria*) the micropylar and/or chalazal cells of the seeds are uncollapsed and air-filled, resembling balloons. In section *Scheidweileria* the surface of the flattened chalaza is pronounced because of deep, collapsed testa cells and an often broadly nipple-shaped operculum.

The other Brazilian or mainly Brazilian sections do not have a characteristic seed structure at the sectional level, and most of their species have seeds that conform to the ordinary begonia seed type. In some cases one or more species within a section may deviate from this ordinary type.

The possible relationship between sections *Ewaldia* and *Scheidweileria,* as suggested by the successive numbering of the two sections in *Die natürlichen Pflanzenfamilien* (Warburg, 1894; Irmscher, 1925), is supported by seed structure. The seeds of the type species *B. lobata* of section *Ewaldia* resemble those of section *Scheidweileria.*

The section *Pritzelia* is quite diverse in seed morphology. Within the section, a number of species observed deviate by having a more pronounced and coarse zigzag cuticular striae.

Seed structure does not provide arguments for a separate section *Bradea* as proposed by Toledo (1946). The seeds of the type species *B. rufosericea* closely resemble those of *B. arborescens* of section *Steineria.*

The seeds of species of section *Latistigma* conform to the ordinary begonia seed type and resemble the seeds of some species of section *Gireoudia,* e.g., *B. cardiocarpa.*

Of the sections mainly confined to the Andean and Guianan regions, five have characteristic seeds. In section *Casparya* the seeds are recognizable by a combination of characters, especially the roughness of the testal surface, the mostly undulated anticlinals, the flat operculum, and sometimes the double structure of the cuticle. On the basis of a combination of these characters, several species groups can be discerned, but they do not match the subsectional classification of Irmscher (1925). Unfortunately, we cannot contribute to the discussion on the status of the former sections *Begoniella* and *Semibegoniella* because no seeds of these taxa could be examined.

Section *Rossmannia* is the only Andean section having narrowly elliptic seeds with a swollen micropylar and an extended chalazal end. The seeds of *B. rossmanniae* resemble those of the *B. cucullata—B. fischeri* group (section *Begonia*) in shape and size, but they differ in the presence of straight anticlinal walls.

Seed structure in section *Hydristyles* is quite diverse. Seed micromorphology provides arguments for the inclusion of section *Warburgina* in section *Hydristyles.* The seeds of *B. comata* resemble seeds of species of section *Hydristyles,* like *B. andina* and *B. unduavensis,* in their elongated testa cells with strongly undulated walls.

The seeds of section *Gobenia* are characterized by an irregular seed shape, a broadly nipple-shaped operculum, and an often flattened chalazal end with more elevated anticlinal walls. The seeds of section *Gobenia* resemble those of section *Scheidweileria.* Seed micromorphology supports the opinion of Smith and Wasshausen (1986) that *B. sodiroi* belongs to section *Gobenia.* The synonymy of *B. sodiroi* with *B. oaxacana* (section *Hexaptera*) as stated by Barkley and Golding (1974) is not supported.

The other mainly Andean sections all have seeds that conform to the ordinary seed type and only differ in details. Seed micromorphology does not contradict a relationship between sections *Lepsia* and *Tittelbachia* and supports the inclusion of section *Huszia* in section *Eupetalum,* as proposed by Smith and Wasshausen (1979, 1986). The seeds of the section type, *B. geraniifolia,* resemble those of a number of species of the former section *Huszia.* The placement of *B. micranthera* in section *Australes* (Smith and Schubert, 1941) also is supported by seed morphology.

Begonia exalata, of the monotypic section *Apteron,* differs in fruit structure and growth form, but the general morphological characters as well as the seed structure indicate a relationship with section *Eupetalum. Begonia trujillensis* was initially placed in section *Apteron* by its author on the basis of the regularly two-parted styles (Smith, 1973; Barkley and Golding, 1974). Seed micromorphology clearly shows that this species belongs to section *Casparya.*

The seeds of the type species of section *Barya, B. monadelpha,* and to a lesser extent the seeds of *B. soror,* agree with those of section *Gobenia* in their somewhat irregular shape and the broadly nipple-shaped opercula.

The elimination of the monotypic Colombian section *Saueria* by synonymy of its type species, *B. sulcata,* with a species of section *Pritzelia,* is supported by seed morphology.

Of the sections mainly confined to the Central American and Caribbean regions and Mexico, only the seeds of the monotypic section *Urniformia* show special characters. *Begonia heydei* is the only Neotropical species having seeds with a smooth cuticle.

The seeds of the large section *Gireoudia* all conform to the ordinary begonia seed type and do not show a distinct grouping of the seeds. The inclusion of section *Auriformia* is not disproved by seed micromorphology. The seeds of the former type species *B. bakeri* (=*B. cardiocarpa*) resemble those of other collections of *B. cardiocarpa* and of *B. involucrata.* Seed morphology does not provide arguments for or against a separate section *Dissepbegonia.* The section most probably should be included in section *Knesebeckia,* as the kind of placentation also is found in some species of this section (Doorenbos et al., 1998).

The seeds of the other three sections all have relatively small seeds and do not show special characters.

The majority of the seeds of all seven sections not restricted to one of the main geographical areas conform to the ordinary seed type. Seed micromorphology generally only provides restricted arguments for delimitation of sections or relationships between these sections. The sections *Ruizopavonia, Doratometra,* and *Begonia* are mutually difficult to delimit (Irmscher, 1949). All three sections are rather heterogenous in seed structure and have species or a group of species with a deviating seed structure. The transfer of *B. filipes, B. humilis,* and *B. hirtella* from section *Begonia* to section *Doratometra* as referred to by Barkley and Golding (1974) is supported by seed micromorphology. The conspecificity of *B. filipes* and *B. hirsuta* as suggested by Burt-Utley (1984) is not supported by seed micromorphology. The seeds of *B. prieurii* and *B. steyermarkii* of section *Doratometra* deviate from the seeds of the other species of this section by the presence of knobbles on the outer periclinal walls and by thicker, distinctly undulated anticlinal walls. The seeds of *B. steyermarkii* resemble those of some species in section *Casparya.*

The seeds of the species of section *Ruizopavonia* are rather heterogenous. The seeds of a number of species, for example, *B. bracteosa* and *B. suprafastigiata,* resemble those of some species of section *Begonia.* The scobiform seeds of *B. cuatrecasiana* resemble those of section *Rossmannia,* and seeds of *B. estrellensis* resemble those of section *Hydristyles.* Seed micromorphology does not support the synonymy of *B. udisilvestris* with *B. carpinifolia* (Barkley and Golding, 1974). *Begonia udisilvestris* most probably does not belong to section *Ruizopavonia.* Doorenbos et al. (1998) placed *B. oaxacana* of the monotypic section *Hexaptera* together with *B. udisylvestris* in section *Parietoplacentalia.* This opinion is supported by the resemblance of the seeds of *B. udisilvestris* to those of *B. oaxacana.*

Seed micromorphology could not provide arguments for or against the inclusion of *B. thiemei* and *B. corredorana* in section *Gireoudia* as indicated by Burt-Utley (1985).

Within section *Begonia,* the *B. cucullata—B. fischeri* group is characterized by a testal pattern of undulated anticlinal walls, a granular to short linear cuticular structure, and, partly, a narrowly ellipsoid or obovate seed shape.

The inclusion of section *Cyathocnemis* in section *Begonia* is supported by seed structure.

Possible Intercontinental Relationships

Our knowledge of the intercontinental relationships of begonias is rather meager. The great majority of *Begonia* sections have a distribution that is restricted to one continent. Warburg (1894) classified all *Begonia* species into African, Asian, and American sections; however, Irmscher (1925) was of the opin-

ion that section *Begoniastrum* was intercontinental, comprising species of American and Asian origin. Baranov and Barkley (1972) changed the name of section *Begoniastrum* to *Begonia,* in accordance with the ICBN, and split off a separate section *Knesebeckia.* According to Barkley and Golding (1974), sections *Begonia* and *Knesebeckia* comprise about 12 and about 10 Asian species, respectively. Serious doubts, however, exist about the validity of the delimitation of these sections. Doorenbos et al. (1998) moved the Asian species of both section *Begonia* and section *Knesebeckia* to section *Diploclinium.*

As shown in this study, the seeds of the American representatives of section *Knesebeckia* are quite diverse in structure. Seeds of the Asian section *Diploclinium* observed by us also conform to the ordinary *Begonia* type: they are mostly relatively small and show some variation in anticlinal walls and cuticular structure. Seeds of the Asian *Knesebeckia* species also show appreciable variation in seed morphology and do not closely resemble the American species of section *Knesebeckia* or those of section *Diploclinium.* Of the Asian species of section *Begonia,* only *B. labordei* Léveillé could be studied by us. The seeds of this species conform to the ordinary begonia seed type and do not show any specific character that points to or against a relation with the American species.

A. De Candolle included in his section *Casparya* a number of Indo-Malaysian species, such as *B. multangula* Blume, *B. robusta* Blume, and *B. silletensis* (A. DC.) C.B. Clarke, now belonging to the Asian section *Sphenanthera* A. DC. The seeds of species in section *Sphenanthera* are relatively small and have a mainly granular structure. The seeds of the above-mentioned species fit well with those of section *Spenanthera.* There are no arguments for a direct relationship of section *Casparya* with Asian species.

As far as we know, no suggestions have been made about intercontinental relationships between Neotropical and African begonias.

Seed Structure in Relation to Dispersal and Growth Form

Field observations on the dispersal of *Begonia* seeds are rare. The great majority of the Neotropical *Begonia* species seems to be wind dispersed (anemochory; see van der Pijl, 1972). Seed dispersal is mostly anemoballistic, i.e., the winged fruit is shaken by wind and the seeds are gradually released through pores or slits. This means of dispersal holds for the majority of the Neotropical sections, including large sections, such as *Begonia, Gireoudia, Knesebeckia,* and *Pritzelia,* which generally grow in a more open and often dry vegetation. Capsular motion may be promoted by elongated frutescences exposed above the leaves, enlargement of the median wing into a vane, or by persistent bracteoles. The seeds of these species are medium-sized and conform to the ordinary seed type.

Special adaptations to wind dispersal are the increase of the surface to volume ratio as seen in narrowly ellipsoid fusi- or scobiform seeds, the decrease of specific gravity (mass) caused by uncollapsed, air-filled testa cells, as in balloon seeds, and promotion of laminar air flow by surface roughness. These adaptations also may occur in varying combinations. Adaptations in seed shape in combination with inflated cells are known in sections *Rossmannia, Solananthera,* and *Trendelenburgia* and in the *B. cucullata—B. fischeri* group of section *Begonia.* Typical balloon seeds also are found in section *Enita,* whereas a more pronounced surface caused by more raised anticlinal walls is seen in seeds of sections *Scheidweileria* and *Gobenia.* Wind dispersal, however, seems neither likely nor effective in species from humid and/or closed-forest vegetations.

On the basis of fruit and seed morphology, it is rather speculative to suggest other types of dispersal in Neotropical begonias. Secondary seed dispersal by rain-wash may occur in the majority of the begonias, including the wind dispersed ones. Rain-wash is supposed to be the most important means of dispersal for most species of the African sections *Filicibegonia, Loasibegonia,* and *Scutobegonia,* growing in the sheltered environment of the tropical rain forest where wind is an ineffective vector in dispersal. Their fruits do not open but rot away. Seeds of species in these sections are small and are often provided with a thick, pronounced, cuticular ornamentation (de Lange and Bouman, 1992). Such a combination of fruit and seed characters is not found among the Neotropical begonias.

A number of Neotropical *Begonia* sections have fruits and seeds that are not adapted to wind dispersal. The species of the epiphytic section *Trachelocarpus* are characterized by solitary, subsessile fruits with narrow wings somewhat hidden underneath the leaves, as expressed by the name *B. rhizocarpa* (=*B. depauperata*), and large seeds with a very pronounced cuticular pattern. The means of seed dispersal is unknown. A combination of accidental dispersal by rain and by adhering to animals (epizoochory) seems to be the most probable way of dispersal.

The species of section *Casparya* act as rattleburrs; their fruits have horns instead of wings, and the seeds are provided with striking cuticular patterns, such as prominent, sometimes plicate foldings or a double structure that might function in dispersal by rain wash. Seeds seem to be dispersed in different ways. Passing animals may catch the horns and shake the fruits, scattering seeds (zooballistics), or seeds may adhere to animals.

None of the Neotropical begonias have fruits adapted to rain ballistics as in the Asian section *Platycentrum,* where the two shorter wings form a cup to catch raindrops. Moreover, none of the Neotropical begonias have fruits or seeds that seem adapted to frugivores or to ant dispersal. Animal-dispersed begonias with fleshy, often colored fruits are known in a number of African sections. These sections show trends toward bigger seeds, loss of cuticular ornamentation, and a thick exotesta, and they may have aril-like appendages (de Lange and Bouman, 1992).

In the Neotropics, seeds without cuticular ornamentation are known only from *B. heydei* (section *Urniformia*). This species, from the wet montane zone of Central America, deviates from

all other begonias by a one-celled ovary with three long, hollow, fleshy horns. Fruit dehiscence and seed release have not been described in detail.

The wingless fruits of *B. exalata* (section *Apteron*) suggest another means of dispersal; however, the seeds are of the ordinary begonia type, and seed micromorphology does not provide an indication for dispersal.

The means of seed dispersal often seems to be related to habitat and growth form (Burt-Utley, 1985). Begonias with special adaptations to wind dispersal are mostly climbers and/or epiphytes or have a tendency to do so. For example, this holds in sections *Enita, Rossmannia*, *Solananthera, Trendelenburgia,* and in species of section *Gobenia*. The rattleburrs of section *Casparya* grow in the wet montane forest, where wind is less effective.

Seed dispersal of the Neotropical begonias, and most probably that of the Asian ones, distinctly differs from seed dispersal in African begonias. In the Neotropical begonias wind dispersal is predominant, and alternative types of dispersal are restricted to a limited number of sections. In Africa only about one-fifth of the *Begonia* species are wind dispersed, almost two-fifths are animal-dispersed, and over two-fifths are dispersed by a combination of rain-wash and epizoochory (de Lange and Bouman, 1992).

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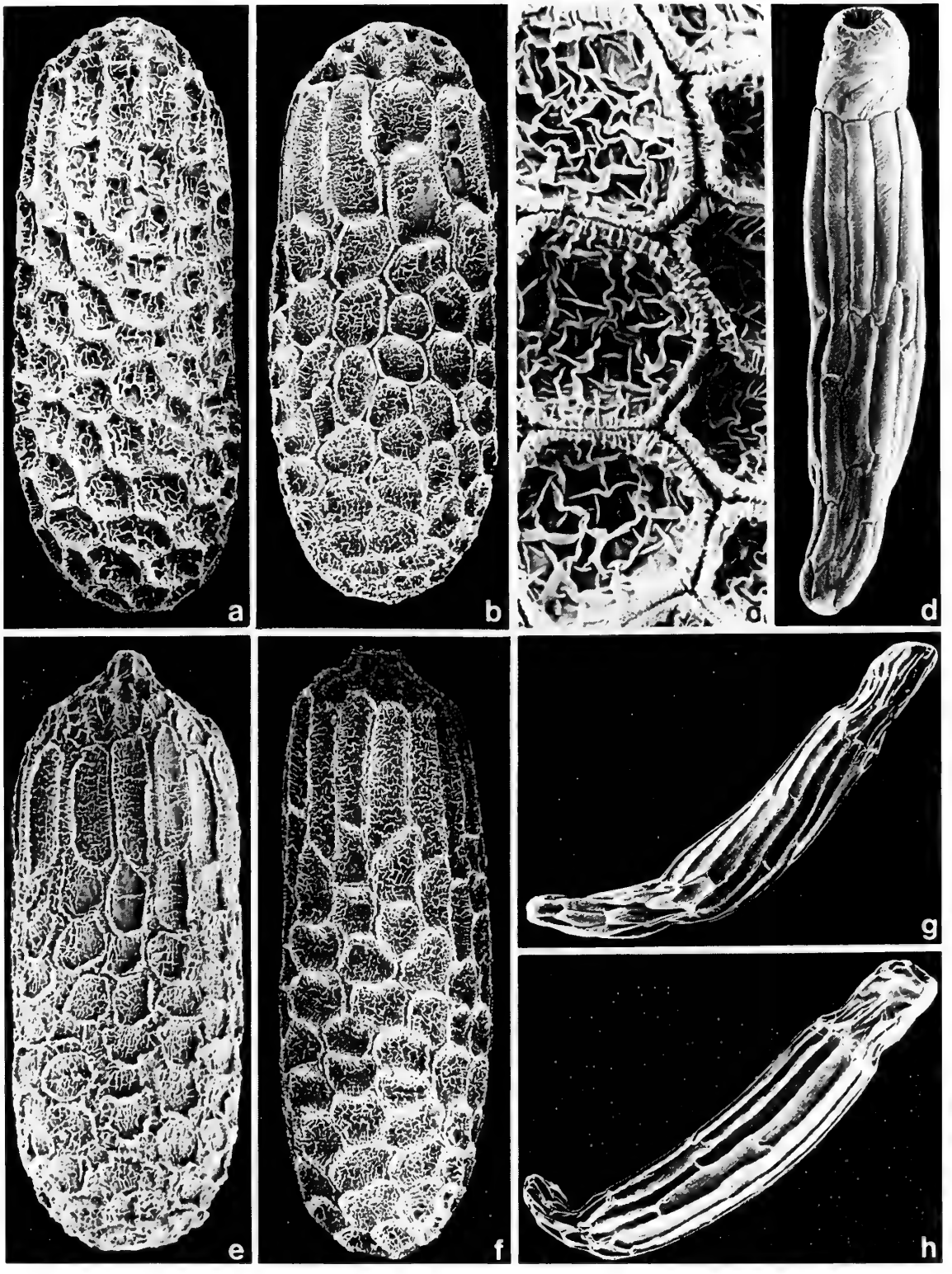

PLATE 1.—Seeds of sections *Trachelocarpus* and *Solananthera: a, B. herbacea* (*Lisedecceales s.n.*), ×125; *b, B. herbacea* var. *ellipticifolia* (*Ule 4240*), ×110, *c,* detail testa, ×500; *d, B. solananthera* (cult.), ×150; *e, B. depauperata* (*Campos Goer 140*), ×130; *f, B. lanceolata* (*Smith & Pereira 15343*), ×100; *g, B. radicans* (*Luederwaldt s.n.*), ×80; *h, B. integerrima* (*Pereira 606*), ×95.

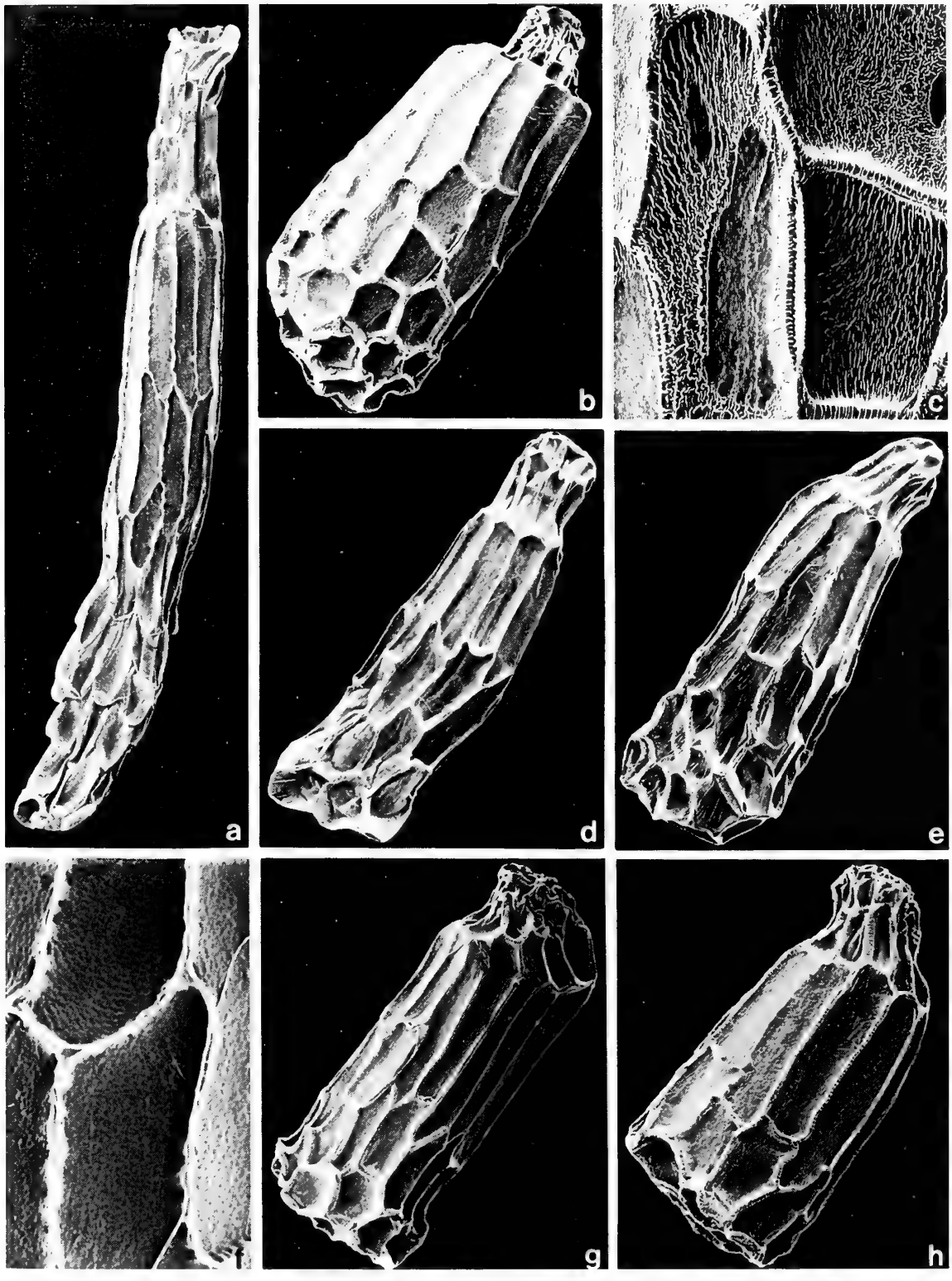

PLATE 2.—Seeds of sections *Trendelenburgia* and *Scheidweileria*: *a, B. fruticosa* (*Martins 8380*), ×100, *f,* detail testa, ×490; *b, B. pentaphylla* (*Maguire c.s. 44596*), ×120, *c,* detail testa, ×480; *d, B. luxurians* (*Hoehne 2370*), ×130; *e, B. digitata* (*Martinelli & Maas 3271*), ×120; *g, B. incisoserrata* (*Hatschbach & Kummran 45532*), ×170; *h, B. parviflora* (*Killip 7837*), ×210.

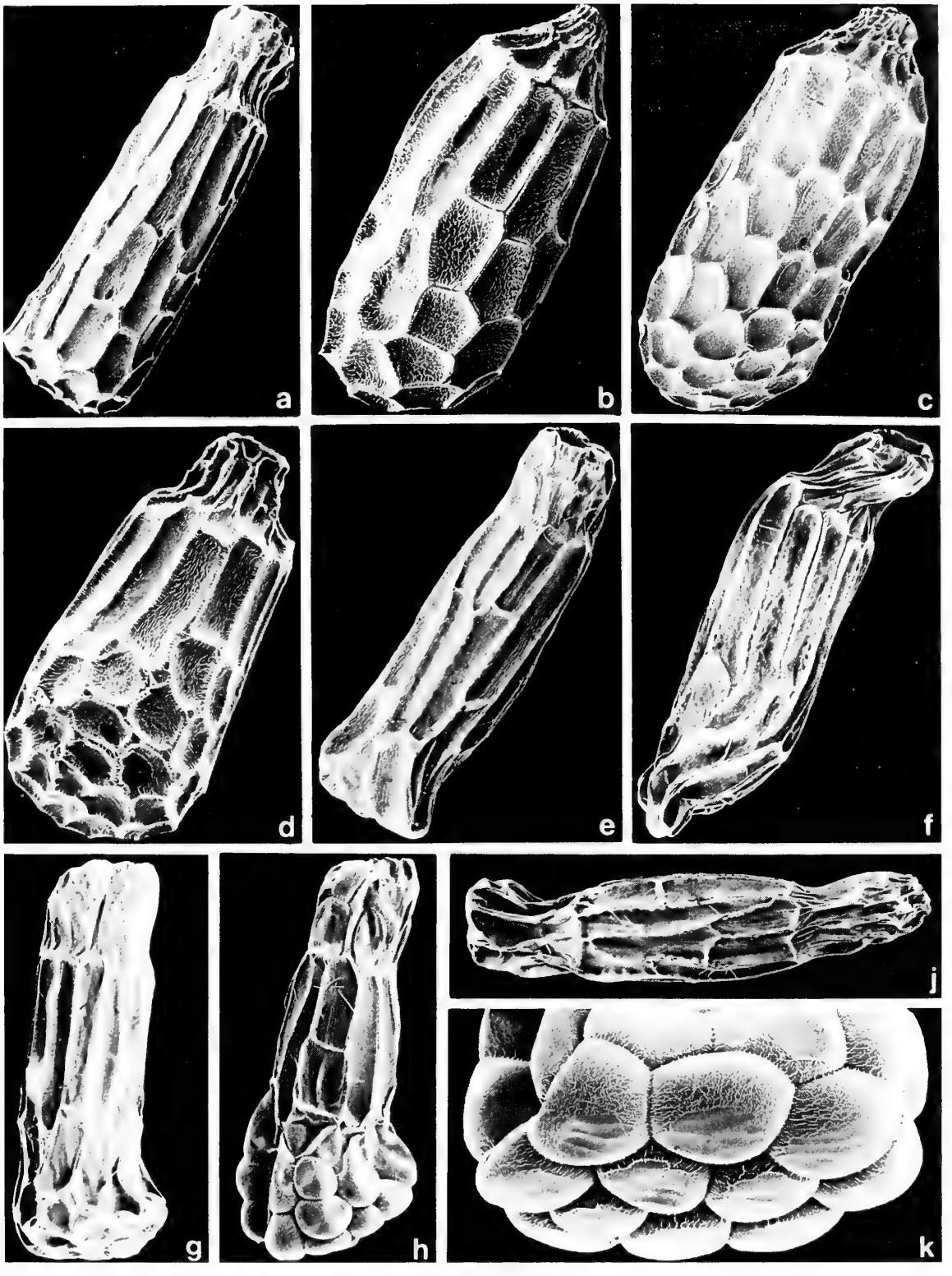

PLATE 3.—Seeds of sections *Ewaldia* and *Enita: a, B. lobata* (*Hatschbach 30073*), ×130; *b, B. scharffii* (*Palacios-Cuezzo 2930*), ×160; *c, B. tomentosa* (*Brade 18572*), ×160; *d, B. rigida* (ABS Seed Fund), ×190; *e, B. convolvulacea* (*Schenck 858*), ×120; *f, B. epibaterium* (*Scott Mori c.s. 12856*), ×140; *g, B. fagifolia* (*Brade 19144*), ×120; *h, B. glabra* var. *glabra* (*Irwin c.s. 54738*), ×180, *k,* detail chalaza, ×280; *j, B. glabra* var. *glabra* (*Laurito 8172*), ×120.

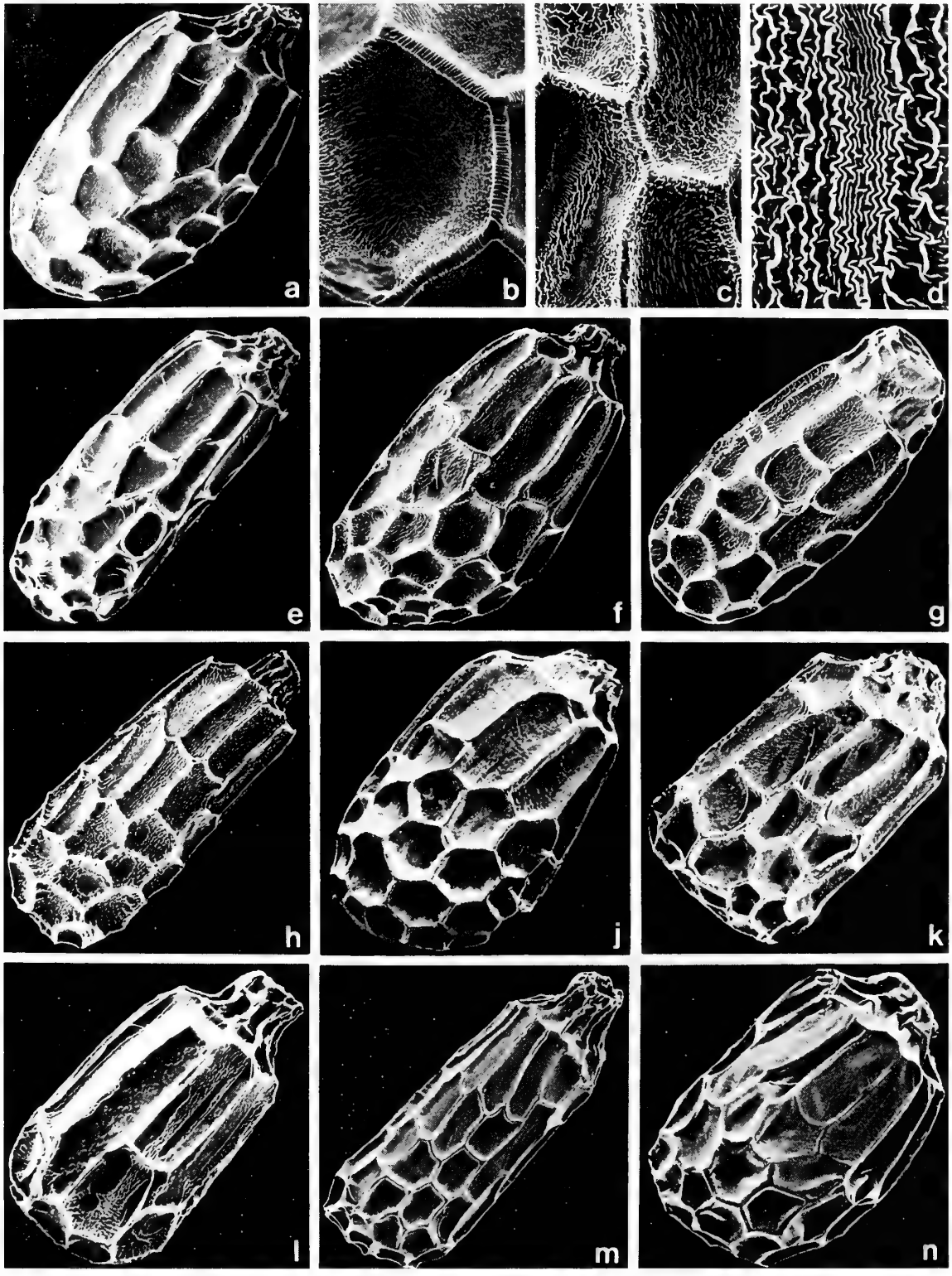

PLATE 4.—Seeds of section *Pritzelia: a, B. dietrichiana* (*Duarte 378*), ×180; *b, B. crispula* (*Boone-Hahn 13*), detail testa, ×510; *c, B. sanguinea* (*Bailey & Bailey 706*), detail testa, ×450, *f,* seed, ×150; *d, B. coccinea* (*Burchell 219A*), detail testa, ×860, *g,* seed, ×120; *e, B. grisea* (*St. Hilaire B 2027*), ×95; *h, B. angulata* var. *angulata* (*Hatschbach 8831*), ×120; *j, B. itaguassuensis* (*Lourteig 3236*), ×150; *k, B. dichotoma* (*Boone-Hahn 25*), ×140; *l, B. acida* (cult., Liège), ×180; *m, B. paranaensis* (*Hatschbach 8941*), ×110; *n, B. olsoniae* (*Pereira 307*), ×110.

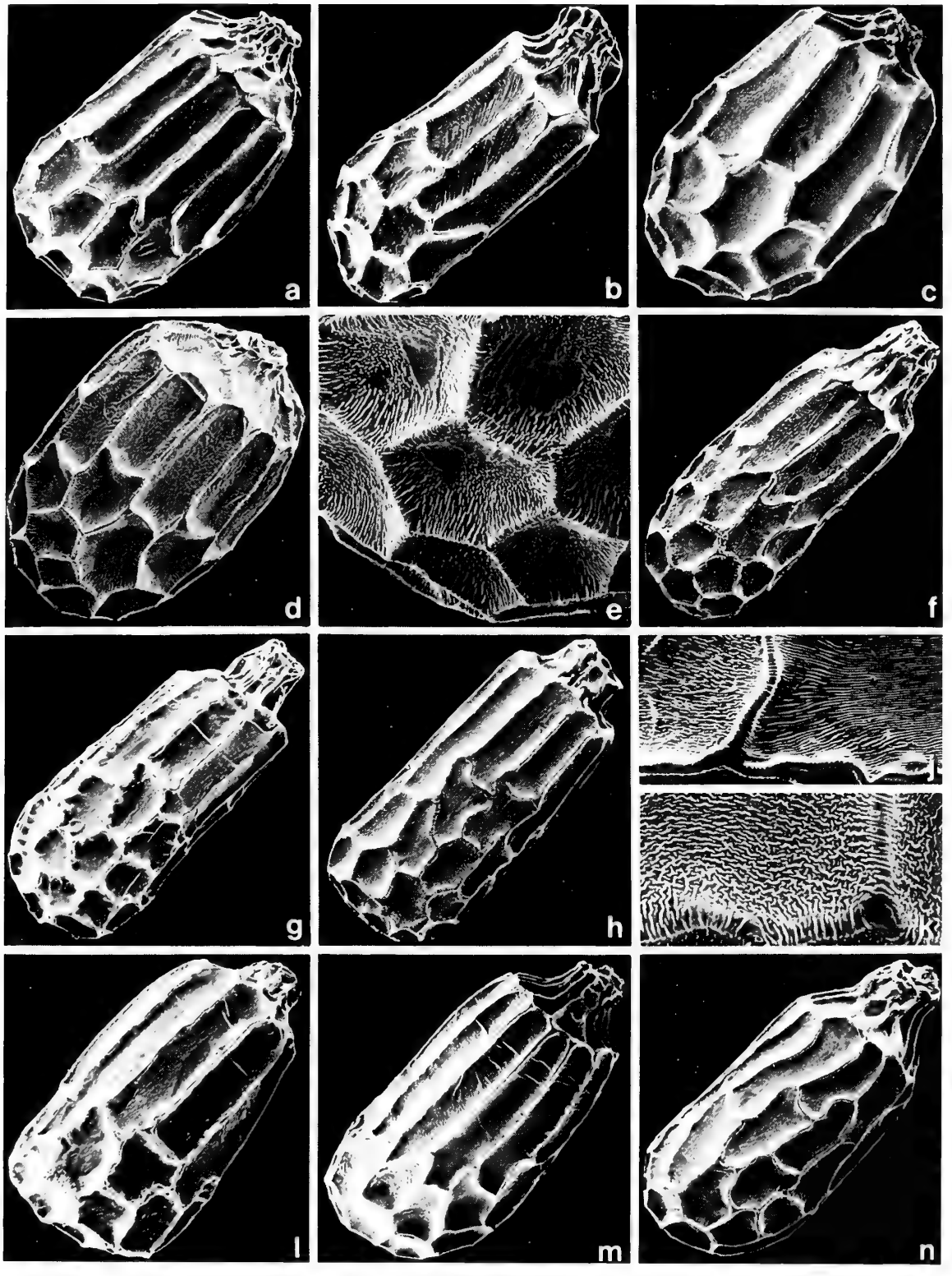

PLATE 5.—Seeds of sections *Pritzelia, Philippomartia, Steineria,* and *Bradea: a, B. bradei* (cult.), ×140; *b, B. hispida* (*Bailey & Bailey 710*) ×130; *c, B. membranacea* (*Curran 170*), ×200; *d, B. leptophylla* (*Mo 4331*), ×170, *e,* detail chalaza, ×440; *f, B. hookerana* (*Occhioni 4788*), ×140, *j,* detail testa, ×760; *g, B. arborescens* var. *arborescens* (*Grisebach s.n.*), ×190; *h, B. polyandra* (*Herb. Hieronymus s.n.*), ×140, *k,* detail testa, ×710; *l, B. oxyphylla* (*Inh. Vien s.n.*), ×190; *m, B. rufosericea* (*Oswaldo Hanro s.n.*), ×160; *n, B. bidentata* (*Peckolt 75*), ×160.

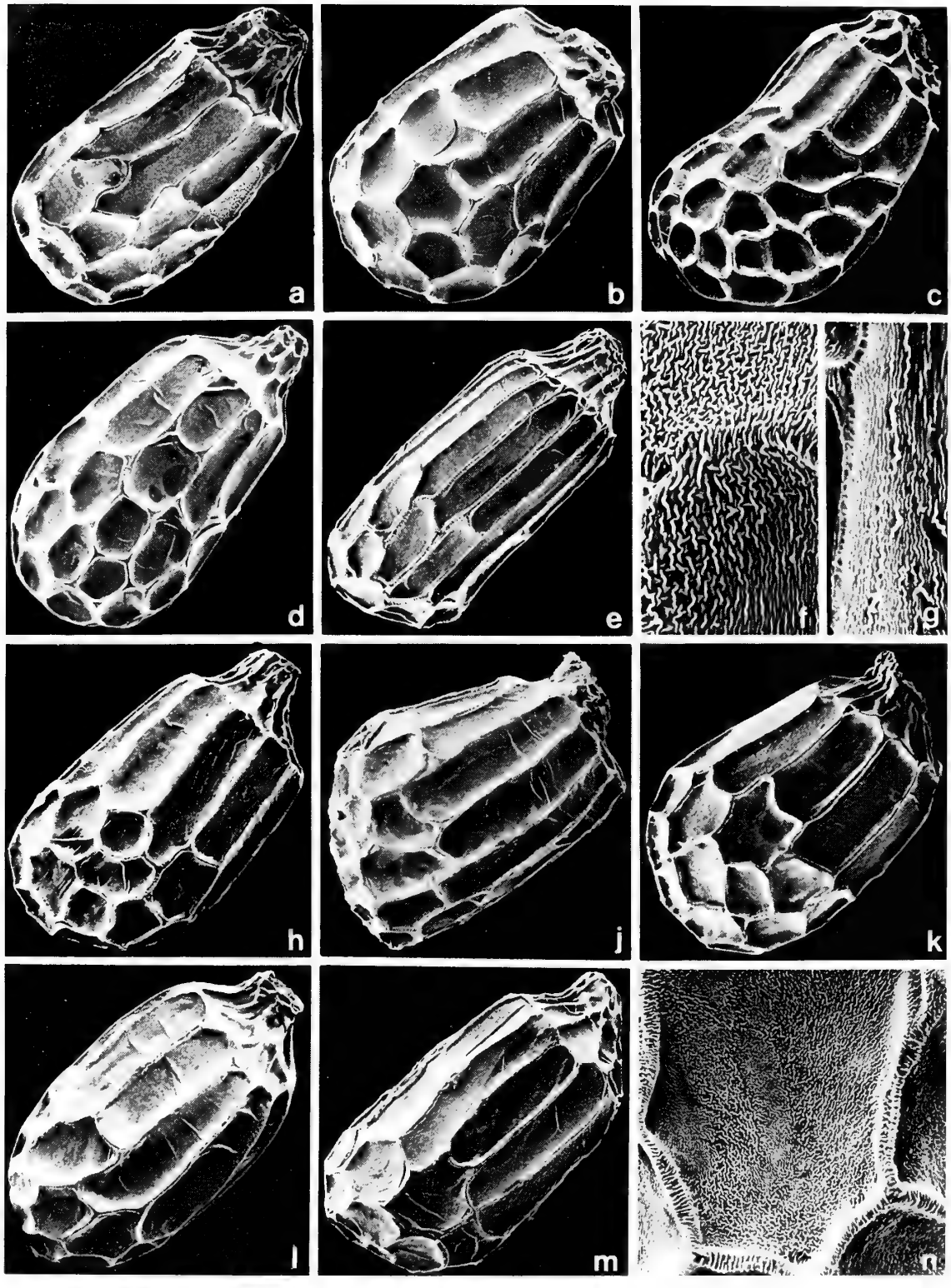

PLATE 6.—Seeds of sections *Bradea, Tetrachia, Gaerdtia, Latistigma,* and *Pereira: a, B. dentatiloba* (*L.B. Smith 1935*), ×160; *b, B. parvifolia* (*d'Alleizette s.n.*), ×130; *c, B. egregia* (*Santos Lima s.n.*), ×120, *g,* detail testa, ×720; *d, B. corallina* (*Boone-Hahn 114*), ×125; *e, B. maculata* (*Maas & Carauta 3149*), ×115, *f,* detail testa, ×1140; *h, B. undulata* (*Gaudichaud 1067*), ×140; *j, B. aconitifolia* (*Glaziou 13389*), ×150; *k, B. leathermaniae* (*Moraes 1056*), ×180, *n,* detail testa, ×560; *l, B. platanifolia* (*Hatschbach 46298*), ×150; *m, B. edmundoi* (*Pereira 366*), ×140.

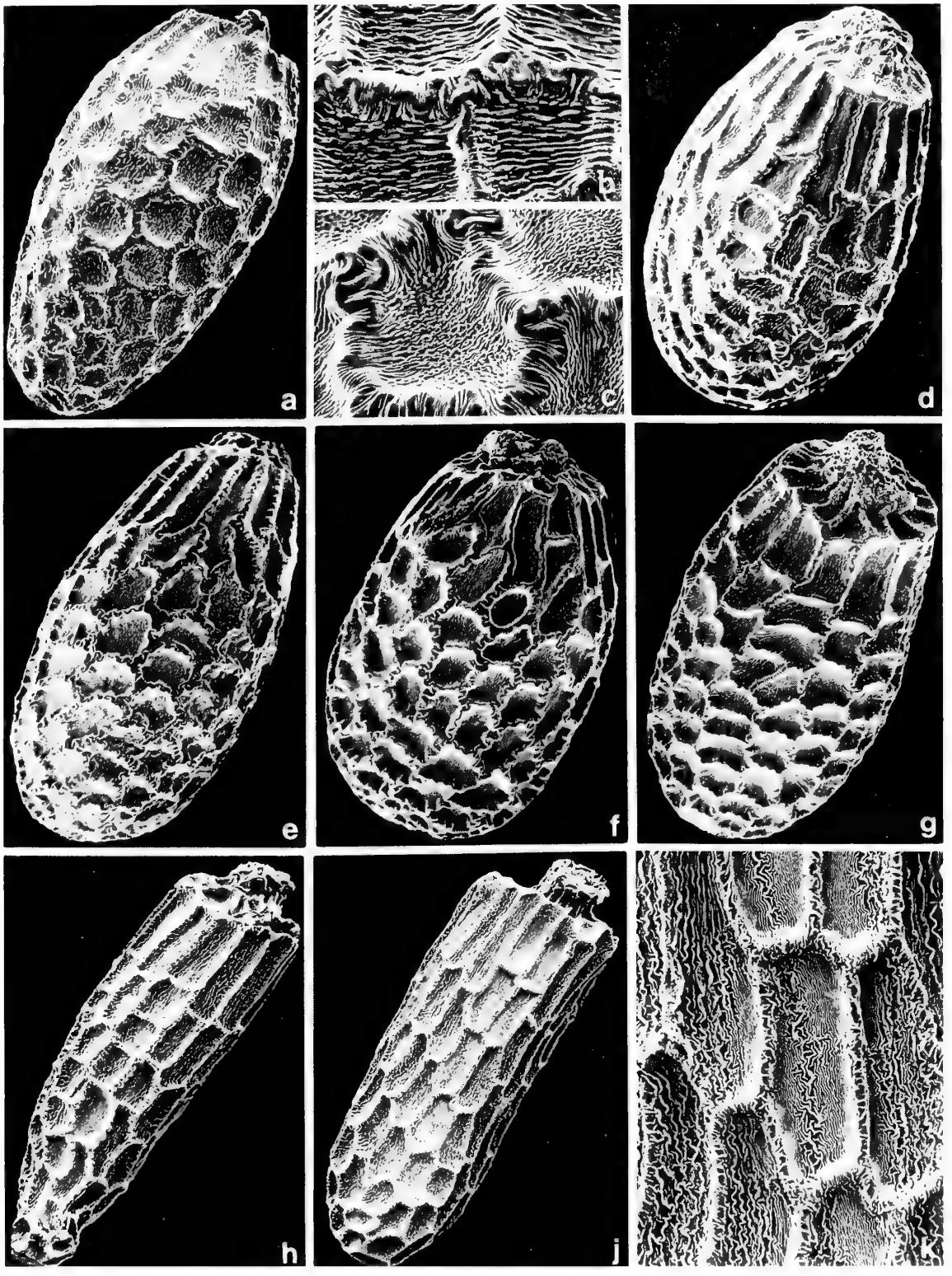

PLATE 7.—Seeds of section *Casparya: a, B. urticae* (*Harling et al. 20465*), ×105, *b,* detail testa, ×340; *c, B. fuchsiiflora* (*Scott Hoover 515*), detail testa, ×620, *f,* seed, ×120; *d, B. urticae* (*Bohlin 975*), ×120; *e, B. longirostris* (*Harling & L. Andersson 11608*), ×130; *g, B. gamolepis* (*Killip & A.C. Smith 16037*), ×130; *h, B. ferruginea* (*Langenheim 3387*), ×85; *j, B. ferruginea* var. *dilatata* (*Garcia-Barriga 12053*), ×115, *k,* detail testa, ×370.

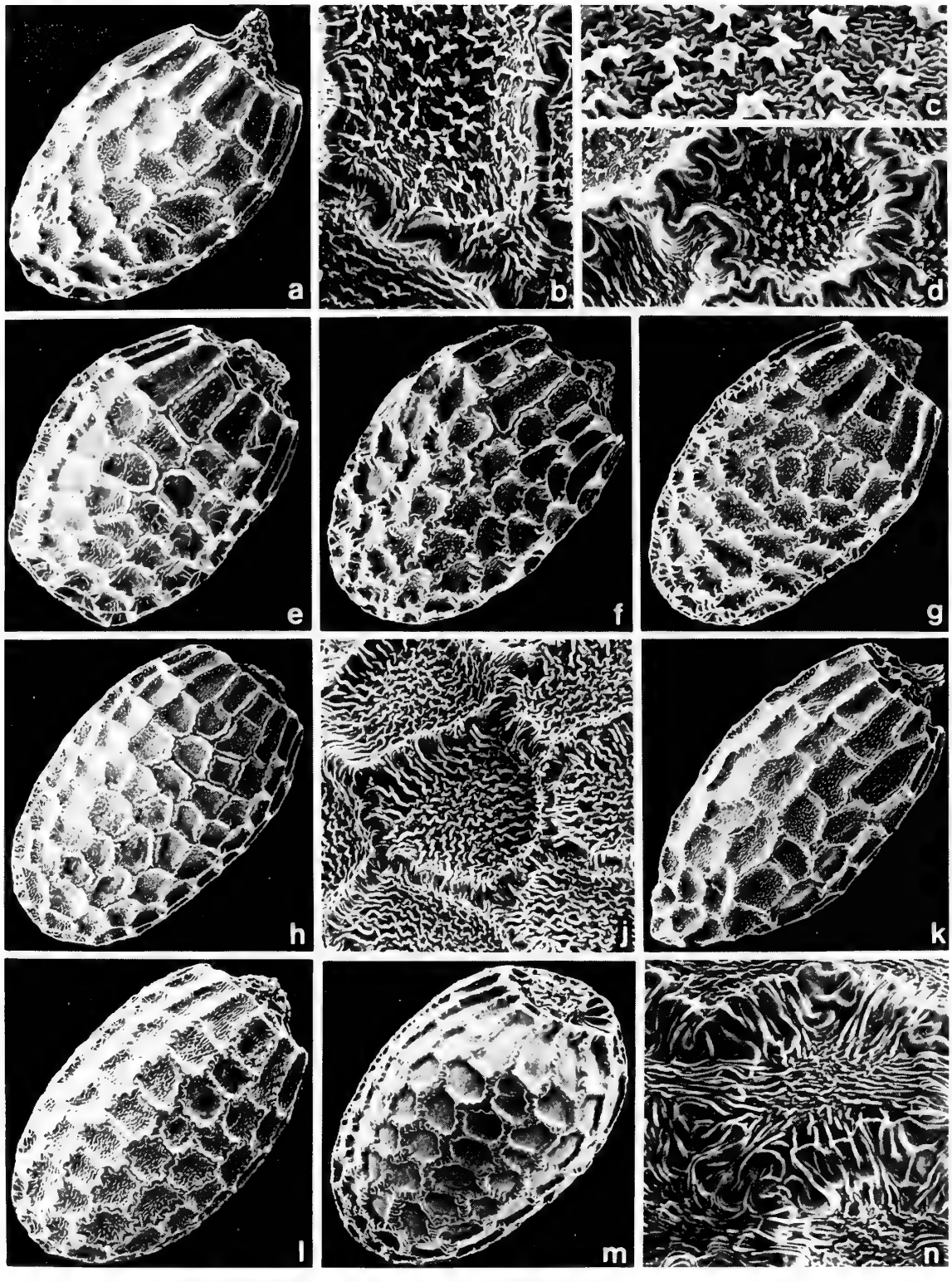

PLATE 8.—Seeds of section *Casparya: a, B. trispathulata* (*Tillett 739-585*), ×130, *b,* detail testa, ×770; *c, B. brevipetala* (*Steyermark & Mehlin 109955*), detail cuticle, ×1690, *d,* detail testa, ×580, *g,* seed, ×120; *e, B. trujillensis* (*Tillett 739-611*), ×125; *f, B. mariae* (*Goldsmith 163*), ×130; *h, B. formosissima* (*Ruiz-Teran & Figueiras 9306*), ×90, *j,* detail testa, ×400; *k, B. lipolepis* (*Goldsmith 167*), ×110; *l, B. toledana* (*Steyermark & Dunsterville 100604*), ×125; *m, B. pectennervia,* seed (*Holm-Nielsen 26762*), ×125, *n,* detail testa (*Holm-Nielsen 26438*), ×620.

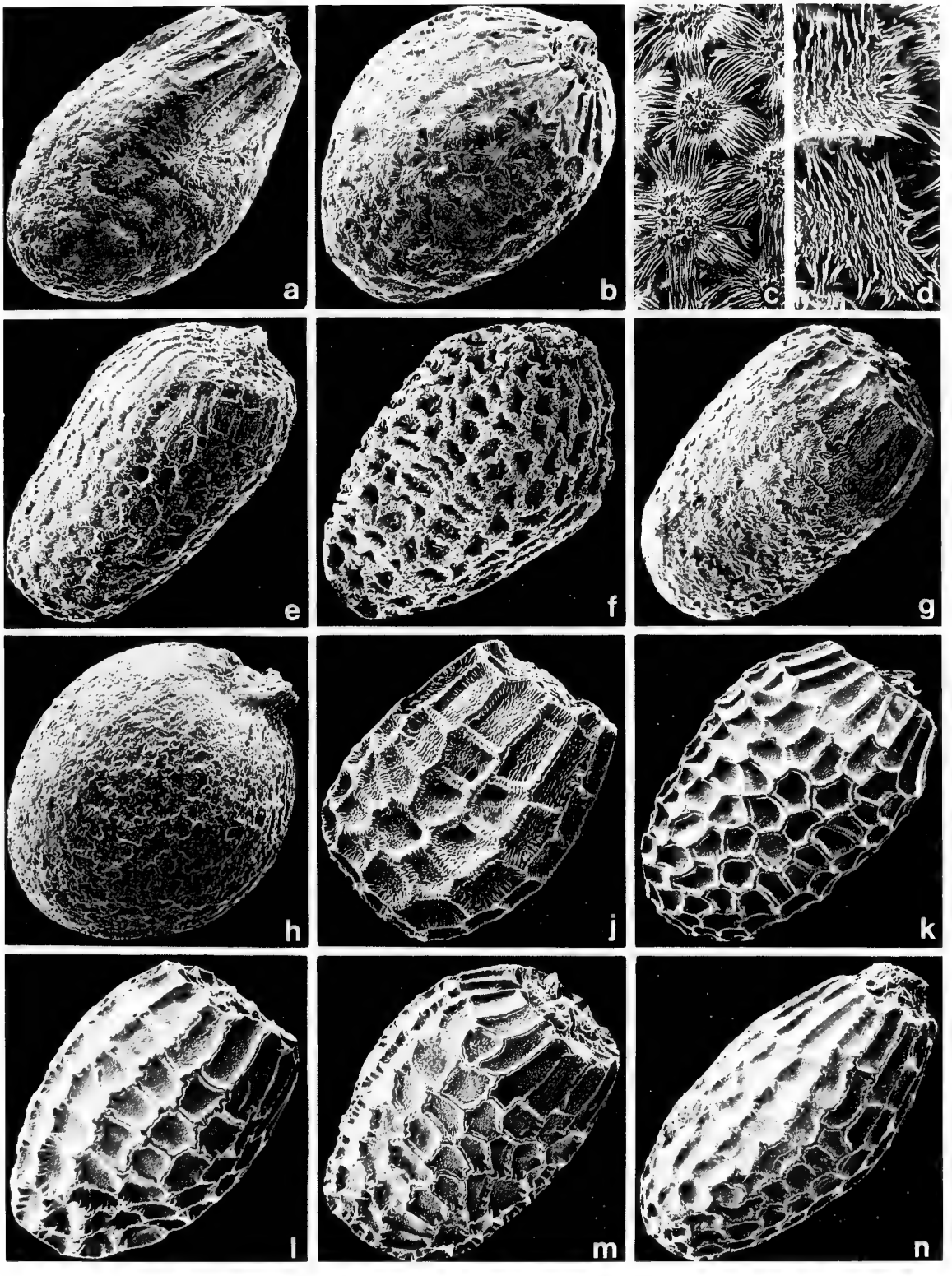

PLATE 9.—Seeds of section *Casparya: a, B. colombiana* (*Schultes & Villarreal 7758*), ×120; *b, B. killipiana* (*Scott Hoover 27*), ×95, *c,* detail testa, ×280; *d, B. trispathulata* (*Steyermark 103480*), detail testa, ×550, *g,* seed, ×140; *e, B. longirostris* (*Lugo 4699*), ×115; *f, B. antioquensis* (*Luteyn 12265*), ×140; *h, B. hexandra* (*Core 1500*), ×110; *j, B. diversistipulata* (*Giacometto 11*) ×150; *k, B. umbellata* (*Killip & Hazen 9165*), ×105; *l, B. montana* (*Funck & Schlim 1044*), ×115; *m, B. formosissima* (*Lopez-Figueiras & Dugarte 29409*), ×100; *n, B. raimondi* (*Raimondi 2982*), ×85.

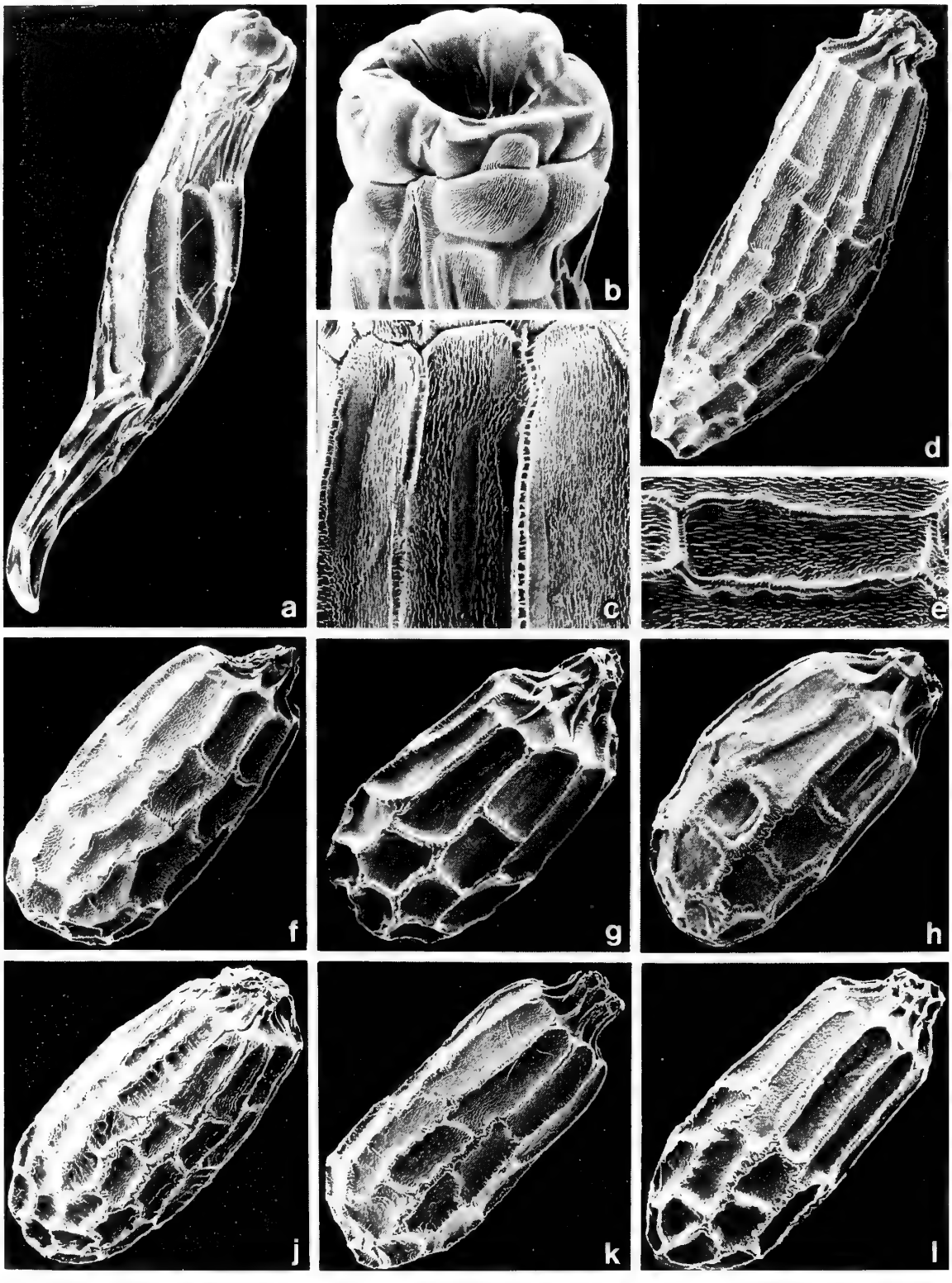

PLATE 10.—Seeds of sections *Rossmannia, Hydristyles,* and *Warburgina: a, B. rossmanniae* (*Holguer Lugo S. 4824*), ×170, *b,* operculum, ×440 (*Holguer Lugo S. 4824*), *c,* detail testa, ×510 (*Vogelmann c.s. 1297*); *d, B. santarosensis* (s.n.), ×150, *e,* detail testa, ×400; *f,* aff. *B. bridgesii* (*Dereims s.n.*), ×150; *g, B. subcaudata* (*Beck 9253*), ×160; *h, B. juntasensis* (*Moore, Salazar, & Smith 8601*), ×180; *j, B. unduavensis* (*Mandon 1089*), ×150; *k, B. andina* (*Williams 1566*), ×140; *l, B. comata* (*Beck 12651*), ×160.

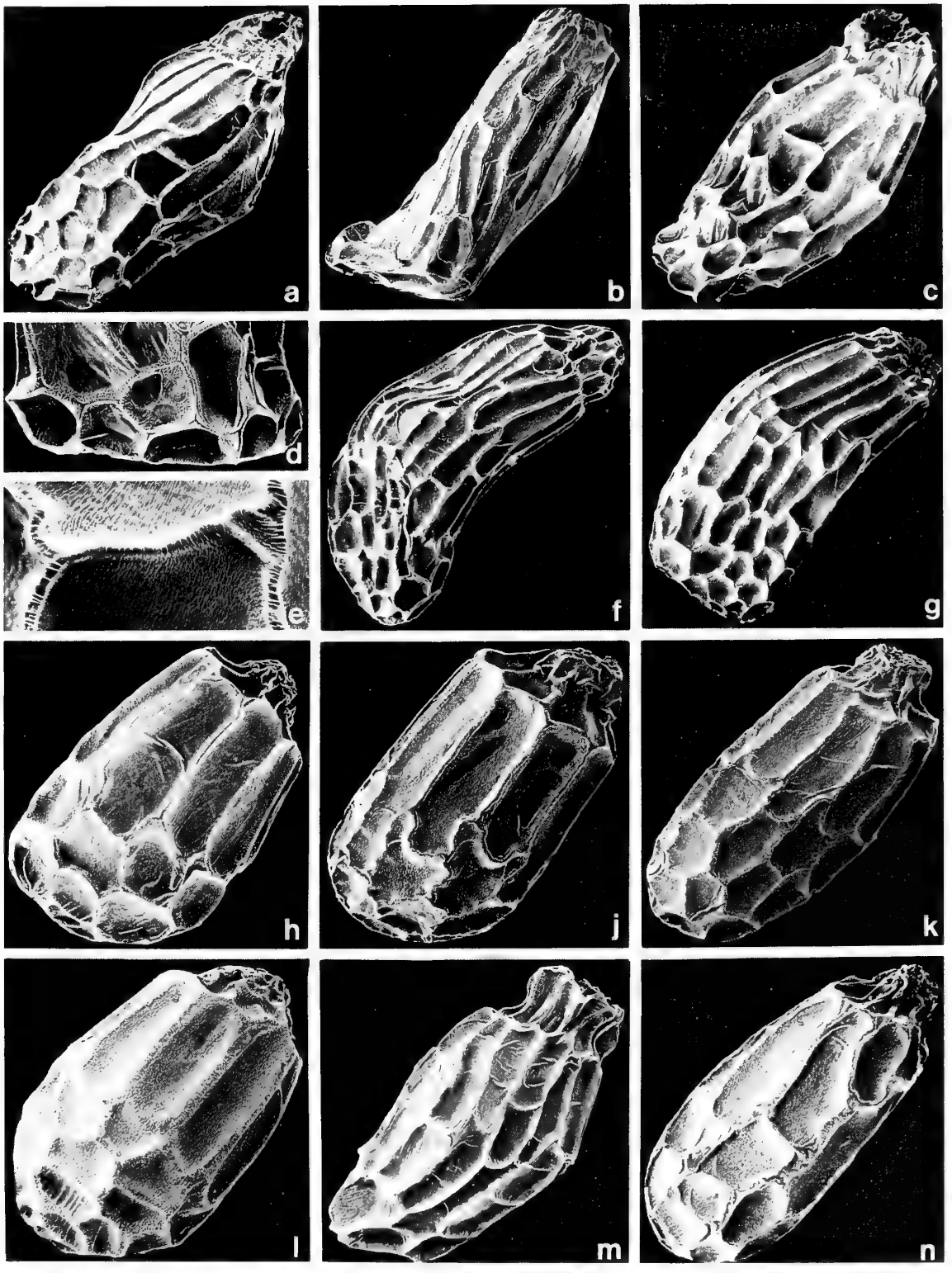

PLATE 11.—Seeds of sections *Gobenia, Meionanthera, Lepsia,* and *Tittelbachia: a, B. maurandiae*, seed (*Camp E 4974*), ×130, *d,* detail chalaza (*André 3315*), ×260; *b, B. pululahuana* (*Davis 500*) ×115; *c, B. secunda* (*Gentry & Shupp 26638*), ×150; *e, B. holtonis,* detail testa (*Uribe Uribe 3878*), ×590, *h,* seed (*Holton 725*), ×170; *f, B. ynesiae* (*Mexia 7706*), ×115; *g, B. sodiroi* (*Holm-Nielsen & Jeppesen 1276*), ×110; *j, B. foliosa* var. *australis* (*Matthias & Taylor 5905*), ×200; *k, B. foliosa* var. *putzeysiana* (*Killip & Smith 19817*), ×120; *l, B. foliosa* var. *rotundata* (*McDougal & Roldan 3540*), ×145; *m, B. microphylla* (*Breteler 4643*), ×125; *n, B. fuchsioides* var. *fuchsioides* (*Killip & Smith 20552*), ×140.

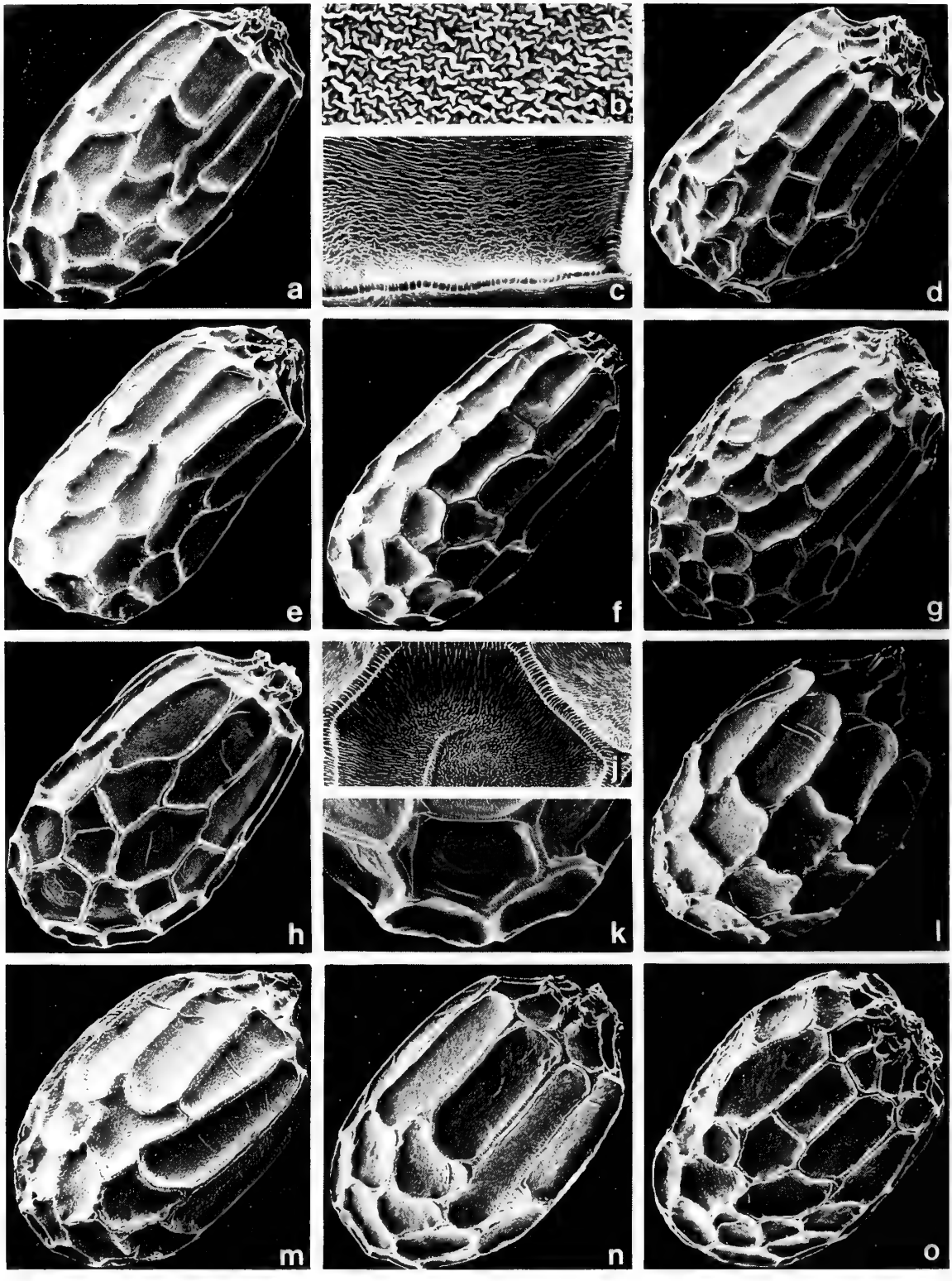

PLATE 12.—Seeds of section *Eupetalum*, including former section *Huszia*: *a*, *B. octopetala* (*Holm-Nielsen c.s. 3404*), ×190, *c*, detail testa, ×790; *b*, *B. pastoensis* (*Lehman 5404*) detail cuticle, ×3340, *d*, seed, ×180; *e*, *B. erythrocarpa* (*Wasshausen & Salas 1194*), ×180; *f*, *B. pleiopetala* (*Buchtien 653*), ×150; *g*, *B. macbrideana* (*Weberbauer 2011*), ×130; *h*, *B. geraniifolia* (*Lourteig 3117*), seed, ×170, *k*, detail chalaza, ×350; *j*, *B. geraniifolia* (*Dowbey s.n.*), detail testa, ×690; *l*, *B. cinnabarina* (*de Michel 16*), ×160; *m*, *B. hydrophylloides* (*Idrobo & Evans Schultes 560*), ×200; *n*, *B. serotina* (*Camp E 3716*), ×200; *o*, *B. pearcei* (*van Veldhuizen 580*), ×170.

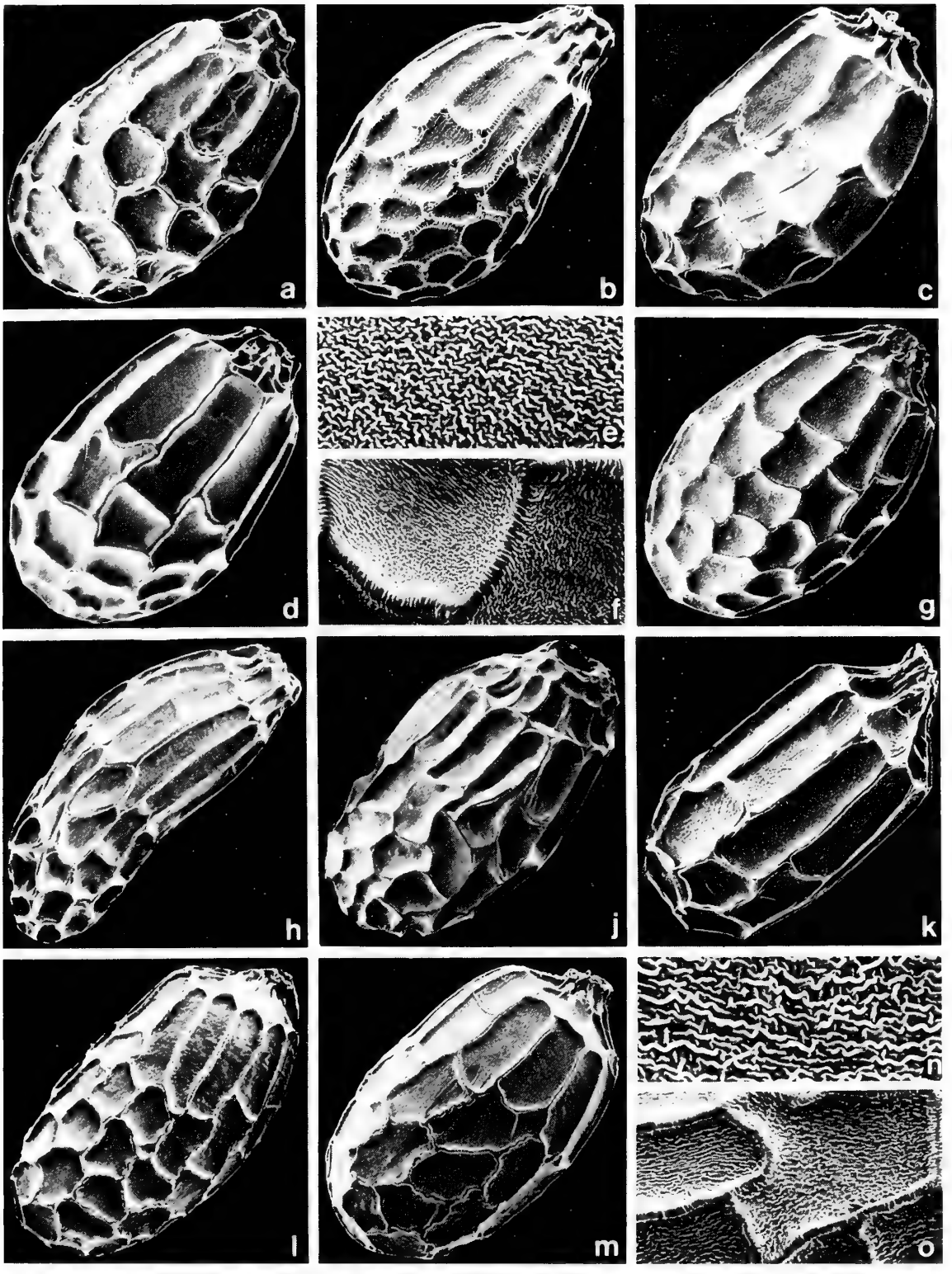

PLATE 13.—Seeds of sections *Eupetalum* (including former section *Huszia*), *Apteron, Barya, Pilderia,* and *Australes: a, B. tumbezensis* (*Weberbauer 7685A*), ×220; *b, B. monophylla* (*Pringle s.n.*), ×190; *c, B. novogranatae* (*Dawe 272*), ×190; *d, B. exalata* (*Sódiro 597*), ×190, *e,* cuticle, ×1970; *f, B. boliviensis* (*Hawkes c.s. 3620*), detail testa, ×740, *g,* seed, ×170; *h, B. monadelpha* (*Weberbauer 6714*), ×120; *j, B. soror* (*Wurdack 1627*), ×130; *k, B. buddleiifolia* (*Holguer Lugo S. 5042*), ×220, *n,* detail cuticle, ×2380; *l, B. tafiensis* (*Venturi 3093*), ×140; *m, B. micranthera* var. *micranthera* (*Petersen & Hjerting s.n.*), ×160; *o, B. micranthera* var. *foliosa* (*West 6216*), detail testa, ×550.

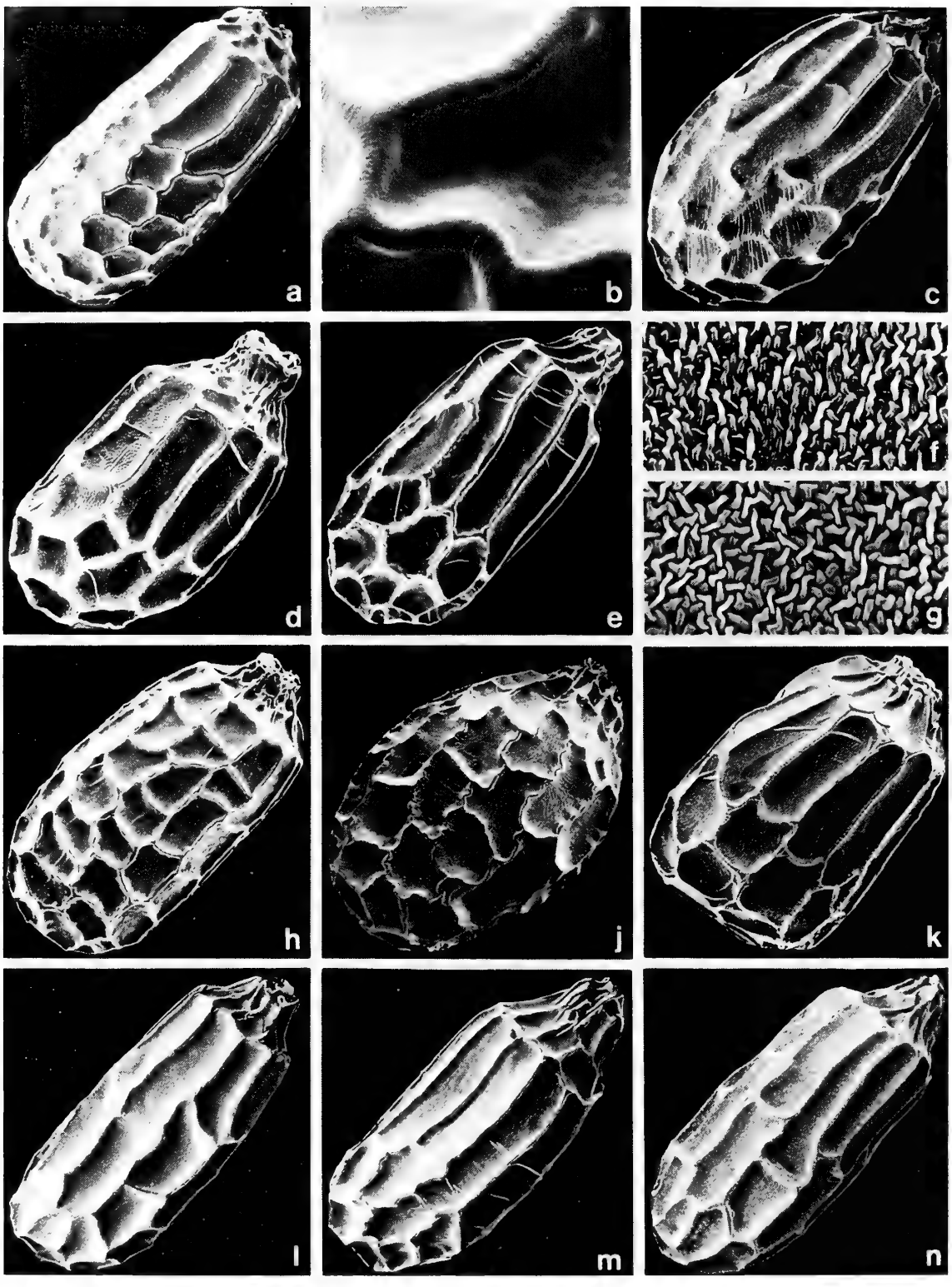

PLATE 14.—Seeds of sections *Urniformia* and *Gireoudia: a, B. heydei* (*Haber & Bello 7645*), ×115, *b,* detail testa, ×870; *c, B. plebeja* (*Taylor 17305*), ×170, *f,* detail cuticle, ×2460; *d, B. jenmannii* (*Maguire & Fanshawe 23081*), ×190; *e, B. multinervia* (*van Veldhuizen 661*), ×180; *g, B. sericoneura* (*van Veldhuizen 392*), detail cuticle, ×2710, *k,* seed, ×180; *h, B. urophylla* (*van Veldhuizen 655*), ×140; *j, B. sartorii* (*Bourgeau 2100*), ×150; *l, B. crassicaulis* (*Steyermark s.n.*), ×160; *m, B. involucrata* (*Standley 34241*), ×190; *n, B. conchifolia* (*Wilbur 24349*), ×160.

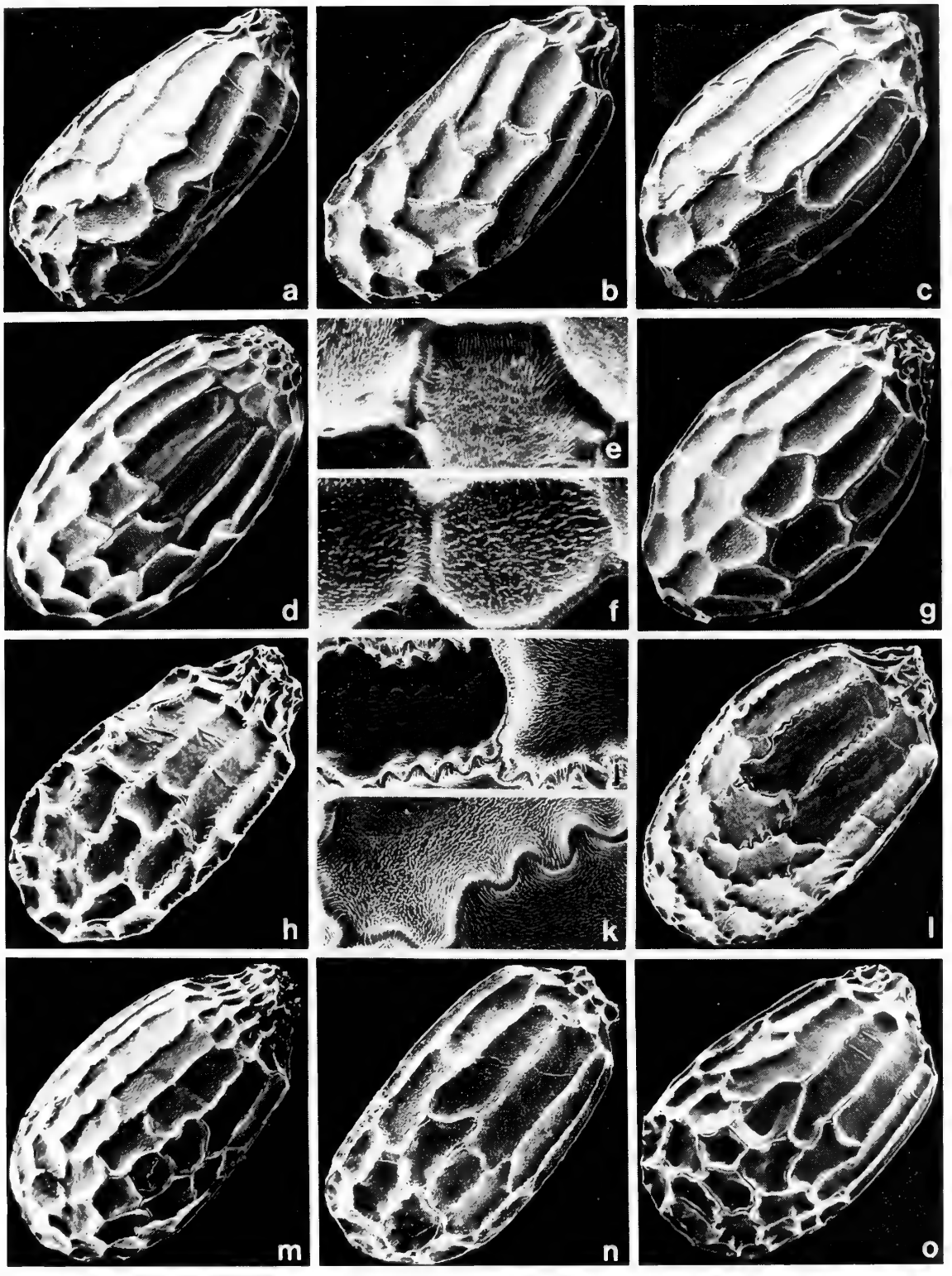

PLATE 15.—Seeds of sections *Gireoudia, Hexaptera, Dissepbegonia, Podandra,* and *Weilbachia: a, B. barkeri* (*Smith 690*), ×160; *b, B. cardiocarpa* (*Utley 5917*), ×180; *c, B. heracleifolia* (*Bourgeau 1583*), ×190; *d, B. oaxacana* (*Davidse et al. 26139*) ×140, *e,* detail testa, ×510 (*McVaugh 10266*); *f, B. palmeri* (*Mexia 219*), detail testa, ×560, *g,* seed, ×190; *h, B. decandra* (*Krug & Urban 1121*), ×180, *j,* detail testa, ×590; *k, B. aridicaulis* (*van Veldhuizen 529*), detail testa, ×830, *l,* seed, ×190; *m, B. purpusii* (*Matuda 5406*), ×140; *n, B. imperialis* (*DTH 5397*), ×145; *o, B. alice-clarkiae* (*van Veldhuizen 497*), ×170.

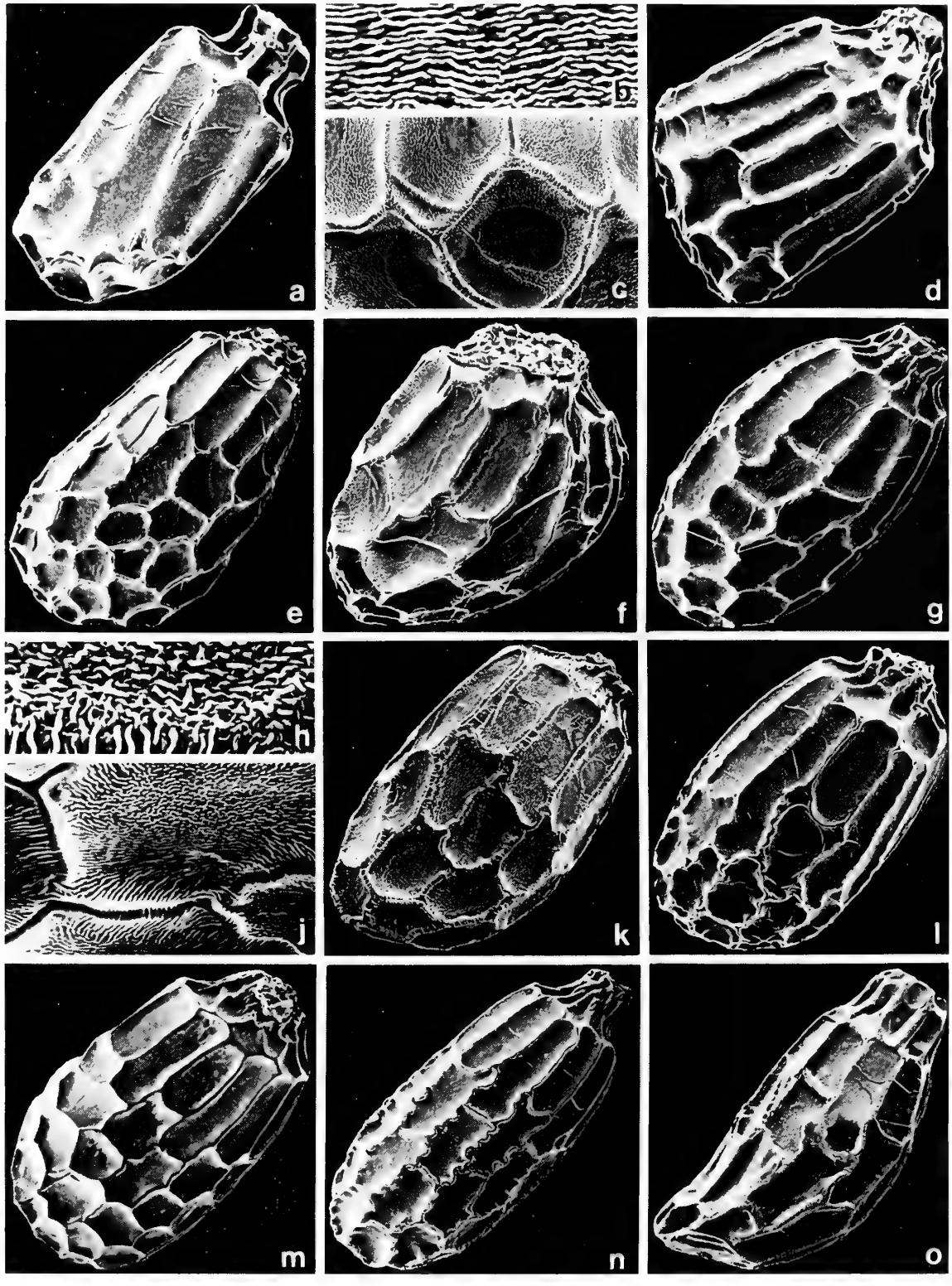

PLATE 16.—Seeds of section *Ruizopavonia: a, B. alnifolia* (*Mocquerys 1219*), ×180, *b,* detail cuticle, ×2620; *c, B. peruviana* (*Sandeman 4378*), detail testa, ×400, *f,* seed, ×190; *d, B. corredorana* (*Skutch 4733*), ×260; *e, B. carpinifolia* (*Kappelle & Monge 3635*), ×140; *g, B. thiemei* (*Calderon 2258*), ×200; *h, B. bracteosa* (*Ellenberg 815*), detail cuticle, ×1640, *k,* seed, ×180; *j, B. udisylvestris* (*Burger & Stolze 5250*), detail testa, ×490, *m,* seed, ×115; *l, B. seemanniana* (*Seemann 1661*), ×200; *n, B. suprafastigiata* (*Weberbauer 7907*), ×145; *o, B. cuatrecasiana* (*Forrero-Jaramillo 2403*), ×180.

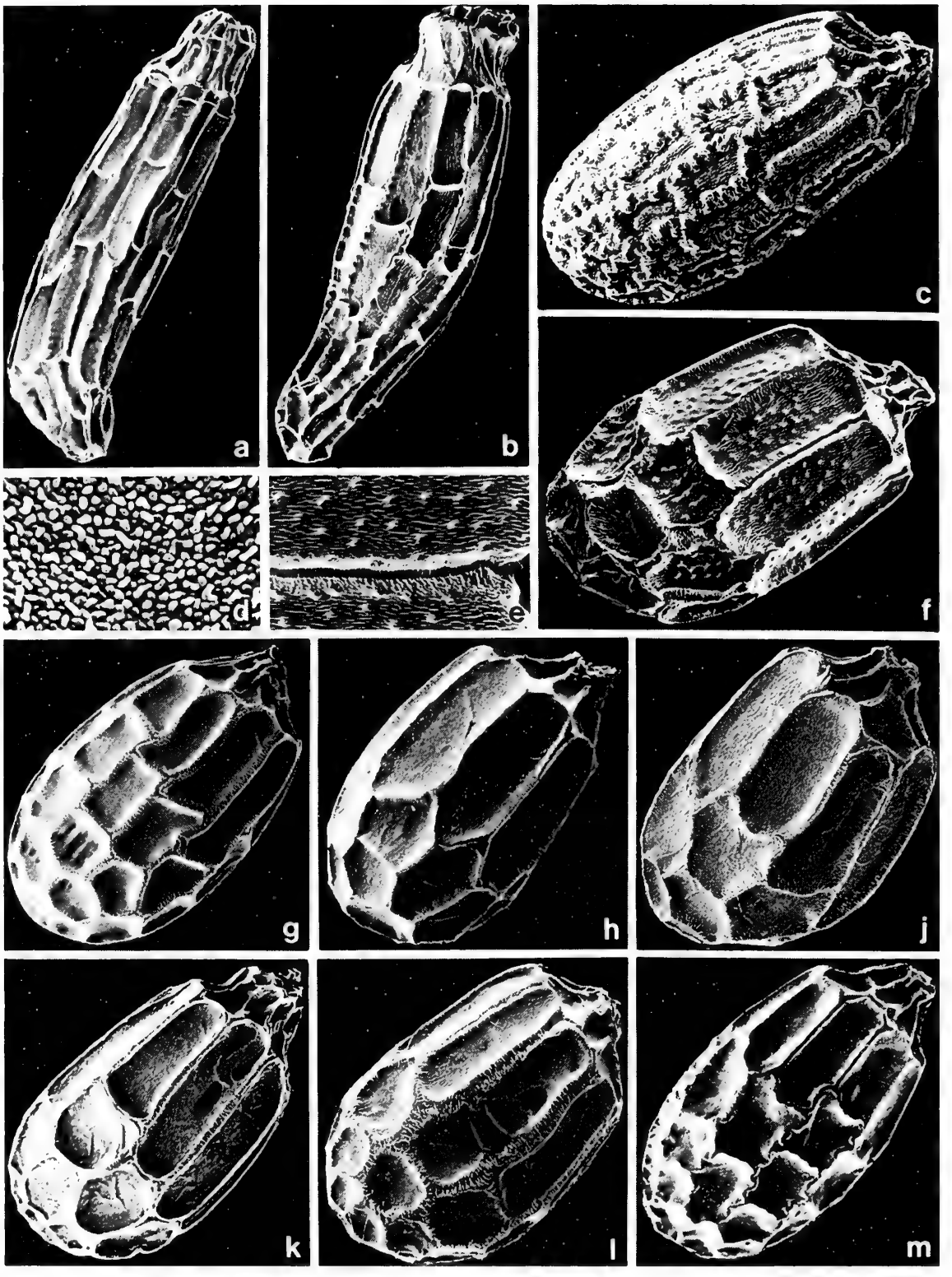

PLATE 17.—Seeds of sections *Ruizopavonia* and *Doratometra: a, B. estrellensis,* ×130 (*Zamora c.s. 512*), *b,* ×145 (*Liesner 1023*); *c, B. steyermarkii* (*Cowan & Soderstrom 1841*), ×200; *d, B. wallichiana* (*Stanford c.s. 972*), detail cuticle, ×2610, *g,* seed, ×180; *e, B. prieurii* (*Irwin c.s. 48113*), detail testa, ×420, *f,* seed, ×200; *h, B. filipes* (*Thiébaut 41*), ×240; *j, B. humilis* (*Egger 1404*), ×210; *k, B. tonduzii* (*Grayum 8132*), ×220; *l, B. hirsuta* (*Herb. Splitgerberianum*), ×190; *m, B. hirtella* (*Lourteig 2308*), ×210.

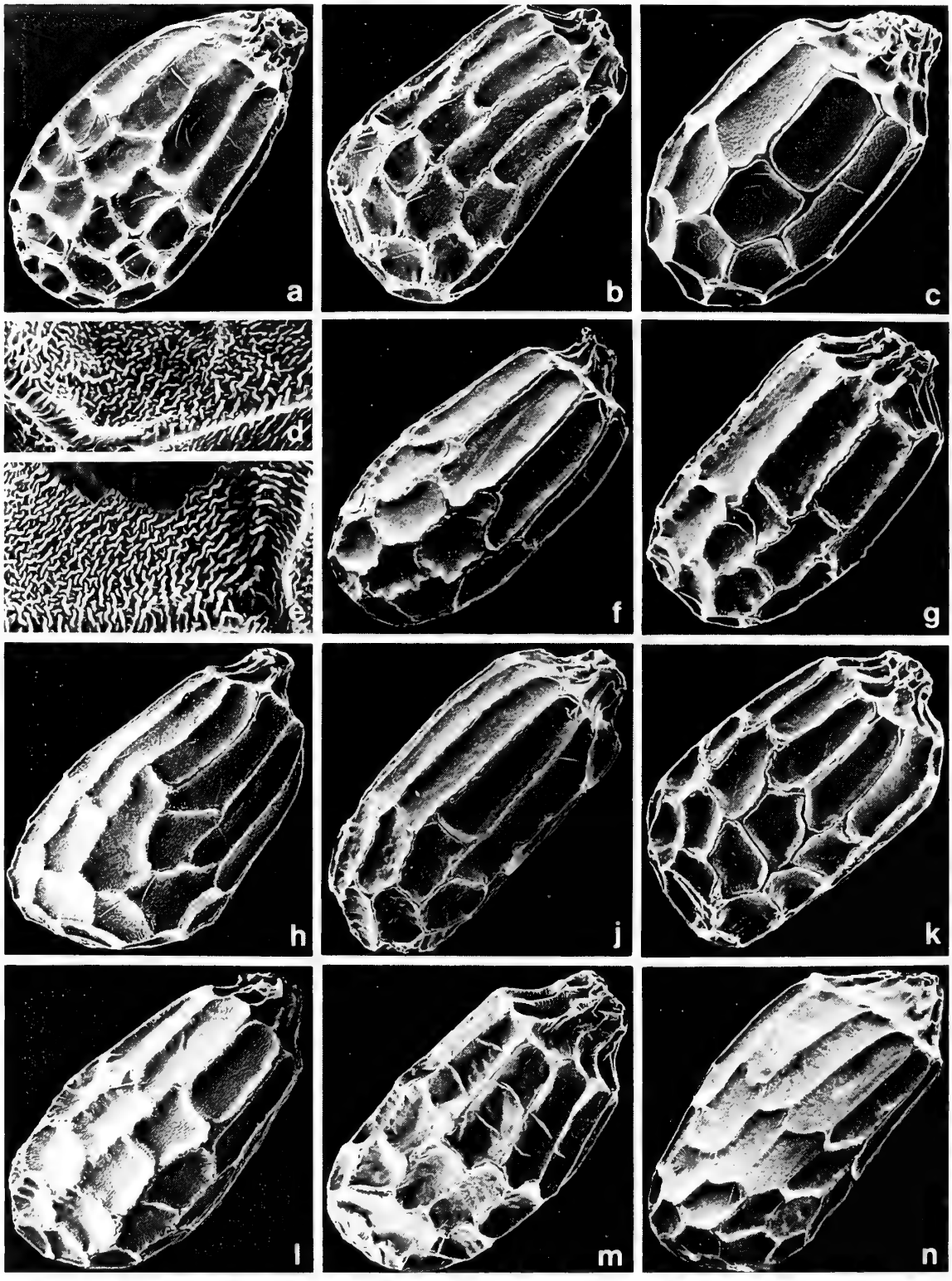

PLATE 18.—Seeds of section *Begonia: a, B. obliqua* (*Duss 973*), ×170, *d,* detail testa, ×1890; *b, B. rotundifolia* (cult., Liège), ×180; *c, B. glandulifera* (*Van Steenis 20304*), ×200; *e, B. plumieri* var. *barahonensis* (*Miguel Fuertes 432*), detail testa, ×1150, *h,* seed, ×160; *f, B. odorata* (*Morton 5066*), ×160; *g, B. retusa* (*Stoffers 3116*), ×200; *j, B. guaduensis* (*Maas & Westra 3877*), ×150; *k, B. cubensis* (*Ziesenhenne s.n.*), ×160; *l, B. cyatophora* (*Mexia 8128*), ×180; *m, B. altoperuviana* (*Weddell 4556*), ×170; *n, B. organensis* (*Sucre c.s. 3005*), ×130.

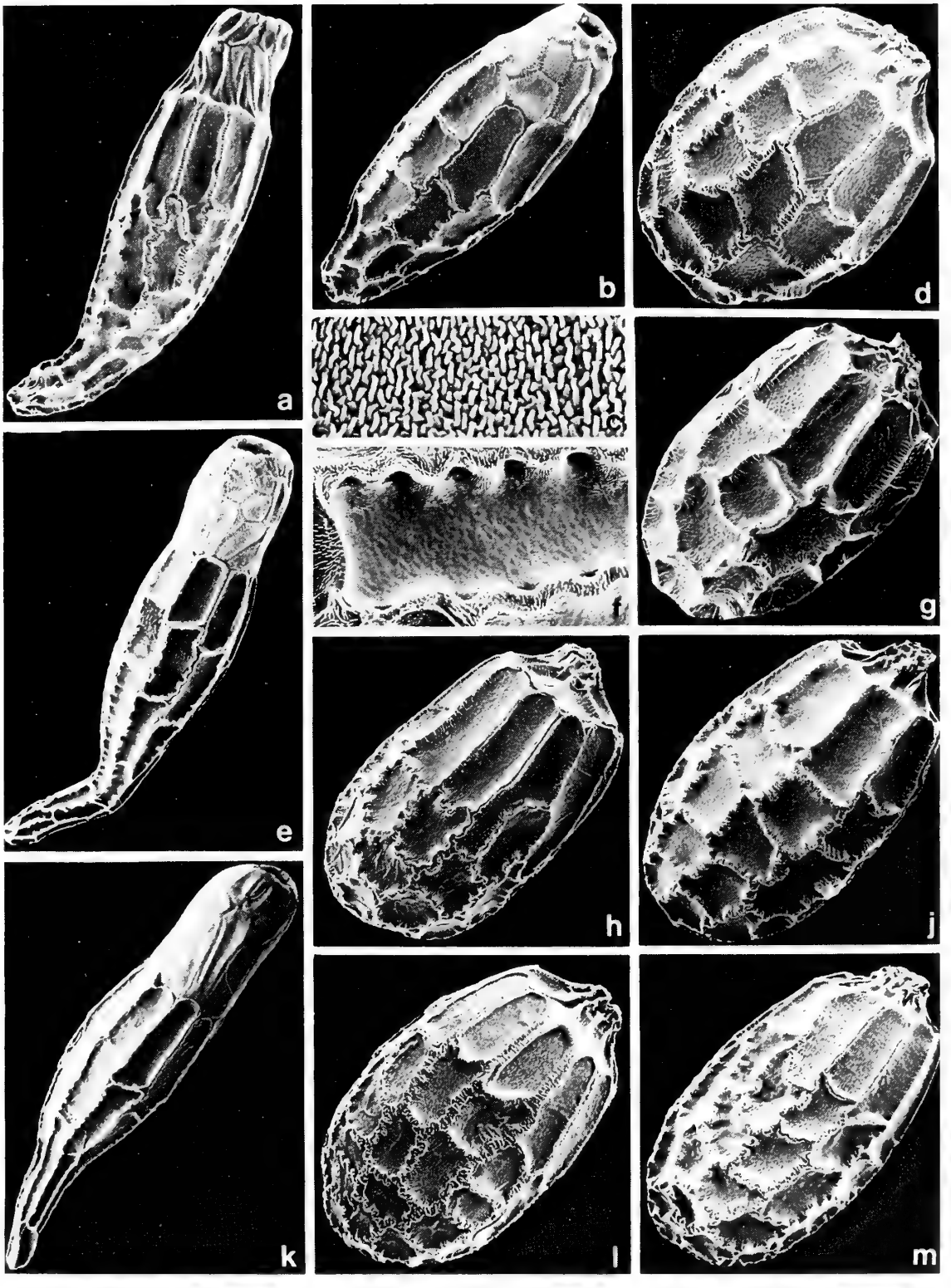

PLATE 19.—Seeds of section *Begonia*: *a, B. cucullata* var. *cucullata*, ×125 (*Irwin c.s. 19961*), *b*, ×125 (*Bartlett 21359*), *c*, detail cuticle, ×1730 (*Bartlett 21359*); *d, B. cucullata* var. *arenosicola* (*Pedersen 10232*), ×190; *e, B. fischeri* var. *fischeri* (*Steyermark & Rabe 96605*), ×100, *f*, detail testa, ×470; *g, B. alchemilloides* (*Irwin c.s. 34478*), ×190; *h, B. balansae* (*Balansa 3281*), ×150; *j, B. descoleana* (*Hatschbach 9944*), ×160; *k, B. fischeri* var. *klugii* (*Klug 3389*), ×115; *l, B. per-dusenii* (*Smith, Klein, & Schnorrenberger 11728*), ×190; *m, B. subvillosa* var. *leptotricha* (*Fiebrig 5354*), ×180.

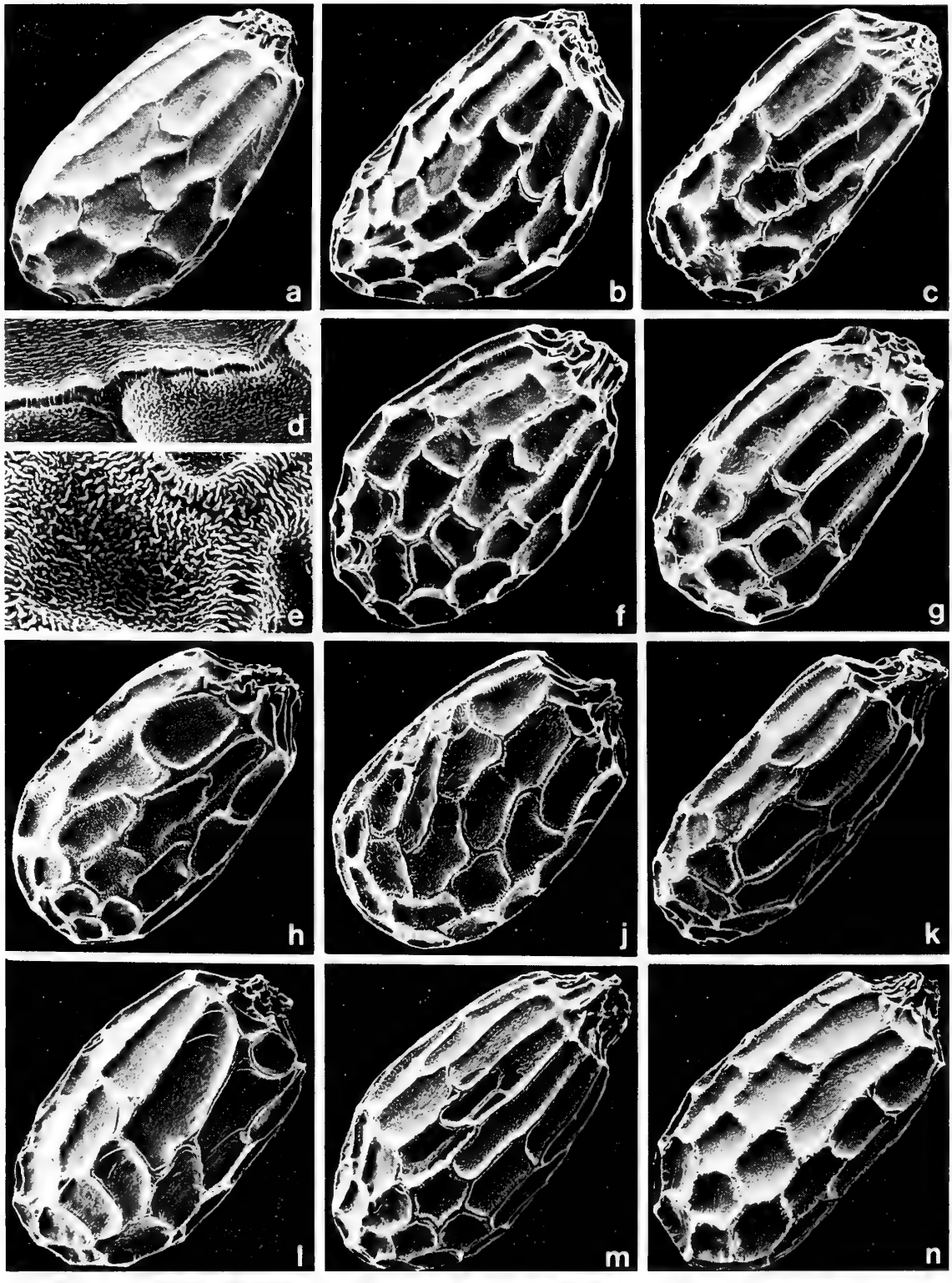

PLATE 20.—Seeds of section *Knesebeckia: a, B. incarnata* (*Liebmann 177*), ×180, *d,* detail testa, ×610; *b, B. kellermannii* (*Ziesenhenne s.n.*), ×140; *c, B. peltata* (*Boom 14288*), ×160; *e, B. gracilis* (*Pringle 11452*), detail testa, ×970, *h,* seed, ×200; *f, B. boissieri* (*van Veldhuizen 747*), ×180; *g, B. ludwigii* (*van Veldhuizen 618*), ×140; *j, B. sandtii* (*Ziesenhenne s.n.*), ×170; *k, B. angustiloba* (*Diguet s.n.*), ×190; *l, B. falciloba* (*Bourgeau 649*), ×170; *m, B. ignea* (*Pittier & Durand 1299*), ×140; *n, B. uniflora* (*Roybal 647*), ×160.

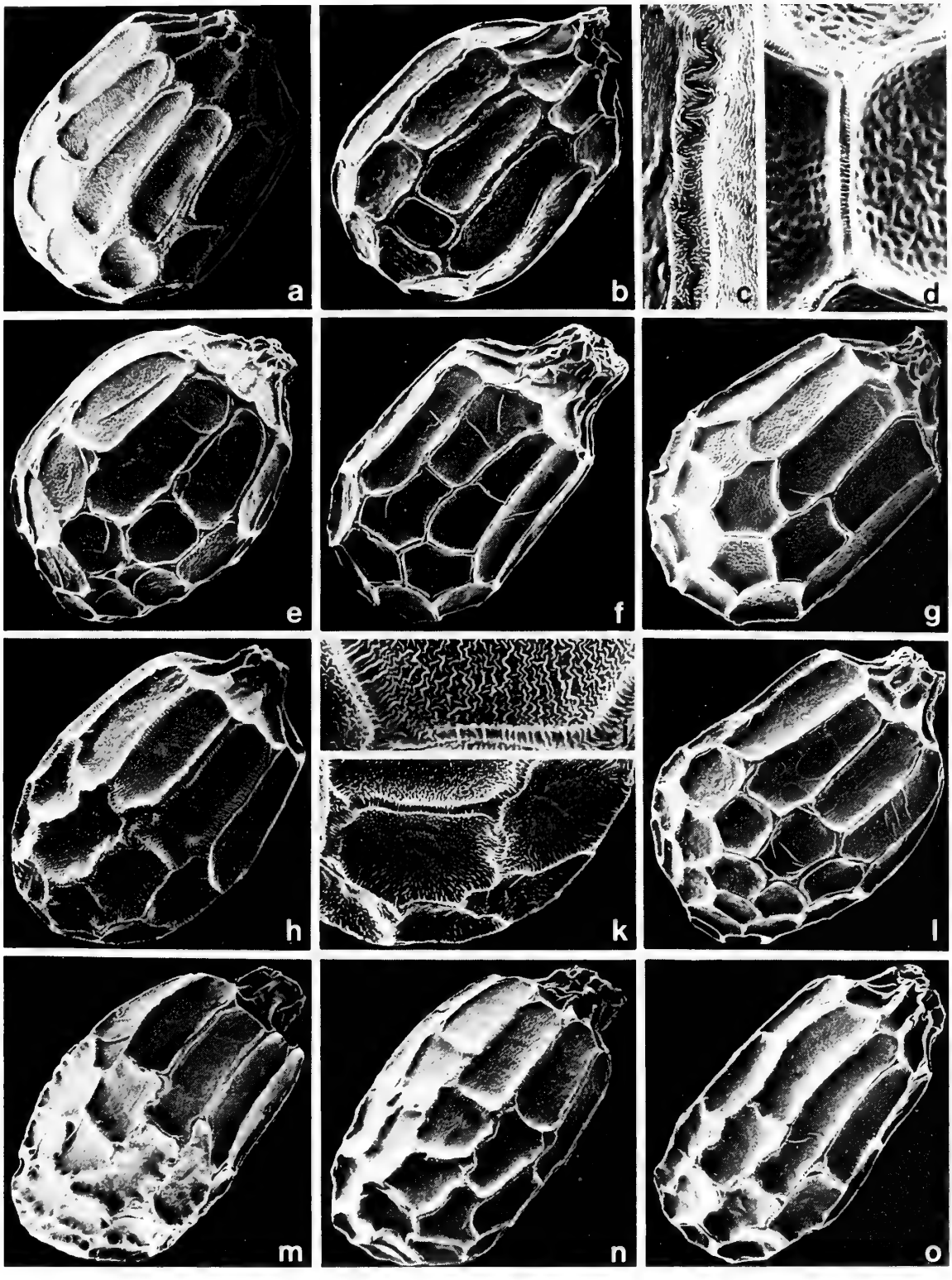

PLATE 21.—Seeds of sections *Knesebeckia* and *Donaldia: a, B. oellgaardii* (*Baker 6396*), ×190; *b, B. maynensis* (*Prance c.s. 7409*), ×220, *c,* detail testa, ×780; *d, B. olbia* (*van Veldhuizen 434*), detail testa, ×610, *g,* seed, ×140; *e, B. wollnyi* (*van Veldhuizen 435*), ×240; *f, B. dichroa* (*Ziesenhenne s.n.*), ×140; *h, B. ulmifolia* (*Hekking 1428*), ×210, *k,* detail chalaza, ×420; *j, B. dasycarpa* (*Glaziou 15388*), detail testa, ×760, *l,* seed, ×160; *m, B. chaetocarpa* var. *chaetocarpa* (*Kuntze s.n.*), ×210; *n, B. chaetocarpa* var. *glabriflora* (*Rusby 690*), ×180; *o, B. bangii* (*Bang 406*), ×180.

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