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RE-ESTABLISHMENT OF BEGONIA CAVALLYENSIS A. CHEV. AND THE ALTITUDINAL VICARIAD BEGONIA FUSICARPA IRMSCH. (SECT. TETRAPHILA A. DC.)

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SUMMARY

Analysis of *B. cavallyensis* A. Chev. leads to the conclusion that this species was mistakenly placed into the synonymy of *B. eminii* Warb. The species is described anew and diagnostic characters are given. *Begonia* species and names at one time or another associated with *B. cavallyensis* are discussed. Among the African *Begonia* species known at present, *B. fusicarpa* Irmsch. is most closely related to *B. cavallyensis*. On morphological, distributional, ecological and palynological grounds the species are considered to be a pair of altitudinal vicariads.

I. INTRODUCTION

In the course of a taxonomic revision of the African *Begonias* belonging to section *Tetraphila* A. DC. our attention was drawn by a specimen originally collected in the Nimba Mountains in Liberia, and now growing in the greenhouse of the Agricultural University at Wageningen. Using the key in HUTCHIN-SON and DALZIEL'S 2nd edition of the Flora of W. Trop. Africa (1954) the plant was identified as *B. eminii* Warb. This identification proved highly unsatisfactory as the plant differed in many characters from our concept of *B. eminii* and, more in particular, from the type material on which *B. eminii* is based. The plant, however, reasonably well fitted the description of *B. cavallyensis* A. Chev., a name which is considered to be a later, heterotypic synonym of *B. eminii* Warb. in HUTCH. and DALZ. (l.c., 1954).

In order to gain information about the variability of the species and its delimitation an analysis was made of all the living and dried material available of *B. cavallyensis*. This material, together with the results of our analysis and all available evidence was compared with that of related taxa and especially with that of all the names, which, at one time or another, have been placed into the synonymy of *B. eminii* Warb. The following validly published names, arranged in chronological order, are involved:

B. eminii Warb., July-Aug. 1895 B. macrostyla Warb., Nov. 1895 B. poggei Warb., Nov. 1895 B. preussii Warb., Nov. 1895 B. warburgii Gilg, 1904 B. rubro-marginata Gilg, 1904 B. alepensis A. Chev., 1912 B. ealensis Irmsch., 1921 B. fusicarpa Irmsch., 1954

Finally we have concluced that *B. cavallyensis* is a distinct species which is here re-described and delimited. At the same time we found that among all the names cited above only *B. fusicarpa* has many characters in common with *B.*

cavallyensis, and is, indeed, very closely related to it. After careful consideration it is maintained here as a vicariad beside *B. cavallyensis*.

2. Begonia cavallyensis A. Chev.

Fig. 1; Phot. 1 and 2; Map 1

Begonia cavallyensis Aug. Chevalier in Bull. Soc. Bot. France 58 (Mém. 8): 176. 1912; A. Chev., Expl. Bot. Afr. Occ. Franc. 1: 297. 1920; Hutch. and Dalz., Fl. W. Trop. Afr. 1st ed. 1(1): 188. 1927; F. R. Irvine, Plants of the Gold Coast: 52. 1930 (cited under the name B. rubro-marginata Gilg); R. Schnell, Vég. et Flore de la Rég. Mont. du Nimba in Mém. de l'Inst. Fr. Afr. Noire 22: 461. 1952 (cited under the name B. rubro-marginata Gilg); Hutch. and Dalz., Fl. W. Trop. Afr. 2nd ed. 1(1): 220. 1954 (in synonymy to B. eminii Warb.; among the material cited only Chevalier no. 21422 belongs to B. cavallyensis); Dalziel, Useful Pl. of W. Trop. Afr. 2nd reprint: 64. 1955 (cited under the name B. rubromarginata Gilg); The Begonian 34: 170. 1967 (phot., as B. eminii Warb.); Adam, Fl. descriptive des Monts Nimba in Mém. Mus. Nat. Hist. Naturelle nouv. sér. B (Bot.) 20: 320, 322-324, pl. 76 and 77. 1971 (the name cited in synonymy to B. eminii Warb., the cited specimens belong to B. cavallyensis); Barkley in The Buxtonian 1, Suppl. 5, The Species of the Begoniaceae 1st ed.: 16, 28, 1972 (in syn. to B. eminii); Barkley and Golding, The Species of the Begoniaceae, 2nd ed.: 19, 34. 1974 (in syn. to B. eminii); Barkley in The Begonian 41: 151 (phot., as B. rubro-marginata). 1974; D. Johansson, Ecol. of Vasc. Epiphytes in W. Afr. rain forest in Acta Phytogeogr. Suecica 59: 41 (excl. the cited distribution in Cameroon), 52 (phot.), 54, 73, 75, 78, 81-82, 84 (phot.), 103, 106, 112, 118. 1974 (everywhere cited under the name B. rubro-marginata Gilg); M. L. Thompson in The Begonian 44: 295 (phot. only). 1977; M. L. Thompson and E. J. Thompson, Begonias, the complete ref. guide: 107, 109, 110, 295, colour phot. 12. 1981.

Misapplied name: *B. fusicarpa* auct. non Irmscher: Adam, loc. cit.: 322, pl. 77. 1971.

Type: Aug. Chevalier no. 21.422 (Ivory Coast: Dyola county in the basin of the upper Cavally River, on the summit of Mt. Dò, near Gouékangouiné, at 950 m alt., holotype and isotype in P).

Diagnostic and differential characters: Monoecious epiphytic erect stem-succulent up to 90 cm tall, confined to the Upper Guinea subdivision of the Guineo-Congolian Region between elevations of ca 500 and 1500 m. Stems thick and with conspicuous scars left by the readily caducous leaves; the internodes usually short, 0.5-3 cm long. Petioles relatively long and thick, $(1-)2-7(-15) \times 0.2-0.5$ cm. Blades ovate, obliquely cordate or obtuse at the base, acute to obtuse at the apex, $4-16(-24) \times 2-10(-15)$ cm; in vivo provided with an up to 4 mm broad contrasting, dark red, almost entire margin. All parts of the living plant scattered with conspicuous whitish, spherical, multicellular trichomes. Inflorescences unisexual, more rarely androgynous. Male inflorescence a (2-)4-15-flowered dichasial cyme; the peduncle 1.5-45(-55) mm long. Female inflorescence a 2-3-flowered cyme; the peduncle very short, 1.5-5.5 mm long. Bracts early caducous. Perianth segments (tepals) 4 (viz. 2 + 2) in flowers of both sexes, the inner pair sometimes missing; the outer pair of tepals pink, the inner pair almost white. Androecium fasciculate, asymmetric; stamens 11-19. Styles 2(3), about half as long as the inner tepals, fused over 0.5-1.5 mm at the base. Stigmas crescent-shaped, the stigmatic tissue on the outer surface continuous from one arm of the crescent to the other. Ovary fusiform, terete in transverse section, 2(3)-celled. Mature fruit $20-50 \times 2-5$ mm, opening by a single lateral slit. Seeds proportionally big, $1.1-1.5 \times 0.6-0.8$ mm, the hilar part embedded into a cup-shaped aril-like structure.

Description: Monoecious sturdy epiphyte growing on forest trees. The stems thick, grey-green to dark red-brown, usually branched, erect, occasionally rooting at the nodes, up to ca 90 cm high, more or less terete, in sicco deeply wrinkled lengthwise, the more woody basal parts of the stem 5-16 mm in diam., the juvenile upper parts densely covered with an indumentum of lepidote-stellate, irregularly shaped, brown transparent hairs. The nodes with marked stipular scars. The internodes short, 4-30 mm, but up to 85 mm in cultivated plants. Axillary buds long, 12-40 mm, acute, red and covered with an indumentum of lepidote-stellate brownish hairs. In vivo the whole plant scattered with conspicuous, sessile, white-transparent, glandular, spherical multicellular trichomes. The trichomes ca 0.2 mm diam., mostly bearing a lepidote-stellate hair on top or lateral. These trichomes are easily rubbed off and eventually disappear in herbarium material.

Stipules large, boat-shaped, $(15-)27-43 \times (4-)13-15$ mm, narrowly oblong to narrowly triangular, acuminate to almost cuspidate at the apex, early caducous, red but often colourless-transparent towards the margins (in vivo), membranous, outside scattered with lepidote-stellate hairs, inside glabrous.

Leaves readily caducous and usually confined to the upper parts of the stem, papery, greenish-brown to red-brown in sicco; in vivo rather thick and somewhat fleshy, green and with a conspicuous up to 4 mm broad dark purplish-red margin and red nerves above, the lower surface pale green to reddish-brown and with red nerves. Petioles relatively long and thick, $8-70(-150) \times 2-5$ mm, furrowed above, otherwise terete, in vivo entirely red or red on the light exposed upper side and green below, covered with indumentum and glandular spherical trichomes, leaving conspicuous big hooflike or transversely broadly elliptic scars on the stem, the scars $2-7 \times 2.5-10$ mm. Blades more or less asymmetric, ovate, 40-160 (-240) \times 20-100(-150) mm, obliquely cordate or obtuse at the base, acute to obtuse at the apex; margin almost entire, undulate; blade in cross-section slightly V-shaped. Older blades with some scattered hairs and glandular trichomes on both sides; younger blades with an indumentum of brownish hairs, especially on the nerves on both sides and with easily caducous glandular trichomes. Nerves wine-red and very prominent on the lower surface, 4-5 on each



side of the midrib.

Inflorescences found in the axils of the leaves or above the scars left by fallen leaves, up to 3 in one axil, most often unisexual, sometimes androgynous, the shed peduncles eventually leaving almost circular scars of 1-2.5 mm diameter in the leaf axils.

Male inflorescence a dichasial cyme, (2-)3-15-flowered; peduncle 1.5-45 (-55) mm long and 0.75-2.5 mm in diam., terete, in vivo red and covered with lepidote-stellate hairs and some glandular trichomes, bearing at the top two opposite membranous, early caducous, brownish bracts (subtending the primary dichasial branches), the bracts $3-5(-10) \times 2-3.5$ mm, ovate with an acute apex, outside with indumentum, inside glabrous; the peduncle branched in two lateral axes; axes (1st order) 1-8(-20) mm long, otherwise similar to the peduncle but with smaller apical bracts; the primary lateral axes usually branched again and the axes of the second order 1-3 mm long with small (1-3.5 \times 0.5-3 mm) bracts at the top. All axes terminated by a flower and in this way the inflorescence usually (3-)7-flowered. Sometimes the branches 2nd order dichasially branched again, resulting in a potentially 15-flowered inflorescence. The axis 3rd order short, ca 1 mm, with very small bracts. In two cases inflorescences were found with axes 4th and 5th order, which would result in a potentially 31-63-flowered inflorescence. However, in these cases some axes and/or flowers were reduced and not developing thereby not resulting in the many flowered dichasium as indicated above (teste Aylmer 49 and Scott Elliot 5721). The terminal flower of the dichasial cyme opening first, followed by the flowers terminating the lateral branches of the first order, etc. The flowers of the axes lower order usually early caducous, while those of higher order are developing. On plants in cultivation occasionally a male inflorescence was found to bear one or two female flowers thus becoming and rogynous. These female flowers are always found on laterals of a dichasium of which the top flower is male (see PHOT. 1).

Male flower supported by a 2-17(-25) mm long 'pedicel' the length of which varies with its place in the cyme. The 'pedicel' (the support of a single male flower) distinctly articulated 0.5-1 mm above the base; the part above the articulation (the perianth-cylinder) 1.5-17(-25) mm long, slender, in vivo pinkish-white, scattered with a few lepidote-stellate hairs and spherical trichomes; the short part below the articulation (the true pedicel) dark pink, otherwise ditto. Flower after anthesis falling in one piece from the articulation, the true pedicel

FIG. 1. Begonia cavallyensis A. Chev. - 1: branch with male inflorescences $(\times \frac{1}{2})$; 2: idem, with male and female inflorescences $(\times \frac{1}{2})$; 3, idem, the nodes showing characteristic scars of fallen leaves and stipules $(\times \frac{1}{2})$; 4: leaf base, underside, with indumentum and spherical trichomes $(\times 2)$; 5: trichomes bearing a lepidote-stellate hair $(\times 20)$; 6: hairs of a leaf $(\times 20)$; 7: trichome-hair $(\times 20)$; 8: σ fl. $(\times 2)$; 9: large stamen, frontal view $(\times 10)$; 10: idem, dorsal view $(\times 10)$; 11: small stamen, frontal view $(\times 10)$; 12: idem, dorsal view $(\times 10)$; 13: Ω fl. $(\times 2)$; 14: tepal, Ω fl., outer side $(\times 2)$; 15: styles and stigmata, lateral view $(\times 10)$; 16: stigma, abaxial side $(\times 10)$; 17: transverse sect. of ovary, ca in the middle $(\times 8)$; 18: young fruit $(\times 2)$; 19: dehised fruit $(\times 1)$; 20: placenta tissue bearing mature seed $(\times 5)$; 21: mature seed $(\times 15)$. - 1, 4-17: living material (J. J. de Wilde 3787); 2: J. J. de Wilde 7395; 3: Leeuwenberg 2957; 18: Leeuwenberg 3870; 19-21:J. J. de Wilde 8789, spirit material.



PHOT. 1. Begonia cavallyensis A. Chev. showing an occasional androgynous inflorescence with a male top flower and two female lateral flowers (J, J, F, E, de Wilde 7395; PHOT, J, W, MUGGE).

staying behind. Perianth-segments (tepals) (2)4; the two bigger outer tepals opposite, $3.5-10(-14) \times 3-8(-11)$ mm, convex, broadly ovate to broadly elliptic, obtuse at apex, outside with a few hairs and glandular trichomes, inside glabrous, pinkish-white with pink veins; the pair of inner tepals alternate with the outer ones, much smaller, $4-7.5 \times 0.7-2.5$ mm, boat-shaped, narrowly obovate, obtuse at apex, glabrous both sides, white, sometimes missing. Androecium fasciculate, asymmetric, stamens 11–19, filaments fused at the base to form a column of ca 0.5–1 mm long, otherwise free, the longest free filaments of the bundle up to 1.2 mm long, the shortest stamens with almost sessile anthers, filaments in vivo pale pink. Anthers yellow, $1-2(-2.2) \times 0.2-0.5(-0.8)$ mm, narrowly obovate, obtuse at the apex, opening more or less laterally, lengthwise, the slits directed towards the centre of the bundle.

Female inflorescence usually a 2-3 flowered dichasial cyme in which the lateral flowers are always subtended by a pair of bracts 2nd order indicating that these flowers are in fact laterals of an otherwise reduced dichasium 2nd order; peduncle short, 1.5-5.5 mm long, in vivo wine-red and with an indumentum of lepidote-stellate hairs and some spherical trichomes, at the top with two opposite bracts (bracts 1st order); the bracts similar to those in the male inflorescence or somewhat smaller; the lateral axes (1st order) 1.5-2.5 mm long, with smaller bracts at the top. Androgynous inflorescence described above under the male ones.



PHOT. 2. Begonia cavallyensis A. Chev.: infructescence with dehisced fruits. All parts scattered with multicellular trichomes (J. J. F. E. de Wilde 8789; PHOT. J. W. MUGGE).

Female flowers sessile. Perianth-segments (tepals) 4 or 2, in the latter case the pair of inner tepals missing; outer tepals convex, $(3-)5-8(-9.5) \times 3-8$ mm, broadly ovate to broadly elliptic; inner tepals (if present) $2-5.5 \times 1-2$ mm, narrowly obovate to obovate; the tepals otherwise similar to the corresponding male flowers. Styles 2(3), often about half as long as the inner tepals, in vivo bright yellow, fused over 1-1.5 mm, otherwise free and spreading. The free parts 0.5-1.5 mm long, glabrous, horseshoe-shaped forked thereupon, the arms of the horseshoe widely spreading, 0.3-1 mm long, on the abaxial (outer) surface densely papillose and this stigmatic glanduliferous tissue forming a continuous band from one arm to the other giving the horseshoe a rather crescent-shaped appearance, the style-arms otherwise glabrous.

Ovary fusiform, tapering towards both sides but especially towards the apex, terete, often somewhat curved. $(6-)10-22(-28) \times 2-3$ mm (the total length of the ovary measured as the part above the subtending bracts), in vivo brown-ish-green to brown-red, covered with a rather dense indumentum of brownish lepidote-stellate hairs and scattered with a few glandular trichomes, the indumentum often more or less disappeared in dried material. Perianth-segments and styles early caducous. The ovary 2(3)-locular, corresponding with the number of the styles. Placentation topographically axile, though morphologically the placentas arise from the ovary-walls, fuse in the centre of the ovary and finally are branched left and right with one branch in each of the 2 locules

(Fig. 1, 17). See also REITSMA, this issue.

Mature fruit in vivo pale red, fusiform, $20-50 \times 2-5$ mm, in sicco attenuated or almost beaked at the apex over 1-3 mm and at the very apex with a disciform scar at the place where the styles and perianth-segments were attached; finally opening by a single lateral slit. The pericarp after dehiscence flattening out and rolling backwards in one piece, fleshy, pale red inside and with two (opposite) longitudinal ridges at the places where the placentas broke away. The seed-bearing placenta tissue bright yellow, forming a fusiform mass and coming loose from the pericarp except for the very base which is devoid of seed-bearing placenta tissue (see PHOT. 2). Both pericarp and placenta tissue very transitory.

Mature seeds glossy light brown, ovoid, obovoid or cylindric with obtuse base and apex, $1.1-1.5 \times 0.6-0.8$ mm; the brittle testa with a conspicuous cellular pattern; the hilar part composed of three transverse rings of very small alveolate cells; the collar cells (sensu BOUMAN and DE LANGE, 1982) much bigger, elongated in longitudinal direction, tetragonal; the remaining testa cells small and in a longitudinal pattern, this pattern becoming more irregular – and the cells smaller – towards the apex. The hilar part of the seed surrounded by a cup-formed arillike structure and connected to the placenta via an up to 1,5 mm long and 0,5 mm broad, flattened funicle.

Notes. 1. In cultivated (clonal) individuals present in the living collection at Wageningen, adventitious roots at the nodes were never observed. However, among the examined herbarium specimens some collections show these roots (e.g. *Adam no. 20851, D. Johansson no. 733*, both in UPS) and others do not. In our opinion, the presence or absence of these roots might depend upon habitat-factors, i.e. a poor food supply and high dynamics in microclimate might lead to the development of aerial roots whereas better nutrition and a steady microclimate (as in the greenhouse) do not induce this development. As such, the occurrence of roots at the nodes has no diagnostic value in this species.

2. A. CHEVALIER (l.c., 1912) in his description of male flowers of *B. cavallyensis* stated: 'sepala 2 suborbicularia; petala 0'. The female flowers are described as having 2 sepals and here the petals are ignored. Individuals in cultivation at Wageningen showed flowers of both sexes having either 2 or 4 perianth-segments even in flowers belonging to a single inflorescence.

Distribution: Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana.

Ecological, biological and distributional notes. In Guinea *B. cavallyensis* was collected in the Fouta-Djallon highlands, in the upper course of the Konkouré River. Although no altitude is stated on the labels, these highlands reach in places over 1400 m. The available collectors' notes mention it to be uncommon and growing as an epiphyte on trees along the rivers (teste *Chevalier no. 25836, Pobéguin nos 1482* and *1651*, all in P). A second locality in Guinea where the species was found are the Nimba Mountains. Here, SCHNELL collected it several times on the south-western ridge at an altitude of ca 1500 m.



MAP 1. Spot distribution map giving localities where B. cavallyensis A. Chev. was collected.

In Sierra Leone it was collected in the northern and south-eastern provinces. No altitudes are given, but the collecting-localities all point to heights above 500 m. DEIGHTON (*no. 709*, K) stated: 'Epiphytic, 1-2 ft high, roots at the nodes and forms large clumps'. MORTON and GLEDHILL (*no. SL 1966-a*, K) found it in the Tingi Mountains as an epiphyte in the forest.

All collections made in Liberia, at least as far as the localities could be traced, originate from the Nimba Mountains. Collectors' notes mention altitudes ranging between 650 and 1300 m and often state that it was found growing as an epiphyte. The living plants of *B. cavallyensis* in cultivation at Wageningen are cloned from a specimen originally collected by H. C. D. DE WIT on Mt Nimba in Liberia in 1960-'61.

From Ivory Coast we examined the type (*Chevalier no. 21.422*, P) and two collections made by LEEUWENBERG (*nos 2957* and *3870*) from the same individual growing on Mt Tonkouï at 1180 m altitude. The latter collector stated that he found it growing as an epiphyte on a branch 2 m above groundlevel in an edge of montane rain-forest. The distribution in Ivory Coast seems confined to the Man-region at altitudes above 900 m.

Finally, from Ghana, only two specimens came to our attention. A specimen distributed by W. H. JOHNSON (no. 129, K) and dated 19-2-1899 only bears the annotation: 'Gold Coast, plant 3 ft high, found in the crutch of huge cotton-tree which had fallen down'. MORTON (no. A 716, GC) collected the species in 1954 at the foot of the Mpraeso Scarp as an epiphyte on the high branches of a tree. No altitude was given. On maps the elevation of this area is indicated to be above 500 m.

Summarizing, the collections of B. cavallyensis presently at hand show a re-

stricted, i.e. endemic distribution in the Upper Guinea subdivision of the Guineo-Congolian Region. Within this area the species is confined to elevations between ca 500 and 1500 m where it grows as an epiphyte in (sub)montane rainforest.

Much more detailed ecological information concerning *B. cavallyensis* is found in D. JOHANSSON (l.c., 1974), who extensively studied the epiphytic flora of the Nimba area, including parts of the Nimba Mts in Liberia. In his publication this information is found under the name *Begonia rubro-marginata* Gilg. Judging from the accompanying photographs and the material cited (*Johansson no. 733*, UPS) this material, without any doubt, belongs to *B. cavallyensis* A. Chev.

According to JOHANSSON the species is common in this area. It grows preferably on the basal and middle parts of the large branches of the phorophyte (i.e. the 'host tree' of the epiphyte), where it is found on humus deposits in open shade to full sun. Among the phorophytes occurring in the Nimba area he records 28 different high forest tree species on which it was observed. Outside the high forest it was found on *Cola nitida*. Several epiphyte communities, rich in epiphytic orchids and ferns with which *B. cavallyensis* is associated, are listed. In the dry season most, if not all, leaves are shed, which is illustrated by Fig. 65 in JOHANSSON's work, and corroborated by herbarium specimens e.g. *Leeuwenberg no. 3870* (WAG) and *Schnell no. 1198* (P). This certainly leads towards reduction of evaporation. JOHANSSON refers to it as a drought tolerant stem succulent in which the thick fleshy stems are suitable for water storage.

Vernacular name and uses: DEIGHTON (no. 709, K) states in his collectors' notes that in Sierra Leone, amongst the Mende tribe, the plant is called 'Gongui', and that the juice is put on wounds, presumably as an antiseptic. This information is cited in DALZIEL, l.c., 1955.

Specimens examined:

GUINEA: Fouta Djallon, between Dalaba and Kouloupa, *Chevalier 25836* (P); Konkouré River, *Pobéguin 1482* (P); ibid., *Pobéguin 1651* (P); Nimba Mountains, *Schnell 1036* (P); ibid., south-western ridge, *Schnell 1198* (P); ibid., *Schnell 1490* (P).

SIERRA LEONE: Falaba, Aylmer 49 (K); sin. loc., Deighton 709 (K); south eastern Prov., Kono Distr., Tingi Mts, above Koyema, Morton and Gledhill SL 1966-a (K); northern Prov., near Makunde, Limba, Scott Elliot 5721 (BM, K).

LIBERIA: sin. loc., Adam 7445 and 7502 (P); Nimba Mts, Adam 20124-bis (P); ibid., Adam 20851 (K, UPS); ibid., Adam 21496 (K, UPS); ibid., Yéképa, Adam 27744 (MO); Mt Barclay, Bunting 27 (BM); Nimba Mts, Sanniquelle Distr., Johansson 733 (UPS); sin. loc., Linder 59 (K).

IVORY COAST: Upper course of the Cavally R., Dyola country, Mt Do, near Gouékangouiné, *Chevalier 21422* (P, 2 sheets, holotype and isotype); Mt. Tonkoui, N.W. of Man, *Leeuwenberg 2957* (WAG); ibid., *Leeuwenberg 3870* (WAG).

GHANA: sin. loc., comm. W. H. Johnson 129 (B, K); Morton A-716 (GC).

CULTA: Agricultural University Wageningen, The Netherlands; from living material originally introduced by H. C. D. de Wit from Mt Nimba, Liberia, J. J. F. E. de Wilde 3397 (WAG); ibid., J. J. F. E. de Wilde 7395 (WAG); ibid., J. J. F. E. de Wilde 8789 (WAG); ibid., van Veldhuizen 502 (WAG).

3. A CHRONOLOGICAL REVIEW OF BEGONIA SPECIES AND NAMES (SECT. TETRAPHILA A. DC.) FORMERLY ASSOCIATED WITH B. CAVALLYENSIS A. CHEV.

Begonia eminii was published by O. WARBURG in ENGLER, Pflanzenwelt Ost-Afr., C (2-3): 282. July-Aug. 1895. It is based on three syntypes, viz. Stuhlmann nos 1453, 1454 and 3828 (all in B). STUHLMANN's specimens are all from Bukoba in Tanzania and remarkably uniform. Since then the species has become known from a large number of African countries. Widespread in the forests of tropical Africa its distribution ranges from Liberia to Kenya, radiating south into Angola and Tanzania, and from sea level up to ca 2200 m altitude.

In HUTCHINSON and DALZIEL'S 2nd edition of the Flora of W. Trop. Africa (l.c., 1954) *B. cavallyensis* was placed into the synonymy of *B. eminii* Warb. This was followed by a number of subsequent authors e.g. ADAM (l.c., 1971) and BARKLEY (l.c., 1972).

B. eminii Warb. is characterized by and differentiated from B. cavallyensis by a number of characters, among which relatively thin stems and long internodes; leaves acute to acuminate at the apex; the leaf-margin coarsely dentate to sinuate, not red; styles 3(2), forked in a sharp angle at the top, the stigmatic tissue slightly spiralled; fruits red and seeds less than 1 mm long. The distributions of both species overlap and there is also an overlap in their altitudinal ranges.

B. macrostyla Warb. was validly published in ENGL., Bot. Jahrb. 22(1): 37. Nov. 1895. The holotype, *Preuss no. 960* (B), was collected in Cameroon, in a forest at Buea at 970 m altitude. The name is cited in synonymy to *B. eminii* Warb. in HUTCHINSON and DALZIEL (l.c., 1954), which was followed by later authors e.g. by BARKLEY (l.c., 1972). *Preuss no. 960*, the type, shows all characters mentioned above for *B. eminii* Warb.; mature seeds, however, are not available. A final decision about the status of the name *B. macrostyla* Warb. awaits further research; but certainly *B. cavallyensis* A. Chev. does not belong to it.

B. poggei Warb. was published simultaneously with the above mentioned *B. macrostyla* Warb. (op cit.: 35. Nov. 1895). It is based on two syntypes, viz. *Pogge no 962* (B) from Zaire and Zenker and Staudt no. 538 (B) from near Yaoundé in Cameroon. WARBURG, the publishing author, already stated in the protologue that it is very closely related to *B. eminii*: 'von der sie nur durch geringe Unterschiede in der Behaarung, Blattform und Blattgrösze getrennt erscheint'. Subsequent authors unanimously place it in synonymy to *B. eminii* Warb. The present authors share this opinion.

B. preussii, published by WARBURG in a single publication together with B. macrostyla and B. poggei (op.cit.: 36. Nov. 1895), is based on Preuss nos 111 and 333 (both in B). Both these syntypes are from Barombi-station in Cameroon $(4^{\circ} 40^{\circ} N.-9^{\circ} 23^{\circ}E.)$. Preuss no. 111 is designated here as the lectotype.

Although the name is cited in synonymy to B. *eminii* Warb. in HUTCHINSON and DALZIEL (l.c., 1954), which was followed by later authors, we are of the

opinion that it represents a distinct taxon. Details on female flowers are unknown. The seeds measure 0.8×0.4 mm. The available evidence, type material and protologue, excludes it from being conspecific with *B. cavallyensis*.

B. warburgii was published by GILG in ENGL., Bot. Jahrb. 34(1): 94. 1904. It is based on *Preuss no. 111* (holotype, B), a specimen which, simultaneously, represents one of the syntypes on which WARBURG based *B. preussii* (see above). In our opinion, and in accordance with our lectotypification, the name *B. warburgii* Gilg constitutes a later homotypic synonym of *B. preussii* Warb.

B. rubro-marginata Gilg in ENGL., Bot. Jahrb. 34(1): 95. 1904 is based on *Conrau no. 80* (holotype, B), collected at Bangwa in Cameroon. Together with for instance *B. mannii* Hook. and *B. komoënsis* Irmsch. it belongs to a group of species which, within section *Tetraphila*, is characterized by simple, subuliform styles. This, in combination with other characters, e.g. short, 5-9 mm long petioles and small leaves devoid of a red margin, does not fit into the circumscription of *B. cavallyensis*.

Doubtless, GILG, in coining the specific epithet 'rubro-marginata' did so to denote the outer pair of perianth-segments which, in the collector's note, are indicated as: 'weisz mit rotem Rande'. The fact that JOHANSSON (l.c., 1974) and others misidentified specimens of *B. cavallyensis* (characterized by distinct red leaf margins) as *B. rubro-marginata* is certainly due to this last specific epithet. The distributions of *B. rubro-marginata* and *B. cavallyensis* do not overlap.

B. alepensis was published by AUG. CHEVALIER in Bull. Soc. Bot. France 58 (Mém. 8): 174. 1912. It is based on Chevalier no. 17482 (holotype and isotype in P), collected near Alépé in Ivory Coast, According to the protologue the fruits are trigonous, equal-sided in transverse section and ivory-white at maturity. The stigmatic parts of the 3 styles are forked, similar to the situation found in B. eminii Warb. Even when fruits are present these fruit characters are often difficult to ascertain on dried herbarium specimens. None the less, in the field they are clear-cut and diagnostic in discriminating between this species and the otherwise closely related B. eminii which is characterized by terete fruits (from personal observation by the second author, who collected B, alepensis several times in Cameroon, teste J. J. de Wilde nos 7499, 7573-A, 7725 and 7864, all in WAG). Trigonous fruits are also known from a few other species in section Tetraphila e.g. B. ebolowensis Engl., and probably B. epiphytica Hook. f. and B. fusialata Warb. The taxonomy of B. epiphytica (1871), B. fusialata (1895) and B. alepensis (1912) is, as yet, not clear; possibly only one taxon is involved. B. ebolowensis Engl. stands apart as a distinct species.

From this it is clear that *B. alepensis* A. Chev. was erroneously placed in synonymy to *B. eminii* Warb. by KEAY in HUTCHINSON and DALZIEL (l.c., 1954), and that, moreover, it is well distinguishable from the terete-fruited *B. cavallyensis* A. Chev. There might be an overlap in distributions.

B. ealensis was published by IRMSCHER in ENGL., Bot. Jahrb. 57(2): 241. 1921. It is based on two syntypes, viz. *Aug. Chevalier nos 28043 and 28046* (P), both collected in Zaire at the Botanic Gardens at Eala in August, 1912. On the collectors' labels it was explicitly marked 'spontané'. According to WILCZEK, in his treatment of the *Begoniaceae* in the Flore du Congo, du Rwanda et du Burundi: 27, 31. 1969, *Chevalier no. 28043* consists of a mixture of *B. eminii* Warb. and *B. alepensis* Chev. In the Paris Herbarium *Chevalier no. 28046* is indicated as the (lecto)type, which is followed here. Accordingly we tentatively agree to WILCZEK's opinion that the name *B. ealensis* Irmsch. is a later heterotypic synonym of *B. eminii* Warb. The difficulties in discriminating between *B. eminii* and *B. alepensis* from dried herbarium specimens are outlined above. Any specific resemblance to *B. cavallyensis* is missing.

Finally *B. fusicarpa* Irmsch., to our knowledge, was never brought into synonymy. Despite this, this taxon is, in our opinion, exactly the one which, among all the above-mentioned species and names, is most closely related to *B. cavallyensis*. After careful consideration, and handicapped by the fact that it was collected only once, it is maintained here as a distinct taxon. For full details see under the species.

4. Begonia fusicarpa Irmsch.

Fig. 2; Map 2

Begonia fusicarpa Irmsch. in Engl., Bot. Jahrb. 76(2): 212. 1954; Hutch. and Dalz., Fl. W. Trop. Afr. 2nd ed. 1(1): 220. 1954 (erroneously cited as *B. fissicar-pa*); Adam, Fl. descriptive des Monts Nimba in Mém. Mus. Nat. Hist. Naturelle nouv. sér. B (Bot.) 20: 322, 324, pl. 77. 1971 (only the name; description, cited material and plate belong to *B. cavallyensis* A. Chev.); Barkley, The Species of the Begoniaceae: 36. 1972 in The Buxtonian 1, suppl. 5; Barkley and Golding, The Species of the Begoniaceae, 2nd ed.: 43. 1974.

Type: *Baldwin no. 11417* (Liberia: Sinoe county, Kulo, on a fallen tree, holotype in K; isotypes: MO, WAG).

Short description (see also remark no. 1): Monoecious epiphyte, to our present knowledge confined to lowland in Liberia under 500 m altitude. Stems probably erect or somewhat bent, 3-6 mm in diam.; internodes 2-4.5 cm long. Leaves rather long persistent, finally falling off and leaving smaller and less conspicuous scars as compared to B. cavallyensis. Petioles 3-6 cm long. Blades narrowly obovate to narrowly elliptic, obtuse and almost symmetric at the base, broadly acute to obtuse at the apex, $13-21 \times 4-6.5$ cm; the margin entire or somewhat sinuate and in the upper half often with a few coarse blunt teeth. The characteristic red margin sometimes faintly visible even on dried specimens of B. cavally ensis and diagnostic for that taxon presumably missing in B. fusicarpa. Multicellular spherical trichomes probably absent. Inflorescences unisexual, axillary. Male inflorescences found in the axils of the terminal leaves, slender, few-flowered, cymose; the peduncle 20-25 mm long. Female inflorescence a 2-5-flowered dichasial cyme; the peduncle very short, up to 4 mm long. The female inflorescences found lower down the stem and sometimes two (or more?) in the axil of a single leaf. Bracts rather early caducous. Perianth-segments



FIG. 2. Begonia fusicarpa Irmsch. – 1: fruiting banch $(\times \frac{1}{2})$; 2: hairs of a leaf $(\times 20)$; 3: $\overset{\circ}{\circ}$ fl., partly reconstructed $(\times 3)$; 4 stamen, frontal view $(\times 20)$; 5: idem, dorsal view $(\times 20)$; 6: and droecium, schematic (magnified); 7: \bigcirc fl., partly reconstructed $(\times 2)$: 8: outer tepal, \bigcirc fl., outer side $(\times 4)$; 9: inner tepal, \bigcirc fl., outer side $(\times 4)$; 10: stigmata of a single flower, abaxial side $(\times 10)$; 11: transverse section of ovary, ca in the middle, partly reconstructed $(\times 8)$; 12: mature fruit $(\times 1)$; 13: surface of pericarp $(\times 10)$; 14: hairs of pericarp $(\times 20)$; 15: part of the placenta bearing a mature seed $(\times 5)$; 16: mature seed $(\times 5)$. – 1–16: Baldwin 11417.



MAP 2. The only hitherto known station where B. fusicarpa Irmsch. was collected.

(tepals) 4 in flowers of both sexes.

Male flower supported by a 2-3 mm long pedicel. The two bigger outer tepals 4×5 mm, broadly ovate; the pair of inner tepals smaller and shorter, 3×2 mm, oblong. Androecium fasciculate, asymmetric; stamens 12–18. Anthers opening lengthwise by means of two more or less lateral slits; the anthers of the outher whorl facing the centre of the bundle, the remaining anthers also directed towards the centre of the bundle (Fig. 2, 6).

Female flower almost sessile. The outer tepals 4.5-5 mm in diam., broadly ovate, the inner tepals smaller, $2.5-3 \times 1-1.3$ mm, oblong. Styles 2, slender, 2.5-3 mm long, about as long as the inner tepals, fused over 1-1.5 mm at the base, above it free and only slightly spreading; the stigmas forked (not crescent-shaped as in *B. cavallyensis*) and the stigmatic tissue not continuous from one arm of the fork to the other. Ovary fusiform, terete in transverse section, 2-celled, $14-18 \times 1-1.5$ mm. Placentation similar to *B. cavallyensis*. Perianth-segments and styles early caducous.

Mature fruit erect, supported by a 1-1.5 mm long pedicel, straight or curved, 3.5-6 cm long by 2-2.5 mm diam.

Mature seeds a bit more slender than those of *B. cavallyensis*, cylindric or obovoid, $1.2-1.5 \times 0.5-0.7$ mm, otherwise almost similar.

Remarks: 1. Our description given above is merely an abstract and translation of the elaborate latin diagnosis produced by IRMSCHER to which we refer. In it differential characters as compared to *B. cavallyensis* are stressed. Since the time that IRMSCHER (1954) published *B. fusicarpa* no additional material or information has become available. This implies that nothing is known about the variability of the species. Dr. F. BOUMAN informed us that he found a minor difference between *B. cavallyensis* and *B. fusicarpa* in a micromorphological character of the seed coat (verbal comm.).

2. Mr. R. G. VAN DEN BERG analysed the pollen of *Begonia* sect. *Tetraphila*, and reports on the two species here under discussion in the following section. His study points to similarities in pollen of *B. cavallyensis* and *B. fusicarpa* and endorses the separation of *B. cavallyensis/B. fusicarpa* from the *B. eminii*-group. 3. The strong similarities in micro- and macromorphology, the allopatric distribution and the altitudinal separation lead us to the conclusion that *B. cavallyensis* and *B. fusicarpa* are to be considered as altitudinal vicariads.

5. PALYNOLOGICAL OBSERVATIONS (BY R. G. VAN DEN BERG)

Within the section *Tetraphila* a number of pollen types is present. Two of these, which are easily distinguished from each other, are characteristic for a large number of species. The 'cavallyensis-type' is a large $(28-30 \mu)$, perprolate grain with a large endoporus bordered by rather heavy costae; a striking character is the presence of a margo: a ca 2μ wide band along the colpi where the striate ornamentation is replaced by an irregular sculpture. This type of pollen is characteristic for: *B. cavallyensis*, *B. fusicarpa*, *B. ebolowensis*, *B. polygonoides*, *B. oxyanthera*, *B. jussiaeicarpa*, *B. sanjeensis*, *B. capillipes* and *B. preussii* (syn.: *B. warburgii*).

The 'eminii-type' is a smaller grain $(20-24 \mu)$, prolate-perprolate, with a small endoaperture with narrow costae and never in possession of a margo. The following species names show this pollen-type: *B. eminii*, *B. alepensis*, *B. epiphytica*, *B. fusialata*, *B. macrostyla*, *B. mannii*, *B. ndongensis*, *B. ealensis*, *B. subalpestris*, *B. poggei* and *B. tatoniana*.

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PLACENTATION IN BEGONIAS FROM THE AFRICAN CONTINENT

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SUMMARY

The author examined the ovaries of 53 *Begonia* species, indigenous to the African continent, i.e. about 39% of the total number of species known from this region. Cross sections of each ovary were made, most of which are illustrated in Figs 4–10.

It appears that the occurrence of different types of placentation in one single ovary, reported by several previous authors, is common in the sections *Mezierea* (Gaud.) Warb., *Tetraphila* A.DC. and *Squamibegonia* Warb. This phenomenon has led to erroneous observations and conclusions in the past.

On the basis of placentation characters the African *Begonias* are divided into two major groups, Group A and Group B. Group A, comprising sections *Mezierea, Tetraphila* and *Squamibegonia*, contains all species with septa which consist partly of sterile placental tissue and in consequence with fundamentally parietal placentation. Somewhat deceptive is the pseudo-axile placentation, occurring in *Squamibegonia* and certain species of *Tetraphila*.

To Group B, comprising sections Sexalaria A.DC., Augustia (Klotzsch) A.DC., Rostrobegonia Warb., Scutobegonia Warb. and Loasibegonia A.DC., belong all species with completely carpellar septa and real axile placentation. Group A and Group B are subdivided into 6 and 2 subgroups respectively. Extrapolating, 35% of the African Begonia species show fundamentally parietal placentation, much more than was assumed before.

Supposing that in the *Begoniaceae* parietal placentation is the primitive condition (according to GAUTHIER, 1950) and given the considerable variation in placentation, this character is useful to provide a better understanding of the evolutionary relationships within the genus *Begonia*.

From this point of view the sections Mezierea, Tetraphila and Squamibegonia are primitive, whereas Sexalaria, Augustia, Rostrobegonia, Scutobegonia and Loasibegonia are relatively advanced.

Placentation characters might, after all, be of great importance for the taxonomy of the genus *Begonia*, provided that they are used cautiously.

I. INTRODUCTION

In the last comprehensive review of the *Begoniaceae* (IRMSCHER, 1925) the genus *Begonia* L. is subdivided in 60 sections, viz. 12 African, 16 Asiatic, 33 American and 1 American-Asiatic section. In Africa 8 sections are continental, 3 are Madagascan and only 1 section occurs on the continent as well as on Madagascar (i.e. *Mezierea* (Gaud.)Warb.). The total number of species within the pan-tropical genus *Begonia* is estimated at about 800; of this number approximately 140 species occur on the African continent according to recent views. This paper deals with the *Begoniaceae* indigenous to this region; Madagascan species have been excluded because of lack of material.

In the taxonomy of *Begonia* form and structure of the ovary, especially the type of placentation, have always played an important role. LINDLEY (1846) segregated the genus Diploclinium from the genus Eupetalum which he newly described in 1835 because of the divided placentae; GAUDICHAUD (1851) created a separate genus Mezierea for Begonias with parietal placentation; KLOTZSCH (1855) used the form of the placentae (divided or entire) as an important character to split Begonia into 41 new genera and IRMSCHER (1925, 1939) finally made use of the same character to subdivide his continental groups of sections. Apparently ovary-characters can supply useful data for a taxonomic division of the Begoniaceae. Some authors however, suggested that the value of the bilobed or simple condition of the placentae used as a taxonomic feature, possibly had been overestimated (DE CANDOLLE, 1859; BUGNON, 1926; SMITH & SCHUBERT, 1943: GAUTHIER, 1950; IRMSCHER, 1961; SMITH, 1973). All note that there are certain species which show both types of placentae, sometimes even in the same ovary. They present this phenomenon as being the exception rather than the rule within Begonia, however.

In the following paragraphs the various types of placentation and their variability in *Begonias* from the African continent are treated. Their use for taxonomy is discussed. This publication intends to be a support and an addition to the research project 'Taxonomic revision of the African *Begoniaceae*' of the Department of Plant Taxonomy, Agricultural University at Wageningen.

2. MATERIAL AND METHODS

In order to analyse the placentation found in African *Begonias* use has been made of the extensive collection of living wild *Begonias* present in the greenhouses of the Department of Horticulture of this University. In some cases only material preserved in alcohol was available.

The 53 *Begonia* species, investigated and discussed here, i.e. about 38% of the total number of species from the African continent, are listed alphabetically in Table 2. These species belong to 8 different sections. Only section *Filicibegonia* A.DC. sensu stricta is not represented. The estimated total number of species and the number of examined species per section are given in Table 1.

Ovaries were collected from flowers just reaching anthesis, hence it may be assumed that they were at a similar phase of development. The ovaries were transversely cut into 2 to 5 pieces which were marked according to their position in the ovary. The pieces were fixed in fixative according to KARPECHENKO, dehydrated to butanol, embedded in paraffin (melting point 54°C) and subsequently sectioned at 15 μ m. The slides with the sections were handled according to the method given in GERLACH (1977). Staining was done in Schiff's leuco-basic fuchsin solution for one hour followed by a counter staining in a 0,1% solution of Fast-Green in 96% ethanol during 5 seconds. The sections were analysed with a Carl Zeiss microscope with objectives 2,5 × , 4 × and 16 × , whereas drawings were made using the drawing device of that firm.

Section		Total number of species			Examined species
		a ¹	b²	¢3	
Augustia (Klotzsch)A.DC.		9	13	13	6
Filicibegonia A.DC.		1	1	2	-
Loasibegonia A.DC.		6	9	5	2
Mezierea (Gaud.)Warb.		5	9	10	5
Rostrobegonia Warb.		7	18	18	3
Scutobegonia Warb.		?	38	50	15
Sexalaria A.DC.		1	1	1	1
Squamibegonia Warb.		7	10	3	3
Tetraphila A.DC.		?	43	35	18
	Total	?	142	137	53

TABLE 1. The estimated number of species according to different authors and the number of species examined per section.

¹ according to IRMSCHER (1925)

² according to BARKLEY (1972a)

³ section Augustia, Rostrobegonia and Sexalaria according to BARKLEY (1972a); section Squamibegonia according to DE WILDE & ARENDS (1980); section Filicibegonia according to HALLÉ (1972); the remaining numbers are estimations by DE WILDE (pers. comm.) and give the most reliable numbers according to recent views.

3. OBSERVATIONS AND INTERPRETATIONS

3.1. Different types of placentation within a single ovary

It appears that in certain groups of *Begonia* species the placentation changes from the bottom to the top of the ovary. It even seems that in these groups this phenomenon is the rule. It concerns nearly all the species of the sections *Tetraphila* A.DC., *Mezierea* (Gaud.)Warb. and *Squamibegonia* Warb. This is surprising as all authors who have signalized this phenomenon consider it rare in *Begonia*. DE CANDOLLE (1859), BUGNON (1926), GAUTHIER (1950) and IRMSCHER (1961) observed entire as well as bifid placentae in the same ovary in certain species. GAUTHIER (1959) described for the first time the occurrence of both axile and parietal placentation, in *Hillebrandia sandwicensis* Oliv. (*Hillebrandia* is a monotypic genus of the *Begoniaceae*). For *Begonia* this has never been published in any detail. Nevertheless it happens to be a common feature in the sections mentioned above. Hence in the following an overall picture will be given to clarify this transition of placentation. This will make the description of the different species-groups (3.2.) and the corresponding drawings (Fig. 4–10) much more comprehensible.

In Fig. 1 the transition of placentation within an ovary is pictured for a repre-

Species	Section*	Herb.no. (all present in WAG)
1. B. alepensis A. Chev.	Tetraphila A.DC.	Breteler & De Wilde 747
2. B. ampla Hook.f.	Squamibegonia Warb.	J. van Veldhuizen 604
3. B. annobonensis A.DC.	Sexalaria A.DC.	J. van Veldhuizen 621
4. B. baccata Hook.f.	Mezierea (Gaud.)Warb.?	De Wilde, Arends & Groenendijk 105
5. B. bonus-henricus J.J. de Wilde	Squamibegonia Warb.	J.J. de Wilde 8404
6. B. cavallyensis Chev.	Tetraphila A.DC.	J. van Veldhuizen 502
7. B. cilio-bracteata Warb.	Scutobegonia Warb.	J. van Veldhuizen 880
8. B. clypeifolia Hook.f.	Scutobegonia Warb.	Breteler 7687
9. B. crateris Exell	Mezierea (Gaud.)Warb.?	Groenendijk 107
10. B. dielsiana Gilg	Scutobegonia Warb.	J. van Veldhuizen 876
11. B. dregei Otto & Dietr.	Augustia Klotzsch	J. van Veldhuizen 477
12. B. ebolowensis Gilg	Tetraphila A.DC.	J.J. de Wilde 7486
13. B. elatostemmoides Hook.f.	Scutobegonia Warb.	J. van Veldhuizen 875
14. B. eminii Warb.	Tetraphila A.DC.	Breteler & De Wilde 695
15. B. engleri Gilg	Rostrobegonia Warb.	J. van Veldhuizen 642
16. B. epiphytica Hook.f.	Tetraphila A.DC.	Arends & Groenendijk 399
17. B. ficicola Irmsch.	Scutobegonia Warb.	J. van Veldhuizen 446
18. B. homonyma Steud.	Augustia Klotzsch	J. van Veldhuizen 476
19. B . johnstonii Oliv.	Rostrobegonia Warb.	J. van Veldhuizen 444
20. B. kisuluana Büttn.	Tetraphila A.DC.	Breteler & De Wilde 702
21. B. komoensis Irmsch.	Tetraphila A.DC.	Breteler 7626
22. B. lacunosa Warb.	Scutobegonia Warb.	Breteler & De Wilde 274
23. B. loranthoides Hook.f. ssp. loranthoides	Tetraphila A.DC.	J. van Veldhuizen 625
24. B. loranthoides ssp. rhopalocarpa (Warb.)J.J. de Wilde	Tetraphila A.DC.	Breteler & De Wilde 205
25. B. macrocarpa Warb.	Scutobegonia Warb.	Bos 10357
26. B. mannii Hook.	Tetraphila A.DC.	Bos 5047
27. B. meyeri-johannis Engl.	Mezierea (Gaud.)Warb.	J.J. de Wilde 8790
28. B. molleri Warb.	Tetraphila A.DC.	J.J. de Wilde 8763
29. B. oxyanthera Warb.	Tetraphila A.DC.	Leeuwenberg 9956
30. B. oxyloba Welw. ex Hook.f.	Mezierea (Gaud.)Warb.	P. Schäfer 6972
31. B. partita Irmsch.	Augustia Klotzsch	J. van Veldhuizen 874

TABLE 2. Alphabetical list of examined *Begonias*, all indigenous to the African continent.

Species	Section*	Herb.no. (all present in WAG)
 B. peperomioides Hook.f. B. poculifera Hook.f. var. poculifera B. poculifera var. teusziana (J.Braun et K. Schum.) J.J. de Wilde B. polygonoïdes Hook.f. B. prismatocarpa Hook.f. B. prismatocarpa Hook.f. B. prismatocarpa Hook.f. B. schultzei land warb. B. schultzei land. and book.f. B. secortana Hook.f. B. secortana Hook.f. B. secortana Hook.f. B. secortana Hook.f. B. subalpestris A.Chev. (= B. macambrarensis Exell) B. subscutata De Wild. 	Scutobegonia Warb. Squamibegonia Warb. Squamibegonia Warb. Tetraphila A.DC. Tetraphila A.DC. Scutobegonia Warb. Augustia Klotzsch Loasibegonia Warb. Scutobegonia Warb. Scutobegonia Warb. Mezierea (Gaud.)Warb. Mezierea (Gaud.)Warb. Augustia Klotzsch Scutobegonia Warb. Tetraphila A.DC. Tetraphila A.DC. Tetraphila A.DC. Augustia Klotzsch Augustia Klotzsch Augustia Klotzsch Loasibegonia Marb. Scutobegonia Warb.	Breteler & De Wilde 369 J. van Veldhuizen 638 Leceuvenberg 10002 Leceuvenberg 8650 J. van Veldhuizen 609 P. Jansen 7878 J. van Veldhuizen 447 L. van Veldhuizen 447 J. van Veldhuizen 616 J. van Veldhuizen 626 J. van Veldhuizen 626 J. van Veldhuizen 626 J. van Veldhuizen 639 J. van Veldhuizen 639 J. van Veldhuizen 639 J. van Veldhuizen 877 Breteler & De Wilde 355 J. van Veldhuizen 878 J. van Veldhuizen 878 J. van Veldhuizen 878 J. van Veldhuizen 878 J. van Veldhuizen 877 Breteler & De Wilde 355 J. van Veldhuizen 877 J. van Veldhuizen 507 J. van V
55. B. wilczekiana N. Hallé	Tetraphila A.DC.	Breteler & De Wilde 335

* The assignment of the species to the different sections is based on information from DE WILDE & ARENDS (1979, 1980) as far as it concerns respectively B. loranthoides Hook.f. and the species of section Squamibegonia Warb., and from BARKLEY (1972b) as regards the remaining species (except B. seychellensis, which was placed in the Ignota-group by BARKLEY).

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FIG. 1. Transition of placentation from the bottom to the top of a single ovary of a fictive species of section *Tetraphila* A.DC.

a-f: different placentation types, corresponding with the level of the cross section in the ovary. For explanation see text.

The arrows in a and b indicate the pollentube-transmitting tissue.

sentative of the section *Tetraphila*. This example is characteristic for many species of this section. Because of the narrowly oblong, fusiform ovaries it is comparatively easy to observe the successive stages.

At the bottom of the ovary (1f) the placentation is axile, although the placentae have not developed completely. In the lowermost part the placentae are often simple, somewhat higher they become bifid. The degree of development in this stage sometimes differs per locule. Slightly higher in the ovary (1e) the placentation is still more or less axile. About midway (1d) the placentae are situated halfway the septa; we call this type of placentation 'septal'. At 1c the situation is different: the locules are not closed any more, the placentation has become parietal. The ovary is three-loculed again at 1b. In the centre, where the septa meet (see arrows in Fig. 1a and 1b), we find tissue consisting of thick-walled cells conducting the pollen-tubes. It appears that species whithout parietal stage (1c) do not possess the thick-walled cells in the top of the ovary, but instead a cavity, the so-called stylar canal. Both the 'pollen-tube transmitting' tissue and the stylar canal conduct the pollen-tubes into the locules. Towards the top (1a) the placentae disappear. The 'pollen-tube transmitting' tissue is clearly visible; it can be followed via the styles into the stigma-papillae.

It must be emphasized that Fig. 1 presents a general outline of the transition of placentation in a specific group of species. Within this group exists a certain variability in the various stages; the parietal stage e.g. may occupy a greater or a smaller part of the ovary or may even be absent. Even within one species some variability might exist although usually of little importance.

One should bear in mind that in other groups of species quite different situations exist. In these groups, however, transition of placentation in a single ovary is, as a rule, of secondary significance and is often completely lacking. In species or species-groups which show axile placentation and bifid placentae it is often found that the placentae are entire at the very base and/or top of the ovary (this phenomenon has been reported before by various authors, see above).

Summarizing it is clear that transition in placentation in a single ovary is a common feature in specific species-groups of African *Begonias*. Were this is the case a single cross section does not give a reliable picture of the over-all placentation.

3.2. Division into species-groups based on placentation characters

3.2.1. Main division and explanation of the criteria used

In the following paragraphs African *Begonia* species divided into main groups (this paragraph) and subgroups (3.2.2. & 3.2.3.) is dealt with. In this presentation only placentation-characters are used. In this way all examined *Begonias* can be divided into two main groups, Group A and Group B. The principal criterion is the nature of the septa viz. whether they consist completely of carpellar tissue, in which case they are called dissepiments (Group B) or they consist partly of placental tissue (Group A).



FIG. 2. Distribution of carpellar and placental tissue in various ovaries. The cross sections are schematic and not on scale:

- a) B. seychellensis Hemsl.
- c) B. baccata Hook.f.
- e) *B. poculifera* Hook.f.
- g) B. sutherlandii Hook.f. (wings omitted)
- b) B. alepensis A.Chev.
- d) B. cavallyensis Chev.
- f) B. princeae Gilg (wings omitted)
- h) B. potamophila Gilg (wings omitted)
- a-e belong to Group A and f-h to Group B; for explanation see text.

In the case of dissepiments the sides of each carpel are fused with those of the adjacent carpels up to the centre of the ovary. In the centre the margins of the same carpel are also fused, which always results in a multilocular ovary with axile placentation. As a consequence the septa and the placentae-bearing centre consist completely of carpellar tissue (see Fig. 2f-2h). In this group of species transition of placentation within one ovary (as described in 3.1.) does not occur. Only at the very bottom or at the very top of the ovary deviations in placentation have been recorded, but this is quite a usual situation in ovaries and should not lead to misinterpretations.

In Group A the sides of the adjacent carpels do not fuse that far, usually only up to or less than halfway the centre of the ovary. As a result the locules are open and the placentation is parietal (see Fig. 2a). The closing of the locules as shown in Fig. 2b-2c seems to be a result of inward outgrowths of the placentae (non-ovuliferous placental tissue). Some formation of sterile placental outgrowths can be seen in Fig. 2a. The type of placentation in which the placentae are arranged halfway the septa will be called 'septal', although the placentation is fundamentally parietal (PURI, 1952). In some species placentation is apparently axile, but the sides of the same carpel are not fused, and the centre of the ovary is filled with placental tissue (see Fig. 2d-2e). As placentation in this case is fundamentally parietal, but axile in topographical sense, we call this 'pseudoaxile' placentation (GAUTHIER, 1959). In such a situation the centre of the ovary will be sometimes open so that placentation becomes parietal instead of pseudoaxile. In species with real axile placentation this never happens.

In most cases it is impossible to discriminate between carpellar and placental tissue. Sometimes, however, a kind of constriction or a vague partition-line can be seen at the possible place of transition of the carpellar tissue into the placental one (see Photo 1,2, *B. cavallyensis* Chev. p. 40). At this very place the septa break at dehiscence of the mature fruit. In the greenhouses at Wageningen this has been observed in *B. cavallyensis* Chev., *B. eminii* Warb., *B. squamulosa* Hook.f., *B. subscutata* De Wild., *B. polygonoides* Hook.f., *B. molleri* Warb., *B. ebolowensis* Gilg, *B. loranthoides* Hook.f. ssp. rhopalocarpa (Warb.)J.J. de Wilde (DE WILDE & ARENDS, 1979), *B. komoensis* Irmsch., *B. subalpestris* A.Chev., and *B. wilczekiana* N. Hallé. Probably it applies to the whole section *Tetraphila*, as all species of this section seem to have dehiscent fruits (notwithstanding IRMSCHER's (1925) and WILCZEK's (1969) statements in their keys!).

In some other species it may be possible to localize the place of transition of carpellar into placental tissue by way of a clear layer of epithelium cells covering the inner surface of the carpellar part of the ovary which is absent or obscure in the placental part.

In this group of species with partly placental septa, transition of placentation within a single ovary is common.

The significant ovary characters of Group A and B are summarized below:

- Group A: all species have septa which consist partly of sterile placental tissue;
 - placentation is topographically parietal, septal or pseudo-axile, but fundamentally always parietal;
 - transition of placentation within a single ovary is a common feature;
 - the placentae are usually not fused at all.

Other ovary-characters are:

- the ovary is usually terete, sometimes triangular or square or lobed in circumference and always unwinged;



FIG. 3. Location of parietal placentation (black regions) in various ovaries. Ovaries not on scale. a-k: schematic ovaries of:

a) B. seychellensisd) B. polygonoides

j) -

g) B. squamulosa (diploid)

B. squamulosa (tetraploid)

b) **B**. oxyloba

k) B. schultzei

- e) B. oxyanthera h) B. molleri
- c) B. meyeri-johannis
- f) B. subalpestris
- i) B. kisuluana

Fig. 4. Ovary cross sections; see also explanatory note Fig. 4-10 p. 51

- A. B. oxyloba Welw. ex Hook.f.; P. Schäfer 6972 (1: \times 3,5; 3: \times 3).
- **B.** B. meyeri-johannis Engl.; De Wilde 8790 (1: \times 4; 3: \times 6).
- C. B. seychellensis Hemsl.; J. van Veldhuizen 539 (1: \times 2; 3: \times 3).
- **D**. *B*. polygonoides Hook.f.; Leeuwenberg 8650 (1: \times 4; 3: \times 6).

- the ovary is 1-4(-7)-locular;
- the fruits are more or less fleshy capsules and often dehisce by slits or valves.

The species incorporated in Group A belong to the sections Mezierea, Tetraphila and Squamibegonia.

Group B: - all species have septa which consist completely of carpellar tissue (dissepiments);

- placentation is always axile;
- transition of placentation within a single ovary hardly occurs;
- the placentae are fused partly (bifid placentae) or completely (entire placentae).

Other ovary-characters are:

- the ovary is nearly always triangular or square in circumference and usually winged;
- the ovary is 3-4-locular;
- the fruits are either dry dehiscent capsules or fleshy fruits which disintegrate at maturity.

The species incorporated in Group B belong to the sections Augustia, Scutobegonia, Loasibegonia, Rostrobegonia and Sexalaria.

3.2.2. Group A subdivided

To Group A belong 26 of the 53 examined species. Most of the species treated here are illustrated by an exact drawing of an ovary in cross section. In 1855 KLOTZSCH dealt in the same way with many of the 194 species he described; however, of the five African species known to him he included only one drawing (viz. *B. dregei* Otto & Dietr.).

Within Group A we recognize six subgroups:

Subgroup A1: the placentation is topographically parietal over more than 60% of the length of the ovary (see Fig. 3). The number of ovules per section varies between 80 and 120. The ovary is round in circumference and 1-, 3-5-locular. Mature fruits do not dehisce (greenhouse observations).

This subgroup contains 3 species, viz.:

B. oxyloba Welw. ex Hook.f. (Fig. 4a)

B. meyeri-johannis Engl. (Fig. 4b)

B. seychellensis Hemsl. (Fig. 4c).

All three species belong to section *Mezierea*, although BARKLEY (1972) puts *B. seychellensis* in category '*Ignota*' (section unknown to him). There are, however, many indications that this species belongs to section Mezierea; its resemblance to *B. oxyloba* is striking.

The occurrence of parietal placentation in this section was already known to GAUDICHAUD (1851) who established *Mezierea* as a genus because of this character.

KLOTZSCH (1855) doubted parietal placentation in B. salaziensis; according to him, GAUDICHAUD's observations could not be correct in view of the fact



FIG. 5. Ovary cross sections; see also explanatory note Fig. 4-10, p. 51.

- A. B. oxyanthera Warb.; Leeuwenberg 9956 (1: × 6,5; 3: × 8,5).
- B. B. kisuluana Büttn.; Breteler & De Wilde 702 (1: × 7; 3: × 8,5).
- C. B. molleri Warb.; De Wilde 8763 (1: × 4; 3: × 4).
- D. B. subalpestris A.Chev.; Arends & Groenendijk 144 (1: \times 4; 3: \times 6).
- E. B. squamulosa Hook. f. (diploid); Breteler & de Wilde 355 (1: ×4; 3: ×4).
- F. B. eminii Warb.; Breteler & de Wilde 695. Rather similar, however mostly 4-locular: B. mannii Hook.: Bos 5047.

that the placentation of all other species was different, viz. axile. DE CANDOLLE (1859) considered parietal placentation a common feature in *Mezierea*. WAR-BURG (1897) and IRMSCHER (1925) shared this view.

From Fig. 4A-C it is evident that the form of the placentae and the arrangement of the ovules are rather different in the species. The ovules of *B. seychellen*sis are very large and variable in shape. *B. meyeri-johannis* is remarkable as sterile placental tissue is completely lacking. In this species the placental tissue is ovulabearing all over.

Subgroup A2: the placentation is topographically parietal over less than 40% of the length of the ovary (see Fig. 3d-i) and often much less. In the remaining part the placentation is septal. The number of ovules per section varies from 12 to 55. The ovary is round in circumference and 1-4-locular. Mature fruits dehisce by valves or slits.

This subgroup contains 6 species, viz.:

B. polygonoides Hook.f. (Fig. 4d)

B. oxyanthera Warb. (Fig. 5a)

B. kisuluana Büttn. (Fig. 5b)

- B. molleri Warb. (Fig. 5c)
- B. subalpestris A. Chev. (= B. macambrarensis Exell; Fig. 5d)
- B. squamulosa Hook.f. (diploid,; Fig. 5e)

These species all belong to section *Tetraphila*. Parietal placentation in this section has not been reported before. WILCZEK (1969) refers to the placentae of 14 *Tetraphila* species (including *B. polygonoides*, *B. kisuluana* and *B. squamulosa*) as being 'centraux, entiers' (placentae in the centre of the ovary, i.e. axile placentation and the placentae entire)! The addition 'diploid' to *B. squamulosa* refers to the differences in placentation between diploid and tetraploid forms of this species (see also Subgroup A5).

Subgroup A3: the placentation is septal in the whole ovary and as a result the ovary is multilocular. Sometimes it is one-locular at the very top, but there the placentae are not well developed or lacking. The number of ovules per section varies between 10 and 50. The ovaries are round or triangular, sometimes square or lobed in circumference and (3-)4(-7)-locular. At maturity the fruits dehisce by valves or slits.

This subgroup contains 8 taxa, viz.:

B. eminii Warb. (Fig. 5f)

B. mannii Hook. (see Fig. 5f)

B. komoensis Irmsch. (Fig. 6a)

B. subscutata De Wild. (see Fig. 6a)

B. spec. (B. spec.nov.?; Fig. 6b)

B. loranthoides Hook.f. ssp. rhopalocarpa (Warb.)J.J. de Wilde

(Fig. 6c) and ssp. loranthoides (see Fig. 6c)

B. epiphytica Hook.f. (Fig. 6d)

B. alepensis A.Chev. (see Fig. 6d)



- FIG. 6. Ovary cross sections; see also explanatory note Fig. 4-10, p. 51.
- A. B. komoensis Irmsch.; Breteler 7626. Rather similar: B. subscutata De Wild.; J. J. de Wilde 7551.
- B. B. spec.nov. (?); Breteler & De Wilde 373.
- C. B. loranthoides Hook.f. ssp. rhopalocarpa (Warb.)J.J. de Wilde; Breteler & De Wilde 205 (2: × 3). Rather similar, however square in outline and fewer ovules per cross section: B. loranthoides Hook.f. ssp. loranthoides.
- D. B. epiphytica Hook.f.; Arends & Groenendijk 399. Very similar: B. alepensis A.Chev.; Breteler & De Wilde 747.
- E. B. baccata Hook.f.; De Wilde, Arends & Groenendijk 105. Very similar: B. crateris Exell; Groenendijk 107.
- F. B. wilczekiana N. Hallé; Breteler & De Wilde 335.

All these taxa belong to section *Tetraphila* (recently *B. loranthoides* Hook.f. and *B. rhopalocarpa* Warb. have been transferred from section *Squamibegonia* to *Tetraphila* and are now treated as two subspecies of *B. loranthoides* Hook.f. (DE WILDE & ARENDS, 1979)).

WILCZEK (1969) erroneously refers to the placentae of *B. alepensis*, *B. subscutata*, *B. mannii* and *B. eminii* as being 'centraux, entiers' (central, entire).

The cross sections of *B. epiphytica* and *B. alepensis* are very similar. These taxa have much in common. It might well be that only one species is involved.

Multilocular ovaries in this subgroup are the rule but exceptions are possible. Our observations show that in the multilocular situation with partly placental septa, the ovary is sometimes open in the centre so that placentation becomes parietal instead of septal (see also Subgroup A4 and A6). Apparently, the fusion of placental tissue in the ovary centre is less solid than that of carpellar tissue (as in Group B).

Subgroup A4: the placentation is septal in the whole ovary and the ovary is (4-)5(-6)-locular. There are (2-)4 placentae per septum and these are very capriciously shaped. The number of ovules per section amounts to 250-300. The ovary is roundish in circumference. The mature fruits dehisce by (4-)5(-6) valves.

This subgroup contains 2 species, viz.:

B. baccata Hook.f. (Fig. 6e)

B. crateris Exell (see Fig. 6e).

DE WILDE & ARENDS (1980) excluded *B. baccata* and *B. crateris* from section *Squamibegonia* and referred them hesitatingly to section *Mezierea*. In our opinion these two species do not fit in any of the nine sections recognized on the African continent. Considering the septal placentation and the dehiscent fruit there are strong affinities to section *Tetraphila*. However, the presence of 4 ovula-bearing placental outgrowths in each locule warrant a separate position.

Cross sections of the ovaries of *B*. baccata and *B*. crateris show a great similarity. Also in this subgroup the centre of the ovary is occasionally open (compare Subgroup A3). The distribution of carpellar and placental tissue of the concerning species, at represented by *B*. baccata is given in Fig. 2c.

Subgroup A5: the placentation is more or less pseudo-axile in the greater part of the ovary. Normally the centre is open in a small part (see Fig. 3j-k), where the placentation becomes topographically parietal. The ovary is 1-, 3- or 4-locular and round in circumference. The number of ovules varies between 20 and 40 per cross section. At maturity the fruits dehisce by valves or slits.

This subgroup contains 3 species, viz.:

B. wilczekiana N.Hallé (Fig. 6f)

B. squamulosa Hook.f. (tetraploid!; Fig. 7a)

B. schultzei Engl. ex R. Wilczek (Fig. 7b)

These three species belong to section *Tetraphila*. They are representatives of the so-called '*B. squamulosa*-complex', a cluster of rather divergent but closely related species-clines, which is very difficult to disentangle taxonomically. In



- FIG. 7. Ovary cross sections; see also explanatory note Fig. 4–10, p. 51.
- A. B. squamulosa Hook.f. (tetraploid); J. van Veldhuizen 878 (1: × 4,5; 3: × 6,5).
- B. B. schultzei Engl. ex R. Wilczek; Breteler & De Wilde 8 (1: × 6,5; 3: × 7,5).
- C. B. ebolowensis Gilg; J.J. de Wilde 7486.
- D. B. cavally ensis Chev.; J. van Veldhuizen 502 (1: \times 5; 3: \times 7).
- E. B. poculifera Hook.f. var. poculifera; J. van Veldhuizen 638 (1: × 3). Nearly identical: B. poculifera Hook.f. var. teusziana (J.Braun et K.Schum.)J.J. de Wilde; Leeuwenberg 1002. Very similar: B. bonus-henricus J.J. de Wilde; J.J. de Wilde 8404.
- F. B. ampla Hook.f.; J. van Veldhuizen 604 (1: \times 2; 3: \times 2).

Subgroup A2 we treated the diploid forms of *B. squamulosa*. It appears that the tetraploid forms of this species differ structurally from the diploid forms (c.f. Fig. 5e and 7a), and show much resemblance to *B. schultzei*, which also is a tetraploid. *B. wilczekiana*, however, is diploid but deviates from the diploid *B. squamulosa*-type. Both in the pseudo-axile and in the parietal situation in this subgroup very little septal tissue of placental origin is present between the placentae and the ovary centre, or none at all. The placentae stretch first in the direction of the ovary-centre and thereafter bend into the locules, so that the septa consist partly of placental tissue (as in *B. cavallyensis*, see Subgroup A6).

Of the three species accommodated in this subgroup only in *B. wilczekiana* the parietal situation is usually completely absent.

Subgroup A6: the placentation is pseudo-axile throughout the ovary. The parietal situation occurs rarely. The ovary is 2-, 3-4(-5)-locular and round or triangular in circumference. The number of ovules varies between 1-6 and between 80-120 per cross section. At maturity the fruits dehisce by one or two lateral slits in which case they are fusiform or they are round, berry-like and indehiscent.

This subgroup contains 5 taxa, viz.:

- B. ebolowensis Gilg (Fig. 7c)
- B. cavallyensis Chev. (Fig. 7d)
- B. poculifera Hook.f. var. poculifera (Fig. 7e) and var. teusziana
- (J. Braun et K. Schum.)J.J. de Wilde (see Fig. 7e)
- B. bonus-henricus J.J. de Wilde (see Fig. 7e)
- B. ampla Hook.f. (Fig. 7f)

B. cavallyensis and B. ebolowensis belong to section Tetraphila, whereas B. bonus-henricus, B. ampla and B. poculifera constitute section Squamibegonia (DE WILDE & ARENDS, 1980).

This subgroup clearly represent two entities: *B. ebolowensis* and *B. cavallyensis* show very few (viz. 1–6) and relatively very large ovules per cross section (also if compared with other species of section *Tetraphila*), while, on the other hand, the species of section *Squamibegonia* contain 80-120 ovules per cross section. Besides this the mature fruits of the former species dehisce by slits, those of section *Squamibegonia* are berry-like and disintegrate. Yet these two entities are treated here together because they share pseudo-axile placentation as a common character. In *B. cavallyensis* the placentae are fused over a considerable part of the ovary-length. After inward extension and fusion with the opposite ones in the centre of the ovary the placentae bend sideward in opposite directions, each into one of the two locules. In consequence the septa partly consist of sterile placental tissue (see Fig. 2d). At the transition from carpellar to sterile placental tissue a kind of interface and a shallow constriction can be seen (Phot. 2, p. 40).

Probably the same applies to *B. ebolowensis*, although a transition-zone in the septa has not been observed in this species. In B. *ebolowensis* the placentae are not fused. On account of the placentation characters just described *B. caval*-



PHOTO 1: Cross section of the ovary of *B. cavallyensis* Chev. (magnif. $50 \times$).



Рното 2: Detail of the transition-zone (magnif. $350 \times$), see inset Рното 1.

lyensis and B. ebolowensis stand apart in section Tetraphila.

In the three species of section Squamibegonia mentioned above the thin septa seem to be of carpellar origin up to the point of the branching of the placentae (see Fig. 2e). In these species the carpellar tissue inside the ovary is covered by a distinct layer of epithelium-cells, whereas this layer is lacking in the placental part. Partial or complete fusion of the placentae is the rule, especially in *B. poculifera* and *B. bonus-henricus. B. ampla* is the only species of this subgroup in which the centre of the ovary is sometimes open. The possibility of an open centre and in consequence a topographically parietal placentation is also present in all other species of this subgroup (cf. Subgroup A3 and A4).

Summarizing the six subgroups of Group A described above are distinguished as follows:

- × Placentation septal, often topographically parietal in a part of the ovary.
 - + Placentation parietal in a part of the ovary
 - + Placentation usually septal in the whole ovary
- × Placentation pseudo-axile, sometimes topographically parietal in a (minor) part of the ovary
 - + Placentation more or less pseudo-axile; usually parietal in a part of the ovary; 20–40 ovules per cross-section; fruits dehiscent Subgroup A5

3.2.3. Group B subdivided

Of the 53 species examined 27 belong to Group B. All the species in this group show completely carpellar septa (dissepiments) and are accordingly characterized by axile placentation. As in paragraph 3.2.2. most of the species dealt with are illustrated by a drawing of an ovary in cross section. On account of the bifid or fused condition of the placentae, Group B can be subdivided into 2 subgroups:

Subgroup B1: the placentae are not fused: distinctly two placentae per locule. The number of ovules per cross section varies between 60 and 430. The ovary is triangular or faintly sexangular in circumference and always winged.



FIG. 8. Ovary cross sections; see also explanatory note Fig. 4-10, p. 51.

- A. B. annobonensis A.DC.; J. van Veldhuizen 621 (1: \times 2,5; 3: \times 3,5).
- B. B. princeae Gilg; P. Jansen 7878. Wings ca 2,5 mm long.
- C. B. engleri Gilg; J. van Veldhuizen 642. Wings 4-8 mm long. Nearly identical: B. johnstonii Oliv.; J. van Veldhuizen 444.
- D. B. sutherlandli Hook.f.; J. van Veldhuizen 543. Wings ca 4 mm long. Very similar: B. partita Irmsch.; J. van Veldhuizen 874 and B. suffruticosa Meissn.; J. van Veldhuizen 507.
- E. B. dregei Otto & Dietr.; J. van Veldhuizen 477. Wings ca 4 mm long. Very similar: B. homonyma Steud.; J. van Veldhuizen 476.
- F. B. thomeana C.DC.; De Wilde, Arends & Groenendijk 141. Wing about 2-5 mm long.

This subgroup contains 4 species, viz.:

B. annobonensis A.DC. (Fig. 8a)

- B. princeae Gilg (Fig. 8b)
- B. engleri Gilg (Fig. 8c)
- B. johnstonii Oliv. (see Fig. 8c)

B. annobonensis belongs to the monotypical section Sexalaria A.DC., B. princeae to section Augustia Klotzsch and B. johnstonii and B. engleri to section Rostrobegonia Warb. The cross sections of the latter two species are very similar.

The bifid or fused condition of the placentae was always an important character in discriminating between the various sections. IRMSCHER (1925) characterized the section Augustia by entire placentae, whereas the species of Rostrobegonia would have bifid placentae. In 1961, however, IRMSCHER in his revision of the sections Augustia and Rostrobegonia came to a different conclusion. Analysing the placentation of many species accommodated in these sections he often found various conditions (viz. bifid, halfway bifid and entire placentae) in one and the same species (e.g. B. princeae). Because of these findings IRMSCHER questioned the validity of both sections but finally kept them apart pending a revision of all African Begoniaceae. Ever since the sections Augustia and Rostrobegonia contain species with bifid as well as entire placentae.

Within Subgroup B1 the four species we examined show little variability in placentation. Sometimes the placentae are fused over a small part at their base as for instance in *B. annobonensis*. In this species the placentae are even fused halfway at the top and at the base of the ovary, but this does not change the basic bifid character of its placentae.

Our observations in this subgroup support the idea that the bifid or fused condition of the placentae supplies a reliable and clear-cut character provided that the situation of the placentae at the top as well as at the very base of the ovary is left out of consideration.

Subgroup B2: the placentae are fused completely: one placenta per locule. The number of ovules per cross section varies between 45 and 400. The ovary is triangular or square in circumference and nearly always winged.

This subgroup contains 22 species accommodated in the sections Scutobegonia (14), Loasibegonia (2), Rostrobegonia (1) and Augustia (5) (Fig. 8d–10f).

It is quite remarkable that WARBURG (1895) as well as IRMSCHER (1925) in their keys attribute bifid placentae to the sections *Scutobegonia* and *Loasibegonia*. All the species of these two sections which we were able to examine clearly show fused placentae!

A further division of this relatively large subgroup based on structural placentation characters as used above, we consider impossible. However, the use of secondary characters such as form of the placentae, number and arrangement of the ovules etc. leads us to distinguish four species-groups (B2-a – B2-d) within this subgroup:

B2-a: placentae unbranched, oblong; the ovules generally regularly arranged in a single layer around the placentae; the number of ovules per cross section



FIG. 9. Ovary cross sections; see also explanatory note Fig. 4-10, p. 51.

- A. B. sciaphila Gilg ex Engl. var. longipedunculata Wilczek; Breteler & De Wilde 261. Wings ca 3 mm long.
- B. B. socotrana Hook.f.; J. van Veldhuizen 449.
- C. B. triflora Irmsch.; Breteler & De Wilde 326.
- D. B. potamophila Gilg; J. van Veldhuizen 609. Wings 1-3 mm long. Rather similar: B. ficicola Irmsch.; J. van Veldhuizen 446 and Begonia aff. B. scapigera Hook.f.; J. van Veldhuizen 877.
- E. B. quadrialata Warb.; Leeuwenberg 12021. Wings ca 1-5 mm long. Rather similar: B. staudtii Gilg var. dispersipilosa Irmsch.; J. van Veldhuizen 445.
- F. B. prismatocarpa Hook.; J. van Veldhuizen 447.

varying between 50 and 100. The ovary is triangular in circumference. This group contains 7 species, viz.:

B. sutherlandii Hook.f. (Fig. 8d)

- B. partita Irmsch. (see Fig. 8d)
- B. suffruticosa Meissn. (see Fig. 8d)
- B. dregei Otto & Dietr. (Fig. 8e)
- B. homonyma Steud. (see Fig. 8e)
- B. thomeana C.DC. (fig. 8f)

B. sciaphila Gilg ex Engl. var. longipedunculata Wilczek (Fig. 9a)

B. partita, B. suffruticosa, B. dregei and B. homonyma belong to section Augustia, B. sutherlandii to section Rostrobegonia (IRMSCHER, 1961), B. thomeana to section Loasibegonia and B. sciaphila var. longipedunculata to section Scutobegonia. The latter differs somewhat from the former species, e.g. in size and arrangement of the ovules.

B2-b: placentae unbranched but sometimes shallowly lobate, strongly thickened; the ovules usually arranged in a single regular layer around the placentae; the number of ovules varying between 50 and 70 per cross section. The ovary is triangular or square in circumference.

This group contains 2 species, viz.:

B. socotrana Hook.f. (Fig. 9b)

B. triflora Irmsch. (Fig. 9c)

B. socotrana traditionally belongs to section *Augustia* and *B. triflora* to section *Scutobegonia*. Among the species admitted to section *Augustia* which we were able to examine, *B. socotrana* is the only one showing thickened placentae. For this reason it occupies an isolated position in this section. WARBURG (1897) erected a subsection *Peltaugustia* for it, which BARKLEY (BARANOV & BARKLEY, 1972) raised to a section.

B2-c: placentae irregular in shape, deeply lobate, sometimes nearly branched, always thickened. The ovules arranged more or less at random, not in a single layer; the number of ovules varying between 45 and 400 per cross section, usually > 100 (over 100). The ovary is triangular or square in circumference.

This group contains 12 species, viz.:

- B. potamophila Gilg (Fig. 9d)
- B. ficicola Irmsch. (see Fig. 9d)
- B. spec. (B. aff. scapigera Hook.f.) (see Fig. 9d)
- B. quadrialata Warb. (Fig. 9e)

B. staudtii Gilg var. dispersipilosa Irmsch. (see Fig. 9e)

B. prismatocarpa Hook. (Fig. 9f)

B. sessilifolia Hook.f. (Fig. 10a)

B. macrocarpa Warb. (Fig. 10b)

B. elatostemmoïdes Hook.f. (Fig. 10c)

B. ciliobracteata Warb. (Fig. 10d)

B. lacunosa Warb. (see Fig. 10d)



FIG. 10. Ovary cross sections; see also explanatory note Fig. 4-10, p. 51.

- A. B. sessilifolia Hook.f.; J. van Veldhuizen 626. Wings ca 3,5 mm long.
- B. B. macrocarpa Warb.; Bos 10357. Wings ca 4 mm long.
- C. B. elatostemmoides Hook.f.; J. van Veldhuizen 875. Wings ca 4 mm long.
- D. B.ciliobracteata Warb.; J. van Veldhuizen 880. Wings ca 2 mm long. Very similar: B. lacunosa Warb.; Breteler & De Wilde 274. Rather similar: B. peperomioides Hook.f.; Breteler & De Wilde 369.
- E. B. clypeifolia Hook.f.; Breteler 7687. Wings ca 1,5 mm long.
- F. B. dielsiana Gilg; J. van Veldhuizen 876. Wings 2-4 mm long.

B. peperomioides Hook.f. (see fig. 10d)

Of these species *B. prismatocarpa* is traditionally placed in section *Loasibegonia*, all others in section *Scutobegonia*. Considering their similarity in placentation *B. potamophila*, *B. ficicola*, *B. spec*. (*B.* aff. *scapigera*), *B. quadrialata* and *B. staudtii* seem closely related. They all show square, 4-locular ovaries and 90–170 ovules per cross section (except for *B. ficicola* which shows about 45 ovules). *B. prismatocarpa* joins this species-cluster with about 50 ovules per cross section. Accordingly *B. elatostemmoides*, *B. sessilifolia* and *B. macrocarpa* form a special cluster characterized by triangular 3-locular ovaries showing 80–110 ovules in a cross section. These species also differ in other characters from the others; it is even doubtful if they belong in *Scutobegonia*. Finally *B. peperomioides*, *B. ciliobracteata* and *B. lacunosa* show a very similar placentation among each other. Here the ovary is triangular and 3-locular too, but the number of ovules in a cross section largely exceeds 110. Especially the latter two species show very much similarity in their placentation having 300–400 ovules in a cross section.

B2-d: placentae branched, more or less treelike. The ovules are arranged at random and number 100-250 per cross section. The ovary is triangular in circumference.

This group contains 2 species, viz.:

B. clypeifolia Hook.f. (Fig. 10e)

B. dielsiana Gilg (Fig. 10f)

Both species belong to section *Scutobegonia*. The cross sections of *B. clypeifolia* and *B. dielsiana* are rather unique because of the small ovules (cf. *B. sciaphila* var. *longipedunculata*, Fig. 9A) and the relatively great deal of empty space in their ovary-cavities.

Summarizing we can distinguish the subgroups of Group B as follows:

• Placentae bifid	pB1
O Placentae fused	ip B2
A more precise division of Subgroup B2 using secondary placentation-cha	arac-
ters leads to:	
+ Placentae unbranched, oblong	B2-a
+ Placentae unbranched, strongly thickened	B2-b
+ Placentae deeply lobate or nearly branched; always thickened	B2-c

3.3. Phylogenetic considerations

Most authors regard axile placentation as the original condition and parietal placentation as derived (PARKIN, 1955; CRONQUIST, 1968; STEBBINS, 1974). However, these authors often indicate certain families or genera in which the development is probably the reverse. PARKIN (1955) for instance points out that this may be true for ovaries with false septa (which happens to be the case in some sections of *Begonia*). PURI (1952) and TAKHTAJAN (1980) state that it is difficult

to decide whether axile or parietal placentation is primitive. REUTER (1926) assumes that parietal placentation is original. IRMSCHER (1939) considers the only Asiatic section of Begonia showing parietal placentation, viz. Coelocentrum Irmsch., as being more advanced than the other Asiatic sections, which all show axile placentation. GAUTHIER (1950), however, concludes after conscientious anatomical investigation of the ovaries of several Begonia species that in the Begoniaceae parietal placentation is the primitive condition. A detailed study of the ovary of Hillebrandia sandwicensis Oliv. by the same author (1959) confirms this idea. Hillebrandia shows parietal placentation and is, moreover, characterized by some very original characters such as a semi-inferior ovary (other Begoniaceae all have inferior ovaries) and a gynoecium open at the top. According to GAUTHIER the union between two adjacent carpels is more intimate and phylogenetically earlier than that between the two margins of the same carpel (GAUTH-IER, 1950, p. 62). This implies within the Begoniaceae a development from parietal placentation as representing the primitive condition towards axile placentation as more advanced. There are indications from other sources which seem to confirm this postulation.

VAN DEN BERG, working on pollen morphology, found that *Begonia* species with parietal placentation show comparatively primitive pollen-types (v.D. BERG, in prep.). In both placentation and pollen-type (v.D. BERG, this issue) *Hillebrandia* resembles *Begonia* section *Mezierea*, which leads us to regard this section as the most primitive among *Begoniaceae* on the African continent.

Accordingly, the sequence of our treatment of the various subgroups discerned (3.2.2.-3.2.3.) is not arbitrary. It is based on GAUTHIER's ideas: primitive subgroups (parietal placentation) are treated first and advanced ones (axile placentation) follow. All species with fundamentally parietal placentation are found in Group A. This group holds the relatively primitive sections, viz. *Mezierea*, *Tetraphila* and *Squamibegonia*. The species characterized by completely carpellar septa (dissepiments) and consequently by real axile placentation constitute the relatively advanced Group B. It appears that the sections *Sexalaria*, *Augustia*, *Rostrobegonia*, *Scutobegonia* and *Loasibegonia* belong here.

Within Group A we ascertain a development in placentation progressing from the parietal condition towards pseudo-axile placentation. Species showing parietal placentation over more than 60% of the length of the ovary are treated in Subgroup A1. This subgroup happens to accommodate all species traditionally placed in section *Mezierea*, which is considered here to represent the most primitive taxon. Going to the Subgroups A3 and A4 via Subgroup A2 we signal a development towards the closing of the ovary in the centre. This, however, not by way of the union of the carpel margins but by fusion of sterile placental outgrowths, resulting in septal placentation. In Subgroup A2 a small part of the ovary still shows parietal placentation, whereas in the Subgroups A3 and A4 the centre is usually closed throughout the ovary. It is evident that the process of fusing of placental tissue in the centre of the ovary proceeds gradually from the base towards the top so that it is always more complete in the lower part of the ovary (cf. Fig. 3). This development culminates in Subgroup A6, containing species with pseudo-axile placentation. In Subgroup A5 we predominantly met with tetraploid representatives of what we call the '*B. squamulosa*-complex'. In the greater part of their ovaries they show a more or less pseudo-axile placentation. In this context it does not seem accidental that the tetraploid forms of this complex, which may be considered as derived from the diploid forms, show pseudo-axile placentation, whereas their diploid counterparts generally show parietal/septal placentation.

In Subgroup A6 the pseudo-axile placentation is more explicit. Sometimes the placentae are even partly or completely fused in a part of the ovary, which is considered to be a derived stage (see also Group B). The species of the section *Squamibegonia* are here regarded as the most advanced in Group A. In this section the inward extension of the fused adjacent carpels is considerable, viz. up to the centre of the ovary. Here, in the very centre the placentae are inserted. In consequence the septa, as we see them, are entirely carpellar (in contrast to *B. cavallyensis* and most probably *B. ebolowensis*). The centre of the ovary, however, is formed by placental tissue (see Fig. 2d-2e and Fig. 11e).

Summarizing we may state that in Group A *Mezierea* is the most primitive section whereas section *Squamibegonia* holds the most advanced types of placentation. Between these two, section *Tetraphila* together with *B. baccata* and *B. crateris* forms a rather wide and variegated link.

As to Group B it is noticeable that here much less structural variation in placentation is found. The placentation is always (real) axile and the placentae are bifid or entire. In the phylogenetic process of fusion of the margins of the same carpel in the centre of the ovary which results in axile placentation, the placentae are first bilamellate and afterwards when the fusion is more complete, simple (GAUTHIER, 1950, p. 62). As a result the sections *Scutobegonia*, *Loasibegonia* and the species of the sections *Augustia* and *Rostrobegonia* which show entire placentae, may be regarded as being more advanced than section *Sexalaria* and the bilamellate species of sections *Augustia* and *Rostrobegonia*.

The different stages illustrating the evolutionary tendencies in the placentation of the *Begoniaceae* on the African continent are outlined in Fig. 11. The sections in which the various stages occur are mentioned. Figures 11 a-g are presented in a linear series only for convenience sake; in reality it is likely that they represent several evolutionary lines along which the developments have taken place.

Going from Fig. 11a to 11g we observe an increasing inward extension of the fused adjacent carpel sides, together with a decline of the placental part of the septa. This process reaches an optimum in section *Tetraphila* and in *B. baccata* and *B. crateris*. As a consequence of this development the placentae are shifting towards the centre of the ovary. This results in a series going from parietal placentation, representing the primitive, basal 'starting point' (Fig. 11a), via septal (Fig. 11b-c) and pseudo-axile placentation (Fig. 11d-e) as intermediate situations to real axile placentation (Fig. 11f-g). This is considered here as the most advanced situation and represents at the moment the final stage in the



FIG. 11. Evolutionary tendencies in placentation in African Begonias. The cross sections are schematic and not on scale.

a-g occur in the following sections/species respectively:

a: Mezierea, Tetraphila partly; b1: Tetraphila, b2: B. baccata and B. crateris; c: Tetraphila; d1 and d2: some species of Tetraphila (B. cavallyensis and B. ebolowensis); e1 and e2: Squamibegonia; f: Sexalaria, Augustia partly, Rostrobegonia partly; g: Augustia partly, Rostrobegonia partly, Scutobegonia, Loasibegonia.

development of the placentae. In Fig. 11 all cross sections of the ovaries are pictured schematically and terete in outline. In reality, however, the situation is different. We found that in the relatively primitive sections *Mezierea*, *Tetraphila* and *Squamibegonia* the ovaries are usually terete in transverse section and apterous. Furthermore these sections show fleshy or even berrylike fruits. The more advanced sections *Sexalaria*, *Augustia*, *Rostrobegonia*, *Scutobegonia* and *Loasibegonia* are characterized by triangular or square ovaries which are usually winged. In addition the fruits of these latter sections tend to be dry capsules although the fruits of the majority of the species belonging to section *Scutobegonia* are fleshy.

4. CONCLUSIONS

1. In the past incorrect observations and unfounded hypotheses sometimes caused by the phenomenon of transition of placentation in a single ovary led to the idea that parietal placentation is rare in *Begonia* and as far as the African representatives are concerned occurs in section *Mezierea* only. Confining ourselves to the African continent it appears that parietal placentation is the rule in the sections *Mezierea*, *Tetraphila* and *Squamibegonia*. This implies that of the circa 137 species known from the African continent, about 48 species show fundamental parietal placentation, i.e. 35%. Topographically the placentation in these species may be parietal, septal or even pseudo-axile. The remaining 65% shows real axile placentation; of these group 11% has bifid placentae (*Sexalaria, Augustia* partly and *Rostrobegonia* partly) and 89% entire placentae (*Augustia* partly, *Rostrobegonia* partly, *Scutobegonia*, *Loasibegonia*).

2. On the ground of placentation-characters the African Begonias can be divided into two major groups, Group A (Mezierea, Tetraphila, Squamibegonia), characterized by septa which consist parly of sterile placental tissue and therefore fundamentally parietal placentation, and Group B (Sexalaria, Augustia, Rostrobegonia, Scutobegonia and Loasibegonia), showing septa which consist completely of carpellar tissue (dissepiments), and axile placentation. None of the current sections is represented in both Group A and Group B. Subdivision into subgroups shows much variation in placentation in Group A (especially in Tetraphila) and little in Group B.

3. The occurrence of different types of placentation in a single ovary is common in the sections with parietal placentation, viz. *Mezierea, Tetraphila* and *Squamibegonia*. In species with axile placentation and bifd placentae, sometimes entire or partly entire placentae occur at the very top or bottom of the ovary; this, however, should not lead to misapprehensions. Transition of placentation as occurring in *Mezierea, Tetraphila* and *Squamibegonia*, may be deceptive and lead to wrong interpretations. Therefore it is always necessary to make cross sections at different levels in an ovary in order to get a general impression of the placentation of the species concerned. In that way the placentation character remains of much value for the taxonomy of *Begonia*. At the species level, however, differences in placentation are often too few and too small to be used as distinguishing characters.

4. It appears that the type of placentation provides an indication for the phylogenetic level of the species, species-group or section. Using this character a better understanding of the evolutionary relationships in the genus is obtained: Group A is relatively primitive and Group B advanced. Within Group A *Mezierea* has to be regarded as the most primitive section, whereas *Squamibegonia* is the least primitive one; *Tetraphila* includes as far as placentation is concerned both very primitive, intermediate and less primitive species. As to Group B it may only be stated that species with entire placentae are more advanced as compared to those with bifid placentae, although in some closely related species-groups both placenta-types occur (e.g. in the current sections *Augustia* and *Rostrobegonia* sensu IRMSCHER, 1961).

The circles in placentae and ovary-wall represent vascular bundles.

N.B. Explanatory note to Fig. 4-10: among the ovaries of species showing different types of placentation within a single ovary, it is always the most parietal situation which is pictured (large drawings). If relevant, different situations occurring towards the top or bottom of the same ovary, are pictured in small drawings. When placentation is the same throughout the ovary, only one cross section is given.

The drawings are not on scale. The magnifications of the small ones are given in the text accompanying the figures.

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POLLEN CHARACTERISTICS OF THE GENERA OF THE BEGONIACEAE

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SUMMARY

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

1. INTRODUCTION

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

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

2. MATERIAL AND METHODS

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

Specimens examined:

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

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

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

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

3. DESCRIPTION OF THE POLLEN TYPES

2	1	Symbogonia	tuno
2.	1.	Symbegoma	Lypc.

Plate 1

Pollen class:	3-zono-colporate, occasionally 4-colporate.
P/E ratio:	Spheroidal.
Apertures:	Ectoaperture – colpus, narrow with straight margins, long but never anastomosing at the poles, endings acute, colpus
	membrane granular, no costae.
	Endoaperture – porus, small, lalongate, elliptical, outline distinct, no costae.
Exine:	Thin, stratification hardly visible with LM, TEM observa-
	tions (Plate 4) show a more or less homogeneous inner
	layer (nexine) on which the variably shaped tooth-like ex-
	crescenses (sexine) are placed; sexine as thick as or thicker
	than nexine, columellae not present, wall thickness uni-
	form.
Ornamentation:	The sculptural elements, which are variously shaped but
	often sharply pointed, are arranged in an irregular pattern.
Outline:	Equatorial view – circular to elliptical.
	Polar view – circular/rounded triangular.
Measurements:	P 12-15 μ m, E 12-14 μ m, P/E 1.0-1.1, exine 0,6-1 μ m, porus 1,5 \times 3 μ m.
Species:	This description is valid for the examined species Symbe- gonia papuana Merr. & Perry, S. sanguinea Warb, and S.
	c.f. strigosa Warb. and a number of samples designated
	as S. spec. Some other samples, determined as S. spec.,
	showed both in their pollen and flower morphology the characteristics of <i>Begonia</i> . Pending further investigation
	it cannot be ruled out beforehand that other pollen types
	can be established within the present circumscription of the genus.
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PLATE 1 SEM: 1. Symbegonia c.f. strigosa Warb. (Van Veldhuizen 689) polar view; 2–4. Symbegonia spec. (Van den Berg, Katik & Cairo NGF 39909) equatorial view; all magnifications ca 2650 ×.

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

Pollen class:	3-zono-colporate.
P/E ratio:	Prolate.
Apertures:	Ectoaperture – colpus, rather narrow, constricted at equa- tor, long but never anastomosing at the poles, endings acute, colpus membrane granular, no costae. Endoaperture – porus, very small, usually somewhat lalon- gate, irregularly shaped or elliptical, outline indistinct, no costae; in cross section protruding endoapertures (raised sexine).
Exine:	Thin, stratification not visible with LM, wall thickness uni- form or slightly thicker at the poles.
Ornamentation:	Finely striate, the lirae running very close together, orien- tation parallel to the colpi or rather variable, often irregu- lar ornamentation at the poles.
Outline:	Equatorial view – elliptical. Polar view – rounded triangular, with invaginated colpi
Measurements:	P 20–22 μ m, E 12–14 μ m, P/E 1.6–1.7, exine 0,5–0.7 μ m, porus $\pm 1 \times 2 \mu$ m.
Species:	Hillebrandia sandwicensis Oliver.
Comments:	This type resembles certain types of <i>Begonia</i> pollen, especially in apertures, overall shape and ornamentation.



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



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

3.3. Begonia type

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

4. **DISCUSSION**

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

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

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

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



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

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

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