*Acta Bot. Neerl.* 44(2), June 1995, p. 139–150

# Diversity and taxonomic value of stigmatic surfaces in Begoniaceae: SEM analysis

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## SUMMARY

The literature does suggest that morphology and arrangement of stigmatic papillae in Begoniaceae might supply diagnostic characters for the discrimination of taxa. To verify this statement the stigmatic surfaces of 65 well-documented species were studied by light and scanning electron microscopy. At least 16 different morphotypes, which could be classified into five groups, were recognized among the, always unicellular, papillae. Some morphotypes were found to be diagnostic at the species level, and in a few cases the taxonomic identity of sections is underlined by the presence of a singular papilla group. It is concluded that in spite of a remarkable variation in detail the overall morphology is very homogeneous and consistent and in general not suitable for sectional delimitation.

*Key-words: Begonia* L., morphology, papillae, stigma, taxonomy.

## INTRODUCTION

Over the years, various aspects of morphology and anatomy of the pantropic genus *Begonia* L. have attracted the attention of a number of researchers across the continents (Hall 1949; Barkley & Hozid 1971; Barkley 1972; Lee 1974; De Wilde & Arends 1980; Bouman & De Lange 1983; Reitsma 1984, 1985; De Lange & Bouman 1985, 1986, 1992; De Wilde 1985, Hoover 1988; Charpentier *et al.* 1989a,b; Arends 1992; Sosef 1994). Notwithstanding this, stigma micromorphology was almost neglected in contemporary *Begonia* literature, apart from the introductory studies of Dumas (1975), Lecocq & Dumas (1975), and Lecocq (1977), who concentrated only on the *Begonia* Tuberhybrida group.

Baranov (1977), using a dissection stereo-microscope, presented his observations on the fresh stigmatic appendages of Begoniaceae. His study was based on 25 mostly New World species of *Begonia* L., covering 17 sections, and on *Hillebrandia sandwicensis* Oliv. Using structural characters of the stigmatic papillae he arranged these into five groups. Perhaps Baranov himself was not very confident about his observations as he commented: 'Understandably the results of this study must be verified' and moreover suggested: 'The real turning point in morphological study of the stigmatic surfaces in the Begoniaceae will be their study and photographing with the help of a scanning microscope'. The present authors proved in several cases that Baranov's observations and interpretations were not always adequate. These cases are detailed (under Results and Discussion) with light microscopy (LM) and scanning electron microscope (SEM) photographs.

The receptive surfaces of mature angiosperm stigmas show considerable diversity in structure and in the amounts of secretion (Heslop-Harrison *et al.* 1975). A general review of these stigma surfaces covering over 1000 species in about 900 genera of some 250 families showed that many features are clearly defined, and it was suggested that some characters could be of taxonomic and phylogenetic significance (Heslop-Harrison & Shivanna 1977). However, these authors did not study the family Begoniaceae closely as only two species of the widely distributed genus *Begonia* L. were examined. The remaining two genera—the monotypic *Hillebrandia* Oliv. and *Symbegonia* Warb. comprising about 12 species—were not mentioned, and only LM data were provided for Begoniaceae.

This paper gives an account of the diversity found in papillar morphology of the stigmatic surfaces of Begoniaceae and its taxonomic implications.

## MATERIALS AND METHODS

Preliminary observations were made with a Zeiss binocular dissecting microscope and a Zeiss—Axiophot LM. Fresh stigmas of fully opened and mature flowers were used (Heslop-Harrison & Shivanna 1977).

For SEM studies, similar stigmas were fixed, dehydrated and dried according to the critical-point technique following Pettitt (1976), sputter-coated with gold-palladium and observed in a JEOL JSM—5200 Scanning Microscope. Spirit material was used in LM and SEM studies for a few species, when fresh material was not available.

The terms stigma and papillae in the present context are defined following Jackson (1971) and Holmes (1979).

The nomenclature of the taxa *grosso modo* follows Smith *et al.* 1986. Voucher specimens collected from the glasshouses are preserved in the Department of Plant Taxonomy—Herbarium Vadense (WAG). Sources and references to vouchered specimens are incorporated in Table 1.

## RESULTS AND DISCUSSION

The present study encompasses 65 species, covering 63 species of *Begonia* assigned to 28 sections, and two species of the genus *Symbegonia*. No *Hillebrandia* specimen could be obtained for study. All taxa were examined in LM and the stigmas of 57 species in SEM. The family comprises *c.* 1000 species. It cannot yet be said that the full range of variation has been explored.

All the species studied (Table 1) were found to have papillate stigmas. The papillae are always unicellular (Fig. 2a), but often show distinctive features implying a potential taxonomic value. Papillar diversity in morphology, arrangement, distribution, cohesion, etc., was noted.

In general, papillar morphology is very diverse: I, capitate; II, conical; III, linear; IV, clavate; V, lageniform; etc. (see also Dulberger 1974). In *Begonia*, there is a clear distinction in the shape of the head of the papillae which may be globose (Fig. 2c), sub-globose, with protuberances as in *B. dewildei*, showing a distinct 'neck' or not, etc. (Table 1, Fig. 1). The stalk may be tapering or cylindric, the base bulbiform or widened apart. The margin in almost all cases is entire. An exception is found in *B. susaniae* where the stalk is distinctly twisted, which probably indicates an apomorphic character state of the species concerned (Fig. 2b). At least 16 different morphotypes

of papillae were recorded, which could be broadly categorized into five groups (Fig. 1, Table 1). These groups are not similar to those distinguished by Baranov. A considerable degree of variation is found in the structure of these stigmatic papillae, not only among the separate groups, but also within each group discerned. We found that some of our categorized groups of papillae are linked to taxonomically recognized sections; e.g. sections *Begonia, Diploclinium, Petermannia, Scutobegonia*, etc. predominantly possess papillae of Group I, and section *Augustia* papillae of Group III. However, in a few cases, different groups of papillae were seen also within a section, e.g. *Gireoudia, Loasibegonia* and *Tetraphila*, which contain species with either capitate or linear papillae. The capitate group (I) is most common among the taxa: of the 65 species studied, 50 species belong to this group, among these are the two species of *Symbegonia*. The taxonomic identity of section *Mezierea*, which is considered to represent a primitive section (De Wilde & Arends 1989) and its affiliation to the section *Baccabegonia* are demonstrated by the presence of conical papillae.

Heslop-Harrison & Shivanna (1977) characterized the stigma type of Begoniaceae as 'dry'. Their conclusion, however, was based on observations of merely two species of *Begonia*. Nonetheless, their conclusion was found correct for the majority of the species examined in the present work. Exceptions are species of the sections *Haagea* and *Petermannia*, and *B. elatostemmoides, B. echinosepala, B. quadrialata, B. ampla, B. elaeagnifolia, B. eminii*, and *B. komoensis*, which exhibit 'hydrophobic exudate', as noted in *B. tuberhybrida* by Lecocq & Dumas (1975). These species can not be considered as 'dry', and fit better in the 'wet' category. In *B. elaeagnifolia*, the secretory fluid was also noted by Arends (1992). Determination of the stigma as 'dry' or 'wet' could not be ascertained for 11 species studied from spirit material. However, in the remaining 54 species living material was available and assessment of this character state was possible. Several other families are similar reported to contain species with either dry or wet stigmas (Heslop-Harrison & Shivanna 1977).

The papillae, in general, remain confined to the stigmatic region. However, an additional situation is found in *B. foliosa, B. acetosa, B. echinosepala, B. ampla, B. arborescens* var. *confertiflora* and *B. fuchsioides*, where the whole style is also papillate (Fig. 3c). In *B. palmata* the stylar papillae are concentrated to form localized spots, presenting a distinct character in the taxon (Fig. 3b). In all these cases, the stigmatic papillae are larger as compared to the stylar ones, while other characters remain similar. The configurations found are characteristic for the taxa concerned.

Baranov (1977) distinguished five groups of stigmatic surfaces among the 25 species of Begoniaceae he examined, seven of which were also included in the present study. He did not examine any species of *Symbegonia*. Unfortunately, the specimens he used were not vouchered except for the monotypic *Hillebrandia*. Our SEM-data considerably contradict Baranov's (1977) stereo-microscope observations with fresh material. These are presented in Table 2 (see also Table 1 and Fig. 1). In no case did we find the papillae packed into 'piles', or in groups, or even in sub-groups. As a rule they are free and scattered irregularly (Fig. 1).

An interesting situation was found in *B. microsperma* of section *Loasibegonia*, considered to be an advanced section of African begonias (Sosef 1994), where the papillae exhibit a synpapillate condition, a connection between their lateral walls (Fig. 1, type IIId, Fig. 3a). This synpapillate condition may present a derived character state

**Table 1.** Taxa studied and morphology of stigmatic papillae in Begoniaceae. 1, Material examined: L, living; S, conserved in spirit. 2, Studied by light microscope (+) and also by scanning electron microscope (++). 3, Stigma: D, dry; W, wet; ?, could not be ascertained from spirit material. 4, Types of papillae; as categorized in Fig. 1. 5, Accession number of living collections: BR, National Botanic Garden of Belgium, Brussels; CPRO, Centre for Plant Breeding and Reproduction Research, DLO, Wageningen; D, Technical University, Delft; K, Royal Botanic Gardens, Kew; PT, Plant Taxonomy Department, WAG. 6. Collector and herbarium number (dry or wet, all present in WAG)

| Genus<br>Section<br>Species | Origin | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|---|
| **Begonia** L. | | | | | | | |
| *Augustia* (Klotzsch) A. DC. | | | | | | | |
| *B. brevibracteata* Kup. | Malawi | L | ++ | D | IIIc | 91 PTMW 019 | J.J.F.E. de Wilde 10700 |
| *B. dregei* Otto & Dietr. | South Africa | L | ++ | D | IIIa | CPRO 89054 | J.v. Veldhuizen 477 |
| *Baccabegonia* Reitsma | | | | | | | |
| *B. baccata* J.D. Hook. | Endemic to São Tomé | S | ++ | ? | IIb | — | Groenendijk 71 |
| *Begonia* | | | | | | | |
| *B. cucullata* Willd. | Brazil | L | ++ | D | Ie | BR 84-2843 | J.v. Veldhuizen 481 |
| *B. fischeri* Schrank | North & South America | L | ++ | D | Id | CPRO 89018 | J.v. Veldhuizen 1471 |
| *B. schmidtiana* Regel | Brazil | L | ++ | D | Id | D 7 | J.v. Veldhuizen 439 |
| *Coelocentrum* Irmsch. | | | | | | | |
| *B. masoniana* Irmsch. | China, Singapore | L | ++ | D | If | BR 55-0133 | J.v. Veldhuizen 1135 |
| *Cristasemen* J.J. de Wilde | | | | | | | |
| *B. thomeana* C. DC. | Gabon, São Tomé | S | ++ | ? | Ib | — | J.v. Veldhuizen 882 |
| *Diploclinium* (Wight) A.DC. | | | | | | | |
| *B. acaulis* Merrill & Perry | New Guinea | S | ++ | ? | Ie | — | J.v. Veldhuizen 484 |
| *B. fenicis* Merrill | Philippines | S | ++ | ? | Ie | — | J.v. Veldhuizen 415 |
| *B. luzonensis* Warb. | Philippines | L | ++ | D | Ia | CPRO 89029 | J.v. Veldhuizen 1407 |
| *B. subnummularifolia* Merrill | Borneo | L | ++ | D | Ib | CPRO 89049 | J.v. Veldhuizen 1411 |
| *Filicibegonia* A. DC. | | | | | | | |
| *B. elatostemmoides* J.D. Hook. | Tropical Central Africa, Gabon | L | ++ | W | Ib | CPRO 90004 | Louis 108 |
| *B. sciaphila* Engl. | Tropical Central Africa, Cameroon, Gabon | L | ++ | D | Id | 84 PTGA 146 | Arends, Louis & De Wilde 334 |
| *Gireoudia Klotzsch* | | | | | | | |
| *B. bowerae* Ziesenhenne | Mexico | L | ++ | D | Ib | CPRO 89009 | J.v. Veldhuizen 1472 |
| *B. heracleifolia* Schlecht. & Cham. | Mexico, Guatemala, Honduras, El Salvador | L | ++ | D | IIIa | CPRO 89148 | J.v. Veldhuizen 1473 |
| *B. hydrocotylifolia* W.J. Hook. | Mexico | L | ++ | D | Ib | CPRO 89023 | J.v. Veldhuizen 422 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Haagea* (Klotzsch) A. DC. | | | | | | | |
| *B. dipetala* Graham | India | L | ++ | W | Ia | CPRO 89136 | J.v. Veldhuizen 1414 |
| *B. malabarica* Lam. | India, Sri Lanka | L | ++ | W | Ia | BR 59-0214, CPRO 89055 | J.v. Veldhuizen 1134 |
| *Lepsia* Klotzsch | | | | | | | |
| *B. foliosa* H.B. & K. | Colombia, Venezuela, Ecuador | L | ++ | D | Id | BR 07-3708, D2 | J.v. Veldhuizen 567 |
| *Liebmannia* Ziesenhenne | | | | | | | |
| *B. alice-clarkiae* Ziesenhenne | Mexico | L | ++ | D | IIIa | CPRO 89111 | J.v. Veldhuizen 497 |
| *Loasibegonia* A. DC. | | | | | | | |
| *B. microsperma* Warb. | Cameroon | L | ++ | D | IIId | CPRO 90060 | J.v. Veldhuizen 446 |
| *B. prismatocarpa* W.J. Hook. | Tropical West Africa | L | ++ | D | IIIc | CPRO 89039, 86 PTCB 433 | J.v. Veldhuizen 447 |
| *B. scutifolia* J.D. Hook. | Tropical Central Africa | L | ++ | D | Ib | CPRO 90055, 84 PTGA 189 | Arends 560 |
| *Mezierea* (Gaud.) Warb. | | | | | | | |
| *B. oxyloba* J.D. Hook. | Tropical Africa & Madagascar | L | ++ | D | IIc | 83 PTGA 714 | J.J.F.E. de Wilde 744 |
| *B. salaziensis* (Gaud.) Warb. | Endemic to Mascarene islands | L | ++ | D | IIa | 86 PTCB 093 | J.J.F.E. de Wilde 9310 |
| *Monopteron* A. DC. | | | | | | | |
| *B. palmata* D. Don | India | S | ++ | ? | Id | — | J.v. Veldhuizen 355 |
| *Peltaugustia* (Warb.) Barkley | | | | | | | |
| *B. socotrana* J.D. Hook. | Socotra | L | ++ | D | IIIc | CPRO 89084 | J.v. Veldhuizen 449 |
| *Petermannia* (Klotzsch) A. DC. | | | | | | | |
| *B. augustae* Irmsch. | New Guinea | L | ++ | W | Id | CPRO 89115 | J.v. Veldhuizen 668 |
| *B. brevirimosa* Irmsch. | New Guinea | L | ++ | W | Id | CPRO 89118 | J.v. Veldhuizen 890 |
| *B. cumingii* A. Gray | Philippines | L | ++ | W | Id | CPRO 89012 | J.v. Veldhuizen 928 |
| *B. serratipetala* Irmsch. | New Guinea | L | ++ | W | Id | CPRO 89045 | J.v. Veldhuizen 384 |
| *Pritzelia* (Klotzsch) A. DC. | | | | | | | |
| *B. acetosa* Vellozo | Brazil | L | ++ | D | Id | CPRO 89110 | J.v. Veldhuizen 1474 |
| *B. echinosepala* Regel | Brazil | L | ++ | W | Ia | CPRO 89138 | J.v. Veldhuizen 1475 |
| *B. epipsila* Brade | Brazil | L | ++ | D | Ie | CPRO 89015 | J.v. Veldhuizen 410 |
| *B. olsoniae* L.B. Smith *et* B.G. Schubert | Brazil | L | ++ | D | Id | BR 68-0350 | J.v. Veldhuizen 408 |
| *Reichenheimia* (Klotzsch) A. DC. | | | | | | | |
| *B. goegoensis* N.E. Brown | Sumatra | L | ++ | D | Id | CPRO 89019 | J.v. Veldhuizen 362 |
| *Rostrobegonia Warb.* | | | | | | | |
| *B. johnstonii* J.D. Hook. | Kenya, Tanganyika | S | ++ | ? | Ib | — | J.J.F.E. de Wilde 11097 |

**Table 1.** (*Continued*).

| Genus<br>Section<br>Species | Origin | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|---|
| *Scutobegonia* Warb. | | | | | | | |
| *B. dewildei* Sosef | Gabon | L | ++ | D | Ic | 84 PTGA 191 | Arends, Louis & De Wilde 700 (Holo.) |
| *B. ferramica* N. Hallé | Gabon | L | + | D | Id | 85 PTGA 198 | Bos, v.d. Laan & Nzabi 10712 |
| *B. potamophila* Gilg | Tropical Central Africa | L | + | D | Ib | CPRO 90061 | J.v. Veldhuizen 609 |
| *B. quadrialata* Warb. | Congo north to Sierra Leone and Guinea | L | ++ | W | Ie | 82 PTGA 481 | Leeuwenberg 12536 |
| *B. staudtii* Gilg | Nigeria, Cameroon | L | ++ | D | Id | 64 PT 00400 | J.v. Veldhuizen 445 |
| *B. susaniae* Sosef | Cameroon, Gabon | S | ++ | ? | Ig | — | De Wilde *c.s.* 10131 |
| *B. vankerckhovenii* De Wild. | Gabon and Zaire | L | + | D | Ib | 84 PTGA 193 | Arends *c.s.* 699 |
| *Sexalaria* A. DC. | | | | | | | |
| *B. annobonensis* A. DC. | Cameroon (coast near Limbe), Principe, São Tomé, Annobon | S | ++ | ? | Ib | — | J.v. Veldhuizen 621 |
| *Solananthera* A. DC. | | | | | | | |
| *B. radicans* Vellozo | Brazil | L | ++ | D | V | CPRO 89040 | J.v. Veldhuizen 1476 |
| *Sphenanthera* A. DC. | | | | | | | |
| *B. roxburghii* A. DC. | India, Burma, Malaya | S | ++ | ? | Ib | — | J.v. Veldhuizen 1114 |
| *Squamibegonia* Warb. | | | | | | | |
| *B. ampla* J.D. Hook | Tropical Africa | L | ++ | W | Id | PT *s.n.* | J.v. Veldhuizen 604 |
| *B. poculifera* J.D. Hook. | Tropical Africa | L | ++ | D | Id | 85 PTGA 048 | J.v. Veldhuizen 638 |
| *Steineria* (Klotzsch) A. DC. | | | | | | | |
| *B. arborescens* Raddi var. *confertiflora* A. DC. | Brazil | L | ++ | D | IIc | CPRO 89011 | J.v. Veldhuizen 1477 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Tetraphila* A. DC. | | | | | | | |
| *B. capillipes* Gilg | Tropical Africa | L | + | D | Id | CPRO 89086, 83 PTGA 713 | J.J.F.E. de Wilde *c.s.* 528 |
| *B. elaeagnifolia* J.D. Hook. | Cameroon, Equatorial Guinea, Gabon, Congo | L | ++ | W | Id | 84 PTGA 192 | J.J.F.E. de Wilde *c.s.* 9127 |
| *B. eminii* Warb. | Tropical East and West Africa | L | ++ | W | Id | CPRO 89096 | J.v. Veldhuizen 473 |
| *B. gabonensis* J.J. de Wilde | Gabon | L | + | D | Id | 84 PTCB 080 | De Wilde 281 (Holo.) |
| *B. horticola* Irmsch. | Congo, Zaire, Uganda, Gabon | L | ++ | D | Ib | 86 PTGA 284 | Breteler & Lemmens 8075 |
| *B. kisuluana* Büttn. | Tropical Central Africa, Uganda, Angola | L | + | D | Id | 85 PTGA 196 | Breteler & De Wilde 702 |
| *B. komoensis* Irmsch. | Tropical Central Africa: Gabon | L | + | W | Id | CPRO 89100 | J.v. Veldhuizen 733 |
| *B. mannii* W.J. Hook. | Tropical Africa | L | ++ | D | IIIa | 69 PT 02641 | Bos 5047 |
| *B. polygonoides* J.D. Hook. | Tropical Africa | L | ++ | D | IIIb | CPRO 89105, 78 PTCI 741 | J.v. Veldhuizen 1118 |
| *B. subscutata* De Wild. | Tropical Africa | L | + | D | Id | 83 PTGA 562 | J.J.F.E. de Wilde 7551 |
| *Tittelbachia* Klotzsch | | | | | | | |
| *B. fuchsioides* W.J. Hook. | Venezuela, Colombia, Mexico | L | ++ | D | Ie | K-037-79-00203 | J.v. Veldhuizen 537 |
| *Weilbachia* (Klotzsch) A. DC. (may include sect. *Liebmannia*) | | | | | | | |
| *B. aridicaulis* Ziesenhenne | Mexico | L | ++ | D | IV | CPRO 89114 | J.v. Veldhuizen 529 |
| **Symbegonia** Warb. | | | | | | | |
| *S. fulvo-villosa* Warb. | New Guinea | S | ++ | ? | Id | — | J.v. Veldhuizen 690 |
| *S. sanguinea* Warb. | New Guinea | S | ++ | ? | Id | — | J.v. Veldhuizen 886 |

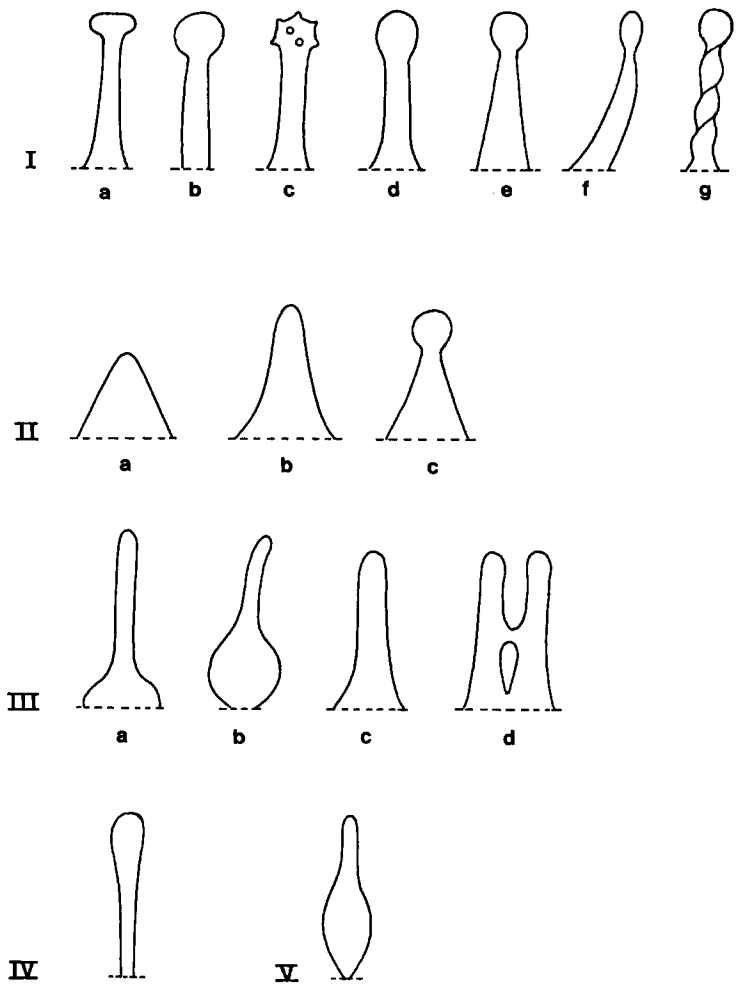


**Fig. 1.** Categories of stigmatic papillae in Begoniaceae (Schematic). Group I, Capitate: (a) stalk cylindric, head discoid; (b) stalk cylindric, head globose; (c) stalk cylindric, head globose with protuberances; (d) stalk cylindric, head sub-globose; (e) stalk tapering, head globose; (f) stalk tapering, head ellipsoid; (g) stalk twisted. Group II, Conical: (a) triangular; (b) elongate; (c) capitate. Group III, Linear: (a) base cushion-shaped; (b) base bulbous; (c) base widened; (d) connected. Group IV, Clavate. Group V, Lageniform.

within the otherwise 'free' papillae common in the whole group, indicating a greater co-ordination among the papillae. In *B. socotrana*, isolated/interrupted rosate papillar arrangement (Fig. 2d) has been noted within the irregularly scattered papillae, which adds to the distinctive characters of the species and upholds the section concerned. Both species of *Symbegonia* studied show very dense, contiguous papillae (Fig. 3d), which may support its generic delimitation.

Type IV is only found in Section *Weilbachia*; type V only in section *Solananthera*.

In conclusion, the data presented here show that the stigmatic surfaces in Begoniaceae are found to be remarkably homogeneous and consistent in respect to their overall characters. All are papillate, and all papillae are unicellular, pointing to the group being a natural taxon. The consistency of the receptive surface in most families was noted by

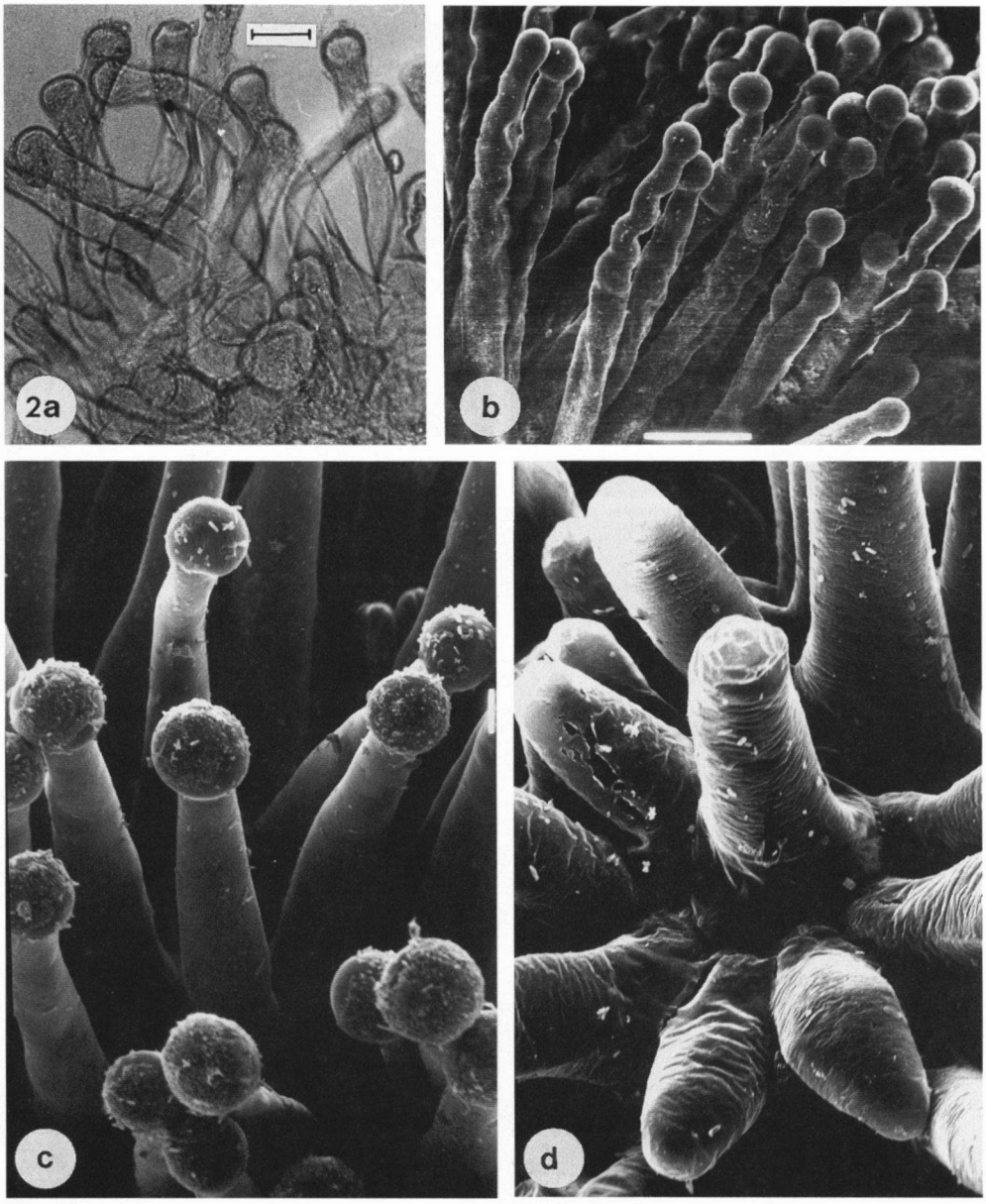


**Fig. 2.** (a) LM and (b–d) SEM photographs. (a) Unicellular capitate papillae in *Begonia vankerckhovenii* (bar=25 μm). (b) Capitate papillae with twisted stalk in *B. susaniae* (bar=50 μm). (c) Capitate papillae with tapering stalk and globose head in *B. quadrialata* (bar=10 μm). (d) Rosately arranged papillae among irregularly scattered ones in *B. socotrana* (bar=10 μm).

Heslop-Harrison & Shivanna (1977), although noteworthy inconsistencies occur in several other families, e.g. Ranunculaceae, Onagraceae, Rosaceae, Liliaceae, Amaryllidaceae, etc. (Heslop-Harrison & Shivanna 1977; Heslop-Harrison 1981). Within this overall homogeneity of the stigmatic surfaces of Begoniaceae a remarkably constant variation in detail is detected, especially by the use of SEM. An increasing

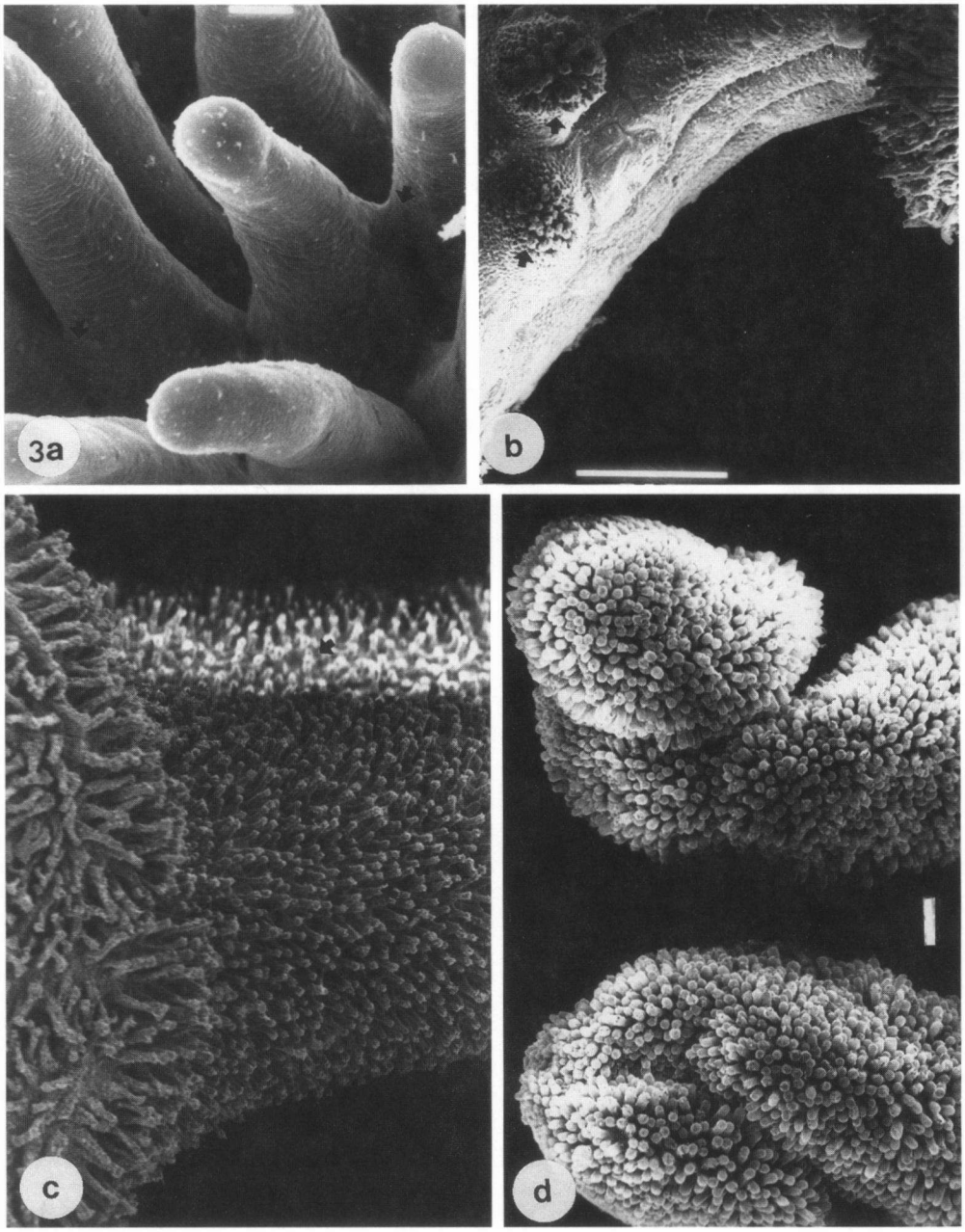


**Fig. 3.** SEM photographs. (a) Connection (arrows) between the lateral walls of papillae in *B. microsperma* (bar=10 μm). (b) Stylar papillae concentrated in localized spots (arrows) in *B. palmata* (bar=500 μm). (c) Stigmatic and stylar (arrows) papillae in *B. ampla* (bar=100 μm). (d) Dense, contiguous papillae in *Symbegonia fulvo-villosa* (bar=100 μm).

coherence of species within sections is found when such detailed characters are considered simultaneously. In particular, some conspicuous character states, e.g. spots of stylar papillae in *B. palmata*, connected papillae in *B. microsperma*, bulbous-based

**Table 2.** Discrepancies between Baranov's observations and the SEM data presented here

| Species | Baranov's observations | Our SEM data |
|---|---|---|
| *Begonia echinosepala* | Wart-like, low conical, papillose 'excrescences' | Capitate papillae |
| *B. roxburghii* | idem | idem |
| *B. goegoensis* | Capitate 'hairs' densely packed into pyramid-like piles | Capitate papillae but not in 'piles' |
| *B. schmidtiana* | idem | idem |
| *B. dipetala* | Irregularly shaped, pinnacle-like excrescences | Capitate papillae |
| *B. mannii* | idem | Linear papillae |
| *B. epipsila* | Rod-like excrescences | Capitate papillae |

ones in *B. polygonoides*, twisted ones in *B. susaniae*, rosate papillae in *B. socotrana*, caps with protuberances in *B. dewildei*, etc. seem to be diagnostic for the species mentioned and are thus of taxonomic value.

## ACKNOWLEDGEMENTS

We are grateful to Prof. Dr L. J. G. van der Maesen for his never-ending and active support in all dimensions, academic and otherwise, and for extending a research fellowship to S.P. on behalf of the Wageningen Agricultural University, The Netherlands, which made possible his stay in The Netherlands and in England to execute this study.

The authors are especially thankful to the Directors of the botanical institutions mentioned in the tables, for providing ample living material. We thankfully acknowledge: Emeritus Prof. Dr J. Doorenbos, Dr M. S. M. Sosef, Dr R. G. van den Berg (Plant Taxonomy Department, WAU), Ir. B. Kroon (CPRO-DLO), for their interest; Dr A. van Aelst, Mr W. van Veenendaal (Department of Plant Cytology and Morphology, WAU) for assistance with the SEM; Mr S. Massalt for printing the microphotographs; Mrs N. Wilders, Mr M. Zevenbergen, Ir. W. Koopman, Ir. X. M. van der Burgt and Ir. J. Kardolus with laboratory and text-editor work; and Mrs J. van Medenbach and Ms M. Wassink for their assistance.

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