A SYSTEMATIC INVESTIGATION OF *BEGONIA* SECTION *SPHENANTHERA* (HASSK.) BENTH. & HOOK.f.

A thesis submitted to the University of Glasgow for the degree of Doctor of Philosophy

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DECLARATION

I hereby declare that this thesis is composed of work carried out by myself unless otherwise acknowledged and cited and the thesis is of my own composition. The research was carried out in the period January 1994 to October 1996. This dissertation has not in whole or in part been previously presented for any other degree.

Under the rules of the *International Code of Botanical Nomenclature*, articles 32 & 33 (Greuter *et al.*, 1994), new taxon names and combinations presented in this thesis are not validly published. Herbarium abbreviations follow *Index Herbariorum* (Holmgren *et al.*, 1981). Abbreviations of taxonomic authors follow *Authors of Plant Names* (Brummit & Powell, 1992) unless otherwise stated.

ABSTRACT

Begonia contains between 900 and 1400 species and is found in most tropical and subtropical regions of the world. The genus is currently divided into c. 80 sections. Several of these are poorly defined and appear not to reflect underlying phylogenetic relationships. This study deals with the systematics of one such taxonomically problematic section from Asia.

Begonia section *Sphenanthera* as currently circumscribed contains 31 species and is differentiated from other sections on the basis that its members are stated to possess leathery or fleshy fruits which are wingless or weakly horned and either indehiscent or dehisce from the centre of the locules. The taxonomic status of many of these species was in need of revision and the section appeared to be polyphyletic.

A revision of the species and infraspecific taxa was conducted based on an extensive morphological study of herbarium and living material. Five new species and a new variety are recognised and some of the existing species are given infraspecific status or synonymised. This revision formed the basis for a cladistic investigation of the section and subsequent revision of the sectional classification.

The cladistic analysis incorporated characters from both traditional and new sources. Morphological, anatomical and molecular data were obtained from the species of section *Sphenanthera* and several potential outgroup sections. A review of the morphological and anatomical characters used in this and past studies is presented. In order to gather molecular data it was necessary to screen several regions of the genome to identify portions with suitable levels of variation for phylogenetic analysis within *Begonia*. The suitability of both sequencing and PCR based restriction site analysis was investigated. Molecular data used in the study was finally obtained from mapped restriction sites of the *trn*C - *trn*D chloroplast region and RFLP patterns from the *psbc*C - *trn*S chloroplast and *nad*4 exon 1 - exon 2 mitochondrial regions.

Section *Sphenanthera* as currently circumscribed is shown to be polyphyletic. The characters used previously to classify the species within this section are shown to be either pleisiomorphic and not suitable for the recognition of higher taxa or homoplastic at this taxonomic level. None of the species have fruit which dehisce from the back of the locules as previously recorded. In order to produce a more

natural classification three new sections and two new subsections of an existing section are proposed. A few species also require moving to sections *Petermannia* and *Platycentrum*. The circumscription of *Sphenanthera* is revised so that it only contains species with two styles and fleshy, 3-locular fruits. This taxon is recognised as a subsection of the section *Platycentrum*. An additional new subsection of section *Platycentrum* is proposed to accommodate *B. balansana* which was previously not allocated to a section. This taxon differs from other species within this section principally in terms of its unique fruit morphology and seed ornamentation. *Begonia trigonocarpa* is also shown to be closely related to section *Platycentrum* and it is suggested that the circumscription of this large section may require changing further in order to accommodate this species. A new monotypic section *Fusiformes* is demarcated by the following combination of characters; fruit fleshy, indehiscent, wingless with parietal placentation, seeds with nipple-shaped opercula. A new section *Blumea* containing five species is demarcated by the following combination of characters; fruit fleshy, 3-locular, indehiscent with axil placentation. A new section *Dioecibegonia* containing eight species is demarcated by the following combination of characters; male flowers with 4 tepals, fruit 4-locular, placentation axile. *Begonia obovoidea* appears to be phylogenetically isolated and may require new sectional status. This taxonomic decision is reserved until the phylogenetic affinities of this species are better known. A taxonomic treatment is presented and includes a key to all the Asian sections and descriptions of the sections, subsections, species and infraspecific taxa treated here. New data relating to the species' distributions, ecologies and uses are presented.

The phylogenetic relationships between the taxa are discussed in relation to their current distributions and ecological niches. Existing hypotheses concerning the place of origin and early evolutionary radiation of the genus are re-evaluated and a new hypothesis is proposed to explain the patterns of variation observed. Many of the taxa treated here appear to have been derived from African ancestors which colonised mainland Asia prior to their differentiation into new higher taxa. The adaptation to different modes of seed dispersal appears to have been particularly important in the evolution of many of the groups.

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Chapter 1
INTRODUCTION

1. INTRODUCTION

1.1. AIMS

The thesis has three main objectives:

- to produce a taxonomic revision of the species and infraspecific taxa currently included in, or associated with, *Begonia* section *Sphenanthera* and to describe new taxa where appropriate.

- to investigate whether *Begonia* section *Sphenanthera* is a natural phylogenetic unit and if not, to produce a revised phylogenetically based classification of these taxa.

- to investigate the phylogenetic affinities, current distributions and ecological preferences of the taxa and use this information to suggest where the group(s) may have originated.

1.2. INTRODUCTION TO THE STUDY

The section *Sphenanthera* was chosen for study as it was not thought to constitute a natural phylogenetic unit and it offers a manageable number of taxa to tackle in a multidisciplinary study such as this. A full revision of the section has never been published and many of the taxa are poorly defined. It was, therefore, proposed to revise all the taxa currently associated with the section and to carry out a cladistic analysis of these species and selected outgroup species with the aim of discovering whether the section constitutes a natural phylogenetic and hence taxonomic unit. If the section, as currently delimited, is un-natural, a revised phylogenetically based classification of the taxa will be produced. The results of the cladistic analysis will be used in combination with distributional and ecological data to suggest where the group(s) may have originated and what speciation processes have probably occurred.

Species level revision was achieved by recognising morphological taxa while higher level classification was based on phylogeny. The different means of constructing classifications at the two taxonomic levels was necessary because at the lower taxonomic levels gene flow causes a complex series of inter relationships

among populations and to a lesser extent among species, while at higher taxonomic levels, reticulation is less common and evolution can be better represented as a hierarchical branching diagram (Hennig, 1966).

Cladistic methodology is the preferred method of phylogenetic reconstruction as it utilises the presence of shared derived character states to reconstruct relationships and attempts to avoid convergent characters by relying on character congruence (Linder, 1988). Classifications based on phylogenetic methods are considered more stable than those based on phenetic ones because the former aims to reconstruct the actual history, of which there can only be one correct answer. Phenetics is based on character similarity, of which there is no true hierarchy and therefore no means of choosing between competing classifications (Donoghue & Cantino, 1988). Classifications based on phylogeny are also thought to have a greater predictive power for additional character distributions (Phillips, 1984). This study was largely based on herbarium material although living plants were also studied in cultivation and in the field (northern Vietnam) where possible. Data used in the cladistic analyses came from a variety of sources, viz. anatomy, micro-morphology of leaf-surfaces and seeds, gross morphology and molecules. A great deal of controversy surrounds the question of whether to combine or analyse separately different data sets (de Queiroz *et al.*, 1995), particularly morphological versus molecular ones (Hillis, 1987; Patterson *et al.*, 1993). Different methods of combination were, therefore, explored to find the effect they had on cladogram topology.

1.3. SYSTEMATIC RESEARCH WITHIN THE BEGONIACEAE

1.3.1. MONOGRAPHIC AND FLORISTIC RESEARCH

The family Begoniaceae Agard is currently composed of three genera, *Begonia* L., *Hillebrandia* Oliv. and *Symbegonia* Warb. *Begonia* is by far the largest of these and contains 900-1400 species (Sosef, 1994) which makes it one of the largest genera of vascular plants (Minelli, 1993). *Symbegonia* contains 12 species and *Hillebrandia* is monotypic (Smith *et al.*, 1986). The species of *Begonia* are widely distributed throughout the tropical and subtropical regions of the world, with the notable exception of subtropical Australia (Heywood, 1978). *Symbegonia* is endemic to New Guinea and *Hillebrandia* is endemic to the Hawaii-archipelago. Many of the species of *Begonia* are narrow endemics and it appears that many

undescribed taxa exist, at least within Asia (pers. obs.). The family contains numerous horticulturally important species and artificial hybrids.

Begonia is currently divided into *c.* 80 sections (Baranov & Barkley, 1974) but a number of these are poorly defined and do not reflect the underlying phylogeny of the genus (Keraudren-Aymonin, 1983; Brouillet, pers. comm.; Doorenbos, pers. comm.; de Wilde, pers. comm.); furthermore, a number of taxa (*e.g. B. amphioxis* Sands, *B. angilogensis* Merr., *B. balansana* Gagnep.) cannot be ascribed to any of the existing sections (Doorenbos, pers. comm.). These problems are particularly acute in south-east Asia and taxa from this region are notoriously difficult to identify (Argent, pers. comm.). The delimitation of most of these sections dates from 1855 when Klotzsch created them as genera in his monograph of the Begoniaceae. The subsequent discovery of many intermediate species means that several of the boundaries recognised by Klotzsch are no longer distinct. The latest currently accepted monograph of the family is that of Irmscher (1925). An illustrated key to the species of Begoniaceae (Smith *et al.*, 1986) has been published, but due to recent taxonomic changes and publication of new taxa it is now outdated. It is generally accepted that research on the delimitation of the sections is urgently required as a sound taxonomic framework is needed to facilitate the identification of members of this large genus and stimulate further taxonomic revision of the species as well as to provide a sound background for comparative evolutionary studies.

Research within the genus reflects this requirement and a number of systematic problems have been investigated within *Begonia*, either by looking at particular characters (*e.g.* anatomy (Fellerer, 1892); chromosome number (Legro & Doorenbos, 1970, 1972, 1974); stem anatomy (Lee, 1974); ovary placentation and anatomy (Reitsma, 1983; Xiao-bai & Fu-hsiung, 1994); pollen morphology (van den Berg, 1985); leaf micromorphology (Cuerrier *et al.*, 1991a & b); seed morphology (de Lange & Bouman, 1992); inflorescence architecture (Goulet *et al.*, 1994); stigmatic surfaces (Panda & Wilde, 1995)) or particular sections (*e.g. Augustia* (Klotzsch) A.DC. and *Rostrobegonia* Warburg (Irmscher, 1961); *Gireoudia* A.DC. (Burt-Utley, 1985); *Trachelocarpus* A.DC. (Karegeannes, 1977)). In recent years the African sections in particular have received a great deal of attention (*e.g. Squamibegonia* Warburg (de Wilde & Arends, 1980); *Mezierea* (Gaud.) Warb. (Klazenga *et al.*, 1994); *Loasibegonia* Warb. and *Scutobegonia* Warb. (Sosef, 1994)) and a number of new sections from this region have been proposed (*e.g. Baccabegonia* Reitsma (Reitsma, 1985); *Cristasemen* J.J. de Wilde

(de Wilde, 1985b)). An in-depth biosystematic study of six species of the African section *Tetraphila* A.DC. (Arends, 1992) was conducted in support of a larger study on this section (de Wilde, pers. comm.). A number of floristic accounts of taxa have also been produced (*e.g.* China (Irmscher, 1939); Venezuala (Smith, 1973); Ecuador (Smith & Wasshausen, 1979); Bhutan, (Grierson, 1991); Taiwan, (Liu & Lai, 1977)). The *Begonia* of Asia have, however, received relatively little attention.

The pollination biology of a wild *Begonia* species from Costa Rica has been studied (Agren & Schemske, 1991; Schemske & Agren, 1995). A study of the origin of a naturally occuring sterile hybrid in Taiwan has also been undertaken (Peng & Chen, 1991). More biosystematic studies within *Begonia* are, however, required, particularly those focusing on speciation mechanisms within the genus.

1.3.2. PHYLOGENETIC RESEARCH

Research into the phylogeny of the Begoniaceae is also being conducted, primarily using molecular techniques (Brouillet, pers. comms.; Peng, pers. comm.; Swensen, pers. comms.), but the findings are so far unpublished. Initial results do, however, suggest that there is a complex relationship between the sections from Asia, America and Africa and that they have undergone relatively recent and rapid differentiation. The current taxonomic seperation of *Begonia* into these three regions, viz. Africa, Asia and the Americas (Irmscher, 1925) appears to be artificial (Brouillet, pers. comm.). *Hillebrandia sandwichensis* Oliv. appears to be the most closely related taxon to *Begonia* and it is hoped that further investigation of this and other related genera will shed some light on the relationships of the *Begoniaceae* with other families (Swensen, pers. comm.).

Very few phylogenetic analyses of *Begonia* have been published and relationships between the sections remain largely speculative (Fellerer, 1892; Irmscher, 1929; de Wilde, 1985a). In a numerical analysis of 55 leaf micromorphological characters from 126 *Begonia* species and *Hillebrandia*, Cuerrier *et al.* (1990, 1991a, 1991b) found that sections from a given continent were phenetically more similar to each other than they were to sections from other continents and that the African and American species both shared more characters with Asian species than they did with each other. In a resulting dendrogram *Begonia roxburghii* (Miq.) A.DC., (currently included in section *Sphenanthera*), occurs in a cluster together with

species of sections *Platycentrum* (Klotzsch) A.DC., *Monopteron* (A.DC.) Warb., *Petermannia* (Klotzsch) A.DC., *Coelocentrum* Irmsch. and *Reichenheimia* (Klotzsch) A.DC. (Cuerrier *et al.*, 1991b). The only published cladistic studies of *Begonia* are of the African sections *Loasibegonia* and *Scutobegonia* (Sosef, 1994) and *Mezierea* (Klazenga *et al.*, 1994) both of which were based on morphological data. The only comprehensive published views on phylogenetic relationships between Asian sections are those presented by Irmscher (1929) who suggests that several independent evolutionary lines occur in this area and have resulted in convergence of fruit locule number, he does not, however, mention where *Sphenanthera* fits into this scheme.

The lack of phylogenetic information for the genus creates a problem when conducting cladistic analyses as appropriate outgroups are difficult to select due to the large number of potential sections to choose from. Morphological convergence is thought to be widespread between many sections of *Begonia* (Irmscher, 1929; de Wilde, 1985a; de Lange & Bouman, 1992) and hence it is important to select closely related outgroup taxa as these are less likely to cause problems associated with homoplasy (Baum & Estabrook, 1996).

Few views regarding intersectional affinities with *Sphenanthera* appear to have been published. De Candolle (1859) groups *Sphenanthera* together with members of the current day South American section *Casparya* (Klotzsch) Warb. to form the genus *Casparya* (Klotzsch) A.DC. This classification was proposed on the basis of their perceived similarity in fruit dehiscence and is no longer accepted. Fellerer (1892) suggests relationships with sections *Bracteibegonia* A.DC., *Huszia* (Klotzsch) A.DC. and *Mezierea* based on shared anatomical and morphological characters and Xiao-bai & Fu-hsiung (1994) suggest affinities with section *Begonia* L. based on anatomical features of the ovaries. *Begonia leprosa* Hance which is currently provisionally included in section *Sphenanthera* (Irmscher, 1939) has in the past been affiliated with *B. delicatula* Parish (Hance, 1883) and *B. houttuynioides* Yü (Yü, 1950) of section *Parvibegonia* A.DC. and *B. henryi* Hemsl. of section *Reichenheimia* (Klotzsch) A.DC. (Hemsley, 1900). Its sectional placement remains problematic.

Unpublished sequence data for the large sub-unit of the ribulose-1,5-bisphosphate carboxylase gene (*rbc*L) (Swensen, pers. comm.) indicates that *B. oxyloba* Welw. ex. Hook. f. (section *Mezierea*) and *B. diadema* Linden ex. Rodig. (section *Platycentrum* (Klotzsch) A.DC.) are closely related to *B. roxburghii*, a species

currently included in section *Sphenanthera*. The perceived wide spread convergence of morphological characters within *Begonia* may mean that such molecular data will be a better means of unravelling phylogenetic relationships at higher taxonomic levels within the genus.

1.4. TAXONOMIC HISTORY OF *BEGONIA* SECTION SPHENANTHERA

The name *Sphenanthera* first appears in a paper by Hasskarl published in 1855. *Sphenanthera* is designated as a genus of *Begoniaceae* with three taxa; *S. robusta* (Blume) Hassk., *S. erosa* (Blume) Hassk. and *S. multangula* (Blume) Hassk. *Sphenanthera robusta* (Blume) Hasskarl is designated as the type of the genus. The genus was said to differ from the genus *Sassae* (currently synonymous with section *Casparya* (Klotzsch) Warb.) by its separated filaments, blunt wedge-shaped anthers, persistent style with spiral stigmatic papillae and shorter fruit.

In 1857 Klotzsch published the first detailed description of the genus *Sphenanthera* Hassk. as follows:

> 'Flores monoici. Masc. Petala 4 biseralia inequalia, exteriora opposita majora oblongo-orbicularia, in centro concava subcarnosa, margine membranacea, extus sparsim hirta, interiora oblongo-obovata minora membranacea, utrinque glabra. Stamina numerosissima; filamenta libera filiformia laxa toro valde pulvinato inserta; antherae oblongo-obovato-cuneiformes, basi attenuatae, apice obtusae, filamentis duplo breviores, loculis lateralibus angustis distantibus infra apicalibus. Fem. Petala 5 supera inequalia biserialia, exteriora 2 elliptica majora in centro concava subcarnosa, margine membranacea, extus sparsim hirta, interiora 3 minora obovata membranacea, utrinque glabra. Ovarium inferum trigonum subturbinatum triloculare sparsim setoso-hirtum, angulis gibbosis vix alatis nunc uno productiore subalato. Ovula in placentis e loculorum angulo centrali geminis crassis conniventim falcatis, utrinque ovuliferis distincte pedicellatis, pedicellis basi conjunctis creberrima, anatropa. Stylus persistens brevis glaber trifidus. Stigmata 3 bifida magis dilata, fascia papillosa bis spiraliter torta, antice ad basin continua cincta. Capsula turbinato-triquetra trilocularis, apice vix producta, primo suberoso-cartilaginea, dein spongioso-membranacea triangularis setoso-hirta, dein glabriuscula, angulis extensis subulato-gibbosis, uno majore, demum ab ima basi secedentibus bipartibilibus. Semina innumerabilia minutissima oblonga laevia obsolete sulcata exalbuminosa.'

An English translation is for the first time set out below:

> Flowers monecious. Male flowers: petals 4, arranged in 2 whorls, unequal; outer ones opposite, larger, oblong-orbicular, concave and rather fleshy in the centre, with a membranous margin, sparsely hairy outside; inner ones oblong-obovate, smaller, membranous, glabrous on both sides. Stamens very numerous; filaments free, filiform, loosely arranged, inserted on a strongly convex torus; anthers oblong-obovate-cuneate, base attenuate, apex obtuse, twice as short as the filaments, with the lateral locules narrow, distant below the apical ones. Female flowers: Petals 5, superior, in 2 unequal whorls, the outer 2 elliptic, larger, concave and rather fleshy in the centre, with a membranous margin, sparsely hairy outside, the inner 3 smaller, obovate, membranous, glabrous on both sides. Ovary inferior, 3-angled, somewhat turbinate, 3-locular, sparsely setose-hairy, with the angles swollen and scarcely winged or sometimes with one angle more extended and somewhat winged. Ovules anatropous, very closely packed together on thick, paired, connivently falcate placentas [arising] from the central angles of the locules, the placentas distinctly pedicellate and bearing ovules on both sides, the pedicels joined at the base. Style persistent, short, glabrous, trifid. Stigmas 3, bifid, more dilated, encircled by a papillate band which is twice spirally twisted and in front is continuous to the base. Capsule turbinate-triquetrous, 3-locular, the apex scarcely produced, at first corky-cartilagenous, thereafter spongy-membranous, triangular, setose-hairy, thereafter almost glabrous, the angles extended and subulate-gibbose, one of them larger, finally splitting apart from the lowest part of the base into 2-parts. Seeds extremely numerous, very minute, oblong, smooth, obsoletely sulcate, without albumen.

The name *Sphenanthera* was said by Klotzsch to be derived from the Greek words σφην (wedge) and ανθηρα (anther) on account of the species' reputedly diagnostic wedge-shaped anthers.

Seven years later de Candolle (1864) demoted Hasskarl's genus to a section of the genus *Casparya* Klotzsch. The latter genus was characterised by axillary placentas and capsules dehiscing longitudinally on the back of the locule along the angles or wings. In addition to Hasskarl's three species, four other taxa were also added to

the "*Sphenanthera* group", although de Candolle was unsure about the taxonomic affinity of three of these.

The circumscription of *Casparya* section *Sphenanthera* (Hassk.) A.DC. presented by de Candolle (1864) does not differ from Hasskarl's genus *Sphenanthera* even though the three species with dubious affinities deviate from the taxa Hasskarl included in *Sphenanthera* in that they all have 4-locular instead of 3-locular fruits. Furthermore, *Casparya? silletensis* A. DC. only has a very short rhizomatous stem unlike Hasskarl's taxa which are tall erect herbs. This does not, however, invalidate *Casparya* section *Sphenanthera* (Hassk.) Warb. as a taxon since De Candolle included its type *S. robusta* (Blume) Hassk.

At the end of de Candolle's treatment of the genus *Casparya*, he described two new sections, *Holoclinium* A.DC. and *Polyschisma* A.DC. Both sections have question marks before their names indicating that de Candolle was unsure about their legitimate taxonomic status. *Casparya* section *Polyschisma* contained a single species, *C. crassicaulis* A.DC. The holotype of this taxon, a Kew specimen annotated 'Jawa De Vriese', is the same specimen as the holotype of *B. multangula* Blume; the taxonomic implications of this are discussed in 5.6.4.1.1 Recently there has been some confusion with regards to the correct identity of *B. crassicaulis* (A.DC.) Warb. Smith & Wasshausen (1984) synonymised the taxon under their *nomen nudum B. pachyrachis* L.B. Smith & D.C. Wasshausen. The holotype of *B. pachyrachis* is however, the holotype of Lindley's *B. crassicaulis* from Guatemala and not de Candolle's taxon from Java. Section *Holoclinium* will be discussed below.

Bentham & Hooker (1867) published an alternative classification of the Begoniaceae in which they synonymized the genus *Casparya* Klotzsch with the genus *Begonia* L. (As the valid publication of the name *Begonia* L. (1753) predates that of *Casparya* Klotzsch (1855) it is the legitimate name of the genus). In this treatment *Begonia* was divided into five series and approximately 40 sections. *Casparya* sections *Sphenanthera* and *Holoclinium* were lumped with *Begonia* sections *Bracteibegonia* and *Trilobaria* and *Mezierea* section *Monopteron* to constitute *Begonia* section *Diploclinium* Wight *sensu* Benth. & Hook. f. Section *Polyschisma* remained of doubtful status. No reason was given for separating section *Diploclinium* from the other sections within the series and it appears that it was only separated as it was Asian in distribution whilst the others are either

African or American. Bentham & Hooker's classification does not appear to have ever been generally accepted.

Warburg in his treatment of the *Begoniaceae* in Engler & Prantl's *Die natürlichen Pflanzenfamilien* (1894) also treated the genus *Casparya* Klotzsch (with its eight sections) as a synonym of the large genus *Begonia* L. In this treatment, the sections of *Casparya* are maintained as distinct taxonomic entities and treated as sections of the genus *Begonia*. *Begonia* section *Sphenanthera* (Hassk.) Warb. was said to contain eight to nine species. The following were cited as representative of the section: *B. robusta* Blume from Java, *B. roxburghii* A.DC. from Burma and the Himalaya and *B. trisulcata* (A.DC.) Warb. from Java.

The section was diagnosed as follows:

> "Male: 4 Blhb., Stf. fast frei, A. länglich, connectiv nicht oder wenig hervorragend; Female: 4-5 Blhb., Gr. 3-4, nicht verwachsen, tief 2spaltig, Narbenpapillen ein continuierliches Schraubenband mit mehreren Windungen. Samenleisten 2spaltig, dick, vom Innenwinkel der Fächer ausgehend. Fr. lederig, dickwandig, zuweilen sogar etwas fleischig, flügellos oder schwach gehörnt, nicht oder sehr spät, und dann auf dem Rücken der Fächer aufreibend. - Kriechende oder aufrechte, selten stengellose große Kräuter oder Halbsträucher mit häufig dickem Rhizom, sehr schiefen handnervigen B. und kurzen Blütenständen. - Etwa 8-9 Arten auf dem östlichen Himalaya, im westlichen Hinterindien und den groben Sundinseln."

An English translation is given below:

> Male flowers: 4 sepals; stamens almost free, anthers oblong, connective not or little projecting. Female flowers: 4-5 sepals, styles 3-4, free, deeply bifid, papillae of the stigma a continuous spiral band with a few twists. Placentae bifid, sometimes somewhat fleshy, placentation axillary. Fruit leathery, thick walled, occasionally slightly fleshy, wingless or weakly horned, indehiscent or dehiscing very late and then from the back of the locule. Plants creeping or erect, rarely acaulescent, large herbs or semi-shrubs, frequently with a thick rhizome; leaves very asymmetric, palmately veined; inflorescences short. About 8-9 species in Eastern Himalayas, Burma, South East Asia and Greater Sunda Islands.

Begonia trisulcata (A.DC.) Warb. had formerly been placed in its own section of *Casparya* by de Candolle, section *Holoclinium* A.DC. This section was erected on

the belief that the species had entire placentae, a state otherwise unknown in the genus *Casparya* Klotzsch. As a result of his studies Warburg, however, found the species to possess divided placentae and, therefore, synonymized *Casparya* section *Holoclinium* A.DC. with *Begonia* section *Sphenanthera* (Hassk.) Warb (Warburg, 1894). The section *Polyschisma* was maintained by Warburg as a taxon of uncertain status.

In the second edition of Engler & Prantl's *Die natürlichen Pflanzenfamilien* Irmscher (1925) retains Warburg's earlier treatment of *Begonia* section *Sphenanthera.* The changes made to the sectional diagnosis are minimal. Irmscher states that the species have 3-4-locular fruits, a fact omitted from Warburg`s description even though this can be deemed to be the case from his list of representative species. Several new taxa are also added to the section and it was said to contain about 21 species. Irmscher lists the following as representative of the section: *B. robusta* Blume from Java; *B. roxburghii* A.DC. from Burma and the Himalayas; *B. handelii* Irmsch. from China; *B. pseudolateralis* Warb. from the Philippines and *B. renifolia* Irmsch. from Sulawesi. Following Warburg the treatment lists *Casparya* section *Holoclinium* A.DC. as a synonym of *Begonia* section *Sphenanthera* (Hassk.) Warb. *Begonia* section *Polyschisma* (A.DC.) Warb. with its single species *B. crassicaulis* (A.DC.) Warb. is maintained as a taxon of uncertain status.

In an alternative classification of the Indian and Burmese *Begoniaceae* proposed by Clarke (1879) in Hooker's *Flora of British India*, the Indian and Burmese species from de Candolle's designation of *Casparya* section *Sphenanthera* (Hassk.) A.DC. along with three new species are formally treated as composing *Begonia* section *Casparya* (Klotzsch) C.B. Clarke.

This taxon is characterised as follows:

> "Stamens numerous, shortly monadelphous; anthers narrowly oblong, connective slightly produced, obtuse. Ovary 4-celled (3-celled in A. De Candolle's species), placentae 2-fid or 2-partite. Fruit more or less fleshy, not dehiscing on the faces; carpels not much compressed, not having their backs produced into a thin wing. (None small: leaves in all very unequal at the base)." (Clarke, 1879 p. 635).

Clarke's classification has fallen into disuse following the general adoption of Warburg's and then Irmscher's later monographic treatments of the complete family.

Irmscher's monograph of the *Begoniaceae* (Irmscher, 1925) remains the most up to date treatment of the Begoniaceae. Table 1.1. provides a summary of past classifications of *Sphenanthera*.

Table 1.1. A summary of the classifications including *Sphenanthera*.

Hasskarl (1855) Klotzsch (1857)	de Candolle (1964)	Bentham & Hooker (1867)	C.B. Clarke (1879)	Warburg(1894)	Irmscher (1925)
Sphenanthera Hassk.	*Casparya* section *Sphenanthera* (Hassk.) A.DC.	*Begonia* series *Diploclinium* (Wight) *sensu* Benth. & Hook. f	*Begonia* section *Casparya* (Klotzsch) C.B. Clarke	*Begonia* section *Sphenanthera* (Hassk.) Warb.	*Begonia* section *Sphenanthera* (Hassk.) Warb
S. robusta (Bl.) Hs. *S. erosa* (M.) Hs. *S. multangula* (Bl.) Hs.	*C. robusta* (Bl.) DC. *C. erosa* (M.) DC. *C. multangula* (Bl.) DC. *C. teysmanniana* (M.) DC. *C? oligocarpa* (DC.) DC. *C? polycarpa* (DC.) DC. *C? silletensis* DC.	= Hasskarl's genus + several *Begonia* sections of A.DC.	*B. roxburghii* DC. *B. silhetensis* Clarke *B. tessaricarpa* Clarke *B. inflata* Clarke *B. dux* Clarke	*B. robusta* Bl. *B. roxburghii* DC. *B. trisulcata* (DC.) W. + 4-5 species not listed	*B. robusta* Bl. *B. handelli* Irm. *B. pseudolateralis* W. *B. renifolia* Irm. *B. trisulcata* (DC.) W. + c. 16 species not listed
	Casparya section *Holoclinium* A.DC. *C. trisulcata* (DC.) DC.				

Key to non conventional author abbreviations used for species in the table due to space constraints.

Blume - **Bl.**, A. de Candolle - **DC.**, C.B. Clarke - **Clarke.**, Hasskarl - **Hs.**, Irmscher - **Irm.**, Miquel - **M.**, Warburg - **W.**

1.5. TAXA CURRENTLY INCLUDED IN OR ASSOCIATED WITH SECTION *SPHENANTHERA*

At the time of the publication of Irmscher's monograph of the Begoniaceae (Irmscher, 1925) the following taxa had been either described and affiliated to *Begonia* section *Sphenanthera* or included within it by subsequent authors:

B. aborensis Dunn, Bull. Misc. Inform., 109, 1920.

B. aptera Blume, Enum. Pl. Javae, 1: 97, 1827.

B. acetosella Craib, Bull. Misc. Inform., 153, 1912.

Diploclinium apterum (Blume) Miq., Fl. Ned. Ind., 1.1: 691, 1856.

B. axillipara Ridley, Trans. Linn. Soc. London, Bot., II, 9: 60, 1916.

B. balansana Gagnep., Bull. Mus. Hist. Nat. (Paris), 25: 194, 1919.

B. burkillii Dunn, Bull. Misc. Inform., 110, 1920.

B. dux C. B. Clarke, in J.D. Hooker, Fl. Brit. Ind., 2: 637, 1879.

B. erosa Blume, Enum. Pl. Javae, 1: 96, 1827.

Platycentrum erosum (Blume) Miq., Fl. Ned. Ind., 1.1:694, 1856.

Sphenanthera erosa (Blume) Hassk., Versl. kon. Akad. Wetensch. 4.139. 1855.

Casparya erosa (Blume) A.DC., Prodr., 15(1): 276, 1864.

B. handelii Irmsch., Akad. Wiss. Wein. Math. Natur. Wiss. K. Anz., 58: 24, 1921.

B. hayatae Gagnep., Bull. Mus. Hist. Nat. (Paris), 25: 282, 1919.

B. aptera sensu Hayata, J. Coll. Sci. Imp. Univ. Tokyo, 30: 122, 1911, non Blume, 1827.

B. inflata C. B. Clarke, in J.D. Hooker, Fl. Brit. Ind., 2: 636, 1879.

B. longifolia Blume, Catalogus, 102, 1825.

Diploclinium longifolium (Blume) Miq., Fl. Ned. Ind., 1.1: 687, 1856.

D. longifolium var. *luxurians* (Blume) Miq. ex Koord., Exkurs.- Fl. Java, 2: 650, 1912, *pro syn. Begonia longifolia* Blume, 1823.

B. multangula Blume var. *multangula*, Enum. Pl. Java, 1: 96, 1827.

B. discolor sensu Blume (1827) *non* R. Brown, Enum. Pl. Java, 96, 1827.

B. grandis Reinw. *ex* Koord., Exkurs.- Fl. Java, 2: 646, 1912, *non* Dryand., 1791; pro syn. *multangula* Blume var. *multangula* 1827.

B. robusta Zoll. *ex* Klotzsch, Bot. Zeitung, 15: 182, 1857, *pro syn.* *Sphenanthera multangula* Klotzsch, 1857; *non* Blume, 1827.

Platycentrum multangulum (Blume) Miq., Fl. Ned. Ind., 1.1: 695, 1856.

Sphenanthera multangula (Blume) Hassk., Versl. kon. Akad. Wetensch. 4.139. 1855.

Casparya multangula (Blume) A.DC., Prodr., 15(1): 275, 1864.

B. multangula Blume var. *glabrata* (Miq.) Miq., Fl. Jungh. 4: 418, '1855', 1857.

Platycentrum multangulum var. *glabrata* Miq., Fl. Ned. Ind., 1.1: 695, 1856.

Sphenanthera multangula var. *glabrata* (Miq.) Klotzsch, Bot. Zeitung., 15: 182, 1857.

Casparya multangula var. *glabrata* (Miq.) A.DC., Prodr., 15(1): 276, 1864.

B. pseudolateralis Warb. in Perkins, Fragm. Fl. Philipp., 51, 1911.

B. aptera Blume var. *calleryana* Fernandez-Villar in Blanco & Mercado, Fl. Filip., ed. 3, 4: 99, 1880.

B. aptera sensu Roxb., Flora Ind., 3: 650, 1832, *non* Blume, 1827.

B. aptera sensu Decne., Nouv. Ann. Mus. Hist. Nat. (Paris), III, 3: 451, 1834, *non* Blume, 1827.

Diploclinium timorense Miq., Fl. Ned. Ind., 1.1: 692, 1856.

Mezierea callaryana herb. ex A.DC., Prod., 15(1): 408, 1864.

M. salaziensis var. *calleryana* A.DC., Prodr., 15(1): 408, 1964.

B. renifolia Irmsch., Bot. Jahrb. Syst., 50: 379, 1913.

B. robusta Blume (1827) var. *robusta*, Enum. Pl. Javae, 1: 96,1827.

B. splendida Rollisson ex Henderson, III. Bouquet, 1, sub. pl. 11, 1857-1859.

Casparya robusta A.DC., Prodr., 15(1): 275, 1864.

Platycentrum robustum (Blume) Miq., Fl. Ned. Ind., 1.1: 694, 1856.

Sphenanthera robusta (Blume) Hassk., Versl. kon. Akad. Wetensch. 4.139. 1855.

Sphenanthera robusta (Blume) Hassk.(1857) var. *viridis* Hasskarl, Hort. Bogor. Descr., 346, 1858.

B. robusta var. *rubra* (A.DC.) Warb., in Engler & Prantl, Nat. Pflanzenfam., 3(6A): 146, 1894.

Casparya robusta var. *rubra* A.DC., Prodr., 15(1): 275, 1864.

B. roxburghii A.DC., Prodr., 15(1): 398, 1864.

B. malabarica sensu Roxb., Fl. Ind., 3: 648, 1832, non Lamarck, 1785.

Casparya oligocarpa A.DC., Ann. Sci. Nat. Bot., IV, 11: 118, 1859.

C. polycarpa A.DC., Ann. Sci. Nat. Bot., IV, 11: 118, 1859.

Diploclinium roxburghii (A.DC.) Miq., Fl. Ned. Ind., 1.1: 692, 1856.

B. sarcocarpa Rid., J. Fed. Malay States Mus., 8(4): 38, 1917.

B. silhetensis (A.DC.) C. B. Clarke, in J.D. Hooker, Fl. Brit. Ind., 2: 636, 1879.

Casparya silletensis A. DC., Prodr., 15(1): 277, 1864.

B. tessaricarpa C. B. Clarke, in J.D. Hooker, Fl. Brit. Ind., 2: 636, 1879.

B. teysmanniana (Miq.) Warb., *nomen nudum*, 1894.

B. teysmanniana Miq., Fl. Ned. Ind., 1.1: 1092, 1858, *pro syn.*

Platycentrum teysmannianum Miq., 1856.

Casparya teysmanniana Miq. ex A.DC., Prodr., 15(1): 276, 1864.

Platycentrum teysmannianum Miq., Fl. Ned. Ind., 1.1: 1092, 1858.

B. tricornis Ridl., J. Roy. Asiat. Soc. Straits Branch, 75: 35, 1917.

B. roxburghii sensu Ridl., J. Fed. Malay States Mus., 4: 20, 1909, *non* A. DC. (1864).

B. trigonocarpa Ridl., Trans. Linn. Soc. London, Bot., II, 9: 38, 1917.

B. trisulcata Warb., in Engler & Prantl, Nat. Pflanzenfam., 3(6A): 142, 1894.

Casparya trisulcata A.DC., Ann. Sci. Nat. Bot., IV, 11: 119, 1859.

Monopteron trisulcatum sensu F.A. Barkley & Golding (1974) *Sphalmate pro Casparya trisulcata* A. DC. (1859).

B. turbinata Ridl., J. Fed. Malay States Mus., 8(4): 37, 1917.

A number of taxa attributed to *Begonia* section *Sphenanthera* have been described since 1925 or were moved to the section after this date and therefore, have never been considered in a monographic context. The following fall into this category;

B. acetosella Craib var. *hirtifolia* Irmsch., Mitt. Inst. Allg. Hamburg, 10: 515, 1939.

B. brachyptera Merr. & Perry, J. Arnold Arbor., 29: 160, 1948.

B. crassirostris Irmsch., Mitt. Inst. Allg. Hamburg, 10: 513, 1939.

B. cristata Warb. ex L.B. Smith & D.C. Wasshausen, Phytologia, 52: 442, pl. 2, 1983.

B. leprosa Hance, J. Bot., 21: 202, 1883.

B. bretschneideriana Hemsl., in W.J. Hooker, Icon. Pl., IV, 27: pl. 2635, 1900.

B. obovoidea Craib, Bull. Misc. Inform., 413, 1930.

B. prostrata Irmsch., Mitt. Inst. Allg. Hamburg, 10: 516, 1939.

B. robusta var. *glabriuscula* (A.DC.) ex F.A. Barkley & Golding, Sp. Begoniaceae, ed. 2: 108, 1974.

Casparya robusta var. *glabriuscula* A.DC., Prodr., 15(1): 275, 1864.

B. robusta var. *hirsutior* (Miq.) Golding & Kareg., Phytologia, 54: 499, 1984.

Diploclinium areolatum Miq., Fl. Ned. Ind., 1.1: 1091, 1858, *non* Miquel, 1856.

Platycentrum robustum var. *hirsutior* Miq., Fl. Ned. Ind., Eerste bijv., 332, 1861.

Casparya robusta var. *rubra* A.DC., Prodr., 15(1): 275, 1864.
B. tetragona Irmsch., Mitt. Inst. Allg. Hamburg, 10: 515, 1939.

The four taxa published by Irmscher (1939) appeared in a paper which also included descriptions of four previously described taxa attributed to section *Sphenanthera* and a key to the Chinese members of *Begonia* section *Sphenanthera*. In this paper Irmscher, with some reservation, put *B. leprosa* Hance and its current synonym, *B. bretschneideriana* Hemsl., in section *Sphenanthera*. Merrill & Perry (1948) published a species from New Guinea, *B. brachyptera*, which they attributed to section *Sphenanthera*. Barkley & Golding (1974) published the varietal name *glabriuscula* (for *Begonia robusta* Blume) as a *comb. nov.* based on de Candolle's taxon *Casparya robusta* var. *glabriuscula*. Barkley & Golding (1974) list two further species as belonging to section *Sphenanthera*, *B. obovoidea* Craib which was described in 1930 but without reference to its sectional affinities and *B. cristata* Warb. ex L.B. Smith & D.C. Wasshausen which was described in 1983. The latter was based on an earlier nomen nudum proposed by Warburg (in herbs. Leiden and Bogor) and later invalidly published by Koorders (1904).

Barkley & Golding (1974) provides a provisional list of all the taxa currently included within the section.

1.6. CURRENT SITUATION AND NOMENCLATURE

A total of 68 species names have been attributed to *Begonia* section *Sphenanthera* (or one of its synonyms), of these, 31 are presently recognised as valid species (see list above). Some of these taxa are not currently affiliated with the section. *Begonia erosa* Blume and its synonyms are presently regarded as being synonymous with *B. tenuifolia* Dryand. (Backer & Bakhuizen, 1963) and are included in section *Platycentrum* (Klotzsch) A.DC. (Barkley & Golding, 1974). *Begonia robusta* Blume var. *rubra* (A.DC.) Warb. is currently regarded as a synonym of *B. muricata* Blume (Smith & Wasshausen, 1984) and included in section *Diploclinium* (R. Wight ex Klotzsch) A.DC. (Barkley & Golding, 1974).

Baranov & Barkley's (1974) 'The sections of the genus *Begonia*' gives the nomenclature of the taxon as '*Begonia* section *Sphenanthera* (Hassk. ex. A.DC.,

1857) A.DC. 1864.' This is incorrect as firstly, Hasskarl validly published the taxon *Sphenanthera* (Hasskarl, 1855) and secondly, de Candolle treated Hasskarl's genus *Sphenanthera* as a section of the genus *Casparya* Klotzsch and not of the genus *Begonia* L. It was Bentham & J.D. Hooker who first treated *Sphenanthera* as a section of *Begonia* in 1867. This publication also lists the type species of section *Sphenanthera* as '*Begonia roxburghii* A.DC., 1864 (*Casparya oligocarpa* A.DC. 1859)'. This is also incorrect as Hasskarl created the genus *Sphenanthera* for *Begonia robusta* Blume and therefore, this species remains the type of *Sphenanthera* regardless of the subsequent changes from a generic to a sectional status.

The correct nomenclature for the section is as follows:
Begonia section *Sphenanthera* (Hassk., 1855) Benth. & Hook. f., 1867.
synonyms: *Sphenanthera* Hassk., 1855, *pro gen.*
Casparya section *Holoclinium* A. DC. 1864.
The type species of the section is *Begonia robusta* Blume.

Proposed taxonomic and nomenclatural changes resulting from the present study are presented in Chapter 5.

1.7. TAXONOMIC CONCEPTS

In the following paragraph taxonomic concepts are reviewed and reasons are presented for recognising particular concepts in the present study.

1.7.1. GENERA AND SECTIONS WITHIN THE BEGONIACEAE

In the case of large genera such as *Begonia* it is often customary to create formal taxonomic subdivisions to make the group more accessible (de Candolle, 1859; Cronquist, 1985). The current International Code of Botanical Nomenclature (Greuter *et al.*, 1994) allows for the recognition of the following infrageneric ranks: subgenus, section, subsection, series and subseries. The two ranks of widest application are section and series. At present the genus *Begonia* is composed of approximately 80 sections, which themselves contain between one and 120+ species. The geographical spread and distinction of these sections within *Begonia* is not uniform. The Americas and Asia both contain relatively large numbers of often morphologically similar sections, while Africa contains a much smaller number of relatively morphologically distinct sections. Infrageneric divisions assist

the classification and identification of unknown taxa as they reduce the total number of taxa an unidentified taxon has to be compared with. In the case of *Begonia*, however, many of the sections appear to be poorly defined *e.g. Sphenanthera* and several sections probably overlap *e.g. Reichenheimia* and *Diploclinium* (Doorenbos, pers. comm.). Furthermore, several species cannot be assigned to any of the existing sections (Doorenbos, pers. comm.). These problems are a hindrance to the users of the classification.

Even in the case of well defined groups of species it is often difficult to distinguish the taxonomic level at which a taxonomic group becomes a family, a genus or an infrageneric taxon. As a result, the delimitation of such taxa differs greatly amongst the angiosperms. The generic concept, for example, encompasses a range of variation from small genera incorporating little variation, such as those in the Apiaceae and the Asteraceae to large genera such as *Begonia* which contain a great deal of variation. The past taxonomic history of the *Begoniaceae* reflects this difficulty as past researchers have variously treated some of the modern day taxa either as genera (*e.g.* Klotzsch, 1855; C. de Candolle, 1908), or as sections of the large genus *Begonia* (*e.g.* Warburg, 1894; Irmscher, 1925). Debate still occurs today with regards to whether some sections of *Begonia* (*e.g. Casparya* Bouman, pers. comm.; *Trachelocarpus* Irmscher, 1925) warrant generic status and whether *Symbegonia* requires demoting to the level of section (de Wilde, 1985a). The current concept of the genus *Begonia* with its *c.* 80 sections is maintained here.

As long as the current concept of the genus is maintained, I would like to revoice Sosef's (1994) plea that authors working on *Begonia* always state the section to which any species belongs. This greatly enhances the information content of a name and thereby assists with the processes of identification and classification of unknown taxa.

In defining new sections in the present study, attempts were made to create natural taxa based on perceived relationships. An effort was also made to create new sections which were roughly comparable in terms of their levels of morphological distinction from existing well defined (and, therefore, presumably natural) sections so that needless disruption of the current classification is avoided.

A review of phylogenetically based classification is presented in 2A.5.

1.7.2. THE SPECIES

The species is often considered the most basic unit of the taxonomic hierarchy (Mayr, 1957). Despite this, the species concept is one of the most controversial areas of classification (Heiser, 1963; Slobodchikoff, 1976; Dobzhansky, 1970; Ghiselin, 1974; Nelson, 1989; Mayr, 1982; Ereshefsky, 1992). Some researchers state that species do not exist in nature (*e.g.* Bessey, 1908; Ehrlich & Raven, 1969; Levin, 1979), although the majority recognise that they do (*e.g.* Babcock, 1931) or that they are at least a necessary concept in classification (*e.g.* Ehrlich & Raven, 1969; Levin, 1979). A number of different species concepts are currently in use and many authors recognise the practical necessity of recognising more than one concept if the huge diversity of life is to be classified (Porter, 1967; Burger, 1975). Many groups, for example, apomictic and clonal organisms and fossils, defy classification in the same sense as sexually reproducing organisms and they often have their own species concepts.

Several general concepts have been proposed for biparental sexually reproducing organisms, *e.g.* the biological species concept (Mayr, 1942, 1963), the recognition species concept (Paterson, 1978, 1985), the cohesion species concept (Templeton, 1989) and others, as reviewed by Slobodchikoff (1976). A great deal of discussion has surrounded the question of whether species should be defined by their isolation mechanisms (the biological species concept (Mayr, 1982)) or the mechanisms which hold them together (the recognition species concept (Paterson, 1978, 1985) and the cohesion species concept (Templeton, 1989)). However, a criticism of all these concepts is that it is usually not practical to investigate the amounts of isolation or cohesion present when defining many species. As a result of this difficulty, these concepts have not generally been applied by taxonomists (although many have claimed to have done so). In recent years a number of cladistically oriented species concepts have been proposed (*e.g.* Cracraft, 1983; Donoghue, 1985). These rely on the idea that species gain unique clusters of characters which cause a loss of interbreeding within a species and hence result in further speciation; species may, therefore, be recognised by the possession of these unique clusters of characters. However, as these diagnostic clusters are not necessarily morphological ones, several such clusters may be recognised within many existing morphologically delimited species. Usage of this concept may, therefore, necessitate a drastic alteration of existing morphological classifications even in cases where the existing classification does not conflict with the groups phylogeny and this inevitably leads to problems of readily identifying species. In order to

produce as little disruption to the current system of classification as is necessary and maintain a system whereby taxa may be readily identified without the use of complex techniques, it would seem more appropriate to treat such divisions of existing morphological taxa as infraspecific variants or perhaps only mention their existence in descriptions of the morphological species. Of all the characters used to define plant species, morphology results in the most widely usable general classifications, as the resulting species are (relatively) easily identified by users from a variety of backgrounds (King, 1993). The practice of defining species in terms of their relative morphological discontinuities has been criticised by Mayr (1963) who agues that firstly, there are often greater differences between individuals or populations than between related species and secondly, some reproductively isolated sympatric populations may be virtually morphologically identical. The former problem at least may be reduced by a detailed knowledge of the group in question and sound taxonomic experience (Crum, 1985). Due to the practical difficulties associated with the other concepts discussed above, the morphological species concept remains the most frequently employed species concept for cataloguing the world's biological diversity (Stuessy, 1990).

Many taxonomists consider the morphological and biological species concepts to be synonymous (Stuessy, 1972) and often use only morphological criteria to define biological species (*e.g.* Sosef, 1994). The two concepts have been defined as follows:

Biological species: 'groups of actually or potentially interbreeding populations which are reproductively isolated from other such groups' (Mayr, 1969).

Morphological species: 'a community, or a number of related communities, whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name' (Regan, 1926).

While it is not always possible to recognise reproductively isolated units using only morphology, the two concepts have been demonstrated to be largely compatible as morphological discontinuity is usually largely a result of common evolutionary descent and reproductive isolation (King, 1993). This approach, therefore, seems reasonable.

In the present study the morphological species concept has been applied because this was most practical as it was based mostly on herbarium material and therefore

the degree of interbreeding or isolation between individuals could not be tested. Phylogenetic species concepts were rejected as they can lead to problems with species identification. In view of the overlap between the morphological species concept and the biological species concept the former is considered to be more practical whilst maintaining biological meaning.

1.7.3. INFRASPECIFIC CATEGORIES

As with the genus and species concepts the delimitation of infraspecific taxa is often fraught with difficulties. A number of infraspecific categories have been proposed for both wild (Hamilton & Reichards, 1992) and cultivated plants (Styles, 1986). The International Code of Botanical Nomenclature (Greuter *et al.*, 1994) recognises the following categories: subspecies, variety, subvariety, form and subform. The code states that these categories must be used strictly in a hierarchical order but does not give any strict guide lines to their delimitation. This has led to a similar situation as occurs with the genus and species concepts whereby the same taxonomic rank may represent very different amounts of variation in different plant families.

Stuessy (1990) attempted to standardise the usage of infraspecific terminology by proposing a list of criteria for recognising subspecies, varieties and forms, the three most commonly utilised infraspecific categories in the angiosperms (Hamilton & Reichards, 1992). Stuessy's guidelines are used as the basis for the recognition of such taxa in the present study and are summarised in Table 1.2.

Table 1.2. Characteristics useful for distinguishing subspecies, varieties and forms in sexually reproducing flowering plants. (Reproduced from Stuessy (1990)).

	Characteristic				
Category	Morphological distinctions	Geographical patterns	Genetic divergence	Likelihood of Natural hybridization	Fertility of hybrids
Subspecies	several conspicuous differences	cohesive; largely allopatric or peripatric	usually markedly multigenic	possible along contact zones	markedly reduced fertility
Variety	one to few conspicuous differences	cohesive; largely allopatric with some overlap	multigenic or with some simple control	probable in overlap region	reduced fertility
Form	usually a single conspicuous difference	sporadic; sympatric	simple control (usually single gene)	always expected	complete fertility

1.8. DELIMITATION OF SPECIES AND INFRASPECIFIC TAXA

The principle method of recognising taxa based on the morphological species concept has traditionally been by the intuitive grouping of individuals into taxa and these into higher taxa, based on the relative similarities of their characters. The subjectivity of this process has sometimes, however, resulted in different classifications being produced by different researchers for the same group of organisms, particularly in groups characterised by inbreeding and asexual reproduction (Stuessy, 1990). Phenetic methods were introduced into systematics in the late 1950's in an attempt to reduce subjectivity in classification with the aims of producing more repeatable and stable classifications (Sneath, 1957; Michener & Sokal, 1957; Sokal & Sneath, 1963). Phenetic methods produce groups based on numerous explicit characters which are treated as equally weighted. Computers are often employed and have had a large impact in aiding the analysis of large, complex data sets. Traditional techniques, however, remain the most popular means of constructing classifications. This is probably because phenetic techniques are time consuming as they require the careful measurement of numerous characters and do not work well in cases where there are large amounts of missing data, as is commonly the case with herbarium material. The introduction of phenetic methods and also more recently, cladistic methods, have, however, greatly influenced traditional taxonomy and in particular have led to an increased emphasis being placed on the application of clearly defined methods and the selection and rigorous description of characters. Other beneficial results of these methods has been an increased desire for large numbers of characters which has often led to the discovery of previously un-utilized sources of taxonomic information and also, the identification of convergently evolved characters and their exclusion from classifications. Phenetic methods were not employed in the current study because of problems associated with large amounts of missing data. However, attempts were made to define clearly the method used to construct the classification and this was based on as many characters as possible. Methods and results are presented in Chapter 5.

Chapter 2
PHYLOGENETIC INVESTIGATION OF *BEGONIA* SECTION *SPHENANTHERA*

SECTION A: INTRODUCTION

2. PHYLOGENETIC INVESTIGATION OF *BEGONIA* SECTION *SPHENANTHERA*

SECTION A: INTRODUCTION

2A.1. INTRODUCTION TO CLADISTIC ANALYSIS

A glossary of cladistic terms is provided at the back of the thesis.

Since Darwin's (1859) publication of a plausible mechanism to explain how organisms evolve, attempts have been made to reconstruct phylogenies by considering the distribution of character states (Coombs *et al.*, 1981). Many such attempts have utilised subjective methods based on intuitive views of character evolution and have, as a result, frequently produced markedly different hypotheses of evolutionary relationship between the same organisms (Stuessy, 1990). In an attempt to make the methods of phylogenetic reconstruction more objective, cladistic methodology was developed within the field of biology as an 'explicit approach that directly reflects evolutionary relationships' (Stuessy, 1990). Hennig (1950, 1966) most coherently formulated cladistic methodology and the basic concepts he presented are still generally accepted today although a number of new ideas and methods have been (and continue to be) developed and incorporated into the methodology. Additionally, many of the original premises formulated by Hennig (1950) have been found to be unnecessary and current cladistic methodology is largely based on the assumptions that each taxon has a unique phylogenetic history and that evolutionary relationships between taxa can be reconstructed by maximising congruence of homologous character states on a branching diagram.

Many different views regarding appropriate cladistic methodology currently exist amongst practitioners and different cladistic procedures, sometimes based on different evolutionary assumptions are practised. Presently, some of the more contentious issues within cladistics include: the conversion of cladograms into classifications (discussed in 2A.5.), the appropriate method of combining information from morphology and molecules (discussed in 2D.1.) and the choice of algorithms for the analysis of large data sets. A number of ideas are generally accepted and the basic procedure usually practised when undertaking a cladistic analysis of a group may be summarised as follows:

a) Select a group for study (the ingroup) based on the assumption that it is monophyletic. (Groups presumed not to be monophyletic may also be investigated

inorder to determine the relative phylogenetic relationships of the included taxa as long as all the probable sistergroup taxa are included in the analyses).
b) Select characters believed to be homologous within the group and which have variable character states, some of which occur in at least two of the terminal taxa.
c) Describe and/or measure character states and use these to construct a data matrix.
d) Select algorithms and generate a cladogram.
e) Root the cladogram. In the past this has been achieved by several different methods. Currently the most accepted method is by outgroup comparison. This is discussed in 2A.3.
f) Assess the original hypotheses concerning character homology and taxon monophyly. Characters and taxa may be temporarily removed at this stage to explore their affect upon cladogram topology.

Very few cladistic studies of *Begonia* have been published and the suspected polyphyletic nature of many of the sections (Brouillet, pers comm.; Doorenbos, pers comm.) reflects the general lack of phylogenetic information for the genus.

Cladistic methodology was used in the current study to explore evolutionary relationships of the section *Sphenanthera* and selected outgroup taxa and to determine which characters are suitable for delimiting sections. The choice of outgroup taxa is explained in 2A.3. Methods of converting cladograms into classifications are discussed in 2A.5. Data were gathered from a variety of sources. Those characters obtained from morphology and anatomy were initially analysed separately to those from molecules (section 2B and 2C respectively). Alternative ways of combining this information are explored and a final cladogram and classification are presented in section 2D.

2A.2. CHARACTERS AND CHARACTER STATES

Cladistic characters are chosen based on their perceived ability to reconstruct evolutionary change in their host organisms. An important consideration when comparing characters and character states is to determine whether they resemble each other because they have evolved from a common ancestor (*i.*e. they are homologous), or because of convergent evolution (*i.*e. they are analogous). Phylogenetic studies should only be based on homologous characters as only these reflect evolutionary relationships accurately. As the determination of homology or

analogy requires prior knowledge of phylogeny, it is only possible to test characters by comparing them with other characters after an analysis has been completed (Bock, 1977). At this stage those characters thought to be analogous, because they are not congruent with other characters, may be temporarily removed and the data set reanalysed to explore their affect upon the analysis. The initial incorporation of analogous characters into an analysis may be lessened by careful developmental and structural studies (Stuessy, 1990). As relatively few characters are generally included in cladistic compared to phenetic analyses, their selection is a particularly important stage of the analysis and one which may markedly affect the outcome of the analyses (Stuessy, 1990). Characters which are highly conserved, possess discrete sub-divisions (states) and also occur in closely related outgroups are considered most appropriate (Stuessy, 1990). Cladists have tended to use qualitative rather than quantitative characters because the latter have been considered either not to 'vary cladistically' (Pimentel & Riggins, 1987) or to be too noisy to allow recovery of a phylogenetic signal (Kraus, 1988). The exclusion of quantitative characters is, however, both subjective and unnecessary. Thiele (1993) for example, demonstrated that separate analyses of quantitative and qualitative character of members of the genus *Banksia* resulted in similar cladograms. Both qualitative and quantitative characters were incorporated in the present study.

2A.3. SELECTION OF POTENTIAL OUTGROUPS

Outgroup comparison is currently one of the most widely used methods of determining character polarity in cladistic analysis (Watrous & Wheeler, 1981). The method identifies the relatively primitive state of a character (its plesiomorphic state) by looking for such states in taxa which are assumed to have ancestors which evolved prior to the evolution of the ingroup and which, therefore, share the primitive (sympleisiomorphic) character state of the ingroup, but not the advanced (apomorphic) state. For an in-depth coverage of the subject see Maddison *et al.* (1984) and Nixon & Carpenter (1993).

Outgroups may also be used to discover whether an ingroup is monophyletic, paraphyletic or polyphyletic, by observing the position of the outgroup taxa relative to the ingroup on the cladogram (Nixon & Carpenter, 1993) (for a definition of these terms see 2A.4.). If more than one outgroup is included in an analysis, their position relative to the ingroup will also give an indication of their relative phylogenetic affinities with the ingroup, as the most closely related

outgroup taxa should occupy the closest position to the ingroup on the cladogram (Maddison *et al.*, 1984).

In the case of phylogenetic investigations which deal with parts of large natural taxa, all possible outgroups cannot be included in the analysis due to the limitations of time. Therefore, those taxa thought to share close phylogenetic affinity to the ingroup should be selected for analysis. Careful selection of outgroup taxa will minimise the risk of polyphyletic taxa being perceived as monophyletic. After the analysis, taxonomic groups may be screened against all existing taxa within a known monophyletic group to confirm that they are characterised by unique synapomorphies.

The basic unit of the outgroup taxa used in these analyses is the species. Sections were not used as outgroups as many of them are believed to be polyphyletic (Brouillet pers. comm.; Doorenbos, pers. comm.). The lack of phylogenetic information for *Begonia* means that it is often difficult to decide on appropriate outgroups. As a result of this lack of phylogenetic information, Sosef (pers. comm.) restricted his search for outgroup taxa in his cladistic study of the African sections *Loasibegonia* and *Scutobegonia* to the other relatively well known African taxa (Sosef, 1994). In view of this difficulty, several potential outgroup taxa within *Begonia* were selected by consulting the known phylogenetic information on the genus. Information was obtained from the following sources: ITS sequence data (Brouillet, pers. comm.), *rbc*L sequence data (Swensen, pers. comm.), morphology (de Candolle, 1859; Irmscher, 1925), anatomy (Fellerer, 1892), style and ovary anatomy (Xiao-bai & Fu-hsiung, 1994), seed micro-morphology (Bouman, pers. comm.) and leaf micro-morphology (Cuerrier *et al.*, 1990). Additional taxa were chosen by looking for species with similar morphological character combinations to the members of section *Sphenanthera*. This was carried out by observation of herbarium material at the Royal Botanic Gardens, Edinburgh and Kew and the Natural History Museum (London) and by consultation of Baranov & Barkley (1974), Reitsma (1983) and Smith *et al.* (1986). Where past authors have suggested affinities between members of section *Sphenanthera* and taxa outside of *Sphenanthera* these latter taxa have also usually been included in the analyses.

As little is known of the phylogenetic relationships among the majority of taxa in *Begonia*, additional outgroup taxa from outside of the genus are also required to help determine character polarity. Evidence from *rbc*L sequence data strongly suggests that the genus *Begonia* is monophyletic and the genus *Hillebrandia* is its

sister group (Swensen, pers. comm.). *Hillebrandia* is, therefore, included as an outgroup in both the morphological and molecular analyses. Molecular data also suggests that the Cucurbitaceae and Datiscaceae are closely related to the Begoniaceae (Swensen *et al.*, 1994). *Datisca* has, therefore, also been included in the morphological analyses. As no living material of this genus could be obtained and it proved difficult to obtain sufficient quantities of PCR product from herbarium material of this taxon for the molecular study, it was not included in the molecular analyses.

Where possible, taxa were chosen which were represented in cultivation. This was because molecular data was only readily obtained from living and silica dried plants (see 2C.2.) and, therefore, only these taxa could be compared in both the morphological and molecular analyses. In order to compare stringently the cladograms produced from the morphological and molecular data, an attempt was made to include the same taxa in both analyses. However, as it was not possible to obtain living material of all the required taxa the effects of missing data and taxa were investigated prior to selecting a final cladogram (see 2D.6.). Replicate species from certain sections were included in the study in order to test both the monophyly of these outgroup taxa and the ability of the characters used in the analysis to group species assigned to previously well defined sections. An attempt was also made to include the type species of each section analysed, so that if future changes are made to the circumscription of the sections they will still be represented in the analysis. The outgroup taxa are shown in Table 2.1. and the specimens used in the analysis are shown in Appendix A and B.

Table 2.1. Sectional membership and distribution of the potential outgroup species included in the study.

Datisca cannibina L.
Hillebrandia sandwichensis Oliv.

Begonia section	species
Asia	
Apterobegonia	*B. delicatula* Parish ex C.B. Clarke (T)
Bracteibegonia	*B. burbidgii* Stapf.
Coelocentrum	*B. masoniana* Irmsch. (*)
Diploclinium	*B. cordifolia* (Wight) Thwaites (T), *B. tayabensis* Merr. (*)
Monopteron	*B. nepalensis* Warb. (T)
Parvibegonia	*B. martabanica* A.DC.(T)
Petermannia	*B. cumingiana* A.DC. (T), *B. brachybotrys* Merr. & Perry, *B. brevirimosa* Irmsch. (*), *B. chlorosticta* Sands (*)
Platycentrum	*B. xanthina* Hook. (T), *B. annulata* K. Koch (*), *B. hatacoa* F. Hamilton ex D. Don (*), *B. sp.* 1 (*), *B. sp.* 2 (*)
Reichenheimia	*B. floccifera* Bedd. (*), *B. goegoensis* N.E. Br. (*)
Ignota	*B. amphioxis* Sands (*), *B. balansana* Gagnep. (*)
Africa	
Augustia	*B. dregei* Otto & Dietrich (T*)
Mezierea	*B. salaziensis* (Gaud.) Warb. (T*),*B. meyeri-johannis* Engler(*)
Rostrobegonia	*B. sutherlandii* Hook. f.(*)
Scutobegonia	*B. prismatocarpa* Hook. (*), *B. quadrialata* Warb. (*)
Squamibegonia	*B. poculifera* Warb. (*)
Tetraphylla	*B. manii* Hook. f. (T*)
Americas	
Casparya	*B. urticae* L. (T)
Solanathera	*B. solananthera* A.DC. (*)
Trachelocarpus	*B. herbacea* Vell. (T*)
Asia & Americas	
Begonia	*B. grandis* Dryand. *subsp. sinensis* (A.DC.) Irmsch.(*), *B. incarnata* Link & Otto (T*)

Key to symbols

(*) Taxon included in molecular analysis (all taxa were included in morphological analysis). [*Begonia acetosella* Craib var. *acetosella* Irmsch., *B. longifolia* Blume, *B. mengyangensis* Tebbitt & K.Y. Guan and *B. roxbrghii* (Miq.) A.DC. from section *Sphenanthera* (Hasskarl) *sensu* Irmsch. were also included in the molecular study.]

(T) Taxon is the type species of its section.

2A.4. MONOPHYLETIC, PARAPHYLETIC AND POLYPHYLETIC GROUPS - SOME DEFINITIONS

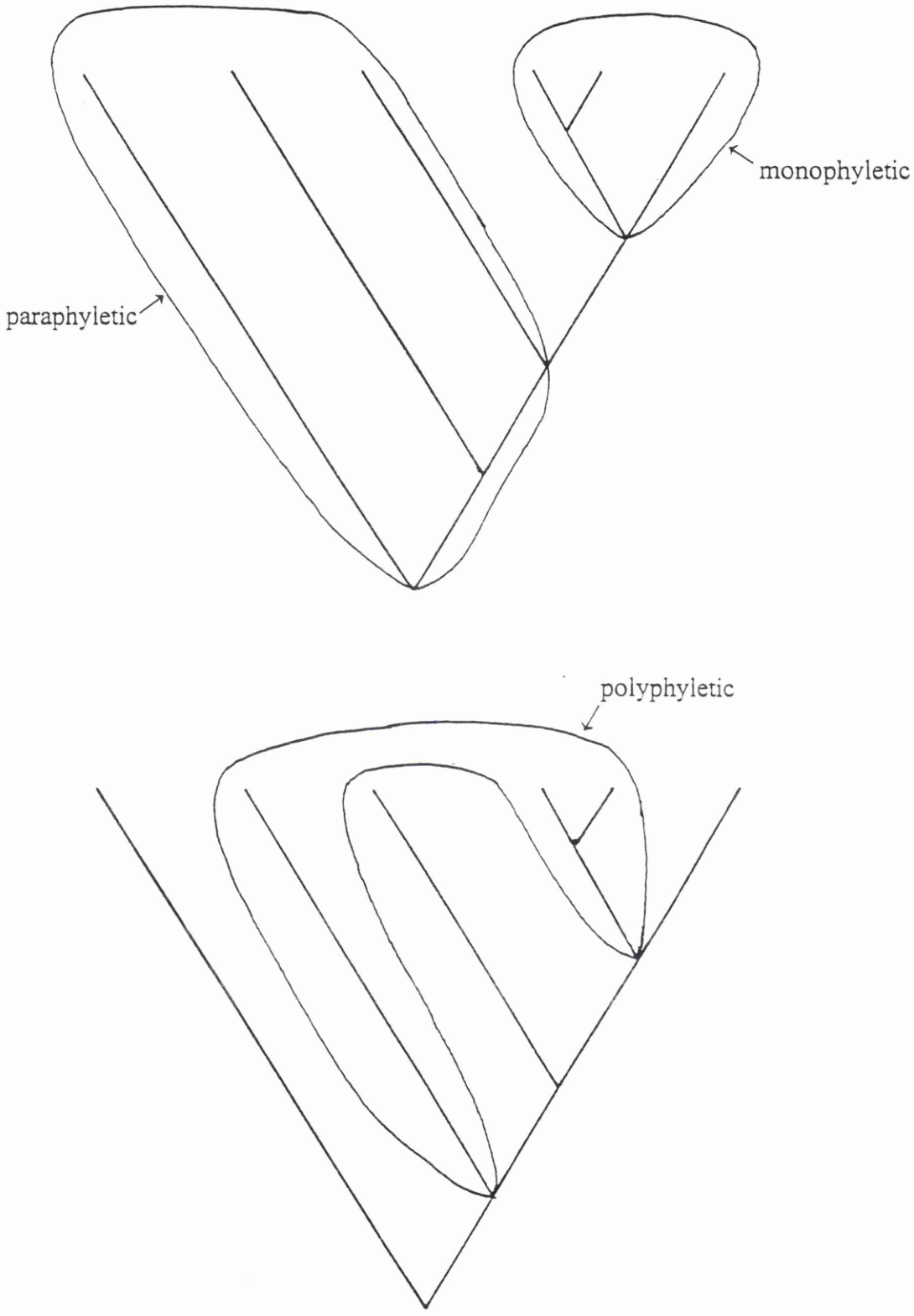
A great deal of attention has been given to the definition of the terms monophyletic, paraphyletic and polyphyletic (Ashlock, 1971, 1972; Nelson, 1971, 1973; Farris, 1974; Platnick, 1977) and much confusion surrounds their application. In order to clarify their present meanings, definitions are presented and illustrated in Figure 2A.1. These definitions follow Hennig (1966).

Monophyletic: A group which includes all descendants of a common ancestor.

Paraphyletic: A group based on symplesiomorphic characters which does not include all the descendants of a common ancestor.

Polyphyletic: A group based on convergent characters rather than common ancestry and which does not include all the descendants of a common ancestor.

Fig. 2A.1. Monophyletic, paraphyletic and polyphyletic groups as defined in the present study



2A.5. CLADISTICS & CLASSIFICATIONS

Classifications offer a means of dealing with the complexity of nature in a way that humans may comprehend. The association, or classification, of organisms into communicable groups on the basis of shared attributes appears to have always been the main objective of taxonomy. In the past many different attributes have been used to classify organisms. Within *Begonia*, for example, taxonomists have erected groups based on both physical appearance and distribution. Irmscher (1925) for example, recognises groups based on morphology and then groups these into three categories, viz. African, Asian and American, which reflect their distribution. The attributes used to construct classifications often differ depending upon the requirements of the user. The system of classification which appears to be used by the Hmong people of northern Vietnam, for example, contrasts with Irmscher's classification as it groups *Begonia* into two categories, those which are eaten and those which are not (pers. obs.) and is, therefore, of more local practical use. The following discussion will focus on general purpose scientific classifications and primarily their means of construction.

As the purpose of classification is transmission of information, the best classification is one which 'combines greatest information content with greatest ease of information retrieval' (Mayr, 1969). Other important qualities of classifications are stability and the ability to predict unknown characters (Rollins, 1965). Much discussion has concerned whether greatest information content may be achieved by constructing classifications using phenetic or cladistic approaches (Gower, 1974; Farris, 1979). The types of information contained within phenetic and cladistic based classifications are, however, different as the former contain information regarding phenetic similarity while the latter contain information regarding phylogeny. Phenetic techniques aim to reduce subjectivity of character choice by incorporating as many characters as possible into an analysis and for this reason are claimed to produce more stable classifications than those produced using traditional methods (Sokal & Sneath, 1963; Sneath & Sokal, 1973). Cladistic techniques should also, however, produce stable classifications as they aim to reflect phylogeny and can, therefore, (unlike phenetic methods) only have one correct answer. Phylogenetic based classifications are generally considered most predictive because the members of natural groups share a common ancestor and, therefore, often share characters in addition to those required for their identification (Cronquist, 1987). Cladistic methodology was used in the current study as it offers

the most objective means of reconstructing phylogeny and classifications based on phylogeny are considered both stable and predictive.

At present, no formal system of phylogenetic (cladistic) taxonomy exists, although a large number of suggestions have been proposed (de Queiroz & Gauthier, 1992). The strict usage of a phylogenetic system of classification would necessitate several fundamental changes to the existing system and probably for this reason has not been readily accepted. Phylogenetic taxonomy if strictly applied, is for example, not compatible with existing concepts of Linnaean binomals, synonymy or the application of taxonomic ranks (de Queiroz & Gauthier, 1992). Many researchers have, therefore, attempted a compromise between disrupting the present traditional system and representing nature as a phylogenetic hierarchy. This has often resulted in the recognition of taxa on the basis of monophyly but a continued application of all the taxonomic concepts of the traditional system to these taxa (de Queiroz & Gauthier, 1992). Other authors, while advocating cladistic methods to reconstruct phylogeny, have argued the value of recognising a certain type of paraphyletic taxon as well as monophyletic taxa (Meacham & Duncan, 1987), especially in cases where several apomorphies exist within a clade and therefore allow the recognition of distinct phenetically recognisable groups (Sosef, 1994). Sytsma & Gottlieb (1986, p.5556) found that chloroplast restriction-site data strongly suggests that the morphologically distinct monotypic genus *Heterogaura* (Onagraceae) evolved from within one section of the genus *Clarkia.* In connection with this observation they state 'mono- and ditypic genera need not stand in a basal position with respect to related and more specious genera, but may be derived from within them.' In another study based on chloroplast site data, Soltis *et al.* (1990) found that the morphologically distinct monotypic genus *Conimitella* (Saxifragaceae) evolved from within the genus *Mitella.* Soltis *et al.* (1990, p.360) conclude that 'restriction site analysis of cpDNA, in conjunction with evidence from crossability and cytology, clearly indicate that *Conimitella williamsii* is a *Mitella.*' The taxonomic treatment of distinct paraphyletic higher taxa is, therefore, far from obvious. Paraphyletic groups delimited by several diagnostic characters are given formal taxonomic rank here. This is because such clusters of characters are believed to represent macro-evolutionary events. As monophyletic taxa maximise phylogenetic information content these are recognised in all other cases. Existing groups which conflict markedly with phylogenetic knowledge (*i.e.* polyphyletic groups and paraphyletic groups defined by plesiomorphic characters) are not accepted. The principles and rules for phylogenetic taxonomy reviewed and proposed by de Queiroz & Gauthier (1992) are rejected as these necessitate

excessive change. This would create an ineffective communication tool because the taxonomic concepts it would recognise would not be comparable with those of past and existing plant classifications.

Chapter 2
PHYLOGENETIC INVESTIGATION OF *BEGONIA* SECTION *SPHENANTHERA*

SECTION B: MORPHOLOGY AND ANATOMY

SECTION 2B: MORPHOLOGY AND ANATOMY

2B.1. INTRODUCTION

Morphology and to a lesser extent anatomy, have traditionally been the major sources of characters used in systematic studies. This is especially true of those studies based on herbarium material. The fact that such characters are relatively easily and cheaply investigated has probably contributed most to their common usage in systematics. The incorporation of macro-morphological characters within classifications based on phylogeny, either during the process of cladogram construction, or later by mapping them onto a cladogram (*e.g.* one produced from molecular characters), is also important as it allows the final classification to be readily used for identification purposes without resorting to complex techniques. Both traditional and new morphological and anatomical characters have been included as sources of data in the current cladistic study. A review of the systematic usage of many of these characters within *Begonia* is presented in 2B.3. Character coding and analysis is explained in 2B.4.1. and the cladograms are discussed in 2B.4.2.

2B.2. MATERIALS AND METHODS

A search of the literature and an independent examination of the plants revealed 40 characters which were potentially phylogenetically informative (Table 2.2.). These characters were then examined in detail in both cultivated (Appendix A) and herbarium (Appendix B) material. In the case of *B. acetosella* Craib, *B. balansana* Gagnepain, *B. handelii* Irmsch. and *B. longifolia* Blume, data was also recorded in the field.

Micro-morphological characters, with the exception of the petiole hairs, anther endothecial wall patterns and seeds (discussed below), were examined under a dissection microscope (Olympus 5240) after soaking in wetting agent for about 10 minutes (in the case of herbarium material). The practice of using steam to soften herbarium material was not utilised in this study as it is known to make *Begonia* specimens very brittle (Klotzsch, 1855). Line drawings were made throughout the study to assist character comparison.

Petiole hair morphology was examined by removing a patch of hairs from mid-way along the petiole and then mounting this on a microscope slide and viewing at x320 magnification under a light microscope.

Endothecial wall thickenings of the anthers were examined as follows: Whole syngenesious anthers were removed from specimens and cleared by soaking for 24 hours in a watch-glass containing 10% NaOH and a few drops of concentrated H_2O_2 (Abuhadra, pers. comm.). Anthers were then removed and placed on a microscope slide and lightly squashed with a cover-slip and viewed at x320 magnification using phase contrast microscopy. Cell wall type was determined from cells mid-way between the ends of the anthers and mid-way from the connective and outer locule wall. Additional dissections of the anthers were made to allow observation of the 3-dimensional structure of the wall thickenings. This was done by teasing the tissue apart using dissecting needles and applying firm downward pressure on the coverslip. Appendix C lists the specimens used in the anatomical study of the anthers.

For examination of seed characters, seeds of the taxa belonging to section *Sphenanthera* and the American outgroups were collected from herbarium material (Appendix D) by gently tapping the fruits. Indehiscent fruit were pierced with a dissecting needle to enable seed collection. Mature seeds were selected using a dissecting microscope and fixed to aluminium pin stubs using Tempfix (Agar Scientific Ltd.). These where then sputter-coated with a thin layer of gold for five minutes in a Emscope Gold Sputter coater and observed in a scanning electron microscope (Leica Cambridge Stereoscan 360). Dirty seeds were cleaned by soaking them in water containing a drop of detergent for 30 minutes and then subjecting them to ultrasonic vibration. These were then left to air dry in a dust free environment containing silica gel for two weeks. Seed ornamentation was determined from the central regions of the testa cells. Seed characters of the African taxa were taken from de Lange & Bouman (1992). Seed characters of *B. balansana* and the Asian outgroup species were taken from electron micrographs housed at the Hugo de Vries Laboratory, University of Amsterdam, The Netherlands.

Table 2.2. Morphological and anatomical characters and character coding used in the analyses

1. Stems woody at base
0) yes
1) no

2. Internode type
0) extended
1) compressed
2) acaulescent

3. Rhizomes or tubers
0) present
1) absent

4. Stipule longevity
0) absent
1) long persisting
2) falling early

5. Stomata clustered
0) no
1) yes

6. Petiole hair morphology
0) stalk unicellular
1) stalk multicellular below, unicellular above
2) stalks multicellular
3) both uni- and multicellular hair types
4) stellate
5) glabrous

7. Female or bisexual inflorescence position
0) arising from leaf axils
1) false petiolar

8. Female peduncle length
0) usually longer than 2 cm
1) 1-2 cm
2) less than 0.5 cm
3) absent

9. Female or bisexual inflorescence type
0) dichasium
1) condensed monochasium
2) raceme
3) flowers solitary
4) panicle

10. Form of sex separation
0) monoecious plants with bisexual inflorescences
1) monoecious plants with unisexual inflorescences
2) dioecious plants or monoecious plants with markedly protrandrous unisexual inflorescences

11. Young male flowers enclosed by large (> 1cm) bracts
0) no
1) yes

12. Male tepal number
0) 10
1) 6
2) 4
3) 2

13. Relative widths of outer and inner male tepals
0) more or less equal
1) inner much thinner than outer

14. Shape of male tepal apex
0) rounded
1) acute

15. Male tepal hair type
0) multicellular
1) unicellular
2) glabrous
3) stellate

16. Male receptacle shape
0) flat or slightly raised
1) rounded or a torus

17. Endothecial wall pattern
0) hoop-shaped
1) U-shaped
2) very thick U-shaped

18. Filament fusion
0) free to base
1) fused at base
2) fused to half-way into a column
3) fused for whole length

19. Anther apex hooded
0) no
1) yes

20. Anther dehiscence position
0) on the inner surface
1) starting from the side of the locule and progressing onto the inner surface
2) via a straight line down side of locule

21. Locules noticibly seperated by connective
0) no
1) yes

TABLE 2.2. (continued)

22. Connective extended at apex
0) no
1) slightly extended
2) markedly extended to shield-like

23. Female tepal number
0) 10
1) 6
2) 5
3) 4
4) 3
5) 2

24. Style number
0) 2
1) 3
2) 4
3) 5
4) 6

25. Style shape
0) bifid
1) shortly bifid
2) many branched
3) entire

26. Style fusion
0) Free
1) Fused at base < 1 mm
2) Fused at base for > 1 mm

27. Stigma position
0) in a band and spiralled
1) in a band and not spiralled
2) covering most of style or all over the style

28. Ovary position
0) partially inferior
1) fully inferior

29. Locule number
0) 2
1) 3
2) 4
3) 5-7

30. Placentation
0) parietal
1) axil

31. Placentae
0) Free and bearing ovules on both surfaces
1) Free and bearing ovules only on outer surfaces
2) Fused

32. Ovary appendages
0) no appendages
1) equal or almost equal wings
2) unequal wings
3) single wing
4) horns-like expanded locules
5) ribs

33. Ovary wing shape
0) tongue shaped
1) equilateral triangle
2) wedge-ridge-shaped
3) rounded
4) isosceles or scalene triangle

34. Fruit orientation
0) pendulous
1) nodding
2) more or less erect

35. Fruit dehiscence
0) between styles
1) via distinct lines next to the wings
2) indehiscent

36. Fruit texture when mature (fresh state)
0) Dry
1) Fleshy to leathery

37. Fruit body shape
0) ovate-elliptic
1) turbinate
2) comma-shaped
3) coronate
4) flask shaped
5) fusiform

38. Seed ornamentation
0) present
1) feint, only on some specimens or absent

39. Operculum shape
0) nipple-shaped
1) obtuse
2) almost flat
3) columnular

40. Number of testa cells along length of seed
0) 5-10
1) 1-4

2B.3. A REVIEW OF THE CHARACTERS INCLUDED IN THE ANALYSES

In the following section, many of the characters are defined, illustrated and discussed in the context of past taxonomic studies and current phylogenetic knowledge of the family. A full list of the morphological and anatomical characters used in the analyses is presented in Table 2.2. The numbering system used below follows this table.

2B.3.1. VEGETATIVE PARTS

1. Stems woody at base:
The majority of *Begonia* species have succulent stems. Woody stems are found in a few African and New World *Begonia* taxa and in *Datisca*. The wood anatomy of *Begonia* and *Datisca* has much in common and supports a close relationship between these taxa (Carlquist, 1985). Irmscher (1925) states that woodiness is rare in *Begonia* but otherwise little mention of this character occurs in the taxonomic literature of the Begoniaceae.

2. Internode type:
In *Begonia*, the length of the internode varies from being so short that the plant appears stemless, through a state where the nodes are almost touching or up to 2 cm apart and finally to a state where they are up to 30 cm or more long. Internode type appears to be closely correlated with plant habit. The latter is, therefore, not included here as a separate character. A few well defined sections, *e.g. Platycentrum*, *Gireoudia* contain more than one of the states recognised here suggesting that at the generic level the character may have evolved multiple times.

4. Stipule longevity:
The stipules of *Begonia* are described by Irmscher (1925) as caducous and leafy or persistent and membranous to occasionally almost leathery. The present study confirms this. The inconsistency with which stipule longevity is recorded in the literature makes it impossible to say whether character states are constant within the sections, although examination of living material suggests that this is generally the case. Stipules are absent in *Datisca*.

5. Stomata arranged in clusters:

A stomatal cluster may be defined as a group of two or more guard cells belonging to one stomatal chamber, where the individual stomata within the cluster group are separated from each other by subsiduary cells (Fellerer, 1892). The morphology and physiological advantages of stomatal clusters in *Begonia* have been discussed in detail (Boghdan & Barkley, 1972) but little taxonomic attention has been given to them. Cuerrier *et al.* (1991a & 1991b) include number of stomata in a cluster as a character in their investigation of leaf micro-morphology within *Begonia*, but do not appear to attribute it much taxonomic significance.

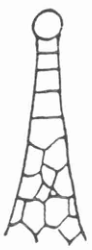
6. Petiole hair morphology:

The large diversity of hair types found in *Begonia* have been classified by Fellerer (1892) as either non-secretary or secretary, a practice followed by Metcalfe & Chalk (1950). Boghdan & Barkley (1969) state that hair characters are too evolutionary plastic to be of taxonomic value within *Begonia*. They also note the occurrence of different hair types on particular parts of the plant. In an analysis of leaf micro-morphological characters Cuerrier *et al.* (1991a) include 12 types of emergence, trichome and hair. The latter study revealed that, several sections were characterised by the presence of a particular hair type, but no firm conclusions could be made due to difficulties with character coding.

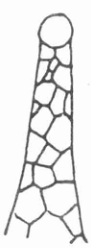
The hair types included in the present study represent only a small amount of the diversity found within *Begonia*. Character coding was also problematic here. The lack of developmental information regarding hairs makes it difficult to decide whether different hair forms should be treated as a single or many characters. This problem was reduced by recording hair characters from mature tissue only and by examining several hairs from many different plants. Several species in this study also showed the occurrence of different hair types on different parts of the plant. Hair type was, therefore, only recorded from the petiole where they are usually most abundant and easily observed. The hair types recognised in the cladistic analysis are illustrated in Figure 2B.1.

Fig. 2B.1. Types of leaf hair

stalk unicellular



stalk multicellular below,
unicellular above



stalk multicellular

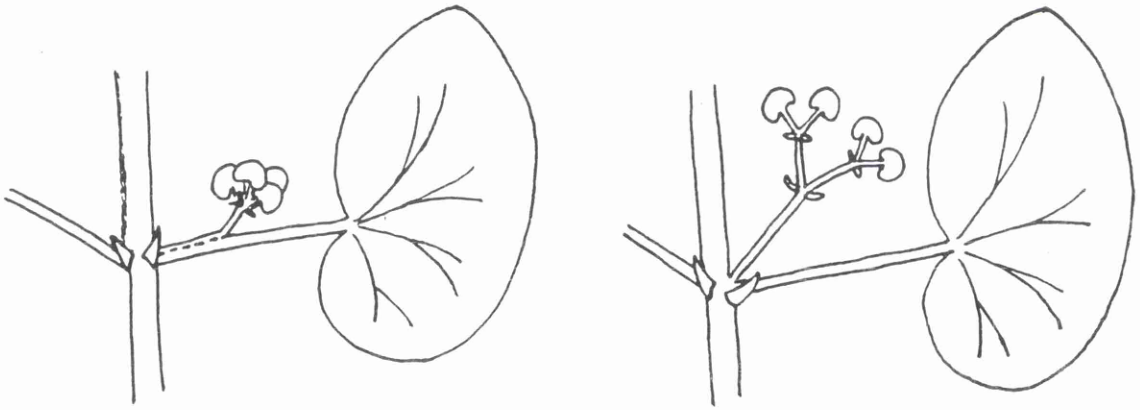
stellate

2B.3.2. INFLORESCENCE

7. Female or bisexual inflorescence position:

The vast majority of species within the Begoniaceae have either true axillary or terminal inflorescences. Some members of section *Petermannia*, *e.g. B. brevirimosa*, however, exhibit a condition whereby the peduncle of the female or bisexual inflorescence is partially fused with the lower portion of the petiole (Fig.2B.2.). In these cases the inflorescence gives the appearance of emerging from half-way along the petiole rather than from the leaf axil and is here termed false petiolar. In the present study, three taxa presently included in section *Sphenanthera*, viz. *B. axillipara*, *B. brachyptera* and *B. pseudolateralis*, exhibit this characteristic. The names *axillipara* and *pseudolateralis* clearly refer to this condition.

Fig. 2B.2. Axillary and false petiolar inflorescences



false petiolar

arising from leaf axils

9. Female or bisexual inflorescence type:

Irmscher (1914) classifies the wide range of inflorescence arrangements found in *Begonia* into two basic forms, cymes and racemes. These are then subdivided into a number of states based on the relative positions of male and female flowers and in the case of cymes whether they are dichasial or cicinnial. Goulet *et al.* (1994) in an analysis of inflorescence architecture of 71 species of *Begonia* recognise nine architectural models, the majority of which are asymmetric in arrangement. Some of the models do not appear to fit readily within Irmscher's (1914) scheme. In section *Gireoudia* a trend from symmetrical to asymmetrical cymes has been reported (Burt-Utley, 1985). Matzke (1938) observed that in *B. cucullata* initially dichasial branches became modified into cincinni. The five inflorescence states observed in the present study are equivalent to Irmscher's broad divisions.

10. Form of sex separation:

Dioecism has only been recorded within *Begonia* from the section *Mezierea* (Klazenga *et al.*, 1994) and doubtfully in *B. aborensis* of section *Sphenanthera* (Dunn, 1920). Examination of herbarium material in the present study suggests that dioecism probably occurs in all the 4-locular taxa of section *Sphenanthera*. This is supported by collectors notes, but cannot be confirmed without observing the development of inflorescences in living plants as it is impossible to differentiate between dioecism and plants with temporally separated unisexual inflorescences. In those species where living material was available, (*B. acetosella*, *B. handelii*, *B. roxburghii*) dioecism is confirmed. *Datisca cannabina* L. is reported to be dioecious (Rieseberg *et al.*, 1992).

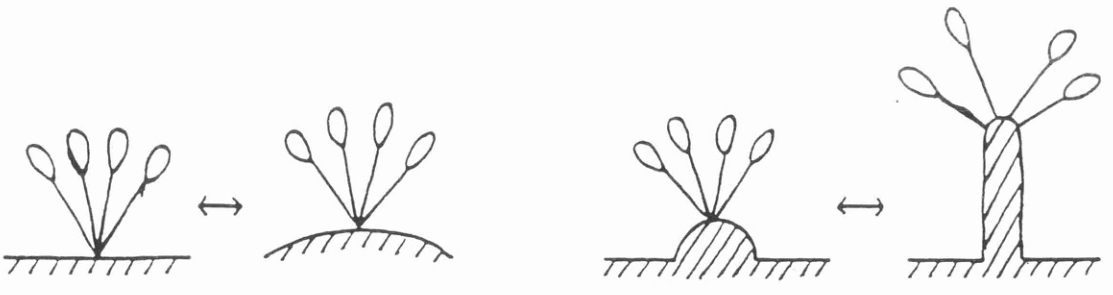
2B.3.3. MALE FLOWERS

11. Young male flowers enclosed by large (>1 cm) bracts:
The majority of taxa have bracts which are usually much shorter than 1 cm, a small number of sections, *e.g. Bracteibegonia*, *Solananthera*, *Squamibegonia*, however, possess characteristically large (>1 cm) bracts which completely surround the young flower buds.

12. & 23. Male & female tepal number:
Klotzsch (1855) considers the number of tepals in flowers of both sexes to be of taxonomic value within the Begoniaceae. De Candolle (1859), however, states that while the female tepal number is of some taxonomic value, the plasticity of male tepal number renders it of little use. In the sections investigated in the present study, male and female tepal numbers were largely conserved, therefore, both sexes were included in the analyses.

16. Male receptacle shape:
This character does not appear to have been given a great deal of attention by past authors. It is included in the study because it appears to have taxonomic significance within section *Sphenanthera* and *Platycentrum*. The character states recognised here are illustrated in Figure 2B.3.

Fig. 2B.3. Male receptacle shapes



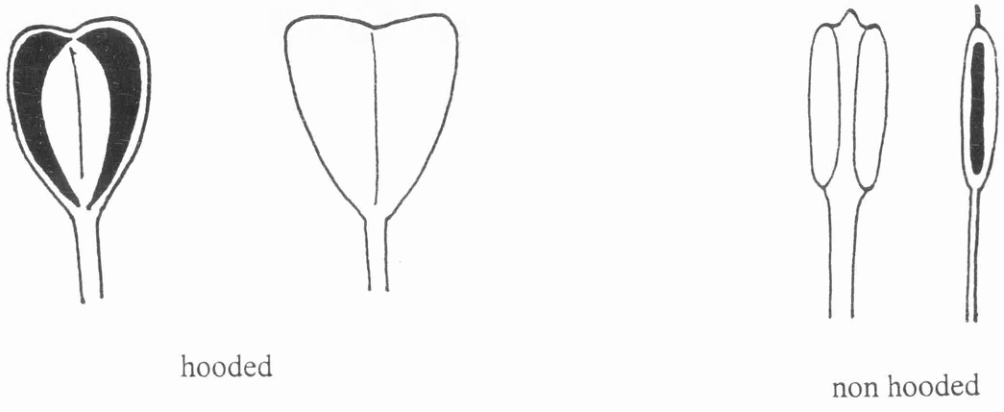
flat or slightly raised

rounded or a torus

17.–22 Stamen characters:

De Candolle (1859) stresses the importance of the form and dehiscence of the anthers, stating that several of the groups established by Klotzsch have something characteristic in the anthers, unfortunately this "something" is not always easy to express. Irmscher (1925) considers stamens to be of systematic value at the sectional level. Clarke (1881), however, considers the characters of the stamen to be of little taxonomic use. A broad scale survey of the stamens of *Begonia* carried out as part of both the present study and a B.Sc. honours project (Cameron MacIver, 1997) found that many of the sections do possess characteristic stamens. Of the sections included within this study *Petermannia* is particularly well characterised by its stamen morphology and anatomy. The character states anther hooded and not hooded are illustrated in Figure 2B.4.

Fig. 2B.4. Hooded and non hooded anthers



The nature of the endothecial wall patterns of *Begonia* are of particular interest as they represent a previously unused source of potential phylogenetic information. A further advantage of the character is that it may be observed from herbarium material. The taxonomic value of wall thickenings in anther cells has long been recognised within the angiosperms as a whole (*e.g.* Meyen, 1828; Purkinje, 1830; Mohl, 1830). In a review of endothecial patterns, Manning (1996) lists 125 families in which this character has been examined, although in almost all of these, only a single, or at the most ten species per family have been studied. Noel (1983) suggests that these patterns may be of greater taxonomic and phylogenetic value than previously realised. The phylogenetic value of the character is, however, usually restricted to the family level because it is often conserved at the generic

level and is thought to exhibit high levels of homoplasy between families (Manning, 1996). Manning (1996) lists a single unnamed species of the Begoniaceae which has been investigated and is said to have U-shaped thickenings and a base plate.

The form of anther thickening present within *Begonia* and *Hillebrandia* is largely constant. Using the terminology of Manning (1996) these may be classified as U-shaped. This study revealed an additional type of thickening in *Begonia*. All the species which were examined from sections *Petermannia* (15), *Tetraphila* (1), *Solananthera* (1), *Bracteibegonia* (1) and three species currently included within *Sphenanthera* were found to possess a distinct type of thickening with thick ribs and well developed base plates. *Datisca cannabina* possesses a type of thickening which is distinct from the Begoniaceae. *Symbegonia* is also of interest (although not included in the present phylogenetic study) as it did not show anthers thickenings in any of the eight taxa examined, a feature which supports its recognition at the generic level. Endothecial wall thickenings are illustrated in Plates 1-2. Appendix C lists the specimens used in the anatomical study of the anthers.

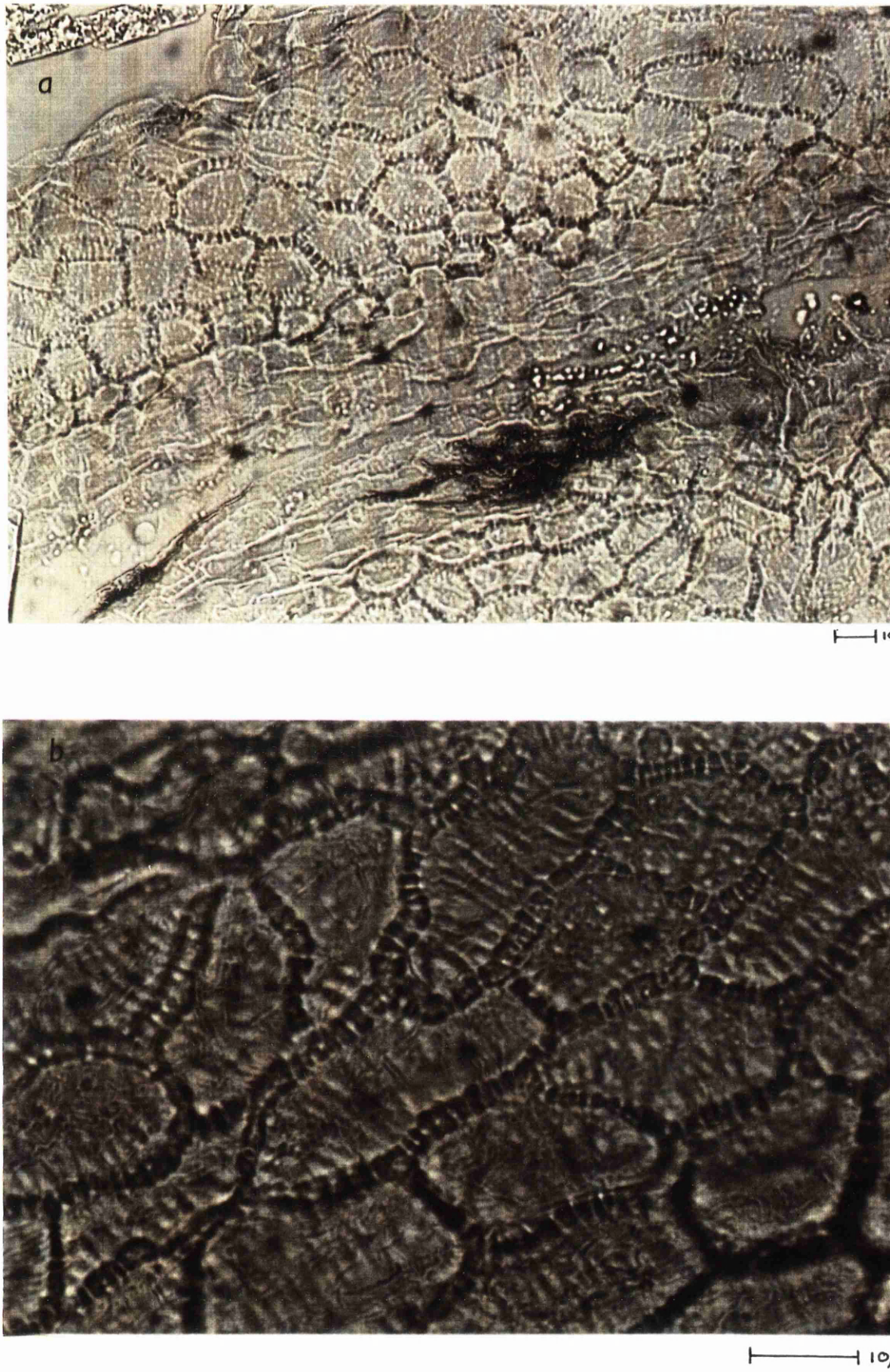


Plate 1. Endothecial wall patterns with distinct base plates (a) *B. axillipara* Ridley (b) *B. brevirimosa* Irmscher (section *Petermannia*)

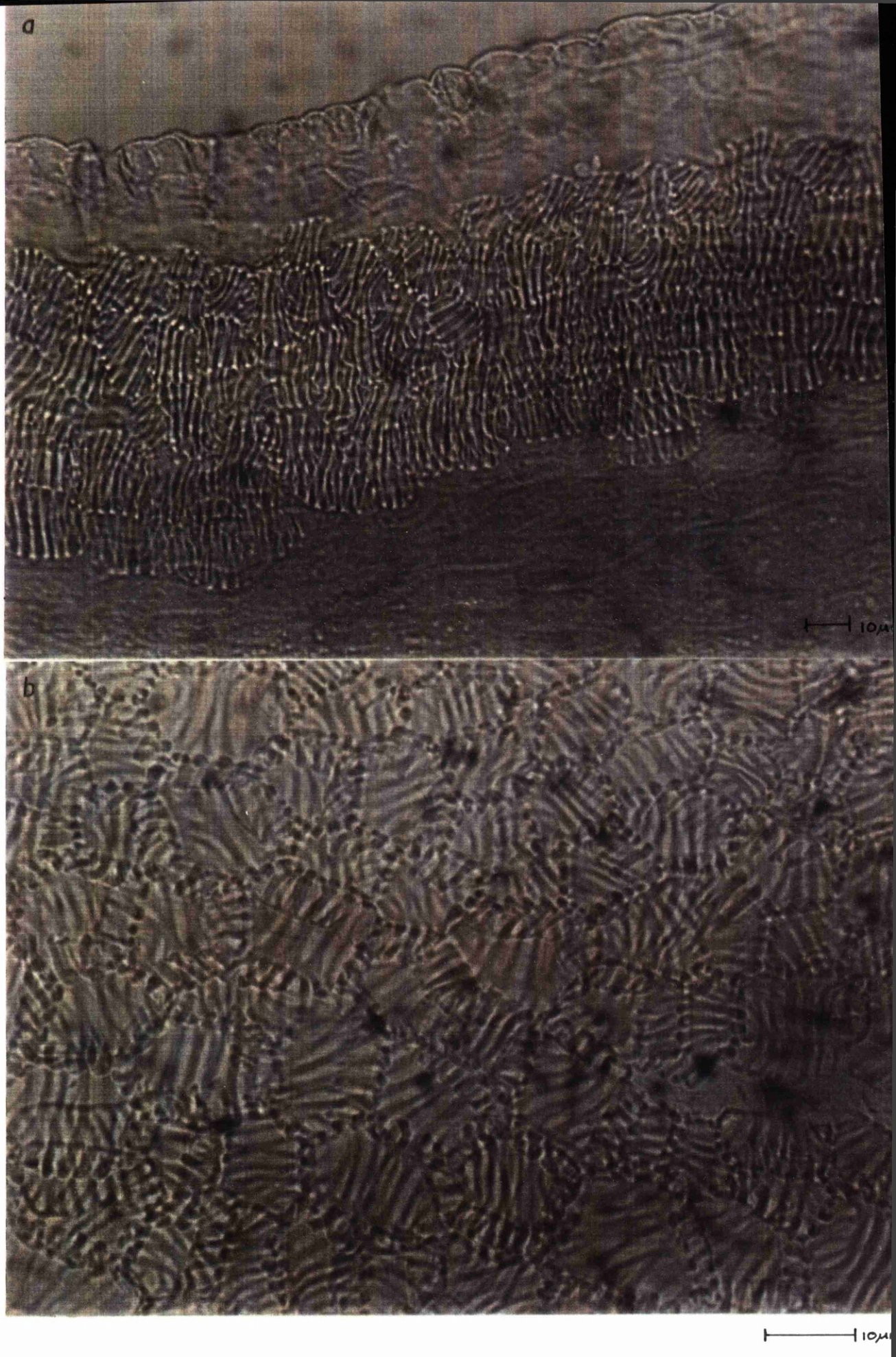


Plate 2. Endothecial wall patterns with U-shaped ribs
(a) *B. roxburghii* (Miq.) A.DC. (b) *B. sutherlandii* Hook. f.
(section *Rostrobegonia*)

2B.3.4. FEMALE FLOWERS

24-27. Style and stigma morphology:
The morphology of the styles and stigma has long been considered of great taxonomic value within *Begonia* (*e.g.* Klotzsch, 1855) and the four characters selected here have often been used in sectional classifications of the genus (*e.g.* de Candolle, 1859; Irmscher, 1925). Clarke (1881) did not, however, attach much importance to the characters of the styles. In addition to those characters of the style and stigma included here, stigmatic papillae have been studied using both the light microscope (Baranov, 1977) and scanning electron microscope (Panda & de Wilde, 1995). However, an in-depth survey of stigmatic papillae morphology within the Begoniaceae carried out by the latter authors found it to be unsuitable for sectional classification.

24. Style number:
In *Begonia* the number of styles is usually 2-3, though some taxa have 4 (sections *Sphenanthera sensu* Irmsch., *Mezierea*, *Squamibegonia*, *Scutobegonia*, *Loasibegonia*, *Gobenia*, *Monopteron* (rarely) and the dubious section *Plurilobaria*). In the case of section *Mezierea*, style number may be either 3 or 5 depending upon the species (Klazenga *et al.*, 1994) and in *B. balansana* (affiliated with section Sphenanthera) from 5-7, although 6 is the most common number (pers. obs.). Style number is usually constant within sections suggesting that the character is of some phylogenetic value. The most frequent style number is given, rather than absolute number as a few of the taxa rarely have variable style numbers, particularly in cultivation. *Hillebrandia* has 5 styles and *Datisca* has 3.

25. Style shape:
An enormous variety of style shapes occur in the Begoniaceae (for a selection of these see Klotzsch (1855) and Irmscher (1925)). Many of these are restricted to particular sections and are, therefore, not all represented here. The bifid styles found in the majority of members of section *Sphenanthera* are of a type possessed by most taxa of *Begonia, Hillebrandia* and *Datisca*, suggesting that the condition is primitive.

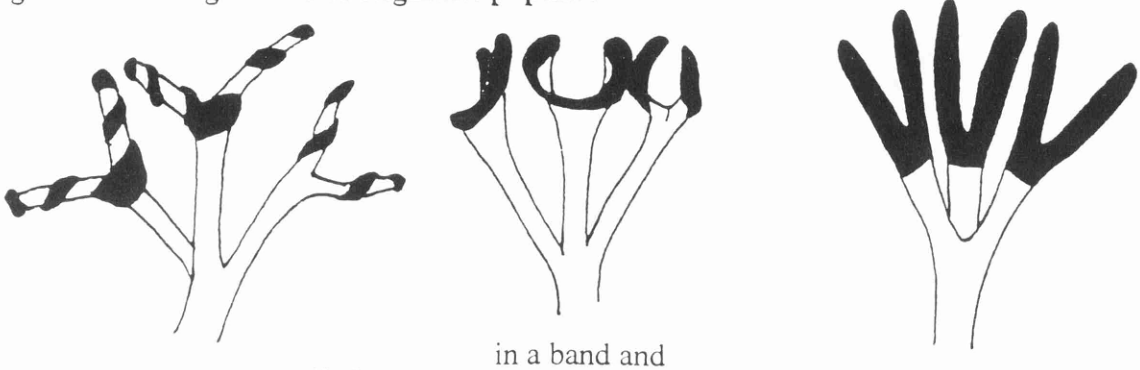
26. Style fusion:

The degree of style fusion is of a continuous nature within *Begonia*. The free styles of members of section *Mezierea* are said to be indicative of their primitive positions within *Begonia* as *Hillebrandia* also has free styles (Xiao-bai & Fu-hsiung, 1994).

27. Stigma position:

The position of the stigmatic papillae on the styles exhibits a great diversity of forms and has been classified into five main states by de Candolle (1859) as follows: a) wide spiral band which joins at the base of the branch division; b) wide spiral band which does not join at the base of the branch division; c) complete coverage of the style branches and joining at base; d) complete coverage of style branches and descending below undivided part of each style; e) contracted around terminal points of branches. Irmscher (1925) recognises the following states: a) spiral band; b) covering all of style; c) ovate; d) lobed; e) kidney-shaped or f) moon-shaped areas. Irmscher's states are consistent with de Candolle's observations. The present study treats de Candolle's first two states as one (as does Irmscher) under the term 'in a band and spiral'. The state expressed by de Candolle as contracted around terminal points of branches and by Irmscher as forming kidney-shaped or moon-shaped areas is here termed 'in a band and not spiral'. De Candolle's two states of complete coverage of style branches are here lumped together (as in Irmscher, 1925) and termed 'covering most or all of style'. It is of interest to note that *B. urticae* L. (section *Casparya*) has a vertical line lacking papillae below the branches, this suggests a condition whereby the band of papillae has spread around the style but not quite touched at its margins. This model of evolution from band to complete coverage of styles is consistent with the fact that the outgroup taxa and the majority of *Begonia* taxa have papillae arranged in bands, from which this condition could have arisen. The states of stigma position recognised here are illustrated in Figure 2B.5.

Fig. 2B.5. Arrangements of stigmatic papillae



in a band and spiralled

in a band and not spiralled

covering all of style

2B.3.5. OVARY & FRUIT

28. Ovary position:

The position of the ovary has traditionally been used within the Begoniaceae to differentiate *Hillebrandia* from *Begonia* and *Symbegonia* (Irmscher, 1925). *Begonia* and *Symbegonia* have fully inferior ovaries while *Hillebrandia* has a partially inferior ovary in which the stamens and perianth are attached a short distance below the top of the ovary. *Datisca* also has a partially inferior ovary.

29. Locule number:

Klotzsch (1855) and subsequent authors attach great importance to the number of locules in the ovary. In the latest classification of the Begoniaceae (Irmscher, 1925) locule number is usually constant within a section, the section *Sphenanthera* being a notable exception, containing taxa with 2-, 3- or 4-locular ovaries. Observation of the locule number in herbarium material of *B. acetosella* (section *Sphenanthera*) shows that it rarely produces both 3- and 4-locular ovaries. The species usually, however, has only 4-locular ovaries. This rare inconsistency in locule number has also been observed in *B. roxburghii* (section *Sphenanthera*) and other species in cultivation (Doorenbos, pers. comm.). Section *Mezierea* is of interest as it contains species with either 3 or 5 locules (Klazenga *et al.*, 1994). Xiao-bai & Fu-hsiung (1994) inferred that section *Platycentrum* which has 2-locules is derived from a 3-locular ancestor. The ovaries of the species examined possessed three dorsal and three outer lateral bundles and three distinct groups of bundles in the centre. This suggests that they are composed of three carpels, two of which are fully developed and the third which does not form a locule.

30.-31. Placentation and placentae:

The divisions between parietal and axile and between divided and entire placentae have been given great significance in many classifications of the Begoniaceae. As early as 1846 Lindley separated the genus *Diploclinium* from the genus *Eupetalum* on the basis of the former possessing divided placentae and the latter entire placentae. Gaudichaud-Beaupré (1841) likewise erected *Mezierea* as a separate genus from *Begonia* based on its parietal placentation, a state not thought to occur within *Begonia*. Klotzsch (1855) and Irmscher (1925) both placed strong emphasis on whether the placentae were divided or entire. Many authors (de Candolle, 1859; Bugnon, 1926; Smith & Schubert, 1946; Gauthier, 1950; Irmscher, 1961; Smith, 1973), however, suggest that the taxonomic distinction between divided and entire placentae has been over emphasised as certain species show both types, sometimes

in the same ovaries. A detailed study of the ovaries of 53 African *Begonia* species was undertaken by Reitsma (1983) in order to assess the characters' taxonomic value. Reitsma concluded that anatomical characters of the ovary are taxonomically informative as long as they are used with caution. The study found parietal placentation to be much more widespread (within the African species) than previously realised and in those taxa in which it occurs a transition from a parietal to an axile condition was found towards the base and in some cases the apex of the fruit. This transition has led to erroneous conclusions in the past, making it imperative that placentation is checked at different levels of the ovary. The African sections *Mezierea*, *Tetraphila* and *Squamibegonia* characteristically contained species with parietal placentation while sections *Sexalaria*, *Augustia*, *Rostrobegonia*, *Scutobegonia* and *Loasibegonia* exhibit true axil placentation. Reitsma (1983) recognised a reticulate evolutionary tendency from true parietal, through pseudo-axile (but still essentially parietal) to true axil placentation within the African taxa. Within the taxa possessing pseudo-axile and true axile placentation a tendency from divided to entire placentae is postulated. Of the three sections characterised by parietal placentation, *Mezierea* was said to be the most primitive as its ovaries possess the greatest amount of parietal tissue found within the three sections and most closely represent the condition found in *Hillebrandia* (which Gauthier (1959) has described in detail).

Parietal placentation is also known to occur outside of Africa, in section *Coelocentrum* (Asia), section *Ewaldia* (Americas) and *B. oaxacana* (Americas) (Barabé *et al.*, 1985). Irmscher (1939) regarded the species of section *Coelocentrum* to be derived from *Begonia* taxa with axile placentation as the former state was otherwise unrecorded within Asia. Xiao-bai & Fu-hsiung (1994), however, state that the fruit anatomy of *B. masoniana* Irmsch., a member of this section, does not support this view. In the present study *B. leprosa* was found to have pseudo-axile placentation, a state previously not recorded for this taxon. In the light of Reitsma's (1983) study, it is possible that more cases of parietal placentation may be recorded within the Asian and American taxa.

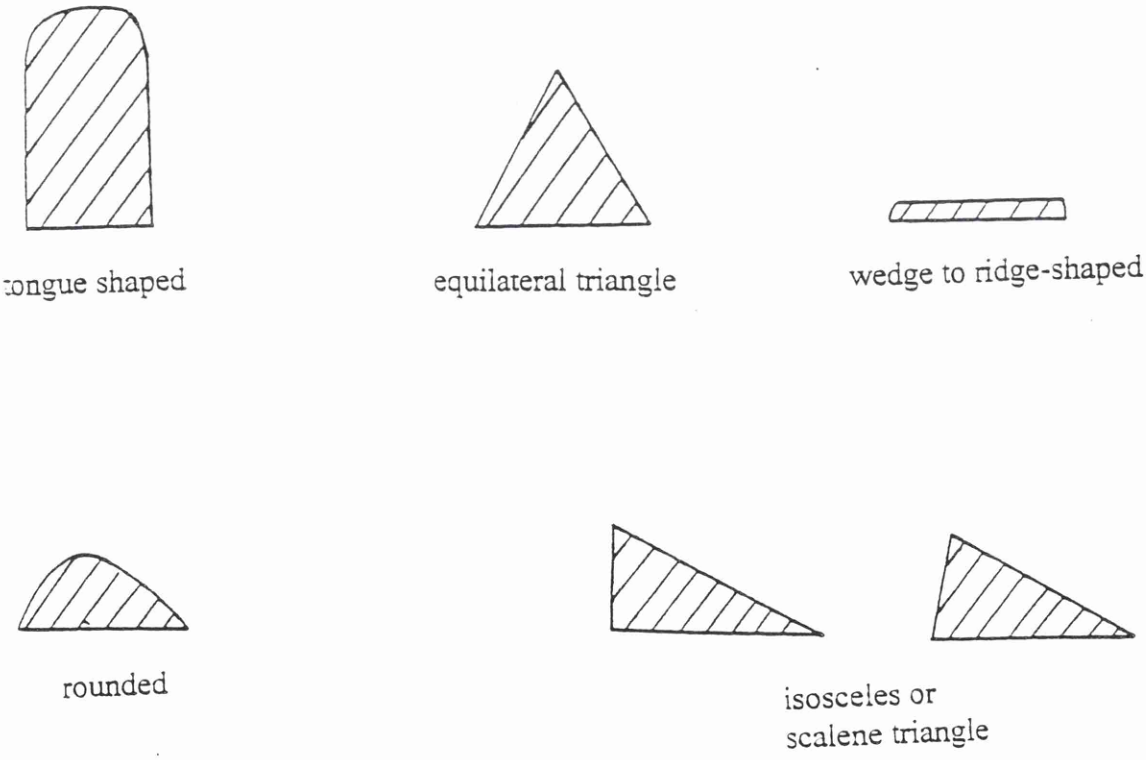
The inclusion of divided or entire placentae as a character is justified regardless of the fact that certain species may possess either state in a single ovary, as this latter condition is the exception rather than the rule and was not observed in the taxa examined here. Following Reitsma (1983), the condition of placentation found in the middle of the ovary is the state which is accepted here. De Candolle (1859) states that the over emphasis of the placentae has lead to inaccuracies in *Begonia*

classification. However, the placentae in the present cladistic study are only one of many equally weighted characters rendering this less of a problem.

32-33. Ovary appendages and ovary wing shape:
Sphenanthera has traditionally been characterised as having wingless or weakly horned fruits (*e.g.* Klotzsch, 1857; Clarke, 1879; Irmscher, 1925). Elsewhere in *Begonia*, wingless fruits are only recorded in sections *Mezierea*, *Squamibegonia*, *Tetraphila*, *Apterobegonia*, *Apteron* and *B. wilsonii* of section *Begonia*. Horned fruits have only been recorded elsewhere in *Casparya*.

Ovary wing shape appears to show a similar situation to anther morphology, in that the wing characteristics of members of many sections are subtly different and difficult to define. Wing shapes recognised in the study are illustrated in Figure 2B.6.

Fig. 2B.6. Ovary wing shapes



34. Fruit orientation:

The orientation of the fruit has received little or no attention from *Begonia* taxonomists including Clarke who otherwise stressed the characters of the fruit in his classification (Clarke, 1879). Three states, viz. pendulous, nodding and erect were observed in the study. These states are believed to be associated with seed dispersal (Bouman, pers. comm.). The majority of *Begonia* species have nodding fruits which are thought to have evolved to assist wind or water dispersal. Such fruits usually have wings which catch the wind or water droplets causing them to shake and thereby release their seeds. Erect fruits are thought to be animal dispersed as they are often fleshy, coloured and usually wingless.

35. Fruit dehiscence:

Many authors (*e.g.* Klotzsch, 1855; de Candolle, 1864; Clarke, 1881) consider that fruit dehiscence is of primary importance to *Begonia* taxonomy. Clarke (1881) even went as far as to base his classification of Indian and Burmese *Begonia* almost entirely on fruit dehiscence. De Candolle (1864) while sinking all but two of Klotzsch's 41 genera into *Begonia* maintained the genus *Casparya* because it had dorsal fruit dehiscence along the angles or wings rather than via elliptic lines on the faces of the fruit, as stated to occur in *Begonia.* Hasskarl's genus *Sphenanthera* was classified as a section of the genus *Casparya* by de Candolle (1864) because he believed them to share a similar method of fruit dehiscence. Clarke (1879) states that the British Indian members of de Candolle's section *Sphenanthera* (of the genus *Casparya*) possess indehiscent fruits or, in the case of *B. roxburghii*, fruits which are irregularly subdehiscent at the angles. The present study found no evidence of dehiscence in all except *B. erosa* and *B. teysmannianum* of de Candolle's *Casparya* section *Sphenanthera* and *B. dux* of Clarke's *Begonia* section *Casparya* (the latter being a species for which Clarke did not observe the fruit). Both these taxa have fruit which dehisce via lines next to the wings. Furthermore, observation of cultivated material of *B. robusta* (Doorenbos, 1980) and *B. roxburghii* (Doorenbos, pers. comm.) suggest that their fruits are indehiscent.

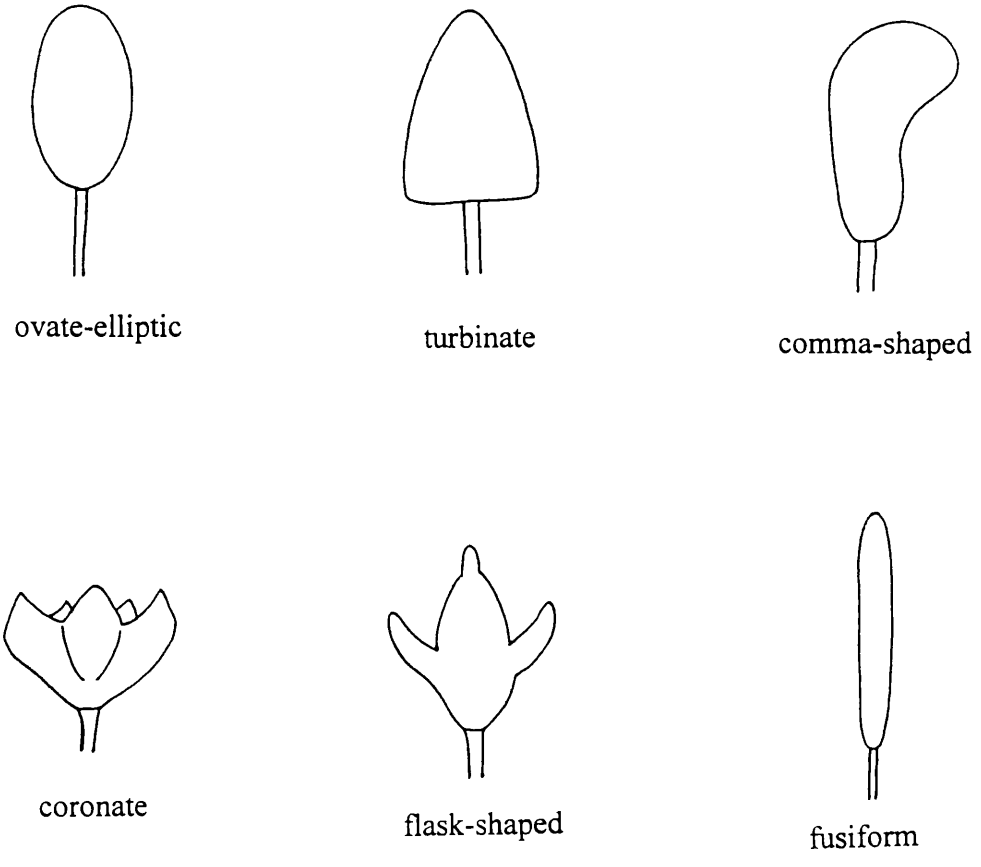
36. Fruit texture when mature (fresh state):

Fruit texture is often difficult to ascertain from herbarium material and for this reason was recorded from the literature, notes on herbarium specimens or personal communication with collectors (Xhangjianhou, Kunming Botanic Garden, P.R. China; Sands, R.B.G. Kew). Fleshy or leathery fruits are infrequent within *Begonia* and are of interest to the present study because in addition to occuring in some

members of section *Sphenanthera*, they are only recorded from the African sections *Mezierea*, *Squamibegonia*, *Tetraphila*, the American species *B. oaxacana* and some members of *Sphenanthera*.

37. Fruit body shape:
A number of different fruit shapes occur within *Sphenanthera* and other *Begonia*. These shapes are often difficult to describe and are, therefore, illustrated in Figure 2B.7. The 'comma shaped' fruits of *B. dux* (section *Sphenanthera*) are shared by many members of the section *Platycentrum*.

Fig. 2B.7. Fruit body shape



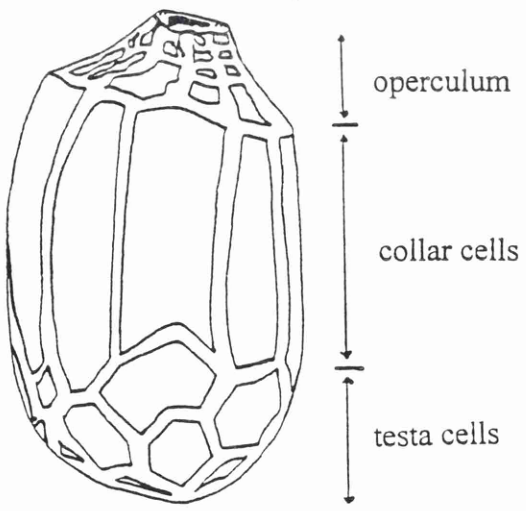
2B.3.6. SEED

39-40. Seed:

The seeds of *Begonia* have been extensively studied using both the scanning electron microscope (Bouman & de Lange, 1982, 1983; Keraudren-Aymonin, 1983; de Lange & Bouman, 1985, 1986, 1992) and the light microscope (Seitner, 1972). The seeds of the African and Madagascan taxa are particularly well documented, but considerably less emphasis has been placed on the American and Asian members of the genus. This imbalance is shortly to be addressed with the proposed publication of broad scale seed surveys of American and Asian taxa (Bouman, pers. comm.).

Morphologically, seeds of the Begoniaceae are unique within the Angiosperms due to the possession of a zone of collar cells between an operculum and unspecialized testa cells (Fig. 2B.8.). The seeds of *Symbegonia* and *Hillebrandia* are virtually indistinguishable from many *Begonia* taxa, although in *Hillebrandia* the micropyle and hilum are sunken in a characteristic crooked, nozzle-like protrusion (Bouman & de Lange, 1983). The seeds of *Datisca* (Datiscaceae) share many similarities (*e.g.* small size, an operculum, cuticular striae) with those of the Begoniaceae, supporting the view that the two are closely related. However, they lack the characteristic collar cells found in the Begoniaceae (Bouman & de Lange, 1983).

Fig. 2B.8. *Begonia* seed morphology



The taxonomic value of seeds within *Begonia* has been demonstrated by de Lange & Bouman (1992). They found that many of the African sections and occasionally species could be delimited by their seed morphologies. Seed diversity appears to be correlated both with method of dispersal and overall morphological diversity of the plant (Bouman, pers. comm.). The morphologically diverse African sections and the most morphologically distinct American (*e.g.* section *Solananthera*) and Asian (*e.g.* section *Lauchea*) sections also possess a high level of diversity in terms of their seed micro-morphology. The levels of diversity in these sections is such that certain seed characters are often restricted to just one section (*e.g.* arils in section *Tetraphila*, distinctive papillae in section *Lauchea*). This form of variation obviously reduces the phylogenetic value of these characters because it does not allow any understanding of inter-sectional relationships. In addition to the presence of these apomorphies the occurrence of trends rather than discrete states in other seed characters and the high levels of convergent evolution, associated with dispersal (Bouman, pers. comm.) also reduce the phylogenetic value of seeds in *Begonia*, especially at higher taxonomic levels. For these reasons, just three of the many characters employed by de Lange & Bouman (1992) to delimit African sections are incorporated in the current phylogenetic study, although other characters which are restricted to single taxa will be discussed elsewhere.

The remaining discussion of seed characters is restricted to those characters utilised in the current study.

38. Seed ornamentation:
Within *Begonia*, seed ornamentation is very variable. The most common type is illustrated in Plate 3a. Ornamentation may also be more pronounced, as occurs in *B. balansana* (associated with section *Sphenanthera*) and the two African sections *Scutobegonia* and *Loasibegonia*. It is faint in some specimens of *B. comorensis* (section *Mezieria*) and absent in *B. meyeri-johannis* (section *Mezeria*), *B. heydei* (section *Urniformia*) and the members of sections *Baccabegonia*, *Squamibegonia* and *Tetraphila*. Lack of seed ornamentation has been associated with presumed animal dispersal (rather than wind or water dispersal) and is associated with a number of morphological characters of the fruits (de Lange & Bouman, 1992). The pronounced ornamentation found in the members of sections *Scutobegonia* and *Loasibegonia* and *B. balansana* presumably helps the seeds of these low growing terrestrial herbs to become air, water or possibly animal borne by increasing their surface area. The difference in micro-morphology of the cuticular patterns found in *B. balansana* compared to the members of sections *Scutobegonia* and

Loasibegonia suggests that these pronounced cuticular ornamentations have evolved more than once and for this reason are not recognised here as a distinct character state.

39. Operculum shape: ▲

The shape of the operculum in the majority of species is described as nipple-shaped (de Lange & Bouman, 1992) (Plate 3b). Some taxa possess opercula which are flat or almost so, (*e.g. B. herbacea* and *B. urticae*) or obtuse, (*e.g.* in sections *Coelocentrum*, *Mezierea*, *Scutobegonia* and *Loasibegonia*). *Hillebrandia* and *Datisca* possess nozzle-like opercula.

40. Number of testa cells along length of seed:

The distinction between 1-4 and 5-10 testa cells is obviously a somewhat artificial division of a continuum but is used here as different species do appear to have either very few testa cells or very many and none of the taxa examined have both few (*i.e.* 1-3) and many (*i.e.* 8-10) testa cells on their seeds. Bouman (pers. comm.) suggests the character directly reflects seed size and, therefore, is of phylogenetic value as the African sections are characterised by particular seed sizes.

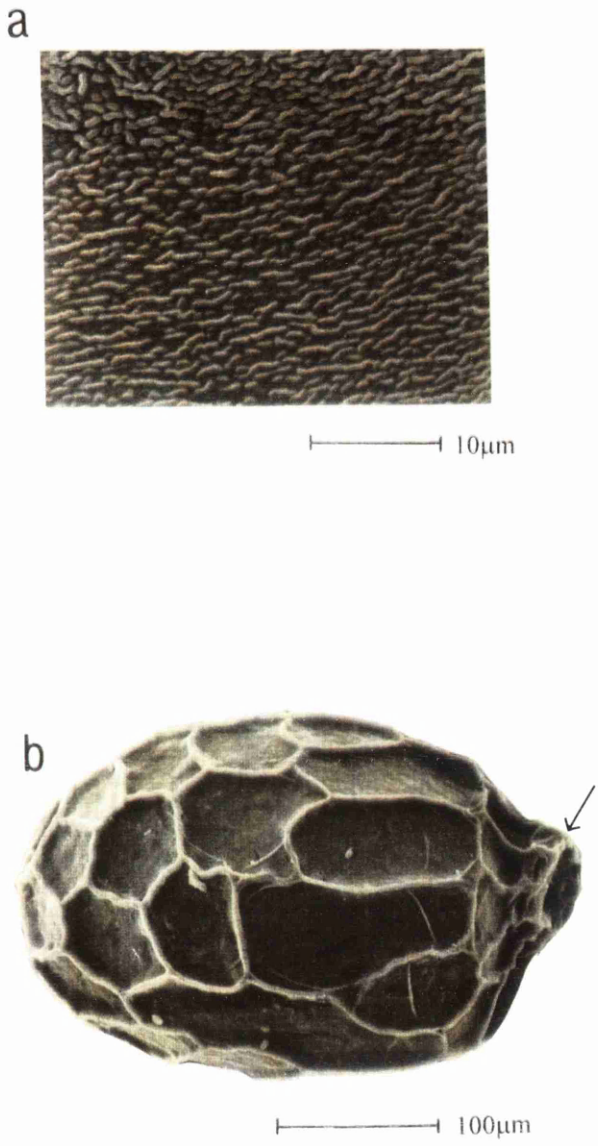


Plate 3. Seed morphology of *B. longifolia* Blume
(a) showing micro-morphology of testa cells
(b) showing nipple shaped operculum

2B.4. THE CLADISTIC ANALYSES

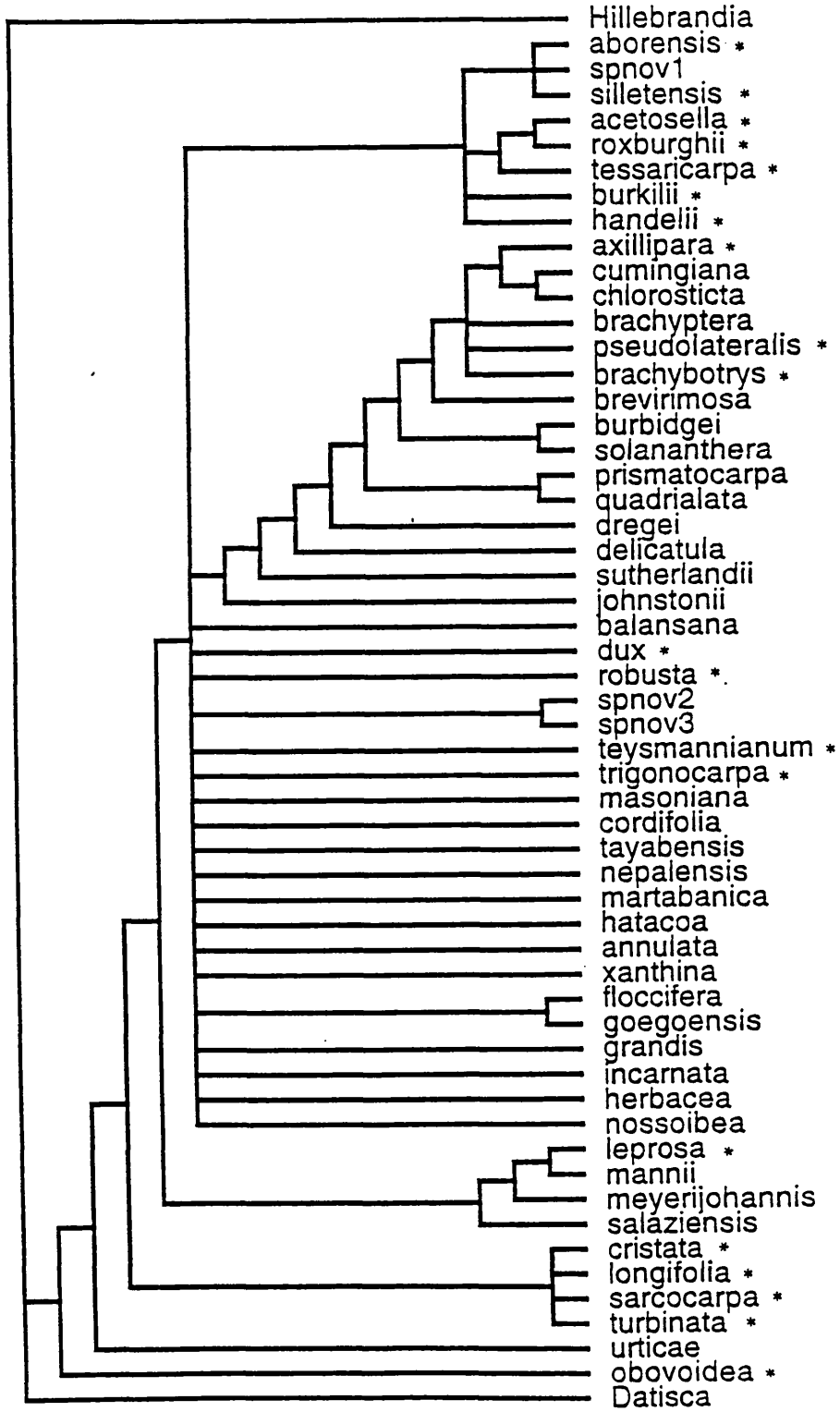
2B.4.1. PROGRAMMES, ANALYSES AND CHARACTER CODING

Heuristic parsimony analyses were performed in PAUP (version 3.1.1.; Swofford, 1993) set for TBR branch-swapping. In analyses with less than 20 taxa, support for clades was inferred by bootstrap (Felsenstein, 1985). In analyses with more than 20 taxa the amount of cladistic signal was inferred by evaluating the skewness of random tree length distributions as bootstrap analysis of the larger data sets proved too time consuming. All characters were unordered and unweighted. Where more than one homologous state of a character occurs in a species these taxa were coded as having both states.

2B.4.2. EXPLORATORY ANALYSES AND CLADOGRAMS

A general heuristic search was conducted upon the full data set (see 2D.2.) with *Hillebrandia sandwichensis* and *Datisca cannibina* as outgroups. This analysis produced 1309 trees with a length of 279, a consistency index (CI) of 0.362 and a retention index (RI) of 0.655. The strict consensus tree of this analysis is shown in Figure 2B.9. The low CI value of 0.362 suggests that a large amount of homoplasy is present within the data, while the RI value of 0.655 suggests that there are few synapomorphies supporting the tree. The low resolution of many of the clades in the strict consensus tree also suggests that there is character conflict in some areas of the tree. This is also supported by the fact that the majority rule consensus tree of this data is much more resolved (Fig. 2B.10.) In order to assess whether the data set contains phylogenetic structure, the amount of skewness present in the graphical distribution of 1000 random tree lengths was calculated in PAUP. The distribution of the tree-lengths of randomly generated trees is commonly used to indicate the phylogenetic information present in a data set. A strong left-skewed distribution indicates that only a few trees occur near to the most parsimonious tree while a symmetrical distribution indicates that many slightly less parsimonious trees occur near to the most parsimonious tree (Huelsenbeck, 1991a). Strongly left skewed distributions, therefore, indicate that the data set is more structured than would be expected from random data. For a data set to be left skewed it must have a g1 value of less than zero. A g1 value of -0.427006 was obtained from the data set. This indicates that it is left skewed and therefore, contains phylogenetic structure.

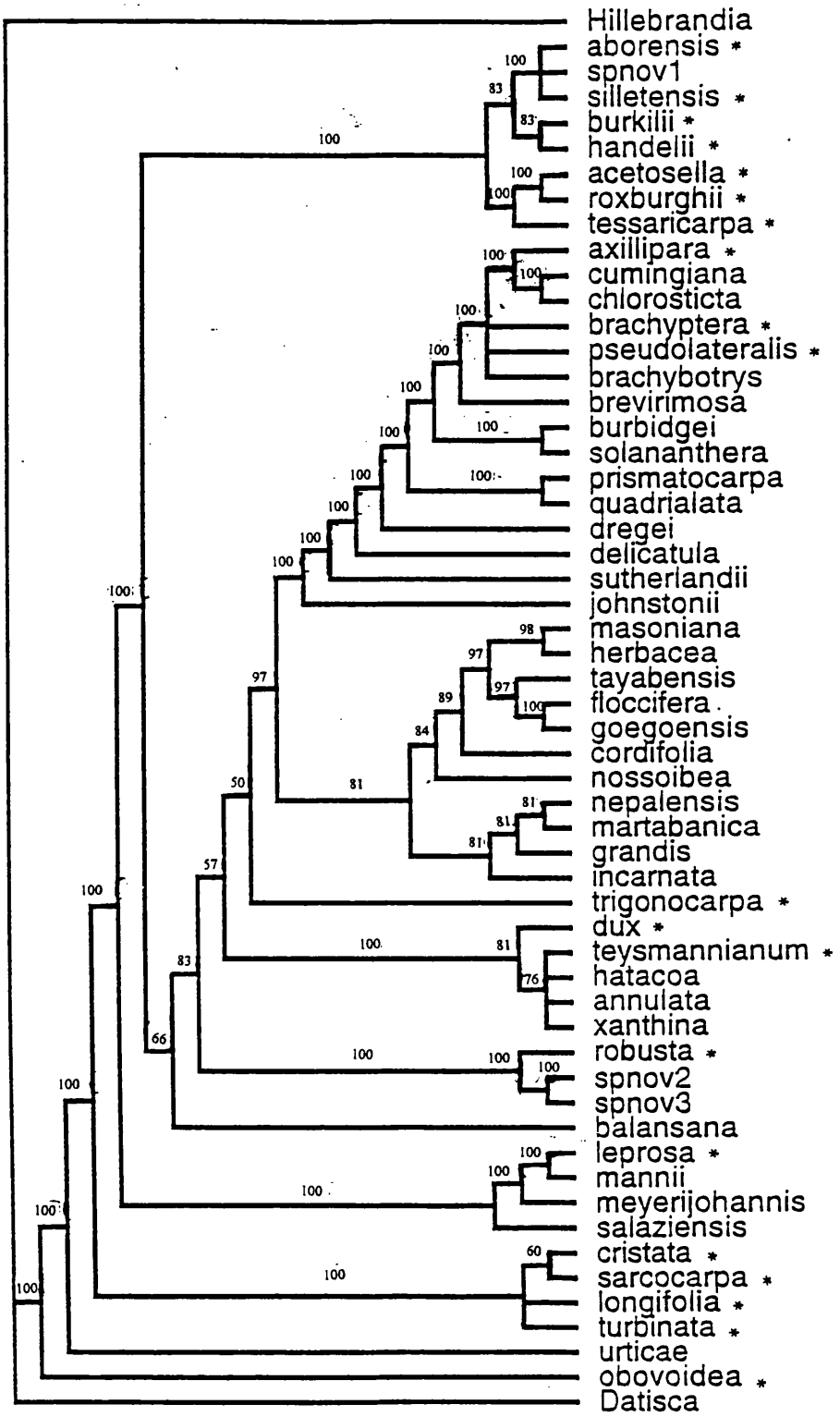
Fig. 2B.9. Strict consensus tree from a Heuristic search of the morphological data set



1309 trees
Length=279
CI=0.362
RI=0.655

* species currently included in section *Sphenanthera*

Fig. 2B.10. Majority rule consensus tree from a Heuristic search of the morphological data set (numbers indicate the percentage frequency that clades appear in the 1309 most parsimonious trees).



* species currently included in section *Sphenanthera*

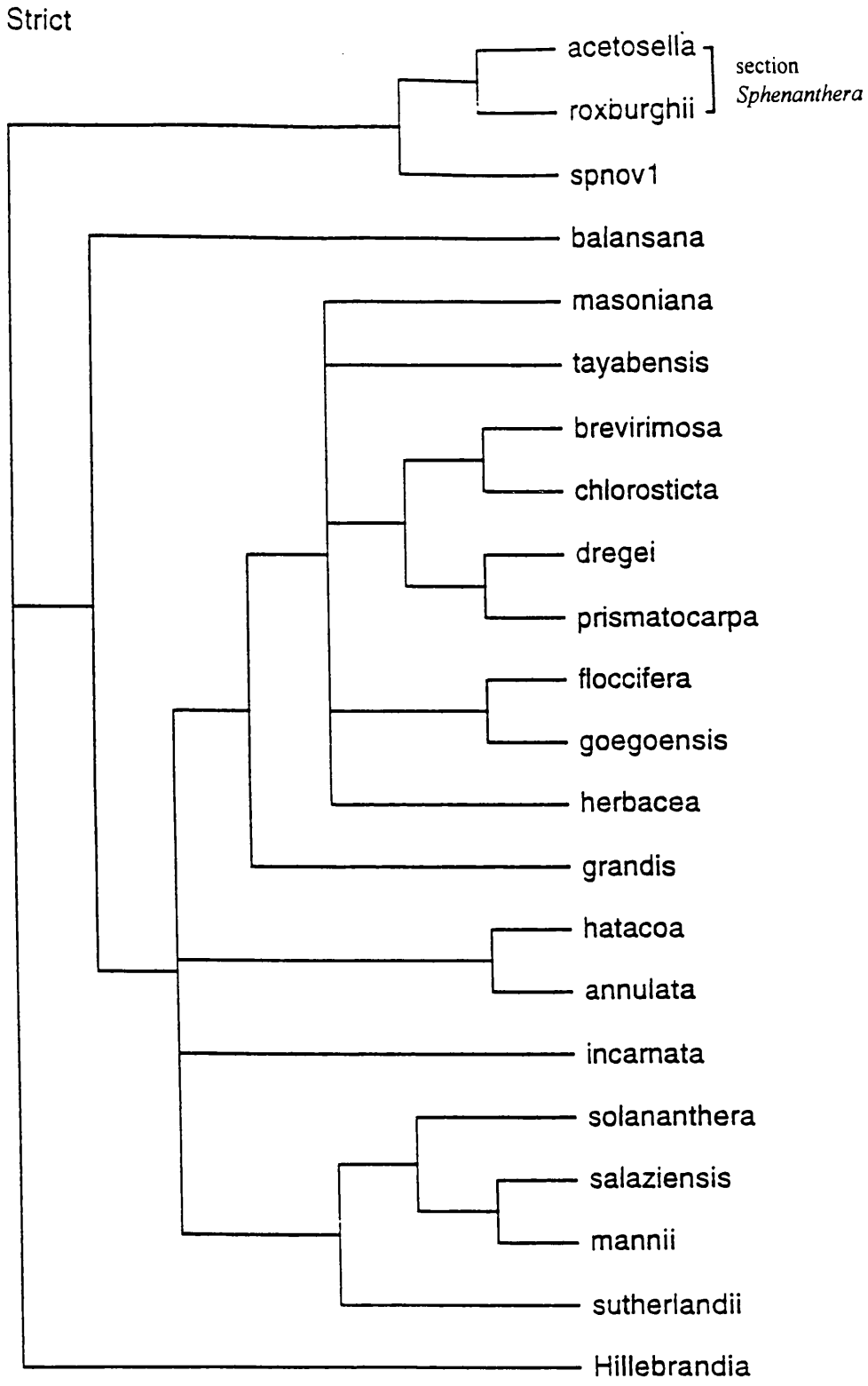
1309 trees
Length=279
CI=0.362
RI=0.655

Molecular data was only available from a subset of the taxa (Table 2.1.) included in the morphological analyses. An heurisitic analysis was, therefore, conducted using only this subset of 22 taxa on the morphological data so that the trees produced from each data set could be later combined, if desired. This analysis resulted in 40 trees with a length of 157, a CI of 0.509 and a RI of 0.528. The strict consensus of these is shown in Figure 2B.11. Bootstrapping was carried out to give an estimate of support for the clades. A general heuristic search with 100 bootstrap replications and a random number seed found that the tree was generally poorly supported as only four clades were supported by more than 50% majority rule bootstrap values (Fig. 2B.12.). The amount of skewness in the tree length distributions of 1000 randomly generated trees was calculated. A g1 value of -0.373979 was obtained. This value suggests that the data set contains phylogenetic information.

Comparison of the strict consensus trees produced from the full data set (Fig. 2B.9.) and a subset of these taxa (Fig. 2B.11.) shows that the removal of taxa results in a change in tree topology. This suggests that the additional taxa in the full data set provide new or additional support for cladistic relationships which are not supported in the analysis of the subset of taxa. The slightly more negative g1 value produced from the analysis of tree length distribution of the full data set compared to those produced from the subset of taxa suggests that the larger data set contains relatively more phylogenetic information compared to the smaller data set. This additional information probably results in the change in tree topology associated with the addition of taxa.

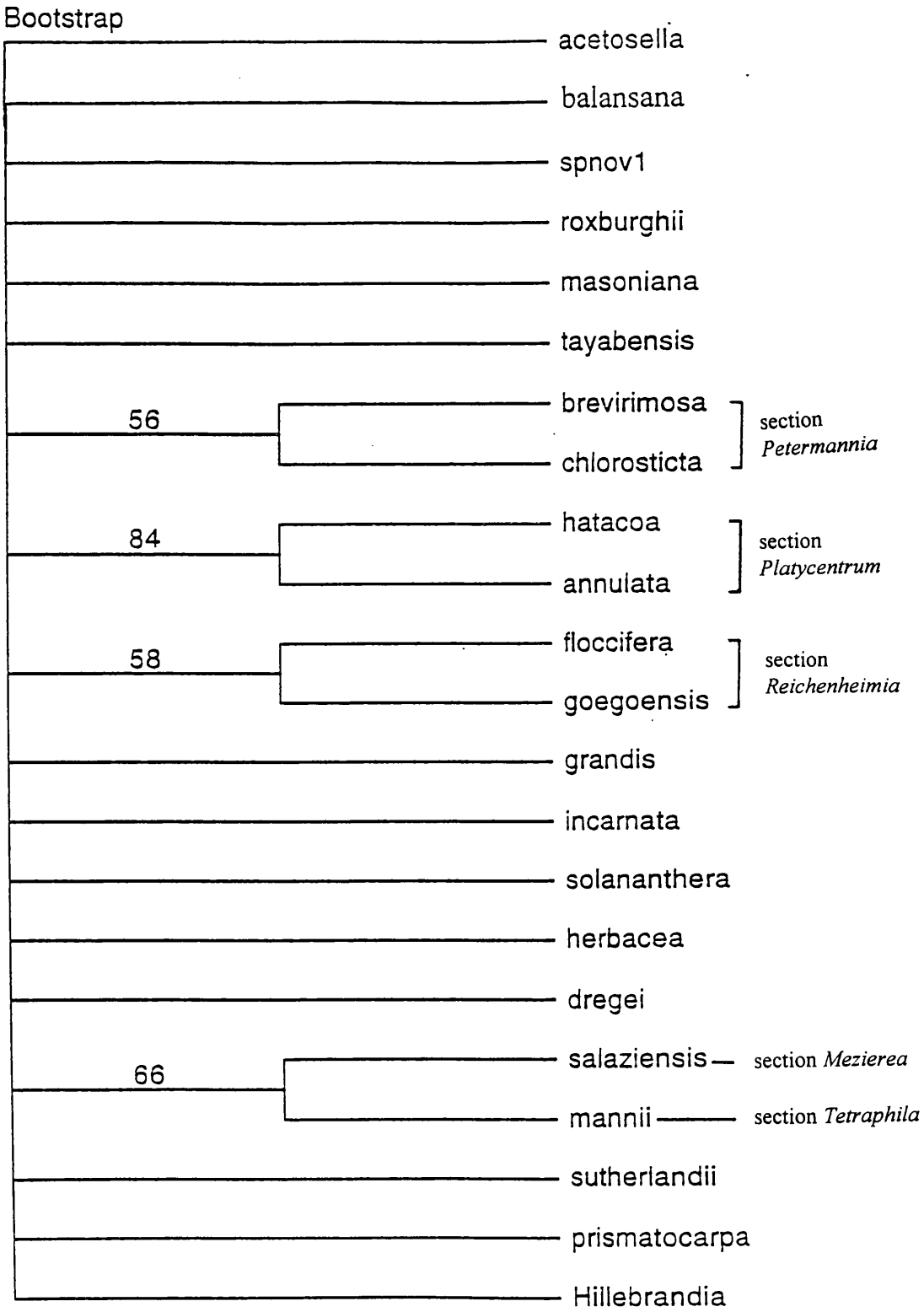
As molecular data was not gathered for *Datisca*, *Hillebrandia* was used solely as the outgroup in the molecular analyses (see 2C.4.2.) and the comparative morphological analysis (above). To test whether the choice of outgroup has an affect upon the tree, a separate analysis was conducted using the full morphological data set and just *Hillebrandia* as the outgroup. The choice of outgroup did not markedly effect the tree topology. It is, therefore, reasonable to use only *Hillebrandia* as a single morphological outgroup.

Fig. 2B.11. Strict consensus tree from a Heuristic search of a subset of taxa from the morphological data set



40 trees
Length=157
CI=0.509
RI=0.528

Fig. 2B.12. 50% majority rule boostrap consensus tree produced from a subset of the morphological data



Chapter 2
PHYLOGENETIC INVESTIGATION OF *BEGONIA* SECTION *SPHENANTHERA*

SECTION C: MOLECULAR DATA

SECTION 2C: MOLECULAR DATA

2C.1. INTRODUCTION

Since the late 1950's molecular techniques have developed rapidly and today molecules are a significant source of data for many phylogenetic studies (Li & Graur, 1991). Some of the properties of molecular data which have led to their widespread use in systematics include: the applicability of molecules to answer questions at all levels of the taxonomic hierarchy, their potential to generate large data sets and the general lack of environmental influence upon their phenotypes (Hillis, 1987). A large array of techniques are presently available and include: DNA-DNA hybridisation, the generation and analysis of DNA fragments (*e.g.* microsatellites, RAPDs and RFLPs) and DNA/RNA sequencing. Hillis *et al.* (1996) provide detailed discussions of these and related techniques.

Rates of molecular evolution differ between organelles (Wolfe *et al.*, 1987), different regions of the genome (*e.g.* Gielly & Taberlet, 1994) and different taxonomic groups (Britten, 1986). It is, therefore, necessary to select a molecular technique which will generate data appropriate to the particular taxonomic questions being posed. Cost and labour time are also considerations when choosing an appropriate technique (Hillis *et al.*, 1996). Hillis *et al.* (1996) state that isozymes/allozymes, restriction enzyme analysis and DNA/RNA sequencing are the techniques most appropriate for the determination of phylogenetic relationships between relatively recently evolved plant species. The low levels of sequence divergence reported from sequence studies of *rbc*L and the nuclear internal transcribed spacer region (ITS) of the 18S-26S ribosomal DNA cistron suggest that within the genus *Begonia*, relatively recent, rapid speciation has occurred. Most systematic studies within angiosperms have focused on the chloroplast genome (for reasons discussed below) and those utilising sequence data have tended to concentrate on *rbc*L, although many other regions of the genome are now frequently used in systematic studies of plants. In angiosperms, chloroplast DNA (cpDNA) has a number of advantages over nuclear and mitochondrial DNA (mtDNA) and ribosomal RNA and this has led to its wider utilisation. Some of the features of cpDNA which make it particularly suitable for molecular systematics include, its conserved gene order which facilitates universal primer design, its lack of recombination and the fact that the complete chloroplast genome has been sequenced for a number of plants (*e.g.* Shinozaki *et al.*, 1986; Ohyama *et al.*,

1986). The rate of sequence evolution of cpDNA is slower than nuclear DNA but faster than mtDNA and is usually most appropriate for investigating systematic questions at the generic (Bachmann, 1992) or familial level (Johnson & Soltis, 1994). The general lack of evolutionary markers in cpDNA at the species level is unfortunate as it reduces the phylogenetic utility of this organelle.

In the majority of angiosperms, chloroplasts and mitochondria are usually maternally inherited (Mogensen, 1996), but see Harris & Ingram (1991) for examples of paternal and biparental inheritance. A cladogram based on cpDNA or mtDNA should parallel that of the organism's phylogeny, but this may not always be the case (Bachmann, 1992). As plastids are usually only passed down the maternal lineage, differences between the cpDNA phylogeny and the organismal phylogeny may occur, for example, as a result of hybridisation. In such situations comparison of the cpDNA data with biparentally inherited nuclear DNA or morphology may highlight discrepancies and identify hybridisation events. In common with other molecular markers, misleading phylogenies may also be obtained as a result of lineage sorting.

Existing molecular systematic studies within the Begoniaceae have concentrated on sequencing the *rbc*L (Swensen, pers. comm.) and ITS regions (Brouillet, pers. comm.). It appears that both regions are too conserved to be of use in determining relationships between closely related species and sections of *Begonia* and are, therefore, of limited value to the current study (Swensen, pers. comm.; Brouillet, pers. comm.). Similar, low intersectional levels of restriction site variation in polymerase chain reaction (PCR) amplified *rbc*L and ORF 106 chloroplast fragments were also found by Rieseberg *et al.* (1992) in a study of the breeding systems of Datiscaceae which included eight species of *Begonia*, from different sections, as outgroups.

In view of the lack of knowledge concerning suitable means of producing molecular data for the current study it was decided to investigate two of the most appropriate techniques. DNA sequencing and restriction analysis were utilised with the aim of finding a source of suitable levels of variation in order to investigate species and sectional level relationships within *Begonia*. A description of the plant material used in the molecular studies is presented in 2C.2. The sequencing study is presented in 2C.3. and the restriction enzyme analysis in 2C.4.

2C.2. PLANT MATERIAL

Many of the species were collected from the National *Begonia* collection housed at the Glasgow Botanic Garden. *Begonia roxburghii*, accession number 2331-54, was a gift from Montreal Botanic Garden. *Hillebrandia sandwichensis*, *B. incarnata*, *B. rhopalocarpa* and *B. sàlaziensis* were a gift from the Royal Botanic Gardens, Kew. Material of an unidentified species of section *Platycentrum* (Yunnan [China]; van der Maesen, 6187) was a gift from Wateringen (The Netherlands). *Begonia acetosella* var. *hirtifolia* and a new species from Yunnan were a gift from Kunming Botanic Garden (P.R. of China). Accessions of *B. acetosella* and *B. balansana* were collected from the wild in the P. R. of Vietnam. Wild material was preserved in silica gel using the method of Chase & Hills (1991) (Appendix Ea). Material of *B. longifolia* and *B. meyeri-johannis* was a gift from Wageningen Agricultural University (The Netherlands). The accession numbers, origins and sectional membership of all taxa included in the molecular studies are given in Appendix A.

Recent studies have demonstrated that it is possible to isolate DNA from herbarium material of sufficient quality to use in molecular studies (*e.g.* Savolainen *et al.*, 1995; Soltis *et al.*, 1996). In view of this, attempts were made to isolate DNA from herbarium material for the purpose of the restriction enzyme analysis. Using microprep procedures (Appendix Eb) and bovine serum albumin (BSA) (which binds to PCR inhibitors such as secondary compounds and phenolics) it was possible to amplify DNA from most herbarium specimens tested. However, the resulting PCR products were not sufficiently concentrated for restriction enzyme analysis and it proved difficult to re-amplify the PCR product. Consequently, herbarium material was not utilised in the study.

2C.3. SEQUENCING

2C.3.1. INTRODUCTION

The comparison of DNA sequences between different organisms is one of the most widely used molecular techniques for phylogenetic purposes (Sanderson & Doyle, 1993). This popularity stems largely from the fact that large data sets may be obtained with relatively little effort. Also this data lends itself readily to phylogenetic analysis and may be easily combined with existing data sets (Hillis *et al.*, 1996). The publication of a number of universal primers for plant DNA (*e.g.* Scoles *et al.*, 1988; White *et al.*, 1990; Taberlet *et al.*, 1991; Demesure *et al.*, 1995;

Vendramin *et al.*, 1996) also means that several regions are readily available for investigation.

The *trn* L (UAA) intron and the intergenic spacer between the *trn* L (UAA) 3' exon and the *trn* F (GAA) gene were investigated, as the two other regions previously examined in *Begonia*, *rbc*L and ITS, were considered to be too conserved for the present study (Swensen, pers. comm.; Brouillet, pers. comm.). The *trn*L region, however, represented a potentially suitable source of variation (Chase, pers. comm.).

The *trn*L intron is non-coding and is, therefore, expected to evolve more rapidly than coding regions, such as *rbc*L (Gielly & Taberlet, 1994). Gielly & Taberlet (1994) found that, on average, the region evolves more than three times faster than *rbc*L. In that study, sequencing produced suitable levels of variation for phylogenetic analysis between closely related grass genera and species of the genus *Gentiana* L. The region has also been demonstrated to exhibit suitable levels of variation for phylogenetic purposes at the generic level in the Saxifragaceae (Vanham *et al.*, 1994) and at the sectional level within the Ranunculaceae (Kita *et al.*, 1995) and Crassulaceae (Mes & Thart, 1994; Vanham *et al.*, 1994; Kim *et al.*, 1996). Gielly *et al.* (1996) demonstrated, that the nuclear rDNA ITS regions (ITS1 & ITS2) in *Gentiana* evolve two or three times faster than the *trn*L intron. The *trn*L region may not be suitable for phylogenetic purposes in the current study, because Brouillet (pers. comm.) suggests that even the ITS regions are too conserved to be of use at the specific level within *Begonia*. However, the suitability of a given gene requires empirically testing for the taxa of interest and Gielly & Taberlet (1996) found that the mutation rate of the *trn*L intron varied even between different lineages of *Gentiana*. Furthermore, this region has been found to exhibit infraspecific variation in *Quercus robur* and *Q. petraea* (Ferris *et al.*, 1993) and *Epipactis helleborine* (Hollingsworth, pers. comm.) demonstrating that it exhibits relatively fast rates of evolution in some taxa.

The species included in the pilot study were chosen as their morphologies suggest that they represent taxa which are both closely and distantly related. These taxa may highlight the taxonomic level at which the *trn*L intron is phylogenetically most informative.

2C.3.2. MOLECULAR TECHNIQUES

Total DNA was isolated from fresh leaf material using a modified CTAB protocol of Doyle & Doyle (1987). Full details of this are given in Appendix Ec. The *trn*F(GAA) and *trn*L(UAA) genes and the intergenic spacer between the *trn*L 3' exon and the *trn*F gene were amplified using the polymerase chain reaction (PCR) with primers C to E and F to D respectively (Taberlet *et al.*, 1991). A primer concentration of 100ng per 1µl was used. Amplification conditions were as follows:

1min. at 94°C,
30 secs. at 50°C,] x 30
1 min. at 75°C.

The double stranded PCR products produced were purified using Promega Wizard minicolumn gene cleaning kits. Single stranded DNA was obtained by asymmetric PCR using a single primer at a concentration of 10ng per 1µl. Amplification conditions used for asymmetric PCR were as above. Single stranded PCR products were purified in an acetate/alcohol mix. Single stranded DNAs were sequenced using the dye primer labelling method on an Applied Biosystems 373 DNA automated sequencer (stretch). Sequences were down loaded onto computer discs for later alignment and analysis. Sequencing, purification and PCR protocols were provided by James Richardson of the R.B.G. Kew and are reproduced in a modified form in Appendix E.

2C.3.3. SEQUENCE ALIGNMENT, PROGRAMMES AND ANALYSES

Sequences were aligned using Sequence Navigator (Applied Biosystems, Inc., 1994) followed by manual adjustment where necessary. The informative sites from the aligned sequences are shown in Appendix F. In the phylogenetic analysis gaps were treated as missing data as they may represent artifacts of the alignment process and are not neccessarily equivalent to insertions and deletions (Olsen, 1988). Phylogenetic analyses were carried out using PAUP 3.1 (Swofford, 1993). A heuristic search and bootstrapping was carried out, as detailed below.

In addition to the six taxa sequenced by the present author six other *Begonia* taxa were sequenced by Zoe Badcock (Glasgow University). These, by permission, are also included in the analyses.

2C.3.4. RESULTS AND DISCUSSION

The study identified 21 informative sites from a total of 995 bases. A branch and bound search carried out on the data obtained five shortest trees all requiring 216 steps. These had a CI of 0.917 and a RI of 0.526. The relationships indicated by the strict consensus of these appears to be phylogenetically meaningful as the Asian and African taxa occur in a separate clade from the American taxa and species presently included in the same section occur within these as subclades (*i.e. B. gracilis* - *B. incarnata* and *B. roxburghii* - *B. balansana*). However, character support for the clades was very low. Bootstrapping was carried out to give an estimate of 'confidence' in the tree topology. A branch and bound search with 100 bootstrap replications and a random number seed was conducted. Bootstrap values were found to be below 50% in all except the *B. herbacea* - *B. obliqua* clade suggesting that there is little support for the tree topology. Felsenstein (1985) states that for a clade to occur within a 95% 'confidence' limit it must be supported by at least three characters. The low bootstrap values are, therefore, due to a low number of characters supporting the clades. In view of the low bootstrap values and small number of informative sites it appears that the *trn*L region does not represent a sufficiently variable region for the study. The lack of obvious alternative regions to sequence made it necessary to explore other sources of molecular data.

2C.4. RESTRICTION ANALYSIS

2C.4.1. INTRODUCTION

Restriction endonucleases (REs) are enzymes that cut DNA at a constant characteristic position within or near a specific recognition sequence, typically 4-6 base pairs (bp) long (Li & Graur, 1991). A restriction enzyme will digest DNA so that homologous sequences are cut into identical restriction fragments. Nucleotide substitutions, deletions and insertions may create new recognition sequences or prevent the recognition of previous recognition sites. Restriction fragments can be sorted according to length by gel electrophoresis and their lengths determined by running against fragments of known size. Differences in restriction fragment patterns are termed restriction fragment length polymorphisms (RFLPs). These banding patterns are routinely used for identification and comparison of DNA sequences (Bachmann, 1992). The approximate position of restriction sites may be determined by using several restriction enzymes singularly and in pairs so that the DNA is digested into overlapping fragments, which may then be fitted together.

The diagramatic representation of restriction sites on a region of DNA is known as a restriction map.

In phylogenetic studies it is important that enzymes with completely independent recognition sequences are used so that the data does not violate the assumptions of the programs used for analysis. To achieve this, Holsinger & Jansen (1993, p.442) recommend that 'the following types of enzymes be avoided in restriction site surveys: (1) those with multiple recognition sequences, (2) those with a recognition sequence identical to another enzyme included in the survey, (3) those with a recognition sequence that differs from that of another enzyme being used by a single nucleotide, and (4) those with a recognition sequence included in that of another enzyme being used.' When analysing restriction site data it is also important to realise that the probability of loosing restriction sites is higher than the probability of gaining sites. In the past, different parsimony methods have been used to attempt to reduce this bias. Three methods of parsimony have been used for the analysis of restriction site data: Wagner, Dollo and weighted parsimony (Holsinger & Jansen, 1993). Wagner parsimony presumes that the gain of a restriction site is as likely as the loss of a restriction site, Dollo parsimony allows a restriction site to be gained only once, but lost many times and Wagner parsimony is intermediate between these two methods. Holsinger & Jansen (1993) recommend that all three methods are compared in an analysis. In the present study only Wagner parsimony was used as this is deemed most appropriate in situations were changes in restriction sites are due largely to insertions and deletions rather than nucleotide substitutions.

Doubts have been expressed concerning the homology of restriction fragments above the specific level and for this reason mapping of restriction sites is often advocated for phylogenetic studies of higher taxa (Holsinger & Jansen, 1993). Bremer (1991, p.50) recommends that fragments of equal length and unknown position on the cpDNA molecule should not be compared for phylogenetic purposes, but states that comparison of fragments from known positions on the genome is acceptable as in this case 'there is a low probability that two non-homologous fragments should have exactly the same size'. In support of this view, Bremer (1991) states that in a study of the *Rubiaceae*, out of 944 fragments of known location on the genome, none were discovered to be non-homologous after mapping. It would also appear that non-homology of identically sized fragments should not be a widespread problem in restriction enzyme analysis based upon PCR amplified fragments because of the relatively low probability of obtaining

non-homologous fragments from a short length of DNA compared with the whole plastid or genome.

In the present study RFLP data was scored for two of the regions studied (see Table 2.3.) as these proved difficult to map. Mapped restriction site data was, however, obtained for the *trn*C [tRNA-Cys (GCA)] - *trn*D [tRNA-Asp (GUC)] region (see Fig. 2C.2.). This was because in *Begonia* several length mutations were found within this region (Plate 4) and these could potentially lead to misleading results due to their over weighting in an RFLP analysis.

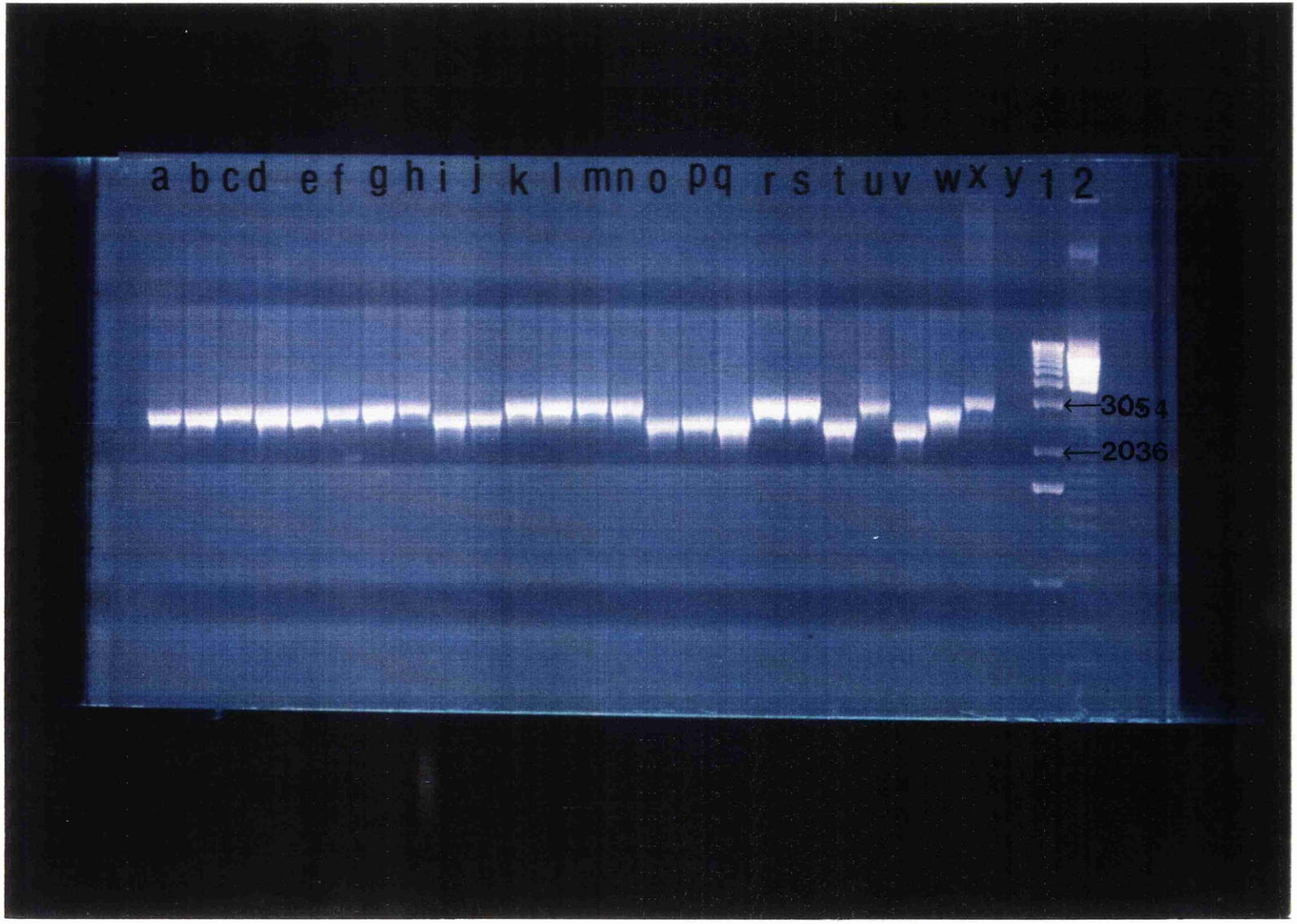


Plate 4. PCR product of the *trn*C - *trn*D intergenic spacer showing length variation in different taxa

Plate 4.

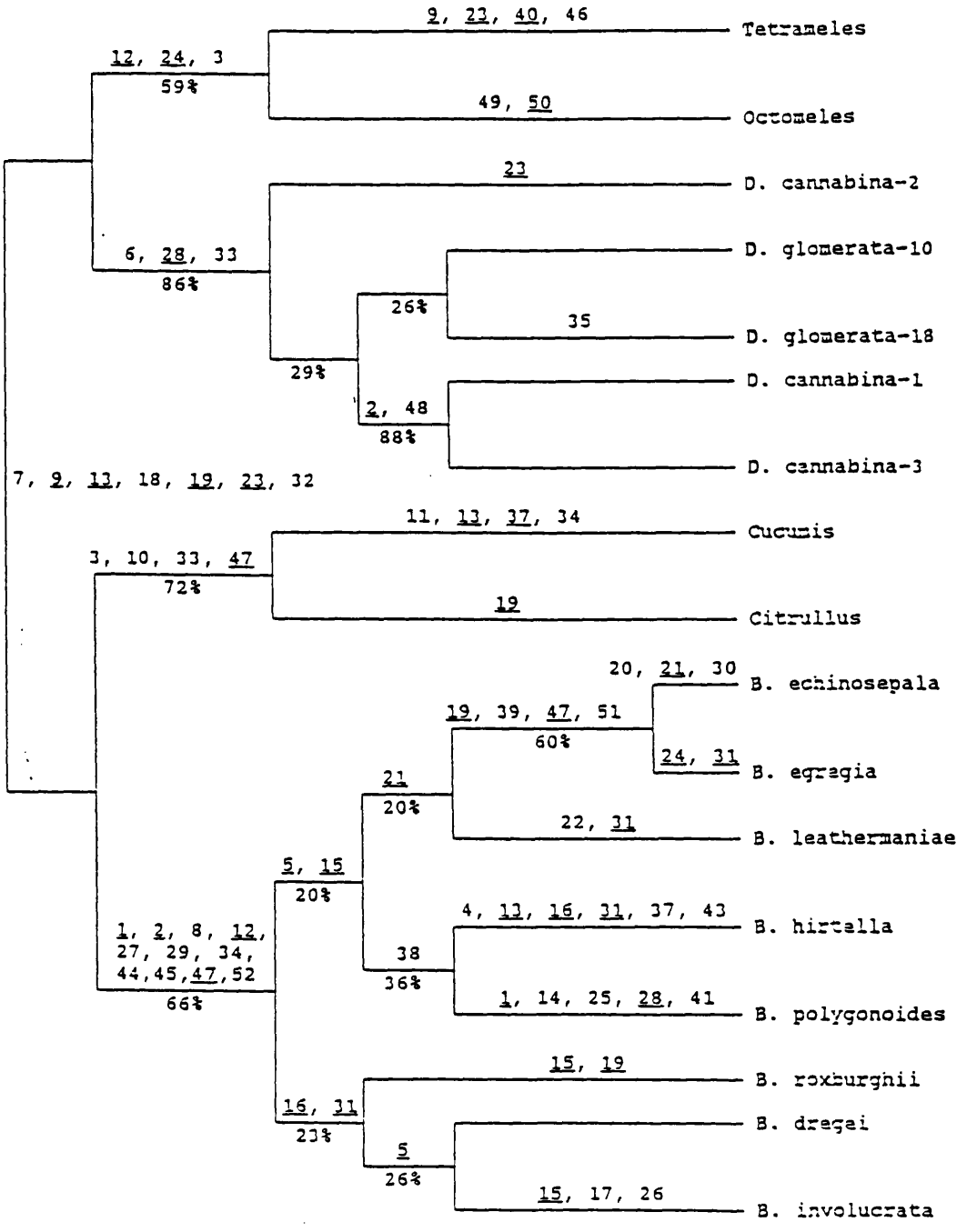
Key to lanes

a) *B. roxburghii*
b) *B. mengyangensis*
c) *B. Platycentrum* sp. 1
d) *B. balansana*
e) *B. tayabensis*
f) *B. salaziensis*
g) *B. annulata*
h) *B. hatacoa*
i) *B. floccifera*
j) *B. goegoensis*
k) *B. chlorosticta*
l) *B. brevirimosa*
m) *B. amphioxis*
n) *B. grandis*
o) *B. incarnata*
p) *B. dregei*
q) *B. sutherlandii*
r) *B. mannii*
s) *B. prismatocarpa*
t) *B. masoniana*
u) *B. solananthera*
v) *B. herbacea*
w) *B. poculifera*
x) *Hillebrandia*
y) -ve
1) 1 kb ladder
2) 123 bp ladder

Few PCR based, restrictriction enzyme studies of plant phylogeny have been published, although a number of population level studies have been conducted using this technique (Ferris *et al.*, 1993; Jordan *et al.*, 1996; Mousadik & Petit, 1996). A study of *Astragalus* by Liston (1992) and a study of the evolution of androdioecy within the Datiscaceae by Rieseberg *et al.* (1992) are perhaps the only published uses of this technique for determining plant phylogeny. Liston (1992) amplified DNA fragments using primers for the chloroplast genes RNA polymerase C1 and RNA polymerase C2 and subjected these to single and double digests using 22 enzymes. Rieseberg *et al.* (1992) amplified cpDNA using primers for the *rbc*L gene and open reading frame 106 (ORF 106) and subjected these to single and double restriction endonuclease digests using 30 enzymes. In addition to the taxa of Datiscaceae, two taxa of Cucurbitaceae and eight species of *Begonia* were also included in the study, as outgroups. In an analysis of the mapped restriction site data, *B. roxburghii*, which is currently included within section *Sphenanthera*, is placed as a sister-species to *B. dregei* and *B. involucrata* (Fig. 2C.1.). The study is, however, largely uninformative with regards the phylogeny of *Begonia* because of the low number of species and the limited geographical area sampled.

The molecular techniques used in the present study are outlined in 2C.4.2., RFLP characters are presented in Table 2.3. and restriction site maps in 2C..2. Cladograms are presented and discussed in 2C.4.4.

Fig. 2C.1. Dollo majority rule consensus tree for Datiscaceae (*Tetrameles*, *Octomeles* & *Datisca*), Cucurbitaceae (*Cucumis* & *Citrullus*) and Begoniaceae (*Begonia*) based on restriction site mutations of PCR-amplified chloroplast DNA fragments (reproduced from Rieseberg *et al.*, 1992).



2C.4.2. MOLECULAR TECHNIQUES

Total DNA was isolated from fresh and silica dried leaf material using a CTAB micro-extraction method. This method is a modified form of the Doyle & Doyle (1987) macro-extraction protocol used in the sequencing study (2C.3.2.). It was necessary to produce a modified version of this protocol for *Begonia* DNA isolation because the original method resulted in DNA of poor quality. Full details of the modified protocol are given in Appendix Eb. This protocol differs from the Doyle & Doyle (1987) protocol in that the ingredients are scaled down so that all stages are carried out in 1.5µl ependorf tubes and by the fact that the leaf material is homogenised using a ground glass rod attached to a domestic power drill. A number of regions were screened with the aim of identifying areas of the genome which exhibit suitable levels of variation for phylogenetic reconstruction within *Begonia*. The following seven primer pairs from Demesure *et al.* (1995) were initially used: *trn*H [tRNA-His (GUG)] - *trn*K [tRNA-Lys (UUU) exon 1], *trn*C [tRNA-Cys (GCA)] - *trn*D [tRNA-Asp (GUC)], *psb*C [psII 44 kd protein] - *trn*S [tRNA-Ser (UGA)], *trn*M [tRNA-Met (CAU)] - *rbc*L [RuBisCO large subunit], *trn*S [tRNA-Ser (UGA)] - *trn*fM [tRNA-fMet (CAU)], *trn*S [tRNA-Ser (GGA)] - *trn*T [tRNA-Thr (UGU)] and *nad*4 exon 1 - *nad*4 exon 2. The first six are chloroplast regions and the seventh is situated in the mitochondria. Both the *trn*S - *trn*fM and *trn*S - *trn*T regions proved difficult to amplify within *Begonia* under a variety of PCR conditions and, therefore, were not used in the study. *Epipactis yongiana* Richards & Porter was used as a positive control in all amplifications, this taxon produced PCR product in all reactions, which suggests that the *trn*S - *trn*fM and *trn*S - *trn*T primer sequences may not be optimum for *Begonia*. Amplification conditions for *trn*H - *trn*K, *psb*C - *trn*S and *trn*C - *trn*D were:

4 mins at 94°C,
58°C for 45 secs.,
92°C for 45 secs., } x 35
72°C for 2 mins.,
72°C for 10 mins.

Conditions for *trn*M - *rbc*L and *nad*4 exon 1-2 amplification were as above, with the exception that the initial annealing temperatures used were 59°C, for the former and 60°C, for the latter. The amplified products were digested using the following 16 restriction enzymes: *Alu* I, *Bam*H I, *Cfo* I, *Cla* I, *Dra* I, *Eco*R I, *Eco*R V, *Hae* III, *Hind* III, *Hinf* I, *Mbo* I, *Msp* I, *Pst* I, *Rsa* I, *Ssp* I, *Taq* I. The recognition sequences of these enzymes are presented in Appendix G. The following species were used to screen for suitable variation using the primer pairs and restriction

enzymes above: *B. brevirimosa*, *B. dregei*, *B. floccifera*, *B. goegoensis*, *B. grandis*, *B. mannii*, *B. roxburghii*, *B. solananthera*, *B. tayabensis*, *B.* section *Platycentrum* 1, *B.* section *Platycentrum* 2. Sectional membership and distribution of these taxa are given in Table 2.1. The only polymorphisms detected for the *trn*M - *rbc*L and *trn*H - *trn*K regions were autapomorphies, therefore, these were not used in the full scale analyses. The region *nad*4 exon 1 - *nad*4 exon 2 was found to exhibit suitable variation when digested with *Bam*H I, *Hinf* I, *Mbo* I and *Taq* I and was, therefore, analysed for these enzymes using the full complement of taxa (Appendix A lists all the taxa included in the study). The region *psb*C - *trn*S was found to exhibit suitable variation when digested with *Alu* I and *Cfo* I and was, therefore, analysed for these enzymes using the full complement of taxa. The region *trn*C - *trn*D was found to exhibit suitable variation when digested with *Alu*I, *Cla* I, *Dra* I, *Eco*RI, *Eco*RV, *Hae* III, *Hind* III, *Mbo* I, *Msp* I, *Rsa* I, *Ssp* I, *Taq* I and was, therefore, analysed for these enzymes using the full complement of taxa. Plate 5 shows the RFLP pattern obtained by digesting the *trn*C - *trn*D fragment with *Dra*I and Plate 6 shows the patterns obtained by digesting the *nad*4 exon 1-2 fragments with a) *Taq*I and b) *Bam*HI. Several length mutations were found to occur in the *trn*C - *trn*D region (see Plate 4) and it was decided to map the restriction sites for this region in order to optimise the cladistic analysis. Restriction site maps are shown in Figure 2C.2. Double digests of all enzymes were carried out with *Eco*RI, *Eco*RV and *Hae*III. Fragment lengths were estimated using 1 Kb and 123bp DNA ladders. In some cases where the relative position of sites was difficult to distinguish, triple and partial digests were also conducted to aid mapping. The restriction sites of *Mbo*I, *Rsa*I and *Taq*I proved difficult to map and were, therefore, not included in the analyses.

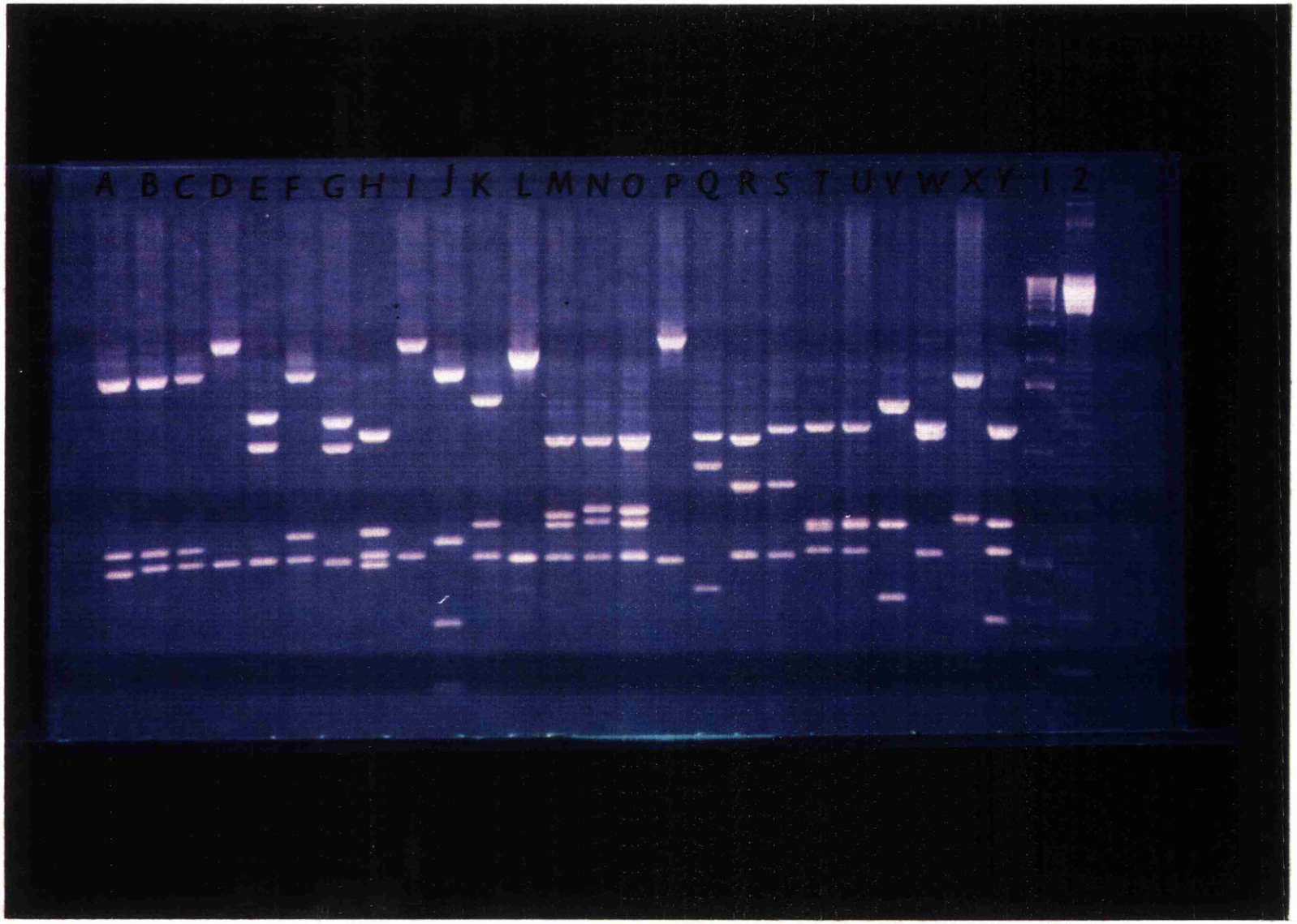


Plate 5. Restriction digest of the chloroplast *trn*C-*trn*D region cut with *Dra*I

Plate 5.

Key to lanes

a) *B. roxburghii*
b) *B. acetosella*
c) *B. mengyangensis*
d) *B. Platycentrum* sp. 1
e) *B. Platycentrum* sp. 2
f) *B. balansana*
g) *B. tayabensis*
h) *B. salaziensis*
i) *B. annulata*
j) *B. hatacoa*
k) *B. floccifera*
l) *B. goegoensis*
m) *B. chlorosticta*
n) *B. brevirimosa*
o) *B. amphioxis*
p) *B. grandis*
q) *B. incarnata*
r) *B. dregei*
s) *B. sutherlandii*
t) *B. mannii*
u) *B. prismatocarpa*
v) *B. masoniana*
w) *B. solananthera*
x) *B. herbacea*
y) *B. poculifera*
1) 1 kb ladder
2) 123 bp ladder

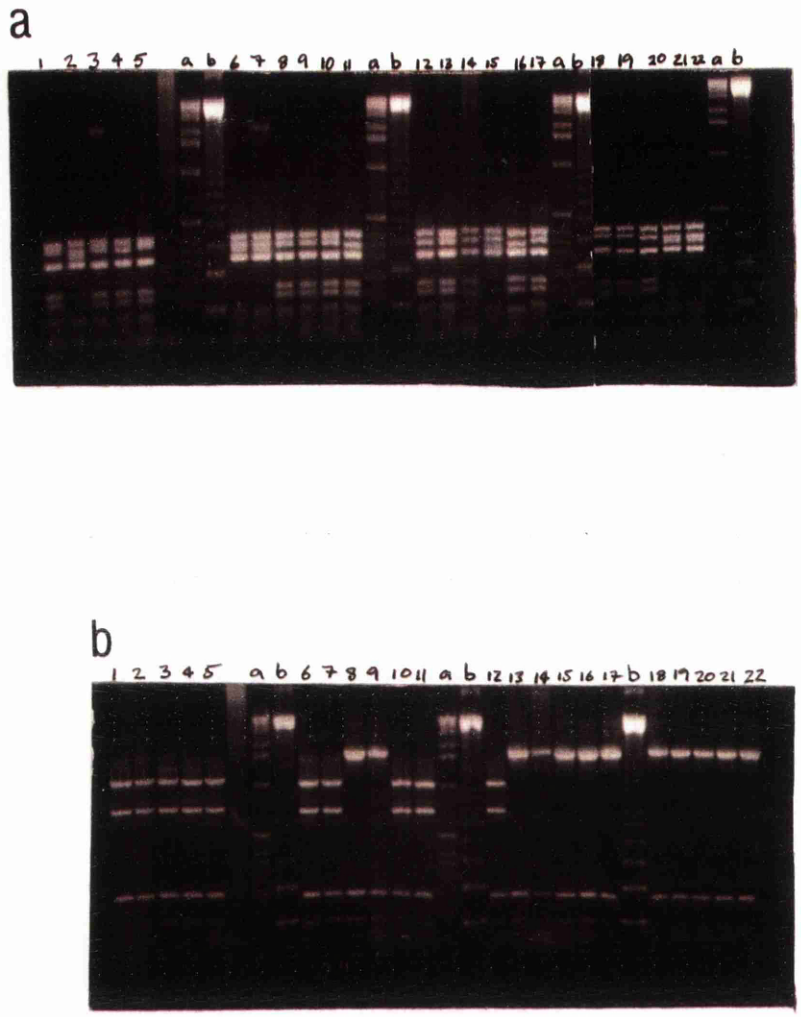


Plate 6. (a) Restriction digest of the *nad*4 exon1-2 region cut with *Taq*I (b) Restriction digest of the *nad*4 exon1-2 region cut with *Bam*HI

Plate 6.

Key to lanes

1) *B. roxburghii*
2) *B. Platycentrum* sp. 1
3) *B. mengyangensis*
4) *B. acetosella*
5) *B. Platycentrum* sp. 2
6) *B. annulata*
7) *B. hatacoa*
8) *B. brevirimosa*
9) *B. chlorosticta*
10) *B. goegoensis*
11) *B. floccifera*
12) *B. masoniana*
13) *B. amphioxis*
14) *B. grandis*
15) *B. tayabensis*
16) *B. prismatocarpa*
17) *B. dregei*
18) *B. mannii*
19) *B. sutherlandii*
20) *B. incarnata*
21) *B. solananthera*
22) *B. herbacea*
a) 1 kb ladder
b) 123 bp ladder

2C.4.3. THE CHARACTERS

Table 2.3. RFLP characters and character coding used in analyses

Characters 1-5 are from the *nad* 4 exon 1 - exon 2 region.
Characters 6-7 are from the *psb*C - *trn*S region.

1. Presence of *Bam*HI restriction site (738 + 1018 = 1756) (Plate 6b)
0) yes
1) no

2. Presence of 123 bp band when restricted with *Hinf* I
0) yes
1) no

3. Presence of *Taq*I restriction site (154 + 190 = 344) (Plate 6a)
0) yes
1) no

4. Presence of 154 bp band when restricted with *Mbo*I
0) yes
1) no

5. Presence of 201 bp band when restricted with *Mbo*I
0) yes
1) no

6. Presence of 230 bp band when restricted with *Alu*I
0) yes
1) no

7. Presence of 615 bp band when restricted with *Cfo*I
0) yes
1) no

Fig. 2C.2. Restriction site maps of the *trn*C - *trn*D intergenic spacer region
All restriction sites are shown for *B. roxburghii*, but only the gain or loss of restriction sites relative to *B. roxburghii* is given for the remaining species. Restriction sites are designated as follows: a, *Msp*I; b, *Eco*RI; c, *Alu*I; d, *Hae*III; e, *Hind*III; f, *Dra*I; g, *Ssp*I; h, *Taq*I; i, *Eco*RV; j, *Cla*I. The mapped restriction site characters (48-63) were recorded from left to right along the sequence. Only synapomorphies were scored.

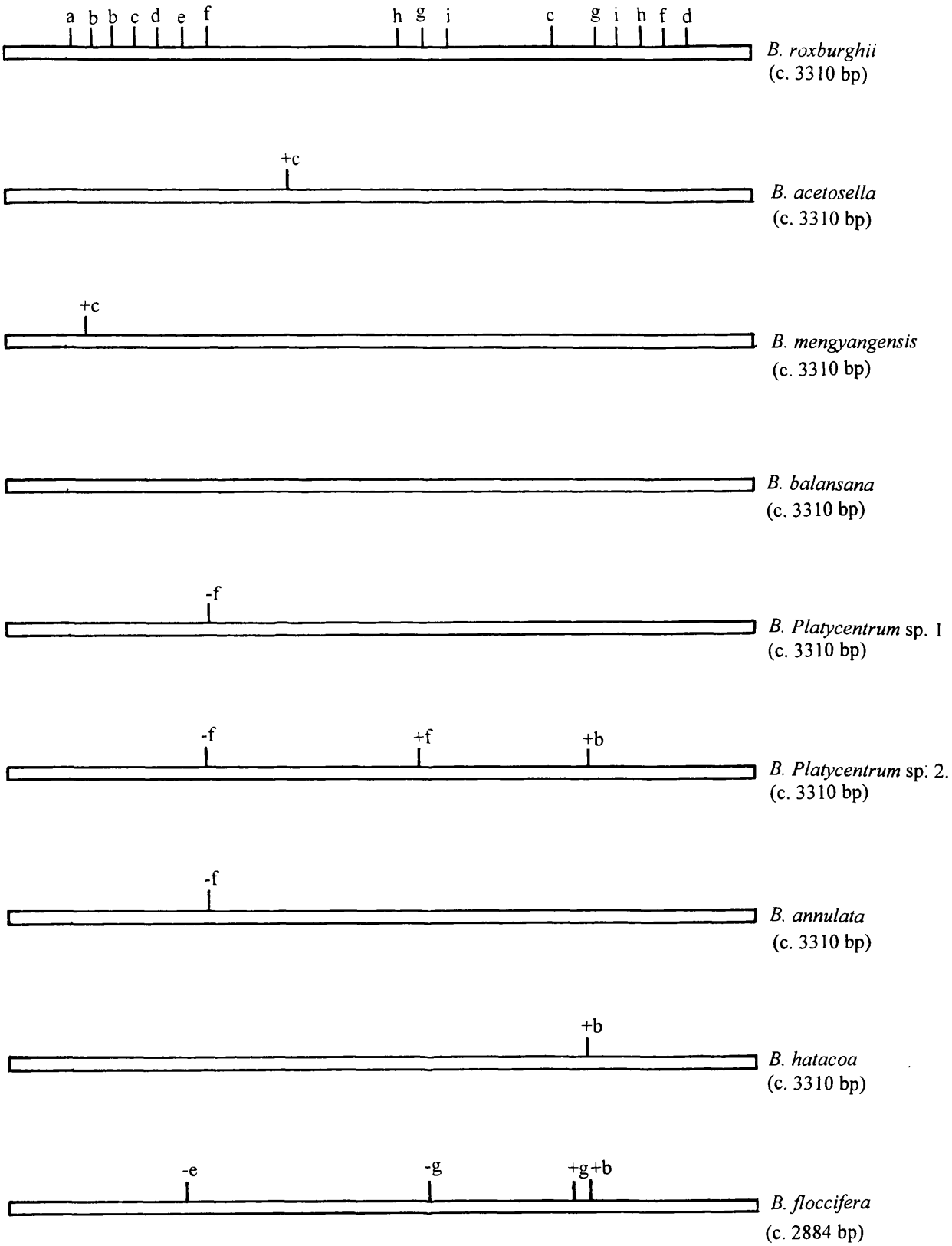


Fig.2C.2. (continued)

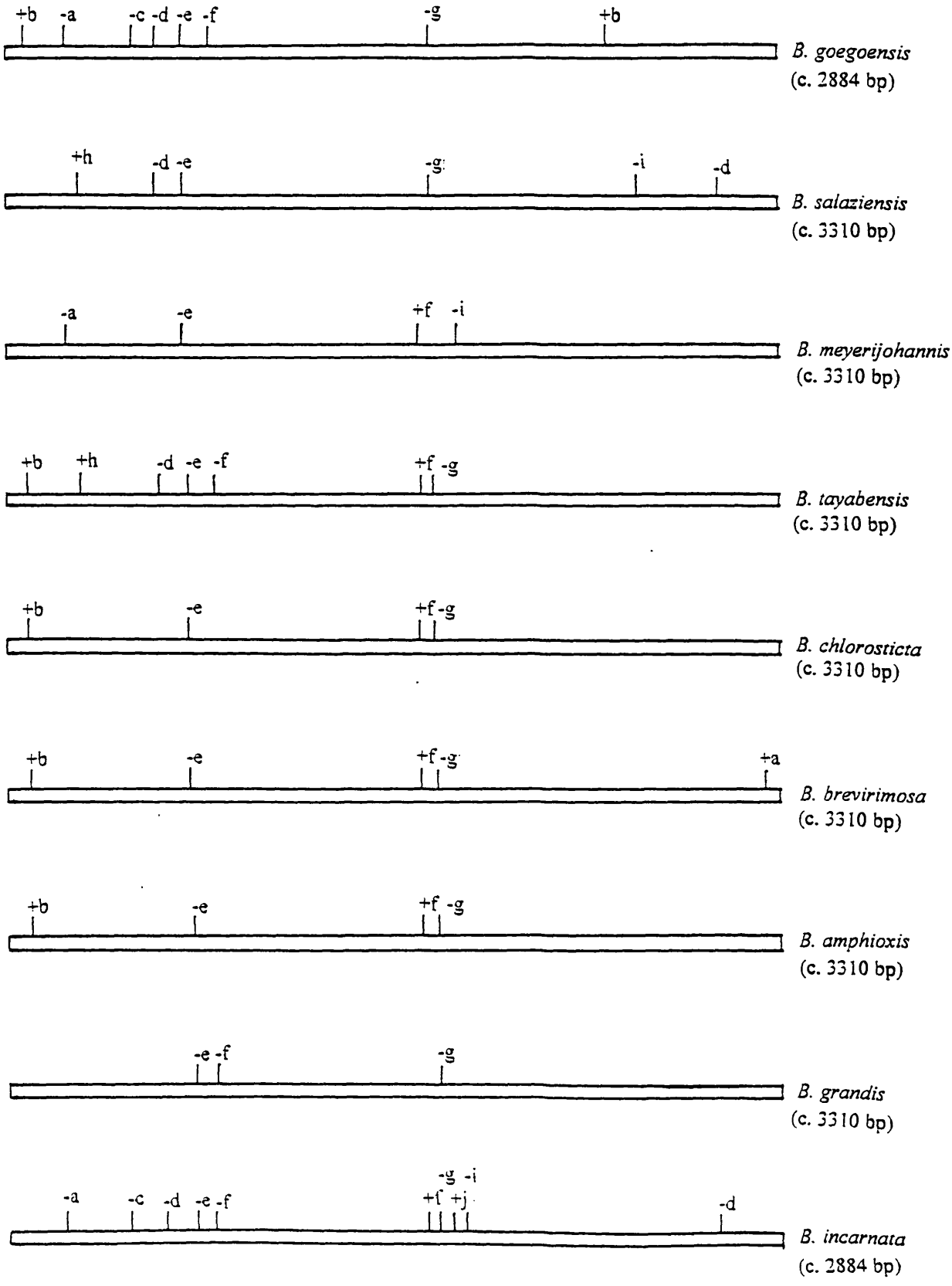
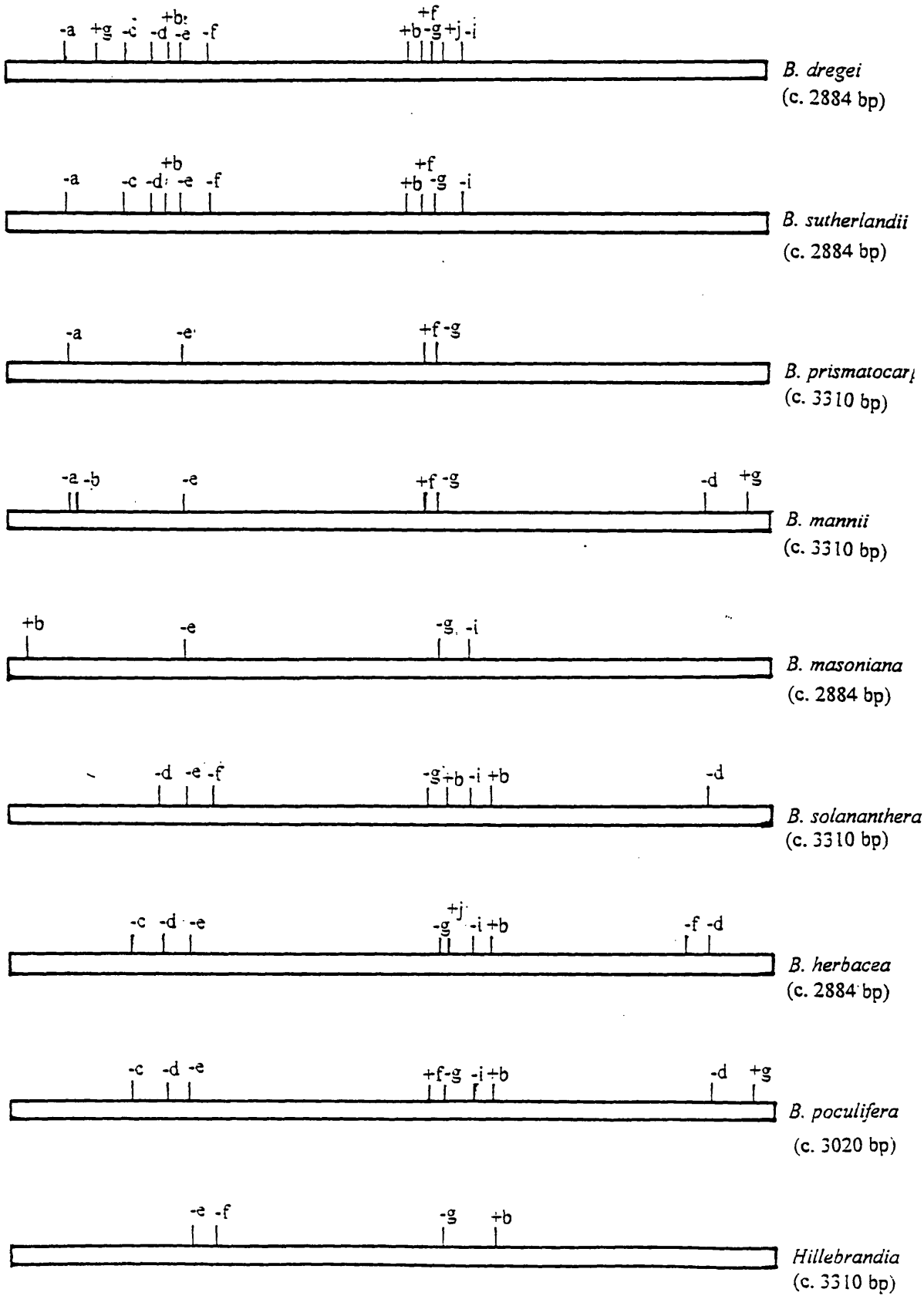


Fig. 2C.2. (continued)



2C.4.4. THE CLADISTIC ANALYSES

2C.4.4.1. PROGRAMMES, ANALYSES AND CHARACTER CODING

Heuristic parsimony analyses were performed in PAUP (version 3.1.1.; Swofford, 1993) set for TBR branch-swapping. Support for clades was inferred by bootstrapping (Felsenstein, 1985). In order to test the affect of taxon sampling on tree topology, separate analyses were carried out using all of the 25 taxa from which molecular data was collected and just the 22 taxa from which morphological data was also collected. The full data set is presented in 2D.2.

2C.4.4.2. EXPLORATORY ANALYSES AND CLADOGRAMS

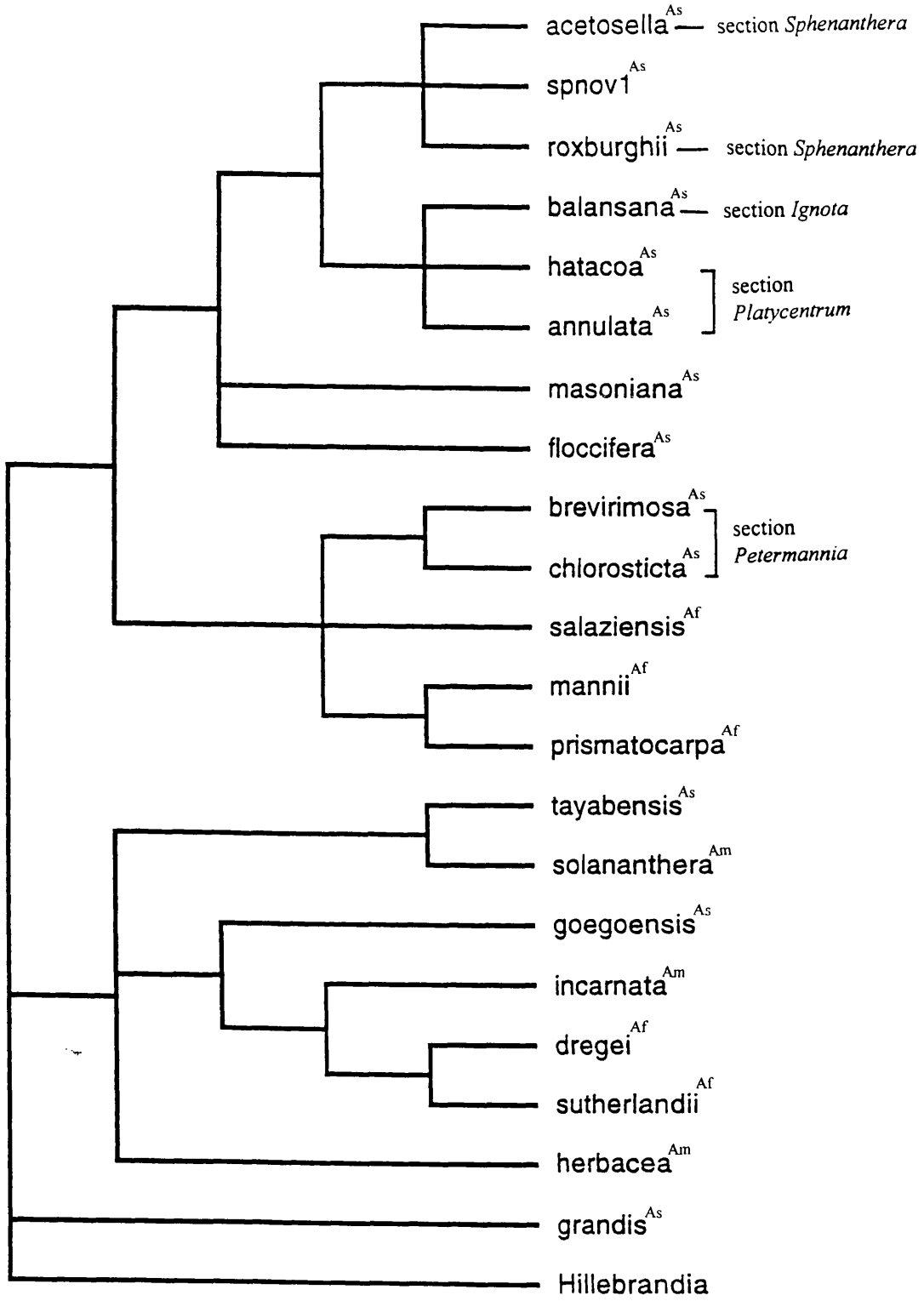
A general heuristic search of the subset of 22 taxa found 2 equally parsimonious trees with a length of 32. These had a CI of 0.500 and a RI of 0.789. A general heuristic search of the subset of 25 taxa found 4 equally parsimonious trees with a length of 51. These had a CI of 0.451 and a RI of 0.767. *Begonia tayabensis* was not included in the analysis as its presence resulted in a marked loss of resolution. Comparison of the analyses incorporating 22 and 25 species (Figs. 2C.3. & 2C.4.) indicates that the addition of taxa does not lead to a marked change in tree topology. Bootstrapping was carried out to give an estimate of support for the clades in the analysis incorporating 22 taxa. A general heuristic search with 100 bootstrap replications and a random number seed found that the most parsimonious tree was generally poorly supported (Fig. 2C.5.). The lack of resolution in this consensus tree may be explained by the small number of characters supporting the clades as can be seen by examining the branch lengths on the two most parsimonious trees (Fig. 2C.6.). As the bootstrap analysis only recognises clades supported by at least three characters it may be suggested that bootstrapping is not a suitable method of analysing the data because it causes an unnecessary lack of resolution because of the low number of characters present in the data set. While it is evident that the clades are supported by few characters, the data is nether the less highly structured as the length of the trees found here is considerably shorter than those generated by random sampling of the data set. The distribution of random tree lengths is left-skewed as indicated by the g1 value of -0.603889. The RI value of 0.789 also suggests that the tree is well supported. Observation of the data in the splits tree program (version 1.0; Huson & Wetzel, 1994) using Hamming distances, however, suggests that it does not have a strong cladistic signal. This can be inferred from the poor fit of the data (22.3%) and the fact that many of the taxa

are related to each other in a reticulate fashion. It is, however, pertinent to note that even in the bootstrap analysis the clade containing the species from section *Sphenanthera* and its sister group *Platycentrum* is well supported and that the two taxa from *Sphenanthera* plus a new species (*B. mengyangensis* Tebbitt & K.Y. Guan) and the two taxa from *Platycentrum* plus *B. balansana* occur within this as well supported sub clades. This suggests that within section *Sphenanthera*, at least *B. roxburghii*, *B. acetosella* and the new species constitute a monophyletic group. It is particularly interesting that the phylogenetic affinities of *B. balansana* with species from section *Platycentrum* are well supported as the phylogenetic affinities of this species were previously unknown (Barkley & Golding, 1974). The molecular data suggest that *B. balansana* is a member of section *Platycentrum*. A clade composed of *B. brevirimosa* and *B. chlorosticta* which are both from section *Petermannia* is also well supported. The phylogenetic affinity of *B. amphioxis* with these members of section *Petermannia* (Fig. 2C.4.) is of note as this species was also previously of unknown phylogenetic affinity (Sands, 1990). *Begonia amphioxis* was initially included within the analyses as its shallowly winged fruits suggest that it may be closely related to members of section *Sphenanthera*. The full analyses of the molecular data (Fig. 2C.4.) clearly indicates that this taxon is not closely related to the members of that section included here but instead is probably a member of section *Petermannia*. The phylogenetic affinities of this species with members of section *Petermannia* is also supported by the fact that *B. amphioxis* possess distinct endothecial wall thickenings and other characteristics of its anthers which are otherwise confined or almost confined to members of this section (MacIver & Tebbitt, unpublished data). The *B. dregei* - *B. sutherlandii* clade is also well supported by bootstrap values (Fig. 2C.3.). These taxa currently belong to sections *Augustia* and *Rostrobegonia* respectively. It is interesting to note that both de Wilde (1985a) and de Lange & Bouman (1992) have suggested that these two sections require merging.

In order to compare stringently the molecular and morphological data only the subset of 22 taxa analysed here are used in subsequent comparisons between these two data sets. The following points suggests that the molecular data set has phylogenetic signal: a) cladogram topology is largely unaffected by the addition of taxa, b) some of the clades are supported by bootstrap values, c) the most parsimonious tree from the analysis of the subset of 22 taxa has a high RI of 0.789.

It should also be noted that many of the clades are consistent with traditional views of *Begonia* classification.

Fig. 2C.3. Strict consensus tree from a Heuristic search of a subset of 22 taxa from the molecular data set



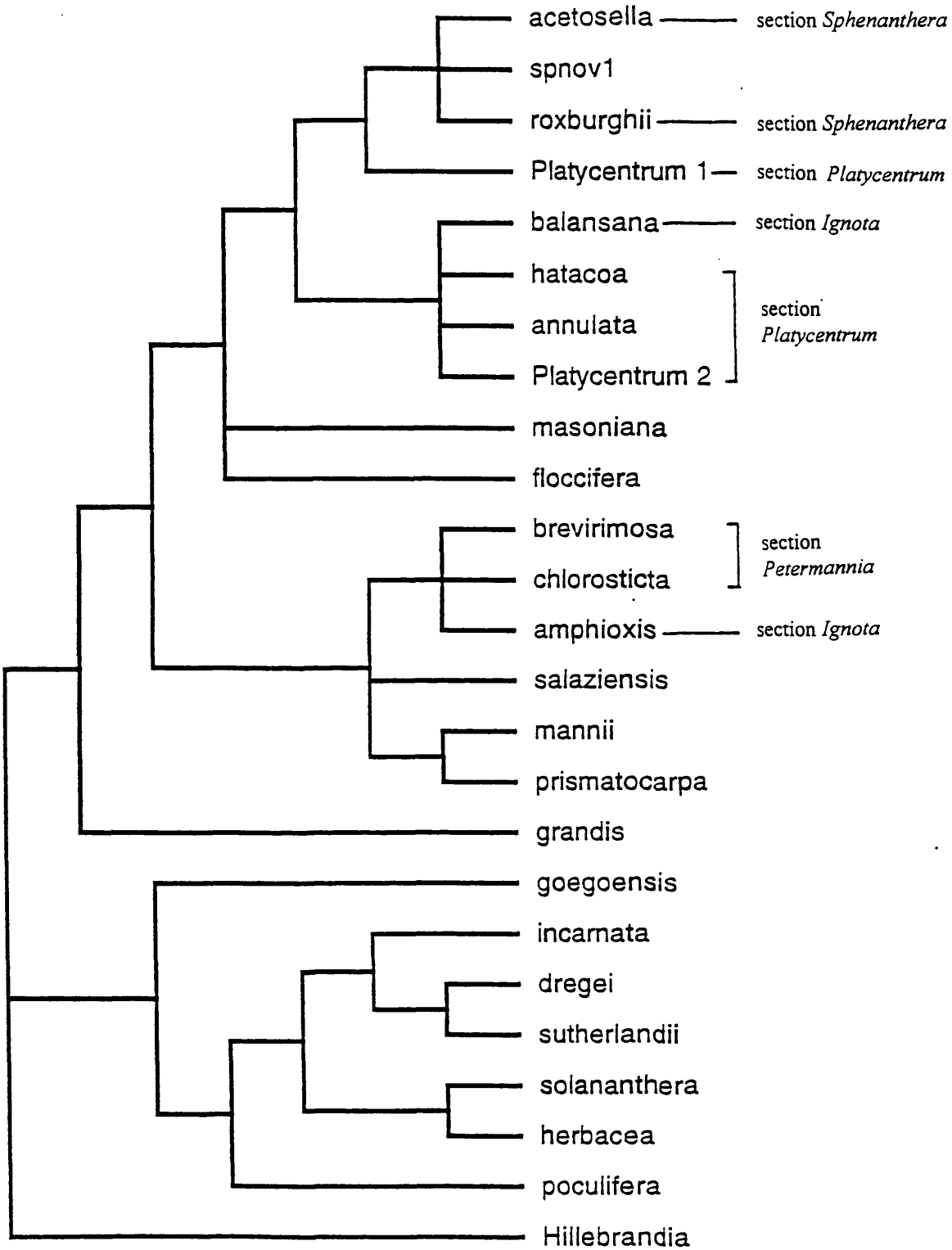
Key

Species' distributions

Af= African, Am= American, As= Asian

2 trees
Length=32
CI=0.500
RI=0.789

Fig. 2C.4. Strict consensus tree from a Heuristic search of a subset of 25 taxa from the molecular data set



4 trees
Length=51
CI=0.451
RI=0.767

Fig. 2C.5. 50% majority rule boostrap consensus tree produced from a subset of 22 taxa included in the molecular study

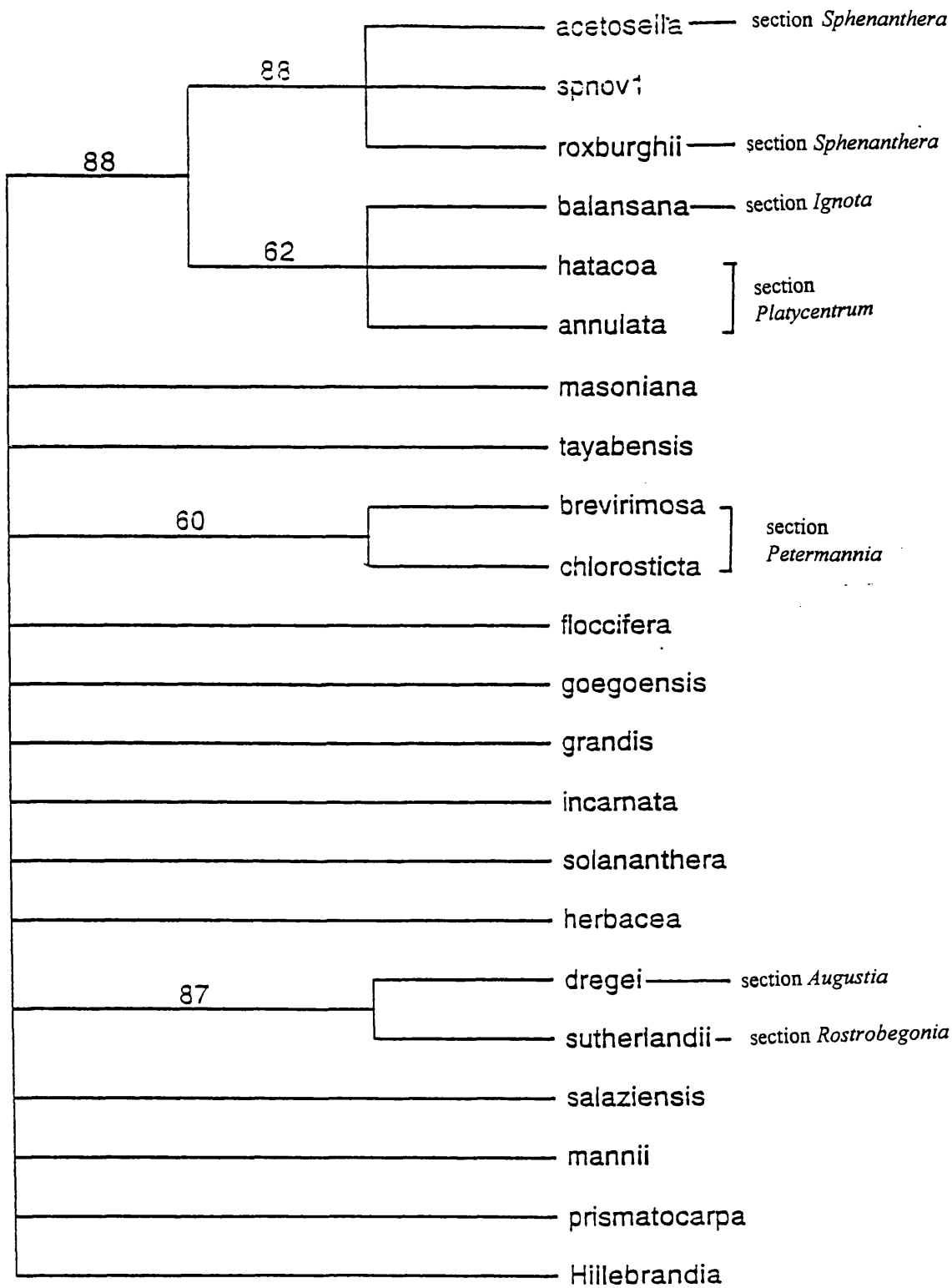
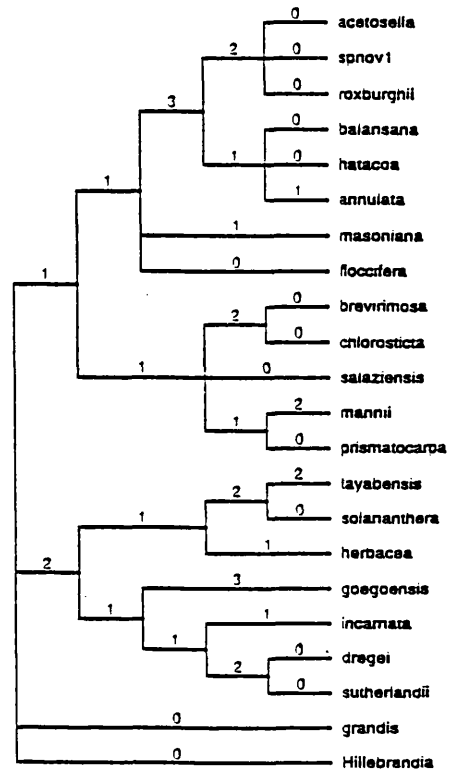
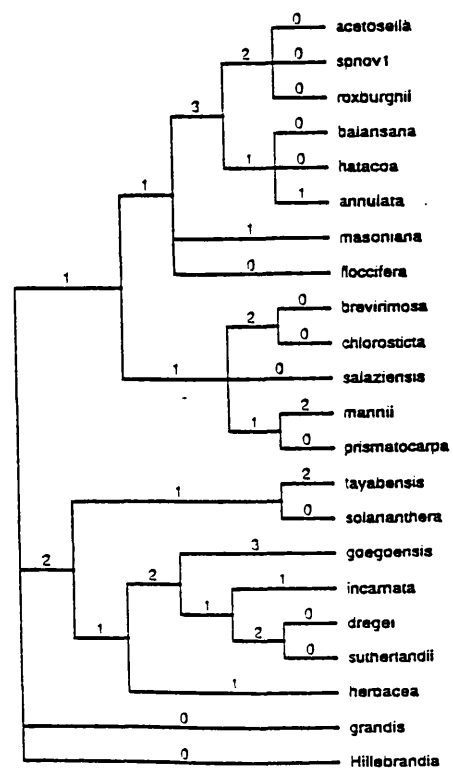


Fig. 2C.6. The two most parsimonious trees produced from an Heuristic analysis of the molecular data - showing character support for the clades





Chapter 2
PHYLOGENETIC INVESTIGATION OF *BEGONIA* SECTION *SPHENANTHERA*

SECTION D: COMBINED AND TOTAL EVIDENCE

SECTION 2D: COMBINED AND TOTAL EVIDENCE

2D.1. INTRODUCTION: SEPARATE OR COMBINED ANALYSES?

Much has been written concerning the relative advantages and disadvantages of morphological and molecular data and the value of each for reconstructing phylogeny (Hillis, 1987; Sytsma, 1990; Doyle, 1992; Donoghue & Sanderson, 1992). The use of morphological data to reconstruct phylogeny in particular, has received a great deal of opposition from practitioners of molecular techniques, who have often claimed that it contains too much homoplasy to be of value (*e.g.* Sytsma *et al.*, 1991). This view now, however, appears to be theoretically unfounded and was probably partially a sociological reaction whereby new molecular techniques were promoted by reducing the perceived value of older techniques (Donoghue & Sanderson, 1992). The value of including information from both molecules and morphology in a phylogenetic analysis is particularly high when they are in general agreement and offer character support at different hierarchical levels as a result of differing rates of evolutionary change (Donoghue & Sanderson, 1992).

Systematists have traditionally treated morphological and molecular data as distinct data sets but such divisions may not always be realistic (Kluge & Wolf, 1993). Before deciding on the appropriate treatment of data from morphology and molecules it is important to determine whether or not the data sets being compared actually represent distinct classes of data. If they do not there is no justification for treating them separately (Miyamoto & Fitch, 1995). In the present study, the strict consensus trees produced separately from the morphological and molecular data sets were compared in order to roughly estimate whether these data sets were different.

The question of how to combine this information when it does represent distinct classes is highly contentious and much discussion has revolved around whether to combine different data sets prior to analysis, to analyse independently different data sets and then choose between them or to analyse the data sets independently and then combine the resulting cladograms (Bull *et al.*, 1993; de Queiroz & Gauthier, 1992). Convincing arguments have been put forward for all three approaches and de Queiroz & Gauthier (1992, p.670) state that 'except in extreme cases where the benefits of one of the approaches disappear it is difficult to say what one should do.' One example of where the choice between methods is said to be more obvious is when sampling error is the only problem. Where this is the case

Hillis (1985) states that data sets should be combined because this generally decreases the chance of the phylogenetic signal being masked by random data. In practise, it may not always be possible to identify the reason for such differences in data sets. In a few situations it is necessary to combine cladograms as methods of combining data do not exist, as for example, when combining character state data and distance data. Where different data sets represent different histories (*e.g.* as a result of lineage sorting), combining data is not appropriate as this approach aims to reconstruct single clades by presenting many characters which have experienced a common ancestry. In this case, combining cladograms offers one possible approach (de Queiroz & Gauthier, 1992). Some of the advantages and disadvantages of each method are briefly outlined below.

The main arguments for combining data centre on the following views: that total evidence should be used in science (Kluge, 1989); that combined data has a greater ability to uncover phylogenetic groups (Hillis, 1985) and, that it has a greater descriptive and explanatory power compared to combined analyses (Miyamoto, 1985). One problem with combining data which may occur when one data set contains significantly more characters than the other (as commonly occurs with molecular and morphological data sets) is that of swamping of the smaller data set's phylogenetic signal (Hillis, 1985; Doyle, 1992). Although it is likely that swamping does occur in some cases, Donoghue & Sanderson (1992) demonstrate that even a few phylogenetically informative characters may have a large influence upon cladogram topology when character support is not uniform.

The available methods of analysing phylogenetic data assume a constant model of evolution and hence homogeneity of data and, therefore, are not suited to analysing heterogeneous data (Bull *et al.*, 1993), thus providing the main argument for combining cladograms. In a simulated analysis of two molecular data sets, with differing evolutionary rates and a known phylogeny, it was found that with increasing amounts of conflicting data, combining data, as opposed to combining cladograms is more likely to give the wrong phylogeny (Bull *et al.*, 1993). Chippendale & Wiens (1994), however, summarise examples where combining data may resolve relationships not present in separate data sets, because separately they have a weak phylogenetic signal and are masked by homoplasy. Consensus cladograms have also been attacked because they weight characters differentially because cladograms are treated as equally weighted regardless of how many characters are used to construct them or support particular clades (Miyamoto, 1985). Kluge (1989) states that the arbitrary nature of selecting a particular

consensus method is an important reason for not using them. De Queiroz *et al.* (1995) suggest that the choice of a particular consensus method, whilst not being defensible in general terms may, however, be justified based on the particular requirement of a study. In this context de Queiroz *et al.* (1995, p.665-6) state as an example that 'it might be argued that strict consensus provides the most conservative assessment of the agreement between trees, or that Adams consensus trees are best at identifying taxa whose position is at odds in two or more trees.'

Arguments for discarding particular sets of data are based on the recognition of 'good' and 'bad' data sets, where such relative terms refer to their ability to reflect true phylogenetic taxon relationships. Ignoring one data set may improve the recovery of the correct phylogeny, as illustrated by the study carried out by Bull *et al.* (1993). This was based on simulated data from two different molecular data sets with different amounts of homoplasy and rates of evolutionary change. It was found that when the data set with less homoplasy was analysed separately it produced a more accurate phylogeny (as judged against a known phylogeny) than when combined with the cladogram constructed from data with high levels of homoplasy. Barrett *et al.* (1991), however, demonstrated that in this same case, weighting could be used to reflect different evolutionary rates and produce further improved results using combined data. The choice of appropriate weights is, however, problematic in practice because in real situations the correct phylogeny is unknown (de Queiroz *et al.*, 1995).

In view of the difficulty in choosing between competing methods it appears that a sensible approach is to firstly carry out statistical analysis on the data sets to determine differences. If the data sets are found to be different, the data should then be explored by conducting separate, combined and different types of consensus analyses. Separate analyses can highlight conflicts resulting from differential rates of evolution, hybridisation, horizontal transfer or lineage sorting and in these situations may indicate that combining data is not appropriate. The final choice of method can then be based on which method gives the most parsimonious explanation of the data.

As molecular data in the present study was only obtained from approximately 70% of those taxa from which morphological data was collected (plus an extra two species for which no morphological data was obtained), it is desirable to explore the affects of missing data and taxa on cladogram topology. Some authors have excluded taxa with missing categories of data (*e.g.* Vrana *et al.*, 1994). If included,

missing data could increase the number of equally parsimonious cladograms obtained, or may cause the wrong cladogram to be chosen (Huelsenbeck, 1991b). Wiens & Reeder (1995) found that cladograms resulting from taxa with missing categories of data were slightly less similar to the known phylogeny or the phylogeny based on the complete data. This decrease in similarity appears to be minor and most nodes are reconstructed correctly. The inclusion of incomplete taxa is favoured because a hypothesis for such taxa which are mostly correct is better than no hypothesis at all. The effects of including those taxa with missing categories of data are discussed in 2D.6.

2D.2. THE DATA

Table 2.4. The cladistic data matrix

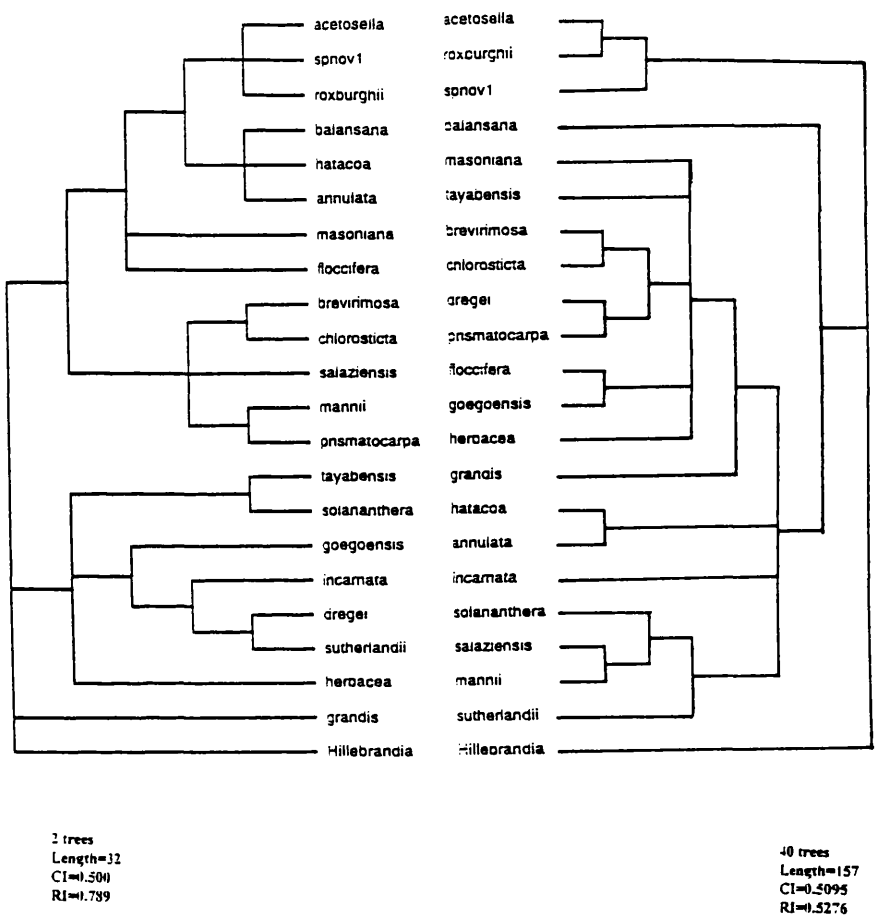
Taxon	1111111111222222222233333333334444444444555555555 56666 12345678901234567890123456789012345678901234567890123456 78 90123
aborensis	1101000002020011100212320201210?221000?????????????????? ?????
acetosella	1012010102021010100212320101210111110001011100010000101101 01011
axillipara	?0?20012?103?0?02010002100011?120?00001?????????????????? ?????
balansana	1001000000021010111012340201310?12130010101011100001011010 1011
brachyptera	10?20012200 3?0?02010002101011101202000 1?????????????????? ?????
burkilii	1101000002021111100212300101210112??0001?????????????????? ?????
cristata	?0?20501000200101002121101011105?1210001?????????????????? ?????
dux	10?1000000020011100212200101010201?12001?????????????????? ?????
handelii	1101000102021011100212320101110112?1000 1?????????????????? ?????
leprosa	1101020001021010100111311111100 0?021500 1?????????????????? ?????
longifolia	1012000 10?020010100212110101110 1?221000 1?????1?????????? ?????
mengyangensis	1101010002020 0?1100212320201210012110001011100010000101101 01011
obovoidea	1002010 20?020011100212110101110 0?020000 1?????????????????? ?????
pseudolateralis	10?20012200 3?0?02010002101011101202000 1?????????????????? ?????
robusta	1001000000020001100212200101110401210001?????????????????? ?????
spnov2	1?0102000002001110021 2?0010111041221000 1?????????????????? ?????
spnov3	1001020000020011100212?0010111040211 2??1?????????????????? ?????
roxburghii	1002000102020010100212320101210 4?1210001011100010000101101 01011
sarcocarpa	?0?20501000200 3 1?0021221010111051 2?10001?????????????????? ?????
silletensis	1101000002020011100212320201210 0?221000 1?????????????????? ?????
tessaricarpa	1001000102020010?0021232010121?412?10001?????????????????? ?????
teysmanniana	?0?2020000020001100212100101010201102001?????????????????? ?????
trigonocarpa	?0?1000000020011?0021221010111?20??10001?????????????????? ?????
turbinata	1012000100020030100212110101110 512?11001?????????????????? ?????
delicatula	1001000000 3?011?1011121121111 00?220001?????????????????? ?????
masoniana	1101020000020011120100410101100201?0001101101110000110111 11011
cordifolia	1201000000021011100111210101110221100001?????????????????? ?????
tayabensis	1101150000021031100110210101110221100001100011100011111011 01011
nepalensis	1002000000031011110211500101010241100001?????????????????? ?????
martabanica	1002000000021011120011201211010221202001?????????????????? ?????
burbidgei	0012050001120010201000210101 1?012211001 1?????????????????? ?????
brachybotrys	1012001220 3?0?02010002101011101201000 1?????????????????? ?????
brevirimosa	1011001020 3?0?12010002101011101211000011010111000011010110 1010
cumingiana	1012001221 3?0?02210002102011101201000 1?????????????????? ?????
chlorosticta	1012000221 3?0?02210002101011101201000?1101011100001101011 01011
hatacoa	1001030000020011100212200101010201102001010101111000010110 100011
annulata	1101030000021001100212200101010201102001010101111000011110 101011
xanthina	1101020000020011100212200101010201102001?????????????????? ?????
floccifera	1101100000 3?0?1120111310101112131100001011011110001101111 100011
goegoensis	1101100000021031?001104101011121 31?000?1001011101111111111 100011
grandis	1002000000021031100111210201110 22?1000011110111100011111110 1011
incarnata	1001000000021011100211210201110221100001111111111111111101 011111
solananthera	0012000000121010211101210101111222?0000111001111001111100010111
urticae	0012110000020000120202112121110 4?2?14020?????????????????? ?????
herbacea	1101000331 3?0?1100100410101 1?12221002011001111011110111010111
dregei	1001000000 3?031100202211211112132100001111011111111101001011011
salaziensis	0012000000021030?102123101011000?2110111111011110001101011010 11
meyerijohannis	0012000002121 0?1?001113301013000?2210110??????0110111101111011
mannii	0012040101021020230012323111200 0?0115111111101111001101011 01101
nossoibea	1201000000 0?1011?102113100011122011000 1?????????????????? ?????
johnstonii	1011000000020011110211210101110222100001?????????????????? ?????
sutherlandii	1001010000020011110211210101110122100001111101111111110100101 11010
prismatocarpa	1002010010 3?0?0121000521211212122205011111011111001101011 01011
quadrialata	1102000010 3?010?2100052121121212220201 1?????????????????? ?????
Hillebrandia	1001010000?0011110021203000030 0?10000311 1??111000111111100011
Datisca	0000000142010120000000110020100 0?0000030?????????????????? ?????
Platycentrum 1	??0111001100001111010 1011
Platycentrum 2	??0101011100001110010 0011
amphioxis	??1010111000011010110 1011
poculifera	??1?1011110111101011 10101

2D.3. COMPARISON OF THE MORPHOLOGICAL AND MOLECULAR CLADOGRAMS

All comparisons of the data sets here are between strict consensus trees containing the same taxa. The strict consensus trees of the morphological and molecular data set are shown in Figure 2D.1., the 50% majority rule bootstrap tree of the morphological data set is shown in Figure 2B.12. and the 50% majority rule bootstrap tree of the molecular data set is shown in Figure 2C.5.

When the strict consensus trees from the two data sets are contrasted their topologies appear to be considerably different (Fig.2D.1.). These data sets, therefore, appear to be distinct. However, in both analyses *B. roxburghii*, *B. acetosella* and a new species form a clade. *Begonia roxburghii* and *B. acetosella* are currently placed within section *Sphenanthera* and it would appear that at least these three taxa form a monophyletic group within this section. This clade is supported by bootstrap values in the molecular analysis but not in the morphological analysis. While the topologies of the strict consensus trees of the two data sets are mostly in conflict it is interesting to note that in the two bootstrap analyses different clades are supported and these do not conflict. The *B. dregei* - *B. sutherlandii* clade is supported in the molecular analysis but not in the morphological analysis. The *B. floccifera* - *B. goegoensis* clade and the *B. salaziensis* - *B. mannii* clades are supported in the morphological analysis but not in the molecular analyses. All these clades are consistent with modern taxonomic thought. The *B. dregei* - *B. sutherlandii* clade probably represents a monophyletic African section (de Wilde, 1985a; de Lange & Bouman, 1992). The *B. floccifera* - *B. goegoensis* clade represent section *Reichenheimia*. *Begonia salaziensis* and *B. mannii* are believed to belong to two closely related African sections (de Wilde, 1985a). Both analyses support the grouping of *B. brevirimosa* and *B. chlorosticta*. These taxa represent section *Petermannia*. It, therefore, appears that the two data sets are to some extent complimentary in the taxonomic groups they support.

Fig. 2D.1. Comparison of the strict consensus trees resulting from the analyses with 22 taxa for the (a) molecular and the (b) morphological data sets.



2D.4. COMBINED CLADOGRAMS

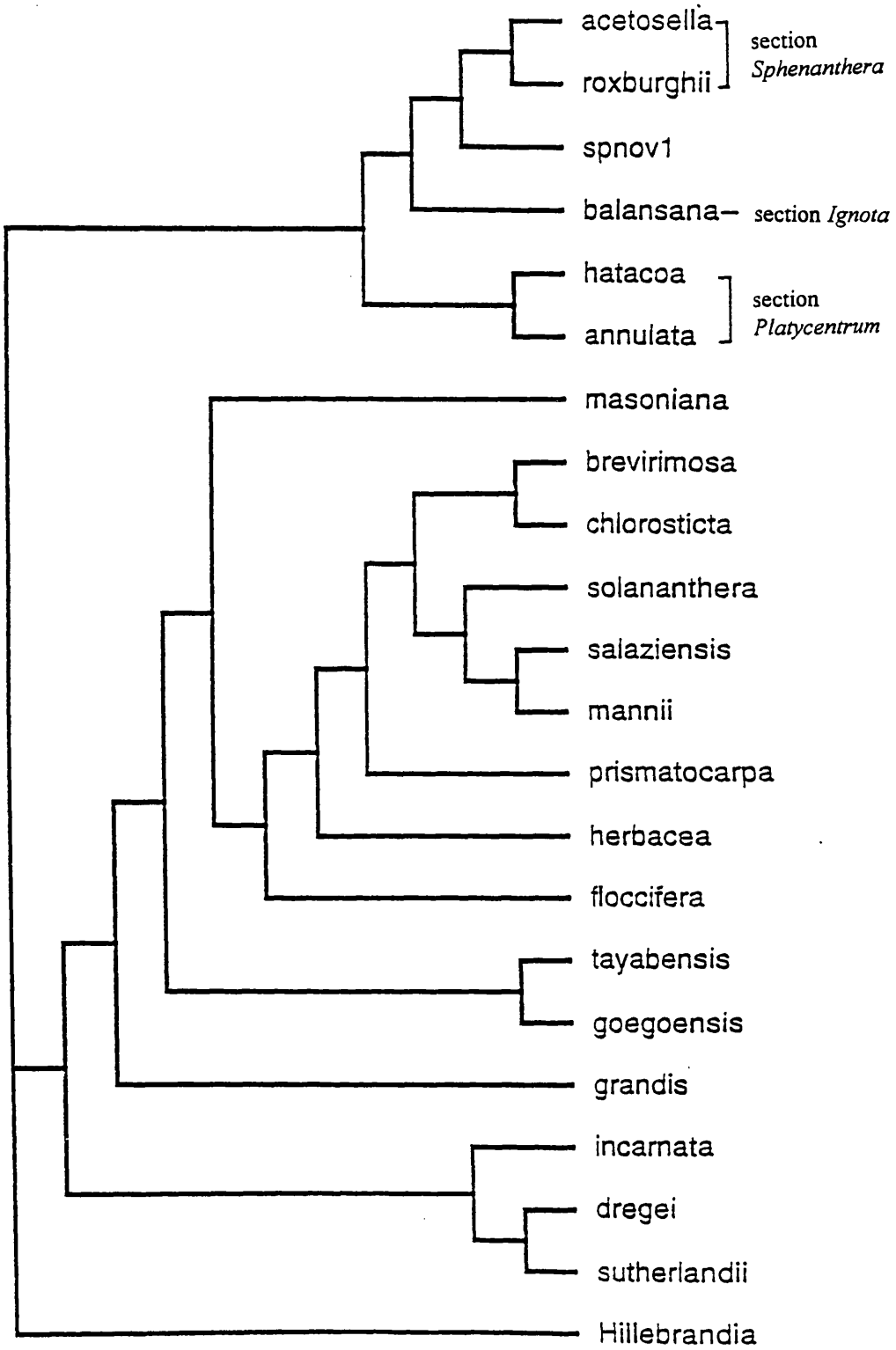
The strict consensus trees from the separate analyses were combined and statistically compared using the computer program COMPONENT (Page, 1993). The strict consensus tree of the combined trees was poorly resolved. This lack of resolution is expected as the trees produced from the separate analyses appear to be considerably different (see 2D.3.). In the strict consensus tree only two clades are resolved. In this tree, the two species of section *Petermannia* appear in a clade and *B. acetosella*, *B. roxburghii* and a new species (*B. mengyangensis* Tebbitt & K.Y. Guan) occur in a unresolved clade. In the semi-strict and Nelson consensus trees an additional clade consisting of the two species from section *Platycentrum* is also resolved. The trees from the two data sets were found to be significantly different upon comparison of the number of triplets resolved and different between the two tree and between each of these trees and random trees. The lack of resolution within the consensus trees produced from the separate trees renders this method of combining the morphological and molecular information of little value to the present study. It is, however, significant to note that the consensus of the trees supports the monophyly of *B. acetosella*, *B. roxburghii* and the new species.

2D.5. COMBINED DATA

Analysis of the combined data for the subset of 22 taxa results in a single tree (Fig. 2D.2.). As the data sets singularly produce more than one tree, this suggests that the two data sets are largely complimentary in the clades they support as previously suggested in 2D.3. A sister group relationship between the members of section *Sphenanthera* included here and members of section *Platycentrum* is supported by the tree produced from the combined data. This relationship was supported by bootstrapping in the molecular analysis (Fig. 2C.5.) but not in the morphological analysis (Fig. 2B.13.). The position of *B. balansana* in the tree produced from the combined data is, however, different from that in the bootstrap analysis of the molecular data. In the tree produced from the combined data *B. balansana* is a sister species of *B. acetosella*, *B. roxburghii* and a new species. In the bootstrap analysis of the molecular data *B. balansana* occurs in an unresolved clade with the two *Platycentrum* species (Fig. 2C.5.). In the strict consensus tree of the morphological data the position of *B. balansana* equally supports a sister species relationship with either the '*Sphenanthera*' or the *Platycentrum* clade (Fig. 2B.12.). It, therefore, appears that in the combined analysis, the morphological data contributes information supporting a closer relationship between *B. balansana* and

the members of '*Sphenanthera*' than between this taxon and the members of section *Platycentrum* and that this information is masked in the separate analysis.

Fig. 2D.2. Strict consensus tree produced from a Heuristic analysis of the combined data subsets



1 tree
Length=207
CI=0.464
RI=0.536

2D.6. THE FINAL CLADOGRAM

The comparisons between the trees produced from combining data and combined trees suggest that combining data is more appropriate in the present study than combining trees because combining the data results in a fully resolved tree, while combining trees results in a largely unresolved tree which clearly contains little phylogenetic information.

A further advantage of combining data compared to combining trees which is relevant to the present thesis is that different data sets with different numbers of taxa can only be combined by combining data. As morphological data was obtained for all the species of section *Sphenanthera* but molecular data was only obtained for a sub set of the section it was necessary to combine the data sets in order to include both data sources in the final analysis.

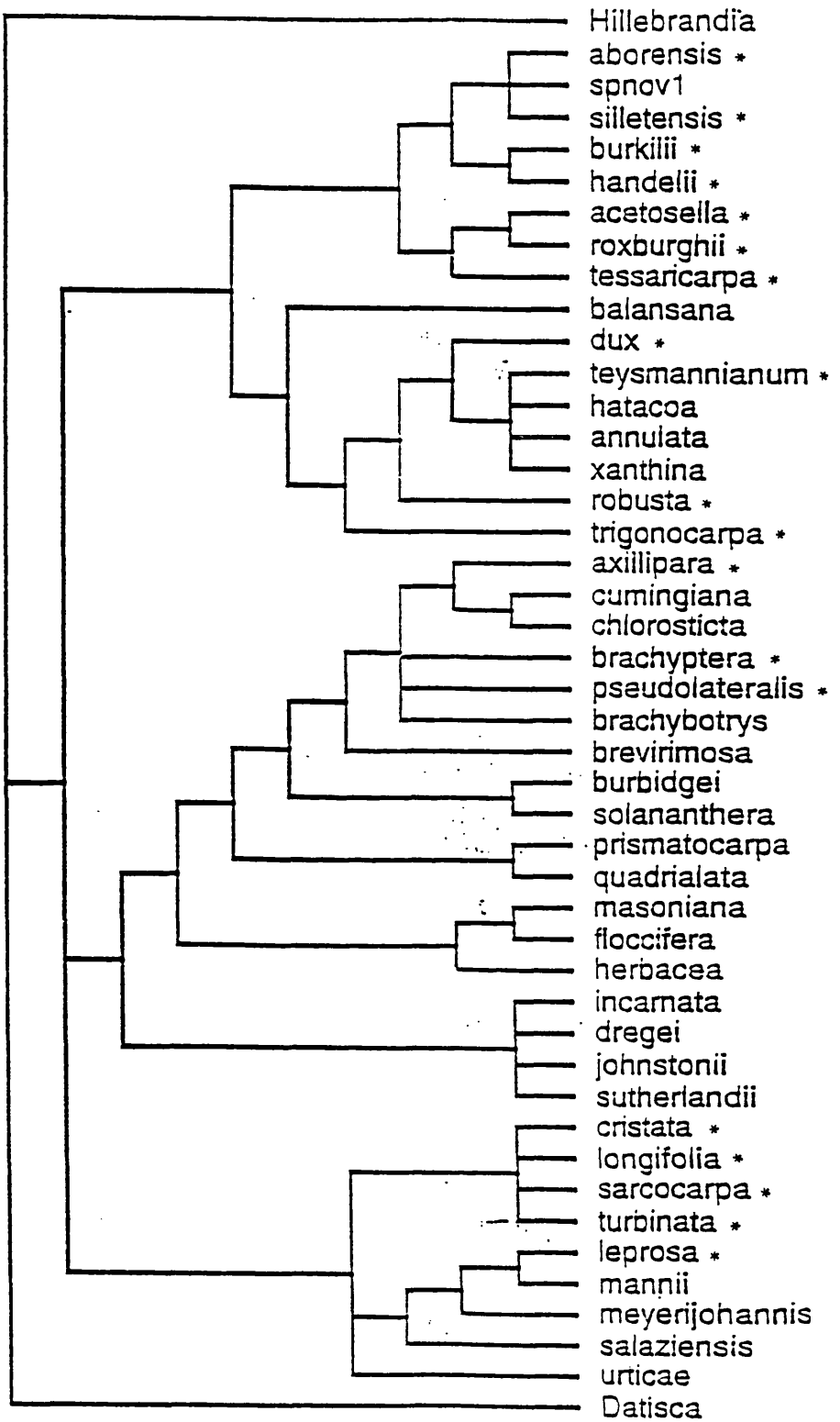
A general heuristic analysis was conducted on the combined data which included all the taxa for which morphological data was present. The analysis was left to run for four days. After this period the analysis was stopped and a strict consensus tree computed. This was found to be poorly resolved and suggests that there is a great deal of character conflict in the data set.

A few of the most poorly known taxa were removed and a further heuristic analysis was conducted. It is possible that some of the characters scored for these taxa are in error because of the low sample numbers examined and this may be causing the lack of resolution in the strict consensus tree. Analysis of this data set resulted in 352 trees with a length of 281 a CI of 0.406 and an RI of 0.661. The amount of cladistic signal was inferred by evaluating the skewness of random tree length distributions. The data is left-skewed as indicated by the g1 value of -0.3999815. This suggests that the data contains phylogenetic information. The RI value of 0.650 also supports this. The strict consensus tree of this data set was, therefore, used as a basis for the revised classification. This tree is shown in Figure 2D.2.

Comparison of the final tree (Fig. 2D.3.) with the strict consensus tree produced from a subset of the taxa in the combined data set (Fig. 2D.2.) indicates that many of the clades are identical or at least similar in the two analyses but that some areas of conflict are also present. One of the most notable of these is in the position of the *B. salaziensis*/*B. mannii* clade. In the analysis of the smaller data set this clade is closely associated with *B. solananthera* and the two species of section

Petermannia, *B. chlorosticta* and *B. brevirimosa*. In the analysis of the larger data set this clade is not closely associated with these taxa but instead is closely associated with taxa which were not included in the smaller analysis. Such differences are probably due to the addition of morphological characters which support new cladistic relationships.

Fig. 2D.3. The final strict consensus tree of the combined data



* species currently included in section *Sphenanthera*

352 trees
Length=281
CI=0.406
RI=0.661

2D.7. CONVERSION OF THE FINAL CLADOGRAM TO A CLASSIFICATION

The distribution of taxa on the final tree indicates that section *Sphenanthera* (Hasskarl) *sensu* Benth. & Hook. f. is polyphyletic (Fig. 2D.3). Therefore, the sectional delimitation of the species previously assigned to this taxon require revision. Some of the characters previously used to delimit *Sphenanthera*, viz. fleshy, wingless indehiscent fruits are plesiomorphic and all occur also in the African section *Mezierea*. Fleshy wingless fruits are also found in section *Tetraphilla* but in this section they are dehiscent. The characters Hasskarl (1855) used to delimit the section, viz. wedge-shaped anthers and persistent styles, are not possessed by many of the species which subsequent authors have included in this taxon and their use in delimiting sections is not supported by the current phylogeny. A revised sectional classification of these species is discussed below in relation to the new phylogenetic evidence presented here.

Begonia axillipara Ridley, *B. brachyptera* Mer. & Per. and *B. pseudolateralis* Warb. occur in a clade which otherwise contains the four members of section *Petermannia* included in the analysis. These three taxa clearly belong to section *Petermannia* and require moving to this section. A number of characters are characteristic of the species of this clade and may be useful in future circumscription of this large section. These include racemose inflorescences, 2 male tepals and very thick anther wall thickenings with base plates. It is also proposed to place *B. amphioxis* Sands in this section as the molecular data indicates that this previously unclassified species is closely related to *B. brevirimosa* and *B. chlorosticta* from this section. This taxon was not included in the combined analysis as only molecular data was collected in the study.

Begonia dux C.B. Clarke and *B. teysmannianum* Irmsch. occur in a clade with all three of the members of section *Platycentrum* included in the study. These two species require moving to this section. The following characters are diagnostic of this clade: fruit 2-locular, with one large and two small wings, styles 2. These characters have traditionally been used to recognise this section. *Begonia robusta*, the type species of section *Sphenanthera*, is a sister species to this clade. In view of the close phylogenetic relationship between this taxon and the members of section *Platycentrum* it is proposed to treat *B. robusta* and hence the section *Sphenanthera* as a subsection of section *Platycentrum*. The only reliable character which separates these two taxa is locule number. All the members of *Platycentrum* have

two locules while *B. robusta* and four other new species which were not included in the final analysis, have three locules. *Begonia trigonocarpa* is also closely related to this clade and may represent either a sixth species of *Sphenanthera* or a new subsection. As this species is only known from a few specimens and a number of other species not included in the study probably also share close phylogenetic affinity to this section no formal taxonomic changes with regard to *B. trigonocarpa* are proposed here. The delimitation of section *Platycentrum* requires further study. As this section contains about 80 species (Barkley & Golding, 1974), such a revision is clearly outwith the scope of the current thesis. *B. balansana* Gagnep. also shares a close relationship to these taxa. The phylogenetic affinity of this species with section *Platycentrum* is particularly well supported by molecular data. These characters include a number of length mutations which were not included in the analyses. The phylogenetic affinities of this taxon were previously unknown and it has not previously been ascribed to a section. It is, therefore, proposed to erect a new subsection of *Platycentrum* for this species. This taxon is particularly distinct as it is the only member of the genus with crown-shaped fruit and 5-7 locules and styles. The seed micro-morphology of this taxon is also distinct as the testa ornamentation of this species is more pronounced than in any other Asian taxon (Bouman, pers comm.).

The clade composed of *B. roxburghii* (Miq.) A.DC. and seven other species represents the group which C.B. Clarke (1879), Warburg (1894), Irmscher (1925) and other authors recognise as section *Sphenanthera*. As this monophyletic clade is characterised by a number of very distinct synapomorphies and it does not contain the type species of *Sphenanthera* it is proposed to recognise it as a new section. This section may be distinguished by the following synapomorphies; stipules persistent, fruit 4-locular, styles 4, or rarely 2 (derived state), dioecious or rarely monoecious with temporal separation of unisexual inflorescences (derived state).

Begonia longifolia Blume, *B. cristata*, *B. sarcocarpa* and *B. turbinata* also belong to a monophyletic clade which does not contain any species of existing sections. It is, therefore, proposed to recognise this clade as a new section. This taxon may be distinguished from other sections of *Begonia* by its member's 3-locular fleshy fruits with axil placentation.

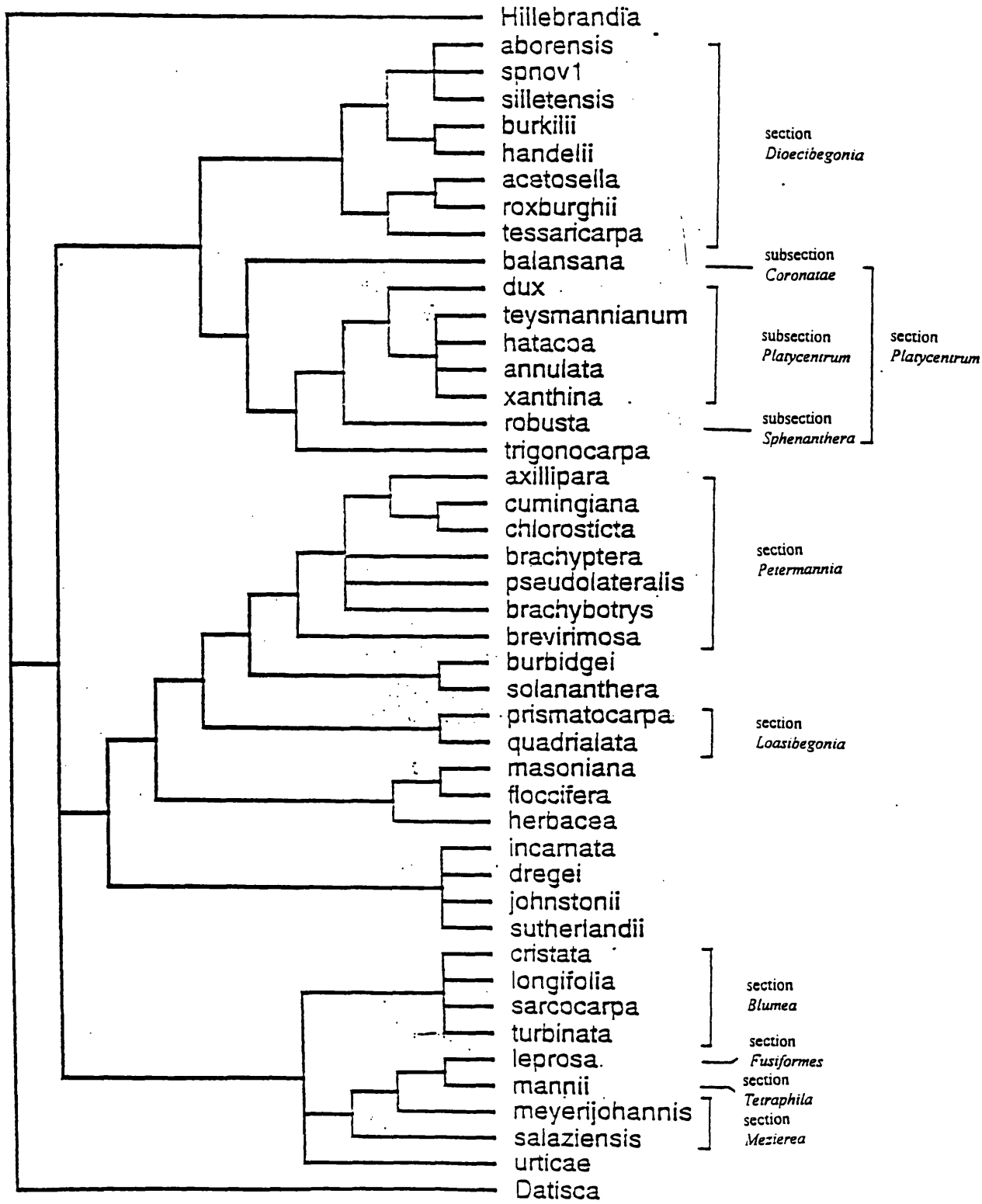
Begonia leprosa Hance occurs in a clade with a number of African taxa from sections *Tetraphila* and *Mezierea*. Within this clade the sister species to *B. leprosa* is *B. mannii* from section *Tetraphila*. As *B. leprosa* possesses a number of

apomorphies not present in the species of section *Tetraphila* it is proposed to erect a new section for this species. Characters which may be used to distinguish this new section from sections *Tetraphila* and *Mezierea* include; seed ornamentation of short striations, operculum of seed nipple-shaped, upper leaf surface with large convex cells, anthers attached to a torus, ovary 3-locular and plant prostrate rather than climbing (the last two characters distinguish this taxon from section *Tetraphila* only).

The creation of monotypic higher taxa has been shown to result in a situation known as Gregg's paradox (Buck & Hull, 1966) whereby the taxonomic content of a monotypic higher taxon is identical to that of a species. Where such taxa are defined on the basis of a large number of apomorphies, as in the above situation with *Begonia* section *Fusiformes*, such higher taxonomic categories may be defended as they serve to highlight the presence of such apomorphies within a species and are, therefore, taxonomically informative.

In Figure 2D.4. the sections of particular interest to the current study are indicated on the final cladogram in order to provide a summary of the revised classification.

Fig. 2D.4. The final tree with higher taxa delimited



352 trees
Length=281
CI=0.406
RI=0.661

Chapter 3
BIOGEOGRAPHY AND POSSIBLE ORIGINS OF THE SECTIONS

CHAPTER 3. BIOGEOGRAPHY AND POSSIBLE ORIGINS OF THE SECTIONS

3.1. INTRODUCTION

Knowledge of the patterns of distribution and the ecological niches occupied by monophyletic taxa may provide an insight into the evolutionary processes responsible for their origin (Platnick & Nelson, 1978). This information can be used to interpret and evaluate phylogenetic hypotheses and classifications. Furthermore, if the distribution of a large number of plant taxa is analysed certain geographical patterns may be identified which may help to reconstruct the vegetational history of a geographical area. The limited distribution, narrow ecological preference and intolerance to changing environmental conditions demonstrated by several *Begonia* species means that they are ideal subjects for biogeographical studies (Sosef, 1994). Sosef (1994), for example, suggested that the present day disjunct distributions shown by the species of the African *Begonia* sections *Loasibegonia* and *Scutobegonia* and a number of other organisms reflect habitat constraints during the last glacial in tropical Africa when lowland rainforests were probably reduced to a number of small refuges.

In this chapter, the final cladogram and resultant classification are discussed in relation to the distribution of taxa in sections *Fusiformes* Tebbitt, *Blumea* Tebbitt, *Dioecibegonia* Tebbitt and *Platycentrum* (Klotzsch) A.DC subsections *Sphenanthera* (Hasskarl) Tebbitt and *Coronatae* Tebbitt. Processes of speciation within these taxa are suggested and related to existing theories on S.E. Asian biogeography.

3.2. DISTRIBUTION OF THE TAXA

In most cases dot maps are provided for the taxa. However, in situations where many collections exist from a particularly well defined region (*e.g.* a mountain range) outline distributions are given. This approach, in addition to highlighting areas from which many collections exist, has the advantage of taking into account the large number of collections for which more precise collecting localities are absent.

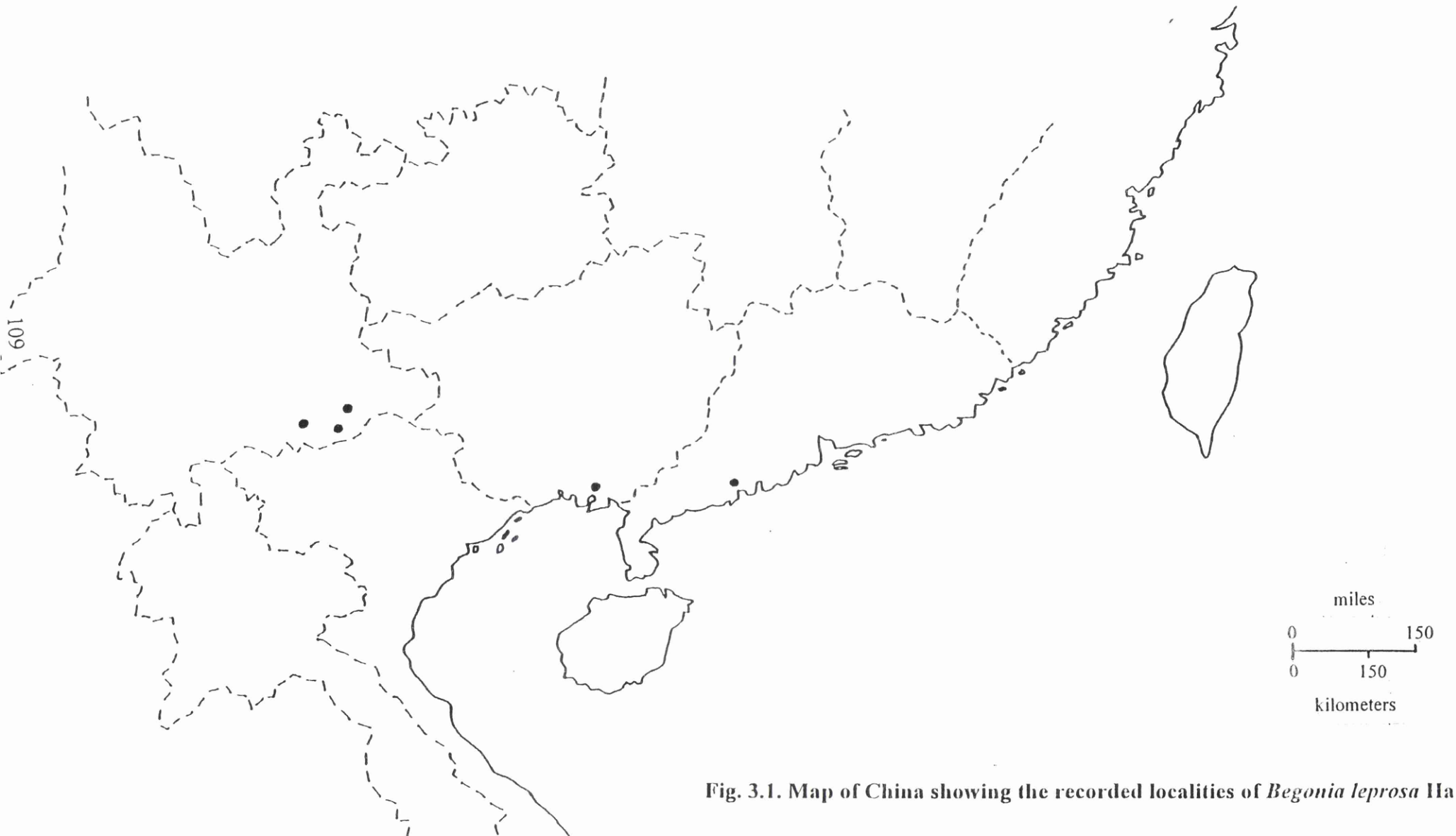


Fig. 3.1. Map of China showing the recorded localities of *Begonia leprosa* Hance

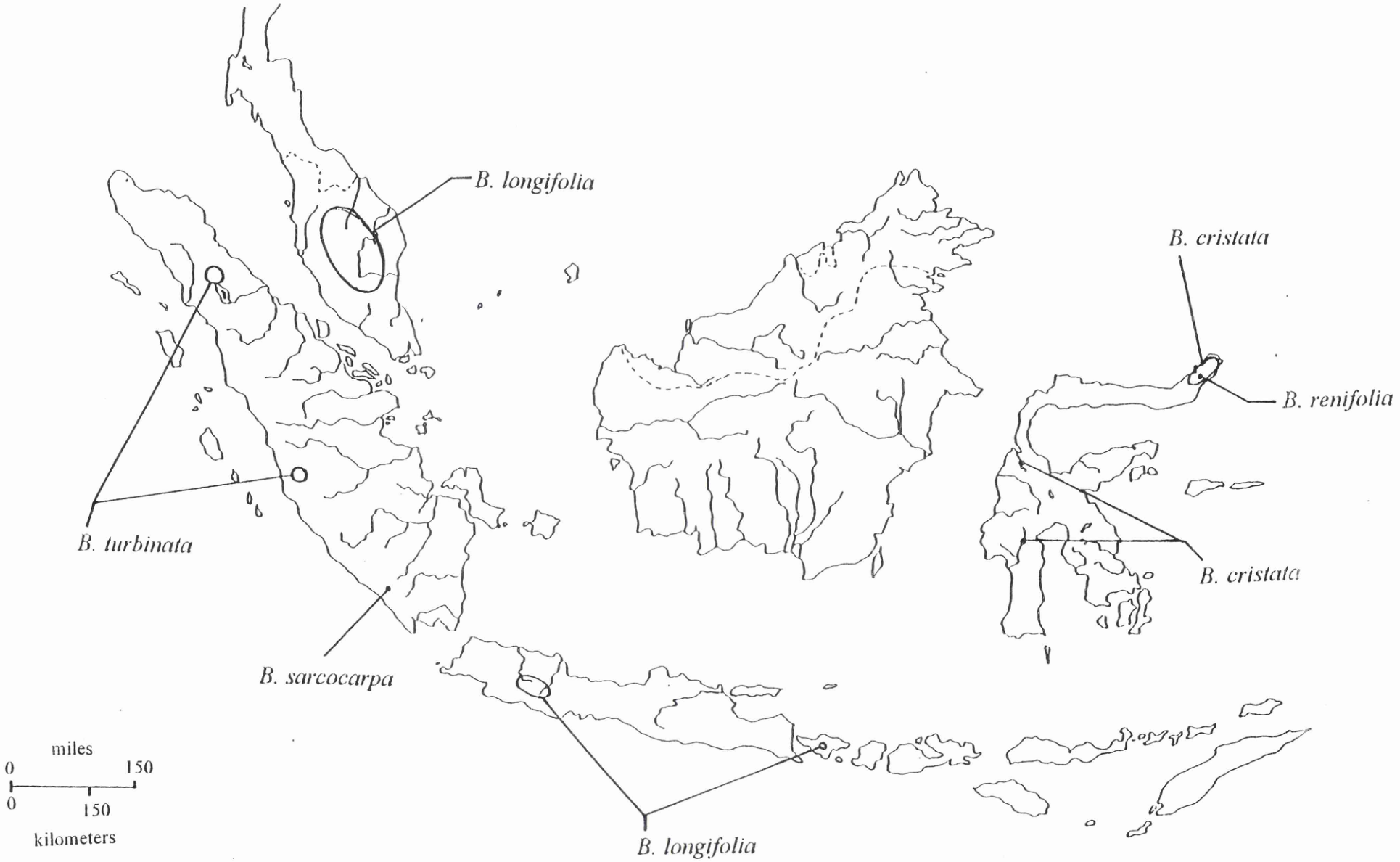


Fig. 3.2. Distribution of the species of *Begonia* section *Blumea* within Indonesia and Malaysia

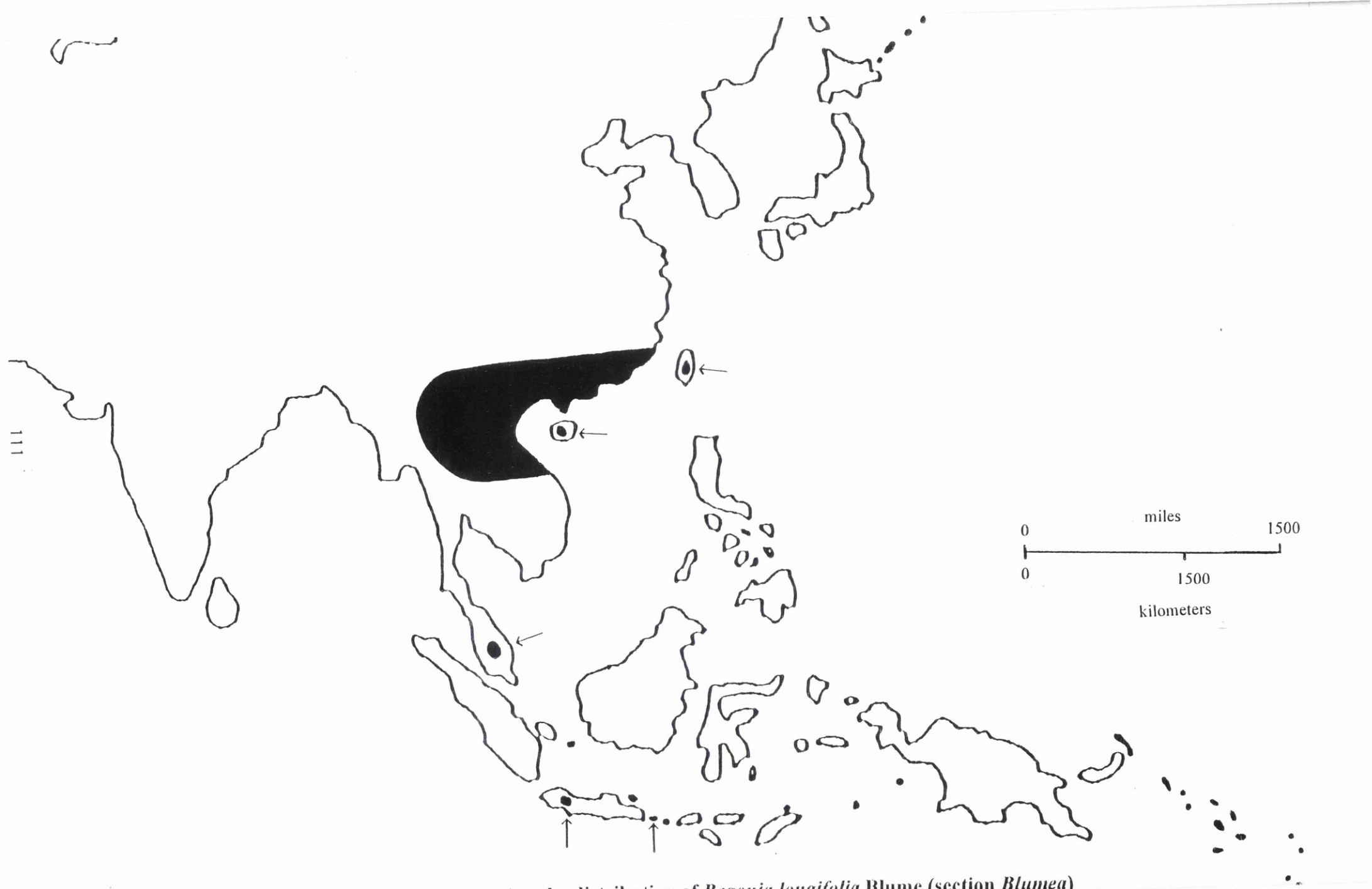


Fig.3.3. Map of Asia showing the distribution of *Begonia longifolia* Blume (section *Blumea*)

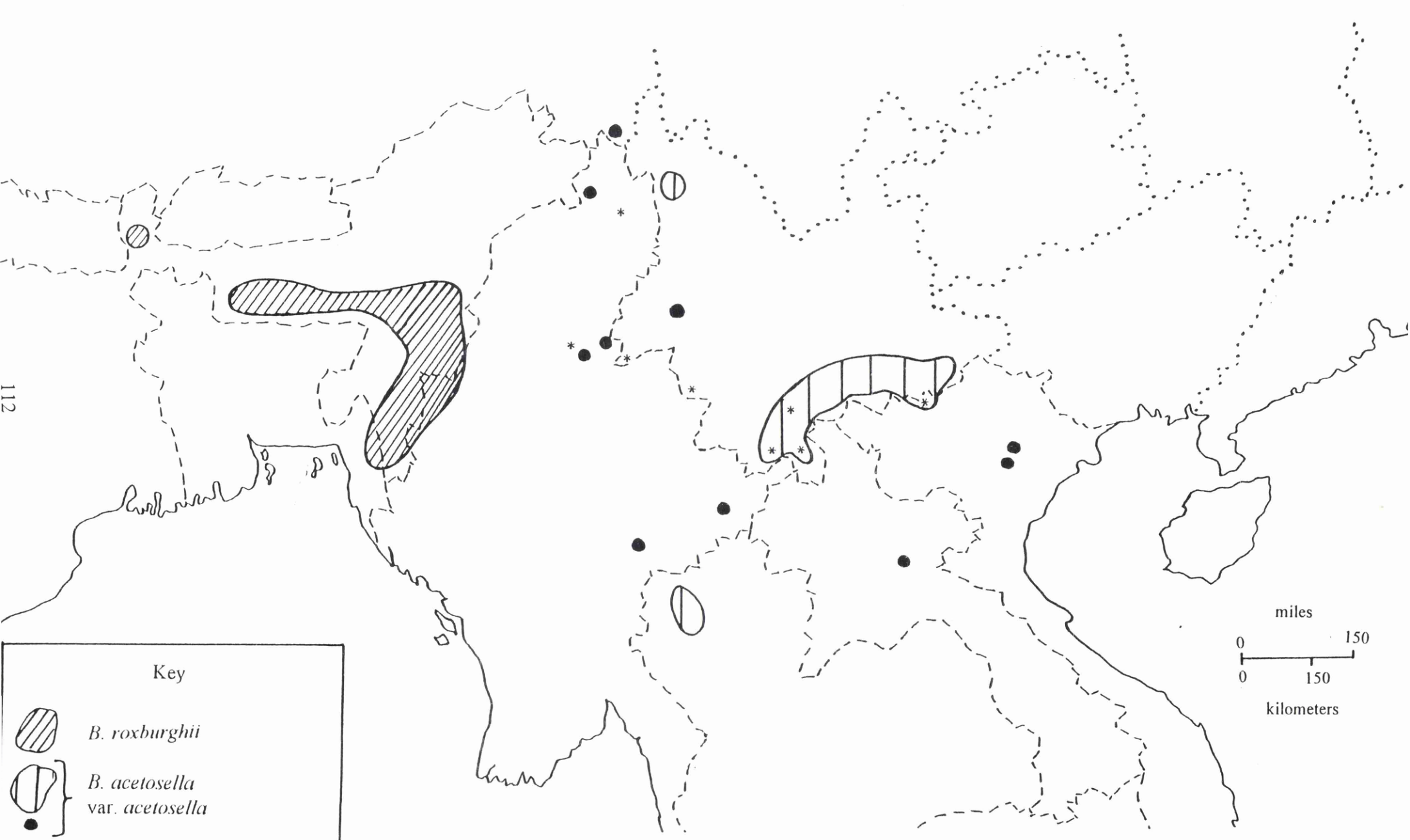


Fig.3.4. Map of mainland south east Asia showing the distributions of *Begonia roxburghii* (Miq) A.DC. and *Begonia acetosella* Craib

Fig.3.5. Map of mainland south east Asia showing the distribution of *Begonia burkillii* Dunn and *Begonia handelii* Irmscher

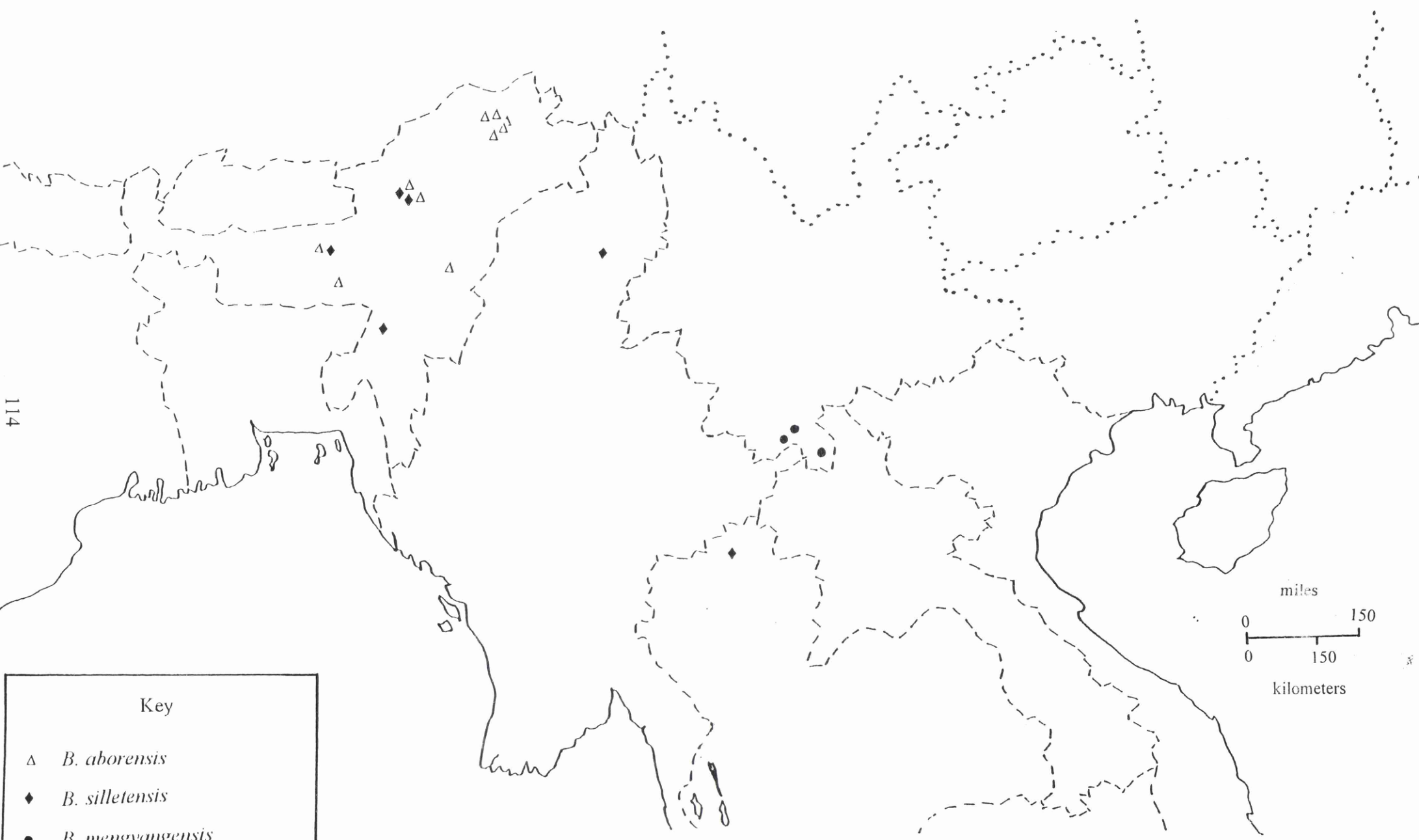


Fig.3.6. Map of mainland south east Asia showing the distribution of *Begonia aborensis* Dunn, *Begonia silletensis* (A.DC.) C.B. Clarke and *Begonia mengyangensis* Tebbitt & K.Y. Guan

Fig.3.7. Map of Vietnam showing the location of Bavi and Tam Dao mountains

3.3. DISTRIBUTION OF THE TAXA IN RELATION TO THE REVISED SECTIONAL CLASSIFICATION

The revised sectional classification is generally well supported by the distributional data as many of the clades are restricted to particular geographical areas. Section *Fusiformes* is restricted to south western China (Fig. 3.1.). The species of the *Blumea* clade are concentrated within Indonesia with one species reaching mainland Asia (Figs. 3.2. & 3.3.) and those from the *Dioecibegonia* clade are restricted to the region between north-eastern India, south-western China and northern Thailand (Figs. 3.4., 3.5. & 3.6.) Section *Platycentrum* subsection *Sphenanthera* (Hasskarl) *sensu* Tebbitt is restricted to islands within S. E. Asia. Section *Platycentrum* subsection *Coronatae* is restricted to a single mountain (Bavi) in north Vietnam (Fig. 3.7.).

3.4. HYPOTHESES OF PAST EVOLUTIONARY PROCESSES BASED ON THE CURRENT DISTRIBUTION AND ECOLOGY OF THE TAXA

3.4.1. SECTION *FUSIFORMES* TEBBITT

The most probable explanation of the occurrence of *B. leprosa* in mainland Asia (Fig. 3.1.) while its sister species and the sister group to this clade occur in Africa (Fig. 2D.3.) is that it has evolved from a taxon which shared a common ancestor with the African taxa and which migrated from Africa into Asia. This idea is discussed in more detail in 3.5.

3.4.2. SECTION *BLUMEA* TEBBITT

All except one of the species from this section are restricted to Indonesia where they mostly appear to have allopatric distributions within the mountains of Sumatra, Java, Bali and Sulawesi (Fig. 3.2.). Many of the taxa exhibit disjunct ranges within particular islands and are probably very under collected. All the taxa are terrestrial forest herbs.

Morphological data suggests that *B. renifolia*, which is known only from a single collection (*Warburg, 15188* (B)), may actually represent an aberrant specimen of *B. cristata*. This view is supported by distributional data as this plant was

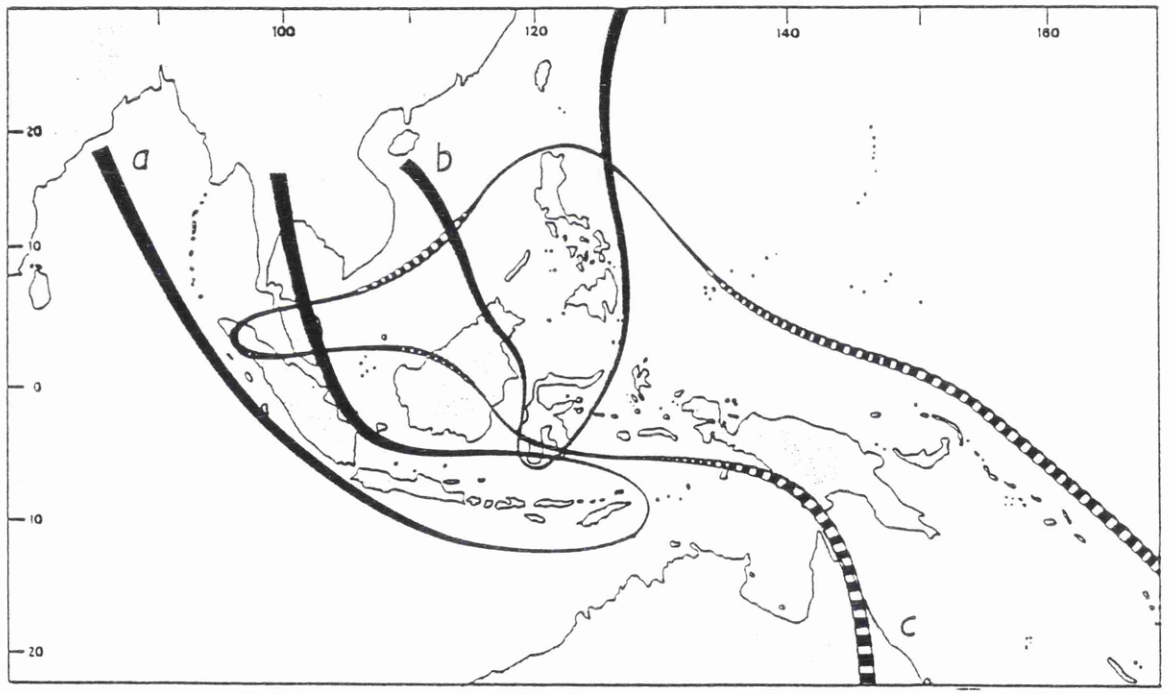
collection in an area were *B. cristata* occurs. A better understanding of the morphological variation present within *B. cristata* is, however, required before the status of the taxa can be resolved.

Begonia longifolia is of interest within the section as, in addition to being found in Indonesia, it also occurs in the highlands of the Malay Peninsula and from an area stretching from north-eastern India and northern Burma to south-western China and Taiwan (Fig. 3.3.). This is one of the largest species distributions in the genus, which contains many species with small ranges. Other species of *Begonia* with comparable distributions include *B. laciniata* Roxb. which is found from Taiwan to India, *B. oxyloba* Welwitsch ex J.D. Hooker from Madagascar and tropical Africa and *B. glabra* Aublet which occurs from Mexico to Ecuador and also in the West Indies. The large distribution of *B. longifolia* may be explained, in part, by its high degree of ecological tolerance. In Vietnam this species grows in a wide range of habitats from primary rainforest to degraded scrub and is found on both acidic and basic soils (pers. obs.). It is, perhaps, still remarkable that material of *B. longifolia* from Indonesia could not be distinguished from material originating from Taiwan and mainland Asia. This is especially true considering that on the other Indonesian islands morphologically distinct species belonging to this section exist. It is possible that the geographically isolated populations within the Malay Peninsula, Sumatra, Java and Bali represent cryptic species. The populations in Java and the Malay highlands were in fact previously recognised as distinct species but in the short descriptions of these taxa no characters are noted which can be used to distinguish them from each other or the mainland plants. Some specimens from Java and Bali do differ from the mainland plants by possessing winged rather than ribbed fruits and inflorescences with wider spaced dichasiums but plants identical to the mainland plants also occur in both these areas, thus rendering these characters useless for delimiting taxa. Future examination of living material may provide additional characters not observed in herbarium material and may support the recognition of distinct taxa. It would also be pertinent to carryout a genetic study of these populations to assess the levels of gene flow occurring between them. Such data could be used to test whether the pattern actually represents a relict distribution rather than the result of chance long distance seed dispersal.

Evidence other than the above morphological data, however, also suggests that the species is genuinely found in both mainland Asia and Indonesia. This comes from the fact that the distribution of *B. longifolia* matches one of the three migration tracts within S.E. Asia proposed by van Steenis (1965) (Fig. 3.8.). These tracts are

based on the distribution of many taxa within this area. As the basal members of the sister group to this clade is composed of taxa from the main-land it may be suggested that *B. longifolia* originated in main-land Asia and from there migrated into Indonesia where it then speciated to produce the other taxa in the section. The fact that the *Blumea* clade is unresolved supports an hypothesis of polychotomous speciation. The minor differences in some plants from Java and Bali compared to main land plants may represent active speciation occuring on the periphery of the species' range. The current disjunct distribution of *B. longifolia* is, therefore, likely to represent a relict distribution.

Fig. 3.8. The migration tracks of van Steenis (reproduced from van Steenis, 1965, Fig. 11) *Begonia longifolia* Blume has a distribution which coincides with track a.



3.4.3. SECTION *DIOECIBEGONIA* TEBBITT

The taxa belonging to this section are distributed between north-eastern India, south-western China and northern Thailand (Figs. 3.4., 3.5. & 3.6.) where they are often restricted to upland broad-leaved evergreen forest. Some species may be occasionally found in scrub or bamboo forest. All species are terrestrial. A number of allopatric sister species can be recognised within the section.

One such pair of allopatric sister species is *B. roxburghii* and *B. acetosella*. *Begonia roxburghii* is found in the mountains around Darjeeling, the mountains surrounding Shillong and the band of mountains composed of the Naga and Mizo Hills and the Brail range of north-eastern India and the Letha range of Burma (Fig. 3.4.). The species is usually found at altitudes between 300-775 m but grows at sea level in Chittagong (Bangladesh) in the south-western part of its range. *Begonia acetosella* is a more eastern species and occurs throughout the mountain range running along the Burma-Yunnan border and down into north eastern Thailand and east along southern Yunnan and northern Vietnam. This species is recorded from altitudes between 400 and 2750m. The range of the two species does not appear to overlap and the lowland area of the Chindwin and Irriwaddy valleys probably provides a barrier to gene flow. *Begonia tessaricarpa*, the sister species to this clade has been collected from a single locality cited as 'East Bengal, Assam'. This distribution is within the range of *B. roxburghii* and is thus concordant with this species' position on the cladogram.

Begonia handelii and *B. burkillii* also represent allopatric sister species. *Begonia burkillii* is found in the Abor Hills of north-eastern India and the Kumon and Mangin ranges of northern Burma. *Begonia handellii* is more south-easterly in its distribution and is found in the mountains from south-western Guandong (China), along the China-Vietnam border and down into northern-eastern Thailand (Fig. 3.5.). The species are both poorly collected but the limited data on their distributions suggests that their ranges do not overlap. As no obvious barriers to dispersal occur between their ranges it may be provisionally suggested that speciation has occurred as a result of climatic selection.

The three remaining species within the section, *B. aborensis*, *B. silletensis* and *B. mengyangensis*, occur within an unresolved clade (Fig. 3.6.). *Begonia mengyangensis* is only known from the Mengyang region of southern Yunnan where it grows in primary forest. The other two species have more north-westerly

distributions. *Begonia aborensis* has only been collected from the Abor Hills of north-eastern India, while *B. silletensis* has been collected from the Abor Hills, northern Burma and northern Thailand (Fig. 3.6.). Both species are poorly represented in herbarium collections and are probably very under collected. It is unlikely, however, that their distributions overlap with *B. mengyangensis* as the region where this species grows is relatively well known botanically as it is situated near the Xishuangbanna botanical field station and a large number of plant collections are available from the area. *Begonia aborensis* and *B. silletensis* are sympatric. These two species may have arisen as a result of habitat specialisation as the former species appears to grow in disturbed scrub and in open situations while the latter grows in primary forest.

Section *Dioecibegonia* probably originated in the mountains of the Himalaya as the molecular data strongly supports a sister group relationship with section *Platycentrum* (Fig. 2C.5.) which is also concentrated here. The ancestor of the two taxa probably diverged as a result of differential selection for seed dispersal mechanisms as discussed in 3.6.

3.4.4. SECTION *PLATYCENTRUM* SUBSECTION *SPHENANTHERA* (HASSKARL) TEBBITT

All the species of this section occur in upland rainforest within Sabah, Sulawesi, Sumatra, Java, Bali and the Lesser Sunda islands. This pattern appears to represent a relict distribution. Further research is, however, required to elucidate the phylogeny and exact distribution of these taxa before any firm conclusions may be reached.

3.4.5. SECTION *PLATYCENTRUM* SUBSECTION *CORONATAE* TEBBITT

The sole member of this subsection is recorded from a single mountain (Bavi) within northern Vietnam (Fig. 3.7.). Many plant species are endemic to the mountain and the general vicinity is botanically relatively well known as it is located near to Hanoi, thus suggesting that the taxon is genuinely restricted in this area to the mountain. The species is locally abundant upon the mountain above 550 m and is found both on the ground and upon cliff faces. It appears to favour situations which are slightly dryer than those occupied by other local *Begonia* taxa. Several species of section *Platycentrum* subsection *Platycentrum* also occur upon

the mountain but do not resemble *B. balansana.* A collection of an unnamed species of subsection *Platycentrum* from the Tam Dao mountain range (*Tebbitt & Khanh, 1* (GLA)), which is situated on the other side of the Red River directly opposite Bavi (Fig. 3.7.), shares a number of morphological characters with *B. balansana*, including a distinctive pattern of venation on the leaf under surface and may represent a closely related species.

3.5. A RE-EVALUATION OF THE PLACE OF ORIGIN AND EARLY EVOLUTION OF THE GENUS *BEGONIA*

The origin and early radiation of the genus *Begonia* remains an enigma. De Wilde & Arends (1989) suggest that Madagascar and the adjacent islands may be the centre of origin for the genus because species of the section *Mezierea*, with reputably the most primitive macro-morphological characters found within *Begonia*, occur there. Cuerrier *et al.* (1991b) suggest that the genus either originated in Asia and from there spread to Africa and the Americas or the genus originated elsewhere and has migrated from Africa and the Americas to Asia. Cuerrier *et al.* (1991b) based their hypotheses on the finding that the begonias of the Americas and Africa are phenetically more similar in terms of their leaf micro-morphologies to those from Asia than they are to each other. In view of the confusion surrounding the origin of the genus and the complex geographical relationships between the sections suggested by preliminary *rbc*L sequence data (Brouillet, pers comm.) the available evidence is re-evaluated here. An understanding of the origin and early distribution of the genus is relevant to the present study as it may help elucidate the origin of the sections described here.

It would appear that the genus was widespread within Gondwanaland at least as early as the mid to late Cretaceous period (100 mya) when Africa, South America and India/Madagascar are thought to have started to separate (Raven & Axelrod, 1974). This can be deduced from the fact that many of the species are believed to have poor dispersal mechanisms (Sosef, 1994) but nether the less occur throughout these regions today. It is unlikely that the genus originated in Asia as previously suggested by Cuerrier *et al.* (1991b) as the distribution of the sections and species within this region suggests that the genus has colonised this area from the west. Evidence for this comes from the fact that the greatest morphological diversity of the genus within Asia is found in the eastern Himalaya and Burma, while relatively little diversity is found in eastern China and Indonesia (pers. obs.). Further more, no species occur naturally in Japan or Australia. In contrast to this limited

distribution within Asia the genus occurs throughout the tropical regions of Africa and Latin America and even occurs on the majority of non-volcanic islands within these regions. The modern Asian sections are, therefore, presumably derived from plants which either migrated into Asia from Africa via the Middle East (which is thought to have been within the tropics until as recently as the Miocene (Cox & Moore, 1993)) and/or, as previously suggested by de Wilde & Arends (1989), were rafted from western Gondwanaland to Laurasia on the Indian fragment of Gondwanaland. The former would appear most likely in view of the fossil evidence which suggests that India experienced large scale extinction of much of its original tropical flora as it passed through a series of climatic belts prior to colliding with Laurasia so that today it is dominated by flowering plants found also in S.E. Asia (Cox & Moore, 1993). Further more, India and Sri Lanka are depauperate in terms of the number of species and sections of *Begonia* represented there compared to elsewhere in mainland Asia.

De Lange & Bouman (1992, p.79) have examined the links between African and Madagascan begonias with those of Sri Lanka and India as suggested by seed morphology and in this context state 'a micromorphological study of the seeds from Ceylon did not reveal any special and manifest relation with the African and Madagascan species'. While no relationships are suggested solely between the African and Asian species by seed morphology it is pertinent to note that the predominantly South African sections *Augustia*, *Rostrobegonia* and *Sexalaria* and the majority of the Madagascan taxa share a seed type indistinguishable from the majority of the Asian and American species (Bouman, pers comm.). De Lange & Bouman (1992, p.78) state that the 'typically African' seed type possessed by section *Mezierea* and other African taxa probably represents a derived condition because 'the seed characters associated with zoochory are a unique feature among the African begonias and not found among the Asiatic and American representatives'. The occurrence of primitive seeds and hence primitive plants in South Africa and Madagascar is also supported by the strong evidence that these areas have provided a refuge to a number of primitive taxa which elsewhere in Africa were wiped out by the increased aridity caused by glaciation (Raven & Axelrod, 1974). The primitive status of this seed morphology is further supported by the fact that *Hillebrandia* possess morphologically very similar seeds.

In view of the fact that Asia is unlikely to represent the cradle of the genus (because of the reasons presented above) it is interesting to note that the molecular data presented here indicates that the South African taxa are closely related to both

the American and some of the Asian taxa, while the other, presumably more derived African taxa, appear to be most closely related to different Asian taxa (Fig. 2C.3.). This suggests that the begonias of Asia are derived both from taxa which evolved prior to the break up of Gondwanaland and also from taxa which evolved on Africa after its separation from South America. This would also explain the complex relationships suggested by *rbc*L and ITS sequence data (Brouillet, pers comm.).

The fact that Cuerrier *et al.* (1991b) found both the American and African taxa to be phenetically more similar to the Asian taxa than they are to each other may also be explained by the hypothesis that originally the genus occurred throughout western Gondwanaland (Africa + South America) and from there migrated into Asia but the subsequent arid conditions within Africa has led to the extinction of many of the lineages in Africa so that today apart from in the refuge areas of South Africa and Madagascar the genus on this continent is represented by locally derived lineages which have given rise to a second introduction of the genus into Asia. It is interesting to note that the majority of those species found in Africa outside of the presumed refuge areas of South Africa and Madagascar possess relatively leathery leaves which may represent a past adaptation to arid conditions.

The species of sections *Blumea*, *Fusiformes*, *Dioecibegonia* and *Platycentrum* examined in the present study are most likely to have evolved from this locally derived African lineage, which is today represented by the following sections *Mezierea*, *Baccabegonia*, *Tetraphila* and *Squamibegonia*. This is supported by the sister group relationship of sections *Blumea* and *Fusiformes* to the African taxa from sections *Mezierea* and *Tetraphila* in the final cladogram. The sections *Dioecibegonia* and *Platycentrum* occur in a monophyletic clade which is unresolved with regard to the clade containing the above African taxa and sections *Blumea*, *Fusiformes* and *Casparya* and the clade containing the rest of the taxa included in the study. It is most likely that the *Dioecibegonia-Platycentrum* clade is more closely related to the *Blumea-Mezierea-Tetraphila-Casparya* clade than it is to the other clade as the species of these two clades share a number of characters which were not included in the analysis due to difficulties with their collection. These characters include the occurrence of fragrant flowers in both the *Dioecibegonia-Platycentrum* clade and section *Mezierea* and the occurrence of leathery leaves in the majority of species from the sections in both clades. Both these characteristics are otherwise very rare within the genus. A preliminary analysis of *rbc*L sequence data also indicates that *B. roxburghii* (*Dioecibegonia*),

B. diadema (*Platycentrum*) and *B. oxyloba* (*Mezierea*) are closely related as these taxa occur in a monophyletic clade characterised by five base substitutions (Swensen, pers comm.).

The presence of *Hillebrandia* on the Hawaiian islands, which have always been isolated, indicates that the seed type possessed by the majority of begonias are potentially capable of long distance dispersal. It is, therefore, likely that the present distribution of the taxa within *Begonia* is a result of a combination of migration, vicariance events (including the break up of Gondwanaland) and at least some chance long distance dispersal.

3.6. POSSIBLE ORIGINS OF THE SECTIONS

Section *Dioecibegonia* probably originated in the mountains of the Himalaya as the molecular data strongly supports a sister group relationship with section *Platycentrum* (Fig. 2C.5.) which is also concentrated here. The occurence of the otherwise rare chromosome number of 2n=22 in both *B. roxburghii* (section *Dioecibegonia*) and the vast majority of species of section *Platycentrum* which have been cytologically examined (Legro & Doorenbos, 1970, 1972, 1974) also supports a close relationship between these taxa. The ancestor of these two taxa probably originated in Africa (as discussed previously) and from there migrated into Asia where they diverged partly as a result of differential selection for seed dispersal mechanisms. The fruits of sections *Dioecibegonia* and the relatively primitive *Platycentrum* subsections *Sphenanthera* and *Coronatae* are adapted to animal dispersal while those of the relatively advanced section *Platycentrum* subsection *Platycentrum* are adapted to water dispersal. Further selection for different modes of dispersal appears to have occurred within section *Dioecibegonia* as the three main clades in this section are characterised by differing fruit presentation. The *B. burkillii* and *B. aborensis* clades contain prostrate species with erect peduncles and fruit which is held *c.* 10 cm from the ground in the case of the former and 10-20 cm from the ground in the latter. The *B. roxburghii-B. acetosella* clade contains erect species which produce their fruit above 60 cm from the ground on short drooping peduncles. *B. tessaricarpa* the sister species to the *B. roxburghii-B. acetosella* clade shares the condition found in the *B. burkillii* clade. The position of this species on the clade suggests that the ancestor of the clade had prostrate stems and erect fruit and that the condition shown by *B. roxburghii* and *B. acetosella* has evolved from this, probably in response to selection for fruit dispersal by different animal vectors.

Section *Blumea* also probably originated in mainland Asia and from there migrated in the Malay Peninsula and Indonesia. Evidence for this comes from the fact that *B. longifolia* shows a relict distribution in mainland Asia, the Malaya Peninsula, Sumatra and Java. This distribution pattern matches one of the migration paths into S.E. Asia which have been proposed by van Steenis (1965) (Fig. 3.8.). The section is probably closely related to sections *Dioecibegonia* and *Platycentrum* as at least the primitive members of these sections all possess fleshy indehiscent fruits.

The occurrence of the morphologically distinct *B. leprosa* (section *Fusiformes*) in south-western China and the close relationship of this taxon with the African section *Tetraphila* suggests that this taxon has diverged in isolation from other begonias following the migration of African taxa into mainland Asia.

Chapter 4
GENERAL DISCUSSION AND CONCLUSIONS

4. GENERAL DISCUSSION AND CONCLUSIONS

4.1. DOES THE STUDY ACHIEVE ITS AIMS?

To answer this question, each of the aims outlined in Chapter 1 will be addressed separately.

a) To produce a taxonomic revision of the species and infraspecific taxa currently included with *Begonia* section *Sphenanthera* and to describe new taxa where appropriate.

The study recognised twenty three distinct species from section *Sphenanthera* (Hassk.) sensu Benth. & Hook. f. including five new species from China, Sumatra (2), Sulawesi and Sabah respectively and a new variety of *B. handelii* Irmsch. from China. The name *Begonia prostrata* Irmsch. is newly combined and treated as a variety of *B. handelii* Irmsch. because the only constant difference between these taxa is in their flower sizes. The name *Begonia multangula* Blume is newly combined and treated as a variety of *B. robusta* Blume because the only constant difference between these taxa is in their hair densities. The specific epithet '*teysmannianum*' is recombined with the genus *Begonia* L from the synonymous genus *Platycentrum* Klotzsch. *Begonia tetragona* Irmsch. is treated as a new synonym of *B. acetosella* var. *acetosella* Craib because continuous variation was found to occur between them. *Begonia crassirostris* Irmsch., *B. hayatae* Gagnep., *B. inflata* C.B. Clarke, *B. tricornis* Ridley, *B. trisulcata* (A.DC.) Warb. and *B. longifolia* var. *luxurians* Miquel ex Koorders are newly synonymysed under the name *B. longifolia* Blume because continuous variation was found to occur between them. The large number of taxa synonymysed with *Begonia longifolia* is probably a result of the fact that these taxa had not previously been examined in a monographic context and were defined in part on their distributions as recognised by political boundaries. *Begonia brachybotrys* Mer. & Per., *B. pseudolateralis* Warb. and *B. erosa* Blume clearly belong to other existing sections and were, therefore, not revised here.

b) To investigate whether *Begonia* section *Sphenanthera* is a natural phylogenetic unit and if not, to produce a revised phylogenetically based classification of these taxa.

This section is found to be polyphyletic. A revised phylogenetic based classification of the taxa ascribed to these taxon is, therefore, presented. Some of the taxa are moved to sections *Platycentrum* and *Petermannia*. The cladistic analyses indicate that *B. robusta*, the type species of section *Sphenanthera* is the sister species of section *Platycentrum*. As this taxon and another four new species can only be distinguished from this taxon in terms of their possession of 3-locular rather than 2-locular fruits it is proposed to treat these species and hence the name *Sphenanthera* as a subsection of section *Platycentrum*. *Begonia balansana* is also shown to be closely related to section *Platycentrum* and a new subsection of *Platycentrum* is also erected for this taxon. A group of species characterised by 4-locular ovaries and persistent stipules occur in a distinct clade and are here named as a new section. This group represents the taxa most past authors have regarded as section *Sphenanthera*. *Begonia leprosa* is closely related to the African section *Tetraphila* but is characterised by a number of distinct apomorphies and is, therefore, given sectional status. Irmscher (1939) had previously suggested that this taxon occupied an isolated phylogenetic position within the Asian begonias. *Begonia cristata*, *B. longifolia*, *B. sarcocarpa* and *B. turbinata* form a distinct monophyletic clade in the cladistic analysis and it is, therefore, proposed to recognise these taxa as a new section. *Begonia renifolia* which is of doubtful taxonomic status and is only known from a single specimen is also provisionally added to this section.

c) To investigate the phylogenetic affinities, current distributions and ecological preferences of the taxa and use this information to suggest where the group(s) may have originated.

The closest phylogenetic affinities of the new taxa and *Sphenanthera* appear to be between themselves and with the African species of sections *Mezierea* and *Tetraphila*. This hypothesis is based on the occurrence of fleshy fruits and leathery leaves in all these taxa and the occurrence of fragrance and parietal placentation in some of the new taxa and the African taxa. Provisional *rbc*L sequence data generated elsewhere also supports this hypothesis. The current distribution of the species and sections within Asia suggests that the genus has colonised this area

from the west. The Asian taxa presumably evolved from African ancestors which probably entered mainland Asia via the Middle East. The Asian taxa presumably evolved in isolation from the African section when the tropical Middle East route was disrupted by continental drift. Within Asia the sister sections *Dioecibegonia* and *Platycentrum* appear to have diverged in response to differing selective pressures associated with seed dispersal. This hypothesis is based on the observation that the species of the former taxon appear to be animal dispersed while the advanced members of the latter taxon appear to be wind dispersed. The majority of the species from section *Dioecibegonia* have probably evolved in response to vicariance events because the majority of the sister species in this section currently have allopatric distributions. *Begonia aborensis* and *B. silletensis* from this section, however, have a sympatric distribution and appear to have evolved in response to preference for different habitats characterised by different light levels. The distribution of the species of section *Platycentrum* subsection *Sphenanthera* suggests that the subsection has a relict distribution. It may be suggested that the species of this section have evolved independently in isolated relict mountain populations of a once widespread species. A similar relict distribution is also exhibited by *B. longifolia* from the new section *Blumea.* It is proposed that this species has given rise to the other members of its section. This is supported by the lack of resolution present in this clade.

4.2. FUTURE WORK

A number of areas which would benefit from future research are identified by the current study. Paramount amongst these would be the collection of sequence data from the *trn*C - *trn*D chloroplast intergenic spacer region. This region appears to exhibit optimum levels of sequence variation for phylogenetic studies within *Begonia.* Such data could provide an insight into specific and sectional level relationships within the genus. The value of such molecular data for phylogenetic studies within the genus is particularly high as morphological data is believed to exhibit high levels of homoplasy within the genus and previous regions which have been sequenced (*rbc*L (Swensen, pers comm.), ITS (Brouillet, pers comm.), *trn*L (present study)) have proved too conserved for such low level phylogenetic research. Sequence data from this region is currently being obtained from species of the section *Begonia* and potential outgroup species by Zoe Badcock (University of Glasgow). Preliminary results suggest that the region does possess suitable

levels of variation for phylogenetic research within the genus (Badcock, pers comm.).

The current research also suggests that the delimitation of section *Platycentrum* requires further investigation as a number of species have been described which do not adequately fit into any of the existing sections but appear to be very closely related to the species of this section. One such species is *B. trigonocarpa* which was investigated in the present study and remains un-ascribed to a section.

The phylogenetic affinities of *B. obovoidea* which was previously ascribed to section *Sphenanthera* (Hasskarl) sensu Benth & Hook. f. (Barkley & Golding, 1974) also require further investigation. This species is morphologically very distinct and shares few obvious morphological synapomorphic characters with other begonias. In view of this, a molecular investigation which included this taxon and several potential outgroup taxa should be conducted.

The occurrence of different types of endothecial wall thickenings within the genus are reported here for the first time. Their distribution appears to be of systematic value and requires investigating in a wide range of species. Such an investigation is currently being under taken by Cameron MacIvor (University of Glasgow). This study has identified a number of types of endothecial thickening within the Begoniaceae, many of which are restricted to a single or a few sections.

Future studies of the species of section *Dioecibegonia* should attempt to investigate the occurrence of a hypodermal layer in the leaves of these taxa. A hypodermis has been observed in *B. silletensis* (Fellerer, 1892) and *B. mengyangensis* (Appendix H). These taxa were found to occur within a clade composed of them selves and one other species, *B. aborensis*. *Begonia roxburghii* which occurs in another clade of this section does not have a hypodermis. In view of the occurrence of this character in the two closely related species but not in the more distantly related species its distribution should be further investigated as it could provide additional phylogenetic information.

Chapter 5
TAXONOMIC TREATMENT

5. TAXONOMIC TREATMENT

5.1. MATERIALS AND METHODS

The delimitation of the specific and infraspecific taxa was carried out using the methods set out in Lawrence (1951), Leenhouts (1968) and Vogel (1987). The taxonomic revision was conducted in the following stages:

1. Consultation with other researchers working on *Begonia* taxonomy and familiarisation with the literature pertaining to section *Sphenanthera*. A list of potentially useful characters was constructed from the above sources, to which additions were made following a preliminary examination of herbarium material. In subsequent stages of the analysis, these characters were examined in each of the specimens (when present) by eye or with an Olympus 5240 dissecting microscope. Drawings of the characters observed in the specimens were made frequently during the course of the analysis to aid comparison.

2. Examination of herbarium material from other institutions (A, B, BM, CAL, E, G, GB, GH, HBG, HK, HN, HNIP, K, K-WALL, KUN, L, M, MO, NY, P, SING, TAI, US, WU).

3. Provisional sorting of material into smallest recognisable morphologically distinct entities for each geographical region. Familiarisation with the material.

4. Temporary exclusion from the analysis of those specimens with doubtful affinity resulting from missing parts.

5. Comparison of entities and subsequent combination of identical entities from different geographical regions where necessary.

6. Examination of total material held in selected herbaria (BM, E, HN, HNIP, HNU, K, KUN) to gain a better understanding of the variation present within each entity.

7. Allocation of taxonomic rank to the entities (see 1.7.).

8. Comparison of entities with original descriptions and descriptions in monographs and floras. Attachment of existing names to entities where possible

(*i.e.* those containing either the type(s) of an existing taxon, or those which accurately fit an existing description but which for some reason have no locatable types). Previously undescribed taxa were given new names.

9. Search for taxa closely resembling those described. This was carried out by examining all the specimens of *Begonia* held within selected herbaria (BM, E, HN, K, KUN, L) known to contain large collections of *Begonia*. This material was analysed using the process outlined above. In the case of the material housed in the two Asian herbaria, stages 6 and 9 were carried out simultaneously due to the difficulties of revisiting these herbaria.

10. Comparison of the descriptions with living plants in cultivation and the field inorder to test the integrity of the taxa.

11. Assignment of those specimens with missing parts temporarily excluded from the analysis to the correct taxa where possible.

Ethnobotanical notes were compiled from annotations on herbarium sheets, the literature and personal communications with local people during field work in Northern Vietnam between the 16th October and the 7th November 1996. During the course of this field work informal talks with villagers from the following areas were conducted; Cuc Phuong (Vinh Phu Province), Tam Dao (Ninh Binh Province) and Sapa (Lao Cai Province). Mr. Nguyen van Tuan and Mr. Wey of the Hanoi College of Pharmacy acted as translators.

5.2. KEY TO THE ASIAN *BEGONIA* SECTIONS (modified from Irmscher (1925) to incorporate taxonomic changes and sections described since his publication).

(Numbers in brackets after certain sections refer to descriptions of these taxa in this thesis).

1a. Placentation parietal.....2
b. Placentation axile.....3
2a. Fruit fleshy, wingless; inflorescence unisexual.....***Fusiformes* (4.4.)**
b. Fruit dry, winged; inflorescence bisexual.....***Coelocentrum***
3a. Placentae undivided in central portion of fruit.....4
b. Placentae divided in central portion of fruit.....6
4a. Male flowers with two tepals.....***Haagea***
b. Male flowers with four tepals.....5
5a. Fruit 2-locular.....***Ridleyella***
b. Fruit 3-locular.....***Reichenheimia***
6a. Fruit 2-locular.....7
b. Fruit more than 2-locular.....12
7a. Anthers opening via pores.....***Heeringia***
b. Anthers opening via slits.....8
8a. Fruits dehiscing along regular cracks next to the wings; large herbs.....9
b. Fruits dehiscing irregularly on the flat side, paper like; delicate herbs.....10
9a. Fruit with 1 wing; erect herbs.....***Monopteron***
b. Fruit with 3 wings, 2 of these often narrow; mostly with short creeping or tuberous rhizomes.....***Platycentrum* subsection *Platycentrum* (4.8.1.)**
10a. Leaves single, sessile; inflorescence appearing to develop out of lamina.....
.....***Monophyllon***
b. Leaves many, petiolate; inflorescence not appearing to develop out of lamina.....11
11a. Leaves in verticillate arrangement, pinnate veined.....***Lauchea***
b. Leaves alternately arranged, palmate veined.....***Parvibegonia***
12a. Fruit 3-locular.....13
b. Fruit more than 3-locular.....24
13a. Styles 2.....***Platycentrum* subsection *Sphenanthera* (4.3.)**
b. Styles more than 2.....14
14a. Styles with long, erect branches.....***Baryandra***
b. Styles not as above.....15

15a. Styles kidney or half-moon shaped.....16
b. Styles bifid.....20
16a. Flowers and fruits surrounded by two large persistent bracts.....17
b. Flowers and fruits not surrounded by two large persistent bracts.....18
17a. Bulbils present in leaf axils.....***Putzeysia***
b. Bulbils absent in leaf axils.....***Bracteibegonia***
18a. Male flowers with 2-tepals; fruit wingless.....***Apterobegonia***
b. Male flowers with 4 tepals; fruit usually winged, rarely wingless.....19
19a. Fruit dehiscing via cracks exactly on the back.....***Alaecida***
b. Fruit dehiscing in regular cracks, next to wings (when these present).....
.....***Begonia***
20a. Fruit fleshy, globose or top-shaped.....***Blumea* (4.5)**
b. Fruit dry, not globose or top-shaped.....21
21a. Fruit dehiscing via cracks exactly on the back.....***Alaecida***
b. Fruit dehiscing via regular cracks next to wings, or paper-like and
irregularly dehiscent.....22
22a. Plant creeping, often epiphytic, mostly rooting the whole length of the plant
.....***Diploclinium***
b. Plant erect or appearing stemless.....23
23a. Male flowers with 2 tepals; fruit wings sub-equal, bulbils absent.....
.....***Petermannia* (4.7.)**
b. Male flowers with 4 tepals; fruit wings usually uneven, bulbils often
present in leaf axils.....***Begonia***
(+ some species currently included in ***Diploclinium***)
24a. Fruit 4-locular, rhomboidal to globose.....***Dioecibegonia* (4.6.)**
b. Fruit (5)-6-(7)-locular, crown-shaped.....
.....***Platycentrum* subsection *coronatae* (4.8.2.)**

5.3. DESCRIPTION AND DELIMITATION OF SECTION *FUSIFORMES* TEBBITT SECTION NOVA

Monoecious, rhizomatous creeping herb, rooting at nodes, *aerial stem* to 2 cm tall. *Stipules* persistent. *Leaves*: *lamina* orbiculate, base slightly oblique to almost regular, lobes overlapping, upper surface with large convex cells, appearing pitted in sicco. *Inflorescences* unisexual dichasiums; *bracts* caducous. *Male flowers*: *tepals* 4; *stamens* c. 75, attached to a torus, *filaments* free, *anthers* elliptic, dehiscing via short diagonal slits arising from the apex on each side of the anther, connective short projecting, but soon drying up. *Female flowers*: *tepals* 4; *ovary* fusiform, wingless, 3-locular, *placentation* pseudo-axillary, *placentas* bifid, bearing ovules on both surfaces; *styles* 3, fan-funnel-shaped, shortly fused at base, stigmatic papillae a continuous band along top of style. *Fruit* grey [at least in sicco] pendulous, fleshy, indehiscent, fusiform. *Seed*: ellipsoid, operculum nipple-shaped, testa cells occupying about half the length of the seed, cuticular ornamentation of short linear foldings.
Type species: *Begonia leprosa* Hance.

The sectional name *fusiformes* refers to the type species' characteristic fusiform fruits.

5.3.1. DESCRIPTION OF THE SPECIES OF SECTION *FUSIFORMES* TEBBITT

5.3.1.1. B. leprosa Hance in J. Bot. 21: 202. 1883; W.Y. Chun & F. Chun in Sunyatsenia. 4: 24. pl.7. 1939. **Plate 7b**.
TYPE: Im umbra rupium, juxta pagum Sam-tin, secus fl. Lien-chan, 230 mill. pass. a Cantone, d. 8.x.1881, leg. *rev. B.C. Henry Herb. prop. no. 22098* (BM! holotype).

SYNONYMY: *B. bretschneiderana* Hemsley in W. J. Hooker, Icon. Pl.. IV. 27. pl. 2635. 1900; Irmscher in Mitt. Inst. Allg. Bot. Hamburg 10: 517. 1939; Chun & Chun in Sunyatsenia. 4: 24. pl. 7. 1939. **TYPE:** *Ford 87* (B! holotype).

ILLUSTRATIONS: Hooker, Ic. Pl. xxvii. t. 2635. 1900. (as *B. bretschneideriana* Hemsl.); Chun & Chun, Sunyatsenia. 4: 24. Plate 7. 1939; Smith *et al.* Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany. No. 60. Fig. 24.22. 1986.

DESCRIPTION: Rhizomatous creeping herb, rooting at nodes, *rhizome* 0.5-1 cm across, *aerial stem* short to 2 cm, simple, internodes short, hairy. *Stipules* persistent, broadly ovate, 8-12 x 2-2.5 mm, apex acute, margin glabrous to sparsely hairy. *Leaves* arising from apical portion of stem; *petioles* 4-8.5 cm, sparsely to densely long haired; *lamina* orbiculate, 4-6 x 4.5-8 cm, apex often shortly acute, base slightly oblique to almost regular, rarely peltate, lobes folded inwards, overlapping, 1.5-3 cm across, sinus 0.5-1 cm, margin entire, both surfaces dull, above with convex cells, appearing pitted in sicco, glabrous, below medium to densely hairy on veins, elsewhere glabrous, hairs c. 0.4 mm long, multicellular with a small glandular head, veins (6)-7, palmate, branched from about halfway. *Inflorescences* arising from apical region of rhizome, a short dichasium, male and female flowers on different inflorescences, male flowers maturing before female, 4-9-flowered; *peduncles* almost absent to 8 cm; *bracts* caducous, 2-6 mm, ovate, margin long ciliate, surfaces glabrous. *Pedicels*: those of male glandular hairy to 12 mm long, those of female flowers glabrous or sparsely minute glandular hairy, 0.5-1 cm long. *Male flowers*: *tepals* white to pink, 4, outer 2 broadly ovate, c. 7 x 8 mm, apex obtuse, inner 2 narrowly ovate, c. 5 x 2.5 mm, apex obtuse; *stamens* c. 75, attached to top of a c. 1 mm torus, *filaments* free, more or less equal, c. 1.6 mm long, *anthers* elliptic, c. 1.2 x 0.75 mm, dehiscing via short transverse slits arising from the apex on each side of the anther, connective short projecting but soon

drying up, apex truncate, locules separated only at apex. *Female flowers*: *tepals* white to pink, 4, outer 2 broadly ovate, c. 5.5 x 6 mm, apex obtuse, inner 2 narrowly ovate, smaller than in male, apex obtuse; *ovary* fusiform, wingless, c. 3.75 x 1.75 mm, 3-locular, *placentation* pseudo-axillary, *placentas* bifid, bearing ovules on both surfaces; *styles* caducous, 3, c. 1.5 mm long, shortly fused at base, fan-funnel-shaped, very shortly branched, stigmatic papillae a continuous band along top of style. *Infructescence* usually 3-fruited; *fruit* pendulous, fleshy, thick-walled in sicco, indehiscent, green, fusiform, c. 13 x 4 mm, wingless, covered with microscopic unicellular hairs with large reddish-black glandular heads.

PHENOLOGY: Flowering and fruiting August to January.

DISTRIBUTION: Southern China (Yunnan, Guangdong).

HABITAT & ECOLOGY: Dense forest at 1200-1500 m, where the taxon grows in moist shady places amongst rocks or on moist cliffs.

NOTES:

1. Hemsley (1900) published the name *B. bretschneiderana* Hemsley for material which is said to differ from *B. leprosa* Hance by having Pedicels which are shorter (rather than longer) than the petioles. The name `*bretschneiderana*` was emended by Irmscher (1939) to `*bretschneideriana*`. Chun & Chun (1939) found that *B. bretschneideriana* Hemsley and *B. leprosa* Hance were conspecific. The present study supports their conclusion.

2. Yü (1950) cites three collections from S.E. Yunnan.

3. Hance (1883) in his original description placed the species in section *Parvibegonia* but went on to say that it was most closely allied to *B. delicatula* Parish (of section *Apterobegonia* Warburg). He states, however, that it differs from the latter in terms of many characters.

SPECIMENS EXAMINED:

P.R. China: GUANGDONG: Kwangtung, iix.1887, *Ford 87* (B [holotype of *B. bretschneideriana* Hemsley]); Lienchow River, 31.iix.1887, *C. Ford s.n.* (Photocopy HK); Kwangtung, Ex. herb. Hongkong Botanic Garden, iix.1887, *Ford s.n.* (HBG photograph); Im umbra rupium, juxta pagum Sam-tin, secus fl. Lien-chan, 230 mill. pass. a Cantone, d. 8.x.1881, leg. *rev. B.C. Henry Herb. prop. no. 22098* (BM holo); Yangchun Xian, Guangdong in moist cliff, 17.x.1935, *C. Wang 38502* (MO).

5.4. DESCRIPTION AND DELIMITATION OF SECTION *BLUMEA* TEBBITT SECTION NOVA

Slender or robust erect herbs to 2 m tall. *Stipules* caducous. *Leaves*: *lamina* lanceolate to broadly elliptic, base asymmetric. *Inflorescences* unisexual or bisexual dichasiums; *bracts* caducous. *Male flowers*: *tepals* 4; *stamens* 25-75, *filaments* free to fused at base, *anthers* linear-elliptic to obovate or wedge-shaped, dehiscing via vertical slits along the sides of the anthers, connective projecting. *Female flowers*: *tepals* 5-6; *ovary* 3-locular, more or less globose to top-shaped, with 3 ribs, narrow wings or obtuse-triangular wings, *placentation* axillary, *placentas* bifid, bearing ovules on both surfaces of the placentae; *styles* 3, bifid, stigmatic papillae arranged in a spiral twisted band. *Fruit* fleshy, green to reddish green, indehiscent. *Seed*: ellipsoid, operculum nipple-shaped, testa cells occupying less than half the length of the seed, cuticular ornamentation of short linear foldings.
Type species: *Begonia longifolia* Blume.

The name *Blumea* commemorates Carl Ludwig Blume (1796-1862) who contributed towards our knowledge of Javan begonias and who named *B. longifolia*, the type species of this section.

5.4.1. KEY TO THE SPECIES OF SECTION *BLUMEA* TEBBITT

1a. Lamina of leaves reniform.....**renifolia**
b. Lamina of leaves lanceolate to broadly elliptic.....2
2a. Female tepals 5; leaves 5-6.5 x 1.2-1.8 cm.....**sarcocarpa**
b. Female tepals 6; leaves 8-22 x 1.8-14 cm.....3
3a. Stems slender, often red tinged; fruit top-shaped.....**turbinata**
b. Stems robust, not usually red tinged; fruit more or less globose.....4
4a. Leaves broadly elliptic, margin remotely shortly and somewhat irregularly bidentate, smaller teeth serrate.....**cristata**
b. Leaves usually lanceolate, larger leaves occasionally broadly elliptic, margin shallowly single toothed to almost entire.....**longifolia**

5.4.2. DESCRIPTIONS OF THE SPECIES OF SECTION *BLUMEA* TEBBITT

5.4.2.1. B. cristata Warburg ex L.B. Smith & D.C. Wasshausen in Phytologia. 52(7): p. 442. 1983; Koorders, Natuurw. Tijdscher. Ned. Indie 63: 90. 1904.
TYPE: N. Celebes, Tomohon, iv.1894, leg. *Sarason 288* (K! holotype).

SYNONYMS: *Begonia cristata* Warburg *nomen nudum* (BM! in sched.)
Begonia cristata Warburg ex Koorders in Natuurw. Tijdscher. Ned. Indie. 63: 90. 1904. *nomen nudum.*

ILLUSTRATIONS: Koorders, Supplement Fl. N.O. Celebes. ii & iii. t. 93. 1922; Smith *et al.* Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany. No. 60. Fig. 27.24. 1986.

DESCRIPTION: Robust, erect branched herb, to 2 m, *stems* 0.4-1.2 cm across, ribbed in sicco, inter-nodes 7-18 cm long, glabrous, dull red. *Stipules* caducous, ovate to narrowly lanceolate, 0.8-2 x 0.2-0.45 cm, apex setose, elsewhere glabrous. *Leaves* alternate; *petioles* 2.5-16.5 cm, 1-3 mm across in sicco, glabrous; *lamina* broadly elliptic, 10-22 x 4-14 cm, apex acute to acuminate, base strongly asymmetric, lobes almost equal, overlapping, lower lobe 4-9.5 mm across, sinus 1-3 cm, margin remotely shortly and somewhat irregularly bidentate, larger teeth angular, smaller teeth serrate, both sides green, below paler, both surfaces glabrous, or below with very sparse microscopic glandular hairs in basal portion, veins 6-7, palmate. *Inflorescences* axillary, a 2-3-branched dichasium, with up to 20 flowers, bearing male and female flowers synchronously on same inflorescence; *peduncles* c. 1 cm, glabrous; *bracts* caducous, narrowly ovate, 4-6 x 2.5 mm. *Pedicels*: those of male flowers sparsely microscopic glandular hairy, 6-7 mm long, those of female flowers glabrous, c. 5 mm long. *Male flowers*: *tepals* white to pale pink, 4, outer 2 broadly ovate to elliptic, concave, 4-8 x 3-5 mm, inner 2 broadly ovate to elliptic, 3-8.5 x 2.8-4.2 mm, outer tepals very sparsely microscopic glandular hairy; *stamens* 25-50, *filaments* fused at base, 1-1.5 mm, those in centre slightly longer than the outer ones, *stamens* wedge-shaped, 1.5-2 mm, connective projecting c. 0.2 mm, apex rounded, dehiscing via longitudinal slits along sides of anther. *Female flowers*: *tepals* white to pale pink, 6, broadly ovate to elliptic, subequal, 3.1-10 x 2.2-6 mm, hairs as in male; *ovary* fleshy, sub-globose, 3-lobed, c. 5 x 6.5 mm, sparsely microscopic glandular hairy, lobes with rounded rib-like to obtuse-triangular wings to 1 mm along centre of each locule, 3-

locular, *placentation* axile, *placentas* bifid, bearing ovules on both surfaces; *styles* caducous, 3, squat, 2.4-4 mm, free or shortly fused at base, bifid from half-way, stigmatic papillae broad, once or twice spirally twisted. *Infructescences* 1-10-fruited; *fruiting pedicels* 0.5-1 cm; *fruit* fleshy, green becoming red, sub-globose, to c. 1 x 1.2 cm, glabrous or with sparse microscopical hairs as in ovary, locules with persistent wart-like remnants of wings [in sicco].

PHENOLOGY: Flowering year-round.

DISTRIBUTION: Sulawesi.

HABITAT & ECOLOGY: Forest at 100-700 m.

NOTES:

1. This species may be Blume`s (1827) *Begonia aptera* (also described from Sulawesi). However, the description of Blume`s species states that his plant has 4-locular fruit while *B. cristata* Warburg ex L.B. Smith & D.C. Wasshausen has 3-locular fruit. Blume did not designate a type so this can not be checked directly. It is likely that Blume made a mistake or an typographic error has occurred as neither I nor past authors have been able to locate any material from Sulawesi with 4-locular fruit. In view of this confusion and the possibility that material of Blume`s species with 4-locular fruit may exist unlocated in a herbarium, *Begonia cristata* must become the accepted name for the taxon with 3-locular fruit.

2. The name *Begonia cristata* was first published by Koorders (1904) based on an earlier unpublished name of Koorders. However, Warburg did not validly publish the name as he neglected to provide a description of the taxon. It was left to Smith & Wasshausen (1983) to designate a holotype, describe and validly publish the name.

3. The specimen labelled 'Sopu valley, c. 80 km s. of Palu, 1000-1250 m, Epiphytic herb, stems patent, c. 1 m long, flowers white, primary forest locally disturbed by rattan collectors, Hennipman, 5633' housed at L probably represents an aberrant plant.

SPECIMENS EXAMINED:

Indonesia: SULAWESI: N. Celebes (Minahassa), Bojong, 1888, leg. *O. Warburg 15187* (2 sheets B); Goeroepaki, *W. Kauderns 61* (L); Goeroepaki, N. Celebes, vid en back i urskogen, 600 m, havet, 27.iii.197, *s.c. s.n.* (NY); Celebes, Tomohon, iv.1894, *Sarason 466* (B); Celebes, Tomohon, 700 m, 6.vi.1954, *A.H.G. Alston 15679* (BM, L); Lokon, etwas Ubrigend Bl. weiss Stengel mit Knoten, *Sarason 488 [38a]* (B); N. Celebes, Tomohon, *Sarason 488 [38]* (B); 22 (B photograph, E, G photograph, US), N. Celebes Lokon, 16.v.1894, leg. *Sarason 278* (K); N. Celebes, Tomohon, iv.1894, leg. *Sarason 288* (K lecto, B photograph); N.E. Celebes (Minahassa), N. slope of Mt. Klabat, c. 500 m, 27.vi.1956, forest, *L.L. Forman 248* (3 sheets K); Utara, 220 km, W. of Manado, *Burley, Turin et al. 3717* (L); G. Lokon, near Tomohon, 600-800 m, 3.vii.1956, forest, *L.L. Forman 371* (2 sheets K, L); N.E. Celebes (Minahassa) G. Masarang, Tomohon, secondary forest edge of crater lake, c. 1200 m, 22.vi.1956, *L.L. Forman 207* (2 sheets K) Celebes, Minahassa, *S.H. Koorders 16244b* (2 sheets L, B drawing, K), *16245* (B drawing), *16245b* (B); Minahassa Province, *Koorders 16248b* (B, L); Celebes ', vii.1840, *Forsten s.n.* (B, 3 sheets L); sine loc., *s.c. s.n.* (B drawing); Selebes expedition, Pasoei-Rante Lemo, 1929, *G. Kjellberg 1627* (B); Selebes, Todjamboe, 800 m, 23.vi., *G. Kjellberg 1750* (B); sine loc., ex Herbario Lugduno-Batavo, *s.c. s.n.* (B); Central Sulawesi, Sopu Valley, c. 80 km. SSE of Palu, c. 1°16's, 120°16'E, 1000 m, 2.v.1979, *E.F. de Vogel 5174* (2 sheets L); Sopu valley, c. 80 km S.of Palu, 1000-1250 m., *Hennipman 5633* (L); Selatan, Gn Rantemario Gowa subcamp, c. 3° 24'S, 120° 00' 30'E, 07-11-1993, 1850 m, *S. Kofman 210* (2 sheets L).

5.4.2.2. B. longifolia Blume in Catalogus. 102. 1823. **Plate 8a.**
TYPE: Salak, *Blume 740* (B! holotype).

SYNONYMS: *Diploclinium longifolium* (Blume) Miquel in Fl. Ned. Ind. 1(1): 687. 1856. **TYPE:** Salak, *Blume 740* (B! holotype).
Diploclinium longifolium var. *luxurians* Miquel ex Koorders in Exkurs. Fl. Java. 2: 650. 1912 *pro syn. Begonia longifolia* Blume, 1823.
Casparya? trisulcata A. DC. in Ann. Sci. Nat. Bot. 4(2): 119. 1859. **TYPE:** *Zollinger 2850* (G! holotype). **synon. nov.**
B. trisulcata (A.DC.) Warburg in Engler & Prantl, Nat. Pflanzenfam. 3(6A): 142. 1894. **TYPE:** *Zollinger 2850* (G! holotype). **synon. nov.**
B. aptera sensu Hayata in J. Coll. Sc. Tokyo. 30 art 1: 122-26. 1911, Icon. Pl. Form. 2: 43. 1912, 6: 21. 1916, Gen. Ind. Fl. Form. 31. 1917; L.B. Smith & D.C. Wasshausen, Phytologia. 54: 467. 1984; Chen Ching-Hsia in Flora of Taiwan. 3: 846-847. 1993, non Decne (1834). **TYPE:** Shintiku, Goshizan, Dec. 1905, leg. *T. Kawakami 1296* (syntype not located), Randaizon, iix.1908, leg. *U. Mori 7121* (syntype not located). **synon. nov.** These specimens were later named *B. hayatae* Gagnepain.
B. hayatae Gagnepain in Bull. Mus. Hist. Nat. Paris 25: 195. 1919; Tang-Shui Liu & Ming-Jou Lai, Flora of Taiwan. 3: 796-797. Pl. 821. 1977. **TYPE:** Shintiku, Goshizan, xii.1905, leg. *T. Kawakami 1296* (syntype not located), Randaizon, iix.1908, leg. *U. Mori 7121* (syntype not located) **synon. nov.**
B. crassirostris Irmscher in Mitt. Inst. Allg. Bot. Hamburg 10: 513. 1939. **TYPE:** Yunnan, Szemao, *Henry 12251* (B!, NY! isosyntypes, K syntype); Yunnan, Shipping, *Henry 13600* (K syntype); Kwangsi, *Ching 7281* (WU syntype); Kwangtung, *Ford 1* (K! syntype); Kwangtung, *Tsiang Ying 1744* (UC syntype, E! syntype); Hainan, *McClure 9325* (K! syntype, MO! isosyntype, PNH syntype); Hainan, *Tsang Wai Tak 278* (UC, E! syntype, G! isosyntype, K! isosyntype, MO! isosyntype); Hainan, *Tsang Wai Tak 536* (UC syntype, B! isosyntype, K! isosyntype, NY! isosyntype). **synon. nov.**
B. inflata C.B. Clarke in J.D. Hooker, Fl. Brit. Ind. 2: 636. 1879; Clarke in J. Linn. Soc. Bot. 18: 115. 1881. **TYPE:** Darjeeling, 3000 ft, *C.B. Clarke 12312A & C* (K! syntypes), Birma?, *Griffith Kew distribution number 2587* (K syntype). **synon. nov.**
B. tricornis Ridley in Journ. Straits Branch Roy. As. Soc. 75: 35. 1917; King, G. in Flora of the Malay Peninsula 1: 854. 1922. **TYPE:** Pahang; Telom, *Ridley 14123* (SING! holotype); Telom, xi.1900, fls. white, erect stemmed, *Ridley s.n.* (K! probable isotype). **synon. nov.**

Begonia roxburghii Ridley in Journ. Fed. Malay States Mus. 4: 20. 1909, non A.DC. 1864 **TYPE:** Pahang: Telom, *Ridley 14123* (SING! holotype); Telom, xi.1900, fls. white, erect stemmed, *Ridley s.n.* (K! isotype). **synon. nov.**

ILLUSTRATIONS: Clarke, Journ. Linn. Soc., London Bot. xviii t. i Fig. 4. 1881 (as *B. inflata* C.B. Clarke); Tang-Shui Liu & Ming-Jou Lai, in Hui-lin Li *et al.* (eds.) Flora of Taiwan. 3: p. 797. 1977 (as *B. hayatae* Gagnepain); Smith *et al.* Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany, No. 60. Fig. 27.25. 1986; Smith *et al,* Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany, No. 60. Fig. 20.8. 1986. (as *B. tricornis* Ridley); Grierson & Long, Flora of Bhutan. 2(1): p. 239 Fig. 29. 1 & m. 1991 (as *B. inflata* C.B. Clarke); Chen Ching-Hsia in Flora of Taiwan. 3: Photo 69. 1993 (as *B. aptera* sensu Hayata).

DESCRIPTION: Monoecious, erect leafy herb to 2 m, lacking rhizomes. *Stem* branched, usually glabrous, occasionally sparsely hairy. *Stipules* deciduous, narrowly lanceolate to lanceolate-subulate, 6-17 x 1.25-3 mm, apex acute, glandular setose, otherwise glabrous, margin entire. *Leaves* alternate; *petioles* 0.7-14 cm, usually glabrous, occasionally sparsely hairy; *lamina* lanceolate to elliptic-acuminate or broadly elliptic, 11-22 x 2.15-10.5 cm, apex gradually long acuminate, base strongly asymmetric, lobes unequal, cordate, lower lobe 1-7.5 cm, inner lobe very short, sinus truncate-3 cm deep, usually 0.5-1.5 cm deep, margin shallowly toothed to almost entire, often slightly wavy, ciliate, above green, below paler green, both surfaces glabrous or veins on lower surface occasionally sparsely microscopic glandular hairy, veins 5-7, palmate. *Inflorescences* axillary, twice branched dichasiums usually 5-7-flowered, occasionally to 10-flowered, male and female flowers occurring on the same or on separate inflorescences; *peduncles* 3-15 mm, glabrous to sparsely hairy; *bracts* caducous, narrowly lanceolate to lanceolate-subulate, 2.25-12 x 0.75-5 mm, apex acute, setose, outer surface sparsely microscopic glandular hairy, margin usually entire, rarely ciliate. *Pedicels* glabrous or microscopic glandular hairy, those of male flowers 0.5-1.3 cm, those of female flowers to 1.4 cm. *Male flowers*: *tepals* usually white, sometimes pale pink, 4, outer 2 broadly ovate or obovate to elliptic, glabrous, 4-10 x 2.5-9 mm, apex rounded, outer surface strongly concave, inner 2 broadly ovate to linear-obovate, 3.5-8.5 x 2-7.8 mm, apex rounded, glabrous; *stamens* 30-60, *filaments* 0.7-1.6 mm long, free to scarcely fused at base, occasionally attached to a raised flowers base to 1.5 mm tall, *anthers* narrow-oblong to linear or elliptic, inner slightly longer than outer, 1-2.6 mm, dehiscing via vertical slits along the sides of the anther,

connective projecting c. 0.2-0.4 mm, apex rounded. *Female flowers*: *tepals* usually white, sometimes pale pink, 6, subequal, inner becoming gradually smaller, glabrous, outer elliptic, 5-16 x 3.6-6 mm, apex rounded, inner elliptic, 4.7-13 x 2.6-4.6 mm, apex rounded; *ovary* globose, 3-lobed, 3-10 x 3-7 mm, with 3 ribs along angles, occasionally with equal wings from centre of each locule, c. 1 mm, triangular, glabrous to very sparsely microscopic glandular hairy, 3-locular, *placentation* axillary, *placentas* bifid, bearing ovules on both surfaces; *styles* deciduous, 3, slender, 3-5 mm tall, fused at base for c. 0.7 mm, bifid from shortly below half-way, branches erect, stigmatic papillae once to thrice spirally twisted. *Infructescences* often 4-fruited; *fruiting pedicels* c. 1 cm; *fruit* green to reddish green, fleshy, pendulous, globose to turbinate, 6-12 x 8-14 mm in dried state, very sparsely microscopic glandular hairy, apex rounded to beak-like.

PHENOLOGY: Flowering year round in Indonesia and the Malay Peninsula but in more northerly latitudes March-October, with most collections between May and September.

DISTRIBUTION: North-eastern India, Bhutan, southern China (Yunnan-Fujian, including Hainan), Taiwan, Burma, northern Thailand, northern & central Vietnam, Malay Peninsula, Sumatra, Java and Bali.

HABITAT & ECOLOGY: Found in a wide range of habitats from primary rain-forest to degraded scrub vegetation, on acidic to basic substrate. Occasionally on limestone cliffs. In full to half shade. In moist conditions but not in seasonally waterlogged areas at altitudes of 120-2000 m.

CULTIVATION: Cultivated at Wageningen Agricultural University and Hanoi College of Pharmacy (Vietnam). Locally cultivated within P.R. Vietnam as an ornamental.

LOCAL NAMES: Chat Chua is a name used in northern Vietnam for this and other edible begonias. Chua Khao appears to be a name of less widespread usage in Vietnam, possibly restricted to the Hmong people of Cuc Phuong National Park (pers. obs.).

USES: Leaves and stem eaten as a vegetable within northern Vietnam.

NOTES:

1. Material from Indonesia has a greater tendency to have more spaced dichasial inflorescences and shortly winged fruit but no infra-specific taxa can be defined.

2. Plants collected from 'wet swamp' on Hainan Island (*Tsang, 26832* (E)) appear stunted.

3. A syntype of *B. inflata* C. B. Clarke [*Griffith 2587* (B, GH, K)] designated by Clarke has written on it 'Birma?', however, in his account of the taxon in Hookers' Flora of British India the locality is given as 'Bhotan?' The locality of the specimen, therefore, remains uncertain.

SPECIMENS EXAMINED:

India: ASSAM: Darjeeling, Rishap, 3000 ft, 2.iix.1870, *C.B. Clarke 12312A* (K syntype of *B. inflata* C.B. Clarke), *12312C* (K syntype of *B. inflata* C.B. Clarke); Assam, Mouth of 'Sireng' (Abor expedition), 700 ft, 30.xii.1911, *I.H. Burkill 37586* (CAL, K). MEGHALAYA: Shillong, Pangu-Minguing, 600-1267 m, 16.v.1958, *R. S. Rao 17711* (CAL).

Bhutan: Shongan Dzong, 28.iix.1915, 3000 ft, *R.E. Cooper 4713* (E).

P.R. China: YUNNAN: sine loc., *Henry 10737* (K); sine loc., Tsang, *Wai-Tak 278* (B); Shih Ping, 5000 ft, *Henry 13600* (K syntype of *B. crassirostris* Irmscher); Yunnan, Mar-li-po, Tung-ting, 1200-1500 m, *K.M. Feng 1354* (B); Gongshan Dulong River, 15000 m, 1979/7/11, *Linqin & Dengxiangfu 790855* (2 sheets KUN); Hekou county, 350-400 m, 91/7/28, *Shui Yuming B91-407* (KUN); Mengla Bubong, 700 m, x.1980, *Zhu Hua 1303* (KUN); Yunnan, Luo Ping, 780 m, 24.xi.1984, *Sunhan 0511* (KUN); Yunnan, Szemao 4500 ft, *A. Henry 12251* (2 sheets B syn, NY isosyn); Mar-li-po, Tung-ting, 1200-1500 m, in mixed forest, 22.xi.1947, *K.M. Feng 13541* (2 sheets KUN); Pingbian, 600 m, 26.iix.1963, *Mao Pingyi 03083* (2 sheets KUN); Xishuangbanna, Mengyang, 750 m, 9.iix.1977, *Tao Guoda 16712* (KUN); Xishuangbanna, Menglun, 600 m, 25.ix.1959, *Institute of Botany Kunming Working Station 59-13217* (KUN); Xishuangbanna, Menglun, 580 m, 23.ix.1959, *Pei Shengji 59-10391* (2 sheets KUN); Xishuangbanna, Yiwu, 660 m, 16.vii.1959, *Li Yanhui 001502* (KUN); Xishuangbanna, Longpa, 1000 m, 18.ix.1960, *Li Yanhui 002662* (KUN); Funing county, 31.x.1958, *Cai Tsitao 58-8975* (2 sheets KUN); Ping-bian county, Yaoshan, 5.vii.1953, *Mao Pingyi 02435* (2 sheets KUN); Xichou county, 1300 m, 15.xii.1939, *W.C. Wang 85747* (KUN); GUANGXI: Guangxi Province, Moxian county, 300 m, 11.v.1957, *Chen Zhaozhou 50518* (KUN); Guangxi Province, Longjin county, 740-880 m, 14.vi.1957, *Chen Shaoqing 12619* (KUN). GUANGDONG: Canton, Yuangshan county, 390 m, 1.vi.1958, *Tang Peixiang 58247* (KUN); Kwangtung, Kung Ping Shan & vicinity,

T'aan Faan, Fang Ch'eng District, *W.T. Tsang 26832* (E, 3 sheets K, P); Lofoushan Mountains, *Tsiang Ying 1744* (E) Ting-wu Shan, *K.C. Ting & K.L. Shih 1137* (L) Lo Fau Shan, 15.iix.1983, 1000 ft, *Ford 1* (K). HAINAN: Kwangtung, Hainan, Ng Chi Ling, 'Tan yah', *N.K. Chun & C.L. Tso 44212* (NY); Hainan, Bak Sa, Forest, 22.iv.1936, *S.K. Lau 26391* (KUN); Hainan, Kwangtung, Hung Mo mountain, *Tsang, Tsang & Fung 47* (NY); Hainan, Kwangtung, Hung Mo Tung, *Tsang & Fung 18156* (NY); Hainan, Hung Mo Shan & vicinity, *Tsang & Fung 622* (K); Hainan, the top of Lin Fa Shan and Vicinity (Lam Ko District), *Tsang, Wai Tak 278* (B drawing, E, G, K, MO); Hainan, Sha Po Shan (Taam Chau District), Tsang, *Wai-Tak 536* (B, K, NY); Hainan, Ngo Ko Shan, near Tsat Cha Village (Ch'ang-kiang District), 12.vi.1933, *S.K. Lau 1928* (BM, NY, P); Hainan, Yaichow, *H.Y. Liang 63076* (NY); Hainan, Yaichow, *H.Y. Liang 63284* (NY); Hainan, Five Finger Mt., *F.A. McClure 9325* (K, MO, NY). FUJIAN: Nanjing county, 500 m, 13.iix.1964, *Xiameng University collecting team 1102* (KUN); S.W. Fukien, Liung Chon San, S. of Shanghang, 725 m, *J. Linsley Gressitt 1677* (BM, MO).

Taiwan: Nantou Hsien, Luku Hsiang, Fenghuangku Bird Park, bamboo plantation on the left side of the entrance station, *Chih-Chia Wang (with C.H. Lin) 1206* (A); Taipei Hsien, Wulai, Tunghou, en route from Mountain control station to guest house, c. 400 m, *Chii-Cheng Liao (with T.Y. Liu & J.N. Wang) 402* (A); Formosa, Uraisya, Taihoku, *S. Sasaki 21531* (NY); Taipei Hsien, sanhsia, Manyuehyuan Waterfall, en route from Chengpai Lodge to Waterfall. Broadleaf forest, *Chii-Cheng Liao 388* (A); Taipei Hsien (County) Cryptomeria Forest to N. Cha-Tien Mt., San Hsia, 800-1300 m, 15.iix.1988, *Tsung-Hsin Hsieh & Chi-Hsing Hsiao s.n.* (NY); Chi Tou?, *s.c. 089* [herbar. W. Schwabe acc. 1987] (B); Taipei Co. Wulai, 25.v.1932, *S. Sasaki s.n.* (TAI); Sintikusyû, Byôritugun, Sansasyô, Kwantpzan-Hoanrin, 500 m, Oobatabu-Taiwansyôbennoki-Tô-Hosobanomidu Kigunsô, Sôhonsô, 28.vii.1940, *T. Suzuki 20532* (TAI); Taipei Co. Tatongshan, 28.vii.1974, *C.M. Kuo 5581* (TAI); Taipei Co. Fushan-Hapen, under wet evergreen forest, 400 m, 13.x.1984, *S.F. Huang 1277* (TAI); Taipei Co. Shiting, Huang-ti-dian, roadside under tree, 12.iix.1984, *T.Y. Tang 43* (TAI); Taipei Co. Houkuntzuchi, in forest, 300 m, 20.iix.1986, *T.C. Huang & K.C. Yang 2100* (TAI); N.E. Horisha, Maibara, dense forest, 2.vii.1912, *W.R. Price 717* (K); Uraisya, Taihoku, 28.iix.1927, *S. Sasaki 21531* (K).

Burma: Upper Burma, Kachin Hills, *S.M. Toppin 4339* (K); Theronliang Tidding valley, 28° 5' N. 96° 17' E, *F. Kingdon-Ward 7936* (K).

Thailand: South of Ka Tha Lai in Pan Paung river valley about 40 km south east of Wangka, 400-800 ft, Kwai Noi River Basin expedition, *C.Y. Wu 838* (A); Siam,

south of Ka Tha Lai in Pan Paung River Valley, abt. 40 km south east of Wangka, 400-800 m, 13-16.vi., leg. *A. Kostermans 838* (K); Kao ' Surat, *Kerr 13256* (K).

P.R. Vietnam: Indochine, Phu-Cho, *s.c. 065* (P); sine loc., *s.c. 758* (HN); sine loc., *s.c. 3690* (5 sheets HN); Hoa Binh Prov. Chinê, 2.iv.1982, *Nguyen Nghia Thin 949* (2 sheets HNU), *892* (2 sheets HNU); Vinh Yên Province, Tam Dao, *Eberhardt 4990* (K, P); Vinh Yên Province, Tam Dao, *Eberhardt 4995* (P); Noi hái, Tam Dáo, 11.x.1959, *s.c. 454* (HNIP); Mount Bavi, *B. Balansa 3757* (2 sheets P); Dò Hoay phué, 9.ix.1980, *B.T.T. Alüoi 164* (HN); Do Hong Phue, 7.ix.1980, *B.T.T. Aluoi 122* (HN); Binh Tri Thien, A Luoi, 7.ix.1980, *D.H. Phu 122* (2 sheets HN); Binh Tri Thien, A Luoi, 9.ix.1980, *D.H. Phuc 164* (HN); Chapa, iv.1925, Herbier de l'École Supérieure d'Agriculture et de Sylviculture (Hanoi), *s.c. s.n.* (B); Thua Thien-Hue Province, Vallée du sông, ', *Eberhardt 3107* (P); Lang bian, Ninh Thuan Province, *Eberhardt 1764* (P); sine loc., *Petelot 1808* (NY).

Malaysia: MALAY PENINSULA: PAHANG: Telom, *Ridley 14123* (2 sheets B photograph, HBG holotype of *B. tricornis* Ridley); *Ridley s.n.* (K); Pahang, Cameron Highlands, c. 3700 ft, 30.iv.1937, *Henderson 32961* (BM, K). PERAK: Tor Camp, Batang Padong, 1800 ft, 1.vi.1923, leg. *Henderson s.n.* 10863 (B drawing); Tanah Runto, P. Tioman, 1500 ft, 8.v.1927, on rocks, *Md Nur 18883* (K, L); Menuang Gasing, *Kloss s.n.* (2 sheets K). SELANGA: Ginting Sempak, 6.iix.1922, *Burkill 9989* (B, K); Ginting Bidai, Selangor, Pahang boundary, iii.1917, *Kloss s.n.* (2 sheets K); 24.ix.14, *Kloss s.n.* (K); Ginting Sempak, Selangor, Pahang boundary, iii.1917, *Ridley, Robinson & loss s.n.* (K); Ginting Sempak, 6.xii.1922, *Burkill 9989* (B, K); sine loc., *Henderson 10863* (B), *11257, 11556, 18883, 21628* (B on same sheet); ' Naug Gating ' Laugat Klaugon, ii.1912, *C.B. Kloss s.n.* (K); Telom, ix.1900, *Ridley s.n.* (K isotype of *B. tricornis* Ridley); Ginting Bindai, 24.ix.1914, *Ridley s.n.* (2 sheets K).

Indonesia: SUMATRA: *s.c. 2125a* (L); Lintang, N.W. Helling, 1150 m, *Bümmemeyer 3551* (L), *3746* (L). JAVA: sine loc., *Blume s.n.* (L); sine loc., *Docker 8724* (B); sine loc., *Koorders s.n.* (L); sine loc., *Koorders 44300* (B); sine loc., *Koorders 27663* (B); sine loc., 24.vii.1919, leg. *S.H. Koorders & A. Koorders 44300* (L); sine loc., *Hallier s.n.* (B); Builenzorg Tjapoes, 22.vi.1896, *Hallier 42* (L); sine loc., *s.c. s.n.* (B); Salak ', ex Herb. Lugduno-Batavo, *s.c. 740* (B lecto); Salak, 2.vi.1996, *H. Raap 174* (L); Batavia, 1000-1520 m, *Van Steenis 12200* (L); Prov. Batavia: Ad decliv. septentr. montis Salak in faucibus torrentis Tjiapus, 6-850 m, 27.i.1894, *V. Schiffner 2268* (L); Salak, *Decloux 740* (L); sine loc., *Zollinger 2850* (G holotype of *B. trisulcata* (A.DC.) Warburg, B isotype, BM isotype, P isotype); sine loc., *Nagel 1844* (B); sine loc., 1858, *Nagel 272* (2 sheets B); sine loc., *ex Herb. Bogorensis 22B* (B); sine loc., *ex Herb. Lugduno-Batavo s.n.*

(2 sheets B); West Java, Tjibodas Gunang Gedah, Bogor, 3.iii.1959, in forest above gardens, *Sinclair 10080* (E); Tjibodas, Hutan Pasir Sintok, primary forest, in gully along water course, 17.vi.1953, *W. Meijer 1456* (L); Pasin Walang naby Nanggerang, 1000 m, 1913, *Backun 8724* (B); sine loc., *Zipp s.n.* (B); Preanger, c. 1000 m, Tjadas-Malang, *Bakhuizen & Brink 2899* (L); Res. Besoeki Panjoer Idjen, *Koorders 1912* (L). BALI: Bedugul forest region, Mt. Batukau complex, *Kostermans, Kuswata, Soegeng & Soepadmo KK&SS92* (L); 08°15'S 115°10'E, Lake Bratan, near Bedugul, 20.vi.1976, *W. Meijer 10551* (2 sheets L); Batu Kau, under forest, 1200 m, 22.iii.1964, *A. Dilmy 991* (L); Batockaoe, 23.i.1935, *C.N.A. de Voogd 2142* (L).

Cultivated: Szemao Hotel, 2000 m, *H. Koyama et al. 1408* (KUN); From Darjeeling SB 1920 where seed was rec'd in 1912 from Mr I.H. Burkill when on the Abor Expedition (K).

5.4.2.3. B. sarcocarpa Ridley in Journal of the Federated Malay States Museum 8(4): 38 1917. **Plate 8b.**

TYPE: Korinchi Expedition, Barong Bharu, W. side Barisan Range, 1914, *H.C. Robinson & C.B. Kloss s.n.* (BM! holotype).

SYNONYMS: *Begonia baccata* Ridley nomen nudum (BM! in sched.) non J.D. Hooker, 1866. **synon. nova.**

DESCRIPTION: Erect herb, stems flexuous with several short branches, internodes short (1.5-2 cm in outer branches), slender, glabrous. *Stipules* caducous, lanceolate-acuminate, 4-5 x c. 1.5 mm, glabrous. *Leaves* alternate; *petioles* 0.7-1.2 cm, slender, glabrous; *lamina* lanceolate-acuminate, clearly oblique, 5-6.5 x 1.2-1.8 cm, apex acuminate, base asymmetric, lobes unequal, lower lobe 0.5-1 cm across, sinus 1.5-2.5 mm deep, margin shortly acute toothed where secondary veins reach the margin, both surfaces glabrous, veins pinnate. *Inflorescences* terminal and in upper leaf axils, once branched dichasiums, 3-4-flowered, male and female flowers present on same inflorescence synchronously; *peduncles* to 6 mm; *bracts* caducous, ovate, 1-2 x 0.6-1.4 mm, glabrous. *Pedicels* to 1.4 cm, glabrous. *Male flowers*: *tepals* 4, glabrous, obovate to elliptic, subequal, outer 2 slightly longer, 5-6 x 2-4.5 mm, apex obtuse; *stamens* c. 75, *filaments* free, linear, central filaments slightly longer, to 1 mm, *anthers* obovate-elliptic, c. 1.3 mm, dehiscing via longitudinal splits along sides of anther, connective projecting c. 0.2 mm, apex rounded. *Female flowers*: *tepals* 5, subequal, elliptic, 5-6.5 x 1.6-2.8 mm, glabrous; *ovary* globose, c. 4 x 4 mm, appearing wingless, wings 3, very short, along centre of locules, c. 0.3 mm long, 3-locular, *placentation* axillary, *placentae* bifid, ovules attached to both sides; *styles* caducous, 3, c. 2.5 mm long, shortly fused at base, branches bifid from 1/3 of length, branches erect, horse-shoe shaped, stigmatic papillae once spirally twisted. *Infructescences* 1-2-fruited, erect; *fruiting pedicels* 8-9 mm; *fruit* fleshy, globose, locules inflated, c. 0.8 x 0.8 cm, wingless but widest part with small protrusions, crowned by remains of style.

PHENOLOGY: Flowering and fruiting in June.

DISTRIBUTION: Sumatra.

HABITAT & ECOLOGY: Montane forest at 1200 m.

NOTES:

1. A Robinson & Kloss specimen which Ridley labelled as the holotype of *Begonia baccata* Ridley is the holotype of *B. sarcocarpa* Ridley. This specimen is illustrated in Plate 8b. It appears that Ridley changed his mind concerning the name of this taxon before its publication as an examination of his bibliography (Henderson & Van Steenis, 1935) and references contained therein indicates that he never published the name *Begonia baccata.* The specimen is very distinct and fits the original description of *B. sarcocarpa* Ridley. Ridley did not designate a type specimen in his description of *B. sarcocarpa* (Ridley, 1917). In addition to a label on which is typed 'Robinson & Kloss Herb. British Museum Sumatra, Korinchi expedition' a piece of paper with 'Japan barong barw no 61' is also fixed to the sheet. This must be a mistake as Barong barw is in Sumatra and is the type locality of Ridley`s *Begonia sarcocarpa.* A label with 'barong barw na 1.42 Japan 8.6.14 (Sumatra, Korinchi Expedition) is also present on another Sumatran taxon, *Begonia trigonocarpa* Ridley, housed at the Natural History Museum.

Smith *et al.* (1986) appear to have been unable to locate any material of this taxon, which also suggests that no type specimen of *B. sarcocarpa* Ridley was originally designated.

2. Known only from holotype.

SPECIMENS EXAMINED:

Indonesia: SUMATRA: Korinchi Expedition, Barong Bharu, W. side Barisan Range, 1914, *H.C. Robinson & C.B. Kloss s.n.* (BM holo).

5.4.2.4. B. turbinata Ridley in Journal of the Federated Malay States Museums. 8(4): 37. (1917).

TYPE: Siolak Daras at 3000 ft, 1914, *Robinson & Kloss s.n.* (BM! holotype, BM! isotype, K! isotype), Sungei Kumbang at 4500 ft, *Robinson & Kloss s.n.* (BM! isotype).

ILLUSTRATIONS: Smith *et al.* Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany. No. 60. Fig. 20.41. 1986.

DESCRIPTION: Erect herb to 2.5 m, stem green, slender, simple or few branched, glabrous. *Stipules* caducous, lanceolate, 0.6-1.3 x 0.3-0.6 cm, apex acuminate, margin entire, glabrous. *Leaves* alternate; *petioles* 2-7 cm long, slender, glabrous; *lamina* lanceolate, 8-16 x 1.8-6.5 cm, apex acuminate, base strongly asymmetric, shallowly cordate, lobes unequal, lower lobe 0.7-2.4 cm, sinus 0-2.4 cm deep, margin toothed, teeth small, forward pointing, ciliate, above green, below paler green, with red veins, both surfaces sparsely microscopic glandular hairy, veins 6, palmate. *Inflorescence* a loose axillary 1-2-branched dichasium, few-flowered, male and female flowers mature on inflorescence synchronously; *peduncles* to 1 cm; *bracts* caducous, ovate-acuminate, c. 6 x 2 mm, very sparsely microscopic glandular hairy. *Pedicels* to 1.7 cm in male flowers, to 1 cm in female flowers. *Male flowers*: *tepals* 4, white to pink, outer 2 orbicular-elliptic, glabrous, 4.6-6 x 3.2-4.4 mm, apex obtuse, inner 2 ovate-elliptic, glabrous, 3.8-5.4 x 2.5-4 mm, apex obtuse; *stamens* c. 25-30, *filaments* linear, free to base, central filaments slightly longer, c. 0.6 mm, *anthers* linear-elliptic, c. 1.5 mm long, dehiscing via vertical slits along side of anther, connective projecting c. 0.2 mm, apex rounded. *Female flowers*: *tepals* 6, white to pink, ovate-elliptic, outer to 8 x 6 mm, apex obtuse, inner to 7 x 3 mm, apex obtuse; *ovary* green, fleshy, top-shaped, locules inflated, with 3 very short wings running along outer angle of locules, these later drying out in fruit to become knob-like protrusions, 3-locular, *placentation* axillary, *placentae* bifid; *styles* caducous, 3, slender, branches bifid, stigmatic papillae once spirally twisted. *Infructescence* 1-4-fruited, orientated at 45° to stem; *fruiting pedicels* to 1.3 cm; *fruit* fleshy, erect, top-shaped, locules inflated, 7-13 x 8-15 cm, wingless, but with knob-like protrusions on angles of locules, crowned by basal part of styles.

PHENOLOGY: All flowering and fruiting specimens examined were collected in March.

DISTRIBUTION: Sumatra.

HABITAT & ECOLOGY: Forest at 854-1371 m.

SPECIMENS EXAMINED:

Indonesia: SUMATRA: Vicinity of Mount Kerinci, Sungei Kering, Kerintji, 2.iii.1954, *A.H.G. Alston 14040* (BM, L); South side of pass between Sungei Penuh & Indrapura, 2800 ft, 8.iii.1954, *A.H.G. Alston 14312* (BM); Korinchi Expedition, Siolak Dras, Korinchi, 3000 ft, 15.iii.1914, *H.C. Robinson & C.B. Kloss s.n.* (BM holo, K iso); Korinchi Expedition, Siolak Dras, Korinchi, 3000 ft, 19.iii.1914, *H.C. Robinson & C.B. Kloss 38* (BM iso); Korinchi Expedition, Sungei Kumbang, 4500 ft, 3.iv.1914, *H.C. Robinson & C.B. Kloss s.n. a.* (BM); Korinchi Expedition, Sungei Kumbang, 4500 ft, 31.iii.14, *H.C. Robinson & C.B. Kloss s.n. b.* (BM iso); Lower slopes of Dolok Si Manoek, Asahan (NW. from Taloen na Oeli, Toba); sine loc., *Rahmat Si Boeea 10246* (K); Berastagi Woods, *H.N. Ridley s.n.* (BM); Deleng Singkoet, north of Berastagi, Karo Plateau, *Bartlett 6595* (NY); Beleng Singkoet, north of Berastagi, Karo Plateau, 24.vi.1927, *Bartlett 8578* (NY); In ravine between Baboeli and Paekas, alt. 4100 ft, 9.i.1932, *W.N. & C.M. Bangham 776* (NY); Trail from Medan Road to top of Sibajak Volcano, 4200-6500 ft, 15.ii.1932, *W.H. & C.M. Bangham 1018* (2 sheets K, NY); Berastagi, West-Hill, 12.ii.1921, *H.N. Ridley s.n.* (K); Berastagi, 1.ii.1921, *H.N. Ridley s.n.* (K).

5.4.3. DOUBTFUL SPECIES

5.4.3.1. B. renifolia Irmscher in Engler, Bot. Jahrb. Syst. 50: 379. 1913.
TYPE: Minahassa, Bojong, *Warburg 15188* (B! holotype).

ILLUSTRATIONS: Smith *et al.* Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany. No. 60. Fig. 29.7. 1986.

DESCRIPTION: Erect herb, stems simple, slender, not flexuous, internodes c. 13 cm, sparsely hairy, hairs glandular, stalks multicellular. *Stipules* caducous, ovate-lanceolate, c. 1.5 x 0.5 cm, apex acuminate, margin very sparsely rusty-red ciliate else where glabrous. *Leaves* few; *petioles* erect, 9.5-12 cm, hairy; *lamina* reniform, 8-9 x 8-10 cm, apex indistinct, base strongly asymmetric, cordate, lower lobe rounded, 4.5-5.5 cm across, margin bidentate, primary teeth present at point of primary vein contact with margin, secondary teeth small, continuous around margin, acute, ciliate, microscopic glandular hairy, above glabrous, below rusty-red pilose on primary veins, elsewhere glabrous, veins 7-8, splitting into three half way along their length. *Inflorescences* a twice branched axillary dichasium, c. 2-3 cm long, few-flowered; *peduncles* 2-2.5 cm, sparsely hairy; *bracts* caducous, ovate, c. 8 x 0.4 mm, apex acuminate, margin very sparsely irregular ciliate. *Flowers.....styles* 3, bifid from half way, branches erect, stigmatic papillae once spirally twisted. *Infructescence* c. 6-fruited; *fruiting pedicels* c. 0.5 cm, erect; *fruit* with thin walls in sicco, subpyramidal, locules inflated-globose, glabrous, wings rudimentary, rib-like, attached to middle portion of locules 3-locular; placentation axillary, *placentas* bifid, bearing ovules on both surfaces.

DISTRIBUTION: Northern Sulawesi.

NOTES:
1. Known only from holotype.
2. This taxon may represent an aberrant specimen of *B. cristata* (Warburg) L.B. Smith & D.C. Wasshausen.

SPECIMENS EXAMINED:
Indonesia: SULAWESI: Minahassa, Bojong, *Warburg 15188* (B holo).

5.5. DESCRIPTION AND DELIMITATION OF SECTION *DIOECIBEGONIA* TEBBITT SECTION NOVA

Dioecious or rarely monoecious and then male inflorescences developing before the female. Robust erect (to 2 m) or prostrate herbs, usually with a creeping rhizome. *Stipules* caducous to deciduous in erect species, persistent in prostrate species. *Leaves*: *lamina* usually leathery, ovate or rarely lanceolate-ovate, base asymmetric. *Inflorescence* dichasial, flowers fragrant, *bracts* usually caducous to deciduous. *Male flowers*: tepals 4; *stamens* 20-100^{+}, *filaments* free or almost so, *anthers* elliptic to obovate, dehiscing via vertical slits along the sides of the anther, connective projecting. *Female flowers*: *tepals* 4; *ovary* 4-locular, rhomboidal to globose, wingless, corniculate, or with short triangular wings, *placentation* axillary, *placentas* bifid, bearing ovules on both surfaces; *styles* 4 or very rarely 2, bifid, slightly fused to fused up to half their length, stigmatic papillae arranged in a spirally twisted band. *Fruit* fleshy, often brightly coloured, indehiscent. *Seed*: ellipsoid, operculum nipple-shaped, testa cells occupying less than half the length of the seed, cuticular ornamentation of short linear foldings.
Type species: *Begonia roxburghii* (Miq.) A.DC.

The name *Dioecibegonia* was chosen as several of the species within this section are dioecious. Dioecy is otherwise very rare within the genus.

5.5.1. KEY TO THE TAXA OF SECTION *DIOECIBEGONIA* TEBBITT

1a. Plant erect, stipules deciduous.....2
b. Plant prostrate or appearing stemless, stipules persistent.....4
2a. Leaves 10-23 cm across, leathery, fruit corniculate.....**roxburghii**
b. Leaves 2.5-12 cm across, never leathery, fruit not corniculate.....3
3a. Leaves glabrous.....**acetosella** var. **acetosella**
b. Leaves hirsute.....**acetosella** var. **hirtifolia**
4a. Styles 2, apex of outer male tepals acute, leaves often blotched.....**burkillii**
b. Styles 4, apex of male tepals obtuse or rarely acute, leaves never blotched.5
5a. Peduncle 0.25-5.5 cm.....6
b. Peduncle 8-25 cm.....8
6a. Fruit with irregular wing-like protrusions.....**mengyangensis**
b. Fruit wingless, lacking wing-like protrusions.....7
7a. Leaves leathery, glabrous.....**silletensis**
b. Leaves not leathery, softly hirsute.....**aborensis**
8a. Fruit corniculate, rhizome short.....**tessaricarpa**
b. Fruit not corniculate, wingless or with short triangular wings, rhizome long creeping.....9
9a. Outer tepal of male flowers 3-5.5 cm long, apex usually acute.....**handelii** var. **handelii**
b. Outer tepal of male flowers 1.2-2.1 cm, apex usually rounded.....10
10a. Rhizome *c.* 1 cm across, leaves; petiole 15-28 cm, lamina 10-20 x 6-16 cm..**handelii** var. **prostrata**
b. Rhizome 0.3-0.45 cm across, leaves; petiole 6-8 cm, lamina 7-9 x 4-5 cm....**handelii** var. **leii**

5.5.2. DESCRIPTIONS OF THE SPECIES OF SECTION *DIOECIBEGONIA* TEBBITT

5.5.2.1. B. aborensis Dunn in Bull. Misc. Inform. 109. 1920. **Plate 9a**.
TYPE: *Burkill 36023* (syntype, not located), *36132* (syntype, not located), *36138* (syntype, not located), *36225* (syntype, not located), *36700* (K! syntype), *36833* (syntype, not located), *36906* (syntype, not located), *37530* (syntype, not located), *37622* (syntype, not located), *37663* (K! syntype), *37794* (syntype, not located), *36825* (syntype, not located).

ILLUSTRATIONS: Clarke, Journ. Linn. Soc. Bot. 18: tab.1. Fig.3. 1880. (as *B. silletensis* C.B. Clarke).

DESCRIPTION: *Dioecious* (?) *herb*, shortly rhizomatous, leaves, peduncles, sepals and fruit softly red hairy or hirsute. *Aerial stem* absent. *Leaves* few, drooping, never leathery, clustered at stem apex; *petioles* c. 80 cm, green, often with white lenticels; *lamina* green on both surfaces, broadly ovate, 10-17 x 10-15 cm, apex shortly acuminate, 30 cm long, margin obscure sinuate, toothed, base oblique, veins 7-9. *Inflorescences* arising from apical region of rhizome, contracted dichasiums; *peduncles* c. 20 cm long; *bracts* caducous, oblong-ovate, 1.4-3 cm long, margin entire, flowers shiny, white with a pink tinge, facing obliquely downwards, fragrant. *Male flowers*: several, *tepals* 4, outer 2 orbicular to ovate, c. 2 x 1.3 cm, inner 2 shorter, narrow obovate, c. 1.3 x 0.5 cm; *stamens* numerous, free, *anthers* c. 2 mm long, locules chestnut-brown, connective black, *anthers* dehiscing via lateral slits along side of anther. *Female flowers*: few, *tepals* 4 or occasionally 6-7, otherwise as in male flowers; *ovary* globose, wingless, *placentation* axillary, *placentae* bifid, bearing ovules upon both surfaces; *styles* 4, c. 7 mm long, bifid, fused just below half way. *Infructescence* erect; *fruit* globose, 1.8 cm across, wingless.

PHENOLOGY: Flowering and fruiting season January to April.

DISTRIBUTION: North eastern India.

HABITAT & ECOLOGY: Burkill (1925 p. 289) states this species 'goes further out on to the Plains than any other in the Abor Hills, occurring in old clearings for instance, under a covering of Saurauja where the sunlight more easily reaches the ground than in the high forest.' Found at altitudes between 274-1158 m.

CULTIVATION: Cultivated at Darjeeling Botanic Garden in the 1920's and possibly still persisting there.

NOTES: Material determined as *Begonia cuboidea* C.B. Clarke *nomen nudum* in herb. Kew is this species.

SPECIMENS EXAMINED:

India: ASSAM: Namsung, 1500 ft, Luckimpore, 17.iv.1885, leg. *C.B. Clarke 37917A* (K); Luckimpore, Hukanjiri, 1000 ft, 16.iv.1885, *C.B. Clarke 37923A* (K), 37923F (K); Abor, *I.H. Burkill 37376* (K); Outer Abor Hills, *Burkill 36700* (K syn), *36825* (K), *37663* (K syn); Dichaing Valley, Abor Hills, 1000-2000 ft, 12.ii.1928, *Kingdon Ward 7854* (2 sheets K); Durrang, Shillong, *Mann 42639* (K); Charduar forest, Darrang Assam, 1887, *Mann s.n.* (K). NAGALAND: East Bengal, Naga Hills, *Griffith* Herbarium of the late East India Company distribution number *2569* (K, B).

Cultivated: From material sent by Burkill from the Abor Hills in 1912 and grown in the Darjeeling B.G. whence specimen sent to Kew in spirit in 1920, *Burkill 4* (K).

5.5.2.2. B. acetosella Craib in Kew Bulletin. 153. 1912; Irmscher, Mitt. Inst. Allg. Bot. Hamburg. 6: 347. 1927.
TYPE: Chiengmai, Doi Sootep, 660-900 m, *Kerr 557* (B! syntype), *1744* (B! isosyntype, 3 sheets E! isosyntypes!, 2 sheets K! syntypes).

SYNONYMS: *B. tetragona* Irmscher in Mitt. Inst. Allg. Bot. Hamburg 10: 515-516. 1939. **TYPE:** Yunnan, Mengtze, S.W. mts., forests, 4000 ft, *Henry 10737A* (B! holotype, E! isotype). **synon. nova.**

ILLUSTRATIONS: Wu (ed.) Wild Flowers of Yunnan, 3-Tropical. p. 70-71. Japan Broadcast Publishing Co. Ltd. 1986; Smith *et al.* Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany, No. 60. Fig. 20.11. 1986. (as *B. tetragona* Irmscher).

DESCRIPTION: *Dioecious*? erect, leafy herb, lacking creeping rhizomes. *Stem* to 2 m, fleshy, green or reddish, swollen at base and nodes, branched, internodes to 20 cm, branches 4-10 mm across, green or often red-tinged particularly at base and on nodes or red throughout, glabrous to microscopic hairy, stem apex usually flexuous. *Stipules* deciduous, greenish-opaque, ovate-lanceolate to lanceolate, 8.5-29 x 1.5-8.5 mm, apex acuminate, glabrous or sparsely microscopic hairy. *Leaves* alternate; *petioles* 1-7 (-17) cm, glabrous to sparsely shortly hairy, hairs glandular, microscopic; *lamina* usually ovate to ovate-lanceolate, larger leaves elliptic-acuminate, 10-27 x 2.5-12 cm, apex acuminate to long acuminate, base strongly asymmetric, lobes unequal, not overlapping, lower lobe 1.7-7.3 cm, sinus truncate [especially in sicco]-12 mm, margin shortly toothed and ciliate or occasionally bidentate, larger teeth to 1 cm deep, above green, below paler green, veins sometimes tinged pink, both surfaces glabrous to sparsely hairy, especially on veins below, veins 5-7, palmate. *Inflorescences* axillary, a once branched or contracted dichasium, flowers often solitary, but up to 5-flowered, flowers fragrant; *peduncles* 1-3 (-50) mm, glabrous; *bracts* deciduous, ovate, 4-10 x 1-3.5 mm, apex acute to glandular setose. *Pedicels* glabrous to sparsely microscopic glandular hairy those of male flowers to 1.4 cm, those of female flowers 4-10 mm. *Male flowers*: *tepals* white, sometimes pink flushed near base inside, 4, outer 2 usually obovate-elliptic, outer surface microscopic glandular hairy, 10-18 x 6-15 mm, apex rounded, inner 2, ovate to elliptic-obovate, 5.5-16 x 3-8.5 mm, apex rounded; stamens yellow, 60-100, *filaments* free, attached to a raised flowers base to 1.5 mm tall, filaments equal, 2-2.6 mm, *anthers* rectangular to obovate, 1.5-3 mm, dehiscing via vertical slits along sides of anther, connective projecting 0.3-1 mm,

apex rounded, often wider than locules. *Female flowers*: *tepals* white to pale pink, microscopic glandular pubescent, 4, usually broadly elliptic, sometimes broadly ovate or almost orbicular, outer 2 6-9.5 x 6-12 mm, outer surface minutely glandular hairy, inner 2 6-7 x 3.5-6 mm, apex usually rounded; *ovary* 4-angled, very rarely 3-angled on same plant, 3-15 x 4-11 mm, wings on central part of each locule, triangular, often narrowly so, microscopically glandular hairy, 4-locular, rarely 3-locular on same plant, *placentation* axillary, *placentas* bifid, bearing ovules on both sides; *styles* caducous to eventually deciduous, 4, slender, c. 5mm long, base fused 0.5-1 mm, bifid from about half-way, branches erect, stigmatic papillae twice spirally twisted. *Infructescence* usually solitary fruited, but sometimes bearing up to 3 fruits; *fruiting pedicels* 10-12.5 mm long; *fruit* fleshy, glossy light green, pendulous, rhomboidal to spherical, 12-15 x c. 17 mm, wings triangular to 5.5 mm, base c. 4 mm wide, apex acute, glabrous.

var. **acetosella**

DIAGNOSIS: Leaves and petioles hairless or almost so.

PHENOLOGY: Flowering January to August. Fruiting year-round.

DISTRIBUTION: Northern Thailand, northern Laos, northern Vietnam, south eastern Tibet, south western China (Yunnan) and north eastern Burma.

HABITAT & ECOLOGY: Shady moist situations by streams in mixed or evergreen forest, usually growing amongst tall vegetation, occasionally in bamboo forest. Mostly on mountains between 800-2750 m, but also frequently collected at altitudes down to c. 400 m.

CULTIVATION: Cultivated at Kunming Botanic Garden (P.R. China), Glasgow Botanic Garden and The Royal Botanic Garden, Edinburgh.

LOCAL NAMES: Hsum hwe (Shaw [or Shau] people, Burma) W.A. Robertson, 273 (K), Som Koi (Laos), A.F.G. Kerr, 20929 (K), Som Kung (Thailand), A.F.G. Kerr, 20325 (BM), Som Kop (Thailand) Bunchuai, 1607 (L), Chi Chua and Cau are names used by the Black Hmong people of North Vietnam for the local edible species of *Begonia*, and for *B. acetosella* in particular, elsewhere in Vietnam these taxa are often called Chat Chua (pers. obs.).

USES: Several indigenous peoples of Northern Vietnam have a variety of medicinal uses for the stem of this taxon including the treatment of fevers, coughs and stomach complaints. The leaves and stems are eaten as a vegetable by the Black Hmong people of North Vietnam. The stem is also widely eaten for its invigorating and thirst quenching properties. The latter practice is particularly popular with children. All parts of the plant have a bitter, acidic taste (pers. obs.). Kerr (1911) in an account of the taxon in Burma says that the 'stem [is] edible and tastes like rhubarb'. Sheets '*W.A. Robertson 791* (B) and *273* (K)' from Burma have written on them 'eaten by Shaus'.

NOTES:

1. *Begonia tetragona* Irmscher is treated as conspecific with *B. acetosella* Craib as a detailed examination of their morphology showed continuous variation of all morphological characters. Irmscher based his taxon on a single collection which represents an extreme variant of *B. acetosella* Craib.

2. Gagnepain (1919) synonymysed *B. acetosella* Craib under Blume's *B. aptera* from Sulawesi (Gagnepain mistakenly gave Java as the origin of Blume's taxon). This treatment is currently widely recognised in the P.R. China even though a number of authors (Irmscher, 1939; Craib, 1931; Wu, 1986) continue to recognise *B. acetosella* Craib as a distinct taxon within China and elsewhere. As no material has since been observed from either Sulawesi or Java which matches the description of *B. aptera* Blume or which resembles *B. acetosella* Craib the latter is maintained here as a distinct taxon from *B. aptera* Blume. Irmscher (1924) states that either the [herbarium] material of Blume's *B. aptera* exists in an undiscovered locality and represents an unknown taxon or, more probably, there has been a mistake in the observation. I am in agreement with this view. If an typographic error has occurred then *B. cristata* Blume would be the best candidate for the taxon.

3. Material lacking fruit is easily confused with *B. longifolia* Blume. The two taxa may be separated on the basis that *B. acetosella* has a considerably shallower leaf sinus than *B. longifolia* and has a tendency to possess flexuous rather than straight upper stems.

SPECIMENS EXAMINED:

Tibet: Medoc, Hanmi, 800-1000 m, 6.iix.1974, *Qinghai-Tibet team 74-4114* (KUN). **China:** YUNNAN: Gongshan county, Duoogjiang, 1350 m, 11.xi.1954, *Feng Kuomei 24182* (KUN); Gongshan county, Dulong jiang, 1700 m, 5.iix.1982,

Qinghai-Tibet team 8910 (KUN); Gongshan County, from Dulong Jiang to Gameilin He, 11.vii.1979, *Lin Qin & Deng Xiangfu 790823* (KUN); Gongshan dulong-shan, 1300-1400 m, 9.iix.1982, *Quinghi-Tibet team 9161* (3 sheets KUN); Yuan Peng chunling, 1200-1300 m, under evergreen broadleaved forest, 7.vi.1974, *Luchan team 1590* (2 sheets KUN); Luchan Song dong, 1630 m, between rock under broad-leaved forest along river, 28.iv.1974, *Luchun team 161* (KUN); Luchung County, Fengshuiling, 13.v.1974, *Luchun team 753* (2 sheets KUN); W. Yunnan, Salwin Valley, lat. 25° 10' N long 98° 50' E, 6000 ft, *G. Forrest 19373* (B, E, K, P); Yünnan Prope vicum Schuidien inter Möngdse et Manho in regionis tropicae fundobambusetorum, 1300 m, *Handel-Mazzetti 6039* (WU); Yunnan, Mengze S.E. Mts., 5000 ft, *Henry 10737* (K, NY); Yunnan, Mengze S.W. Mts., 4000 ft, *Henry 10737A* (B holotype of *B. tetragona* Irmsch., K iso); Szemao, s.c., *12251A* (NY); Yingdong County Yunnan, Li Yue he, 1620 m, in wood and along river, 19.v.1963, *Wquanan 9257* (2 sheets KUN); Changyuan county, Long tou shan, 800-850 m, 13.vi.1974, *Li Yuanhui 011930* (KUN); Guizhou Xingren, 28.iix.1960, Chang Zhisong 8823 (KUN); Guizhou Anshun, 820 m, 12.vii.1959, *Anshun team 80* (KUN); Yunnan, You-louh Shan, Che-li Hsien, 1150 m, ravine side, ix.1936, *C.W. Wang 78142* (2 sheets KUN); Yunnan, Fo-Hai, 1300 m, ravine, water side, *C.W. Wang 74858* (KUN); Lan-Tsang Hsien, 2200 m, rock precipice, v.1936, *C.W. Wang 76844* (KUN); Pingbian, Daeeshan, 1100 m, 22.vi.1956, *Institute of Botany Kunming Work Station 3716* (KUN); Pingbian, Daeeishan, 1230 m, 1.vi.1958, *Hu Yueying & Wen shao keng 580434* (KUN); Pingbian xinli xiang, 1200 m, 18.vii.1953, *Institute of Botany Kunming Working Station 02602* (2 sheets KUN); Pingbian, Magaqi, 1600 m, 10.xii.1939, *Wang, Chang & Liu 83000* (KUN); Pingbian, Damuga, 1600 m, 14.xii.1939, *C.W. Wang 83070* (4 sheets KUN); Jingdong, Meeng-Piann, 1600 m, under forest near stream, 25.iv.1940, *M.K. Li 3391* (KUN); Jinghong, Guanping, 930 m, 19.v.1978, *Zhangjianho 18505* (KUN); Mnglian county, north of town, 18.iix.1973, *Menglian expedition group 010237* (KUN); Jingdong, 1500 m, under woods by stream, 26.iv.1940, *M.K. Li 3422* (KUN); Jingdong, Meeng-Piann, 1600 m, under forest near stream, 25.iv.1940, *M.K. Li 3391* (KUN); Menglian county, North of town, 18.iix.1973, *Menglian expedition group 010237* (KUN); Yunnan, Xishuanbanna, 1957, *Kunming Institute 57947* (KUN); Xishuangbanna, Nannuoshan, 1400 m, 2.iii.1957, *Sino-Soviet Union team 5608* (KUN); Xishuangbanna, Menghai, Mengsong, 6.iii.1957, *Sino-Soviet Union team 7040* (2 sheets KUN); Xishuangbanna, Mengyeng, Mengnai, 850 m, 30.iii.1957, *Sino-Soviet Union team 5767* (KUN); Xishuangbanna, Mengyang, 1100 m, 4.iv.1957, *Sino-Soviet Union team 5837* (3 sheets KUN); Xishuangbanna, Pueen da kaihe, 850 m, 14.iix.1977, *Tao guo da et*

al. 17938 (KUN); Xishuangbanna, Menglun, 620 m, 17.iii.1959, *Yunnan Tropical Biological Resources Field Expedition 000922* (KUN); Xishuangbanna, from Pueen to Guanping, 1000 m, 14.iix.1977, *Tao Guodo 16997* (KUN); Xishuangbanna, Xiaolaqi, 3.ix.1975, *Tao Guodo 013770* (2 sheets KUN); Xishuangbanna, Yuleshan, 21.iii.1975, *Tao Guado 013643* (KUN); Mar Li po, 26.v.1962, *Fengkuo Mei 22828* (2 sheets KUN); Mar-li -po, Sze-tai-po, Loa-chun-shan, 1300-1500 m, in mixed forest, 20.xii.1947, *K.M. Feng 13953* (2 sheets KUN, E).

Burma: Upper Burmah, Valley of the Taping, Lat. 24° 30', shady situations by streams, *G. Forrest 12155* (E); Putao District, 500-6000 ft, General in subtropical jungle but ascends behind Konglu to 6500 ft, 12.ix.1920, *R.A. 1503* (E); Bhamo, 7.iv.1912, *Lace 5759* (2 sheets K, E); Mong hau, trans Salween, 2100 ft, moist evergreen rainforest on the waters edge, limestone, 17.iii.1911, *W.A. Robertson 273* (2 sheets K); Möng Nai, ' Salween, 2100 ft, 17.iv.1911, *W.A. Robertson 791* (B); Southeastern Shan States, Keng Tung territory, valley of the Meh Len, between Muang Hpyak and Pang Sop Lao, 525-690 m, 27-28.i.1922, *J.F. Rock 2124* (B, NY); Yomzalum, 3000 ft, iii.1880, *s.c. s.n.* (HBG).

Thailand: Northeastern, Loei, Phu Luang, 8.ii.1968, *leg. Bunchuai 1607* (L); Doi Pu Ka, 1500-1600 m, *A.F.G. Kerr 4940* (BM, K); Chiengmai, *A.F.G. Kerr 1744* (B isosyn, 3 sheets E isosyn., 2 sheets K syntypes, L isosyn); Doi Chiengdao, Me Na Lao drainage, c. 550 m, 20.iii.1950, *H.B.G. Garrett 1288* (2 sheets K, 3 sheets L); Doi Chiengdao, Me Na Lao drainage, c. 550 m, 4.iv.1955, *H.B.G. Garret 1450* (A, K, L); Doi Sutep, 24.iii.1937, H.G. Deignam 1550 (A); Doi Sootep, Chiengmai, 2200-3000 ft, *A.F.G. Kerr 557* (B iso); Muang district, Chiang Mai Province, Doi sutep-Pui National Park, Shristian Hill, south of Doi Sutep temple, *Maxwell 90-290* (E topo, L topo), 89-323 (L); Kao Paga Paw, Chaing apum, c. 400 m, 4.iii.1931, *A.F.G. Kerr 20325* (BM); Northern Teen Tok 10 km N. of Doi Chieng Dao, at 600 m, 3.iix., *K. Larson, T. Santisuk & E. Warncke 3098* (E); Siam, Doi Sutape, Chengmai, N. Siam, 10/2/26, *D.J. Collins 1221* (K); Siam, Hue Sala, 500 m, 10.iii.1921, *A.F.G. Kerr 5075* (K); Siam, Doi Wao, 3000 ft, 24.ii.1912, evergreen jungle, *A.F.G. Kerr 2440A* (K), *2440* (K); sine loc., 21.iii.1909, *A.F.G. Kerr 557* (2 sheets K).

Laos: Tawieng Chieng kwang [Xiang Khoang], 1900 m, evergreen forest, 6.iv.1932, *A.F.G. Kerr 20929* (BM, 2 sheets K).

P.R.Vietnam: sine loc., *s.c., 3690* (5 sheets HN); sine loc., *s.c. 758* (HN); sine loc., *N.H. Hien 2879* (HN); Sapa, *Chinese study group 2879* (HN); 2 km to Sapa, 1550-1600 m, 11.xii.1964, *Sino-Vietnam team & C.Y. Wu 379* (KUN); Prov. Sontây, Mont Bavi, 400 et 800 m., 24.ii.1941, *Petelot 7084* (2 sheets B); Bavi

Mountain, 800-1000 m, 8.i.1965, *Sino-Vietnam team 1190* (KUN); Tam Dao, ix.1908, *D'Alleizette s.n.* (L).

var. **hirtifolia** Irmscher in Mitt. Inst. Allg. Bot. Hamburg 10: 515. 1939.
TYPE: Yunnan, Szemao, forests, 4500 ft, *Henry 12251A* (B! holotype, E! isotype, 2 sheets K! isotype).

DIAGNOSIS: Differs from var. *acetosella* in that its leaves and petioles are hairy.

CULTIVATION: In cultivation at Kunming Botanic Garden (P.R. China).

NOTES: The specimen 'Yunnan, Szemao forests, 4500 ft, *A. Henry 12251A*' (B, 2 sheets K, MO) was determined as an isosyntype of *B. crassirostris* Irmscher by Irmscher. This collection is, however, designated as the type of *B. acetosella* var *hirtifolia* Irmscher by Irmscher (1939) and is clearly a distinct taxon.

SPECIMENS EXAMINED:
P.R. China: YUNNAN: Cangyuan County Yunnan, 1100-1200 m, wet areas under bamboo forest along stream, 20.vi.1975, *Liyanhui 013380* (KUN); Ruili Denga, 9000 m, 26.iv.1961, *Zhouxun 563* (2 sheets KUN); Yuan Yang, panzhihua, 1200 m, 30.v.1974, *Lu Chun 1187* (2 sheets KUN); Fo-Hai, 1540 m, thickets, v.1936, *C.W. Wang 74269* (2 sheets KUN); Tsang-Yuan, 1250 m, ravine, rock crevice, v.1936, *C.W. Wang 73184* (2 sheets KUN); Yunnan, Szemao forests, 4500 ft, *A. Henry 12,251A* (B holo, 2 sheets K iso, KUN klepto MO iso); Xishuangbanna, Mengyang, 1100 m, 26.iii.1957, *Sino-Soviet Union expedition team 5692* (2 sheets KUN); Xishuangbanna, Menghan Jingha, 540 m, 5.v.1955, *Feng Guomei 20726* (KUN).
Burma: Myelleyiana between Nimgama and Lamkang, 700-2580 ft, 1.iv.1953, *Tha Hla & Chit Koko 3724* (K); Upper Burma, Kachin Hills, *Captain S.M. Toppin 4299* (K).

5.5.2.3. B. burkillii Dunn in Kew Bulletin. 110. 1920. **Plates 11a & b.**

TYPE: *Burkill 36121* (syntype, not located), *36315* (syntype, not located), *36910* (syntype, not located), *37121* (syntype, not located), *37139* (K! syntype, B! isosyntype), *37375* (syntype, not located), *37455* (K! syntype), *37706* (syntype, not located).

DESCRIPTION: Rhizomatous creeping herb, rooting at nodes, *rhizome* 2.5-6 mm across, *aerial stem* short, 1-6 cm long, usually simple, glabrous. *Stipules* persistent, ovate to ovate-lanceolate, 0.5-1.7 x 0.3-0.75 cm, apex setose, margin entire, surfaces glabrous. *Leaves* erect, arising from apical portion of stem; *petioles* 2.5-25 cm, glabrous or occasionally with scattered microscopic hairs with large black glandular heads and unicellular stalks; *lamina* blue-green, lanceolate-ovate to ovate, to 20 x 8.5 cm, apex shortly acuminate, base strongly asymmetric, lower lobe 1.7-6.5 cm across, sinus to 2.2 cm deep, margin entire to wavy toothed, above green, usually with either alternate radiating bands of light and dark or white blotches, below green, both surfaces usually glabrous, occasionally with microscopic glandular hairs, veins usually 7, palmate. *Inflorescences* a twice branched or contracted dichasium, often several arising from apical portion of rhizome in leaf axils, each bearing 1-8 flowers, uni-sexual, female inflorescences appearing after male; *peduncles* slender to 6.5 cm; *bracts* deciduous, membranous, linear-elliptic to elliptic, 0.6-2 x 0.1-0.4 cm, apex acute. *Pedicels* sparsely microscopic glandular hairy, in male flowers 0.8-3.5 cm. *Male flowers*: *tepals* 4, white or flushed pink, ovate, 1-2.5 x 0.7-1.6 cm, apex acute, microscopic glandular hairy, inner 2 narrowly elliptic, 1-2 x 0.5-0.65 cm, apex acute; *stamens* c. 50, *filaments* free, on a raised base, inner slightly longer, 1-2.5 mm, *anthers* elliptic-obovate, 1.5-2 mm, dehiscing via vertical slits along sides of anther, connective projecting 0.25-0.5 mm, apex rounded. *Female flowers*: *tepals* 4; *ovary*..... 4-locular, thin walled in dried state, *placentae* bifid; *styles* 2, fused at base, bifid [Dunn, 1920]. *Infructescences* c. 4-fruited; *fruiting pedicels* 4.5-7 cm; *fruit* erect, rhomboid, c. 2 x 1 cm in dried state, microscopic glandular hairy, wings arising in central part of each locule, triangular, 2-5 x 3-5 mm, crowned by basal part of caducous style.

PHENOLOGY: Flowering season February to May.

DISTRIBUTION: North eastern India & northern Burma.

HABITAT & ECOLOGY: Locally common. Growing on rocks by streams in deep shade. Found at altitudes between 213-1188 m. Apparently requiring more moisture than other local begonias (Burkill, 1925).

NOTES:

1. New to Burma.

SPECIMENS EXAMINED:

India: ASSAM: Eastern Himalaya, Outer Abor Hills [Renging camp], 1911-12, *I.H. Burkill 36720* (B, K); Abor Expedition [near the Shile & Janak streams], *I.H. Burkill 37139* (B isosyn, K syn); sine loc. [near the Shile & Janak streams], *I.H. Burkill 37455* (K syn); Assam, Dihang Valley; Pasighat, 1000-2000 ft, 10.ii.1928, *F. Kingdon Ward 7822* (B, 2 sheets K).

Burma: Kachin Hills, *S.M. Toppin 4276* (K), *4137* (K), *4371* (K); Katha District, Kadu Hill, 3500 ft, 22.ii.1910, *Lace 5105* (B, K, 2 sheets E).

5.5.2.4. B. handelii Irmscher in Akad. Wiss. Wien. Math. Natur. Wiss. K. Anz. 58: 24-25. 1921. Chun, W.Y. & F. Chun, Sunyatsenia. 4: 22. pl. 9. 1939.
TYPE: Tonkin Indochinae Gallicae Laogai ad fines prov. Yünnan, in regionis tropicae bambusetis valleculae Ngoikoden ad Phomei, ca. 150 m, 2.xi.1914, Handel-Mazzetti 12 (WU! holotype, B! isotype, E! isotype).

DESCRIPTION: *Dioecious* or rarely *monoecious*, rhizomatous creeping herb, rooting at nodes, *rhizome* short, to 30 cm long, c. 1 cm across, *aerial stem* short, 1-10 (-30) cm long, simple or shortly 2-3-branched, inter-nodes usually 1-4 cm, very sparsely microscopic glandular hairy. *Stipules* persistent, oblong-ovate to ovate-lanceolate, 0.9-2.3 x 0.3-1 cm, apex acute, long setose, margin entire, surfaces glabrous. *Leaves* few; *petioles* green, fleshy, 15-28 cm, c. 6 mm across, usually glabrous to sparsely glandular hairy, rarely densely reddish glandular hairy, stalks unicellular; *lamina* erect, fleshy to almost-leathery, ovate, 10-20 x 6-16 cm, apex shortly acuminate, base strongly asymmetric, lobes unequal, not overlapping, lower lobe 4-9 cm across, sinus 0.5-2.5 cm deep, margin usually shortly angular lobed, sometimes wavy, shortly toothed, teeth blunt or acute, above bright green, below paler green, both sides glabrous or with sparse microscopic glandular hairs, hairs mostly narrow and multicellular but scattered squat multicellular hairs also present, veins 7-8, palmate, below slightly raised, pale green or tinged purple. *Inflorescences* arising from apical region of rhizome, a condensed dichasium, unisexual, usually several per stem, 1-7-flowered, flowers fragrant; *peduncle* short 0.25-5.5 cm; *bracts* at least long persistent, variable, oblong to ovate lanceolate, 1.8-1.55 x 0.5-0.8 cm, apex acute, margin entire, glabrous or sparsely ciliate, sparsely microscopic reddish glandular hairy, margin glabrous or sparsely ciliate. *Pedicels* microscopically glandular hairy, those of male flowers 3.5-11 cm long, those of female 1.5-8 cm long. *Male flowers*: *tepals* white to pink, 4, outer 2 broadly ovate to elliptic, 1.5-5.5 x 1.6-2.2 cm, apex acute to rounded, inner 2 oblong to ovate, 0.65-3 x 0.3-1 cm, apex obtuse, receptacle slightly raised; *stamens* 35-100^{+}, *filaments* free to scarcely fused at base, almost equal, 1.4-3.5 mm long, *anthers* linear-elliptic-oblong, 1.8-3.5 x 0.7-0.8 mm, dehiscing via vertical splits along side of anther, connective projecting 0.25-0.5 mm, apex obtuse. *Female flowers*: *tepals* white to pink, 4, outer 2 ovate to elliptic, 3-27 x 2.2-19 cm, apex obtuse, inner 2 linear to oblong-ovate, 0.2-1.4 x 0.5-0.8 cm, apex obtuse; *ovary* fleshy, globose-obovate, 0.5-1.6 x 0.6-1.5 cm, almost 4-angular, usually with very short triangular wings in upper half, microscopic glandular hairy, 4-locular, *placentation* axillary, *placentas* bifid, bearing ovules on both surfaces; *styles* caducous, 4, erect, slender, 5-6 mm long, base fused for 0.5-2 mm, bifid from half

way, branches erect, stigmatic papillae once spirally twisted in a broad band. *Infructescences* 1-4-fruited; *fruiting pedicels* 2-4 cm; *fruit* fleshy, erect, green when young, becoming purple tinged and finally red, erect, obovate-top-shaped, 1-1.8 x 0.9-1.6 cm, microscopic, glandular hairy, wings triangular to rib-like, to 2.5 mm long.

var. handelii

ILLUSTRATIONS: Chun & Chun, Sunyatensia 4: 1-2. p. 22. 1939; Barabé, The Begonian 47: 10. p.268-270. 1980; Smith *et al.*, Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany, No. 60. Fig. 26.6. 1986.

DIAGNOSIS: *Male flowers*: *outer tepals* 3-5.5 cm long, apex usually acute.

PHENOLOGY: Flowering December-July. Fruiting year-round.

DISTRIBUTION: Southern China (Yunnan, Guangxi, Guangdong), northern Vietnam, northern Laos, northern Burma, northern Thailand.

HABITAT & ECOLOGY: In moist acidic conditions on rocks or ground in evergreen broad leaved forest. In half sun or full shade. Type locality in moist shady places amongst rocks in dwarf bamboo and shrub forest.

CULTIVATION: Occasionally cultivated. Requires warm, humid conditions. Easily propagated via stem cuttings (Yü, 1950).

LOCAL NAMES: Thuhaiduong Handel (Vietnam).

NOTES:

1. In the P.R. China this taxon has been confused with *B. balansana* Gagnepain. However, the two taxa may be readily separated by a large number of characters including locule number, fruit shape and leaf venation. *Begonia balansana* is not known to occur in the P.R. China and given its very restricted distribution (within the P.R. Vietnam) is unlikely to do so.

2. This taxon often has very large female outer perianth segments (to 5.5 cm long). Irmscher (1921) states that they are the largest of any known Asian species.

3. Barabé (1980) states that the vascular anatomy of the flowers shows them to have a double perianth differentiated as both calyx and corolla.

SPECIMENS EXAMINED:

P.R. Vietnam: Prov. Tonkin, Indochinae Gallicae, Laogai ad finer prov. Yünnan, in regionis tropicae bambusetis, c. 150 m, 2.xi.1914, *Handel-Mazzetti 12* (WU holo, E Iso); Tonkin nackst der Yunnan-Grenze Tropischer Dschungel im Talchen Ngoi koden bei Phomoi nächst Laokay, 180 m, leg Aufg.ii.1914, *Handel-Mazzetti s.n.* 2.iix.1914 (B iso).

Cultivated: Jardin Botanique de Montréal, Pl. de Loogee's Green., Danielson, Conn., N. Cornellier, 12.i.1960, *s.c. 1747-57* (B).

var. **prostrata** (Irmscher) Tebbitt **comb. nova.**

DIAGNOSIS: *Rhizome c.* 1 cm across. *Stipules* 0.9-2.3 x 0.3-1 cm. *Leaves*: *petioles* 15-28 cm; *lamina* 10-20 x 6-16 cm, sinus 0.5-2.5 cm deep. *Inflorescences*: those of male 1-7-flowered. *Pedicels* of male flowers 3.5-11 cm. *Male flowers*: *tepals* 4, outer 2, broadly ovate, apex rounded, 1.5-2.1 cm.

NOTES:

1. Toppin's letters (housed at E) indicate that of his collection number 4137 originated from north west Burma.
2. Irmscher annotated a few specimens of *B. handelii* var. *prostrata* (housed at B) as *B. brachyblasta* Irmscher and *B. pastica* Irmscher, these names were never published.
3. *Begonia handelii* and its synonyn *B. prostrata* were not previously recognised from Laos or Thailand.

SPECIMENS EXAMINED:

Burma: *Wehrli s.n.* (2 sheets Z); sine loc., *S.M. Toppin 4137* (E).

P.R. China: YUNNAN: *Wang 2526* (B); Szemao, *Henry 11628B* (NY); Si-chour-hsien, Shiang-ping-shan, 1600 m, in mixed forests, 3.ix.1947, *K.M. Feng 11607* (B); Marlipo, Szetaipo (Loa-chün-shan), 1300-1500 m, in mixed forest, *K.M. Feng 13894* (E). GUANGXI: Pingnan Xian, Guangxi by side of brook, 26.xii.1936, *C. Wang 40767* (MO). GUANGDONG: Xinyi Xian, Guangdong in stream side by ravine, 21.iii.1931, *C. Wang 31748* (MO).

P.R. Vietnam: sine loc., *s.c. 4482* (2 sheets HN); sine loc., *s.c. 3454* (3 sheets HN); Lan-Tsang Hsien, ravine, rock crevice, 1300 m, v.1936, *C.W. Wang 76618* (KUN); Van Son, Woodland in valley, 370-400 m, 4.i.1964, *Sino-Vietnam expedition team 954* (KUN); sine loc., *s.c. 3454* (3 sheets HN); sine loc., *s.c. 4482* (HN); Moc chau; suan nha, *H.T. Dung 197* (HN); Vinh Phu, Tam Dao, on rock under evergreen broadleaved forest, 4.ii.1962, *Sino-Vietnam expedition team 1982* (KUN); Tam Dao, *s.c. 4570* (2 sheets HN); Tam Dao, 1000-1100 m, 8.ii.1965, *Sino-Vietnam expedition team 2070* (KUN).
Laos: Tatom, Chieng kwang [Xiang Khoang], c. 200 m, 1.iv.1932, on banks in evergreen forests, *A.F.G. Kerr 21772* (K).
Thailand: Doi Pae Poe, about 90 km NV of Tak, 17° 17' N 98° 25' E, 1380 m, 14.iii.1968, succulent herb common on granitic rock in streams, *Bertel Hansen & Tem Smitinand 12905* (E, L); Between Fang and Chiengrai evergreen forest, moist slope, 900 m, ii.1928, *Th. Sorensen, Kai Larsen & Bertel Hansen 1804* (E, GB, L).

var. **leii** Tebbitt **var. nova.**
TYPE: Hainan: Pak Shik Ling and vicinity, Ku Tung Village, Ching Mai District, rare, moist gentle slope, sandy soil, forest, roadside, herb erect, fl. powder white, fragrant, 12.iii.1933, *C.I. Lei 441* (B holo, K iso, NY iso).

DIAGNOSIS: Differs in terms of its smaller parts. *Rhizomes* 3-4.5 mm across. *Stipules* 0.8-1.2 cm x 2.75-4 mm. *Leaves*: *petioles* 6-8 cm; *lamina* 7-9 x 4-5 cm, sinus 0.5-1 cm deep. *Inflorescences* c. 5-flowered. *Pedicels* of male flowers c. 3 cm. *Male flowers*: *tepals* 4, outer 2, broadly ovate, apex rounded, c. 1.2 x c. 1.1 cm.

SPECIMENS EXAMINED:
P.R. China: HAINAN: Pak Shik Ling and vicinity, Ku Tung Village, Ching Mai District, rare, moist gentle slope, sandy soil, forest, roadside, herb erect, fl. powder white, fragrant, 12.iii.1933; *C.I., Lei 441* (B holo, K iso, NY iso).

5.5.2.5. **B. mengyangensis** Tebbitt & K.Y. Guan **sp. nova. Plates 10a & b.**

TYPE: Xishuangbanna, on way from Puurem to Mengyang, bottom of valley in wet area in slope facing north dense forest, 21.iv.1957, *Sino-Soviet Union expedition 9633* (KUN! holotype, KUN! isotype).

DESCRIPTION: *Dioecious*, robust, rhizomatous herb, 20-50 cm tall. *Rhizomes* short, 1.5-4 cm across, red in cross section, roots fibrous. *Stipules*..... *Leaves* arising from rhizome; *petioles* green with white lenticels, red at base, 30-55 x to 1.5 cm [in fresh state], shortly white hairy; *lamina* leathery, arising from apical region of rhizome, broadly ovate, 14-27 x 20-27 cm, apex acuminate, base slightly asymmetric, lobes almost equal, sinus 4.5-11 cm deep, lobes overlapping in fresh state, margin shallowly and remotely toothed to entire, above shiny green, glabrous, below hairy, particularly on veins, veins 8, palmate. *Inflorescences* arising from rhizome, contracted dichasiums, occasionally with a single flower below the rest, flowers fragrant, few, c. 7; *peduncles* 10-15 cm shortly hairy; *bracts* deciduous, membranous, narrowly to broadly ovate, 0.8-2 x 0.2-1.2 cm, both surfaces glabrous, margin shortly ciliate. *Pedicels*: those of male flowers 12-35 mm. *Male flowers*: *tepals* white, flushed pink, 4, outer 2, broadly elliptic, c. 15 x 10-15 mm, outer surface hairy, inner 2 membranous, c. 10 x 12 mm; *stamens* c. 60, *filaments* free to base, c. 2 mm, attached to a raised flowers base c. 1 mm high, *anthers* elliptic, c. 2.2 mm, dehiscing via vertical slits along side of anther, connective shortly projecting, apex rounded. *Female flowers*:.....*ovary* 4-locular, *placentation* axillary, *placentae* bifid, bearing ovules on both surfaces; *styles* long persisting but eventually deciduous, 4, fused at base for 1.5-2 mm, bifid from just above base, stigmatic papillae once spirally twisted. *Fruiting pedicels* to 3 cm, green, erect; *fruit* fleshy, globose, 1-2 x (0.5)1-2 cm, 4-locular, almost wingless or with 4 blunt triangular wings (often on same plant), wings 2-3 x 3-5 mm at angles, shortly hairy.

PHENOLOGY: Flowering in April.

DISTRIBUTION: South western China (Yunnan).

HABITAT & ECOLOGY: Wet, shady areas in primary tropical forest amongst tall herbaceous vegetation.

CULTIVATION: Cultivated at Kunming Botanic Garden (P.R. China) and Glasgow Botanic Gardens.

SPECIMENS EXAMINED:

P.R. China: YUNNAN: Xishuangbanna, Cheli liusha he, along riverside wet areas in shady forest, 600-800 m, 30.iv.1957, *Sino-Soviet Union expedition 9834* (KUN); Xishuangbanna, Mengla, Mengyang, in valley under dense forest in wet areas, 1200 m, 5.iv.1957, *Sino-Soviet Union expedition 5869* (3 Sheets KUN); Xishuangbanna, on way from Puurem to Mengyang, bottom of valley in wet area in slope facing north dense forest, 21.iv.1957, *Sino-Soviet Union expedition 9633* (KUN holo, KUN iso); Mengla, Mengxin he, in valley, alt. 570 m, 19.iii.1977, *Xhangjianhou 13666* (KUN).

HYBRIDS: An unnamed artificial hybrid between *B. mengyangensis* x *B. masoniana* Irmscher is grown at the Kunming Botanic Garden.

5.5.2.6. B. roxburghii (Miq.) A. DC. in Prodr. 15(1): 398. 1864; S. Kurz, Journal of the Asiatic Society of Bengal 2: 107. 1877; C.B. Clarke, Fl. Brit. Ind. 2: 635. 1879; F. B. Forbes, J. Linn. Soc. Bot. 23: 322. 1886; F. Gagnepain in M.H. Lecomte, Flore Generale L'lind Chine 8: 1119. 1921; Grierson, A.J.C. & D.G. Long, Flora of Bhutan 2(1): p. 239. Fig. 29: n & o. 1991. **Plate 12a.**
TYPE: Chittagong alt., 0-1000 ft, *Hooker fil. et Thompson s.n.* (K! lectotype, chosen here).

SYNONYMS: *B. malabarica* sensu Roxburgh in Fl. Ind., 3; 648, 1832. excluding syn. Dryander. **TYPE:** not located.
Diploclinium roxburghii Miquel in Fl. Ind. Bat., 1.1; 692, 1855. **TYPE:** not located.
Casparya? oligocarpa A. DC. in Ann. Sci. Nat. Bot., 4, 11; 118, 1859 **TYPE:** *Hooker.fil. & Thompson s.n.* (not located).
Casparya? polycarpa A. DC. in Ann. Sci. Nat. Bot., 4, 11; 118, 1859 **TYPE:** *Hooker.fil. & Thompson s.n.* (not located).

ILLUSTRATIONS: Clarke, Journ. Linn. Soc., Bot. 18: tab.1. Fig. 1. 1880; Leatherman, The Begonian 15: 9. p. 201. 1948; Carrell, The Begonian 16: 5. p.105. no. 6. 1949; Baranov, The Begonian (July). 1979; Thompson & Thompson, Begonias the complete reference guide, Fig. 20, Times books. 1981; Barabé & Chrétien, Bull. Soc. Bot. Fr. 130. Lettres Bot. 307-316. 1983; Smith *et al.* Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany. No. 60. Fig. 34.14. 1986; Grierson & Long, Flora of Bhutan 2: 1. Fig. 29. 1991.

DESCRIPTION: *Dioecious*, shortly rhizomatous, tall erect herb, stems branched, inter-node length variable, red-spotted, thick, often ribbed in dried state, microscopic glandular hairy, becoming sparse with age. *Stipules* caducous, lanceolate, 7-12 x 2-3.5 mm, apex setose, margin entire, densely microscopic glandular hairy. *Leaves* alternate; *petioles* 7-29 cm, hairs as in leaf lamina; *lamina* leathery or almost so, broadly ovate, 16-25 x 10-23 cm, apex acuminate, base strongly asymmetric, lower lobe 6.5-13 cm across, sinus 1.2-4.5 cm deep, margin remotely toothed, both surfaces green, sparsely to densely microscopic glandular hairy, veins 7-8, palmate. *Inflorescences* short axillary contracted dichasiums, usually not exceeding 2 cm and usually hidden by leaves, rarely to 10 cm and clearly dichasial; *peduncles* almost absent to 6 mm, microscopic glandular hairy, few-flowered, flowers fragrant; *bracts* caducous, lanceolate, c. 5 x 2.5 mm,

microscopic glandular hairy, stalks unicellular. *Pedicels* microscopic glandular hairy, c.1 cm, or those of female flowers occasionally to 2 cm. *Male flowers*: *tepals* white, sometimes pink tinged, 4, outer 2 ovate, deeply concave, 1-1.7 x 1-1.1 cm, apex obtuse, outer surface sparsely to densely microscopic glandular hairy, inner 2 obovate, 1.1-1.2 x 0.7-0.8 cm, apex obtuse; *stamens* 25-50, *filaments* free to base, inner longer, c. 4 mm, linear, *anthers* obovate-oblong, c. 1.5 mm, dehiscing via a slit down the sides of the anther, connective projecting 0.2 mm, apex rounded. *Female flowers*: *tepals* white, sometimes pink tinged, 4, larger than male, outer 2 obovate to oblong, 6-1.8 x 0.6-1.8 mm, apex obtuse, pubescent as in male, inner 2 oblong, 0.7-1.4 x 0.45-0.8 mm, apex obtuse; *ovary* fleshy, top-shaped to elliptic, 0.3-1 x 0.6-0.8 cm, densely microscopic glandular hairy, 4-angular, 4-locular, *placentation* axillary, *placentas* bifid, bearing ovules on both surfaces, angles of locules corniculate; *styles* caducous, 4, fused at base for 0.5 mm, bifid from half way, branches erect, c. 0.5 mm, stigmatic papillae spirally twisted. *Infructescences* 1-3-fruited; *fruiting pedicels* to 2 cm long; *fruit* fleshy, thick-walled even in sicco, top-shaped to elliptic, 0.9-1.5 x 0.75-1.5 cm, sparsely microscopic glandular hairy, angles of locules corniculate. 2n = 22 (Legro & Doorenbos, 1972).

PHENOLOGY: Flowering season June to September. Fruiting season year-round.

DISTRIBUTION: North eastern India, Bhutan, Bangladesh, Burma.

HABITAT & ECOLOGY: Usually at altitudes of 300-775 m but found at sea level in Chittagong [Bangladesh].

CULTIVATION: Occasionally cultivated.

NOTES:

1. Hara & Williams (1975) record the species from Nepal and cites the specimen '*Williams 349*' as a example. Examination of this material (at BM), however, found it not to be *B. roxburghii* (Miq.) A.DC. It is, therefore, unlikely that the species occurs in Nepal.

2. Forbes & Hemsley (1886) list *B. roxburghii* from China; Kwangtung; Lofaushan (Ford!). Herb. Kew. Examination of this material has shown it to be *B. longifolia* Blume. *Begonia roxburghii* is not, therefore, validly recorded from China.

3. As no types have been designated in the literature and no designated type specimens were located in the herbaria in which Miquel and A. De Candolle deposited their material (G, G-DC, K, L, P, U), the specimen "Hab. Khasia, Regio

trop. alt. 2-4000 ft, J.D. Hooker & T. Thomson, s.n. (K)" has been designated here as a lectotype of *Begonia roxburghii* (Miq.) A.DC.

This specimen was chosen as it has been determined by both A. De Candolle and C.B. Clarke.

SPECIMENS EXAMINED:

India: SIKKIM: sine loc., *J.D. Hooker s.n.*, (3 sheets K); sine loc., *Thomson s.n.* (M); sine loc., T. *Thomson s.n.* (B); Sikkim Reg trop., 2-4000 ft, *J.D. Hooker & T. Thomson s.n.* (B drawing); Singtam, 15.v.1867, *N.C. Majumder & R.M. Dutta 286* (CAL); sine loc., 1857, *T. Thomson s.n.* (B, B drawing); Mongpo 5.x.1884, leg. *C.B. Clarke 36195b* (G); Mongpo, 1000 ft, Sikkim, 5.x.1884, *C.B. Clarke 36195c* (BM); Mongpo, 1000 ft, Sikkim, 5.x.1884, leg. *C.B. Clarke 36195d* (B); sine loc., Gamble 3885A (K); Mongpo, 2000 ft, Darjeeling, 24.ix.1875, *C.B. Clarke 24798a* (BM); Darjeeling, *Clarke 9093* (K); Mendong, 5000 ft, Sikkim, 21.x.1869, *Clarke 9478a* (E); Runject, 500 ft, Darjeeling, 20.ix.1869, *C.B. Clarke 9299* (BM). ASSAM: sine loc., *Jenkins s.n.* (B, M); sine loc., *Griffith s.n.* (3 sheets K); sine loc., *Jenkins 178* (B); sine loc., *s.c. 575* (K); *s.c. 575* (2 sheets K); Khorungoma, 3500 ft, 2.vi.1951, *Thakur Rup Chand 4672* (L); Lushai Hills; *Parry 186* (K); sine loc., *s.c. 264* (2 sheets K); sine loc., *Hamilton 2052* (E); N. Cachar Hills ' of Circuit House, Haflong, 2500 ft, 1.iix.1908, *W.G. Craib 116* (CAL); Cachar, North of Circuit House, Haflong, *G. Craib s.n.* (K); Cachar, Shapore, *s.c. s.n.* (K); Assam, Garo Hills, Tura Mountain ', 4000 ft, 6.xi.1929, *Mrs N.E. Parry 866* (K); Mabru Manipur 3-4000 ft, xi.1907, leg. *A. Meebold 5861* (B). NAGALAND: Henima, Naga Hills, 5000 ft, 9.ix.1935, *N.L. Bor 6417* (K). KHASIA: sine loc., *J.D. Hooker & Thomson 1605* (2 sheets K); sine loc., *s.c. s.n.* herb. Hook. (4 sheets B, 3 sheets K); sine loc., *Clarke 5462* (K); Khasia, *J.D. Hooker & Thomson s.n.* (M); Khasia, regio trop., alt., 2-4000 ft, *J.D. Hooker & T. Thomson s.n.* (B, K); Khasia, 2-4000 ft, *J.D. Hooker & T. Thomson s.n.* (B drawing); Khasia, below Nunklow, *s.c. s.n.* (K); Khasia, Chuwe; *J.D. Hooker & Thomson 877* (K); Khasai, Jaiwtia Hills, 4000 ft, April, *T. Yandall s.n.* (K).

Bangladesh: Chittagong; *J.D. Hooker & Thomson 296* (K); Chittagong, regio trop 0-1000 ft, *J.D. Hooker & T. Thomson s.n.* (K); East Bengal, *Griffith, Herbarium of the late East India Company distribution number 2561* (B, KUN).

Burma: sine loc., *Griffith s.n.* (K); Burma, Mawlaik Distr. 500 ft, 12.i.1926, *Po Chin 198* (B).

Cultivated: Kultivert im Botanischen Garten Berlin-Dahlem 14.ix.1981., Acc. no. 104-41-79-80, leg. *Schwerdtfeger 10666* (2 sheets B), *10666a* (B).

HYBRIDS: A hybrid has been reported from cultivation between *B. roxburghii* x *B. inflata* (=*B. longifolia*) (Legro & Doorenbos, 1974). The following specimen is intermediate between these two taxa and thought to represent this hybrid; Jardin Botanique de Montréal from N. Mason, Norfolk , Engl., 2331-54 (2 sheets B).

5.5.2.7. B. silletensis (A.DC.) C.B. Clarke in J.D. Hooker Fl. Brit. Ind. 2: 636. 1879. as 'silhetensis'. **Plate 9b**.
TYPE: Sillet Mts. ', *Wallich 9107* (G syntype, 2 sheets K-WALL! syntype, BM! isosyntype).

SYNONYMS: *Casparya? silletensis* A.DC. in Prod. 15(1): *277*. 1864.
TYPE: *Wallich 9107* (G holotype, K-WALL! isotype, BM! isotype).

ILLUSTRATIONS: Clarke in J. Linn. Soc. Bot. 18: 115. 1881; Smith *et al.*, Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany, No. 60. Fig. 23.14. 1986.

DESCRIPTION: *Dioecious* (?) rhizomatous perennial herb, *rhizome* short, c. 1 cm across, roots fibrous, aerial stem absent. *Stipules* persistent, lanceolate, 1.4-2.1 x c. 0.4 cm, apex acute, margin entire, surfaces glabrous. *Leaves* few, drooping; *petioles* 22-43 cm; *lamina* ovate, 10-17 x 10-15 cm, apex shortly acuminate, base strongly asymmetric, lower lobe 5-8 cm across, sinus 3-4.5 cm deep, margin wavy, shortly regular toothed, both surfaces green, glabrous, veins 7-9, palmate. *Inflorescences* arising from apical region of rhizome, contracted or once branched dichasiums, usually 1-10-flowered, flowers fragrant; *peduncles* 8-11 cm; *bracts* caducous, ovate to elliptic, c. 1.1 x 0.2 cm, margin entire, surfaces glabrous. *Pedicels*: those of male flowers 1-2 cm, those of female flowers 4-5 cm. *Male flowers*: *tepals* white, greenish white or pink, 4, outer 2 ovate, oblong or obovate, concave, thick, 4.5-15 x c. 10 mm, apex blunt, thick, inner 2 ovate-obovate, 3.4-17.5 x 7.5-8 mm, apex rounded; *stamens* 100^{+}, *filaments* free, attached to raised base, inner slightly longer, 1.75-2.5 mm, *anthers* linear, 1.75-2.75 mm, dehiscing via vertical wavy slits down sides of the anther, projecting 0.5 mm, apex obtuse. *Female flowers*: *tepals* 4, white or pink, oblong to obovate, apex rounded, outer slightly longer; *ovary* globose, c. 1 x 1 cm, circular in cross-section, 4-locular, *placentation* axillary, *placentae* bifid, bearing ovules on both surfaces, rhomboidal in cross section, c. 4 x 4 mm, ovules attached on both surfaces; *styles* caducous, 4, very broad, base 0.5 cm across, 0.8-1.2 cm long, fused just below half way,bifid, stigmatic papillae twice spirally twisted. *Infructescences* 1-2-fruited; *fruiting pedicels* c. 3.5 cm; *fruit* globose, 2.3 x 1.5 cm, walls thick c. 2.5 mm, usually cork-like in texture, rarely leathery, apical part crowned by basal part of deciduous styles.

DISTRIBUTION: North eastern India.

NOTES:

1. Material determined as the type of *Begonia spherocarpa* C.B. Clarke *nomen nudum* at herb. K. is this species. Wallich proposed the unpublished name Begonia gigantea for this species based on the collection '*Wallich 3677B*' (not located).

2. New to Burma and Thailand.

SPECIMENS EXAMINED:

India: ASSAM: Sylhit District, vii.1823, *Wallich 9107* (BM, 2 sheets K-Wall.); Chanduar Forest, *Mann 7/87* (K); Luckimpore, Makum 300 ft, 12.iv.1885, *Clarke 37805* [determined as B. sphaerocarpa sp. nov. by C.B. Clarke] (K); Namchung, 155 ft, Luchimpore, 18.iv.1885, *Clarke 37937A* [determined as *B. sphaerocarpa* sp. nov. by C.B. Clarke] (K); Cachar, moist shade of Shapose Bomara, Nov. 1873, *Keenan sn.* (K); Katakhal Forest, *Mann sn.* (K).

Burma: Nammeen to Namma, Myitkina District, 1000 ft, 7.iii.1910, *Lace 5170* (E).

Thailand: Northern Chiengmai, Trang, ca. 800 m, 11.vi.1960, herb scattered in evergreen forest, by stream, fruits purplish red, angular, *T. Smitinand & H. ST. John 6832* (K).

5.5.2.8. B. tessaricarpa C. B. Clarke in J.D. Hooker, Fl. Brit. Ind. 2: 636. 1879.

TYPE: East Bengal, Assam, *Griffith Herbarium of the late East India Company Distribution no. 2586* (K! holotype).

ILLUSTRATIONS: Clarke, Journ. Linn. Soc., Botany 18: tab.1. Fig.2. 1880; Smith *et al.*, Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany. No. 60. Fig. 8.45. 1986.

DESCRIPTION: *Dioecious*? shortly rhizomatous creeping herb, rooting at nodes, *rhizome* short, c. 0.5 cm across in dried state, *aerial stem* 0.5 cm long, slender, simple, sparsely microscopic glandular hairy. *Stipules* persistent, lanceolate c. 2.6 x 2 mm, apex acute, margin entire, sparsely glandular, microscopic hairy. *Leaves* few: *petioles* to 30 cm, slender, densely microscopic glandular hairy, especially near leaves; *lamina* ovate, clearly oblique, 8-8.5 x 5.5-6.5 cm, apex acute, base strongly oblique, lobes unequal, lower lobe c. 4 cm, sinus c. 0.75 cm deep, margin shortly toothed, above green, below paler green, above very sparsely microscopic hairy, below sparsely microscopic glandular hairy. *Inflorescences* short axillary once or twice branched dichasiums, few-flowered; *peduncles* 0.5-1 cm, densely glandular hairy, hairs short; *bracts* caducous, lanceolate, c. 9 x 2.5 mm, apex acute, margin entire, surfaces glabrous. *Pedicels* densely microscopic glandular hairy, those of male flowers 0.5-1.7 cm, those of female flowers c. 1.6 cm. *Male flowers*: *tepals* 4, outer 2 elliptic, c. 6.5 x 3 mm, apex obtuse, inner 2 narrowly obovate elliptic, c. 5.5 x 2.4 mm, apex obtuse; *stamens* 20-25, *filaments* free to base, attached to slightly raised flowers base, almost equal, c. 1.4 mm, *anthers* elliptic, c. 2 mm, dehiscing via vertical slits along each side of anther, connective projecting c. 0.2 mm, apex obtuse. *Female flowers*: *tepals* 4, broadly elliptic, c. 7 x 5 mm, apex obtuse, very sparsely microscopic glandular hairy; *ovary* top-shaped, c. 6 x 5.5 mm, corniculate on angles, horns c. 0.5 mm, 4-angular, densely short hairy, 4-locular, *placentation*..... *styles* caducous, 4, slender, c. 3 mm long, shortly fused at base, bifid from just below half way, branches erect, stigmatic papillae 3 times spirally twisted. *Infructescences* 3-fruited; *fruiting pedicels* 4 cm long; *fruit* leathery, walls thin in sicco, erect, top-shaped, narrowing to base, c. 1 x 1 cm, angles of locules corniculate, surface with scattered short hairs.

DISTRIBUTION: North eastern India.

NOTES:

1. Known only from holotype.

2.Clarke (1879) is his description says that he suspects the specimen may be no more than a stunted form of *B. roxburghii* (Miq.) A.DC. On account of the differences in fruit morphology, peduncle length, size of male tepals and general habit between the taxa the two are retained as separate species.

SPECIMENS EXAMINED:

India: ASSAM: East Bengal, Assam, *Griffith Herbarium of the late East India Company Distribution no. 2586* (K holo).

5.6. TAXA MOVED TO SECTION *PLATYCENTRUM* (KLOTZSCH) A.DC.

5.6.1. CIRCUMSCRIPTION OF SECTION *PLATYCENTRUM* (KLOTZSCH) A.DC. (from Baranov & Barkley, 1974).

A. de Candolle in Ann. Sci. Nat., Bot. 4. 11. 134 (1859).
'*Staminate flowers*; *tepals* four, filaments below united more or less into a high thick column, anthers oblong, longer than the filaments, connective often extended. *Pistillate flowers*; *tepals* four to six (as an exception eight), *styles* 2 [rarely 5-7], not persistent, united below, twice-divided, branches twisted, stigmatic surfaces continuous, helical, band-shaped, *placentae* two- or seldom many-times divided. *Fruit* 2-celled [rarely 3 or 5-7-celled], drooping, with three unequal wings, one of them in most cases considerably lengthened. Stemless herbs, mostly with thick, creeping rhizome, seldom with erect, slender stem, leaves palmately (seldom palmate-pinnately) veined.'
Type species: *Begonia xanthina* W.J. Hooker.

The name *Platycentrum* is derived from the Greek words *Platy* meaning broad and *centrum* meaning centre and refers to the broad central wing possessed by most species from this section.

5.6.2. CIRCUMSCRIPTION OF SECTION *PLATYCENTRUM* (KLOTZSCH) A.DC. SUBSECTION *PLATYCENTRUM*

DIAGNOSIS: *Fruit* 2-locular; *styles* 2. *Seed*: testa ornamentation of short linear foldings.

5.6.2.1. THE SPECIES MOVED TO SUBSECTION *PLATYCENTRUM*

5.6.2.1.1. B. erosa Blume was originally included in the genus *Sphenanthera* by Hasskarl (1855) but was subsequently moved to section *Platycentrum* by Backer & Bakhuizen (1963). As this taxon undisputedly belongs within section *Platycentrum* on account of its two styles and two-locular fruit which possess one long and two short wings it is not described here and was not included in the cladistic analysis.

5.6.2.1.2. B. dux C.B. Clarke in J.D. Hooker, Fl. Brit. Ind. 2: 637. 1879. **Plate 12b.**
TYPE: Moulmein, Moolee alt. 6000 ft, *Parish s.n.* (K! holotype).

ILLUSTRATIONS: Smith *et al.* Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany, No. 60. Fig. 27.33. 1986.

DESCRIPTION: *Monoecious* erec herb to 60 cm high, *stem* succulent, 0.5 cm across (in sicco), inter-nodes long, stem, bracts and upper leaf surface sparsely minute glandular hairy, leaf under surface glabrous. *Stipules* persistent [C.B. Clarke, 1879], ovate-lanceolate, c. 16 x 12 (at base) mm, very sparse microscopic glandular hairy. *Leaves* drooping; *petioles* erect, 2.5-10.5 cm, glabrous; *lamina* ovate-acuminate, asymmetrical, 8.5-18 x 3.5-11 cm, base strongly asymmetric, lobes unequal, lower lobe 3-5 cm, sinus 1-4 cm deep, margin somewhat angular, irregularly toothed or serrate, ciliate, veins 6, palmate, deep shiny green on both sides, above very sparsely microscopic glandular hairy, below glabrous, veins 6, palmate. *Inflorescences* in upper leaf axils, once or twice branched dichasiums, 4-8-flowered, male flowers developing before or synchronous with females; *peduncle* 0.5-13 cm; *bracts* deciduous, to 1 cm, ovate lanceolate, margin entire, surfaces almost glabrous. *Pedicels* glabrous, those of male 1.5-4.5 cm, those of female flowers c. 1.5 cm. *Male flowers*: *tepals* 4, pale white with a pink margin, glabrous to sparsely hairy, outer 2 elliptic to broadly elliptic, 1-2.5 x 1.7-2.4 cm, apex obtuse, inner 2 elliptic, 0.8-1.9 x 0.3-1.4 cm, apex obtuse; *stamens* c. 100, arranged in a dense cone, attached at all heights to a torus, torus 0.5-2 mm high, broad based, *filaments* free, slightly longer in centre, *anthers*, elliptic to angular-obovate,1-1.6 mm long, dehiscing via vertical obovate slits along sides of anther, connective projecting c. 0.2 mm, apex rounded. *Female flowers*: *tepals* 5, pale white with a rose margin, almost equal, elliptic to obovate, c. 1.5 x 0.75 cm, apex obtuse, glabrous; *ovary* elliptic, c. 1 x 0.55 cm, 3-winged, one wing much longer, longest triangular-ovate, apex blunt, c. 1 x 0.5-0.8 cm (width at half-way position), base of wing 0.7 cm across, smaller wings broadly elliptic, apex blunt, c. 0.3 x 0.7 cm, 2-locular, *placentation* axillary, *placentae* bifid; *styles* deciduous, 2, squat, c. 0.4 cm long, bifid from slightly below half way, branches wide spreading, stigmatic papillae once spirally twisted. *Infructescences*.....

DISTRIBUTION: Southern Burma and north eastern India.

HABITAT & ECOLOGY: Forest between 1370-1828 m.

NOTES:

1. New to India.

SPECIMENS EXAMINED:

Burma: Moulmein, Moolee alt. 6000 ft, *Parish s.n.* (K holo); Burma, Mooley ', 4500 ft, *R. H. Beddome 3196* (BM); Burma, Mooley it ', 6000 ft, *R. H. Beddome 3197* (BM); Mooley it ', 4500 ft, *R.H. Beddome s.n.* (HBG drawing); sine loc., *R. H. Beddome s.n.* (K).

India: ASSAM: ', *R. H. Beddome 3194* (BM).

5.6.2.1.3. B. teysmannianum (Miquel) Tebbitt **comb. nova.**

TYPE: mont. Talang by Solok, *H. Bünnemeyer 1104* (BO holotype).

SYNONYMS: *Platycentrum teysmannianum* Miquel in Fl. Ned. Ind. 1.1: p. 1092, 1855. **TYPE:** mont. Talang by Solok, *H. Bünnemeyer 1104* (BO holotype).
Casparya teysmanniana Miquel ex A.DC. Prodr. 15(1): 276. 1864. **TYPE:** mont. Talang by Solok, *H. Bünnemeyer 1104* (BO holotype).
Begonia teysmanniana Miq. nomen nudum (herb BO in sched.). **TYPE:** mont. Talang by Solok, *H. Bünnemeyer 1104* (BO holotype).

DESCRIPTION: *Monoecious*, robust, erect herb, stems fleshy, branched. *Stipules* deciduous, thin, dry membranous, ovate-oblong, apex mucronate. *Leaves*: *petioles* 4-13 cm, sparsely to densely minute hairy, hairs as in leaf-lamina; *lamina* ovate, 10-25 x 10-24 cm, apex acuminate, base strongly asymmetric, lobes unequal, lower lobe 13.5-24.3 cm long, margin usually shortly angular irregular lobed, sharply bidentate, ciliate, both surfaces sparsely to densely glandular setose, especially on veins below, 0.2-1 mm long. *Inflorescences* in upper most leaf axils, few-flowered, twice branched dichasiums, male and female flowers occurring on same inflorescence; *peduncles* 7.5-21.5 cm; *bracts* caducous, ovate, c. 1.8 mm long, apex acuminate, margin ciliate, concave. *Pedicels* c. 3 cm. *Male flowers*: *tepals* 4, outer 2 hairy, broadly elliptic, c. 2.3 x 2 cm, apex obtuse, inner 2 obovate, c. 2 x 1 cm, apex obtuse; *stamens* c. 70, *filaments* c. 3 mm long, attached to a torus at all lengths, *anthers* obovate, c. 2 mm long, dehiscing via longitudinal slits along sides of anther, connective projecting c. 0.4 mm long, aex rounded. *Female flowers*: *tepals* 6 [Irmscher in herb. B], obovate, outer 12-30 x 0.9-1.8 cm, apex obtuse, inner 10-22 x 1.1-5.5 cm, apex obtuse; *ovary* obovate, unequally 3-winged, 2-locular, *placentation* axillary, *placentas* bifid, bearing ovules on both sides; *styles* deciduous, 2, shortly fused at base, bifid from about half-way, branches erect, stigmatic papillae once spirally twisted. *Fruit* leathery, obovate, c. 3 x 1.4 cm, dehiscing along a transverse line next to largest wing, wings 3, 2 small 7-8 mm, third much larger, elliptic, sides parallel, apex rounded.

PHENOLOGY: Specimens examined flowering April and October and fruiting in March.

DISTRIBUTION: Sumatra.

HABITAT & ECOLOGY: Montane forest.

NOTES:

1. All the specimens observed were fragmentary and consist of parts taken off specimens from Bogor (BO) herbarium.

SPECIMENS EXAMINED:

INDONESIA: SUMATRA: Riang, Mont Talang by Solok, leg. *Teysmann 1104.4B* (drawing of holotype B); W. Sumatra, N.W. Helling, Talaman, 1900 m, *H.A.B. Bünnemeyer 887A* (B drawing); Sumatra WK, Saras Talang ', *Bünnemeyer 5091* (B); W. Sumatra Z Helling, Koerintji Peak, 4.iii.1920, *H.A.B. Bünnemeyer 8419* (B); W. Sumatra, S. Koerintji, 1750 m, 17.iv.1920, *H.A.B. Bünnemeyer 9540* (2 sheets B); W. Sumatra, S. Koerintji, 1860 m, 21.iv.1920, *H.A.B. Bünnemeyer 9648* (B); W. Sumatra, Sg. Koerintji, 2000 m, *H.A.B. Bünnemeyer 9266* (B); W. Sumatra, S. Koerintgi, 2100 m, 1.v.20, *H.A.B. Bünnemeyer 9884* (B); W. Sumatra, *H.A.B. Bünnemeyer 5391* (B); W. Sumatra, *H.A.B. Bünnemeyer 8419* (B); sine loc., *H.A.B. Bünnemeyer 8064* (B); sine loc., *H.A.B. Bünnemeyer 8219* (B); sine loc., *H.A.B. Bünnemeyer 8461* (B); sine loc., *H.A.B. Bünnemeyer 9207* (B).

5.6.3. CIRCUMSCRIPTION OF SECTION *PLATYCENTRUM* SUBSECTION *CORONATAE* TEBBITT SUBSECTION NOVA

DIAGNOSIS: *Fruit* 5-7-locular; *styles* (5)-6-(7). *Seed*: testa ornamentation of pronounced short linear foldings.
Type species: *Begonia balansana* Gagnepain.

The name *coronatae* is in reference to the type species' characteristic crown shaped fruits.

5.6.3.1. THE SPECIES OF SUBSECTION *CORNATAE* TEBBITT

5.6.3.1.1. B. balansana Gagnepain in Bull. Mus. Hist. Nat. (Paris). 25: 194. 1919. **Plates 13a & b, 14a & b.**
TYPE: Forests du Mont Bavi sur le bow der torrents, janvier 1887, *B. Balansa 3758* (P! syntype, K! isosyntype); sine loc. 1885-1889, *B. Balansa 3758* (P! isosyntype); Vallée de Lankok (mont-Bavi), sur le bow des torrents, octobre, 1887, *B. Balansa 3764* (P! syntype, K! isosyntype).

ILLUSTRATIONS: Smith *et al.*, Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany, No. 60. Fig. 23.13. 1986.

DESCRIPTION: *Monoecious* rhizomatous herb, rhizome creeping, rooting at nodes, *rhizomes* 4-5 x c. 5 mm across, *aerial stem* 1-1.5 cm long, with short, soft, pink hairs. *Stipules* persistent, ovate-acute, 8-17 x 6-11 mm, apex acute, margin ciliate, especially near apex, above red-villose. *Leaves* arising from apical portion of rhizome; *petioles* 9-35 cm long, c. 5 mm thick, fleshy, with short, soft pink hairs; *lamina* ovate-obtuse, 12-16 x 8-15 cm, apex acute or somewhat rounded, base strongly asymmetric, lobes uneven, not overlapping, lower lobe 2-6.5 cm across, sinus c. 2 cm deep, margin often undulate, ciliate, above shiny green with darker veins, below paler green, both surfaces glabrous or veins and veinlets beneath sparsely to densely short pink hairy, veins 6-8, palmate, branched, apices with 2-5 secondary veinlets usually strongly conspicuous. *Inflorescences* once or twice branched dichasiums, male flowers maturing before female, 2-8-flowered; *peduncles* 8-12 cm; *bracts* deciduous, resembling stipules, glabrous, 10-15 mm. *Pedicels* pinkish downy hairy, in male flowers to 20 mm. *Male flowers*: *tepals* 4, pink or very rarely white, outer 2 ovate to orbicular, 13-17 x 8-16 mm, apex

obtuse, microscopic glandular hairy, inner 2 elliptic, 6-10 x 4-6.5 mm, apex obtuse; *stamens* c. 65, stamen mass globose, anthers asymmetric hatchet shaped, *filaments* free, almost equal, c. 2.5 mm, attached to a torus at all heights, torus 1-1.5 mm tall, thick, *anthers* asymmetrically elliptic, c.1 mm long, lacking connective apically so that locules adpressed at apex, dehiscing via a transverse slits along sides of anther. *Female flowers*: *tepals* 4, pink, very rarely white, inner gradually getting smaller, ovate to obovate, 11 x 8 mm to 9 x 5 mm; *ovary* coronate, c.1 x 1 mm, wall c. 1 mm thick [in fresh state], wingless, apex swollen into a column, locules (5-)6(-7), *placentation* axillary, *placentae* bifid, bearing ovules on both surfaces; *styles* caducous, (5-)6(-7), fused at base for c. 1 mm, stigmas bifid, branches erect, strongly contorted, stigmatic papillae once spirally twisted on branches, confined to top of styles between branches. *Infructescences* 2- or 4-fruited; *fruiting pedicels* green, curved downwards, c. 1.5 cm long; *fruit* fleshy, coronate, c. 4 x 6.5-10 mm, apex swollen into a column.

PHENOLOGY: Flowering and fruiting year-round.

DISTRIBUTION: Northern Vietnam, where endemic to Mount Bavi.

RECOGNITION: The combination of 5-7-locular, unwinged fruits and usually conspicuous veins and veinlets on the leaf under surface are diagnostic of this very distinct species.

HABITAT & ECOLOGY: Montane forest above 550 m. In moist or somewhat dry conditions on rocks or soil usually in half-sun.

CULTIVATION: Previously cultivated at Glasgow Botanic garden.

LOCAL NAMES: Thuhaiduong Balansa (Vietnam).

NOTES:

1. Gagnepain`s original spelling of the name was ``balansaeana``. Smith *et al.* (1986) use the modern spelling without an a before the e. This practice is followed here.

2. A drawing of a transverse section of the ovary of 'Balansa 3758 (P)' shows the specimen to possess entire placentae. Numerous sections of fruit in the field, however, indicate that the species consistently has bifid placentae. Therefore, it appears that Balansa's collection was either an aberrant collection or the artist made

a mistake. The Balansa specimen was not re-checked due to the paucity of this type material.

3. This species has been confused with *B. handelii* Irmscher in the P.R. China but the two taxa may be very readily separated (see notes under *B. handelii*).

4. The species is vulnerable to extinction as the single montane forest in which it grows is under threat from deforestation notwithstanding its status as a National Nature Reserve. A further threat exists in the form of collection by tourists who up-root a great number of plants due to their decorative appearance.

SPECIMENS EXAMINED:

P.R. Vietnam: Forests du Mont Bavi sur le bow der torrents, i.1887, *B. Balansa 3758* (P syn, K isosyn); sine loc. 1885-1889, *B. Balansa 3758* (P isosyn); Vallée de Lankok (mont-Bavi), sur le bow des torrents, x.1887, *B. Balansa 3764* (P syntype, K isosyn); Mont Bavi- forets bows de torrents, juillet 1908, , *s.n.* (L).

5.6.4. CIRCUMSCRIPTION OF SUBSECTION *SPHENANTHERA* (HASSK.) TEBBITT

Robust erect or prostrate rhizomatous herbs. Stem and leaves glabrous or densely long glandular hairy. *Stipules* persistent. *Leaves*: *lamina* ovate to almost orbicular, margin almost entire to somewhat irregularly 5-8-lobed, base asymmetric. *Inflorescences* axillary, homogamous dichasiums, *bracts* caducous, usually conspicuous. *Male flowers*: *tepals* 4; *stamens* 65-75, *filaments* free, attached to a torus, *anthers* elliptic to wedge-shaped, dehiscing via vertical slits at sides of anthers, connective projecting. *Female flowers*: *tepals* 5; *ovary* 3-locular, globose, locules usually inflated to form wings, *placentation* axillary, *placentas* bifid, bearing ovules on both surfaces; *styles* 2, bifid, stigmatic papillae arranged in a once spirally twisted band. *Fruit* fleshy, often brightly coloured, indehiscent. *Seed*: ellipsoid, operculum nipple-shaped, testa cells occupying less than half the length of the seed, cuticular ornamentation of short linear foldings.
Type species: *Begonia robusta* Blume.

The name *Sphenanthera* was said by Klotzsch to be derived from the Greek words σφην (wedge) and ανθηρα (anther) on account of the species' reputedly diagnostic wedge-shaped anthers.

5.6.4.1. DESCRIPTION OF SELECTED SPECIES OF SUBSECTION *SPHENANTHERA* (HASSK.) TEBBITT

Three new species from Sabah, Sumatra and Sulawesi are awaiting description by Tebbitt and Sands. The Sumatran species is illustrated in **Plate 7a.**

5.6.4.1.1. B. robusta Blume in Enum. Pl. Javae. 1: 96. 1827; Hasskarl, Pl. Java Rar. 242. 1848; Mueller, Ann. Bot. Syst. 4: 929. 1857; Koorders, Exkur. Fl. Java. 2: 646. 1912; Backer & Van Den Brink, Flora of Java. 1: 313. 1963.
TYPE: Jawa, *Lobb s.n.* (K!).

SYNONYMS: *Platycentrum robustum* Miquel in Fl. Ned. Ind. 1.1: 694. 1856. **TYPE:** Jawa, *Lobb s.n.* (K!).
Sphenanthera robusta (Blume) Hasskarl in Versl. Kon. Akad. Wetensch. 4. 1855: 135-141; Klotzsch in Bot. Zeitung. 15: 181. 1857. **TYPE:** Jawa, *Lobb s.n.* (K!).
S. robusta var. *viridis* Hasskarl in Hort. Bogor. Descr. 346. 1858. **TYPE:** not located.
Begonia splendida hort. Rollisson ex Henderson in Illus. Bouquet. 1. sub. pl. 11. 1864. **TYPE:** not located.
Casparya robusta A.DC. in Prodr. 15(1): 275. 1864. **TYPE:** Jawa, *Lobb s.n.* (K!).

DESCRIPTION: Robust herb to 2 m tall, shortly rhizomatous, *rhizome* c. 1 cm across. *Stem* branched, glabrous or with a covering of long glandular hairs, hairs often dense, red, internodes 4.5-10.5 cm, branches 0.5-1.7 cm across. *Stipules* persistent, lanceolate, ovate-lanceolate or ovate, rarely triangular-lanceolate, 1-3.7 x 0.9-2.4 cm, apex acute, long setose to 7.5 mm, outer surface glabrous or with long hairs throughout, hairs often dense along mid-rib, inner surface glabrous. *Leaves* alternate; *petioles* 10-40 cm, glabrous, with sparse short hairs or with dense long glandular hairs throughout, these often red; *lamina* medium green above, greyish green below, in outline ovate to almost orbicular, 10-25 x 10-35 cm, usually somewhat irregularly 5-8-lobed, sometimes almost entire, especially in juvenile plants, lobes narrowly to broadly triangular, to 7 cm deep, apices acute to obtuse, base asymmetric, lower lobe 7-14 cm across, sinus 2-9 cm deep, narrow to wide in dried state, margin entire, ciliate, both surfaces glabrous, with sparse short hairs or with long glandular hairs, these often dense, especially on veins, long hairs when present usually interspersed with microscopic glandular hairs, veins (7-)8(-9), palmate. *Inflorescences* axillary, twice branched dichasiums, homogamous, 12-

22-flowered, not projecting above leaves, flowers white or sometimes pink-tinged; *peduncles* 5-22 cm, covered with long glandular hairs, often densely so; *bracts* caducous, usually conspicuous, broadly elliptic to obovate, 0.55-2.5 x 0.2-1 cm, apex acute, setose, margin irregularly long ciliate, outer surfaces glabrous to long glandular hairy. *Pedicels* densely glandular hairy, those of male flowers 0.5-2 cm, those of female flowers 0.6-1.1 cm. *Male flowers*: *tepals* 4, outer 2 broadly elliptic-elliptic, outer surface densely hairy especially in central region, 0.8-1.55 x 0.7-1.2 cm, apex rounded, inner 2 elliptic, 0.7-1.65 x 0.45-0.85 cm; *stamens* 65-75, *filaments* free, attached at all heights to a 1.5-2 mm tall torus, 4-5 mm, inner filaments slightly longer than outer, *anthers* elliptic to wedge-shaped, c. 1.5 mm, dehiscing via vertical slits along sides of anthers, connective projecting 0.2-0.25 mm, apex rounded. *Female flowers*: *tepals* 5, outer shortly glandular hairy, particularly in central regions of outer segments, elliptic to obovate, 0.85-2 x 6.5-1.1 cm, apex rounded; *ovary* 3-angled, locules globose, 4-8.5 x 4.5-7 mm, locules inflated to form wings, one wing usually longer than the other two, longest wing rounded with more or less straight sides, 4-4.5 x 4-4.5 mm, shortest wings rounded, c. 2.5 x c. 4.5 mm, locules glabrous or densely glandular hairy, hairs mostly long, becoming shorter near base of styles, 3-locular, *placentation* axillary, *placentas* bifid, bearing ovules on both surfaces; *styles* greenish yellow, deciduous, 2, 5.25-6.5 mm tall, bifid from near base, branches erect, stigmatic papillae arranged in a once spirally twisted band. *Infructescences* densely glandular hairy throughout, c. 14.5 cm, not projecting through the leaves, 7-8-fruited; *fruiting pedicels* 1-1.6 cm; *fruit* green, fleshy, indehiscent, remaining on plant for many months, erect, sparsely glandular hairy-medium glandular hairy and microscopic glandular hairy, 3-angled, locules globose, 0.7-1.5 x 1.15-1.75 cm, with one longer wing and two shorter wings or ribs, longest wing rounded, 2.5-5 x 4-5 mm, shorter wings or ribs to 4 mm long.

var. **robusta**

ILLUSTRATIONS: Koorders, Flora Tjibodas. iii. II. t. 3. 1918; Fotsch, Die Begonien. 61. 1933; Schimper & Faber, Pflanzen-Geogr. ed. 3. i. 442. 1935; Doorenbos, The Begonian. 47 (August), p. 213. 1980.

DIAGNOSIS: Leaves and petioles covered with long glandular hairs, often densely so, hairs often red.

PHENOLOGY: Flowering and fruiting year-round.

DISTRIBUTION: Java, Bali, Lesser Sunda Islands.

HABITAT & ECOLOGY: Primary forest. Marshy grassland in low, mossy forest.

CULTIVATION: Not presently known from cultivation. Both varieties were grown in the Netherlands in the 1970's but have since been lost from cultivation (Doorenbos, 1980). Buxton (1946) states that 'the plant many begonia lovers know as *B. robusta* is really *B. ingrami* (*B. nitida* x *B. fuchsioides*)'.

LOCAL NAMES: Hariang (Sunda Language) ['W. Java, Tjibodas, *D.R. Pleyte 111* (L)'].

SPECIMENS EXAMINED:

Indonesia: JAVA: sine loc., *Blume s.n.* (NY isotype of *B. grandis* Blume); sine loc., *Blume s.n.* (4 sheets L); sine loc., *Kathas s.n.* (2 sheets L); sine loc., *s.c. 12832* (L); sine loc., *s.c. s.n.* [Herb. Lugd. Bat. no. 94454-202] (L); sine loc., Koorders s.n. (L); sine loc., *s.c. 13947* (L); sine loc., 8.iix.1982, *Balgooy 4279* (L); sine loc., 17.xii.1925, leg. *Dansen s.n.* (L); sine loc., *Warburg 298* (B); sine loc., Nov. 81, *Warburg s.n.* (B); sine loc., *Zollinger 439Z* (B); sine loc., *Engler 4637* (B); sine loc., *' 387* (B); sine loc., 1858, *Jagor 46B* (2 sheets B); Tjibodas 19.6.22, leg. *Burkill 8163* (HBG); Tjibodas, Gunong Gedeh Boror, West Java, by path in forest above gardens, 3.iii.1959, *J. Sinclair 10075* (3 sheets E, K); West Java, Tjibodas, ii.1890, *Lehmann 63* (2 sheets B); Tjibodas ', 1400-1700 m, 12.iii.1950, *Ooststroom 12938* (L); ' Tjibodas (Gede), c.1450 m, 8.v.1950, *Ooststroom 13971* (L); Tjibodas, Boerlage s.n. (L); Res. Preanger, Tjibodas, 1400 m, 6.xi.1896, *Koorders 25968B* (L); Res Preanger, Tjibodas, Mons Gede, 18.x.98, *Koorders 31834B* (L); Tjibodas ', Gede, 12.ii.1899, *', 280* (L); Mt. Gede, 14.ii.1915, *H.N. Ridley s.n.* (K); Gede, Tjibodas, 26.vi.1924, leg. *C. de ' 650* (L); nr. Salak, 17.ii.1915, *H.N. Ridley s.n.* (2 sheets K); Kawak ' Woods, 1.ii.1915, *H.N. Ridley s.n.* (K); Pangerango, 4500-9000 ft, frequens, leg. *Kurz s.n.* (K); W. Java, Tjibodas, area II, 24.v.1948, 1600 m, Primary forest, *D.R. Pleyte 111* (L); West Java, Tjibodas, Regenwald, 1450 m, 19.i.1906, leg. *A. Engler 4637* (B); Gedeh Binneniveg n. Tjibussun, 17.iv.1932, leg. *A Ke 59* (L); Gede, 3-5000 ft, *s.c. s.n.* (L); Preanger, Reg. Tjibodas', c. 2000 m, 17.xii.1925, *Vansen 6161* (L); Preanger Reg. G. Windae, 24.iv.1909, *Soeganderedja 86* (L); Java Prov. Preanger. Apud

fontes calidos supra beureum prope Tjibodas (Mons Gede), 2140 m, 2.v.1894, *V. Schiffer 2265* (L); Res. Preanger, takoka, 1000 m, 9.ix.1899, *Koorders 32878B* (L); ', Tjibodas (Gede), c. 1500 m, 8.v.1950, *Ooststroom 13946* (L); Cibodas, from the garden to Gunung Gede (until 2100 m alt.), 30.xii.1977, *Aya Nitta 15113* (L); Res. Batavia, G. Salak, 700 m, 23.ix.1896, *Koorders 24465* (L); Sallak, *s.c. s.n.* (L); Prov. Batavia. Ad decliv. septentr. montis Pangerango apud locum dictum Artja, 1000-1500 m, 6.iv.1894, *V. Schiffner 2271* (L); Prov. Batavia. Ad decliv. septentr. montis Pangerango apud locum dictum "Artja" In Silva primigenia, 11-1200 m, 7.iv.1894, *V. Schiffner 2267* (L); Versaiit N du Salak, c. 1100 m, s.c. 57 (L); W. Java, N. Salak above Tjalobak, c. 800 m, 25.xi.1940, *De Voogd s.n.* (L); Katjana, 22.iv.09, *Soegandi 93* (L); Tjiburrum, 1916, *Bourlage s.n.* (2 sheets L); Tambak, Mt. Lawu, C. Java, 26.xi.1982, *J.J. Afriastini 486* (L); Mt. Malabar Java, 19.x.1861, *T. Anderson s.n.* (K); Malabar, *Kathal s.n.* (L); Gn. Luhur, W. of Tugu on Bogor-Puncak Rd., 1700 m, depleted forest, common in damp undergrowth, 8.iix.1982, *V. Balgooy & Mogea 4279* (L); South East Java, 1880, *H.O. Forbes 856* (B, BM); Tjisaroeo-Zuid, c. 1200 m, 26.ii.1950, *Ooststroom 12832* (L); Gn. Halimun Area, Nirmala Estate, W. Java, Remnant rainforest alt. 1100 m, 1.x.1985, *Van Balgooy 5206* (2 sheets L). BALI: Kleine Soenda Eilanden, G. Abang, 1600-1800 m, *Van Steenis 8059* (K). LESSER SUNDA ISLANDS: sine loc., 16.vi.1973, leg. *Father E. Schmutz 3231a* (L).

HYBRIDS: An artificial hybrid between *B. robusta* Bl. and an unnamed *Begonia* taxon is reputably in cultivation under the name *B.* x *leopoldii* Verschaffelt (syns. B. 'Bettina Rothschild', B. 'Fire-flush') (Doorenbos, 1980).

var **multangula** (Blume) Tebbitt **comb. nova.**

TYPE: Jawa, *De Vriese s.n.* (K! holotype).

SYNONYMS: *Begonia multangula* Blume in Enum. Pl. Java. 1: 96. 1827; Backer & Van Den Brink, Flora of Java. 1: 313. 1963. **TYPE:** Jawa, *De Vriese s.n.* (K!).
Begonia discolor sensu Blume in Enum. Pl. Java. 1: 96. 1827, non R. Brown (1813), Koorders, Exkurs. Fl. Java. 2: 646. 1912. **synon. nova.**
Platycentrum multangulum (Blume) Miquel in Fl. Ned. Ind. 1.1: 695. 1856. **TYPE:** Jawa, *De Vriese s.n.* (K!). **synon. nova.**
Platycentrum multangulum var. *glabrata* (Miquel) R. Brown in Fl. Ned. Ind. 1.1: 695. 1856. **TYPE:** not located. **synon. nova.**

Sphenanthera multangularis (Blume) Hasskarl in Versl. Kon. Akad. Wetensch. 4: 135-141. 1855.

Sphenanthera multangula (Blume) Klotzsch in Bot. Zeitung. 15: 181. 1857. **TYPE:** Jawa, *De Vriese s.n.* (K!). **synon. nova.**

Sphenanthera multangula var. *glabrata* (Miquel) Klotzsch in Bot. Zeitung. 15: 182. 1857. **TYPE:** Jawa, *De Vriese s.n.* (K!). **synon. nova.**

Begonia robusta sensu Zollinger ex Klotzsch in Bot. Zeitung. 15: 182. 1857. pro syn. *Sphenanthera multangula* Klotzsch, 1857. **synon. nova.**

Begonia multangula var. *glabrata* Miquel in Fl. Jungh. 4: 418. 1857. **TYPE:** not located. **synon. nova.**

Casparya multangula (Blume) A.DC. in Prodr. 15(1): 275. 1864. **TYPE:** Jawa, *De Vriese s.n.* (K!). **synon. nova.**

Casparya multangula var. *glabrata* (Miquel) A.DC. in Prodr. 15(1): 276. 1864. **TYPE:** not located. **synon. nova.**

Casparya robusta var. *glabriuscula* A.DC. in Prodr. 15(1): 275. 1864. **TYPE:** *Zollinger 2844* (G!). **synon. nova.**

Begonia grandis Reinwardt ex Koorders in Exkurs.-Fl. Java. 2: 646. 1912, pro syn. *Sphenanthera multangula* Klotzsch (1857). **synon. nova.**

Begonia robusta var. *glabriuscula* (A.DC.) ex F.A. Barkley & J. Golding in Sp. Begoniaceae, ed. 2: 108. 1974. **TYPE:** *Zollinger 2844* (G!). **synon. nova.**

ILLUSTRATIONS: Doorenbos, The Begonian. 47 (August). p.214. 1980.

DIAGNOSIS: Leaves and petioles glabrous to short downy hairy, occasionally with a few scattered longer hairs.

DISTRIBUTION: Java, Bali, Lesser Sunda Islands.

LOCAL NAMES: Lungar (Mangari language) ['Flores, Ruteng, Sanoh Poco Gurung, 1700m, 17.vi.1975, *J.F. Veldkamp 7040* (L)].

NOTES:

1. Some confusion presently exists with regards to the correct identity of *Begonia crassicaulis* (A.DC.) Warburg (here treated as a synonym of *B. robusta* var. *multangula* (Blume) Tebbitt).

The first valid publication of the name 'crassicaulis' appears in de Candolle's (1864). Here, the taxon is treated as a species of the genus *Casparya*. De Candolle

erected the section *Polyschisma* for the taxon. He was presumably unsure of the correct taxonomic status of the taxon as he put a question mark before the name *Polyschisma*. Warburg (1894) in a later revision of the Begoniaceae synonymised the genus *Casparya* under the genus *Begonia*. *Begonia crassicaulis* (A.DC.) Warburg was maintained as the only species in *Begonia* section Polyschisma (A.DC.) Warburg. The section remained of uncertain taxonomic status.

The taxonomic status of *B. crassicaulis* (A.DC.) Warburg remained unchanged until Smith and Wasshausen (1984) synonymised the taxon under their nomen numen *Begonia pachyrhachis* L.B. Smith & D.C. Wasshausen.

The holotype of *B. pachyrhachis* L.B. Smith & D.C. Wasshausen is, however, the holotype of Lindley's *B. crassicaulis* from Guatemala and not Warburg's taxon from Java. Therefore, *B. crassicaulis* (A.DC.) Warburg is not a synonym of *B. pachyrachis* Smith & Wasshausen. The holotype of *B. crassicaulis* (A.DC.) Warburg is sheet 'Jawa, *De Vriese*' and is housed at Kew. This sheet is also Blume's holotype of *B. multangula* Blume. The latter taxon must, therefore, be treated as a synonym of *B. multangula* Blume and hence also as a synonym of *B. robusta* var. *multangula* (Blume) Tebbitt.

The sheet 'Jawa *De Vriese*' also has the name *Polyschisma crassicaulis* A.DC. on it. This name is unpublished and is not, therefore, treated as a synonym.

SPECIMENS EXAMINED:

Indonesia: JAVA: sine loc., *Zollinger 2844* (B, G); sine loc., *Koorders s.n.* (5 sheets L); sine loc., Aug., *Koorders 1402* (2 sheets L); ', *Reinwardt 1721* (L); ', 1.i.1915, *H.N. Ridley s.n.* (K); Preanger, leg. *O. Warburg 11298* (B); Pengalongan, Preanger, vii.186, *Warburg 11298* (B); Preang. Reg., 1000 m, 2.iix.1929, *C.A. Wisse 1123* (L); Res. Preanger, Tjibodas, 2400 m, 1.xi.1898, leg. *S.H. Koorders 32001B* (L); Res. Preanger Reg. G. Mandalagiri, alt. 1550 m, 31.iii.1920, leg. *H.Y. Ham 271* (L); Preanger Reg., Tjibodas bova ', c. 2000 m, 17.xii.1925, *Vansen 6101* (L); ', ' Mt. Helling, 21.x.1928, *D.T.H. 5397* (L); Pasoeroean, 30.x.1922, *J.D. Dorgelo 1245* (L); Res. Pasoeroean, Tosari, 1750 m, 31.x.1892, leg. *Koorders 37866B* (B, L); Res. Pasoeroean Soember tangkil, 400-500 m, 28.vi.1896, leg. *Koorders 23046B* (L); Res. Temarang, Telomojo, 10.vi.1897, leg. *S.H. Koorders 27665B* (L); Res. Temarang Telomojo, 16.v.1899, leg. *Koorders 35890B* (L); Besoeki O. Helling G. Taroeb (Lamongan) route top naar Tiris, 1600 m alt., 12.vii.1938, leg. *Van Steenis 10774* (L); South East Java, 1880, *H.O. Forbes 857a*

(B); Java (Buitenzorg.) Kandang Baelak, 20. vii.1898, leg. *M. Fleischer s.n.* (2 sheets B); Telagabodas auf Patocha Preanger Java, ix.1881, *Warburg 3330* (B); Manau near Ruteng, 1500 m, 26.iv.1965, *Kostermans & Wirawan 668* (L); Ruteng, Sanoh Poco Gurung, 1700 m, 17.vi.1975, marshy ground in low, somewhat mossy forest. Edge of marsh, *J.F. Veldkamp 7040* (L); Cheribon, G. Tjeremai, 1800 m, 21.xii.1940, *Van Steenis 12829* (L); Putueha, *Koorders s.n.* (L); Mt. Ijen, E. Java, primary forest scattered, 14.ii.1984, *J.J. Afriastinii 1457* (L). BALI: Batoekaoe, 1300 m, 23.i.1935, leg. *de Voogd 2140* (2 sheets L). LESSER SUNDA ISLANDS: Flores, Leg. *Father J.A.J. Verheijen s.n.* (L).

5.6.4.2. SPECIES WITH UNCONFIRMED MEMBERSHIP OF SUBSECTION *SPHENANTHERA* (HASSK.) TEBBITT

5.6.4.2.1. B. macintyrensis Tebbitt sp. nova.

TYPE: Sumatra: Sibayak Volcano, Woods, Berastagi, Feb. 1921, *Ridley s.n.* (K holotype); Berastagi, woods, 15.ii.1921, *H.N. Ridley s.n.* (K isotype).

The species is named in honour of M.L. MacIntyre who established the National Collection of *Begonia* housed at Glasgow Botanic Garden.

DESCRIPTION: *Monoecious* erect herb to at least 10 cm, *stems* slender, very sparsely microscopic glandular hairy. *Stipules* persistent, ovate-lanceolate, 1.2-1.6 x 0.4-0.6 cm, apex setose, margin entire, sparsely microscopic glandular hairy. *Leaves* alternate; *petioles* 7-17 cm long, slender, sparsely microscopic glandular hairy; *lamina* ovate, 8.5-9 x 5-6.5 cm, apex acuminate, base strongly asymmetric, cordate, lobes unequal, lower lobe rounded, 2.75-3.25 cm across, sinus 5-8.5 mm deep, margin never lobed, serrately toothed, ciliate, both surfaces sparsely microscopic glandular hairy, veins c. 8, palmate. *Inflorescènces* once branched dichasiums, few-flowered, bearing male and female flowers synchronously; *peduncles* 3.7-7 cm long; *bracts* caducous, outer c. 1.5 x 0.6 cm, inner c. 7.5 x 3 mm, surfaces glabrous, margins long ciliate. *Pedicels*..... *Male flowers*: *tepals* 4, white, tipped pink, outer 2 ovate, glandular hairy, 10-11.5 x c. 5.5 mm, apex obtuse, inner 2 elliptic, glabrous, 8-9 x 4-5 mm, apex obtuse; *stamens* c. 60, *filaments* linear, free to base, c. 1.5 mm long, attached to a raised flowers base, *anthers* linear-elliptic, c. 1 mm long, dehiscing via a vertical slit along each side of anther, connective projecting c. 0.4 mm, apex rounded. *Female flowers*:..... *Infructecences* 2-fruited; *fruiting pedicels* c. 1.5 cm, erect; *fruit* fleshy, globose, 1-1.4 x 1-1.4 cm, sparsely microscopic glandular hairy, 3-locular, wings rounded, attached along entire length of fruit, more or less equal, to 2.75 mm.

PHENOLOGY: Specimens observed were said to be flowering and fruiting in February.

DISTRIBUTION: Sumatra.

RECOGNITION: Lamina of leaves broadly ovate, 8.5-9 x 5-6.5 cm, margin serrate. Fruit globose with short triangular wings.

HABITAT & ECOLOGY: Montane forest.

NOTES:

1. The specimens observed have all been determined by H.N. Ridley as *Begonia trigonocarpa* Ridley. They differ, however, in terms of a number of morphological characteristics as shown in Table 5.1. and are, therefore, recognised here as a new species.
2. This taxon is provisionally placed within section *Sphenanthera* (Hasskarl) *sensu* Tebbitt. Its affinity to the other members of this section cannot be confirmed until further material bearing female flowers is located.

SPECIMENS EXAMINED:

Indonesia: SUMATRA: Sibayak Volcano, Woods, Berastagi, Feb 1921, *Ridley s.n.* (K); Berastagi, woods, 15.ii.1921, *H.N. Ridley s.n.* (K).

Table 5.1. Characters which separate *Begonia macintyrensis* Tebbitt from *B. trigonocarpa* Ridley.

CHARACTER	TAXON	
	B. trigonocarpa Ridley	***B. macintyrensis*** Tebbitt
Leaf size	10-16 x 7-13 cm	8.5-9 x 5-6.5 cm
Leaf margin	shallowly angular lobed	serrate, not lobed
Inflorescence type	2-3-branched dichasium	once branched dichasium
Number of flowers	several (c. 10)	few (c. 5)
Fruit shape	elliptic-globose	globose
Fruit wings	very unequal	equal or almost so

5.7. TAXA MOVED TO SECTION *PETERMANNIA* (KLOTZSCH) A.DC.

5.7.1. CIRCUMSCRIPTION OF SECTION *PETERMANNIA* (KLOTZSCH) A.DC. (from Baranov & Barkley, 1974).

A. de Candolle in Ann. Sci. Nat., Bot. 4, 11; 128 (1859).
'*Staminate flowers*: *tepals* two, *filaments* mostly affixed in a more or less circular fashion to a conical column, *anthers* obovate, approximately the length of the filaments. *Pistillate flowers*: *tepals* five, *styles* three, two-lobed, not persistent, stigmatic papillae form continuous helical bands, placentae two-divided. *Fruit* three-celled, with three subequal wings. Mostly erect semi-shrubs with pinnately or palmate-pinnately veined leaves, inflorescences terminal or opposite to the leaves, paniculate or few-flowered.'
Type species: *Begonia cumingiana* A.DC.

Petermannia was named in honour of Wilhelm Ludwig Petermann (1806-1855).

5.7.2. THE SPECIES MOVED TO SECTION *PETERMANNIA*

5.7.2.1. ***Begonia brachyptera*** Mer. & Per. and ***B. pseudolateralis*** Warb. clearly belong to section *Petermannia*, as currently circumscribed. They both possess a combination of male flowers with two tepals, anthers with endothecial base plates, female flowers with five tepals, bifid placentae, 3-locular ovaries and racemose inflorescences. However, no clear cut morphological discontinuities could be found between *B. brachyptera*, *B. brachybotrys* (which is currently included in section *Petermannia*) and *B. pseudolateralis*. *Begonia brachyptera* Mer. & Per. and *B. brachybotrys* Mer. & Per. are both said to occur in New Guinea while *B. pseudolateralis* Warb. is stated to occur throughout the Philippines. Plants from Mindanao in the Philippines, the islands of Moluccas and the islands North of New Guinea are particularly difficult to identify. Plants from elsewhere in the Philippines fit the description of *B. pseudo-lateralis* and are morphologically distinct from the main land New Guinea plants. However, even on main land New Guinea, *B. brachyptera*, *B. brachybotrys* can not be readily distinguished. These plants are also morphologically similar to *B. megacarpa* Mer. & Per. of section *Petermannia* but may be readily distinguished from this taxon, in part by this species larger fruit. Due to the difficulty in defining species boundaries between these taxa and because they clearly belong to section *Petermannia* they were not described here. Cladistic data for these taxa were only collected from the type

specimens and those specimens seen by the authors of the species. Further study is required to resolve whether these species are distinct or require merging.

B. brachyptera Mer. & Per.
SPECIMENS EXAMINED IN CLADISTIC ANALYSIS:
New Guinea: *Clemens 40896* (A Holo), *41205* (A), *6327* (A), *40750* (A).

B. pseudolateralis Warb.
SPECIMENS EXAMINED IN CLADISTIC ANALYSIS:
PHILLIPPINES: LUZON ISLAND: Prov. Isabela, Malunu, *Warburg 11792* (B); Prov. Tayabas, Sampoloc, *Warburg 13086* (B); Prov. Tayabas, Sampoloc, *Warburg 13086* (B); MINDORO ISLAND: Baco River, *Merrill 991* (L).

5.7.2.2. B. axillipara Ridley in Trans. Linn. Soc. London. Bot. 10:1. 60-61. 1916.
TYPE: Dutch New Guinea: Utakwa River to Mt. Garstesz, Canoe Camp, 10.xi.1912, *C. B. Kloss s.n.* (BM! holotype).

ILLUSTRATIONS: Smith *et al.* Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany, No. 60. Fig. 12.11. 1986.

DESCRIPTION: *Monoecious*, erect herb, at least 30 cm [lower portion of stem missing], *stems* c. 5 mm thick, branched above, glabrous. *Stipules* caducous, oblong. *Leaves* alternate; *petioles* 6-10 cm, slender, sparsely microscopic glandular hairy; *lamina* membranous, ovate, 9-10.5 x 6.5-8 cm, apex acute, base strongly asymmetric, cordate, lobes unequal, lower lobe rounded, 3-3.5 cm, margin shortly toothed, teeth ciliate, hairs microscopic, glandular, stalks multicellular, bright green on both sides, above glabrous, below with sparse microscopic red glandular hairs, stalks unicellular, veins 7, palmate, *Inflorescences* axillary, 1-2-flowered, male flowers borne in upper leaf axils, females in lower leaf axils; *peduncles* very short, to 2 mm; *bracts* deciduous, white, oblong, apex truncate or obtuse, 5 mm long, concealed. *Pedicels* slender, glabrous, those of male flowers to 1.4 cm long, those of female flowers c. 1.3 cm. *Male flowers*: *tepals* 2, orbicular, off-white with a pink margin, c. 5 x 5 mm; stamens 25-30, *filaments* free to base, slender, more or less equal, *anthers* elliptic-oblong, to 1 mm, apex obtuse, locules touching, connective not projecting, dehiscing via longitudinal slits along under surface of

anther. *Female flowers*: *tepals* 5, off-white with a pink margin, outer 2 oblong, truncate, c. 4 x 3 mm, inner 3 narrower; *ovary* succulent, elliptic c. 4 x 3 mm, shortly winged, wings c. 1 x 1.5 mm basal half and pedicels covered with microscopic red glandular hairs, stalks unicellular, 3-locular; *styles* caducous 3, c. 1.5 mm, fused at base, bifid, branches erect, stigmatic papillae yellowish, once spirally twisted. *Infructescences* c. 18 mm long, 1-fruited, *fruit*.....

PHENOLOGY: The only known example of the taxon was flowering and fruiting in October-November.

DISTRIBUTION: New Guinea.

RECOGNITION: The combination of membranous leaves, inflorescences 1-2-flowered, very short peduncles and succulent, short winged ovaries distinguish this species from other members of section *Petermannia*.

HABITAT & ECOLOGY: Forest at 45 m.

NOTES:

1. Known only from holotype.

SPECIMENS EXAMINED:

New Guinea: Utakwa River to Mt. Garstesz, Canoe Camp, 10.xi.1912, *C.B. Kloss s.n.* (BM holo).

5.8. SPECIES NOT ALLOCATED TO A SECTION

5.8.1. B. trigonocarpa Ridley in Trans. Linn. Soc. London, Bot. 11. 9: 38. 1917; Ridley, J. Fed. Malay States Mus. 8(4): 38. 1917.

TYPE: Korinchi Expedition, Sungei Kumbang, 4500 ft, I.IV.14, *H.C. Robinson & C.B. Kloss 29* (K! holotype, BM! isotype).

ILLUSTRATIONS: Smith *et al.,* Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany. No. 60. Fig. 28.11. 1986.

DESCRIPTION: Erect herb to at least 30 cm tall, stems branched, slender, very sparsely microscopic glandular hairy. *Stipules* persistent, lanceolate, 1-1.4 x 0.4-0.5 cm, apex mucronate, margin entire, surfaces sparsely microscopic reddish glandular hairy. *Leaves* alternate; *petioles* 6-17 cm, slender, sparsely microscopic glandular hairy; *lamina* ovate, 10-16 x 7-123cm, apex acuminate, base strongly asymmetric, cordate, lobes unequal, lower lobe rounded, 4.5-8.5 cm across, sinus 1.5-3.5 cm deep, margin shallowly irregular angular lobed, lobes to 1.5 cm deep, green with red veins, both surfaces sparsely microscopic glandular hairy, veins 7, palmate. *Inflorescences* in upper-most leaf axils, 2-3-branched dichasiums, c. 10-flowered, male and female flowers on inflorescence synchronously; *peduncles* 4-12 cm, sparsely microscopic glandular hairy; *bracts* caducous, ovate, c. 6 x 3 mm, margin ciliate, surfaces glabrous. *Pedicels* 0.9-1.1 cm. *Male flowers*: *tepals* 4, outer 2 fleshy, white tinged with pink, elliptic, c. 6.5 x 4.5 mm, apex obtuse, minutely reddish glandular hairy, inner 2 obovate, glabrous, c. 6 x 3 mm, apex obtuse; *stamens* c. 50, *filaments* free, slender, inner longer than outer,1-2 mm, *anthers* linear-elliptic, c. 2 mm, narrow, dehiscing via vertical slits along sides of anther, connective projecting c. 0.2 mm, apex rounded. *Female flowers*: *tepals* 5, white tinged with pink, elliptic, inner gradually getting smaller, 6.5-9.5 x 2.5-4 mm, apex obtuse, outer microscopic reddish glandular hairy, inner glabrous; *ovary* elliptic-globose, 0.3-0.75 mm long, 3-angled, two angles very shortly winged, third with a rounded triangular wing to 4 mm, 3-locular, *placentation* axillary, *placentae*.....; *styles* 3, caducous, slender, c. 0.4 mm long, base fused for c. 0.5 mm, bifid from just below half-way, branches erect, stigmatic papillae twice spirally twisted. *Infructescence* 2-4-fruited; *fruiting pedicels* 1-2 cm; *fruit* succulent, erect, elliptic-

globose, to 1.5 x 1.4 cm, very sparsely microscopic glandular hairy, wings as in ovary.

PHENOLOGY: All specimens examined were flowering in April. A single specimen was fruiting in February.

DISTRIBUTION: Sumatra.

RECOGNITION: The only species in the genus with the following combination of characters: *Leaves* ovate, irregular, short angular lobed. *Peduncles* 4-5 cm long. *Fruit* fleshy, 3-locular; *styles* 3.

HABITAT & ECOLOGY: Montane forest at 1370 m.

NOTES:

1. *Begonia trigonocarpa* cannot be placed in any section as these are currently defined. The species is closely related to sections *Platycentrum* Hasskarl. The circumscription of this section probably requires redefining so that it accommodates such taxa as *B. trigonocarpa.*
2. A Robinson & Kloss specimen collected on the 8.6.1914 in addition to having Barong barw as the locality, also has Japan written on it. This must be a mistake as Ridley described the taxon from Sumatra and Robinson and Kloss were collecting in Sumatra on this date. The same confusion over the collection locality also occurs with a specimen of *Begonia sarcocarpa* Ridley collected during the same expedition.

SPECIMENS EXAMINED:

INDONESIA: SUMATRA: Korinchi Expedition, Sungei Kumbang, 4500 ft, 1.iv.1914, *H.C. Robinson & C.B. Kloss 29* (K holo, BM iso); Korinchi Expedition, Sungei Kumbang, 4500 ft, 14.iv.1914, *H.C. Robinson & C.B. Kloss 30* (BM); sine loc., *s.c. s.n.* (K); Korinchi Expedition, Barong Bharu, *H.C. Robinson & C.B. Kloss 1.42* (BM).

5.8.2. B. obovoidea Craib in Kew Bulletin. 413. 1930.
TYPE: Nam Chut Ranawng, c. 75 m, 28.i.1927, Kam Kung, by streams in evergreen forest, *Kerr 12902* (K! holotype).

ILLUSTRATIONS: Smith *et al.*, Begoniaceae Part I: Illustrated Key Part II: Annotated Species List. Smithsonian Contributions to Botany. No. 60. Fig. 4.39. 1986.

DESCRIPTION: *Monoecious*, erect stemmed herb, stem simple, red, lower nodes rooting, at first sparsely hairy becoming glabrous. *Stipules* caducous..... *Leaves* alternate; *petioles* c. 17 cm long, microscopic glandular hairy; *lamina* thin, in outline orbicular or 4-angled orbicular, palmately 7-9-lobed, lobes lanceolate or broadly lanceolate, c. 10 cm deep, apices acute, base symmetric, broadly cordate, margin irregularly sparsely toothed or almost entire, both surfaces microscopic glandular hairy particularly on veins below, veins 7, veinlets few, conspicuous below. *Inflorescences* short axillary dichasiums, bearing both male and female flowers, *bracts*..... *Pedicels* c. 8 mm long, microscopic hairy. *Male flowers*: *tepals* 4, white, outer 2, sub-elliptic, c. 7 x 5 mm, apex obtuse, dorsal surface pubescent, inner 2 elliptic, c. 5 x 2.5 mm, glabrous; *stamens* c. 100, *filaments* free to base, *anthers* linear, c. 2 mm long, dehiscing via a vertical slit down sides of anther, connective short projecting, apex obtuse. *Female flowers*: *tepals* 6, white, almost elliptic, outer surfaces microscopic glandular hairy, c. 5.8 x 4.3 mm; *ovary* oblong, c. 0.7 x 0.65 cm, densely microscopic glandular hairy, with short membranous wings which become attenuate along pedicels, 3-locular; *styles* caducous, 3, c. 3.5 mm tall, free, bifid from half-way, base of branches funnel-shaped, branches erect, stigmatic papillae once spirally twisted on ends of branches, confined to top of lower funnel-shaped portion. *Infructescence* 1-(2?)-fruited; *fruiting pedicels* c. 2.5 cm long, erect; *fruit* oblong, c. 1.6 x 1.3 cm.

DISTRIBUTION: Burma and India.

RECOGNITION: The only species in the genus with large palmately lobed leaves and obovoid shortly winged capsules, wings tapering along pedicels.

HABITAT & ECOLOGY: By streams in evergreen forest.

USES: Craib (1930) states that the stems are edible.

NOTES:

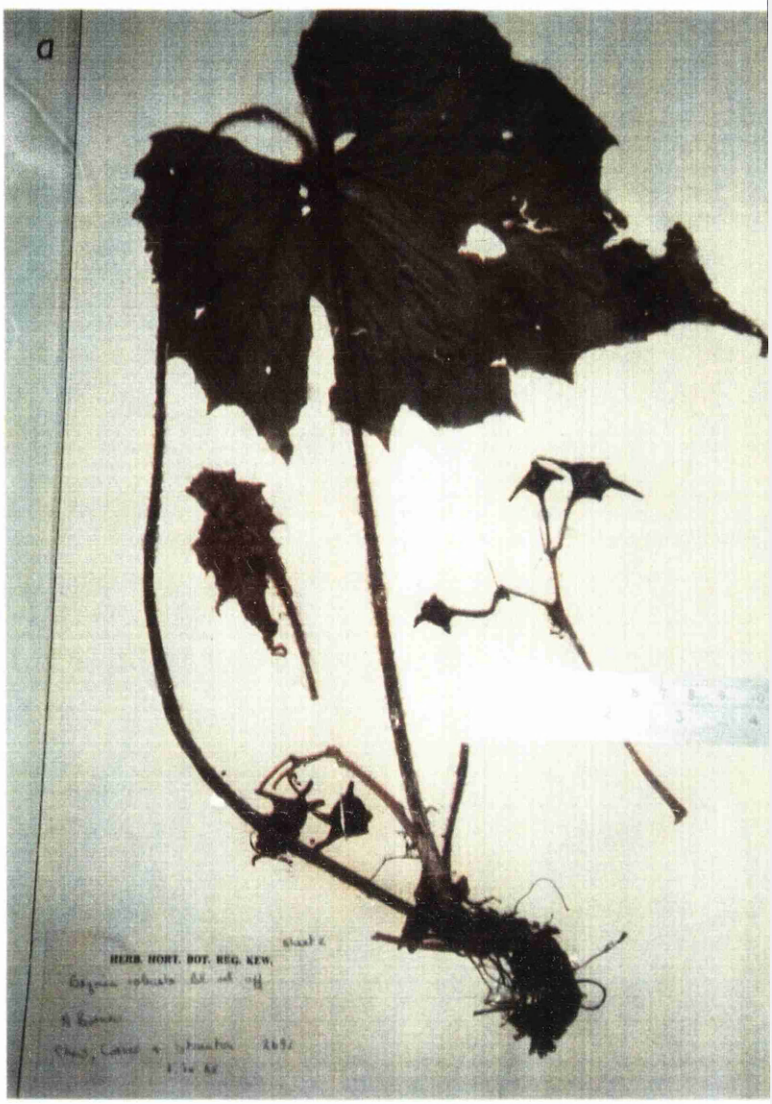
1. New to India.

2. The fruit morphology of this species is similar to that of many species of section *Petermannia*. This similarity appears to be the result of convergent evolution as the species is otherwise quite different from the members of this section.

SPECIMENS EXAMINED:

Burma: Tavoy ' head waters, 1500 ft, 29.xi.1921, *P.T., Russell 2254* (K); Ranawng; Nam Chut, 18.i.1922, *Kerr 12902* (K holo); Kao Naung, Surat, *W.S. Kurz 13367* (K); Burma (south) Tenasserim Division, Tavoy District, Hills South of Paungdaw Power Station, scattered, gregarious in undergrowth especially in damp wet and loose soil along streams, 1800 ft, 6.ix.1961, *J. Keenan, U Tun Aung & R.H. Rule 1425* (E).

India: Naga Hills, Kegurina, *Clarke 41183A* (K).



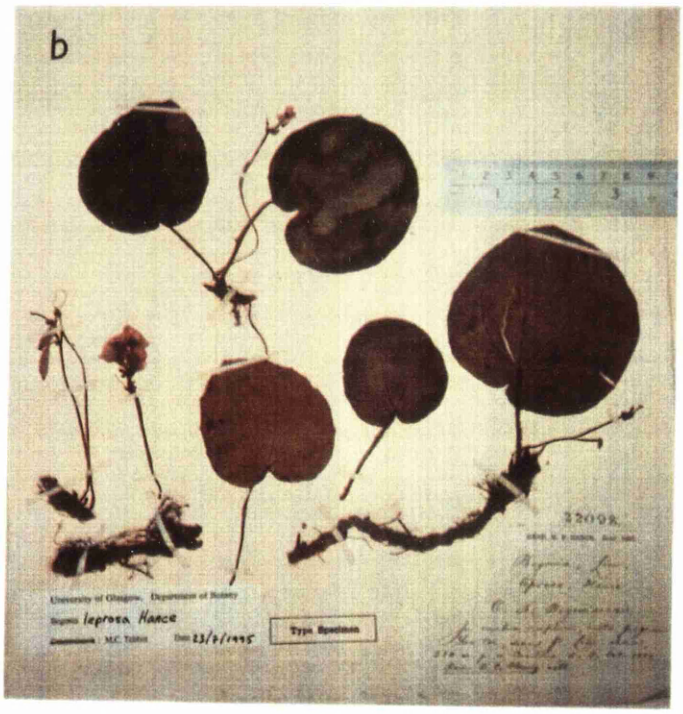


Plate 7. (a) Unnamed species of subsection *Sphenanthera* (Hasskarl) *sensu* Tebbitt
(b) Holotype specimen of *Begonia leprosa* Hance (section *Fusiformes*)

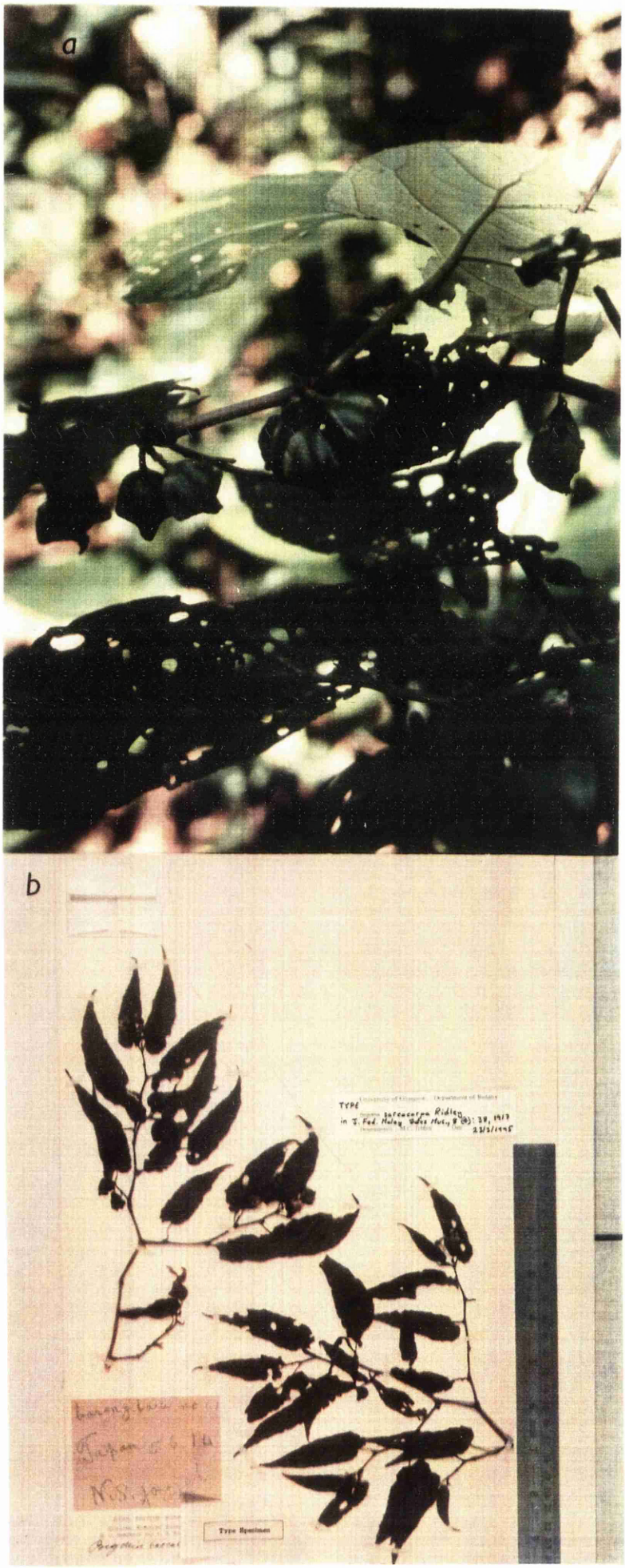


Plate 8. (a) Fruit of *Begonia longifolia* Blume (section *Blumea*)
(b) Holotype specimen of *Begonia sarcocarpa* Ridley (section *Blumea*)

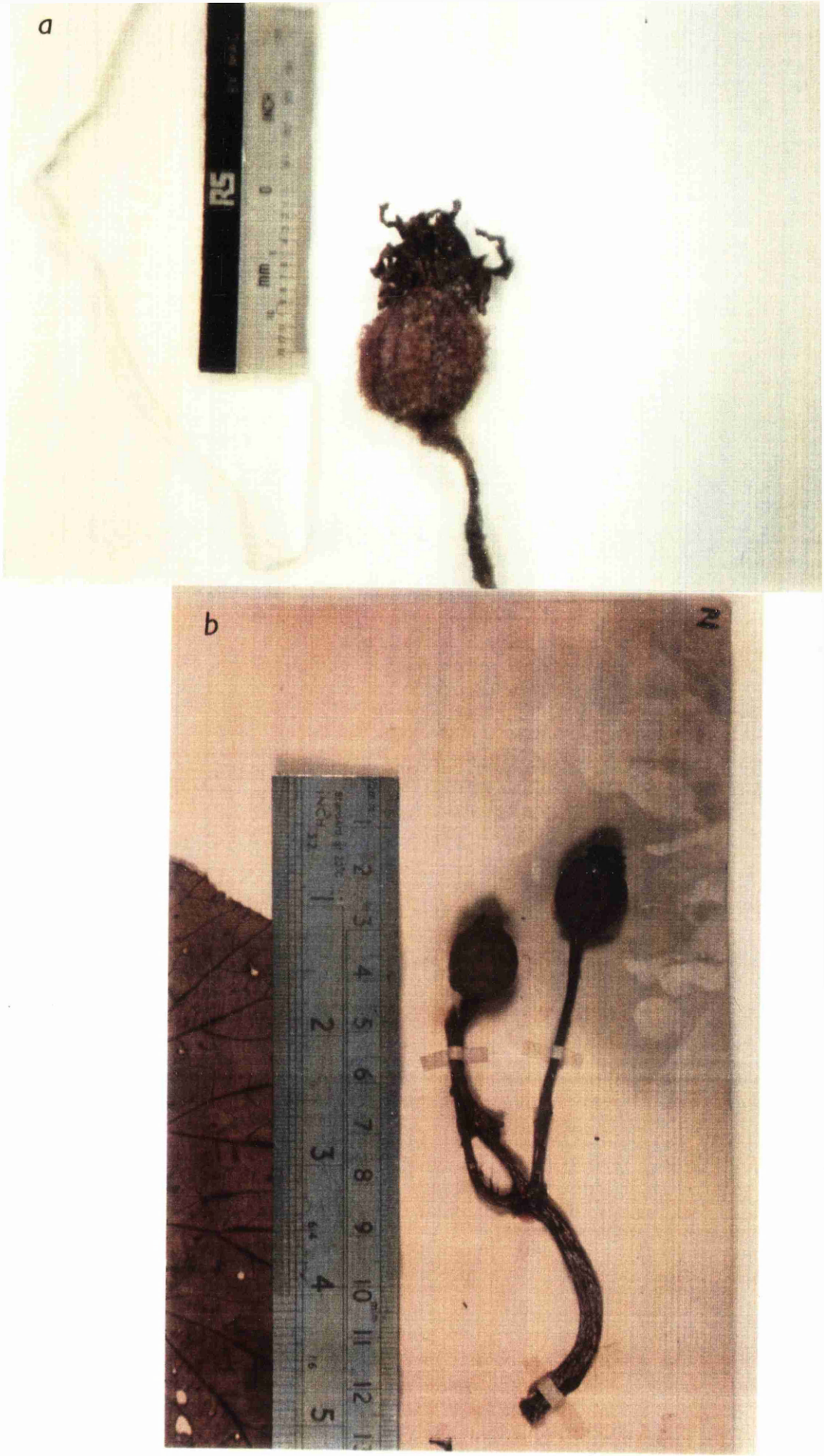


Plate 9. (a) Fruit of *Begonia aborensis* Dunn (section *Dioecibegonia*)
(b) Fruit of *Begonia silletensis* C.B. Clarke (section *Dioecibegonia*)

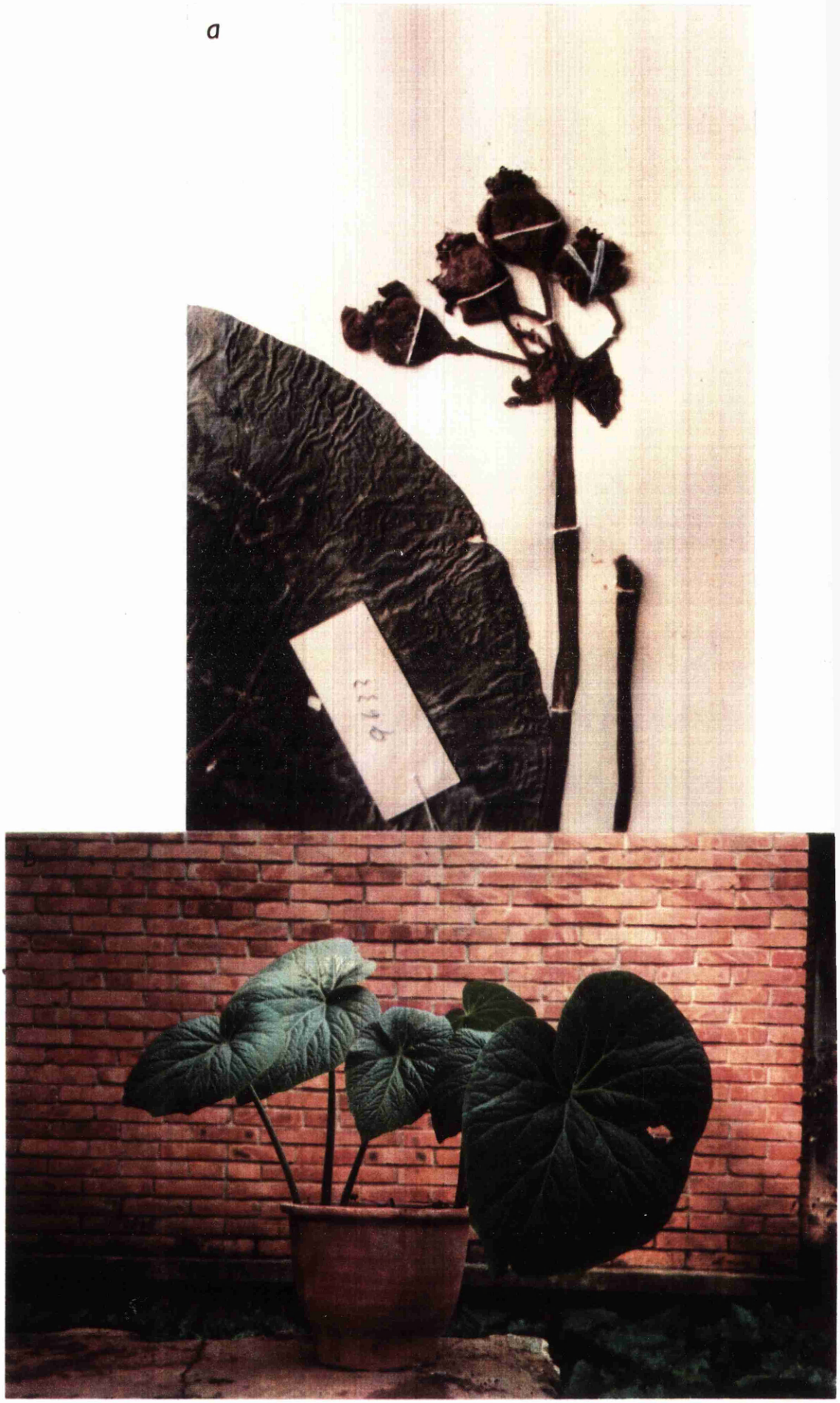
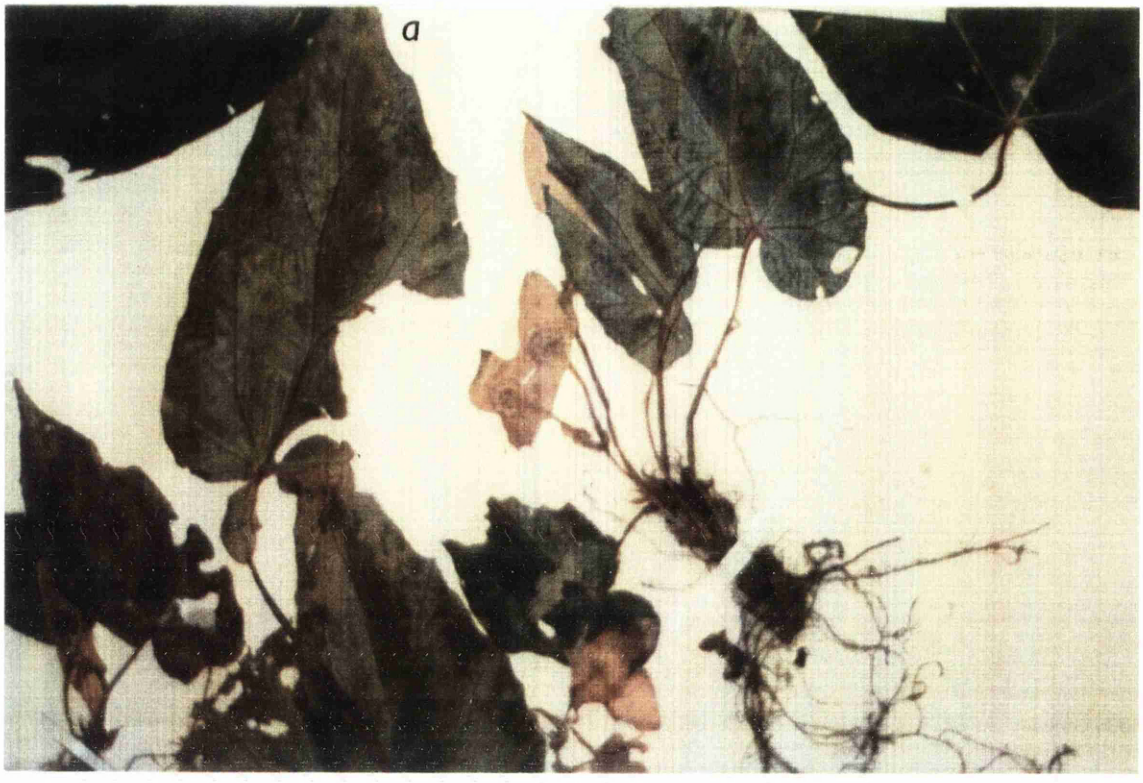


Plate 10. *Begonia mengyangensis* Tebbitt & K.Y. Guan (section *Dioecibegonia*) (a) Fruit (b) whole plant



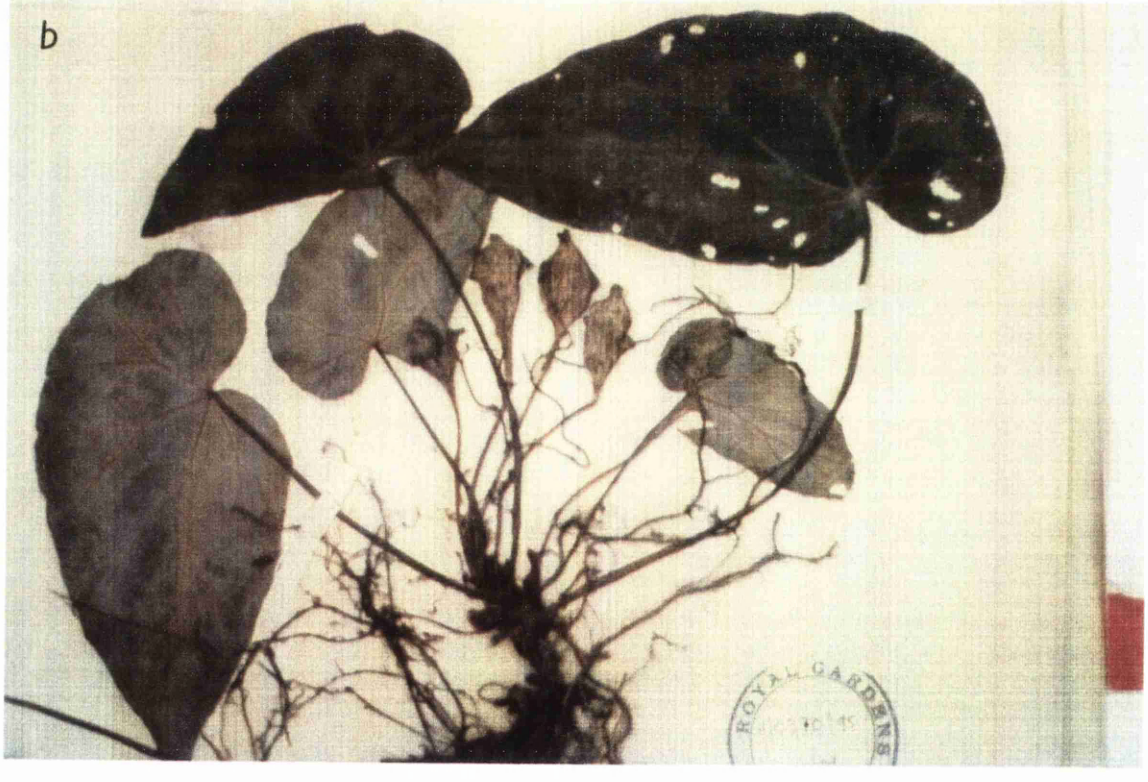


Plate 11. *Begonia burkillii* Dunn (section *Dioecibegonia*)
(a) showing male flowers (b) showing fruit

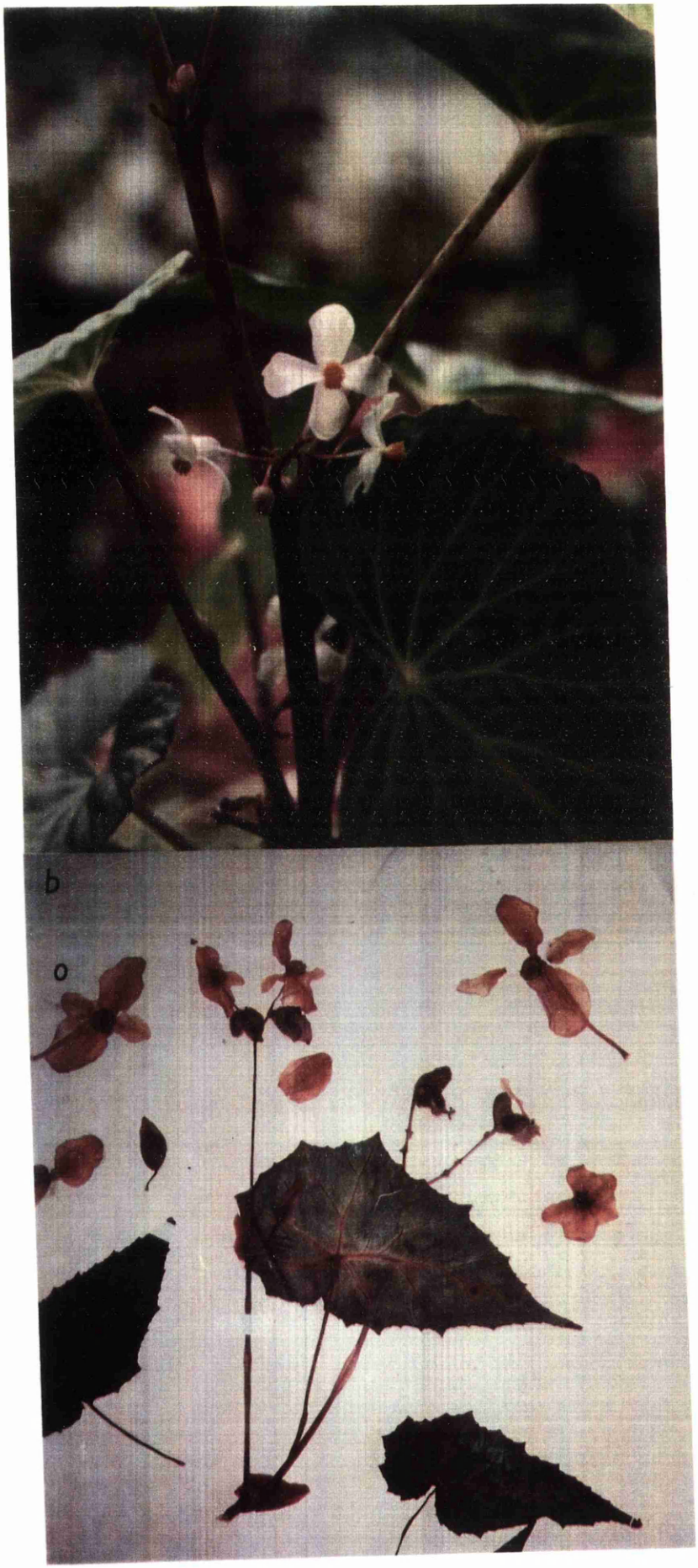


Plate 12. (a) *Begonia roxburghii* (Miq.) A.DC. (section *Dioecibegonia*) showing characteristically short inflorescence and male flowers (b) *Begonia dux* C.B. Clarke (section *Platycentrum* subsection *Platycentrum*) showing fruits

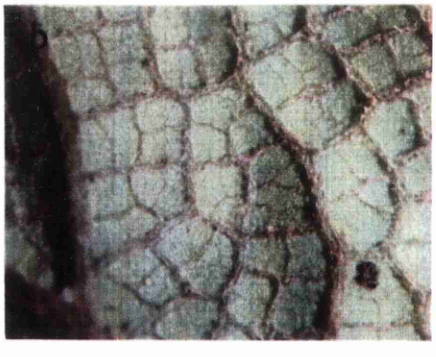


Plate 13. *Begonia balansana* Gagnepain (section *Platycentrum* subsection *coronatae*) (a) showing male flowers (b) showing distinctive veination on leaf under surface

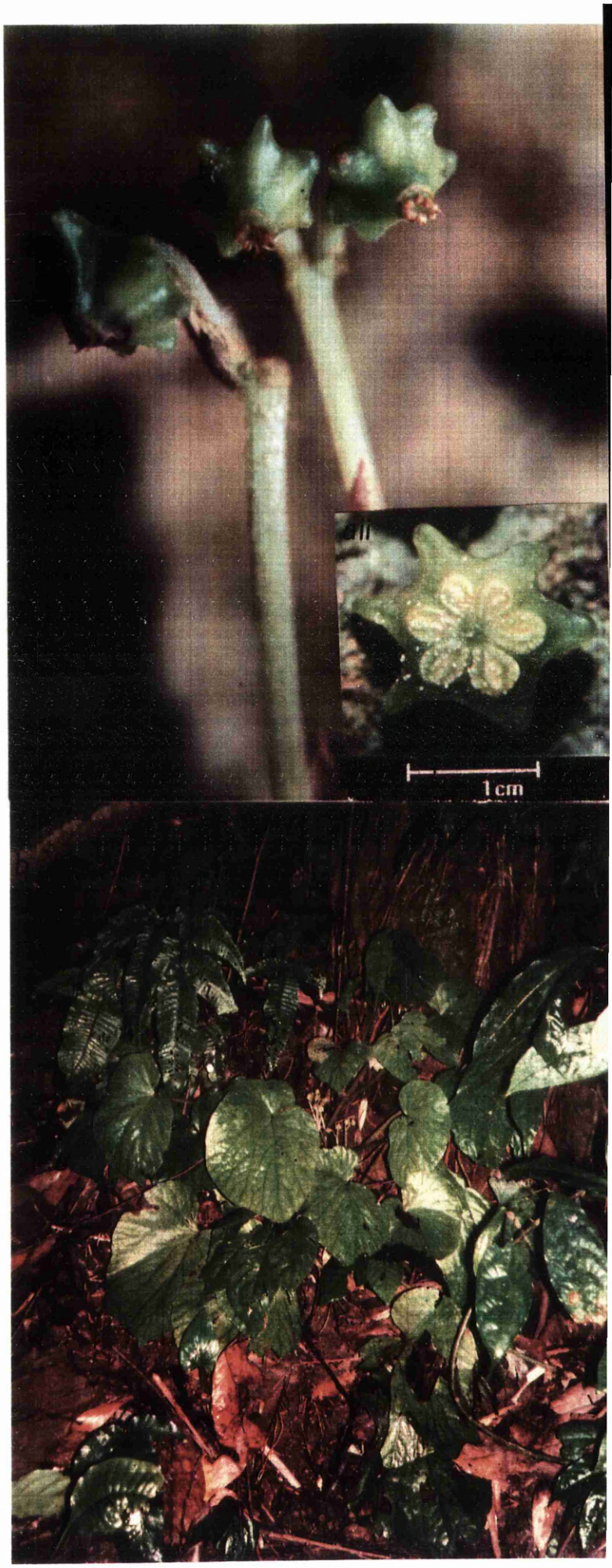


Plate14. *Begonia balansana* Gagnepain (section *Platycentrum* subsection *coronatae*): (ai) diagnostic crown-shaped fruits (aii) section of fruit showing bifid placentae (b) Habitat

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GLOSSARY

GLOSSARY: Cladistic terms

Apomorphy - relatively derived state of a character (Hennig, 1966).

Autapomorphy - an apomorphy peculiar to one monophyletic taxon (Hennig, 1966).

Cladistics - the method of determining branching patterns of evolution by using the principle of parsimony to optimise congruence of synapomorphies.

Character - a homologous feature of an organism that can be used for taxonomic purposes (Stuessy, 1990) (see example below).

Character state - a homologous divisible property of a character (Stuessy, 1990). *e.g.* the character placentation has the states parietal and axil.

Clade - a monophyletic group.

Cladogram - a branching diagram that is constructed by cladistic principles and methods (Camin & Sokal, 1965).

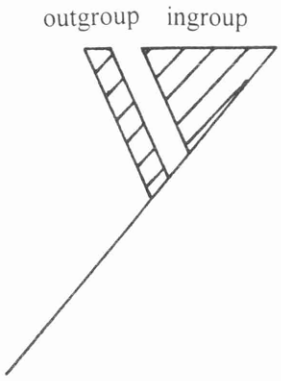
Convergence - development of similar characters or states in different lineages but without a common direct ancestry (Simpson, 1961).

Homoplasy - resemblance not due to inheritance from a common ancestor (Simpson, 1961).

Homology - the same character or character state which has evolved from a common ancestor.

Ingroup - a monophyletic study group (illustrated below).

Example of an ingroup and an outgroup



Monophyletic - A group in which all members have the same ancestor and which includes all descendants of that ancestor (Hennig, 1966).

Outgroup - a group which has its closest evolutionary relationships outside of the ingroup (illustrated above).

Parallelism - Independent attainment of apomorphy in two independent lines, but from the same ancestor (Hecht, 1976).

Paraphyletic - A group based on symplesiomorphic characters in which all members have the same ancestor but which does not include all the descendants of that ancestor (Hennig, 1966).

Parsimony - The principle that the most economical solution is to be preferred to all others.

Plesiomorphy - relatively primitive state of a character (Hennig, 1966).

Polyphyletic - A group based on convergent characters rather than common ancestry in which all members have the same ancestor but which does not include all the descendants of that ancestor (Hennig, 1966).

Reversal - a reversion from an apomorphous state to the plesiomorphous state .

Sistergroup - the most closely related group cladistically to a clade (Hennig, 1966 in Stuessy, 1990).

Synapomorphy - a shared derived state of a character.

Sympleisiomorphy - a shared primitive state of a character.

Topology - the shape of a cladogram, with the relative positions of the branches but not taking the positions of the postulated character changes into account (Linder, 1988).

APPENDIX A: Living accessions included in the sudy

SPECIES	SOURCE	ACCESSION NUMBER
Hillebrandia sandwichensis	R.B.G. Kew	1977-8
Begonia acetosella	Glasgow (S.W. China)	003-152-95
B. acetosella	Glasgow (Vietnam)	001-073-96
B. amphioxis	Glasgow	007-156-94
B. annulata	Glasgow	003-124-82
B. balansana	Glasgow	002-152-95
B. brevirimosa	Glasgow	004-042-83
B. chlorosticta	Glasgow	001-167-94
B. dregei	Glasgow	002-082-91
B. floccifera	Glasgow	030-099-89
B. goegoensis	Glasgow	011-125-57
B. grandis	Glasgow	002-009-82
B. grandis	Glasgow	004-085-80
B. handelii	Montreal	1747-57
B. hatacoa	Glasgow	004-005-89
B. herbacea	Glasgow	001-122-95
B. incarnata	R.B.G. Kew	1977-3589
B. longifolia	Wageningen	Yunnan, *Van der Maesen 6187*
B. mannii	Glasgow	008-067-80
B. masoniana	Glasgow	001-007-56
B. meyeri-johannis	Wageningen	*Quené & van der Wege 48 & 49*
B. prismatocarpa	Glasgow	002-121-78
*B. quadrialata**	R.B.G. Kew	1984-122
B. rhopalocarpa	R.B.G. Kew	1982-3056
B. roxburghii	Glasgow	004-093-79
B. roxburghii	Montreal	2331-54
B. salaziensis	R.B.G. Kew	1986-412
B. solananthera	Glasgow	020-123-70
B. sutherlandii	Ansells garden centre	none
B. tayabensis	Glasgow	006-035-89
B. sp. nov. China	Kunming	001-152-95
B. *Platycentrum* species 1	Wateringen	002-096-95
B. *Platycentrum* species 2	Glasgow	004-151-95

Explanation of table: The accession marked * was only included in the morphological analyses, all other accessions were included in both the morphological and molecular analyses.

Key to place names:

Ansells Garden Centre - Ansells Garden Centre, High Street, Horningsea, Cambs.

R.B.G. Edinburgh - Royal Botanic Garden Edinburgh, Inverleith Row, Edinburgh, EH3 5LR.

Glasgow - Glasgow Botanic Garden, 730, Great Western Road, G12 OUE.

R.B.G. Kew - Royal Botanic Gardens Kew, Richmond, Surrey, TW9 3AB.

Montreal - Jardin botanique, 4101, rue Sherbrooke Est, Montréal, Québec, H1X 2B2.

Wageningen - Botanical centre, Wageningen Agricultural University, P.O.B. 8010 6700 ED Wageningen, The Netherlands.

Wateringen - Gaelstraat 9, 2291 SG Wateringen, The Netherlands.

APPENDIX B: Herbarium specimens examined as outgroup taxa in the morphological cladistic analyses

***Datisca cannabina* L.**

INDIA: Himachal Pradesh, Lahul, Udaipur, 2800m, 11/8/90; *Mc Beath, 2450* (E), 2251 (E): Above Shadipur, 5000ft., 19/4/02; *Drummond, 14369* (E): Kawaou; *Wallich, 4664* (E-GL). RUSSIA: Leninsky district, Varzob River Valley, 48 km. N of Dushanbe, above Khushyori, 1500-2000m, 1/8/1985; *Elias, Murray & Newcombe, 10019* (E).

***Hillebrandia sandwicensis* Oliver**

HAWAII: E.Maui, Haleakala Crater, Koolau Gap, Wailau Waterfall, October 1910, *J.F. Rock 8631* (K); Hawlsl Kauai, Kokee, 1100m, 31-5-82, *V. Balgooy 4244* (2 sheets K); Hanalei, Kauai, 11/66, *H. Mann & W.T. Brigham s.n.* (K); Kauai, Baha Nolokai naui, *Hillebrand s.n.* (K type); Molokai Pohohca, June 1912, *C.N. Forbes, 85* (K): Molokai, Waikolu gorge along pipeline trail near tunnel, July 13, *L.M. Cranwell & C. Skottsberg 2627* (K); Wet gullies region between Waikalu Valley and probably northern base of Puu alii, Molokai T. Hawaii, open wet slope, April 10 1928, *Otto Degener 9760* (K); Wanyaku Valley, *Mann 466* (2 sheets K types?); *sine loc.*, *Hillebrand s.n.* (K type); Hawaii; Sinclair s.n. (K).

***B. annulata* K. Koch**

E. Bhutan 26' O 'N 92° O 'E, *F. Kingdon-Ward 6444* (K); E. Himalaya, Boolom, *Griffith* Kew Distribution no. *2571* (2 sheets K); Polly Badgeley 5700 Kohima, 7 Nov. 1885, leg. *C. B. Clarke 41801A* (K).

***B. brachybotrys* Merrill & Perry**

NEW GUINEA: Musom village, road to Mt. Jasop Lae subprovince, Morobe Province, 600m. lat. 6°45'S long. 147°00'E, secondary forest, 19/6/78, *P. Katik LAE 70827* (A, K); Mt. Yungat, N. slopes Bewani Mts., 14 km SSW of Bewani, Bewani sub province, W.S.P. 800m, lat. 3°8'S long. 141°06'E, lower montane forest on steep slopes, 20/9/82, *J. Wiakabu et al. LAE 50578* (K).

***B. burbidgei* Stapf.**

SABAH: Mt. Kinabalu, Pinosuk Plateau, 6°-6°03'N, 116° 37-41'E, Sungei Bembangan, 5000', 16/8/61, riverside, *W.L. Chew, E.J.H. Corner, A. Stainton 1309* (K); Mt. Kinabalu, Eastern Shoulder, 6°05'N, 116°36-40'E, Camp 2, 6500', 16/6/61, mossy forest, *W.L. Chew, E.J.H. Corner & A. Stainton 1043* (K); Kambarangoh, Kinabalu, mossy forest, 7000', 19/5/67, *W.R. Price 197* (K), *246* (K); North Borneo, Sandakan, Ranau, Ulu Liwago, Kinabalu, 7500', 7/3/1961, *W. Meijer SAN 24136* (K); Kinabalu, at 7600', *G.D. Haviland 1188* (K holo & Iso);

Mt. Kinabalu, Eastern Shoulder, 6°05'N, 116°36-40'E, 9500', 18/7/61, *W.L. Chew, E.J.H. Corner & A. Stainton 866* (K); Mt. Kinabalu, Ulu Liwagu and Ulu Mesilau, 6°N, about 116°35'E, *W.L. Chew, E.J.H. Corner & A. Stainton 2685* (K); Kinabalu National Park, Kinabalu W. route from park HQ, c. 6°05'N, 116°30'E, *Argent 1604* (E); Kinabalu N.P., Mesilau Ridge, Sinclair 259 (E); Mt. Kinabalu on descent, 6,100ft., 15/6/1957, *Sinclair 9211* (E).

B. cordifolia (Wight) Thwaites

INDIA: Peninsula Indine Orientalis, Malabar, June 1836, *Wight 1030* (K holo); *sine loc.*, 'Herb. *Wight* 1857' *s.n.* (K); Malabar, June 1836, *Wight 835* (E). SRI LANKA: Ceylon, Arawakumbra, bet. Lunugala and Bible, Badulla District, soil pockets and crevices on wet rocky slopes, also on hard gravelly road banks, shade, frequent, 1972 Dec. 15., 450m, *A. H. M. Jayasuriya & D. D. Tiruvengadum 1006* (2 sheets K); Kotatalawa, between Mahiyangana and Uraniya, Badulla District, on somewhat rocky banks, shady, reddish brown earth, common, 160 m, 1972 Dec. 15, *A. H. M. Jayasuriya & D. D. Tiruvengadum 1007* (K); Hasalaka, Kandy District, 80° 56'N 7° 21'E, on shady wayside banks, reddish brown earth, common, 100 m, 1972 Dec. 15, *A. H. M. Jayasuriya & D. D. Tiruvengadum 1008* (K); Ududaha (mile 39), Bintenna Pass, Kandy District, on shady road banks and on forest floor, common, 150 m, 1974 Jan. 19, *A. H. M. Jayasuriya, H. N. Moldenke & D. B. Sumithraarachchi 1420* (K); Near villa unya, 3.1.28, *A. H. Gaston 1645* (K); Ceylon, *Thwaites 3584* (K).

B. cumingiana A. DC.

PHILIPPINES: Prov. Albay Luzon, *Cunng 856* (K); Prov. Albay, Luzon, 1841, *s.c. 856* (K); Albay-Camarines, Luzon, June 1908, *H. M. Curran 12260* (K); Infauta, Luzon, *s.c. 2916* (K); Luzon, Cuming, s.c. 856 (E iso).

B. delicatula Parish *ex* C.B. Clarke

BURMA: Moulmein, 1862, *Parish*, herb. *mstr.* no. *297* (K holo).

B. dregei Otto & Dietrich

SOUTH AFRICA: Inanda, Natal, *J. M. Wood 1197* (K); Natal, Inanda, frequent in bush at Inanda heights, *H. G. Fihweichustr 31899* (K); Inandra, Natal, *J. M. Wood s.n.* (K); Inanda, 450ft., 4/4/48, *Posi* 61 (E); Natal ', *Billiard & Burtt 5657* (E, K); Port Shepstone distr., 900ft., 21/12/1965, *Hilliard & Burtt 3390* (E); Uvongo side river Kloof forest on moist rocks, 23/11/72, *R. G. Strey 11051* (K).

CULTIVATED: Cape, Transkei, Port St. James, *Strey 6655* (E); Transkei Lusikisiki dist., Lupatana, *Strey 10223* (E).

B. floccifera Beddome

INDIA: Madras, Oct 1919, ' *10842* (K); ', *Beddome 217* (K); On roads near Kodamadi, Tinnevelly Hills, Jan 1933, *Barnes 201* (K); CULTIVATED: Peradeniya gardens in glasshouse 3/7/'28, *J.J. Senanatna 2* (K); Received as cutting in 1969 from Rudolf Ziesenhenne, California, acc. no. 691803, *s.c. C11072* (E).

B. grandis Dryander

P.R. CHINA: Kweichow Province, China, wet shaded rocky slope, 900m, 9/17/1931, *A.N. Steward, C.Y. Chiao & H.C. Cheo 638* (K); Kweichow, *s.c. 638* (K); Shantung Province, Tai Ching Kung, Lao Shan, 30m, Aug. 13 1930, *C.Y. Chiao 2907* (K); Tien Mou Shan, Chekiang, Aug. 21 '24, *R.C. Chiang 5159* (K); Kwangtung Province, Aug 1887, *C. Ford 85* (K), *86* (K); Hupeh, Changyang, *Henry 6236A* (K); Nan-T'O and mountains to northward Ichang, *A. Henry 2110* (K); Ichang and immediate neighbourhood, *A. Henry 2228* (K).

B. hatacoa F. Hamilton ex D. Don

INDIA: East Himalaya, *Griffith* Kew Distribution no. *2565* (K); Sikkim, Darjeeling 5000', Sept 1879, *J. S. Gamble 7083* (K); Darjeeling, Tista, June 20 1960, leg. *H. Hara, H. Kanai, G. Murata, M. Togashi & T. Tuyama 88174* (K); Rishap, Darjeeling, 4000', 28 July 1870, *C.B. Clarke 12252A* (K); Darjeeling, Tukoar road, 6000', Aug 1874, *J. S. Gamble 3889/150* (K); Rungbee, 4000 Darjeeling, 3 July 1870, *C. B. Clarke 12146A* (K); Darjeeling 1923, *J. M. Cowan s.n.* (K); Mongpo, 3000', Oct 1872, *J. S. Gamble 3888A* (K); Regio trop, alt. 3-4000', *J.D. Hooker & T Thompson s.n.* (10 sheets K); North Cachas Hills, 4000, May 1968, *T. Yandall 79* (K); Haflong, W Cachar Hills Assam, 2500', 25 Aug 1908, *Craib s.n.* (K); Khasia, Uni wai, 3500', 23 Oct 1871, *C.B. Clarke 15869* (K).

B. herbacea Vellozo

BRAZIL: Evirons of Rio Janeiro, 1982, com. *A. Glaziou 14236* (K); Rio, 1892, *A. Glaziou 19821* (K).

B. johnstonii Oliver

TANZANIA: Tanganyika, Lushoto District, 24/5/1953, *R.B. Drummond & J.H. Hemsley 2728* (2 sheets K), *2765* (2 sheets K); Tanganyika, Uluguno, 'Mongood', 4500', rocks below forest, April 18th 1930, *Bruce 1069* (K); Tanganyika T., 20/4/35, *Bruce 1129* (K); Tanzania, Kilosa Distr. Ukaguru Mts. Ihanga rock, c. 6° 26'S, 37°03'E, steep, sometimes vertical rock with *Aloe*, *Kalanchoe*, *Senecio mannii*, *Urogentias* etc. Below the rock secondary scrub with much *Bidens*, *Veronica* etc. at the margin of *Pinus* plantation, c. 1450m, 2/6/1978, *M. Thulin & B. Mhoro 2862* (K); Tanzania, Iringa Distr. N. part of Gologolo Mts. 7°40'S 36° 53'E, In wet grass near stream, c. 1500m, 13/9/1970, *M. Thulin & B. Mhoro 957* (K); Tanzania, T6 Morogoro District, Kanga Mt., 0600S, 3743E, montane forest, 780m, 5/7/1983, *R.M. Polhill & J.c. & J.M. Lovett 4965* (K); Marangu, 1600m, October 1893, *G. Volkens 1241* (E, K); Kilimanjaro, 5-6000', *H.H. Johnston s.n.* (K type); Lutindi Peak, E. Usambaras, *C. Holst 3381* (K); Kenya, Meru, Karita River below road bridge nr. Boma, *P. Archer B8038* (K type).

B. mannii J.D. Hooker

NIGERIA: south boundary of Boje enclave near pillar 33, in small stream valley in H.F., 14 May 1946, *A.P.D. Jones 5810* (K); Uyo District, Eket, along the road to James town, 4/10/64, *B.O. Daramola 55280* (K); Obodu, forest, 5000', May 26 1962, *W. Head 97* (K); Ondo, Idanre, Orosun, in main tongue of forest on eastern side of Orosun, c. 2800', epiphytic herb, scrambling over low branches of trees and also on vertical faces of moss covered boulders, *R.W.J. Kerry 22683* (K); Obudu Cattle ranch, South eastern state, 6°24'N, 9°25'E, c. 1.5 miles south of hotel, Epiphyte on shrubs, *J. Lowe 2663* (K); Calabar, Oban group forest reserve, near Aningeje on Calabar-Mamfe road, lowland rainforest, margin of forest, 13/1/59, *R.W.J. Keay 37731* (K); Calabar, Oban enclave near mile 50, roadside, 25/1/57, leg. *C.F.A. Onochie 36161* (K); River Old Calabas, epiphytic on trees, Feb. 03, *G. Mann 2317* (2 sheets K) Old Calabar, 1862, ' 23 (E). SIERRA LEONE: Daru (Tunkia chiefdom), climber, epiphytic on oil palm, 27/10/31, *J.D. Fisher 83* (K). CAMEROON: sine loc., 1912, *Zenker 4501* (E); Bule counrty, Oct. 1895, *Bates 404* (E). CULTIVATED: Cult at Kew British Cameroons, Mbonge, *J.O. Wright s.n.* (3 sheets K).

B. martabanica A. DC.

INDIA: *sine loc.*, *Lobb 175* (K). BURMA: Moulmein, *Lobb 393* (2 sheets K, types); Moulmein, 1837, *Helfer* Kew Distribution no. *2575* (K).

B. meyeri-johannis Engler

ZAIRE: Prov. Kivu Territ. Rutshuru, Parc National Albert, forêt ombrophile, 2000 m, Septembre 1952, *de Witte 8143* (K); Kivu, à l'W de Tshibinda, 2000-2400 m, leg. *H. Humbert 7447* (K); Parc national Albert, *de Witte 1415* (K). RWANDA: 16 Feb 1980, *Briedson 408* (2 sheets K); route Butare-Cyangugu env. de Rwasenkoko préfective Gikongoro, 2000 m, forêt de montagne, 28 Mai 1981, *G. Troupin 16263* (K); Kamiranjovu territoire; Shanugu, forêt de vallée, 2000 m, 17 Mars 1956, *A. R. Christiaensen 1397* (K); Ancienne route Nyongwe-territoire. Shangugu, forêt de montagne, 2200 m, 27 Septembre, 1956, *A. R. Christiaensen 1856* (K); Route Bukavu-Astrida-territoire, Shangugu, talus, 2390m, 23 Juillet 1959, *A. Léonard 5070* (K); Forêt du Rugege (Cyangugu), Marais du Kamiransovu, aux env. du km 104 de la route Butane-Cyangugu, alt. env. 1920 m, marais à cypéracées (env. 40 cm d'eau), 25 Juillet 1974, *P. Auquier 3403* (K). KENYA: Ruweujni forest, 4000ft., Feb. 1934, *Pearson s.n.* (E); Kinga Mts., *Goetze 1213* (E); ', Sept. 1893, *Volkens 993* (E).

B. nepalensis Warb.

NEPAL: Napalia 1892, *Wallich 3677* (K). INDIA: Sikkim, 3-6000', *J. D. Hooker sn.* (9 sheets K); Sikkim, 500', 4 March 1871, *C. B. Clarke 13943* (K); Sikkim Himalaya, Gt. Ringeet Valley, 800', Nov. 18th 1874, *Coh. 1073* (K); Darjeeling, Siaoke, Feb. 1873, *Gamble 3874A* (K); Darjeeling, 15/1/77, *Gamble 2413A* (K); Darjeeling, Panchkilla 1000, 1 Dec 1875, *C. B. Clarke 26496* (K); Darjeeling ' 1500, 14 Nov 1870, *C. B. Clarke 13743A* (K); East Himalaya, Darjeeling, *Griffith* Kew distribution no. *2572* (K); Tista, 1000ft., 23/2/1919, *Cave s.n.* (3 sheets E); Pankabari, 1000ft., 11/12/1917, *Cave s.n.* (E); Chula Chuli, 1000ft., 4/2/85, *Stainton 8906* (E).

B. nossibea A.DC.

MADAGASCAR: Nossibe, Mai 1879, *leg. J.M. Hildebrandt 2995* (K), *2995a* (K). COMORES: Mohilla Island Comores Isles, April 1861, *J. Kirk s.n.* (K).

B. prismatocarpa W.J. Hooker

CAMEROON: Cameroons, Basosi, Kumba Div., Bambe-Muen cetar path, roch in damp shady place near water, 29/10/46, leg. *Dundas 15329* (K). EQUATORIAL GUINEA: Bioko, Musola, *Mann 563* (K holo); Bioko, Caldera, San Carlos, above Ruiché, *Thorold 79A* (K).

B. quadrialata Warb.

NIGERIA: Ogoja Province Oji River, alt. 400', shaded damp rocks on side of river, 17.14.1955, *R. H. Stone 2* (K); Province Ogoja, District Ikom, Afri River Forest reserve, near Aboabam, marshy ground by stream under high forest, 9/12/50, leg. *R.W.J. Keay 28188* (K); South-Eastern Nigeria, south boundary of Boje enclave near pillar 33, on sand in flat valley under H.F. shade, 14 May 1946, *A.P.D. Jones Forest Herbarium Ibadan no. 5809* (K). LIBERIA: Nimba, *P. Adames 765* (K); Western Province, vonjama District, Soplima, Nov. 1. 1947, *J.T. Baldwin, Jr. 10024* (K); Sinoe Co. Duo, common throughout region, March 11 1948, *J.T. Baldwin, Jr. 11351* (K); Eastern Province, Webo District, Nyaake (Webo), June 25 1947, *J.T. Baldwin, Jr. 6111* (K); Sinoe Co., about 25 miles up Sangwin River near Truo, March 12 1948, *J.T. Baldwin, Jr. 11377* (K); Sinoe Basin, *A Whyte s.n.* (K); Njagbela (Valunia) on vertical earth cutting at side of path through forest, 18/7/52, *F.C. Deighton 5795* (K).

B. salaziensis (Gaud.) Warb.

sine loc., *Bojer s.n.* (E).

B. solananthera A. DC.

BRAZIL: Brasiliae, Mandiorra, *Bridel s.n.* (K holo).

B. sutherlandii J.D. Hooker

TANZANIA: Tanganyika, Iringa district, *R. Polhill & S. Paulo 1629* (K); Tanganyika, Songea District, *E. Milne-Redhead & P. Taylor 8471A* (K); Tanganyika, 14/1/1957, *H.M. Richards 7767* (2 sheets K); Tanganyika, Mbeya District, middle fishing camp, Kiwira River, 2100m, 26/1/1963, growing on a tree trunk in dense forest, *M. Richards 17617* (K); Rungwe district, Kiejo Volcano, west face, volcanic lavas and ashes of 1800 AD in lava block niches, *Hepper, Field & B. Mhoro 5387* (K); Matagoro Hills just S.W. of Songea on rocks by stream side, 1410m, 3/2/1956, *E. Milne-Redhead & P. Taylor 8471* (2 sheets K). CULTIVATED: Raised from Burtt, 5995, collected from Natal in 1969, accession no. 69 0419, *s.c. C6317* (E).

B. tayabensis Merrill

PHILIPPINES: Umiray, Province of Tayabas, Luzon, May-June, 1917, *M. Ramos & G. Edano 29054* (K).

B. urticae L.

COLOMBIA: Columbia, *E. F. André K1072* (K); Columbia, Departamento de Cundanamarca, E of Bogota, Paramo de Carchi, Abajo-Penazul, cloud region, alt. 2800-3000 m, July 9 1963, *D. D. Saejarto & R. Martin 12* (K); Tolima, W.S.W. of Fresno, 3000m, 28/1/78, *Archibold 4092* (E). ECUADOR: Napo-Pastasa, E.N.E. of cayambe Mountain, alt. 10700', scrub by Oriente trail, 6.12.61, *P. C. D. Cazalet & T. D. Pennington s.n.* (K); Province Loja, Parque Nacional Podocarpus, S. of Loja. wet montane forest at the 'Centro de Informacisn' E. of Nudo de Cajanuma (79°10'W 04° 05'S) alt. 2850- 2950 m, 21-22 Feb. 1985, *B. Øllgaard 57812* (K); Clusia forest with Anthurium and tree ferns dominating forest floor, Bosque de Pongo, cloud forest, 2900 m, west facing, 25 km s/sw Cuenca, Azuay, 27 Aug. 1986, *V. Fleming 64* (K); Prov. Napa; S. of El Playán de San Fransisco on the slopes of cero mirador. Espeletia paramo. (77°39'W 0° 34'N) alt. 3600-3800 m, 29 Dec. 1980, *L. Holm-Nielson, J. Jaramillo & F. Coello 29964* (K); Prov. NAPO, Upper slopes of Guagra Ureu. NE exposed montane forest (77°44'W 0° 28'S) alt. 2600 m, 26 sept. 1980, *L. Holm-Nielson, J. Jaramillo & F. Coello & E. Azanza 27075* (K); San Florencio, 22 Jun. 76, 1580 m, *E. F. André 3748* (K); Chuquioibamba, *K 1071* (K); South America, 11000', Azuay, *Pearce s.n.* (K); Yangana, 18 Dec. 1876, *F. André 4584* (K); Above El Encano, Laguna La Cocha, del Putumayo, above 12000ft, 11/8/1939, *Balls 7503* (E).

B. xanthina W.J. Hooker

NEPAL: *sine loc.*, *Wallich s.n.* (K). INDIA: Sikkim, Regio subtrop., 4-5000', *J. D. Hooker s.n.* (K); Sikkim, 5-7000' Regio trop., *J. D. Hooker s.n.* (K); Sikkim, Nov. 1880, *Gamble 9971* (K); Khasia Hills, 4-5000', 1886, *Mann s.n.* (K). BHUTAN: Dumsong, 6000', 22 Sept 1869, *C. B. Clarke 9271A* (K), *9271B* (K); Balukpung-Bomdila Road, July 1970, 3-4000', *T. Yandall s.n.* (K).

APPENDIX C: Herbarium and living specimens examined in the anatomical study of the anthers

INGROUP

Begonia

aborensis: *Griffith 2569* (K)

acetosella Larsen et al. 3098 (E); *Lace 5759* (E); *Forrest 12155* (E); *Larsen Santisuk & Warncke 3098* (E)

axillipara: *Boden & Kloss s.n.* (BM)

balansana: wild collected

brachyptera: *Clemens 41205* (A)

burkillii: *Lace 5105* (2 sheets E)

cristata: *Alston 15679* (BM)

dux: *Beddome 3197* (BM)

handelii: *Toppin 4137* (E); *Rock 2072* (E); *MacGregor 1239* (E)

leprosa: *Wang 38502* (MO)

longifolia Md Nur 32961 (BM); *Tsang & Fung 622* (K); Tsang 26832 (E)

mengyangensis: *Sino-Soviet Union expedition 5869* (KUN)

obovoidea: *Kurzz 13367* (K)

pseudolateralis: *Elmer 13494* (E)

robusta: *Forbes 856* (BM); *Sinclair 10,075* (E)

roxburghii: 004-093-79 Glasgow Botanic Garden (living); 2331-54 Glasgow Botanic Garden (living)

sarcocarpa: *Robinson & Kloss s.n.* (BM)

silletensis: *Lace 5170* (E); *Mann s.n.* (K)

tessaricarpa: *Griffith, 2586* (K)

teysmannianum: *Bünnemeyer 9266* (B)

trigonocarpa: *Ridley, s.n.* (K)

turbinata: *Alston 14040* (BM)

sp. nov. Sumatra: *Ridley s.n.* (K)

sp. nov. Sabah: *Clemens 33882* (BM)

OUTGROUP

Datisca cannibina: *MacBeath 2251* (E), *Drummond 14369* (E)
Hillebrandia sandwichensis: *Rock 8631* (K)
Begonia
annulata: 003-124-82 Glasgow Botanic Garden (living)
brachybotrys: *Brass 14112* (BM)
brevirimosa: 004-042-83 Glasgow Botanic Garden (living)
burbidgei: *Argent 1604* (E)
cordifolia: *Wight 835* (E)
cumingiana: *s.c. 856*v1P (K)
chlorosticta: 001-167-94 Glasgow Botanic Garden (living)
delicatula: *Parish 297* (K)
dregei: *Hilliard & Burtt 3390* (E); *Hilliard & Burtt 5657* (E)
floccifera: *s.c. C11072 (E)*
goegoensis: 011-125-57 Glasgow Botanic Garden (living)
grandis: 002-009-82 Glasgow Botanic Garden (living)
hatacoa: 004-005-89 Glasgow Botanic Garden (living)
herbacea: *s.c. C14250* (E)
incarnata: *M. Nee 26392* (NY)
johnstonii: *Volkens 1241* (E)
mannii: *Bates 404* (E)
masoniana: 001-007-56 Glasgow Botanic Garden (living)
meyeri-johannis: *Pearson s.n.* (E); *Volkens 993* (E)
nepalensis: Pakabari, *Cave s.n.* (E); Tista, *Cave s.n.* (2 sheets E)
prismatocarpa: 002-121-78 Glasgow Botanic Garden (living)
quadrialata: 1984-122 R.B.G., Kew (living)
solananthera: 020-123-70 Glasgow Botanic Garden (living)
salaziensis: *Bojer s.n.* (E)
sutherlandii: *s.c. C6317* (E)
tayabensis: 006-035-89 Glasgow Botanic Garden (living)
urticae: *Balls 7503* (E); *Archibald 4092* (E)
xanthina: *Wallich s.n.* (K)

APPENDIX D: Herbarium specimens examined in micro-morphological study of seeds

TAXON	COLLECTION
B. aborensis	*Burkill 4* (K)
B. aborensis	*Burkill 36700* (K)
B. acetosella	China, *Henry 10, 737A* (K)
B. acetosella	Thailand, *Maxwell 90-290* (E)
B. c.f. brachyptera	New Guinea, *s.c. 9743* (L)
B. c.f. brachyptera	New Guinea, *Ramos 22017* (L)
B. burkillii	India, *Burkill 36720* (K)
B. cristata	*Koorders 162443* (L)
B. cristata	Goeroepaki, 27/3/1917, *s.c. s.n.* (NY)
B. cristata	Sarason, *s.c. 278* (K)
B. handelii	S.W.China, *Feng 11607* (B)
B. herbacea	Living: Glasgow, 001-122-95
B. incarnata	Living: R.B.G. Kew, 1977-3589
B. leprosa	*Wang 38502* (MO)
B. longifolia	Java, *Sinclair 10080* (E)
B. longifolia	Java, *Nagel 1844* (B)
B. longifolia	Java, *Koorders 44300* (B)
B. longifolia	Malay Peninsula, *Burkill 9989* (B)
B. longifolia	Malay Peninsula, *Ridley 18883* (B)
B. longifolia	Malay Peninsula, *Md Nur 32961* (BM)
B. longifolia	Burma, *Griffith 2587* (B)
B. longifolia	Bhutan, *Cooper 4713* (E)
B. longifolia	Hainan, *Lau 1928* (NY)
B. longifolia	S. China, *Tsang 26832* (E)
B. longifolia	Taiwan, *Chi Tou s.n.* (B)
B. obovoidea	*Russel 2254* (K)
B. c.f. pseudolateralis	*Henty 14820* (L)
B. renifolia	*Warburg 15188* (B)
B. robusta	Java, *Afriastinii 1457* (L)
B. robusta	Java, *Ooststroom 13946* (L)
B. robusta	*Schiffner 2267* (L)
B. robusta	Java, *Vansen 6101* (L)
B. roxburghii	N.E. India, *Parry 866* (K)
B. roxburghii	N.E. India, *Clarke 36195c* (BM)
B. roxburghii	Burma, *J.D. Hooker & Thompson 296* (K)

B. silletensis	*Clarke 37917A* (K)
B. silletensis	Cachar, *Keenan s.n.* (K)
B. tessaricarpa	*Griffith 2586* (K)
B. teysmannianum	ex. Herb. Bogor, *s.c. 753* (B)
B. teysmannianum	*s.c. 8219* (B)
B. trigonocarpa	*sine loc., s.c. s.n.* (K)
B. turbinata	*Alston 14041* (BM)
B. turbinata	*Robinson & Kloss s.n.* (BM)
B. turbinata	*Ridley s.n.* (BM)
B. turbinata	*Bartlett 8578* (NY)
B. urticae	Colombia, *Balls 7503* (E)
B. sp. nov. Sabah	*Clemens s.n.* (BM)

APPENDIX E: Molecular protocols

a. Preservation of field-collected leaf material using silica gel
b. DNA micro-isolation
c. DNA macro-isolation
d. Polymerase Chain Reaction (PCR)
e. Minicolumn gene cleaning (cleaning PCR products)
f. Cycle sequencing (Asymetric PCR)
g. Cleaning cycle sequencing products
h. Digestion of DNA with restriction enzymes

a. Preservation of field-collected leaf material using silica gel

Method follows Chase & Hills (1991).

1. Place c. 6g of fresh leaves in small (10 x 14 cm) resealable plastic bags. If leaves do not fit without folding them tear them first (do not cut) into smaller (c. 6 x 6 cm) pieces.

2. Add about 50 grams of 28-200 mesh size, grade 12 (fine) silica gel (Sigma Chemicals) and about 10 g of indicating gel (colour changes from blue to pink above 20% relative humidity) to the bags and shake well until the gel is distributed between the layers of leaves. Place these bags within larger (13 x 21 cm) resealable plastic bags.

3. Check samples after 12 hours to see if they are dry by bending leaves, dry leaves may be snapped easily and leave a clean break while samples not yet ready will just bend or leave a ragged break .

4. When samples are dry remove most of silica gel (for reuse) and add about three grams of fresh indicating gel. Place dried samples in an air tight container.

b. DNA micro-isolation

Method is a modified version of Doyle & Doyle (1987) (see Appendix Ec)

1. Preheat 400 µl CTAB + 0.8 µl 2β-mercaptoethanol per sample at 60°C. Remove leaf material and store in liquid nitrogen.

2. Place $1cm^2$ of leaf material into a 1.5 µl eppendorf tube and add 400 µl of the preheated buffer and a pinch of acid washed sand.

3. Homogenise using a (sterile) ground glass rod attached to a domestic power drill.

4. Add a pinch of PVPP and incubate for 30 mins at 60°C.

5. Add 400 µl chloroform isoamyl alcohol (24:1), shake and shake gently for 40 mins.

6. Spin down samples at 8000g for 10 mins.

7. Gently remove the supernatant with a medium-bore pastette (yellow tip) and repeat the chloroform extraction, this time mixing for 20 mins.

8. Take the supernatant and transfer to another 1.5 µl eppendorf tube. Precipitate DNA by adding 2/3 volume freezer cold isopropanol and leave at -20°C overnight.

9. Spin down solution at 8000 g for 10 mins. Pour off overlying liquid, invert the tube and leave pellet to air dry for 30 mins.

10. Add 200 µl wash buffer and leave for 2-3 hrs; shake very gently at 15 min intervals.

11. Spin down sample at 8000 g for 10 mins. Pour off overlying liquid, invert the tube and leave the pellet to air dry for 1-2 hrs.

12. Re-suspend pellet in 300 µl of TE.

13. Check concentration of DNA by running 5 µl of sample against a DNA standard on a 1.8% agarose gel. Store at -20°C.

c. DNA macro-isolation

Method follows Doyle & Doyle (1987)

1. Preheat 5 ml 2xCTAB + 10 µl 2β-mercaptoethanol per sample at 60°C. It is wise to pre-heat more buffer than is required in case some of the samples require dilution. Remove about 6 g of leaf material from each plant, discard midribs and place lamina in a small resealable bag, wrap in aluminium foil and freeze in liquid nitrogen.

2. Gently crumble the leaf tissue in the bag over a cold pestle of liquid nitrogen. Add 2 spatulas of fine sand and grind the frozen leaf in liquid nitrogen. Make sure that the material is thoroughly ground into a fine powder, then add 0.5 ml volume of PVPP powder into the pestle and mix.

3. Scrape the powder into a universal tube and add 5 ml of the preheated CTAB-buffer, mix gently, avoid leaving dry material around the rim of the tube.

4. Incubate for 30 mins at 60°C.

5. Add an equal volume of chloroform isoamyl alcohol (24:1), mix by shaking for 2-5 mins, transfer to polypropylene centrifuge tubes, balance the tubes using chloroform isoamyl alcohol and spin at 12500 g for 10 mins.

6. Remove the supernatant with a wide-bore pastette (cut off P1000 Gilson tip), and repeat the chloroform extraction.

7. Take the supernatant and transfer to a universal tube using a wide-bore pastette. Precipitate the DNA by adding 2/3 volume freezer cold isopropanol and rocking gently. Leave DNA overnight in a -20°C freezer to maximise precipitation .

8. Spin down the solution at 700g for 5 mins to collect the pellet. Add 5 ml wash buffer. Leave for at least 20 mins. The DNA can be left overnight at this stage if required.

9. Spin down the solution at 700 g for 5 mins to form a pellet. Pour off overlying liquid, invert the tube and leave the pellet to air dry for 1-2 hours.

10. Re-suspend pellet in 1 ml of TE. If the pellet will not re-suspend immediately, it can be left overnight to dissolve. Furthermore the addition of an extra 2 mls of TE and / or gentle heating (65°C for 30 mins) may help.

11. Add 1 µl 10 mg / ml RNAse to each 1 ml TE / DNA mixture and incubate for 60 mins at 37°C.

12. Dilute with 2 volumes TE (if only 1 ml was added at step 10) and add 0.3 ml of 3M Sodium acetate (pH 8.0). Mix thoroughly until the solution is homogeneous. Then add 2.5 volumes of freezer cold ethanol, and rock gently to precipitate the DNA. Keep rocking the tube until the DNA does not fall rapidly to the base of the tube.

13. Spin down the solution at 700 g for 5 mins to form a pellet. Pour off overlying liquid and leave to air dry. Re-suspend pellet in 0.5-1 ml of TE. Divide sample into two and store at -20^{o}C.

14. Check concentrations of DNA by running out 5 µl of sample against a DNA concentration standard on a 1.8% agarose gel.

Pestles and mortars are washed for 20-30 mins in 0.25M HCl, rinse in water and air dry.

REAGENTS:

CTAB BUFFER

2% CTAB
20 mM EDTA
100 mM Tris-HCl pH 8.0
1.4 M NaCl

+ 0.2% β-mercaptoethanol (add just before use)

WASH BUFFER

76% Ethanol
10 mM Ammonium acetate

PVPP - Polyvinyl polypyrrolidone. Keep 0.5 ml volumes in eppendorf tubes.

d. Polymerase Chain Reaction (PCR)

1. Fill out PCR experiment sheet. Keep ingredients on ice.

2. Make up a master mix including every ingredient except the template DNA. Each reaction should amount to a volume of 50 or 100 µl. The amount of water added depends on the amount of the other ingredients added. Ingredients should be added in the following order:

PCR water (autoclaved distilled H_2O)
dNTP's
NH_4
primers
$MgCl_2$
Dimethylsulfoxide (DMSO) (optimal)
bovine serum albumen (BSA) (optimal)
Taq (Enzyme)

Vortex mix.

3. Divide master mix into individual reaction mixes and add template DNA to each.

4. Spin down individual mixes briefly to ensure that no solutions are left on the sides of the tubes. Add 2 drops of mineral oil.

5. Load tubes into PCR machine (see 2B.3.2. and 2B.4.1. for reaction conditions and times used here).

6. Check levels of PCR products by running out 5-10 µl of sample against a DNA standard on a 1.6% agarose gel.

e. Minicolumn Gene Cleaning (cleaning PCR products)

Required:
80% iso-propanol
PCR water
1 3 ml luer-lock syringe per prep
1 Wizard minicolumn per prep
1.5 ml and 0.5 ml eppendorf tubes
Direct purification buffer
Magic PCR preps resin.

1. Aliquot 100 µl of direct purification buffer into a 1.5 ml tube (this is kept at -20°C and requires thawing before use). Add PCR prep and vortex.

2. Add 1 ml magic resin and vortex 3 times during 1 minute (DNA binds to this resin allowing other compounds to be washed out).

3. For each prep prepare Wizard minicolumn: remove plunger from 3 ml disposable syringe and attach the barrel to the luer lock extension of each minicolumn. Label/number each minicolumn.

4. Pipette the resin/DNA mix into the syringe barrel. Insert the plunger slowly, and gently push the slurry into the minicolumn until plunger reaches bottom of barrel.

5. Detach the syringe from the minicolumn and then remove plunger; reattach the syringe barrel to the minicolumn. Pipette 2 ml of 80% iso-propanol into the syringe to wash the column; insert plunger and gently push it through. Do one at a time.

6. Remove the syringe and transfer the minicolumn to a (re-usable) lidless 1.5 ml tube. Centrifuge for 20 seconds at 12500 g to dry the resin.

7. Transfer minicolumn to a new lidless labelled eppendorf tube. Pipette 50 µl of PCR water to each minicolumn. Tap down on bench top to make sure water is in resin. Leave for up to 30 minutes. Centrifuge for 20 seconds at 12500 g to elute DNA.

5. Add 1 drop of mineral oil.

6. Load tubes into PCR machine (see 2B.3.2. and 2B.4.1. for reaction conditions and times).

g. Cleaning cycle sequencing products

1. For each reaction prepare a 1.5 ml eppendorf tube for each sample containing:
2 µl 3M sodium acetate pH 4.6
50 µl Absolute alcohol

2. Transfer the entire 20 µl contents of the sequencing reaction tube to the 1.5 ml tube containing the acetate/alcohol mix. Vortex and place on ice for 10 mins.

3. Spin at 17000 g for 25 mins.

4. Drain off the solution.

5. Wash the pellet with 300 µl 70% ethanol and spin at 17000 g for 15 mins.

6. Drain ethanol and dry in spinvac for 30 mins at 60^{o} C.

7. This dried sample may be stored in a -20^{o} C freezer wrapped in foil.

h. Digestion of DNA with restriction enzymes

Method follows Hillis *et al.* (1996)

Best results, particularly with double digests, were obtained using Pharmacia Biotech restriction enzymes and the 'one-phor-all buffer plus' system which allowed all the reactions to be carried out using a single standard buffer. Enzyme activities are dependant upon temperature, pH and salt concentrations (Na^+, K^+, Mg^{2+}) and the use of this universal buffer system helps to achieve optimal reaction conditions with a variety of different enzymes.

i. Single Digests

1. A final reaction volume of 20 µl is made up by adding the following to each sterile 0.5 µl eppendorf tube:

buffer
PCR product
restriction enzyme
PCR water

When not in use restriction enzymes must be stored at -20° C. The volume of restriction enzyme added should always be less than 10 % as at higher concentrations the glycerol they are stored in can affect their activity .

2. Mix ingredients and incubate at 37° C (or 60 ° C + cover with a drop of mineral oil for *Taq* I) for approximately four hours.

3. Remove from incubator and store at -20° C until required.

EXAMPLE:

2 or 4 µl 10x buffer stock (as manufacturers instructions)
13.3 µl DNA sample (for typical concentrations *e.g.* Plate 4 but depends on DNA concentration)
0.1-0.33 µl restriction enzyme (depends on enzyme concentration)
PCR water (make up to 20 µl volume)

ii. Double Digests

As with the single digests the total reaction volume should be 20 µl. To compensate for the additional volume of the second restriction enzyme reduce the volume of water accordingly.

Universal buffers allow for most enzymes to be added concurrently but in the case of *Taq* I, which has a higher temperature requirement than the other enzymes used here, single digests are carried out at 37° C before adding this enzyme and incubating at 60 °C. Samples are left for 5-12 hours to digest.

EXAMPLE:

2 or 4 µl 10x buffer stock
13.3 µl DNA sample
0.1-0.33 µl restriction enzyme 1
0.1-0.33 µl restriction enzyme 2
PCR water (make up to 20 µl volume)

APPENDIX F: Informative sites of *trn* L sequences

```
maynensis       GAnnAGCCGnAnnGATnTn
roxburghii      ..CT.nGGACGCCA.ACCC
balansana       ..TTT.GGAAnCCA.AAAC
gracilis        nnnn..GG.n.nn.nnCAn
grandis         ..CT..GGACGCC.CCCCC
herbacea        ..CT..GA.A.AC.C.AA-
incarnata       ..nT..GG.C--------C
masoniana       TTAT..GG.CGCC..CCCC
obliqua         nnCT.TGA.nGAC..nnAT
ulmifolia       TTTC...G.C.AT...A.C
handelii        ..CTT.GGACGAT..CnAT
mannii          ..CC.T.G.CGCC..nnCC
```

APPENDIX G: Recognition sequences of restriction enzymes used in the study

*Alu*I	AG*CT
*Cfo*I	GCG*C
*Hae*III	GG*CC
*Mbo*I	*GATC
*Msp*I	C*CGG
*Rsa*I	GT*AC
*Taq*I	T*CGA
*Hinf*I	G*ANTC
*Bam*HI	G*GATCC
*Cla*I	AT*CGAT
*Dra*I	TTT*AAA
*Eco*RI	G*AATTC
*Eco*RV	GAT*ATC
*Hind*III	A*AGCTT
*Pst*I	CTGCA*G
*Ssp*I	AAT*ATT
*Xba*I	T*CTAGA

* denotes position cut

APPENDIX H: Leaf and petiole anatomy of selected members of *Begonia* section *Sphenanthera* (Hassk.) *sensu* Irmscher and outgroup taxa

Introduction:

Detailed studies of leaf anatomy of *Begonia* have been conducted by both Fellerer (1892) and Cuerrier *et al.* (1990, 1991a & 1991b). The findings of these and other authors suggests that anatomical features of the leaves are of taxonomic significance at the specific and sectional level within the genus. Fellerer (1892) included the following members of section *Sphenanthera sensu* Irmscher in his study: *B. robusta*, *B. multangula*, *B. roxburghii*, *B. silletensis* and *B. trisulcata* (=*B. longifolia sensu* Tebbitt). His study suggest that leaf anatomy may provide characters of taxonomic significance with regards the classification of this section.

A few species from sections *Sphenanthera*, *Platycentrum* and *Petermannia* were examined in the present study with the aim of determining the taxonomic value of leaf anatomy in these taxa. Characters with taxonomic potential are reported. An in depth survey of section *Sphenanthera sensu* Irmscher and outgroups was not conducted here because of the general lack of fresh or pickled leaf material. It is not possible to obtain suitable anatomical sections from herbarium material. It is hoped that if leaf material of further species becomes available such characters may be of value for future research.

Materials and methods:

The following taxa were examined in the study: *B. chlorosticta*, *B. hatacoa*, *B. Platycentrum* sp. 1, *B. Platycentrum* sp. 2, *B. mengyangensis* and three accessions of *B. roxburghii*. Accession numbers of these species are given in Appendix A. Petioles and central and marginal portions of the lamina were sectioned using standard paraffin wax techniques and stained with Heidenheim's haematoxylin with fast green counterstain. Material was observed at x400 under a light microscope.

Results and discussion:

The following characters were found to have taxonomic potential within the taxa studied:

1) Number of schlerenchyma layers in the petiole:

There appears to be a trend from 2-5 layers of relatively large schlerenchya cells in *B. chlorosticta*, *B. hatacoa*, *B. Platycentrum* sp. 1 and *B. Platycentrum* sp. 2 (Plate 15a), to 5-6 layers of relatively small schlerenchyma cells in *B. mengyangensis* and the three accessions of *B. roxburghii* (Plate 15b). This trend reflects the relatively close relationship of *B. mengyangensis* and *B. roxburghii* as suggested by both the

molecular and morphological studies presented here and may be of taxonomic value.

2) Distribution and number of vascular bundles within the petiole

The arrangement of vascular tissue within the petiole of *B. roxburghii* appears to be distinct from the other species examined here. The vascular bundles of Begonia roxburghii appear to be more numerous and arranged closer to the centre of the petiole than in the other species examined. This requires further investigation in additional taxa.

3) Presence or absence of a hypodermis:

The genus *Begonia* has traditionally been the classical example of the multi-layered epidermis (*e.g.* Fellerer, 1892; Habertlandt, 1928; Metcalfe & Chalk, 1979; Bogdan & Barkley, 1969). In the present study, the only species found to have a hypodermis was *B. mengyangensis*. This species has a one layered hypodermis (see illustration). Within section *Sphenanthera* sensu Irmscher the only other species reported to have a hypodermis is *B. silletensis* (Fellerer, 1892). In the present morphological based cladistic analysis, *B. silletensis* and *B. mengyangensis* occur together in an unresolved clade composed of themselves and *B. aborensis*. It would, therefore, appear that this character has taxonomic value. The leaf anatomy of *B. aborensis* has not been investigated to date so it is unknown whether the character is a synapomorphy of this clade.

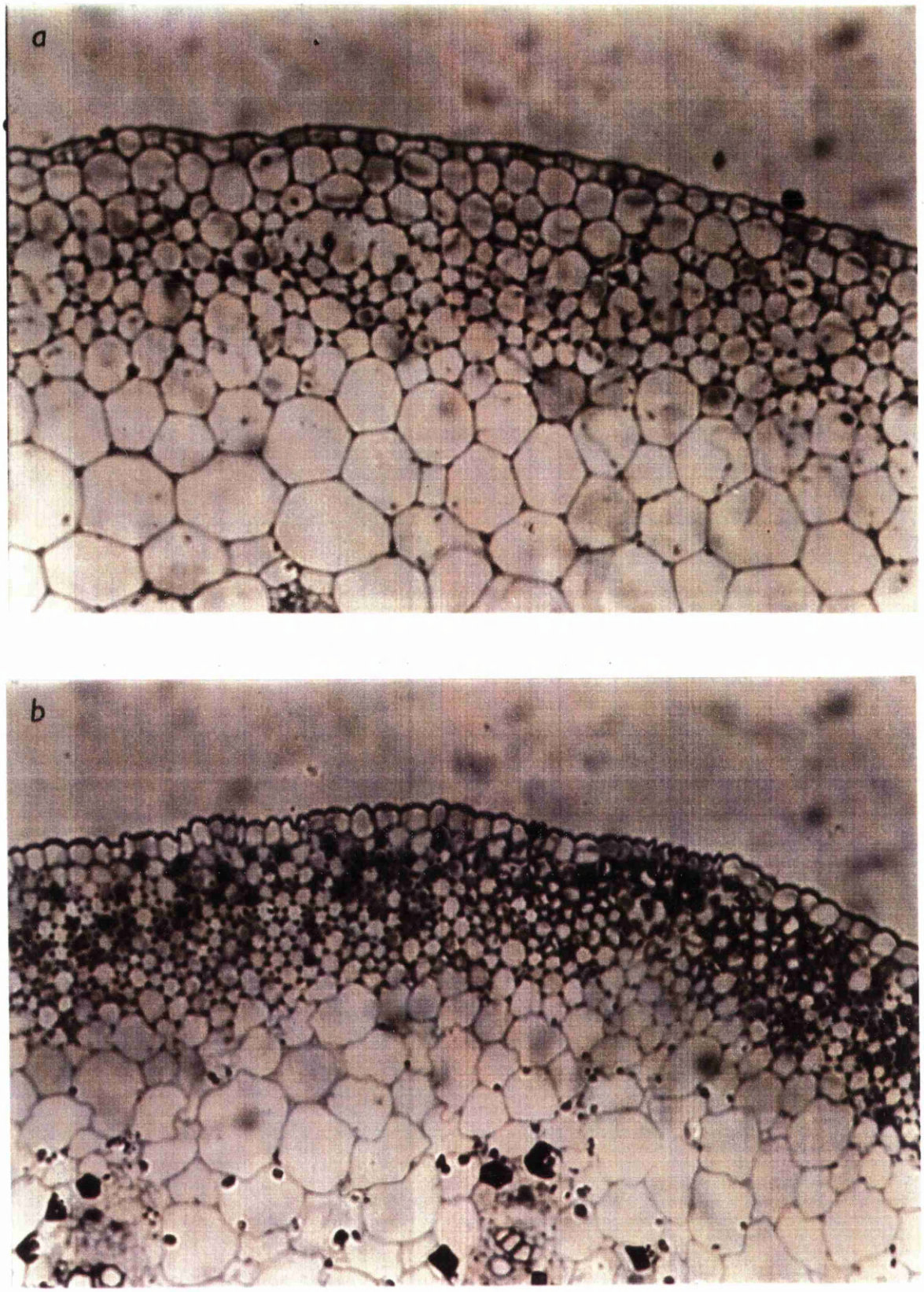


Plate 15. Transverse sections of petioles (a) *Begonia chlorosticta* Sands (section *Petermannia*) with c. 6 layers of relatively large schlerenchyma cells (b) *Begonia roxburghii* (Miq.) A.DC. with c. 8 layers of relatively small schlerenchyma cells

Transverse section of *Begonia mengyangensis* Tebbitt & K.Y. Guan leaf showing hypodermis