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The sections of *Begonia*
including descriptions, keys and species lists

(Studies in Begoniaceae VI)

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1 Historical review

The first description of a plant of what we now call *Begonia* to appear was Francisco Hernandez' 'Totocaxoxo coyollin' from Mexico (1651). The second was 'Tsjeria-nariampuli' from Malabar described by Henricus van Rheede in 1689. Six years later Plumier described six species from the Caribbean Islands of the genus he was the first to name *Begonia*. Tournefort published these descriptions in 1700. For Linnaeus, who had never seen any material of it, *Begonia* was dubious. In his Species Plantarum of 1753 he reduced the six species of Plumier to one, which he gave the name *Begonia obliqua*. (All descriptions and pictures of *Begonia* published up to 1763 have been reproduced by Barkley, 1968).

The number of species known to the world expanded slowly. In 1791 Dryander, the first monographer of the genus, described 21 species and mentioned another 9 'species obscurae'. Fifty years later Steudel in the 2nd edition of his Nomenclator Botanicus listed 140 species names (and 36 synonyms). By that time it had become clear that *Begonia* was a large genus. As early as 1818 Robert Brown wrote 'the extensive genus *Begonia*, which it is perhaps expedient to divide'.

The first to take this to heart was John Lindley, who in 1846 distinguished the genera *Begonia* with one placenta in each locule of the ovary, *Diploclinium* with two placentae per locule and *Eupetalum* with four tepals. Meanwhile, Gaudichaud had proposed the genus *Mezierea* (ignored by Lindley) for a species from Réunion.

The author who went furthest in this direction was Klotzsch. In 1854 and 1855 he published the results of a meticulous study of a large and for the time representative collection of *Begonia* species. On the basis of this study he distinguished no less than 37 genera of *Begoniaceae* in addition to the four of Lindley and Gaudichaud. Although the great merit of Klotzsch' work was - and still is - generally recognized, subsequent authors have not followed his subdivision of the family.

Alphonse de Candolle, who in 1864 published the second - and so far the last - monograph of the *Begoniaceae*, has only three genera: *Mezierea* with 3, *Casparya* with 23, and *Begonia* with 323 species (and 31 'species dubiae'). *Mezierea* is divided into 2, *Casparya* into 8, and *Begonia* into 61 sections, and of these 34 correspond to genera of Klotzsch.

In 1894 Warburg reviewed the *Begoniaceae* for Engler's 'Natürliche Pflanzenfamilien'. He was the first to group the sections of *Begonia* according to continent and divided the genus, in which he included *Casparya* and *Mezierea*, into 12 African, 15 Asian, and 31 American sections, and 3 dubious ones, rejecting 17 of de Candolle's sections but adding 6 new ones.

In the second edition of Engler's monumental work, Irsmscher (1925) greatly expanded Warburg's treatment but in general followed his taxonomy. *Begonia* is divided into 12 African, 16 Asian, and 32 American sections, one section (*Begoniastrum*) with Asian as well as American representatives, and still 3 uncertain sections. Irsmscher's subdivision and key have been used by most subsequent authors, sometimes including the printing errors (which Irsmscher himself corrected in 1929, p. 93) and generally without observing the subsequent changes in Irsmscher's own ideas.

Meanwhile the number of species, put by Warburg at more than 400 and by Irsmscher at more than 760, kept expanding, every collecting trip into territory rich in begonias revealing new ones. Repeatedly species were described that could not be fitted into one of the sections recognized by Irsmscher. He himself had already written on the subject of genera within the *Begoniaceae* 'Wenn man beginnt, einzelne morphologisch besonders abweichende Sektionen als Gattungen abzutrennen ... kommen schliesslich noch andere mit gleichem Recht im Frage und man weiss nicht, wo man Halt machen soll' [When one starts to separate single morphologically aberrant sections as genera ... finally other ones should be considered similarly, and one does not know where to stop]. He must have realized that the same holds true for sections, only more so, for he is very reluctant to describe new sections himself. He proposes two new ones in 1929 and one more in 1939. In later papers he provisionally attaches aberrant species to the nearest section or leaves the classification undecided. In one of the latter cases (Irsmscher, 1953: 95) he writes: 'doch sehe ich auch in diesem Falle von der Aufstellung einer neuen Gruppe zunächst ab, da ich z.Zt. mit der Neuordnung der bekannten Sektionen beschäftigt bin' [I refrain also in this case from the erection of a new group, as I am at the moment working on a rearrangement of the known sections]. It is unfortunate that he never published this rearrangement. We only know that he intended to have vegetative characters play a decisive role as well.

In 1972 F.A. Barkley made an effort to classify all known species according to the sections of A. de Candolle and subsequent

authors. In the same year he published, together with A. Baranov, a list of all known sections of *Begonia*, their accepted names and synonyms together with a short description, where possible based on Irmscher (1925). In addition they recorded the type species of each section, and where this was not yet available, they indicated a lectotype species for accepted as well as rejected section names. Of both publications a revised edition appeared in 1974. The list of species had been much improved through collaboration with J. Golding. The list of sections could also have done with some revision, but except that the order of both authors had been reversed there were only minor changes.

In 1986 'The Begoniaceae' by Lyman B. Smith et al. appeared with a key to all known species, the great majority also pictured, as a rule by a photograph of the type specimen. The species list and relevant literature citations have been prepared with meticulous care by J. Golding and Ms C.E. Karegeannes. This book will be an indispensable work of reference for years to come, but it does not mention sections. Probably because the contention "there are too many gaps in our knowledge to allow us to arrange the species of *Begonia* by sections" (Smith & Schubert, 1946: 6) was still held to be valid.

Be that as it may, when dealing with a genus the size of *Begonia* it is inevitable that one feels the need of a system to survey this multitude of species, preferably one which gives an insight into their natural relationships. As such the traditional grouping of species into sections presents itself and has been used, especially by authors whose work is only indirectly connected with taxonomy, e.g. Cuerrier et al. (anatomy) or Bouman & de Lange (seed micromorphology), who felt the need to discuss the variation they observed in relation to this classification. Until now, the list of species and sections of Baranov & Barkley (1974) has often been used, as it was the most recent, although it was in many ways unsatisfactory. In this way not only some of the inaccuracies of these authors are perpetuated, but the system on which it is largely based, that of Irmscher (1925), got a longer life than Irmscher himself would have wished.

2 Goals of the present study

In the course of their former work with *Begonia*, the present authors became convinced that grouping the species into sections is a useful way to get an insight into the existing variation within this extensive genus. It also became obvious, however, that the descriptions of the sections would have to be brought up-to-date and their delimitation in many cases to be revised.

The purpose of the present study is to draw up an inventory of the sections of *Begonia* that have so far been proposed and to establish to what extent all known species can be fitted into these sections. We may expect that there will turn out to be at the same time too few and too many sections, and that apart from the species that cannot be classified for lack of information there will be quite a few that do not fit any existing section. We have, however, deliberately refrained from describing new sections as we are convinced that this should be based on sound revisional work at the species level.

We do not start with the illusion that we will be able to propose a balanced system for the classification of *Begonia* species. We hope, however, to show in more detail than has been done before the state of the art of the present system, and note the limits of its usefulness by specifying its imperfections and indicating which steps should be taken to further improve it.

3 Methods

We started from the consideration that the merits and shortcomings of the existing subdivision of *Begonia* can only be judged when one tries to apply it to every species so far described. It was a great help to this study that the book of L.B. Smith et al. (1986), giving a complete and reliable list of these species and important literature citations, was available. This work has also been followed in matters of synonymy, except when more recent publications were at hand. Some unpublished information concerning African species, which have been the object of study for two of the present authors, has also been taken into account.

In view of the size of the genus and the limited time and manpower available, an exhaustive study of the existing herbarium material was impossible. Except for the majority of the African species, the data were gathered from literature, supplemented with

herbarium material that was available at Wageningen (WAG): mainly voucher material of a collection of living begonias that in its heyday comprised 350 species. The original publication (protologue) is only cited for sections and other supraspecific taxa. For those of the species the reader is referred to L.B. Smith et al. (1986) and for those described after 1986 to the Index Kewensis. When no other citation is given, data on leaf anatomy are taken from Fellerer (1892) or Cuerrier et al. (1991), on pollen (only available for African species) from van den Berg (1985), on seed micromorphology from de Lange & Bouman (1986, 1992 and in press) and on chromosome numbers from Legro & Doorenbos (1969, 1971, 1973). The identification and nomenclature in the latter has been revised with voucher material at WAG.

As was to be expected, not all species could be accommodated with certainty in the existing sections. In many cases descriptions were inadequate, either because the studied material was incomplete, or because the author had refrained from recording all particulars he could have noted. In these cases the species has been placed in the most plausible section. Often the opinion of the original author has been followed, also when he had omitted some essential characteristics, e.g. the number of placentae.

A different cause of uncertainty are the exceptions, i.e. the species which show all the characteristics of a particular section but one. An example is *B. malmquistiana* which is a typical member of sect. *Petermannia* except for the fact that it has a 2-locular ovary. Only for this reason its author (Irmscher, 1913, 1925) placed it in sect. *Platycentrum*, but later (Irmscher, 1929: 90-91) he considered a place in sect. *Petermannia* more satisfactory after all. The present authors have followed this example, e.g. in the case of *B. paulensis* (placed in sect. *Pritzelia* despite its divided placentae), *B. pavonina* (in sect. *Platycentrum* in spite of the undivided placentae), *B. decandra* (in sect. *Begonia* in spite of the aberrant stamens), and so on. For the latter species A. de Candolle had created a special section, which is incorporated here in sect. *Begonia*. The same has happened with a few other small sections.

When characterizing sections there is of course no getting away from properties used in the original description. In addition we have, as far as we could, used new criteria, e.g. the structure of the inflorescence (studied in detail by Irmscher (e.g. 1925) but cursorily treated by many other authors), protogynous vs protandrous inflorescences, leaf anatomy, seed micromorphology, chromosomes etc.,

but literature on these aspects is still frugal.

As very few species of *Begonia* occur over a wide area, knowledge of geographic origin is very useful in the identification process. To a lesser extent this holds true also for sections. A. de Candolle uses it right at the onset of his key to the sections, and so do Warburg (1894) and Irmischer (1925), who also group the sections according to continent. According to the latter there is one section (*Begoniastrum*, nowadays *Begonia*) which occurs in two continents viz. America and Asia. We will discuss this problem under sect. *Diploclinium*. To our reasoning to keep the American and Asian species in separate sections, we add here that there are also other cases where sections from different continents show close affinities, particularly sect. *Begonia* vs sect. *Augustia* and *Rostrobegonia* (compare e.g. *B. cowelli* from Cuba with *B. dregei*, especially the form '*suffruticosa*'). This, by the way, supports Irmischer's conviction that the species of the section *Begonia* are closest to the archetype of the genus (Irmischer, 1939: 489). There are also affinities between Asian and African sections, e.g. *Diploclinium* and *Quadrilobaria*, and *Reichenheimia* and *Nerviplantentaria*.

As also in our conception sectional distribution is always limited to one of the continents, we considered it useful to present, next to general keys, keys for each continent.

To describe each section in a standardized way all relevant literature was scanned to obtain characters used to delimit the sections (see the next chapter). Each character was critically reviewed and eventually a list of 63 was drawn up on which the present authors agreed that they were significant at sectional level. A form was then designed on which the presence or absence (or rare occurrence) of each character (or as many as possible) could be tagged. Subsequently, these data were entered in a DELTA (Descriptive Language for Taxonomy; Dallwitz, Paine & Zurcher, 1993) format and standard descriptions were extracted. When a character is not mentioned in a description, it means that no information on this character could be obtained for that particular section.

The DELTA files render it possible to identify a certain species to the sectional level by a computer-assisted multi-entry method. Those who are using the DELTA program and interested to receive the DELTA *Begonia* files are suggested to contact the authors.

The DELTA files have also been used, in combination with the PANKEY programs (developed by R.J. Pankhurst), to generate identification keys (see chapter 5).

4 Character list

This chapter lists all plant morphological characters as defined for the DELTA files, and from which the botanical descriptions were generated. Now and again it was found useful to present an explanation about a character and/or its expressions, or of the sense in which it was used by us. The value of the various characters for the delimitation of sections is often indicated. When appropriate, annotations have been added on the geographic distribution of character expressions, or the combinations thereof.

1. **Plant:** growth form

- terrestrial
- epiphytic

The discrimination between terrestrial and epiphytic was found useful for the African sections *Squamibegonia* and *Tetraphila* which are almost strictly epiphytic. In America this is reported for *Trachelocarpus* and *Urniformia*.

2. **Plant:** longevity

- annual
- perennial

Annual *Begonia* species, i.e. short-lived species that survive periods of unfavourable conditions as seeds, are comparatively rare. The species of section *Doratometra* fall in this category as well as some species of section *Begonia*. The latter section contains both annual and perennial species and so do some others (e.g. *Knesebeckia* and *Rostrobegonia*). It is often hard to tell how long the life-span of a plant is. This is also difficult when a species survives with tubercles.

3. **Plant:** habit

- rhizomatous (e.g. fig. 22, 31, 40)
- with an upright stem (e.g. fig. 1, 11, 27, 42)
- with rhizomes from which upright stems arise (e.g. fig. 30)
- lianescent (e.g. fig. 8, 43)
- acaulescent (e.g. fig. 14, 24, 33)

Plant form is used in the horticultural classification system of *Begonia* (see Thompson & Thompson, 1981). This leads to groups of species characterised as 'cane-like', 'fibrous-rooted' and so on, analogous in habit but often containing species non-

related in a taxonomic sense. For sectional delimitation habit is sometimes a useful character, but many sections comprise species of various habits.

4. **Tubers:** presence

- absent
- present (e.g. fig. 1, 3, 10, 14)

The base of the stem, the rhizomes or parts of the roots may thicken to form a tuber. In 8 sections all species are tuberous, whereas in 11 other sections only a part of the constituent species show tubers or tuberous rhizomes. For above-ground bulbils see #6.

5. **Stem:** consistency

- herbaceous
- woody (at least at base)

Although the formation of true wood does not occur within *Begonia*, the stem of many species is ligneous at base. This feature is rarely used for sectional delimitation, but e.g. all species of the sections *Baccabegonia* and *Nervioplacentaria* have woody stem bases.

6. **Tubercles (or cormlets):** presence

- absent
- present

Propagules in which the food is stored in the stem while the leaves are rudimentary are characteristically found in leaf axils of section *Quadriperigonia*, in the monotypic section *Putzeysia*, and incidentally in sections *Diploclinium* and *Rostrobegonia*. Bulbils, propagules in which leaflike organs act as storage organs, are found only in the monotypic section *Peltaugustia*.

7. **Stipules:** persistence

The leaves of *Begoniaceae* are always stipulate. When the stipules are still present at the base of mature leaves they are indicated as persistent. The character generally appeared to be not useful for sectional discrimination.

8. **Stipules:** margin

- entire
- dentate

The margin is called entire when it is not incised in any way; if otherwise it is classified as dentate.

9. **Junction of petiole and leaf blade:** with/without a tuft of hairs

- without a tuft of hairs
- with a tuft of hairs (e.g. fig. 37, 42)

The character is supposed to deal with all kinds of trichomes, including scales. In some species there are only a few hairs or scales, whereas in others there is a conspicuous tuft. Following Irmscher (1961) this character is used to distinguish section *Augustia* from *Rostrobegonia*. In sections like e.g. *Platycentrum* and *Knesebeckia* this tuft of hairs is found only in part of the species.

10. **Leaves:** arrangement

- close and distichous
- alternate
- opposite
- whorled (e.g. fig. 10)

In a large majority of the sections the leaf arrangement is alternate. Distichous leaves are found in some species with creeping stems (very pronounced in *B. thelmae*, which has not yet been classified) and in horizontal laterals of e.g. cane-types of *Pritzelia*. The upper leaves of *B. sibthorpioides* (sect. *Heeringia*) and some species of *Petermannia* are distinctly opposite. Whorled leaves are found in acaulescent species. The monotypic section *Lauchea* has a whorl of leaves at the top of a stem with alternate leaves.

11. **Leaves:** number

- 1 or 2
- more than 2

Restriction of the leaves to 1 or 2 is comparatively rare in *Begonia*. On Madagascar, however, the phenomenon is found in the sections *Erminea*, *Muscibegonia* and especially in *Quadrilobaria*. In Asia species with only 1 or 2 leaves are found in sections *Alicida*, *Diploclinium*, *Heeringia*, *Monophyllum*, *Parvibegonia* and *Reichenheimia*. In America it is very rare (2 species of section *Eupetalum*?).

12. **Leaves:** position relative to petiole

- straight (e.g. fig. 38, 49)
- oblique
- transverse (e.g. fig. 2, 9)

The position is straight when the midrib of the blade is in a direct line with and a continuation of the petiole. It is oblique when the midrib extends from the petiole at an angle of around 45 degrees. It is transverse when the midrib stands at an almost right angle with the petiole.

13. **Leaves:** symmetry

- symmetric (e.g. fig. 10, 13, 49)
- asymmetric (e.g. fig. 3, 12, 26, 32)

Leaves with dissimilar leaf-halves are characteristic for *Begonia*, hence the German name Schiefblätter for the family. Nevertheless, in 12 sections all the constituent species show symmetric leaves, and in 21 sections both species with symmetric and species with asymmetric leaves occur.

14. **Leaves:** peltate or not

- peltate (e.g. fig. 18, 22, 40)
- not peltate

In peltate leaves the petiole is not attached to the margin but to the middle (or more to the side) of the blade. Species with peltate leaves are found in 21 sections, but within these sections they usually occur side by side with species with basifixed leaves. The monotypic sections *Peltaugustia* and *Tetrachia*, and *Ridleyella* with two species, show peltate leaves. In *Gobenia* twelve species out of a total of 14 are peltate.

15. **Leaves:** division

- simple
- palmately lobed (fig. 23)
- palmatifid
- palmatisect
- palmately compound (fig. 39)
- pinnatifid (fig. 15)
- bipinnatifid or further divided

In simple leaves the blade is not divided or lobed in any way. 'Palmately lobed' signifies that the blade is lobed or divided in a hand-like fashion to less than about the middle. In 'palmatifid'

leaves the blade is divided in a similar way for halfway down or more, and in 'palmatisect' leaves the various elements of the blade are free almost down to the base. 'Pinnatifid' leaves show blades cleft in a pinnate rather than palmate way. 'Bipinnatifid' is used when the divisions of a pinnatifid blade are themselves pinnately cleft again.

In most sections the leaves are simple or lobed; further incised leaves occur in only 14 species found throughout the sections. Truly palmately compound leaves are rare; *Scheidweilera* is the only section that is characterised by them.

16. Venation: type

- palmate (e.g. fig. 2, 8, 22, 23)
- palmate-pinnate (e.g. fig. 12, 38)
- pinnate (e.g. fig. 11, 30, 41, 48)

In 15 sections all species have a palmate venation, in 12 sections the venation is always pinnate and in only 6 sections the venation is always palmate-pinnate. In 5 sections all three character states occur, while the remaining sections show two character states.

17. Indumentum of scales: presence

- absent
- present (fig. 45, 47)

Scales referred to here are thin, dry and membranous outgrowths of epidermal origin (trichomes). They can be more or less circular or stellate in outline (not to be confused with stellate hairs #18). In the African sections *Baccabegonia* (2 spp.), *Squamibegonia* (3 spp.) and *Tetraphila* (30 spp.) all species show scales, whereas they are also found in 2 of the 19 species of the African section *Loasibegonia*. Among the Asian and American sections such scales are unknown.

18. Indumentum of stellate hairs: presence

- absent
- present

Stellate or star-shaped hairs have a 'stipe', although sometimes very short, with radiating branches. In Asia 2 species of *Parvibegonia* and in South America a few species of *Knesebeckia* and *Pritzelia* possess stellate hairs.

19. Inflorescence: position

- axillary (e.g. fig. 1, 47)
- terminal (fig. 30, 34)
- at the base of the leaf blade

In a majority of the sections (45) the inflorescences are always implanted in a leaf axil. In 10 other sections species exist in which the inflorescences are axillary, next to species with terminal inflorescences, the latter forming a strong minority. Terminal inflorescences are the rule in *Parvibegonia*, *Quadriperigonia* and in the small or monotypic sections *Bracteibegonia*, *Heeringia*, *Pilderia* and *Rossmannia*. Section *Monophyllon* (2 spp.) represents an exception as the inflorescences arise from the base of the single leaf blade.

20. Inflorescence: general arrangement

- racemose (fig. 29, 30, 34)
- cymose

In *Begoniaceae* the axillary inflorescences are as a rule cymose. The flowers in these inflorescences are basically arranged in compound dichasia which, by reduction, often become monochasial at the apex. Racemose inflorescences are usually terminal with cymose lateral branches, i.e. they are thyrsoid. Racemose inflorescences are confined to a few sections, viz. *Parvibegonia*, *Petermannia*, *Pilderia*, *Rossmannia*, to some species of *Diploclinium* and, probably, *Semibegoniella*.

21. Inflorescence: sexuality

- only bisexual
- bisexual and male
- bisexual and female
- separate male and female (fig. 29, 47)

The sexuality of the inflorescence of *Begonia* is of taxonomic interest. Four character states are distinguished. Most sections have bisexual inflorescences, containing both staminate and pistillate flowers. The bisexual nature of an inflorescence is sometimes difficult to observe as the female flowers may not develop before the male ones have dropped, as in e.g. section *Pritzelia*, or the male flowers may not develop before the female ones have dropped their perianth segments, as in section *Petermannia*. In such cases inflorescences may have been described erroneously as unisexual.

When both bisexual and male inflorescences are present, the latter ones sometimes develop on specific branches and/or under specific conditions. This situation occurs in certain species of *Rostrobegonia*, *Tetraphila*, *Petermannia* and *Casparya*.

Bisexual and female inflorescences have been reported from a few species of *Tetraphila*, *Diploclinium* and *Petermannia*.

Species with separate male and female inflorescences are rare within *Begonia*. They can either occur on the same plant (monoecious), as is characteristic for section *Trachelocarpus* and is observed in some species of section *Tetraphila*, or on separate plants (dioecious), as in some species of *Mezierea*, *Tetraphila* and *Sphenanthera*.

22. Inflorescence: distribution of sexes

- with male flowers basal and female flowers distal (e.g. fig. 11)
- with male flowers distal and female flowers basal (fig. 29)

In most species the cymose inflorescence carries as a rule male central flowers with the lateral female ones produced only in a distal position. In species with a raceme of cymes, the lower cymes are as a rule female and the distal ones male. This is observed in the large section *Petermannia* and a few smaller ones, and in scattered species elsewhere.

23. Inflorescence: protandrous or protogynous

- protandrous (e.g. fig. 11)
- protogynous (fig. 29)

The terms protandrous and protogynous are used here in a wide sense, viz. for bisexual inflorescences in which staminate flowers reach anthesis and shed pollen before pistillate flowers reach maturity and vice versa. The terms are also applied in cases in which separate unisexual (either male or female) inflorescences occur on one plant.

24. Bisexual inflorescence: type

- dichasial (e.g. fig. 27, 32, 40)
- monochasial (e.g. fig. 1)
- dichasial at base, monochasial at apex (e.g. fig. 11, 12, 14)

Basically the inflorescence of *Begonia* is cymose, i.e. composed of a false dichotomy in which the first flower to open terminates the primary axis. Generally, two lateral axes arise from beneath the top flower, each again terminated by a flower. The inflo-

rescence resulting from this simple ramification is called a dichasium. In 18 out of the 63 sections the inflorescences are always neatly dichasial.

In case only one of each pair of laterals develops this is called monochasial branching, the resulting inflorescence being a monochasium. In only a few sections the inflorescences are always completely monochasial, viz. in section *Filicibegonia*, *Loasibegonia*, *Scutobegonia*, *Heeringia*, *Eupetalum* and *Semi-begoniella*.

Mostly, however, bisexual inflorescences in *Begonia* are dichasially branched at the base but monochasially towards the top. This is characteristic for 26 sections.

25. Male inflorescence: type

- dichasial
- monochasial
- dichasial at base, monochasial at apex
- consisting of solitary flowers

Purely male inflorescences have been reported in only 14 sections. They usually show dichasial branching, but in a few sections this changes into monochasial towards the apex. Purely monochasial male inflorescences are rare and not always incontestable. The same holds true for inflorescences consisting of solitary male flowers.

26. Female inflorescences: type

- dichasial
- monochasial
- dichasial at base, monochasial at apex
- consisting of solitary flowers

It is not surprising that purely female inflorescences are encountered in the same sections and species as the male ones. There are, however, considerably more sections with solitary female flowers than with solitary male ones.

27. Inflorescences: number of female flowers

- 1 female flower
- 2 female flowers
- 3 female flowers
- more than 3 female flowers

The total number of female flowers in an inflorescence was

considered to supply a fairly unambiguous character. Analysis of the available data shows that for the 16 African and Malagasy sections our knowledge on this character is quite adequate. For a majority of the extra-African sections, however, this knowledge is often insufficient, sometimes non-existent.

28. Inflorescence axis: development

- strongly reduced (fig. 22, 23, 45, 47)
- not reduced

In Africa the sections *Filicibegonia*, *Loasibegonia*, *Scutobegonia* and *Squamibegonia* show strongly reduced axes, and also in section *Tetraphila* reduced axes are common. Outside Africa strongly contracted axes are comparatively rare, but nevertheless occur in several sections. The small section *Trachelocarpus* is characterized by it.

29. Bracts: persistence

- persistent (during flowering) (e.g. fig. 45)
- caducous (e.g. fig. 2)

Modified leaves present in the inflorescence and supporting the flower-bearing axes are called bracts. In 24 sections all species show persistent bracts, in 10 sections they are always early caducous and in 27 sections both states occur.

30. Bracteoles: presence and number

- absent
- 1
- 2
- 3

Bracteoles are foliaceous structures implanted on the flower-stalk (pedicel). They are often denoted as 'prophylls', in German as 'Vorblätter'. Bracteoles are absent in almost all 16 African and Malagasy sections, occur rarely in Asia (although they may sometimes be overlooked as they can be very small) but are common in America. The presence or absence of bracteoles is often diagnostic at sectional level, but in 16 sections both states occur. When bracteoles are present, their number is usually 2. One is not rare, but 3 is very uncommon. Whether the number of bracteoles has any significance on species or even sectional level is not clear yet.

31. **Bracteoles: position**

- inserted directly below the ovary (fig. 9, 11, 12, 18)
- spaced from the base of the ovary (fig. 16, 50)
- inserted on the ovary (fig. 36)

The first two character states are commonly found in *Begonia*. Whether the third case, where the bracteoles are adnate to the ovary, really occurs, specifically in the small sections *Rossmannia* and *Warburgina*, is not clear as the reports are conflicting.

32. **Perianth segments: colour**

- white or pink
- red
- orange
- yellow

In flowers of *Begoniaceae* it is difficult to distinguish calyx and corolla, but anatomical research shows that the two types of perianth whorls are present. For that reason we prefer to use the term 'perianth segments' in stead of 'tepals' because the latter suggests that no such distinction can be made.

In a very large majority of the sections the colour of the perianth segments is white and/or pink, and among these 17 sections contain also red-flowering species. The small section *Barya* is characterised by its pendant, red-coloured flowers. Orange-coloured begonias are comparatively rare: only few species in the sections *Baryandra*, *Eupetalum*, *Gaerdtia*, *Petermannia*, *Platycentrum* and *Augustia*. In Africa yellow flowers are rather common, viz. in the sections *Loasibegonia* and *Scutobegonia*, *Cristasemen* and *Augustia*. In America and Asia there are only a few yellow-flowering begonias, viz. in the sections *Eupetalum* and *Platycentrum*.

33. **Outer perianth segments: shape**

- rounded at apex (e.g. fig. 2)
- acute at apex (e.g. fig. 3)

Rounded perianth segments are more common than acute ones. The shape of the apex is generally not diagnostic at sectional level as both states occur in many (21) sections. Only in sections *Barya*, *Parietoplacentalia* and *Urniformia* the apex is always acute. There are also a few cases in which the male perianth segments are rounded, but the female ones acute.

34. **Male flower:** number of perianth segments
As a rule this number is constant within species. At sectional level it appears that in 14 sections the number of perianth segments in the male flowers is always 2, in 25 sections it is 4 or sometimes higher, and 21 sections comprise species with 2 and others with 4 segments. Species in which the male flowers show 3 segments are rare: a few are found in *Reichenheimia* and in *Ridleyella*. The number of 5 occurs rarely but in several sections; in *Eupetalum* exceptionally up to 11 perianth segments can be encountered.
35. **Male flower perianth segments:** fusion
- free
- partially fused (fig. 41)
Among the 10 species found in section *Semibegoniella* some show perianth segments fused at base in both the male and female flowers, some only in the male flowers, whereas in other species the segments are free.
36. **Androecium:** symmetry
- actinomorphic (e.g. fig. 19)
- zygomorphic (e.g. fig. 2, 45)
The collectivity of the stamens of a flower, the androecium, is often of diagnostic value for *Begonia* sections; less often it can be used to distinguish species within sections. When the androecium is zygomorphic all stamens are generally positioned in the same direction, resembling a bunch of bananas.
It appears that among the 63 sections 36 invariably show an actinomorphic androecium. In 6 other sections the androecium is either actinomorphic or zygomorphic and in only 12 sections it is always zygomorphic. In 9 sections the arrangement of the stamens is still unknown to us, a conspicuously high number given the importance of the character.
37. **Filaments:** length
- equal (e.g. fig. 33)
- unequal (e.g. fig. 2, 45)
Judged are the free parts of the filaments in the androecium. In the African and Malagasy sections an actinomorphic androecium is generally correlated with the filaments being of equal length, while in zygomorphic androecia they are unequal. For

many of the Asian sections the character is not described as our information is inadequate. In the American sections the above observed correlation is much less distinct.

38. **Filaments:** fusion

- free (e.g. fig. 2, 19)
- partly fused (e.g. fig. 3)
- entirely fused (fig. 18)

Sections exclusively composed of species with free filaments are in the minority. It is sometimes difficult to judge whether the filaments are free though implanted on a low torus or fused at the extreme base. In Africa sections *Baccabegonia* and *Sexalaria* are characterized by free filaments. In Asia only section *Ridleyella*, composed of two or three species, shows this state. In America next to section *Ruizopavonia* (c. 36 spp.), also the smaller or monotypic sections *Rossmannia* (1 sp.), *Scheidweileria* (6 spp.), *Tetrachia* (6 spp.), *Trendelenburgia* (1 sp.) and *Warburgina* (1 sp.) are characterized by free filaments. Sections with variously fused filaments (c. 50) are predominant. About half of these, however, contain also species in which the filaments are free. Species with entirely fused filaments are rare and found scattered in various sections. This state is diagnostic at sectional level only in the monotypic Asian section *Heeringia* (actually the only Asian species with entirely fused filaments) and the American section *Trachelocarpus*.

39. **Anthers:** shape

- circular to elliptic (fig. 12)
- obovate (fig. 31)
- oblong (e.g. fig. 2, 25)
- broadly triangular (fig. 16)

Given the often irregular 3-dimensional shape of the anthers, only the shape of their outline is circumscribed here. Oblong anthers are found in 42 sections, obovate ones in 34. Circular to elliptic anthers are less common. Broadly triangular anthers characterize the monotypic Asian section *Heeringia*, and are found in some of the species of the American section *Gobenia*. Anther shape can be diagnostic at sectional level, e.g. to separate *Begonia* from *Knesebeckia* and *Quadribegonia*, or *Pritzelia* from *Gaerdtia*, but often 2 or more states occur within one section, especially in Africa.

40. **Anthers:** relative length

- longer than the filament (fig. 32)
- about as long as the filament (fig. 1, 33)
- shorter than the filament (fig. 3, 51)

Considered is the length of the anther (excluding the connective) in relation to the length of the free part of its filament. Most commonly, 2 or more states occur within a single section. In 12 sections the anthers are always longer than the filaments, in 7 sections they always equal the length of these, and in 6 sections the anthers are always shorter than the filaments.

41. **Anthers:** dehiscence

- with apical pores
- with short pore-like slits (less than half of the anther length) (fig. 31)
- with longitudinal slits (more than half of the anther length) (e.g. fig. 2, 8)

In Africa pore-like slits are characteristic for the monotypic section *Peltaugustia* and some species of *Tetraphila*. In Asia part of the representatives of the large sections *Diploclinium*, *Petermannia* and *Reichenheimia* show anthers that dehisce with short pore-like slits. In America this state is rare; it is characteristic for *Trachelocarpus* and found in a few species of *Knesebeckia* and *Solananthera*. Anthers opening with distinct apical pores are quite rare in *Begonia*. In Africa the phenomenon is absent, in Asia it is only found in the monotypic section *Heeringia*, and in America it occurs in section *Solananthera*.

42. **Anthers:** position openings

- openings lateral (e.g. fig. 23, 30, 42)
- openings unilateral (e.g. fig. 8, 15)

The anthers of *Begonia* species have two anther cells. The openings (see #41) to release the pollen are either placed on the periphery of the anther (lateral), or they may both be found on one side (unilateral). When the openings are situated on the periphery at the base but bend towards each other towards the top this is always classified as unilateral.

The lateral position is found in 40 sections, unilateral ones in 22 sections, 7 of which show both types.

43. **Anthers:** apex hooded or not
- apex hooded (e.g. fig. 15)
- apex not hooded

In some sections tissue from the rear and side of the anther expands to form a 'cap' over the top of the anther openings. The presence of this cap is usually correlated with a unilateral position of the opening slits of the anther. In Africa hooded anthers are quite common. In describing American and Asian *Begonia* species authors often did not mention this feature and for that reason we lack correct information for 17 sections. In Asia a hooded apex is only reported for the small section *Haagea*. In America it also seems to be poorly represented.

44. **Connective:** extension
- extended (e.g. fig. 6, 9)
- not extended (e.g. fig. 2, 3)

Species with extended connectives are rather rare in Africa, and mainly found in sections *Augustia* and *Rostrobegonia*. In Asia extension of the connective is more common, particularly in the sections *Platycentrum* and *Sphenanthera*. In America extended connectives are found in all or some species of 24 sections. Filiform connective extension, as found among species of section *Casparya*, is comparatively rare.

45. **Female flower:** number of perianth segments

The number of perianth segments in female flowers is of comparatively large taxonomic significance. In 31 sections the female flowers show a definite number of segments, viz. 2 segments (9 sections), 3 (3 sections), 4 (5 sections), 5 (12 sections), and 6 (2 monotypic sections). In the remaining 32 sections the number of segments is not fixed. In section *Diploclinium* it even ranges from 2 to 6. Species with more than 6 segments in the female flowers occur in sections *Eupetalum* (rarely up to 9), *Gobenia* and *Pritzelia* (both rarely up to 7).

46. **Female flower perianth segments:** fusion

- free
- partially fused (fig. 41, 45)

Partially fused perianth segments are rare (see also #35). In all 3 species of the African section *Squamibegonia* the two perianth segments of the female flowers are fused at base to form what is

called a 'perianth cylinder'. This narrow tube connects the top of the ovary with the free parts of the segments (de Wilde & Arends, 1980). In Asia fusion of perianth segments does not seem to occur. Among the 10 species of the American section *Semibegoniella* a number shows 4 to 6 partially fused female perianth segments, similar to the situation found in the male flowers. In other species of this section they are free, but there is also a species with free female but fused male perianth segments.

47. **Ovary or fruit: number of wings**

Ovaries of *Begonia* are usually winged. A number of 3 wings is by far the most common situation, but ovaries without wings or with 1, 2, 4, 5, 6 or even 7 wings also occur. Within sections, and even within species, the number of wings is not always constant, e.g. in the monotypic section *Sexalaria* it may vary between 3 and 7. Wingless fruits are primarily found among the African sections *Baccabegonia*, *Mezierea*, *Squamibegonia* and *Tetrachia*. Their fruits are also more or less fleshy. Outside Africa more or less wingless, berry-like fruits are only found among species in the Asian section *Sphenanthera*. Wingless capsular fruits are encountered in some species of section *Filicibegonia*. Likewise in the African sections *Loasibegonia* and *Scutobegonia* a few species are characterized by wingless fruits. The monotypic Asian section *Apterobegonia* has wingless capsular fruits, and so do a few species of the large Asian sections *Diploclinium* and *Petermannia*. Also in Asia, section *Monopteron*, comprising only 2 species, shows fruits in which only one wing is strongly developed.

In the Neotropics, the monotypic section *Tetrachia* has 4 wings and the same holds for some species of section *Gobenia*. In section *Weilbachia* species occur with 1-winged fruits.

48. **Wings: equal or not**

- equal or subequal in fruit (e.g. fig. 7)

- unequal in fruit (e.g. fig. 11, 21)

During fruit maturation one or more wings may enlarge. Usually the presence of more or less equal or unequal wings is characteristic for a section; in only 16 sections both states occur.

49. **Wings: hook-like or not**

- developed into hooks (fig. 6, 41, 50)

- not hook- or spine-like

In case the wings of the fruit develop into horn-, hook-, or spine-like structures their tip is usually narrowed towards its apex and somewhat curved inwards. The phenomenon is not known from African *Begonia* species. In Asia, it occurs in some species of section *Sphenanthera*. In America, most species of *Casparya* and *Semibegoniella* develop hook-like wings, whereas in the monotypic section *Urniformia* the fruit bears 3 hollow horns.

50. **Locules:** number

In a number of African sections, e.g. in *Meziera*, *Squamibegonia* and *Tetraphila* the type of placentation may change from axillary at the bottom to parietal at the top of a single ovary. As a result the number of locules may be interpreted differently depending on the level at which an ovary is sectioned. In order to standardize this the number of locules relates to a transverse section at about midway.

A number of 3 locules is characteristic for 40 out of the 63 sections. Only 8 sections have 2 locules, 7 of these are from Asia. As a rule the number of locules is quite constant within species, by way of exception it may vary considerably. Within the 2 species of the African section *Baccabegonia* the number of locules varies between 4 and 7. This also occurs in *Tetraphila*, e.g. *B. loranthoides* with 4-8 locules and *B. mannii* with 4 or 5. In all 12 species of the Asian section *Coelocentrum* the ovaries show a parietal placentation and thus are 1-locular.

51. **Placentation:** type

- parietal (fig. 7, 23)
- septal (fig. 2)
- axillary

When the placentation is parietal, the placentae are borne on the ovary wall or on outgrowths of the wall, a rare phenomenon in *Begonia*. In Africa it is found in *Meziera* and *Tetraphila*. In the latter the other two types of placentation also occur. In Asia parietal placentation is limited to the section *Coelocentrum*. In America it is confined to the 3 species of section *Parietoplacentalia* which show all three types of placentation, sometimes even in a single ovary.

Septal placentation, in which the placentae are borne on the

septa, is rare as well, though commonly found in the African sections *Baccabegonia*, *Mezierea* and *Tetraphila*. In these sections, however, the placentation is fundamentally parietal, and the partition of the ovary is the result of fusion of inward outgrowths of placental tissue in its centre. Septal placentation has not been recorded from Asia. In the New World the phenomenon is reported from a single species in section *Knesebeckia*, viz. *B. cavum*.

In all other sections the placentation is axillary, viz. the placentae are borne on the central axis of the ovary.

52. Placental branches: number per locule

The form of the placentae in the locules, either entire, bifid or yet otherwise has always played an important role in the classification of *Begonia*. The character is fairly constant but in some species the placentae may be simple at the bottom of the cavity to become bifid somewhat higher up. For this reason, preferably, the number of placental branches is judged from a transverse section of the ovary about halfway its length (see also # 50).

In 18 sections all species have one placenta per locule, 32 sections all have two. *Doratometra* comprises species with both simple and bifid placentae. In 10 other sections species with an aberrant number of placentae occur as an exception, whereas 3 sections accommodate species with exceptionally 4 placentae.

53. Ovules: presence between placental branches

- present between placental branches

- absent between placental branches

When two or more placentae are present per locule these are usually covered with ovules on both surfaces. However, in some rare cases the surfaces facing each other are devoid of ovules. This is found in the African section *Squamibegonia* and in the Neotropical section *Solananthera* and most of the species of *Gaerdtia*.

54. Styles: number

A majority of the sections (41 out of 63) consistently shows 3 styles. In Asia all species of sections *Heeringia*, *Lauchea*, *Monophyllon*, *Parvibegonia*, *Platycentrum* consistently have 2 styles.

In the Asiatic section *Sphenanthera* (c. 25 spp.) the species usually show 3 or 4 styles, a few, however, have 2. In the small Afri-

can section *Baccabegonia* the number of styles varies between 4 and 7, and between 2 and 6 in *Tetraphila*. In the Neotropics 2 styles is limited to some species of *Weilbachia*, although all species of this section have 2 locules. The monotypic section *Tetrachia* has 4 locules and 4 styles. *Hydristyles* has 3 locules but 4–6 styles and the same holds true for some species of *Eupetalum*.

55. Styles: fusion

- free
- fused less than halfway (fig. 8, 15)
- fused more than halfway (fig. 47)

The distinction of these three character states is rather arbitrary. The character is polymorphous especially among the species in large sections such as *Rostrobegonia*, *Diploclinium*, *Parvibegonia*, *Platycentrum*, *Casparya* and *Knesebeckia*.

56. Styles: shape

- simple
- 2-lobed (fig. 13)
- forked once (e.g. fig. 2)
- forked more than once (fig. 8)

Species with simple styles are rare and never the only type within a section, as demonstrated in sections *Tetraphila*, *Parvibegonia* and *Gireoudia*. A minority is formed by sections in which all species show 2-lobed styles. In 25 sections all species show styles which are forked once. Merely in the monotypic section *Cristasemen* and in sections *Hydristyles* (9 spp.) and *Semibegoniella* (10 spp.) all species exhibit styles that are forked more than once. Many more sections, however, are variable in style shape.

57. Styles: persistence

- persistent in fruit (fig. 12, 19, 42)
- caducous in fruit (e.g. fig. 7, 22)

This character is often supposed to present a stable character among species and higher taxa in *Begoniaceae*. Klotzsch (1855) highly valued this character and used it to divide the family into two tribes, viz. the *Stephanocarpeae* with persistent styles and the *Gymnocarpeae* with deciduous styles.

We found persistent styles in 25 sections, caducous ones in 21 sections, whereas in 14 sections both character states occur. The

persistency of styles can only be determined when mature fruits are available, which is often not the case.

58. **Stigmas:** kidney-shaped or not

- not kidney-shaped
- kidney-shaped (fig. 8)

Among its manifold expressions the stigma is sometimes kidney-shaped, i.e. crescent-shaped with the ends rounded. In 10 small sections all species show kidney-shaped stigmas. In 15 sections part of the species, usually only a few, show this character. In a majority of the sections kidney-shaped stigmas are absent.

59. **Stigmas:** position on style

- in a band and spiralled (e.g. fig. 2, 3, 12)
- in a band and not spiralled (fig. 24)
- all over the style (fig. 42)
- contracted near the style apex (fig. 14)

Most common is the situation in which the stigmatic tissue forms a distinctly spiralled band around the style apex. In 50 sections all or at least a part of the species show this state. Less common is a situation in which the stigmatic tissue is band-shaped but not spiralled. The condition in which the stigmatic tissue is distributed all over the style is rare. It occurs in the African sections *Sexalaria*, in which, however, the stylar part is extremely short, and in *Squamibegonia*. This state has never been reported from Asia. In America *B. fuchsioides* of the small section *Lepsia* shows this state. Finally, a few sections are known in which the stigma is contracted near the style apex. In Africa this is found in a few species of section *Tetraphila*. In Asia this condition seems to be absent. In the Neotropics it is reported for a number of species of the sections *Casparya*, *Doratometra*, *Eupetalum* and *Ruizopavonia*.

60. **Fruits:** berry-like or not

- berry-like (fig. 2, 23, 44, 45, 47)
- not berry-like

As a rule the fruits in *Begonia* are dry capsules. A few sections, however, are characterized by berry-like (baccate), pulpy or fleshy fruits. Notably in Africa this phenomenon is comparatively common, viz. in *Baccabegonia*, *Mezierea*, *Squamibegonia* and *Tetraphila*. In Asia fleshy fruits are characteristic for

Sphenanthera. In the Neotropics red and fleshy fruits are described for the 3 species in section *Parietoplacentalia*.

61. **Fruits: dehiscence**

- not dehiscent (fig. 23, 44, 45)
- irregularly dehiscent (fig. 2)
- dehiscent near the back of the locules (fig. 47)
- dehiscent near the septa
- dehiscent both near the back of the locules and near the septa (fig. 42)
- at the back of the carpels (through the wings)

Apparently little information is available on this character. Out of the 29 Neotropical sections we found data on only 10 sections, for the 18 Asian sections on only 11. For Africa data are still lacking for the Malagasy sections *Erminea* and *Muscibegonia*.

In Africa indehiscent fruits characterize the sections *Loasibegonia*, *Mezierea*, *Scutobegonia*, *Squamibegonia* and with a few exceptions *Filicibegonia*. In these sections the fruits finally disintegrate to release the seeds. The Asian section *Sphenanthera* shows fleshy fruits that are either indehiscent or irregularly dehiscent dependent on the species. Examples of Neotropical species showing indehiscent fruits did not come to our attention. More or less irregularly dehiscent fruits are found in the African section *Baccabegonia* and in a few species of section *Tetraphila*. In Asia this state is described for the small sections *Apterobegonia*, *Lauchea*, *Monophyllon*, *Parvibegonia* and for some of the species of section *Sphenanthera*. In America it is not known.

Dehiscence by slits that arise on or near the back of the locules appears to be the commonest way to release the seeds. In Africa 9 out of the 16 sections release, or are assumed to release, the seeds in this way, whereas in Asia and the Neotropics it is the predominant mode of dehiscence.

Dehiscence of the fruits by slits formed near the septa has as yet not been reported. Dehiscence both near the back of the locules and near the septa is only observed in Africa in the monotypic section *Cristasemen* and in a few species of section *Filicibegonia*. Dehiscence of the fruit through the back of the carpels (through the wings) is characteristic for the Asian section *Alicida* and the American sections *Casparya* and *Semibegoniella*.

62. Fruits: position

- more or less erect (fig. 2, 22, 48)
- pendulous (fig. 1, 8)
- nodding (fig. 7, 25)
- recurved towards the substrate (fig. 40)

This feature should be observed in specimens with mature fruits. Provided these are present, their position presents a useful discriminating character at sectional level.

In many sections all species included show erect fruits, in others they are always pendulous. In a limited number of sections, however, both erect and pendulous fruited species are accommodated.

Nodding fruits make an angle of usually more than 90 degrees with the supporting pedicel. It may, however, be difficult to differentiate pendulous from nodding and in some cases there may be a certain overlap. Nodding fruits are characteristic for the African sections *Muscibegonia*, *Nervioplacentalia* and for some species in section *Quadrilobaria*. In Asia nodding fruits are found in many, perhaps all species of *Coelocentrum*, *Monophyllon*, *Parvibegonia*, *Platycentrum* and *Ridleyella*.

Remarkably little is known about the fruit position in many of the American sections. Nodding fruits are mentioned for species in several sections, but seem to predominate only in *Cyathocnemis* and *Weilbachia*.

Fruits which are recurved towards the substrate by the curving of both the peduncle and the pedicel have so far only been described for section *Scutobegonia*.

63. Fruits: presence of a beak

- without or with an indistinct beak
- with a distinct beak (fig. 48)

The fruit apex may be elongated and narrowed into a slender beak-shaped point. To judge the character mature fruits are usually needed.

In the African sections *Filicibegonia*, *Loasibegonia* and *Scutobegonia* a minority of the species is characterized by beaked fruits. In Asia the 2 small sections *Lauchea* and *Monopteron* and 1 species of *Sphenanthera* have distinctly beaked fruits. In the Neotropics species with beaked fruits are reported for the sections *Parietoplacentalia*, *Semibegoniella* and *Trachelocarpus*.

5 Keys

Keys may serve two different goals. The most obvious one is the identification of an unknown specimen: "To which taxon does my plant belong?". This requires the key to be user-friendly, i.e. ideally to ask for easily observed and straightforward characters. The couplets lead the user to a certain taxon, in our case a section, and he/she can be pretty sure his/her plant belongs there. The second reason to use a key is of a more scientific nature: "How can the group concerned best be subdivided?". Such an analytical key will show a certain grouping of the taxa or 'relationships' between the taxa, related ones keying out closely together. It starts with characters considered most important in the context of a taxonomic subdivision of the total group concerned. Ease of observation is of no or much less concern in such analytical keys, but they tend to have fewer couplets.

We decided to present both 'user-friendly' keys and 'analytical' keys to the sections of *Begonia*. Additional keys are presented for each continent. Exceptions within a section (see chapter 8 for our definition of 'exception') were not taken into account in any of the keys. The 'user-friendly' keys were originally prepared using the PANKEY software (Pankhurst, 1988), after which they were edited and slightly altered manually whenever necessary.

5.1 User-friendly keys

5.1.1 General user-friendly key to all sections

- 1 - Locules 1 or 2.....2
 - Locules 3 to 7.....12
- 2 - Fruit more or less erect, or pendulous.....3
 - Fruit nodding.....7
- 3 - Ovary or fruit wingless; plants epiphytic; indumentum of scales present.....sect. **Tetraphila**
 - Ovary or fruit with 1 or 3 wings; plants terrestrial; indumentum of scales absent.....4
- 4 - Ovary or fruit with 1 wing; stipules early caducous; venation palmate-pinnate; male flower with 2 perianth segments; anthers about as long as the filaments.....sect. **Monopteron**
 - Ovary or fruit with 3 wings; stipules persistent; venation palmate or pinnate; male flower with 4 perianth segments; anthers longer than the filaments or shorter than the filaments.....5
- 5 - Tubers absent; plants with upright stems; stem woody (at least at base); leaves transverse, asymmetric; bisexual inflorescence dichasial at base, monochasial at apex; outer perianth segments acute at apex; anthers obovoid, shorter than the filaments, connective extended; female flower with 3 perianth segments; styles 3; fruit fleshy.....sect. **Parietoplacentalia**
 - Tubers present; plants with rhizomes from which upright stems arise; stem herbaceous; leaves straight, symmetric; bisexual inflorescence dichasial or monochasial; outer perianth segments rounded at apex; anthers circular to elliptic or oblong or broadly triangular, longer than the filaments, connective not extended; female flower with 4 or 5 perianth segments; styles 2; fruit not fleshy.....6
- 6 - Stipules entire; leaves whorled, venation pinnate; inflorescence axillary, dichasial; androecium actinomorphic, filaments fused below, anthers circular to elliptic or oblong; styles forked once, persistent in fruit, stigma not kidney-shaped; fruit pendulous, with a distinct beak.....sect. **Lauchea**
 - Stipules dentate; leaves alternate or opposite, venation palmate; inflorescence terminal, monochasial; androecium zygomorphic, filaments entirely fused, anthers broadly triangular, styles 2-lobed, caducous in fruit, stigma kidney-shaped; fruit more or

- less erect, without or with an indistinct beak.....sect. **Heeringia**
- 7 - Inflorescence at the base of the leaf blade ...sect. **Monophyllon**
 - Inflorescence axillary or terminal.....8
- 8 - Inflorescence terminal.....sect. **Parvibegonia**
 - Inflorescence axillary9
- 9 - Locules 1; placentation parietalsect. **Coelocentrum**
 - Locules 2; placentation axillary.....10
- 10 - Androecium actinomorphic; female flower with 5 perianth segments; stigma not kidney-shaped.....sect. **Platycentrum**
 - Androecium zygomorphic; female flower with 2 to 4 perianth segments; stigma kidney-shaped11
- 11 - Leaves oblique; anthers longer than the filaments, dehiscent with laterally positioned longitudinal slits; female flower with 2 perianth segments; styles fused more than halfway; placental branches 2 per locule.....sect. **Weilbachia**
 - Leaves transverse; anthers about as long as the filaments, dehiscent with unilaterally positioned longitudinal slits; female flower with 3 or 4 perianth segments; styles fused less than halfway; placental branches 1 per locule.....sect. **Ridleyella**
- 12 - Placental branches 1 per locule13
 - Placental branches 2 to 4 per locule.....41
- 13 - Female flower with 2 perianth segments14
 - Female flower with 3 to 6 perianth segments19
- 14 - Anthers dehiscent with laterally positioned longitudinal slits, apex not hoodedsect. **Reichenheimia**
 - Anthers dehiscent with unilaterally positioned longitudinal slits, apex hooded.....15
- 15 - Plants lianescent; styles forked more than once; wings unequal in fruit.....sect. **Cristasemen**
 - Plants rhizomatous or with upright stems; styles 2-lobed or forked once; wings equal or subequal in fruit16
- 16 - Fruit pendulous; plants with upright stems17
 - Fruit more or less erect or recurved towards the substrate; plants rhizomatous.....18
- 17 - Venation palmate-pinnate; inflorescence dichasial at base, monochasial at apex, axes not reduced; androecium actinomorphic, filaments equal, anthers about as long as or shorter than the filaments; styles fused more than halfway or free, forked once, persistent in fruit, stigma not kidney-shaped, in a band and spiralled.....sect. **Haagea**
 - Venation pinnate; inflorescence monochasial, axes strongly

- reduced; androecium zygomorphic, filaments unequal, anthers longer than the filaments; styles fused less than halfway, 2-lobed, caducous in fruit, stigma kidney-shaped, in a band and not spiralled.....sect. **Filicibegonia**
- 18 - Fruit recurved towards the substrate.....sect. **Scutobegonia**
 - Fruit more or less erect.....sect. **Loasibegonia**
- 19 - Tubers present.....20
 - Tubers absent.....25
- 20 - Connective extended.....21
 - Connective not extended.....22
- 21 - Stem usually upright, usually 10-50 cm; fruit narrowed towards the apex.....sect. **Augustia**
 - Plant acaulescent or with short stems; fruit truncate at apex.....
sect. **Erminea**
- 22 - Anthers obovoid.....sect. **Reichenheimia**
 - Anthers oblong.....23
- 23 - Stem woody (at least at base); leaves asymmetric; inflorescence with more than 3 female flowers; styles persistent in fruit.....
sect. **Nervioplacentaria**
 - Plant acaulescent or stem herbaceous; leaves symmetric; inflorescence with 1 to 3 female flowers; styles caducous in fruit.....24
- 24 - Stamens 3 or 4; anthers longer than the filaments.....
sect. **Muscibegonia**
 - Stamens 6 or more; anthers about as long as the filaments.....
sect. **Erminea**
- 25 - Wings developed into hooks.....26
 - Wings not hook- or spine-like.....27
- 26 - Plants epiphytic; stipules early caducous; venation palmate-pinnate; anthers obovoid, about as long as the filaments, dehiscent with laterally positioned longitudinal slits; female flower with 3 perianth segments; styles forked once.....
sect. **Urniformia**
 - Plants terrestrial; stipules persistent; venation pinnate; anthers circular to elliptic or oblong, longer or shorter than the filaments, dehiscent with unilaterally positioned longitudinal slits; female flower with 4 to 6 perianth segments; styles forked more than once.....sect. **Semibegoniella**
- 27 - Stem herbaceous.....28
 - Stem woody (at least at base).....35
- 28 - Plants epiphytic; leaves whorled; inflorescence axes strongly

- reduced.....sect. **Trachelocarpus**
- Plants terrestrial; leaves alternate; inflorescence axes not reduced.....29
- 29 - Inflorescence racemose; lateral inflorescences monochasial.....sect. **Pilderia**
- Whole inflorescence cymose.....30
- 30 - Junction petiole and leaf blade with a tuft of hairs.....31
- Junction petiole and leaf blade without a tuft of hairs.....32
- 31 - Anthers usually shorter than the filaments.....sect. **Rostrobegonia**
- Anthers usually longer than the filaments.....sect. **Pritzelia**
- 32 - Plants annual.....sect. **Doratometra**
- Plants perennial.....33
- 33 - Plants with bulbils; female flower with 6 perianth segments.....sect. **Peltaugustia**
- Plants without bulbils; female flower with (2-)3-5 perianth segments.....34
- 34 - Anthers oblong, usually longer than the filaments, connective extended.....sect. **Pritzelia**
- Anthers obovoid, usually as long as or shorter than the filaments, connective not extended.....sect. **Reichenheimia**
- 35 - Bracteoles absent.....36
- Bracteoles 2.....37
- 36 - Plants epiphytic, rhizomatous; stipules dentate; leaves whorled, symmetric; venation pinnate; inflorescence separate male and female, the axes strongly reduced; filaments entirely fused, anthers obovoid, with short pore-like slits (less than 0.5 of the anther length), connective extended; female flower with 3 perianth segments; styles caducous in fruit; wings equal or subequal in fruit; fruit more or less erect, with a distinct beak...sect. **Trachelocarpus**
- Plants terrestrial, with upright stems or with rhizomes from which upright stems arise; stipules entire; leaves alternate, asymmetric; venation palmate or palmate-pinnate; inflorescence bisexual, the axes not reduced; filaments free or fused below, anthers oblong, with longitudinal slits (more than 0.5 of the anther length), connective not extended; female flower with 4 or 5 perianth segments; styles persistent in fruit; wings unequal in fruit; fruit nodding, without or with an indistinct beak.....sect. **Nervi-placentaria**
- 37 - Leaves palmately compound.....sect. **Scheidweilera**

- Leaves entire or lobed.....39
- 38 - Leaves palmatifid; anthers globose, shorter than the filaments; chalazal end of seeds flattened.....
.....sect. **Scheidweileria** (*B. parviflora*)
- Leaves entire or lobed; anthers oblong, longer than the filaments; chalazal end of seeds not flattened.....39
- 39 - Plants lianescent.....sect. **Wageneria**
- Plants with upright stems.....40
- 40 - Bracteoles spaced from the base of the ovary; male flower with free perianth segments; filaments free, anthers with short pore-like slits (less than 0.5 of the anther length); styles free, persistent in fruit; wings equal or subequal in fruit.....
.....sect. **Trendelenburgia**
- Bracteoles inserted directly below the ovary; male flower with partially fused perianth segments; filaments fused below, anthers with longitudinal slits (more than 0.5 of the anther length); styles fused less than halfway, caducous in fruit; wings unequal in fruit.....sect. **Lepsia**
- 41 - Ovary or fruit wingless (though sometimes triangular with blunt to sharp edges).....42
- Ovary or fruit with 3 to 7 distinct wings.....47
- 42 - Indumentum of scales present.....43
- Indumentum of scales absent.....45
- 43 - Male flower with 4 perianth segments; venation palmate-pinnate or pinnate; female flower with 4 perianth segments.....
.....sect. **Tetraphila**
- Male flower with 2 perianth segments; venation palmate; female flower with 2 perianth segments.....44
- 44 - Plants epiphytic; inflorescence axes strongly reduced; bracts persistent (during flowering); filaments fused below, anthers dehiscent with unilaterally positioned longitudinal slits, apex hooded; perianth segments partially fused; stigma all over the style; placentation axillary, ovules absent between placental branches; fruit not dehiscent.....sect. **Squamibegonia**
- Plants terrestrial; inflorescence axes not reduced; bracts caducous; filaments free, anthers dehiscent with laterally positioned longitudinal slits, apex not hooded; perianth segments free; stigma in a band and spiralled; placentation septal, ovules present between placental branches; fruit irregularly dehiscent.....sect. **Baccabegonia**
- 45 - Styles fused more than halfway; plants with rhizomes from

- which upright stems arise; inflorescence protogynous; styles 2-lobed, stigma kidney-shaped, in a band and not spiralled.....sect. **Apterobegonia**
- Styles fused less than halfway or free; plants rhizomatous or with upright stems or lianescent; inflorescence protandrous; styles forked once, stigma not kidney-shaped, in a band and spiralled.....46
 - 46 - Styles fused less than halfway.....sect. **Sphenanthera**
 - Styles free.....sect. **Mezierea**
 - 47 - Venation pinnate48
 - Venation palmate or palmate-pinnate.....61
 - 48 - Wings equal or subequal in fruit.....49
 - Wings unequal in fruit.....53
 - 49 - Styles caducous in fruit.....50
 - Styles persistent in fruit.....51
 - 50 - Inflorescence with male flowers basal and female flowers distal; anthers dehiscent with laterally positioned longitudinal slits; styles forked more than once, stigma in a band and not spiralled or contracted near style apex; fruit with hooks, dehiscent at the back of the carpels (through the hooks).....sect. **Casparya**
 - Inflorescence with male flowers distal and female flowers basal; anthers dehiscent with unilaterally positioned longitudinal slits; styles 2-lobed or forked once, stigma in a band and spiralled; fruit without hooks, dehiscent near the wings.....sect. **Petermannia**
 - 51 - Female flower with 6 perianth segments; styles 4; ovary or fruit with 4 wings; locules 4.....sect. **Tetrachia**
 - Female flower with 5 perianth segments; styles 3; ovary or fruit with 3 wings; locules 3.....52
 - 52 - Plants with rhizomes from which upright stems arise; stems herbaceous; inflorescence terminal, racemose; bracts persistent; bracteoles inserted directly below the ovary; filaments free, anthers oblong, dehiscent with unilaterally positioned longitudinal slits.....sect. **Bracteibegonia**
 - Plants rhizomatous or with upright stems; stems woody (at least at base); inflorescence axillary, cymose; bracts caducous; bracteoles spaced from the base of the ovary; filaments fused below, anthers obovate, dehiscent with laterally positioned longitudinal slits.....sect. **Gaerdtia**
 - 53 - Inflorescence racemose.....54

- Inflorescence cymose.....55
- 54 - Leaves symmetric; inflorescence with male flowers basal and female flowers distal, protandrous; bracteoles 2, conspicuous; anthers circular to elliptic, dehiscent with laterally positioned longitudinal slits, connective extended; female flower with 2 perianth segments; styles persistent in fruit...sect. **Rossmannia**
- Leaves asymmetric; inflorescence with male flowers distal and female flowers basal, protogynous; bracteoles absent or inconspicuous; anthers obovoid or oblong, dehiscent with unilaterally positioned longitudinal slits, connective not extended; female flower with 4 or 5 perianth segments; styles caducous in fruit...
.....sect. **Petermannia**
- 55 - Inflorescence bisexual and male or bisexual and female or separate male and female.....56
- Inflorescence bisexual.....57
- 56 - Bracteoles 3.....sect. **Warburgina**
- Bracteoles absent.....sect. **Petermannia**
- 57 - Connective not extended.....58
- Connective extended.....60
- 58 - Inflorescence protogynous; styles caducous in fruit.....
.....sect. **Petermannia**
- Inflorescence protandrous; styles persistent in fruit.....59
- 59 - Plants annual; fruit pendulous.....sect. **Doratometra**
- Plants perennial; fruit nodding.....sect. **Donaldia**
- 60 - Leaves pinnately veined; styles caducous in fruit.....
.....sect. **Ruizopavonia**
- Leaves palmately veined; styles persistent in fruit.....
.....sect. **Begonia**
- 61 - Tubers present.....62
- Tubers absent.....79
- 62 - Styles free.....63
- Styles fused less than or more than halfway.....72
- 63 - Plants with rhizomes from which upright stems arise; tubercles in groups, enveloped by bracts; inflorescence axes strongly reduced.....sect. **Putzeysia**
- Plants rhizomatous or with upright stems or acaulescent; tubercles (if present) not enveloped by bracts; inflorescence axes not reduced.....64
- 64 - Bisexual inflorescence monochasial or dichasial at base and monochasial at apex.....65
- Bisexual inflorescence dichasial.....68

- 65 - Junction petiole and leaf blade with a tuft of hairs.....
.....sect. **Rostrobergonia**
- Junction petiole and leaf blade without a tuft of hairs66
- 66 - Fruit nodding.....67
- Fruit more or less erect or pendulous.....sect. **Knesebeckia**
- 67 - Anthers dehiscent with laterally positioned longitudinal slits,
connective not extended.....sect. **Eupetalum**
- Anthers dehiscent with unilaterally positioned longitudinal slits,
connective extendedsect. **Augustia** (*B. princae*)
- 68 - Plants rhizomatous or acaulescent69
- Plants with upright stems70
- 69 - Plants rhizomatous; filaments unequal; fruit pendulous.....
.....sect. **Diploclinium**
- Plants acaulescent or rhizomatous; filaments equal; fruit
more or less erect or nodding.....sect. **Quadrilobaria**
- 70 - Junction petiole and leaf blade with a tuft of hairs.....
.....sect. **Rostrobergonia**
- Junction petiole and leaf blade without a tuft of hairs71
- 71 - Asian species.....sect. **Diploclinium**
- African speciessect. **Augustia** (*B. princae*)
- 72 - Fruit nodding.....73
- Fruit more or less erect, pendulous or recurved towards the
substrate.....74
- 73 - Plants with upright stems; female flower with 5 perianth
segments; wings unequal in fruit; fruit dehiscent near the wings
.....sect. **Quadriperigon**
- Plants rhizomatous or with rhizomes from which upright stems
arise; female flower with 4 perianth segments; wings equal or
subequal in fruit; fruit dehiscent through the wings.....
.....sect. **Alicida**
- 74 - Perianth segments red; filaments unequal, fused into a long
columnsect. **Barya**
- Perianth segments white, pink, orange or yellow; filaments
subequal, free or fused below75
- 75 - Junction petiole and leaf blade with a tuft of hairs
.....sect. **Rostrobergonia**
- Junction petiole and leaf blade without a tuft of hairs76
- 76 - Bisexual inflorescence monochasial or dichasial at base and
monochasial at apex.....sect. **Knesebeckia**
- Bisexual inflorescence dichasial77
- 77 - Fruit dehiscent at the back of the carpels (through the wings)....

-sect. **Alicida**
- Fruit dehiscent near the back of the locules78
78 - Two placentae per loculesect. **Diploclinium**
- One placenta per locule.....sect. **Augustia**
79 - Female flower with 2 to 4 perianth segments.....80
- Female flower with 5 or 6 perianth segments95
80 - Junction petiole and leaf blade with a tuft of hairs.....81
- Junction petiole and leaf blade without a tuft of hairs84
81 - Female flower with 2 perianth segments.....sect. **Gireoudia**
- Female flower with 3 or 4 perianth segments82
82 - Plants rhizomatous and climbing; leaves transverse
.....sect. **Baryandra**
- Plants with upright stems; leaves straight or oblique83
83 - Bisexual inflorescence dichasial at base, monochasial at apex;
connective not extended; styles 2-lobed, stigma kidney-shaped,
all over the style.....sect. **Sexalaria**
- Bisexual inflorescence dichasial or monochasial; connective
extended; styles forked once or more than once, stigma not
kidney-shaped, in a band and spiralledsect. **Rostrobegonia**
84 - Plants annualsect. **Doratometra**
- Plants perennial.....85
85 - Female flower with 2 or 3 perianth segments86
- Female flower with 4 perianth segments90
86 - Androecium zygomorphic.....sect. **Gireoudia**
- Androecium actinomorphic87
87 - Fruit fleshysect. **Parietoplacentalia**
- Fruit not fleshy88
88 - Stem upright89
- Stem rhizomatoussect. **Diploclinium**
89 - Leaves transverse; petioles 0.25—1 times as long as the leaf
bladesect. **Cyathocnemis**
- Leaves straight; petioles 0.2 times as long as the leaf blade or
lesssect. **Ruizopavonia**
90 - Fruit fleshy, not or irregularly dehiscent ...sect. **Sphenanthera**
- Fruit dry, dehiscent at the back of the locules, near or through
the wings.....91
91 - Fruit dehiscent through the wings92
- Fruit dehiscent near the wings93
92 - Plants with upright stems 30—400 cm high; venation palmate-
pinnate; anthers oblong; styles forked more than once, caducous
in fruitsect. **Casparya**

- Plants rhizomatous or with rhizomes from which short (up to 8 cm) stems arise; venation palmate; anthers obovoid; styles 2-lobed or forked once, persistent in fruit.....sect. **Alicida**
- 93 - Inflorescence with male flowers distal and female flowers basal, protogynous.....sect. **Petermannia**
- Inflorescence with male flowers basal and female flowers distal, protandrous.....94
- 94 - Stem upright.....sect. **Ruizopavonia**
- Stem rhizomatous.....sect. **Diploclinium**
- 95 - Bracteoles absent96
- Bracteoles 1, 2 or 3106
- 96 - Anthers dehiscent with unilaterally positioned longitudinal slits.....97
- Anthers dehiscent with laterally positioned longitudinal slits.....101
- 97 - Junction petiole and leaf blade with a tuft of hairs.....sect. **Rostrobegonia**
- Junction petiole and leaf blade without a tuft of hairs98
- 98 - Stems lianescent or scandent; ovules absent between placental branches.....sect. **Solananthera**
- Stems upright; ovules present between placental branches99
- 99 - Plants annual; bracteoles presentsect. **Doratometra**
- Plants perennial; bracteoles absent.....100
- 100 - Inflorescence protogynous, with male flowers distal and female flowers basal.....sect. **Petermannia**
- Inflorescence protandrous, with male flowers basal and female flowers distal.....sect. **Diploclinium**
- 101 - Junction petiole and leaf blade with a tuft of hairs102
- Junction petiole and leaf blade without a tuft of hairs.....103
- 102 - Stigma kidney-shaped, all over the style.....sect. **Sexalaria**
- Stigma not kidney-shaped, in a band and spiralledsect. **Rostrobegonia**
- 103 - Perianth segments red; filaments unequal, fused into a long column.....sect. **Barya**
- Perianth segments white or pink; filaments equal or subequal, free or connate104
- 104 - Plants annual.....sect. **Doratometra**
- Plants perennial105
- 105 - Bisexual inflorescence monochasial or dichasial at base and monochasial at apex.....sect. **Knesebeckia**
- Bisexual inflorescence dichasial.....sect. **Diploclinium**

106 - Bracteoles spaced from the base of the ovary.....	107
- Bracteoles inserted directly below the ovary.....	114
107 - Junction petiole and leaf blade with a tuft of hairs; bracteoles conspicuous.....	sect. Rostrobegonia
- Junction petiole and leaf blade without a tuft of hairs; bracte- oles absent or inconspicuous.....	108
108 - Plants lianescent.....	sect. Solananthera
- Plants rhizomatous or with upright stems.....	109
109 - Filaments fused below.....	110
- Filaments free.....	111
110 - Stem woody (at least at base).....	sect. Gaerdtia
- Stem herbaceous.....	sect. Diploclinium
111 - Leaves transverse.....	112
- Leaves straight or oblique.....	113
112 - Styles forked more than once.....	sect. Hydristyles
- Styles forked once.....	sect. Diploclinium
113 - Plants suffrutescent, stems woody at base; leaves pinnately veined; female flowers with bracteoles.....	sect. Ruizopavonia
- Plants herbaceous; leaves palmately veined; flowers without bracteoles.....	sect. Diploclinium
114 - Junction petiole and leaf blade with a tuft of hairs.....	115
- Junction petiole and leaf blade without a tuft of hairs.....	116
115 - Anthers oblong, connective extended; styles caducous.....sect. Rostrobegonia
- Anthers obovate, connective not extended; styles persistent.....sect. Knesebeckia
116 - Plants lianescent.....	sect. Gobenia
- Plants rhizomatous or with upright stems.....	117
117 - Styles caducous in fruit.....	sect. Ruizopavonia
- Styles persistent in fruit.....	118
118 - Plants perennial.....	119
- Plants annual.....	120
119 - Anthers circular to elliptic or obovoid, about as long as or shorter than the filaments.....	sect. Knesebeckia
- Anthers oblong, longer than the filaments.....	sect. Begonia
120 - Fruit with unequal wings.....	sect. Begonia
- Fruit with equal or subequal wings.....	sect. Doratometra

5.1.2 *User-friendly key to the American sections*

- 1 - Female flower with 2 or 3 perianth segments.....2
- Female flower with 4 to 6 perianth segments.....10
- 2 - Androecium zygomorphic.....3
- Androecium actinomorphic.....4
- 3 - Stigma kidney-shaped; locules 2sect. **Weilbachia**
- Stigma not kidney-shaped; locules 3.....sect. **Gireoudia**
- 4 - Male flower with 4 perianth segments5
- Male flower with 2 perianth segments7
- 5 - Plants epiphytic; wings developed into hooks; placental branches 1 per locule.....sect. **Urniformia**
- Plants terrestrial; wings not hook- or spine-like; placental branches 2 per locule.....6
- 6 - Leaves straight; venation palmate-pinnate or pinnate; bracteoles 2; filaments free, anthers circular to elliptic or oblong; fruit not berry-like, without or with an indistinct beak.....
-sect. **Ruizopavonia**
- Leaves transverse; venation palmate; bracteoles absent; filaments fused below, anthers obovoid; fruit berry-like, with a distinct beak.....sect. **Parietoplacentalia**
- 7 - Anthers obovoid; plants rhizomatous; stipules dentate; leaves whorled; inflorescence separate male and female, the axes strongly reduced; anthers dehiscent with short pore-like slits (less than 0.5 of the anther length); wings equal or subequal in fruit; placental branches 1 per locule.....sect. **Trachelocarpus**
- Anthers circular to elliptic or oblong; plants with upright stems; stipules entire; leaves alternate; inflorescence bisexual, the axes not reduced; anthers dehiscent with longitudinal slits (more than 0.5 of the anther length); wings unequal in fruit; placental branches 2 per locule.....8
- 8 - Leaves transverse; venation palmate.....sect. **Cyathocnemis**
- Leaves straight; venation palmate-pinnate or pinnate.....9
- 9 - Inflorescence axillary, cymose; styles caducous in fruit.....
-sect. **Ruizopavonia**
- Inflorescence terminal, racemose; styles persistent in fruit.....
-sect. **Rossmannia**
- 10 - Placental branches 1 per locule11
- Placental branches 2 per locule20
- 11 - Inflorescence terminal, racemose; bracteoles inserted directly below the ovarysect. **Pilderia**

- Inflorescence axillary, cymose, bracteoles spaced from the base of the ovary12
- 12 - Plants rhizomatous or lianescent13
 - Plants with upright stems14
- 13 - Plants lianescent; anthers dehiscent with laterally positioned longitudinal slits; styles freesect. **Wageneria**
 - Plants rhizomatous; anthers dehiscent with unilaterally positioned longitudinal slits; styles fused less than halfway.....sect. **Pritzelia**
- 14 - Wings developed into hooks; styles forked more than once.....sect. **Semibegoniella**
 - Wings not hook- or spine-like; styles forked once.....15
- 15 - Leaves pinnately veined16
 - Leaves palmately veined.....18
- 16 - Anthers dehiscent with short pore-like slits (less than 0.5 of the anther length)sect. **Trendelenburgia**
 - Anthers dehiscent with longitudinal slits (more than 0.5 of the anther length)17
- 17 - Stomata in large groups; cystoliths absent; no stellate hairs; Colombia to Peru.....sect. **Lepsia**
 - Stomata single or in small groups; cystoliths present or if absent stellate hairs present; Brazil.....sect. **Pritzelia**
- 18 - Leaves palmately compoundsect. **Scheidweileria**
 - Leaves entire or lobedsect. **Pritzelia**
- 19 - Plants perennial.....sect. **Pritzelia**
 - Plants annual.....sect. **Doratometra**
- 20 - Wings equal or subequal in fruit21
 - Wings unequal in fruit24
- 21 - Female flower with 6 perianth segments; male flower with 2 perianth segments; androecium zygomorphic; styles 4; ovary or fruit with 4 wings; locules 4.....sect. **Tetrachia**
 - Female flower with 4 or 5 perianth segments; male flower with 4 perianth segments; androecium actinomorphic; styles 3; ovary or fruit with 3 wings; locules 3.....22
- 22 - Female flower with 4 perianth segments; styles forked more than once, caducous in fruit; fruit more or less erect.....sect. **Casparya**
 - Female flower with 5 perianth segments; styles 2-lobed or forked once, persistent in fruit; fruit pendulous.....23
- 23 - Bracteoles spaced from the base of the ovary; anthers obovoid, about as long as or shorter than the filaments, connective not

	extended.....	sect. Gaerdtia
	- Bracteoles inserted directly below the ovary; anthers oblong, longer than the filaments, connective extended....	sect. Begonia
24	- Tubers present.....	25
	- Tubers absent.....	30
25	- Inflorescence terminal.....	26
	- Inflorescence axillary.....	27
26	- Fruit nodding.....	sect. Quadriperigonia
	- Fruit pendulous.....	sect. Knesebeckia
27	- Perianth segments red or yellow.....	28
	- Perianth segments white or pink.....	29
28	- Outer perianth segments rounded at apex; styles free; fruit nodding.....	sect. Eupetalum
	- Outer perianth segments acute at apex; styles fused less than halfway; fruit pendulous.....	sect. Barya
29	- Fruit pendulous.....	sect. Knesebeckia
	- Fruit nodding.....	sect. Eupetalum
30	- Plants rhizomatous or lianescent.....	31
	- Plants with upright stems.....	33
31	- Plants rhizomatous; leaves asymmetric.....	sect. Begonia
	- Plants lianescent; leaves symmetric.....	32
32	- Stem herbaceous; bracts caducous; anthers oblong, dehiscent with apical pores or short pore-like slits (less than 0.5 of the anther length); styles forked once, caducous in fruit; ovules absent between placental branches.....	sect. Solananthera
	- Stem woody (at least at base); bracts persistent (during flowering); anthers obovoid or broadly triangular, dehiscent with longitudinal slits (more than 0.5 of the anther length); styles 2-lobed, persistent in fruit; ovules present between placental branches.....	sect. Gobenia
33	- Stigmas all over the style.....	sect. Lepsia
	- Stigmas in a band and spiralled.....	34
34	- Inflorescence separate male and female.....	sect. Warburgina
	- Inflorescence bisexual.....	35
35	- Styles caducous in fruit.....	sect. Ruizopavonia
	- Styles persistent in fruit.....	36
36	- Perianth segments red.....	sect. Barya
	- Perianth segments white or pink.....	37
37	- Styles 3 or more, forked more than once.....	sect. Hydristyles
	- Styles 3, 2-lobed or forked once.....	38
38	- Fruit nodding.....	sect. Donaldia

- Fruit pendulous.....39
- 39 - Anthers oblong40
- Anthers circular to elliptic or obovoid.....sect. **Knesebeckia**
- 40 - Plants usually perennial, not self-pollinating.....sect. **Begonia**
- Plants annual, self-pollinatingsect. **Doratometra**

5.1.3 User-friendly key to the African sections

- 1 - Female flower with 2 perianth segments.....2
- Female flower with 3 to 6 perianth segments6
- 2 - Inflorescence axes not reduced3
- Inflorescence axes strongly reduced17
- 3 - Fruit dehiscent near the back of the locules or dehiscent both near the back of the locules and near the septa; stipules persistent; ovary or fruit with 3 wings; fruit not berry-like4
- Fruit not or irregularly dehiscent; stipules early caducous; ovary or fruit wingless; fruit berry-like5
- 4 - Plants acaulescent or rhizomatous; leaves straight; inflorescence dichasial; perianth segments white or pink; androecium actinomorphic, filaments equal, anthers circular to elliptic or oblong, dehiscent with laterally positioned longitudinal slits, apex not hooded; styles free, 2-lobed or forked once; placental branches 2 per locule; fruit dehiscent near the back of the locules, more or less erect or noddingsect. **Quadrilobaria**
- Plants lianescent; leaves transverse; inflorescence dichasial at base, monochasial at apex; perianth segments yellow; androecium zygomorphic, filaments unequal, anthers obovoid, dehiscent with unilaterally positioned longitudinal slits, apex hooded; styles fused less than halfway, forked more than once; placental branches 1 per locule; fruit dehiscent both near the back of the ocules and near the septa, penduloussect. **Cristasemen**
- 5 - Indumentum of scales or stellate hairs absent; styles free; fruit not dehiscentsect. **Mezierea**
- Indumentum of scales and stellate hairs present; styles fused less than halfway; fruit irregularly dehiscent....sect. **Baccabegonia**
- 6 - Ovary or fruit wingless (though sometimes sharply triangular); fruit berry-like7
- Ovary or fruit with 3 to 7 wings; fruit not berry-like8
- 7 - Plants epiphytic; indumentum of scales present; anthers dehiscent with unilaterally positioned longitudinal slits or pore-like

- slits; styles fused less than or more than halfway; fruit irregularly dehiscent or dehiscent near the back of the locules.....sect. **Tetraphila**
- Plants terrestrial; indumentum of scales absent; anthers dehiscent with laterally positioned longitudinal slits; styles free; fruit not dehiscent.....sect. **Mezierea**
- 8 - Leaves peltate (at least the lower ones)9
- Leaves not peltate.....10
- 9 - Plants acaulescent or with short upright stems; flower without bracteoles; anthers with longitudinal slits (more than 0.5 of the anther length), apex not hooded.....sect. **Erminea** (*B. marojejyensis*)
- Plants with an upright stem; flower with 2 bracteoles; anthers with short pore-like slits (less than 0.5 of the anther length), apex hooded.....sect. **Peltaugustia**
- 10 - Bisexual inflorescence dichasial at base, monochasial at apex; stigma all over the stylesect. **Sexalaria**
- Bisexual inflorescence dichasial or monochasial; stigma in a band, spiralled or not spiralled11
- 11 - Plants acaulescent or rhizomatous12
- Plants with upright stems or with rhizomes from which upright stems arise.....14
- 12 - Male flower with 2 perianth segments; styles free; placental branches 2 per locule.....sect. **Quadrilobaria**
- Male flower with 4 perianth segments; styles fused less than or more than halfway; placental branches 1 per locule.....13
- 13 - Stamens 3 or 4; anthers longer than the filaments.....sect. **Muscibegonia**
- Stamens 6 or more; anthers about as long as the filaments.....sect. **Erminea**
- 14 - Stem woody (at least at base); fruit nodding.....sect. **Nerviplantaria**
- Stem herbaceous; fruit more or less erect or pendulous.....15
- 15 - Junction petiole and leaf blade with a tuft of hairs; placental branches usually 2 per locule (occasionally 1 in *B. rostrata*).....sect. **Rostrobegonia**
- Junction petiole and leaf blade without a tuft of hairs; placental branches usually 1 per locule (occasionally 2 in *B. princae* and always 2 in *B. tayloriana*)16
- 16 - Stem 10-50 cm (except in *B. pygmaea*); connective extended; fruit not narrowed towards the apex.....sect. **Augustia**

- Plants acaulescent or with a very short stem; connective not extended; fruit narrowed towards the apex.....sect. **Erminea**
- 17 - Plants epiphytic; stem woody (at least at base); indumentum of stellate scales present; perianth segments partially fused; stigma all over the style; placental branches 2 per locule; fruit berry-like.....sect. **Squamibegonia**
- Plants terrestrial; stem herbaceous; indumentum of stellate scales absent; perianth segments free; stigma in a band, spiralled or not; placental branches 1 per locule; fruit not berry-like....18
- 18 - Plants with upright stems; venation pinnate; styles 2-lobed; fruit pendulous.....sect. **Filicibegonia**
- Plants rhizomatous; venation palmate or palmate-pinnate; styles forked once; fruit more or less erect or recurved towards the substrate.....19
- 19 - Fruit recurved towards the substrate.....sect. **Scutobegonia**
- Fruit more or less erect.....sect. **Loasibegonia**

5.1.4 User-friendly key to the Asian sections

- 1 - Locules 1 or 22
- Locules 3 or 49
- 2 - Inflorescence at the base of the leaf blade....sect. **Monophyllon**
- Inflorescence axillary or terminal3
- 3 - Fruit more or less erect; stipules dentate; filaments entirely fused, anthers broadly triangular.....sect. **Heeringia**
- Fruit pendulous or nodding; stipules entire; filaments free or fused below, anthers circular to elliptic or obovoid or oblong...
.....4
- 4 - Male flower with 2 perianth segments; stem woody (at least at base); ovary or fruit with 1 wingsect. **Monopteron**
- Male flower with 3 or 4 perianth segments; stem herbaceous; ovary or fruit with 3 wings.....5
- 5 - Styles 36
- Styles 2 or 4.....7
- 6 - Bracts caducous; filaments free; locules 2; placentation axillary, placental branches 1 per locule.....sect. **Ridleyella**
- Bracts persistent (during flowering); filaments fused below; locules 1; placentation parietal, placentas bifid.....
.....sect. **Coelocentrum**
- 7 - Leaves whorled; venation pinnate; styles persistent in fruit;

fruit pendulous	sect. Lauchea	
- Leaves alternate; venation palmate or palmate-pinnate; styles caducous in fruit; fruit nodding		8
8 - Inflorescence axillary, cymose	sect. Platycentrum	
- Inflorescence terminal, racemose	sect. Parvibegonia	
9 - Placental branches 1 per locule		10
- Placental branches 2 per locule		11
10 - Venation palmate; anthers dehiscent with laterally positioned longitudinal slits, apex not hooded	sect. Reichenheimia	
- Venation palmate-pinnate; anthers dehiscent with unilaterally positioned longitudinal slits, apex hooded	sect. Haagea	
11 - Bulbils in leaf axil present	sect. Putzeysia	
- Bulbils in leaf axil absent		12
12 - Inflorescence with male flowers distal and female flowers basal		13
- Inflorescence with male flowers basal and female flowers distal		15
13 - Plants rhizomatous or with upright stems or lianescent; styles caducous in fruit	sect. Petermannia	
- Plants with rhizomes from which upright stems arise; styles persistent in fruit		14
14 - Venation pinnate; filaments free, anthers oblong; female flower with 5 perianth segments; styles fused less than halfway, stigma in a band and spiralled; ovary or fruit with 3 wings	sect. Bracteibegonia	
- Venation palmate; filaments fused below, anthers obovoid; female flower with 4 perianth segments; styles fused more than halfway, stigma in a band and not spiralled; ovary or fruit wingless	sect. Apterobegonia	
15 - Perianth segments orange	sect. Baryandra	
- Perianth segments white or pink		16
16 - Leaves symmetric		17
- Leaves asymmetric		18
17 - Fruit dehiscent on both sides of the wings	sect. Diploclinium	
- Fruit dehiscent through the wings	sect. Alicida	
18 - Plants with rhizomes from which upright stems arise; venation pinnate; styles 2-lobed, stigma kidney-shaped	sect. Bracteibegonia	
- Plants rhizomatous or with upright stems; venation palmate or palmate-pinnate; styles forked once, stigma not kidney-shaped		19

- 19 - Fruit fleshy, not or irregularly dehiscent.....sect. **Sphenanthera**
- Fruit dry, dehiscent near the wings.....sect. **Diploclinium**

5.2 Analytical keys

5.2.1 General analytical key to all sections

- 1 - Fruit fleshy, more or less berry-like.....2
- Fruit dry, leathery or papery8
- 2 - Fruit dehiscent with valves.....3
- Fruit not or irregularly dehiscent4
- 3 - Male flower with 2 perianth segments.....sect. **Baccabegonia**
- Male flower with 4 perianth segments.....sect. **Tetraphila**
- 4 - Stellate hairs and scales present.....sect. **Squamibegonia**
- Stellate hairs or scales absent.....5
- 5 - Female flower with 3 perianth segments.....
-sect. **Parietoplacentaria**
- Female flower with 2, 4, 5 or 6 perianth segments6
- 6 - Placentation parietal or septal.....sect. **Mezierea**
- Placentation axillary.....7
- 7 - Inflorescence axillary; male flower with 4 perianth segments....
-sect. **Sphenanthera**
- Inflorescence axillary and terminal; male flower with 2 perianth segments.....sect. **Apterobegonia**
- 8 - Fruit not or irregularly dehiscent9
- Fruit regularly dehiscent.....15
- 9 - Ovary or fruit with 2 locules.....10
- Ovary or fruit with 3 or 4 locules.....12
- 10 - Plant with 1 or 2 leaves; inflorescence at the base of the leaf blade.....sect. **Monophyllon**
- Plant with more than 2 leaves; inflorescence axillary or terminal11
- 11 - Leaves whorled, venation pinnate.....sect. **Lauchea**
- Leaves alternate, venation palmate or palmate-pinnate.....
-sect. **Parvibegonia**
- 12 - Male flower with 2 perianth segments; 1 placenta per locule.....
-13
- Male flower with 4 perianth segments; 2 placentae per locule....
-sect. **Sphenanthera**

13 - Stem upright.....	sect. Filicibegonia	
- Plants rhizomatous.....		14
14 - Mature fruit erect.....	sect. Loasibegonia	
- Mature fruit recurved towards the substrate.....		
	sect. Scutobegonia	
15 - Fruit dehiscent through the wings which are hooked- or horn-shaped		16
- Fruit dehiscent on both sides of the wings.....		19
16 - Plants small, rhizomatous; styles persistent.....	sect. Alicida	
- Plant medium high, with upright stems; styles caducous.....		17
17 - Plants epiphytic; female flower with 3 perianth segments.....		
	sect. Urniformia	
- Plants terrestrial; female flower with (2-)4(-6) perianth segments.....		18
18 - 1 placenta per locule; stamens 4-6.....	sect. Semibegoniella	
- 2 placentae per locule; stamens many.....	sect. Casparya	
19 - Ovary or fruit with 1 locule; placentation parietal.....		
	sect. Coelocentrum	
- Ovary or fruit with 2 or more locules; placentation axillary.....		20
20 - Ovary or fruit with 2 locules.....		21
- Ovary or fruit with 3 or 4 locules.....		25
21 - Male flower with 2 perianth segments.....	sect. Monopteron	
- Male flower with 3 or 4 perianth segments		22
22 - 1 placenta per locule	sect. Ridleyella	
- 2 placentae per locule		23
23 - Anthers dehiscent with pores	sect. Heeringia	
- Anthers dehiscent with slits		24
24 - Female flower with 2(-4) perianth segments...sect. Weilbachia		
- Female flower with (3 or) 5(-6) perianth segments.....		
	sect. Platycentrum	
25 - Ovary or fruit with 4 locules.....		26
- Ovary or fruit with 3 locules.....		27
26 - Plant lianescent.....	sect. Gobenia	
- Plant with upright stems.....	sect. Tetrachia	
27 - Female flower with 2 perianth segments		28
- Female flower with 3 or more perianth segments		35
28 - 1 placenta per locule.....		29
- 2 placentae per locule.....		31
29 - Plant lianescent; flowers yellow	sect. Cristasemen	
- Plant with upright stems; flowers white or pink.....		30

- 30 - Style 2-lobed, stigma kidney-shaped, not spiralled.....sect. **Filicibegonia**
 - Style forked, stigma in a spiralled band.....sect. **Haagea**
- 31 - Inflorescence thyrsoïd; bracteoles longer than the fruit.....sect. **Rossmannia**
 - Inflorescence cymose; bracteoles shorter than the fruit.....32
- 32 - Plant rhizomatoussect. **Gireoudia**
 - Plant with upright stems.....33
- 33 - Leaves straight, venation pinnate.....sect. **Ruizopavonia**
 - Leaves transverse, venation palmate34
- 34 - Androecium zygomorphic.....sect. **Gireoudia**
 - Androecium actinomorphic.....sect. **Cyathocnemis**
- 35 - Plant lianescent or climbing.....36
 - Plant at most scandent or creeping40
- 36 - Flowers orange; female flower with 4 perianth segments.....sect. **Baryandra**
 - Flowers white or pink; female flower with 5 perianth segments.....37
- 37 - 1 placenta per locule; seed with a 'crown' (micropylar or chalazal end inflated).....sect. **Wageneria**
 - 2 placentae per locule; seed without a 'crown'38
- 38 - Leaves peltate; perianth segments of female flower smaller than those of male flower.....sect. **Gobenia**
 - Leaves not peltate; perianth segments of female flower not smaller than those of male flower39
- 39 - Inflorescence unisexual; seeds ellipsoid.....sect. **Petermannia**
 - Inflorescence bisexual; seeds elongatedsect. **Solananthera**
- 40 - Plant dioecious (?); flowers 1-3 together on a peduncle.....sect. **Warburgina**
 - Plant monoecious41
- 41 - Female flowers sessile on the rhizome, male flowers in long-peduncled umbel-like cymes; plant epiphytic.....sect. **Trachelocarpus**
 - Female flowers not sessile42
- 42 - Plant with bulbils or cormels.....43
 - Plant without bulbils or cormels46
- 43 - Plant with bulbils at base of stem; anthers dehiscent with pores.....sect. **Peltaugustia**
 - Plant with cormels in leaf axils; anthers dehiscent with slits...44
- 44 - Clusters of cormels enveloped by bracts.....sect. **Putzeysia**
 - Clusters of cormels not enveloped by bracts.....45

45 - Filaments connate (East Asian species).....
.....	sect. Diploclinium (group II)
- Filaments free (Mexican species).....	sect. Quadriperigonía
46 - Plant acaulescent or rhizomatous.....	47
- Plant ascendent or with upright stems.....	54
47 - Plant acaulescent	48
- Plant rhizomatous.....	53
48 - 1 placenta per locule.....	49
- 2 placentae per locule	50
49 - Stamens 3 or 4; seed papillate.....	sect. Muscibegonia
- Stamens 6 or more; seed smooth.....	sect. Erminea
50 - Male flower with 2 perianth segments	sect. Quadrilobaria
- Male flower with 4 or more perianth segments.....	51
51 - Female flower with 5 or 6 perianth segments..	sect. Eupetalum
- Female flower with 3 or 4 perianth segments	52
52 - Leaves asymmetrical; anthers oblong.....	sect. Quadrilobaria
- Leaves symmetrical; anthers obovate
.....	sect. Diploclinium (group III)
53 - Female flower with 3 or 4 perianth segments.....
.....	sect. Reichenheimia
- Female flower with 5 perianth segments	sect. Pritzelia
54 - 1 placenta per locule.....	55
- 2 placentae per locule	65
55 - Male flower with 2 perianth segments [for <i>B. dregei</i> (sect. <i>Augustia</i>) with 2 or 4 perianth segments follow 60].....	56
- Male flower with 4 perianth segments.....	60
56 - Tubers absent.....	57
- Tubers present	59
57 - Inflorescence racemose.....	sect. Pilderia
- Inflorescence cymose.....	58
58 - Plant annual	sect. Doratometra
- Plant perennial	sect. Nervi-placentaria
59 - Stem woody at base; fruit nodding, wings rounded.....
.....	sect. Nervi-placentaria
- Stem herbaceous; fruit pendulous, wings triangular.....
.....	sect. Augustia
60 - Plant annual, self-pollinating.....	sect. Doratometra
- Plant perennial, not self-pollinating.....	61
61 - Leaves compound; seed with flattened ends.....
.....	sect. Scheidweileri
- Leaves simple, entire or lobed; seeds without flattened ends...62	

- 62 - Cystoliths present, or if absent hairs stellate (predominantly Brazil)63
 - Cystoliths absent; hairs not stellate (Colombia to Peru).....64
- 63 - Anthers dehiscent with apical pore-like slits; seeds about 8 times as long as broad.....sect. **Trendelenburgia**
 - Anthers dehiscent with long slits; seeds 1.7–2.6 times as long as broadsect. **Pritzelia**
- 64 - Inflorescence terminal, a raceme of cymes.....sect. **Pilderia**
 - Inflorescence axillary, cymosesect. **Lepsia**
- 65 - Male flower with 2 perianth segments66
 - Male flower with 4 perianth segments71
- 66 - Inflorescence protogynoussect. **Petermannia**
 - Inflorescence protandrous67
- 67 - Leaves straight, venation pinnate.....68
 - Leaves transverse, venation palmate or pinnate-palmate.....69
- 68 - Bracts and styles persistent.....sect. **Donaldia**
 - Bracts and styles caducous.....sect. **Ruizopavonia**
- 69 - Tubers present; female flower without bracteoles.....
 -sect. **Augustia**
 - Tubers absent; female flower with bracteoles70
- 70 - Styles 3–6, forked more than once.....sect. **Hydristyles**
 - Styles 3, forked once71
- 71 - Inflorescence protogynoussect. **Petermannia**
 - Inflorescence protandrous.....72
- 72 - Filaments connate into a long column; perianth segments lanceolate.....sect. **Barya**
 - Column absent or short; perianth segments ovate.....73
- 73 - Top of petiole with a tuft of hairs74
 - Top of petiole without a tuft of hairs.....76
- 74 - Anthers obovatesect. **Knesebeckia**
 - Anthers oblong75
- 75 - Connective extended; styles forked, not persistent, stigma spiralled.....sect. **Rostropegonia**
 - Connective not extended; styles 2-lobed, persistent, stigma all over the stylesect. **Sexalaria**
- 76 - Tubers present77
 - Tubers absent.....79
- 77 - Inflorescence terminal, thyrsoid.....
 -sect. **Diploclinium** (group II)
 - Inflorescence axillary, cymose.....78
- 78 - Styles multibranchedsect. **Eupetalum**

- Styles bifid.....sect. **Knesebeckia**
- 79 - Leaves straight, venation pinnate.....80
 - Leaves transverse, venation palmate or palmate-pinnate.....82
- 80 - Styles caducous.....sect. **Ruizopavonia**
 - Styles persistent.....81
- 81 - Anthers oblong; placentae with ovule on 2 sides.....
 -sect. **Donaldia**
 - Anthers obovate; no ovules between placentae....sect. **Gaerdtia**
- 82 - Anthers oblong, longer than the filaments.....sect. **Begonia**
 - Anthers obovate, as long as or shorter than the filaments.....83
- 83 - Inflorescence terminal, thyrsoïd.....
 -sect. **Diploclinium** (group II)
 - Inflorescence axillary, cymose.....sect. **Knesebeckia**

5.2.2 Analytical key to the American sections

- 1 - Fruit dehiscent through the wings, which are usually hook- or horn-like.....2
 - Fruit dehiscent on both sides of the wings.....4
- 2 - Plant epiphytic; female flower with 3 perianth segments.....
 -sect. **Urniformia**
 - Plant terrestrial; female flower with (2-)4(-6) perianth segments.....3
- 3 - 1 placenta per locule; stamens 4-6.....sect. **Semibegoniella**
 - 2 placentae per locule; stamens many.....sect. **Casparya**
- 4 - Ovary or fruit with 2 or 4 locules.....5
 - Ovary or fruit with 3 locules.....7
- 5 - Ovary or fruit with 2 locules.....sect. **Weilbachia**
 - Ovary or fruit with 4 locules.....6
- 6 - Plant lianescent.....sect. **Gobenia**
 - Plant with upright stems.....sect. **Tetrachia**
- 7 - Female flower with 2 perianth segments.....8
 - Female flower with 3 or more perianth segments.....12
- 8 - Inflorescence thyrsoïd; bracteoles longer than the fruit.....
 -sect. **Rossmannia**
 - Inflorescence cymose; bracteoles shorter than the fruit.....9
- 9 - Plant rhizomatous.....sect. **Gireoudia**
 - Plant with upright stems.....10
- 10 - Leaves straight, venation pinnate.....sect. **Ruizopavonia**
 - Leaves transverse, venation palmate.....11

- 11 - Androecium actinomorphic.....sect. **Cyathocnemis**
 - Androecium zygomorphic.....sect. **Gireoudia**
- 12 - Plant lianescent or climbing.....13
 - Stem upright or prostrate.....15
- 13 - 1 placenta per locule; seed with a 'crown' (micropylar or
 chalazal end inflated).....sect. **Wageneria**
 - 2 placentae per locule; seed without a crown14
- 14 - Leaves peltate; perianth segments of female flower smaller than
 those of male flower; seeds about 2.2 times as long as broad
sect. **Gobenia**
 - Leaves not peltate; perianth segments of female flower equal to
 those of male flower; seeds about 6 times as long as broad
sect. **Solananthera**
- 15 - Male and female flowers in separate inflorescences.....16
 - Inflorescence bisexual.....17
- 16 - Male and female flowers in clusters of 1-3 on a peduncle.....
sect. **Warburgina**
 - Male flowers in long-peduncled, umbel-like cymes, female
 flowers sessile on the rhizomesect. **Trachelocarpus**
- 17 - Inflorescence a raceme of cymes.....18
 - Inflorescence cymose.....19
- 18 - Plant with cormels; stems upright, not branched; leaves
 palmately veinedsect. **Quadriperigonia**
 - Plant without cormels; stems ascendent, branched; leaves
 pinnately veined.....sect. **Pilderia**
- 19 - Female flower with 3 perianth segments; fruit fleshy.....
sect. **Parietoplacentalia**
 - Female flower with 4 or more perianth segments; fruit dry
20
- 20 - Plant acaulescent or rhizomatous.....21
 - Plant with upright stems.....22
- 21 - Plant acaulescent; tubers present.....sect. **Eupetalum**
 - Plant rhizomatous; tubers absent.....sect. **Pritzelia**
- 22 - 1 placenta per locule.....23
 - 2 placentae per locule28
- 23 - Male flower with 2 perianth segments.....sect. **Doratometra**
 - Male flower with 4 perianth segments24
- 24 - Plant annual, self-pollinating.....sect. **Doratometra**
 - Plant perennial, not self-pollinating.....25
- 25 - Leaves compound; seed with a flattened end
sect. **Scheidweilera**

- Leaves simple, entire or lobed; seed without a flattened end...26
- 26 - Cystoliths absent; hairs not stellate.....sect. **Lepsia**
- Cystoliths present or, when absent, stellate hairs present.....27
- 27 - Anthers dehiscent with pores; seeds about 8 times as long as broad.....sect. **Trendelenburgia**
- Anthers dehiscent with longitudinal slits; seeds ellipsoid, 1.7–2.6 times as long as broad.....sect. **Pritzelia**
- 28 - Male flower with 2 perianth segments29
- Male flower with 4 perianth segments32
- 29 - Leaves straight, venation pinnate.....30
- Leaves transverse, venation palmate or palmate-pinnate31
- 30 - Bracts and styles persistent.....sect. **Donaldia**
- Bracts and styles caducous.....sect. **Ruizopavonia**
- 31 - Styles 3–6, irregularly branched.....sect. **Hydristyles**
- Styles 3, forked once.....sect. **Cyathocnemis**
- 32 - Perianth segments lanceolate; filaments connate into a long column.....sect. **Barya**
- Perianth segments ovate; filaments free or connate into a short column.....33
- 33 - Petiole with a tuft of hairs at the apex.....sect. **Knesebeckia**
- Petiole without a tuft of hairs at apex34
- 34 - Tubers present.....35
- Tubers absent.....36
- 35 - Styles bifid.....sect. **Knesebeckia**
- Styles multifid.....sect. **Eupetalum**
- 36 - Leaves straight, venation pinnate.....37
- Leaves transverse, venation palmate or palmate-pinnate39
- 37 - Styles caducoussect. **Ruizopavonia**
- Styles persistent.....38
- 38 - Anthers oblong; placentae with ovules on both sides.....
-sect. **Donaldia**
- Anthers obovoid; no ovules in between the placentae.....
-sect. **Gaerdtia**
- 39 - Anthers oblong, longer than the filaments.....sect. **Begonia**
- Anthers obovoid, as long as or shorter than the filaments.....
-sect. **Knesebeckia**

5.2.3 Analytical key to the African sections

- 1 - Fruit fleshy, berry-like.....2
- Fruit dry, leathery or papery5
- 2 - Fruit dehiscent with valves.....3
- Fruit not or irregularly dehiscent.....4
- 3 - Male flower with 2 perianth segments.....sect. **Baccabegonia**
- Male flower with 4 perianth segments.....sect. **Tetraphila**
- 4 - Stellate scales present; inflorescence axes reduced; bracts persistent even in fruitsect. **Squamibegonia**
- Stellate scales absent; inflorescence axes not reduced; bracts caducous.....sect. **Mezierea**
- 5 - Fruit not or irregularly dehiscent6
- Fruit regularly dehiscent.....8
- 6 - Stem upright.....sect. **Filicibegonia**
- Plant rhizomatous7
- 7 - Mature fruit erect.....sect. **Loasibegonia**
- Mature fruit recurved towards the substratesect. **Scutobegonia**
- 8 - Female flower with 2 perianth segments.....9
- Female flower with 3-6 perianth segments.....11
- 9 - Plant acaulescent or rhizomatous; androecium actinomorphic; placentae 2 per loculesect. **Quadrilobaria**
- Plant with upright stems; androecium zygomorphic; 1 placenta per locule.....10
- 10 - Plant lianescent; flowers yellowsect. **Cristasemen**
- Stem upright; flowers white or pinksect. **Filicibegonia**
- 11 - Plant acaulescent or rhizomatous.....12
- Plant with upright stems.....14
- 12 - 1 placenta per locule.....13
- 2 placentae per locule (as far as known)....sect. **Quadrilobaria**
- 13 - Stamens 3 or 4; seed papillate.....sect. **Muscibegonia**
- Stamens 6 or more; seed smoothsect. **Erminea**
- 14 - 2 placentae per locule15
- 1 placenta per locule.....17
- 15 - Petiole without a tuft of hairs at the apex.....sect. **Augustia**
- Petiole with a tuft of hairs at the apex.....16
- 16 - Style 2-lobed, stigma kidney-shaped, not spiralled.....sect. **Sexalaria**
- Style forked, stigma not kidney-shaped, spiralledsect. **Rostrobegonia**

- 17 - Fruits nodding, with rounded wings.....sect. **Nervi**placentaria
 - Fruits more or less erect or pendulous, with obtriangular wings 18
- 18 - Stem with bulbils at base; leaves peltate (at least the lower ones)sect. **Peltaugustia**
 - Stem without bulbils; leaves not peltate.....sect. **Augustia**

5.2.4 Analytical key to the Asian sections

- 1 - Fruit fleshy, somewhat berry-like; wings fleshy or absent.....2
 - Fruit dry; wings leathery or papery3
- 2 - Inflorescence terminal; male flowers with 2 perianth segments..
 -sect. **Apterobegonia**
 - Inflorescence axillary; male flower with 4 perianth segments
 -sect. **Sphenanthera**
- 3 - Fruit not or irregularly dehiscent; locules 2.....4
 - Fruit regularly dehiscent; locules 1-36
- 4 - Leaves 1 or 2; inflorescence at the base of the leaf
 -sect. **Monophyllon**
 - Leaves more than 2; inflorescence terminal or axillary5
- 5 - Leaves whorled, venation pinnatesect. **Lauchea**
 - Leaves alternate, venation palmate or palmate-pinnate
 -sect. **Parvibegonia**
- 6 - Fruit dehiscent through the wings.....sect. **Alicida**
 - Fruit dehiscent on both sides of the wings.....7
- 7 - Ovary or fruit with 1 locule; placentation parietal.....
 -sect. **Coelocentrum**
 - Ovary or fruit with 2 or 3 locules; placentation axillary.....8
- 8 - Ovary or fruit with 2 locules.....9
 - Ovary or fruit with 3 locules.....11
- 9 - 1 placenta per loculesect. **Ridleyella**
 - 2 placentae per locule10
- 10 - Inflorescence terminal, monochasial; anthers dehiscent with pores.....sect. **Heeringia**
 - Inflorescence axillary, dichasial at base, monochasial at apex; anthers dehiscent with longitudinal slits.....sect. **Platycentrum**
- 11 - Stem absent or plant rhizomatous.....12
 - Stem upright or lianescent.....13
- 12 - 1 placenta per loculesect. **Reichenheimia** (group I & III)
 - 2 placentae per loculesect. **Diploclinium** (group I & III)

13 - Stem lianescent or climbing.....	14
- Stem upright	15
14 - Flowers orange; female flower with 4 perianth segments.....	
.....sect. Baryandra	
- Flowers white or pink; female flower with 5 perianth segments.	
.....sect. Petermannia	
15 - 1 placenta per locule.....	16
- 2 placentae per locule	17
16 - Tubers absent; leaves transverse, venation palmate-pinnate.....	
.....sect. Haagea	
- Tubers present; leaves straight, venation pinnate.....	
.....sect. Reichenheimia (group II)	
17 - Plant with cormels.....	18
- Plant without cormels	19
18 - Cluster of cormels enveloped by bracts.....	sect. Putzeysia
- Cormels not enveloped by bracts	
.....sect. Diploclinium (group II)	
19 - Male flowers with 2 perianth segments.....	sect. Petermannia
- Male flowers with 4 perianth segments	20
20 - Inflorescence protogynous	sect. Petermannia
- Inflorescence protandrous	21
21 - Venation pinnate.....	sect. Bracteibegonia
- Venation palmate or palmate-pinnate	
.....sect. Diploclinium (group II)	

6 Taxonomic treatments

6.1 Generic description of *Begonia*

Begonia L.

Sp. Pl. 2: 1056 (1753); Gen. Pl., ed. 5: 475 (1754), type species: *B. obliqua* L.
(for synonyms see Smith & Schubert, 1958).

Terrestrial or epiphytic, perennial or more rarely annual, monoecious or very rarely dioecious herbs, sometimes shrubs; stems herbaceous, often succulent, or woody, frequently rhizomatous, or plants tuberous and either acaulescent or short-stemmed, rarely lianoid or climbing with adventitious roots. Leaves arranged spirally, stipulate, petiolate, asymmetric or exceptionally symmetric, sometimes peltate, entire to pinnatifid or rarely even bipinnatifid or palmately compound, pinnately or palmately veined, glabrous or pubescent, rarely with stellate hairs or scale-like trichomes; sometimes with bulbils in the leaf axils. Inflorescence unisexual or androgynous, usually cymose, sometimes racemose or racemose with cymose branches, rarely 1-flowered, protandrous or protogynous; cymes dichasial and/or monochasial, sometimes with strongly reduced axes, when bisexual the central flower male and lateral flowers female; bracts persistent or not, bracteoles often present. Flowers unisexual. Male flowers with 2 or (3-)4(-8), almost free to variously fused perianth segments; androecium with 3 to many stamens, actinomorphic or zygomorphic and then sometimes the stamens arranged into several rows like an amphitheatre; filaments free or variously fused into a column; anthers with 2 thecae, opening lengthwise with slits, with pore-like slits or more rarely with terminal pores, connective frequently extended. Female flowers with 2-6(-9) free or partially fused, often unequal perianth segments which are sometimes persistent in fruit; ovary inferior, with (1-)3-4(-7) often unequal wings or horns, more rarely wingless, broadly obovoid or ovoid to globose or fusiform in shape, triangular, square or terete in circumference, (1-)2-3(-6)-locular, the locules sometimes incomplete; placentation axillary or less often parietal or septal, occasionally changing from the bottom of the ovary towards the top, placental branches 1-2(-4) per locule; styles (2-)3-4(-7), persistent or caducous, often partly fused, once or more

times forked towards the apex or more rarely simple, stigmatic tissue generally in a continuous band coiled around the arms, less often kidney-shaped or in an uncoiled band or distributed all over the style. Fruit a capsule, rarely berry-like and fleshy, usually loculicidal, more rarely indehiscent. Seed characterized by a ring of collar cells below the micropylar-hilar part which acts as an operculum during germination.

A pantropical genus (few species in the warm temperate zone) with about 1400 species at the moment classified in 63 sections.

6.2 Alphabetical treatment of the sections

sect. **Alicida** C.B. Clarke

Fl. Brit. India 2: 637 (1879), lectotype species (Barkley & Baranov, 1972): *B. alicida* C.B. Clarke.

Plants terrestrial, perennial, rhizomatous or with rhizomes from which upright stems arise; tubers absent or present; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire. **Leaves** alternate, 1 or 2 or more than 2, straight, symmetric, not peltate, simple; venation palmate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary and terminal, dichasial (or thyrsoid?), bisexual, with male flowers basal and female flowers distal, protandrous, with the central flower of the cyme male, lateral flower(s) female (doubtful); inflorescence axes not reduced; bracts persistent (during flowering). **Flower** without bracteoles (? , not described); perianth segments white or pink, outer ones rounded at apex. *Male flower* with 4 free perianth segments; filaments fused below, anthers obovate (or ovate), connective not extended. *Female flower* with 4 free perianth segments; ovary or fruit with 3 wings, wings equal or subequal in fruit, locules 3, placentation axillary, placental branches 2 per locule; styles 3, fused less than or more than halfway, 2-lobed or forked once, persistent in fruit, stigma kidney-shaped or not, in a band and spiralled or not spiralled. **Fruit** dehiscent at the back of the carpels (through the wings), without or with an indistinct beak.

DISTRIBUTION: Asia: Myanmar (Burma).

IMPORTANT LITERATURE: Clarke (1879, 1880).

TAXONOMIC COMMENTS: So far, the protologues of the three species of this section, without pictures, are all that is known. Consequently, some characters are unknown or not clear; particularly the inflorescence deserves further study.

SPECIES LIST: 3 species: *B. alicida* C.B. Clarke, *B. tricuspida* C.B. Clarke, *B. triradiata* C.B. Clarke.

sect. **Apterobegonia** Warb.

in Engl. & Prantl, Die Natürl. Pflanzenfam. (ed. 1) 3, 6a: 143 (1894), type species: *B. delicatula* Parish ex C.B. Clarke.

Plants terrestrial, perennial, with rhizomes from which upright stems arise; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight, asymmetric, not peltate, simple; venation palmate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary and terminal, dichasial, bisexual, with male flowers distal and female flowers basal (?), protogynous (?); inflorescence axes not reduced; bracts persistent (during flowering). **Flower** without bracteoles; outer perianth segments rounded at apex. *Male flower* with 2 free perianth segments; filaments fused below (implanted on a column), anthers obovate, connective not extended. *Female flower* with 4 free perianth segments; ovary or fruit wingless, locules 3, placentation axillary (?), placental branches 2 per locule; styles 3, fused more than halfway, 2-lobed, persistent in fruit (?), stigma kidney-shaped, in a band and not spiralled. **Fruit** irregularly dehiscent, more or less erect (?), without or with an indistinct beak.

DISTRIBUTION: Asia: Myanmar (Burma).

IMPORTANT LITERATURE: Clarke (1879).

TAXONOMIC COMMENTS: There seems to be just one specimen and just one description of the only species.

SPECIES LIST: A single species: *B. delicatula* Parish ex C.B. Clarke.

Prodr. 15(1): 384 (1864). — *Augustia* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 124 (1854), lectotype species (Barkley & Baranov, 1972): *Augustia dregei* (Otto & Dietr.) Klotzsch = *B. dregei* Otto & Dietr. (homotypic synonym).

Plants terrestrial, perennial, with upright stems; tubers present; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire or dentate; junction petiole and leaf blade without or rarely with a tuft of hairs (occasionally in *B. dregei* and *B. sutherlandii*). **Leaves** alternate, more than 2, straight to oblique, symmetric or asymmetric, not peltate, simple to palmately lobed or rarely palmatifid; venation palmate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary and terminal, dichasial or monochasial, bisexual or rarely bisexual and male (*B. sutherlandii* occasionally), protandrous, with 1 to 3 or rarely more than 3 female flowers, the central flower of the cyme male, lateral flower(s) female; inflorescence axes not reduced; bracts persistent (during flowering) or caducous. **Flower** without bracteoles (rarely 1 or 2 in *B. homonyma*); perianth segments white or pink or rarely orange or yellow (*B. sutherlandii*), outer ones rounded at apex. **Male flower** with 2 or 4 free perianth segments; androecium actinomorphic (but often not described), filaments equal or unequal, free to fused below or rarely entirely fused, anthers circular or obovate to oblong, about as long as or shorter than or rarely longer than the filaments, dehiscent with laterally or unilaterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective extended. **Female flower** with (3–)5 free perianth segments; ovary or fruit with 3 wings, wings equal to unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 1 per locule or rarely 2 (*B. princae*, *B. tayloriana*); styles 3, free to fused more than halfway, forked once or rarely 2-lobed, persistent or caducous in fruit, stigma not or rarely kidney-shaped, in a band and spiralled or rarely not spiralled. **Fruit** not berry-like, dehiscent near the back of the locules, more or less erect or pendulous, without or with an indistinct beak.

DISTRIBUTION: Africa: tropical East Africa, from eastern Dem. Rep. Congo and Tanzania to South Africa, one species in Angola.

LEAF ANATOMY: Stomata single; hypoderm absent; no cystoliths (*B. dregei*).

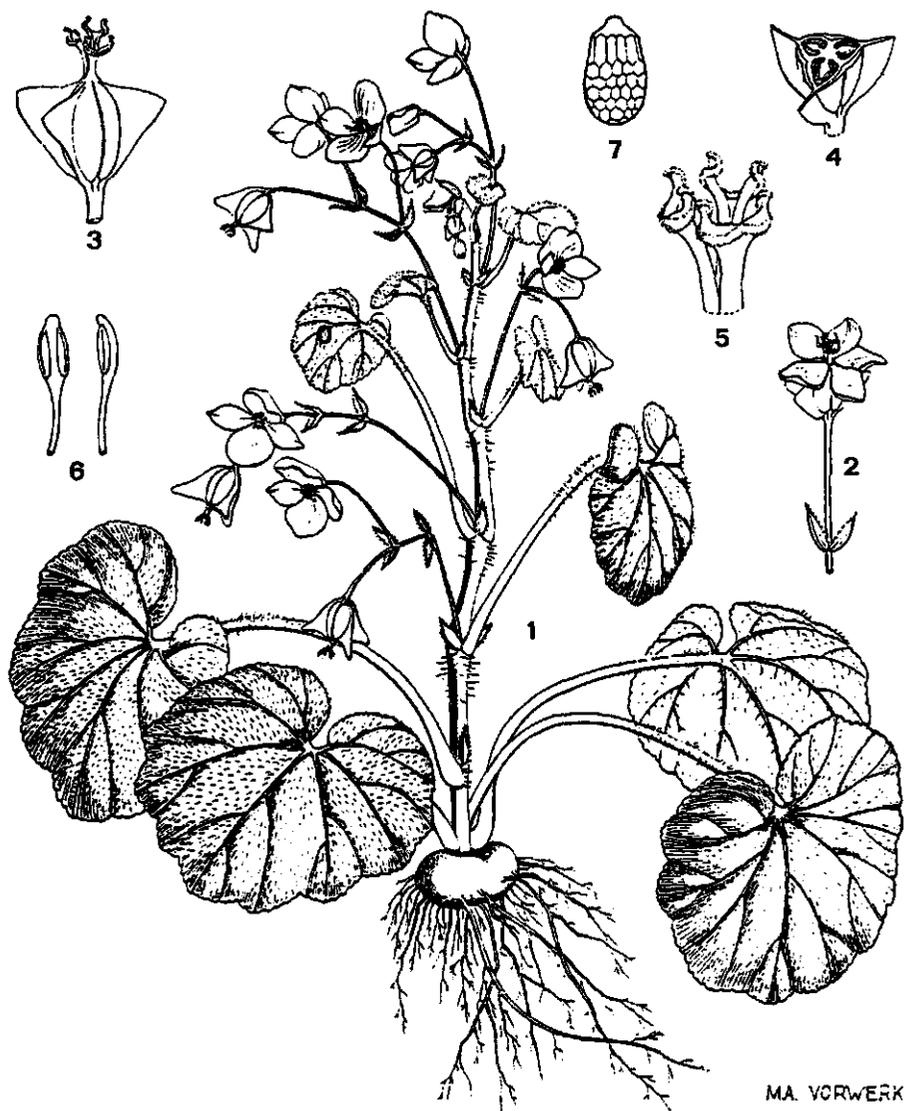


Fig. 1. Sect. *Augustia*. *B. geranioides* — 1, plant habit; 2, female flower; 3, ovary and styles; 4, ovary in transverse section; 5, styles; 6, stamens; 7, seed. Reproduced from Hilliard (1976): fig. 44.

SEED MICROMORPHOLOGY: Seeds ellipsoid, 450–520 x 265–305 μm ; length/width ratio 1.7; ratio collar to seed length about 1:2.3; anticlinal walls between collar cells straight or almost straight, those between the testa cells straight; operculum almost flat, nipple-shaped; cuticular ornamentation linear.

CHROMOSOMES: $2n = 26$ (*B. sutherlandii*); $2n = 56$ (*B. dregei*, *B. homonyma*, *B. princeae*).

IMPORTANT LITERATURE: Irmscher (1961), Hilliard (1976), Kupicha (1978), Wilczek (1969).

TAXONOMIC COMMENTS: See sect. *Rostrobegonia* and sect. *Peltaugustia*.

SPECIES LIST: 12 species: *B. angolensis* Irmscher, *B. brevibracteata* Kupicha, *B. dregei* Otto & Dietr., *B. geranioides* Hook. f., *B. homonyma* Steud., *B. princeae* Gilg, *B. pygmaea* Irmscher, *B. riparia* Irmscher, *B. stolzii* Irmscher, *B. sutherlandii* Hook. f., *B. tayloriana* Irmscher, *B. wakefieldii* Gilg ex Engl.

sect. **Baccabegonia** Reitsma

Fig. 2

Agric. Univ. Wageningen Papers 84-3: 97 (1985), type species: *B. baccata* Hook. f.

Plants terrestrial, perennial, with upright stems; tubers absent; stem woody (at least at base); tubercles in leaf axil absent; stipules early caducous, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, oblique or transverse, asymmetric, peltate or not, simple; venation palmate; indumentum of scales and stellate hairs present. **Inflorescence** axillary, dichasial at base, monochasial at apex, bisexual, protandrous, with up to 30 female flowers, the central flower of the cyme male, lateral flowers female; inflorescence axes not reduced; bracts caducous. **Flower** without bracteoles; perianth segments white or pink, outer ones rounded at apex. *Male flower* with 2 free perianth segments; androecium zygomorphic, filaments unequal, free, anthers obovate, longer than to shorter than the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective not extended. *Female flower* with 2 free

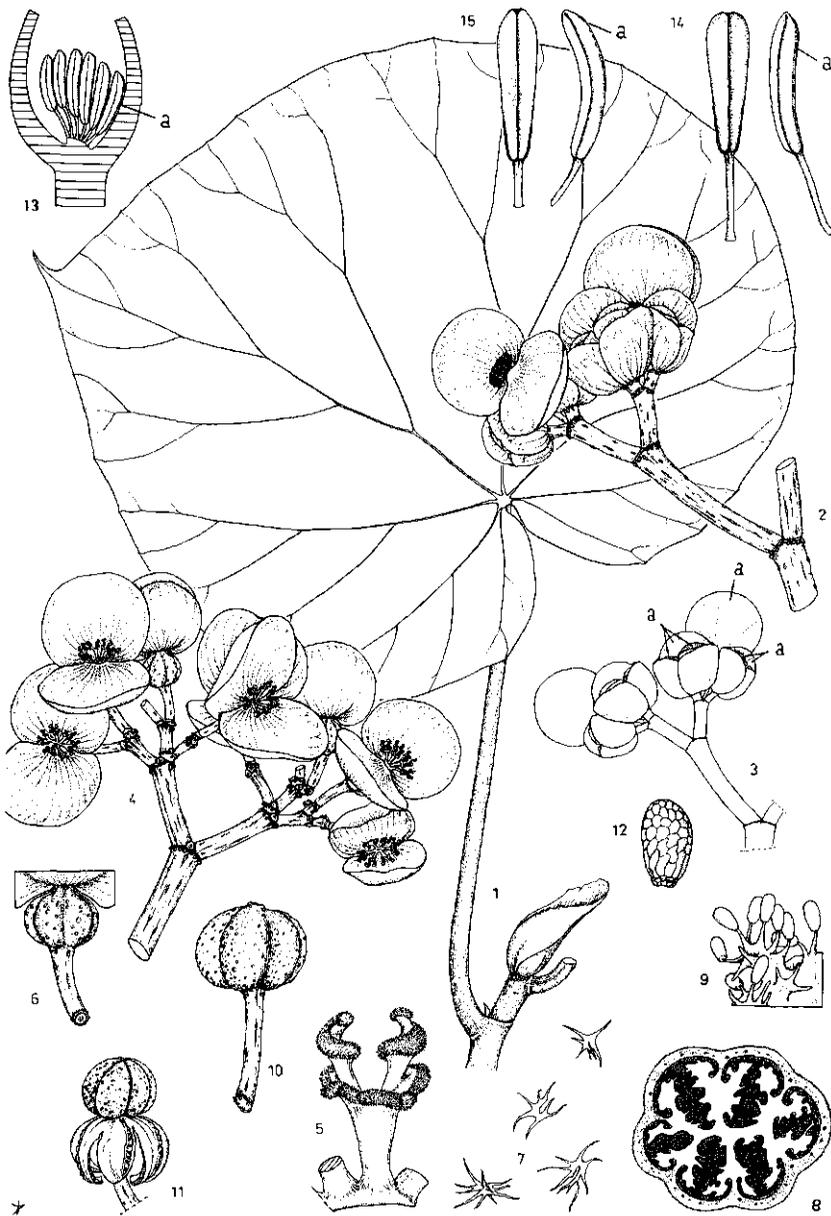


Fig. 2. Sect. *Baccabegonia*. *B. baccata* — 1, leaf; 2, inflorescence with male flowers; 3, androgynous inflorescence with male flowers (a) reaching anthesis first; 4, inflorescence with female flowers; 5, style; 6, ovary; 7, stellate scales; 8, ovary in transverse section; 9, placenta with ovules; 10, fruit; 11, dehisced fruit; 12, seed; 13, male flower in longitudinal section; 14 stamens in dorsal and lateral view; 15, stamens in ventral and lateral view. Drawing by Miss Ike Zewald.

perianth segments; ovary or fruit wingless, locules (4-)5-6(-7), placentation septal, placental branches 2-4 per locule, ovules present between placental branches; styles 4-6(-7), fused less than halfway, forked once, caducous in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** berry-like, irregularly dehiscent (by valves from the apex to the base), more or less erect, without a beak.

DISTRIBUTION: Africa: endemic on São Tomé.

SEED MICROMORPHOLOGY: Seeds ellipsoid, 550-630 x 300-330 µm; length/width ratio 1.9; ratio collar to seed length 1:2.9; anticlinal walls between collar cells slightly curved, those between testa cells curved; testa cells shallow; operculum obtusate; anticlinal boundaries flat; cuticular ornamentation almost absent.

CHROMOSOMES: $2n = 36$.

IMPORTANT LITERATURE: Reitsma (1985).

TAXONOMIC COMMENTS: The pedicels are characteristically more or less elongated in fruit. The endemic occurrence of the section on the oceanic island São Tomé might be explained by long-distance dispersal of the seeds by birds from the continent. Afterwards the section survived under favourable island conditions during the period that their near relatives on the mainland became extinct under the influence of Pleistocene climatic conditions.

SPECIES LIST: 2 species: *B. baccata* Hook. f., *B. crateris* Exell.

sect. **Barya** (Klotzsch) A. DC.

Fig. 3

Ann. Sci. Nat., Bot. 4, 11: 122 (1859). — *Barya* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 122 (1854), type species: *Barya monadelpha* (Ruiz ex Klotzsch) Klotzsch = *Begonia monadelpha* Ruiz & Pavon ex A. DC. (homotypic synonym).

Plants terrestrial, perennial, with upright stems; tubers absent or present; stem herbaceous or woody (at least at base); tubercles in leaf axil absent; stipules persistent or early caducous, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, oblique to transverse, asymmetric, not peltate, simple or

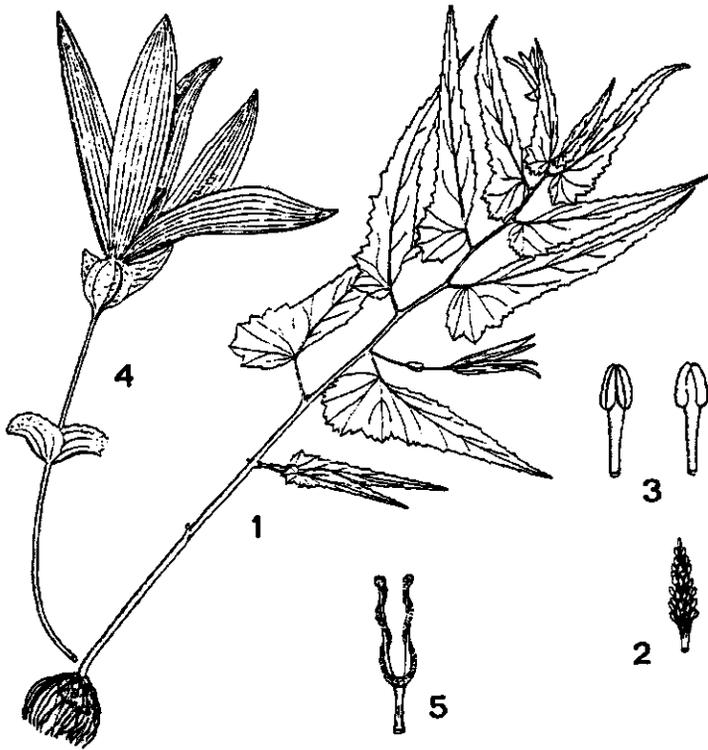


Fig. 3. Sect. *Barya*. *B. boliviensis* — 1, plant habit; 2, androecium; 3, stamens; 4, female flower; 5, style. Reproduced from Smith & Schubert (1941): p. 83, fig. 1.

palmately lobed; venation palmate or palmate-pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary (possibly terminal in *B. soror*), dichasial or monochasial, bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not or strongly reduced (*B. soror*); bracts persistent (during flowering) or caducous. **Flower** without bracteoles; perianth segments red, outer ones acute at apex. *Male flower* with 4 free perianth segments; androecium actinomorphic, filaments unequal, fused below (into a long column), anthers circular to elliptic or oblong (ovate in *B. boliviensis*), shorter than or rarely longer than the free part of the filaments (*B. soror*), dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective extended or not. *Female flower* with 5 or 6 free perianth segments; ovary or fruit with 3 wings, wings

unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles 3, fused less than halfway, forked once, persistent in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, pendulous (at least in *B. boliviensis*), without or with an indistinct beak.

DISTRIBUTION: America: 1 species in Bolivia, 2 species in Peru.

LEAF ANATOMY: Stomata single; hypoderm absent; no cystoliths (*B. boliviensis*, *B. monadelpha*).

SEED MICROMORPHOLOGY: Seed narrowly ellipsoid to ellipsoid, mean length from 510 μm (*B. monadelpha*) to 355 μm (*B. boliviensis*), length/width ratio 2.7 and 1.5 resp.

CHROMOSOMES: The only species that is well-known, *B. boliviensis*, does not only have the same number of chromosomes as several other tuberous species, viz. $2n = 28$, but when hybridized with the latter (e.g. *B. veitchii* or *B. pearcei*) gives a fertile offspring, which is evidence of a close relationship, closer perhaps than with the other species of *Barya*.

TAXONOMIC COMMENTS: The three species that constitute this small section are similar in habit and linked by the pendant flowers with acute, slender tepals that do not spread out fully, and especially by the filaments which are of considerable, but unequal length and joined to a stretched column. On closer inspection, the species show considerable differences, and the section may not be as natural as it seems. According to A. DC., *B. boliviensis* has 2 bracteoles whereas *B. monadelpha* has none. The material of *B. boliviensis* at WAG has no bracteoles and it seems likely that A. DC. meant the bracts.

SPECIES LIST: 3 species: *B. boliviensis* A. DC., *B. monadelpha* Ruiz & Pavon ex A. DC., *B. soror* Irmscher.

sect. **Baryandra** A. DC.

Ann. Sci. Nat., Bot. 4, 11: 122 (1859), type species: *B. oxysperma* A. DC.

Plants terrestrial, perennial, rhizomatous (and climbing); tubers

absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade with a tuft of hairs (not conspicuous). **Leaves** more than 2, transverse, asymmetric, not peltate, simple; venation palmate; indumentum of scales absent (but with indumentum of fimbriate-ciliate paleae), stellate hairs absent. **Inflorescence** axillary, dichasial, bisexual, with male flowers basal and female flowers distal, protandrous, with the central flower of the cyme male, lateral flower(s) female; inflorescence axes not reduced; bracts caducous. **Flower** without bracteoles; perianth segments orange, outer ones rounded at apex. *Male flower* with 4 free perianth segments; androecium actinomorphic, filaments unequal, fused below (into a column), anthers circular to elliptic or ovate, shorter than the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective not extended. *Female flower* with 4 free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles 3, fused less than halfway, forked once (branches long, erect), caducous in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, without or with an indistinct beak.

DISTRIBUTION: Asia: The Philippines.

SEED MICROMORPHOLOGY: Seeds fusiform, long acuminate.

CHROMOSOMES: $2n = 28$ (not certain).

TAXONOMIC COMMENTS: Merrill (1912) doubted whether this section could be distinguished from *Diploclinium*. It is upheld here because of the following characters: flowers orange, tepals remaining half-open, filaments fused below into a column, style branches long and erect, seed fusiform. The fimbriate-ciliate hair-like structures are characteristic but occur also in *B. calcicola* of the section *Diploclinium*.

SPECIES LIST: A single species: *B. oxysperma* A. DC.

sect. **Begonia**

Fig. 4

Type species: *B. obliqua* L.

Begonia sect. *Begoniastrum* A. DC., Ann. Sci. Nat., Bot. 4, 11: 123 (1859), lectotype species (Barkley & Baranov, 1972): *B. meridensis* A. DC. (should be *B. obliqua* L.)

Begonia sect. *Begoniastrum* subsect. *Eubegonia* Warb. in Engl. & Prantl, Die Natürl. Pflanzenfam. (ed. 1) 3, 6a: 149 (1894), type species: *B. obliqua* L.

Begonia sect. *Podandra* A. DC., Ann. Sci. Nat., Bot. 4, 11: 122 (1859), type species: *B. decandra* Pavon ex A. DC.

Plants terrestrial, perennial or annual (at least 4 species), with upright stems or less often rhizomatous or rarely with rhizomes from which upright stems arise (at least 1 species) or acaulescent (2 species); tubers absent or rarely present (*B. balansae*, *B. cowellii*?); stem herbaceous or woody (at least at base); tubercles in leaf axil absent; stipules persistent or early caducous, entire or dentate; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, transverse or less often straight, asymmetric or rarely symmetric (2 or 3 species), not peltate, simple or rarely palmately lobed (*B. balansae*, *B. exigua*); venation palmate or less often palmate-pinnate (7 species) or pinnate (4 species); indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial or dichasial at base and monochasial at apex (or possibly monochasial in *B. cowellii*), bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced or rarely partly reduced (*B. saxicola*); bracts persistent (during flowering) or caducous. **Flower** with 2(-3) bracteoles inserted directly below the ovary; perianth segments white or pink, outer ones rounded at apex. **Male flower** with 4 free perianth segments; androecium actinomorphic, filaments equal or unequal, free or rarely fused below, anthers oblong, longer than the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective extended or rarely not (*B. decandra*). **Female flower** with 5 free perianth segments; ovary or fruit with 3 wings, wings unequal or less often equal or subequal in fruit (4 species), not hook- or spine-like, locules 3, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles 3, free or fused less than halfway, forked once or rarely more than once (*B. repens*), persistent or rarely caducous in fruit (*B. pensilis*), stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, dehiscent near the back of the locules, pendulous (always?), without or with an indistinct beak.

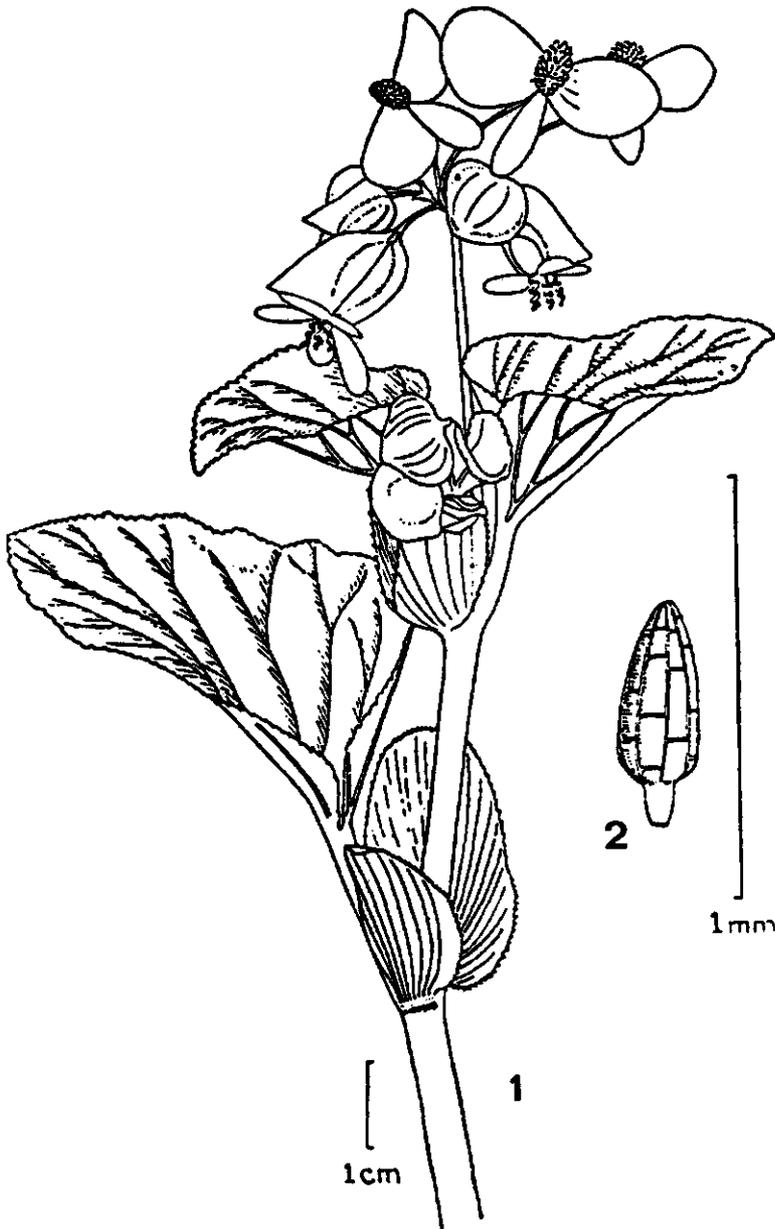


Fig. 4. Sect. *Begonia*. *B. cucullata* var. *hookeri* (A. DC.) L.B. Smith & Schubert — 1, flowering stem; 2, seed. Reproduced from Smith & Smith (1961): p. 26, est. 6.

DISTRIBUTION: America: mainly the West Indies and Brazil.

LEAF ANATOMY: Stomata in (often large) groups; hypoderm absent or present on both sides; cystoliths absent.

SEED MICROMORPHOLOGY: 16 species have been studied. On the whole the seeds confirm to the usual type, varying from 360 x 195 μm to 555 x 255 μm (length/width 1.8–2.2). In *B. cucullata* and *B. fischeri*, however, other seed types were observed. Their seeds are much longer (670 and 795 μm resp.) mainly as a result of an extended chalazal end, narrow (length/width 3.6–5.5) and often J-shaped.

CHROMOSOMES: $2n = 34$ (*B. cucullata*, *B. fischeri*, *B. mollicaulis*, *B. schmidtiana*, *B. subvillosa*); $2n = 52$ (*B. cubensis*, *B. odorata*, *B. rotundifolia*); $2n = 78$ (*B. minor*); $2n = 156$ (*B. acutifolia*).

TAXONOMIC COMMENTS: The species of Klotzsch's genus *Begonia* were classified by A. de Candolle in the section *Begoniastrum* of the genus *Begonia* which he treated in a much wider sense. Warburg extended *Begoniastrum* with A. DC.'s sections *Moschkowitzia* and *Knesebeckia*, but limited it to the Neotropical species. Irmscher followed Warburg but extended the section again with a number of Asian species which Warburg had put in *Diploclinium* subsect. *Knesebeckia*. It was Irmscher's opinion "dasz nach dem morphologischen Verhalten die amerikanischen und asiatischen *Begoniastrum*-Formen dem Urtypus der Gattung recht nahe kommen, von dem zweifellos zahlreiche hochspezialisierte endemische Sektionen ihren Ausgangspunkt genommen haben" (Irmscher, 1925: 569), and again "Sie [sect. *Begoniastrum*] stellt unter den Asiatischen Begonien hinsichtlich den Blütenverhältnisse eine des im wenigsten abgeleiteten Gruppen dar und kann als Ausgangspunkt für manche andere spezialisierte Habitus- und Blütenprägung angesehen werden" (Irmscher, 1939: 489). As large numbers of new species were described, many by Irmscher himself, the delimitation of the section became problematic, and he wrote "Erst deren Gesamtbearbeitung wird erweisen, ob sie im alten Umfang aufrecht zu erhalten ist oder eine Aufteilung erforderlich sein wird" (Irmscher, 1949: 604). It is a pity that Irmscher never got around to this general treatment. That he would have split up *Begoniastrum* is clear from his article on *Begonia* in Parey's *Blumengaertnerei* (1960) where he treats the

section *Knesebeckia* separate from *Begoniastrum*. In the present publication section *Begonia* (as the section has to be called according to the nomenclatural rules) does not include *Knesebeckia*. The species of the former sect. *Moschkowitzia*, characterized by a.o. 2 male perianth segments, have been transferred to sect. *Cyathocnemis* and *Ruizopavonia*. The monotypic section *Podandra* ('habitu et capsula sect. *Begoniastrum* sed staminibus omnino diversa' - A. DC., 1864) is included in *Begonia*. Its peculiar anthers (linear, standing off horizontally from the top of a 2 mm long column) are to be found also in *B. thelmae* and *B. hoehneana*, but the three species can not be united in a separate section, however, and for the moment it seems best to regard *B. decandra* as an aberrant species within sect. *Begonia*. As already discussed in chapter 3 sect. *Begonia*, like all other sections, has been limited to one continent. In this respect Warburg has been followed.

SPECIES LIST: 62 species: *B. abbottii* Urban, *B. acutifolia* Jacq., *B. admirabilis* Brade, *B. albidula* Brade, *B. alcarrasica* J. Sierra Calzado, *B. alchemilloides* Meisner ex A. DC., *B. azuensis* Urb. & Ekman, *B. balansae* C. DC., *B. banoensis* J. Sierra Calzado, *B. bissei* J. Sierra Calzado, *B. bolleana* Urb. & Ekman, *B. brachypoda* O.E. Schulz, *B. bullata* Urb. & Ekman, *B. cowellii* Nash, *B. cubensis* Hassk., *B. cucullata* Willd., *B. decandra* Pav. ex A. DC., *B. descoleana* L.B. Smith & Schubert, *B. domingensis* A. DC., *B. dominicalis* A. DC., *B. eciliata* O.E. Schulz, *B. ekmanii* Houghton ex L.B. Smith & Schubert, *B. exigua* Irmscher, *B. exilis* O.E. Schulz, *B. fischeri* Schrank, *B. glaberrima* Urb. & Ekman, *B. harlingii* L.B. Smith & Wasshausen, *B. hassleri* C. DC., *B. jamaicensis* A. DC., *B. lanstyakii* Brade, *B. leivae* J. Sierra Calzado, *B. leuconeura* Urb. & Ekman, *B. libanensis* Urb., *B. lindmanii* Brade, *B. linearifolia* J. Sierra Calzado, *B. lomensis* Britton & Wilson, *B. maestrensis* Urb., *B. minor* Jacq., *B. mollicaulis* Irmscher, *B. notiophila* Urb., *B. obliqua* L., *B. odorata* Willd., *B. organensis* Brade, *B. pensilis* L.B. Smith & Wasshausen, *B. per-dusenii* Brade, *B. platyptera* Urb., *B. plumieri* A. DC., *B. purdieana* A. DC., *B. pycnantha* Urb. & Ekman, *B. repens* Lam., *B. retusa* O.E. Schulz, *B. rotundifolia* Lam., *B. schenckii* Irmscher, *B. schmidtiana* Regel, *B. schulziana* Urb. & Ekman, *B. squamipes* Irmscher, *B. stenotepala* L.B. Smith & Schubert, *B. stipulacea* Willd., *B. subvillosa* Klotzsch, *B. venosa* Skan ex Hook. f., *B. vincentiana* O.E. Schulz, *B. wrightiana* A. DC.

Species whose membership is doubtful: 5 species: *B. glandulifera*

Griseb., *B. konder-reisiana* L.B. Smith & R.C. Smith, *B. lucidissima* J. Golding & Karegeannes, *B. sciadiophora* L.B. Smith & Schubert, *B. tiliifolia* C. DC.

sect. **Bracteibegonia** A. DC.

Fig. 5

Ann. Sci. Nat., Bot. 4, 11: 127 (1859), lectotype species (Barkley & Baranov, 1972): *B. bracteata* Jack.

Plants terrestrial, perennial, with rhizomes from which upright stems arise; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** more than 2, straight or transverse, asymmetric, not peltate, simple; venation pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** terminal, a raceme of cymes, bisexual; inflorescence axes not reduced (or slightly reduced in *B. aberrans*); bracts persistent (during flowering). **Flower** without or with 2 bracteoles inserted directly below the ovary; perianth segments white or pink (possibly red in *B. bracteata*), outer ones rounded at apex. **Male flower** with 2 (*B. aberrans*) or 4 free perianth segments; androecium actinomorphic, filaments free (possibly fused below in *B. bracteata*), anthers oblong, dehiscent with unilaterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective not extended. **Female flower** with 5 free perianth segments; ovary or fruit with 3 wings, wings equal or subequal in fruit, not hook- or spine-like, locules 3, placentation axillary (probably), placental branches 2 per locule, ovules present between placental branches (probably); styles 3, fused less than halfway, 2-lobed, persistent in fruit, stigma kidney-shaped, in a band and spiralled. **Fruit** not berry-like, more or less erect (probably), without or with an indistinct beak.

DISTRIBUTION: Asia: Sumatra and Java.

LEAF ANATOMY: Stomata single (very rarely 2–3); hypoderm absent; no cystoliths (*B. lepida*).

TAXONOMIC COMMENTS: Alphonse de Candolle (1859) erected this section for 2 closely related species: *B. bracteata* and *B. lepida*. They differed from the 6 species (and 4 with a question mark) of section *Petermannia* in seven respects. The third species to be placed



Fig. 5. Sect. *Bracteibegonia*. *B. lepida* — flowering stem. Redrawn by Mrs. Wil Wessel-Brand from van Steenis (1972): plate 5.4.

in section *Bracteibegonia*, *B. burbidgei* (1894), was already much closer to *Petermannia* and the many new species described since then in both sections gradually bridged the gap. Nevertheless *Bracteibegonia* is upheld here because the inflorescences which are few-flowered and bisexual do not show the separation between a basal female and distal male portion, as is so characteristic for *Petermannia*. It should be added, however, that we know the inflorescence of *B. lepida* only from a picture in C.G.G.J. van Steenis' Mountain flora of Java (1972: plate 5, fig. 4).

SPECIES LIST: 3 species: *B. aberrans* Irmscher, *B. bracteata* Jack, *B. lepida* Blume.

Species whose membership is doubtful: *B. divaricata* Irmscher.

sect. *Casparya* (Klotzsch) Warb.

Fig. 6

in Engl. & Prantl, Die Natürl. Pflanzenfam. (ed. 1) 3, 6a: 146 (1894). — *Casparya* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 127 (1854), lectotype species (here proposed): *Casparya coccinea* Klotzsch = *B. urticae* L. f. (heterotypic synonym).

Stibadotheca Klotzsch ('*Stiradotheca*', printing error), Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 127 (1854), lectotype species (Baranov & Barkley, 1974): *S. ferruginea* (L. f.) Klotzsch = *B. ferruginea* L. f. (homotypic synonym)

Sassea Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 128 (1854), lectotype species (Baranov & Barkley, 1972): *S. urticae* (L. f.) Klotzsch = *B. urticae* L. f. (homotypic synonym)

Isopteryx Klotzsch, Abh. Kön. Akad. Wiss. Berlin '1854': 252 (1855), type species: *I. umbellata* (Humb., Bonpl. & Kunth) Klotzsch = *B. umbellata* Humb., Bonpl. & Kunth. (homotypic synonym)

Casparya sect. *Aetheopteryx* A. DC., Prodr. 15(1): 271 (1864), type species: *C. trispathulata* A. DC. = *B. trispathulata* (A. DC.) Warb. (homotypic synonym)

Casparya sect. *Andiphila* A. DC., Prodr. 15(1): 271 (1864), lectotype species (Baranov & Barkley, 1974): *C. trianaei* A. DC. = *B. trianaei* (A. DC.) Warb. (homotypic synonym)

All five synonyms appear as sections of *Casparya* in A. DC. (1864) and (except *Isopteryx*) as subsections of section *Casparya* in Warburg (1894).

Plants terrestrial, perennial, with upright stems; tubers absent; stem herbaceous or woody (at least at base); tubercles in leaf axil absent; stipules persistent or early caducous, entire or dentate (fimbriate-serrulate); junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight to transverse, symmetric or asymmetric, not peltate or rarely peltate, simple; venation palmate-pinnate or pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, bisexual or separate male and female or rarely bisexual and male, with male flowers basal and female flowers distal, protandrous or protogynous; female inflorescence consisting of solitary flowers; inflorescence axes strongly reduced or not; bracts persistent (during flowering) or caducous. **Flower** without or with 2 bracteoles implanted directly under the ovary; perianth segments white, pink or red, outer ones rounded or acute at apex. *Male flower* with 4 or rarely 2 (*B. gamolepis*) free perianth segments; androecium actinomorphic, filaments free or rarely fused below, anthers oblong, longer than or

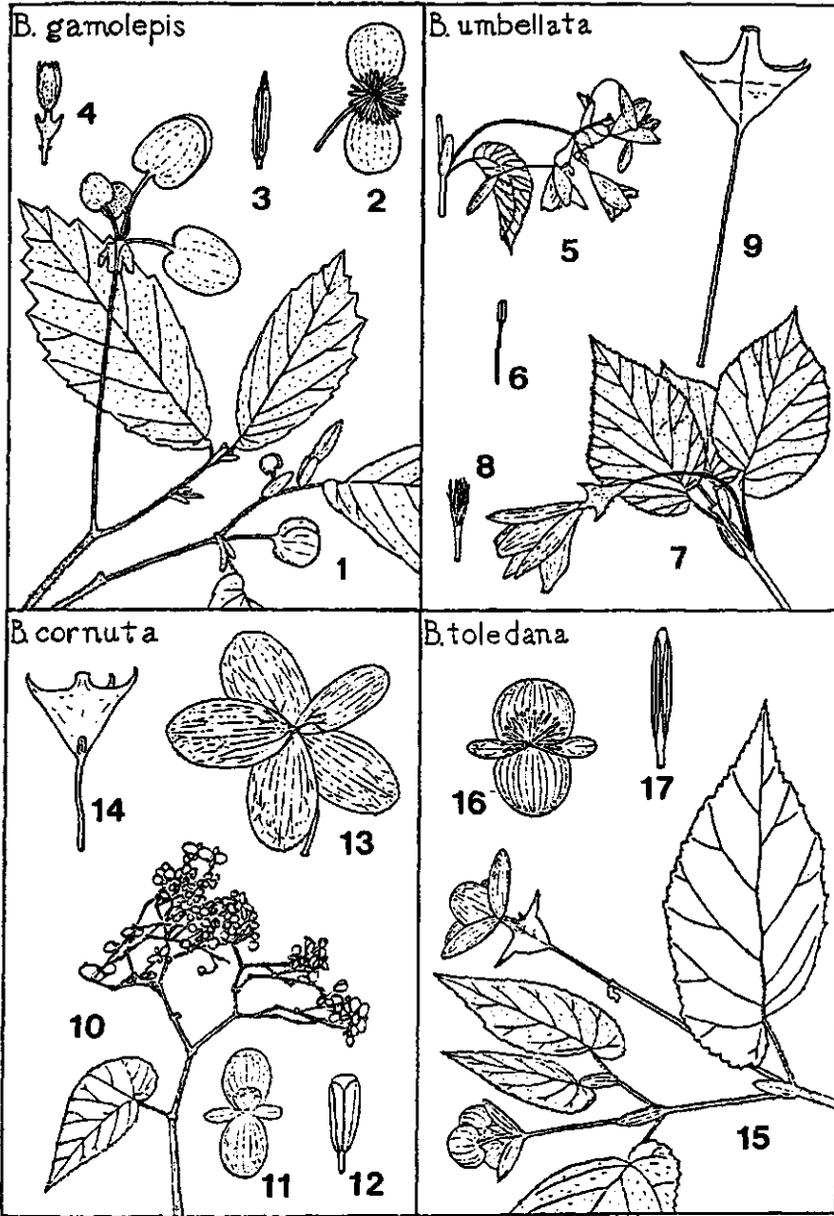


Fig. 6. Sect. *Casparya*. *B. gamolepis* — 1, flowering stem; 2, male flower; 3, stamen; 4, female flower. *B. umbellata* — 5, stem with male inflorescence; 6, stamen; 7, stem with female inflorescence; 8, styles; 9, fruit. *B. cornuta* — 10, flowering stem; 11, male flower; 12, stamen; 13, female flower; 14, fruit. *B. toledana* — 15, flowering stem; 16, male flower; 17, stamen. Reproduced from Smith & Schubert (1946): p. 19, tab. 45.

rarely about as long as (*B. columbiana*) or shorter than the filaments (*B. umbellata*), dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective extended or rarely not. *Female flower* with 4 or rarely 2 (*B. gamolepis*) free perianth segments; ovary or fruit with 3 wings, wings equal or subequal in fruit, developed into hooks or rarely not, locules 3, placentation axillary, placental branches 2 or rarely 1 per locule (possibly in *B. diffusa*), ovules present between placental branches; styles 3, free or fused less than halfway or rarely fused more than halfway (possibly in *B. toledana*), forked more than once (better: irregularly branched) or rarely forked once (*B. trujillensis*), caducous in fruit, stigma not kidney-shaped, in a band and not spiralled or contracted near the style apex. **Fruit** not berry-like, dehiscent at the back of the carpels (through the wings), more or less erect (?), usually with a distinct beak.

DISTRIBUTION: America: Central and Andean America, from Costa Rica to Peru.

LEAF ANATOMY: Stomata in groups; hypoderm absent; cystoliths absent.

SEED MICROMORPHOLOGY: Seed very diverse. According to Bouman & de Lange (in press), characterized by the roughness of the testal surface, the generally undulating anticlinals, the flat operculum, and sometimes the double structure of the cuticular ornamentation and the absence of a distinct collar. On the basis of seed structure these authors distinguish 7 groups whereas 4 species could not be classified. Mean length varies from 390 μ m in *B. diversistipulae* to 880 μ m in *B. ferruginea*; mean length/width ratio from 1.6 in *B. trispathulata* to 3.0 in *B. ferruginea*.

IMPORTANT LITERATURE: Smith & Schubert (1946).

TAXONOMIC COMMENTS: Barkley & Baranov (1972) appointed *B. urticae* L.f. as a lectotype, but Klotzsch did not classify this species in *Casparya* but in *Sassea*. We therefore suggest *Casparya coccinea* Klotzsch as the lectotype which, according to L.B. Smith et al. is synonymous with *B. urticae*. *Casparya* is a group of American species characterized by fruits which open at the back of the locules and usually have no wings but horns. Klotzsch classified them in four

genera. Alphonse de Candolle maintained *Casparya* as a genus with the other three genera of Klotzsch as sections, to which he added two other American sections and an Asian one. Subsequent authors, notably Warburg (1894) and Irmscher (1926), reduced *Casparya* to a section of *Begonia* with American species only. Meanwhile Oliver erected the genus *Begoniella* (1873) and Casimir de Candolle created *Semibegoniella* (1908) for species with fruits similar to those of sect. *Casparya* but with a more or less sympetalous perianth. In 1955, Smith & Schubert included both genera in *Casparya*. As there are other distinguishing characters apart from the connate tepals, however, we feel that a separate section is warranted, as will be discussed below. In *B. chlorolepis*, *B. diversistipulata*, *B. trispathulata* and, less pronounced in *B. trapa*, the hooks on the fruit are flattened in a horizontal plane. As A. de Candolle already remarked, this does not occur elsewhere in *Begonia*, but as these four species do not seem to have other characteristics that set them apart, there is at the moment no reason to revive A. de Candolle's section *Aetheopteryx*.

Most species of *Casparya* appear to be hard to grow. This is one of the reasons why there is little information on the development of the inflorescences. The dried material gives the situation at a given moment which is difficult to interpret. Pictures show inflorescences that are either monosexual, dichasial (e.g. *B. gehrigeri* = *B. trapa*, L.B. Smith 1973: 222), monosexual, the male monochasial, the female with solitary flowers which appear to be protogynous (e.g. *B. toledana*, Smith & Schubert 1946: 27), or bisexual, di- to monochasial, protandrous (e.g. *B. cornuta*, Smith & Schubert 1946: 27). This could be a criterion for further subdivision, but for the moment the data are still too fragmentary.

SPECIES LIST: 24 species: *B. brevipetala* (A. DC.) Warb., *B. chlorolepis* L.B. Smith & Schubert, *B. colombiana* L.B. Smith & Schubert, *B. cornuta* L.B. Smith & Schubert, *B. diffusa* L.B. Smith & Schubert, *B. diversistipulata* Irmscher, *B. ferruginea* L. f., *B. formosissima* Sandwith, *B. fuchsiiflora* (A. DC.) A.L. Baranov & F.A. Barkley, *B. gamolepis* L.B. Smith & Schubert, *B. hirta* (Klotzsch) L.B. Smith & Schubert, *B. lipolepis* L.B. Smith, *B. mariae* L.B. Smith, *B. montana* Warb., *B. raimondii* Irmscher, *B. toledana* L.B. Smith & Schubert, *B. trapa* L.B. Smith & Schubert, *B. trianae* (A. DC.) Warb., *B. trispathulata* (A. DC.) Warb., *B. trujillensis* L.B. Smith, *B. umbellata* Humb., Bonpl. & Kunth, *B.*

ursina L.B. Smith & Schubert, *B. urticae* L. f., *B. vareschii* Irmischer.

sect. **Coelocentrum** Irmischer

Fig. 7

Mitt. Inst. Bot. Hamb. 10: 553 (1939), lectotype species (Barkley & Baranov, 1972): *B. porteri* Léveillé & Vaniot.

Plants terrestrial, perennial, rhizomatous; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent or early caducous, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, transverse, asymmetric, not peltate or rarely peltate (*B. setulosa-peltata*, *B. umbraculifolia*), simple; venation palmate or palmate-pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial or dichasial at base and monochasial at apex, bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts persistent (during flowering) or not. **Flower** without bracteoles; perianth segments free, white or pink (in *B. masoniana* greenish with brown), outer ones rounded at apex. **Male flower** with 4 perianth segments; androecium actinomorphic, filaments equal or unequal, fused below (into a short column), anthers obovate, about as long as the filaments, dehiscent with laterally or unilaterally positioned (at the top) slits (more than 0.5 of the anther length), connective not extended. **Female flower** with 3 or rarely 4 (*B. setulosa-peltata*) or 5 (*B. obsolescens*) perianth segments; ovary or fruit with 3 wings, wings equal to unequal in fruit, not hook- or spine-like, locules 1, placentation parietal, placentae 3, placental branches 2 (branched in *B. lanternaria*); styles 3, fused less than halfway or free, forked once or rarely 2-lobed (*B. porteri*, *B. umbraculifolia*), persistent or caducous in fruit. **Fruit** not berry-like, nodding.

DISTRIBUTION: Asia: eastern China.

LEAF ANATOMY: Stomata single; hypoderm absent; no cystoliths (*B. masoniana*).

CHROMOSOMES: $2n = 30$ (*B. masoniana*).

IMPORTANT LITERATURE: Irmischer (1939), Wu & Ku (1997).

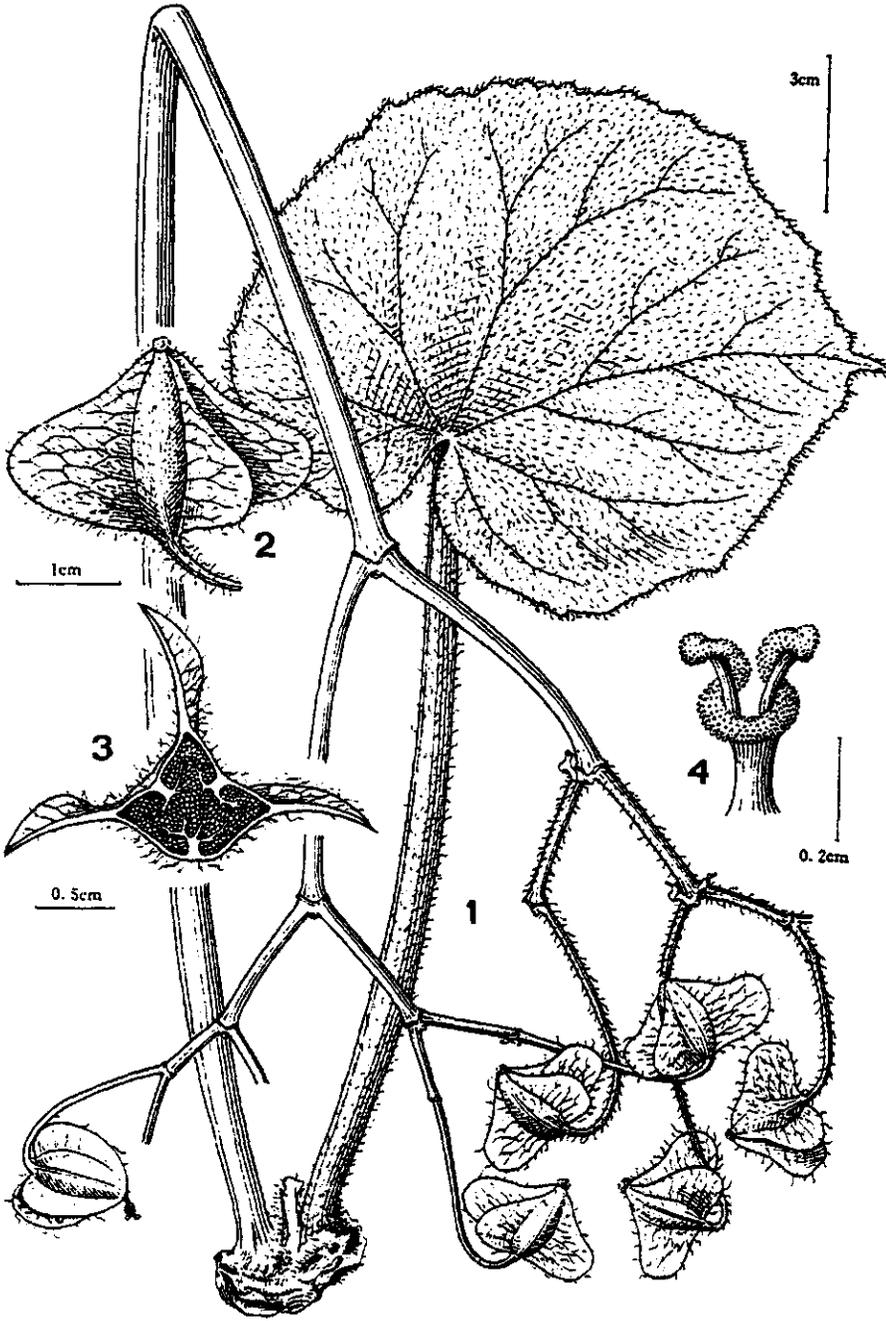


Fig. 7. Sect. *Coelocentrum*. *B. guangxinensis* — 1, plant habit; 2, fruit; 3, transverse section of fruit; 4, style. Reproduced from Wu & Ku (1997): p. 47, fig. 27.

SPECIES LIST: 12 species: *B. biflora* Ku, *B. cirrosa* L.B. Smith & Wasshausen, *B. daxinensis* Ku, *B. guangxinensis* Ku, *B. lanternaria* Irmscher, *B. masoniana* Irmscher, *B. morsei* Irmscher, *B. obsolescens* Irmscher, *B. ornithophylla* Irmscher, *B. porteri* Léveillé & Vaniot, *B. setulosa-peltata* Wu, *B. umbraculifolia* Y. Wan & B.N. Chang.

sect. **Cristasemen** J.J. de Wilde

Fig. 8

Agric. Univ. Wageningen Papers 84-3: 115 (1985), type species: *B. thomeana* C. DC.

Plants terrestrial, perennial, lianescent (climbing with adventitious roots like ivy, *Hedera helix* L.); tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, transverse, symmetric to asymmetric, not peltate, simple; venation palmate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial at base, monochasial at apex, bisexual, protandrous, with 1–2(–3) female flowers, the central flower of the cyme male, lateral flower(s) female; inflorescence axes not reduced; bracts persistent (during flowering). **Flower** without bracteoles; perianth segments yellow, outer ones rounded at apex. *Male flower* with 2 free perianth segments; androecium zygomorphic, filaments unequal, fused below, anthers obovate, longer than to about as long as the filaments, dehiscent with unilaterally positioned longitudinal slits (more than 0.5 of the anther length), apex hooded, connective not extended. *Female flower* with 2 free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 1 per locule; styles 3, fused less than halfway, forked more than once, persistent in fruit, stigma kidney-shaped, in a band and not spiralled. **Fruit** not berry-like, dehiscent both near the back of the locules and near the septa, pendulous, without or with an indistinct beak.

DISTRIBUTION: Africa: on the island of São Tomé and in Gabon.

LEAF ANATOMY: Stomata single; hypoderm absent; no cystoliths (see also Sosef, 1994).

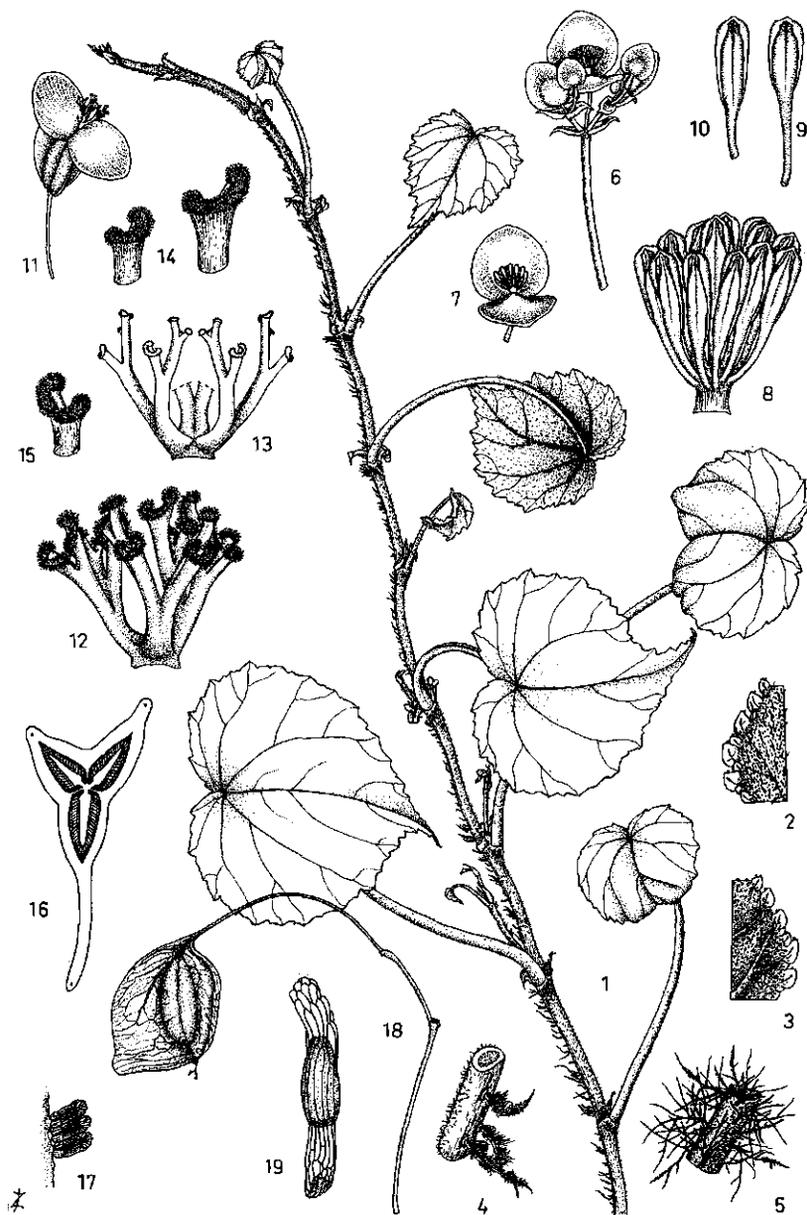


Fig. 8. Sect. *Cristasemen*. *B. thomeana* — 1, plant habit; 2, margin of developing leaf, upper side; 3, idem, lower side; 4-5, parts of stem with adventitious roots; 6, inflorescence; 7, male flower; 8, androecium; 9-10, stamens; 11, female flower; 12, styles; 13, schematic representation of 2 styles; 14-15, stigmas; 16, ovary in transverse section; 17, ovules on placenta; 18, fruit; 19, seed. Drawing by Miss Ike Zewald.

SEED MICROMORPHOLOGY: Seeds narrowly ellipsoid to narrowly cylindrical, 940–1290 x 210–260 μm , ratio length/width 4.6; micropylar and chalazal ends of seeds composed of blown-up, air-filled cells; operculum massive; hilum sunken; collar cells with sunken anticlinal boundaries; testa cells with striate cuticular ornamentation (see also de Wilde, 1985b).

CHROMOSOMES: $2n = 38$.

IMPORTANT LITERATURE: de Wilde (1985b).

TAXONOMIC COMMENTS: The fruiting peduncle and especially the pedicel are much elongated in fruit.

SPECIES LIST: A single species: *B. thomeana* C. DC.

sect. **Cyathocnemis** (Klotzsch) A. DC.

Fig. 9

Prodr. 15, 1: 332 (1864). — *Cyathocnemis* Klotzsch (1854), Abh. Akad. Berlin '1854': 220 (1855), type species: *Cyathocnemis obliqua* (Ruiz ex Klotzsch) Klotzsch = *B. cyathophora* Poeppig & Endlicher (heterotypic synonym).
Moschkowitzia Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 127 (1854), type species: *Moschkowitzia fagopyroides* (Kunth) Klotzsch = *B. denticulata* Humb., Bonpl. & Kunth (heterotypic synonym).
Begonia sect. *Ruizopavonia* A. DC. p.p.

Plants terrestrial, perennial, with upright stems; tubers absent; stem herbaceous or woody (at least at base); tubercles in leaf axil absent; stipules early caducous or less often persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, transverse, asymmetric, not peltate, simple or less often palmately lobed (*B. pseudoglauca*, *B. viridiflora*); venation palmate or rarely palmate-pinnate (*B. viridiflora*); indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial or dichasial at base and monochasial at apex, bisexual, with male flowers basal and female flowers distal, protandrous, axes not reduced; bracts usually caducous. **Flower** without or with 2 or 3 (caducous) bracteoles implanted at the base of the ovary; perianth segments white, pink or red, outer ones rounded or rarely acute at apex (*B. subspinulosa*). *Male flower* with 2 free perianth segments; androecium actinomorphic, filaments unequal, anthers oblong, longer than or shorter than the filaments, dehiscent with laterally

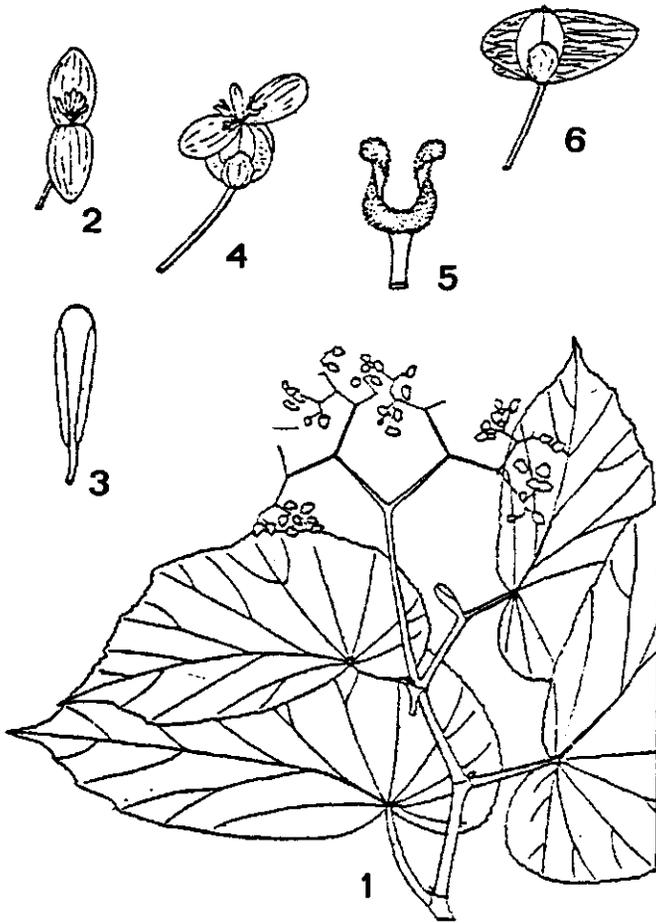


Fig. 9. Sect. *Cyathocnemis*. *B. magdaleneae* — 1, flowering branch; 2, male flower; 3, stamen; 4, female flower; 5, style; 6, fruit with bracteole. Reproduced from Smith & Schubert (1946): t. 10.

positioned longitudinal slits (more than 0.5 of the anther length), connective extended. *Female flower* with 2 or rarely 3 (*B. magdaleneae*) or 5 (*B. denticulata*, *B. wagnerana*) free perianth segments; ovary or fruit with 3 wings, wings unequal or rarely equal or subequal in fruit (*B. tribracteata*), not hook- or spine-like, locules 3, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles 3, free or fused less than halfway, forked once or less often more than once (*B. glauca*), caducous in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, nodding.

DISTRIBUTION: America: the Andean region.

LEAF ANATOMY: Stomata in groups; hypoderm absent but present on both sides in *B. viridiflora*; cystoliths present in *B. glauca*, absent in *B. cyathophora*, *B. glauca*, *B. pseudoglauca*, *B. subciliata*, *B. viridiflora* and *B. wagnerana*.

SEED MICROMORPHOLOGY: No special characters (*B. altoperuviana*, *B. cyathophora*).

CHROMOSOMES: $2n = 52$ (*B. roezlii*).

TAXONOMIC COMMENTS: In 1854 Klotzsch proposed the genus *Cyathocnemis* for a *Begonia* with two tepals in both male and female flowers, bifid placentas and the inflorescence supported by a cup of fused bracts. In 1859, A. de Candolle described several Peruvian *Begonia* species with similar characters but free bracts which he put, together with other species, in a new section, *Ruizopavonia*, apparently considering the fused bracts of sufficient importance to keep *Cyathocnemis*, which he had reduced to sectional status, separate. The present authors do not share this opinion, however, and have brought such species of *Ruizopavonia* with transverse, more or less palmate leaves and *B. cyathophora* together in a section.

SPECIES LIST: 17 species: *B. altoperuviana* A. DC., *B. bracteosa* A. DC., *B. brevicordata* L.B. Smith & Schubert, *B. cryptocarpa* L.B. Smith & Schubert, *B. cyathophora* Poepp. & Endl., *B. glauca* (Klotzsch) Ruiz & Pav. ex A. DC., *B. laxa* L.B. Smith & Schubert, *B. lophoptera* Rolfe, *B. lucifuga* Irmscher, *B. magdalenae* L.B. Smith & Schubert, *B. pseudoglauca* Irmscher, *B. roezlii* Regel, *B. subciliata* A. DC., *B. subspinulosa* Irmscher, *B. suprafastigiata* Irmscher, *B. tribracteata* Irmscher, *B. viridiflora* A. DC.

Species whose membership is doubtful: 5 species: *B. albo-maculata* C. DC. ex Huber, *B. denticulata* Humb., Bonpl. & Kunth, *B. machrisiana* L.B. Smith & Schubert, *B. nubicola* L.B. Smith & Schubert, *B. wagnerana* Hook.

sect. **Diploclinium** (Lindl.) A. DC.

Fig. 10

Ann. Sci. Nat., Bot. 4, 11: 129 (1859). — *Diploclinium* Lindl., Veg. Kingdom: 319 (1846), type species: *Diploclinium evansianum* (Andrews) Lindl. = *B.*

grandis Dryander (heterotypic synonym).

Begonia sect. *Trilobaria* A. DC., Ann. Sci. Nat., Bot. 4, 11: 131 (1859), type species: *B. ovalifolia* A. DC.

Plants terrestrial, perennial, rhizomatous or with upright stems; tubers absent or present; stem herbaceous; tubercles in leaf axil absent or rarely present (*B. grandis*, *B. notata*, *B. pedunculosa*); stipules persistent or early caducous, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate or rarely close and distichous (*B. pedunculosa*), 1 or 2 (group III) or more than 2, straight to transverse, symmetric or asymmetric, not peltate or rarely peltate, simple or rarely palmatifid (*B. aceroides*, *B. collisiae*, *B. garrettii*); venation palmate or palmate-pinnate; indumentum of scales or stellate hairs absent but fimbriate-ciliate paleae rarely present (*B. calcicola*). **Inflorescence** axillary or pseudoterminal or terminal, a cyme or a raceme of cymes, bisexual or rarely bisexual and female (*B. minicarpa*, *B. yunnanensis*?) or separate male and female (*B. minjemensis*), with male flowers basal and female flowers distal or rarely with male flowers distal and female flowers basal (*B. longinoda*?, *B. minicarpa*, *B. yunnanensis*?), protandrous or rarely protogynous (*B. minicarpa*, *B. minjemensis*?, *B. yunnanensis*?); bisexual and male inflorescence dichasial; female inflorescence monochasial (?) or consisting of solitary flowers; inflorescence axes not reduced or rarely reduced (*B. flagellaris*, *B. leptoptera*); bracts persistent (during flowering) or caducous. **Flower** with 0(-2) bracteoles spaced from the base of the ovary; perianth segments white or pink, outer ones rounded at apex. *Male flower* with 4 or rarely 2 (5 species) or 5 (*B. hernandioides*) free perianth segments; androecium actinomorphic, filaments unequal, free or fused below, anthers circular to obovate or rarely oblong, shorter than or rarely longer than the filaments, dehiscent with laterally or unilaterally positioned short pore-like slits (less than 0.5 of the anther length) or longitudinal slits (more than 0.5 of the anther length), connective not extended or rarely extended. *Female flower* with 3-5 or rarely with 2 (7 species) free perianth segments; ovary or fruit with 3 wings or rarely wingless (*B. wilsonii*) or with 6 wings (*B. suborbiculata*), wings equal to unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 2 per locule or rarely 1 per locule (*B. concanensis*, *B. fimbriatipula*, *B. labordei*, *B. wilsonii*), ovules present between placental branches; styles 3, free or fused less than halfway or rarely fused more than halfway (*B. putii*), forked once or rarely more than once (*B. klemmei*), persistent or caducous

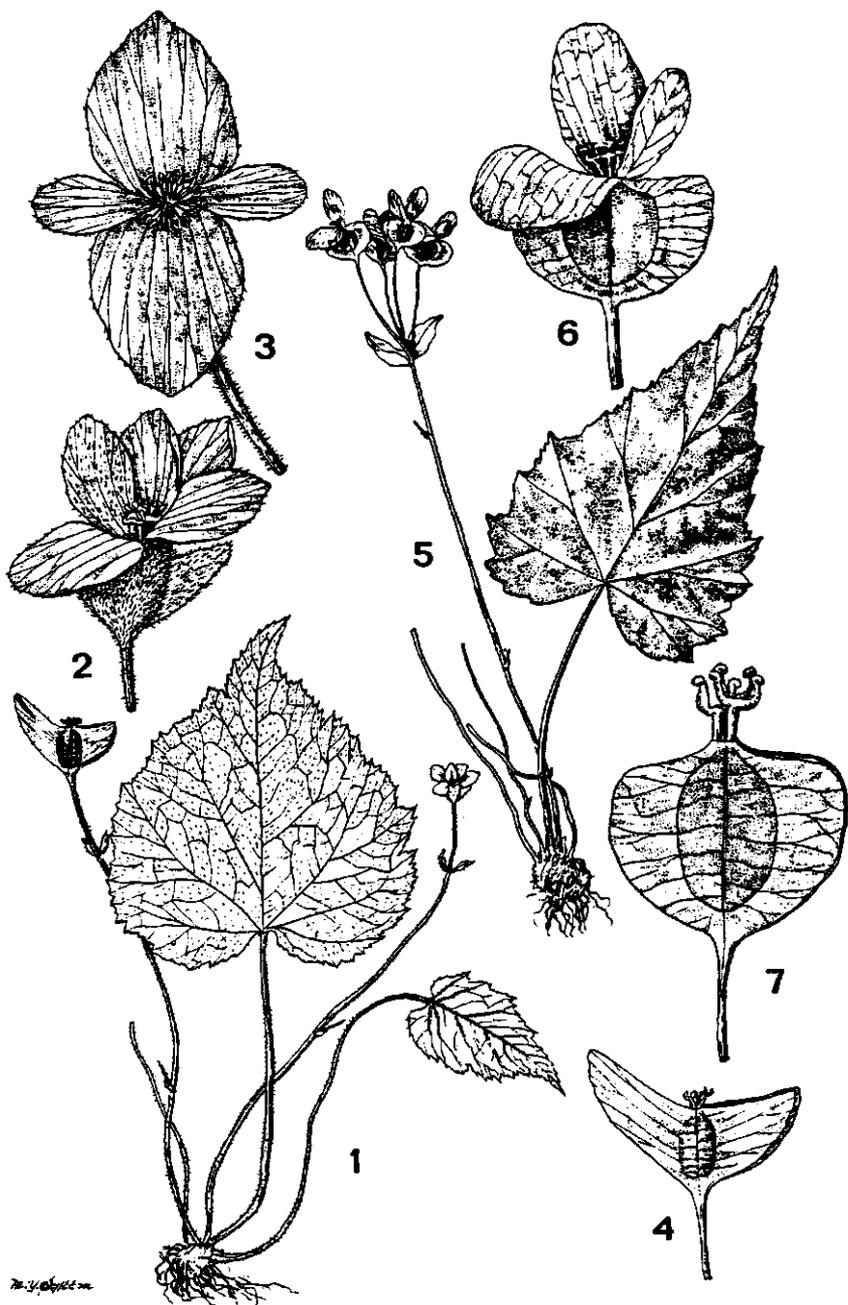


Fig. 10. Sect. *Diploclinium*. *B. picta* — 1, plant habit; 2, female flower; 3, male flower; 4, fruit. *B. dioica* — 5, plant habit; 6, female flower; 7, fruit. Reproduced from Ghazanfar & Aziz (1976): p. 2, fig. 1.

in fruit, stigma not kidney-shaped or rarely kidney-shaped (*B. aceroides*), in a band and spiralled or rarely not spiralled (*B. brassii*). **Fruit** not berry-like, dehiscent near the wings, pendulous, without or with an indistinct beak.

DISTRIBUTION: Asia: From India and Sri Lanka to the Himalayas, Indo-China, China, Taiwan, the Malesian region and Fiji.

LEAF ANATOMY: Stomata single and in groups; hypoderm present or absent; cystoliths absent (14 species studied).

CHROMOSOMES: $2n = 22$ (*B. picta*, *B. fimbriatipula*), $2n = 26$ (*B. grandis*), $2n = 28$ (3 species), $2n = 32$ (preliminary count, *B. subnummularifolia*), $2n = 36$ (*B. ravenii*, Peng & Chen, 1988), $2n = 38$ (*B. taiwaniana*, Peng & Chen, 1991), $2n = 44$ (*B. nigritarum*).

TAXONOMIC COMMENTS: This large and polymorphous section is a show-case of the difficulties one meets when trying to delimit sections. Paradoxically, the section which shows the greatest similarity to *Diploclinium* is also the easiest to separate: the placentae of *Reichenheimia* are undivided whereas those of *Diploclinium* are bifid. At the same time, this is the only difference between the 2 sections. *Platycentrum* and *Parvibegonia* differ from *Diploclinium* in having 2-locular fruits, but in this case there are additional differences. The differences with such *Petermannia* species that have repent and scandent stems are less obvious, as witnessed by the fact that *B. aequata*, *B. gracilipes* and *B. lagunensis*, here placed in *Petermannia*, were classified into *Diploclinium* by Merrill (1912). In this case the inflorescence is the distinguishing characteristic. The Asiatic species classified hitherto in the sections *Begonia* or *Knesebeckia* (rather similar and often united) present the greatest problems. When Irmscher's (1925) diagnoses of *Diploclinium* and *Begonia* (incl. *Knesebeckia*) are set side by side, the differences are the number of female tepals (3 or 4 in *Diploclinium*, 5 or 6 in *Begonia*), the shape of the anthers (obovate in the former, oblong in the latter) and the habit of the plants: species of *Diploclinium* are 'herbs, generally with a tuberous rhizome, without or with a usually short thick stem ...', while species of *Begonia* are 'usually erect (rarely somewhat scandent) herbs or semi-shrubs, never stemless ... sometimes with a tuberous stem base ...'. Later (1927, in a discussion of *B. labordei*) Irmscher added that *Begonia* is characterised by racemose, articulate

inflorescences, persistent styles and unequal wings on the fruit while *Diploclinium* has a purely cymose inflorescence, caducous styles and subequal wings. Many species are not difficult to place in either of the sections thus described, but one is left with dozens of others which are in one way or another intermediate. This leaves us no other option than to combine the 2 sections (*Begonia* so far as Asian species are concerned), although this leads to a very heterogeneous group. For ease of survey, this group has been divided into creeping, erect and stemless species. This is not as straightforward as it seems: authors differ greatly in what they call 'stemless' and several species vary in this respect. It is not suggested, however, that the division given here could be the basis for a classification in subsections or even sections. This would require a detailed study of the numerous species of *Diploclinium*, many of which are now known only from the protologue. Particular attention should be paid to the structure of the inflorescence, which so far most authors have described in very vague terms.

Group I: stem rhizomatous, often fleshy; leaves occasionally peltate (3 species), often symmetrical; inflorescence dichasial, very rarely a raceme of cymes (*B. longiscapa*); male flowers with 4 tepals, rarely 2 (*B. yappii*) or 5 (*B. hernandioides*); filaments connate at base or free, anthers usually obovate, sometimes oblong or elliptic (*B. flagellaris*), connective rarely protruding (*B. festiva*, *B. kaniensis*); female flowers usually with 4 or 5 tepals, sometimes with 3 or 6; styles more or less free or shortly united, branched at about half their length or nearer to the top.

Group II (incl. most Asian species formerly brought to *Begonia* and *Knesebeckia*): stem erect, often tuberous; leaves rarely peltate (*B. josephii*), symmetrical or asymmetrical; inflorescence axillary, cymose, sometimes the upper cymes forming a corymbose inflorescence (*B. asperifolia* a.o.), sometimes a raceme of cymes (*B. modestiflora* a.o.); male flowers with 4 perianth segments, rarely with 2 (*B. cehengensis*, *B. ravenii*); filaments sometimes free but usually more or less united, anthers usually obovate, sometimes oblong to elliptic, connective rarely protruding (*B. wengeri*, *B. yunnanensis*); female flowers usually with 5 perianth segments, less often with 3, rarely with 2 (*B. cehengensis*, *B. ravenii*, *B. rongjiangensis*), 4 (*B. hymenocarpa*) or 6 (*B. miranda*); styles usually more or less free, branched halfway or nearer to the top, usually persistent?

Group III (incl. some Asiatic species grouped hitherto in sect.

Begonia): plant usually tuberous, stem much reduced or absent; leaves occasionally peltate (*B. subperfoliata*), usually more or less symmetrical; inflorescence dichasial, the first branching(s) sometimes non-dichasial, rarely clearly racemose (*B. labordei*); male flowers with 4 perianth segments, rarely with 2 (2 species); filaments more or less united, rarely free (*B. wilsonii*), anthers usually obovate, rarely oblong (*B. incerta*), connective rarely protruding (*B. minjemensis*, *B. soluta*); female flowers usually with 4 perianth segments, less often with 3, rarely with 2 (3 species) or 5 (*B. incerta*); styles usually free (long united in *B. labordei* and *B. putii*), branched halfway or closer to the top, usually persistent in fruit.

SPECIES LIST:

Group I, 55 species: *B. acuminatissima* Merr., *B. alba* Merr., *B. alvarezii* Merr., *B. anisoptera* Merr., *B. arnotiana* (Wight) A. DC., *B. bartlettiana* Merr. & L.M. Perry, *B. biliranensis* Merr., *B. calcicola* Merr., *B. cavaleriei* Léveillé, *B. collisiae* Merr., *B. colorata* Warb., *B. copelandii* Merr., *B. cordifolia* (Wight) Thwaites, *B. elmeri* Merr., *B. fengii* Ku, *B. fenicis* Merr., *B. festiva* Craib, *B. flagellaris* Hara, *B. gitingensis* Elmer, *B. gulingingensis* Huang & Shui, *B. hasskarliana* (Miq.) A. DC., *B. havilandii* Ridley, *B. hernandioides* Merr., *B. incondita* Craib, *B. inversa* Irmscher, *B. isabelensis* Quisumb. & Merr., *B. kaniensis* Irmscher, *B. klemmei* Merr., *B. lancilimba* Merr., *B. longinoda* Merr., *B. longiscapa* Warb., *B. longovillosa* A. DC., *B. luzonensis* Warb., *B. malipoensis* Huang & Shui, *B. manillensis* A. DC., *B. mindorensis* Merr., *B. nigritarum* (Kamel) Steud., *B. obtusifolia* Merr., *B. parva* Merr., *B. pinamalayensis* Merr., *B. pingbiensis* Wu, *B. rotundilimba* Huang & Shui, *B. ruboides* Hu, *B. rubrifolia* Merr., *B. rufipila* Merr., *B. serpens* Merr., *B. sharpeana* F. Muell., *B. sino-vietnamica* Wu, *B. subcyclophylla* Irmscher, *B. sublobata* Jack, *B. subnummularifolia* Merr., *B. suborbiculata* Merr., *B. trichochila* Warb., *B. vanoverberghii* Merr., *B. vitiensis* A.C. Smith.

Species whose membership of Group I is doubtful: 15 species: *B. beccarii* Warb., *B. caespitosa* Jack, *B. calcarea* Ridley, *B. carnosula* Ridley, *B. castilloi* Merr., *B. lansbergeae* L. Lind. & Rodigas, *B. leprosa* Hance, *B. neopurpurea* L.B. Smith & Wasshausen, *B. orbiculata* Jack, *B. promethea* Ridley, *B. pyrrha* Ridley, *B. scintillans* Dunn, *B. tonkinensis* Gagnep., *B. xinyiensis* Ku, *B. yappii* Ridley.

Group II, 39 species: *B. adscendens* C.B. Clarke, *B. alveolata* Yü, *B. anceps* Irmscher, *B. asperifolia* Irmscher, *B. brassii* Merr. &

L.M. Perry, *B. cehengensis* Ku, *B. clavicaulis* Irmscher, *B. coptidimontana* Wu, *B. discreta* Craib, *B. fimbristipula* Hance, *B. fordii* Irmscher, *B. garrettii* Craib, *B. glechomifolia* Hu, *B. grandis* Dryander, *B. hymenocarpa* Wu, *B. imitans* Irmscher, *B. josephii* A. DC., *B. leptoptera* Hara, *B. lushaiensis* C.E.C. Fischer, *B. minicarpa* Hara, *B. miranda* Irmscher, *B. modestiflora* Kurz, *B. morifolia* Yü, *B. murina* Craib, *B. notata* Craib, *B. parvuliflora* A. DC., *B. pedunculosa* Wall., *B. picta* J.E. Smith, *B. ravenii* C.I. Peng & Y.K. Chen, *B. rhodophylla* Wu, *B. rongjiangensis* Ku, *B. rubella* Buch.-Ham. ex D. Don, *B. satrapis* C.B. Clarke, *B. surculigera* Kurz, *B. taliensis* Gagnep., *B. wadei* Merr. & Quisumb., *B. wenshanensis* Hu, *B. yui* Irmscher, *B. yunnanensis* Léveillé.

Species whose membership of Group II is doubtful: 7 species: *B. concanensis* A. DC., *B. geoffrayi* Gagnep., *B. howii* Merr. & Chun, *B. oligandra* Merr. & L.M. Perry, *B. subviridis* Craib, *B. taiwaniana* Hayata, *B. wengeri* C.E.C. Fischer.

Group III, 23 species: *B. acaulis* Merr. & L.M. Perry, *B. aceroides* Irmscher, *B. coronensis* Merr., *B. dentato-bracteata* Wu, *B. dioica* Buch.-Ham. ex D. Don, *B. guishanensis* Huang & Shui, *B. incerta* Craib, *B. ionophylla* Irmscher, *B. kerrii* Craib, *B. labordei* Léveillé, *B. lithophila* Wu, *B. minjemensis* Irmscher, *B. moumeinensis* C.B. Clarke, *B. muliensis* Yü, *B. ovatifolia* A. DC., *B. putii* Craib, *B. saxifragifolia* Craib, *B. soluta* Craib, *B. subperfoliata* Parish ex Kurz, *B. summoglabra* Yü, *B. tribenensis* C.R. Rao, *B. wilsonii* Gagnep., *B. woodii* Merr.

Species whose membership of Group III is doubtful: 3 species: *B. hymenophylloides* F.K. Ward ex L.B. Smith & Wasshausen, *B. xingyiensis* Ku, *B. xishuiensis* Ku.

sect. **Donaldia** (Klotzsch) A. DC.

Fig. 11

Ann. Sci. Nat., Bot. 4, 11: 127 (1859). — *Donaldia* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 127 (1854), lectotype species (Barkley & Baranov, 1972): *Donaldia ulmifolia* (Willd.) Klotzsch = *B. ulmifolia* Willd. (homotypic synonym).

Plants terrestrial, perennial, with upright stems; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent or rarely early caducous (*B. jairii*), entire; junction petiole and leaf blade without a tuft of hairs. Leaves alternate, more than 2, straight, symmetric or asymmetric, not peltate, simple; venation pinnate;

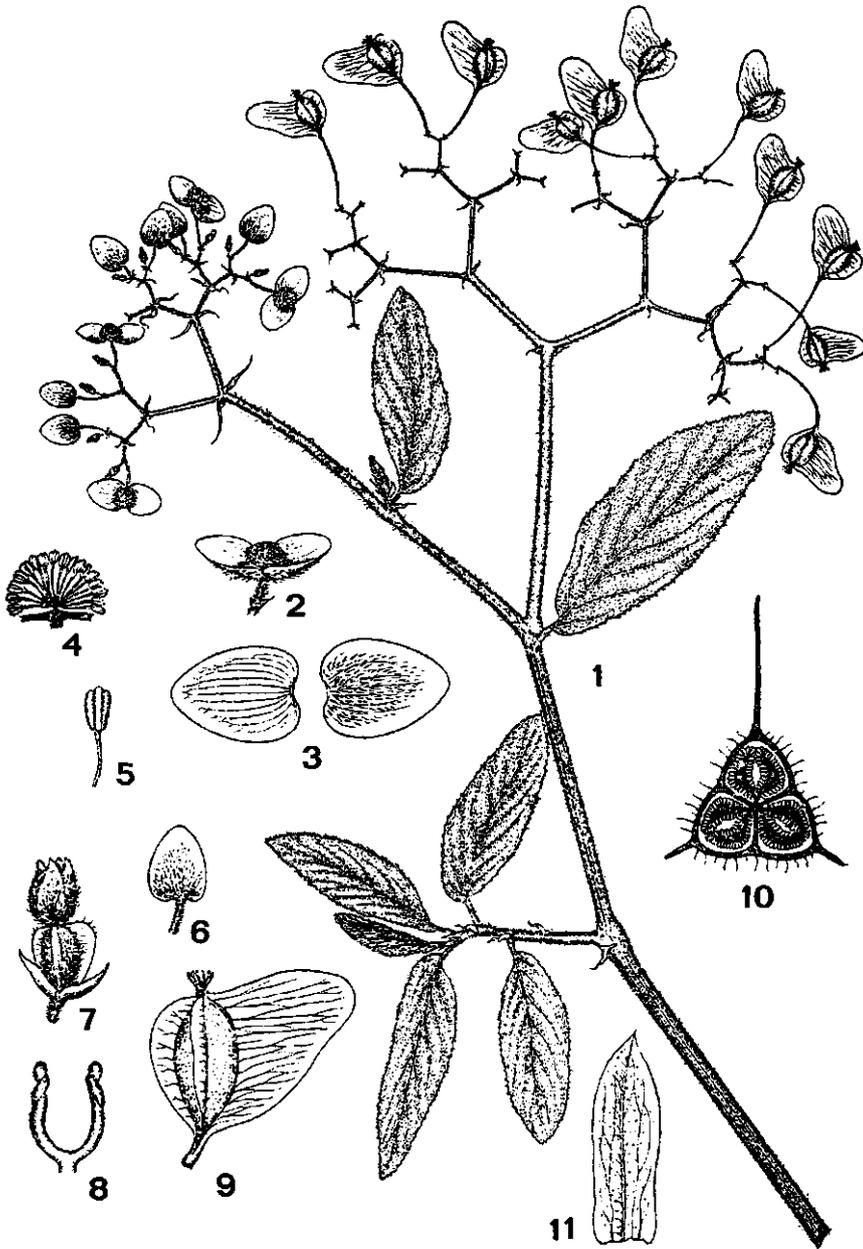


Fig. 11. Sect. *Donaldia*. *B. jairii* — 1, flowering stem; 2, male flower; 3, perianth segments of male flower; 4, androecium; 5, stamen; 6, young male flower; 7, female flower; 8, style; 9, fruit; 10, ovary in transverse section; 11, stipule. Reproduced from Brade (1950): est. 5.

indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial at base and monochasial at apex, bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts persistent (during flowering). **Flower** with 2 bracteoles inserted directly below the ovary or rarely without bracteoles (*B. egleri*); perianth segments white or pink, outer ones rounded or rarely acute at apex (in male flowers of *B. burle-marxii* and *B. ulmifolia*). *Male flower* with 2 or 4 free perianth segments; androecium actinomorphic, filaments equal, free or fused below, anthers circular to elliptic or oblong, shorter than or about as long as the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective not extended (or very little). *Female flower* with 5 free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles 3, fused less than halfway (to nearly free), forked once, persistent in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, nodding (in two species; others unknown), without or with an indistinct beak.

DISTRIBUTION: America: Brazil; one species spread throughout South America (and also introduced and naturalized in Asia) as a weed.

LEAF ANATOMY: Stomata single or few together; hypoderm absent or consisting of one layer; cystoliths absent or present and opalescent.

SEED MICROMORPHOLOGY: Seeds conform to the usual type. Those of *B. ulmifolia* measure 290 x 190 μm (3 species studied).

CHROMOSOMES: $2n = 30$ (*B. ulmifolia*).

TAXONOMIC COMMENTS: The characters which distinguish this section from sect. *Begonia*, viz. pinnate leaves and 2 male tepals, bring *Donaldia* close to *Ruizopavonia*, from which it differs by the 5 female tepals, and perhaps by a lower, spreading habit. The species of *Donaldia* are found in Brazil, except for the type species *B. ulmifolia* which occurs in Venezuela, Guyana and Trinidad but tends to follow man and is naturalized as far as Sri Lanka. *B. bangii* and *B.*

chaetocarpa were placed by their author O. Kuntze in *Donaldia*, but the latter has two female tepals and multifid styles and *B. bangii* has only been cursorily described. Therefore, both are tentatively relegated to sect. *Ruizopavonia*.

SPECIES LIST: 7 species: *B. burle-marxii* Brade, *B. dasycarpa* A. DC., *B. eglerti* Brade, *B. heloisana* Brade, *B. jairii* Brade, *B. saxicola* A. DC., *B. ulmifolia* Willd.

sect. **Doratometra** (Klotzsch) A. DC.

Fig. 12

Prodr. 15, 1: 383 (1864). — *Doratometra* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 126 (1854), type species: *Doratometra wallichiana* (Lehmann) Klotzsch = *B. wallichiana* Lehmann (homotypic synonym; non Steudel 1840, nomen nudum).

Begonia sect. *Poecilia* A. DC., Ann. Sci. Nat., Bot. 4, 11: 142 (1859), lectotype species (Barkley & Baranov, 1972): *B. humilis* Dryander.

Hoffmannella Klotzsch ex A. DC., Prodr. 15(1): 299 (1864), type species: *Hoffmannella rosea* Klotzsch ex A. DC. = *B. semiovata* Liebm. (heterotypic synonym).

Plants terrestrial, often annual, stems upright or ascending (*B. subcostata*); tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs (present in *B. prieurii*?). **Leaves** alternate, more than 2, straight or transverse (*B. hirtella*, *B. wallichiana*), symmetric or asymmetric, not peltate, simple; venation palmate to pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial or dichasial at base and monochasial at apex (inflorescences of *B. steyermarkii* are 2-flowered), bisexual; inflorescence axes not reduced; bracts persistent (during flowering). **Flower** with 2 bracteoles inserted directly below the ovary or rarely without bracteoles (*B. wallichiana*); perianth segments white or pink, outer ones rounded at apex. *Male flower* with 2 or 4 free perianth segments; androecium actinomorphic, filaments equal, free or fused below (into a short column) or rarely entirely fused (*B. steyermarkii*), anthers circular to oblong or obovate, longer than or shorter than the filaments, dehiscent with laterally or unilaterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective extended or not. *Female flower* with 4 or 5 free or rarely partially fused (*B. steyermarkii*) perianth segments; ovary or fruit with 3 wings, wings usually unequal in fruit,

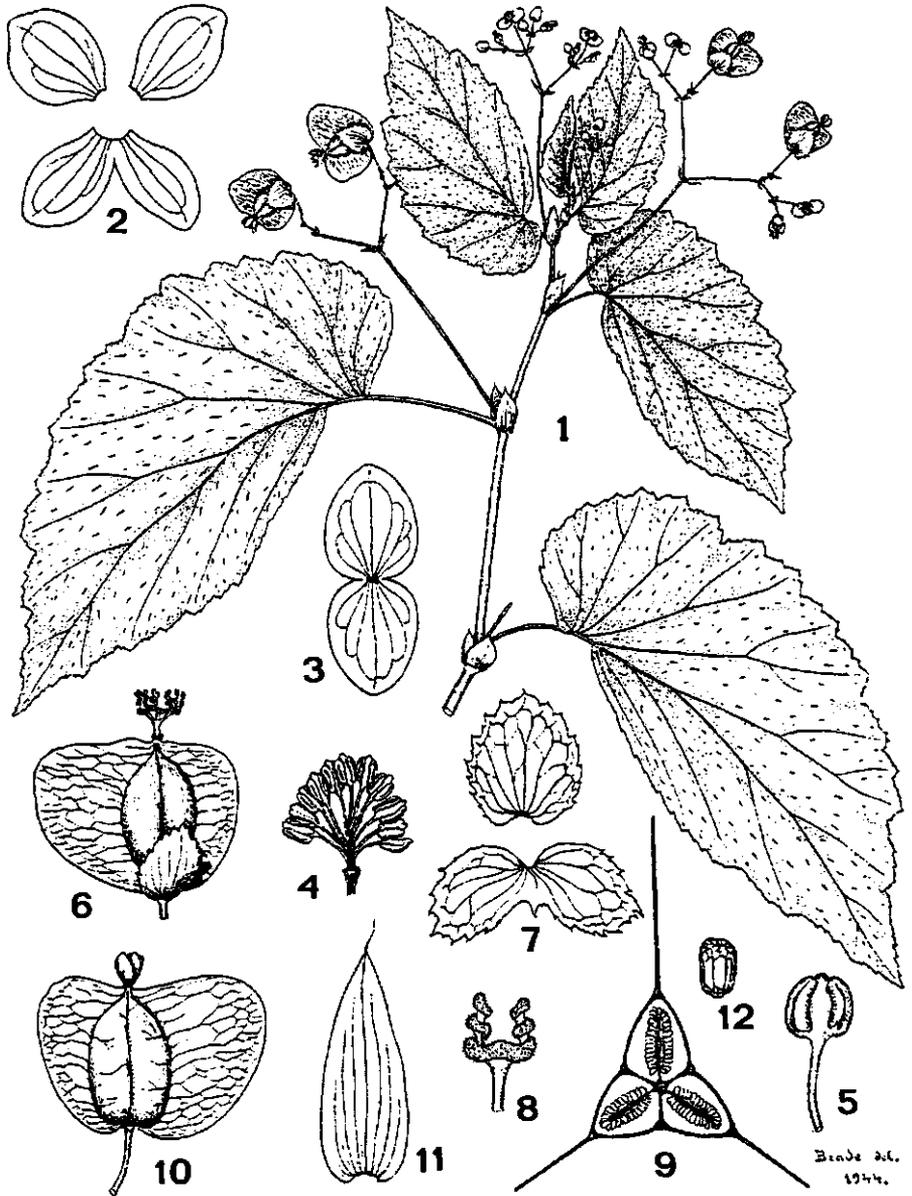


Fig. 12. Sect. *Doratometra*. *B. alemanii* — 1, flowering stem; 2, perianth segments of female flower; 3, perianth segments of male flower; 4, androecium; 5, stamen; 6, fruit with bracteole; 7, bracteoles of female flower; 8, style; 9, ovary in transverse section; 10, fruit; 11, stipule; 12, seed. Reproduced from Brade (1945): est. 1.

not hook- or spine-like, locules 3, placentation axillary, placental branches 1 or 2 per locule, ovules present between placental branches; styles 3, free or fused less than halfway, usually forked once or rarely multifid (*B. subcostata*), persistent in fruit, stigma not kidney-shaped, usually in a band and spiralled. **Fruit** not berry-like, dehiscent near the back of the locules (on both sides of the wings), pendulous.

DISTRIBUTION: America: throughout Central and South America, some as weeds.

LEAF ANATOMY: Stomata single (*B. wallichiana*) or in groups (*B. filipes*, *B. hirtella*, *B. humilis*, *B. prieurii*, *B. semiovata*); hypoderm absent; no cystoliths.

SEED MICROMORPHOLOGY: Seeds of *B. wallichiana* are 340 x 195 μm , the collar cells comparatively short, testa cells isodiametric. Those of *B. filipes* (235 μm), *B. humilis* and *B. semiovata* are smaller; in *B. hirsuta* and *B. hirtella* the cell walls are more undulated than in *B. wallichiana*. Seed of *B. prieurii* is ornamented with little knobs and that of *B. steyermarkii* has thicker, distinctly undulate anticlinal walls.

CHROMOSOMES: $2n = 26$ (*B. wallichiana*); $2n = 34$ (*B. hirtella*; Piton (1962) counted 36); $2n = 60$ (*B. humilis* var. *porterana* A. DC.).

TAXONOMIC COMMENTS: At first sight a homogeneous section of short-lived (annual?) species with inconspicuous flowers in small inflorescences, which in some species, perhaps even in all, are self-pollinating. Apart from these similarities in habit and ecology, however, these species show a considerable variation in morphological characters, e.g. the number of tepals, shape of the anthers, placentae and seeds. *B. hirtella* forms a link to section *Begonia*, also by its chromosome number.

SPECIES LIST: 8 species: *B. alemanii* Brade, *B. filipes* Benth., *B. hirsuta* Aubl., *B. hirtella* Link, *B. humilis* Dryand., *B. prieurii* A. DC., *B. semiovata* Liebm., *B. wallichiana* Lehman.

Species whose membership is doubtful: 2 species: *B. steyermarkii* L.B. Smith & Schubert, *B. subcostata* Rusby.

Ann. Sci. Nat., Bot. 4, 11: 143 (1859), type species: *B. erminea* L'Hér.

Plants terrestrial, perennial, acaulescent or with short upright stems; tubers present; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2 or rarely 1 or 2 (*B. androrangensis*), straight, symmetric, not peltate or rarely peltate (*B. marojejyensis*), simple or rarely palmatifid (*B. lemurica*) or bipinnatifid or further divided (*B. monicae*); venation palmate, palmate-pinnate or pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial, bisexual, protandrous, with 1–2(–3) female flowers, the central flower of the cyme male, lateral flower(s) female; inflorescence axes not reduced; bracts persistent (during flowering) or caducous. **Flower** without bracteoles; perianth segments white or pink, outer ones rounded at apex (but always elliptic or narrowly so). *Male flower* with 4 free perianth segments; androecium actinomorphic or zygomorphic, filaments equal or unequal, fused below, anthers oblong, about as long as the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective not extended or rarely extended (*B. marojejyensis*). *Female flower* with (4–)6 free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 1 per locule; styles 3, fused less than or rarely more than halfway, 2-lobed or forked once, caducous in fruit, stigma sometimes kidney-shaped, in a band and spiralled or not. **Fruit** not berry-like, (presumably dehiscent near the back of the locules), more or less erect or pendulous, without or with an indistinct beak (but more or less narrowed towards the apex which seems diagnostic when compared with sect. *Augustia*).

DISTRIBUTION: Africa: Madagascar.

SEED MICROMORPHOLOGY: Seeds ellipsoid, mean length (475–)550–600 μm , length/width ration 2.0–2.2; operculum nipple- to broadly nipple-shaped with a sunken hilum and composed of many cells; cuticular ornamentation finely striate.

CHROMOSOMES: $2n = 38$ (*B. bogneri*).

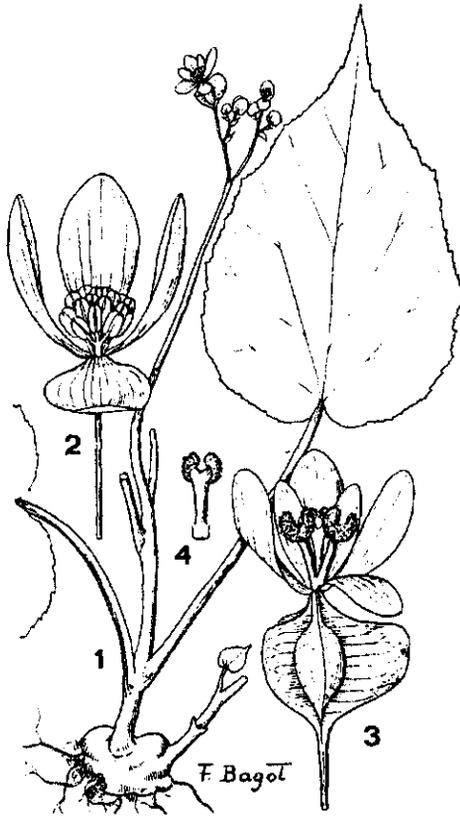


Fig. 13. Sect. *Erminea*. *B. erminea* — 1, plant habit; 2, male flower; 3, female flower; 4, style. Reproduced from Keraudren-Aymonin (1983); p. 25, pl. 5.

IMPORTANT LITERATURE: Keraudren-Aymonin, 1983.

TAXONOMIC COMMENTS: Hardly distinguishable from sect. *Muscibegonia* and possibly identical with it. Kept separate because of the unique seed micromorphology of sect. *Muscibegonia*. *B. bosseri* Keraudren may belong here; it has its inflorescence at the base of the leaf blade, like in the Asian section *Monophyllon*, and anthers on very short filaments.

SPECIES LIST: 12 species: *B. androrangensis* Humbert, *B. antongilensis* Humbert ex Bosser & Keraudren-Aymonin, *B. betsimisaraka* Humbert ex Bosser & Keraudren-Aymonin, *B. bogneri* Ziesenh., *B. erminea* L'Hér., *B. keraudrenae* Bosser, *B. lemurica* Keraudren, *B. marojejyensis* Humbert, *B. monicae* Aymonin & Bosser, *B. nana*

L'Hér., *B. razafinjohanyi* Aymonin & Bosser, *B. tsimihety* Humbert ex Bosser & Keraudren-Aymonin.

Species whose membership is doubtful: *B. bosseri* Keraudren.

sect. **Eupetalum** (Lindl.) A. DC.

Fig. 14

Prodr. 15, 1: 280 (1864). — *Eupetalum* Lindl., Nat. Syst. ed. 2: 440 (1836), type species: *Eupetalum petalodes* Lindl. = *B. geraniifolia* Hook. (heterotypic synonym).

Begonia sect. *Begoniella* A. DC., Ann. Sci. Nat., Bot. 4, 11: 120 (1859), lectotype species (Barkley & Baranov, 1972): *B. gracillima* A. DC.

Huszia Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 121 (1854). — *Begonia* sect. *Huszia* (Klotzsch) A. DC., Ann. Sci. Nat., Bot. 4, 11: 121 (1859), lectotype species (Barkley & Baranov, 1972): *B. octopetala* L'Hér.

Begonia sect. *Australes* L.B. Smith & Schubert, Darwiniana 5: 80 (1941), lectotype species (Barkley & Baranov, 1972): *B. micranthera* Griseb.

Plants terrestrial, with upright stems or acaulescent; tubers present; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire or rarely denticulate (*B. weberbaueri*); junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate or whorled, more than 2 or rarely 1 or 2 (*B. monophylla*, *B. sleumeri*), straight or rarely transverse, symmetric or asymmetric, not peltate, simple or palmately lobed (in about 4 species) or rarely palmatifid (*B. tafiensis*, *B. weberbaueri*); venation palmate or rarely palmate-pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, monochasial, bisexual (in *B. sleumeri* inflorescences possibly 1-flowered), with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts persistent (during flowering) or caducous. Flower without or rarely with 2 bracteoles spaced from the base of the ovary; perianth segments white, pink, red or orange (*B. cinnabarina*) or yellow (*B. lutea*, *B. pearcei*), outer ones rounded at apex. *Male flower* with 4–5(–11) free perianth segments; androecium actinomorphic, filaments free or fused below, anthers circular to elliptic or obovate, shorter than or rarely longer than the filaments (*B. davisii*, *B. froebelii*, *B. pleiopetala*), dehiscent with laterally positioned, longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective not extended or rarely extended. *Female flower* with (4–)5–6(–9) free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 2 or rarely 1 (*B. lutea*) per locule, ovules present

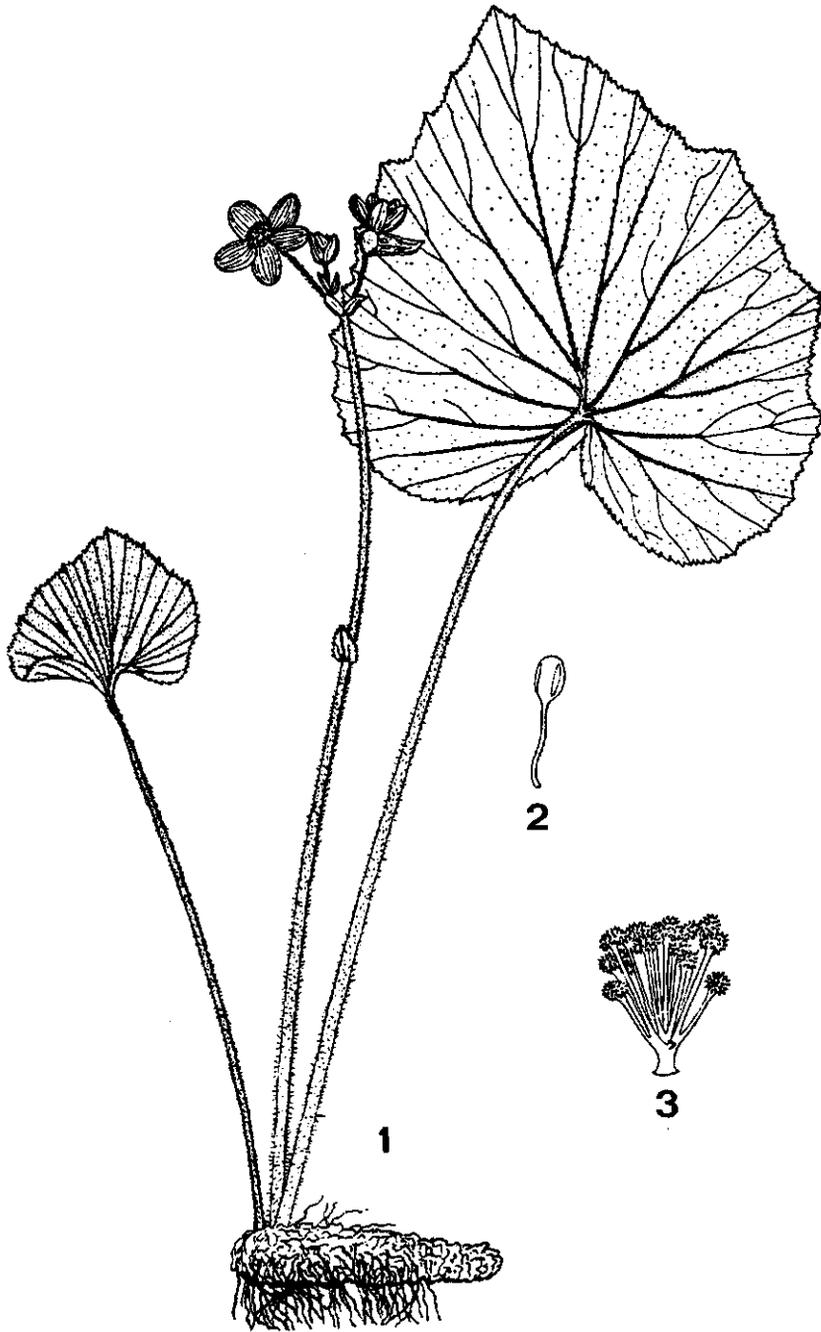


Fig. 14. Sect. *Eupetalum*. *B. rubricaulis* — 1, plant habit; 2, stamen; 3, styles. Reproduced from Smith & Schubert (1941): p. 86, tab. 5.

between placental branches; styles 3(-5), free or rarely fused less than halfway (*B. rubricaulis*), forked once or more than once or rarely 2-lobed (*B. baumannii*), persistent in fruit, stigma in a band and spiralled or rarely contracted near style apex. **Fruit** not berry-like, nodding (but often unknown), without or with an indistinct beak.

DISTRIBUTION: America: the Andean region and one species (*B. monophylla*) in Mexico.

LEAF ANATOMY: Stomata single (in groups of 2 (or more?) in *B. froebelii*); hypoderm usually present (absent in *B. froebelii*); cystoliths absent (*B. cinnabarina*, *B. geraniifolia*, *B. novogranatae*, *B. octopetala*, *B. rubricaulis*, *B. tominana*).

SEED MICROMORPHOLOGY: All species examined have the ordinary type of *Begonia* seed. The mean size varies from 340 x 180 to 455 x 300 μm . The seed shows a dense cuticular pattern of short zigzag and crow's foot striae. The seeds of *B. monophylla* differ by a broad nipple-shaped operculum, broader anticlinal walls and a coarser cuticular pattern.

CHROMOSOMES: $2n = 26$ (*B. cinnabarina*, *B. pearcei*); $2n = 28$ (*B. davisii*, *B. froebelii*, *B. micranthera*, *B. monophylla* (also $2n = 56$), *B. octopetala*).

TAXONOMIC COMMENTS: Klotzsch (1855) grouped the species that are now popularly known as the tuberous begonias ('einjährige Kräuter mit dicken, perennierenden Knollen und groszen Blüten' - Irmscher, 1925: 580) into three genera: *Barya* with one species, *Eupetalum* with three and *Huszia* with two. A. de Candolle, who reduced these genera to the status of sections, added 10 species to *Huszia*. Misled by the fact that the latter have all forked styles, he wrote 'styli ... bifido-conchiformis' in his diagnosis of *Huszia*, although the styles of the first two species described are many-branched. This error had a long life: it was repeated by Warburg (1894) and Irmscher (1926) and even by Baranov & Barkley (1974). Meanwhile, however, Irmscher had put things right (1949: 615-616). He discussed the possibility of limiting section *Huszia* to species with a much-branched style and putting the others in a separate section, but rejects this idea because the new section would

not be sufficiently distinct from either *Huszia* or *Begoniastrum* (which for Irmscher at that time included *Knesebeckia*). At a much earlier date A. DC. (1864) had divided *Huszia* into two subsections according to the number of petals: *Pluripetalae* and *Paucipetalae*. In the much-used key of Irmscher (1926) *Eupetalum* differs from *Huszia* by its upright stems and multi-branched styles. This leaves the tuberous species with showy flowers, upright stems and bifid styles, for which Smith & Schubert (1941) erected the section *Austerales*. In the present paper the species of this section have been divided over *Eupetalum* and *Knesebeckia*. We must admit that this is rather arbitrary: some forms of *B. micranthera* could just as well have been put into *Knesebeckia*. Some species do not quite fit, e.g. *B. froebelii* with oblong to linear anthers, and *B. lutea* with entire placentas, but as there seem to be no other characters that stand out against classification in *Eupetalum* we think it is not wise to erect new (mini)-sections.

SPECIES LIST: 27 species: *B. aequatorialis* L.B. Smith & Schubert, *B. anemoniflora* Irmscher, *B. baumannii* Lemoine, *B. cinnabarina* Hook., *B. clarkei* Hook. f., *B. davisii* Hook. f., *B. froebelii* A. DC., *B. geraniifolia* Hook., *B. gracillima* A. DC., *B. herrerae* L.B. Smith & Schubert, *B. macra* A. DC., *B. micranthera* Griseb., *B. neoharlingei* L.B. Smith & Wasshausen, *B. novogranatae* A. DC., *B. octopetala* L'Hér., *B. pearcei* Hook. f., *B. pleiopetala* A. DC., *B. polypetala* A. DC., *B. rosacea* Putz., *B. rubricaulis* Hook., *B. sleumeri* L.B. Smith & Schubert, *B. tafiensis* Lillo, *B. tenuicaulis* A. DC., *B. tominana* J. Golding, *B. tumbezensis* Irmscher, *B. veitchii* Hook. f., *B. weberbaueri* Irmscher.

Species whose membership is doubtful: 4 species: *B. fulgens* Lemoine, *B. lutea* L.B. Smith & Schubert, *B. monophylla* Pav. ex A. DC., *B. xerophyta* L.B. Smith & Wasshausen.

sect. **Filicibegonia** A. DC.

Fig. 15

Prodr. 15, 1: 392 (1864), type species: *B. aspleniifolia* Hook. f. ex A. DC.
Begonia sect. *Scutobegonia* Warb. series *Longicaules* Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenw. Afr. 3, 2: 616 (1921), lectotype species (here proposed): *B. elatostemmoides* Hook. f.

Plants terrestrial, perennial, with upright stems; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent or



Fig. 15. Sect. *Filicibegonia*. *B. asplenifolia* — 1, plant base with roots and fructing stem; 2, stipule; 3, perianth segment of male flower; 4, androecium; 5, styles; 6, fruit; 7, seed. Reproduced from Hallé (1972): p. 364, pl. 3.

early caducous, entire or dentate; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight, asymmetric, not peltate, simple or pinnatifid or rarely bipinnatifid or further divided; venation usually pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, bisexual or rarely bisexual and male or bisexual and female, protandrous; bisexual, male and female inflorescence monochasial; inflorescence with 1 female flower (rarely aberrantly 2), the central flower of the cyme male, lateral flower female; inflorescence axes strongly reduced; bracts persistent (during flowering) or rarely caducous. **Flower** without bracteoles; perianth segments white or pink, outer ones rounded or acute at apex. *Male flower* with 2 free perianth segments; androecium zygomorphic, filaments unequal, fused below, anthers circular to elliptic or oblong, longer than the filaments, dehiscent with unilaterally positioned longitudinal slits (more than 0.5 of the anther length), apex hooded, connective not extended. *Female flower* with 2 free perianth segments; ovary or fruit with 3(-4) wings (sometimes almost wingless), wings equal or subequal in fruit, not hook- or spine-like, locules 3(-4), placentation axillary, placental branches 1 per locule; styles 3(-4), fused less than halfway, 2-lobed, caducous in fruit, stigma kidney-shaped, in a band and not spiralled. **Fruit** not berry-like, not dehiscent (but disintegrating) or more rarely dehiscent both near the back of the locules and near the septa, pendulous, without or with an indistinct beak or rarely with a distinct beak.

DISTRIBUTION: Africa: from Guinea through tropical Africa to eastern Dem. Rep. Congo and south to Angola.

LEAF ANATOMY: Stomata single; hypoderm absent; no cystoliths (Sosef, 1994). Cuerrier et al. (1990) observed stomata in small groups for *B. auriculata* and cystoliths in *B. macrocarpa*. The first may be a different interpretation of the irregularly distributed stomata, the second requires confirmation.

SEED MICROMORPHOLOGY: Seeds ellipsoid, 265–350 x 175–250 μm , length/width ratio 1.4–1.6; collar cells with undulating anticlinal walls; operculum nipple- or broadly nipple-shaped, rarely obtuse; cuticula with a double ornamentation of short zigzag to star-shaped foldings intermingled with shortly linear to granular structures (see Lange, A. de & F. Bouman, 1992).

CHROMOSOMES: $2n = 36-38$, c. 72 (Arends, unpublished data).

TAXONOMIC COMMENTS: Closely related to the sections *Loasi-begonia* and *Scutobegonia*, but easily distinguished by its upright stems, distinctly kidney-shaped stigmas, and dry, disintegrating fruits.

SPECIES LIST: 8 species (and probably some undescribed ones): *B. aspleniifolia* Hook. f. ex A. DC., *B. auriculata* Hook. f., *B. elatostemmoides* Hook. f., *B. gossweileri* Irmscher, *B. macrocarpa* Warb., *B. minutifolia* N. Hallé, *B. sciaphila* Gilg ex Engl., *B. sessilifolia* Hook. f.

sect. **Gaerdtia** (Klotzsch) A. DC.

Fig. 16

Ann. Sci. Nat., Bot. 4, 11: 128 (1859). — *Gaerdtia* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 123 (1854), lectotype species (Barkley & Baranov, 1972): *Gaerdtia maculata* (Raddi) Klotzsch = *B. maculata* Raddi (homotypic synonym).

Begonia sect. *Pereira* Brade, Rodriguesia 18: 33 (1945), type species: *B. edmundoi* Brade.

Plants terrestrial, perennial, with upright stems; tubers absent; stem woody (at least at base); tubercles in leaf axil absent; stipules persistent or early caducous, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight to transverse, asymmetric, not peltate or rarely peltate (*B. lubbersii*), simple; venation pinnate or rarely palmate-pinnate (*B. pseudo-lubbersii*); indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial or dichasial at base and monochasial at apex, bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts caducous. **Flower** with 2 (caducous) bracteoles spaced from the base of the ovary; perianth segments white or pink or rarely red (*B. corallina*, *B. maculata* p.p.?) or orange (*B. dichroa*), outer ones rounded or acute at apex. *Male flower* with 4 free perianth segments; androe-cium actinomorphic, filaments unequal (always?), fused below, anthers obovate, usually shorter than or less often about as long as the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded or rarely hooded (*B. albo-picta*, *B. maculata*), connective not extended. *Female flower* with 5 free perianth segments; ovary or fruit with 3 wings,

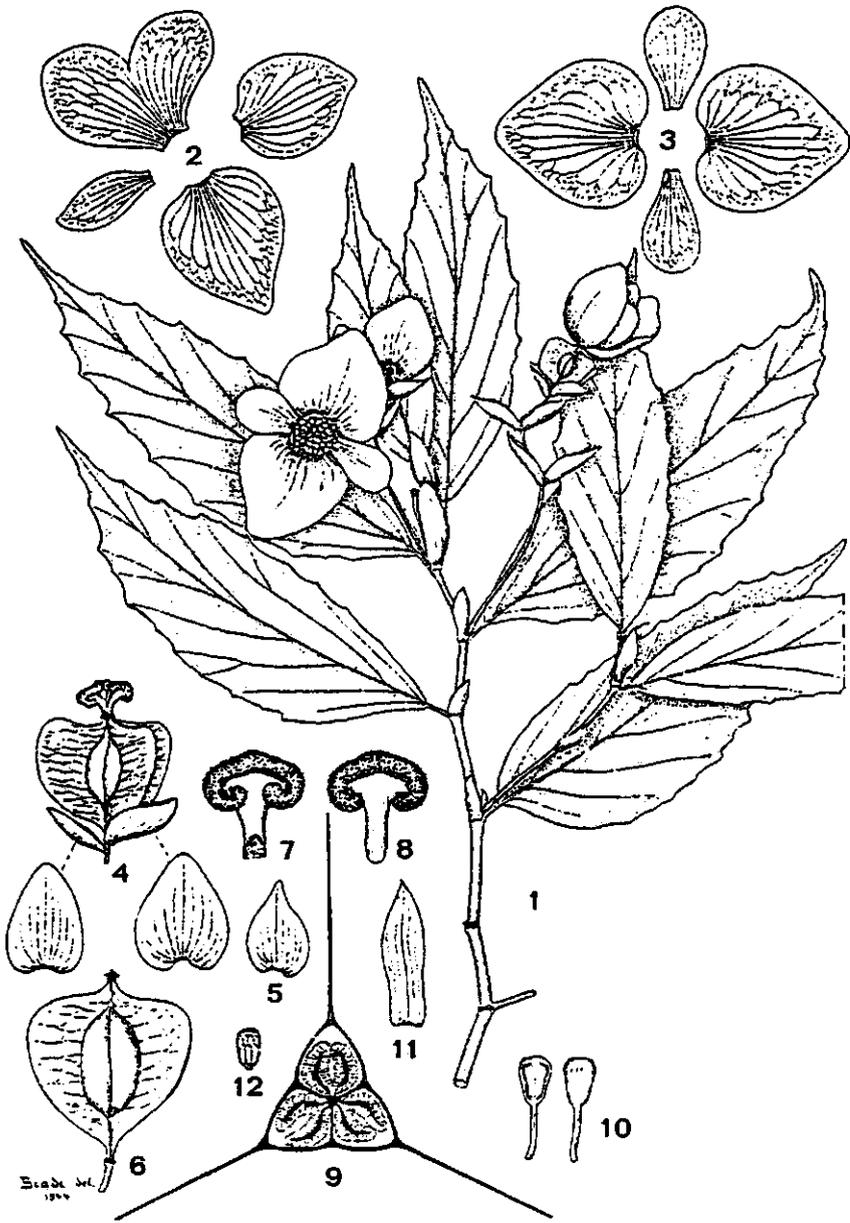


Fig. 16. Sect. *Gaerdtia*. *B. edmundoi* — 1, flowering stem; 2, perianth segments of female flower; 3, perianth segments of male flower; 4, ovary and bracteoles; 5, bracteole of male flower; 6, fruit; 7, stigma ventral view; 8, stigma dorsal view; 9, ovary in transverse section; 10, stamens; 11, stipule; 12, seed. Reproduced from Brade (1945): est. 6.

wings equal or subequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 2 or rarely 1 (*B. edmundoi*) per locule, ovules absent or rarely present (*B. dichroa*) between placental branches; styles 3, free or fused less than halfway, 2-lobed or forked once, persistent in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, pendulous, without or with an indistinct beak.

DISTRIBUTION: America: eastern Brazilian region.

LEAF ANATOMY: Stomata single; hypoderm absent; no cystoliths. Stone cells present in the stem (*B. albo-picta*, *B. corallina*, *B. dichroa*, *B. kunthiana*, *B. maculata*, *B. salicifolia*, *B. undulata*).

SEED MICROMORPHOLOGY: Seeds ellipsoid in *B. corallina* (495 μm long) and *B. undulata* (460 μm long), elliptic or narrowly elliptic, 565 x 290 μm with relatively long collar cells (290 μm) in *B. maculata*.

CHROMOSOMES: $2n = 56$ (*B. albo-picta*, *B. corallina*, *B. dichroa*, *B. edmundoi*, *B. maculata*, *B. undulata*).

TAXONOMIC COMMENTS: The distinction of the genus, and later the section, *Gaerdtia* was mainly based on the placentae, which were bifid with the ovules on the outside. Otherwise 'habito omnino sect. *Pritzelia*' as A. DC. wrote in 1861. He did not yet know that the similarity goes even further: such species of *Pritzelia* that are close to *Gaerdtia* also have the same number of chromosomes (56) and crosses can easily be made, often resulting in fertile hybrids. Many cultivars of the group, known in the USA as 'cane begonias', originated in this way. That *Gaerdtia* is nevertheless upheld here, is on account of differences in the anthers which in *Gaerdtia* are elliptic to obovate and usually much shorter than (at most as long as) the filaments, the connective reduced, whereas in *Pritzelia* they are oblong to linear, longer than the filaments, with an extended connective. Anatomically, *Pritzelia* is characterized by cystoliths, which are absent in *Gaerdtia*. *Gaerdtia* is extended here by two species that fit perfectly within the section except for the placentae. In *B. edmundoi*, for which Brade erected the section *Pereira*, these are entire. In *B. dichroa* they are bifid with ovules on both sides; for this reason this species was previously placed in *Knesebeckia*.

SPECIES LIST: 11 species: *B. albo-picta* Bull., *B. corallina* Carr., *B. dichroa* Sprague, *B. edmundoi* Brade, *B. kunthiana* Walp., *B. lubbersii* E. Morr., *B. macduffieana* L.B. Smith & Schubert, *B. maculata* Raddi, *B. pseudolubbersii* Brade, *B. salicifolia* A. DC., *B. undulata* Schott.

sect. **Gireoudia** (Klotzsch) A. DC.

Fig. 17

Ann. Sci. Nat., Bot. 4, 11: 133 (1859). — *Gireoudia* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 125 (1854), lectotype species (Barkley & Baranov, 1972): *Gireoudia involucrata* (Liebm.) Klotzsch = *B. involucrata* Liebm. (homotypic synonym).

Magnusia Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 125 (1854). — *Begonia* sect. *Magnusia* (Klotzsch) A. DC., Prodr. 15, 1: 333 (1864), type species: *Magnusia maxima* Klotzsch = *B. fusca* Liebm. (heterotypic synonym).

Begonia sect. *Psathuron* A. DC., Ann. Sci. Nat., Bot. 4, 11: 131 (1859), type species: *B. pinetorum* A. DC.

Begonia sect. *Auriformia* Houghton in Ziesenh., The Begonian 41: 13 (1974), type species: *B. bakeri* C. DC. = *B. cardiocarpa* Liebm. (heterotypic synonym).

Rachia Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 124. — *Begonia* sect. *Rachia* (Klotzsch) A. DC., Ann. Sci. Nat., Bot. 4, 11: 131 (1859), lectotype species (Barkley & Baranov, 1972): *Rachia incana* (Lindl.) Klotzsch = *B. peltata* Otto & Dietr. var. *auriformis* J. Golding (heterotypic synonym).

Plants terrestrial, perennial, rhizomatous or with upright stems; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent or early caducous, entire; junction petiole and leaf blade without or less often with a tuft of hairs (in about 5 species). **Leaves** alternate or whorled (more or less), more than 2, usually oblique to transverse or rarely straight, asymmetric or symmetric (in about 7 species), not peltate or less often peltate (in about 7 species), simple or less often palmately lobed (in about 8 species) or palmately compound (*B. carolineifolia*, *B. thiemei*); venation palmate or rarely palmate-pinnate (*B. buseyi*, *B. plantaginea*); indumentum of scales absent but indumentum of fimbriate-ciliate paleae sometimes present, stellate hairs absent. **Inflorescence** axillary, dichasial or dichasial at base and monochasial at apex (often asymmetrical to unilateral (at least 17 species; in *B. quaternata* the lower nodes are 3–5-radiate; in *B. knoopii* the first node may be 3-radiate), bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not or strongly reduced (outer internodes sometimes reduced in *B. corredorana*, *B. involucrata* and *B. vestita*); bracts persistent

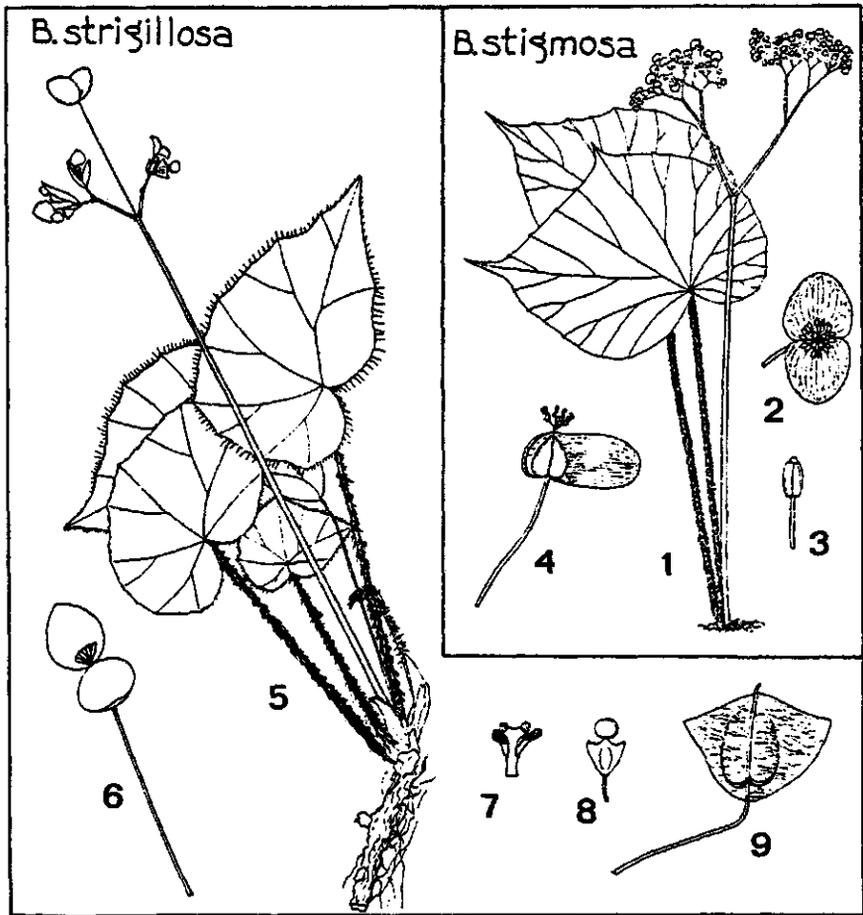


Fig. 17. Sect. *Gireoudia*. *B. stigmosa* — 1, plant habit; 2, male flower; 3, stamen; 4, fruit. *B. strigillosa* — 5, plant habit; 6, male flower; 7, style; 8, female flower; 9, fruit. Reproduced from Smith & Schubert 1958: p. 50, fig. 15.

(during flowering) or caducous. **Flower** usually without or rarely with 2 bracteoles inserted directly below the ovary; perianth segments white or pink, outer ones rounded or rarely acute at apex (*B. cardiocarpa*, *B. lyman-smithii*). **Male flower** with 2(–4) free perianth segments; androecium zygomorphic, filaments unequal, free or fused below (on a short column), anthers oblong or obovate (8 species) or rarely circular to elliptic (*B. quaternata*), usually longer than to about as long as or rarely shorter than the filaments (*B. quaternata*), dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective

extended or not. *Female flower* with 2 free perianth segments; ovary or fruit with 3 wings, wings equal to unequal in fruit, not hook- or spine-like, locules (2-)3 (2 or 3 in *B. dressleri*), placentation axillary, placental branches (1-)2 per locule, ovules present between placental branches; styles (2-)3 (2 or 3 in *B. dressleri*), usually fused less than or sometimes more than halfway (5 species) or free (2 species), 2-lobed or forked once or less often simple (6 species), persistent or caducous in fruit, stigma usually lunate and not spiralled, less often in a band and spiralled. **Fruit** not berry-like, dehiscent near the back of the locules, without or with an indistinct beak.

DISTRIBUTION: America: Central America.

LEAF ANATOMY: Anatomical data available for 28 species. Stomata in small groups (2-5), sometimes intermingled with single ones; Fellerer (1892) mentions 4 species with solitary stomata only but this has been confirmed only for *B. hydrocotylifolia*. In *B. multinervia* the groups are larger (3-8). Hypoderm is always present, usually on both sides of the leaf. Cystoliths are probably absent. Fellerer l.c. found no hypoderm in *B. fusca*, but Cuerrier et al. (1991a) did. He observed cystoliths in *B. involucrata*, *B. multinervia* and *B. urophylla* which Cuerrier et al. did not see (they did not examine *B. urophylla*).

SEED MICROMORPHOLOGY: Bouman & de Lange (in press) found that 16 species 'confirm to the ordinary seed type'. Seeds ellipsoid, up to 445 µm long (*B. crassicaulis*) with a length/width ratio of about 2; anticlinal walls mostly straight or slightly curved; cuticular ornamentation mainly granular or short zigzag.

CHROMOSOMES: Chromosomes have been counted for 30 species. In all cases the chromosome number was 28.

IMPORTANT LITERATURE: Burt-Utley (1985).

TAXONOMIC COMMENTS: Burt-Utley (1985) suggested *B. plebeja* Liebm. as the type species of *Gireoudia* Klotzsch instead of *B. involucrata* but in our opinion Article 8 of the Code does not leave this possibility.

As A. DC. already remarked, sect. *Rachia* is intermediate between

Gireoudia and *Knesebeckia*. Warburg included it in *Gireoudia*. Irmscher (1926) followed this example but in 1960 put *B. peltata* into *Knesebeckia*. Burt-Utley, citing Irmscher, did not include *B. peltata* and *B. kellermanii* in her study of Middle American *Gireoudia*. In the present study these two species are included in *Gireoudia* again on account of the similarity in inflorescence and leaf anatomy.

SPECIES LIST: 66 species: *B. barkeri* Knowl. & Westc., *B. bettinae* Ziesenh., *B. bowerae* Ziesenh., *B. breedlovei* K. Burt-Utley, *B. buseyi* K. Burt-Utley, *B. cardiocarpa* Liebm., *B. carolineifolia* Regel, *B. carrieae* Ziesenh., *B. chiapensis* K. Burt-Utley, *B. chivatoa* Ziesenh., *B. conchifolia* A. Dietr., *B. corredorana* C. DC., *B. corzoensis* Ziesenh., *B. crassicaulis* Lindl., *B. cristobalensis* Ziesenh., *B. croatii* K. Burt-Utley, *B. dressleri* K. Burt-Utley, *B. fusca* Liebm., *B. garagarana* C. DC., *B. glandulifera* Hook., *B. heracleifolia* Cham. & Schlecht., *B. hispidivillosa* Ziesenh., *B. huberti* Ziesenh., *B. hydrocotylifolia* Otto ex Hook., *B. involucrata* Liebm., *B. jaliscana* K. Burt-Utley, *B. karwinskyana* A. DC., *B. kellermanii* C. DC., *B. kenworthyae* Ziesenh., *B. knoopii* Ziesenh., *B. kortisiae* Ziesenh., *B. lindleyana* Walp., *B. louis-williamsii* K. Burt-Utley, *B. lyman-smithii* K. Burt-Utley & J.F. Utley, *B. manicata* Brongn., *B. mariti* K. Burt-Utley, *B. mazae* Ziesenh., *B. morii* K. Burt-Utley, *B. multinervia* Liebm., *B. multistaminea* K. Burt-Utley, *B. nelumbiifolia* Cham. & Schlecht., *B. peltata* Otto & Dietr., *B. philodendroides* Ziesenh., *B. pinetorum* A. DC., *B. plantaginea* L.B. Smith & Schubert, *B. plebeja* Liebm., *B. polygonata* Liebm., *B. pringlei* S. Wats., *B. pruinata* (Klotzsch) A. DC., *B. pudica* L.B. Smith & Schubert, *B. quaternata* L.B. Smith & Schubert, *B. rafael-torresii* K. Burt-Utley, *B. rhizocaulis* (Klotzsch) A. DC., *B. roseibractea* Ziesenh., *B. sarcophylla* Liebm., *B. serico-neura* Liebm., *B. sousae* K. Burt-Utley, *B. sparsipila* Baker, *B. squarrosa* Liebm., *B. stigmosa* Lindl., *B. strigillosa* A. Dietr., *B. tacanana* Ziesenh., *B. thiemei* C. DC. ex J.D. Smith, *B. urophylla* Hook., *B. vestita* C. DC., *B. xilitlensis* K. Burt-Utley.

Species whose membership is doubtful: 2 species: *B. mucronistipula* C. DC., *B. setulosa* Bertol.

Ann. Sci. Nat., Bot. 4, 11: 119 (1859), lectotype species (Barkley & Baranov, 1972): *B. maurandiae* A. DC.

Plants terrestrial or epiphytic (*B. secunda?*), perennial, lianescent; tubers absent; stem woody (at least at base); tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, usually straight, symmetric, peltate or rarely not peltate (*B. maurandiae* partly, *B. secunda*), simple; venation palmate-pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, cymose, bisexual (?), of several species only male flowers are known; whether this means that female flowers develop later on the same inflorescence or that the inflorescences are purely male is not clear), with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced or rarely strongly reduced (*B. hitchcockii*); bracts persistent (during flowering). **Flower** with 2 bracteoles inserted directly below the ovary; perianth segments white or pink or red (on the outside), outer ones rounded or rarely acute at apex (*B. maurandiae*, *B. truncicola*). *Male flower* with 4 or rarely 5 (*B. truncicola?*) free perianth segments; androecium actinomorphic, filaments equal, fused below or entirely fused, anthers obovate or broadly triangular, longer than the filaments, with longitudinal slits (more than 0.5 of the anther length), connective extended or not. *Female flower* with 5–6(–7) free perianth segments; ovary or fruit with 3–4 wings, wings unequal in fruit, not hook- or spine-like, locules 3–4, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles 3–4, free or fused less than halfway, 2-lobed, persistent in fruit, stigma kidney-shaped or not, in a band and spiralled. **Fruit** not berry-like, without or with an indistinct beak.

DISTRIBUTION: America: the Andean region.

LEAF ANATOMY: Stomata single; hypoderm absent; no cystoliths (*B. maurandiae*).

SEED MICROMORPHOLOGY: Seed irregularly ellipsoid; length 420–555 μm ; length/width ratio 2.5–3.0; operculum broadly nipple-shaped; chalazal end often flattened (5 species examined).



Fig. 18. Sect. *Gobenia*. *B. geminiflora* — 1, plant habit; 2, male flower; 3, female flower. Reproduced from Smith & Wasshausen (1979): p. 251, pl. 4.

IMPORTANT LITERATURE: Smith & Wasshausen (1986).

TAXONOMIC COMMENTS: In many respects *Gobenia* is a homogeneous section, set apart from other sections by the flexuous, climbing stems with peltate leaves, female flowers with 5–7 very small tepals and 3- or 4-celled ovaries which are covered by the

bracteoles and develop into capsules with very unequal wings (of course there are exceptions, as everywhere in *Begonia*). The inflorescences are axillary, 3- to many-flowered dichasia which in four (possibly more) species are borne on special branches in the axils of leaves. On these branches the leaves are suppressed but for the stipules. In some species the inflorescence is reduced to either one female flower or one or three male ones. In the latter case it is not clear whether the plant bears only male or female flowers or both, and if the latter, it bears them on different inflorescences or on the same, with a time interval between the two.

SPECIES LIST: 14 species: *B. dodsonii* L.B. Smith & Wasshausen, *B. geminiflora* L.B. Smith & Wasshausen, *B. hitchcockii* Irmscher, *B. maurandiae* A. DC., *B. pululahuana* C. DC., *B. rubrotincta* L.B. Smith & Schubert, *B. secunda* L.B. Smith & Wasshausen, *B. segregata* L.B. Smith & Schubert, *B. sodiroi* C. DC., *B. spadiciflora* L.B. Smith & Schubert, *B. tropaeolifolia* A. DC., *B. truncicola* Sod. ex C. DC., *B. wurdackii* L.B. Smith & Schubert, *B. ynesiae* L.B. Smith & Wasshausen.

Species whose membership is doubtful: 1 species: *B. grandibracteolata* Irmscher.

sect. **Haagea** (Klotzsch) A. DC.

Fig. 19

Prodr. 15, 1: 391 (1864). — *Haagea* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 125 (1854), type species: *Haagea dipetala* (Graham) Klotzsch = *B. dipetala* Graham (homotypic synonym).

Plants terrestrial, perennial, with upright stems; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight to transverse, asymmetric, not peltate, simple; venation palmate-pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial at base and monochasial at apex, bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts persistent (during flowering) or caducous. **Flower** without bracteoles; perianth segments white or pink, outer ones rounded at apex. *Male flower* with 2 free perianth segments; androecium actinomorphic, filaments equal, fused below (into a short column), anthers obovate or oblong, about as long as to shorter than the

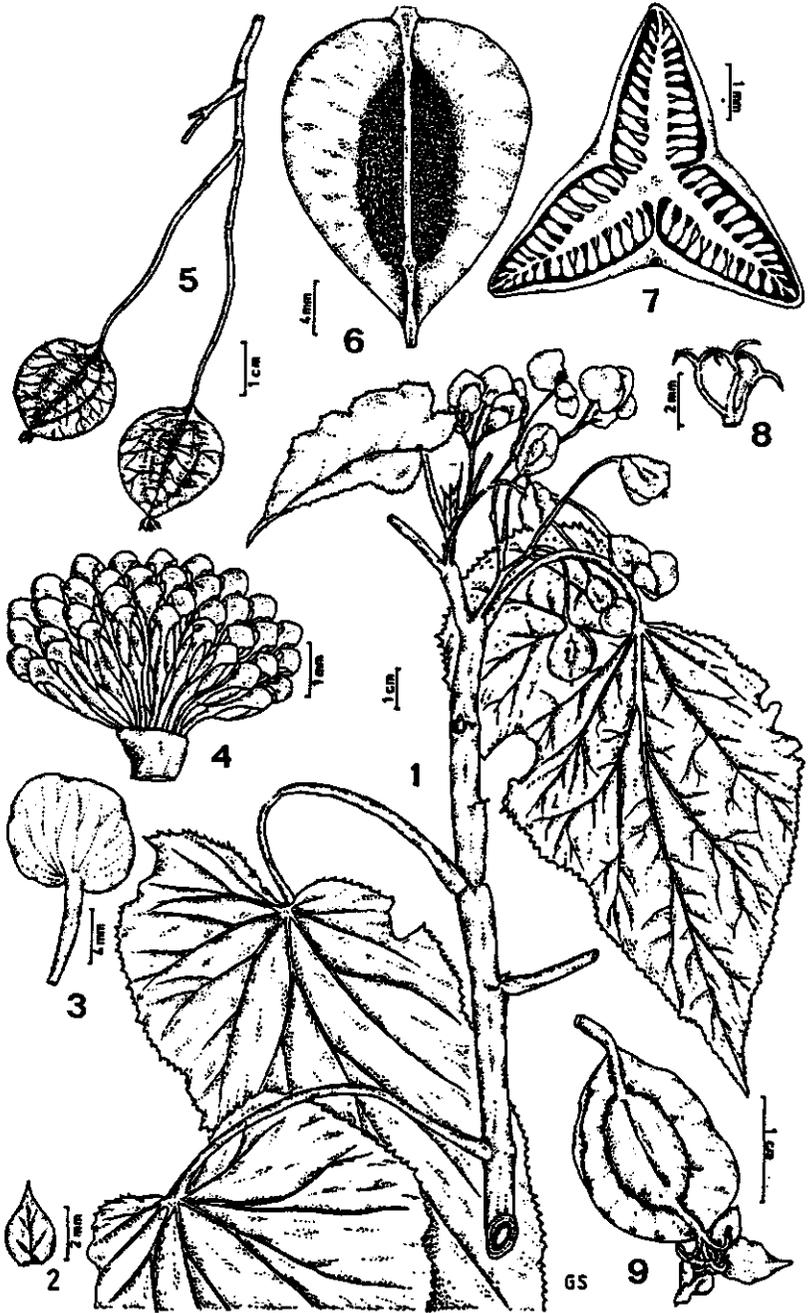


Fig. 19. Sect. *Haagea*. *B. dipetala* — 1, flowering stem; 2, bract; 3, young male flower; 4, androecium; 5, fruits; 6, young fruit; 7, ovary in transverse section; 8, styles; 9, female flower. Reproduced from Matthew (1982): pl. 306.

filaments, dehiscent with unilaterally positioned longitudinal slits (more than 0.5 of the anther length), apex hooded. *Female flower* with 2 free perianth segments; ovary or fruit with 3 wings, wings equal or subequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 1 per locule; styles 3, free, forked once, persistent in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, pendulous, without or with an indistinct beak.

DISTRIBUTION: Asia: India and Sri Lanka.

LEAF ANATOMY: Stomata single; hypoderm absent; no cystoliths.

CHROMOSOMES: $2n = 30$ & 60 .

TAXONOMIC COMMENTS: Authors from A. de Candolle (1864) to Smith & Wasshausen (1986) include a second species: *B. malabarica* A. DC. However, this is a later homonym of *B. malabarica* Lamk which outdates the first by 81 years. As clearly it merges into *B. dipetala*, we join the two species here, leaving it to others to solve the problem if and how to subdivide *B. dipetala*.

SPECIES LIST: A single variable species: *B. dipetala* R. Grah.

sect. **Heeringia** Irmscher

Mitt. Inst. Allgem. Bot. Hamburg 8: 158 (1929), type species: *B. sibthorpioides* Ridley.

Plants terrestrial, perennial, with rhizomes from which upright stems arise; tubers present (tuberous rhizome); stem herbaceous; tubercles in leaf axil absent; stipules persistent, dentate; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate or opposite (the upper pair), 1 or 2 or more than 2, straight, symmetric, not peltate, simple; venation palmate; indumentum of scales or stellate hairs absent. **Inflorescence** terminal, monochasial, bisexual, with 1 female flower; inflorescence axes not reduced. **Flower** without bracteoles; perianth segments white or pink, outer ones rounded at apex. *Male flower* with 4 free perianth segments; androecium zygomorphic, filaments equal, entirely fused, anthers broadly triangular (rough to densely tomentose due to whitish short

protuberances), longer than the filaments, dehiscent with unilaterally positioned apical pores, connective not extended. *Female flower* with 5 free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 2, placentation axillary (?), placental branches 2 per locule, ovules present between placental branches; styles 2, fused to almost halfway, 2-lobed, caducous in fruit, stigma kidney-shaped, in a band and not spiralled. **Fruit** not berry-like, more or less erect, without or with an indistinct beak.

DISTRIBUTION: Asia: Peninsular Malaysia.

SPECIES LIST: A single species: *B. sibthorpioides* Ridley.

sect. **Hydristyles** A. DC.

Ann. Sci. Nat., Bot. 4, 11: 132 (1859), lectotype species (Barkley & Baranov, 1972): *B. bridgesii* A. DC.

Begonia sect. *Ruizopavonia* A. DC. p.p.

Plants terrestrial, perennial, with upright stems; tubers absent; stem herbaceous or woody (at least at base); tubercles in leaf axil absent; stipules persistent or rarely early caducous (*B. bridgesii*), entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, transverse, asymmetric, not peltate, simple; venation palmate or palmate-pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary or terminal (pseudo-terminal in *B. andina*?), cymose, bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts persistent (during flowering) or caducous. **Flower** with 2 bracteoles (or none?, often not described) spaced from the base of the ovary; perianth segments white or pink, outer ones rounded at apex. *Male flower* with 2 or rarely 4 (*B. ophiogyna*) free perianth segments; androecium actinomorphic, filaments free, unequal or subequal, anthers oblong, usually longer than or about as long as or rarely shorter than the filaments (*B. unduavensis*), dehiscent with laterally positioned (?) longitudinal slits (more than 0.5 of the anther length), connective extended. *Female flower* with 5(-6) free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles 3 or 4 or 6, fused less than halfway, forked

more than once, persistent in fruit, stigma not kidney-shaped, in a band and spiralled (in as far as there is room for spirals). **Fruit** not berry-like, without or with an indistinct beak.

DISTRIBUTION: America: mainly Bolivia.

LEAF ANATOMY: Stomata single; hypoderm absent; no cystoliths (*B. andina*).

SEED MICROMORPHOLOGY: Seeds quite diverse; mean size 340 x 175 μm (*B. juntasensis*) to 630 x 205 μm (*B. santarosensis*); anticlinal walls weakly to strongly undulate (5 species studied).

CHROMOSOMES: $2n = 52$ (unidentified species, *B. andina*?).

TAXONOMIC COMMENTS: In 1926 it was still easy for Irmscher to separate the sections *Hydristyles* and *Ruizopavonia*, both with 2 male perianth segments but the former with 5 female perianth segments and multifid styles, the latter with 2 female perianth segments and bifid styles. Since then several newly discovered species in the section *Ruizopavonia* with multifid styles have reduced the usefulness of this character for the delimitation of *Hydristyles*. The number of female perianth segments remains a distinctive character, however, and so does Bolivia as the area of distribution. Species with similar transverse, palmate leaves and 2 male perianth segments, but with 2 female perianth segments formerly brought to *Ruizopavonia* (now *Cyathocnemis*) occur mainly in Peru. It should be noted that of about half the species of *Hydristyles* only incomplete descriptions are available.

SPECIES LIST: 9 species: *B. andina* Rusby, *B. bridgesii* A. DC., *B. fissistyla* Irmscher, *B. juntasensis* Kuntze, *B. peltigera* Irmscher, *B. santarosensis* Kuntze, *B. subcaudata* Rusby ex L.B. Smith & Schubert, *B. unduavensis* Rusby, *B. unilateralis* Rusby.

Species whose membership is doubtful: 1 species: *B. ophiogyna* L.B. Smith & Schubert.

sect. **Knesebeckia** (Klotzsch) A. DC.

Fig. 20

Ann. Sci. Nat., Bot. 4, 11: 125 (1859). — *Knesebeckia* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 122 (1854), lectotype species

- (Barkley & Baranov, 1972): *Knesebeckia incarnata* (Link & Otto) Klotzsch = *B. incarnata* Link & Otto (homotypic synonym).
Begonia sect. *Apteron* C. DC., Bull. Herb. Boiss. 2, 8: 326 (1908), type species: *B. exalata* C. DC.
Begonia sect. *Cylindrobegonia* L.B. Smith & Schubert, Contr. Gray Herb. 127: 25 (1939), type species: *B. cylindrata* L.B. Smith & Schubert.
Begonia sect. *Dissepbegonia* Ziesenh., The Begonian 15: 20 (1948), type species: *B. cavum* Ziesenh.
Begonia sect. *Latistigma* A. DC., Ann. Sci. Nat., Bot. 4, 11: 127 (1859), lectotype species (Barkley & Baranov, 1972): *B. aconitifolia* A. DC.

Plants terrestrial, perennial or rarely annual (*B. viscida*), with upright stems or rarely rhizomatous (*B. serotina*; *B. uniflora* is procumbent); tubers absent or present; stem herbaceous or possibly woody (at least at base); tubercles in leaf axil absent or rarely present (*B. weberlingii*); stipules persistent or early caducous, entire or dentate; junction petiole and leaf blade without or less often with a tuft of hairs. **Leaves** alternate, more than 2 (several species flower in leafless condition), straight to transverse, asymmetric or symmetric (in about 5 species), peltate or not, simple or palmately lobed; venation palmate or rarely palmate-pinnate (in about 5 species) or rarely pinnate (*B. longimaculata*, *B. maynensis*); indumentum of scales absent, stellate hairs absent or rarely present (*B. kuhlmannii*, *B. santos-limae*). **Inflorescence** axillary or rarely terminal (3 species?), bisexual or rarely separate male and female (*B. extranea*, *B. viscida*), with male flowers basal and female flowers distal, protandrous; bisexual inflorescence usually dichasial at base and monochasial at apex or rarely monochasial (possibly also dichasial); inflorescence axes not reduced or rarely strongly reduced (*B. wollnyi*); bracts persistent (during flowering) or caducous. **Flower** without or with 2 bracteoles inserted directly below the ovary; perianth segments white or pink or rarely red (*B. weddelliana*), outer ones rounded or acute at apex. *Male flower* usually with 4 or rarely 2 (*B. aconitifolia*) free perianth segments; androecium actinomorphic, filaments free or fused below (into a column), anthers circular to elliptic or obovate or rarely oblong (*B. incarnata*), usually shorter than or rarely about as long as the filaments (4 species), dehiscent with laterally positioned, usually longitudinal slits (more than 0.5 of the anther length) or rarely short pore-like slits (less than 0.5 of the anther length; 3 species), apex usually not hooded or rarely hooded (*B. olbia*), connective usually not extended or less often extended (5 species). *Female flower* with 5 free perianth segments; ovary or fruit with 3 wings or rarely with 1 wing (*B.*

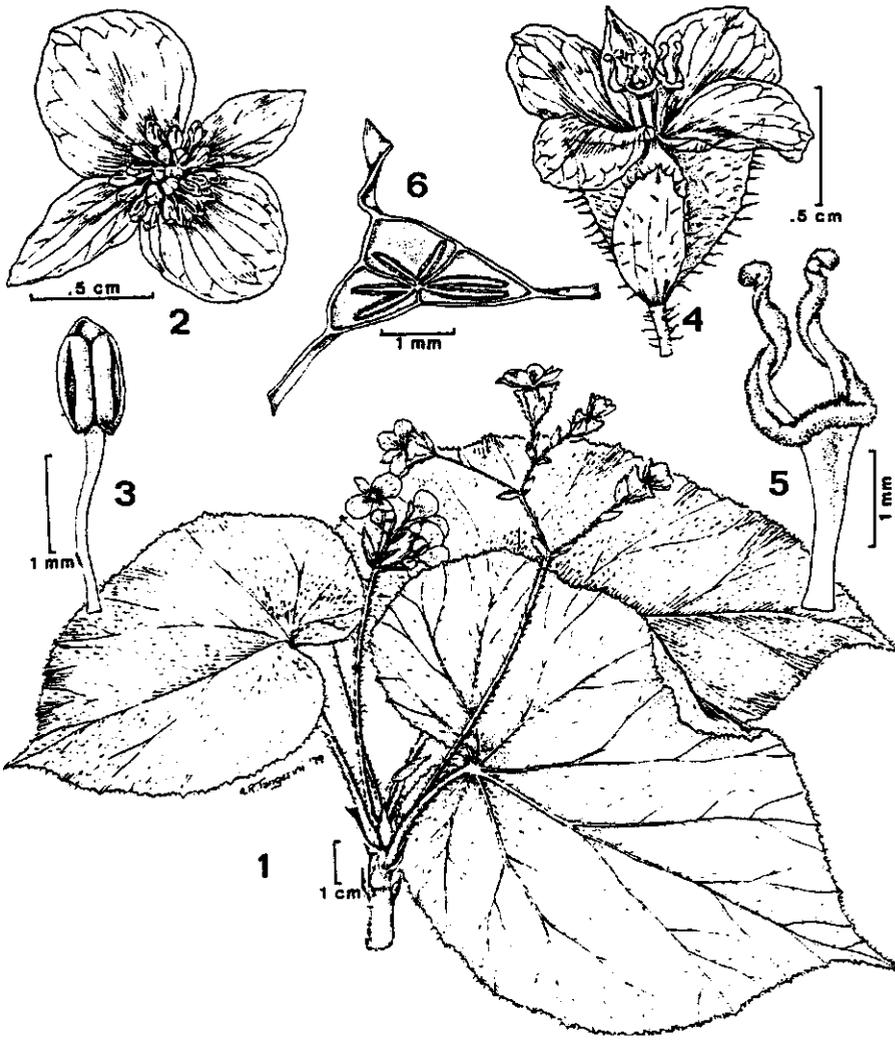


Fig. 20. Sect. *Knesebeckia*. *B. sparreana* — 1, plant habit; 2, male flower; 3, stamen; 4, female flower; 5, style; 6, ovary in transverse section. Reproduced from Smith & Wasshausen (1986): p. 47, fig. 9.

cylindrata, *B. hintoniana*) or wingless (*B. exalata*), wings unequal in fruit, not hook- or spine-like, locules 3, placentation usually axillary or rarely septal (*B. cavum*), placental branches 2 per locule, ovules present between placental branches; styles 3, fused less than halfway or free or rarely fused more than halfway (*B. parcifolia*), 2-lobed or forked once or rarely forked more than once (*B. longimaculata*, *B.*

wollnyi), usually persistent or rarely caducous in fruit (*B. cylindrata*), stigma usually not kidney-shaped or rarely kidney-shaped (*B. hintoniana*), usually in a band and spiralled or rarely not spiralled (*B. incarnata*). **Fruit** not berry-like, pendulous, without or with an indistinct beak.

DISTRIBUTION: America: throughout Central and mostly eastern South America (Mexico to Bolivia).

LEAF ANATOMY: Stomata single; hypoderm absent; cystoliths absent.

SEED MICROMORPHOLOGY: Confirms to the usual type. Seeds ellipsoid, mean length from 280 μm (*B. maynensis*) to 440 μm (*B. aconitifolia*), length/width ratio 1.5 to 2.0 (11 species studied).

CHROMOSOMES: $2n = 28$ (*B. acerifolia*, *B. cavum*, *B. falciloba*, *B. ludwigii*, *B. uniflora*, *B. viscida*, *B. wollnyi*); $2n = 56$ (*B. ignea*, *B. olbia*); $2n = 60$ (*B. aconitifolia*, *B. leathermaniae*).

TAXONOMIC COMMENTS: Klotzsch set up the genus *Knesebeckia* in 1854 for 6 American and 1 Asian species; already in 1855 the number had grown to 13. A. DC. treated *Knesebeckia* as a section of *Begonia*; in his Prodrômus he distinguished 19 American species and 6 Asian ones. Warburg (1894) reduced *Knesebeckia* to a subsection of *Begonia*(*strum*) and so did Irmscher (1926). In subsequent publications (e.g. Irmscher 1949, 1953a) he even ignored the subsection altogether, but in 1960 he uses *Knesebeckia* again as a section in its own right. Of the other sections mentioned, *Apteron*, *Cylindrobegonia* and *Dissepbegonia* are monotypic and differ from *Knesebeckia* in only one character. Section *Latistigma* used to be a well-defined group but is now joined with *Knesebeckia* by species such as *B. olbia* and *B. barkleyana*.

SPECIES LIST: 50 species: *B. acerifolia* Humb., Bonpl. & Kunth, *B. aconitifolia* A. DC., *B. arrogans* Irmscher, *B. barkleyana* L.B. Smith, *B. bifurcata* L.B. Smith & Schubert, *B. brachyclada* Urb. & Ekman, *B. cavum* Ziesenh., *B. cebadillensis* Houghton ex L.B. Smith & Schubert, *B. compacticaulis* Irmscher, *B. crinita* Oliver ex Hook. f., *B. cuernavacensis* Ziesenh., *B. cylindrata* L.B. Smith & Schubert, *B. erythrocarpa* A. DC., *B. exalata* C. DC., *B. extranea*

L.B. Smith & Schubert, *B. falciloba* Liebm., *B. fernaldiana* L.B. Smith & Schubert, *B. hintoniana* L.B. Smith & B.G. Schubert, *B. hydrophyloides* L.B. Smith & Schubert, *B. ignea* Warzewicz, *B. incarnata* Link & Otto, *B. kuhlmannii* Brade, *B. lachaoensis* Ziesenh., *B. leathermaniae* T. O'Reilly & C. Karegeannes, *B. longimaculata* Irmscher, *B. ludwigii* Irmscher, *B. mayasiana* L.B. Smith & Schubert, *B. maynensis* A. DC., *B. michoacana* L.B. Smith & Schubert, *B. microcarpa* A. DC., *B. nemoralis* L.B. Smith & Schubert, *B. oellgaardii* L.B. Smith & Wasshausen, *B. olbia* Kerchove, *B. parcifolia* C. DC., *B. parodiana* L.B. Smith & Schubert, *B. pastoensis* A. DC., *B. piurensis* L.B. Smith & Schubert, *B. platanifolia* Schott, *B. relicta* L.B. Smith & Schubert, *B. santoslimae* Brade, *B. serotina* A. DC., *B. sparreana* L.B. Smith & Wasshausen, *B. stenocardia* L.B. Smith & Schubert, *B. triramosa* Irmscher, *B. uniflora* S. Wats., *B. velata* L.B. Smith & Schubert, *B. viscida* Ziesenh., *B. weberlingii* Irmscher, *B. weddelliana* A. DC., *B. wollnyi* Herzog.

Species whose membership is doubtful: 5 species: *B. asympeltata* L.B. Smith & Wasshausen, *B. brandbygeana* L.B. Smith & Wasshausen, *B. lugonis* L.B. Smith & Wasshausen, *B. mariannensis* Wasshausen & McLellan, *B. molinana* K. Burt-Utley.

sect. **Lauchea** (Klotzsch) A. DC.

Prodr. 15, 1: 353 (1864). — *Lauchea* Klotzsch, Abh. Akad. Berlin '1854': 241 (1855), type species: *Lauchea verticillata* (Hook.) Klotzsch = *B. adenopoda* Lem. (heterotypic synonym).

Plants terrestrial, perennial, with rhizomes from which upright stems arise; tubers present; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** whorled, more than 2, straight, symmetric, not peltate, simple; venation pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial (in the description of A. DC., but in Hooker's drawing it is a raceme of monochasia), bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts persistent (during flowering). **Flower** without bracteoles; perianth segments white or pink, outer ones rounded at apex. *Male flower* with 4 free perianth segments; androecium actinomorphic, filaments fused below, anthers circular to elliptic (according to A. DC.) or oblong

(according to Clarke), longer than the filaments, apex not hooded (probably), connective not extended. *Female flower* with usually 4 or rarely 5 free perianth segments; ovary or fruit with 3 wings (2 very narrow), wings unequal in fruit, not hook- or spine-like, locules 2, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles 2, fused less than halfway, forked once, persistent in fruit, stigma not kidney-shaped. **Fruit** not berry-like, irregularly dehiscent, pendulous, with a distinct beak.

DISTRIBUTION: Asia: Myanmar (Burma).

LEAF ANATOMY: Stomata single; hypodermi absent; cystoliths absent; scleroids absent.

SEED MICROMORPHOLOGY: The margins of the areolae of the testa beaded due to minute papillae.

SPECIES LIST: 2 species: *B. adenopoda* Lem., *B. burmensis* L.B. Smith & Wasshausen.

sect. **Lepsia** (Klotzsch) A. DC.

Fig. 21

Ann. Sci. Nat., Bot. 4, 11: 139 (1859). — *Lepsia* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 123 (1854), lectotype species (Barkley & Baranov, 1972): *Lepsia foliosa* (Humb., Bonpl. & Kunth) Klotzsch = *B. foliosa* Humb., Bonpl. & Kunth. (homotypic synonym).

Tittelbachia Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 126 (1854). — *Begonia* sect. *Tittelbachia* (Klotzsch) A. DC., Prodr. 15, 1: 291 (1864), lectotype species (Barkley & Baranov, 1972): *Tittelbachia fuchsoides* (Hook.) Klotzsch = *B. fuchsoides* Hook. (homotypic synonym).

Plants terrestrial, perennial, with upright stems (in *B. foliosa* sometimes scandent); tubers absent; stem woody (at least at base) (in *B. confinis* completely herbaceous?); tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight, symmetric, not peltate, simple or pinnatifid (subtrilobed in *B. confinis*); venation pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, cymose, bisexual or rarely separate male and female (in certain forms of *B. foliosa*?); inflorescence axes not reduced; bracts persistent (during flowering). **Flower** with 2 bracteoles inserted directly below the ovary (or somewhat lower); perianth

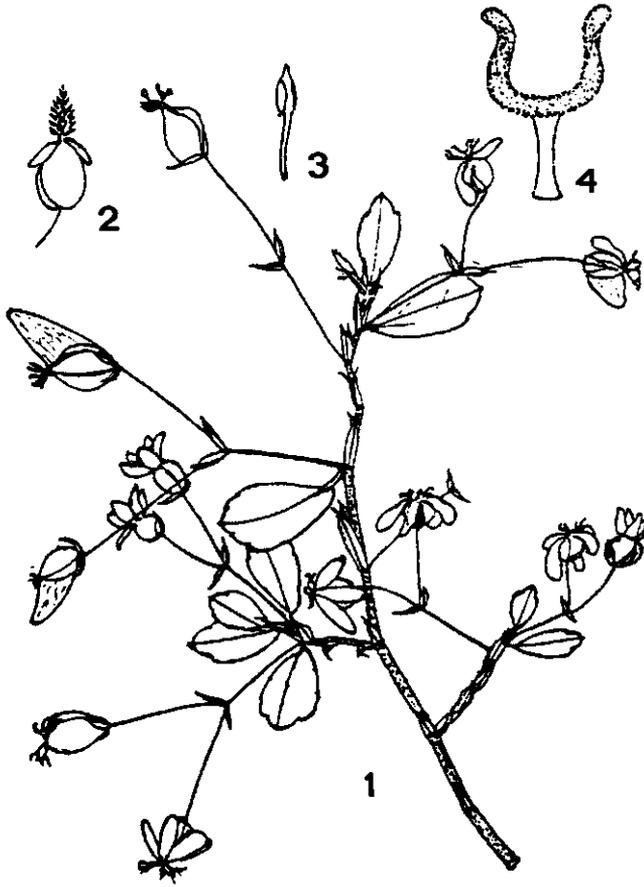


Fig. 21. Sect. *Lepsia*. *B. microphylla* — 1, flowering stem; 2, male flower; 3, stamen; 4, style. Reproduced from Smith & Schubert (1946): p. 188, tab. 15.

segments white or pink or rarely red (sometimes in *B. fuchsioides*), outer ones rounded or acute at apex. *Male flower* with 4 free perianth segments; androecium actinomorphic, filaments usually unequal or equal (*B. confinis*, *B. fuchsioides*), fused below, anthers circular to elliptic or oblong, longer than or about as long as the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective extended or rarely not extended (*B. confinis*). *Female flower* with 5 free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 1 per locule or 2 (*B. fuchsioides*, always?), ovules present between placental branches (in *B. fuchsioides*); styles 3, fused

less than halfway, forked once, caducous in fruit (*B. confinis*), stigma not kidney-shaped, in a band and spiralled or all over the style (*B. fuchsioides*). **Fruit** not berry-like, pendulous (*B. fuchsioides*), without or with an indistinct beak.

DISTRIBUTION: America: Colombia, Venezuela and Peru.

LEAF ANATOMY: Stomata in groups; hypoderm absent (*B. foliosa*) or comprising 1–2 layers (*B. foliosa*, *B. fuchsioides*); no cystoliths.

SEED MICROMORPHOLOGY: Seed of the prevalent type. Mean length 355–580 μm (also within *B. foliosa*). Three species examined.

CHROMOSOMES: $2n = 60$ (*B. foliosa* (Piton, 1962), *B. fuchsioides*); $2n = 84$ (*B. foliosa*).

TAXONOMIC COMMENTS: Although the species concerned are very similar, the sections *Lepsia* and *Tittelbachia* have long been kept separate because of the differences in placentas (entire in *Lepsia*, bifid in *Tittelbachia*) and in stigmas (forming a spiral band in *Lepsia*, covering the whole style in *Tittelbachia*). Smith & Schubert (1946: 196) showed that the former character is unreliable in this case and found only spiral stigmas in wild material of *B. fuchsioides*. Consequently, they not only united the two sections but even reduced *B. fuchsioides* to a variety of *B. foliosa* (later, Smith & Wasshausen raised it to the status of species again). It should be noted that *B. fuchsioides* as originally described (and as it is still being grown) is also distinguished by large inflorescences of bright red flowers with fleshy tepals (A. DC. writes 'carnosis'). In our opinion it is a cultivar whose relationship to the wild species deserves closer study.

SPECIES LIST: 4 species: *B. confinis* L.B. Smith & Wasshausen, *B. foliosa* H. B. & K., *B. fuchsioides* Hook., *B. microphylla* A. DC.

Species whose membership is doubtful: 2 species: *B. complicata* (Hassk.) A. DC., *B. praerupta* Irmscher.

sect. **Loasibegonia** A. DC.

Fig. 22

Prodr. 15, 1: 389 (1864), type species: *B. prismatocarpa* W.J. Hooker.
Begonia sect. *Scutobegonia* Warb. series *Cordifolia* Engl., in Engl. & Drude, Veg.

der Erde 9, Die Pflanzenwelt Afr. 3, 2: 616 (1921), type species: *B. pseudo-viola* Gilg.

Begonia sect. *Scutobegonia* Warb. series *Euscutatae* Engl., l.c. 617 p.p., lectotype species (Sosef, 1994): *B. quadrialata* Warb.

Plants terrestrial, perennial, rhizomatous; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire or dentate; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight to transverse, symmetric or asymmetric, peltate or not, simple or rarely palmately lobed (*B. prismatocarpa*); venation usually palmate or rarely palmate-pinnate; indumentum of scales usually absent or rarely present and stellate, stellate hairs absent. **Inflorescence** axillary, monochasial, bisexual, protandrous, with 1 female flower (rarely aberrantly up to 3), the central flower of the cyme male, lateral flower female; inflorescence axes strongly reduced; bracts persistent (during flowering). **Flower** without bracteoles; perianth segments yellow or white or pink, outer ones rounded at apex. *Male flower* with 2 free perianth segments; androecium zygomorphic, filaments unequal, fused below, anthers oblong, longer than to about as long as the filaments, dehiscent with unilaterally positioned longitudinal slits (more than 0.5 of the anther length), apex hooded, connective not extended. *Female flower* with 2 free perianth segments; ovary or fruit wingless or with 3 or 4 wings, wings equal or subequal in fruit, not hook- or spine-like, locules 3 or 4, placentation axillary, placental branches 1 per locule; styles 3 or 4, fused less than halfway, forked once, caducous in fruit, stigma not kidney-shaped or kidney-shaped, in a band and spiralled or not. **Fruit** not berry-like, not dehiscent, more or less erect, usually without or with an indistinct beak or rarely with a distinct beak.

DISTRIBUTION: Africa: from Guinea eastward to Dem. Rep. Congo, Rwanda and Burundi, south to northern Angola.

LEAF ANATOMY: Stomata single; hypoderm absent; no cystoliths (see Sosef, 1994).

SEED MICROMORPHOLOGY: Seeds ellipsoid, 265–420 x 165–215 μm , length/width ratio 1.5–1.6; operculum broadly nipple-shaped to obtuse; collar cells with straight to undulate anticlinal walls; anti-clinals thick and with transverse cuticular hatching; cuticular ornamentation prominent, with a double structure of star-shaped or zigzag foldings elevated from a fine labyrinth-like structure.

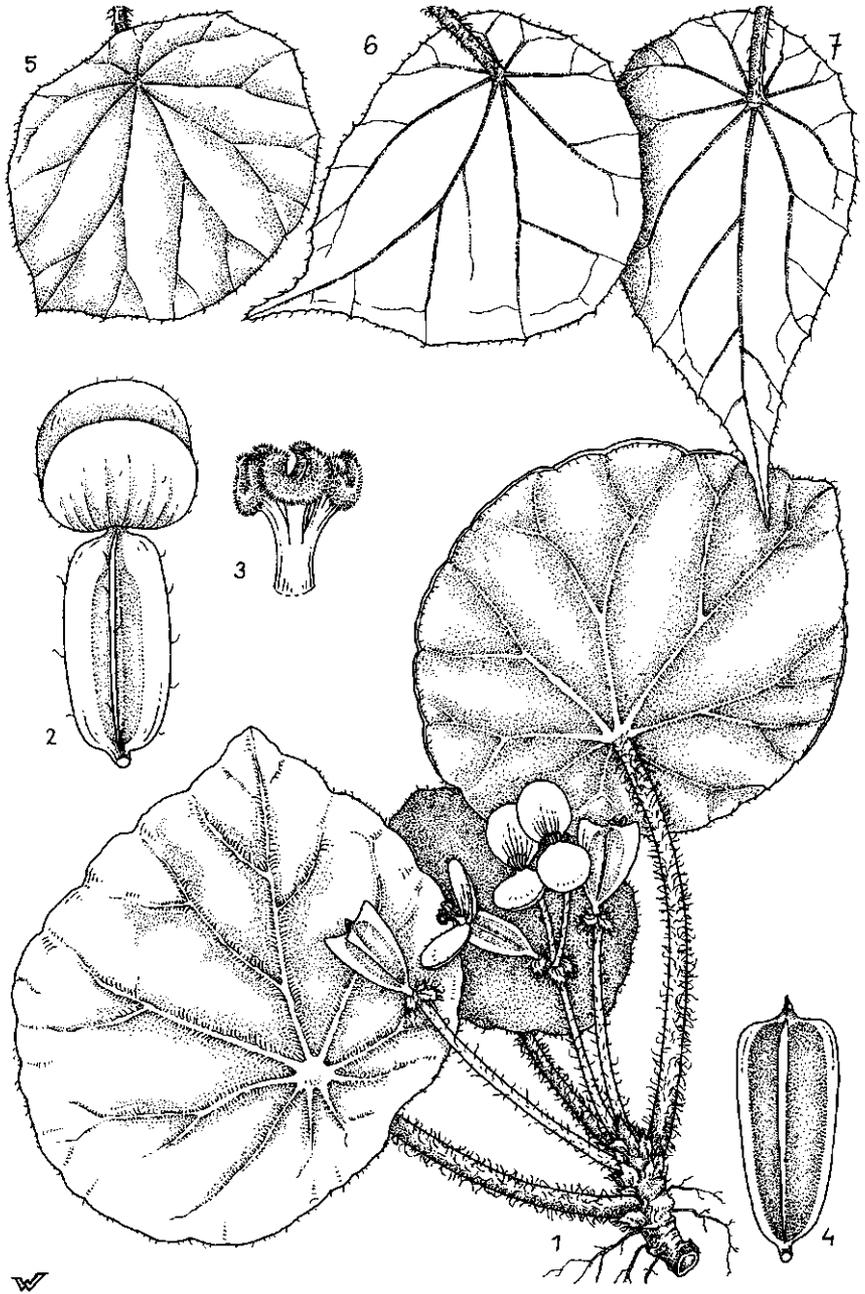


Fig. 22. Sect. *Loasibegonia*. *B. quadrialata* — 1, plant habit; 2, female flower; 3, styles; 4, fruit; 5-6 leaf shapes; 7, leaf of subsp. *dusenii* (Warb.) Sosef. Drawing by Mrs. Wil Wessel.

CHROMOSOMES: $2n = 26$ (*B. potamophila*); $2n = 32$ (*B. prismatocarpa*); $2n = 34$ (*B. staudtii*); $2n = 34 + 4B$ (*B. microsperma*); $2n = 52$ (*B. quadrialata* subsp. *nimbaensis*).

IMPORTANT LITERATURE: Sosef (1994).

TAXONOMIC COMMENTS: This section is very closely related to sect. *Scutobegonia* Warb. In sect. *Loasibegonia* the mature fruit is held in a more or less erect position, the tertiary veins lack a sclerenchymatous sheath and the ovary/fruit is narrowly oblong to very broadly obovate, whereas in sect. *Scutobegonia* the mature fruit is generally recurved towards the substrate, the tertiary veins have a (sometimes weakly developed) sclerenchymatous sheath, and the ovary/fruit is broadly obovate to very shallowly obtriangular, or rarely spindle-shaped.

SPECIES LIST: 19 species: *B. adpressa* Sosef, *B. atroglandulosa* Sosef, *B. duncan-thomasii* Sosef, *B. gentilii* De Wild., *B. heterochroma* Sosef, *B. letouzeyi* Sosef, *B. microsperma* Warb., *B. minuta* Sosef, *B. potamophila* Gilg, *B. prismatocarpa* Hook., *B. pseudoviola* Gilg, *B. pulcherrima* Sosef, *B. quadrialata* Warb., *B. salisburyana* Irmscher, *B. scapigera* Hook. f., *B. schaeferi* Engl., *B. scutifolia* Hook. f., *B. staudtii* Gilg, *B. stellata* Sosef.

sect. **Mezierea** (Gaud.) Warb.

Fig. 23

in Engl., Nat. Pflanzenfam. (ed. 1) 3, 6a: 139 (1894). — *Mezierea* Gaud., Voy. Bonite Atlas, tab. 32 (1841), type species: *Mezierea salaziensis* Gaud. = *B. salaziensis* (Gaud.) Warb.

Mezierea sect. *Aneupteron* A. DC., Prodr. 15, 1: 407 (1864), type species: *Mezierea salaziensis* Gaud. = *B. salaziensis* (Gaud.) Warb.

Begonia sect. *Exalabegonia* Warb. in Wittmack, Gartenflora 49: 2, 282 (1900), type species: *B. heddei* Warb. = *B. oxyloba* Welw. ex Hook. f. (heterotypic synonym).

Plants terrestrial, perennial, usually with upright stems or rarely lianescent; tubers absent; stem usually woody (at least at base) or rarely herbaceous; tubercles in leaf axil absent; stipules early caducous, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, oblique or transverse, asymmetric, not peltate, usually simple or rarely palmately lobed; venation palmate or palmate-pinnate; indumentum of scales or

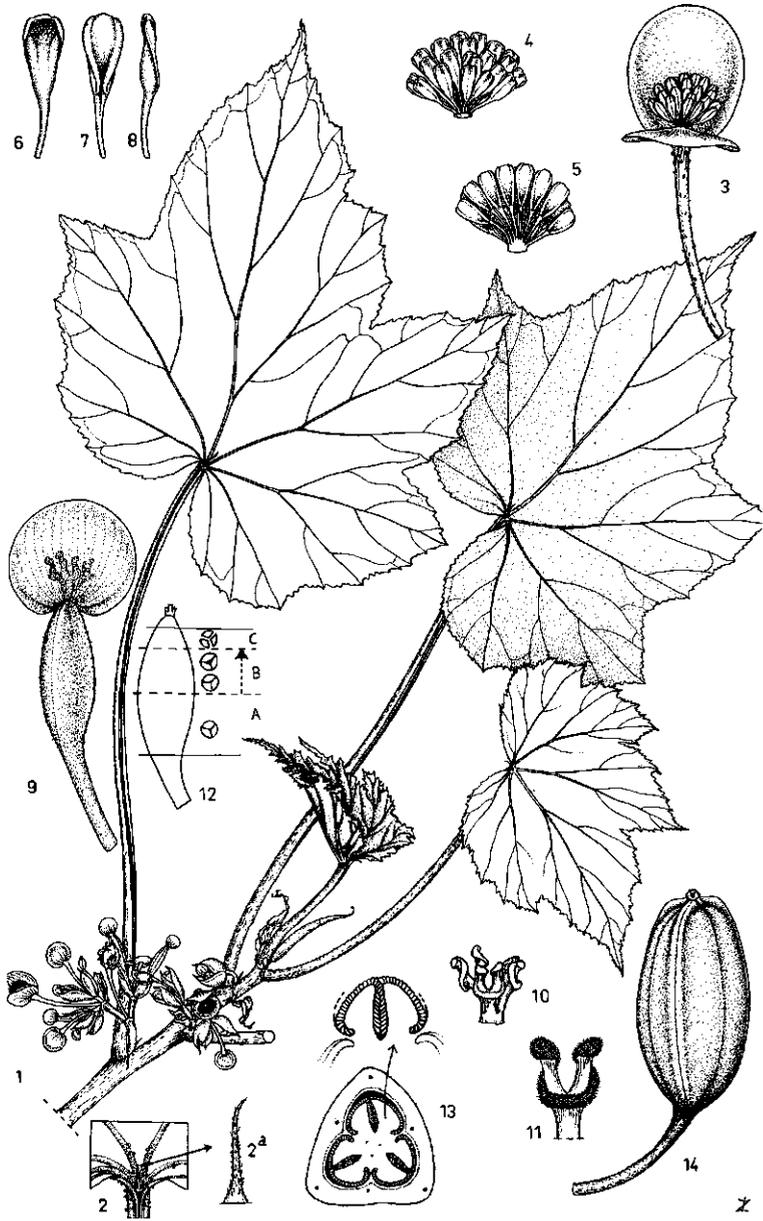


Fig. 23. Sect. *Mezierea*. *B. oxyloba* — 1, flowering stem; 2, base of upper leaf surface and single trichome; 3, male flower; 4, androecium frontal view; 5, androecium dorsal view; 6-8, stamens in ventral, dorsal and lateral view; 9, female flower; 10, styles; 11, stigma; 12, scheme of ovary with different modes of placentation; 13, ovary in transverse section, halfway along its length; 14, fruit. Drawing by Miss Ike Zewald.

stellate hairs absent. **Inflorescence** axillary, usually bisexual or rarely separate male and female, protandrous; bisexual inflorescence dichasial or dichasial at base and monochasial at apex; male and female inflorescence dichasial; inflorescence with up to 9 female flowers, the central flower of the cyme male, lateral flower(s) female; inflorescence axes not reduced; bracts caducous. **Flower** without bracteoles; perianth segments white or pink, outer ones rounded at apex. *Male flower* with 2 or 4 or rarely 3 free perianth segments; androecium actinomorphic or zygomorphic, filaments usually unequal or rarely equal, usually fused below or rarely free, anthers obovate or oblong, longer than to shorter than the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective usually not extended or rarely extended. *Female flower* with 2 or 4 free perianth segments; ovary or fruit wingless, locules 3 or 5, placentation parietal or septal or rarely axillary, placental branches 2 per locule, ovules present between placental branches; styles 3 or 5, free, forked once, usually persistent or rarely caducous in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** berry-like, not dehiscent, more or less erect, without or with an indistinct beak.

DISTRIBUTION: Africa: throughout tropical Africa and in Madagascar, the Seychelles, the Comores and the Mascarene Islands.

LEAF ANATOMY: Stomata single; hypoderm absent; no cystoliths (*B. salaziensis*).

SEED MICROMORPHOLOGY: Seeds rather variable, ellipsoid, 380–800 x 200–475 μm , length/width ratio 1.7–2.2; anticlinal walls of collar cells straight; operculum broadly nipple-shaped to obtusate; hilum usually sunken; cuticular ornamentation absent to present and composed of a double structure.

CHROMOSOMES: $2n = 26$ (*B. seychellensis*).

IMPORTANT LITERATURE: de Wilde & Arends (1989), Klazenga, de Wilde & Quené (1994).

TAXONOMIC COMMENTS: *B. meyeri-johannis* Engl. is aberrant as it represents a lianescent woody climber. The species is supposed to be dioecious but undeniably monoecious individuals do also occur.

The sections *Baccabegonia*, *Mezierea* and *Squamibegonia* are thought to be closely affiliated. This is based on arguments provided by pollen morphology, placentation, and the presence of apterous, berry-like fruits in all three sections.

SPECIES LIST: 6 species: *B. comorensis* Warb., *B. humberitii* Keraudren-Aymonin, *B. meyeri-johannis* Engl., *B. oxyloba* Welw. ex Hook. f., *B. salaziensis* (Gaud.) Warb., *B. seychellensis* Hemsl.

sect. **Monophyllon** A. DC.

Ann. Sci. Nat., Bot. 4, 11: 135 (1859), type species: *B. prolifera* A. DC.

Plants terrestrial, perennial, with upright stems; tubers present; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** 1 or 2, straight or transverse, symmetric or asymmetric, not peltate, simple; venation palmate; indumentum of scales or stellate hairs absent. **Inflorescence** at the base of the leaf blade, dichasial, bisexual; inflorescence axes not reduced; bracts persistent (during flowering). **Flower** without bracteoles; perianth segments white or pink, outer ones rounded at apex. *Male flower* with 4 free perianth segments; filaments fused below, anthers obovate or oblong, longer than the filaments, connective not extended. *Female flower* with 5 perianth segments; ovary or fruit with 3 wings, wings very unequal in fruit, locules 2, placental branches 2 per locule; styles 2, fused less than halfway, 2-lobed or forked once, caducous in fruit. **Fruit** not berry-like, irregularly dehiscent, nodding, without or with an indistinct beak.

DISTRIBUTION: Asia: Myanmar (Burma) and Peninsular Malaysia.

LEAF ANATOMY: Stomata single or in small groups; hypoderm absent; no cystoliths; no scleroids (*B. prolifera*).

TAXONOMIC COMMENTS: The section is characterized by the unusual position of the inflorescence. But for this character the species could be accommodated in section *Parvibegonia*.

SPECIES LIST: 2 species: *B. paleacea* Kurz, *B. prolifera* A. DC.

sect. **Monopteron** (A. DC.) Warb.

in Engl. & Prantl., Die Natürl. Pflanzenfam. (ed. 1) 3, 6a: 142 (1894). — *Meziera* sect. *Monopteron* A. DC., Prodr. 15, 1: 406 (1864), lectotype species (Barkley & Baranov, 1972): *Meziera nepalensis* A. DC. = *B. nepalensis* (A. DC.) Warb. (homotypic synonym).

Begonia subgenus *Platycentrum* sect. *Elasticae* C.B. Clarke, Journ. Linn. Soc. Bot. 18: 118 (1880), type species: *B. gigantea* Wallich = *B. nepalensis* (A. DC.) Warb. (homotypic synonym).

Plants terrestrial, perennial, with rhizomes from which upright stems arise; tubers absent; stem woody (at least at base); tubercles in leaf axil absent; stipules early caducous, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** more than 2, straight, asymmetric, not peltate, simple; venation palmate-pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial, bisexual, with male flowers basal and female flowers distal, protandrous, with the central flower of the cyme male, lateral flower(s) female; inflorescence axes not reduced; bracts persistent (during flowering) or caducous. **Flower** without bracteoles; perianth segments white or pink, outer ones rounded or acute at apex. *Male flower* with 2 free perianth segments; androecium actinomorphic, filaments equal (probably), fused below, anthers obovate, about as long as the filaments, dehiscent with unilaterally positioned short pore-like slits (less than 0.5 of the anther length) or longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective not extended. *Female flower* with 4 free perianth segments; ovary or fruit with 1 wing, wings very unequal in fruit (2 not developed), not hook- or spine-like, locules 2, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles usually 2 or sometimes 3, fused less than halfway or free, forked once or more than once (*B. nepalensis*), persistent in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, dehiscent on one side of the 2 undeveloped wings, pendulous, with a distinct beak.

DISTRIBUTION: Asia: Nepal and Bhutan.

CHROMOSOMES: Legro et al. (1971) found $2n = 16$ chromosomes for *B. nepalensis*, but Sharma & Bhattacharyya (1961) found much higher numbers (28–42). *B. griffithiana* has $2n = 22$.

SPECIES LIST: 2 species: *B. griffithiana* (A. DC.) Warb., *B. nepalensis* (A. DC.) Warb.

sect. **Muscibegonia** A. DC.

Fig. 24

Ann. Sci. Nat., Bot. 4, 11: 143 (1859), type species: *B. perpusilla* A. DC.

Plants terrestrial, perennial, acaulescent; tubers present; tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight, symmetric, not peltate, simple; venation palmate-pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial, bisexual, protandrous, with 1 or 2 female flowers, the central flower of the cyme male, lateral flower(s) female; inflorescence axes not reduced; bracts persistent (during flowering). **Flower** without bracteoles; perianth segments white or pink, outer ones rounded at apex (but elliptic or narrowly so). *Male flower* with 4 free perianth segments; androecium actinomorphic, filaments equal, fused below or entirely fused, anthers oblong, longer than the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective not extended. *Female flower* with 4 or 5 free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 1 per locule; styles 3, fused less than halfway, forked once, caducous in fruit, stigma not kidney-shaped, in a band and spiralled or not. **Fruit** not berry-like, (probably dehiscent near the back of the locules), pendulous or nodding, without or with an indistinct beak.

DISTRIBUTION: Africa: Madagascar.

SEED MICROMORPHOLOGY: Seeds subglobose, 270–360 µm long, length/width ratio 1.2–1.3; each cell with a peculiar, central papilla; anticlinal walls undulate; cuticular ornamentation linear.

IMPORTANT LITERATURE: Keraudren-Aymonin (1983).

TAXONOMIC COMMENTS: Two species of small herbs. Very closely related to sect. *Erminea*, see remarks made there.

SPECIES LIST: 2 species: *B. kalabenonensis* Humbert ex Keraudren-Aymonin & Bosser, *B. perpusilla* A. DC.

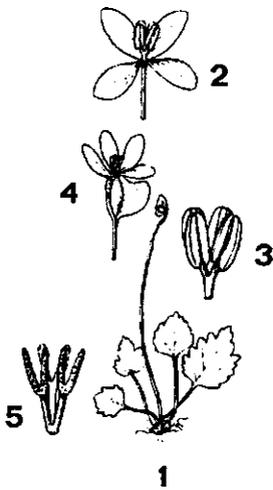


Fig. 24. Sect. *Muscibegonia*. *B. perpusilla* — 1, plant habit; 2, male flower; 3, androecium; 4, female flower; 5, styles. Reproduced from Keraudren-Aymonin (1983): p. 25, pl. 5.

sect. *Nervioplacentaria* A. DC.

Fig. 25

Ann. Sci. Nat., Bot. 4, 11: 144 (1859), lectotype species (Barkley & Baranov, 1972): *B. lyallii* A. DC.

Plants terrestrial, perennial, with upright stems or with rhizomes from which upright stems arise; tubers absent or present; stem woody (at least at base); tubercles in leaf axil absent; stipules persistent or early caducous, entire; junction petiole and leaf blade without a tuft of hairs (? , not recorded for most species). **Leaves** alternate, more than 2, straight, asymmetric, not peltate, simple or palmately lobed; venation palmate or palmate-pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial, bisexual, protandrous, with more than 3 female flowers, the central flower of the cyme male, lateral flower(s) female; inflorescence axes not reduced; bracts persistent (during flowering) or caducous (often conspicuous). **Flower** without bracteoles; perianth segments white or pink, outer ones rounded at apex. *Male flower* with usually 2 or rarely 4 free perianth segments; androecium actinomorphic, filaments equal, usually free or rarely fused below (*B. coursii*, *B. cladocarpoides*), anthers oblong, longer than to shorter than the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective not extended (usually very slightly protruding beyond the anther cells).

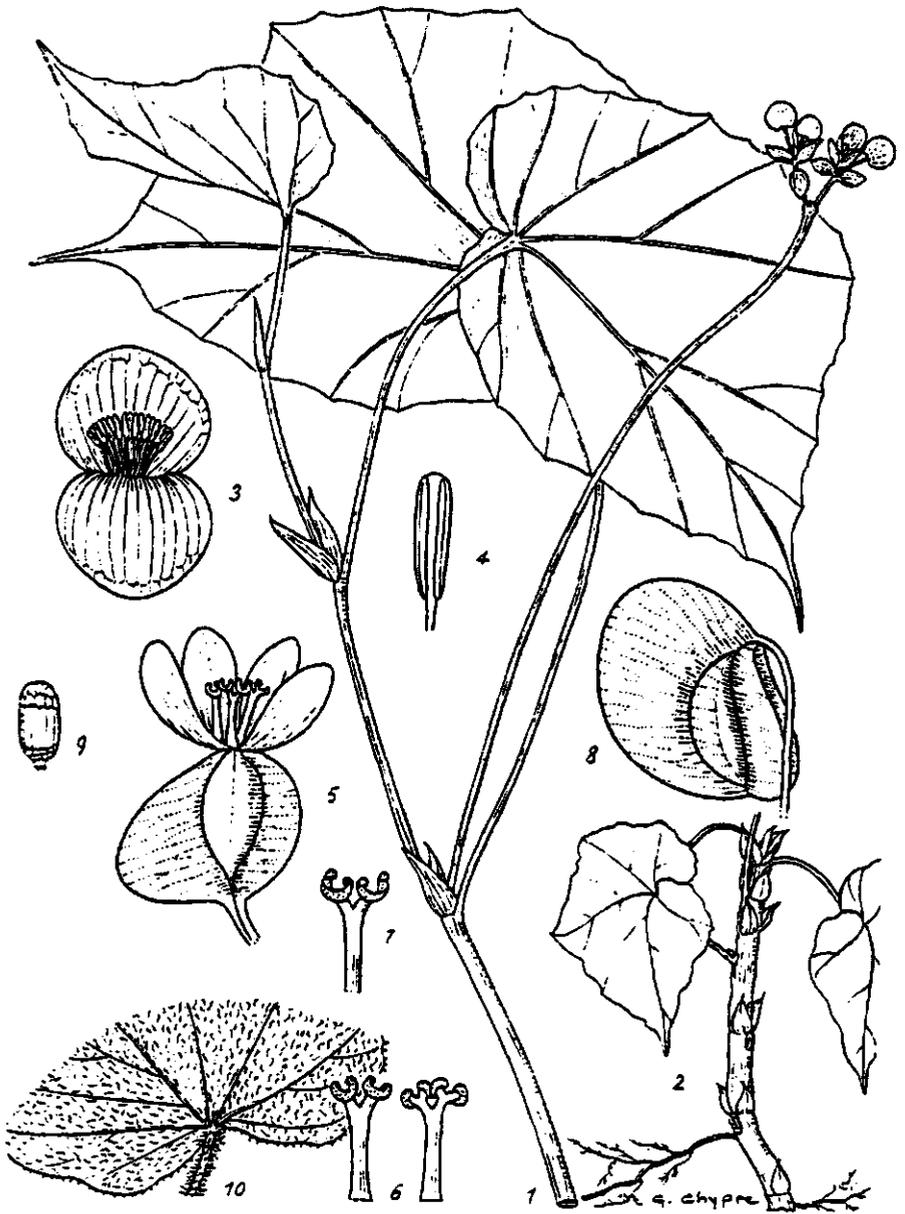


Fig. 25. Sect. *Nerviplantentaria*. *B. hyalii* — 1, flowering stem; 2, base of plant; 3, male flower; 4, stamen; 5, female flower; 6, young styles; 7, style; 8, fruit; 9, seed; 10, base part of lower leaf surface. Reproduced from Keraudren-Aymonin (1983): p. 75, pl. 22.

Female flower with 4 or 5 free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 1 per locule (only known for *B. lyallii*); styles 3, fused more than halfway to free, forked once or more than once, persistent in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, dehiscent near the back of the locules, nodding, without or with an indistinct beak.

DISTRIBUTION: Africa: Madagascar.

SEED MICROMORPHOLOGY: Seeds ellipsoid; collar cells large; testa cells few; operculum nipple-shaped; anticlinal walls straight; cuticular ornamentation composed of linear or zigzag foldings.

IMPORTANT LITERATURE: Irmscher (1925), Keraudren-Aymonin (1983).

TAXONOMIC COMMENTS: Very similar to sect. *Quadrilobaria*, probably only distinct because of its developed, basally woody stems. Deviating from sect. *Augustia* by the nodding fruits with rounded, not obtriangular wings. *B. mangorensis* may belong here, but its male flowers have 4 perianth segments and the fruit bears subequal wings.

SPECIES LIST: 7 species: *B. baronii* Baker, *B. cladocarpoides* Humbert ex Aymonin & Bosser, *B. coursii* Humbert ex Keraudren, *B. lyallii* A. DC., *B. madecassa* Keraudren, *B. majungaensis* Guillaumin, *B. marnieri* Keraudren.

Species whose membership is doubtful: *B. mangorensis* Humbert ex Bosser & Keraudren-Aymonin.

sect. **Parietoplacentalia** Ziesenh.

Fig. 26

The Begonian 36: 36 (1969), type species: *B. candollei* Ziesenh.
Begonia sect. *Hexaptera* Ziesenh., The Begonian 41: 13 (1974), type species: *B. serrulatoala* C. DC. = *B. oaxacana* A. DC. (heterotypic synonym).

Plants terrestrial, perennial, with upright stems; tubers absent; stem woody (at least at base; ?); tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, transverse, asymmetric, not

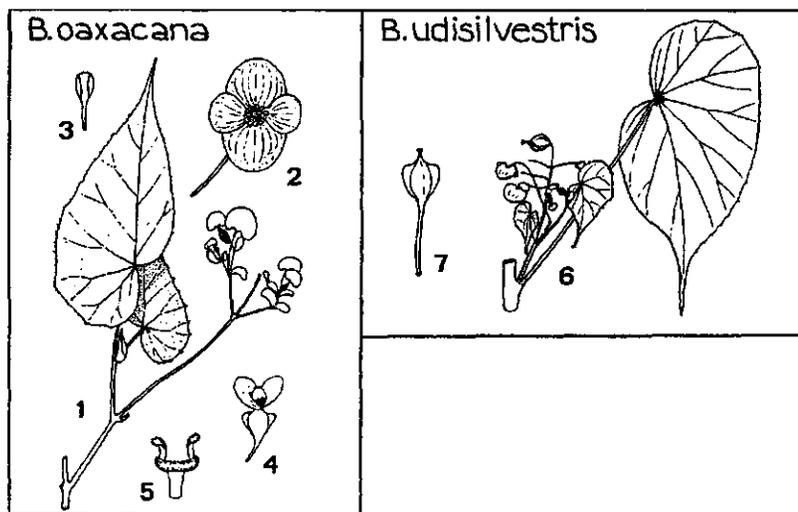


Fig. 26. Sect. *Parietoplacentalia*. *B. oaxacana* — 1, flowering stem; 2, male flower; 3, stamen; 4, female flower; 5, style. *B. udisilvestris* — 6, flowering stem; 7, fruit. Reproduced from Smith & Schubert (1958): p. 59, fig. 18.

peltate, simple; venation palmate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial at base and monochasial at apex (?), bisexual, with male flowers basal and female flowers distal (?), protandrous (?); inflorescence axes not reduced; bracts persistent (during flowering). **Flower** without bracteoles (?); perianth segments white or pink, outer ones acute at apex. *Male flower* with 4 free perianth segments; androecium actinomorphic, filaments unequal, fused below, anthers obovate, shorter than the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective extended (but little). *Female flower* with 3 free perianth segments; ovary or fruit with 3 wings, wings equal to unequal in fruit, not hook- or spine-like, locules 1 (*B. candollei*; generally?) or (2–)3 (occasionally in *B. oaxacana* and *B. udisilvestris*), placentation parietal or septal or axillary, placental branches 2 per locule, ovules present between placental branches; styles 3, shortly fused or fused more than halfway (?), forked once, caducous in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** berry-like (? , 'red and fleshy'), more or less erect or pendulous (possibly in *B. candollei*), with a distinct beak, dehiscent through the wings (?).

DISTRIBUTION: America: Central America.

LEAF ANATOMY: Stomata single; hypoderm absent; cystoliths absent. (*B. oaxacana*, *B. udisilvestris*).

SEED MICROMORPHOLOGY: The seeds of *B. oaxacana* are ellipsoid, 480 x 255 μm ; operculum nipple-shaped or broadly nipple-shaped; walls thickened, anticlinal boundaries always flat; cuticular structure variable, mostly faintly linear. *B. udisilvestris* is similar: 545 x 295 μm , anticlinal boundaries flat, without cuticular ornamentation.

CHROMOSOMES: $2n = 28$ (*B. udisilvestris*).

TAXONOMIC COMMENTS: The three species which form this section differ from *Knesebeckia*, in which *B. oaxacana* and *B. udisilvestris* have hitherto been placed, a.o. in the three female tepals, the narrow-winged, beaked fruit and the placentation. In the two species just mentioned the ovary has usually three but sometimes 2 locules with axillary but partly also septal or parietal placentation. In *B. candollei* so far only parietal placentas have been observed. According to C. de Candolle, the fruits of *B. udisilvestris* dehisce at the angles; he accordingly placed it in section *Casparya*. The dehiscence of the fruits of the other two species has not yet been described.

SPECIES LIST: 3 species: *B. candollei* Ziesenh., *B. oaxacana* A. DC., *B. udisilvestris* C. DC.

sect. **Parvibegonia** A. DC.

Fig. 27

Ann. Sci. Nat., Bot. 4, 11: 136 (1859), lectotype species (Barkley & Baranov, 1972): *B. martabanica* A. DC.

Begonia sect. *Dysmorphia* A. DC., Ann. Sci. Nat., Bot. 4, 11: 136 (1859), type species: *B. crenata* Dryand.

Plants terrestrial, perennial, with upright stems or with rhizomes from which upright stems arise (probably but not described) or rarely rhizomatous (*B. crenata*, *B. thaipingensis*); tubers absent or present; stem herbaceous; tubercles in leaf axil absent or present; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2 (but never many) or rarely 1 or 2, straight or transverse, asymmetric or

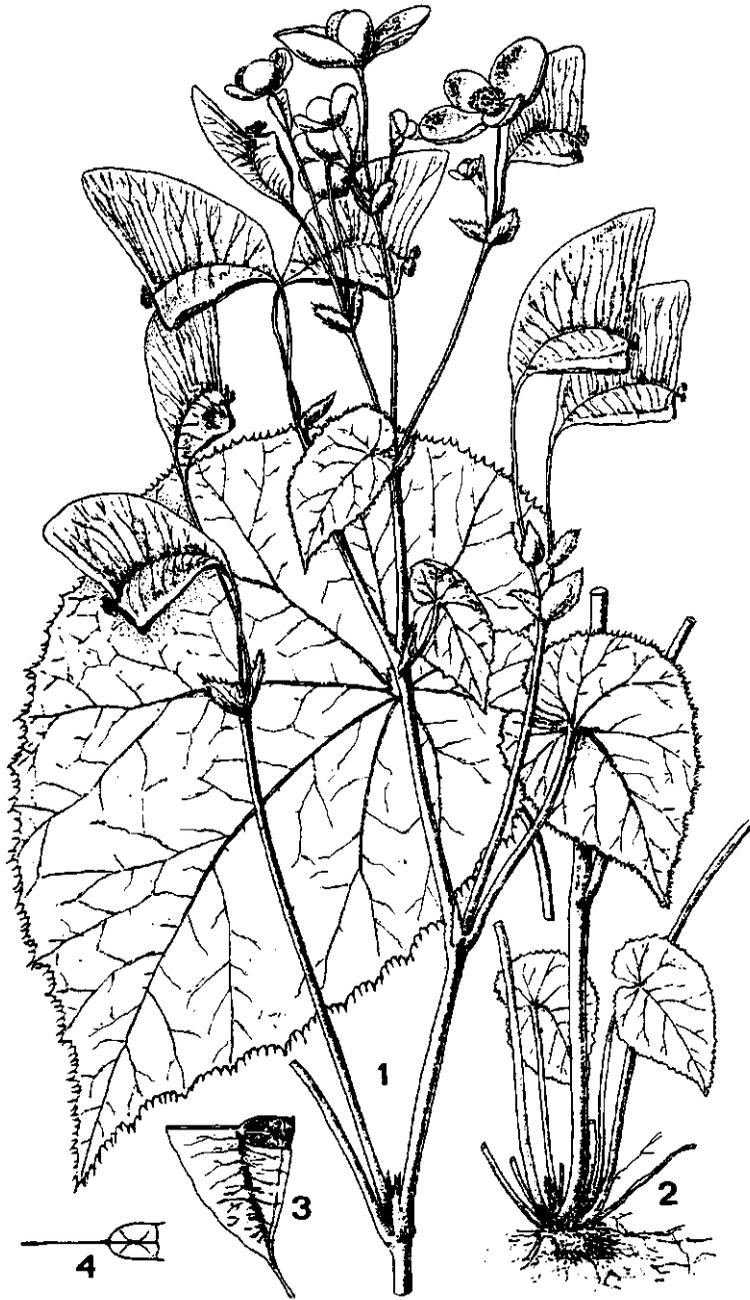


Fig. 27. Sect. *Parvibegonia*. *B. wattii* — 1, flowering stem; 2, plant base; 3, fruit in transverse section; 4, schematic presentation of ovary in transverse section. Reproduced from Clarke (1889): pl. 11.

rarely symmetric, not peltate, simple; venation palmate or palmate-pinnate; indumentum of scales absent, stellate hairs absent or rarely present (*B. andamensis*, *B. sinuata*). **Inflorescence** terminal, racemose, bisexual, with male flowers basal and female flowers distal, protandrous; lateral inflorescences dichasial at base and monochasial at apex or rarely entirely monochasial or entirely dichasial; inflorescence with 1 or 2 female flowers, the central flower of the cyme male, lateral flower(s) female; inflorescence axes not reduced; bracts persistent (during flowering) or rarely caducous (*B. rimarum*, *B. socia*). **Flower** without or rarely with 1 or 2 bracteoles (*B. aliciae*) spaced from the base of the ovary; perianth segments white or pink, outer ones rounded at apex. *Male flower* usually with 4 or rarely 2 (*B. flaccidissima*) free perianth segments; androecium actinomorphic or rarely zygomorphic (*B. aliciae*), filaments fused below or rarely free (*B. grata*), anthers obovate or rarely oblong (*B. aliciae*, *B. crenata*), about as long as or longer than the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length) or rarely unilaterally positioned short pore-like slits (less than 0.5 of the anther length; *B. sinuata*), connective not extended or rarely extended (*B. brevicaulis*). *Female flower* with 4–6 or rarely 2 (*B. flaccidissima*) free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 2, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles 2, free or fused less than or rarely more than halfway (*B. parishii*, *B. peii*), 2-lobed or forked once or rarely simple (*B. socia*?), caducous or rarely persistent in fruit (*B. crenata*), stigma kidney-shaped or not, in a band and spiralled or not. **Fruit** not berry-like, irregularly dehiscent, nodding or rarely upright (*B. peii*), without or with an indistinct beak.

DISTRIBUTION: Asia: from India to the Himalayas, Indo-China and Malaysia.

LEAF ANATOMY: Stomata single or in groups (*B. guttata*); hypoderm absent; no cystoliths; no scleroids (5 species studied.)

CHROMOSOMES: $2n = 56$ (*B. crenata*).

IMPORTANT LITERATURE: Irmscher (1929).

TAXONOMIC COMMENTS: The species of this section have 2-locular fruits and bifid placentae, like those of sect. *Platycentrum*, but they differ from the latter in being smaller and more slender plants, sometimes tuberous, with inflorescences consisting of a raceme of dichasia ending in monochasia, anthers whose connective is not extended, and fruits that do not open by slits. The species list below contains several species, however, which do not answer to this description in one or two respects. It seems probable that on closer study some may have to be moved to *Platycentrum*, or vice versa.

SPECIES LIST: 29 species: *B. aliciae* C.E.C. Fischer, *B. andamensis* Parish ex C.B. Clarke, *B. brevicaulis* A. DC., *B. canarana* Miq., *B. crenata* Dryand., *B. curtisii* Ridley, *B. debilis* King, *B. demissa* Craib, *B. flaccidissima* Kurz, *B. grantiana* Craib, *B. grata* Geddes ex Craib, *B. guttata* Wall. ex A. DC., *B. haniffii* Burkill, *B. leucantha* Ridley, *B. martabanica* A. DC., *B. parishii* C.B. Clarke, *B. peii* Wu, *B. phoeniogramma* Ridley, *B. procrdifolia* Wall. ex A. DC., *B. rimarum* Craib, *B. rupicola* Miq., *B. sinuata* Wall. ex Meissner, *B. socia* Craib, *B. tenuifolia* Dryand., *B. thaipingensis* King, *B. vagans* Craib, *B. variabilis* Ridley, *B. wattii* C.B. Clarke, *B. zollingeriana* A. DC.

sect. **Peltaugustia** (Warb.) Barkley

Fig. 28

Phytologia 24: 156 (1972). — *Begonia* sect. *Augustia* A. DC. subsect. *Peltaugustia* Warb. in Engl., Nat. Pflanzenfam. (ed. 1) 3, 6a: 140 (1894), type species: *B. socotrana* Hook. f.

Plants terrestrial, perennial, with upright stems; tubers absent but small bulbils present at the base of the plant; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, transverse, symmetric, peltate or not (within the same plant), simple; venation palmate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary and terminal, dichasial, bisexual, protandrous, with 1 female flower, the central flower of the cyme male, lateral flower female; inflorescence axes not reduced; bracts persistent (during flowering). **Flower** with 2 bracteoles spaced from the base of the ovary; perianth segments pink, outer ones rounded at apex. *Male flower* with 4 free perianth segments; androecium actinomorphic, filaments equal, free, anthers obovate, about as long as the



Fig. 28. Sect. *Peltaugustia*. *B. socotrana*. Reproduced from Hooker (1881): p. 8, fig. 1.

filaments, dehiscent with unilaterally positioned short pore-like slits (less than 0.5 of the anther length), apex hooded, connective not extended. *Female flower* with 6 free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 1 per locule; styles 3, fused less than halfway, forked once, persistent in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, dehiscent near the back of the locules, pendulous, without or with an indistinct beak.

DISTRIBUTION: Africa: endemic on the island of Socotra.

LEAF ANATOMY: Stomata in groups; hypoderm present on upper side; no cystoliths.

SEED MICROMORPHOLOGY: Seed ellipsoid, 425–450 x 225–265 μm , length/width ratio 1.8; ratio collar to seed length 1:3.3; anticlinal cell walls of testa cells undulate; operculum obtuse; anticlinal boundaries sunken; cuticular ornamentation composed of undulate striae.

CHROMOSOMES: $2n = 28$.

IMPORTANT LITERATURE: Irmscher, 1961.

TAXONOMIC COMMENTS: This section is closely related to sect. *Augustia*, and was even included in the latter by Irmscher (1961). It differs, however, in the presence of bulbils (unique in the genus?), the peltate leaves, the unilaterally dehiscent, hooded anthers, and the distinct type and dark purple colour of the seeds. These differences warrant the species distinction at sectional level.

SPECIES LIST: A single species: *B. socotrana* Hook. f.

sect. **Petermannia** (Klotzsch) A. DC.

Fig. 29

Ann. Sci. Nat., Bot. 4, 11: 128 (1859). — *Petermannia* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 124 (1854), lectotype species (Barkley & Baranov, 1972): *Petermannia cumingiana* Klotzsch = *B. cumingiana* (Klotzsch) A. DC. (homotypic synonym).

Plants terrestrial, perennial, usually with upright stems or less often rhizomatous or rarely lianescent; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent or early caducous, entire or rarely dentate (*B. eberhardtii*); junction petiole and leaf blade without a tuft of hairs. **Leaves** close and distichous or alternate (rarely subopposite), more than 2, straight or transverse, asymmetric, usually not peltate or rarely peltate (*B. baramensis* if it belongs to *Petermannia*), usually simple or rarely pinnatifid (*B. incisa*, *B. pinnatifida*, *B. serratipetala*) or bipinnatifid or further divided (*B. bipinnatifida*, *B. humilicaulis*); venation palmate to pinnate;

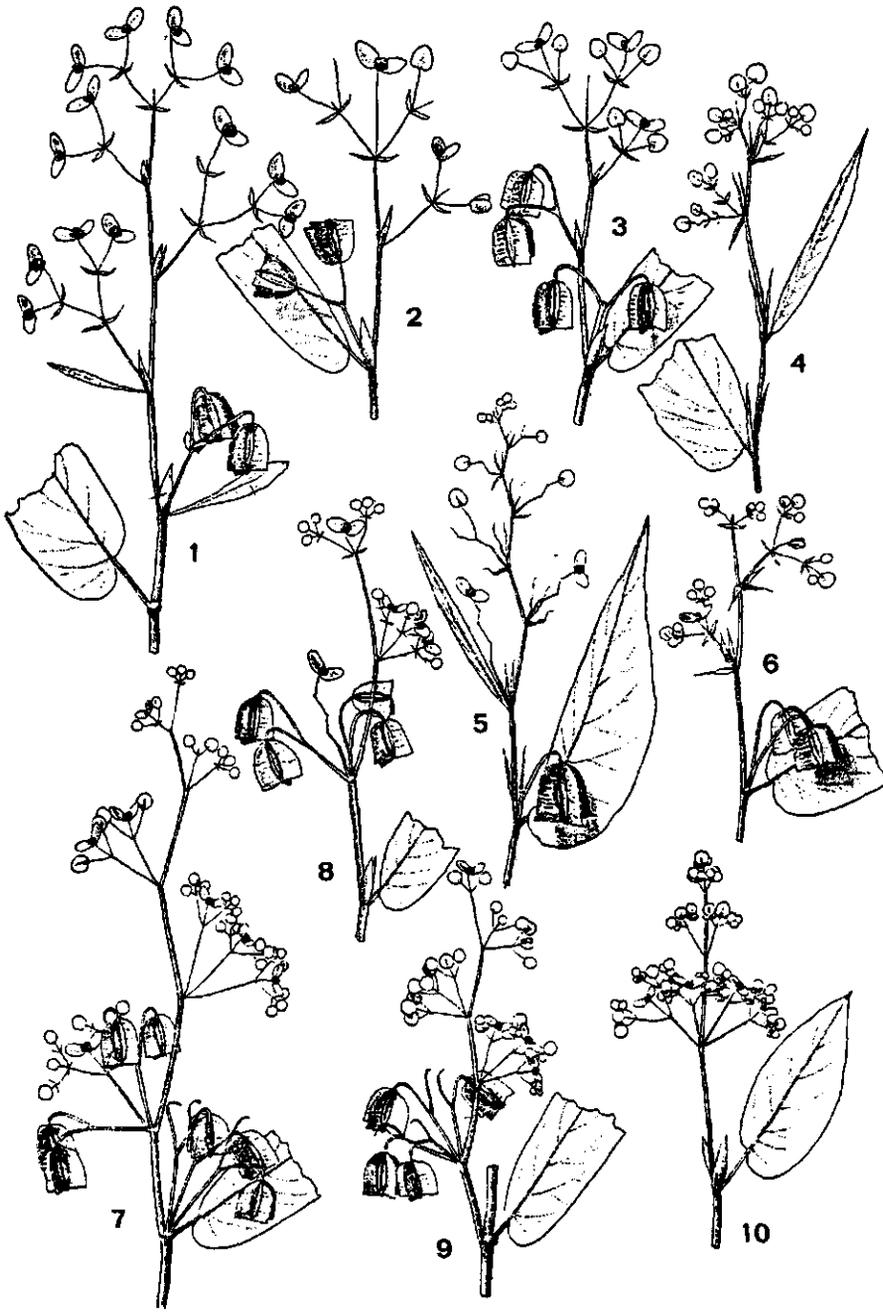


Fig. 29. Sect. *Petermannia*. Various inflorescence types of *B. hirsuticaulis* (1-3), *B. filibracteosa* (4-5), *B. gilgiana* (6), and *B. naumoniensis* (7-10). Reproduced from Irmscher (1914): p. 565, fig. 2.

indumentum of scales or stellate hairs absent. **Inflorescence** an axillary cyme (or of solitary flowers) or a terminal raceme of cymes, usually bisexual or separate male and female, with male flowers distal and female flowers basal, protogynous; male inflorescence or male part of inflorescence usually dichasial at base and monochasial at apex or rarely consisting of solitary flowers; female inflorescence or female part of inflorescence dichasial or consisting of solitary flowers or with 2 female flowers (terminal male flower aborted) or rarely with 3 or more female flowers; inflorescence axes not or strongly reduced; bracts persistent (during flowering) or caducous. **Flower** usually without or rarely with 1 or 2 bracteoles (*B. montis-bismarckii*, *B. monantha*) spaced from the base of the ovary; perianth segments usually white or pink or rarely red or orange, outer ones rounded or acute (usually only in female flowers) at apex. *Male flower* usually with 2 or less often with 4 or very rarely 5 (*B. sarawakensis*) free perianth segments; androecium actinomorphic or zygomorphic, filaments equal or unequal, free or fused below, anthers obovate or oblong, longer than or shorter than the filaments, dehiscent with unilaterally positioned short pore-like slits (less than 0.5 of the anther length) or longitudinal slits (more than 0.5 of the anther length), connective not extended. *Female flower* with 5 or rarely with 2 (*B. casiguranensis*), 3 (4 species), 4 (5 species) or 6 (2 species?) free perianth segments; ovary or fruit usually with 3 wings or rarely wingless (*B. axillipara*), wings equal to unequal in fruit, usually not hook- or spine-like or rarely developed into hooks (*B. brachyptera*), locules usually 3 or rarely 2 (*B. malmquistiana*, *B. fruticella*), placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles 3, fused less than halfway or free, usually forked once or rarely 2-lobed or forked more than once (*B. brevipes*), caducous in fruit, stigma usually not kidney-shaped or rarely kidney-shaped, in a band and spiralled. **Fruit** not berry-like, dehiscent near the wings, usually pendulous or rarely more or less erect, without or with an indistinct beak.

DISTRIBUTION: Asia: Malesia.

LEAF ANATOMY: Stomata single; hypoderm absent (4 species) or on both sides (*B. cumingii*); no cystoliths.

CHROMOSOMES: $2n = 30$ (7 species), $2n = 44$ (3 species).

IMPORTANT LITERATURE: Imscher (1914).

TAXONOMIC COMMENTS: The section is one of the largest of the genus, and there are probably dozens of species still awaiting description, particularly in Borneo and New Guinea. Most species are frutescent, 50 to 200 cm high, but about 25 are repent, rooting at the nodes, with or without ascendent laterals, sometimes scandent. Because of this habit Merrill (1912) classified 3 of the latter species in sect. *Diploclinium*, from which they differ in their inflorescence, however. *Petermannia* is closest to *Bracteibegonia* and *Sphenanthera*. The differences with the former have already been discussed. *Sphenanthera*, as hitherto understood, is a distinct section but some intermediate species cause it to merge into *Petermannia*. Species with small axillary inflorescences and fruits with wings reduced to ridges have been classified here in *Petermannia* when protogynous, in *Sphenanthera* when protandrous, but as descriptions of inflorescences are often vague there are a few question marks.

SPECIES LIST: 193 species: *B. adenodes* Imscher, *B. aequata* A. Gray, *B. affinis* Merr., *B. agusanensis* Merr., *B. albobracteata* Ridley, *B. altissima* Ridley, *B. angustilimba* Merr., *B. apayaoensis* Merr., *B. articulata* Imscher, *B. artior* Imscher, *B. atricha* (Miq.) A. DC., *B. augustae* Imscher, *B. axillaris* Ridley, *B. axillipara* Ridley, *B. barbellata* Ridley, *B. beryllae* Ridley, *B. bifolia* Ridley, *B. binuangensis* Merr., *B. bipinnatifida* J.J. Smith, *B. bolsteri* Merr., *B. bonthainensis* Hemsl., *B. borneensis* A. DC., *B. brachybotrys* Merr. & L.M. Perry, *B. brevipes* Merr., *B. brevirimosa* Imscher, *B. burbidgei* Stapf, *B. calliantha* Merr. & L.M. Perry, *B. capituliformis* Imscher, *B. carnosa* Teijsm. & Binnend., *B. casiguranensis* Quisumb. & Merr., *B. caudata* Merr., *B. cauliflora* M.J.S. Sands, *B. celebica* Imscher, *B. chlorosticta* M.J.S. Sands, *B. ciliifera* Merr., *B. cincinnifera* Imscher, *B. clemensiae* Merr. & L.M. Perry, *B. cognata* Imscher, *B. congesta* Ridley, *B. consanguinea* Merr., *B. contracta* Warb., *B. crispipila* Elmer, *B. cumingiana* A. DC., *B. cumingii* A. Gray, *B. cuneatifolia* Imscher, *B. densiretis* Imscher, *B. diffusiflora* Merr. & L.M. Perry, *B. djamuensis* Imscher, *B. dolichotricha* Merr., *B. dosedlae* A. Gilli, *B. eberhardtii* Gagnep., *B. edanoi* Merr., *B. elatostematoides* Merr., *B. elatostemma* Ridley, *B. eliasii* Warb., *B. erythrogyna* M.J.S. Sands, *B. esculenta* Merr., *B. everettii* Merr., *B. fasciculata* Jack, *B. fasciculiflora* Merr., *B. filibracteosa* Imscher, *B. flacca* Imscher, *B. flexicaulis* Ridley, *B. flexula*

Ridley, *B. fruticella* Ridley, *B. gemella* Warburg ex L.B. Smith & Wasshausen, *B. gilgiana* Irmscher, *B. glabricaulis* Irmscher, *B. gracilipes* Merr., *B. grandipetala* Irmscher, *B. halconensis* Merr., *B. herveyana* King, *B. hirsuticaulis* Irmscher, *B. hispidissima* Zipp. ex Koord., *B. holttumii* Irmscher, *B. horsfieldii* Miq. ex A. DC., *B. hullettii* Ridley, *B. humboldtiana* L.S. Gibbs, *B. humilicaulis* Irmscher, *B. imbricata* M.J.S. Sands, *B. imperfecta* Irmscher, *B. incisa* A. DC., *B. inostegia* Stapf, *B. insularum* Irmscher, *B. isoptera* Dryander ex J.E. Smith, *B. isopteroidea* King, *B. jagorii* Warb., *B. kelliana* Irmscher, *B. kerstingii* Irmscher, *B. kinabaluensis* M.J.S. Sands, *B. koordersii* Warb. ex L.B. Smith & Wasshausen, *B. lacera* Merr., *B. laevis* Ridley, *B. lagunensis* Elmer, *B. lancifolia* Merr., *B. latistipula* Merr., *B. lauterbachii* Warb., *B. ledermannii* Irmscher, *B. lepidella* Ridley, *B. leptantha* C.B. Robinson, *B. leucosticta* Warb., *B. loheri* Merr., *B. longibractea* Merr., *B. longiseta* Irmscher, *B. longistipula* Merr., *B. macgregorii* Merr., *B. malachosticta* M.J.S. Sands, *B. malindangensis* Merr., *B. malmquistiana* Irmscher, *B. masarangensis* Irmscher, *B. mearnsii* Merr., *B. media* Merr. & L.M. Perry, *B. megacarpa* Merr., *B. megalantha* Merr., *B. merrittii* Merr., *B. mindanaensis* Warb., *B. monantha* Warb., *B. montis-bismarckii* Warb., *B. moszkowskii* Irmscher, *B. multidentata* Warb., *B. muru-densis* Merr., *B. mystacina* L.B. Smith & Wasshausen, *B. naumoniensis* Irmscher, *B. negrosensis* Elmer, *B. novoguineensis* Merr. & L.M. Perry, *B. oblongata* Merr., *B. oblongifolia* Stapf, *B. oligantha* Merr., *B. otophora* Merr. & L.M. Perry, *B. oxyura* Merr. & L.M. Perry, *B. padangensis* Irmscher, *B. palawanensis* Merr., *B. panayensis* Merr., *B. papuana* Warb., *B. parvilimba* Merr., *B. pediophylla* Merr. & L.M. Perry, *B. peekelii* Irmscher, *B. pendula* Ridley, *B. pentaphragmifolia* Ridley, *B. perryae* L.B. Smith & Wasshausen, *B. pilosa* Jack, *B. pinnatifida* Merr. & L.M. Perry, *B. platyphylla* Merr., *B. pleioclada* Irmscher, *B. propinqua* Ridley, *B. pryeriana* Ridley, *B. pseudisoptera* Irmscher, *B. pubescens* Ridley, *B. quercifolia* A. DC., *B. racemosa* Jack, *B. ramosii* Merr., *B. randiana* Merr. & L.M. Perry, *B. rhodantha* Ridley, *B. rieckei* Warb., *B. rizalensis* Merr., *B. rubida* Ridley, *B. salomonensis* Merr. & L.M. Perry, *B. samarensis* Merr., *B. sarasinorum* Irmscher, *B. sarawakensis* Ridley, *B. sarmentosa* L.B. Smith & Wasshausen, *B. serraticauda* Merr. & L.M. Perry, *B. serratipetala* Irmscher, *B. simulans* Merr. & L.M. Perry, *B. sogerensis* Ridley, *B. somervillei* Hemsl., *B. sorsogonensis* Elmer, *B. sphenocarpa* Irmscher, *B. spilotophylla* F. Muell., *B. stilandra* Merr. & L.M. Perry, *B. strachwitzii* Warb. ex Irmscher, *B.*

strictinervis Irmscher, *B. strictipetiolaris* Irmscher, *B. subelliptica* Merr. & L.M. Perry, *B. subprostrata* Merr., *B. subtruncata* Merr., *B. suffrutescens* Merr. & L.M. Perry, *B. sympodialis* Irmscher, *B. tafaensis* Merr. & L.M. Perry, *B. tawaensis* Merr., *B. tenericaulis* Ridley, *B. timorensis* (Miq.) J. Golding & C. Karegeannes, *B. torricellensis* Warb., *B. urdanetensis* Elmer, *B. vandewateri* Ridley, *B. walteriana* Irmscher, *B. waryana* Irmscher, *B. weberi* Merr., *B. weigallii* Hemsl., *B. wenzelii* Merr., *B. xiphophylla* Irmscher, *B. zamboangensis* Merr.

Species whose membership is doubtful: 7 species: *B. baramensis* Merr., *B. brachyptera* Merr. & L.M. Perry, *B. hainanensis* W.Y. Chun & F. Chun, *B. holosericea* Teijsm. & Binnend., *B. lunatistyla* Irmscher, *B. promethea* Ridley, *B. warburgii* K. Schum. & Lauterb.

sect. **Pilderia** (Klotzsch) A. DC.

Fig. 30

Ann. Sci. Nat., Bot. 4, 11: 141 (1859). — *Pilderia* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 127 (1854), type species: *Pilderia urticaefolia* Klotzsch = *B. buddleiifolia* A. DC. (heterotypic synonym).

Plants terrestrial, perennial, with an upright or ascendent stem; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight, asymmetric, not peltate, simple; venation pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** terminal, a raceme of monochasia, lateral inflorescences bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts persistent (during flowering). **Flower** with 2 bracteoles inserted directly below the ovary; perianth segments white or pink, obtuse. *Male flower* with 2 or 4 free perianth segments; androecium actinomorphic, filaments fused below, anthers oblong, shorter than the filaments, dehiscent with laterally positioned, longitudinal slits (more than 0.5 of the anther length), connective extended (slightly). *Female flower* with 4 or 5 free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 3, placentation axillary (?), placental branches 1 per locule; styles 3, free, forked once, persistent in fruit (?), stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, without or with an indistinct beak.

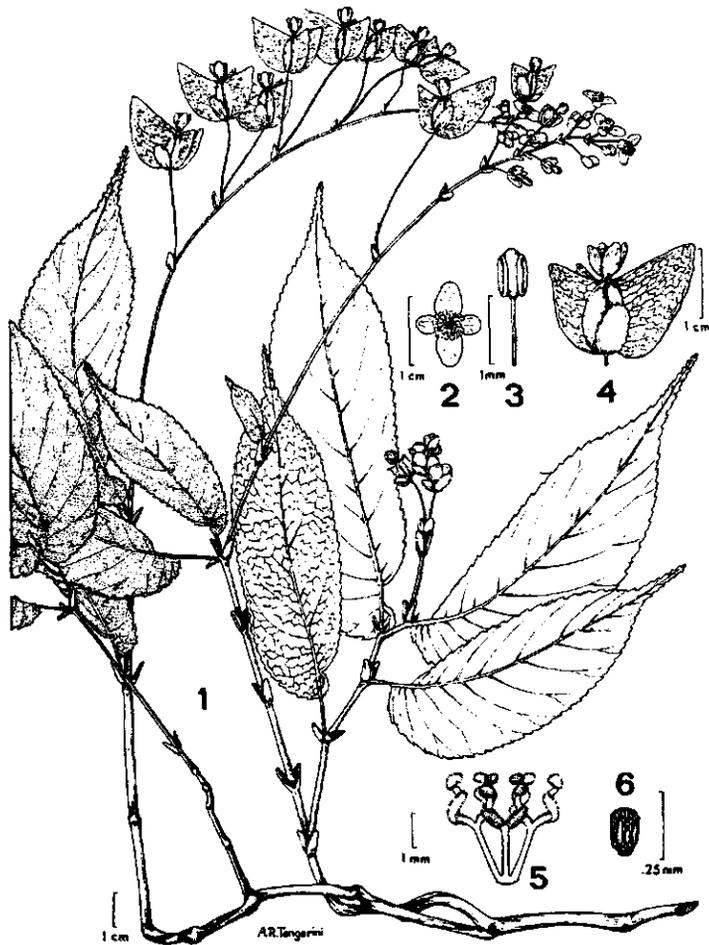


Fig. 30. Sect. *Pilderia*. *B. buddleiifolia* – 1, plant habit; 2, male flower; 3, stamen; 4, fruit; 5, styles; 6, seed. Reproduced from Smith & Wasshausen (1986): 12, fig. 1.

DISTRIBUTION: America: Andean region (Colombia and Venezuela to Peru).

LEAF ANATOMY: Stomata single or in groups of 2 or 3; hypoderm absent; cystoliths absent.

SEED MICROMORPHOLOGY: The seeds of *Pilderia* are of the prevalent type, about 285 x 150 µm or somewhat larger.

TAXONOMIC COMMENTS: There is general agreement that the inflorescence of *B. buddleiifolia* is a raceme of monochasial cymes. The description and pictures of the latter (Irmscher, 1914: 560; Smith & Schubert, 1946: 101; Smith, 1973: 223) diverge markedly, however. Apparently the distribution of the staminate and pistillate flowers is very variable. *B. buddleiifolia* is further characterized by straight, penninerved leaves, short, oblong anthers and undivided placenta. C. de Candolle put his *B. pilderifolia* in the same section, but although this has similar leaves, its cymose inflorescences and linear anthers show that it has to be classified in another section (possibly *Pritzelia*, although it does not seem to have cystoliths). It may be that *B. jenmanii* belongs here, as it has a similar habit and the same type of inflorescence as in *B. buddleiifolia*. Its leaves are transverse, palmate and broadly ovate in outline, however, and there are no bracteoles. Its placenta have not been described.

SPECIES LIST: A single species: *B. buddleiifolia* A. DC.

Species whose membership is doubtful: 1 species: *B. jenmanii* Tutin.

sect. **Platycentrum** (Klotzsch) A. DC.

Fig. 31

Ann. Sci. Nat., Bot. 4, 11: 134 (1859). — *Platycentrum* Klotzsch, Abh. Kön. Akad. Wiss. Berlin '1854': 243 (1855), type species: *Platycentrum xanthina* (Hook.) Klotzsch = *B. xanthina* Hook. (homotypic synonym).

Plants terrestrial, perennial, rhizomatous or with upright stems or with rhizomes from which upright stems arise; tubers usually absent or rarely present; stem herbaceous; tubercles in leaf axil absent; stipules persistent or early caducous, entire; junction petiole and leaf blade usually without or rarely with a tuft of hairs (*B. circumlobata*). **Leaves** alternate, more than 2, symmetric or asymmetric, not peltate, usually simple or sometimes palmately lobed or rarely palmately compound (*B. hemsleyana*); venation palmate or palmate-pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial at base and monochasial at apex, bisexual, with male flowers basal and female flowers distal, protandrous, with 1 female flower, the central flower of the cyme male, lateral flower(s) female; inflorescence axes not reduced; bracts persistent (during flowering) or caducous. Flower usually without or rarely with 1 or 2 bracteoles (*B. psilophylla*) spaced from the base of

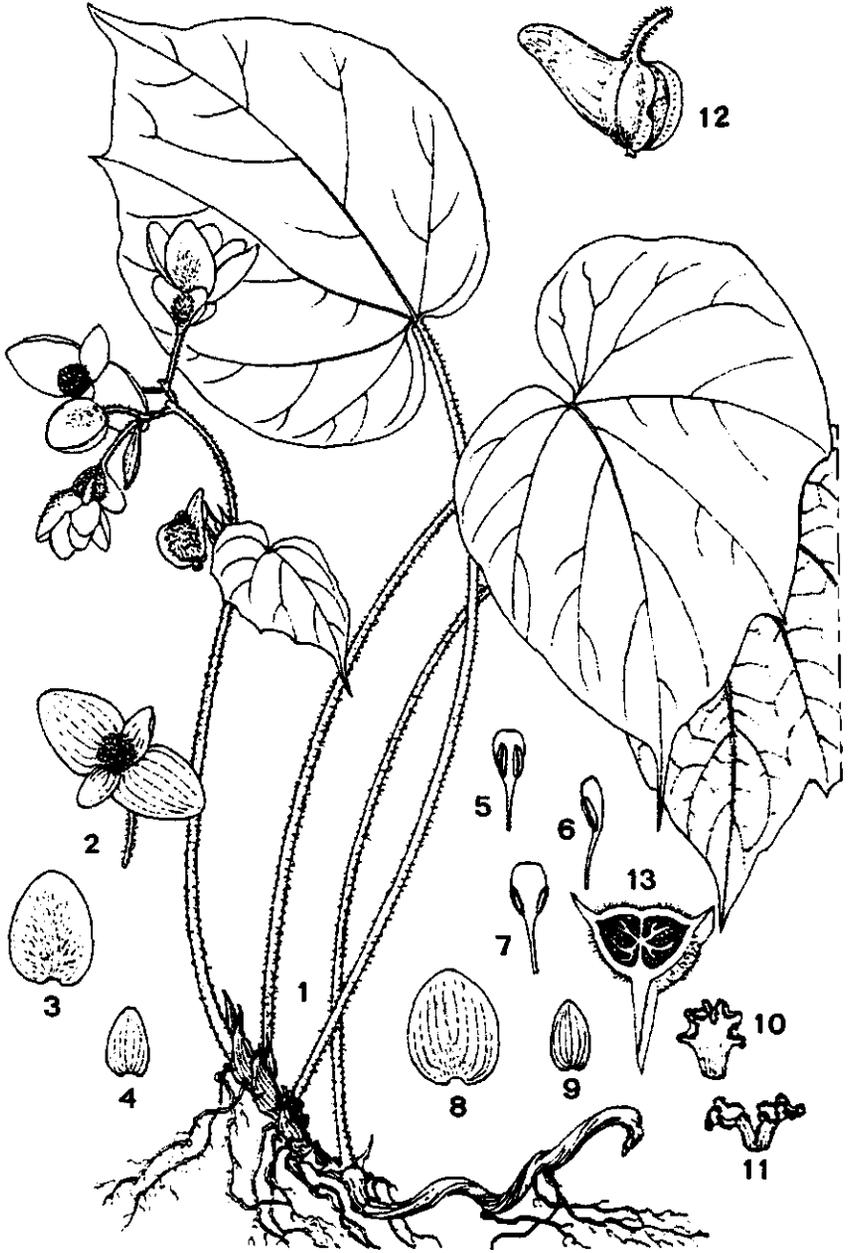


Fig. 31. Sect. *Platycentrum*. *B. daweshanensis* — 1, plant habit; 2, male flower; 3, outer perianth segment of male flower; 4, inner perianth segment of male flower; 5-7, stamens in frontal, lateral and dorsal view; 8, outer perianth segment of female flower; 9, inner perianth segment of female flower; 10-11, styles; 12, fruit; 13, ovary in transverse section. Reproduced from Huang & Shui (1994): p. 338, fig. 5.

the ovary; perianth segments usually white or pink or rarely red (*B. chitoensis*, *B. duclouxii*, *B. sikkimensis*) or orange (*B. cathayana*) or yellow (*B. edulis*?, *B. flaviflora*, *B. xanthina*), outer ones rounded at apex. *Male flower* with 4 free perianth segments; androecium actinomorphic, filaments equal or unequal, usually fused below (into a column) or less often free, anthers obovate or oblong, longer than to shorter than the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), connective usually extended or rarely not extended. *Female flower* with 5 or rarely with 3 (3 species), 6 (*B. lipingensis*) or 8 (*B. tarokoensis*) free perianth segments; ovary or fruit with 3 wings, wings very unequal in fruit, not hook- or spine-like, locules 2, placentation axillary, placental branches (1-)2(-4) per locule (1 in *B. pavonina*, more than 2 in *B. venusta*), ovules present between placental branches; styles usually 2 or rarely 4, usually free or fused less than halfway or rarely fused more than halfway (*B. rockii*, *B. siamensis*), usually 2-lobed or forked once or rarely forked more than once, caducous in fruit, stigma usually not kidney-shaped or rarely kidney-shaped (*B. mengtzeana*, *B. scitifolia*), in a band and spiralled. **Fruit** not berry-like, nodding, dehiscent on one or both sides of the 2 narrow wings.

DISTRIBUTION: Asia: from India to the Himalayas, Indo-China, China, Taiwan and Malesia.

LEAF ANATOMY: Stomata single or in small groups (rarely, *B. palmata*); hypoderm absent; no cystoliths (16 species studied).

CHROMOSOMES: $2n = 22$ (15 species), $2n = 44$ (*B. venusta*, and several cultivars of *B. rex*).

TAXONOMIC COMMENTS: The difficulties in assigning species with 2-locular fruits and bifid placentae either to *Parvibegonia* or to *Platycentrum* have already been discussed under the former section. Against other sections, however, *Platycentrum* appears to be well-defined. One soon learns to recognise its representatives and only rarely meets a species with every appearance of a *Platycentrum* that differs in a single essential character, e.g. undivided placentae (*B. pavonina*) or a 3-locular ovary (*B. setifolia*). The latter is here placed in *Diploclinium*, although Irmscher put it in *Platycentrum*. The remarkable case of *B. robusta* will be discussed under section *Sphenanthera*.

SPECIES LIST: 96 species: *B. adenostegia* Stapf, *B. aenea* Linden & André, *B. aequilateralis* Irmscher, *B. algaia* L.B. Smith & Wasshausen, *B. alpina* L.B. Smith & Wasshausen, *B. amabilis* Linden, *B. annulata* K. Koch, *B. areolata* Miq., *B. argentea* Linden, *B. augustinei* Hemsl., *B. baviensis* Gagnep., *B. beddomei* Hook. f., *B. brevisetulosa* Wu, *B. cathayana* Hemsl., *B. cathcartii* Hook. f. & Thoms., *B. chishuiensis* Ku, *B. circumlobata* Hance, *B. collina* Irmscher, *B. cucurbitifolia* Wu, *B. dawuishanensis* Huang & Shui, *B. decora* Stapf, *B. deliciosa* Linden ex Fotsch, *B. diadema* Linden ex Rodigas, *B. dielsiana* E. Pritz. ex Diels, *B. digyna* Irmscher, *B. discrepans* Irmscher, *B. dryadis* Irmscher, *B. duclouxii* Gagnep., *B. edulis* Léveillé, *B. emeiensis* Hu, *B. flaviflora* Hara, *B. formosana* (Hayata) Masamune, *B. forrestii* Irmscher, *B. foveolata* Irmscher, *B. fraseri* Kiew, *B. gagnepainiana* Irmscher, *B. goniotis* C.B. Clarke, *B. hatacoa* Buch.-Ham. ex D. Don, *B. hemsleyana* Hook. f., *B. houttuynioides* Yü, *B. integrifolia* Dalz., *B. iridescens* Dunn, *B. klossii* Ridley, *B. kouytcheouensis* Guillaumin, *B. lacerata* Irmscher, *B. laminariae* Irmscher, *B. limprichtii* Irmscher, *B. lipingensis* Irmscher, *B. littleri* Merr., *B. longanensis* Wu, *B. longicaulis* Ridley, *B. longiciliata* Wu, *B. longipedunculata* J. Golding & C. Karegeannes, *B. lowiana* King, *B. macrotoma* Irmscher, *B. maguanensis* Huang & Shui, *B. maxwelliana* King, *B. megaptera* A. DC., *B. mengtzeana* Irmscher, *B. obversa* C.B. Clarke, *B. palmata* D. Don, *B. paucilobata* Wu, *B. paupercula* King, *B. pedatifida* Léveillé, *B. perakensis* King, *B. poecila* C. Koch, *B. proluxa* Craib, *B. psilophylla* Irmscher, *B. purpureofolia* Huang & Shui, *B. reflexisquamosa* Wu, *B. repenticaulis* Irmscher, *B. rex* Putz., *B. rheifolia* Irmscher, *B. rhoephila* Ridley, *B. robinsonii* Ridley, *B. rockii* Irmscher, *B. rubropunctata* Huang & Shui, *B. sandalifolia* C.B. Clarke, *B. scitiifolia* Irmscher, *B. scortechinii* King, *B. siamensis* Gagnep., *B. sikkimensis* A. DC., *B. smithiae* Geddes, *B. smithiana* Yü ex Irmscher, *B. tampinica* Burkill ex Irmscher, *B. tarokoensis* M.J. Lai, *B. teysmanniana* (Miq.) Warb., *B. thomsonii* A. DC., *B. tiomanensis* Ridley, *B. truncatiloba* Irmscher, *B. tsaii* Irmscher, *B. tsoongii* Wu, *B. venusta* King, *B. versicolor* Irmscher, *B. villifolia* Irmscher, *B. xanthina* Hook.

Species whose membership is doubtful: 14 species: *B. austrotaiwanensis* Y.K. Chen & C.I. Peng, *B. beccariana* Ridley, *B. chitoensis* T.S. Liu & M.J. Lai, *B. dux* C.B. Clarke, *B. erosa* Blume, *B. gesnerioides* Huang & Shui, *B. gungshaniensis* Wu, *B. langbianensis* E.G. Baker, *B. megalophyllaria* Wu, *B. oreodoxa* Chun & Chun, *B.*

pavonina Ridley, *B. polytricha* Wu, *B. pseudodryadis* Wu, *B. setifolia* Irmscher.

sect. **Pritzelia** (Klotzsch) A. DC.

Fig. 32

- Ann. Sci. Nat., Bot. 4, 11: 137 (1859). — *Pritzelia* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 126 (1854), lectotype species (Barkley & Baranov, 1972); *Pritzelia fischeri* Klotzsch = *B. dietrichiana* Irmscher (homotypic synonym).
- Wageneria* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 126 (1854). — *Begonia* sect. *Wageneria* (Klotzsch) A. DC. p.p.
- Ewaldia* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 123 (1854). — *Begonia* sect. *Ewaldia* (Klotzsch) A. DC., Prodr. 15, 1: 372 (1864), lectotype species (Barkley & Baranov, 1972); *Ewaldia lobata* (Schott) Klotzsch = *B. lobata* Schott (homotypic synonym).
- Nephromischus* Klotzsch, Index Sem. Hort. Berol. App.: 1 (1855), type species: *Nephromischus rutilans* (Van Houtte) Klotzsch = *B. rutilans* Van Houtte (homotypic synonym).
- Saueria* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 122 (1854). — *Begonia* sect. *Saueria* (Klotzsch) A. DC., Prodr. 15, 1: 288 (1864), type species: *Saueria sulcata* (Scheidweiler) Klotzsch = *B. dichotoma* Jacq. (heterotypic synonym).
- Steineria* Klotzsch, Abh. Akad. Berlin '1854': 184 (1855). — *Begonia* sect. *Steineria* (Klotzsch) A. DC., Ann. Sci. Nat., Bot. 4, 11: 140 (1859), lectotype species (Barkley & Baranov, 1972); *Steineria ferruginea* Klotzsch = *B. hookeriana* Gardner (heterotypic synonym).
- Begonia* sect. *Philippomartia* A. DC., Ann. Sci. Nat., Bot. 4, 11: 139 (1859), lectotype species (Barkley & Baranov, 1972); *B. neglecta* A. DC.
- Begonia* sect. *Plurilobaria* A. DC., Ann. Sci. Nat., Bot. 4, 11: 136 (1859), type species: *B. schlumbergeriana* Lemaire.
- Begonia* sect. *Dasystyles* A. DC., Ann. Sci. Nat., Bot. 4, 11: 143 (1859), type species: *B. frigida* A. DC.
- Begonia* sect. *Bradea* Toledo, Arq. Bot. Est. S. Paulo n.s. Form. Maior 2, 3: 61 (1946), type species: *B. rufosericea* Toledo.
- Begonia* sect. *Gehrtia* Toledo, Arq. Bot. Est. S. Paulo n.s. Form. Maior 2, 3: 62 (1946), type species: *B. adiantiformis* Toledo = *B. itatinensis* Irmscher ex Brade (heterotypic synonym).

Plants terrestrial, perennial, rhizomatous or with upright stems; tubers absent; stem herbaceous or woody (at least at base); tubercles in leaf axil absent; stipules persistent or early caducous, usually entire or rarely denticulate (about 4 species); junction petiole and leaf blade without or with a tuft of hairs (*B. collaris* and *B. caraguatatubensis* have collar-shaped trichomes). **Leaves** alternate, more than 2, symmetric or asymmetric, usually not peltate or sometimes peltate (about 7 species), usually simple or less often palmately lobed; venation palmate to pinnate; indumentum of scales

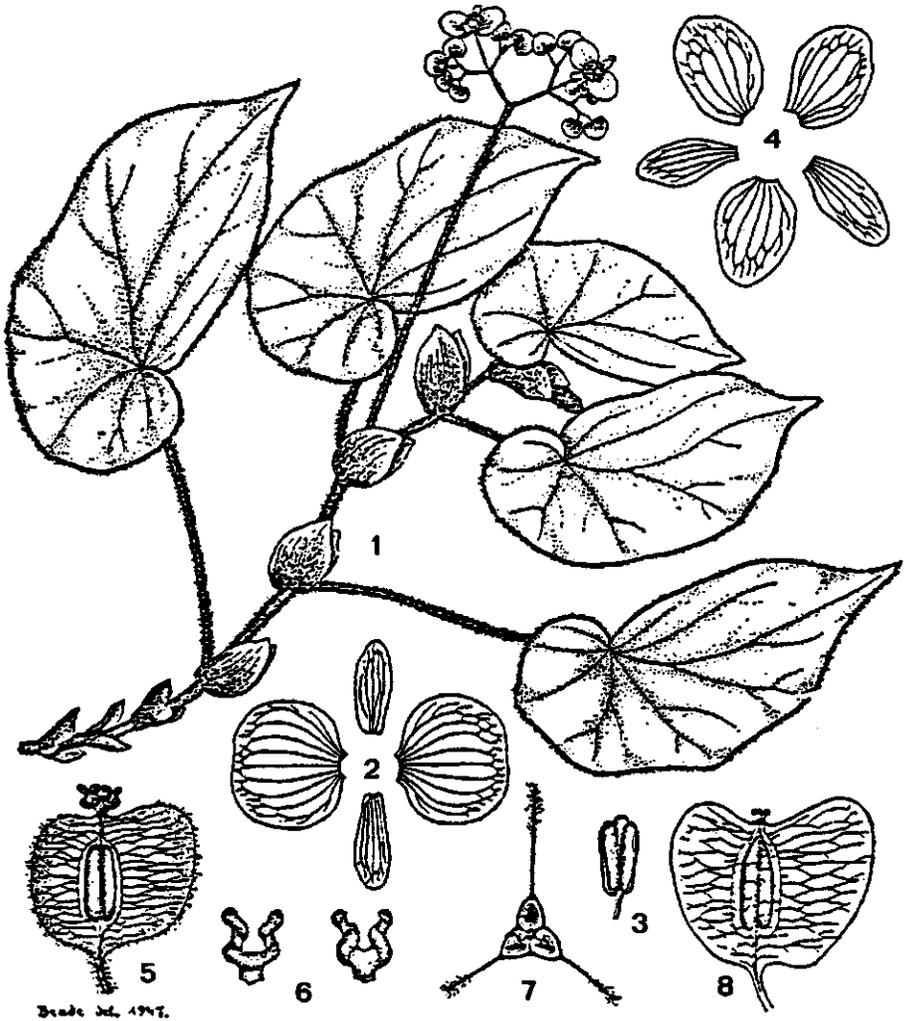


Fig. 32. Sect. *Pritzelia*. *B. epipsila* — 1, flowering stem; 2, perianth segments of male flower; 3, stamen; 4, perianth segments of female flower; 5, young fruit; 6, styles; 7, ovary in transverse section; 8, mature fruit. Reproduced from Brade (1948): p. 240, est. 1.

absent, stellate hairs usually absent or less often present (6 species), fimbriate-ciliate paleae sometimes present (5 species). **Inflorescence** axillary, dichasial or dichasial at base and monochasial at apex, bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts persistent (during flowering) or caducous. **Flower** with 2 bracteoles (rarely 1

or none?, often not described) spaced from the base of the ovary; perianth segments usually white or pink or rarely red (*B. coccinea*), outer ones rounded or acute at apex (usually only in female flowers). *Male flower* with usually 4 or rarely 2 (*B. fellereriana*, *B. umbraculifera*) free perianth segments; androecium actinomorphic, filaments usually equal or unequal (?), usually free or rarely fused below (5 species), anthers oblong, usually longer than or rarely about as long as the filaments (4 species), dehiscent with laterally or more or less unilaterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective extended. *Female flower* with 5(-7) (up to 6 in *B. parvifolia* and up to 7 in *B. schlumbergeriana*) free perianth segments; ovary or fruit with 3 wings (up to 5 in *B. schlumbergeriana*), wings equal to unequal in fruit, not hook- or spine-like, locules 3 (occasionally 4 in *B. schlumbergeriana*), placentation axillary, placental branches 1 or rarely 2 per locule (*B. kautskyana*, *B. paulensis*); styles 3 (sometimes 4 in *B. schlumbergeriana*), fused less than halfway, forked once, usually persistent in fruit or (rarely?) caducous in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, without or with an indistinct beak.

DISTRIBUTION: America: South America, predominantly in Brazil.

LEAF ANATOMY: Stomata single or in (usually small) groups; hypoderm often on the upper as well as the lower side of the leaf, but also on the upper side only or absent; astrosclereids have been reported in 5 species (out of more than 40); cystoliths always present, except in *B. fellereriana* and *B. grisea*.

SEED MICROMORPHOLOGY: Mean length 310–620 μm ; length/width ratio 1.7–2.6; operculum nipple-shaped; cuticular pattern fine to coarse (very coarse in *B. coccinea*; 28 spp. studied). In some species of the former section *Ewaldia* (e.g. *B. lobata*) the seed resembles that of sect. *Scheidweileria*, a.o. in the flattened chalaza.

CHROMOSOMES: $2n = 38$ (7 species); $2n = 56$ (31 species); $2n = 48$ (*B. princeps*, *B. scabrada*); $2n = 68$ (*B. dichotoma*).

TAXONOMIC COMMENTS: The species of *Pritzelia* as presented here show considerable diversity ranging from rhizomatous to shrubby and even tree-like. Scandent, tuberous or annual species are

lacking, however. The linking characters are the entire placentae and the presence of cystoliths in the leaf cells. The diversity within the section is an invitation to further division, but on the basis of the available evidence we see no way to split up *Pritzelia*. On the contrary, we have united several former sections, either because in our opinion the differences within *Pritzelia* were never sufficient to warrant sectional status, or else because the original differences have been bridged by species discovered since. One of these characteristics is whether the stigmatic papillae cover the stigma completely or leave the part between the twist of the spiral uncovered, which has been used by authors from Klotzsch to Barkley to separate sect. *Pritzelia* and sect. *Wageneria* on one hand from *Ewaldia*, *Steineria* and related genera/sections on the other. *Plurilobaria* and *Dasystyles*, both monotypic, seem very distinct, but closer study reveals that the species concerned were described from cultivated material, and the aberrant characters are such as are often found in interspecific hybrids. It seems undesirable, therefore, to erect a special section for them. The entire placentae show that at least one of the parent species belonged in *Pritzelia*. According to Fellerer (1892: 171–172) *B. grisea* and *B. parvipeltata* β *bahiensis* A. DC. (homotypic synonym of *B. fellereriana* Irmscher) have no cystoliths; he suggested a separate section. Irmscher added *B. ruhlandiana* to these exceptions, but wrote (1953a: 69) "Tatsächlich nehmen alle drei Arten eine Sonderstellung ein, doch sehe ich hier davon ab, eine neue Gruppe für sie zu schaffen, sondern verschiebe dies bis zur endgültigen Neuordnung aller Sektionen" [Indeed, all three species take a special position but I refrain to erect a new group for them here, and postpone this until the final rearrangement of all sections]. This he apparently never got around to. Two other aberrant species are *B. kautskyana* and *B. paulensis*. Both have bifid placentae which would place them in sect. *Begonia*, but their habit and other characteristics (*B. kautskyana* has stellate scales, *B. paulensis* has cystoliths) suggest that their closest relatives are in sect. *Pritzelia*.

SPECIES LIST: 122 species: *B. acetosa* Vell., *B. acida* Vell., *B. altamiroi* Brade, *B. angularis* Raddi, *B. angulata* Vell., *B. apparicioi* Brade, *B. arborescens* Raddi, *B. bahiensis* A. DC., *B. bidentata* Raddi, *B. biguassuensis* Brade, *B. bonitoensis* Brade, *B. boraceiensis* Handro, *B. boucheana* (Klotzsch) A. DC., *B. bradei* Irmscher, *B. brevilobata* Irmscher, *B. campos-portoana* Brade, *B. capanemae* Brade, *B. caraguatatubensis* Brade, *B. catharinensis* Brade, *B. cocci-*

nea Hook., *B. collaris* Brade, *B. compta* Bull, *B. concinna* Schott, *B. cornitepala* Irmscher, *B. crispula* Brade, *B. curtii* L.B. Smith & Schubert, *B. densifolia* Irmscher, *B. dichotoma* Jacq., *B. dietrichiana* Irmscher, *B. echinosepala* Regel, *B. epipsila* Brade, *B. falcifolia* Hook. f., *B. fernando-costae* Irmscher, *B. fiebrigii* C. DC., *B. fluminensis* Brade, *B. forgetiana* Hemsl., *B. friburgensis* Brade, *B. frigida* A. DC., *B. fuscocaulis* Brade, *B. gardneri* A. DC., *B. gehrtii* Irmscher, *B. grisea* A. DC., *B. handroi* Brade, *B. heringeri* Brade, *B. hilariana* A. DC., *B. hispida* Schott, *B. hookeriana* Gardn., *B. huegelii* (Klotzsch) Hort. Berol. ex A. DC., *B. inculta* Irmscher, *B. insularis* Brade, *B. isopterocarpa* Irmscher, *B. itaguassuensis* Brade, *B. itatiaiensis* Brade, *B. itatinensis* Irmscher ex Brade, *B. itupavensis* Brade, *B. jocelinoi* Brade, *B. juliana* Loefgr. ex Irmscher, *B. larorum* L.B. Smith & Wasshausen, *B. lealii* Brade, *B. lineolata* Brade, *B. listada* L.B. Smith & Wasshausen, *B. longibarbata* Brade, *B. magdalenensis* Brade, *B. membranacea* A. DC., *B. metallica* W.G. Smith, *B. moysesii* Brade, *B. neglecta* A. DC., *B. neocomensium* A. DC., *B. nuda* Irmscher, *B. obscura* Brade, *B. occhionii* Brade, *B. odeteiantha* Handro, *B. olsoniae* L.B. Smith & Schubert, *B. otophylla* L.B. Smith & Schubert, *B. oxyphylla* A. DC., *B. paleata* A. DC., *B. paranaensis* Brade, *B. parilis* Irmscher, *B. parvifolia* Schott, *B. parvistipulata* Irmscher, *B. paulensis* A. DC., *B. peltifolia* Schott, *B. peristegia* Stapf, *B. pernambucensis* Brade, *B. petasitifolia* Brade, *B. pickelii* Irmscher, *B. pilgeriana* Irmscher, *B. piresiana* Handro, *B. polyandra* Irmscher, *B. princeps* A. DC., *B. pulchella* Raddi, *B. ramentacea* Paxt., *B. reniformis* Dryand., *B. riedelii* A. DC., *B. rigida* Linden ex Regel, *B. rubropilosa* A. DC., *B. rufa* Thunb., *B. rufosericea* Toledo, *B. ruhlandiana* Irmscher, *B. rupium* Irmscher, *B. rutilans* Hort. Van-Houtte ex A. DC., *B. sanguinea* Raddi, *B. saxifraga* A. DC., *B. scabrida* A. DC., *B. scharffiana* Regel, *B. scharffii* Hook. f., *B. schlumbergeriana* Lem., *B. sementacea* Hort., *B. solimutata* L.B. Smith & Wasshausen, *B. solitudinis* Brade, *B. spinibarbis* Irmscher, *B. stenolepis* L.B. Smith & R.C. Smith, *B. stenophylla* A. DC., *B. subacida* Irmscher, *B. sylvatica* Meisner ex A. DC., *B. teuscheri* Linden ex André, *B. toledoana* Handro, *B. tomentosa* Schott, *B. umbraculifera* Hook., *B. valdensium* A. DC., *B. valida* Goebel, *B. vicina* Irmscher.

Species whose membership is doubtful: 13 species: *B. cariocana* Brade ex L.B. Smith & Wasshausen, *B. cordata* Vell., *B. declinata* Vell., *B. dentatiloba* A. DC., *B. erecta* Vell., *B. fellereriana* Irmscher, *B. garuvae* L.B. Smith & R.C. Smith, *B. kautskyana* O.

Handro, *B. obovatistipula* C. DC., *B. peruibensis* O. Handro, *B. pilderifolia* C. DC., *B. rotunda* Vell., *B. verruculosa* L.B. Smith.

sect. **Putzeysia** (Klotzsch) A. DC.

Prodr. 15, 1: 314 (1864). — *Putzeysia* Klotzsch, Abh. Kön. Akad. Wiss. Berlin '1854': 254 (1855), type species: *Putzeysia gemmipara* (Hook. f. & Thomson) Klotzsch = *B. gemmipara* Hook. f. & Thomson (homotypic synonym).

Plants terrestrial, perennial, with rhizomes from which upright stems arise; tubers present; stem herbaceous; tubercles in leaf axil present (in large clusters enveloped by bracts); stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight, asymmetric, not peltate, simple or palmately lobed to palmatifid; venation palmate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial, bisexual (or plants occasionally dioecious); inflorescence axes strongly reduced; bracts persistent (during flowering). **Flower** with 2 bracteoles spaced from the base of the ovary; perianth segments white or pink, outer ones rounded at apex. *Male flower* with 4 free perianth segments; androecium zygomorphic, filaments fused below, anthers obovate, longer than the filaments, connective not extended. *Female flower* with 5 free perianth segments; ovary or fruit with 3 wings, wings equal or subequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles 3, free, 2-lobed, caducous in fruit, stigma kidney-shaped. **Fruit** not berry-like, dehiscent near the wings, without or with an indistinct beak.

DISTRIBUTION: Asia: India (Sikkim).

LEAF ANATOMY: Stomata single; hypoderm absent; no cystoliths.

SEED MICROMORPHOLOGY: Seeds with adpressed papillae.

TAXONOMIC COMMENTS: Characterized by the clusters of tubercles which arise in some axils instead of inflorescences and the peculiar seeds. In other respects this species could be a member of *Diploclinium* II.

SPECIES LIST: A single species: *B. gemmipara* Hook. f. & Thomson.

sect. **Quadrilobaria** A. DC.

Fig. 33

Ann. Sci. Nat., Bot. 4, 11: 130 (1859), lectotype species (Barkley & Baranov, 1972): *B. nossibea* A. DC.

Plants terrestrial, perennial, acaulescent or rhizomatous; tubers absent or present; tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, 1 or 2 or more than 2, straight, symmetric or asymmetric, usually not peltate or rarely peltate (*B. decaryana*), simple to palmatifid or rarely palmatisect; venation palmate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial, bisexual, protandrous, with 1 to more than 3 female flowers, the central flower of the cyme male, lateral flower(s) female; inflorescence axes not reduced; bracts usually caducous or rarely persistent (during flowering). **Flower** without bracteoles; perianth segments white or pink, outer ones rounded at apex (those of the male flowers always more or less circular). *Male flower* with 2 free perianth segments; androecium actinomorphic, filaments equal, fused below (from almost free to almost entirely fused), anthers usually oblong or rarely circular to elliptic, usually longer than to about as long as or rarely shorter than the filaments (*B. tsaratananensis*), dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective usually not extended or rarely extended (*B. bernieri*). *Female flower* with 2 or 4 free perianth segments; ovary or fruit with 3 wings, wings equal to unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 2 per locule (but often not recorded); styles 3, free, 2-lobed or forked once, persistent or caducous in fruit, stigma usually not kidney-shaped or rarely kidney-shaped, usually in a band and spiralled or rarely not spiralled. **Fruit** not berry-like, dehiscent near the back of the locules, more or less erect to nodding, without or with an indistinct beak.

DISTRIBUTION: Africa: Madagascar.

LEAF ANATOMY: Stomata single; hypoderm absent; no cystoliths (*B. bernieri*, *B. boiviniana*, *B. goudotii*, *B. nossibea*).

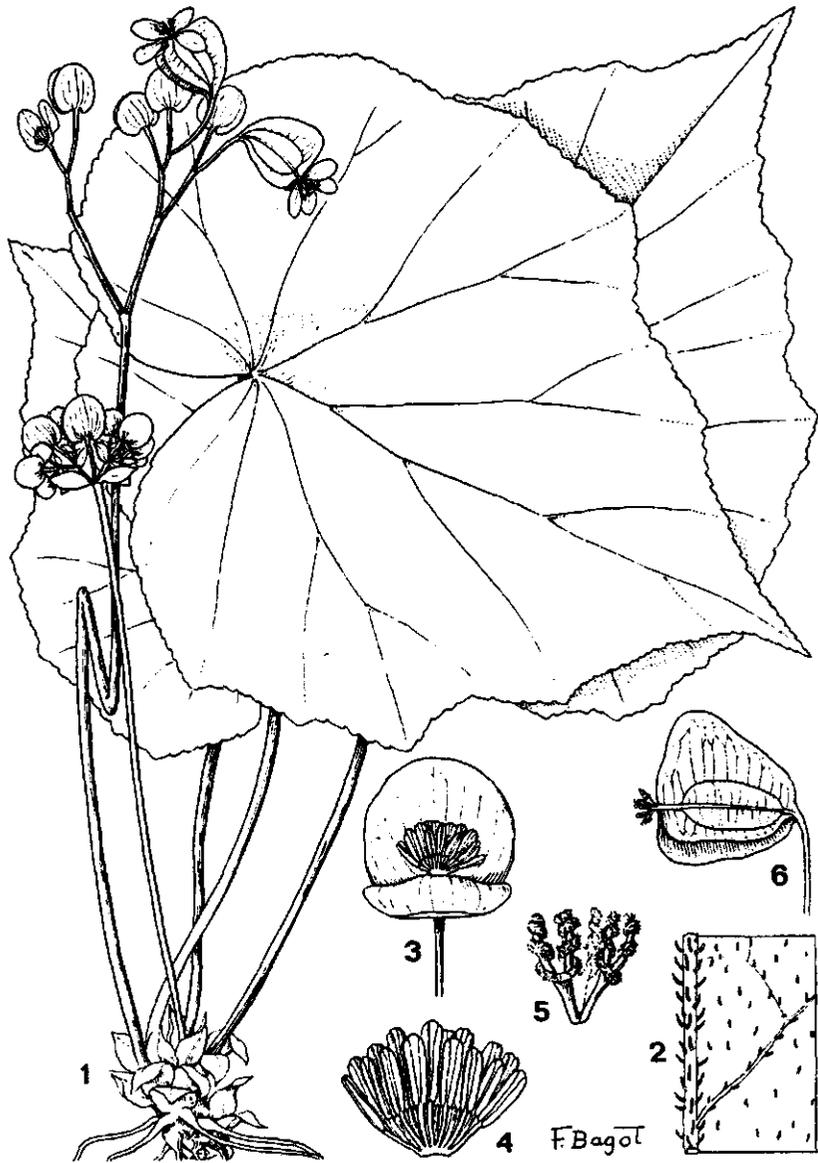


Fig. 33. Sect. *Quadrilobaria*. *B. nossibeae* — 1, plant habit; 2, detail of lower leaf surface; 3, male flower; 4, androecium; 5, styles; 6, fruit. Reproduced from Keraudren-Aymonin (1983): p. 43, pl. 13.

SEED MICROMORPHOLOGY: Seeds ellipsoid to subglobose; collar cells comparatively long; testa cells often few; anticlinal walls straight to undulate.

CHROMOSOMES: $2n = 38$ (*B. francoisii*).

IMPORTANT LITERATURE: Keraudren-Aymonin (1983).

TAXONOMIC COMMENTS: Very close to sect. *Rostrobegonia*, *Augustia*, and *Nervioplacentaria*. Differing from sect. *Rostrobegonia* by the male flowers with 2 tepals and the lack of a stem, from sect. *Augustia* by the 2 placentae (but unknown for many species). For differences with sect. *Nervioplacentaria* see under that section.

SPECIES LIST: 19 species: *B. anjuanensis* Humbert ex Keraudren-Aymonin & Bosser, *B. ankaranensis* Humbert ex Keraudren-Aymonin & Bosser, *B. antsingyensis* Humbert ex Keraudren-Aymonin & Bosser, *B. antsiranensis* Aymonin & Bosser, *B. bagotiana* Humbert ex Keraudren-Aymonin & Bosser, *B. bekopakensis* Aymonin & Bosser, *B. bernieri* A. DC., *B. boiviniana* A. DC., *B. decaryana* Humbert ex Keraudren-Aymonin & Bosser, *B. francoisii* Guillaumin, *B. goudotii* A. DC., *B. heteropoda* Baker, *B. isalensis* Humbert ex Keraudren-Aymonin & Bosser, *B. leandrii* Humbert ex Keraudren-Aymonin & Bosser, *B. mananjebensis* Humbert ex Bosser & Keraudren-Aymonin, *B. neoperrieri* Humbert ex Keraudren-Aymonin & Bosser, *B. nossibea* A. DC., *B. sambiranensis* Humbert ex Keraudren-Aymonin & Bosser, *B. tsaratananensis* Aymonin & Bosser.

sect. **Quadriperigon** Ziesenh.

Fig. 34

The Begonian 35: 257 (1968), type species: *B. abaculoides* Ziesenh. = *B. boissieri* A. DC. (heterotypic synonym).

Begonia sect. *Knesebeckia* (Klotzsch) A. DC. p.p.

Begonia sect. *Begoniastrum* subsection *Euknesebeckia* Warb. in Engl. & Prantl, Die Natürl. Pflanzenfam. (ed. 1) 3, 6a: 149 (1894) p.p., type species: *B. monoptera* Link & Otto = *B. balmisiana* Balmis (heterotypic synonym).

Plants terrestrial, perennial or annual (?), with upright stems; tubers usually present or rarely absent (*B. gracilis*, *B. biserrata*?); stem herbaceous; tubercles in leaf axil absent or present; stipules persistent or early caducous, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight to transverse, symmetric or asymmetric (in at least 6 species (possibly more) the lower leaves are symmetric, the upper asymmetric), not peltate, simple or palmately lobed or rarely palmatifid; venation

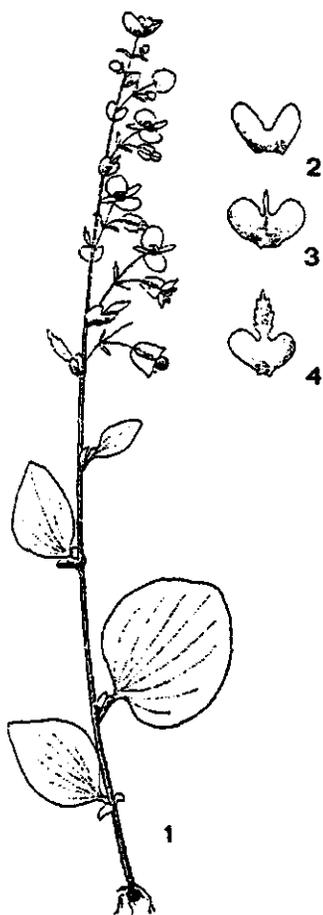


Fig. 34. Sect. *Quadriperigonia*. *B. angustiloba* — 1, plant habit; 2-4, reduced leaves and adnate stipules in the inflorescence. Reproduced from Irmischer (1914): p. 560, fig. 1.1.

usually palmate or rarely palmate-pinnate (*B. dealbata*, *B. sandtii*); indumentum of scales or stellate hairs absent. **Inflorescence** terminal, a raceme of cymes, the cymes bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts persistent (during flowering) or caducous. **Flower** without or with 2 bracteoles spaced from the base of the ovary; perianth segments white or pink, outer ones usually rounded or rarely acute at apex. *Male flower* with usually 4 or rarely 2 (*B. fusibulba*) free perianth segments; androecium actinomorphic, filaments equal (?), usually fused below or rarely free (*B. pedata*), anthers obovate, shorter than the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length),

apex not hooded, connective not extended. *Female flower* with usually 5 or rarely 2 (*B. fusibulba*) or 4 (*B. dealbata*?) free perianth segments; ovary or fruit usually with 3 wings or rarely 1 wing (*B. balmisiana*), wings usually unequal or rarely equal or subequal in fruit (*B. boissieri*), not hook- or spine-like, locules 3, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles 3, usually fused less than halfway or rarely free (*B. fusibulba*), 2-lobed or forked once or rarely more than once (occasionally in *B. boissieri*), persistent in fruit, stigma usually not kidney-shaped or rarely kidney-shaped (*B. fusibulba*), in a band and spiralled. **Fruit** not berry-like, nodding (recorded for only few species), without or with an indistinct beak.

DISTRIBUTION: America: Mexico and one aberrant species in Peru.

LEAF ANATOMY: Stomata single (7 species) or in groups (*B. balmisiana*); hypoderm absent (6 species), present on both sides in *B. angustiloba*; cystoliths absent.

SEED MICROMORPHOLOGY: The seeds conform to the prevalent type in *Begonia*. The size is rather small (300 μm long in *B. gracilis* and 340 μm in *B. sandtii*); cuticular ornamentation granular or short zigzag (3 species studied).

CHROMOSOMES: $2n = 28$ (*B. biserrata*, *B. bulbillifera*, *B. gracilis*, *B. uruapensis*); $2n = 42$ (*B. balmisiana*); $2n = 56$ (*B. bulbillifera*, *B. gracilis*).

TAXONOMIC COMMENTS: Ziesenhenné erected section *Quadriperigonia* for his *B. abaculoides* because the specimen on which it was founded had 4 female perianth segments. It was subsequently shown to belong to *B. boissieri* which usually has 5 female perianth segments. This is a representative of a rather homogeneous group of Mexican *Begonia*s, characterized by a terminal, thyrsoid inflorescence and often (how often is not exactly known) a geophytic habit and propagation not only by seed but also by tubercles. These species were hitherto brought to section *Begoniastrum* subsection *Knesebeckia* but are here grouped into a separate section, for which the - somewhat unfortunate - name *Quadriperigonia* is the taxonomically correct one.

SPECIES LIST: 17 species: *B. angustiloba* A. DC., *B. anodifolia* A. DC., *B. balmisiana* Balmis, *B. biserrata* Lindl., *B. boissieri* A. DC., *B. bulbilifera* Link & Otto, *B. dealbata* Liebm., *B. fusibulba* C. DC., *B. gracilis* Humb., Bonpl. & Kunth, *B. macdanielsii* Standley, *B. palmeri* S. Wats., *B. pedata* Liebm., *B. portillana* S. Wats., *B. rhodochlamys* L.B. Smith & Schubert, *B. sandtii* Houghton ex Ziesenh., *B. thyrsoides* Irmscher, *B. uruapensis* Sessé & Moc.

Species whose membership is doubtful: 2 species: *B. ornithocarpa* Standley, *B. racemiflora* Ortigies ex C. Chev.

sect. **Reichenheimia** (Klotzsch) A. DC.

Fig. 35

Prodr. 15, 1: 385 (1864). — *Reichenheimia* Klotzsch, Abh. Kön. Akad. Wiss. Berlin '1854': 174 (1855), lectotype species (Barkley & Baranov, 1972): *Reichenheimia thwaitesii* (Hook.) Klotzsch = *B. tenera* Dryand. (heterotypic synonym).

Mitscherlichia Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 124 (1854). — *Begonia* sect. *Mitscherlichia* (Klotzsch) A. DC., Prodr. 15, 1: 389 (1864), lectotype species (Barkley & Baranov, 1972): *Mitscherlichia albo-coccinea* (Hook.) Klotzsch = *B. albo-coccinea* Hook. (homotypic synonym).

Begonia sect. *Uniplacentales* C.B. Clarke p.p.

Begonia subgenus *Aschisma* C.B. Clarke p.p.

Plants terrestrial, perennial, usually rhizomatous or rarely with upright stems; tubers absent or present; stem herbaceous; tubercles in leaf axil usually absent (rarely at the leaf edge in *B. harmandii* and *B. intermixta*); stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, 1 or 2 or more than 2, straight or transverse, symmetric or asymmetric, peltate or not, usually simple or rarely palmatifid (*B. brandisiana*); venation palmate; indumentum of scales or stellate hairs absent. **Inflorescence** usually axillary or rarely terminal (*B. hymenophylla*), dichasial or monochasial, often dichasial at base and monochasial at apex, usually (perhaps always) bisexual, usually protandrous or possibly protogynous (*B. pierreii*, *B. speluncae*, perhaps others), with the central flower of the cyme male, lateral flower(s) female; inflorescence cymose or rarely racemose, axes not reduced or rarely strongly reduced (*B. morelii*, *B. tenera*, others?); bracts usually persistent (during flowering). **Flower** usually without or rarely with 1 or 2 bracteoles (*B. albo-coccinea*, *B. coriacea*, *B. morelii*) spaced from the base of the ovary; perianth segments usually white or pink or rarely red (*B. bonii*, *B. coriacea*, possibly *B. trichopoda*), outer

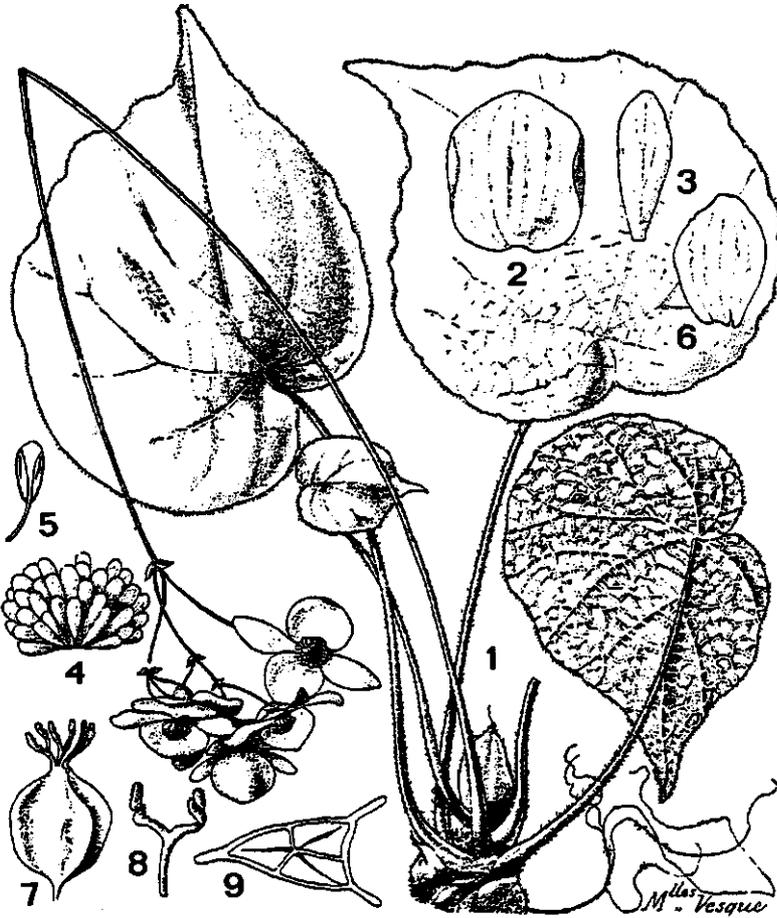


Fig. 35. Sect. *Reichenheimia*. *B. bonii* — 1, plant habit; 2-3, outer and inner perianth segment of male flower; 4, androecium; 5, stamen; 6, outer perianth segment of female flower; 7, ovary; 8, style; 9 ovary in transverse section. Reproduced from Gagnepain (1921): p. 1117, fig. 131.

ones rounded at apex (emarginate in *B. brandisiana*). *Male flower* with 4 or less often 2 free perianth segments; androecium actinomorphic, filaments usually fused below or rarely free (about 9 species), anthers obovate, usually about as long as the filaments, usually dehiscent with laterally or rarely unilaterally positioned (*B. intermixta*, *B. pumilio*, others?) short pore-like slits (less than 0.5 of the anther length) or longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective not extended. *Female flower* with 3 or 4 or rarely 2 (5 species), 5 (5 species) or 6 (*B. pierrei*)

free perianth segments; ovary or fruit with 3 wings, wings usually equal or subequal or rarely unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 1 per locule; styles 3, free or fused less than halfway, 2-lobed or forked once, usually caducous or less often persistent in fruit, stigma kidney-shaped or not, in a band and spiralled or not. **Fruit** not berry-like, dehiscent near the wings, usually pendulous, without or with an indistinct beak.

DISTRIBUTION: Asia: from India and Sri Lanka to the Himalayas, Indo-China, China and the Malesian region.

LEAF ANATOMY: Stomata single or in small groups; hypoderm present or absent; no cystoliths (8 species studied).

CHROMOSOMES: $2n = 30$ (*B. morelii*, *B. rajah*), $2n = 32$ (*B. floccifera*), $2n = 34$ (*B. goegoensis*).

TAXONOMIC COMMENTS: *Reichenheimia* differs from *Diploclinium* only in the number of placentae. Both sections are polymorphous but the variability follows more or less the same pattern. To show the similarity more clearly the species have been divided into three groups in the same way as *Diploclinium*. The analogies are obvious. For easy survey a further division of *Reichenheimia* might be advisable. An in depth study of this group will have to show if this is feasible. (It is not suggested that the following division deserves taxonomic status).

Group I: stem rhizomatous, often fleshy; leaves often (i.e. in about half the number of species) peltate, usually asymmetrical; inflorescence cymose; male flowers with 4 perianth segments, rarely with 2; female flowers with 3 or 4 perianth segments, rarely with 2 or 5; styles free, rarely long connate, more often forked than lobed.

Group II: stem erect from a tuberous base; leaves not peltate, straight and symmetrical, at least the basal ones; inflorescence cymose; male perianth segments 2 or 4; female perianth segments 4 or 5, rarely 2.

Group III: tuberous, stem absent or very short; leaves sometimes peltate, usually symmetrical; inflorescence cymose or racemose; male flower with 4 perianth segments, rarely with 2; anthers shortly connate; female flowers with 4 perianth segments, rarely with 2, 3, 5 or 6; styles free, stigmas 2-lobed to globular.

SPECIES LIST:

Species whose membership of the section is doubtful: 1 species:

B. strigulosa A. DC.

Group I, 22 species: *B. albo-coccinea* Hook., *B. bonii* Gagnep., *B. brevicaulis* Ku non A. DC., *B. coriacea* Hassk., *B. corneri* R. Kiew, *B. filiformis* Irmscher, *B. floccifera* Bedd., *B. foxworthyi* Burkill ex Ridley, *B. goegoensis* N.E. Br., *B. gueritziana* L.S. Gibbs, *B. ignorata* Irmscher, *B. lobbii* A. DC., *B. mollis* A. DC., *B. muricata* Blume, *B. nurii* Irmscher, *B. nymphaeifolia* Yü, *B. peninsulae* Irmscher, *B. rajah* Ridley, *B. stictopoda* (Miq.) A. DC., *B. sudjanae* Jansson, *B. sychnantha* L.B. Smith & Wasshausen, *B. tayabensis* Merr.

Species whose membership of Group I is doubtful: 6 species: *B. fibrosa* C.B. Clarke, *B. forbesii* King, *B. peltatifolia* Li, *B. speluncae* Ridley, *B. stelzneri* (Klotzsch) Warb., *B. vuijckii* Koord.

Group II, 5 species: *B. brandisiana* Kurz, *B. cardiophora* Irmscher, *B. phrixophylla* Blatter & McCann, *B. trichocarpa* Dalz., *B. trichopoda* Miq.

Group III, 13 species: *B. chingii* Irmscher, *B. harmandii* Gagnep., *B. henryi* Hemsl., *B. hymenophylla* Gagnep., *B. intermixta* Irmscher, *B. morelii* Irmscher ex Karegeannes, *B. nivea* Parish ex Kurz, *B. parvula* Léveillé & Vaniot, *B. pierrei* Gagnep., *B. pumilio* Irmscher, *B. subpeltata* Wight, *B. tenera* Dryand., *B. wangii* Yü.

Species whose membership of Group III is doubtful: 1 species: *B. rabilii* Craib.

sect. **Ridleyella** Irmscher

Mitt. Inst. Allgem. Bot. Hamburg 8: 105 (1929), type species: *B. eiromischa* Ridley.

Plants terrestrial, perennial, rhizomatous; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** more than 2, transverse, asymmetric, peltate, simple; venation palmate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial at base and monochasial at apex, bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts caducous. **Flower** without bracteoles; perianth segments white or pink, outer ones rounded at apex. *Male flower* with 3 or 4 free perianth segments; androecium

zygomorphic, filaments free, anthers obovate, about as long as the filaments, dehiscent with unilaterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded. *Female flower* with 3 or 4 free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 2, placentation axillary, placental branches 1 per locule; styles 3, fused less than halfway, persistent in fruit, stigma kidney-shaped. **Fruit** not berry-like, nodding, without or with an indistinct beak.

DISTRIBUTION: Asia: Thailand and Peninsular Malaysia.

IMPORTANT LITERATURE: Imscher (1929).

TAXONOMIC COMMENTS: The (annual?) dwarf species *B. pumila* Craib may also belong here because of its peltate leaves, 2-locular fruit, and undivided placentae, but it differs from the other two in having an upright stem, caducous stipules, symmetric leaves, 5 tepals in the female flower, 2 styles, and a fruit with subequal wings.

SPECIES LIST: 2 species: *B. eiromischa* Ridley, *B. kingiana* Imscher.

Species whose membership is doubtful: 1 species: *B. pumila* Craib.

sect. **Rossmannia** (Klotzsch) A. DC.

Fig. 36

Prodr. 15, 1: 333 (1864). — *Rossmannia* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 125 (1854), type species: *Rossmannia repens* Klotzsch = *B. rossmanniae* A. DC. (homotypic synonym).

Plants terrestrial or epiphytic, perennial, with upright stems (subscandent); tubers absent; stem herbaceous (?); tubercles in leaf axil absent; stipules early caducous, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight, symmetric, not peltate, simple; venation pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** terminal, racemose (a raceme of cymes); lateral inflorescences bisexual, with male flowers basal and female flowers distal (?), protandrous (?); inflorescence axes not reduced; bracts caducous. **Flower** with 2 bracteoles inserted directly below the ovary; perianth segments white, pink or red, outer ones rounded at apex. *Male flower* with 2 free perianth segments;

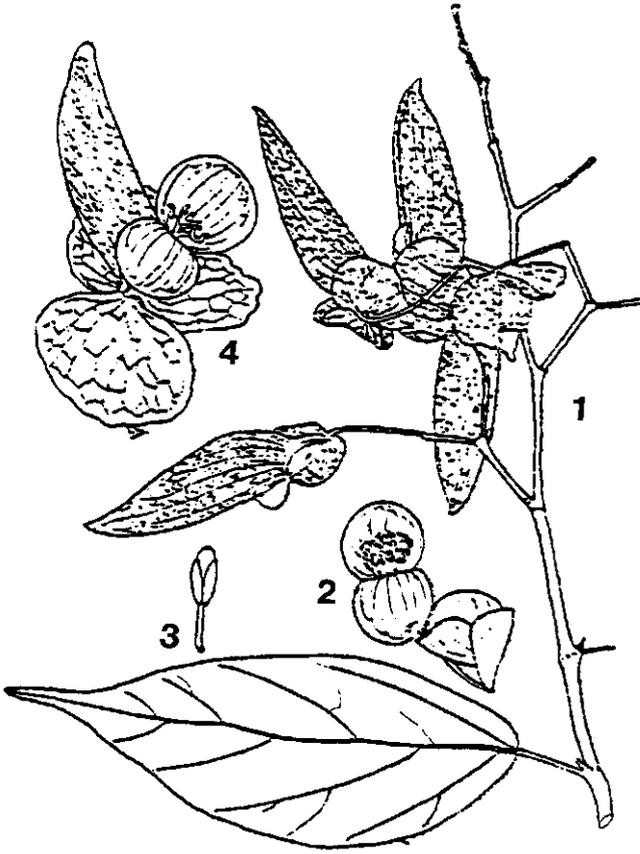


Fig. 36. Sect. *Rossmannia*. *B. rossmanniae* — 1, fruiting stem; 2, male flower and bracts; 3, stamen; 4, female flower and bracteoles. Reproduced from Smith & Schubert (1946): p. 101, tab. 2.

androecium actinomorphic, filaments unequal, free, anthers circular to elliptic, shorter than the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective extended. *Female flower* with 2 free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles 3, fused less than halfway, forked once, persistent in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, without or with an indistinct beak.

DISTRIBUTION: America: the Andean region.

LEAF ANATOMY: Stomata single and in groups; hypoderm absent; cystoliths absent.

SEED MICROMORPHOLOGY: Seed narrowly ellipsoid, mean size 675 x 140 μm , micropylar end swollen, composed of air-filled cells, chalazal end extended.

TAXONOMIC COMMENTS: A monotypic section related to *Ruizopavonia* (with which it was united by Smith & Schubert, 1946: 103), but differing in the thyrsoid inflorescence, the ellipsoid rather than oblong anthers, and the pistillate bracteoles which are longer than, and accrescent to the fruit. *Rossmannia* differs from *Pilderia*, which also has a thyrsoid inflorescence, in a.o. the number of perianth segments.

SPECIES LIST: A single species: *B. rossmanniae* A. DC.

sect. **Rostrobegonia** Warb.

Fig. 37

in Engl. & Prantl, Die Natürl. Pflanzenfam. (ed. 1) 3, 6a: 141 (1894), type species: *B. rostrata* Welw. ex Hook. f.

Plants terrestrial, annual or perennial, usually with upright stems or rarely rhizomatous (*B. schliebenii*); tubers absent or present; stem herbaceous; tubercles in leaf axil usually absent or rarely present; stipules persistent or early caducous, usually entire or rarely dentate; junction petiole and leaf blade usually with or rarely without a tuft of hairs (*B. rumpiensis*, *B. sonderana*). **Leaves** alternate, more than 2, straight or oblique, asymmetric, not peltate, simple to palmately lobed or rarely palmatifid; venation palmate or palmate-pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary and terminal, usually bisexual or rarely bisexual and male (*B. wollastonii*), protandrous; bisexual inflorescence usually dichasial or rarely monochasial; male inflorescence dichasial (when present); inflorescence with 1 to more than 3 female flowers, the central flower of the cyme male, lateral flower(s) female; inflorescence axes not reduced; bracts persistent (during flowering) or caducous. **Flower** without or with 2 bracteoles inserted directly below or spaced from the base of the ovary;

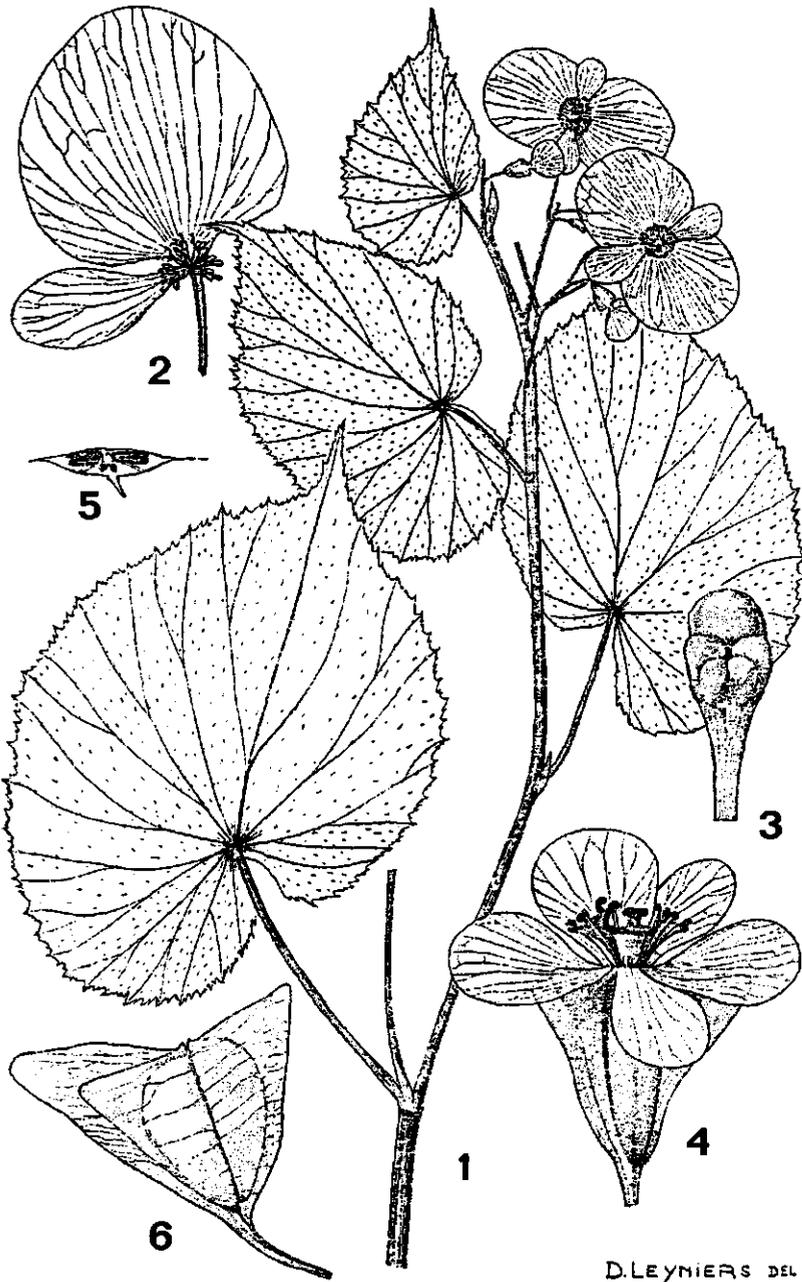


Fig. 37. Sect. *Rostrobegonia*. *B. wollastonii* — 1, flowering stem; 2, male flower (2 perianth segments removed); 3, stamen; 4, female flower; 5, ovary in transverse section; 6, fruit. Reproduced from Wilczek (1969): p. 49, pl. 5.

perianth segments white, pink or red, outer ones rounded at apex. *Male flower* with (2–)4 free perianth segments; androecium usually actinomorphic or rarely zygomorphic, filaments equal or unequal, free or fused below, anthers usually oblong or circular to elliptic or rarely obovate, usually shorter than or occasionally about as long as the filaments, dehiscent with laterally or unilaterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective usually extended or rarely not extended (*B. bequaertii*). *Female flower* with (3–)5 free perianth segments; ovary or fruit with 3 wings, wings equal to unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 1 or 2 per locule, ovules present between placental branches (but often not recorded); styles 3, usually fused less than halfway or free or rarely fused more than halfway, usually forked once or rarely forked more than once (*B. keniensis*, *B. wollastonii*), usually caducous or rarely persistent in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, dehiscent near the back of the locules, more or less erect or pendulous, without or with an indistinct beak.

DISTRIBUTION: Africa: throughout tropical Africa towards southern Africa.

LEAF ANATOMY: Stomata in small groups (2–6?); hypoderm absent; no cystoliths (*B. johnstonii*).

SEED MICROMORPHOLOGY: Seeds ellipsoid, 345–685 x 185–400 μm , length/width ratio 1.7–2.2; ratio collar to seed length 1:2.2–3.0; longitudinal walls of collar cells straight, those of testa cells undulating to slightly curved; operculum nipple- to broadly nipple-shaped; anticlinal boundaries flat; cuticle of collar and testa cells granular to shortly linear or more prominently zigzag.

CHROMOSOMES: $2n = 26$ (*B. engleri*, *B. johnstonii*); $2n = 38$ (*B. keniensis*, *B. rostrata*).

IMPORTANT LITERATURE: Imscher (1961), Hilliard (1976), Kupicha (1978), Wilczek (1969).

TAXONOMIC COMMENTS: Closely related to sect. *Augustia* and possibly identical with it. Imscher showed that the criterion of undivided against divided placentae does not hold. He suggested a

different species grouping, based mainly on the presence or absence of bristles at the top of the petiole. Although weakly based, following some rearrangement of species the grouping of Irmscher is maintained here.

SPECIES LIST: 10 species: *B. bequaertii* Robyns & Lawalrée, *B. engleri* Gilg, *B. johnstonii* Oliv. ex Hook. f., *B. keniensis* Gilg ex Engl., *B. nyassensis* Irmscher, *B. rostrata* Welw. ex Hook. f., *B. rumpiensis* Kupicha, *B. schliebenii* Irmscher, *B. sonderana* Irmscher, *B. wollastonii* E.G. Baker.

sect. **Ruizopavonia** A. DC.

Fig. 38

Ann. Sci. Nat., Bot. 4, 11: 132 (1859), lectotype species (Barkley & Baranov, 1972): *B. alnifolia* A. DC.
Begonia sect. *Meionanthera* A. DC., Ann. Sci. Nat., Bot. 4, 11: 141 (1859), type species: *B. holtonis* A. DC.

Plants terrestrial, perennial, with upright stems (at least 10 species scandent or subscandent); tubers absent; stem herbaceous or woody (at least at base); tubercles in leaf axil absent; stipules persistent or early caducous, usually entire or rarely denticulate (*B. buchtienii*); junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight, usually asymmetric or rarely symmetric (*B. cuatrecasasiana*, *B. estrellensis*), not peltate, simple; venation usually pinnate or rarely palmate-pinnate (*B. buchtienii*, *B. consobrina*, *B. varistyla*); indumentum of scales or stellate hairs absent. **Inflorescence** axillary (pseudo-terminal in 6 species), dichasial or dichasial at base and monochasial at apex, bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts usually caducous or rarely persistent (during flowering). **Flower** with 2 bracteoles usually spaced from the base of or rarely inserted directly below the ovary; perianth segments usually white or pink or rarely red, outer ones usually rounded or rarely acute at apex. *Male flower* with 2 or 4 free perianth segments; androecium actinomorphic, filaments equal or unequal, free, anthers usually oblong or rarely circular to elliptic or obovate (*B. meridensis*), dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), connective usually extended or rarely not extended (*B. holtonis*). *Female flower* with 2–5 free perianth segments; ovary or fruit with 3 wings, wings



Fig. 38. Sect. *Ruizopavonia*. *B. convallariodora* — 1, flowering stem; 2, male flower; 3, stamen; 4, female flower; 5 style; 6, fruit. Reproduced from Smith & Schubert (1961): p. 165, fig. 19.

unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 2 per locule or rarely 1 per locule (*B. holtonis* in part), ovules present between placental branches; styles 3, fused less than halfway or free, forked once or more than once or rarely 2-lobed (*B. rubiginosipes*, *B. seemanniana*), caducous in fruit or rarely persistent (4 species), stigma not kidney-shaped, usually in a band and spiralled or rarely not (*B. prionophylla*) or contracted near the style apex (*B. obtecticaulis*, *B. varistyla*). **Fruit** not berry-like, dehiscent near the back of the locules, pendulous (or nodding?), without or with an indistinct beak.

DISTRIBUTION: America: Central America and the Andean region from Venezuela to Bolivia; two species in Brazil.

LEAF ANATOMY: Stomata single (*B. prionophylla*, *B. seemanniana*) or in groups (*B. alnifolia*, *B. carpinifolia*, *B. holtonis*, *B. peru-*

viana); hypoderm absent, but present on both sides in *B. holtonis*; cystoliths present (*B. carpinifolia*, *B. glaucoides*) or absent (*B. alnifolia*, *B. cooperi*, *B. estrellensis*, *B. holtonis*, *B. peruviana*, *B. seemanniana*).

SEED MICROMORPHOLOGY: Seeds comparatively small, mean length up to 415 μm ; anticlinals curved, undulating; cuticular structure fine, consisting of linear or undulating striae.

CHROMOSOMES: *B. barrigae*, *B. convallariodora*, *B. cooperi*, *B. guaduensis* and *B. holtonis* have been studied, but all that can be said is that the chromosomes are very numerous ($2n = 78-104?$).

IMPORTANT LITERATURE: Irmischer (1949: 570-603).

TAXONOMIC COMMENTS: Like many sections of neotropical *Begonia*, *Meionanthera*, *Ruizopavonia* and *Hydristyles* shade off into each other. Moreover, *Meionanthera* is very close to *Lepsia*, *Ruizopavonia* is related to *Donaldia*, and all sections mentioned accommodate species that might also be, and often have been, placed into section *Begonia*. The gaps that existed between these sections at the time of Alphonse de Candolle's monograph have since been filled in as new species were described and more became known about the variability within known species. In the course of the present study it became clear that the easiest place to make a division was now in the middle of the section *Ruizopavonia*. The species of this section fall into two groups: group I with straight, pinnate leaves with petioles one fifth of the lamina or less, and group II with transverse, palmate leaves with petioles 1/4 to 1 x as long as the lamina. Group II has so far only been reported from Peru and Bolivia, whereas species of group I not only occur in these countries but reach much further north through Ecuador, Colombia and Panama to Costa Rica; there are also two representatives in Brazil. Traditionally, *Meionanthera* has only one species, *B. holtonis* with entire placentas. It appears, however, that the placentas may also be bilamellate or intermediate (Smith & Schubert, 1946: 186), which means that *B. holtonis* can be accommodated in group I of *Ruizopavonia*. Group II of *Ruizopavonia* has been united with *Cyathocnemis*. Group I of *Ruizopavonia* includes the lectotype species so it retains the name.

SPECIES LIST: 32 species: *B. alnifolia* A. DC., *B. bangii* Kuntze,

B. barrigae L.B. Smith & Schubert, *B. besleriifolia* Schott, *B. buchtienii* Irmscher, *B. carpinifolia* Liebm., *B. chaetocarpa* Kuntze, *B. conso-brina* Irmscher, *B. convallariodora* C. DC., *B. cooperi* C. DC., *B. cuatrecasasiana* L.B. Smith & Schubert, *B. cymbalifera* L.B. Smith & Schubert, *B. dugandiana* L.B. Smith & Schubert, *B. estrellensis* C. DC., *B. extensa* L.B. Smith & Schubert, *B. glaucoides* Irmscher, *B. guaduensis* Humb., Bonpl. & Kunth, *B. holtonis* A. DC., *B. juni-nensis* Irmscher, *B. lignescens* Morton, *B. meridensis* A. DC., *B. multiflora* Benth., *B. oblanceolata* Rusby, *B. obtecticaulis* Irmscher, *B. peruviana* A. DC., *B. pilosella* Irmscher, *B. prionophylla* Irmscher, *B. rubiginosipes* Irmscher, *B. seemanniana* A. DC., *B. tonduzii* C. DC., *B. varistyla* Irmscher, *B. xylopoda* L.B. Smith & Schubert.

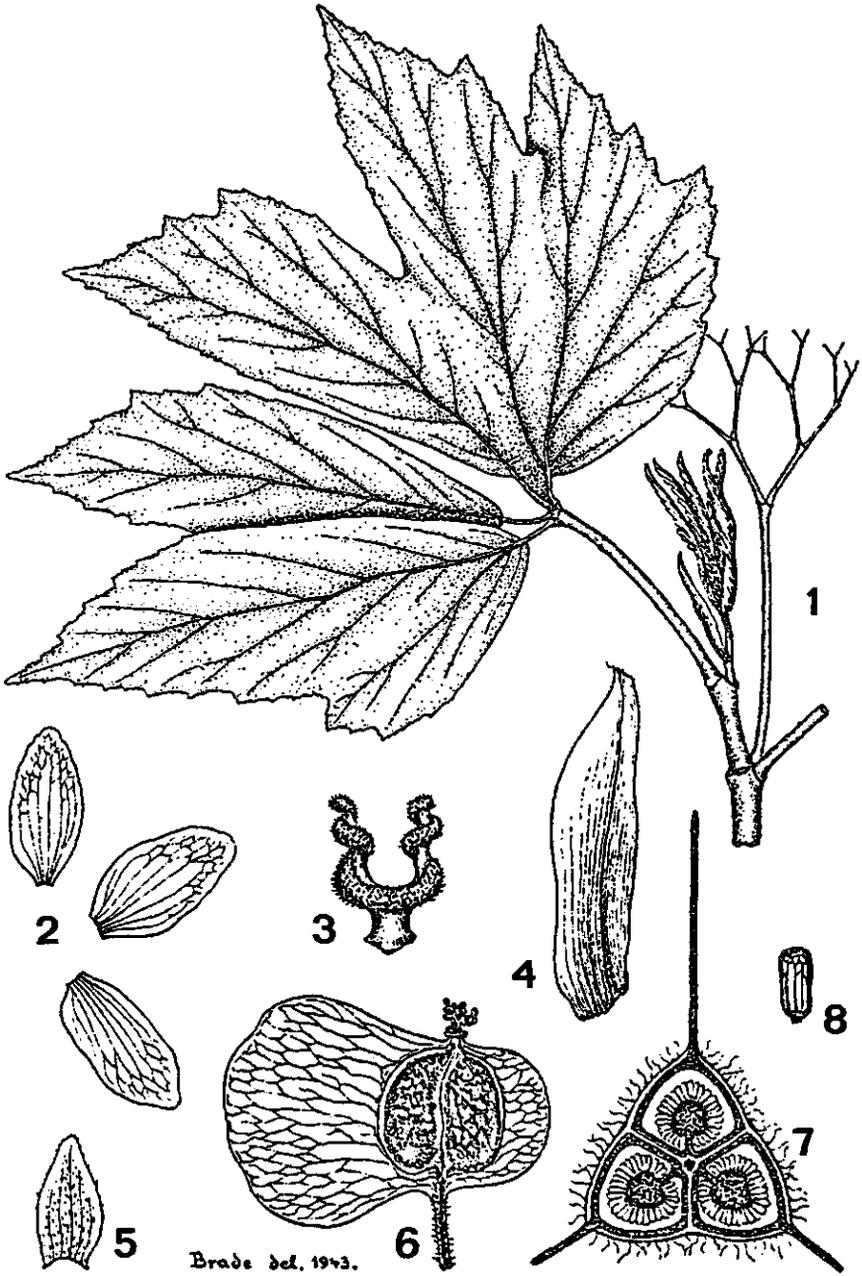
Species whose membership is doubtful: 3 species: *B. gesnerioides* L.B. Smith & Schubert, *B. leptostyla* Irmscher, *B. opuliflora* Putz.

sect. **Scheidweileria** (Klotzsch) A. DC.

Fig. 39

Prodr. 15, 1: 370 (1864). — *Scheidweileria* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 123, lectotype species (Barkley & Baranov, 1972): *Scheidweileria muricata* (Scheidw.) Klotzsch = *B. pentaphylla* Walp. (homotypic synonym).

Plants terrestrial, with upright stems; tubers absent; stem woody (at least at base); tubercles in leaf axil absent; stipules early caducous, dentate; junction petiole and leaf blade without or with a tuft of hairs. **Leaves** alternate, more than 2, not peltate, usually palmately compound or rarely palmately lobed (*B. parviflora*); indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial at base and monochasial at apex, bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts caducous. **Flower** with 2 bracteoles spaced from the base of the ovary; perianth segments white or pink, outer ones rounded at apex. *Male flower* with 4 free perianth segments; androecium actinomorphic, filaments unequal, free (but on a low 'torus'), anthers circular to oblong, about as long as or shorter than the filaments, dehiscent with unilaterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective extended. *Female flower* with 5 free perianth segments; ovary or fruit with 3 wings, wings usually equal or subequal or rarely unequal in fruit (*B. semidigitata*), not hook- or spine-like, locules 3, placentation axillary, placental branches 1 per



Brade del. 1943.

Fig. 39. Sect. *Scheidweilera*. *B. semidigitata* — 1, flowering stem (flowers not drawn); 2, female perianth segments; 3, style; 4, stipule; 5, outer side of perianth segment; 6, fruit; 7, ovary in transverse section; 8, seed. Reproduced from Brade (1945): est. 4

locule; styles 3, free, forked once, eventually caducous in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, without or with an indistinct beak.

DISTRIBUTION: America: Brazil, one species from Colombia to Bolivia.

LEAF ANATOMY: Stomata single; hypoderm on the upper side only; astrosclereids and cystoliths present (*B. digitata*, *B. incisoserrata*, *B. luxurians*, *B. parviflora*, *B. pentaphylla*).

SEED MICROMORPHOLOGY: Seed ellipsoid (length/width ratio 1.8) to narrowly elliptic (length/width ratio 2.3); mean length from 315 µm in *B. parviflora* to 640 µm in *B. pentaphylla*; anticlinal walls straight; testa cells of chalaza deep; chalaza flattened on one side.

CHROMOSOMES: $2n = 56$ (*B. incisoserrata*, *B. luxurians*).

TAXONOMIC COMMENTS: *Scheidweilera* is very close to *Pritzelia*, especially to the species formerly brought to *Ewaldia*, e.g. *B. lobata*, but differs in the compound leaves (although those of *B. parviflora* are only lobed), the anthers which are shorter or about as long as the filaments and the seeds with flattened chalazal ends.

SPECIES LIST: 6 species: *B. digitata* Raddi, *B. incisoserrata* A. DC., *B. luxurians* Scheidw., *B. parviflora* Poepp. & Endl., *B. pentaphylla* Walp., *B. semidigitata* Brade.

sect. **Scutobegonia** Warb.

Fig. 40

in Engl. & Prantl, Die Natürl. Pflanzenfam. (ed. 1) 3, 6a: 140 (1894), type species: *B. lacunosa* Warb.

Begonia sect. *Scutobegonia* series *Brevicaules* Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenwelt Afr. 3, 2: 616 (1921), lectotype species (Sosef, 1994): *B. hirsutula* Hook. f.

Begonia sect. *Scutobegonia* series *Euscutatae* Engl. l.c. 617 p.p.

Plants terrestrial, perennial, rhizomatous; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire or dentate; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight to transverse, symmetric or asymmetric, peltate or not, simple; venation palmate or palmate-

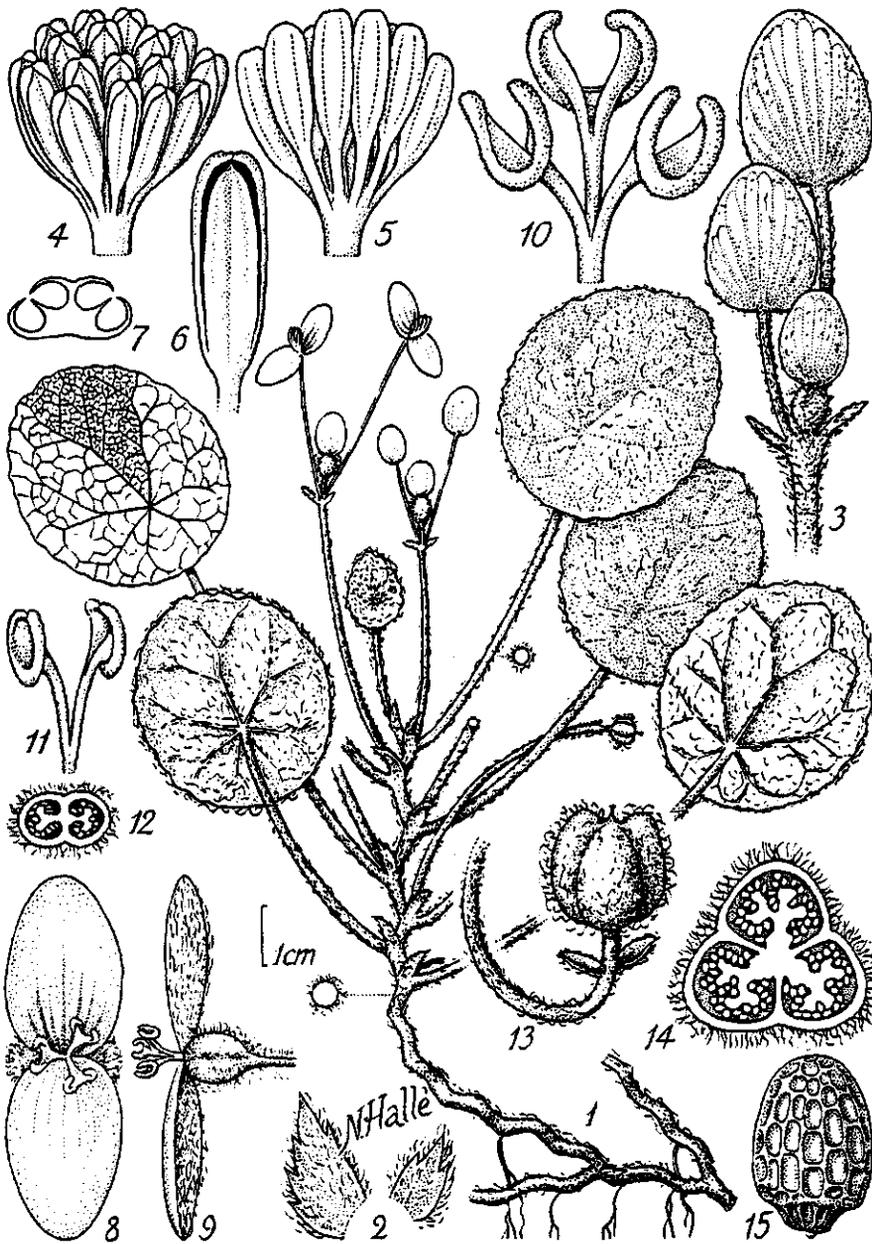


Fig. 40. Sect. *Scutobegonia*. *B. ferramica* — 1, plant habit; 2, stipules; 3, young inflorescence; 4-5 androecium in frontal and dorsal view; 6, stamen; 7, anther in transverse section; 8-9, female flower; 10, styles; 11 & 12, styles and ovary in transverse section of aberrant 2-locular ovary; 13, fruit; 14, ovary in transverse section; 15, seed. Reproduced from Hallé (1967): p. 510, pl. 2.

pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, monochasial, bisexual, protandrous, usually with 1 female flower (rarely aberrantly up to 3), the central flower of the cyme male, lateral flower(s) female; inflorescence axes strongly reduced; bracts persistent (during flowering). **Flower** without bracteoles; perianth segments yellow, white or pink, outer ones rounded at apex. *Male flower* with 2 free perianth segments; androecium zygomorphic, filaments unequal, fused below, anthers oblong, longer than to about as long as the filaments, dehiscent with unilaterally positioned longitudinal slits (more than 0.5 of the anther length), apex hooded, connective not extended. *Female flower* with 2 free perianth segments; ovary or fruit usually with 3 or 4 wings or rarely wingless, wings equal or subequal in fruit, not hook- or spine-like, locules 3 or 4 (rarely aberrantly 2), placentation axillary, placental branches 1 per locule (though often tree-like branched); styles (2-)3-4, fused less than halfway, forked once, caducous in fruit, stigma usually not kidney-shaped or rarely kidney-shaped, usually in a band and spiralled or rarely not spiralled. **Fruit** not berry-like, not dehiscent, usually recurved towards the substrate, usually without or with an indistinct or rarely with a distinct beak.

DISTRIBUTION: Africa: from Ivory Coast east to eastern Dem. Rep. Congo, south to the border between Dem. Rep. Congo and Angola.

LEAF ANATOMY: Stomata single; hypoderm absent; no cystoliths (see Sosef, 1994).

SEED MICROMORPHOLOGY: Seeds ellipsoid, 275-390 x 155-230 μm , length/width ratio 1.3-1.9; ratio collar to seed length 1:2.3-2.9; longitudinal anticlinal walls straight to strongly undulate; operculum broadly nipple-shaped to obtusate; anticlinal boundaries with cross hatching; cuticular ornamentation prominent, often composed of a double structure of star-shaped or zigzag foldings on a labyrinth-like structure.

IMPORTANT LITERATURE: Sosef (1994).

TAXONOMIC COMMENTS: Closely related to sect. *Loasibegonia* A. DC., for distinguishing characters see under that section.

SPECIES LIST: 21 species: *B. aggeloptera* N. Hallé, *B. anisosepala* Hook. f., *B. ciliobracteata* Warb., *B. clypeifolia* Hook. f., *B. dewildei* Sosef, *B. erectocaulis* Sosef, *B. erectotricha* Sosef, *B. ferramica* N. Hallé, *B. hirsutula* Hook. f., *B. lacunosa* Warb., *B. laportefolia* Warb., *B. mbangaensis* Sosef, *B. mildbraedii* Gilg, *B. peperomioides* Hook. f., *B. scutulium* Hook. f., *B. susaniae* Sosef, *B. vankerckhovenii* De Wild., *B. vittariifolia* N. Hallé, *B. wilksii* Sosef, *B. zairensis* Sosef, *B. zenkeriana* L.B. Smith & Wasshausen.

sect. **Semibegoniella** (C. DC.) Barkley & Baranov

Fig. 41

Buxtonian 1, Suppl. 1: 7 (1972) — *Semibegoniella* C. DC., Bull. Herb. Boiss. 2, 8: 307 (1908), lectotype species (Barkley & Baranov, 1972): *Semibegoniella sodiroi* C. DC. = *B. longirostris* Benth. (heterotypic synonym).

Begoniella Oliv., Trans. Linn. Soc. 28: 513 (1873), type species: *Begoniella whitei* Oliv. = *B. oliveri* L.B. Smith & Schubert.

Casparya sect. *Andiphila* A. DC., Ann. Sci. Nat., Bot. 4, 11: 116 (1859) p.p.

Plants terrestrial, perennial, with upright stems; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight, asymmetric, not peltate, simple; venation pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, cymose (also racemose?), usually bisexual or rarely separate male and female, with male flowers basal and female flowers distal, protandrous; bisexual inflorescence monochasial; male inflorescence dichasial; female inflorescences 1(–2?)-flowered; inflorescence axes not reduced; bracts persistent (during flowering) or caducous. **Flower** without or with 2 (caducous) bracteoles inserted directly below the ovary; perianth segments white, pink or red, outer ones rounded or acute at apex. *Male flower* with 4 free or partially fused perianth segments; stamens 4 or 6, filaments equal or unequal, free or fused below, anthers circular to oblong, shorter than or longer than the filaments, dehiscent with unilaterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective extended or not. *Female flower* with 4(–6) free or partially fused perianth segments; ovary or fruit with 3 wings, wings equal or subequal in fruit, developed into hooks, locules 3, placental branches 1 per locule; styles 3, fused less than halfway, forked more than once, caducous in fruit. **Fruit** not berry-like, dehiscent at the back of the carpels (through the wings), more or less erect, usually with a

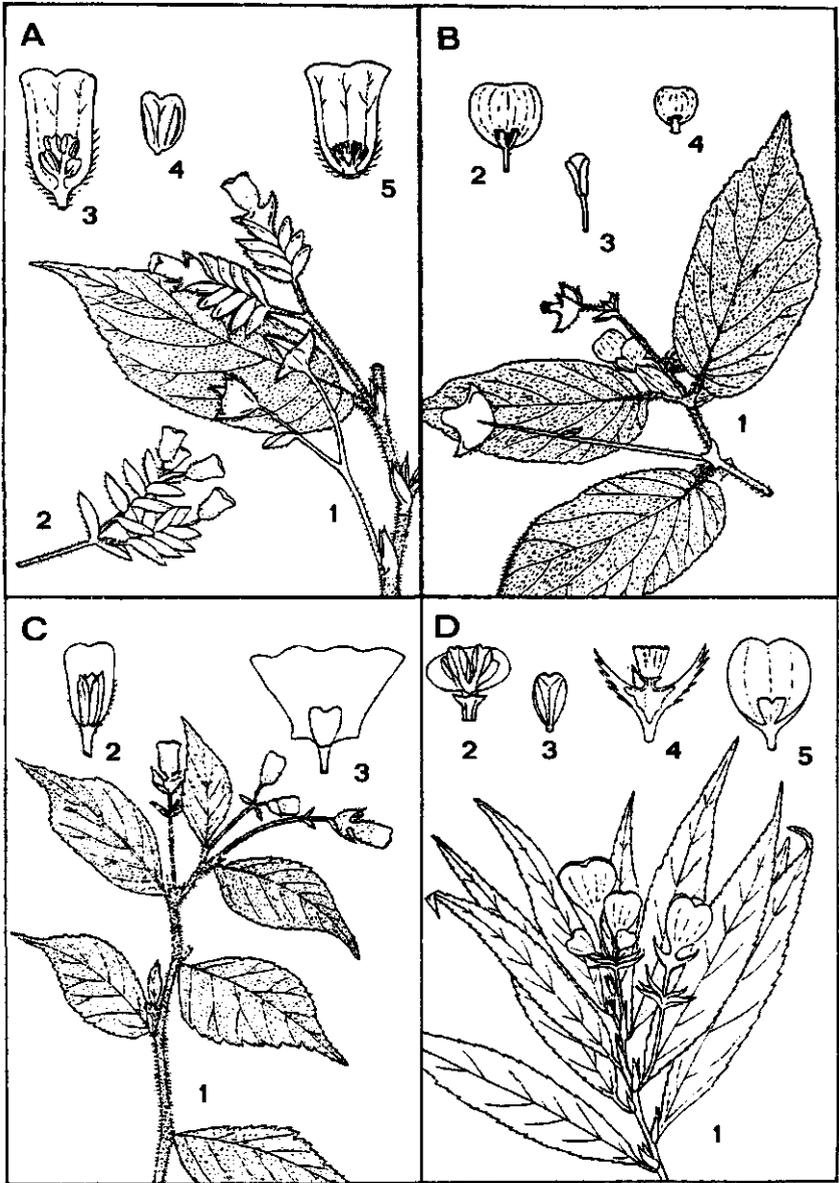


Fig. 41. Sect. *Semibegoniella*. A: *B. oliveri* — 1, flowering stem; 2, inflorescence; 3, opened male flower; 4, stamen; 5, opened female flower. B: *B. libera* — 1, fertile stem; 2, opened male flower; 3, stamen; 4, opened female flower. C: *B. kalbreyeri* — 1, flowering stem; 2, opened male flower; 3, opened female flower showing inner perianth. D: *B. irmscheri* — 1, flowering stem; 2, opened male flower; 3, stamen; 4, fruit; 5, opened female flower showing inner perianth. Reproduced from Smith & Schubert (1946): p. 207, tab. 18.

distinct or rarely without or with an indistinct beak (*B. oliveri*).

DISTRIBUTION: America: from Colombia to Peru.

LEAF ANATOMY: Epidermal cells collenchymatous; stomata in groups; hypoderm absent; cystoliths absent (*B. longirostris*).

SEED MICROMORPHOLOGY: Seed ellipsoid with a flattened micropylar end; length about 600 μm , width about 300 μm ; anticlinal walls strongly undulated; cuticular pattern consisting of undulating striae (*B. longirostris*).

TAXONOMIC COMMENTS: Taken together, *Casparya* and *Semibegoniella* are quite distinct from the other sections of *Begonia*, but to separate the two is less easy. One reason is that the data are insufficient. As yet, the placentae of ten species of *Semibegoniella* are unknown; should any of these turn out to have bifid placentae this species probably has to be moved to *Casparya*. The placentae of *B. valvata* are 'bicornutis'. On the basis of the available evidence an additional difference between section *Casparya* and *Semibegoniella* is that in *Casparya* there are numerous stamens, but in *Semibegoniella* there are only 4 or 6 (4 short and 2 longer ones). The inflorescences of the species of *Semibegoniella* show a similar wide range of variation as those of *Casparya* (see there). In four species the inflorescence is covered by densely imbricate, apparently distichous bracts, which hide its structure.

SPECIES LIST: 13 species: *B. hexandra* Irmscher, *B. holmnielseniana* L.B. Smith & Wasshausen, *B. irmscheri* L.B. Smith & Schubert, *B. kalbreyeri* (Oliv.) L.B. Smith & Schubert, *B. killipiana* L.B. Smith & Schubert, *B. lehmannii* (Irmscher) L.B. Smith & Schubert, *B. libera* (L.B. Smith & Schubert) L.B. Smith & Schubert, *B. longirostris* Benth., *B. napoensis* L.B. Smith & Wasshausen, *B. oliveri* L.B. Smith & Schubert, *B. pectennervia* L.B. Smith & Wasshausen, *B. tetrandra* Irmscher, *B. valvata* L.B. Smith & Schubert.

sect. **Sexalaria** A. DC.

Fig. 42

Ann. Sci. Nat., Sér. 4 (Bot.) 11, 2: 127 (1859), type species: *B. annobonensis* A. DC.



Fig. 42. Sect. *Sexalaria*. *B. annobonensis* — 1, flowering stem; 2, upper leaf surface; 3, leaf margin with indumentum; 4, tuft of hairs on junction petiole and leaf blade; 5, male flower; 6, ditto, outer perianth segment, lateral view; 7-8, stamens frontal and lateral view; 9, female flower; 10, stigmas; 11, ovary in transverse section; 12-16, fruits from various collections, schematic frontal views added; 17, branch with dehisced fruits; 18, seed; 19-20, small already fruiting plants. Drawing by Miss Ike Zewald.

Plants terrestrial, annual, with upright stems; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules early caducous, entire; junction petiole and leaf blade with a tuft of hairs. **Leaves** alternate, more than 2, oblique, asymmetric, not peltate, simple; venation palmate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial at base and monochasial at apex, bisexual, protandrous, with up to 8 female flowers, the central flower of the cyme male, lateral flower(s) female; inflorescence axes not reduced; bracts caducous. **Flower** with 2 bracteoles; perianth segments white or pink, outer ones rounded at apex. *Male flower* with 4 free perianth segments; androecium actinomorphic, filaments unequal, free, anthers oblong, longer than or about as long as the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective not extended. *Female flower* with (4-)5-6 free perianth segments; ovary or fruit with 3-6(-7) wings, wings unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles 3, fused less than halfway, 2-lobed, persistent in fruit, stigma almost kidney-shaped, all over the style. **Fruit** not berry-like, dehiscent near the back of the locules, more or less erect, without or with an indistinct beak.

DISTRIBUTION: Africa: coastal Cameroon, Principe, São Tomé, Pagalú (Annobon), not known from Bioko.

SEED MICROMORPHOLOGY: Seeds ellipsoid, 370-430 x 235-250 μm , length/width ratio 1.6; collar cells elongate, ratio collar to seed length 1:2.4; anticlinal walls straight or slightly curved; operculum nipple-shaped; anticlinal boundaries flat; collar and testa cells with a short, undulating and striate to granular cuticular structure.

CHROMOSOMES: $2n = 22$.

IMPORTANT LITERATURE: de Wilde (1985a).

TAXONOMIC COMMENTS: The decision to merge sect. *Sexalaria* (1859) with sect. *Rostrobegonia* (1895) and possibly also with sect. *Augustia* (1864) is still pending. The chromosome number in combination with the shape of the styles, and the distribution of the stigmatic tissue, may present features to maintain the monotypic sect.

Sexalaria.

SPECIES LIST: A single species: *B. annobonensis* A. DC.

sect. *Solananthera* A. DC.

Fig. 43

Ann. Sci. Nat., Bot. 4, 11: 128 (1859), lectotype species (Barkley & Baranov, 1972): *B. solananthera* A. DC.

Plants terrestrial, perennial, lianescent (scandent); tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent or early caducous, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight, symmetric, not peltate, simple; venation palmate-pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial, bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts caducous. **Flower** without or with 2 bracteoles spaced from the base of the ovary; perianth segments usually white or pink or rarely red (*B. radicans* in cultivation), rounded at apex. *Male flower* with 4 free perianth segments; androecium actinomorphic, filaments equal, fused below (into a short column), anthers oblong to linear, longer than the filaments, dehiscent with unilaterally positioned apical pores or short pore-like slits (less than 0.5 of the anther length), apex \pm hooded, connective slightly extended. *Female flower* with 5 free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 2 per locule, ovules absent between placental branches; styles 3, free, forked once, caducous in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, more or less erect (?), without or with an indistinct beak.

DISTRIBUTION: America: eastern Brazil.

LEAF ANATOMY: Stomata single; hypoderm absent; no cystoliths.

SEED MICROMORPHOLOGY: Seeds comparatively long (755–1060 μm) and slender, length/width ratio 5.2–6.2; chalazal end extended; cuticular pattern consisting of long undulating striae.

CHROMOSOMES: $2n = 56$ (*B. radicans*, *B. solananthera*).



Fig. 43. Sect. *Solananchera*. *B. radicans* — 1, flowering stem; 2, perianth segments of female flower; 3, ovary; 4, ovary in transverse section; 5, style; 6, fruit; 7, seed; 8, perianth segments of male flower; 9, androecium; 10, stamen. Reproduced from Brade (1944): est. 3.

IMPORTANT LITERATURE: Irmscher (1953a).

SPECIES LIST: 3 species: *B. integerrima* Spreng., *B. radicans* Vell., *B. solananthera* A. DC.

sect. *Sphenanthera* (Hassk.) Warb.

Fig. 44

in Engl. & Prantl, Die Natürl. Pflanzenfam. (ed. 1) 3, 6a: 141 (1894). — *Sphenanthera* Hassk., Versl. Akad. Wetensch. Amsterdam 4: 139 (1855). — *Casparya* sect. *Sphenanthera* (Hassk.) A. DC., Ann. Sci. Nat., Bot. 4, 11: 118 (1859), type species: *Sphenanthera robusta* (Blume) Hassk. ex Klotzsch = *B. robusta* Blume (homotypic synonym).

Casparya sect. *Holoclinium* A. DC., Ann. Sci. Nat., Bot. 4, 11: 118 (1859). — *Begonia* sect. *Holoclinium* (A. DC.) Warb. in Engl. & Prantl, Die Natürl. Pflanzenfam. (ed. 1) 3, 6a: 142 (1894), type species: *Casparya trisulcata* A. DC. = *B. trisulcata* (A. DC.) Warb. (homotypic synonym).

Casparya sect. *Polyschisma* A. DC., Ann. Sci. Nat., Bot. 4, 11: 119 (1859). — *Begonia* sect. *Polyschisma* (A. DC.) Warb., in Engl. & Prantl, Die Natürl. Pflanzenfam. (ed. 1) 3, 6a: 149 (1894), type species: *Casparya crassicaulis* A. DC. = *B. crassicaulis* (A. DC.) Warb. non Lindl. = *B. pachyrhachys* L.B. Smith & Wasshausen (homotypic synonym).

Plants terrestrial, perennial, rhizomatous or with upright stems; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent or early caducous, entire; junction petiole and leaf blade usually without or rarely with a tuft of hairs (*B. robusta*). **Leaves** alternate, more than 2, oblique to transverse or rarely straight (\pm 3 species), asymmetric, not peltate, usually simple or rarely palmatifid (*B. obovoidea*); venation palmate or palmate-pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, cymose, usually bisexual or rarely separate male and female (these species all dioecious), with male flowers basal and female flowers distal, protandrous; bisexual and male inflorescence dichasial or dichasial at base and monochasial at apex; female inflorescence monochasial or consisting of solitary flowers; inflorescence with the central flower of the cyme male, lateral flower(s) female; inflorescence axes strongly reduced or not (but usually shorter than the petiole); bracts persistent (during flowering) or caducous. **Flower** usually without or rarely with 1 or 2 bracteoles (*B. renifolia*) spaced from the base of the ovary; perianth segments white or pink. *Male flower* with 4 free perianth segments; androecium actinomorphic, filaments free or fused below, anthers oblong (or linear), usually longer than the filaments, dehiscent with laterally positioned longitudinal slits (more

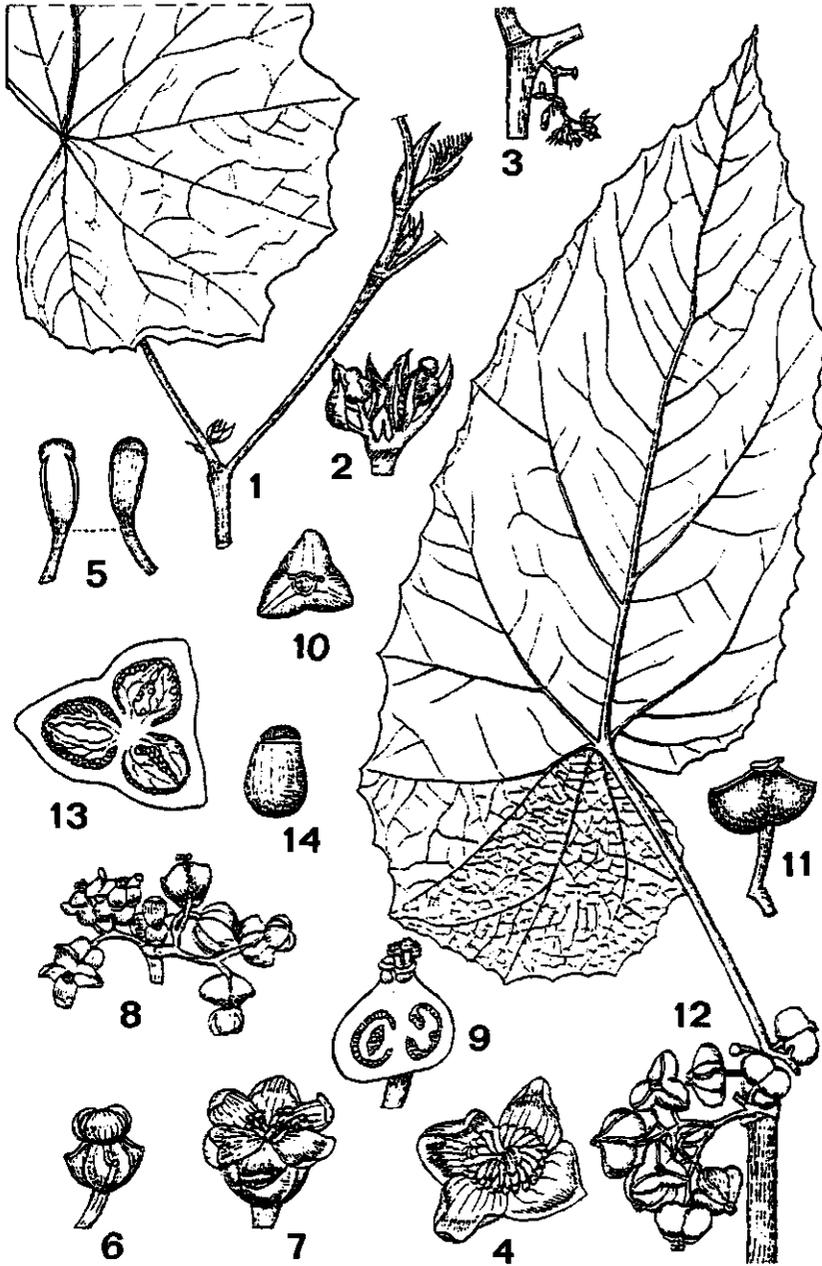


Fig. 44. Sect. *Sphenanthera*. *B. cristata* — 1-3, stem with young inflorescences; 4, male flower; 5, stamens; 6-8, female flowers; 9, ovary in longitudinal section; 10-12 fruits; 13, fruit in transverse section; 14, seed. Reproduced from Koorders (1922): pl. 93.

than 0.5 of the anther length), connective extended. *Female flower* with usually 4 or rarely 5 (*B. robusta*, *B. multangula*) or 6 (*B. hayatae*, *B. cristata*, *B. crassirostris*) free perianth segments; ovary or fruit usually wingless or with 3 or 4 wings or rarely with 2 wings (*B. burkillii* has 2 horns), wings when present usually equal or subequal or rarely unequal in fruit (*B. robusta*), usually developed into hooks or rarely not hook- or spine-like, locules 3 or 4, placentation axillary, placental branches usually 2 or rarely 4 per locule (*B. tetragona*), ovules present between placental branches; styles (2-)3-4, fused less than halfway, usually forked once or rarely more than once (*B. tetragona*), persistent or caducous in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** berry-like or not (but always fleshy), not or irregularly dehiscent, more or less erect or pendulous or rarely nodding (*B. robusta*), usually without or with an indistinct or rarely with a distinct beak (*B. crassirostris*).

DISTRIBUTION: Asia: from India to the Himalayas, Indo-China, China, Taiwan and Malesia east to the Moluccas.

LEAF ANATOMY: Stomata single; hypoderm absent (but present on upper side in *B. silletensis*); no cystoliths (5 species studied).

CHROMOSOMES: $2n = 22$ (*B. roxburghii*); $2n = 88$ (possibly in *B. robusta*).

TAXONOMIC COMMENTS: Hasskarl erected the genus *Sphenanthera* for *Begonia robusta*, which therefore is the type species. Unfortunately, it differs rather strikingly from other species in the section: the peduncle is erect and longer than the petiole of the supporting leaf, and the fruit has 3 very unequal wings, the longest sometimes reaching 2 cm. In fact, if it did not have a 3-locular ovary, one would not hesitate to put *B. robusta* in *Platycentrum*. Fruits with reduced wings are characteristic for *Sphenanthera* and have led authors to place species into it on the strength of this quality alone, where they differed strikingly in other features. These species have been transferred to *Diploclinium* and *Petermannia*.

SPECIES LIST: 26 species: *B. aborensis* Dunn, *B. acetosella* Craib, *B. aptera* Blume, *B. burkillii* Dunn, *B. crassirostris* Irmscher, *B. cristata* Warb. ex Koord., *B. handelii* Irmscher, *B. hayatae* Gagnep., *B. heteroclinis* Miq. ex Koord., *B. inflata* C.B. Clarke, *B. longifolia*

Blume, *B. multangula* Blume, *B. obovoidea* Craib, *B. pachyrhachis* L.B. Smith & Wasshausen, *B. prostrata* Irmscher, *B. pseudolateralis* Warb., *B. renifolia* Irmscher, *B. robusta* Blume, *B. roxburghii* A. DC., *B. sarcocarpa* Ridley, *B. silletensis* (A. DC.) C.B. Clarke, *B. tessaricarpa* C.B. Clarke, *B. tetragona* Irmscher, *B. tricornis* Ridley, *B. trigonocarpa* Ridley, *B. turbinata* Ridley.

Species whose membership is doubtful: 1 species: *B. trisulcata* (A. DC.) Warb.

sect. **Squamibegonia** Warb.

Fig. 45

in Engl., Die Natürl. Pflanzenfam. (ed. 1) 3, 6a: 139 (1894), type species: *B. ampla* Hook. f.

Plants epiphytic, perennial, with upright stems; tubers absent; stem woody (at least at base); tubercles in leaf axil absent; stipules early caducous, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight or oblique, usually asymmetric or rarely symmetric, not peltate, simple to palmately lobed; venation palmate; indumentum of scales and stellate hairs present. **Inflorescence** axillary, usually dichasial at base and monochasial at apex or rarely monochasial, bisexual, with male flowers basal and female flowers distal, protandrous, rarely with 1 to usually up to 8 female flowers, the central flower of the cyme male, lateral flower(s) female; inflorescence axes strongly reduced; bracts persistent (even in fruit). **Flower** without bracteoles; perianth segments white or pink, outer ones rounded at apex. *Male flower* with 2 free perianth segments; androecium zygomorphic, filaments unequal, fused below, anthers obovate or oblong, longer than the filaments, dehiscent with unilaterally positioned longitudinal slits (more than 0.5 of the anther length), apex hooded, connective not extended. *Female flower* with 2 partially fused perianth segments; ovary or fruit wingless, locules 4(-5), placentation axillary, placental branches 2 per locule, ovules absent between placental branches; styles 4(-5), fused less than halfway, forked once, usually caducous or rarely persistent in fruit, stigma not kidney-shaped, all over the style (but a spiralled band with longer stigmatic papillae present). **Fruit** berry-like, not dehiscent, more or less erect, without or with an indistinct beak.

DISTRIBUTION: Africa: east of the Dahomey-gap; from Nigeria

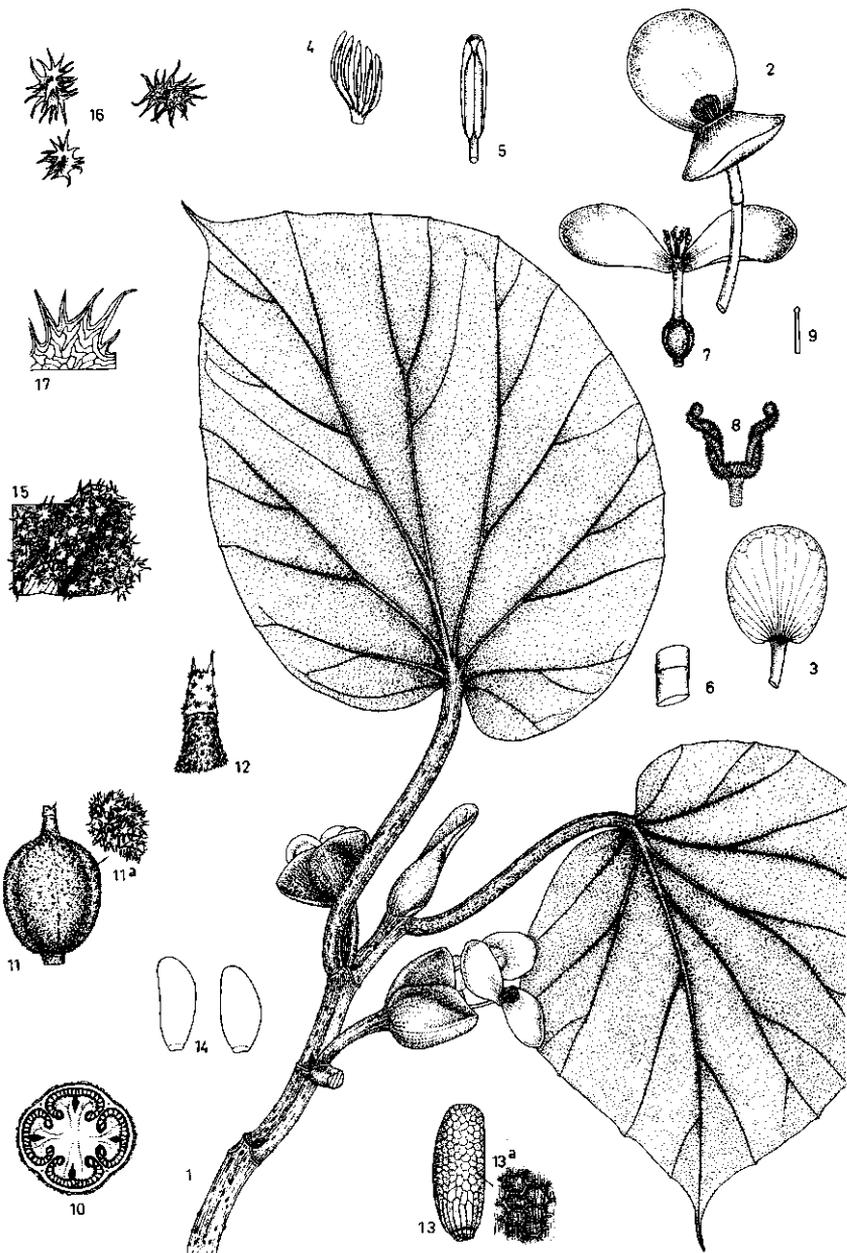


Fig. 45. Sect. *Squamibegonia*. *B. ampla* — 1, flowering stem; 2, male flower; 3, perianth segment of male flower; 4, androecium; 5, stamen; 6, female flower; 7, style; 8, ovary in transverse section; 9, mature fruit with indumentum; 10, seed with detail of testa; 11, detail of lower leaf surface; 12, various stellate scales; 13, detail of stellate scale. Drawing by Miss Ike Zewald.

through central Africa east to Uganda, Rwanda, Burundi and Tanzania, south to Angola, also on the islands in the Gulf of Guinea.

LEAF ANATOMY: Sessile, globose, multicellular, whitish or brownish black trichomes (Meyensche Perldrüsen) sometimes present on the stipules.

SEED MICROMORPHOLOGY: Seeds ellipsoid to narrowly ellipsoid, 670–780 x 275–315 µm, length/width ratio 2.4; ratio collar to seed length 1:4.6; anticlinal walls of collar cells almost straight, those of testa cells straight to curved; testa cells in irregular rows; operculum obtusate; cuticle not ornamented.

CHROMOSOMES: $2n = 36-40$ (45).

IMPORTANT LITERATURE: Bouman & de Lange (1982), de Wilde & Arends (1980).

TAXONOMIC COMMENTS: 1. Additional characters: In female flowers a distinct perianth tube is always present between the apex of the ovary and the base of the free perianth segments. 2. Endozoochorous long-distance seed dispersal is presented as the explanation for the occurrence of *B. ampla* on Principe, São Tomé and Pagalú (Annobon).

SPECIES LIST: 3 species: *B. ampla* Hook. f., *B. bonus-henricus* J.J. de Wilde, *B. poculifera* Hook. f.

sect. **Tetrachia** Brade

Fig. 46

Rodriguesia 18: 21 (1945), type species: *B. quadrilocularis* Brade = *B. egregia* N.E. Brown (heterotypic synonym).

Plants terrestrial, perennial, with upright stems; tubers absent; stem woody (at least at base); tubercles in leaf axil absent; stipules early caducous, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight, asymmetric, peltate (always?, marginally), simple; venation pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial, bisexual, with male flowers basal and female flowers distal, protandrous, with the central flower of the cyme male, lateral

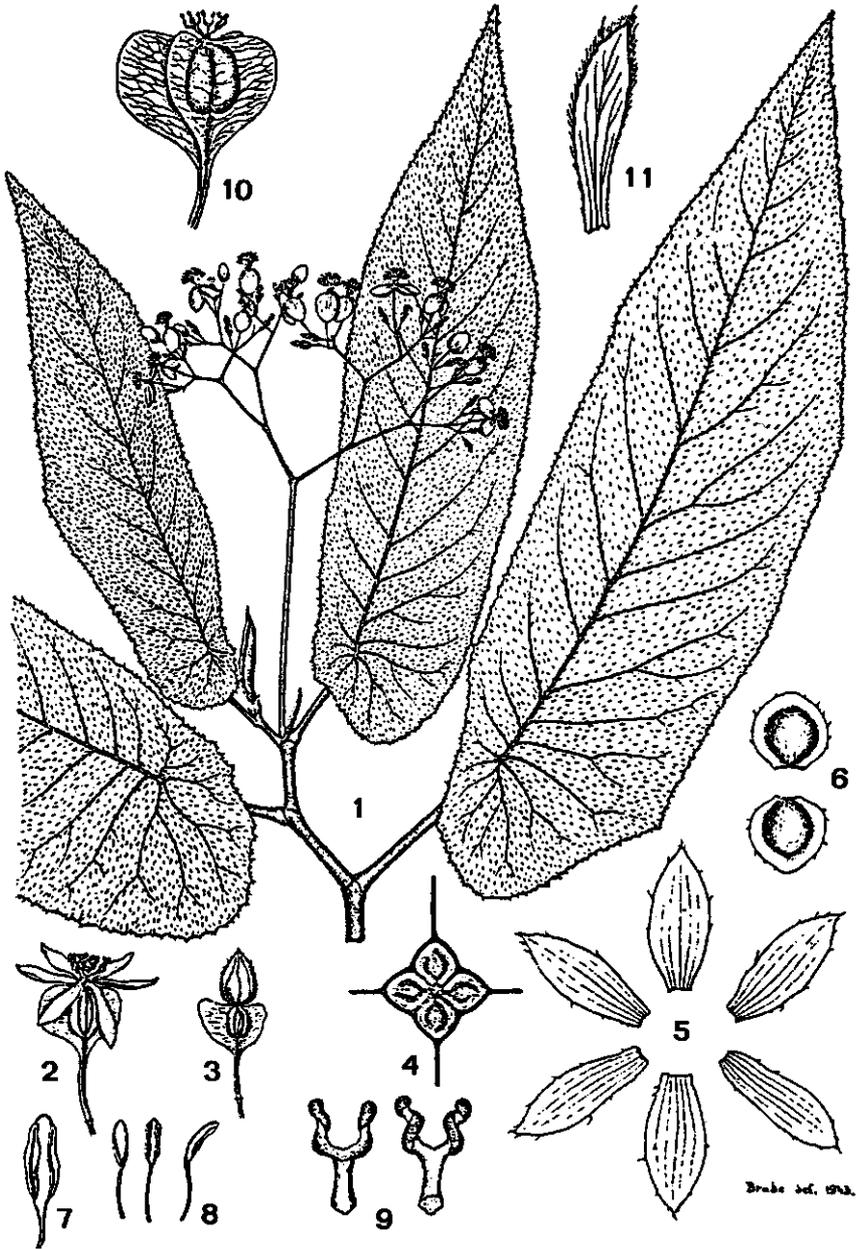


Fig. 46. Sect. *Tetrachia*. *B. egregia* — 1, flowering stem; 2, female flower; 3, young female flower; 4, ovary in transverse section; 5, perianth segments of female flower; 6, perianth segments of male flower; 7-8, stamens; 9, styles; 10, fruit; 11, stipule. Reproduced from Brade (1945): est. 6.

flower(s) female; inflorescence axes not reduced; bracts caducous. **Flower** with 2 bracteoles spaced from the base of the ovary; perianth segments white or pink, outer ones rounded at apex (male flowers) or acute at apex (female flowers). *Male flower* with 2 free perianth segments; androecium zygomorphic, filaments equal, free, anthers oblong to lanceolate, shorter than the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective not extended. *Female flower* with 6 free perianth segments; ovary or fruit with 4 wings, wings equal or subequal in fruit, not hook- or spine-like, locules 4, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles 4, free, forked once, persistent in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, without a beak.

DISTRIBUTION: America: eastern Brazil.

SEED MICROMORPHOLOGY: Seeds ellipsoid; mean measurements 530 x 275 μm ; collar cells 190 μm ; no distinguishing characters.

CHROMOSOMES: $2n =$ possibly 52.

SPECIES LIST: A single species: *B. egregia* N.E. Br.

sect. **Tetraphila** A. DC.

Fig. 47

Prodr. 15, 1: 517 (1864), type species: *B. mannii* Hook.

Begonia sect. *Fusibegonia* Warb. in Engl., Die Natürl. Pflanzenfam. (ed. 1) 3, 6a: 141 (1894), lectotype species (Barkley & Baranov, 1972): *B. eminii* Warb.

Begonia sect. *Fusibegonia* series *Subaequilaterales* Engl. in Engl. & Drude, Veg. der Erde 9, Die Pflanzenw. Afr. 3, 2: 618 (1921), lectotype species (here designated): *B. polygonoides* Hook. f.

Begonia sect. *Fusibegonia* series *Inaequilaterales* Engl. in Engl. & Drude, l.c.: 620 (1921), lectotype species (here designated): *B. eminii* Warb.

Begonia sect. *Irmshera* Ziesenh., The Begonian 38, 7: 161 (1971), type species: *B. mauricei* Ziesenh. = *B. loranthoides* Hook. f. subsp. *loranthoides* (heterotypic synonym).

Plants usually epiphytic or rarely terrestrial, perennial, rhizomatous or with upright stems; tubers absent; stem herbaceous or woody (at least at base); tubercles in leaf axil absent; stipules persistent or early caducous, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight or

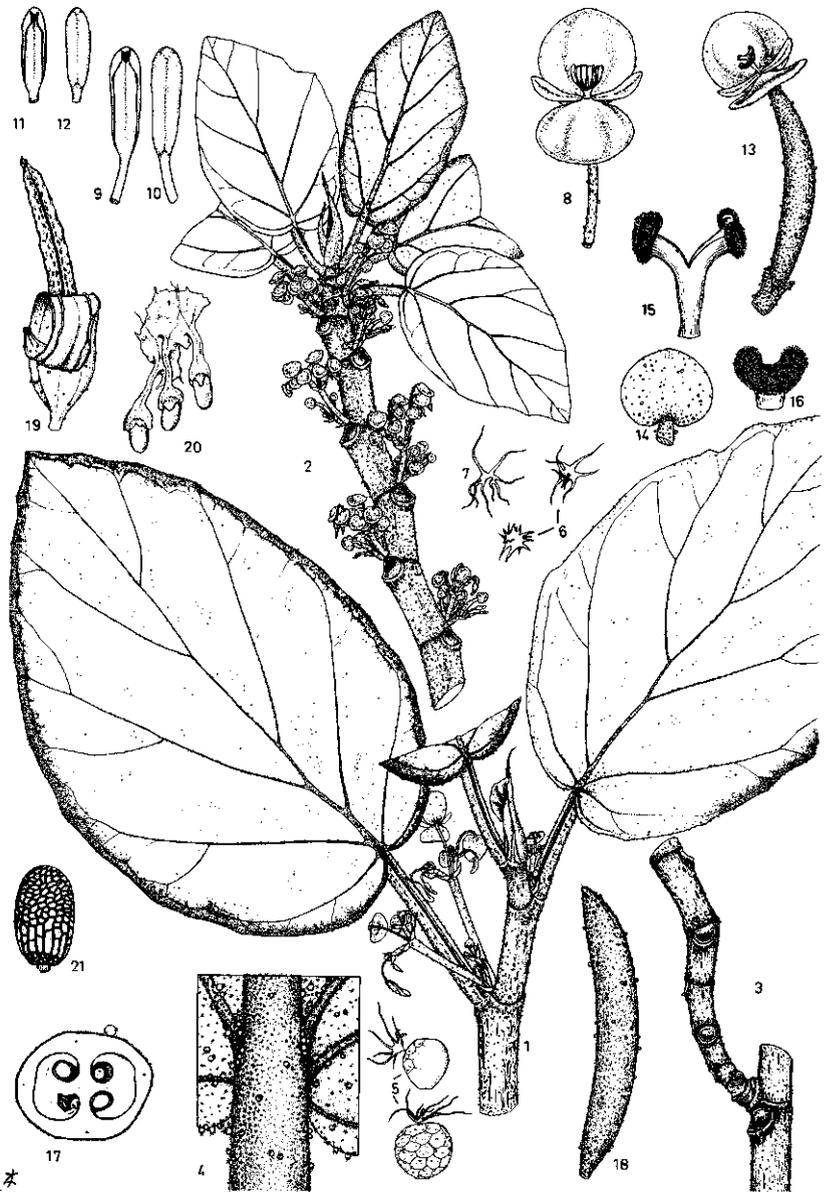


Fig. 47. Sect. *Tetraphila*. *B. cavallyensis* — 1, stem with male inflorescences; 2, stem with male and female inflorescences; 3, old stem with scars of fallen leaves and stipules; 4, detail of lower leaf surface; 5, spherical trichomes bearing a stellate scale; 6-7, stellate scales; 8, male flower; 9-12, stamens in frontal and dorsal view; 13, female flower; 14, perianth segment of female flower; 15, styles; 16, stigma; 17, ovary in transverse section (about halfway up); 18, young fruit; 19, dehiscent fruit; 20, placenta bearing mature seeds; 21, seed. Drawing by Miss Ike Zewald.

oblique, symmetric or asymmetric, usually not peltate or rarely peltate, simple (sometimes distinctly sinuate); venation palmate-pinnate to pinnate or rarely palmate; indumentum of scales (often stellately shaped) present, stellate hairs absent. **Inflorescence** axillary, cymose, bisexual or separate male and female or rarely bisexual and male or bisexual and female, with male flowers basal and female flowers distal, protandrous; bisexual inflorescence dichasial or dichasial at base and monochasial at apex; male inflorescence dichasial at base and monochasial at apex; female inflorescence dichasial or dichasial at base and monochasial at apex or consisting of solitary flowers; inflorescence with (1–)3 or more than 3 female flowers, in bisexual inflorescences the central flower of the cyme male, lateral flower(s) female; inflorescence axes usually strongly reduced or rarely not reduced; bracts usually caducous or rarely persistent (during flowering). **Flower** without bracteoles; perianth segments usually white or pink or rarely red, outer ones rounded at apex. *Male flower* with 4 free perianth segments; androecium actinomorphic or zygomorphic, filaments usually unequal or rarely equal, usually fused below or rarely free or entirely fused, anthers obovate or oblong, longer than to shorter than the filaments, dehiscent with unilaterally positioned usually longitudinal slits (more than 0.5 of the anther length) or rarely short pore-like slits (less than 0.5 of the anther length), apex hooded or not, connective usually not extended or rarely extended. *Female flower* with usually 4 or rarely 2 free perianth segments; ovary or fruit wingless, locules 2–4(–5), placentation parietal or septal or rarely axillary, placental branches 2 per locule, ovules present between placental branches; styles 2–4(–6), usually fused less than halfway or rarely more than halfway, simple or 2-lobed or forked once, usually caducous in fruit or rarely persistent in fruit, stigma usually not kidney-shaped or rarely kidney-shaped, in a band and spiralled or not or contracted near the style apex. **Fruit** berry-like, usually dehiscent near the back of the locules or rarely irregularly dehiscent, more or less erect, usually without or with an indistinct beak or rarely with a distinct beak.

DISTRIBUTION: Africa: from Guinea and Sierra Leone through tropical Africa east to Tanzania and south to Angola.

LEAF ANATOMY: Stomata in groups; hypoderm present; no cystoliths (4 species studied; also Arends, 1992).

SEED MICROMORPHOLOGY: Seeds ellipsoid to narrowly ellipsoid,

500–2100 μm long, arillate; anticlinal walls often thick, cuticle without ornamentation.

CHROMOSOMES: $2n = (34), 36\text{--}39, 71\text{--}76$. The latter numbers are considered as tetraploid. Some species contain tetraploid chromosomal races morphologically almost indistinguishable from the diploid ones (see Arends, 1992).

IMPORTANT LITERATURE: Arends (1992), de Wilde (in prep.).

TAXONOMIC COMMENTS: The fleshy fruits are often brightly coloured, white, pink, or red, and are dehiscent. At dehiscence the fleshy seed-bearing orange to yellow placenta tissue becomes exposed and seed dispersal is most probably endozoochorous by birds. Wild bees visiting male flowers have been observed and are assumed to act as a vector in deceit pollination by which the pistils of the female flowers mimic the androecium.

SPECIES LIST: 28 species: *B. capillipes* Gilg, *B. cavallyensis* A. Chev., *B. ebolowensis* Engl., *B. elaeagnifolia* Hook. f., *B. eminii* Warb., *B. furfuracea* Hook. f., *B. fusialata* Warb., *B. fusicarpa* Irmscher, *B. horticola* Irmscher, *B. karperi* J.C. Arends, *B. kisuluana* Büttn., *B. komoensis* Irmscher, *B. longipetiolata* Gilg, *B. loranthoides* Hook. f., *B. mannii* Hook., *B. molleri* Warb., *B. oxyanthera* Warb., *B. pelargoniiflora* J.J. de Wilde & J.C. Arends, *B. polygonoides* Hook. f., *B. preussii* Warb., *B. rubromarginata* Gilg, *B. rubronervata* De Wild., *B. rwandensis* J.C. Arends, *B. squamulosa* Hook. f., *B. subalpestris* A. Chev., *B. subscutata* De Wild., *B. tatoniana* R. Wilczek, *B. zimmermannii* Peter ex Irmscher.

sect. **Trachelocarpus** (C. Müller) A. DC.

Fig. 48

in Martius, Fl. Bras. 4 (1): 381 (1861). — *Trachelocarpus* C. Müller in Walp., Ann. Bot. 4: 909 (1857), type species: *Trachelocarpus rhizocarpus* C. Müller = *B. depauperata* Schott (heterotypic synonym).

Trachelanthus Klotzsch, Abh. Akad. Berlin '1854': 202 (1855), non *Trachelanthus* G. Kunze (Boraginaceae), lectotype species (Barkley & Baranov, 1972): *Trachelanthus rhizocarpus* Klotzsch = *B. depauperata* Schott (heterotypic synonym).

Plants epiphytic, perennial, rhizomatous; tubers absent; tubercles in leaf axil absent; stipules persistent, dentate; junction

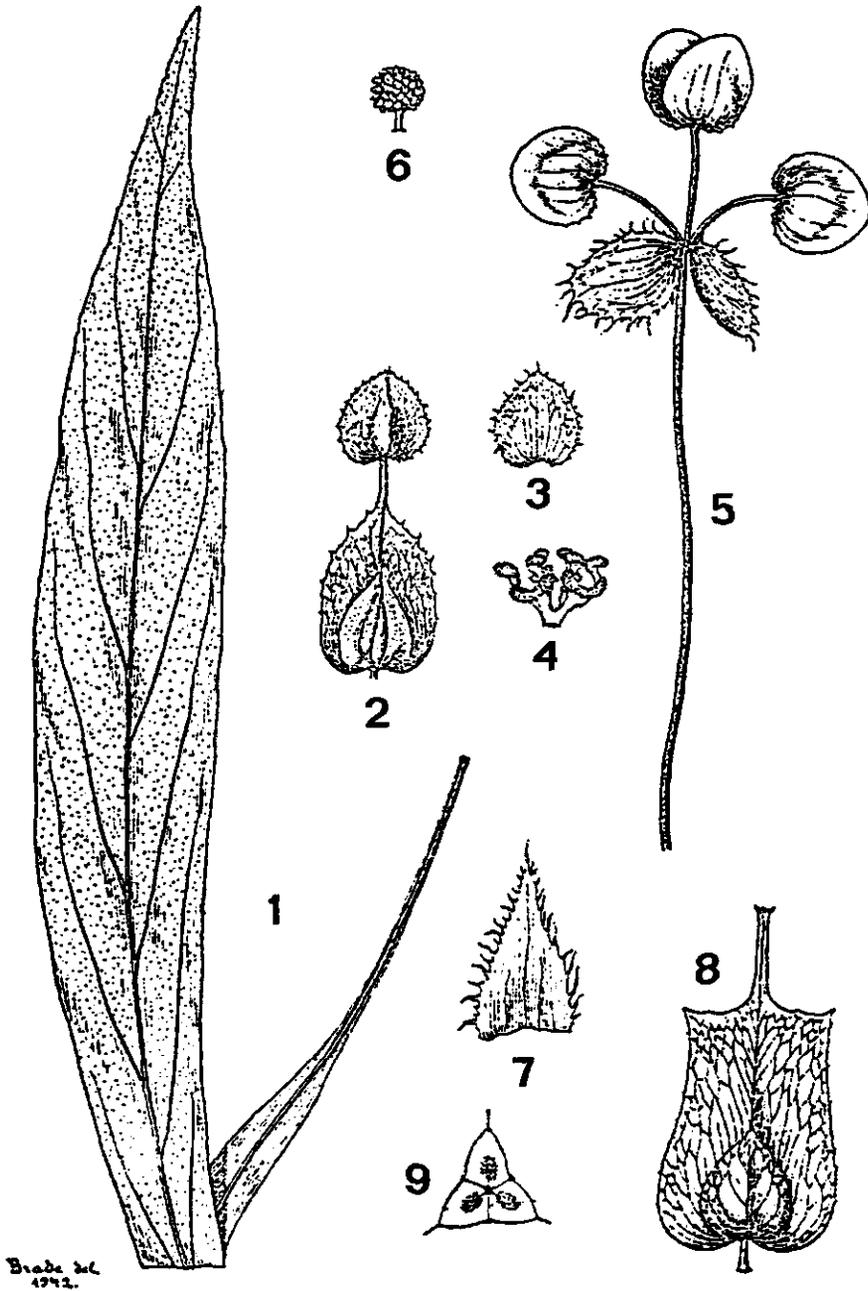


Fig. 48. Sect. *Trachelocarpus*. *B. angraensis* — 1, leaf; 2, female flower; 3, perianth segment of female flower; 4, styles; 5, inflorescence with male flowers; 6, androecium; 7, stipule; 8, fruit; 9, ovary in transverse section. Reproduced from Brade (1943): est. 2.

petiole and leaf blade without a tuft of hairs. **Leaves** whorled, more than 2, straight, symmetric, not peltate, simple; venation pinnate; indumentum of scales or stellate hairs absent (the indumentum consists of pearl-glands: 'Meyenschen Perldrüsen'). **Inflorescence** axillary, separate male and female; male inflorescence dichasial; female inflorescence consisting of solitary flowers; inflorescence axes strongly reduced; bracts persistent (during flowering). **Flower** without bracteoles; perianth segments white or pink, outer ones rounded (in male flowers) or acute at apex (in female flowers). *Male flower* with 2 free perianth segments; androecium actinomorphic, filaments equal, entirely fused (into a column), anthers obovate, dehiscent with laterally positioned short pore-like slits (less than 0.5 of the anther length), apex not hooded, connective extended. *Female flower* with 3 free perianth segments; ovary or fruit with 3 wings, wings equal or subequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 1 per locule; styles 3, fused less than to about halfway, forked once, caducous in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, dehiscent by curved splits at both sides of the septae, more or less erect, with a distinct beak.

DISTRIBUTION: America: eastern Brazil.

LEAF ANATOMY: Stomata single; hypoderm absent, but Barkley & Hozid (The Begonian 38: 135–142, 1971) picture a well-developed hypoderm in *B. herbacea*; no cystoliths (*B. depauperata*, *B. herbacea*, *B. lanceolata*).

SEED MICROMORPHOLOGY: Seeds ellipsoid to narrowly ellipsoid, comparatively large (300 x 320 µm to 1030 x 410 µm); operculum obtuse, composed of many small cells; cuticula shows a net-like structure of erect or folding-over pleats.

CHROMOSOMES: $2n = 56$ (*B. fulvo-setulosa*, *B. herbacea*, *B. lanceolata*, *B. velloziana*).

IMPORTANT LITERATURE: Irmischer (1953a).

TAXONOMIC COMMENTS: Descriptions of some of the older species are either inadequate or based on fragmentary material. This has given rise to nomenclatural problems which have not all been solved

in a satisfactory way. Closer study will probably reveal that the number of species can be reduced, possibly even drastically.

SPECIES LIST: 6 species: *B. angraensis* Brade, *B. depauperata* Schott, *B. fulvo-setulosa* Brade, *B. herbacea* Vell., *B. lanceolata* Vell., *B. velloziana* Walp.

sect. **Trendelenburgia** (Klotzsch) A. DC.

Fig. 49

in Martius, Fl. Bras. 4 (1): 377 (1861). — *Trendelenburgia* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 123 (1854), type species: *Trendelenburgia fruticosa* Klotzsch = *B. fruticosa* (Klotzsch) A. DC.

Plants terrestrial, perennial, with upright stems (\pm scandent); tubers absent; stem woody (at least at base); tubercles in leaf axil absent; stipules persistent, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight, symmetric, not peltate, simple; venation pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial at base and monochasial at apex (?), bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts persistent (during flowering). **Flower** with 2 bracteoles spaced from the base of the ovary; perianth segments white or pink, outer ones rounded at apex (?). *Male flower* with 4 free perianth segments; androecium actinomorphic, filaments equal, free, anthers oblong, about as long as the filaments, dehiscent with laterally positioned apical slits (less than 0.5 of the anther length), apex not hooded, connective extended. *Female flower* with 4–6 free perianth segments; ovary or fruit with 3 narrow wings, wings equal or subequal in fruit, not hook- or spine-like, locules 3, placentation axillary, placental branches 1 per locule; styles 3, free, forked once, persistent in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, without or with an indistinct beak.

DISTRIBUTION: America: eastern Brazil.

LEAF ANATOMY: Stomata in groups; hypoderm present on both sides; astrosclereids present; cystoliths small, brown.

SEED MICROMORPHOLOGY: Seeds with a mean length of 1450 μm and mean width of 180 μm , the most slender seed found so far in



Fig. 49. Sect. *Trendelenburgia*. *B. fruticosa* — 1, flowering stem; 2, stamen; 3, female flower; 4, fruit. Reproduced from Smith & Smith (1971): p. 19, est. 4.

Begonia; micropylar and chalazal end composed of blown-up air-filled cells; anticlinal walls undulating; cuticle faintly pitted.

TAXONOMIC COMMENTS: So far, a single species with the habit of a *Lepsia* but differing in distribution (*Lepsia* is confined to the Andean region), anthers which open with pore-like apical slits and characteristic seeds.

SPECIES LIST: A single species: *B. fruticosa* A. DC.

sect. **Urniformia** Houghton ex Ziesenh.

Fig. 50

The Begonian 41: 12 (1974), type species: *B. pittieri* C. DC. = *B. heydei* C. DC. (heterotypic synonym).

Plants epiphytic, perennial, with upright stems; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules early caducous, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, straight, asymmetric, not peltate, simple; venation palmate-pinnate; indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial, bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts persistent (during flowering). **Flower** with 2 bracteoles spaced from the base of the ovary; perianth segments white or pink, outer ones acute at apex. *Male flower* with 4 free perianth segments; androecium actinomorphic, filaments unequal, fused below (into a column), anthers obovate, about as long as the filaments, dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective slightly extended. *Female flower* with 3 free perianth segments; ovary or fruit with 3 wings, wings equal or subequal in fruit, developed into hooks (or horns), locules 3, placentation axillary, placental branches 1 per locule; styles 3, fused less than halfway, forked once, caducous in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, the horns splitting at the base when ripe (C. DC.).

DISTRIBUTION: America: Central America.

LEAF ANATOMY: Cystoliths absent.

SEED MICROMORPHOLOGY: Seeds ellipsoid, mean measurements

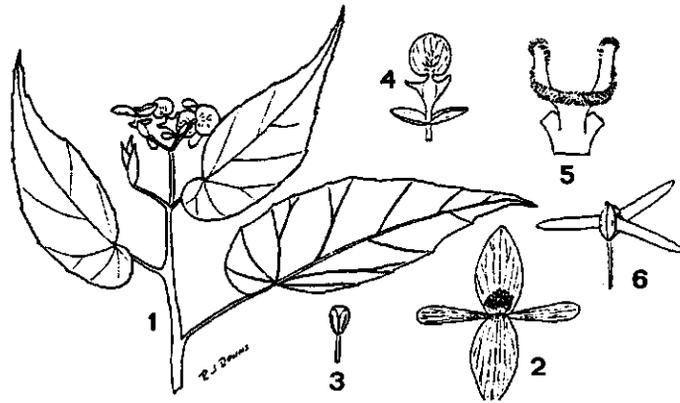


Fig. 50. Sect. *Urniformia*. *B. heydei* — 1, flowering stem; 2, male flower; 3, stamen; 4, female flower and bracteoles; 5, style; 6, fruit. Reproduced from Smith & Schubert (1961): p. 172, fig. 24.

585 x 280 μm ; collar cells 205 μm long. The only neotropical species having seeds with a smooth cuticle.

CHROMOSOMES: $2n =$ probably 28.

TAXONOMIC COMMENTS: Casimir de Candolle put *B. pittieri* and *B. triloba* (synonyms of *B. heydei*) in *Casparya* on account of the horned wings, but it is not known yet if the fruits dehisce in a way similar to *Casparya* as well.

SPECIES LIST: A single species: *B. heydei* C. DC.

sect. **Wagneria** (Klotzsch) A. DC.

Fig. 51

Ann. Sci. Nat., Bot. 4, 11: 137 (1859). — *Wagneria* Klotzsch, Monatsber. Kön. Preuss. Akad. Wiss. Berlin 1854: 126 (1854), lectotype species (Barkley & Baranov, 1972): *Wagneria fagifolia* (Fischer ex Otto & Dietr.) Klotzsch = *B. fagifolia* Fischer ex Otto & Dietr. (homotypic synonym).

Begonia sect. *Enita* Brade, Rodriguesia 32: 160 (1957), type species: *B. convolvulacea* (Klotzsch) A. DC.

Plants terrestrial, perennial, lianescent (or scandent); tubers absent; stem woody (at least at base); tubercles in leaf axil absent; stipules usually persistent or rarely early caducous (*B. aeranthos*), entire; junction petiole and leaf blade without a tuft of hairs. **Leaves**

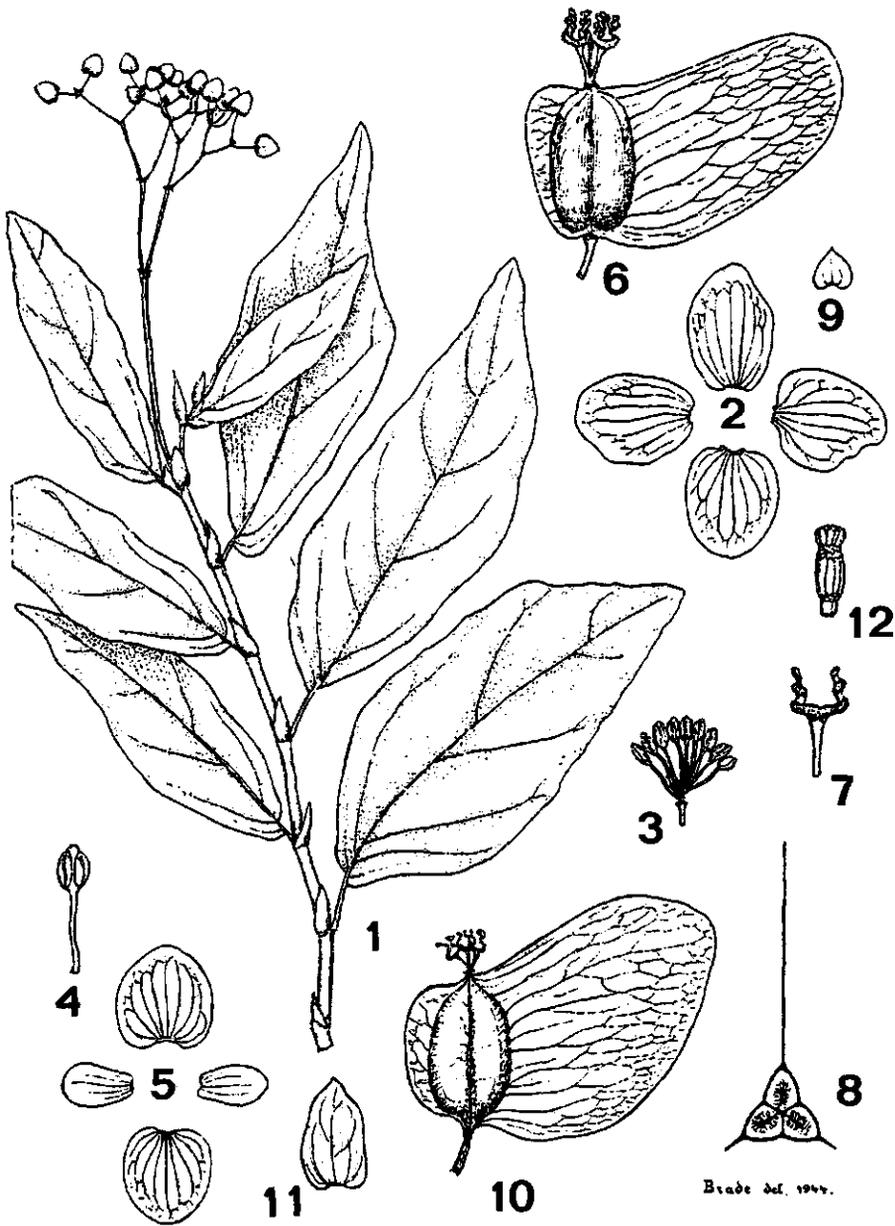


Fig. 51. Sect. *Wageneria*. *B. inconspicua* — 1, flowering stem; 2, perianth segments of male flower; 3, androecium; 4, stamen; 5, perianth segments of female flower; 6, ovary and styles; 7, style; 8, ovary in transverse section; 9, bracteole of female flower; 10, fruit; 11, stipule; 12, seed. Reproduced from Brade (1945): p. 31, est. 4.

alternate, more than 2, straight, symmetric, usually not peltate or rarely peltate (subpeltate in *B. aeranthos*), simple; venation usually pinnate or rarely palmate (*B. convolvulacea*); indumentum of scales or stellate hairs absent. **Inflorescence** axillary, dichasial at base and monochasial at apex, bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced; bracts usually persistent (during flowering) or rarely caducous (*B. polygonifolia*). **Flower** with 2 bracteoles spaced from the base of the ovary; perianth segments white or pink, outer ones rounded or occasionally acute at apex (in female flowers only). *Male flower* with 4 free perianth segments; androecium actinomorphic, filaments equal, free (rarely fused below in *B. inconspicua*?), anthers oblong or rarely ovate (*B. inconspicua*), usually longer than or rarely shorter than the filaments (*B. inconspicua*), dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective usually not extended or rarely extended (*B. inconspicua*). *Female flower* with 5 free perianth segments; ovary or fruit with 3 wings, wings unequal in fruit (usually 2 marginal), not hook- or spine-like, locules 3, placentation axillary, placental branches 1 per locule; styles 3, free, forked once, persistent in fruit, stigma not kidney-shaped, in a band and spiralled. **Fruit** not berry-like, without or with an indistinct beak.

DISTRIBUTION: America: throughout Central and South America except for the Guianas.

LEAF ANATOMY: Stomata single and in pairs and hypoderm present only at the upper side (*B. convolvulacea*, *B. epibaterium*), or stomata in groups and hypoderm present on both sides (*B. fagifolia*, *B. glabra*, *B. polygonifolia*); cystoliths present.

SEED MICROMORPHOLOGY: Seeds with mean measurements of 495 x 170 μm (*B. epibaterium*) to 675 x 195 μm (*B. convolvulacea*); cells at the micropylar and/or chalazal ends inflated, forming a 'crown'; collar and other testa cells elongated.

CHROMOSOMES: $2n = 38$ (*B. glabra*, *B. fagifolia*, *B. convolvulacea*).

TAXONOMIC COMMENTS: When Klotzsch described the genus *Wageria* in 1854 he distinguished no less than 16 species. Seven of

these are still recognised and of these three are shrubs or small trees and the other four are scandent. The latter are also characterized by their seeds. Alphonse de Candolle maintained *Wagneria* as a section of *Begonia*, but Warburg and later Irmscher incorporated it in the section *Pritzelia*. In 1945, Brade suggested that the scandent species merited a separate section which he called *Enita*, and described in 1957. At that time he mentioned only one species, *B. convolvulacea*, which automatically became the type species of the new section. Barkley & Baranov (1972) indicated *B. fagifolia*, a similar scandent species, as the lectotype of *Wagneria*, and proceeded to put *Wagneria* as a synonym under *Enita*. Owing to this rather unfortunate choice of a lectotype, however, the name *Enita* has to give way to the older *Wagneria*. The three non-scandent species remain in *Pritzelia*.

SPECIES LIST: 8 species: *B. aeranthos* L.B. Smith & Schubert, *B. convolvulacea* (Klotzsch) A. DC., *B. epibaterium* Mart. ex A. DC., *B. fagifolia* Fisch. ex Otto & Dietr., *B. glabra* Aubl., *B. inconspicua* Brade, *B. polygonifolia* A. DC., *B. smilacina* A. DC.

sect. **Warburgina** O. Kuntze

Rev. Gen. 3, 2: 105 (1893), type species: *B. comata* O. Kuntze.

Plants terrestrial, perennial, with upright stems; tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules persistent. **Leaves** more than 2, asymmetric, not peltate, simple; venation pinnate. **Inflorescence** cymose (?), separate male and female (?); bracts persistent (during flowering). **Flower** with 3 bracteoles inserted on the ovary; perianth segments white or pink, outer ones rounded at apex. *Male flower* with 2 free perianth segments; filaments unequal, free, anthers oblong. *Female flower* with 4 perianth segments; ovary or fruit with 3 wings, wings unequal in fruit, not hook- or spine-like, locules 3, placental branches 2 per locule, ovules present between placental branches; styles fused less than halfway, forked once, stigma in a band and spiralled. **Fruit** not berry-like.

DISTRIBUTION: America: Bolivia.

LEAF ANATOMY: Cystoliths present.

SEED MICROMORPHOLOGY: Seeds ellipsoid to narrowly ellipsoid; mean size 420 x 120 µm; testa cells somewhat elongated, with strongly undulated walls.

TAXONOMIC COMMENTS: *Warburgina* has much in common with *Ruizopavonia*, but is maintained here because of the peculiar inflorescence. There may also be a difference in habit.

SPECIES LIST: A single species: *B. comata* O. Kuntze.

sect. **Weilbachia** (Klotzsch & Oersted ex Klotzsch) A. DC. **Fig. 52**

Ann. Sci. Nat., Bot. 4, 11: 134 (1859). — *Weilbachia* Klotzsch & Oersted ex Klotzsch, Abh. Akad. Berlin '1854': 240 (1855), lectotype species (Barkley & Baranov, 1972): *Weilbachia reptans* Klotzsch = *B. ludicra* A. DC. (heterotypic synonym), see notes.

Begonia sect. *Liebmannia* Ziesenh., The Begonian 43: 64 (1976), type species: *B. alice-clarkiae* Ziesenh.

Plants terrestrial, perennial, usually rhizomatous or rarely with upright stems (*B. alice-clarkiae*, *B. purpusii*); tubers absent; stem herbaceous; tubercles in leaf axil absent; stipules usually persistent or rarely early caducous, entire; junction petiole and leaf blade without a tuft of hairs. **Leaves** alternate, more than 2, usually oblique, usually asymmetric or rarely symmetric (*B. francisiae*, *B. reptans*), usually not peltate or rarely peltate, usually simple or occasionally palmately lobed; venation usually palmate or rarely palmate-pinnate (*B. aridicaulis*, *B. reptans*); indumentum of scales or stellate hairs absent. **Inflorescence** axillary, monochasial or dichasial at base and monochasial at apex, bisexual, with male flowers basal and female flowers distal, protandrous; inflorescence axes not reduced (?); bracts usually caducous or rarely persistent (during flowering; *B. lynceorum*). **Flower** usually without or rarely with 2 bracteoles (*B. davidsoniae*) spaced from the base of the ovary; perianth segments white or pink, outer ones rounded at apex. *Male flower* with 2 or 4 free perianth segments; androecium zygomorphic, filaments unequal, free (rarely fused below?), anthers obovate or oblong, usually longer than or rarely shorter than the filaments (*B. davidsoniae*), dehiscent with laterally positioned longitudinal slits (more than 0.5 of the anther length), apex not hooded, connective extended. *Female flower* with 2(–4) (3 in *B. pustulata* and *B. trichosepala*, 4 in *B. davidsoniae*) free perianth segments; ovary or fruit with 1 or 3 wing(s), wings

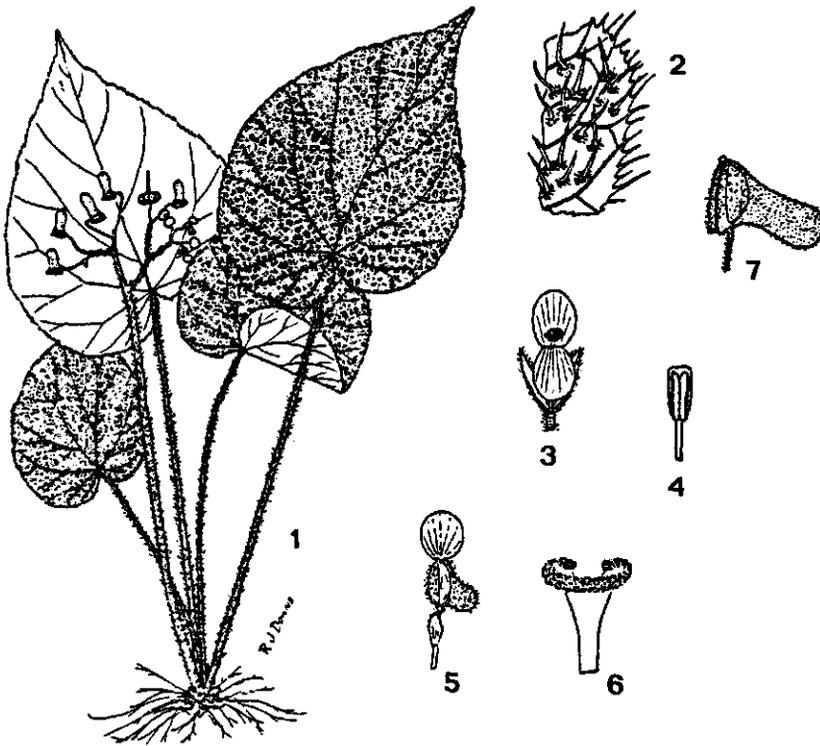


Fig. 52. Sect. *Weilbachia*. *B. pustulata* — 1, plant habit; 2, detail of upper leaf surface; 3, male flower and bracteoles; 4, stamen; 5, female flower and bracteoles; 6, style; 7, fruit. Reproduced from Smith & Schubert (1961): p. 180, fig. 27.

unequal in fruit, not hook- or spine-like, locules 2, placentation axillary, placental branches 2 per locule, ovules present between placental branches; styles (2-)3, usually fused more than or rarely less than halfway (*B. assurgens*), 2-lobed, stigma kidney-shaped, usually in a band and not spiralled or rarely spiralled (*B. davidsoniae*). **Fruit** not berry-like, dehiscent near the back of the locules, nodding, without or with an indistinct beak.

DISTRIBUTION: America: Central America.

LEAF ANATOMY: Stomata single; hypoderm absent; cystoliths absent (*B. imperialis*, *B. ludicra*, *B. pustulata*, *B. violifolia*). According to Neubauer (1967), *B. mexicana* has stomata in groups of 1-3(-4) and a 1-layered hypoderm on both sides of the leaf. Another indication that *B. mexicana* is of hybrid origin?

SEED MICROMORPHOLOGY: Seeds ellipsoid; mean size from 320 x 195 μm in *B. aridicaulis* to 415 x 215 μm in *B. pustulata* (6 species examined). The seeds confirm to the ordinary type.

CHROMOSOMES: $2n = 28$ (*B. alice-clarkiae*, *B. aridicaulis*, *B. imperialis*, *B. ludicra*, *B. purpusii*, *B. violifolia*).

TAXONOMIC COMMENTS: The genus *Weilbachia* was erected for two species: *W. pustulata* and *W. reptans*. Baranov & Barkley (1972) appointed the latter as the lectotype, but equalled it, like Klotzsch had done, with *Begonia reptans* Benth. A. DC. had already pointed out in 1864, however, that *W. reptans* Klotzsch was not *B. reptans* Benth. and called the former species *B. liebmannii* A. DC. In 1961 Smith & Schubert showed that this taxon is synonymous with *B. ludicra* A. DC. Although it shows many *Weilbachia* characters, *B. alice-clarkiae* was put into a separate section by its author because the stems are upright, not rhizomatous as in the other species. Other sections, e.g. *Gireoudia*, also accommodate both upright and rhizomatous species, so that there seems to be as yet no reason to follow Ziesenhennes example. *Weilbachia* is very close to *Gireoudia*, differing mainly in the 2-locular instead of 3-locular ovary. In addition, many species of *Weilbachia* have long, rather thin, stolon-like rhizomes. Based on this character a number of species have been classified in *Weilbachia*, although the ovaries have not yet been described: *B. brevicyma*, *B. confusa*, *B. copeyana*, *B. davidsoniae*, *B. popenoei* and *B. reptans*. Should the ovary of any of these turn out to be 3-locular, the species concerned may have to be moved to *Gireoudia*.

Begonia acutiloba was described by Liebmann from male material. Nearly a century later Smith & Schubert (1946) thought they had found a female specimen, which they described. This seems to be a *Weilbachia* (the number of locules is not mentioned). Burt-Utley (1985), however, doubts if the male and female specimens belong to the same species.

B. mexicana was collected by G.H.H. Karsten in Mexico in 1894. He is cited as the author, but a description by his hand could not be traced. The first publication of the species was by Fotsch in 1938; a much better description is that of Irmscher in Parey's *Blumengartneri* (1960). He puts it in the section *Weilbachia*. In view of the sterile flowers we consider it to be a hybrid.

SPECIES LIST: 14 species: *B. acutiloba* Liebm., *B. alice-clarkiae*

Ziesenh., *B. aridicaulis* Ziesenh., *B. assurgens* Irmscher apud Weberling, *B. calderonii* Standley, *B. fimbriata* Liebm., *B. francisiae* Ziesenh., *B. imperialis* Lem., *B. ludicra* A. DC., *B. lyniceorum* K. Burt-Utley, *B. mexicana* Karst. ex Fotsch, *B. purpusii* Houghton ex Ziesenh., *B. pustulata* Liebm., *B. violifolia* A. DC.

Species whose membership is doubtful: 9 species: *B. brevicyma* C. DC., *B. carletonii* Standley, *B. confusa* L.B. Smith & Schubert, *B. copeyana* C. DC., *B. davidsoniae* Standley ex L.B. Smith & Schubert, *B. popenoei* Standley, *B. reptans* Benth., *B. trichosepala* C. DC., *B. valerioi* Standley.

7 Species not attributable to any existing section

B. amphioxus Sands from Sabah has the habit of an erect *Petermannia* species, the male inflorescences being dichasial, the female flowers solitary. It differs in the lanceolate, peltate leaves, the female flowers with 3-4(-5), often more or less united perianth segments and 2-locular fruits with 2 subequal wings. Its author puts it in *Platycentrum* on account of the 2-celled fruit but in this section the fruit always has 1 long and 2 short wings, and the inflorescences are bisexual.

B. angilogensis Merr. is apparently rather large and scandent. This, in combination with the 2-locular fruits with 2 wings, 1 up to 25 mm, the other up to 4 mm wide, set it apart from any of the known sections. The flowers are unknown, the placentae have not yet been described.

B. antaisaka Humbert and the very similar *B. tanala* Humbert could be fitted into sect. *Augustia* except for their almost symmetric leaves with pinnate venation and elongated fruits, and their occurrence on Madagascar from which no 'true' *Augustia* species have been recorded to date. Moreover, their seed type is clearly aberrant from that of sect. *Augustia*. The seeds perfectly fit those of the Malagasy section *Erminea* from which the two species differ however in their erect stems, equal wings and different shape of the fruit.

B. archboldiana Merr. & L.M. Perry is very similar to, if not conspecific with, *B. physandra*. See the comments on that species.

B. balansana Gagnep. has the habit and flowers of a rhizomatous

Reichenheimia species, but is strikingly different in its fruits which have 5-7 locules and no wings but 5-7 horns. The dehiscence of the fruit has not yet been described.

- B. boisi* Gagnep. could be regarded as a caulescent species of *Reichenheimia* but there is no other species in this section of similar habit and leaf shape. It differs from *Petermannia* in the protandrous inflorescence and the undivided placentae. If one does not know its Asian origin one could presume it belongs to the Neotropical section *Pritzelia*, but it differs in the lunate stigmas and the chromosome number ($2n = 30$).
- B. chuniana* Wu from Hainan was initially interpreted by Chun & Chun as *B. handelii* Irmischer from the Chinese-Vietnamese border; their picture is reproduced by L.B. Smith et al. (1986: plate 26.6). The species appears to have male and female flowers in separate inflorescences. The male inflorescences are cymose with strongly reduced axes. Male and female flowers have 4 tepals; the fruit is bilocular with 2 wings. Wu classifies it in *Platycentrum* where it obviously does not belong.
- B. floribunda* Ku was classified by its author in *Platycentrum*, probably on account of the 2-locular ovary, but is very different in its peltate leaves, peduncles shorter than the petioles with up to 5 or 6 dichasial branchings, and the very small flowers with 2 perianth segments in the male as well as in the female flowers.
- B. herteri* Irmischer is a dwarf tuberous begonia with yellow flowers. The characteristics are consistent with section *Begonia*, in which section it was provisionally placed by Irmischer, but as he already remarked, habit and flower colour set it apart.
- B. hoehniana* Irmischer is a creeping species with \pm kidney-shaped leaves on long petioles, characterised in particular by its anthers which spread out from the top of a long column. On account of its entire placentae Irmischer placed it in *Pritzelia* but noted its isolated position in this section.
- B. humillima* L.B. Smith & Wasshausen is a very distinct species from Venezuela with creeping stems, bullate leaves, racemose male and uniflorous female inflorescences, male flowers with 4 perianth segments, anthers on a column, female flowers with 5 perianth segments, placentae entire.
- B. iucunda* Irmischer from Congo (Brazzaville) and the Dem. Rep. Congo was placed by its author in section *Scutobegonia* because of its male and female flowers with 2 yellow perianth segments. The upright plants carry small tubers, solitary axillary flowers,

a zygomorphic androecium, 3 forked styles with spiralled stigmatic tissue, more or less erect fruits with 3 unequal wings. The seeds are reminiscent of those of sect. *Filicibegonia*, but deviate in several characteristics. The species presumably takes up an isolated position in the affinity of sect. *Filicibegonia*.

- B. lecomtei* Gagnep. has the habit of a rhizomatous *Diploclinium* but with 4 male and 2 female perianth segments, linear anthers with the connective 1 mm extended, 4 free styles with lyrate, contorted stigmas and a 4-locular ovary.
- B. leptophylla* Taubert is a dwarf species with tuberous rhizomes, thin stems, straight, orbicular leaves without cystoliths and entire placentae. Taubert suggests it might belong to section *Pritzelia*, but this is not very convincing.
- B. malabarica* Lamk non A. DC. (*B. fallax* A. DC.) is very similar in habit to *B. dipetala* of section *Haagea* but has 4 male and 3 female perianth segments and bifid placentae. A. DC. classified it in section *Trilobaria*, later incorporated in *Diploclinium*, but it looks out of place in this section, if only because of its shrubby habit.
- B. militaris* L.B. Smith & Schubert is placed by its authors in section *Begonia* on account of the number of perianth segments (4 male and 5 female) but in view of the plant habit (slender, creeping rhizomes, long-petioled, peltate leaves and erect, 1-sided inflorescences) this does not seem satisfactory.
- B. physandra* Merr. & L.M. Perry is a New Guinean species that fits in with section *Diploclinium* (group I), but on examination of a living plant we found that the ovary had 2 locules. Should this observation be confirmed, a separate section for this species should be considered. This would probably also concern the closely related *B. archboldiana*.
- B. tanala* Humbert see *B. antaisaka*.
- B. thelmae* L.B. Smith is characterized by a creeping stem with straight, distichous leaves, erect, few-flowered, racemose inflorescences, oblong anthers spreading out from the top of a column, multifid styles and entire placentae. In some respects (creeping stem, spreading anthers) it is reminiscent of *B. hoehniana*.

8 Relationships between the sections

8.1 Methods

Apart from an analytical key as presented in chapter 5, relationships between taxa can be studied and visualized by other methods as well. There are roughly speaking two 'categories' of methods: numerical taxonomy and cladistics. Especially the latter method is very popular nowadays to study evolutionary relationships. However, the authors do not think cladistic methods can be applied to the taxa (sections) treated here. Each description, and thus the data per taxon, concerns an entire section. Many of these sections will probably be paraphyletic groups, or even polyphyletic ones. This poses unsolvable theoretical problems to the application of cladistic methods in our case. These can be partly overcome by analyzing the data (character states) of one or more representative species for each section, but the present data were not gathered in that manner. Therefore, we decided to apply numerical methods only. These methods are not primarily suitable to represent evolutionary relationships, but show a scheme of relationships based on similarities. The outcome should therefore not be interpreted in an evolutionary context, but merely be seen as a tool to obtain some insight in the complexity of the sectional relationships.

The DELTA package (Dallwitz, Paine & Zurcher, 1993) provides the possibility to calculate similarities between all sections directly from the DELTA files containing the coded descriptions. For unordered multistate characters the contribution of each character k to the distance D between section i and j is calculated as follows:

$$D_{ijk} = 0.5(|P_{ilk}-P_{jlk}| \dots + |P_{isk}-P_{j sk}| \dots + |P_{ink}-P_{jnk}|)$$

where P_{isk} is the probability of item i having state s of character k , and n is the number of states of character k . For ordered multistate and numerical characters the contribution of each character to the distance is calculated as:

$$D_{ijk} = |X_{ik}-X_{jk}| / R_k$$

where X_{ik} is the value of item i for character k and R_k is the range of the possible values for all included items.

The values were calculated with exclusion of all rare characters occurring within a section. Such 'exceptions' have been defined as follows:

- in a section of 5 to 14 species any character occurring only occasionally within a single species;
- in a section of 15 to 44 species any character occurring in a single species only;
- in a section of 45 to 99 species any character occurring in 1 or 2 species only;
- in a section of 100 or more species any character occurring in 1, 2 or 3 species only.

The resulting similarity, or in our case dissimilarity, matrix was entered in the program NTSYS-pc (Rohlf, 1993). A standard agglomerative clustering method (SAHN option) was applied yielding a phenogram, the cophenetic values calculated and the correlation between the two matrices determined. The latter two actions will provide a measure of the fit of the dissimilarity matrix to the phenogram, hence a measure of the 'firmness' of the phenogram.

8.2 Results and discussion

General remarks

The resulting phenogram is shown in fig. 53. The correlation r between the original dissimilarity matrix and the matrix containing the cophenetic values based on this phenogram (the normalized Mantel statistic Z) is only 0.727, which indicates the fit is 'poor'. This could already be expected from several other features of the phenogram. First of all, some 90% of all correlations lie between 0.3 and 0.1, hence most agglomerations are based on very small differences between the taxa. From the fact that even no correlation passes the value of 0.4, it can be deduced that most of the characters we used are not unique for a certain section and even that the sections themselves are rather variable.

Specific remarks

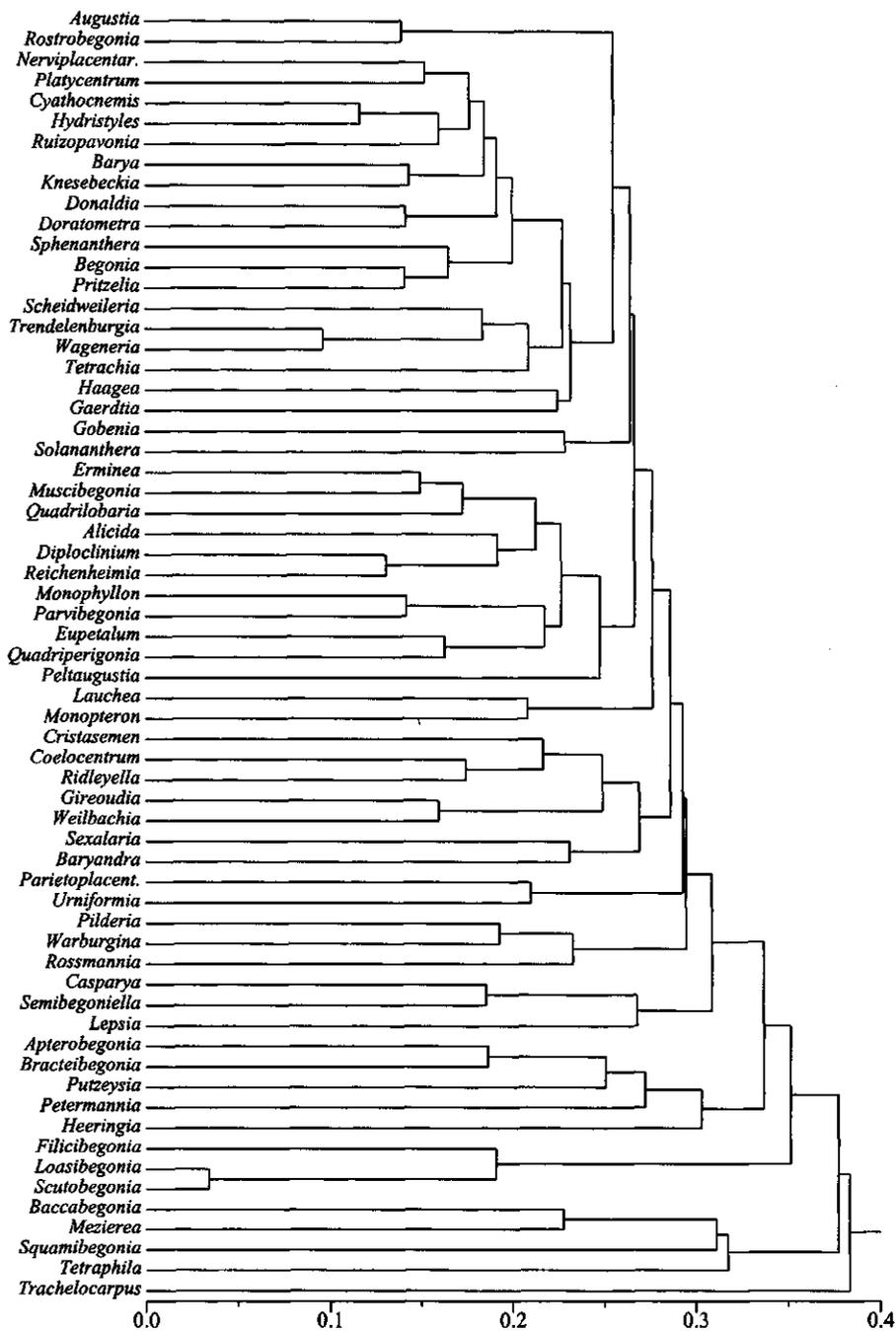


Fig. 53. Phenogram of all *Begonia* sections.

In view of the important role geographic origin has played in the past in the delimitation of sections within *Begonia*, it is interesting to see that in the present dendrogram, drawn up without the geographic origin being taken into account, the sections show a tendency to group themselves according to continent. Therefore, a discussion of the dendrogram per continent, as presented below, seems the most appropriate way to shed some light on this complex figure.

Africa: The African sections are dispersed across the dendrogram in four groups and four separate sections. To start with the latter: *Peltaugustia*, *Sexalaria* and *Cristasemen* are all morphologically isolated, monotypic sections without obvious counterparts on other continents. The sections with which they are paired do not show obvious relationships with them either. The Malagasy section *Nervi-placentaria* is grouped together with the Asian section *Platycentrum*, but there is very little similarity between the two. The continental African sections *Augustia* and *Rostrobegonia*, which indeed show many similarities and are even kept separate on rather feeble grounds, form a distinct group, and so do the likewise rather similar Malagasy sections *Erminea*, *Muscibegonia* and *Quadrilobaria*. One would expect, however, that the two groups would appear closer together. Most remarkable is the group of African sections comprising *Baccabegonia*, *Mezierea*, *Squamibegonia* and *Tetraphila*. These are split off very early and are therefore recognized as an aberrant group within the genus. This is indeed so because of their berry-like fruits, parietal placentation and (except for *Mezierea*) the indumentum of scales. The fourth group of African sections is split off directly after the latter one and contains the sections *Filicibegonia*, *Loasibegonia* and *Scutobegonia*. These also do not appear to have close relatives within the genus. Section *Filicibegonia* was treated as the sister-group of the other two sections in a phylogenetic study by Sosef (1994); a choice supported by the present results.

Asia: The 18 Asian sections are spread out over the dendrogram in two groups of 5, two groups of 2 and four solitary sections. The large section *Platycentrum* unexpectedly turns up next to the African section *Nervi-placentaria*, with which there are no obvious similarities, and is remote from *Parvibegonia*, from which it is sometimes difficult to distinguish. The section *Sphenanthera* is also in an unexpected position between American sections, but then it is a

rather aberrant Asian section and its species are very divergent. Another 'odd man out' among Asian sections is the monotypic *Haagea* which is indeed morphologically closer to the Brazilian sections with which it is grouped here than with its sympatric sections.

Alicida, *Diploclinium* and *Reichenheimia* show many similarities, especially the latter two which differ mainly in the placentae. These two large sections will probably have to be divided after which one can imagine that the resulting parts will end up elsewhere in the dendrogram and relationships with sections like *Quadriperigonia* and possibly some of the Malagasy ones will be emphasized. *Monophyllon* and *Parvibegonia*, closely related, are situated close to *Diploclinium*. In the past, relations between these sections and *Platycentrum* have been emphasized but perhaps too much weight has been given to the 2-locular ovary and more attention should be paid to the inflorescence. The very small sections *Lauchea* and *Monopteron* also have a 2-locular ovary; they differ strikingly in plant size.

The Asian sections *Coelocentrum* and *Ridleyella* are an unlikely pair, the one with parietal placentation (very uncommon in *Begonia*) with divided placentae, the other with a 2-locular ovary with entire, axillary placentae. In fact, *Ridleyella* looks like a 2-locular *Reichenheimia*, while one would expect that the species of *Coelocentrum* would be remote from other sections on account of their placentation. The relation between these two sections with either the African *Cristasemen* or the American *Gireoudia* and *Weilbachia* is not obvious and the same can be said of the relation between *Baryandra* and the African *Sexalaria*, both monotypic.

Finally, the second group of 5 Asian sections is very diverse with only *Bracteibegonia* and *Petermannia* showing obvious similarities. One would expect *Apterobegonia* and particularly *Putzeysia* to be close to *Diploclinium*. *Heeringia*, monotypic like the latter two, has several characteristics in common with these but stands apart on account of its 2-locular ovaries and certain peculiarities of the male flowers.

Overlooking the Asian sections one must conclude that the relationships are still far from clear. This might be related with the comparatively poor state of our knowledge of especially the Asian begonias. Perhaps a further division of large and divergent sections like *Diploclinium* and *Petermannia* would elucidate matters. It should also be remembered that there are 7 Asian species that could not yet

be classified in an existing section.

America: The American sections are clustered in a large group of 16 (*Cyathocnemis* to *Solananthera*), interspersed with only 2 Asian sections, a smaller group of 8, two 'pairs' and one isolated section. The group of 16 brings together sections that are undoubtedly related, and one would have expected that the two 'pairs' and *Lepsia* would also be attached to this group. The group of 8 unites sections that are further removed.

In the upper part of the dendrogram one finds *Cyathocnemis*, *Hydristyles* and *Ruizopavonia*, three closely related and not always easily distinguished sections. They are followed by *Barya* and *Knesebeckia*, which are in many ways similar to each other, although the only species of *Barya* which is well known is genetically close to *Eupetalum*, and *Knesebeckia* hitherto comprised *Quadriperigonina*. It is reasonable that *Eupetalum* and *Quadriperigonina* stand next to each other, but one would not expect them to be so far away from the sections mentioned. The same can be said of *Gireoudia* and *Weilbachia*, of which particularly *Gireoudia* shows many similarities to *Knesebeckia*.

The succession from *Donaldia* to *Pritzelia* - apart from *Sphenanthera* - is conceivable, except that in the past *Pritzelia* has been considered to be related to *Scheidweilera* and *Wageneria* rather than to *Begonia*, although there are also connections with this section. *Tetrachia* is somewhat apart on account of its 4-locular ovary, whereas *Gaerdia* which has characters in common with *Knesebeckia* as well as with *Pritzelia*, and is peculiar in the ovules usually occurring only on one side of the placenta lobes, is still further away. The surprising position of *Haagea* has already been discussed. *Gobonia* and *Solananthera*, both characteristic, are conform in that they are both lianescent.

Parietoplacentaria and *Urniformia* form an unlikely pair, although both have three perianth segments in the female flower, which is rare in America. *Pilderia*, *Warburgina* and *Rossmannia* are small sections of which the first and the third have a thyrsoid inflorescence, which is very uncommon in America but does occur in several Asian sections which in the dendrogram are not too far away. How *Warburgina*, which elsewhere we thought to be close to *Ruizopavonia*, came to key out here is not clear.

Casparya and *Semibegoniella* are clearly aberrant and rightly appear side by side. Klotzsch (1855) and Alphonse de Candolle

(1864) brought the species that were known at the time to a genus, *Casparya*, and still one might argue in favour of such a classification. Finally, *Trachelocarpus*, the most isolated section in this dendrogram, is one that in its habit and the morphology of its inflorescence and flowers is indeed much at variance with the others.

9 Alphabetical list of species

The list presented below gives all accepted *Begonia* species, their continent, distribution and section. It is based on the impressive work of Smith et al. (1986) and made up-to-date until 1998. When a certain name was accepted by Smith et al. but proved to be synonymous with another name afterwards, this is indicated in this list as well.

- Begonia abbottii* Urban; America: Haiti; *Begonia*
Begonia aberrans Irmscher; Asia: Indonesia (Sumatra); *Bractebegonia*
Begonia aborensis Dunn; Asia: India (Himalaya); *Sphenanthera*
Begonia abyssinica Cufodontis = *B. wollastonii* Bak.
Begonia acaulis Merr. & L.M. Perry; Asia: New Guinea; *Diploclinium* III
Begonia acerifolia Humb., Bonpl. & Kunth; America: Ecuador; *Knesebeckia*
Begonia aceroides Irmscher; Asia: Thailand; *Diploclinium* III
Begonia acetosa Vell.; America: Brazil; *Pritzelia*
Begonia acetosella Craib; Asia: China (Yunnan), Burma, Thailand; *Sphenanthera*
Begonia acida Vell.; America: Brazil; *Pritzelia*
Begonia aconitifolia A. DC.; America: Brazil (Rio de Janeiro); *Knesebeckia*
Begonia acuminatissima Merr.; Asia: The Philippines (Balut, Mindanao); *Diplo-*
clinium I
Begonia acutifolia Jacq.; America: Cuba, Jamaica; *Begonia*
Begonia acutiloba Liebm.; America: Mexico (Oaxaca), Guatemala; *Weilbachia*
Begonia adenodes Irmscher; Asia: Borneo (Sarawak); *Petermannia*
Begonia adenopoda Lem.; Asia: Burma; *Lauchea*
Begonia adenostegia Stapf; Asia: Borneo (Sabah); *Platycentrum*
Begonia admirabilis Brade; America: Brazil (Espírito Santo); *Begonia*
Begonia adolfi-friderici Gilg = *B. poculifera* Hook. f.
Begonia adpressa Sosef; Africa: Cameroon; *Loasibegonia*
Begonia adscendens C.B. Clarke; Asia: India (Nagaland); *Diploclinium* II
Begonia aenea Linden & André; Asia: India (Assam, cult.?): *Platycentrum*
Begonia aequata A. Gray; Asia: The Philippines (Luzon); *Petermannia*
Begonia aequatorialis L.B. Smith & Schubert; America: Ecuador (3 prov.);
Eupetalum
Begonia aequilateralis Irmscher; Asia: Peninsular Malaysia; *Platycentrum*
Begonia aeranthos L.B. Smith & Schubert; America: Ecuador (Morona-Santiago);
Wageneria
Begonia affinis Merr.; Asia: The Philippines; *Petermannia*
Begonia aggeloptera N. Hallé; Africa: Gabon; *Scutobegonia*
Begonia agusanensis Merr.; Asia: The Philippines (Mindanao); *Petermannia*
Begonia alba Merr.; Asia: The Philippines; *Diploclinium* I
Begonia albido-setulosa Hassk. = *B. hirtella* Link
Begonia albidula Brade; America: Brazil (Espírito Santo); *Begonia*
Begonia albobracteata Ridley; Asia: Indonesia (Irian Jaya); *Petermannia*
Begonia albo-coccinea Hook.; Asia: India; *Reichenheimia* I
Begonia albomaculata C. DC. ex Huber; America: Peru (Lorato), Ecuador (El Oro),

Pichincha); *Cyathocnemis* ?
Begonia albo-picta Bull; America: Brazil; *Gaerdia*
Begonia alcarrasica J. Sierra Calzado; America: Cuba; *Begonia*
Begonia alchemilloides Meisner ex A. DC.; America: Brazil (Minas Gerais);
Begonia
Begonia alemanni Brade; America: Brazil (Rio de Janeiro); *Doratometra*
Begonia alepensis A. Chev. = *B. fusialata* Warb.
Begonia algaia L.B. Smith & Wasshausen; Asia: China (Kiangsi); *Platycentrum*
Begonia alicae-clarkiae Ziesenh.; America: Mexico (Chiapas); *Weilbachia*
Begonia aliciae C.E.C. Fischer; Asia: India; *Parvibegonia*
Begonia alicida C.B. Clarke; Asia: Burma (Moulmein); *Alicida*
Begonia alnifolia A. DC.; America: Colombia (Norte de Santander); *Ruizopavonia*
Begonia alpina L.B. Smith & Wasshausen; Asia: Peninsular Malaysia; *Platycentrum*
Begonia altamiroi Brade; America: Brazil (Espírito Santo); *Pritzelia*
Begonia altissima Ridley; Asia: Indonesia (Sumatra); *Petermannia*
Begonia altoperuviana A. DC.; America: Peru, Bolivia; *Cyathocnemis*
Begonia alvarezii Merr.; Asia: The Philippines (Luzon); *Diploclinium* I
Begonia alveolata Yü; Asia: China (Yunnan); *Diploclinium* II
Begonia amabilis Linden; Asia: India (Assam, prob. cultivar); *Platycentrum*
Begonia amphioxus M.J.S. Sands; Asia: Borneo (Sabah); ? (new section?)
Begonia ampla Hook. f.; Africa: Central Africa; *Squamibegonia*
Begonia anaimalaiensis Bedd.; Asia: India (Tamil Nadu); ? (placentae unknown)
Begonia anceps Irmscher = *B. alveolata* Yü
Begonia andamensis Parish ex C.B. Clarke; Asia: Burma (Andaman Islands);
Parvibegonia
Begonia andina Rusby; America: Bolivia (Chimborazo); *Hydrisryles*
Begonia androrangensis Humbert; Africa: Madagascar; *Erminea*
Begonia anemoniflora Irmscher; America: Peru (Tarma); *Eupetalum*
Begonia anemonoides Azara ex Steud.; ?; ?; ?
Begonia angilogensis Merr.; Asia: The Philippines (Luzon); ? (new section?)
Begonia angolensis Irmscher; Africa: Angola; *Augustia*
Begonia angraensis Brade; America: Brazil (Rio de Janeiro); *Trachelocarpus*
Begonia angularis Raddi; America: Brazil (Rio de Janeiro, Minas Gerais); *Pritzelia*
Begonia angulata Vell.; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia angustilimba Merr.; Asia: Borneo; *Petermannia*
Begonia angustiloba A. DC.; America: Mexico; *Quadriperigonia*
Begonia anisoptera Merr.; Asia: The Philippines (Mindanao); *Diploclinium* I
Begonia anisosepala Hook. f.; Africa: Cameroon, Equatorial Guinea, Gabon;
Scutobegonia
Begonia anjuanensis Humbert ex Keraudren-Aymonin & Bosser; Africa: Madag-
 ascar; *Quadrilobaria*
Begonia ankaranensis Humbert ex Keraudren-Aymonin & Bosser; Africa: Madag-
 ascar; *Quadrilobaria*
Begonia annobonensis A. DC.; Africa: Cameroon, Principe, São Tomé, Pagalú
 (Annobon); *Sexalaria*
Begonia annulata K. Koch; Asia: India (Himalaya); *Platycentrum*
Begonia anodifolia A. DC.; America: Mexico; *Quadriperigonia*
Begonia antaisaka Humbert ex Bosser & Keraudren-Aymonin; Africa: Madagascar;
 ? (new section?)
Begonia antioquiensis (A. DC.) Warb. = *B. urticae* L.
Begonia antongilensis Humbert ex Bosser & Keraudren-Aymonin; Africa: Madag-
 ascar; *Erminea*

Begonia antsingyensis Humbert ex Keraudren-Aymonin & Bosser; Africa: Madagascar; *Quadrilobaria*
Begonia antsiranensis Aymonin & Bosser; Africa: Madagascar; *Quadrilobaria*
Begonia apayaoensis Merr.; Asia: The Philippines; *Petermannia*
Begonia apparicioi Brade; America: Brazil (Espírito Santo); *Pritzelia*
Begonia aptera Blume; Asia: Indonesia (Sulawesi); *Sphenanthera*
Begonia arborescens Raddi; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia archboldiana Merr. & L.M. Perry; Asia: New Guinea; ? (new section?)
Begonia areolata Miq.; Asia: Indonesia (Java); *Platycentrum*
Begonia argentea Linden; Asia: India (cult. ?); *Platycentrum*
Begonia argyrocoelis Herincq; Asia: ?; ? (obscure species)
Begonia aridicaulis Ziesenh.; America: Mexico (Oaxaca); *Weilbachia*
Begonia arnotiana (Wight) A. DC.; Asia: India (Courtallum); *Diploclinium* I
Begonia arrogans Irmscher; America: Peru (Jurin); *Knesebeckia*
Begonia articulata Irmscher; Asia: Borneo (Sarawak); *Petermannia*
Begonia artior Irmscher; Asia: Borneo (Sarawak); *Petermannia*
Begonia ascotiensis J.B. Weber; America: ?; hybrid of *B. fuchsoides* (x *B. cucullata* ?)
Begonia asperifolia Irmscher; Asia: China (Yunnan); *Diploclinium* II
Begonia aspleniifolia Hook. f. ex A. DC.; Africa: Gabon; *Filicibegonia*
Begonia assurgens Irmscher apud Weberling; America: El Salvador; *Weilbachia*
Begonia asympeltata L.B. Smith & Wasshausen; America: Ecuador (Los Rios);
Knesebeckia ?
Begonia atricha (Miq.) A. DC.; Asia: Indonesia (Sumatra); *Petermannia*
Begonia atroglandulosa Sosef; Africa: Equatorial Guinea, Gabon, Congo, Dem. Rep. Congo; *Loasibegonia*
Begonia augustae Irmscher; Asia: New Guinea; *Petermannia*
Begonia augustinei Hemsl.; Asia: China (Yunnan); *Platycentrum* ?
Begonia auriculata Hook. f.; Africa: Gabon; *Filicibegonia*
Begonia austrotaiwanensis Y.K. Chen & C.I. Peng; Asia: Taiwan; *Platycentrum* ?
Begonia axillaris Ridley; Asia: Indonesia (Lingga Archipelago); *Petermannia*
Begonia axillipara Ridley; Asia: Indonesia (Irian Jaya); *Petermannia*
Begonia azuensis Urban & Ekman; America: Sto. Domingo; *Begonia*
Begonia baccata Hook. f.; Africa: São Tomé; *Baccabegonia*
Begonia bagotiana Humbert ex Keraudren-Aymonin & Bosser; Africa: Madagascar;
Quadrilobaria
Begonia bahiensis A. DC.; America: Brazil (Bahia); *Pritzelia*
Begonia balansae C. DC.; America: Paraguay (Guaira); *Begonia*
Begonia balansana Gagnep.; Asia: Indo-China; ? (new section?)
Begonia balmisiana Balmis; America: Mexico (Mexico, Michoacan); *Quadriperigonia*
Begonia banaoensis J. Sierra Calzado; America: Cuba; *Begonia*
Begonia bangii O. Kuntze; America: Bolivia (La Paz, Cochabamba); *Ruizopavonia*
Begonia baramensis Merr.; Asia: Borneo (Sarawak); *Petermannia* ?
Begonia barbellata Ridley; Asia: Peninsular Malaysia; *Petermannia*
Begonia barkeri Knowl. & Westc.; America: Mexico; *Gireoudia*
Begonia barkleyana L.B. Smith; America: Brazil (Paraná); *Knesebeckia*
Begonia baronii Baker; Africa: Madagascar; *Nervioplacentaria*
Begonia barrigae L.B. Smith & Schubert; America: Colombia (Cundinamarca);
Ruizopavonia
Begonia bartlettiana Merr. & L.M. Perry; Asia: New Guinea; *Diploclinium* I
Begonia batesii C. DC. = *B. potamophila* Gilg

Begonia baumannii Lemoine; America: Bolivia (Cochabamba); *Eupetalum*
Begonia baviensis Gagnep.; Asia: Indo-China; *Platycentrum*
Begonia beccariana Ridley; Asia: Indonesia (Sumatra); *Platycentrum* ?
Begonia beccarii Warb.; Asia: Borneo; *Diploclinium* I ?
Begonia beddomei Hook. f.; Asia: India (Assam); *Platycentrum*
Begonia bekopakensis Aymonin & Bosser; Africa: Madagascar; *Quadrilobaria*
Begonia bequaertii Robyns & Lawalrée; Africa: Dem. Rep. Congo; *Rostrobegonia*
Begonia bernieri A. DC.; Africa: Madagascar; *Quadrilobaria*
Begonia beryllae Ridley; Asia: Borneo (Sarawak); *Petermannia*
Begonia besleriifolia Schott; America: Brazil (Espírito Santo); *Ruizopavonia*
Begonia betsimisaraka Humbert ex Bosser & Keraudren-Aymonin; Africa: Madag-
 ascar; *Erminea*
Begonia bettinae Ziesenh.; America: Mexico (Chiapas); *Gireoudia*
Begonia bidentata Raddi; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia biflora T.C. Ku; Asia: China (Yunnan); *Coelocentrum*
Begonia bifolia Ridley; Asia: Indonesia (Sumatra); *Petermannia*
Begonia bifurcata L.B. Smith & Schubert; America: Peru (Piura); *Knesebeckia*
Begonia biguassuensis Brade; America: Brazil (Sta Catarina); *Pritzelia*
Begonia biliranensis Merr.; Asia: The Philippines; *Diploclinium* I
Begonia binuangensis Merr.; Asia: The Philippines; *Petermannia*
Begonia bipinnatifida J.J. Smith; Asia: Indonesia (Irian Jaya); *Petermannia*
Begonia biserrata Lindl.; America: Mexico (Guerrero, Oaxaca), Guatemala, El
 Salvador; *Quadriperigonia*
Begonia bissei J. Sierra Calzado; America: Cuba; *Begonia*
Begonia bogneri Ziesenh.; Africa: Madagascar; *Erminea*
Begonia boisianana Gagnep.; Asia: Indo-China; ? (new section?)
Begonia boissieri A. DC.; America: Mexico (Guerrero); *Quadriperigonia*
Begonia boiviniana A. DC.; Africa: Madagascar; *Quadrilobaria*
Begonia boliviensis A. DC.; America: Bolivia (Chuquisaca, Santa Cruz, Tarija);
Barya
Begonia bolleana Urban & Ekman; America: Haiti; *Begonia*
Begonia bolsteri Merr.; Asia: The Philippines (Mindanao); *Petermannia*
Begonia bonii Gagnep.; Asia: Vietnam; *Reichenheimia* I
Begonia bonitoensis Brade; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia bonthainensis Hemsl.; Asia: Indonesia (Sulawesi); *Petermannia*
Begonia bonus-henricus J.J. de Wilde; Africa: Cameroon, Equatorial Guinea
 (Bioko); *Squamibegonia*
Begonia boraceiensis Handro; America: Brazil (São Paulo); *Pritzelia*
Begonia borneensis A. DC.; Asia: Borneo; *Petermannia*
Begonia bosseri Keraudren; Africa: Madagascar; *Erminea* ?
Begonia boucheana (Klotzsch) A. DC.; America: Venezuela (Caracas); *Pritzelia*
Begonia bowerae Ziesenh.; America: Mexico (Oaxaca); *Gireoudia*
Begonia brachybotrys Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia brachyclada Urban & Ekman; America: Haiti; *Knesebeckia*
Begonia brachypoda O.E. Schulz; America: Haiti; *Begonia*
Begonia brachyptera Merr. & L.M. Perry; Asia: Papua New Guinea; *Petermannia* ?
Begonia bracteata Jack; Asia: Indonesia (Sumatra); *Bracteibegonia*
Begonia bracteosa A. DC.; America: Peru (Junin); *Cyathocnemis*
Begonia bradei Irmscher; America: Brazil (São Paulo); *Pritzelia*
Begonia brandbygeana L.B. Smith & Wasshausen; America: Ecuador (Morona-
 Santiago); *Knesebeckia* ?
Begonia brandisiana Kurz; Asia: Burma; *Reichenheimia* II

Begonia brassii Merr. & L.M. Perry; Asia: New Guinea; *Diploclinium* II
Begonia breedlovei Burt-Utley; America: Mexico (Chiapas); *Gireoudia*
Begonia brevibracteata Kupicha; Africa: Malawi; *Augustia*
Begonia brevicaulis A. DC.; Asia: Himalaya; *Parvibegonia*
Begonia brevicaulis T.C. Ku non A. DC.; Asia: China (Yunnan); *Reichenheimia* I
Begonia brevicordata L.B. Smith & Schubert; America: Peru (Cuzco); *Cyathocnemis*
Begonia brevicyma C. DC.; America: Panama; *Weilbachia* ?
Begonia brevilobata Irmscher; America: Brazil (São Paulo); *Pritzelia*
Begonia brevipes Merr.; Asia: The Philippines (Luzon); *Petermannia*
Begonia brevipetala (A. DC.) Warb.; America: Venezuela (Merida); *Casparyia*
Begonia brevirimosa Irmscher; Asia: New Guinea; *Petermannia*
Begonia brevisetulosa C.Y. Wu; Asia: China (Sichuan); *Platycentrum*
Begonia bridgesii A. DC.; America: Bolivia (Cochabamba); *Hydristyles*
Begonia brongniartiana Lem.; ?; ?; ?
Begonia brogniartii Lem.; ?; ?; ?
Begonia buchholzii Gilg = *B. preussii* Warb.
Begonia buchtienii Irmscher; America: Bolivia (Cochabamba); *Ruizopavonia*
Begonia buddleiifolia A. DC.; America: Colombia to Peru; *Pilderia*
Begonia bufoderma L.B. Smith & Wasshausen; ?; ?; ? (flowers not described)
Begonia bui-montana Yamamoto; Asia: Taiwan; ? natural hybrid
Begonia bulbillifera Link & Otto; America: Mexico; *Quadriperigonia*
Begonia bullata Urban & Ekman; America: Haiti; *Begonia*
Begonia burbidgei Stapf; Asia: Borneo (Sabah); *Petermannia*
Begonia burkei Hort.; Asia: Burma ?; ?
Begonia burkillii Dunn; Asia: India (Himalaya); *Sphenanthera*
Begonia burle-marxii Brade; America: Brazil (Pernambuco); *Donaldia*
Begonia burmensis L.B. Smith & Wasshausen; Asia: Burma; *Lauchea*
Begonia buseyi Burt-Utley; America: Panama; *Gireoudia*
Begonia caespitosa Jack; Asia: Indonesia (Sumatra); *Diploclinium* I ?
Begonia calcarea Ridley; Asia: Borneo (Sarawak); *Diploclinium* I ?
Begonia calcicola Merr.; Asia: The Philippines (Luzon); *Diploclinium* I
Begonia calderonii Standley; America: El Salvador, Guatemala; *Weilbachia*
Begonia calliantha Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia calophylla Gilg ex Engl. = *B. anisosepala* Hook. f.
Begonia cameroonensis L.B. Smith & Wasshausen = *B. ciliobracteata* Warb.
Begonia campos-portoana Brade; America: Brazil (Sta Catarina); *Pritzelia*
Begonia canarana Miq.; Asia: India (Mangalor); *Parvibegonia*
Begonia candollei Ziesenh.; America: Mexico (Chiapas); *Parietoplacentalia*
Begonia capanemae Brade; America: Brazil (Sta Catarina); *Pritzelia*
Begonia capensis L. f.; ?; ?; ?
Begonia capillipes Gilg; Africa: Cameroon, Equatorial Guinea, Gabon; *Tetraphila*
Begonia capituliformis Irmscher; Asia: Indonesia (Sulawesi); *Petermannia*
Begonia caragatatubensis Brade; America: Brazil (São Paulo); *Pritzelia*
Begonia cardiocarpa Liebm.; America: Honduras, Nicaragua; *Gireoudia*
Begonia cardiophora Irmscher; Asia: Thailand; *Reichenheimia* II
Begonia cariocana Brade ex L.B. Smith & Wasshausen; America: Brazil (Rio de Janeiro); *Pritzelia* ?
Begonia carletonii Standley; America: Panama; *Weilbachia* ?
Begonia carnosa Teijsm. & Binnend.; Asia: Indonesia (Sulawesi); *Petermannia*
Begonia carnosula Ridley; Asia: Peninsular Malaysia; *Diploclinium* I ?
Begonia carolineifolia Regel; America: Mexico (Chiapas, Veracruz); *Gireoudia*

Begonia carpinifolia Liebm.; America: Costa Rica, Panama; *Ruizopavonia*
Begonia carrieae Ziesenh.; America: Mexico (Chiapas); *Gireoudia*
Begonia casiguranensis Quisumb. & Merr.; Asia: The Philippines; *Petermannia*
Begonia castaneifolia Otto & Dietr.; America: Brazil; ? (no flowers)
Begonia castilloi Merr.; Asia: The Philippines; *Diploclinium* I ?
Begonia cataractarum J. Braun et K. Schum. = *B. polygonoides* Hook. f.
Begonia catharinensis Brade; America: Brazil (Sta Catarina); *Pritzelia*
Begonia cathayana Hemsl.; Asia: China (Yunnan); *Platycentrum*
Begonia cathcartii Hook. f. & Thoms.; Asia: India (Sikkim); *Platycentrum*
Begonia caudata Merr.; Asia: The Philippines; *Petermannia*
Begonia cauliflora M.J.S. Sands; Asia: Borneo (Sabah); *Petermannia*
Begonia cavaleriei Léveillé; Asia: China (Yunnan, Kweitschou); *Diploclinium* I
Begonia cavallyensis A. Chev.; Africa: Guinea to Ivory Coast; *Tetraphila*
Begonia cavum Ziesenh.; America: Mexico (Oaxaca); *Knesebeckia*
Begonia cebadillensis Houghton ex L.B. Smith & Schubert; America: Guatemala,
 El Salvador; *Knesebeckia*
Begonia cehengensis T.C. Ku; Asia: China (Guizhou); *Diploclinium* II
Begonia celebica Irmscher; Asia: Indonesia (Sulawesi); *Petermannia*
Begonia cerasiphylla L.B. Smith & Wasshausen; America: Brazil; ? (insufficient
 data)
Begonia chaetocarpa O. Kuntze; America: Bolivia (La Paz, Cochabamba); *Ruizo-*
pavonia
Begonia chiapensis Burt-Utley; America: Mexico (Chiapas); *Gireoudia*
Begonia chingii Irmscher; Asia: China (Kwangsi); *Reichenheimia* III
Begonia chishuiensis T.C. Ku; Asia: China (Guizhou); *Platycentrum*
Begonia chitoensis T.S. Liu & M.J. Lai; Asia: Taiwan; *Platycentrum* ?
Begonia chivatoa Ziesenh.; America: Mexico (Oaxaca); *Gireoudia*
Begonia chlorolepis L.B. Smith & Schubert; America: Colombia (Magdalena);
Casparya
Begonia chlorosticta M.J.S. Sands; Asia: Borneo (Sarawak); *Petermannia*
Begonia chuniana C.Y. Wu; Asia: China (Hainan); new section?
Begonia cilifera Merr.; Asia: The Philippines (Mindanao); *Petermannia*
Begonia ciliobracteata Warb.; Africa: Nigeria, Cameroon; *Scutobegonia*
Begonia cincinnifera Irmscher; Asia: Borneo (Sarawak); *Petermannia*
Begonia cinnabarina Hook.; America: Bolivia (Acero, Cordillera); *Eupetalum*
Begonia circumlobata Hance; Asia: China (Kwantung); *Platycentrum*
Begonia cirrosa L.B. Smith & Wasshausen; Asia: China; *Coelocentrum*
Begonia cladocarpa Baker = *B. oxyloba* Welw. ex Hook. f.
Begonia cladocarpoides Humbert ex Aymonin & Bosser; Africa: Madagascar;
Nervioplacentaria
Begonia clarkei Hook. f.; America: Peru, Bolivia; *Eupetalum*
Begonia clavicaulis Irmscher; Asia: China (Yunnan); *Diploclinium* II
Begonia clemensiae Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia clypeifolia Hook. f.; Africa: Equatorial Guinea, Gabon, Congo; *Scuto-*
begonia
Begonia coccinea Hook.; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia cognata Irmscher; Asia: Borneo (Sarawak); *Petermannia*
Begonia collaris Brade; America: Brazil (Minas Gerais); *Pritzelia*
Begonia collina Irmscher; Asia: Peninsular Malaysia; *Platycentrum*
Begonia collisiae Merr.; Asia: The Philippines; *Diploclinium* I
Begonia colombiana L.B. Smith & Schubert; America: Colombia (Putumayo);
Casparya

Begonia colorata Warb.; Asia: The Philippines (Mindanao); *Diploclinium* I
Begonia comata O. Kuntze; America: Bolivia (Cochabamba); *Warburgina*
Begonia comorensis Warb.; Africa: Comores; *Mezierea*
Begonia compacticaulis Irmscher; America: Ecuador (Chimborazo, Cotopaxi);
Knesebeckia
Begonia comperei Wilczek = *B. hirsutula* Hook. f.
Begonia complicata (Hassk.) A. DC.; America: cult. Hort. Bogor, Indonesia;
Lepsia ?
Begonia compta Bull; America: Brazil; *Pritzelia*
Begonia concanensis A. DC.; Asia: India (Bombay); *Diploclinium* II
Begonia conchifolia A. Dietr.; America: Costa Rica, Panama; *Gireoudia*
Begonia concinna Schott; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia confinis L.B. Smith & Wasshausen; America: Venezuela (Zulia); *Lepsia*
Begonia confusa L.B. Smith & Schubert; America: Guatemala; *Weilbachia* ?
Begonia congesta Ridley; Asia: Borneo (Sarawak); *Petermannia*
Begonia consanguinea Merr.; Asia: Borneo (Sarawak); *Petermannia*
Begonia consobrina Irmscher; America: Ecuador; *Ruizopavonia*
Begonia contracta Warb.; Asia: The Philippines (Luzon); *Petermannia*
Begonia convallariodora C. DC.; America: Mexico, Panama; *Ruizopavonia*
Begonia convolvulacea (Klotzsch) A. DC.; America: Brazil (Ceara, Bahia, Rio de
Janeiro); *Wageneria*
Begonia cooperi C. DC.; America: Costa Rica; *Ruizopavonia*
Begonia copelandii Merr.; Asia: The Philippines (Mindanao); *Diploclinium* I
Begonia copeyana C. DC.; America: Costa Rica; *Weilbachia* ?
Begonia coptidi-montana C.Y. Wu; Asia: China (Yunnan); *Diploclinium* II
Begonia corallina Carr.; America: Brazil; *Gaerdia*
Begonia cordata Vell.; America: Brazil; *Pritzelia* ?
Begonia cordifolia (Wight) Thwaites; Asia: India, Sri Lanka; *Diploclinium* I
Begonia coriacea Hassk.; Asia: Indonesia (Java); *Reichenheimia* I
Begonia corneri R. Kiew; Asia: Peninsular Malaysia (Trengganu); *Reichenheimia* I
Begonia cornitepala Irmscher; America: Brazil (São Paulo); *Pritzelia*
Begonia cornuta L.B. Smith & Schubert; America: Colombia (Cundinamarca);
Casparya
Begonia coronensis Merr.; Asia: The Philippines (Calamian Islands); *Diploclinium*
III
Begonia corredorana C. DC.; America: Costa Rica, Panama; *Gireoudia*
Begonia corzoensis Ziesenh.; America: Mexico (Chiapas); *Gireoudia*
Begonia coursii Humbert ex Keraudren; Africa: Madagascar; *Nervioplacentaria*
Begonia cowellii Nash; America: Cuba; *Begonia*
Begonia crassicaulis Lindl.; America: Guatemala; *Gireoudia*
Begonia crassipes Gilg ex Engl. = *B. longipetiolata* Gilg
Begonia crassirostris Irmscher; Asia: China; *Sphenanthera*
Begonia crateris Exell; Africa: São Tomé; *Baccabegonia*
Begonia crenata Dryand.; Asia: India (Malabar); *Parvibegonia*
Begonia crinita Oliver ex Hook. f.; America: Bolivia; *Knesebeckia*
Begonia crispipila Elmer; Asia: The Philippines (Luzon); *Petermannia*
Begonia crispula Brade; America: Brazil (Espírito Santo, Minas Gerais); *Pritzelia*
Begonia cristata Warb. ex Koord.; Asia: Indonesia (Sulawesi); *Sphenanthera*
Begonia cristobalensis Ziesenh.; America: Guatemala; *Gireoudia*
Begonia croatii Burt-Utley; America: Panama; *Gireoudia*
Begonia cryptocarpa L.B. Smith & Schubert; America: Colombia (Magdalena);
Cyathocnemis

Begonia cuatrecasasiana L.B. Smith & Schubert; America: Colombia (Valle);
Ruizopavonia
Begonia cubensis Hassk.; America: Cuba; *Begonia*
Begonia cucullata Willd.; America: Brazil; *Begonia*
Begonia cucurbitifolia C.Y. Wu; Asia: China (Yunnan); *Platycentrum*
Begonia cuernavacensis Ziesenh.; America: Mexico (Morelo); *Knesebeckia*
Begonia cultrata Irmscher = *B. capillipes* Gilg
Begonia cumingiana A. DC.; Asia: The Philippines (Luzon); *Petermannia*
Begonia cumingii A. Gray; Asia: The Philippines (Luzon); *Petermannia*
Begonia cuneatifolia Irmscher; Asia: Indonesia (Sulawesi); *Petermannia*
Begonia curtii L.B. Smith & Schubert; America: Brazil (Espírito Santo); *Pritzelia*
Begonia curtisii Ridley; Asia: Thailand; *Parvibegonia*
Begonia cyathophora Poepp. & Endl.; America: Peru; *Cyathocnemis*
Begonia cylindrata L.B. Smith & Schubert; America: Mexico (Mexico); *Knesebeckia*
Begonia cymbalifera L.B. Smith & Schubert; America: Colombia (Putumayo, Caldas); *Ruizopavonia*
Begonia dasycarpa A. DC.; America: Brazil (Bahia); *Donaldia*
Begonia davidsoniae Standley ex L.B. Smith & Schubert; America: Panama; *Weilbachia* ?
Begonia davisii Hook. f.; America: Peru; *Eupetalum*
Begonia daweshanensis Huang & Shui; Asia: China (Yunnan); *Platycentrum*
Begonia daxinensis T.C. Ku; Asia: China (Guangxi); *Coelocentrum*
Begonia dealbata Liebm.; America: Mexico (Oaxaca); *Quadriperigonia*
Begonia debilis King; Asia: Peninsular Malaysia (Perak); *Parvibegonia*
Begonia decandra Pavon ex A. DC.; America: Puerto Rico; *Begonia*
Begonia decaryana Humbert ex Keraudren-Aymonin & Bossier; Africa: Madagascar; *Quadrilobaria*
Begonia declinata Vell.; America: Brazil (Rio de Janeiro?); *Pritzelia* ?
Begonia decora Stapf; Asia: Peninsular Malaysia; *Platycentrum*
Begonia delicatula Parish ex C.B. Clarke; Asia: Burma; *Apterobegonia*
Begonia deliciosa Linden ex Fotsch; Asia: ?; *Platycentrum*
Begonia demissa Craib; Asia: Thailand; *Parvibegonia*
Begonia densifolia Irmscher; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia densiretis Irmscher; Asia: Borneo (Sarawak); *Petermannia*
Begonia dentatiloba A. DC.; America: Brazil (Rio de Janeiro); *Pritzelia* ?
Begonia dentato-bracteata C.Y. Wu; Asia: China (Yunnan); *Diploclinium* III
Begonia denticulata Humb., Bonpl. & Kunth; America: Venezuela; *Cyathocnemis* ?
Begonia depauperata Schott; America: Brazil (Rio de Janeiro); *Trachelocarpus*
Begonia descoleana L.B. Smith & Schubert; America: Argentina, Brazil (Sta Catarina, Paraná); *Begonia*
Begonia dewildei Sosef; Africa: Gabon; *Scutobegonia*
Begonia diadema Linden ex Rodigas; Asia: ?; *Platycentrum*
Begonia dichotoma Jacq.; America: Venezuela, Colombia; *Pritzelia*
Begonia dichroa Sprague; America: Brazil; *Gaerdia*
Begonia dielsiana E. Pritz. ex Diels; Asia: China (Szechuan); *Platycentrum*
Begonia dietrichiana Irmscher; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia diffusa L.B. Smith & Schubert; America: Colombia (Santandes); *Casparya*
Begonia diffusiflora Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia digitata Raddi; America: Brazil (Rio de Janeiro, Minas Gerais); *Scheidweilleria*
Begonia digyna Irmscher; Asia: China (Fokien); *Platycentrum*

Begonia dioica Buch.-Ham. ex D. Don; Asia: India (Sikkim), Nepal; *Diploclinium*

III

Begonia dipetala R. Grah.; Asia: India; *Haagea*

Begonia discrepans Irmscher; Asia: China (Yunnan); *Platycentrum*

Begonia discreta Craib; Asia: Thailand; *Diploclinium* II

Begonia divaricata Irmscher; Asia: Indonesia (Sumatra); *Bracteibegonia* ?

Begonia diversistipulata Irmscher; America: Colombia (Magdalena); *Casparya*

Begonia djamuensis Irmscher; Asia: New Guinea; *Petermannia*

Begonia dodsonii L.B. Smith & Wasshausen; America: Ecuador (Pichincha);

Gobonia

Begonia dolichotricha Merr.; Asia: The Philippines; *Petermannia*

Begonia domingensis A. DC.; America: Sto Domingo, Haiti; *Begonia*

Begonia dominicalis A. DC.; America: Dominica; *Begonia*

Begonia donkelaariana Lem.; America: Mexico ?; ?

Begonia dosedlae A. Gilli; Asia: Papua New Guinea; *Petermannia*

Begonia dregei Otto & Dietr.; Africa: South Africa; *Augustia*

Begonia dressleri Burt-Utley; America: Panama; *Gireoudia*

Begonia dryadis Irmscher; Asia: China (Yunnan); *Platycentrum*

Begonia dubia Haworth; America: Brazil; ? (no flowers)

Begonia duclouxii Gagnep.; Asia: China (Yunnan); *Platycentrum*

Begonia dugandiana L.B. Smith & Schubert; America: Colombia (Tolima); *Ruizo-*

pavonia

Begonia duncan-thomasi Sosef; Africa: Cameroon; *Loasibegonia*

Begonia dusenii Warb. = *B. quadrialata* Warb. subsp. *dusenii* (Warb.) Sosef

Begonia dux C.B. Clarke; Asia: Burma; *Platycentrum* ?

Begonia eberhardtii Gagnep.; Asia: Indo-China (Amman); *Petermannia*

Begonia ebolowensis Engl.; Africa: Cameroon, Equatorial Guinea, Gabon, Dem.

Rep. Congo; *Tetraphila*

Begonia echinosepala Regel; America: Brazil (Sta Catarina, Parará); *Pritzelia*

Begonia ciliata O.E. Schulz; America: Trinidad; *Begonia*

Begonia edanoi Merr.; Asia: The Philippines; *Petermannia*

Begonia edmundoi Brade; America: Brazil (Rio de Janeiro); *Gaerdtia*

Begonia edulis Léveillé; Asia: China; *Platycentrum*

Begonia egléri Brade; America: Brazil (Pernambuco); *Donaldia*

Begonia egregia N.E. Br.; America: Brazil (Rio de Janeiro); *Tetrachia*

Begonia eiiromischa Ridley; Asia: Peninsular Malaysia; *Ridleyella*

Begonia ekmanii Houghton ex L.B. Smith & Schubert; America: Cuba; *Begonia*

Begonia elaeagnifolia Hook. f.; Africa: Cameroon, Equatorial Guinea, Gabon,

Congo; *Tetraphila*

Begonia elatostematoides Merr.; Asia: The Philippines; *Petermannia*

Begonia elatostemma Ridley; Asia: Borneo (Sarawak); *Petermannia*

Begonia elatostemmoides Hook. f.; Africa: Cameroon, Gabon, Congo, Dem. Rep.

Congo; *Filicibegonia*

Begonia eliasii Warb.; Asia: New Guinea; *Petermannia*

Begonia elmeri Merr.; Asia: The Philippines; *Diploclinium* I

Begonia emeiensis C.M. Hu; Asia: China (Sichuan, Heilongjiang); *Platycentrum*

Begonia eminii Warb.; Africa: Central & East Africa; *Tetraphila*

Begonia engleri Gilg; Africa: Tanzania; *Rostrobegonia*

Begonia epibaterium Mart. ex A. DC.; America: Brazil (Bahia); *Wageneria*

Begonia epipsila Brade; America: Brazil (Rio de Janeiro); *Pritzelia*

Begonia erecta Vell.; America: Brazil; *Pritzelia* ?

Begonia erectocaulis Sosef; Africa: Gabon; *Scutobegonia*

Begonia erectotricha Sosef; Africa: Gabon; *Scutobegonia*
Begonia eriocaulon Neumann; ?; ?; ?
Begonia erminea L'Hér.; Africa: Madagascar; *Erminea*
Begonia erosa Blume; Asia: Indonesia (Java); *Platycentrum* ?
Begonia erythrocarpa A. DC.; America: Ecuador, Peru, Bolivia; *Knesebeckia*
Begonia erythrogyna M.J.S. Sands; Asia: Borneo (Sabah); *Petermannia*
Begonia esculenta Merr.; Asia: The Philippines; *Petermannia*
Begonia estrellensis C. DC.; America: Costa Rica, Panama; *Ruizopavonia*
Begonia everetti Merr.; Asia: The Philippines (Negros); *Petermannia*
Begonia exalata C. DC.; America: Ecuador (Bolívar, Pinchincha); *Knesebeckia*
Begonia exigua Irmscher; America: Brazil; *Begonia*
Begonia exilis O.E. Schulz; America: Haiti; *Begonia*
Begonia extensa L.B. Smith & Schubert; America: Colombia (Boyaca); *Ruizo-*
pavonia
Begonia extranea L.B. Smith & Schubert; America: Mexico (Jalisco); *Knesebeckia*
Begonia fabulosa L.B. Smith & Wasshausen; America: Brazil; ? (data improbable)
Begonia fagifolia Fisch. ex Otto & Dietr.; America: Brazil (Rio de Janeiro);
Wageneria
Begonia falcifolia Hook. f.; America: Peru; *Pritzelia*
Begonia falciloba Liebm.; America: Mexico (Oaxaca); *Knesebeckia*
Begonia fallax A. DC. = *B. malabarica* Lamk non A. DC.
Begonia fasciculata Jack; Asia: Indonesia (Sumatra); *Petermannia*
Begonia fasciculiflora Merr.; Asia: The Philippines (Mindanao); *Petermannia*
Begonia fellereriana Irmscher; America: Brazil (Bahia); *Pritzelia* ?
Begonia fenchihuensis S.S. Ying = *B. bui-montana* Yamamoto
Begonia fengii T.C. Ku; Asia: China (Yunnan); *Diploclinium* I
Begonia fenicis Merr.; Asia: The Philippines (Batanes Islands), Taiwan?; *Diplo-*
clinium I
Begonia fernaldiana L.B. Smith & Schubert; America: Mexico (Guerrero);
Knesebeckia
Begonia fernando-costae Irmscher; America: Brazil (São Paulo); *Pritzelia*
Begonia ferramica N. Hallé; Africa: Gabon; *Scutobegonia*
Begonia ferruginea L. f.; America: Colombia, Venezuela; *Casparya*
Begonia festiva Craib; Asia: Thailand; *Diploclinium* I
Begonia fibrosa C.B. Clarke; Asia: Burma; *Reichenheimia* I ?
Begonia ficicola Irmscher = *B. microsperma* Warb.
Begonia fiebrigii C. DC.; America: Paraguay; *Pritzelia*
Begonia filibracteosa Irmscher; Asia: New Guinea; *Petermannia*
Begonia filicifolia N. Hallé = *B. asplenifolia* Hook. f.
Begonia filiformis Irmscher; Asia: China (Kiangsi); *Reichenheimia* I
Begonia filipes Benth.; America: Panama, Costa Rica, Colombia; *Doratometra*
Begonia fimbriata Liebm.; America: Mexico (Oaxaca); *Weilbachia*
Begonia fimbristipula Hance; Asia: China (Kanton); *Diploclinium* II
Begonia fischeri Schrank; America: Central and South America; *Begonia*
Begonia fissistyla Irmscher; America: Bolivia (Yungas); *Hydristyles*
Begonia flacca Irmscher; Asia: Indonesia (Sulawesi); *Petermannia*
Begonia flaccidissima Kurz; Asia: Burma; *Parvibegonia*
Begonia flagellaris Hara; Asia: Nepal; *Diploclinium* I
Begonia flava Marais = *B. sutherlandii* Hook. f.
Begonia flaviflora Hara; Asia: India, Burma; *Platycentrum*
Begonia flexicaulis Ridley; Asia: New Guinea; *Petermannia*
Begonia flexula Ridley; Asia: Indonesia (Sumatra); *Petermannia*

Begonia floccifera Bedd.; Asia: India; *Reichenheimia* I
Begonia floribunda T.C. Ku; Asia: China (Guangxi); new section?
Begonia fluminensis Brade; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia foliosa Humb., Bonpl. & Kunth; America: Colombia, Venezuela, Ecuador;
Lepsia
Begonia forbesii King; Asia: Peninsular Malaysia; *Reichenheimia* I ?
Begonia fordii Irmscher; Asia: China (Kwantung); *Diploclinium* II
Begonia forgetiana Hemsl.; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia formosana (Hayata) Masamune; Asia: Taiwan; *Platycentrum*
Begonia formosissima Sandwith; America: Venezuela (Merida); *Casparya*
Begonia forrestii Irmscher; Asia: China (Yunnan); *Platycentrum*
Begonia foveolata Irmscher; Asia: India (Bengal); *Platycentrum*
Begonia foxworthyi Burkill ex Ridley; Asia: Peninsular Malaysia; *Reichenheimia* I
Begonia fragilis Baker = *B. goudotii* A. DC.
Begonia francisiae Ziesenh.; America: Mexico (Chiapas); *Weilbachia*
Begonia francoisii Guillaumin; Africa: Madagascar; *Quadrilobaria*
Begonia fraseri Kiew; Asia; Peninsular Malaysia; *Platycentrum*
Begonia friburgensis Brade; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia frigida A. DC.; ? culta, probably a hybrid; ?; *Pritzelia*
Begonia froebelii A. DC.; America: Ecuador (5 prov.); *Eupetalum*
Begonia fruticella Ridley; Asia: New Guinea; *Petermannia*
Begonia fruticosa A. DC.; America: Brazil (Rio de Janeiro to Rio Grande do Sul),
 Argentina (Misiones); *Trendelenburgia*
Begonia fuchsiflora (A. DC.) Baranov & F.A. Barkley; America: Ecuador;
Casparya
Begonia fuchsoides Hook.; America: Colombia; *Lepsia*
Begonia fulgens Lemoine; America: Bolivia; *Eupetalum* ?
Begonia fulvo-setulosa Brade; America: Brazil (São Paulo); *Trachelocarpus*
Begonia furfuracea Hook. f.; Africa: Cameroon, Equatorial Guinea (Bioko);
Tetraphila
Begonia fusca Liebm.; America: Mexico (Chiapas, Oaxaca, Veracruz), Guatemala,
 Honduras; *Gireoudia*
Begonia fuscocaulis Brade; America: Brazil (Sta Catarina); *Pritzelia*
Begonia fusialata Warb.; Africa: West & Central Africa; *Tetraphila*
Begonia fusibulba C. DC.; America: Mexico (San Luis Obispo); *Quadriperigonia*
Begonia fusicarpa Irmscher; Africa: Liberia; *Tetraphila*
Begonia gagnepainiana Irmscher; Asia: China (Yunnan); *Platycentrum*
Begonia gamolepis L.B. Smith & Schubert; America: Colombia (Santander);
Casparya
Begonia garagarana C. DC.; America: Panama; *Gireoudia*
Begonia gardneri A. DC.; America: Brazil (Minas Gerais); *Pritzelia*
Begonia garrettii Craib; Asia: Thailand; *Diploclinium* II
Begonia garuuae L.B. Smith & R.C. Smith; America: Brazil (Sta Catarina); *Pritzelia*
 ?
Begonia gehrtii Irmscher; America: Brazil (São Paulo ?); *Pritzelia*
Begonia gemella Warb. ex L.B. Smith & Wasshausen; Asia: New Guinea; *Peter-*
mannia
Begonia geminiflora L.B. Smith & Wasshausen; America: Ecuador (Pichincha);
Gobenia
Begonia gemmipara Hook. f. & Thoms.; Asia: India (Sikkim); *Putzeysia*
Begonia gemmirhiza Lévillé; Asia: China; ? (only leaves known)
Begonia gentilii De Wild.; Africa: Dem. Rep. Congo; *Loasibegonia*

Begonia geoffrayi Gagnep.; Asia: Cambodia; *Diploclinium* II ?
Begonia geraniifolia Hook.; America: Peru (Lima); *Eupetalum*
Begonia geranioides Hook. f.; Africa: South Africa; *Augustia*
Begonia gesnerioides L.B. Smith & Schubert; America: Peru (San Martin); *Ruizopavonia* ?
Begonia gesnerioides Huang & Shui; Asia: China (Yunnan); *Platycentrum* ?
Begonia gilgiana Irmscher; Asia: New Guinea; *Petermannia*
Begonia gilgii Engl. = *B. sessilifolia* Hook. f.
Begonia gitingensis Elmer; Asia: The Philippines (Sibuyan); *Diploclinium* I
Begonia glaberrima Urban & Ekman; America: Haiti; *Begonia*
Begonia glabra Aubl.; America: Mexico, West Indies, Guatemala to Peru; *Wagneria*
Begonia glabricaulis Irmscher; Asia: New Guinea; *Petermannia*
Begonia gladiifolia Engl. = *B. longipetiolata* Gilg
Begonia glandulifera Griseb.; America: Trinidad, Venezuela (Sucre); *Begonia* ?
Begonia glandulosa Hook.; America: Mexico; *Platycentrum*
Begonia glauca (Klotzsch) Ruiz & Pavon ex A. DC.; America: Peru (Huanuco);
Cyathocnemis
Begonia glaucoides Irmscher; America: Peru (Huanuco); *Ruizopavonia*
Begonia glechomifolia C.M. Hu; Asia; China (Guangxi); *Diploclinium* II
Begonia goegoensis N.E. Br.; Asia: Indonesia (Sumatra); *Reichenheimia* I
Begonia goniotis C.B. Clarke; Asia: Burma; *Platycentrum*
Begonia gossweileri Irmscher; Africa: Congo, Angola (Cabinda); *Filicibegonia*
Begonia goudotii A. DC.; Africa: Madagascar; *Quadrilobaria*
Begonia gracilicaulis Irmscher = *B. macrocarpa* Warb.
Begonia gracilipes Merr.; Asia: The Philippines (Luzon); *Petermannia*
Begonia gracilipetiolata De Wild. = *B. longipetiolata* Gilg
Begonia gracilis Humb., Bonpl. & Kunth; America: Mexico (Oaxaca); *Quadriperigonia*
Begonia gracillima A. DC.; America: Peru; *Eupetalum*
Begonia grandibracteolata Irmscher; America: Peru; *Gobenia* ?
Begonia grandipetala Irmscher; Asia: Indonesia (Sulawesi); *Petermannia*
Begonia grandis Dryander; Asia: China, Japan; *Diploclinium* II
Begonia grantiana Craib; Asia: Thailand; *Parvibegonia*
Begonia grata Geddes ex Craib; Asia: Thailand; *Parvibegonia*
Begonia griffithiana (A. DC.) Warb.; Asia: India (Khasia), Bhutan; *Monopteron*
Begonia grisea A. DC.; America: Brazil (Minas Gerais); *Pritzelia*
Begonia groenewegensis Hort. ex K. Koch & G.A. Fintelmann; Asia: ?; ?
Begonia guaduensis Humb., Bonpl. & Kunth; America: Colombia, Venezuela, Ecuador, Peru; *Ruizopavonia*
Begonia guangxinensis C.Y. Wu; Asia; China (Guangxi); *Coelocentrum*
Begonia guatemalensis Van Houtte ex Galeotii; America: ?; ?
Begonia gueritziana L.S. Gibbs; Asia: Borneo (Sabah); *Reichenheimia* I
Begonia guishanensis Huang & Shui; Asia: China (Yunnan); *Diploclinium* III
Begonia gulinqingensis Huang & Shui; Asia: China (Yunnan); *Diploclinium* I
Begonia gungshaniensis C.Y. Wu; Asia; China (Yunnan); *Platycentrum* ?
Begonia guttata Wall. ex A. DC.; Asia: Thailand, Peninsular Malaysia; *Parvibegonia*
Begonia hainanensis W.Y. Chun & F. Chun; Asia: China (Hainan); *Petermannia* ?
Begonia halconensis Merr.; Asia: The Philippines (Mindanao); *Petermannia*
Begonia handelii Irmscher; Asia: Indo-China, China (Yunnan); *Sphenanthera*
Begonia handroi Brade; America: Brazil (São Paulo); *Pritzelia*

Begonia haniffii Burkill; Asia: Thailand; *Parvibegonia*
Begonia harlingii L.B. Smith & Wasshausen; America: Ecuador (Los Rios);
Begonia
Begonia harmandii Gagnep.; Asia: Vietnam; *Reichenheimia* III
Begonia hasskarliana (Miq.) A. DC.; Asia: Indonesia (Sumatra); *Diploclinium* I
Begonia hassleri C. DC.; America: Argentina (Misiones); *Begonia*
Begonia hatocoa Buch.-Ham. ex D. Don; Asia: Nepal; *Platycentrum*
Begonia haullevilleana De Wild. = *B. poculifera* Hook. f.
Begonia havilandii Ridley; Asia: Borneo (Sarawak); *Diploclinium* I
Begonia hayatae Gagnep.; Asia: Taiwan; *Sphenanthera*
Begonia heloisana Brade; America: Brazil (Ceará); *Donaldia*
Begonia hemsleyana Hook. f.; Asia: China; *Platycentrum*
Begonia henryi Hemsl.; Asia: China (Yunnan); *Reichenheimia* III
Begonia heracleifolia Cham. & Schlecht.; America: Mexico, Guatemala, Honduras;
Gireoudia
Begonia herbacea Vell.; America: Brazil; *Trachelocarpus*
Begonia heringeri Brade; America: Brazil (Minas Gerais); *Pritzelia*
Begonia hernandioides Merr.; Asia: The Philippines (Luzon); *Diploclinium* I
Begonia herrerae L.B. Smith & Schubert; America: Peru (Cuzco); *Eupetalum*
Begonia herteri Irmscher; America: Brazil (Rio de Janeiro); ? (new section?)
Begonia herveyana King; Asia: Peninsular Malaysia; *Petermannia*
Begonia heterochroma Sosef; Africa: Cameroon, Gabon; *Loasibegonia*
Begonia heteroclina Miq. ex Koord.; Asia: Indonesia (Sulawesi); *Sphenanthera*
Begonia heteropoda Baker; Africa: Madagascar; *Quadrilobaria*
Begonia hexandra Irmscher; America: Colombia (Cauca); *Semibegoniella*
Begonia heydei C. DC.; America: Costa Rica, Guatemala, Panama; *Urniiformia*
Begonia hilariana A. DC.; America: Brazil (Sta Catarina); *Pritzelia*
Begonia hintoniana L.B. Smith & B.G. Schubert; America: Mexico (Mexico);
Knesebeckia
Begonia hirsuta Aubl.; America: Guyana; *Doratometra*
Begonia hirsuticaulis Irmscher; Asia: New Guinea; *Petermannia*
Begonia hirsutula Hook. f.; Africa: Ghana to Dem. Rep. Congo; *Scutobegonia*
Begonia hirta (Klotzsch) L.B. Smith & Schubert; America: Peru (Huanuco, Junin);
Casparya
Begonia hirtella Link; America: West Indies, Colombia to Brazil; *Doratometra*
Begonia hispida Schott; America: Brazil (Sta Catarina); *Pritzelia*
Begonia hispidissima Zipp. ex Koord.; Asia: Indonesia (Sulawesi); *Petermannia*
Begonia hispidivillosa Ziesenh.; America: Mexico (Oaxaca); *Gireoudia*
Begonia hitchcockii Irmscher; America: Ecuador (Tungurahua); *Gobenia*
Begonia hochbaumii Hort. ex E. Otto; Asia: ?; ?
Begonia hoehneana Irmscher; America: Brazil (São Paulo); ? (new section?)
Begonia holmnielseniana L.B. Smith & Wasshausen; America: Ecuador (Napó);
Semibegoniella
Begonia holosericea Teijsm. & Binnend.; Asia: Indonesia (Ternate); *Petermannia* ?
Begonia holtonis A. DC.; America: Colombia, Ecuador; *Ruizopavonia*
Begonia holtumii Irmscher; Asia: Peninsular Malaysia; *Petermannia*
Begonia homonyma Steud.; Africa: South Africa; *Augustia*
Begonia hookeriana Gardn.; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia horsfieldii Miq. ex A. DC.; Asia: Indonesia (Sumatra); *Petermannia*
Begonia horsticola Irmscher; Africa: Congo, Dem. Rep. Congo, Uganda; *Tetraphila*
Begonia houttuynioides Yü; Asia: China; *Platycentrum*
Begonia howii Merr. & Chun; Asia: China (Hainan); *Diploclinium* II ?

Begonia huberti Ziesenh.; America: Mexico (Chiapas); *Gireoudia*
Begonia huegelii (Klotzsch) Hort. Berol. ex A. DC.; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia hullettii Ridley; Asia: Borneo (Sarawak); *Petermannia*
Begonia humbertii Keraudren-Aymonin; Africa: Madagascar; *Mezierea*
Begonia humboldtiana L.S. Gibbs; Asia: New Guinea; *Petermannia*
Begonia humilicaulis Irmscher; Asia: Indonesia (Sulawesi); *Petermannia*
Begonia humilis Dryand.; America: West Indies to Peru and Brazil; *Doratometra*
Begonia humillima L.B. Smith & Wasshausen; America: Venezuela (Yaracuy); ?
 (new section?)
Begonia hydrocotylifolia Otto ex Hook.; America: Mexico; *Gireoudia*
Begonia hydrophylloides L.B. Smith & Schubert; America: Colombia (Cundinamarca); *Knesebeckia*
Begonia hymenocarpa C.Y. Wu; Asia: China (Guangxi); *Diploclinium* II
Begonia hymenophylla Gagnep.; Asia: Laos; *Reichenheimia* III
Begonia hymenophylloides F.K. Ward ex L.B. Smith & Wasshausen; Asia: ?;
Diploclinium III ?
Begonia hypogaea Winkler = *B. laportefolia* Warb.
Begonia ignea Warzewicz; America: Guatemala, Costa Rica; *Knesebeckia*
Begonia ignorata Irmscher; Asia: Peninsular Malaysia; *Reichenheimia* I
Begonia imbricata M.J.S. Sands; Asia: Borneo (Sabah); *Petermannia*
Begonia imitans Irmscher; Asia: China (Szechuan); *Diploclinium* II
Begonia imperfecta Irmscher; Asia: Indonesia (Sulawesi); *Petermannia*
Begonia imperialis Lem.; America: Mexico; *Weilbachia*
Begonia incarnata Link & Otto; America: Mexico; *Knesebeckia*
Begonia incerta Craib; Asia: Thailand; *Diploclinium* III
Begonia incisa A. DC.; Asia: The Philippines (Luzon); *Petermannia*
Begonia incisoserrata A. DC.; America: Brazil (São Paulo to Minas Gerais);
Scheidweileria
Begonia incondita Craib; Asia: Thailand; *Diploclinium* I
Begonia inconspicua Brade; America: Brazil (Ceará); *Wageneria*
Begonia inculca Irmscher; America: Brazil (Espírito Santo); *Pritzelia*
Begonia inflata C.B. Clarke; Asia: India; *Sphenanthera*
Begonia inostegia Stapf; Asia: Borneo (Sabah); *Petermannia*
Begonia insularis Brade; America: Brazil (Sta Catarina); *Pritzelia*
Begonia insularum Irmscher; Asia: Indonesia (Sangir Island); *Petermannia*
Begonia integerrima Spreng.; America: Brazil (Rio de Janeiro, Minas Gerais, São Paulo); *Solananthera*
Begonia integrifolia Dalz.; Asia: India; *Platycentrum*
Begonia intermixta Irmscher; Asia: Thailand, Peninsular Malaysia; *Reichenheimia* III
Begonia inversa Irmscher; Asia: Indonesia (Sumatra); *Diploclinium* I
Begonia involucrata Liebm.; America: Costa Rica, Nicaragua, Panama; *Gireoudia*
Begonia ionophylla Irmscher; Asia: Indonesia (Sumatra); *Diploclinium* III
Begonia iridescens Dunn; Asia: India (Himalaya); *Platycentrum*
Begonia irmscheri L.B. Smith & Schubert; America: Colombia (Choco); *Semi-begoniella*
Begonia isabelensis Quisumb. & Merr.; Asia: The Philippines; *Diploclinium* I
Begonia isalensis Humbert ex Keraudren-Aymonin & Bosser; Africa: Madagascar;
Quadrilobaria
Begonia isoptera Dryander ex J.E. Smith; Asia: Indonesia (Java); *Petermannia*
Begonia isopterocarpa Irmscher; America: Brazil (Rio Grande do Sul); *Pritzelia*

Begonia isopteroidea King; Asia: Peninsular Malaysia; *Petermannia*
Begonia itaguassuensis Brade; America: Brazil (Espírito Santo); *Pritzelia*
Begonia itatiaiensis Brade; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia itatinensis Irmscher ex Brade; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia itupavensis Brade; America: Brazil (Paraná); *Pritzelia*
Begonia iucunda Irmscher; Africa: Congo, Dem. Rep. Congo; ? (new section?)
Begonia jagorii Warb.; Asia: The Philippines (Luzon); *Petermannia*
Begonia jairii Brade; America: Brazil (Paraíba); *Donaldia*
Begonia jaliscana Burt-Utley; America: Mexico (Jalisco); *Gireoudia*
Begonia jamaicensis A. DC.; America: Jamaica; *Begonia*
Begonia jenmanii Tutin; America: Guyana; *Pilderia* ?
Begonia jocelinoi Brade; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia johnstonii Oliv. ex Hook. f.; Africa: Kenya, Uganda, Tanzania; *Rostro-*
begonia
Begonia josephii A. DC.; Asia: India (Sikkim, Khasia); *Diploclinium* II
Begonia juliana Loefgr. ex Irmscher; America: Brazil (São Paulo); *Pritzelia*
Begonia juninensis Irmscher; America: Peru (Junin); *Ruizopavonia*
Begonia juntasensis O. Kuntze; America: Bolivia (La Paz, Cochabamba);
Hydristyles
Begonia jussiaeicarpa Warb. = *B. oxyanthera* Warb.
Begonia kalabenonensis Humbert ex Keraudren-Aymonin & Bosser; Africa: Mada-
 gascar; *Muscibegonia*
Begonia kalbreyeri (Oliv.) L.B. Smith & Schubert; America: Colombia (Antiqua,
 Caldes); *Semibegoniella*
Begonia kaniensis Irmscher; Asia: New Guinea; *Diploclinium* I
Begonia karwinskyana A. DC.; America: Mexico (Hidalgo); *Gireoudia*
Begonia karperi Arends; Africa: Gabon; *Tetraphila*
Begonia kautskyana O. Handro; America: Brazil (Espírito Santo); *Pritzelia* ?
Begonia kellermanii C. DC.; America: Guatemala; *Gireoudia*
Begonia kelliana Irmscher; Asia: New Guinea; *Petermannia*
Begonia keniensis Gilg ex Engl.; Africa: Kenya, Uganda; *Rostrobegonia*
Begonia kenworthyae Ziesenh.; America: Mexico (Chiapas); *Gireoudia*
Begonia keraudrenae Bosser; Africa: Madagascar; *Erminea*
Begonia kerrii Craib; Asia: Thailand; *Diploclinium* III
Begonia kerstingii Irmscher; Asia: New Guinea; *Petermannia*
Begonia khasiana C.B. Clarke; Asia: India (Khasia); ? (insufficient data)
Begonia killipiana L.B. Smith & Schubert; America: Colombia (Cauca); *Semi-*
begoniella
Begonia kinabaluensis M.J.S. Sands; Asia: Borneo (Sabah); *Petermannia*
Begonia kingiana Irmscher; Asia: Peninsular Malaysia; *Ridleyella*
Begonia kisuluana Büttn.; Africa: Nigeria to Uganda, south to Angola; *Tetraphila*
Begonia klainei Pierre ex Pellegrin = *B. hirsutula* Hook. f.
Begonia klemmei Merr.; Asia: The Philippines (Luzon); *Diploclinium* I
Begonia klossii Ridley; Asia: Peninsular Malaysia; *Platycentrum*
Begonia knoopii Ziesenh.; America: Mexico (Chiapas); *Gireoudia*
Begonia komoensis Irmscher; Africa: Gabon; *Tetraphila*
Begonia konder-reisiana L.B. Smith & R.C. Smith; America: Brazil (Sta Catarina);
Begonia ?
Begonia koordersii Warb. ex L.B. Smith & Wasshausen; Asia: Indonesia (Sula-
 wes); *Petermannia*
Begonia kortsiae Ziesenh.; America: Mexico (Oaxaca); *Gireoudia*
Begonia kouy-tcheouensis Guillaumin; Asia: China (Kweichow); *Platycentrum*

Begonia kuhlmannii Brade; America: Brazil (Rio de Janeiro); *Knesebeckia*
Begonia kunthiana Walp.; America: Venezuela; *Gaerdtia*
Begonia labordei Lévillé; Asia: China (Szechuan, Yunnan), Burma; *Diploclinium*
 III
Begonia lacera Merr.; Asia: The Philippines; *Petermannia*
Begonia lacerata Irmscher; Asia: China (Yunnan); *Platycentrum*
Begonia lachaoensis Ziesenh.; America: Mexico (Oaxaca); *Knesebeckia*
Begonia lacunosa Warb.; Africa: Cameroon, Gabon, Congo, Angola (Cabinda),
 Dem. Rep. Congo; *Scutobegonia*
Begonia laevis Ridley; Asia: Indonesia (Sumatra); *Petermannia*
Begonia lagunensis Elmer; Asia: The Philippines (Luzon); *Petermannia*
Begonia laminariae Irmscher; Asia: China (Yunnan); *Platycentrum*
Begonia lanceolata Vell.; America: Brazil (Rio de Janeiro, São Paulo); *Trachelo-*
carpus
Begonia lancifolia Merr.; Asia: The Philippines; *Petermannia*
Begonia lancilimba Merr.; Asia: The Philippines; *Diploclinium* I
Begonia langbianensis E.G. Baker; Asia: N. Vietnam; *Platycentrum* ? (no flowers)
Begonia lansbergeae L. Lind. & Rodigas; Asia: ?; *Diploclinium* I ? (no flowers)
Begonia lanstykii Brade; America: Brazil (Rio de Janeiro); *Begonia*
Begonia lanternaria Irmscher; Asia: China; *Coelocentrum*
Begonia laportefolia Warb.; Africa: Cameroon; *Scutobegonia*
Begonia larorum L.B. Smith & Wasshausen; America: Brazil (São Paulo); *Pritzelia*
Begonia latistipula Merr.; Asia: The Philippines; *Petermannia*
Begonia lauterbachii Warb.; Asia: New Guinea; *Petermannia*
Begonia laxa L.B. Smith & Schubert; America: Venezuela (Sucre); *Cyathocnemis*
Begonia lealii Brade; America: Brazil (Pernambuco); *Pritzelia*
Begonia leandrii Humbert ex Keraudren-Aymonin & Bosser; Africa: Madagascar;
Quadrilobaria
Begonia leathermaniae T. O'Reilly & Karegeannes; America: Bolivia; *Knesebeckia*
Begonia lecomtei Gagnep.; Asia: Indo-China; ? (new section?)
Begonia ledermannii Irmscher; Asia: New Guinea; *Petermannia*
Begonia lehmannii (Irmscher) L.B. Smith & Schubert; America: Colombia (Cauca);
Semibegoniella
Begonia leivae J. Sierra Calzado; America: Cuba; *Begonia*
Begonia le-maouti Hort. ex Vallerand; ?; ?; ? (female flowers not described)
Begonia lemurica Keraudren; Africa: Madagascar; *Erminea*
Begonia lepida Blume; Asia: Indonesia (Java); *Bracteibegonia*
Begonia lepidella Ridley; Asia: Indonesia (Sumatra); *Petermannia*
Begonia leprosa Hance; Asia: China (Canton); *Diploclinium* I ?
Begonia leptantha C.B. Robinson; Asia: The Philippines (Polillo); *Petermannia*
Begonia leptophylla Taub.; America: Brazil (Goyaz); ? (new section?)
Begonia leptoptera Hara; Asia: Nepal; *Diploclinium* II
Begonia leptostyla Irmscher; America: Bolivia; *Ruizopavonia* ? (no flowers)
Begonia lethomasiae Wilczek = *B. ebolowensis* Engl.
Begonia letouzeyi Sosef; Africa: Cameroon, Gabon, Congo; *Loasibegonia*
Begonia leucantha Ridley; Asia: Peninsular Malaysia (Perak); *Parvibegonia*
Begonia leuconeura Urban & Ekman; America: Haiti; *Begonia*
Begonia leucosticta Warb.; Asia: The Philippines (Luzon); *Petermannia*
Begonia libanensis Urban; America: Cuba; *Begonia*
Begonia libera (L.B. Smith & Schubert) L.B. Smith & Schubert; America: Colombia (Valle); *Semibegoniella*
Begonia lignescens Morton; America: Costa Rica; *Ruizopavonia*

Begonia limprichtii Irmscher; Asia: China (Szechuan); *Platycentrum*
Begonia lindleyana Walp.; America: Guatemala (hybrid?); *Gireoudia*
Begonia lindmanii Brade; America: Brazil (Mato Grosso); *Begonia*
Begonia linearifolia J. Sierra Calzado; America: Cuba; *Begonia*
Begonia lineolata Brade; America: Brazil (Sta Catarina); *Pritzelia*
Begonia lipingensis Irmscher; Asia: China (Kweichow); *Platycentrum*
Begonia lipolepis L.B. Smith; America: Venezuela (Táchira); *Casparya*
Begonia listada L.B. Smith & Wasshausen; America: Paraguay?; *Pritzelia*
Begonia lithophila C.Y. Wu; Asia: China (Yunnan); *Diploclinium* III
Begonia littleri Merr.; Asia: The Philippines (Basilan); *Platycentrum*
Begonia lobata Schott; America: Brazil (Rio de Janeiro, Minas Gerais); *Pritzelia* =
B. rufa Thunb.?
Begonia lobbii A. DC.; Asia: Indonesia (Java); *Reichenheimia* I
Begonia loheri Merr.; Asia: The Philippines (Luzon); *Petermannia*
Begonia loloensis Gilg = *B. elatostemmoides* Hook. f.
Begonia lomensis Britton & Wilson; America: Cuba; *Begonia*
Begonia longanensis C.Y. Wu; Asia: China (Guangxi); *Platycentrum*
Begonia longibarbata Brade; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia longibractea Merr.; Asia: The Philippines; *Petermannia*
Begonia longicaulis Ridley; Asia: Peninsular Malaysia; *Platycentrum*
Begonia longiciliata C.Y. Wu; Asia: China (Guizhou); *Platycentrum*
Begonia longifolia Blume; Asia: Indonesia (Java); *Sphenanthera*
Begonia longimaculata Irmscher; America: Peru; *Knesebeckia*
Begonia longinoda Merr.; Asia: The Philippines (Luzon); *Diploclinium* I
Begonia longipedunculata J. Golding & Karegeannes; Asia: Indonesia (Sumatra);
Platycentrum
Begonia longipetiolata Gilg; Africa: Nigeria to Dem. Rep. Congo; *Tetraphila*
Begonia longirostris Benth.; America: Colombia (Caldas, Valle), Ecuador; *Semi-*
begoniella
Begonia longiscapa Warb.; Asia: The Philippines (Leyte); *Diploclinium* I
Begonia longiseta Irmscher; Asia: Borneo (Sarawak); *Petermannia*
Begonia longistipula Merr.; Asia: The Philippines (Mindanao); *Petermannia*
Begonia longovillosa A. DC.; Asia: The Philippines (Luzon); *Diploclinium* I
Begonia lophoptera Rolfe; America: Peru (Pozuzu); *Cyathocnemis*
Begonia loranthoides Hook. f.; Africa: Cameroon to Dem. Rep. Congo, São
Tomé, Príncipe; *Tetraphila*
Begonia louis-williamsii Burt-Utley; America: Guatemala; *Gireoudia*
Begonia lowiana King; Asia: Peninsular Malaysia; *Platycentrum*
Begonia lubbersii E. Morr.; America: Brazil; *Gaerdia*
Begonia lucidissima J. Golding & Karegeannes; America: Paraguay (Asuncion);
Begonia ?
Begonia lucifuga Irmscher; America: Peru (Junin); *Cyathocnemis*
Begonia ludicra A. DC.; America: Mexico (Oaxaca), Guatemala, Panama;
Weilbachia
Begonia ludwigii Irmscher; America: Ecuador (Chimborazo); *Knesebeckia*
Begonia lugonis L.B. Smith & Wasshausen; America: Ecuador (Pastaza); *Knese-*
beckia ?
Begonia lunatistyla Irmscher; Asia: Borneo (Sarawak); *Petermannia* ?
Begonia lushaiensis C.E.C. Fischer; Asia: India (Misoram); *Diploclinium* II
Begonia lutea L.B. Smith & Schubert; America: Colombia (Meta, Vaupes);
Eupetalum ?
Begonia luxurians Scheidw.; America: Brazil (São Paulo to Minas Gerais);

Scheidweileria

- Begonia luzonensis* Warb.; Asia: The Philippines (Luzon); *Diploclinium* I
Begonia lyallii A. DC.; Africa: Madagascar; *Nervioplacentaria*
Begonia lyman-smithii Burt-Utley & Utley; America: Mexico (Oaxaca); *Gireoudia*
Begonia lynceorum Burt-Utley; America: Mexico (Veracruz); *Weilbachia*
Begonia macahensis Glaziou; America: Brazil (Rio de Janeiro); ?
Begonia macambrensis Exell = *B. subalpestris* A. Chev.
Begonia macdanielsii Standley; America: Mexico (Guerrero); *Quadriperigonia*
Begonia macduffteana L.B. Smith & Schubert; America: Brazil (Para); *Gaerdia*
Begonia macgregorii Merr.; Asia: The Philippines; *Petermannia*
Begonia machrisiana L.B. Smith & Schubert; America: Brazil (Goias); *Cyathocnemis* ?
Begonia macra A. DC.; America: Colombia (Cundinamarca); *Eupetalum*
Begonia macrocarpa Warb.; Africa: West & Central Africa; *Filicibegonia*
Begonia macrotis Vis.; ?; ?; ?
Begonia macrotoma Irmscher; Asia: China (Yunnan); *Platycentrum*
Begonia maculata Raddi; America: Brazil (Rio de Janeiro); *Gaerdia*
Begonia madecassa Keraudren; Africa: Madagascar; *Nervioplacentaria*
Begonia maestrensis Urban; America: Cuba; *Begonia*
Begonia magdalenae L.B. Smith & Schubert; America: Colombia (Magdalena);
Cyathocnemis
Begonia magdalenensis Brade; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia maguanensis Huang & Shui; Asia: China (Yunnan); *Platycentrum*
Begonia majungaensis Guillaumin; Africa: Madagascar; *Nervioplacentaria*
Begonia malabarica Lamk non A. DC.; Asia: India, Sri Lanka; new section?
Begonia malachosticta M.J.S. Sands; Asia: Borneo (Sabah); *Petermannia*
Begonia malindangensis Merr.; Asia: The Philippines (Mindanao); *Petermannia*
Begonia malipoensis Huang & Shui; Asia: China (Yunnan); *Diploclinium* I
Begonia malinquistiana Irmscher; Asia: New Guinea; *Petermannia*
Begonia mananjebensis Humbert ex Bosser & Keraudren-Aymonin; Africa: Madagascar; *Quadrilobaria*
Begonia mangorensis Humbert ex Bosser & Keraudren-Aymonin; Africa: Madagascar; *Nervioplacentaria* ?
Begonia manicata Brongn.; America: Mexico, Guatemala, Honduras, Nicaragua;
Gireoudia
Begonia manillensis A. DC.; Asia: The Philippines (Luzon); *Diploclinium* I
Begonia mannii Hook.; Africa: West & Central Africa; *Tetraphila*
Begonia maracayuensis Parodi; America: Paraguay (Canendiyu); ?
Begonia mariae L.B. Smith; America: Venezuela (Merida); *Casparya*
Begonia mariannensis Wasshausen & McLellan; America: Trinidad; *Knesebeckia* ?
Begonia mariti Burt-Utley; America: Mexico (Oaxaca); *Gireoudia*
Begonia marnieri Keraudren; Africa: Madagascar; *Nervioplacentaria*
Begonia marojejyensis Humbert; Africa: Madagascar; *Erminea*
Begonia martabanica A. DC.; Asia: Peninsular Malaysia, Burma; *Parvibegonia*
Begonia masarangensis Irmscher; Asia: Indonesia (Sulawesi); *Petermannia*
Begonia masoniana Irmscher; Asia: ? cult. Singapore; *Coelocentrum*
Begonia maurandiae A. DC.; America: Colombia, Ecuador; *Gobenia*
Begonia maxwelliana King; Asia: Peninsular Malaysia; *Platycentrum*
Begonia mayasiana L.B. Smith & Schubert; America: Peru; *Knesebeckia*
Begonia maynensis A. DC.; America: Ecuador, Peru; *Knesebeckia*
Begonia mayombensis Irmscher = *B. lacunosa* Warb.
Begonia mazae Ziesenh.; America: Mexico (Chiapas); *Gireoudia*

Begonia mbangaensis Sosef; Africa: Cameroon; *Scutobegonia*
Begonia mearnsii Merr.; Asia: The Philippines (Mindanao); *Petermannia*
Begonia media Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia megacarpa Merr.; Asia: The Philippines (Leyte); *Petermannia*
Begonia megalantha Merr.; Asia: The Philippines; *Petermannia*
Begonia megalophyllaria C.Y. Wu; Asia: China (Yunnan); *Platycentrum* ? (flowers
unknown)
Begonia megaptera A. DC.; Asia: India, Nepal, Burma; *Platycentrum*
Begonia membranacea A. DC.; America: Brazil; *Pritzelia*
Begonia mengtzeana Irmscher; Asia: China (Yunnan); *Platycentrum*
Begonia meridensis A. DC.; America: Venezuela (Merida, Sucre, Amazon); *Ruizo-*
pavonia
Begonia merrittii Merr.; Asia: The Philippines (Luzon); *Petermannia*
Begonia metallica W.G. Smith; America: Brazil (cult. ?); *Pritzelia*
Begonia mexicana Karst. ex Fotsch; America: Mexico (hybrid?); *Weilbachia*
Begonia meyeri-johannis Engl.; Africa: East Africa; *Mezierea*
Begonia meysselliana Linden; Asia?; Indonesia (Sumatra)?; ? (no flowers)
Begonia michoacana L.B. Smith & Schubert; America: Mexico (Michoacan);
Knesebeckia
Begonia micranthera Griseb.; America: Argentina (Salta, Tucumán); *Eupetalum*
Begonia microcarpa A. DC.; America: Colombia (Valle, Huila, Caqueta), Ecuador?;
Knesebeckia
Begonia microphylla A. DC.; America: Colombia (Santander); *Lepsia*
Begonia microptera Hook. f.; Asia: Borneo; ?
Begonia microsperma Warb.; Africa: Cameroon; *Loasibegonia*
Begonia mildbraedii Gilg; Africa: West & Central Africa; *Scutobegonia*
Begonia militaris L.B. Smith & Schubert; America: Guatemala; ? (new section?)
Begonia mindanaensis Warb.; Asia: The Philippines; *Petermannia*
Begonia mindorensis Merr.; Asia: The Philippines; *Diploclinium* I
Begonia minicarpa Hara; Asia: India, Nepal; *Diploclinium* II
Begonia minjemensis Irmscher; Asia: New Guinea; *Diploclinium* III
Begonia minor Jacq.; America: Jamaica; *Begonia*
Begonia minuta Sosef; Africa: Cameroon; *Loasibegonia*
Begonia minutifolia N. Hallé; Africa: Gabon; *Filicibegonia*
Begonia miranda Irmscher; Asia: China (Yunnan); *Diploclinium* II
Begonia modestiflora Kurz; Asia: Burma; *Diploclinium* II
Begonia molinana Burt-Utley; America: Honduras; *Knesebeckia* ?
Begonia molleri Warb.; Africa: São Tomé; *Tetraphila*
Begonia mollicaulis Irmscher; America: Brazil?; *Begonia*
Begonia mollis A. DC.; Asia: Indonesia; *Reichenheimia* I
Begonia monadelpha Ruiz & Pavon ex A. DC.; America: Peru (Amazonas, Liber-
tad, Hubnuco, Cuzco); *Barya*
Begonia monantha Warb.; Asia: New Guinea; *Petermannia*
Begonia monicae Aymonin & Bossier; Africa: Madagascar; *Erminea*
Begonia monophylla Pavon ex A. DC.; America: Mexico (Morelos, Guerrero,
Mexico); *Eupetalum* ?
Begonia montana Warb.; America: Venezuela (Merida, Táchira); *Casparya*
Begonia montis-bismarckii Warb.; Asia: New Guinea; *Petermannia*
Begonia morelii Irmscher ex Karegeannes; Asia: ?; *Reichenheimia* III
Begonia morifolia Yü; Asia: China (Yunnan); *Diploclinium* II
Begonia morii Burt-Utley; America: Panama; *Gireoudia*
Begonia morsei Irmscher; Asia: China; *Coelocentrum*

Begonia moszkowskii Irmscher; Asia: New Guinea; *Petermannia*
Begonia mouleimensis C.B. Clarke; Asia: Burma; *Diploclinium* III
Begonia moysesii Brade; America: Brazil (São Paulo); *Pritzelia*
Begonia mucronistipula C. DC.; America: Panama; *Gireoudia* ?
Begonia multiensis Yü; Asia: China (Sikang, Yunnan); *Diploclinium* III
Begonia multangula Blume; Asia: Indonesia (Java); *Sphenanthera*
Begonia multidentata Warb.; Asia: New Guinea; *Petermannia*
Begonia multiflora Benth.; America: Colombia; *Ruizopavonia*
Begonia multinervia Liebm.; America: Costa Rica, Panama; *Gireoudia*
Begonia multistaminea Burt-Utley; America: Mexico (Veracruz); *Gireoudia*
Begonia muricata Blume; Asia: Indonesia (Java); *Reichenheimia* I
Begonia murina Craib; Asia: Thailand; *Diploclinium* II
Begonia murudensis Merr.; Asia: Borneo (Sarawak); *Petermannia*
Begonia mutabilis Harland; ?; ?; ?
Begonia mystacina L.B. Smith & Wasshausen; Asia: New Guinea; *Petermannia*
Begonia nana L'Hér.; Africa: Madagascar; *Erminea*
Begonia napoensis L.B. Smith & Wasshausen; America: Ecuador (Napó); *Semi-*
begoniella
Begonia naumoniensis Irmscher; Asia: New Guinea; *Petermannia*
Begonia ndongensis Engl. = *B. mannii* Hook.
Begonia neglecta A. DC.; America: Brazil (Bahia); *Pritzelia*
Begonia negrosensis Elmer; Asia: The Philippines (Negros); *Petermannia*
Begonia nelumbiifolia Cham. & Schlecht.; America: Mexico (Chiapas) to Colombia;
Gireoudia
Begonia nemoralis L.B. Smith & Schubert; America: Mexico (Michoacán); *Knese-*
beckia
Begonia neocomensium A. DC.; America: Brazil (Bahia); *Pritzelia*
Begonia neoharlingei L.B. Smith & Wasshausen; America: Ecuador (Loja);
Eupetalum
Begonia neoperrieri Humbert ex Keraudren-Aymonin & Bosser; Africa: Mada-
 gascar; *Quadrilobaria*
Begonia neopurpurea L.B. Smith & Wasshausen; Asia: The Philippines; *Diplo-*
clinium I ?
Begonia nepalensis (A. DC.) Warb.; Asia: India (Sikkim), Nepal; *Monopteron*
Begonia nicolai-hallei Wilczek = *B. longipetiolata* Gilg
Begonia nigritarum (Kamel) Steud.; Asia: The Philippines; *Diploclinium* I
Begonia nivea Parish ex Kurz; Asia: Burma; *Reichenheimia* III
Begonia northiana Hort. ex Gentil; ?; ?; ?
Begonia nossibeae A. DC.; Africa: Madagascar; *Quadrilobaria*
Begonia notata Craib; Asia: Thailand; *Diploclinium* II
Begonia notiophila Urban; America: Haiti; *Begonia*
Begonia novogranatae A. DC.; America: Colombia (Cundinamarca); *Eupetalum*
Begonia novoguineensis Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia nubicola L.B. Smith & Schubert; America: Venezuela (Amazonas);
Cyathocnemis ?
Begonia nuda Irmscher; America: Brazil (São Paulo); *Pritzelia*
Begonia nummulariifolia Putzeys; America: Colombia (Norte de Santander); ?
Begonia nurii Irmscher; Asia: Peninsular Malaysia; *Reichenheimia* I
Begonia nyassensis Irmscher; Africa: Malawi; *Rostrobegonia*
Begonia nymphaeifolia Yü; Asia: China (Yunnan); *Reichenheimia* I
Begonia oaxacana A. DC.; America: Mexico, Guatemala, Costa Rica, El Salvador;
Parietoplacentalia

Begonia oblanceolata Rusby; America: Bolivia (Cochabamba); *Ruizopavonia*
Begonia obliqua L.; America: Martinique; *Begonia*
Begonia oblongata Merr.; Asia: The Philippines; *Petermannia*
Begonia oblongifolia Stapf; Asia: Borneo (Sarawak); *Petermannia*
Begonia obovatistipula C. DC.; America: Paraguay; *Pritzelia* ?
Begonia obovoidea Craib; Asia: Thailand; *Sphenanthera*
Begonia obscura Brade; America: Brazil (Espírito Santo); *Pritzelia*
Begonia obsolescens Irmscher; Asia: China; *Coelocentrum*
Begonia obtecticaulis Irmscher; America: Peru; *Ruizopavonia*
Begonia obtusifolia Merr.; Asia: The Philippines; *Diploclinium* I
Begonia obversa C.B. Clarke; Asia: India; *Platycentrum*
Begonia occhionii Brade; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia octopetala L'Hér.; America: Ecuador, Peru (Lima); *Eupetalum*
Begonia odeteiantha Handro; America: Brazil (São Paulo); *Pritzelia*
Begonia odorata Willd.; America: Guadeloupe; *Begonia*
Begonia oellgaardii L.B. Smith & Wasshausen; America: Ecuador (Napó); *Knesebeckia*
Begonia olbia Kerchove; America: Brazil; *Knesebeckia*
Begonia oligandra Merr. & L.M. Perry; Asia: New Guinea; *Diploclinium* II ?
Begonia oligantha Merr.; Asia: The Philippines; *Petermannia*
Begonia oligocarpa A. DC. ex Koord.; Asia: India; ? (nomen)
Begonia oligophylla Blume ex Miq. = *Chirita asperifolia* (Blume) Burt (Gesneriaceae)
Begonia oliveri L.B. Smith & Schubert; America: Colombia (Choco); *Semibegoniella*
Begonia olsoniae L.B. Smith & Schubert; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia ophiogyna L.B. Smith & Schubert; America: Colombia (Magdalena); *Hydristyles* ?
Begonia opuliflora Putz.; America: Panama; *Ruizopavonia* ?
Begonia opulifolia Loud.; ?; ?; ?
Begonia orbiculata Jack; Asia: Indonesia (Sumatra); *Diploclinium* I ?
Begonia orchidiflora Griff.; Asia: India; ? (imperfectly described)
Begonia oreodoxa W.Y. Chun & F. Chun; Asia; China (Yunnan); *Platycentrum*
(female flowers unknown)
Begonia organensis Brade; America: Brazil (Rio de Janeiro); *Begonia*
Begonia ornithocarpa Standley; America: Mexico (Nayarit); *Quadriperigon* ? (no flowers)
Begonia ornithophylla Irmscher; Asia: China; *Coelocentrum*
Begonia otophora Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia otophylla L.B. Smith & Schubert; America: Venezuela (Sucre); *Pritzelia*
Begonia ovatifolia A. DC.; Asia: India (Sikkim, Khasia); *Diploclinium* III
Begonia oxyanthera Warb.; Africa: Nigeria, Cameroon, Equatorial Guinea (Bioko); *Tetraphila*
Begonia oxyloba Welw. ex Hook. f.; Africa: tropical Africa, Madagascar; *Meziera*
Begonia oxyphylla A. DC.; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia oxysperma A. DC.; Asia: The Philippines (Luzon); *Baryandra*
Begonia oxyura Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia pachyrhachis L.B. Smith & Wasshausen; Asia: Indonesia (Java?); *Sphenanthera*
Begonia padangensis Irmscher; Asia: Indonesia (Sumatra); *Petermannia*
Begonia palawanensis Merr.; Asia: The Philippines (Palawan); *Petermannia*
Begonia paleacea Kurz; Asia: Burma; *Monophyllon*

Begonia paleata A. DC.; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia palmata D. Don; Asia: India, Nepal, Burma, China; *Platycentrum*
Begonia palmatiloba Linden & André; America: ?; ?
Begonia palmeri S. Wats.; America: Mexico; *Quadriperigonia*
Begonia panayensis Merr.; Asia: The Philippines (Panay); *Petermannia*
Begonia paniculata Parodi; America: Paraguay; ?
Begonia pantherina Putz. ex Linden; America: ?; ?
Begonia papillaris Hort. Paris ex Cels; ?; ?; ?
Begonia papuana Warb.; Asia: New Guinea; *Petermannia*
Begonia paraguayensis Parodi; America: Paraguay (Cordillera); ?
Begonia paranaensis Brade; America: Brazil (Paraná); *Pritzelia*
Begonia parcifolia C. DC.; America: Ecuador (El Oro, Loja); *Knesebeckia*
Begonia parilis Irmscher; America: Brazil (Sta Catarina); *Pritzelia*
Begonia parishii C.B. Clarke; Asia: Burma; *Parvibegonia*
Begonia parodiana L.B. Smith & Schubert; America: Argentina (Salta); *Knese-*
beckia
Begonia parva Merr.; Asia: The Philippines (Luzon); *Diploclinium* I
Begonia parviflora Poepp. & Endl.; America: Colombia, Ecuador, Peru, Bolivia;
Scheidweileri
Begonia parvifolia Schott; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia parvilimba Merr.; Asia: The Philippines; *Petermannia*
Begonia parvistipulata Irmscher; America: Brazil (Sta Catarina); *Pritzelia*
Begonia parvula Léveillé & Vaniot; Asia: China (Yunnan); *Reichenheimia* III
Begonia parvuliflora A. DC.; Asia: Burma; *Diploclinium* II
Begonia pastoensis A. DC.; America: Colombia (Nariño); *Knesebeckia*
Begonia patula Haw. = *B. fischeri* Schrank
Begonia paucilobata C.Y. Wu; Asia: China (Yunnan); *Platycentrum*
Begonia paulensis A. DC.; America: Brazil (São Paulo); *Pritzelia*
Begonia paupercula King; Asia: Peninsular Malaysia; *Platycentrum*
Begonia pavonina Ridley; Asia: Peninsular Malaysia; *Platycentrum* ?
Begonia pearcei Hook. f.; America: Bolivia (La Paz?); *Eupetalum*
Begonia pectennervia L.B. Smith & Wasshausen; America: Ecuador; *Semibego-*
niella
Begonia pedata Liebm.; America: Mexico (Oaxaca); *Quadriperigonia*
Begonia pedatifida Léveillé; Asia: China (Szechuan, Hupeh, Kweichow); *Platy-*
centrum
Begonia pediophylla Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia pedunculosa Wall.; Asia: India (Khasia, Bhutan); *Diploclinium* II
Begonia peekelii Irmscher; Asia: Papua New Guinea (Bismarck Archipelago);
Petermannia
Begonia peii C.Y. Wu; Asia: China (Yunnan); *Parvibegonia*
Begonia pelargoniflora J.J. de Wilde & Arends; Africa: Cameroon, Equatorial
Guinea (Bioko); *Tetraphila*
Begonia peltata Otto & Dietr.; America: Mexico, Guatemala; *Gireoudia*
Begonia peltatifolia Li; Asia: China (Hainan); *Reichenheimia* I ?
Begonia peltifolia Schott; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia peltigera Irmscher; America: Peru; *Hydristyles*
Begonia pendula Ridley; Asia: Borneo (Sarawak); *Petermannia*
Begonia peninsulae Irmscher; Asia: Peninsular Malaysia; *Reichenheimia* I
Begonia pensilis L.B. Smith & Wasshausen; America: St Vincent; *Begonia*
Begonia pentaphragmifolia Ridley; Asia: New Guinea; *Petermannia*
Begonia pentaphylla Walp.; America: Brazil (Rio de Janeiro); *Scheidweileri*

Begonia peperomioides Hook. f.; Africa: Gabon; *Scutobegonia*
Begonia perakensis King; Asia: Peninsular Malaysia; *Platycentrum*
Begonia per-dusenii Brade; America: Brazil (Sta Catarina); *Begonia*
Begonia peristegia Stapf; America: Brazil?; *Pritzelia*
Begonia pernambucensis Brade; America: Brazil (Pernambuco); *Pritzelia*
Begonia perpusilla A. DC.; Africa: Madagascar; *Muscibegonia*
Begonia perrieri Bois; Africa: Madagascar; ? (imperfectly known)
Begonia perryae L.B. Smith & Wasshausen; Asia: The Philippines (Luzon); *Petermannia*
Begonia peruibensis O. Handro; America: Brazil (São Paulo); *Pritzelia* ?
Begonia peruviana A. DC.; America: Peru (Huanuco, Junin, Cuzco); *Ruizopavonia*
Begonia petasitifolia Brade; America: Brazil (Bahia); *Pritzelia*
Begonia philodendroides Ziesenh.; America: Mexico (Oaxaca, Chiapas); *Gireoudia*
Begonia phoeniogramma Ridley; Asia: Peninsular Malaysia; *Parvibegonia*
Begonia phrixophylla Blatter & McCann; Asia: India; *Reichenheimia* II
Begonia physandra Merr. & L.M. Perry; Asia: New Guinea; ? (new section?)
Begonia pickelii Irmscher; America: Brazil (Pernambuco); *Pritzelia*
Begonia picta J.E. Smith; Asia: India; *Diploclinium* II
Begonia pierreii Gagnep.; Asia: Indo-China; *Reichenheimia* III
Begonia pilderifolia C. DC.; America: Brazil (Ceara); *Pritzelia* ?
Begonia pilgeriana Irmscher; America: Brazil (Sta Catarina); *Pritzelia*
Begonia pilosa Jack; Asia: Indonesia (Sumatra); *Petermannia*
Begonia pilosella Irmscher; America: Peru (Cuzco); *Ruizopavonia*
Begonia pinamalayensis Merr.; Asia: The Philippines; *Diploclinium* I
Begonia pinetorum A. DC.; America: Mexico (Veracruz, Chiapas, Oaxaca);
Gireoudia
Begonia pingbiensis C.Y. Wu; Asia: China (Yunnan), Vietnam; *Diploclinium* I
Begonia pinnatifida Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia piperoides Linden; ?; ?; ?
Begonia piresiana Handro; America: Brazil (São Paulo); *Pritzelia*
Begonia piurensis L.B. Smith & Schubert; America: Ecuador (Azuay); *Knesebeckia*
Begonia plantaginea L.B. Smith & Schubert; America: Mexico (Chiapas); *Gireoudia*
Begonia platanifolia Schott; America: Brazil; *Knesebeckia*
Begonia platyphylla Merr.; Asia: The Philippines; *Petermannia*
Begonia platyptera Urban; America: Haiti; *Begonia*
Begonia plebeja Liebm.; America: Mexico, Central America; *Gireoudia*
Begonia pleioclada Irmscher; Asia: Borneo (Sarawak); *Petermannia*
Begonia pleiopetala A. DC.; America: Peru (Huancabamba, Sandia), Bolivia (La Paz); *Eupetalum*
Begonia plumieri A. DC.; America: Sto Domingo; *Begonia*
Begonia poculifera Hook. f.; Africa: Nigeria to Tanzania and Angola; *Squamibegonia*
Begonia poecila C. Koch; Asia: India (Himalaya); *Platycentrum*
Begonia polyandra Irmscher; America: Brazil (Sta Catarina); *Pritzelia*
Begonia polygonata Liebm.; America: Mexico, Honduras; *Gireoudia*
Begonia polygonifolia A. DC.; America: Brazil; *Wagneria*
Begonia polygonoides Hook. f.; Africa: West & Central Africa; *Tetraphila*
Begonia polypetala A. DC.; America: Peru; *Eupetalum*
Begonia polytricha C.Y. Wu; Asia: China (Yunnan); *Platycentrum* ? (fruits unknown)
Begonia popenoei Standley; America: Honduras; *Weilbachia* ?
Begonia porteana Van Geert; Asia: ?; ?

Begonia porteri Léveillé & Vaniot; Asia: China; *Coelocentrum*
Begonia portillana S. Wats.; America: Mexico; *Quadriperigonia*
Begonia potamophila Gilg; Africa: Cameroon, Gabon, Congo; *Loasibegonia*
Begonia praerupta Irmscher; America: Colombia (El Cauca); *Lepsia* ?
Begonia preseriana Hort.; ?; ?; ?
Begonia prieurii A. DC.; America: Guyana; *Doratometra*
Begonia preussii Warb.; Africa: Nigeria, Cameroon, Equatorial Guinea (Bioko);
Tetraphila
Begonia princeae Gilg; Africa: Central, East & southern Africa; *Augustia*
Begonia princeps A. DC.; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia pringlei S. Wats.; America: Mexico; *Gireoudia*
Begonia prionophylla Irmscher; America: Peru (Huanuco); *Ruizopavonia*
Begonia prismatocarpa Hook.; Africa: Ivory Coast, Cameroon, Equatorial Guinea
(Bioko); *Loasibegonia*
Begonia procrifolia Wall. ex A. DC.; Asia: Burma (Martaban); *Parvibegonia*
Begonia prolifera A. DC.; Asia: Burma, Peninsular Malaysia; *Monophyllon*
Begonia promixa Craib; Asia: Thailand; *Platycentrum*
Begonia promethea Ridley; Asia: Borneo (Sarawak); *Petermannia* ?
Begonia propinqua Ridley; Asia: Borneo (Sarawak); *Petermannia*
Begonia prostrata Irmscher; Asia: China (Yunnan); *Sphenanthera*
Begonia pruinata (Klotzsch) A. DC.; America: Costa Rica; *Gireoudia*
Begonia pryeriana Ridley; Asia: Borneo (Sarawak); *Petermannia*
Begonia pseudisoptera Irmscher; Asia: Peninsular Malaysia; *Petermannia*
Begonia pseudodryadis C.Y. Wu; Asia: China (Yunnan); *Platycentrum* ? (female
flowers unknown)
Begonia pseudoglauca Irmscher; America: Peru (Huanuco); *Cyathocnemis*
Begonia pseudolateralis Warb.; Asia: The Philippines; *Sphenanthera*
Begonia pseudolubbersii Brade; America: Brazil (Rio de Janeiro); *Gaerdtia*
Begonia pseudoviola Gilg; Africa: Cameroon; *Loasibegonia*
Begonia psilophylla Irmscher; Asia: China (Yunnan); *Platycentrum*
Begonia pubescens Ridley; Asia: Borneo (Sarawak); *Petermannia*
Begonia pudica L.B. Smith & Schubert; America: Mexico (Hidalgo); *Gireoudia*
Begonia pulchella Raddi; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia pulcherrima Sosef; Africa: Rwanda, Burundi; *Loasibegonia*
Begonia pululahuana C. DC.; America: Ecuador (Napo, Pichincha); *Gobenia*
Begonia pumila Craib; Asia: Thailand; *Ridleyella* ?
Begonia pumilio Irmscher; Asia: Thailand; *Reichenheimia* III
Begonia purdieana A. DC.; America: Jamaica; *Begonia*
Begonia purpureofolia Huang & Shui; Asia: China (Yunnan); *Platycentrum*
Begonia purpusii Houghton ex Ziesenh.; America: Mexico (Chiapas); *Weilbachia*
Begonia pustulata Liebm.; America: Mexico (Oaxaca); *Weilbachia*
Begonia putii Craib; Asia: Thailand; *Diploclinium* III
Begonia putzeysii Hort.; ?; ?; ?
Begonia pycnantha Urban & Ekman; America: Haiti; *Begonia*
Begonia pygmaea Irmscher; Africa: Zambia; *Augustia*
Begonia pyrrha Ridley; Asia: Borneo (Sarawak); *Diploclinium* I ?
Begonia quadrialata Warb.; Africa: West & western Central Africa; *Loasibegonia*
Begonia quaternata L.B. Smith & Schubert; America: Costa Rica, Panama;
Gireoudia
Begonia quercifolia A. DC.; Asia: The Philippines; *Petermannia*
Begonia quietamensis L.B. Smith & Schubert = *B. novogranatae* A. DC.
Begonia rabilii Craib; Asia: Thailand; *Reichenheimia* III ?

Begonia racemiflora Ortigies ex C. Chev.; America: Mexico; *Quadriperigonina* ?
Begonia racemosa Jack; Asia: Indonesia (Sumatra); *Petermannia*
Begonia radicans Vell.; America: Brazil (Rio de Janeiro to Rio Grande do Sul);
Solananthera
Begonia rafaël-torresii Burt-Utley; America: Mexico (Oaxaca); *Gireoudia*
Begonia raimondii Irmscher; America: Peru (Janin); *Casparya*
Begonia rajah Ridley; Asia: Peninsular Malaysia; *Reichenheimia* I
Begonia ramentacea Paxt.; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia ramosa Sosef = *B. schaeferi* Engl.
Begonia ramosii Merr.; Asia: The Philippines (Luzon); *Petermannia*
Begonia randiana Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia ravenii C.I. Peng & Y.K. Chen; Asia: Taiwan; *Diploclinium* II
Begonia raynallorum Wilczek = *B. ciliobracteata* Warb.
Begonia razafinjohanyi Aymonin & Bosser; Africa: Madagascar; *Erminea*
Begonia reflexisquamata C.Y. Wu; Asia: China (Yunnan); *Platycentrum*
Begonia relicta L.B. Smith & Schubert; America: Mexico; *Knesebeckia*
Begonia renifolia Irmscher; Asia: Indonesia (Sulawesi); *Sphenanthera*
Begonia reniformis Dryand.; America: Brazil (Ceara to São Paulo); *Pritzelia*
Begonia repens Lamk; America: Haiti; *Begonia*
Begonia repenticaulis Irmscher; Asia: China (Yunnan); *Platycentrum*
Begonia reptans Benth.; America: Mexico; *Weilbachia* ?
Begonia retusa O.E. Schulz; America: Caribbean Islands; *Begonia*
Begonia rex Putz.; Asia: India (Himalaya); *Platycentrum*
Begonia rheifolia Irmscher; Asia: Peninsular Malaysia; *Platycentrum*
Begonia rhizocaulis (Klotzsch) A. DC.; America: Mexico ?; *Gireoudia*
Begonia rhodantha Ridley; Asia: New Guinea; *Petermannia*
Begonia rhodochlamys L.B. Smith & Schubert; America: Mexico (Michoacan);
Quadriperigonina
Begonia rhodophylla C.Y. Wu; Asia: China (Yunnan); *Diploclinium* II
Begonia rhoephila Ridley; Asia: Peninsular Malaysia; *Platycentrum*
Begonia rieckei Warb.; Asia: New Guinea; *Petermannia*
Begonia riedelii A. DC.; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia rigida Linden ex Regel; America: Brazil; *Pritzelia*
Begonia rimarum Craib; Asia: Thailand; *Parvibegonia*
Begonia riparia Irmscher; Africa: Tanzania; *Augustia*
Begonia rizalensis Merr.; Asia: The Philippines (Luzon); *Petermannia*
Begonia robinsonii Ridley; Asia: Peninsular Malaysia; *Platycentrum*
Begonia robusta Blume; Asia: Indonesia (Java); *Sphenanthera*
Begonia rockii Irmscher; Asia: Burma; *Platycentrum*
Begonia rodwellii Hort.; ?; ?; ?
Begonia roezlii Regel; America: Peru; *Cyathocnemis*
Begonia rongjiangensis T.C. Ku; Asia: China (Guizhou); *Diploclinium* II ?
Begonia rosacea Putz.; America: Colombia (Cundinamarca, Meta?); *Eupetalum*
Begonia roseibractea Ziesenh.; America: Mexico (Oaxaca); *Gireoudia*
Begonia rossmanniae A. DC.; America: Colombia, Peru, Ecuador; *Rossmannia*
Begonia rostrata Welw. ex Hook. f.; Africa: West & Central Africa; *Rostrobegonia*
Begonia rotunda Vell.; America: Brazil; *Pritzelia* ? (no flowers)
Begonia rotundifolia Lamk; America: West Indies; *Begonia*
Begonia rotundilimba Huang & Shui; Asia: China (Yunnan); *Diploclinium* I
Begonia roxburghii A. DC.; Asia: India, Nepal, Burma; *Sphenanthera*
Begonia rubella Buch.-Ham. ex D. Don; Asia: Nepal; *Diploclinium* II
Begonia rubida Ridley; Asia: Borneo (Sarawak); *Petermannia*

Begonia rubiginosipes Irmscher; America: Peru (Junin); *Ruizopavonia*
Begonia ruboides C.M. Hu; Asia: China (Yunnan); *Diploclinium* I
Begonia rubricaulis Hook.; America: Argentina (Jujuy, Tucumán); *Eupetalum*
Begonia rubrifolia Merr.; Asia: The Philippines; *Diploclinium* I
Begonia rubromarginata Gilg; Africa: Nigeria, Cameroon; *Tetraphila*
Begonia rubronervata De Wild.; Africa: Dem. Rep. Congo; *Tetraphila*
Begonia rubropilosa A. DC.; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia rubropunctata Huang & Shui; Asia: China (Yunnan); *Platycentrum*
Begonia rubrosetulosa A. DC.; Asia: Indonesia? (cult. Hort. Bogor); = *B. malab-*
rica Lamk non A. DC.?
Begonia rubrotincta L.B. Smith & Schubert; America: Peru (Amazonas); *Gobenia*
Begonia rufa Thunb.; America: Brazil (Minas Gerais); *Pritzelia*
Begonia rufipila Merr.; Asia: The Philippines (Luzon); *Diploclinium* I
Begonia rufosericea Toledo; America: Brazil (São Paulo); *Pritzelia*
Begonia ruhlandiana Irmscher; America: Brazil (Bahia); *Pritzelia*
Begonia rumpiensis Kupicha; Africa: Malawi; *Rostrobegonia*
Begonia rupicola Miq.; Asia: Indonesia (Java); *Parvibegonia*
Begonia rupium Irmscher; America: Brazil (Sta Catarina); *Pritzelia*
Begonia rutilans Hort. Van-Houtte ex A. DC.; America: Brazil ?; *Pritzelia*
Begonia rwandensis Arends; Africa: Dem. Rep. Congo, Rwanda; *Tetraphila*
Begonia salaziensis (Gaud.) Warb.; Africa: Réunion, Mauritius; *Meziera*
Begonia salicifolia A. DC.; America: Brazil (Rio de Janeiro); *Gaerdnia*
Begonia salisburyana Irmscher; Africa: Nigeria; *Loasibegonia*
Begonia salomonensis Merr. & L.M. Perry; Asia: The Solomon Islands (Ulawa);
Petermannia
Begonia samarensis Merr.; Asia: The Philippines (Samar); *Petermannia*
Begonia sambiranensis Humbert ex Keraudren-Aymonin & Bosser; Africa: Mada-
gascar; *Quadrilobaria*
Begonia sandalifolia C.B. Clarke; Asia: Burma; *Platycentrum*
Begonia sandtii Houghton ex Ziesenh.; America: Mexico (Oaxaca or Guerrero);
Quadriperigonia
Begonia sanguinea Raddi; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia sanjeensis Wilczek = *B. ebolowensis* Engl.
Begonia santarosensis O. Kuntze; America: Bolivia (Cochabamba); *Hydristyles*
Begonia santos-limae Brade; America: Brazil (Rio de Janeiro); *Knesebeckia*
Begonia sarasinorum Irmscher; Asia: Indonesia (Sulawesi); *Petermannia*
Begonia sarawakensis Ridley; Asia: Borneo (Sarawak); *Petermannia*
Begonia sarcocarpa Ridley; Asia: Indonesia (Sumatra); *Sphenanthera*
Begonia sarcophylla Liebm.; America: Mexico, Guatemala; *Gireoudia*
Begonia sarmentacea Hort. ex Brilmayer = *B. sementacea* Hort.
Begonia sarmentosa L.B. Smith & Wasshausen; Asia: Philippines; *Petermannia*
Begonia satrapis C.B. Clarke; Asia: India (Sikkim); *Diploclinium* II
Begonia saxicola A. DC.; America: Brazil (Bahia); *Donaldia*
Begonia saxifraga A. DC.; America: Brazil (Bahia); *Pritzelia*
Begonia saxifragifolia Craib; Asia: Thailand; *Diploclinium* III
Begonia scabrida A. DC.; America: Venezuela (Fed. Distr., Sucre); *Pritzelia*
Begonia scabridoidea L.B. Smith & Wasshausen; America: ?; ?
Begonia scapigera Hook. f.; Africa: Nigeria, Cameroon, Gabon, Congo; *Loasibe-*
gonia
Begonia schaeferi Engl.; Africa: Nigeria, Cameroon; *Loasibegonia*
Begonia scharffiana Regel; America: Brazil (Sta Catarina, cult. ?); *Pritzelia*
Begonia scharffii Hook. f.; America: Brazil (Sta Catarina, cult. ?); *Pritzelia*

Begonia schenckii Irmscher; America: Brazil (Sta Catarina); *Begonia*
Begonia schlechteri Gilg = *B. laportefolia* Warb.
Begonia schliebenii Irmscher; Africa: Tanzania; *Rostrobegonia*
Begonia schlumbergeriana Lem.; America: ? probably a hybrid; *Pritzelia*
Begonia schmidiana Regel; America: Brazil; *Begonia*
Begonia schulziana Urban & Ekman; America: Haiti; *Begonia*
Begonia sciadiophora L.B. Smith & Schubert; America: Guatemala; *Begonia* ?
Begonia sciaphila Gilg ex Engl.; Africa: Cameroon, Gabon, Angola (Cabinda);
Filicibegonia
Begonia scintillans Dunn; Asia: India (Arunachal Pradesh); *Diploclinium* I ?
Begonia scitifolia Irmscher; Asia: China (Yunnan); *Platycentrum*
Begonia scortechinii King; Asia: Peninsular Malaysia; *Platycentrum*
Begonia scutifolia Hook. f.; Africa: Cameroon, Equatorial Guinea, Gabon, Angola
(Cabinda), Dem. Rep. Congo; *Loasibegonia*
Begonia scutulium Hook. f.; Africa: Gabon; *Scutobegonia*
Begonia secunda L.B. Smith & Wasshausen; America: Ecuador (Pichincha);
Gobenia
Begonia seemanniana A. DC.; America: Costa Rica, Panama; *Ruizopavonia*
Begonia segregata L.B. Smith & Schubert; America: Colombia (Nariño), Ecuador
(Carchi); *Gobenia*
Begonia sementacea Hort.; America: Brazil; *Pritzelia*
Begonia semidigitata Brade; America: Brazil (Rio de Janeiro); *Scheidweilera*
Begonia semiovata Liebm.; America: Mexico and Guyana to Peru; *Doratometra*
Begonia sericoneura Liebm.; America: Mexico (Chiapas, Oaxaca); *Gireoudia*
Begonia serotina A. DC.; America: Ecuador (4 prov.); *Knesebeckia*
Begonia serpens Merr.; Asia: The Philippines; *Diploclinium* I
Begonia serraticauda Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia serratipetala Irmscher; Asia: New Guinea; *Petermannia*
Begonia sessilantha Warb. = *B. preusii* Warb.
Begonia sessilifolia Hook. f.; Africa: Cameroon to Congo, incl. Equatorial Guinea
(Bioko); *Filicibegonia*
Begonia setifolia Irmscher; Asia: China (Yunnan); *Platycentrum* ?
Begonia setulosa Bertol.; America: Guatemala; *Gireoudia* ?
Begonia setulosa-peltata C.Y. Wu; Asia: China (Guangxi); *Coelocentrum*
Begonia seychellensis Hemsl.; Africa: Seychelles; *Meziera*
Begonia sharpeana F. Muell.; Asia: New Guinea; *Diploclinium* I
Begonia siamensis Gagnep.; Asia: Thailand, Laos; *Platycentrum*
Begonia sibthorpioides Ridley; Asia: Peninsular Malaysia; *Heeringia*
Begonia sikkimensis A. DC.; Asia: India (Sikkim); *Platycentrum*
Begonia silletensis (A. DC.) C.B. Clarke; Asia: India; *Sphenanthera*
Begonia simulans Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia sino-vietnamica C.Y. Wu; Asia: China (Guangxi); *Diploclinium* I
Begonia sinuata Wall. ex Meissner; Asia: India, Burma, Thailand, Peninsular
Malaysia; *Parvibegonia*
Begonia sleumeri L.B. Smith & Schubert; America: Argentina (Jujuy); *Eupetalum*
Begonia smilacina A. DC.; America: Brazil (Amada); *Wageneria*
Begonia smithiae Geddes; Asia: Thailand; *Platycentrum*
Begonia smithiana Yü ex Irmscher; Asia: China (Kweichow); *Platycentrum*
Begonia socia Craib; Asia: Thailand; *Parvibegonia*
Begonia socotrana Hook. f.; Africa: Socotra; *Peltaugustia*
Begonia sodiroi C. DC.; America: Ecuador (4 prov.); *Gobenia*
Begonia sogerensis Ridley; Asia: New Guinea; *Petermannia*

Begonia solanthera A. DC.; America: Brazil (Rio de Janeiro); *Solanthera*
Begonia soli-mutata L.B. Smith & Wasshausen; America: Brazil (Pará, cult.);
Pritzelia
Begonia solitudinis Brade; America: Brazil (Sta Catarina); *Pritzelia*
Begonia soluta Craib; Asia: Thailand; *Diploclinium* III
Begonia somervillei Hemsl.; Asia: The Solomon Islands; *Petermannia*
Begonia sonderana Irmscher; Africa: Zambia, Mozambique, South Africa; *Rostro-*
begonia
Begonia soror Irmscher; America: Peru (Amazonas); *Barya*
Begonia sorsogonensis Elmer; Asia: The Philippines (Luzon); *Petermannia*
Begonia sousae Burt-Utley; America: Mexico (Veracruz); *Gireoudia*
Begonia spadiciflora L.B. Smith & Schubert; America: Colombia (Antiquia);
Gobenia
Begonia sparreana L.B. Smith & Wasshausen; America: Ecuador (Morona-
Santiago); *Knesebeckia*
Begonia sparsipila Baker; America: hybrid ?; *Gireoudia*
Begonia speluncae Ridley; Asia: Borneo (Sarawak); *Reichenheimia* I ? (placentae
unknown)
Begonia sphenocarpa Irmscher; Asia: Indonesia (Sulawesi); *Petermannia*
Begonia spilotophylla F. Muell.; Asia: New Guinea; *Petermannia*
Begonia spinibarbis Irmscher; America: Brazil (São Paulo); *Pritzelia*
Begonia squamipes Irmscher; America: Brazil (Sta Catarina); *Begonia*
Begonia squamulosa Hook. f.; Africa: Equatorial Guinea, Gabon, Dem. Rep.
Congo; *Tetraphila*
Begonia squarrosa Liebm.; America: Mexico (Oaxaca); *Gireoudia*
Begonia staudtii Gilg; Africa: Nigeria, Cameroon; *Loasibegonia*
Begonia stellata Sosef; Africa: Cameroon; *Loasibegonia*
Begonia stelzneri (Klotzsch) Warb.; Asia: Sri Lanka; *Reichenheimia* I ?
Begonia stenocardia L.B. Smith & Schubert; America: Colombia (Choco); *Knese-*
beckia
Begonia stenolepis L.B. Smith & R.C. Smith; America: Brazil (Sta Catarina);
Pritzelia
Begonia stenophylla A. DC.; America: Brazil (São Paulo); *Pritzelia*
Begonia stenotepala L.B. Smith & Schubert; America: Peru; *Begonia*
Begonia steyermarkii L.B. Smith & Schubert; America: Venezuela (Bolivar);
Doratometra ?
Begonia stictopoda (Miq.) A. DC.; Asia: Indonesia (Sumatra); *Reichenheimia* I
Begonia stigmosa Lindl.; America: Mexico; *Gireoudia*
Begonia stilandra Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia stipulacea Willd.; America: cult.; *Begonia*
Begonia stipularis Spreng.; America: Brazil; ? (no flowers)
Begonia stolzii Irmscher; Africa: Tanzania; *Augustia*
Begonia strachwitzii Warb. ex Irmscher; Asia: Indonesia (Sulawesi); *Petermannia*
Begonia strictinervis Irmscher; Asia: New Guinea; *Petermannia*
Begonia strictipetiolaris Irmscher; Asia: Indonesia (Sulawesi); *Petermannia*
Begonia strigillosa A. Dietr.; America: Mexico (Chiapas), Guatemala, El Salvador,
Costa Rica; *Gireoudia*
Begonia strigulosa A. DC.; Asia: ? cult. Hort. Bogor; *Reichenheimia* ?
Begonia subacida Irmscher; America: Brazil (Bahia); *Pritzelia*
Begonia subalpestris A. Chev.; Africa: São Tomé; *Tetraphila*
Begonia subcaudata Rusby ex L.B. Smith & Schubert; America: Bolivia (La Paz);
Hydristyles

Begonia subciliata A. DC.; America: Peru (Ayacucho, Junin); *Cyathocnemis*
Begonia subcostata Rusby; America: Colombia (Magdalena); *Doratometra* ?
Begonia subcyclophylla Irmscher; Asia: New Guinea; *Diploclinium* I
Begonia subelliptica Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia sublobata Jack; Asia: Indonesia (Sumatra); *Diploclinium* I
Begonia subnummularifolia Merr.; Asia: Borneo; *Diploclinium* I
Begonia suborbiculata Merr.; Asia: The Philippines (Palawan); *Diploclinium* I
Begonia subpeltata Wight; Asia: India; *Reichenheimia* III
Begonia subperfoliata Parish ex Kurz; Asia: Burma; *Diploclinium* III
Begonia subprostrata Merr.; Asia: The Philippines; *Petermannia*
Begonia subscutata De Wild.; Africa: Cameroon to Congo and Dem. Rep. Congo;
Tetraphila
Begonia subspinulosa Irmscher; America: Peru (Cuzco); *Cyathocnemis*
Begonia subtilis Irmscher = *B. pseudoviola* Gilg
Begonia subtruncata Merr.; Asia: The Philippines (Luzon); *Petermannia*
Begonia subvillosa Klotzsch; America: Brazil, Paraguay; *Begonia*
Begonia subviridis Craib; Asia: Thailand; *Diploclinium* II ?
Begonia sudjanae Jansson; Asia: Indonesia (Sumatra); *Reichenheimia* I
Begonia suffrutescens Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia summoglabra Yü; Asia: China (Yunnan); *Diploclinium* III
Begonia sunorchis C. Chev.; America: hybrid ?; ?
Begonia suprafastigiata Irmscher; America: Peru (Cuzco); *Cyathocnemis*
Begonia surculigera Kurz; Asia: India (Akyab); *Diploclinium* II
Begonia susaniae Sosef; Africa: Cameroon, Gabon; *Scutobegonia*
Begonia sutherlandii Hook. f.; Africa: Dem. Rep. Congo, Tanzania, Zambia,
Mozambique, South Africa; *Augustia*
Begonia sychnantha L.B. Smith & Wasshausen; Asia: Indonesia (Sumatra);
Reichenheimia I
Begonia sylvatica Meisner ex A. DC.; America: Brazil (Bahia, Espirito Santo);
Pritzelia
Begonia sympodialis Irmscher; Asia: Borneo (Sarawak); *Petermannia*
Begonia tacanana Ziesenh.; America: Mexico (Chiapas); *Gireoudia*
Begonia tafaensis Merr. & L.M. Perry; Asia: New Guinea; *Petermannia*
Begonia tafiensis Lillo; America: Argentina (Tucumán); *Eupetalum*
Begonia taiwaniana Hayata; Asia: Taiwan; *Diploclinium* II ?
Begonia taliensis Gagnep.; Asia: China (Yunnan); *Diploclinium* II
Begonia tampinica Burkill ex Irmscher; Asia: Peninsular Malaysia; *Platycentrum*
Begonia tanala Humbert ex Bosser & Keraudren-Aymonin; Africa: Madagascar; ?
(new section?)
Begonia tarokoensis M.J. Lai; Asia: Taiwan; *Platycentrum*
Begonia tascellezii Hort.; ?; ?; ?
Begonia tatoniana Wilczek; Africa: Central Africa; *Tetraphila*
Begonia tawaensis Merr.; Asia: Borneo (Sabah); *Petermannia*
Begonia tawabensis Merr.; Asia: The Philippines; *Diploclinium* I
Begonia tayloriana Irmscher; Africa: Tanzania; *Augustia*
Begonia tenera Dryand.; Asia: Sri Lanka; *Reichenheimia* III
Begonia tenericaulis Ridley; Asia: Indonesia (Sumatra); *Petermannia*
Begonia tenuicaulis A. DC.; America: Bolivia (Larecaja, Caupolicán); *Eupetalum*
Begonia tenuifolia Dryand.; Asia: Indonesia (Java); *Parvibegonia*
Begonia tessaricarpa C.B. Clarke; Asia: India (Assam); *Sphenanthera*
Begonia tetragona Irmscher; Asia: China (Yunnan); *Sphenanthera*
Begonia tetrandra Irmscher; America: Peru; *Semibegoniella*

Begonia teuscheri Linden ex André; America: hybrid?; *Pritzelia*
Begonia teysmanniana (Miq.) Warb.; Asia: Indonesia (Sumatra); *Platycentrum*
Begonia thaipingensis King; Asia: Peninsular Malaysia; *Parvibegonia*
Begonia thelmae L.B. Smith & Wasshausen; America: Brazil (cult.); ? (new section?)
Begonia thiemei C. DC. ex J.D. Smith; America: Mexico (Chiapas, Veracruz); *Gireoudia*
Begonia thomeana C. DC.; Africa: São Tomé, Gabon; *Cristasemen*
Begonia thomsonii A. DC.; Asia: India (Khasia); *Platycentrum*
Begonia thyrsoides Irmscher; America: Peru (Cuzco); *Quadriperigonia*
Begonia tiliifolia C. DC.; America: Colombia (Cauca), Ecuador (Cotopaxi); *Begonia* ?
Begonia timorensis (Miq.) J. Golding & Karegeannes; Asia: Indonesia (Timor); *Petermannia*
Begonia tiomanensis Ridley; Asia: Peninsular Malaysia; *Platycentrum*
Begonia toledana L.B. Smith & Schubert; America: Colombia, Venezuela; *Casparya*
Begonia toledoana Handro; America: Brazil (São Paulo); *Pritzelia*
Begonia tomentosa Schott; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia tominana J. Golding; America: Bolivia (Tomina); *Eupetalum*
Begonia tonduzii C. DC.; America: Costa Rica; *Ruizopavonia*
Begonia tonkinensis Gagnep.; Asia: China; *Diploclinium* I ?
Begonia torricellensis Warb.; Asia: New Guinea; *Petermannia*
Begonia trapa L.B. Smith & Schubert; America: Venezuela (Merida); *Casparya*
Begonia trianae (A. DC.) Warb.; America: Colombia (Norte de Santander, Cundinamarca); *Casparya*
Begonia tribenensis C.R. Rao; Asia: Nepal; *Diploclinium* III
Begonia tribracteata Irmscher; America: Peru (Ayacucho); *Cyathocnemis*
Begonia trichocarpa Dalz.; Asia: India; *Reichenheimia* II
Begonia trichochila Warb.; Asia: The Philippines (Luzon); *Diploclinium* I
Begonia trichopoda Miq.; Asia: Indonesia (Sumatra); *Reichenheimia* II
Begonia trichosepala C. DC.; America: Guatemala; *Weilbachia* ?
Begonia tricornis Ridley; Asia: Peninsular Malaysia; *Sphenanthera*
Begonia tricuspudata C.B. Clarke; Asia: Burma (Moulmein); *Alicida*
Begonia triflora Irmscher = *B. scutifolia* Hook. f.
Begonia trigonocarpa Ridley; Asia: Indonesia (Sumatra); *Sphenanthera*
Begonia triradiata C.B. Clarke; Asia: Burma; *Alicida*
Begonia triramosa Irmscher; America: Ecuador (Chimbarazo); *Knesebeckia*
Begonia trispathulata (A. DC.) Warb.; America: Colombia?, Venezuela (Aragua, Lara, Trujillo); *Casparya*
Begonia trisulcata (A. DC.) Warb.; Asia: Indonesia (Java); *Sphenanthera* ?
Begonia tropaeolifolia A. DC.; America: Colombia (Cundinamarca), Ecuador; *Gobenia*
Begonia trujillensis L.B. Smith; America: Venezuela (Trujillo); *Casparya*
Begonia trullifolia Guillaumin; Africa: Madagascar; ? (imperfectly known)
Begonia truncatiloba Irmscher; Asia: China (Yunnan); *Platycentrum*
Begonia truncicola Sod. ex C. DC.; America: Ecuador (Carchi, Pichincha); *Gobenia*
Begonia tsaii Irmscher; Asia: China (Yunnan); *Platycentrum*
Begonia tsaratananensis Aymonin & Bosser; Africa: Madagascar; *Quadrilobaria*
Begonia tsimihety Humbert ex Bosser & Keraudren-Aymonin; Africa: Madagascar; *Erminea*
Begonia tsoongii C.Y. Wu; Asia: China (Guangxü); *Platycentrum*
Begonia tumaitesii Hort.; ?; ?; ?

Begonia tumbezensis Irmscher; America: Peru (Tumber); *Eupetalum*
Begonia turbinata Ridley; Asia: Indonesia (Sumatra); *Sphenanthera*
Begonia udisilvestris C. DC.; America: Guatemala to Nicaragua; *Parietoplacentalia*
Begonia ulmifolia Willd.; America: Venezuela, Guyana, Trinidad; *Donaldia*
Begonia umbellata Humb., Bonpl. & Kunth; America: Colombia (Tolima, Caldas,
 Cauca); *Casparya*
Begonia umbraculifera Hook. f.; America: Brazil; ? (hybrid)
Begonia umbraculifolia Y. Wan & B.N. Chang; Asia: China (Guangxi); *Coelocentrum*
Begonia unduavensis Rusby; America: Bolivia (La Paz, Cochabamba); *Hydristyles*
Begonia undulata Schott; America: Brazil (Rio de Janeiro); *Gaerdtia*
Begonia uniflora S. Wats.; America: Mexico (San Luis Potosi); *Knesebeckia*
Begonia unilateralis Rusby; America: Bolivia; *Hydristyles*
Begonia urdanetensis Elmer; Asia: The Philippines; *Petermannia*
Begonia urophylla Hook.; America: Guatemala to Colombia; *Gireoudia*
Begonia ursina L.B. Smith & Schubert; America: Colombia (Magdalena); *Casparya*
Begonia urticae L. f.; America: Costa Rica to Peru; *Casparya*
Begonia uruapensis Sessé & Moc.; America: Mexico (Mexico); *Quadriperigon*
Begonia vagans Craib; Asia: Thailand; *Parvibegonia*
Begonia valdensium A. DC.; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia valerioi Standley; America: Costa Rica; *Weilbachia* ? (no female flowers)
Begonia valida Goebel; America: Brazil (Rio de Janeiro); *Pritzelia*
Begonia validissima Hort.; ? (nomen subnudum); ?; ?
Begonia valvata L.B. Smith & Schubert; America: Ecuador (Morona-Santiago);
Semibegoniella
Begonia vandewateri Ridley; Asia: New Guinea; *Petermannia*
Begonia vankerckhovenii De Wild.; Africa: Gabon, Dem. Rep. Congo; *Scutobegonia*
Begonia vanoverberghii Merr.; Asia: The Philippines (Luzon); *Diploclinium* I
Begonia vareschii Irmscher; America: Venezuela (Barinas); *Casparya*
Begonia variabilis Ridley; Asia: Peninsular Malaysia; *Parvibegonia*
Begonia varistyla Irmscher; America: Bolivia (Santa Cruz); *Ruizopavonia*
Begonia veitchii Hook. f.; America: Peru (Cuzco, Apurimac); *Eupetalum*
Begonia velata L.B. Smith & Schubert; America: Peru (Piura); *Knesebeckia*
Begonia velloziana Walp.; America: Brazil; *Trachelocarpus*
Begonia venosa Skan ex Hook. f.; America: Brazil (Rio de Janeiro); *Begonia*
Begonia venusta King; Asia: Peninsular Malaysia; *Platycentrum*
Begonia verruculosa L.B. Smith; America: Venezuela (Sucre); *Pritzelia* ?
Begonia versicolor Irmscher; Asia: China (Yunnan); *Platycentrum*
Begonia vestita C. DC.; America: Costa Rica, Panama; *Gireoudia*
Begonia vicina Irmscher; America: Brazil (São Paulo); *Pritzelia*
Begonia villifera Hort.; ?; ?; ?
Begonia villifolia Irmscher; Asia: China (Yunnan); *Platycentrum*
Begonia vincentiana O.E. Schulz; America: St Vincent; *Begonia*
Begonia violifolia A. DC.; America: Mexico (Chiapas?); *Weilbachia*
Begonia viridiflora A. DC.; America: Peru (Huanuco); *Cyathocnemis*
Begonia viscida Ziesenh.; America: Mexico (Oaxaca); *Knesebeckia*
Begonia vitiensis A.C. Smith; Asia: Fiji; *Diploclinium* I
Begonia vittariifolia N. Hallé; Africa: Gabon; *Scutobegonia*
Begonia vuijckii Koord.; Asia: Indonesia (Java); *Reichenheimia* I
Begonia wadei Merr. & Quisumb.; Asia: The Philippines (Coron); *Diploclinium* II
Begonia wagnerana Hook.; America: Brazil or Venezuela; *Cyathocnemis* ?

Begonia wakefieldii Gilg ex Engl.; Africa: Kenia, Tanzania; *Augustia*
Begonia wallichiana Lehman; America: Brazil; *Doratometra*
Begonia walteriana Irmscher; Asia: Borneo (Labuan); *Petermannia*
Begonia wangii Yü; Asia: China (Yunnan); *Reichenheimia* III
Begonia warburgii K. Schum. & Lauterb.; Asia: New Guinea; *Petermannia* ?
Begonia waryana Irmscher; Asia: New Guinea; *Petermannia*
Begonia warszewiczii Neuman = *B. conchifolia* A. Dietr.
Begonia wattii C.B. Clarke; Asia: India (Himalaya); *Parvibegonia*
Begonia weberbaueri Irmscher; America: Peru (Cajamarca); *Eupetalum*
Begonia weberi Merr.; Asia: The Philippines (Mindanao); *Petermannia*
Begonia weberlingii Irmscher; America: El Salvador; *Knesebeckia*
Begonia weddelliana A. DC.; America: Bolivia (Yungas); *Knesebeckia*
Begonia weigallii Hemsl.; Asia: The Solomon Islands; *Petermannia*
Begonia wengeri C.E.C. Fischer; Asia: India (Mizoram); *Alicida* ?
Begonia wenshanensis C.M. Hu; Asia: China (Yunnan); *Diploclinium* II
Begonia wenzelii Merr.; Asia: The Philippines (Leyte); *Petermannia*
Begonia wilczekiana N. Hallé = *B. elaeagnifolia* Hook. f.
Begonia wilksii Sosef; Africa: Gabon; *Scutobegonia*
Begonia wilsonii Gagnep.; Asia: China (Szechuan); *Diploclinium* III
Begonia wollastonii E.G. Baker; Africa: Dem. Rep. Congo, Uganda; *Rostro-*
begonia
Begonia wollnyi Herzog; America: Bolivia (La Paz, Yungas, Sta Cruz); *Knese-*
beckia
Begonia woodii Merr.; Asia: The Philippines (Palawan); *Diploclinium* III
Begonia wrightiana A. DC.; America: Cuba; *Begonia*
Begonia wurdackii L.B. Smith & Schubert; America: Peru (Amazonas); *Gobenia*
Begonia xanthina Hook.; Asia: India; *Platycentrum*
Begonia xerophyta L.B. Smith & Wasshausen; America: Ecuador (Loja);
Eupetalum ?
Begonia xilitlensis Burt-Utley; America: Mexico (San Luis Potosi); *Gireoudia*
Begonia xingyiensis T.C. Ku; Asia: China (Guizhou); *Diploclinium* III
Begonia xinyiensis T.C. Ku; Asia: China (Guangdong); *Diploclinium* III ? (female
flowers unknown)
Begonia xiphophylla Irmscher; Asia: Borneo (Sarawak); *Petermannia*
Begonia xishuiensis T.C. Ku; Asia: China (Guizhou); *Diploclinium* III ?
Begonia xylopoda L.B. Smith & Schubert; America: Colombia (Putumayo); *Ruizo-*
pavonia
Begonia yappii Ridley; Asia: Peninsular Malaysia; *Diploclinium* I ?
Begonia ynesiae L.B. Smith & Wasshausen; America: Ecuador (Carchi, Pichincha);
Gobenia
Begonia yui Irmscher; Asia: China (Yunnan); *Diploclinium* II
Begonia yunnanensis Léveillé; Asia: China (Yunnan); *Diploclinium* II
Begonia zairensis Sosef; Africa: Dem. Rep. Congo; *Scutobegonia*
Begonia zamboangensis Merr.; Asia: The Philippines (Mindanao); *Petermannia*
Begonia zenkeriana L.B. Smith & Wasshausen; Africa: Cameroon; *Scutobegonia*
Begonia zimmermannii Peter ex Irmscher; Africa: Tanzania; *Tetraphila*
Begonia zollingeriana A. DC.; Asia: Indonesia (Java); *Parvibegonia*

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