

Dividing and conquering the fastest-growing genus: Towards a natural sectional classification of the mega-diverse genus *Begonia* (Begoniaceae)

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Abstract The pantropical genus *Begonia* is the sixth-largest genus of flowering plants, including 1870 species. The sections of *Begonia* are used frequently as analogues to genera in other families but, despite their taxonomic utility, few of the current sections have been examined in the light of molecular phylogenetic analyses. We present herein the largest, most representative phylogeny of *Begonia* published to date and a subsequent provisional sectional classification of the genus. We utilised three plastid markers for 574 species and 809 accessions of *Begonia* and used *Hillebrandia* as an outgroup to produce a dated phylogeny. The relationships between some species and sections are poorly resolved, but many sections and deeper nodes receive strong support. We recognise 70 sections of *Begonia* including 5 new sections: *Astrothrix*, *Ephemeria*, *Jackia*, *Kollmannia*, and *Stellandrae*; 4 sections are reinstated from synonymy: *Australes*, *Exalabegonia*, *Latistigma* and *Pereira*; and 5 sections are newly synonymised. The new sectional classification is discussed with reference to identifying characters and previous classifications.

Keywords *Begonia*; dating; phylogenetics; sectional classification

Supplementary Material The Electronic Supplement (Table S1) and DNA sequence alignment are available from <https://doi.org/10.12705/672.3.S1> and <https://doi.org/10.12705/672.3.S2>, respectively; an Excel table showing species names, voucher information, GenBank accession numbers and alignment name for each terminal is available from <https://doi.org/10.12705/672.3.S3>

■ INTRODUCTION

Big genera remain the largest black holes in plant taxonomy (Frodin, 2004), which has a detrimental effect in related fields including evolutionary biology, biogeography, and conservation. Around 57 angiosperm genera have more than 200 species with the ten largest each containing more than 1250 species (Frodin, 2004). In the decade to 2015, 2064 species were published in these genera (Fig. 1), accounting for ca. 10% of species described in this timeframe (Bebber & al., 2010). The size of mega-diverse genera makes it unfeasible for a single taxonomist to monograph them within a career. Monographic work has instead tended to focus upon smaller plant groups (Wood & al., 2015), while taxonomists working on very large genera have largely focused on geographic or infrageneric groups (Atkins & al., 2013). The problems associated with geography-focussed taxonomy are well documented (Stace, 1991) thus we recommend putting future efforts into delimiting natural infrageneric groups through collaboration as advocated by Van Welzen & al. (2009). We suggest this will stimulate monographic work within large genera and help plug the taxonomic black hole.

Begonia L. is one of the ten largest genera of plants (Frodin, 2004) and species number has increased faster than in any other genus from 2005 to 2015 (Fig. 1). The 341 new species published within this timeframe were not the result of a single work or group, with species published by 73 authors in 119 journal articles covering species from 29 countries across three continents. In 2015 alone, 105 *Begonia* species were published, more than in any other year since 1859 when Alphonse de Candolle

published a treatment of the Begoniaceae C.Agardh. (Candolle, 1859). The number of accepted species of *Begonia* currently stands at 1870 species (Hughes & al., 2015–) and is likely to rise to well over 2000. The number of undescribed species from Borneo alone is estimated at over 300 (Julia & Kiew, 2014) and large parts of the taxonomic and geographic range of *Begonia* have not been covered in monographs or Floras since the 1850s (e.g., Brazil, India, *B.* sect. *Knesebeckia* (Klotzsch) A.DC., *B.* sect. *Begonia*). A stable, natural infra-generic classification of *Begonia* is required to aid systematic work within the genus.

The author who progressed furthest towards a generic classification within the family was Klotzsch, who described 39 genera in two publications (Klotzsch, 1854, 1855). The majority of genera were relegated to sections of *Begonia* by Candolle (1859, 1864). In the context of a group whose species number was growing rapidly, in which the genera were poorly defined, and in which many of the species remained poorly known, Candolle concluded assigning new species to genera would remain problematic and result in considerable nomenclatural instability (Candolle, 1864). Candolle maintained only *Casparya* Klotzsch and *Mezierea* Gaudich. at the generic level. These genera were distinguished from *Begonia* by their apical fruit dehiscence and parietal placentation respectively, but these were later reduced to sections by Bentham and Hooker, who considered these characters weak (Bentham & Hooker, 1867). *Symbegonia* Warb. (Warburg, 1894) and *Semibegoniella* C.DC. (Candolle, 1908) were described to accommodate species with tepals fused into a lobed corolla tube. *Semibegoniella* was reduced to a section by Barkley & Baranov (1972) as species intermediate between the type and members of *B.* sect. *Casparya* had

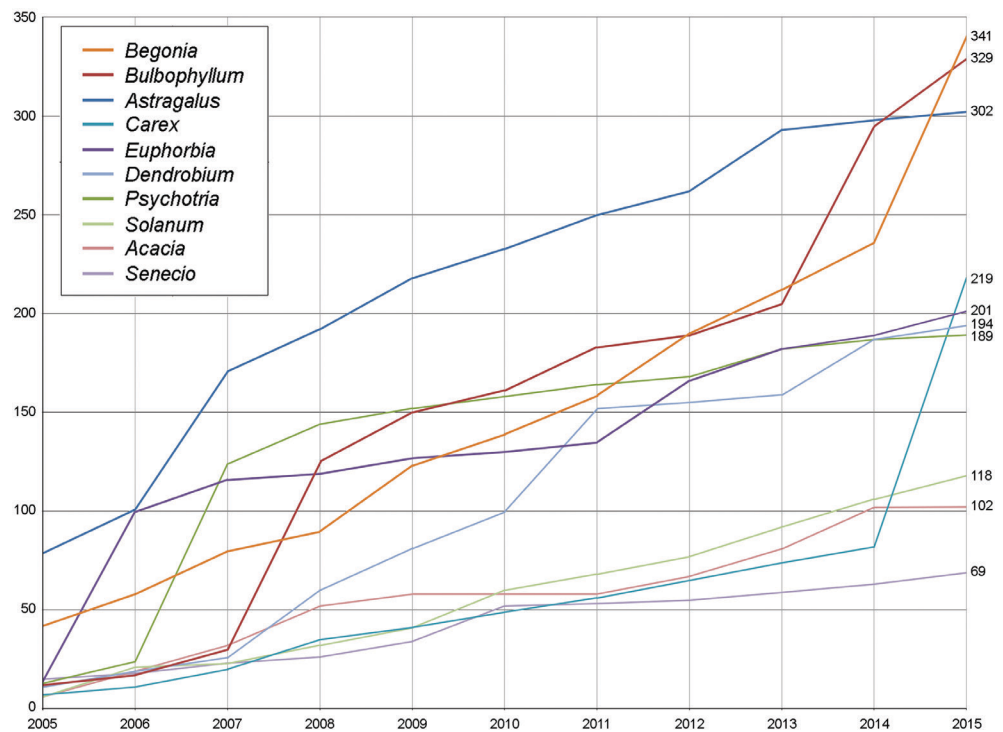


Fig. 1. Accumulation of species in the ten largest plant genera from 2005 to 2015. Data from the International Plant Names Index (IPNI, 2016).

by then been discovered and Forrest & Hollingsworth (2003) reduced *Symbegonia* to a section as molecular data showed it was highly nested within *Begonia*. Further sampling of both taxa and DNA regions (Forrest & al., 2005; Thomas & al., 2011; Moonlight & al., 2015) has shown that none of the previously recognised genera form a sister relationship with *Begonia*, with the exception of *Hillebrandia* Oliv.

Subsequently, only *Begonia* and *Hillebrandia* are currently recognised at the generic level, with *Hillebrandia* being both phylogenetically and morphologically distinct from *Begonia* (Clement & al., 2004). Barkley & Baranov (1972) and Doorenbos & al. (1998) later classified the majority of known species of *Begonia* into sections and it is the latter work that is primarily followed today. Doorenbos & al. recognised 63 sections in 1998 and a further five have since been described (De Wilde & Plana, 2003; Forrest & Hollingsworth, 2003; Gu & al., 2007; Hughes & Takeuchi, 2015; Shui & al., 2002). All sections are restricted to a single continent with the notable exceptions of *B. sect. Tetraphila* A.DC. (De Wilde & al., 2011), which is present in both Africa and Asia, and *B. sect. Doratometra* (Klotzsch) A.DC., which is present in both South America and Asia (Radbouchoom & al., 2017), although the Asian range may be the result of an introduction in the latter case (Radbouchoom & al., 2017). The replacement of the generic classification of the Begoniaceae with one which is largely based on sections has downsides as well as benefits. It means the species binomials do not convey as much information about species relationships; a further disadvantage is that stating sectional placement is not a nomenclatural requirement, and hence species can be published “stateless” within the genus. However, a significant advantage of a sectional classification over a generic classification is that taxonomic instability does not produce nomenclatural instability. Species can be moved among sections with no impact upon their generic name or authority string (McNeill & al., 2012), a situation which is very welcome at present given that some of the sections are in a state of flux.

The current morphological classification of Doorenbos & al. (1998) has served us well up to this point, but as our knowledge of *Begonia* phylogeny has improved and species become better known due to a resurgence of taxonomic activity in the genus, some improvements can be made. Doorenbos & al. were unable to assign ca. 50 poorly known species to section, only tentatively assigned a further ca. 80 species to a section, and suggested new sections would be required to encompass another 19 species. In addition a number of more recently published species have not been assigned to section by their authors (e.g., *B. caparaoensis* E.L.Jacques & L.Kollmann) or have been assigned to sections that do not follow the circumscriptions of Doorenbos & al. (1998) (e.g., *B. acuitipala* K.Y.Guan & D.K.Tian). Furthermore, the majority of the classification system remains untested by molecular phylogenetic methods and published phylogenies suggest a number of sections are paraphyletic (e.g., *B. sect. Begonia* [Moonlight & al., 2015]; *B. sect. Platycentrum* (Klotzsch) A.DC. [Thomas & al., 2011]) or polyphyletic (e.g., *B. sect. Diploclinium* (Lindl.) A.DC. [Thomas & al., 2011]; *B. sect. Knesebeckia* [Moonlight & al., 2015]). A phylogenetic update

to the sectional classification of *Begonia* is required to work towards a natural sectional classification of *Begonia*. By natural classification, we mean one which is based on phylogeny, and also informed by morphology. We aim to delimit monophyletic sections where possible, and indeed this has proved feasible for most of the genus. There has been much debate about the acceptance of paraphyletic groups in classifications, and whether one should even attempt classifications based on monophyly. Paraphyletic groups are seen as either “bad taxonomy” (Ebach & al., 2006) or a fundamental consequence of evolution which need to be reflected in a practical taxonomy (Brummit, 2006). We are not fundamentally opposed to paraphyletic groups and have taken a pragmatic approach to sectional delimitation, based on the evidence at hand in terms of phylogeny, morphology and biogeography. We have left some sections as paraphyletic where this has either retained some utility for identification, or where it has not been possible to manufacture a taxonomy based on monophyly.

We have based this updated classification on a chloroplast DNA phylogeny, for two reasons. Firstly, the taxon sampling available for the chloroplast DNA regions we have used is superior to that for nuclear DNA (specifically, ITS). The current sampling for ITS is heavily biased towards a small number of sections, and is particularly lacking in sampling in the Neotropics. Secondly, it is not possible to align ITS sequences with certainty across the genus as many base positions in the spacers are saturated with substitutions. Hybridisation and ensuing phylogenetic incongruence has been found in *Begonia*, but this is overwhelmingly limited to gene exchange between species within the same section (Hughes & al., 2015c). The results we present here are congruent with the only genus-wide phylogenetic study based on ITS and morphology (Forrest & al., 2005), but that lacks sufficient resolution to make a useful comparison. We consider the chloroplast DNA phylogeny presented here to be the best estimate of *Begonia* evolutionary history to date.

While it is not the principle goal of our analysis, we recognise that a dated phylogeny will be of significant utility to authors studying the timing of evolutionary and biogeographic events in either *Begonia* or across multiple groups. The most comprehensive dated phylogeny of the Begoniaceae to date included 268 taxa (Moonlight & al., 2015); this study doubles this number and broadens the phylogenetic sampling considerably. While the divergence time estimation methods used in Moonlight & al. (2015) are relatively robust to incomplete sampling (Drummond & al., 2012), a sampling increase of this magnitude may reduce the variance on the inferred ages of some nodes.

This study aims to:

- (1) Produce a well-sampled, well-resolved and dated phylogeny of the Begoniaceae;
- (2) Identify well-supported clades and assess how they relate to the sections of *Begonia*;
- (3) Recircumscribe natural sections where our sampling allows and identify sections or clades requiring further taxonomic and phylogenetic work to achieve a natural sectional classification of *Begonia*.

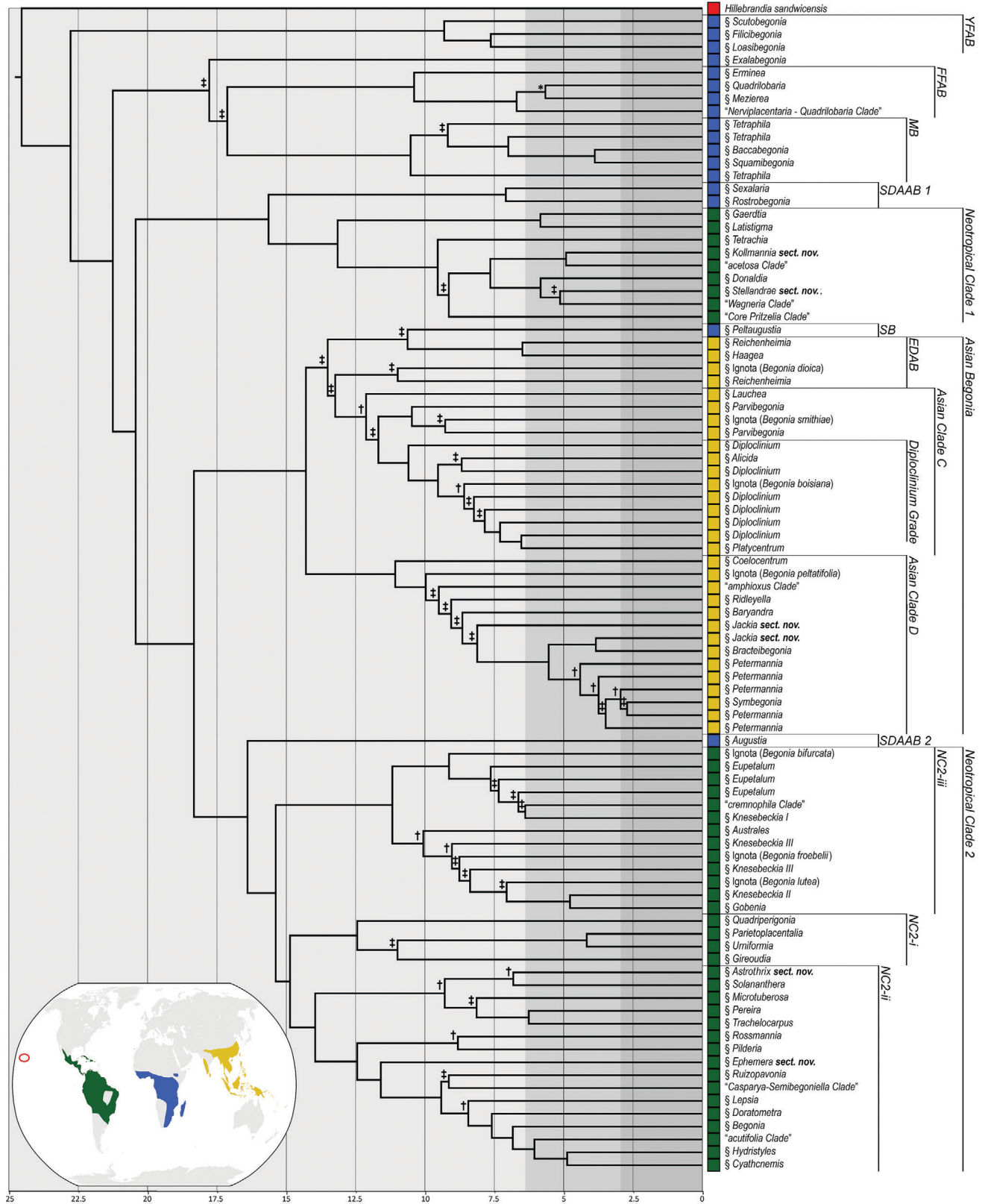


Fig. 2. Maximum-clade-credibility chronogram of BEAST analysis of the Begoniaceae. Node heights indicate mean ages. Rectangles beside taxon names indicate distributions: red, Hawaii; green, Americas; blue, Africa including Socotra; gold, Asia. Geological epochs are indicated by background colour: light grey, Miocene (23.0–5.3 Ma); mid-grey, Pliocene (5.3–2.6 Ma); dark grey, Holocene and Pleistocene (2.6–0 Ma). Asterisks indicate posterior clade probabilities <0.85, crosses indicate ML bootstrap values <75, double crosses indicate posterior clade probabilities <0.85 and ML bootstrap values <75. See the Results section for explanation of the clade acronyms.

■ MATERIALS AND METHODS

Plant material. — The dataset comprises 802 accessions of 574 species of the Begoniaceae including *Hillebrandia sandwicensis*, and 51 African (27%), 239 Asian (24%), and 283 Neotropical (40%) species of *Begonia* (see Appendix 1). All accessions were identified by experts in *Begonia* taxonomy, with reference to the most up to date taxonomy provided by Hughes & al. (2015–). Sampling focussed upon the inclusion of as many currently accepted sections of *Begonia* as possible with further emphasis placed upon the type of all published sections. We sampled species from 57 of the 68 currently accepted sections of *Begonia*. Types of section names were included from 66 of the 103 published sections of *Begonia* (see Electr. Suppl.: Table S1). In total, 1195 sequences were newly generated for this study.

DNA extraction, amplification and sequencing. — Total genomic DNA was extracted from silica-dried or fresh material using Qiagen DNeasy Plant Mini Kits or QiaXtractor high-throughput purification (Qiagen, Germantown, Maryland, U.S.A.) in accordance with the manufacturer's protocols.

Three non-coding plastid DNA regions were chosen for amplification (*ndhA* intron, *ndhF-rpl32* spacer, *rpl32-trnL* spacer) and the primers used were as in Thomas & al. (2011). The *ndhA* intron and *ndhF-rpl32* spacer were amplified in 13.6 µl reactions containing 0.5 µl of template, 0.75 µl of both forward and reverse primers, 0.1 µl of Phusion polymerase (Thermo Fisher Scientific, Waltham, Massachusetts, U.S.A.), 8.125 µl of ddH₂O, 2.5 µl of 10× reaction buffer, 1.25 µl of dNTPs, and 0.75 µl of DMSO. The *rpl32-trnL* spacer was amplified in 12.5 µl reactions containing 0.5 µl of template, 0.75 µl of both forward and reverse primers, 0.1 µl of Phusion polymerase (Thermo Fisher Scientific), 8.5 µl of ddH₂O, 2.5 µl of 10× reaction buffer, and 0.25 µl of dNTPs. The PCR temperature profile included: template denaturation at 95°C for 5 min; 34 cycles of denaturation at 98°C for 30 s, primer annealing at 50°C for 30 s, primer extension at 72°C for 30 s; and a final stage primer extension at 72°C for 10 min. PCR products were purified using ExoSAP-IT (Invitrogen/Life Technologies, Carlsbad, California, U.S.A.). Sequencing PCRs used the same primers as for amplification, in 10 µl reactions using BigDye sequencing kits (Invitrogen/Life Technologies). Samples were then sent to GenePool at the University of Edinburgh for sequencing.

Phylogenetic analyses. — Sequences were edited with Geneious Pro v.7.1 (Biomatters, 2014) and aligned by hand in BioEdit v.7.2.5 (Hall, 1999). Phylogenetic and divergence-time estimations were carried out with an uncorrelated lognormal relaxed clock in BEAST v.1.8.3 (Drummond & al., 2012). No fossil data suitable for the calibration of divergence time estimation analyses exists within the Begoniaceae, thus we use a single secondary calibration point derived from a fossil-calibrated, Cucurbitales-Fagales wide analysis (Thomas & al., 2012). The age of the *Begonia* crown group was estimated at 24 Ma (\pm 3.57 Myr) with a normal distribution. Models of molecular evolution were determined upon a maximum-likelihood topology with jModelTest v.2 (Darriba & al., 2012), resulting in the selection of a GTR+I+ Γ model. A tree prior of birth-death incomplete sampling was selected. Four sets of two searches

each comprising two MCMC (Markov chain Monte Carlo) chains were run for between 3.2×10^7 and 3.4×10^7 generations on the Cipres Science Gateway (Miller & al., 2010) and sampled every 10,000 generations. Time-series plots were analysed in Tracer v.1.8.3 (Rambaut & Drummond, 2009) to ensure adequate sample size (>200) for all parameters and convergence of parameters. Runs were combined in LogCombiner v.1.8.3 and the maximum clade credibility (MCC) chronogram was selected in TreeAnnotator v.1.8.3 (Drummond & al., 2012). Preliminary analyses were run with identical parameters on data for each DNA region. No well-supported incongruence was present among the three trees, so we proceeded with the combined analysis. Maximum likelihood (ML) phylogenetic analysis was carried out using RAxML (Stamatakis & al., 2008), with 100 rapid bootstrap inferences followed by a thorough ML search (10 replicates), using a gamma distribution of rates and a proportion of invariant sites.

■ RESULTS

Phylogenetic analyses. — The maximum-clade-credibility (MCC) chronogram of the Begoniaceae (Fig. 2) resolves broadly the same relationships as resolved in previous cpDNA analyses (Plana, 2003; Goodall-Copestake & al., 2010; Thomas & al., 2011; Moonlight & al., 2015). Selected clade-specific posterior probabilities and ages are presented in Table 1. African *Begonia* is resolved as an early-diverging grade with a single clade of

Table 1. Bayesian posterior probabilities (PP), ML bootstrap support values (BS) and divergence time estimates (95% highest posterior density, HPD) for selected clades from a phylogeny of global *Begonia* (see Fig. 2).

Clade	PP	BS	Mean divergence age (95% HPD) [Ma]
Begoniaceae	–	–	24.57 (33.03–16.76)
<i>Begonia</i>	1.00	100	22.80 (30.41–16.14)
YFAB	1.00	100	9.34 (14.59–4.92)
FFAB	1.00	100	10.54 (15.45–6.73)
MB	1.00	100	10.42 (15.40–5.34)
SDAAB 1 & NC1	1.00	100	15.67 (21.78–10.40)
SDAAB 1	1.00	100	7.11 (11.58–3.71)
NC1	1.00	100	13.18 (18.30–8.76)
Asian <i>Begonia</i>	1.00	100	14.32 (14.9–9.23)
Asian Clade C	0.98	72	12.15 (16.66–7.79)
Asian Clade D	1.00	94	11.10 (15.39–7.28)
SDAAB 2 & NC2	1.00	100	16.42 (21.89–10.66)
SDAAB 2	1.00	100	5.05 (9.55–2.13)
NC2	1.00	92	15.41 (20.92–10.43)
NC2-i	1.00	85	12.47 (17.87–7.98)
NC2-ii	1.00	100	13.98 (18.70–9.00)
NC2-iii	1.00	96	11.20 (16.00–7.53)

Asian *Begonia* (including Socotran *Begonia* [SB]) and two clades of Neotropical *Begonia* (each as sister to a clade of Seasonally Dry Adapted African *Begonia* [SDAAB]) nested within.

We resolve Yellow-flowered African *Begonia* (YFAB) as sister to the remainder of *Begonia* (PP: 1.0; BS: 100). The relationships among early-diverging clades of African *Begonia* were unresolved in earlier analyses (Plana, 2003; Goodall-Copestake & al., 2010; Moonlight & al., 2015).

The second dichotomy within *Begonia* resolves African *Begonia* (excluding SDAAB and SB) as sister to the remainder of the genus, although there is poor support for both this clade (PP: 0.74; BS: 56) and the relationships among its major subclades (PP: 0.48; BS: 19). This relationship was unresolved in earlier analyses (Plana, 2003; Goodall-Copestake & al., 2010). Within this clade, we resolve *B. sect. Exalabegonia* Warb. as sister to the reciprocally monophyletic fleshy-fruited African *Begonia* (FFAB) and Malagasy *Begonia* (MB).

The majority of Asian *Begonia* is resolved within two clades. Asian Clade C and Asian Clade D as identified by Thomas & al. (2011). We resolve Asian Clade C as nested within a grade we informally name as Early Diverging Asian *Begonia* (EDAB), which also includes SB. The relationships within EDAB, and among major Asian clades are poorly supported.

We replicate the results of Moonlight & al. (2015) in resolving Neotropical Clade 1 (NC1) and Neotropical Clade 2 (NC2) as sister to SDAAB 1 and SDAAB 2 respectively (both PP: 1.0; BS: 100). Within NC2, we resolve the same three major subclades as Moonlight & al. (2015) and informally name them: NC2-i, containing Central American and Mexican species; NC2-ii, cane-like Andean and Caribbean species nested within a diverse South American grade; NC2-iii, primarily western South American tuberous, rhizomatous, and scandent species. We resolve NC2-i as sister to NC2-ii, with both sister to NC2-iii.

Divergence time estimates. — We estimate a much younger date (24.6 [33.0–16.8] Ma) for the divergence of *Begonia* and *Hillebrandia* than that found by Clement & al. (2004) (50.9 [62.8–39.0] to 64.7 [80.1–49.3]). However, the dates we estimate within the genus *Begonia* (see our Table 1) are similar to those of previous analyses (see table 1 in Moonlight & al., 2015 and table 1 in Thomas & al., 2012). We estimate ages for all major clades of 1–3 Ma older than previous estimates, with the exception of NC1, which is estimated as 13.2 (18.3–8.8) Ma compared to 14.5 (20.1–9.0) Ma in Moonlight & al. (2015).

DISCUSSION

With few exceptions, species in the Begoniaceae are easily recognisable as such. The majority of species share a more or less asymmetric leaf; and dry, trilobular fruits while all share an inferior ovary and a ring of collar cells on the seed (De Lange & Bouman, 1999). Debate regarding the classification of species within the family has historically focused upon the delimitation of genera and, more recently, sections.

All previous sectional and generic classifications of *Begonia* and the Begoniaceae have their merits with respects to particular sections or clades of *Begonia*, but we see little value in their

comparative assessment. We limit our discussion to the currently accepted sectional classification of *Begonia* by Doorenbos & al. (1998) and its subsequent updates (Forrest & Hollingsworth, 2003; De Wilde & Plana, 2003; Rubite & al., 2013; Hughes & Takeuchi, 2015; Moonlight & Jara-Muñoz, 2017; Moonlight & al., 2017b). We accept previously accepted sections where the rules of nomenclature require and refer only to previous classifications where they best fit the results of our phylogenetic analyses.

In updating the sectional classification of *Begonia* to take into account information from molecular phylogenetic analyses we have reached an often-uneasy compromise among conflicting criteria: monophyly, stability and utility. It is unlikely that if we were to design a sectional classification without the burden of history, we would have settled upon that which we present. However, even given our often incomplete knowledge, particularly with regards to phylogenetic taxon sampling, the classification we present represents a significant advance from previous sectional classifications of *Begonia*. In this discussion, we reference both sampled and unsampled species and sections, highlighting clades and sections we consider in need of further work to achieve a completed sectional classification of *Begonia*.

Divergence time estimates

The divergence of *Begonia* and *Hillebrandia*. — (Fig. 2). The sister relationship between *Hillebrandia* and *Begonia* is well established (Clement & al., 2004), and our use of the former as an outgroup confirms the most early-diverging lineages of *Begonia* are African. Our analyses suggest the two genera diverged 24.6 (33.0–16.8) Ma, much more recently than the range of 50.9 to 64.7 Ma found by Clement & al. (2004). Our divergence time estimates are congruent with a hypothesis of *Begonia* and *Hillebrandia* diverging during the Oligocene when suitable habitat was available for Begoniaceae species in the Hawaiian archipelago. The Hawaiian distribution of *Hillebrandia* may therefore be best explained by a single dispersal from Africa to Hawaii and not a boreotropical or Malaysian-Pacific origin as suggested by Clement & al. (2004). However, our divergence time analyses are based upon a single, secondary calibration point at the base of *Begonia* and therefore of limited utility outside the genus.

Divergence time estimates within *Begonia*. — (Table 1). Divergence time estimates for all major clades within *Begonia* are largely in line, and certainly within the margin of error, of the previous most densely sampled and dated phylogeny of *Begonia* (Moonlight & al., 2015) (Table 1). In general, we find dates for major clades 1–3 Ma older than those in Moonlight & al. (2015). This is likely because taxon sampling, both in terms of species number and the phylogenetic diversity of those species, is significantly higher in this paper. Indeed, the clades where we see greatest increase in divergence time estimates are those where sampling density has increased most significantly. For example, we now sample almost three times as many species in NC2 as Moonlight & al. (2015), and the mean divergence time estimation for this group has increased from 12.5 (17.2–7.97) Ma to 15.4 (20.9–10.4) Ma. Conversely, the number of species in NC1 has less than doubled and this is the

only major clade whose divergence time estimate has decreased (from 14.5 [20.1–8.9] Ma to 13.2 [18.3–8.8] Ma). It is possible that the divergence time estimates of large, undersampled clades (such as *B. sect. Petermannia* (Klotzsch) A.DC.) may increase given further species-level sampling while relatively well-sampled clades will remain stable.

Phylogenetic relationships and sectional monophyly

African *Begonia* (including Malagasy and Socotran *Begonia*) (Figs. 3, 4). — Sectional delimitation within African *Begonia* has remained relatively stable compared to that of Asian and American *Begonia*. This is due to a combination of factors. Most notably fewer species occur in Africa and the morphological gaps between clades are larger (presumably because extinction rates have been higher here due to a combination of the relatively long time that *Begonia* has existed in Africa coupled with large-scale climatic changes). African *Begonia* systematics has also benefitted greatly from having a particularly large group of researchers (mostly based in the Netherlands) concentrate their efforts in this geographical area (e.g., De Wilde, 1985a). Other geographical regions are yet to receive the same degree of attention by monographers. The majority of the continent's sections have been included in recent revisions (*B. sect. Augustia* (Klotzsch) A.DC. [Irmscher, 1961]; *B. sect. Baccabegonia* J.M.Reitsma [Reitsma, 1985]; *B. sect. Chasmophila* J.J.de Wilde & Plana [De Wilde & Plana, 2003]; *B. sect. Cristasemen* J.J.de Wilde [De Wilde, 1985b]; *B. sect. Loasibegonia* A.DC. [Sosef, 1994]; *B. sect. Mezierea* (Gaudich.) Warb. [Klazenga & al., 1994]; *B. sect. Peltaugustia* (Warb.) F.A.Barkley [Hughes & Miller, 2002]; *B. sect. Rostrobegonia* Warb., [Irmscher, 1961]; *B. sect. Scutobegonia* Warb. [Sosef, 1994]; *B. sect. Squamibegonia* Warb. [De Wilde & Arends, 1980]; *B. sect. Tetrastylis* [De Wilde, 2002]) or floristic treatments (Malagasy *Begonia* [Keraudren, 1983]) and members of all currently accepted sections except *B. sect. Muscibegonia* A.DC. have further been included in molecular phylogenetic studies (Plana, 2003; Plana & al., 2004). Our sampling includes some species not included in these studies and *vice versa* but the sectional relationships and major clades resolved in the studies are identical, thus we discuss the monophyly of sections of African *Begonia* with reference to all three phylogenies.

• **Yellow-flowered African *Begonia* (YFAB) (Fig. 3).** — We resolve a well-supported clade containing all sampled YFAB species as sister to the rest of *Begonia*. Included are all sampled members of *B. sect. Filicibegonia* A.DC., *B. sect. Loasibegonia* and *B. sect. Scutobegonia* as reciprocally monophyletic groups with *B. sect. Scutobegonia* resolved as sister to the two other sections. This mirrors the results of Plana (2003) and Plana & al. (2004) despite little overlap in sampled species between theirs and our study. We, therefore, recognise existing circumscriptions of these three sections. We further note the monotypic *B. sect. Chasmophila* was resolved as sister to this clade and that *B. sect. Cristasemen* was resolved as sister to the wider clade by Plana (2003) and Plana & al. (2004). Species in both of these sections have yellow flowers and are recognised as currently circumscribed.

• ***Begonia* sect. *Exalabegonia* (Fig. 3).** — *Begonia* sect. *Mezierea* was recognised as polyphyletic by Plana (2003) and Plana & al. (2004) with Malagasy species resolved within a clade of Malagasy sections and the two mainland African species (*B. meyeri-johannis* Engl., *B. oxyloba* Welw. ex Hook.f.) resolved as a separate clade at the unresolved base of their tree. We achieve greater resolution and resolve the two mainland species, treated here as *B. sect. Exalabegonia*, as sister to a clade including all Malagasy sections as sister to FFAB.

• **Malagasy *Begonia* (MB) (Fig. 3).** — Both our and previous studies resolve a clade containing all sampled species of MB, with *B. sect. Erminea* A.DC. as sister to the remainder of MB. We resolve as sister to *B. sect. Erminea* a clade containing Malagasy species of *B. sect. Mezierea* and all sampled species of *B. sect. Nerviplacentaria* A.DC. and *B. sect. Quadrilobaria* A.DC. From both our sampling and Plana (2003) it is clear that *B. sect. Quadrilobaria* is not monophyletic: *B. goudotii* A.DC. as sister to *B. sect. Mezierea* and *B. nossibea* as nested within *B. sect. Nerviplacentaria*.

• **Fleshy-fruited African *Begonia* (FFAB) (Fig. 3).** — We resolve a clade including all sampled species of *B. sect. Tetrastylis*, *B. sect. Squamibegonia*, and *B. sect. Baccabegonia*, which together include all of FFAB except *B. sect. Mezierea*. The relationship between these sections is poorly resolved, and like Plana (2003) and Plana & al. (2004), we resolve *B. sect. Squamibegonia* and *B. sect. Baccabegonia* as sister clades nested within *B. sect. Tetrastylis*.

• **Seasonally Dry Adapted African *Begonia* (SDAAB) (Fig. 3).** — The three sections of SDAAB are resolved into two well-supported clades. The first of these (SDAAB 1) contains all sampled members of *B. sect. Sexalaria* A.DC. and *B. sect. Rostrobegonia* resolved as sister groups, with both sister to NC1. The second (SDAAB 2) contains all sampled members of *B. sect. Augustia*, as sister to NC2.

• **Socotran *Begonia* (Fig. 4).** — *Begonia* sect. *Peltaugustia* is resolved as a monophyletic group within early-diverging Asian *Begonia* as shown by previous studies (Thomas & al., 2011, 2012; Moonlight & al., 2015).

Early-diverging Asian *Begonia* (Fig. 4). — Like previous studies, we resolve Asian *Begonia* as monophyletic with Socotran *Begonia* nested within. The majority of Asian species are resolved in two major clades: clades C and D as defined by Thomas & al. (2011). The remainder of Asian and Socotran *Begonia* are resolved within a number of smaller clades as a grade with Asian *Begonia* clade C nested within. The relationships within this clade are poorly resolved.

• ***Begonia* sect. *Haagea* (Fig. 4).** — The monotypic *B. sect. Haagea* (Klotzsch) A.DC. represented by *B. dipetala* is resolved as sister to the type of the polyphyletic *B. sect. Reichenheimia* (Klotzsch) A.DC. (see below). Collectively these two sections are resolved as sister to Socotran *Begonia*.

• **Tuberous *Begonia* sect. *Reichenheimia* (Fig. 4).** — We resolve the section as polyphyletic. *Begonia thwaitesii* Hook. was previously considered as a subspecies of another Sri Lankan endemic (*B. tenera* Dryand.) as *B. tenera* var. *thwaitesii* (Hook.) Jayasuriya. Following field observations of both taxa by one of the authors, we consider them as distinct at species level.

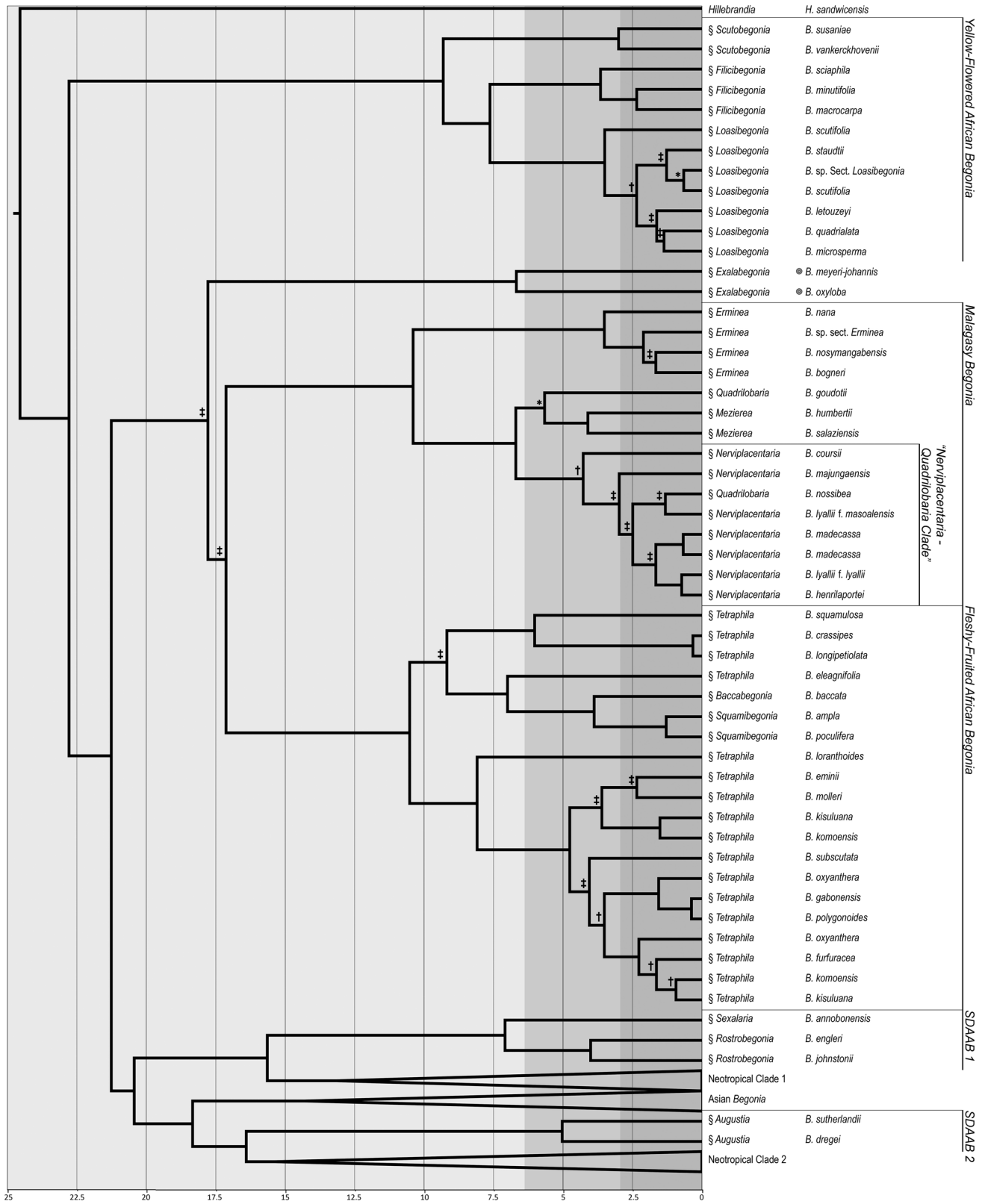


Fig. 3. Maximum-clade-credibility chronogram of BEAST analysis of the Begoniaceae focusing on African taxa. Node heights indicate mean ages. Geological epochs are indicated by background colour: light grey, Miocene (23.0–5.3 Ma); mid-grey, Pliocene (5.3–2.6 Ma); dark grey, Holocene and Pleistocene (2.6–0 Ma). Asterisks indicate posterior clade probabilities < 0.85, crosses indicate ML bootstrap values < 75, double crosses indicate posterior clade probabilities < 0.85 and ML bootstrap values < 75. Circles indicate species placed in sections different to their previous placement.

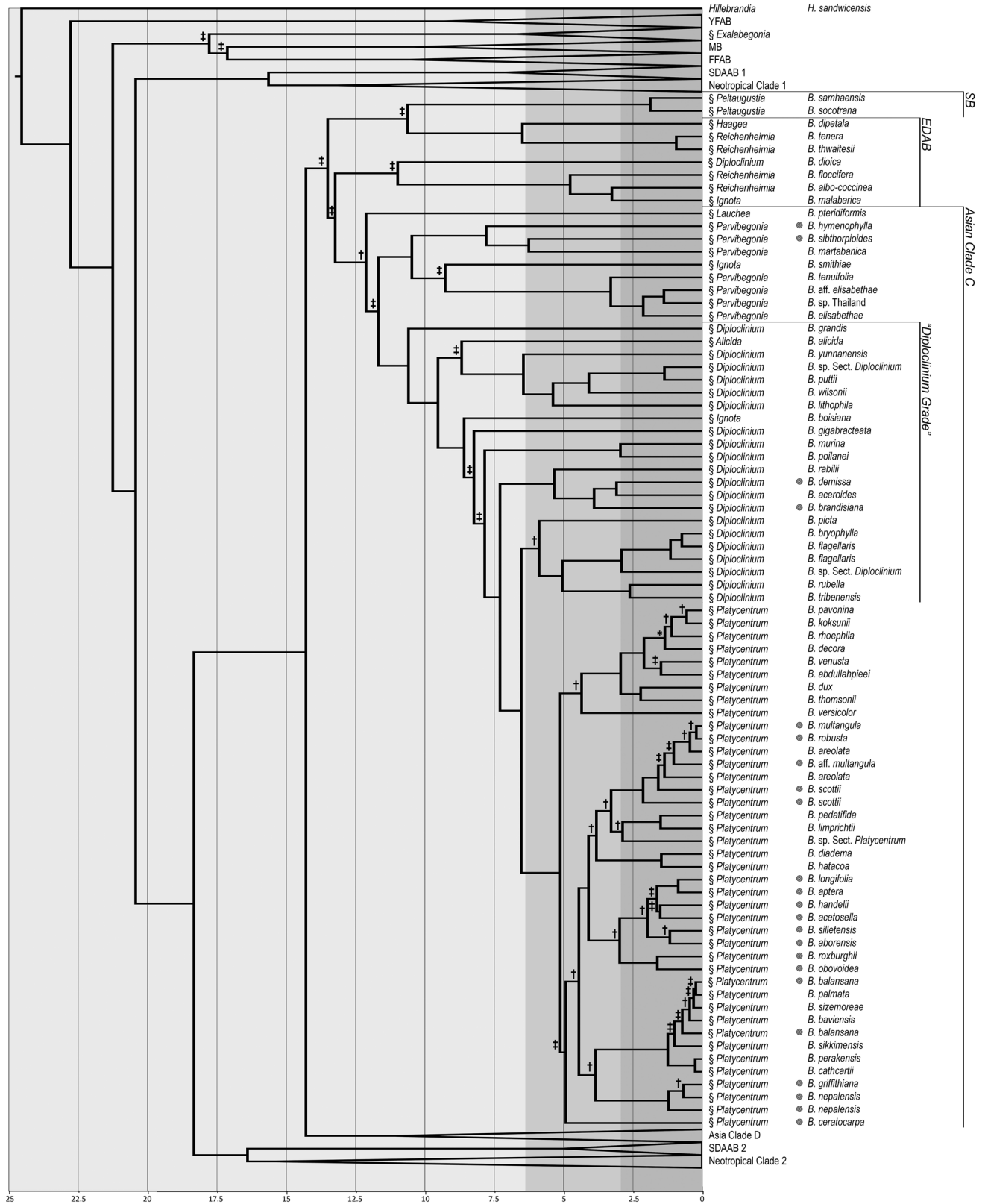


Fig. 4. Maximum-clade-credibility chronogram of BEAST analysis of the Begoniaceae focusing on Early-diverging Asian *Begonia* and Asian *Begonia* Clade C. Node heights indicate mean ages. Geological epochs are indicated by background colour: light grey, Miocene (23.0–5.3 Ma); mid-grey, Pliocene (5.3–2.6 Ma); dark grey, Holocene and Pleistocene (2.6–0 Ma). Asterisks indicate posterior clade probabilities <0.85, crosses indicate ML bootstrap values <75, double crosses indicate posterior clade probabilities <0.85 and ML bootstrap values <75. Circles indicate species placed in sections different to their previous placement.

Begonia thwaitesii is the type of *B. sect. Reichenheimia*. The section as circumscribed in Doorenbos & al. (1998) includes both rhizomatous species, which are most diverse in Malesia, and tuberous species, which are most diverse on mainland Asia. We create *B. sect. Jackia* sect. nov. to encompass the rhizomatous species (see below) but our sampling of tuberous species is poor and those species we do sample are resolved as polyphyletic. *Begonia albococcinea* Hook. and *B. floccifera* Bedd. are resolved with the unassigned *B. malabarica* Lam. and *B. hymenophylla* Gagnep. in a clade with members of *B. sect. Parvibegonia* A.DC. and *B. brandisiana* Kurz in the “Diploclinium grade”. The placement of the remainder of the section remains unclear.

- *Begonia dioica* (Fig. 4). – We resolve *B. dioica* Buch-Ham. ex D.Don within early-diverging Asian *Begonia*, although its position as sister to three Indo–Sri Lankan species is poorly supported (PP: 0.22; BS: 59).

Asian *Begonia* (Clade C) (Fig. 4). — Clade C contains primarily mainland Asian species including the “Diploclinium grade” and the “Platycentrum-Sphenanthera clade”.

- *Begonia pteridiformis* (Fig. 4). – We resolve *B. pteridiformis* Phutthai as sister to a clade containing *B. sect. Parvibegonia*, the “Diploclinium grade”, and the “Platycentrum-Sphenanthera clade”.

- *Begonia sect. Parvibegonia* (Fig. 4). – We resolve a clade containing all sampled species of *B. sect. Parvibegonia* and *B. smithiae* Geddes as sister to the “Diploclinium grade”.

- The “Diploclinium grade” (Fig. 4). – The majority of species of *B. sect. Diploclinium* were sampled; *B. demissa* Craib; *B. boisiana* Gagnep.; *B. brandisiana*; and *B. alicida* C.B.Clarke, the type of *B. sect. Alicida* C.B.Clarke, are resolved as a grade with the “Platycentrum-Sphenanthera clade” (see below) nested within. This is largely consistent with previous studies (Rajbhandary & al., 2011; Thomas & al., 2011, 2012), and the group was informally named “Diploclinium grade” by Rajbhandary & al. (2011). We follow this notation. We resolve the type of *B. sect. Diploclinium*, *B. grandis* Dryand., as sister to the rest of the clade. Our placement of *B. sect. Alicida* within the “Diploclinium grade” is poorly supported and does not match that observed by the ITS phylogeny presented in Rajbhandary & al. (2011), who resolved the section as sister to *B. sect. Parvibegonia* and *B. smithiae*.

- The “Platycentrum-Sphenanthera clade” (Fig. 4). – That *B. sect. Platycentrum* and *B. sect. Sphenanthera* (Hassk.) Warb. form a clade in which both sections are polyphyletic has been demonstrated repeatedly (Tebbit & al., 2006; Rajbhandary & al., 2011; Thomas & al., 2011, 2012). We confirm both this and the findings of Rajbhandary & al. (2011) that both species of *B. sect. Monopteron* (A.DC.) Warb., *B. griffithiana* (A.DC.) Warb. and *B. nepalensis* (A.DC.) Warb., are nested within this clade. We synonymise *B. sect. Sphenanthera* and *B. sect. Monopteron* with *B. sect. Platycentrum* while recognising a “Sphenanthera group” within *B. sect. Platycentrum*.

Asian *Begonia* (Clade D) (Figs. 5, 6). — Clade D is most diverse in Malesia but also includes the predominantly Chinese *B. sect. Coelocentrum* Irmsch.

- *Begonia sect. Coelocentrum* (Fig. 5). – *Begonia sect. Coelocentrum* in our analysis forms a clade including *B. leprosa*

Hance, the type of *B. sect. Leprosae* (T.C.Ku) Y.M.Shui. This is consistent with the section as recircumscribed by Chung & al. (2014) and we follow their delimitation of *B. sect. Coelocentrum* with *B. sect. Leprosae* treated as a synonym. Chung & al. further noted that *B. bataiensis* Kiew and *B. longicarpa* K.Y.Guan & D.K.Tian, included within *B. sect. Leprosae* by Shui & al. (2002), do not fall within their *B. sect. Coelocentrum*. Here we treat *B. bataiensis* as unassigned to section due to its isolated phylogenetic position in Chung & al. (2014), and *B. longicarpa* as belonging to *B. sect. Platycentrum* based on its phylogenetic placement in Rajbhandary & al. (2011) and Chung & al. (2014). We confirm the multiple origin of fleshy fruits with *Begonia* (Thomas & al., 2011), which is especially prevalent in *B. sect. Coelocentrum* and sect- *Platycentrum*.

- *Begonia peltatifolia* (Fig. 5). – *Begonia peltatifolia* H.L.Li was treated as a doubtful member of *B. sect. Reichenheimia* I by Doorenbos & al. (1998) and *B. sect. Diploclinium* by Gu & al. (2007). It differs considerably from both sections as circumscribed here, in being a relatively large rhizomatous species with very succulent leaves. Given its isolated phylogenetic position here and in the phylogeny of Chung & al. (2014), we treat *B. peltatifolia* as unassigned to section.

- The “*Begonia amphioxus* clade” (Fig. 5). – A number of Bornean and mainland Asian members of *B. sect. Petermannia* are resolved in a well-supported clade as sister to most of the remaining Malesian *Begonia* in Clade D. We resolve Vietnamese *B. cucphuongensis* H.Q.Nguyen & Tebbit in this clade, a species that was unassigned to section upon its description and considered most similar to the unplaced *B. boisiana*. This hypothesis is unsupported by our analysis (*B. boisiana* is placed in the “Diploclinium grade”). We also include *B. amphioxus* Sands within this group, which as originally assigned to *B. sect. Platycentrum* (Sands, 1990). Doorenbos & al. (1998) later treated this species as a possible new section, while Tebbit & Maciver (1999) noted morphological and phylogenetic similarities between it and *B. sect. Petermannia*. We informally name species within this clade the “*Begonia amphioxus* clade” and treat them within *B. sect. Petermannia*.

- *Begonia sect. Ridleyella* (Fig. 5). – *Begonia kingiana* Irmsch. and *B. speluncae* Ridl. are resolved as sister to the remainder of Asian *Begonia*. *Begonia kingiana* is our only sampled species of *B. sect. Ridleyella* Irmsch. sensu Doorenbos & al. (1998). Although we could not include the extinct *B. eriomischia* Ridl., the type of the section, we are confident it would fall within this group given its peltate leaves and retuse stamens. We transfer *B. speluncae* to *B. sect. Ridleyella*.

- *Begonia sect. Baryandra* (Fig. 5). – *Begonia sect. Baryandra* A.DC. was recently recircumscribed to include a group consisting of largely Philippines species previously in *B. sect. Diploclinium* (Rubite & al., 2013). This was based upon nrITS data, which resolved the recircumscribed section as a monophyletic group far removed from the type of *B. sect. Diploclinium*. We resolve the same clade and follow the circumscription of Rubite & al. (2013).

- *Begonia sect. Jackia* sect. nov. (Fig. 6). – *Begonia sect. Reichenheimia* sensu Doorenbos & al. (1998) is resolved in our analysis as polyphyletic (Fig. 2). A large number of rhizom-

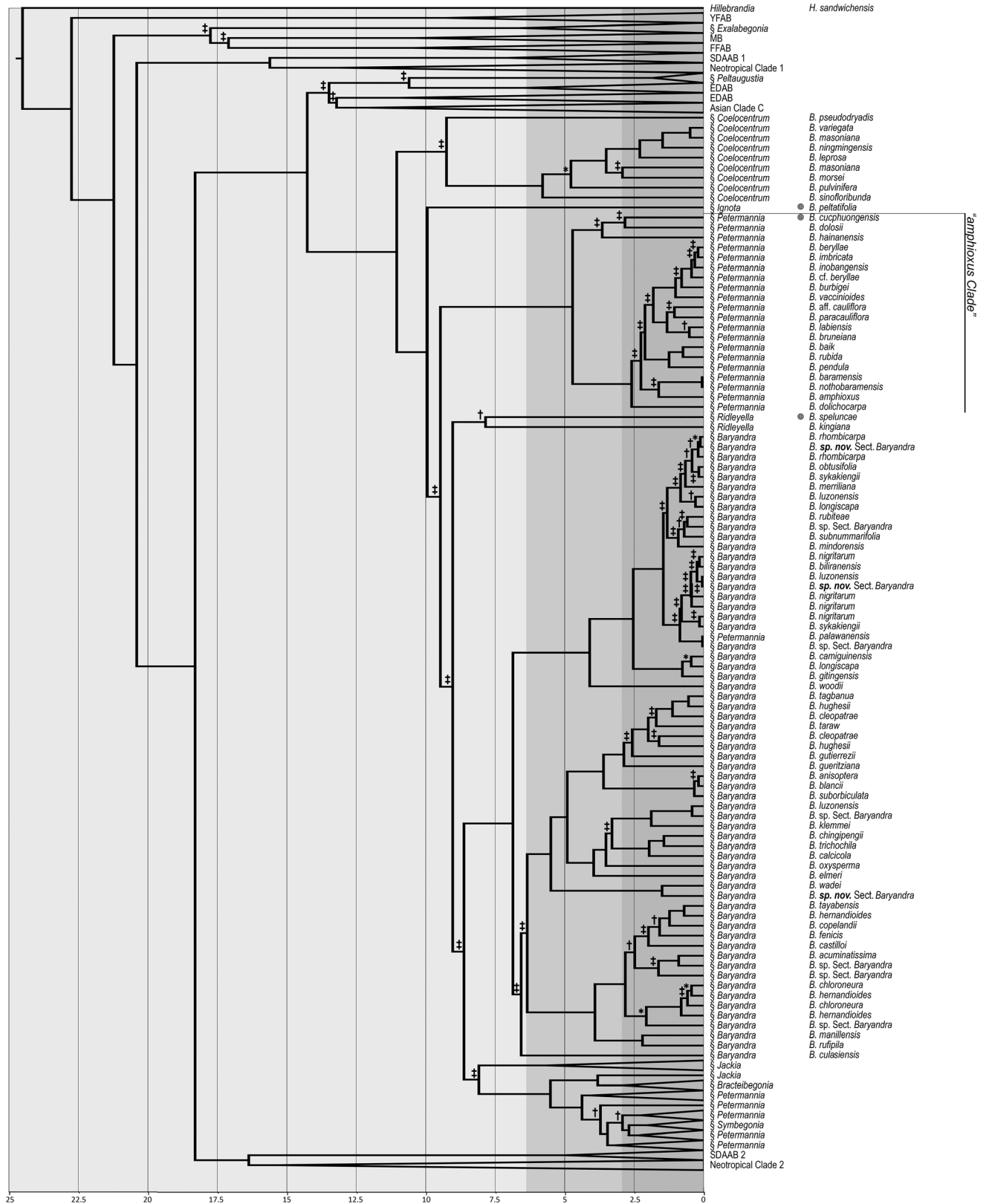


Fig. 5. Maximum-clade-credibility chronogram of BEAST analysis of the Begoniaceae focusing on Asian *Begonia* Clade D (part 1). Node heights indicate mean ages. Geological epochs are indicated by background colour: light grey, Miocene (23.0–5.3 Ma); mid-grey, Pliocene (5.3–2.6 Ma); dark grey, Holocene and Pleistocene (2.6–0 Ma). Asterisks indicate posterior clade probabilities <0.85, crosses indicate ML bootstrap values <75, double crosses indicate posterior clade probabilities <0.85 and ML bootstrap values <75. Circles indicate species placed in sections different to their previous placement.

atous Malaysian and Sumatran species previously assigned to this section are resolved in a clade sister to the remainder of *B. sect. Petermannia* and all sampled species of *B. sect. Bracteibegonia* A.DC. and *B. sect. Symbegonia*. (Warb.) L.L.Forrest & Hollingsw. This rhizomatous clade is distant both geographically and phylogenetically from the type of *B. sect. Reichenheimia*, *B. thwaitesii* from Sri Lanka. Species within the Malaysian and Sumatran clade further differ from the remainder of *B. sect. Reichenheimia* in their rhizomatous (vs. tuberous) habit and we include them here in *B. sect. Jackia* sect. nov.

A single species of *B. sect. Jackia*, *B. olivacea* Ardi, is resolved as sister to *B. sect. Bracteibegonia*. *Begonia olivacea* is a Sumatran endemic which morphologically clearly fits in *B. sect. Jackia* and not *B. sect. Bracteibegonia*. We suggest chloroplast capture is the most likely cause of the unexpected placement of *B. olivacea* and we include it here within *B. sect. Jackia*.

• *Begonia* sect. *Bracteibegonia* (Fig. 6). – All sampled species currently classified within *B. sect. Bracteibegonia* are resolved as a monophyletic group sister to the remainder of *B. sect. Petermannia* and *B. sect. Symbegonia*. However, further sampling is needed of the potentially dozens of species which are currently in *B. sect. Petermannia*, but which may fit better into *B. sect. Bracteibegonia* following a better understanding of how to define these sections morphologically. Our concept of this section follows Hughes & al. (2015b) and includes species with hairy stems, a low-growing spreading habit, short petioles, leaf lamina base often cuneate, short peduncles, a lax and fasciculate androecium, fruits which often have bristles or hairs and pistillate flowers with persistent tepals.

• The “Petermannia-Symbegonia clade” (Fig. 6). – The majority of *B. sect. Petermannia* is resolved as a grade with *B. sect. Symbegonia* nested within. It has been clear since it was transferred from a genus that *B. sect. Symbegonia* is nested within *B. sect. Petermannia* (Forrest & Hollingsworth, 2003).

The clade of *B. sect. Petermannia* containing *B. sect. Symbegonia* includes species from Malesia both west and east of Wallace’s line. We informally name this group the “Petermannia-Symbegonia clade” and suggest further study is required to determine whether this group should be split up to allow the continued recognition of *B. sect. Symbegonia*.

• Unsampled Asian *Begonia*. – We have been unable to sample members of four sections of Asian *Begonia*: *B. sect. Apterobegonia* Warb., *B. sect. Monophyllon* A.DC., *B. sect. Oligandrae* M.Hughes & W.N.Takeuchi, and *B. sect. Putzeysia* (Klotzsch) A.DC. The affinities of two of these sections appear clear and are discussed above (*B. sect. Monophyllon*, *B. sect. Putzeysia*) but those of the remainder are less apparent. *Begonia* sect. *Apterobegonia* is a monotypic section of unknown affinity and we retain its sectional status. The affinity of *B. sect. Oligandrae* may lie with *B. sect. Symbegonia* as discussed by Hughes & Takeuchi (2015).

We also did not sample any members of the six species of the “calcareo group”, as defined by Kiew & al. (2016), and they have not been included in previous phylogenetic analyses. We follow Kiew & al. (2016) and do not assign these species to section.

Neotropical Clade 1 (Fig. 7). — Neotropical Clade 1 (NC1) as defined by Moonlight & al. (2015) contains the majority of American species from east of Amazonia and a small number of widespread groups found throughout the Americas. The major clades and their branching order replicates those described by Moonlight & al., but we double the number of sampled species within this clade. NC1 can be split into three major clades: two clades of “cane-like” Brazilian *Begonia*; a clade we informally name the “core Pritzelia clade”; and *B. sect. Wageria* (Klotzsch) A.DC. and *B. sect. Donaldia* (Klotzsch) A.DC. nested within a grade of small groups of phylogenetically and morphologically distinct species we describe as *B. sect. Kollmannia* sect. nov. and *B. sect. Stellandrae* sect. nov.

• *Begonia* sect. *Gaerdia* (Fig. 7). – The majority of species in *B. sect. Gaerdia* (Klotzsch) A.DC. including the type are resolved in a monophyletic group including *B. coccinea* Hook., which was previously classified in *B. sect. Pritzelia* (Klotzsch) A.DC.

• *Begonia* sect. *Latistigma* (Fig. 7). – All sampled Brazilian species of *B. sect. Knesebeckia*, as circumscribed by Doorenbos & al. (1998), are only distantly related to the type of the section (*B. incarnata* Link & Otto). We resolve a group of species including *B. aconitifolia* A.DC., the type of *B. sect. Latistigma* A.DC., which we reinstate, as sister to *B. sect. Gaerdia*.

• *Begonia* sect. *Tetrachia* (Fig. 7). – We resolve *B. sect. Tetrachia* Brade as sister to the remainder of NC1, although this placement is poorly supported. Relationships within *B. sect. Tetrachia* are also poorly supported.

• The “*Begonia acetosa* clade” (Fig. 7). – We resolve as sister to *B. sect. Kollmannia* sect. nov. a well-supported clade containing two rhizomatous species currently classified in *B. sect. Pritzelia*: *B. acetosa* Vell. and *B. subacida* Irmsch. This relationship is well supported.

• *Begonia* sect. *Kollmannia* sect. nov. (Fig. 7). – We resolve *B. thelmae* L.B.Sm. & Wassh. and *B. jaguarensis* L.Kollmann & al. as sister to the “*Begonia acetosa* clade”.

• *Begonia* sect. *Donaldia* (Fig. 7). – *Begonia* sect. *Donaldia* is resolved as sister to a clade containing *B. sect. Stellandrae* sect. nov., and the “*Wageria* clade”. Both this clade and its relationships to related sections are well supported, and we also resolve *B. dichotoma* Jacq. and *B. scabrida* A.DC. within the clade.

• *Begonia* sect. *Stellandrae* sect. nov. (Fig. 7). – We resolve *B. hoehneana* as sister to the “*Wageria* clade”, although this position is poorly supported.

• The “*Wageria* clade” (Fig. 7). – All sampled species of *B. sect. Wageria* are resolved within a clade sister to *B. sect. Stellandrae* sect. nov. This clade is remarkable within *Begonia* for the lack of sequence divergence among its species, indicated in Fig. 7 by the short branch lengths and poor support for the majority of relationships within the clade. A number of species of *B. sect. Pritzelia* are also resolved within this clade, which is highly supported.

• The “core Pritzelia clade” (Fig. 7). – The majority of species in *B. sect. Pritzelia* are resolved in a clade containing *B. dietrichiana* Irmsch., the type of *B. sect. Pritzelia*. We further resolve *B. sect. Scheidweilaria* (Klotzsch) A.DC.; the monotypic *B. sect. Trendelenbergia* (Klotzsch) A.DC.; and *B. venosa*

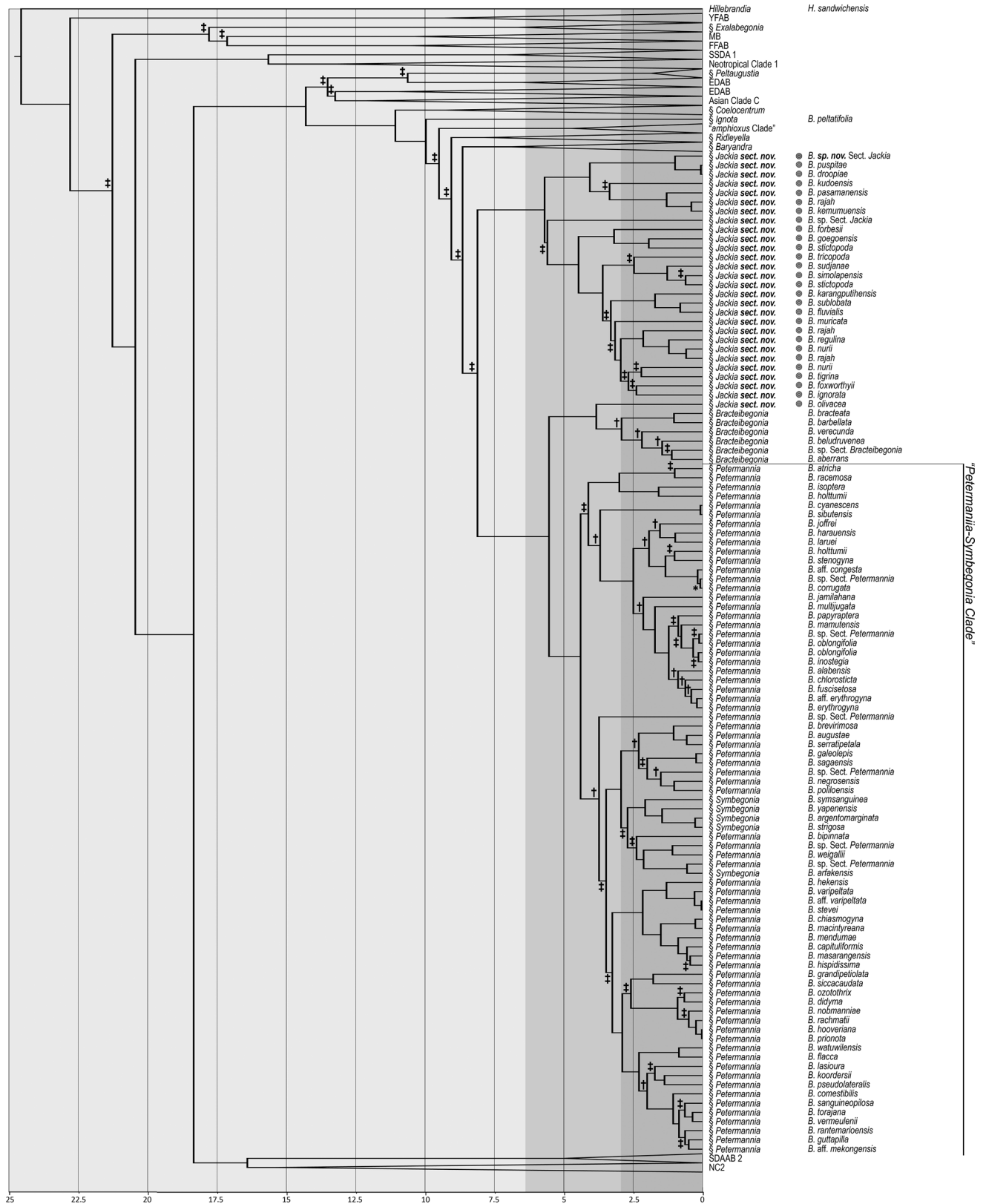


Fig. 6. Maximum-clade-credibility chronogram of BEAST analysis of the Begoniaceae focusing on Asian *Begonia* Clade D (part 2). Node heights indicate mean ages. Geological epochs are indicated by background colour: light grey, Miocene (23.0–5.3 Ma); mid-grey, Pliocene (5.3–2.6 Ma); dark grey, Holocene and Pleistocene (2.6–0 Ma). Asterisks indicate posterior clade probabilities < 0.85, crosses indicate ML bootstrap values < 75, double crosses indicate posterior clade probabilities < 0.85 and ML bootstrap values < 75. Circles indicate species placed in sections different to their previous placement.

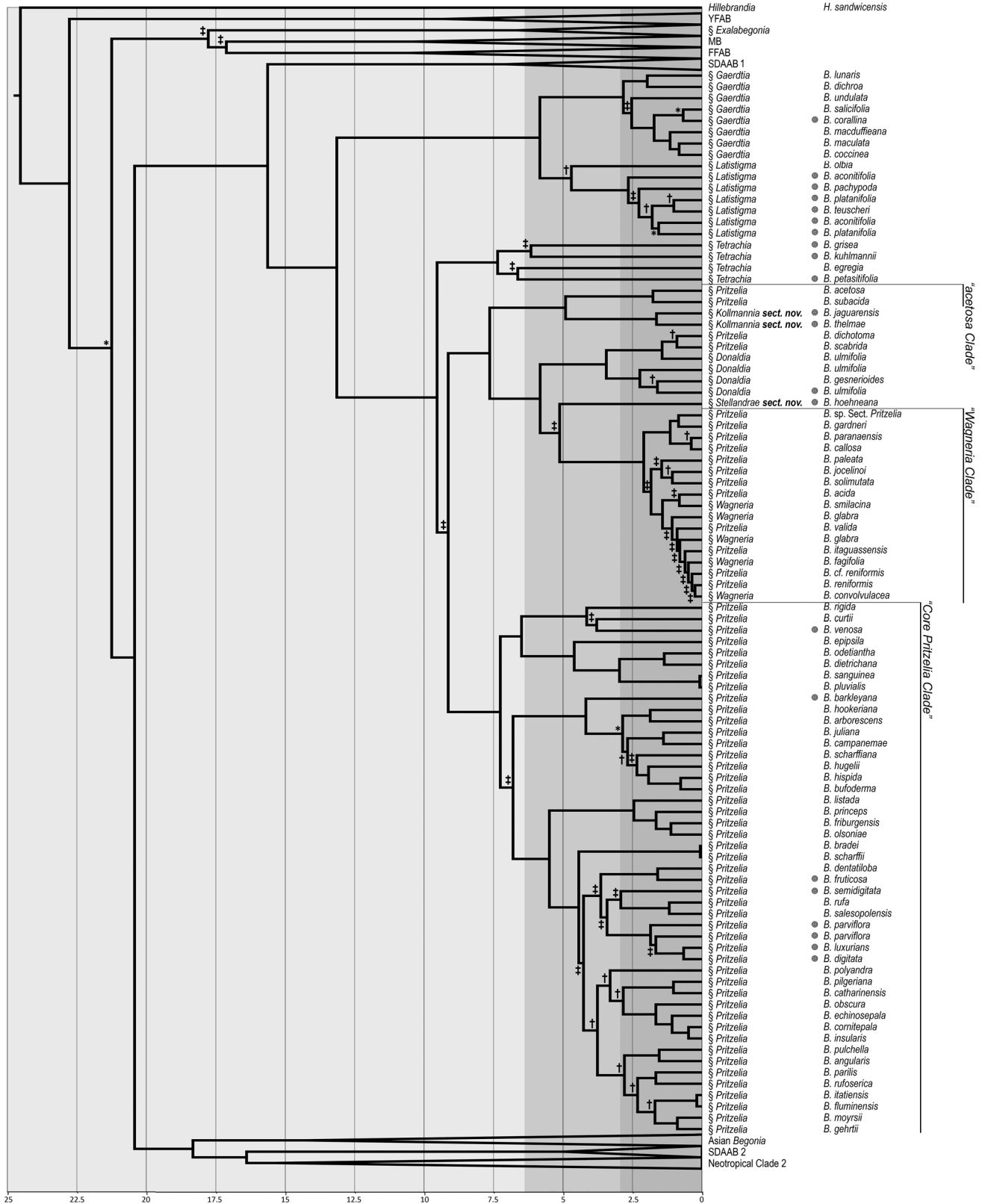


Fig. 7. Maximum-clade-credibility chronogram of BEAST analysis of the Begoniaceae focusing on Neotropical Clade 1. Node heights indicate mean ages. Geological epochs are indicated by background colour: light grey, Miocene (23.0–5.3 Ma); mid-grey, Pliocene (5.3–2.6 Ma); dark grey, Holocene and Pleistocene (2.6–0 Ma). Asterisks indicate posterior clade probabilities <0.85, crosses indicate ML bootstrap values <75, double crosses indicate posterior clade probabilities <0.85 and ML bootstrap values <75. Circles indicate species placed in sections different to their previous placement.

Skan ex Hook.f. within this clade, and we transfer all to *B.* sect. *Pritzelia*. This clade is well supported and informally named the “core *Pritzelia* clade”.

Neotropical Clade 2 (Figs. 8–10). — Neotropical Clade 2 (NC2) as defined by Moonlight & al. (2015) contains a small number of species and sections from eastern South America and the vast majority of species and sections from the remainder of the Americas. The relationships we observe within NC2 replicate those found by Moonlight & al. but our markedly improved sampling has allowed us to recircumscribe and describe a number of sections within the clade. The clade, NC2 can be split into three main clades: a largely Central American and Mexican clade (NC2-i); an eastern South American, Caribbean, and western South American clade of primarily cane-like species (NC2-ii); and a western South American clade of primarily rhizomatous and tuberous species (NC2-iii).

NC2-i (Fig. 8). — This clade is well supported, as is the sub-clade containing our much-expanded sampling of *B.* sect. *Gireoudia*.

- Tuberous Central American and Mexican *Begonia* (Fig. 8). — Our sampling of northern Central American and Mexican tuberous *B.* sect. *Knesebeckia* and *B.* sect. *Quadriperigon* Ziesenh. is poor, and we sample only a single species from each. *Begonia gracilis* Kunth of *B.* sect. *Quadriperigon* is resolved as sister to rhizomatous Central American and Mexican *Begonia*. This section is morphologically homogeneous and it is likely monophyletic. We recognise the section as circumscribed by Doorenbos & al. (1998).

From Central American and Mexican *B.* sect. *Knesebeckia* we sample only the type of the section (*B. incarnata*), which is nested within rhizomatous Central American and Mexican *Begonia*. This placement is surprising, given the many morphological differences between these two sections and we suggest it is unlikely to be representative of the species’ true affinities.

- Fleshy-fruited Central American and Mexican *Begonia* (Fig. 8). — We resolve *B. oaxacana* A.DC. and *B. heydei* C.DC., the type of *B.* sect. *Parietoplacentalia* Ziesenh. and the monotypic *B.* sect. *Urniformia* Ziesenh. respectively, as sister to the remainder of NC2. The sister relationship of these two sections is well supported but their placement is poorly supported.

- Rhizomatous Central American and Mexican *Begonia* (Fig. 8). — All sampled species of *B.* sect. *Gireoudia* (Klotzsch) A.DC. and *B.* sect. *Weilbachia* (Klotzsch & Oersted ex Klotzsch) A.DC. are resolved in a well-supported clade. We resolve *B.* sect. *Weilbachia* as polyphyletic within a paraphyletic *B.* sect. *Gireoudia* and newly synonymise *B.* sect. *Weilbachia* with *B.* sect. *Gireoudia*.

NC2-ii (Fig. 9). — The branching order among the early-diverging clades of NC2-ii is well-resolved and all major clades are well supported. We resolve a clade containing five well-supported, early-diverging clades from eastern South America of which three correspond to currently recognised sections: *B.* sect. *Solananthera* A.DC.; *B.* sect. *Trachelocarpus* (Müll.Berol.) A.DC.; and *B.* sect. *Microtuberosa* Moonlight & Tebbitt. We recognise *B.* sect. *Solananthera* and *B.* sect. *Trachelocarpus* as delimited by Doorenbos & al. (1998) and *B.* sect. *Microtuberosa* as delimited by Moonlight & al. (2017b). We also resolve a clade

of Brazilian members of *B.* sect. *Knesebeckia* with thyrsoid inflorescences, which we describe as the new section *Astrothrix* sect. nov., and a clade of members of *B.* sect. *Gaerdia*, for which we reinstate *B.* sect. *Pereira* Brade. These five sections are sister to a large clade of cane-like species most diverse in the Caribbean and Andes but with representatives throughout the Americas. This group includes *B.* sect. *Ruizopavonia* A.DC.; *B.* sect. *Casparya* (Klotzsch) Warb.; *B.* sect. *Semibegoniella* (C.DC.) Baranov & Barkley; *B.* sect. *Doratometra*; *B.* sect. *Begonia*; *B.* sect. *Hydristyles* A.DC. and *B.* sect. *Cyathocnemis* (Klotzsch) A.DC. and is exceptional among *Begonia* in the large levels of sequence divergence among clades and species, and appears to have an elevated rate of sequence evolution.

- *Begonia* sect. *Astrothrix* sect. nov. (Fig. 9). — We resolve a clade containing two species (*B. santos-limae* Brade, *B. bulatifolia* L.Kollmann) of *B.* sect. *Knesebeckia*. Together with four unsampled species, these species have been recognised as forming a morphologically and geographically distinct group within *B.* sect. *Knesebeckia* (Kollmann, 2009; Kollmann & Peixoto, 2012).

- *Begonia* sect. *Pereira* (Fig. 9). — A fourth eastern South American clade contains *B. edmundoi* Brade, *B. lubbersii* E.Morren, and *B. pseudolubbersii* Brade, all recognised by Doorenbos & al. (1998) in *B.* sect. *Gaerdia*. We reinstate *B.* sect. *Pereira*, typified by *B. edmundoi*, to include these species.

- *Begonia* sect. *Pilderia* and sect. *Rossmannia* (Fig. 9). — We resolve a clade containing *B.* sect. *Pilderia* (Klotzsch) A.DC. as circumscribed by Moonlight and Jara (Moonlight & Jara-Muñoz, 2017) as sister to the monotypic *B.* sect. *Rossmannia* A.DC. These sections are together resolved as sister to the remainder of NC2-ii.

- *Begonia* sect. *Ephemer* sect. nov. (Fig. 9). — A well-supported clade containing the majority of sampled South American members of *B.* sect. *Begonia* is resolved as sister to the remainder of NC2-ii. *Begonia hirtella* Link, treated by Doorenbos & al. (1998) in *B.* sect. *Doratometra*, is included in this clade.

- *Begonia* sect. *Ruizopavonia* (Fig. 9). — The relationships between the next three early-diverging, well-supported clades within NC2-ii remain unresolved. The first of these contains primarily species treated by Doorenbos & al. within *B.* sect. *Ruizopavonia*; however, this section is polyphyletic. Species resolved within this clade share raised veins on the underside of the leaves, elliptic or oblong anthers longer than the filaments, and fewer than five tepals in the female flower (except *B. tiliifolia* and *B. harlingii*). We therefore recircumscribe *B.* sect. *Ruizopavonia* to include those species with these characters.

- Horn-fruited Andean *Begonia* (Fig. 9). — *Begonia* sect. *Casparya* and *B.* sect. *Semibegoniella* together form a distinctive group of Andean species with horn-like fruits that dehisc along the back of the locules. The two sections were distinguished by Doorenbos & al. (1998) by the connate tepals of *B.* sect. *Semibegoniella*, its less numerous stamens, and its simple placentae (usually bifid in *B.* sect. *Casparya*). While we note that our results suggest the two sections may not be reciprocally monophyletic, we refrain from making formal changes to their circumscriptions while we await more detailed morphological and molecular data (A. Jara, unpub. data).

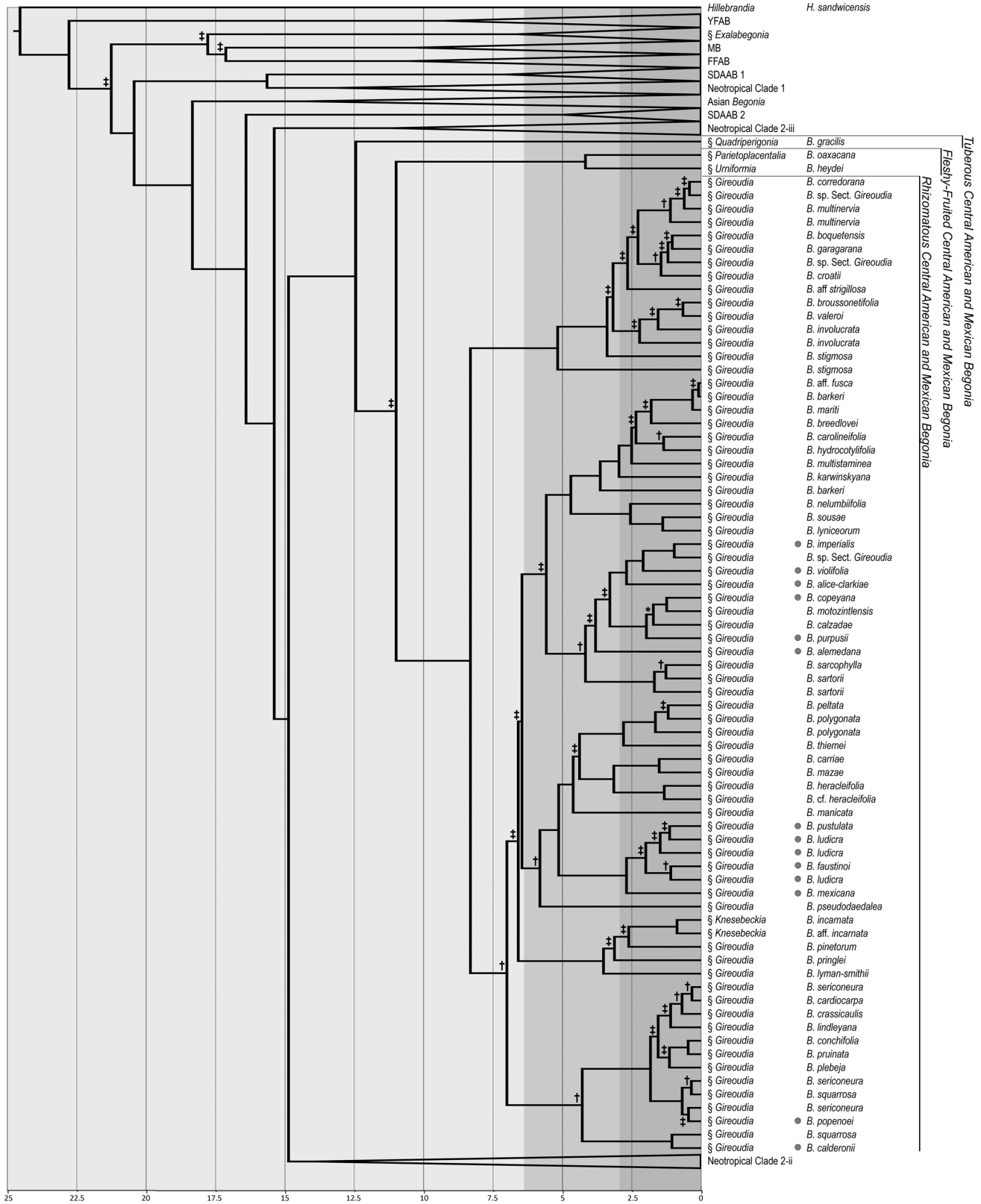


Fig. 8. Maximum-clade-credibility chronogram of BEAST analysis of the Begoniaceae focusing on Neotropical Clade 2-i. Node heights indicate mean ages. Geological epochs are indicated by background colour: light grey, Miocene (23.0–5.3 Ma); mid-grey, Pliocene (5.3–2.6 Ma); dark grey, Holocene and Pleistocene (2.6–0 Ma). Asterisks indicate posterior clade probabilities < 0.85, crosses indicate ML bootstrap values < 75, double crosses indicate posterior clade probabilities < 0.85 and ML bootstrap values < 75. Circles indicate species placed in sections different to their previous placement.

• *Begonia* sect. *Lepsia* (Fig. 9). – The remainder of *Begonia* sect. *Ruizopavonia* is resolved in a clade including *B. holtonis* A.DC., the type of *B. sect. Meionanthera* A.DC., and *B. foliosa* Kunth, the type of *B. sect. Lepsia* (Klotzsch) A.DC.

• *Begonia* sect. *Doratometra* (Fig. 9). – Three species of *Begonia* sect. *Doratometra* are resolved as sister to the remainder of NC2-ii. We do not sample *B. wallichiana* Lehm., the type of the section, but reproduce the circumscription of the section of Doorenbos & al. (1998) with the exception of *B. hirtella* Link, which was treated by Doorenbos & al. in *B. sect. Doratometra* and we include in *B. sect. Ephemera* sect. nov. (see discussion above).

• Caribbean *Begonia* sect. *Begonia* (Fig. 9). – All sampled Caribbean species of *B. sect. Begonia* are resolved as a grade with the remainder of NC2-ii nested within. The first dichotomy within this grade separates all sampled species of Caribbean *B. sect. Begonia* (except *B. acutifolia* Jacq.) from the remainder of NC2-ii (including *B. acutifolia*). The second dichotomy resolves *B. acutifolia* as sister to Bolivian *Begonia* and *B. sect. Cyathocnemis*.

• Bolivian *Begonia* (Fig. 9). – The Bolivian species of *Begonia* are among the most poorly known of the genus, with most known species described with incomplete descriptions, few having been covered in floristic accounts, and several other species awaiting description (P.W. Moonlight, unpub. data; M.C. Tebbitt, unpub. data). The members of *B. sect. Hydristyles* (which is almost restricted to Bolivia), monotypic *B. sect. Warburgina* O.Kuntze, and the Bolivian members of *B. sect. Ruizopavonia* are particularly problematic. The only species of these groups we sample (*B. fissistyla* Irmsch.) is not nested within any other sections and as sister to *B. rubriflora* L.Kollmann, which was described as a member of *B. sect. Begonia* from cultivated material of uncertain origins presumed to be from Argentina. We cannot speculate upon the placement of the remainder of the species of Bolivian *B. sect. Hydristyles*, *B. sect. Ruizopavonia* or *B. sect. Warburgina*.

• *Begonia* sect. *Cyathocnemis* (Fig. 9). – The final clade of NC2-ii contains primarily species of *B. sect. Cyathocnemis*. We also resolve *B. obtecticaulis* Irmsch. within this clade.

NC2-iii (Fig. 10). — We increase the sampling within NC2-iii from seven species in Moonlight & al. (2015) to over 50 in our current analysis. Much of the clade remains poorly resolved but we resolve a number of clear, reciprocally monophyletic clades within it. All species included are Andean and the majority are rhizomatous or tuberous members of *B. sect. Knesebeckia* and *B. sect. Eupetalum* (Lindl.) A.DC., although the scandent *B. sect. Gobenina* A.DC. is also nested within this clade.

• *Begonia bifurcata* (Fig. 10). – Northern Andean *B. bifurcata* L.B.Sm. & B.G.Schub. is resolved as sister to a primarily northern Andean clade including *B. sect. Barya* (Klotzsch) A.DC., the “cremnophila group”, *B. sect. Eupetalum* and *B. sect. Knesebeckia* group I. This relationship is well supported.

• Northern Andean *Begonia* sect. *Eupetalum* (Fig. 10). – We resolve a well-supported clade including all sampled species with multifid styles as sister to a clade containing the simple-styled “cremnophila group”, *B. sect. Knesebeckia* I and *B. sect. Barya*. Resolved as the most early-diverging clade of this sister group

are *B. geraniifolia* Hook. and *B. weberbaueri* Irmsch., which also have simple styles, but the placement of this clade is poorly supported. Our result is not inconsistent with *B. geraniifolia*, *B. weberbaueri*, and *B. sect. Eupetalum* forming a clade but we note our analyses do not strictly support this hypothesis.

• The “cremnophila clade” (Fig. 10). – We resolve a moderately well-supported clade containing *B. cremnophila* Tebbitt, *B. speculum* Moonlight & Tebbitt and *B. urubambensis* Tebbitt as sister to *B. sect. Knesebeckia* group I. The position of this clade is poorly supported and its affinity to *B. sect. Knesebeckia* group I and *B. sect. Eupetalum* remains unclear. These species are superficially very different, but share characters including their asymmetric, cymose inflorescences; four, unequal male tepals; anther morphology; five subequal female tepals; and stigmatic papillae morphology. We informally name this group of species the “cremnophila group”.

• *Begonia* sect. *Knesebeckia* group I and *B. sect. Barya* (Fig. 10). – We resolve a clade containing a number of species of the “acerifolia group” as defined by Tebbitt (2016); and *B. monadelphina* Ruiz & Pav. ex A.DC., the type of *B. sect. Barya*. The clade is well-supported but there is no support for relationships among subclades.

• *Begonia* sect. *Australes* (Fig. 10). – We resolve all sampled South American tuberous and caulescent members of *B. sect. Eupetalum* (sensu Doorenbos & al., 1998) with bifid styles within a well-supported clade. This clade corresponds to and includes the type of former *B. sect. Australes. Begonia boliviensis* A.DC. of *B. sect. Barya* is also resolved within this clade.

• *Begonia* sect. *Knesebeckia* group III (Fig. 10). – The remainder of Andean *B. sect. Knesebeckia* are resolved in two clades, the “maynensis group” as defined by Moonlight & al. (2017a) and part of the “acerifolia group” as defined by Tebbitt (2016): *B. arrogans* Irmsch., *B. ludwigii* Irmsch., *B. serotina* A.DC. and *B. wollnyi* Herzog, the tuberous species *B. piurensis* L.B.Sm. & B.G.Schub. and *B. parcifolia* C.DC. Together with *B. froebelii* A.DC., these two clades form a grade within which a clade containing *B. lutea* L.B.Sm. & B.G.Schub., *B. sect. Knesebeckia* group II, and *B. sect. Gobenina* is nested. The relationship between these clades and their close relatives are poorly supported and results are not inconsistent with *B. sect. Knesebeckia* III forming a monophyletic group, although we find no particular support for this hypothesis.

• *Begonia lutea* (Fig. 10). – *Begonia lutea* is resolved as sister to a clade containing *B. sect. Knesebeckia* group II and *B. sect. Gobenina* A.DC. as reciprocally monophyletic groups. This placement is poorly supported.

• *Begonia* sect. *Gobenina* (Fig. 10). – *Begonia* sect. *Gobenina* forms a well-supported clade including all sampled species of the section resolved as sister to *B. sect. Knesebeckia* group II. Relationships within *B. sect. Gobenina* are poorly supported.

• *Begonia* sect. *Knesebeckia* group II (Fig. 10). – Resolved as sister to *B. sect. Gobenina* are two undescribed limestone endemics from the Alto Mayo region of northern Perú. These species best fit Doorenbos & al.’s (1998) circumscription of *B. sect. Knesebeckia* and we informally name this clade *B. sect. Knesebeckia* group II.



Fig. 9. Maximum-clade-credibility chronogram of BEAST analysis of the Begoniaceae focusing on Neotropical Clade 2-ii. Node heights indicate mean ages. Geological epochs are indicated by background colour: light grey, Miocene (23.0–5.3 Ma); mid-grey, Pliocene (5.3–2.6 Ma); dark grey, Holocene and Pleistocene (2.6–0 Ma). Asterisks indicate posterior clade probabilities <0.85, crosses indicate ML bootstrap values <75, double crosses indicate posterior clade probabilities <0.85 and ML bootstrap values <75. Circles indicate species placed in sections different to their previous placement.

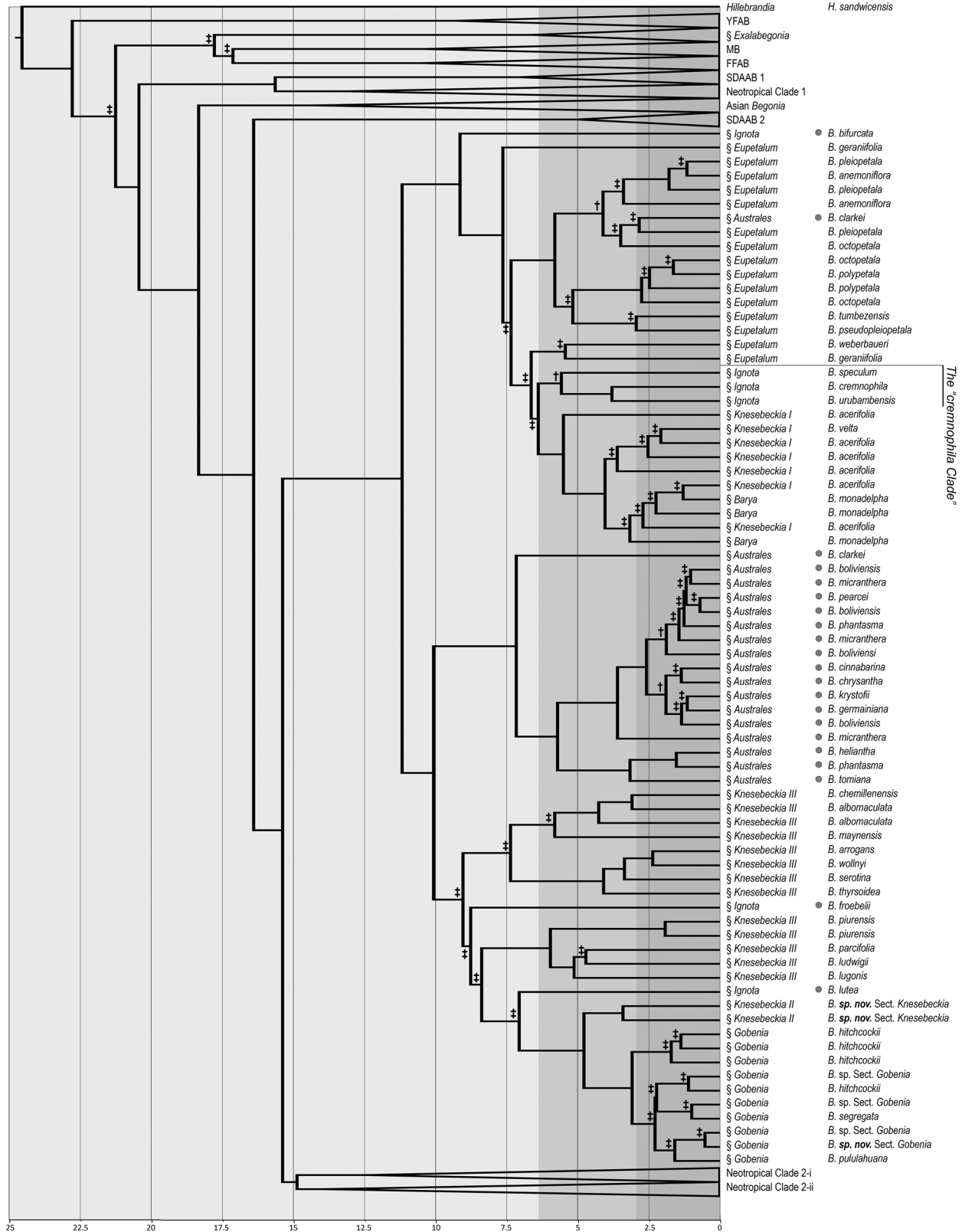


Fig. 10. Maximum-clade-credibility chronogram of BEAST analysis of the Begoniaceae focusing on Neotropical Clade 2-iii. Node heights indicate mean ages. Geological epochs are indicated by background colour: light grey, Miocene (23.0–5.3 Ma); mid-grey, Pliocene (5.3–2.6 Ma); dark grey, Holocene and Pleistocene (2.6–0 Ma). Asterisks indicate posterior clade probabilities <0.85, crosses indicate ML bootstrap values <75, double crosses indicate posterior clade probabilities <0.85 and ML bootstrap values <75. Circles indicate species placed in sections different to their previous placement.

■ TAXONOMIC TREATMENT

Begonia* sect. *Alicida C.B.Clarke in Hooker, Fl. Brit. India 2: 637. 1879 ≡ *Begonia* subg. *Alicida* (C.B.Clarke) C.B.Clarke in Bot. J. Linn. Soc. 18: 116. 1881 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 2. 1972): *Begonia alicida* C.B.Clarke. — [Fig. 13A]¹

Species list. – 4 species: *B. alicida* C.B.Clarke, *B. tricuspida* C.B.Clarke, *B. triradiata* C.B.Clarke, *B. vagans* Craib.

Distribution. – ASIA: Myanmar, Thailand.

Taxonomic notes. – Our placement of *B. sect. Alicida* within the “Diploclinium grade” does not match that observed by Rajbhandary & al. (2011), who resolved *B. alicida* as sister to a clade of *B. sect. Parvibegonia*. Given the conflict between datasets, we refer to the description in Doorenbos & al. (1998: 64) and follow the circumscription therein.

Begonia* sect. *Apterobegonia Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 143. 1894 – Type: *Begonia deliculata* Parish ex C.B.Clarke. — [Fig. 13B]

Species list. – 2 species: *B. deliculata* Parish ex C.B.Clarke, *B. phuthaii* M.Hughes.

Distribution. – ASIA: Myanmar, Thailand.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 65) and follow the circumscription therein.

Begonia* sect. *Astrothrix Moonlight, **sect. nov.** – Type: *Begonia bullatifolia* L.Kollmann. — [Fig. 15A]

Description. – Acaulescent, rhizomatous herbs, perennial, with an indumentum of stellate hairs. Stipules persistent. Leaves alternate, basifixed or peltate, blade subsymmetrical or asymmetrical, veins palmate. Inflorescence axillary, thyrsoid, protandrous, bracts deciduous or persistent. Male flowers: with 4 free perianth segments; stamens 20 to 50, filaments fused for less than half their length or free to the base (*B. espiritosantensis*), anthers obovate, dehiscing via lateral slits, connective not projecting or slightly projecting. Female flowers: bracteoles absent or 2 at the base of the ovary, with 5 to 6 free perianth segments; ovary and fruit with 3 wings, wings unequal, 3-locular, placentas axile, bifid, bearing ovules on both surfaces; styles 3, free to base, bifid, stigmatic papillae in a once spirally twisted band. Fruit a capsule.

Species list. – 5 species: *B. bullatifolia* L.Kollmann, *B. espiritosantensis* E.L.Jacques & Mamede, *B. fragae* L.Kollmann & Peixoto, *B. leopoldinensis* L.Kollmann, *B. santos-limae* Brade.

Distribution. – AMERICAS: Brazil (Espírito Santo, Rio de Janeiro).

Etymology. – The epithet is from the Greek *astro-* (starry) and *thrix* (hairs), referring to the stellate indumentum shared by all species in the section.

Taxonomic notes. – *Begonia* sect. *Astrothrix* represents a geographically and morphologically distinct group of species previously classified within *B. sect. Knesebeckia*. The section

is distinguished from other current and former members of *B. sect. Knesebeckia* by their unique combination of a rhizomatous habit, stellate indumentum, and thyrsoid inflorescence.

The section may be most easily confused with *B. sect. Tetrachia* as both share a stellate indumentum, basifixed or peltate leaves, and both usually have 5 free female and 4 male perianth segments. These two sections are best distinguished by their inflorescence structure (cymose in *B. sect. Tetrachia*; thyrsoid in *B. sect. Astrothrix*).

Begonia* sect. *Augustia (Klotzsch) A.DC., Prodr. 15(1): 384. 1864 ≡ *Augustia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 124. 1854 – Type (designated by Barkley & Baranov, in Buxtonian 1(Suppl. 1): 2. 1972): *Augustia dregei* (Otto & Dietr.) Klotzsch ≡ *Begonia dregei* Otto & Dietr. — [Fig. 11A]

Species list. – 12 species: *B. angolensis* Irmsch., *B. brevibracteata* Kupicha, *B. dregei* Otto & A.Dietr., *B. geranioides* Hook.f., *B. homonyma* Steud., *B. princeae* Gilg, *B. pygmaea* Irmsch., *B. riparia* Irmsch., *B. stolzii* Irmsch., *B. sutherlandii* Hook.f., *B. tayloriana* Irmsch., *B. wakefieldii* Gilg ex Engl.

Distribution. – AFRICA: Angola, Democratic Republic of the Congo, Kenya, Malawi, Mozambique, South Africa, Swaziland, Tanzania, Zaire, Zimbabwe.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 66) and follow the circumscription therein.

Begonia* sect. *Australes L.B.Sm. & B.G.Schub. in Darwiniana 5: 80. 1941 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 2. 1972): *Begonia micranthera* Griseb. — [Fig. 15B]

Species list. – 20 species: *B. barborkae* Halda, *B. baumannii* Lem., *B. boliviensis* A.DC., *B. chrysantha* Tebbitt, *B. cinnabarina* Hook., *B. clarkei* Hook.f., *B. crinita* Oliv. ex Hook.f., *B. fulgens* Lem., *B. germaineana* Tebbitt, *B. heliantha* Tebbitt, *B. herrerae* L.B.Sm. & B.G.Schub., *B. krystofii* Halda, *B. micranthera* Griseb., *B. pearcei* Hook.f., *B. phantasma* Tebbitt, *B. sleumeri* L.B.Sm. & B.G.Schub., *B. tafiensis* Lillo, *B. tominana* Golding, *B. veitchii* Hook.f., *B. weddelliana* A.DC.

Description. – Caulescent or rarely acaulescent (in some populations of *B. clarkei*), tuberous herbs, perennial. Stipules usually persistent, rarely deciduous (in some populations of *B. micranthera*). Leaves alternate, basifixed, blade usually asymmetrical, rarely symmetrical to subsymmetrical, veins palmate or palmate-pinnate. Inflorescence axillary, cymose, protandrous, bracts persistent. Male flowers: with 4 free perianth segments; stamens 15 to 150, filaments on a rounded receptacle or arranged along a 0.1–2.5 cm long column, anthers ellipsoid, cuboid, or obovoid, dehiscing via lateral slits, connective not projecting or slightly projecting. Female flowers: bracteoles usually absent or rarely 2 at the base of the ovary, with 5 or rarely 6 free perianth segments; ovary and fruit usually with 3 wings, wings unequal, rarely wings reduced to ribs, usually 3-locular, rarely 4-locular (in some populations of *B. micranthera*), placentas axile, bifid, bearing ovules on both surfaces; styles usually 3, rarely 4 (in some populations of *B. micranthera*), free or slightly fused at base, usually bifid

1 Colour plates are ordered geographically and collected at the end of the Taxonomic Treatment (p. 308 ff.).

or rarely 2-lobed (in some populations of *B. clarkei*), stigmatic papillae usually in a spirally twisted band. Fruit a capsule.

Distribution. – AMERICAS: Argentina (Catamarca, Jujuy, Salta, Tucumán), Bolivia, Ecuador, Peru.

Taxonomic notes. – *Begonia* sect. *Australes* as circumscribed here includes all tuberous and caulescent members of *B. sect. Eupetalum* sensu Doorenbos & al. (1998) with bifid styles. We also include *B. boliviensis* in this section, which was previously treated in *B. sect. Barya*. This species possesses the characteristic features of *B. sect. Australes* but differs in its columnar androecium and red, forward projecting tepals. These characters appear to be adaptations to hummingbird pollination independent of those of *B. sect. Barya*. We transfer *B. boliviensis* into *B. sect. Australes*.

We note two collections of *B. clarkei* from Cuzco, Perú are resolved within *B. sect. Eupetalum* allied to *B. pleiopetala* A.DC. These collections are from near the northern end of the range of *B. clarkei* and *B. sect. Australes* where the species occurs sympatrically with *B. pleiopetala* (which is herein recognised in a more narrowly defined *B. sect. Eupetalum*). We propose recent chloroplast capture as a possible explanation for the observed disagreement between molecules and morphology and continue to classify *B. clarkei* within *B. sect. Australes* since this species is caulescent and has bifid styles.

Begonia* sect. *Baccabegonia Reitsma in Agric. Univ. Wagenin-gen Pap. 84(3): 97. 1985 – Type: *Begonia baccata* Hook.f. — [Fig. 11B]

Species list. – 2 species: *B. baccata* Hook.f., *B. crateris* Exell.

Distribution. – AFRICA: São Tomé and Príncipe (São Tomé).

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 68) and follow the circumscription therein.

Begonia* sect. *Barya (Klotzsch) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 122. 1859 ≡ *Barya* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 122. 1854 – Type: *Barya monadelpha* (Ruiz ex Klotzsch) Klotzsch ≡ *Begonia monadelpha* Ruiz & Pav. ex A.DC. — [Fig. 15C]

Species list. – 2 species: *B. monadelpha* Ruiz & Pav. ex A.DC., *B. soror* Irmsch.

Distribution. – AMERICAS: Ecuador, Peru.

Taxonomic notes. – We follow the circumscription of Doorenbos & al. (1998: 70), although *B. boliviensis* is transferred to *B. sect. Australes* (see above). We refer to the description therein but note the section no longer includes tuberous species.

Begonia* sect. *Baryandra A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 122. 1859 – Type: *Begonia oxysperma* A.DC. — [Fig. 13C]

Species list. – 64 species: *B. acclivis* Coyle, *B. acuminatissima* Merr., *B. alba* Merr., *B. alvarezii* Merr., *B. angilogenis* Merr., *B. anisoptera* Merr., *B. bernadusii* V.S. Guanah, *B. biliranensis* Merr., *B. blancii* M.Hughes & C.I Peng, *B. calcicola* Merr., *B. camiguinensis* Elmer, *B. castilloi* Merr.,

B. chingipengii Rubite, *B. chloroneura* P. Wilkie & Sands, *B. cleopatrae* Coyle, *B. collisiae* Merr., *B. colorata* Warb., *B. copelandii* Merr., *B. coronensis* Merr., *B. culasiensis* C.I Peng, Rubite, C.W.Lin & K.F.Chung, *B. diwolii* Kiew, *B. doloisii* Rimi, *B. elmeri* Merr., *B. fenicis* Merr., *B. gitingensis* Elmer, *B. gueritziana* Gibbs, *B. gutierrezii* Coyle, *B. hernandioides* Merr., *B. hughesii* Rubite & C.I Peng, *B. isabelensis* Quisumb. & Merr., *B. klemmei* Merr., *B. lancilimba* Merr., *B. longinoda* Merr., *B. longiscapa* Warb., *B. luzonensis* Warb., *B. manillensis* A.DC., *B. merrilliana* C.I Peng, Rubite, C.W.Lin & K.F.Chung, *B. mindorensis* Merr., *B. moneta* C.I Peng, Rimi & C.W.Lin, *B. neopurpurea* L.B.Sm. & Wassh., *B. nigritarum* (Kamel) Steud., *B. obtusifolia* Merr., *B. oxysperma* A.DC., *B. parva* Merr., *B. rubiteae* M.Hughes, *B. rubrifolia* Merr., *B. rufipila* Merr., *B. serpens* Merr., *B. sharpeana* F.Muell., *B. simunii* Rimi, *B. subnummularifolia* Merr., *B. suborbiculata* Merr., *B. sykakiengii* Rubite, C.I Peng, C.W.Lin & K.F.Chung, *B. tagbanua* M.Hughes, C.I Peng & Rubite, *B. tandangii* C.I Peng & Rubite, *B. taraw* M.Hughes, C.I Peng & Rubite, *B. tayabensis* Merr., *B. titoevangelistae* D. Tandang & Rubite, *B. trichocheila* Warb., *B. vanoverberghii* Merr., *B. vespiopropinqua* F.Y.Chong, *B. wadei* Merr. & Quisumb., *B. wilkiei* Coyle, *B. woodii* Merr.

Distribution. – ASIA: Indonesia (Kalimantan, Moluccas), Japan (Nansei-Shoto), Malaysia (Sabah, Sarawak), Philippines, Papua New Guinea, Taiwan.

Taxonomic notes. – We refer to the description in Rubite & al. (2013: 4) and follow the circumscription therein.

Begonia* sect. *Begonia – Type: *Begonia obliqua* L. — [Fig. 15D]

= *Begonia* sect. *Podandra* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 122. 1859 – Type: *B. decandra* Pav. ex A.DC.

– *Begonia* “sect. *Begoniastrum*” A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 123. 1859, not validly published (Art. 22.2).

– *Begonia* (“sect. *Begoniastrum*”) “subsect. *Eubegonia*” Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 149. 1894, not validly published (Art. 21.3 & 22.2).

Species list. – 41 species: *B. abbotii* Urb., *B. acutifolia* Jacq., *B. alcarrasica* J.Sierra, *B. azuensis* Urb. & Ekman, *B. banaoensis* J.Sierra, *B. bissei* J.Sierra, *B. bolleana* Urb. & Ekman, *B. brachyclada* Urb. & Ekman, *B. brachypoda* O.E.Schulz, *B. bullata* Urb. & Ekman, *B. cowellii* Nash, *B. cubensis* Hassk., *B. decandra* Pav. ex A.DC., *B. domingensis* A.DC., *B. eciliata* O.E.Schulz, *B. exilis* O.E.Schulz, *B. glaberrima* Urb. & Ekman, *B. jamaicensis* A.DC., *B. leivae* J.Sierra, *B. leuconeura* Urb. & Ekman, *B. libanensis* Urb., *B. linearifolia* J.Sierra, *B. lomensis* Britton & P.Wilson, *B. maestransis* Urb., *B. minor* Jacq., *B. notiophila* Urb., *B. obliqua* L., *B. odorata* Willd., *B. pensilis* L.B.Sm. & Wassh., *B. platyptera* Urb., *B. plumieri* A.DC., *B. purdieana* A.DC., *B. purpurea* Sw., *B. pycnantha* Urb. & Ekman, *B. repens* Lam., *B. retusa* O.E.Schulz, *B. rotundifolia* Lam., *B. schulziana* Urb. & Ekman, *B. stipulacea* Willd., *B. vincentina* O.E.Schulz, *B. wrightiana* A.DC.

Species whose membership is doubtful. – 5 species: *B. admirabilis* Brade, *B. konderreisiana* L.B.Sm. & R.C.Sm., *B. lindmanii* Brade, *B. lanstykii* Brade, *B. lucidissima* Golding & Kareg.

Distribution. – AMERICAS: Cuba, Dominica, Dominican Republic, Grenada, Guadeloupe, Haiti, Jamaica, Martinique, Montserrat, Puerto Rico, Saint Kitts & Nevis, Saint Lucia, Saint Vincent, Trinidad-Tobago. — Doubtful species: Brazil (Bahia, Espírito Santo, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Rio de Janeiro, Santa Catarina, São Paulo), Paraguay.

Taxonomic notes. – All sampled non-Caribbean species of *B. sect. Begonia* are only distantly related to the type of the section and are transferred to other sections (see *B. sect. Ephemera* *sect. nov.*; the “core Pritzelia clade”) with the exception of an unsampled group of many-flowered eastern South American species. We assign these species doubtfully to *B. sect. Begonia*, recognising a much-diminished section restricted to the Caribbean.

The placement of *B. acutifolia* as sister to the remainder of NC2-ii resolves *B. sect. Begonia* as paraphyletic with the remainder of NC2-ii nested within. *Begonia acutifolia* is a Cuban species most similar to a number of other Cuban species that differ from the remainder of Caribbean *B. sect. Begonia* in their relatively straight, lanceolate leaves (e.g., *B. banoensis* J.Sierra, *B. cubensis* Haask., *B. maestrensis* Urb.). We sample only *B. acutifolia* of this poorly known group and assign all species to *B. sect. Begonia*.

We refer to the description in Doorenbos & al. (1998: 74), which fits *B. sect. Begonia* despite its significantly reduced circumscription.

Begonia* sect. *Bracteibegonia A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 127. 1859 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 2. 1972): *Begonia bracteata* Jack. – [Fig. 13D]

Species list. – 13 species: *B. aberrans* Irmsch., *B. barbellata* Ridl., *B. beludruvenea* M.Hughes, *B. bracteata* Jack, *B. fasciculata* Jack, *B. flexula* Ridl., *B. horsfieldii* Miq. ex A.DC., *B. jackiana* M.Hughes, *B. lepida* Blume, *B. lepidella* Ridl., *B. pilosa* Jack, *B. triginticollium* Girm., *B. verecunda* M.Hughes

Distribution. – ASIA: Indonesia (Java, Sumatra), Malaysia (Peninsular Malaysia).

Taxonomic notes. – Our concept of this section follows Hughes & al. (2015b) and includes species with hairy stems, a low-growing spreading habit, leaves with short petioles, short peduncles, a lax and fasciculate androecium and fruits which often have bristles or hairs and pistillate flowers with persistent tepals. Many species from Borneo currently classified in *B. sect. Petermannia* have this suite of characters and may need to be transferred to *B. sect. Bracteibegonia* following further research. However, given the flood of new taxa in *B. sect. Petermannia* published during the writing of this paper (e.g., Ardhaka & Ardi, 2016; Julia & Kiew, 2016; Julia & al., 2016), we thought it premature to attempt a recircumscription of these two sections.

Begonia* sect. *Casparya (Klotzsch) Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 146. 1894 ≡ *Casparya* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 127. 1854 ≡ *Begonia* subg. *Casparya* (Klotzsch) C.B.Clarke in Bot. J. Linn. Soc. 18: 115. 1881 – Type

(designated by Doorenbos & al. in Wageningen Agric. Univ. Pap. 98(2): 80, 1998): *Casparya coccinea* Klotzsch = *Begonia urticae* L.f. — [Fig. 15E]

= *Stibadotheca* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 127. 1854 (“*Stiradotheca*”) ≡ *Casparya* *sect. Stibadotheca* (Klotzsch) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 116. 1859 ≡ *Begonia* (*sect. Casparya*) *subsect. Stibadotheca* (Klotzsch) Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 146. 1894 – Type (designated by Baranov & Barkley in Buxtonian 1(Suppl. 1): 2. 1972): *Stibadotheca ferruginea* (L.f.) Klotzsch ≡ *Begonia ferruginea* L.f.

= *Sassea* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 128. 1854 ≡ *Begonia* (*sect. Casparya*) *subsect. Sassea* (Klotzsch) Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 146. 1894 – Type (designated by Baranov & Barkley in Buxtonian 1(Suppl. 1): 2. 1972): *Sassea urticae* (L.f.) Klotzsch = *Begonia urticae* L.f.

= *Isopteryx* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 127. 1854 (“*Isopterys*”) ≡ *Casparya* *sect. Isopteryx* (Klotzsch) A.DC., Prodr. 15(1): 270. 1864 – Lectotype (designated Swart, ING Card 10021. 1960): *Isopteryx umbellata* (Kunth) Klotzsch ≡ *Begonia umbellata* Kunth.

= *Casparya* *sect. Aetheopteryx* A.DC., Prodr. 15(1): 271. 1864 ≡ *Begonia* (*sect. Casparya*) *subsect. Aetheopteryx* (A.DC.) Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 146. 1894 – Type: *Casparya trispathulata* A.DC. ≡ *Begonia trispathulata* (A.DC.) Warb.

= *Casparya* *sect. Andiphila* A.DC., Prodr. 15(1): 271. 1864 ≡ *Begonia* (*sect. Casparya*) *subsect. Andiphila* (A.DC.) Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 146. 1894 – Type (designated by Baranov & Barkley in Buxtonian 1(Suppl. 1): 3. 1972): *Casparya trianae* A.DC. ≡ *Begonia trianae* (A.DC.) Warb.

Species list. – 28 species: *B. antioquiensis* (A.DC.) Warb., *B. brevipetala* (A.DC.) Warb., *B. chlorolepis* L.B.Sm. & B.G.Schub., *B. colombiana* L.B.Sm. & B.G.Schub., *B. cornuta* L.B.Sm. & B.G.Schub., *B. diffusa* L.B.Sm. & B.G.Schub., *B. diversistipulata* Irmsch., *B. ferruginea* L.f., *B. formosissima* Sandwith, *B. fuchsiiflora* (A.DC.) F.A.Barkley & Baranov, *B. gamolepis* L.B.Sm. & B.G.Schub., *B. hirta* (Klotzsch) L.B.Sm. & B.G.Schub., *B. liesneri* Burt-Utley & Utley, *B. lipolepis* L.B.Sm., *B. mariae* L.B.Sm., *B. montana* (A.DC.) Warb., *B. nevadensis* Dorr, *B. raimondii* Irmsch., *B. solaniflora* Jara, *B. toledana* L.B.Sm. & B.G.Schub., *B. trianae* (A.DC.) Warb., *B. trispathulata* (A.DC.) Warb., *B. trujillensis* L.B.Sm., *B. umbellata* Kunth, *B. ursina* L.B.Sm. & B.G.Schub., *B. urticae* L.f., *B. vareschii* Irmsch., *B. wilburi* Burt-Utley & Utley

Distribution. – AMERICAS: Colombia, Costa Rica, Ecuador, Panamá, Perú, Venezuela.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 80) and follow the circumscription therein.

Begonia* sect. *Chasmophila J.J.de Wilde & Plana in Edinburgh J. Bot. 60(2): 122. 2003 – Type: *Begonia iucunda* Irmsch. *Species list.* – 1 species: *B. iucunda* Irmsch.

Distribution. – AFRICA: Democratic Republic of the Congo, Republic of the Congo.

Taxonomic notes. – We refer to the description in De Wilde & Plana (2003: 122) and follow the circumscription therein.

Begonia* sect. *Coelocentrum Irmsch. in Mitt. Inst. Allg. Bot. Hamburg 10: 553. 1939 – Type (designated by Baranov & Barkley in Buxtonian 1(Suppl. 1): 3. 1972): *Begonia porteri* H.Lév. & Vaniot. — [Fig. 13E]

= *Begonia* sect. *Leprosae* (T.C.Ku) Y.M.Shui in Bot. Bull. Acad. Sin. 43(4): 321. 2002 – Type: *B. leprosa* Hance.

Species list. – 69 species: *B. arachnoidea* C.I Peng, Yan Liu & S.M.Ku, *B. asteropyrifolia* Y.M.Shui & W.H.Chen, *B. aurantiflora* C.I Peng, Yan Liu & S.M.Ku, *B. auritistipula* Y.M.Shui & W.H.Chen, *B. austroguangxiensis* Y.M.Shui & W.H.Chen, *B. babeana* Aver. & H.Q.Nguyen, *B. bamaensis* Yan Liu & C.I Peng, *B. biflora* T.C.Ku, *B. ×breviscapa* C.I Peng, Yan Liu & S.M. Ku, *B. calciphila* C.I Peng, *B. chongzuoensis* Yan Liu, S.M.Ku & C.I Peng, *B. circularis* C.I Peng & C.W.Lin, *B. cirrosa* L.B.Sm. & Wassh., *B. crystallina* Y.M.Shui & W.H.Chen, *B. curvicarpa* S.M.Ku, C.I Peng & Yan Liu, *B. cylindrica* D.R.Liang & X.X.Chen, *B. daxinensis* T.C.Ku, *B. debaoensis* C.I Peng, Yan Liu & S.M.Ku, *B. fangii* Y.M.Shui & C.I Peng, *B. ferox* C.I Peng & Yan Liu, *B. filiformis* Irmsch., *B. fimbribracteata* Y.M.Shui & W.H.Chen, *B. guangxiensis* C.Y.Wu, *B. guixiensis* Yan Liu, S.M.Ku & C.I Peng, *B. huangii* Y.M.Shui & W.H.Chen, *B. jingxiensis* D.Fang & Y.G.Wei, *B. kui* C.I Peng, *B. langsonensis* C.I Peng & C.W.Lin, *B. lanternaria* Irmsch., *B. leipongensis* D.K.Tian, L.H.Yang & C.Li, *B. leprosa* Hance, *B. liuyanii* C.I Peng, S.M.Ku & W.C. Leong, *B. locii* C.I Peng, C.W.Lin & N.H. Nguyen, *B. longa* C.I Peng & W.C. Leong, *B. longgangensis* C.I Peng & Yan Liu, *B. longistyla* Y.M.Shui & W.H.Chen, *B. luochengensis* S.M.Ku, C.I Peng & Yan Liu, *B. luzhaiensis* T.C.Ku, *B. masoniana* Irmsch., *B. melanobullata* C.I Peng & C.W.Lin, *B. montaniformis* C.I Peng, C.W.Lin & N.H. Nguyen, *B. morsei* Irmsch., *B. nahangensis* Aver. & H.Q.Nguyen, *B. ningmingensis* D.Fang, Y.G.Wei & C.I Peng, *B. obliquefolia* S.H.Huang & Y.M.Shui, *B. ornithophylla* Irmsch., *B. pengii* S.M.Ku & Yan Liu, *B. phuthoensis* H.Q.Nguyen, *B. picturata* Yan Liu, S.M.Ku & C.I Peng, *B. platycarpa* Y.M.Shui & W.H.Chen, *B. porteri* H.Lév. & Vaniot, *B. pseudodaxinensis* S.M.Ku, Yan Liu & C.I Peng, *B. pseudodryadis* C.Y.Wu, *B. pseudoleprosa* C.I Peng, Yan Liu & S.M.Ku, *B. pulvinifera* C.I Peng & S.M.Ku, *B. retinervia* D.Fang, D.H.Qin & C.I Peng, *B. rhynchocarpa* Y.M.Shui & W.H.Chen, *B. rugosula* Aver., *B. semiparietalis* Yan Liu, S.M.Ku & C.I Peng, *B. setulosopeltata* C.Y.Wu, *B. sinofloribunda* Dorr, *B. sonlaensis* Aver., *B. subcoriacea* C.I Peng, Yan Liu & S.M.Ku, *B. ufoides* C.I Peng, Y.H.Qin & C.W.Lin, *B. umbraculifolia* Y.Wan & B.N.Chang, *B. variegata* Y.M.Shui & W.H.Chen, *B. variifolia* Y.M.Shui & W.H.Chen, *B. wangii* T.T.Yu, *B. zhengyiana* Y.M.Shui

Distribution. – ASIA: China (Guangdong, Guangxi, Guizhou, Yunnan), Vietnam.

Taxonomic notes. – We refer to the description in Chung & al. (2014) and follow the circumscription therein.

Begonia* sect. *Cristasemen J.J.de Wilde in Agric. Univ. Wageningen Pap. 84(3): 115. 1984 – Type: *Begonia thomeana* C.DC. – [Fig. 11D]

Species list. – 1 species: *B. thomeana* C.DC.

Distribution. – AFRICA: Gabón, São Tomé and Príncipe (São Tomé).

Taxonomic notes. – We refer to the description in De Wilde (1985a: 115) and follow the circumscription therein.

Begonia* sect. *Cyathocnemis (Klotzsch) A.DC., Prodr. 15(1): 332. 1864 ≡ *Cyathocnemis* Klotzsch in Abh. Königl. Akad. Wiss. Berlin 1854: 220. 1855 – Type: *Cyathocnemis obliqua* Klotzsch ≡ *Begonia cyathophora* Poepp. & Endl. — [Fig. 15F]

= *Moschkowitzia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 127. 1854 – Type: *Moschkowitzia fagopyroides* (Kunth) Klotzsch = *Begonia denticulata* Kunth.

Species list. – 18 species: *B. altoperuviana* A.DC., *B. bracteosa* A.DC., *B. brevicordata* L.B.Sm. & B.G.Schub., *B. cryptocarpa* L.B.Sm. & B.G.Schub., *B. cyathophora* Poepp. & Endl., *B. falcifolia* Hook.f., *B. laxa* L.B.Sm. & B.G.Schub., *B. lophoptera* Rolfe, *B. lucifuga* Irmsch., *B. magdalenae* L.B.Sm. & B.G.Schub., *B. obtecticaulis* Irmsch., *B. pseudoglaucia* Irmsch., *B. roezlii* Regel, *B. stenotepala* L.B.Sm. & B.G.Schub., *B. subciliata* A.DC., *B. subspinulosa* Irmsch., *B. suprafastigiata* Irmsch., *B. tribracteata* Irmsch.

Species whose membership is doubtful. – 4 species: *B. denticulata* Kunth, *B. machrisiana* L.B.Sm. & B.G.Schub., *B. nubicola* L.B.Sm. & B.G.Schub., *B. wagneriana* (Klotzsch) Hook.

Distribution. – AMERICAS: Bolivia, Colombia, Peru. — Doubtful species: Brazil (Amazonas, Goiás), Venezuela.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 88) and follow the circumscription therein with the exclusion of *B. viridiflora* A.DC. (see *B. sect. Ruizopavonia*) and the addition of *B. obtecticaulis*. The female flowers of this species were unknown in 1998 but match those of *B. sect. Cyathocnemis* (P.W. Moonlight, unpub. data). Our sampling lacks northern Andean species (e.g., *B. denticulata* Kunth., *B. nubicola* L.B.Sm. & B.G.Schub.) and the single Brazilian species (*B. machrisiana* L.B.Sm. & B.G.Schub.) so we follow Doorenbos & al. (1998) in doubtfully assigning these species to the section.

Begonia* sect. *Diploclinium (Lindl.) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 129. 1859 ≡ *Diploclinium* Lindl., Veg. Kingd., ed. 2: 319. 1847 – Type: *Diploclinium evansianum* (Andrews) Lindl. = *Begonia grandis* Dryand. — [Fig. 13F]

= *Begonia* sect. *Trilobaria* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 131. 1859 – Type: *Begonia ovatifolia* A.DC.

– *Begonia* “subg. *Eubegonia*” C.B.Clarke in Bot. J. Linn. Soc. 18: 117. 1881, not validly published.

Species list. – 85 species: *B. acutitepala* K.Y.Guan & D.K.Tian, *B. adscendens* C.B.Clarke, *B. alveolata* T.T.Yu, *B. anceps* Irmsch., *B. arborea* Y.M.Shui, *B. arnottiana* (Wight) A.DC., *B. asperifolia* Irmsch., *B. brandisiana* Kurz, *B. burmensis* L.B.Sm. & Wassh., *B. cavaleriei* H.Lév., *B. cehengensis*

T.C.Ku, *B. concanensis* A.DC., *B. coptidi-montana* C.Y.Wu, *B. cordifolia* (Wight) Thwaites, *B. demissa* Craib, *B. dentatobracteata* C.Y.Wu, *B. dioica* Buch.-Ham. ex D.Don, *B. discreta* Craib, *B. exposita* Phutthai & M.Hughes, *B. fengii* T.C.Ku, *B. festiva* Craib, *B. fimbriatipula* Hance, *B. flagellaris* H.Hara, *B. fordii* Irmsch., *B. fulgurata* C.I Peng, C.W.Lin & Phutthai, *B. garrattii* Craib, *B. gigabracteata* H-Z.Li & H.Ma, *B. glechomifolia* C.M.Hu ex C.Y.Wu & T.C.Ku, *B. grandis* Dryand., *B. guaniana* H.Ma & Z.D.Weï, *B. guishanensis* S.H.Huang & Y.M.Shui, *B. howii* Merr. & Chun, *B. hymenocarpa* C.Y.Wu, *B. imitans* Irmsch., *B. incerta* Craib, *B. incondita* Craib, *B. jayaensis* Kiew, *B. josephii* A.DC., *B. kanburiensis* Phutthai, *B. labordei* H.Lév., *B. leptoptera* H.Hara, *B. lithophila* C.Y.Wu, *B. lowiana* King, *B. lushaiensis* C.E.C.Fischer, *B. malipoensis* S.H.Huang & Y.M.Shui, *B. mashanica* D.Fang & D.H.Qin, *B. minicarpa* H.Hara, *B. morifolia* T.T.Yu, *B. modestiflora* Kurz, *B. muliensis* T.T.Yu, *B. murina* Craib, *B. notata* Craib, *B. obsolescens* Irmsch., *B. ovatifolia* A.DC., *B. parvuliflora* A.DC., *B. pedunculosa* Wall., *B. pengchengii* Phutthai & M.Hughes, *B. picta* Sm., *B. poilanei* Kiew, *B. pseudosubperfoliata* Phutthai & M.Hughes, *B. putii* Craib, *B. rabilii* Craib, *B. ravenii* C.I Peng & Y.K.Chen, *B. rhodophylla* C.Y.Wu, *B. rongjiangensis* T.C.Ku, *B. rotundilimba* S.H.Huang & Y.M.Shui, *B. rubella* Buch.-Ham. ex D.Don, *B. ruboides* C.M.Hu ex C.Y.Wu & T.C.Ku, *B. satrapis* C.B.Clark, *B. saxifragifolia* Craib, *B. scintillans* Dunn, *B. sino-vietnamica* C.Y.Wu, *B. soluta* Craib, *B. suboblata* D.Fang & D.H.Qin, *B. subperfoliata* Parish ex Kurz, *B. subviridis* Craib, *B. summoglabra* T.T.Yu, *B. surculigera* Kurz, *B. taliensis* Gagnep., *B. tonkinensis* Gagnep., *B. tribenensis* C.R.Rao, *B. wengeri* C.E.C.Fischer, *B. wenshanensis* C.M.Hu ex C.Y.Wu, *B. wilsonii* Gagnep., *B. yui* Irmsch.

Species whose membership is doubtful. – 16 species: *B. acaulis* Merr. & L.M.Perry, *B. alta* Aver., *B. bartlettiana* Merr. & L.M.Perry, *B. clavicaulis* Irmsch., *B. havilandii* Ridl., *B. hymenophylloides* Kingdon-Ward ex L.B.Sm. & Wassh., *B. kaniensis* Irmsch., *B. longovillosa* A.DC., *B. minjemensis* Irmsch., *B. miranda* Irmsch., *B. pyrrha* Ridl., *B. subcyclophylla* Irmsch., *B. vitiensis* A.C.Sm., *B. xingyiensis* T.C.Ku, *B. xinyiensis* T.C.Ku, *B. xishuensis* T.C.Ku

Distribution. – ASIA: Bhutan, China (Guangdong, Guangxi, Guizhou, Hainan, Sichuan, Yunnan), India (Arunachal Pradesh, Assam, Darjeeling, Kerala, Manipur, Meghalaya, Mizoram, Nagaland, Sikkim, Tamil Nadu, Tripura), Laos, Malaysia (Peninsular Malaysia), Myanmar, Nepal, Pakistan, Papua New Guinea, Sri Lanka, Taiwan, Thailand, Vietnam, West Papua. — Doubtful species: Fiji (Santo Island, Vanua Levu), Indonesia (West Papua), Malaysia (Sarawak), Papua New Guinea, Philippines.

Taxonomic notes. – Merging *B. sect. Diploclinium*, *B. sect. Platycentrum* and *B. sect. Sphenanthera* to produce a monophyletic section is impractical and would result in a highly polymorphic section distinguished by no obvious morphological characters. It is more feasible to split *B. sect. Diploclinium* into its constituent clades and search for morphological characters distinguishing those clades. Our current sampling is too low to permit this thus we recognise a paraphyletic *B. sect. Diploclinium* and acknowledge that further morphological and

phylogenetic work is required to recircumscribe the section into natural groups.

Begonia boisiana is also phylogenetically placed within the “Diploclinium grade”. This is a morphologically aberrant species for the grade (e.g., it differs by its entire placentae and shrubby habit) and has a conflicting placement in a phylogeny composed of both nuclear and chloroplast data, where it appears in a clade with *B. sect. Coelocentrum* and *sect. Petermannia* (Chung & al., 2014). This species was unplaced to section by Doorenbos & al. (1998), which we follow here.

The similarity between *B. brandisiana*, *B. burmensis* L.B.Sm. & Wassh. and *B. demissa* was noted by Hughes (2008), but the three species have been placed in different sections by Doorenbos & al. (1998): *B. brandisiana* in *B. sect. Reichenheimia*, *B. burmensis* in *B. sect. Lauchea*, and *B. demissa* in *B. sect. Parvibegonia*. The three species are not only morphologically similar but also do not fit easily into any of the three sections currently used to accommodate them. We transfer *B. brandisiana*, *B. demissa*, and *B. burmensis* into *B. sect. Diploclinium*, based on the position of the first two taxa in the “Diploclinium grade”.

Begonia dioica was treated by Doorenbos & al. (1998) within *B. sect. Diploclinium* and was resolved within the “Diploclinium grade” (see below) in an ITS phylogeny by Rajbhandary & al. (2011) as sister to *B. ravenii* C.I Peng & Y.K.Chen. *Begonia dioica* fits well morphologically in with the remainder of *B. sect. Diploclinium* in being tuberous with almost symmetric leaves. We consider it likely that the early-diverging position of *B. dioica* within Asian *Begonia* is correct and that the slightly incongruent position in the ITS phylogeny could be due to later hybridisation. Until further data becomes available on its phylogenetic placement, and further species in *B. sect. Diploclinium* are sampled, we leave *B. dioica* in *B. sect. Diploclinium*.

Begonia* sect. *Donaldia (Klotzsch) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 141. 1859 ≡ *Donaldia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 127. 1854 – Lectotype (designated Swart, ING Card 09630. 1959): *Donaldia ulmifolia* (Willd.) Klotzsch ≡ *Begonia ulmifolia* Willd. — [Fig. 15G]

Species list. – 3 species: *B. gesnerioides* L.B.Sm. & B.G.Schub., *B. saxicola* A.DC., *B. ulmifolia* Willd.

Distribution. – AMERICAS: Brazil (Acre, Alagoas, Bahia, Ceará, Espírito Santo, Minas Gerais, Pará, Paraíba, Pernambuco, Rio de Janeiro, Sergipe), Colombia, French Guiana, Guyana, Peru, Suriname, Trinidad-Tobago, Venezuela.

Taxonomic notes. – The number of species in *B. sect. Donaldia* has fallen greatly since 1998, all other species having been synonymised with either *B. saxicola* A.DC. or *B. ulmifolia* Willd. (Jacques & Mamede, 2005). We recognise this diminished section with the addition of *B. gesnerioides* L.B.Sm. & B.G.Schub., which we resolve within the section. *Begonia gesnerioides* was tentatively assigned to *B. sect. Ruizopavonia* A.DC. by Doorenbos & al. (1998) but both type collection and specimens collected at its type locality appear indistinguishable from *B. ulmifolia* and are likely the same species (P.W. Moonlight, unpub. data).

Also resolved within *B.* sect. *Donaldia* are *B. dichotoma* Jacq., including both a Colombian and a Venezuelan collection, and *B. scabrida* A.DC. Neither species can be morphologically grouped with *B.* sect. *Donaldia* to the exclusion of the members of *B.* sect. *Pritzelia* resolved within the “Wageneria clade”. These two species are the only Colombian and Venezuelan members of this group we sampled. We consider it highly likely that an ancestor of *B. scabrida* and *B. dichotoma* hybridised with a member of *B.* sect. *Donaldia* resulting in chloroplast capture. This may extend to the other three Venezuelan close relatives of these species: *B. boucheana* (Klotzsch) A.DC., *B. otophylla* L.B.Sm. & B.G.Schub., and *B. verruculosa* L.B.Sm. Given the clear morphological similarities between these species and the “Wageneria clade”, which are not shared by *B.* sect. *Donaldia*, we retain all as members of *B.* sect. *Pritzelia*.

We refer to the description in Doorenbos & al. (1998: 98) and follow the circumscription therein.

Begonia* sect. *Doratometra (Klotzsch) A.DC., Prodr. 15(1): 383. 1864 ≡ *Doratometra* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 126. 1854 – Type: *Doratometra wallichiana* (Lehm.) Klotzsch ≡ *Begonia wallichiana* Lehm. — [Fig. 15H]

= *Begonia* sect. *Poecilia* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 142. 1859 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 3. 1972): *Begonia pavoniana* A.DC. = *Begonia humilis* Dryand.

= *Hoffmannella* Klotzsch ex. A.DC., Prodr. 15(1): 299. 1864 – Type: *Hoffmannella rosea* Klotzsch ex. A.DC. = *Begonia semiovata* Liebm.

Species list. – 8 species: *B. bernicei* Aymard & G.A.Romero, *B. hirsuta* Aubl., *B. humilis* Dryand, *B. prieurii* A.DC., *B. semiovata* Liebm., *B. steyermarkii* L.B.Sm. & B.G.Schub., *B. subcostata* Rusby, *B. wallichiana* Lehm.

Distribution. – AMERICAS: Brazil (Acre, Bahia, Ceará, Espírito Santo, Minas Gerais, Pará, Parana, Pernambuco, Rio de Janeiro, Roraima, Santa Catarina, São Paulo), Colombia, Costa Rica, Ecuador, French Guiana, Guadeloupe, Guatemala, Guyana, Honduras, Jamaica, Martinique, Mexico (Hidalgo, Oaxaca, Querétaro, San Luis Potosi, Tamaulipas, Veracruz), Nicaragua, Panama, Peru, Saint Vincent, Suriname, Trinidad and Tobago, Venezuela.

ASIA: Vietnam (*B. wallichiana*).

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 99) and follow the circumscription therein with the exception of *B. hirtella* (see below). We note the unusual South American and Vietnamese distribution of *B. wallichiana* Lehm. Given the weedy nature of this species its occurrence in Asia is likely the result of human introduction rather than a natural, long-distance dispersal event.

Begonia* sect. *Ephemer Moonlight, **sect. nov.** – Type: *Begonia exigua* Irmsch. — [Fig. 15I]

Description. – Caulescent, rhizomatous (*B. delicata* Gregório & J.A.S.Costa) or erect succulent herbs, annual. Stipules persistent. Leaves alternate, basifixed, blade subsymmetrical to asymmetrical, veins palmate to palmate-pinnate.

Inflorescence axillary, few flowered, cymose, bracts persistent. Male flowers: with 2 or 4 free perianth segments; stamens 3 to numerous, free or filaments fused at the base or united in a column, anthers oblong, dehiscent via lateral slits, connective produced. Female flowers: bracteoles 2 or 3 at the base of the ovary, with 5 free perianth segments; ovary and fruit with 3 wings, wings subequal or unequal, 3-locular, placentas axile, bifid, bearing ovules on all surfaces; styles 3, free, bifid, stigmatic papillae in a spirally twisted band. Fruit a capsule.

Species list. – 14 Species: *B. alchemilloides* Meisn. ex A.DC., *B. balansae* C.DC., *B. cacauicola* L.B.Sm. ex S.F. Smith & Wassh., *B. cucullata* Willd., *B. delicata* Gregório & J.A.S.Costa, *B. descoleana* L.B.Sm. & B.G.Schub., *B. exigua* Irmsch., *B. fischeri* Schrank, *B. hassleri* C.DC., *B. hirtella* Link, *B. mollicaulis* Irmsch., *B. obovatistipula* C.DC., *B. per-dusenii* Brade, *B. subvillosa* Klotzsch.

Distribution. – AMERICAS: Argentina (Buenos Aires, Chaco, Corrientes, Entre Ríos, Formosa, Jujuy, Misiones, Salta, Santa Fe, Santa Cruz, Tucumán), Bolivia, Brazil (Acre, Bahia, Distrito Federal, Durango, Espírito Santo, Goiás, Minas Gerais, Mato Grosso, Mato Grosso do Sul, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Roraima, Santa Catarina, São Paulo, Tocantins), Colombia, Costa Rica, Cuba, Ecuador, El Salvador, Guatemala, Guyana, Honduras, Jamaica, México (Chiapas, Hidalgo, Oaxaca, San Luis Potosí, Tabasco, Veracruz), Nicaragua, Panama, Paraguay, Peru, Uruguay, Venezuela.

Etymology. – The epithet is from the Greek *ephēmeros* (fleeting), referring to the annual life cycle of all species in this section, which is highly unusual in *Begonia*.

Taxonomic notes. – The species we treat in *B.* sect. *Ephemer* were treated in *B.* sect. *Begonia* or sect. *Doratometra* (*B. hirtella* Link) by Doorenbos & al. (1998) and share an annual life history; a succulent, upright habit (1 rhizomatous species); persistent stipules, bracts, and bracteoles; and few-flowered cymose inflorescences.

Despite the high support for this clade, it has proven difficult to find characters that distinguish *B.* sect. *Ephemer* from *B.* sect. *Doratometra* but the majority of species are larger and more robust than those of the latter section. Those species most similar to those of *B.* sect. *Doratometra* (e.g., *B. hirtella* and *B. fischeri* Schrank) can be distinguished by their combination of 4 male tepals, 5 female tepals, and bifid placentae. These characters are all found within *B.* sect. *Doratometra* but not in combination. We note that many of the species of *B.* sect. *Doratometra* are poorly known and highly variable. A revision of this group is long overdue, and may help further distinguish these two sections. Some species we treat within *B.* sect. *Doratometra* may later prove to be members of *B.* sect. *Ephemer*.

Begonia* sect. *Erminea A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 143. 1859 – Type: *Begonia erminea* L'Hér. — [Fig. 11C]

Species list. – 14 species: *B. androrangensis* Humb. ex Keraudren & Bossier, *B. antongilensis* Humb. ex Keraudren & Bossier, *B. betsimisaraka* Humb. ex Keraudren & Bossier, *B. bogneri* Ziesenh., *B. erminea* L'Hér., *B. keraudrenae* Bossier, *B. lemurica* Keraudren, *B. marojejyensis* Humb., *B. monicae*

Aymonin & Bosser, *B. nana* L'Hér., *B. nosymangabensis* Scherber. & Duruiss., *B. pteridoides* Scherber. & Duruiss., *B. razafinjohanyi* Aymonin & Bosser, *B. tsimihety* Humb. ex Keraudren & Bosser.

Species whose membership is doubtful. – 1 species: *B. bosseri* Keraudren.

Distribution. – AFRICA: Madagascar.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 102) and follow the circumscription therein. We likewise doubtfully assign *B. bosseri* Keraudren to this section (see Doorenbos & al., 1998 for discussion).

Begonia* sect. *Eupetalum (Lindl.) A.DC., Prodr. 15(1): 280. 1864 ≡ *Eupetalum* Lindl., Intr. Nat. Syst. Bot., ed. 2: 440. 1836 – Type: *Eupetalum petalodes* Lindl. = *Begonia geraniifolia* Hook. — [Fig. 15J]

= *Begonia* sect. *Begoniella* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 120. 1859 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 3. 1972): *Begonia gracillima* A.DC. = *Begonia pleiopetala* A.DC.

= *Huszia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 121. 1854 ≡ *Begonia* sect. *Huszia* (Klotzsch) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 121. 1859 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 4. 1972): *Huszia octopetala* (L'Hér.) Klotzsch ≡ *Begonia octopetala* L'Hér.

Species list. – 16 species: *B. aequatorialis* L.B.Sm. & B.G.Schub.*; *B. anemoniflora* Irmsch.*; *B. anemonoides* Azara; *B. geraniifolia* Hook.; *B. macra* A.DC.*; *B. marinae* Tebbitt*; *B. neoharlingii* L.B.Sm. & Wassh.; *B. novogranatae* A.DC.*; *B. octopetala* L'Hér.*; *B. pleiopetala* A.DC.*; *B. polypetala* A.DC.*; *B. pseudopleiopetala* Tebbitt*; *B. rosacea* Putz.*; *B. rubricaulis* Hook.*; *B. tumbezensis* Irmsch.*; *B. weberbaueri* Irmsch. — [*The “octopetala group”]

Distribution. – AMERICAS: Argentina (Jujuy, Salta, Tucumán), Bolivia, Colombia, Ecuador, Peru, Venezuela.

Taxonomic notes. – The circumscription of *B. sect. Eupetalum* adopted by Doorenbos & al. (1998) was an uneasy alliance of geophytic Andean species. The majority were previously included as members of two synonymised sections. Smith & Schubert (1941) described *B. sect. Australes* to encompass caulescent, southern Andean species with bifid styles whereas *B. sect. Huszia* included acaulescent, northern Andean species with multifid styles. Doorenbos & al. (1998) united both groups with geophytic Andean species fitting neither category, including *B. weberbaueri* Irmsch. and *B. geraniifolia*, the type of *B. sect. Eupetalum*, the latter of which possesses both multifid styles and an upright stem. We proceed by recognising a reduced circumscription of *B. sect. Eupetalum* including only *B. sect. Huszia*, *B. geraniifolia*, and *B. weberbaueri* but recognise that further work is required to resolve the relationships among these taxa.

Begonia lutea was doubtfully included in *B. sect. Eupetalum* by Doorenbos & al. (1998), differing from his circumscription of the section in its entire placentae. The species further differs from our circumscription in its bifid styles and yellow tepals, and is resolved as distantly related to all species included in the section. We treat *B. lutea* as unassigned to section.

Begonia* sect. *Exalabegonia Warb. in Gartenflora 49: 2. 1900 – Type: *Begonia heddei* Warb. = *Begonia oxyloba* Welw. ex Hook.f. — [Fig. 11E]

Description. – Caulescent herbs, erect or scandent, perennial. Stipules deciduous. Leaves alternate, basifixed, blade subsymmetric, veins palmate. Inflorescence axillary, a symmetrical cyme, unisexual (*B. meyeri-johannis*) or bisexual (*B. oxyloba*), bracts persistent. Male flowers: with 2 or 4 free perianth segments; stamens 7–100, filaments fused for <1 mm their length or free to base, anthers obovate to oblong or elliptical, dehiscing via lateral slits, connective not projecting or slightly projecting (*B. oxyloba*). Female flowers: bracteoles absent, with 2–4 free perianth segments; ovary and fruit indehiscent, wingless, 3- to 5-locular, placentas parietal for >60% of the ovary, bifid, bearing ovules on all surfaces; styles 3–5, free to base, bifid, stigmatic papillae in a spirally twisted band. Fruit a berry.

Species list. – 2 species: *B. meyeri-johannis* Engl., *B. oxyloba* Welw. ex Hook.f.

Distribution. – AFRICA: Angola, Burundi, Cameroon, Democratic Republic of the Congo, Equatorial Guinea (Bioko, Equatorial Guinea), Gabón, Ghana, Guinea, Ivory Coast, Kenya, Liberia, Madagascar, Malawi, Mozambique, Nigeria, Republic of the Congo, Rwanda, Sierra Leone, Togo, Uganda.

Taxonomic notes. – Plana (2003) discussed at length the possibility of creating a section to include mainland *B. oxyloba* and *B. meyeri-johannis*, but was unable to find characters that link the two species to the exclusion of Malagasy *B. sect. Mezierea*. However, given the addition of further molecular evidence supporting the polyphyly of this group, we consider it prudent to separate Malagasy and mainland species into two sections. *Begonia oxyloba* is the type of *B. sect. Exalabegonia* thus we reinstate this section to include *B. oxyloba* and *B. meyeri-johannis*.

Begonia* sect. *Filicibegonia A.DC., Prodr. 15(1): 392. 1864 – Type: *Begonia aspleniifolia* Hook.f. ex A.DC. — [Fig. 11F]

= *Begonia* (sect. *Scutobegonia*) ser. *Longicaules* Engl. in Engler & Drude, Veg. Erde 9(3, 2): 616. 1921 – Type (designated by Doorenbos & al. in Wageningen Agric. Univ. Pap. 98(2): 107. 1998): *Begonia elatostemmoides* Hook.f.

Species list. – 8 species: *B. aspleniifolia* Hook.f. ex A.DC., *B. auriculata* Hook.f., *B. elatostemmoides* Hook.f., *B. gossweileri* Irmsch., *B. macrocarpa* Warb., *B. minutifolia* N.Hallé, *B. sciaphila* Gilg ex Engl., *B. sessilifolia* Hook.f.

Distribution. – AFRICA: Angola, Cameroon, Democratic Republic of the Congo, Equatorial Guinea (Bioko), Gabón, Republic of the Congo.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 107) and follow the circumscription therein.

Begonia* sect. *Gaerdtia (Klotzsch) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 128. 1859 ≡ *Gaerdtia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 123. 1854 – Type (designated by Barkey & Baranov in Buxtonian 1(Suppl. 1): 4. 1972): *Gaerdtia maculata* (Raddi) Klotzsch ≡ *Begonia maculata* Raddi. — [Fig. 15K]

Species list. – 8 species: *B. coccinea* Hook., *B. corallina* Carrière, *B. dichroa* Sprague, *B. kunthiana* Walp., *B. lunaris*

E.L.Jacques, *B. macduffieana* L.B.Sm. & B.G.Schub., *B. maculata* Raddi, *B. undulata* Schott

Distribution. – AMERICAS: Brazil (Espírito Santo, Minas Gerais, Pará, Rio de Janeiro, São Paulo).

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 80) and recognise a reduced circumscription of the section (as discussed under *Begonia* sect. *Pereira* below). *Begonia coccinea* is resolved within the *B.* sect. *Gaertdia* and differs from the remainder of the section only in having entire placentae and thus we transfer it into the section.

Begonia* sect. *Gireoudia (Klotzsch) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 133. 1859 ≡ *Gireoudia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 4. 1972): *Gireoudia involucrata* (Liebm.) Klotzsch ≡ *Begonia involucrata* Liebm. — [Fig. 15L]

= *Rachia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 124. 1854 ≡ *Begonia* sect. *Rachia* (Klotzsch) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 131. 1859 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 4. 1972): *Rachia incana* (Lindl.) Klotzsch = *Begonia peltata* Otto & A.Dietr.

= *Weilbachia* Klotzsch & Oerst. ex Klotzsch in Abh. Königl. Akad. Wiss. Berlin 1854: 239. 1855 ≡ *Begonia* sect. *Weilbachia* (Klotzsch & Oerst. ex Klotzsch) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 134. 1859, **syn. nov.** – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 8. 1972): *Weilbachia reptans* Klotzsch = *Begonia ludicra* A.DC.

= *Begonia* sect. *Auriformia* Ziesenh. in Begonian 41: 13. 1974 – Type: *Begonia bakeri* C.DC. = *Begonia cardiocarpa* Liebm.

= *Begonia* sect. *Liebmannia* Ziesenh. in Begonian 43: 64. 1976 – Type: *Begonia alice-clarkiae* Ziesenh.

= *Begonia* sect. *Psathuron* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 131. 1859 – Type: *Begonia pinetorum* A.DC.

Species list. – 110 species: *B. acutiloba* Liebm., *B. agubuenensis* Burt-Utley & Utley, *B. alice-clarkiae* Ziesenh., *B. almedana* Burt-Utley & Utley, *B. aridicaulis* Ziesenh., *B. assurgens* Irmsch., *B. barkeri* Knowles & Wescott, *B. barsalouxiae* Standl. & L.H.J.Williams, *B. bettinae* Ziesenh., *B. boqueronensis* Burt-Utley & Utley, *B. bowerae* Ziesenh., *B. breedlovei* Burt-Utley, *B. broussonetiifolia* A.DC., *B. buseyi* Burt-Utley, *B. calderonii* Standl., *B. calzadae* Burt-Utley & Utley, *B. campanensis* Burt-Utley & Utley, *B. cardiocarpa* Liebm., *B. carletonii* Standl., *B. carolineifolia* Regel, *B. carrieae* Ziesenh., *B. chiapensis* Burt-Utley, *B. chivatoa* Ziesenh., *B. conchifolia* A.Dietr., *B. confusa* L.B.Sm. & B.G.Schub., *B. copeyana* C.DC., *B. corredorana* C.DC., *B. corzoensis* Ziesenh., *B. crassicaulis* Lindl., *B. cristobalensis* Ziesenh., *B. croatii* Burt-Utley, *B. dressleri* Burt-Utley, *B. erythrotricha* C.DC., *B. faustinoi* Burt-Utley & Utley, *B. fimbriata* Liebm., *B. fonsecae* Standl., *B. fortunensis* Burt-Utley & Utley, *B. fusca* Liebm., *B. garagarana* C.DC., *B. gentryi* Burt-Utley & Utley, *B. glandulosa* Hook., *B. heracleifolia* Schldl. & Cham.,

B. hispidavillosa Ziesenh., *B. hondurensis* Burt-Utley & Utley, *B. hubertii* Ziesenh., *B. hydrocotylifolia* Otto ex Hook., *B. imperialis* Lem., *B. involucrata* Liebm., *B. jaliscana* Burt-Utley, *B. jarmilae* Halda, *B. karwinskyana* A.DC., *B. kenworthyae* Ziesenh., *B. knoopii* Ziesenh., *B. kortsiae* Ziesenh., *B. lindleyana* Walp., *B. louis-williamsii* Burt-Utley, *B. ludicra* A.DC., *B. lyman-smithii* Burt-Utley & Utley, *B. lynceorum* Burt-Utley, *B. makrinii* Burt-Utley & Utley, *B. manicata* Brongn. ex Cels, *B. mariti* Burt-Utley, *B. matudae* Burt-Utley & Utley, *B. mazaе* Ziesenh., *B. mcphersonii* Burt-Utley & Utley, *B. mexicana* G.Karst ex Fotsch, *B. militaris* L.B.Sm. & B.G.Schub., *B. morii* Burt-Utley, *B. morrisiorum* Rekah Morris & P.D.McMillan ex Rekah Morris, *B. motozintlensis* Burt-Utley & Utley, *B. mucronistipula* C.DC., *B. multinervia* Liebm., *B. multistaminea* Burt-Utley, *B. nelumbiifolia* Schldl. & Cham., *B. panamensis* Burt-Utley & Utley, *B. peltata* Otto & A.Dietr., *B. philodendroides* Ziesenh., *B. pinetorum* A.DC., *B. plantaginea* L.B.Sm. & B.G.Schub., *B. plebeja* Liebm., *B. polygonata* Liebm., *B. popenoei* Standl., *B. pringlei* S. Watson, *B. pruinata* (Klotzsch) A.DC., *B. pseudodaedalea* P.D.McMillan & Rekah Morris, *B. pseudopeltata* Burt-Utley & Utley, *B. pudica* L.B.Sm. & B.G.Schub., *B. purpusii* Houghton ex Ziesenh., *B. pustulata* Liebm., *B. quaternata* L.B.Sm. & B.G.Schub., *B. rafael-torresii* Burt-Utley, *B. reptans* Benth., *B. rhizocaulis* (Klotzsch) A.DC., *B. roseibractea* Ziesenh., *B. sartorii* Liebm., *B. sericoneura* Liebm., *B. skutchii* Burt-Utley & Utley, *B. sousae* Burt-Utley, *B. sparsipila* Baker f., *B. squarrosa* Liebm., *B. stigmosa* Lindl., *B. strigillosa* A.Dietr., *B. suku-tensis* Burt-Utley & Utley, *B. thiemei* C.DC., *B. trichosepala* C.DC., *B. turrialbae* Burt-Utley & Utley, *B. urophylla* Hook., *B. vestita* C.DC., *B. violifolia* A.DC., *B. xilitlensis* Burt-Utley.

Species whose membership is doubtful. – 1 Species: *B. setulosa* Bertol.

Distribution. – AMERICAS: Belize, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, México (Chiapas, Colima, Durango, Guerrero, Hidalgo, Jalisco, Distrito Federal, México State, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, Quintana Roo, San Luis Potosí, Sinaloa, Tabasco, Tamaulipas, Veracruz, Yucatán), Nicaragua, Panama, Venezuela.

Taxonomic notes. – All sampled species of *B.* sect. *Gireoudia* and *B.* sect. *Weilbachia* (Klotzsch & Oersted ex Klotzsch) A.DC. are resolved in a well-supported clade. We resolve *B.* sect. *Weilbachia* as polyphyletic within a paraphyletic *B.* sect. *Gireoudia*. *Begonia* sect. *Gireoudia* and *B.* sect. *Weilbachia* encompass mainly rhizomatous but also upright species, and differ primarily in locule number (3 in *B.* sect. *Gireoudia*; 2 in *B.* sect. *Weilbachia*). Species in *B.* sect. *Weilbachia* also tend to be smaller and often have thin, elongated rhizomes although others (e.g., *B. popenoei* Standl.) have large rhizomes more typical of *B.* sect. *Gireoudia*. Given the morphological similarity of these two sections, and the polyphyly of *B.* sect. *Weilbachia* within *B.* sect. *Gireoudia*, we conclude bilocular fruits have evolved multiple times within the clade and newly synonymise *B.* sect. *Weilbachia* with *B.* sect. *Gireoudia*.

We refer to the descriptions in Doorenbos & al. (1998) of *B.* sect. *Gireoudia* (p. 113) and *B.* sect. *Weilbachia* (p. 214).

Begonia sect. **Gobenia** A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 119. 1859 – Type (designated by Barkley & Baranov, in Buxtonian 1(Suppl. 1): 4. 1972): *B. maurandiae* A.DC. — [Fig. 16A]

Species list. – 16 species: *B. aeranthos* L.B.Sm. & B.G.Schub., *B. dodsonii* L.B.Sm. & Wassh., *B. geminiflora* L.B.Sm. & Wassh., *B. hederacea* A.DC., *B. hitchcockii* Irmsch., *B. maurandiae* A.DC., *B. pululahuana* C.DC., *B. rubrotincta* L.B.Sm. & B.G.Schub., *B. secunda* L.B.Sm. & Wassh., *B. segregata* L.B.Sm. & B.G.Schub., *B. sodiroi* C.DC., *B. spadiciflora* L.B.Sm. & B.G.Schub., *B. tropaeolifolia* A.DC., *B. truncicola* Sodiro ex C.DC., *B. wurdackii* L.B.Sm. & B.G.Schub., *B. ynesiae* L.B.Sm. & Wassh.

Distribution. – AMERICAS: Colombia, Ecuador, Peru.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 117) and follow the circumscription therein with the addition of *B. aeranthos* L.B.Sm. & B.G.Schub. This species was treated by Doorenbos & al. (1998) in *B.* sect. *Wageneria* but differs only from the traditional members of *B.* sect. *Gobenia* in minor characters.

Begonia sect. **Haagea** (Klotzsch) A.DC., Prodr. 15(1): 391. 1864 ≡ *Haagea* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854 – Type: *Haagea dipetala* (Graham) Klotzsch ≡ *Begonia dipetala* Graham. — [Fig. 13G]

Species list. – 1 species: *B. dipetala* Graham.

Distribution. – ASIA: India (Karnataka, Kerala, Tamil Nadu), Sri Lanka.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 119) and follow the circumscription therein.

Begonia sect. **Hydristyles** A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 132. 1859 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 4. 1972): *Begonia bridgesii* A.DC. — [Fig. 16B]

Species list. – 10 species: *B. andina* Rusby, *B. bridgesii* A.DC., *B. fissistyla* Irmsch., *B. juntasensis* Kuntze, *B. peltigera* Irmsch., *B. rubriflora* L.Kollmann, *B. santarosensis* Kuntze, *B. subcaudata* Rusby ex L.B.Sm. & B.G.Schub., *B. unduavensis* Rusby, *B. unilateralis* Rusby.

Species whose membership is doubtful. – 1 species: *B. ophiogyna* L.B.Sm. & B.G.Schub.

Distribution. – AMERICAS: Argentina, Bolivia, Peru. — Doubtful species: Colombia.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 119) and follow the circumscription therein with the addition of the previously-unplaced Argentinian *B. rubriflora* L.Kollmann. This species is phylogenetically placed within the section.

Begonia sect. **Jackia** M.Hughes, **sect. nov.** – Type: *Begonia sublobata* Jack. — [Fig. 13H]

Description. – Acaulescent rhizomatous herbs, perennial, glabrous or hairy. Stipules persistent. Leaves basifixed or peltate, asymmetric to subsymmetric, veins palmate. Inflorescence axillary, a dichasial cyme, bracts deciduous. Male flowers: with

2 or 4 free perianth segments; stamens numerous, filaments fused into a column, anthers obovate, dehiscing via lateral slits, connective retuse. Female flowers: with 2, 3 or 4 free perianth segments, ovary and fruit with 3 wings, wings subequal, 3-locular, placentas axile, entire, bearing ovules on both surfaces; styles 3, free, bifid, stigmatic papillae in a once-spirally twisted band. Fruit a capsule, usually recurved at maturity.

Species list. – 53 species: *B. andersonii* Kiew & S.Julia, *B. bimaensis* Undaharta & Ardhaka, *B. bonii* Gagnep., *B. caespitosa* Jack, *B. cladotricha* M.Hughes, *B. coriacea* Hassk., *B. corneri* Kiew, *B. droopiae* Ardi, *B. fluvialis* M.Hughes, *B. forbesii* King, *B. foxworthyi* Burkill ex Ridl., *B. gesneriifolia* Aver., *B. goegoensis* N.E.Br., *B. halabanensis* M.Hughes, *B. hasskarliana* (Miq.) A.DC., *B. hosensis* C.W.Lin & C.I Peng, *B. ignorata* Irmsch., *B. inversa* Irmsch., *B. ionophylla* Irmsch., *B. karangputihensis* Girm., *B. kemumuensis* M.Hughes, *B. korthalsiana* Miq. ex M.Hughes, *B. kudoensis* Girm., *B. lengguanii* Kiew, *B. lilliputana* M.Hughes, *B. lob-bii* A.DC., *B. longipedunculata* Golding & Kareg., *B. lugrae* Ardhaka & Undaharta, *B. minuscula* Aver., *B. mollis* A.DC., *B. muricata* Blume, *B. natunaensis* C.W.Lin & C.I Peng, *B. nurii* Irmsch., *B. olivacea* Ardi, *B. orbiculata* Jack, *B. pasamanensis* M.Hughes, *B. pseudomuricata* Girm., *B. puspitae* Ardi, *B. rajah* Ridl., *B. raoensis* M.Hughes, *B. reginula* Kiew, *B. sendangensis* Ardi, *B. simolapensis* Ardi, *B. stictopoda* (Miq.) A.DC., *B. sublobata* Jack, *B. sudjanae* C.-A.Jansson, *B. sumbawaensis* Girm., *B. sychnantha* L.B.Sm. & Wassh., *B. tambelanensis* (Irmsch.) Kiew, *B. tigrina* Kiew, *B. trichopoda* Miq., *B. vietnamensis* H.Q.Nguyen & C.I Peng, *B. yappii* Ridl.

Distribution. – ASIA: China (Guangxi, Jiangxi), Indonesia (Bali, Java, Kalimantan, Lesser Sunda Islands, Sumatra), Malaysia (Peninsular Malaysia, Sarawak), Vietnam.

Etymology. – In honour of William Jack (1795–1822), a pioneering botanist from Scotland who collected in Penang, Singapore and Sumatra.

Taxonomic notes. – Created to hold Southeast Asian species previously in *B.* sect. *Reichenheimia*, the type of which (*B. thwaitesii*) is a tuberous species endemic to Sri Lanka in early-diverging Asian *Begonia* and not associated with the rhizomatous species we move here to *B.* sect. *Jackia*. The only species phylogenetically sampled here from *B.* sect. *Reichenheimia* (*B. albo-coccinea*, *B. floccifera*, *B. tenera*, *B. thwaitesii*) are placed in early-diverging Asian *Begonia*. The non-Malesian species we include in *B.* sect. *Jackia* from continental Southeast Asia and China fit here reasonably well morphologically, but given their geographic location they may not be closely related and further phylogenetic data is needed to confirm this.

Begonia sect. **Kollmannia** Moonlight, **sect. nov.** – Type: *B. jaguarensis* L.Kollmann, R.S.Lopes & Peixoto. — [Fig. 16C]

Description. – Caulescent, semi-erect to repent herbs, perennial. Stipules persistent. Leaves alternate, basifixed, blade asymmetrical, veins palmate-pinnate. Inflorescence axillary, racemose, bracts persistent. Male flowers: with four free perianth segments; stamens 6 to 8, filaments fused into a column for around half their length, anthers oblong, dehiscing via lateral

slits, connective projecting. Female flowers: bracteoles 2 at the base of the ovary, with 5 free perianth segments; ovary and fruit with 3 wings, wings subequal, 3-locular, placentas axile, entire, bearing ovules on all surfaces; styles 3, united at the base, bifid, stigmatic papillae in a spirally twisted band. Fruit a capsule.

Species list. – 2 species: *B. jaguarensis* L.Kollmann, R.S.Lopes & Peixoto, *B. thelmae* L.B.Sm. & Wassh.

Distribution. – AMERICAS: Brazil (Espírito Santo).

Etymology. – The epithet honours Ludovic Jean Charles Kollmann, who has described more than 80 species of Brazilian plants including the type of *B. sect. Kollmannia* and 14 other species of *Begonia*.

Taxonomic notes. – Upon its description, Smith & Wasshausen (1981) were only able to classify *B. thelmae* L.B.Sm. & Wassh. to section by extending the boundaries of *B. sect. Begoniastrum* A.DC. (a superfluous name for *B. sect. Begonia*). Doorenbos & al. (1998) were unable to assign the species to any of their sections. The recently described *B. jaguarensis* L.Kollmann & al. shares with *B. thelmae* its creeping habit; fimbriate stipules; few-flowered, racemose inflorescences; and androecium united on a column. We create *B. sect. Kollmannia* to include these two species. *Begonia sect. Kollmannia* is most similar to *B. hoehneana* of the monotypic *B. sect. Stellandrae* sect. nov., which differs in its reniform leaf blades, and cymose inflorescences.

We describe the placentae of *B. sect. Kollmannia* as entire but note the discussion in Kollmann & al. (2015) regarding the placentae of *B. thelmae*. Like Kollmann & al. (2015), we only observe entire placentae in cultivated specimens but are aware that this character may vary in wild populations.

Begonia* sect. *Knesebeckia (Klotzsch) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 125. 1859 ≡ *Knesebeckia* Klotzsch, Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 122. 1854 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 4. 1972): *Knesebeckia incarnata* (Link & Otto) Klotzsch ≡ *Begonia incarnata* Link & Otto. — [Fig. 16D, core *Knesebeckia*; Fig. 16E, *Knesebeckia* group I; Fig. 16F, *Knesebeckia* group II; Fig. 16G, *Knesebeckia* group III]

= *Begonia* sect. *Apteron* C.DC. in Bull. Herb. Boissier 2(8): 326. 1908 – Type: *Begonia exalata* C.DC.

= *Begonia* sect. *Cylindribegonia* L.B.Sm. & B.G.Schub. in Contr. Gray Herb. 127: 25. 1939 – Type: *Begonia cylindrata* L.B.Sm. & B.G.Schub.

= *Begonia* sect. *Dissepbegonia* Ziesenh. in Begonian 15: 20. 1948 – Type: *Begonia cavum* Ziesenh.

Species list (core *Knesebeckia*). – 23 species: *B. cavum* Ziesenh., *B. cebadillensis* Houghton ex L.B.Sm. & B.G.Schub., *B. cuernavacensis* Ziesenh., *B. cylindrata* L.B.Sm. & B.G.Schub., *B. extranea* L.B.Sm. & B.G.Schub., *B. falciloba* Liebm., *B. fernaldiana* L.B.Sm. & B.G.Schub., *B. gracilioides* Burt-Utley & Utley, *B. hintoniana* L.B.Sm. & B.G.Schub., *B. ignea* (Klotzsch) Warsz. ex A.DC., *B. incarnata* Link & Otto, *B. lachaoensis* Ziesenh., *B. macvaughii* Burt-Utley & Utley, *B. martinezii* Burt-Utley & Utley, *B. michoacana* L.B.Sm. & B.G.Schub., *B. monophylla* Pav. ex A.DC., *B. nemoralis* L.B.Sm.

& B.G.Schub., *B. relictata* L.B.Sm. & B.G.Schub., *B. tenuis* Burt-Utley & Utley, *B. tlapensis* Burt-Utley & Utley, *B. uniflora* S.Watson, *B. viscida* Ziesenh., *B. weberlingii* Irmsch.

Species whose membership is doubtful. – 4 species: *B. barkleyana* L.B.Sm., *B. molinana* Burt-Utley, *B. misteriosa* L.Kollmann & A.Fontana, *B. stenocardia* L.B.Sm. & B.G.Schub.

Species list (*Knesebeckia* group I). – 2 species: *B. acerifolia* Kunth*, *B. velata* L.B.Sm. & B.G.Schub.*

Species list (*Knesebeckia* group II). – 3 species: *B. exalata* C.DC., *B. microcarpa* A.DC., *B. pastoensis* L.B.Sm. & B.G.Schub.

Species list (*Knesebeckia* group III). – 20 species: *B. albomaculata* C.DC.**, *B. arrogans* Irmsch.*, *B. brandbygeana* L.B.Sm. & B.G.Schub., *B. chemillenensis* Moonlight & Tebbitt**, *B. gorgonea* Tebbitt, *B. hydrophylloides* L.B.Sm. & B.G.Schub., *B. leathermaniae* O'Reilly & Kareg*, *B. ludwigii* Irmsch.*, *B. lugonis* Wassh., *B. maynensis* A.DC.**, *B. oellgaardii* L.B.Sm. & Wassh., *B. parcifolia* C.DC., *B. parodiana* L.B.Sm. & B.G.Schub., *B. piurensis* L.B.Sm. & B.G.Schub., *B. scorpiocaulis* Moonlight & Tebbitt**, *B. serotina* A.DC.*, *B. sparreana* L.B.Sm. & Wassh., *B. thyrsoides* Irmsch., *B. tiramosa* Irmsch., *B. wollnyi* Herzog*

[*The “acerifolia group”; **the “maynensis group”]

Distribution (core *Knesebeckia*). – AMERICAS: Costa Rica, El Salvador, Guatemala, Mexico (Chiapas, Colima, Guerrero, Jalisco, México Distrito Federal, México State, Michoacán, Nayarit, Nuevo León, Oaxaca, Veracruz), Panamá. — Doubtful species: AMERICAS: Bolivia, Brazil (Espírito Santo, Paraná, Santa Catarina), Colombia; Honduras, Venezuela.

Distribution (*Knesebeckia* group I). – AMERICAS: Bolivia, Ecuador, Peru.

Distribution (*Knesebeckia* group II). – AMERICAS: Colombia, Ecuador, Peru.

Distribution (*Knesebeckia* group III). – AMERICAS: Argentina (Salta), Bolivia, Brazil (Acre), Ecuador, Peru.

Taxonomic notes. – Central American and Mexican *B. sect. Knesebeckia* is similar to *B. sect. Quadriperigonina* in its tuberous, upright habit but differs in its axillary, cymose inflorescences. We sample only a single species of this group (*B. incarnata*, the type of the section name), which is resolved within *B. sect. Gireoudia*. This placement is surprising and we continue to recognise Central American and Mexican *B. sect. Knesebeckia* and suggest further sampling of the 22 other species in *B. sect. Knesebeckia* to confirm the placement of the group.

All sampled South American members of *B. sect. Knesebeckia* are distantly related to *B. incarnata*. The section has been used as a “taxonomic dustbin”, including species with vastly different habits lacking synapomorphies. We recognise a much-reduced section including only Central American and Mexican species; reinstate the synonymised *B. sect. Latistigma* (see below); describe a new section (see *B. sect. Astrothrix*); and transfer species into existing sections (see *B. sect. Tetrachia* below).

We further identify three numbered groups of *B. sect. Knesebeckia*. Informally naming numbered groups within sections of *Begonia* has precedence. Doorenbos & al. (1998) identified three morphological groups within both *B. sect.*

Diploclinium and *B. sect. Reichenheimia* for “ease of survey”. We justify our inclusion of informal numbered groups upon similar grounds, although our groups are phylogenetic rather than morphological and we note that these groups are unlikely to remain assigned to *B. sect. Knesebeckia* in the future.

Begonia sect. Knesebeckia group I includes *B. acerifolia* Kunth and *B. velata* L.B.Sm. & B.G.Schub., which form part of the informally named “acerifolia group” of *B. sect. Knesebeckia* (Tebbutt, 2016). *Begonia monadelpha*, the type of *B. sect. Barya*, differs from these two species primarily in its red, tubular flowers and columnar androecium, an apparent adaptation to hummingbird pollination. Together, these three species form a clade but we have been unable to identify synapomorphies that distinguish these species from the remainder of the “acerifolia group” (see *B. sect. Knesebeckia* group III), and are accordingly reluctant to recircumscribe *B. sect. Barya*. We compromise by recognising *B. sect. Barya* and informally naming the remainder of the clade *B. sect. Knesebeckia* group I. Further morphological and phylogenetic work on the *B. acerifolia* group is required before formal changes are proposed.

Our sampling of *B. sect. Knesebeckia* group II is limited to two undescribed species from northern Peru. These species share their upright stems with lower portions trailing and rooting at the nodes; simple, glandular indumentum; cymose inflorescences; paired bracteoles; four male and five female flower tepals; columnar androecia; equal-winged ovaries and fruits; and lobed stigmas. These characters are shared with three Ecuadorian and Colombian species: *B. exalata* C.DC., *B. microcarpa* A.DC., and *B. pastoensis* A.DC. *Begonia exalata* is the type of *B. sect. Apterion* C.DC., but we refrain from reinstating the section to include these species while we await the description of the two undescribed Peruvian species and phylogenetic confirmation of their proposed relationship with *B. exalata*.

We have been unable to identify synapomorphies that unite *Begonia sect. Knesebeckia* group III to the exclusion of the members of *B. sect. Knesebeckia* group I. In particular, the polyphyly of the morphologically well-defined “acerifolia group” is unexpected and may be the result of chloroplast capture. We refrain from describing this group as a section and await further work to identify synapomorphies for the group and to confirm its monophyly.

Five unsampled South American species do not fall within any of these groups and are doubtfully assigned to *B. sect. Knesebeckia*. *Begonia molinana* is doubtfully assigned because its fragmentary type collection lacks the characters required to assign it to section.

Begonia bifurcata is resolved as sister to a clade containing *B. sect. Eupetalum*, *B. sect. Cremnophila*, and *B. sect. Knesebeckia* group I. This species is most similar to *B. froebelii* (see *B. sect. Australes*) and its placement in our phylogeny is surprising. We refrain from describing a small section for *B. bifurcata* and treat it as unplaced to section while we await further phylogenetic data.

We refer to the description in Doorenbos & al. (1998: 123), which fits *B. sect. Knesebeckia* despite its significantly reduced circumscription.

Begonia sect. Latistigma A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 119. 1859 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 5. 1972): *Begonia aconitifolia* A.DC. — [Fig. 16H]

Description. – Caulescent, erect suffrutescent herbs, perennial. Stipules deciduous. Leaves alternate, basifixed, blade asymmetrical, palmatifid, veins palmate. Inflorescence axillary, cymose, bracts deciduous. Male flowers: with 2–4 free perianth segments; stamens ca. 50, free, anthers obovate, dehiscent via lateral slits, connective not projecting. Female flowers: bracteoles absent, with 5 free perianth segments; ovary and fruit with 3 wings, wings subequal or unequal, 3-locular, placentas axile, bifid, bearing ovules on all surfaces; styles 3, free, bifid, stigmatic papillae in a spirally twisted band. Fruit a capsule.

Species list. – 5 species: *B. aconitifolia* A.DC., *B. olbia* Kerch., *B. pachypoda* L.Kollmann & Peixoto, *B. platanifolia* Schott, *B. teuscheri* Linden ex André.

Distribution. – Brazil (Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo).

Taxonomic notes. – We treat a number of species previously included within *B. sect. Knesebeckia* as belonging to the reinstated *B. sect. Latistigma*. These species are recognised by their upright habit with swollen stem bases, palmately dissected leaves, and large flowers. All are restricted to the Mata Atlântica of Brazil.

Begonia sect. Laucha (Klotzsch) A.DC., Prodr. 15(1): 353. 1864 ≡ *Laucha* Klotzsch in Abh. Akad. Berlin 1854: 241. 1855 – Type: *Laucha verticillata* (Hook.) Klotzsch ≡ *Begonia adenopoda* Lem. — [Fig. 13I]

= *Begonia sect. Dysmorphia* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 136. 1859 – Type: *Begonia crenata* Dryand.

= *Begonia sect. Papyracea* C.B.Clarke in Hooker, Fl. Brit. India, 2: 649. 1879 – **Type (designated here):** *Begonia adenopoda* Lem.

Species list. – 5 species: *B. adenopoda* Lem., *B. crenata* Dryand., *B. namkadingensis* C.J.Yang, Souladeth & Tagane, *B. pteridiformis* Phutthai, *B. tenasserimensis* Phutthai & M.Hughes

Distribution. – ASIA: Myanmar, Thailand.

Taxonomic notes. – *Begonia pteridiformis* and *B. tenasserimensis* were placed originally in *B. sect. Parvibegonia* on account of their tuberous habits and bilocular fruit with one enlarged wing and bifid placentae (Phutthai & Sridith, 2010; Phutthai & Hughes, 2017). These characters are shared with *B. namkadingensis* C.J.Yang & al., which was described as unplaced to section (Yang & al., 2018), and *B. adenopoda*, the type of *B. sect. Laucha*. All these species further share an unusual fruit morphology (covered in glandular hairs, with the largest wing being fleshy; Fig. 13I) and symmetric lanceolate leaves. We recognise an expanded *B. sect. Laucha* including *B. namkadingensis*, *B. pteridiformis* and *B. tenasserimensis* but excluding *B. burmensis* (see *B. sect. Diploclinium*).

Begonia sect. Lepsia (Klotzsch) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 141. 1859 ≡ *Lepsia* Klotzsch in Ber. Bekanntm.

Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 123. 1854 – Type: *Lepsia microphylla* Klotzsch = *Begonia foliosa* Kunth. — [Fig. 16I]

= *Tittelbachia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 126. 1854 ≡ *Begonia* sect. *Tittelbachia* (Klotzsch) A.DC., Prodr. 15(1): 291. 1864 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 8. 1972): *Tittelbachia fuchsoides* (Hook.) Klotzsch = *Begonia foliosa* Kunth.

= *Begonia* sect. *Meionanthera* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 141. 1859 – Type: *Begonia holtonis* A.DC.

Species list. – 8 species: *B. barrigae* L.B.Sm. & B.G.Schub., *B. confinis* L.B.Sm. & Wassh., *B. foliosa* Kunth, *B. guaduensis* Kunth, *B. holtonis* A.DC., *B. meridensis* A.DC., *B. opuliflora* Putz., *B. praerupta* Irmsch.

Distribution. – AMERICAS: Brazil (Amazonas, Mato Grosso, Para, Rondônia), Colombia, Ecuador, Guyana, Panamam Peru, Suriname, Venezuela.

Taxonomic notes. – *Begonia* sect. *Lepsia* sensu Doorenbos & al. (1998) was a small section of shrub-like northern Andean species. We transfer a number of former members of *B. sect. Ruizopavonia* into this section. The redefined *B. sect. Lepsia* differs from *B. sect. Ruizopavonia* in having smooth leaf undersurfaces with indistinct primary and secondary veins, globose or subglobose anthers shorter than the filaments (except *B. foliosa*), and five tepals in the female flower. Included in the species we transfer is *B. holtonis*, the type of *B. sect. Meionanthera*. This section was described in the same publication as *B. sect. Lepsia* (Candolle, 1859) so neither name has priority. We treat *B. sect. Lepsia* as the accepted name to maintain nomenclatural stability as *B. sect. Lepsia* was previously accepted.

Begonia sect. *Loasibegonia* A.DC., Prodr. 15(1): 389. 1864 – Type: *Begonia prismatocarpa* Hook. — [Fig. 11G]

= *Begonia* (sect. *Scutobegonia*) ser. *Cordifolia* Engl. in Engler & Drude, Veg. Erde 9(3, 2): 616. 1921 – Type: *Begonia pseudoviola* Gilg.

= *Begonia* (sect. *Scutobegonia*) ser. *Euscutatae* Engl. in Engler & Drude, Veg. Erde 9(3, 2): 617. 1921 – Type (designated by Sosef in Wageningen Agric. Univ. Pap. 94(1): 136. 1994): *Begonia quadrialata* Warb.

Species list. – 21 species: *B. adpressa* Sosef, *B. aequatoguineensis* Sosef & Nguema, *B. atroglandulosa* Sosef, *B. duncanthomasii* 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* Irmsch., *B. scapigera* Hook.f., *B. schaeferi* Engl., *B. scutifolia* Hook.f., *B. sosefiana* J.J.de Wilde & Valk., *B. staudtii* Gilg, *B. stellata* Sosef.

Distribution. – AFRICA: Angola, Burundi, Cameroon, Democratic Republic of the Congo, Equatorial Guinea, Gabón, Ghana, Guinea, Ivory Coast, Liberia, Nigeria, Republic of the Congo, Rwanda, Sierra Leone, Togo.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 131) and follow the circumscription therein.

Begonia sect. *Mezierea* (Gaudich.) Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 139. 1894 ≡ *Mezierea* Gaudich., Voy. Bonite, Bot. 3: t. 32. 1841 – Type: *Mezierea salaziensis* Gaudich. ≡ *Begonia salaziensis* (Gaudich.) Warb. — [Fig. 11H]

= *Mezierea* sect. *Aneupteron* A.DC., Prodr. 15(1): 407. 1864 – Type: *Mezierea salaziensis* Gaudich. ≡ *Begonia salaziensis* (Gaudich.) Warb.

Species list. – 4 species: *B. comorensis* Warb., *B. humbertii* Keraudren, *B. salaziensis* (Gaudich.) Warb., *B. seychellensis* Hemsl.

Distribution. – AFRICA: Comoros, Madagascar, Mauritius, Réunion, Seychelles.

Taxonomic notes. – Malagasy and Indian Ocean *B. sect. Mezierea* appears monophyletic and we re-circumscribe the section to include only these species, which represent all fleshy-fruited Malagasy species excluding *B. masoalaensis* M.Hughes. This species differs from *B. sect. Mezierea* in its tuberous habit and axile placentation, and Hughes (2011) suggest it may be more closely related to other Malagasy sections with these characters (e.g., *B. sect. Erminea* or *B. sect. Nerviplacentaria*). We follow Hughes (2011) in not assigning this species to section while we await further molecular data.

Begonia sect. *Microtuberosa* Moonlight & Tebbitt in Eur. J. Taxon. 281: 4. 2017 – Type: *Begonia elachista* Moonlight & Tebbitt. — [Fig. 16J]

Species list. – 1 species: *B. elachista* Moonlight & Tebbitt.

Distribution. – AMERICAS: Peru.

Taxonomic notes. – We refer to the description in Moonlight & al. (2017: 4) and follow the circumscription therein.

Begonia sect. *Monophyllon* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 135. 1859 – Type: *Begonia prolifera* A.DC. — [Fig. 13J]

Species list. – 2 species: *B. paleacea* Kurz, *B. prolifera* A.DC.

Distribution. – ASIA: Malaysia (Peninsular Malaysia), Myanmar, Singapore, Thailand.

Taxonomic notes. – *Begonia* sect. *Monophyllon* A.DC. includes two species, *B. paleacea* and *B. prolifera*, which are small, tuberous plants with 2-locular fruits similar to those in *B. sect. Parvibegonia*. It is differentiated from *B. sect. Parvibegonia* by inflorescences arising from the base of the leaves whereas those of *B. sect. Parvibegonia* are terminal. We retain *B. sect. Monophyllon* as a separate section awaiting further molecular evidence, refer to the description in Doorenbos & al. (1998: 136), and follow the circumscription therein.

Begonia sect. *Muscibegonia* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 143. 1859 – Type: *Begonia perpusilla* A.DC.

Species list. – 2 species: *B. kalabenonensis* Humb. ex Keraudren & Bosser, *B. perpusilla* A.DC.

Distribution. – AFRICA: Madagascar.

Taxonomic notes. – We note the similarity of this unsampled section to *B. sect. Erminea*, which is separated only by its seed morphology (Doorenbos & al., 1998). Further phylogenetic work is required to determine whether the two sections should

remain distinct. We refer to the description in Doorenbos & al. (1998: 138) and follow the circumscription therein.

Begonia* sect. *Nervi-placentaria A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 144. 1859 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 5. 1972): *Begonia lyallii* A.DC. — [Fig. 11I]

Species list. – 10 species: *B. baronii* Baker, *B. cladocarpoides* Humb. ex Aymonin & Bosser, *B. coursii* Humb. ex Keraudren, *B. henrilaportei* Scherber. & Duruiss., *B. lyallii* A.DC., *B. madecassa* Keraudren, *B. majungaensis* Guillaumin, *B. mangorensis* Humb. ex Keraudren & Bosser, *B. marnieri* Keraudren, *B. perrieri* Bois

Distribution. – AFRICA: Madagascar.

Taxonomic notes. – The similarity between *B.* sect. *Nervi-placentaria* and *B.* sect. *Quadrilobaria* has long been noted, with the former only differing in its basally woody stems (Doorenbos & al., 1998). We refer to the description in Doorenbos & al. (1998: 139), reproduce the existing circumscriptions of these sections, and echo Plana (2003) in advocating for further work to determine the phylogenetic and morphological boundaries of these sections. We further assign *B. perrieri* Bois to *B.* sect. *Nervi-placentaria* (unassigned by Doorenbos & al., 1998) because of its affinity to caulescent members of the section (e.g., *B. madecassa* Keraudren and *B. majungaensis* Guillaumin).

Begonia* sect. *Oligandrae M.Hughes & W.N.Takeuchi in Phytotaxa 197(1): 38. 2015 – Type: *Begonia oligandra* Merr. & L.M.Perry. — [Fig. 13K]

Species list. – 5 species: *B. brassii* Merr. & L.M.Perry, *B. chambersiae* W.N.Takeuchi, *B. oligandra* Merr. & L.M.Perry, *B. pentandra* W.N.Takeuchi, *B. sandsiana* W.N.Takeuchi.

Distribution. – ASIA: Indonesia (West Papua), Papua New Guinea.

Taxonomic notes. – We refer to the description in Hughes & Takeuchi (2015: 38) and follow the circumscription therein.

Begonia* sect. *Parietoplacentalia Ziesenh. in Begonian 36: 36. 1969 – Type: *Begonia candollei* Ziesenh. = *B. oaxacana* A.DC. — [Fig. 16K]

= *Begonia* sect. *Hexaptera* Ziesenh. in Begonian 41: 13. 1974 – Type: *Begonia serrulatoala* C.DC. = *Begonia oaxacana* A.DC.

Species list. – 3 species: *B. oaxacana* A.DC., *B. udisilvestris* C.DC., *B. yunckeri* Standl.

Distribution. – AMERICAS: Costa Rica, El Salvador, Guatemala, Honduras, México (Chiapas, Guerrero, Hidalgo, Jalisco, Puebla, Veracruz), Nicaragua, Panama.

Taxonomic notes. – *Begonia* sect. *Parietoplacentalia* and *B.* sect. *Urniformia* share an erect to semi-scandent habit; an inflorescence structure with male flowers basal and female flowers distal; male flowers with four tepals; female flowers with three tepals; and fleshy fruit. The fruit of *B.* sect. *Parietoplacentalia* differ in their beaked rather than horned fruit with bipartite rather than entire placentation. We refer to the description in Doorenbos & al. (1998: 143) and follow the circumscription therein.

Begonia* sect. *Parvibegonia A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 136. 1859 = *Begonia* subg. *Parvibegonia* (A.DC.) C.B.Clark in Bot. J. Linn. Soc. 18: 115. 1881 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 5. 1972): *Begonia martabanica* A.DC. — [Fig. 13L]

= *Begonia* sect. *Heeringia* Irmsch. in Mitt. Inst. Allg. Bot. Hamburg 8: 158. 1929, **syn. nov.** – Type: *Begonia sibthorpioides* Ridl.

Species list. – 28 species: *B. andamensis* Parish ex C.B.Clark, *B. bella* Phutthai, *B. brevicaulis* A.DC., *B. canarana* Miq., *B. carnosula* Ridl., *B. elisabethae* Kiew, *B. erosa* Blume, *B. flaccidissima* Kurz, *B. geoffrayi* Gagnep., *B. grantiana* Craib, *B. grata* Geddes ex Craib, *B. integrifolia* Dalzell, *B. martabanica* A.DC., *B. parishii* C.B.Clark, *B. phamiana* Kiew, *B. phoeniogramma* Ridl., *B. procrudifolia* Wall. ex A.DC., *B. pumila* Craib., *B. rimarum* Craib, *B. rupicola* Miq., *B. sibthorpioides* Ridl., *B. sinuata* Wall. ex Meisn., *B. socia* Craib, *B. tenuifolia* Dryand., *B. thaipingensis* King, *B. variabilis* Ridl., *B. wattii* C.B.Clark, *B. zollingeriana* A.DC.

Distribution. – ASIA: Cambodia, India (Andaman Islands, Karnataka, Manipur, Meghalaya, Mizoram, Nagaland), Indonesia (Bali, Java, Sumatra), Laos, Malaysia (Peninsular Malaysia), Myanmar, Nepal, Thailand, Vietnam.

Taxonomic notes. – The placement of *B. smithiae* in this section in both our phylogeny and Rajbhandary & al. (2011) is unusual as it is rhizomatous (not tuberous) and has 3-locular fruit (not 2-locular). We treat this species as unplaced to section, rather than assigned to *B.* sect. *Platycentrum* as in Doorenbos & al. (1998). We also resolve *B. hymenophylla* of *B.* sect. *Reichenheimia* in this clade, which fits morphologically with the exception of the fruits having 3 locules. *Begonia hymenophylla* is perhaps most similar to *B. sibthorpioides* Ridl., the type of *B.* sect. *Heeringia* Irmsch., which is also resolved within *B.* sect. *Parvibegonia*. Both differ slightly from core *B.* sect. *Parvibegonia* in their diminutive size and monochasial inflorescence structure (as opposed to dichasia ending in monochasia), but otherwise the small, tuberous habit fits well. We reclassify both species in *B.* sect. *Parvibegonia* and newly synonymise *B.* sect. *Heeringia* with *B.* sect. *Parvibegonia*.

Begonia* sect. *Peltaugustia (Warb.) Barkley in Phytologia 24: 156. 1972 = *Begonia* (sect. *Augustia*) subsect. *Peltaugustia* Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 140. 1894 – Type: *Begonia socotrana* Hook.f. — [Fig. 11J]

Species list. – 2 species: *B. samhaensis* M.Hughes & A.G.Mill., *B. socotrana* Hook.f.

Distribution. – AFRICA: Yemen (Socotra).

Taxonomic notes. – We refer to the description in Hughes & Miller (2002: 277) and follow the circumscription therein.

Begonia* sect. *Pereira Brade in Rodriguésia 18: 33. 1945 – Type: *Begonia edmundoi* Brade. — [Fig. 16L]

Description. – Caulescent, erect suffrutescent herbs, one species with a subterranean tubercule-like structure (*B. caparaensis*), perennial. Stipules deciduous or persistent. Leaves alternate, peltate or rarely basifixed (*B. pseudolubbersii*), blade subsymmetrical to asymmetrical, veins pinnate or

palmate-pinnate. Inflorescence axillary, cymose, bracts deciduous. Male flowers: with 4 free perianth segments; stamens 30–100, free or fused for less than half their length, anthers obovate, dehiscent via lateral slits, connective not extended or slightly-projecting. Female flowers: bracteoles 1–2 or absent, with 5 free perianth segments; ovary and fruit with 3 wings, wings subequal or unequal, 3-locular, placentas axile, bifid, bearing ovules on all surfaces or only the outside surfaces; styles 3, free, one- or two-lobed, the lobes flattened, stigmatic papillae in a twisted band. Fruit a capsule.

Species list. – 5 species: *B. caparaoensis* E.L.Jacques & L.Kollmann, *B. edmundoi* Brade, *B. jureiensis* S.J.Gomes & Mamede, *B. lubbersii* E. Morren, *B. pseudolubbersii* Brade.

Distribution. – AMERICAS: Brazil (Minas Gerais, Rio de Janeiro, São Paulo).

Taxonomic notes. – The species we treat in *B.* sect. *Pereira* published by 1998 were all treated within *B.* sect. *Gaerdtia* by Doorenbos & al. (1998) while those published subsequently were left unassigned by their respective authors (Gomes da Silva & Mamede, 2000; Jacques & Kollmann, 2009). They differ from the species we treat in *B.* sect. *Gaerdtia* in their usually peltate leaves (basifixed in *B. pseudolubbersii*) with palmate-pinnate venation (rather than pinnate); and their flattened, reniform stigmas (rather than bifid). *Begonia edmundoi* Brade is the type of *B.* sect. *Pereira* thus we reinstate this section to include these species.

Begonia* sect. *Petermannia (Klotzsch) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 128. 1859 ≡ *Petermannia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 124. 1854 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 6. 1972): *Petermannia cumingiana* Klotzsch ≡ *B. cumingiana* (Klotzsch) A.DC. — [Fig. 14A]

Species list. – 416 species: *B. abbreviata* C.I.Peng, *B. acidulenta* S.Julia & Kiew, *B. addrinii* S.Julia & Kiew, *B. adenodes* Irmsch., *B. adliniana* Rimi, *B. aequata* A.Gray, *B. affinis* Merr., *B. agusanensis* Merr., *B. aiensis* C.W.Lin & C.I.Peng, *B. aketa-jawensis* Ardi & D.C.Thomas, *B. alabensis* Kiew, *B. albobracteata* Ridl., *B. amidalae* C.W.Lin & C.I.Peng, *B. amphioxus* Sands, *B. androturba* Coyle, *B. angustilimba* Merr., *B. anseriana* C.W.Lin & C.I.Peng, *B. anthonyi* Kiew, *B. apayaoensis* Merr., *B. apiensis* Kiew & S.Julia, *B. armykapii* S.Julia & C.Y.Ling, *B. articulata* Irmsch., *B. artior* Irmsch., *B. atricha* (Miq.) A.DC., *B. augustae* Irmsch., *B. awongii* Sands, *B. axillaris* Ridl., *B. axillipara* Ridl., *B. bahakensis* Sands, *B. baik* C.W.Lin & C.I.Peng, *B. baikoides* S.Julia & C.Y.Ling, *B. bakunensis* S.Julia, *B. baramensis* Merr., *B. basintaliana* Rimi, *B. baturongensis* Kiew, *B. bayae* S.Julia & Kiew, *B. beccarii* Warb., *B. belagaensis* S.Julia, *B. benaratensis* S.Julia, *B. bengohensis* S.Julia, *B. berhamanii* Kiew, *B. beryllae* Ridl., *B. bintang* Rimi, *B. binuangensis* Merr., *B. bipinnatifida* J.J.Sm., *B. bolsteri* Merr., *B. bonthainensis* Hemsl., *B. borneensis* A.DC., *B. bosuangiana* S.Julia, *B. brachybotrys* Merr. & L.M.Perry, *B. brangbosangensis* Girm., *B. brevipes* Merr., *B. brevirimosa* Irmsch., *B. bruneiana* Sands, *B. burbidgei* Stapf, *B. calliantha* Merr. & L.M.Perry, *B. capituliformis* Irmsch., *B. carnosa* Teijsm. & Binn., *B. casiguranensis* Quisumb. &

Merr., *B. caudata* Merr., *B. cauliflora* Sands, *B. celata* S.Julia & Kiew, *B. celebica* Irmsch., *B. chaiana* Kiew & S.Julia, *B. chiasmogyna* M.Hughes, *B. chlorandra* Sands, *B. chlorosticta* Sands, *B. chongii* Sands, *B. ciliifera* Merr., *B. cincinnifera* Irmsch., *B. clemensiae* Merr. & L.M.Perry, *B. cognata* Irmsch., *B. comestibilis* D.C.Thomas & Ardi, *B. compacta* S.Julia & Kiew, *B. congesta* Ridl., *B. conipila* Irmsch. ex Kiew, *B. conigeriae* S.Julia & Kiew, *B. consanguinea* Merr., *B. contracta* Warb., *B. corrugata* Kiew & S.Julia, *B. crassa* S.Julia & Kiew, *B. crispipila* Elmer, *B. crockerensis* S.Julia, *B. cucphuongensis* H.Q.Nguyen & Tebbitt, *B. cumingiana* (Klotzsch) A.DC., *B. cumingii* A.Gray, *B. cuneatifolia* Irmsch., *B. cyanescens* Sands, *B. danumensis* F.Y.Chong, *B. darthaderiana* C.W.Lin & C.I.Peng, *B. densiretis* Irmsch., *B. devexa* S.Julia & Kiew, *B. didyma* D.C.Thomas & Ardi, *B. diffusiflora* Merr. & L.M.Perry, *B. dimorpha* S.Julia, *B. dinosauria* C.W.Lin & C.I.Peng, *B. divaricata* Irmsch., *B. divergens* Kiew & S.Julia, *B. djamuensis* Irmsch., *B. dolichobracteata* Girm., *B. dolichocarpa* Girm., *B. dolichotricha* Merr., *B. dosedlae* Gilli, *B. duhungensis* Girm., *B. eberhardtii* Gagnep., *B. edanoi* Merr., *B. edgariana* S.Julia & Kiew, *B. elatostematoides* Merr., *B. elatostemma* Ridl., *B. eliasii* Warb., *B. erythrogyna* Sands, *B. esculenta* Merr., *B. eutricha* Sands, *B. everettii* Merr., *B. fasciculiflora* Merr., *B. felis* C.W.Lin & C.I.Peng, *B. filibracteosa* Irmsch., *B. flacca* Irmsch., *B. flammea* Rimi, *B. flavovirens* Kiew & S.Julia, *B. flexicaulis* Ridl., *B. fruticella* Ridl., *B. fuscisetosa* Sands, *B. galeolepis* Ardi & D.C.Thomas, *B. gambutensis* Ardi & D.C.Thomas, *B. gelasensis* Rimi & Kimahim, *B. gemella* Warb. ex L.B.Sm. & Wassh., *B. geniculata* Jack, *B. georgei* Coyle, *B. gibbsiae* Irmsch. ex Sands, *B. gilgiana* Irmsch., *B. glabricaulis* Irmsch., *B. gomantongensis* Kiew, *B. gracilipes* Merr., *B. grandipetala* Irmsch., *B. gusilii* Rimi, *B. guttapilla* D.C.Thomas & Ardi, *B. hainanensis* Chun & F.Chun, *B. harauensis* M.Hughes, *B. hekensis* D.C.Thomas, *B. heliostrophe* Kiew, *B. heteroclinis* Miq. ex Koord., *B. hexaptera* Sands, *B. hidirii* Tawan, Ipor & Meekiong, *B. hirsuticarpa* C.W.Lin & C.I.Peng, *B. hirsuticaulis* Irmsch., *B. hirtitepala* S.Julia & Kiew, *B. hispidissima* Zipp. ex Koord., *B. holosericea* (Teijsm. & Binn.) Teijsm. & Binn., *B. holosericeoides* Ardi & D.C.Thomas, *B. holttumii* Irmsch., *B. hooveriana* Wiriad., *B. hullettii* Ridl., *B. humboldtiana* Gibbs, *B. humericola* Sands, *B. humilicaulis* Irmsch., *B. ignita* C.W.Lin & C.I.Peng, *B. imbricata* Sands, *B. imperfecta* Irmsch., *B. incisa* A.DC., *B. incompta* Kiew, *B. inobongensis* Kiew, *B. inopinata* V.S.Guanih, *B. inostegia* Stapf, *B. inostegioides* F.Y.Chong, *B. insueta* D.C.Thomas & Ardi, *B. insularum* Irmsch., *B. iridifolia* C.W.Lin & C.I.Peng, *B. isoptera* Dryand. ex Sm., *B. isopteroidea* King, *B. jagorii* Warb., *B. jamilahana* Y.W. Low, Joffre & Ariffin, *B. jamilahanuiana* S.Julia & Kiew, *B. jamilyana* Rimi, *B. jaranpusangensis* Girm., *B. jenginensis* S.Julia & Kiew, *B. jiewhoei* Kiew, *B. joffrei* S.Julia, *B. johariana* S.Julia & C.Y.Ling, *B. jugamensis* S.Julia & Kiew, *B. julaihihana* S.Julia & C.Y.Ling, *B. juliasangii* Kiew, *B. kachak* K.G.Pearce, *B. kasutensis* K.G.Pearce, *B. keeana* Kiew, *B. keithii* Kiew, *B. kelliana* Irmsch., *B. kerstingii* Irmsch., *B. kiamfeeii* Kiew & S.Julia, *B. kibambangensis* V.S.Guanih & F.Y.Chong, *B. kinabaluensis* Sands, *B. kinahimiae* Rimi, *B. kipandiensis* S.Julia,

B. koordersii Warb. ex L.B.Sm. & Wassh., *B. kuchingensis* C.W.Lin & C.I Peng, *B. kurakura* Tawan, Ipor & Meekiong, *B. labiensis* (Sands) S.Julia, *B. lacera* Merr., *B. lacustris* Irmsch. ex Peekel, *B. lagunensis* Elmer, *B. lailana* Kiew & Geri, *B. lambii* Kiew, *B. lambirensis* Kiew & S.Julia, *B. lamriana* Rimi, *B. lamxayiana* Souvann., *B. lancifolia* Merr., *B. laruei* M.Hughes, *B. lasioura* D.C.Thomas & Ardi, *B. latistipula* Merr., *B. lauterbachii* Warb., *B. lawii* C.W.Lin & C.I Peng, *B. layang-layang* Kiew, *B. lazat* Kiew & Reza Azmi, *B. ledermannii* Irmsch., *B. leptantha* C.B.Rob., *B. leucochlora* Sands, *B. leucosticta* Warb., *B. leucotricha* Sands, *B. lichenora* C.W.Lin & C.I Peng, *B. linauensis* S.Julia, *B. littleri* Merr., *B. loheri* Merr., *B. lombokensis* Girm., *B. longibractea* Merr., *B. longiseta* Irmsch., *B. longistipula* Merr., *B. ltahensis* Girm., *B. lucychongiana* S.Julia & Kiew, *B. lunatistyla* Irmsch., *B. macgregorii* Merr., *B. macintyreana* M.Hughes, *B. madaiensis* Kiew, *B. magentifolia* Kiew & S.Julia, *B. magnicarpa* C.W.Lin & C.I Peng, *B. malachosticta* Sands, *B. malindangensis* Merr., *B. malmquistiana* Irmsch., *B. mamutensis* Sands, *B. manuselaensis* Ardhaka & Ardi, *B. mariaensis* Rimi & Simun, *B. masarangensis* Irmsch., *B. matangensis* S.Julia & Kiew, *B. mearnsii* Merr., *B. media* Merr. & L.M.Perry, *B. megacarpa* Merr., *B. megalantha* Merr., *B. mekongensis* Girm. & Wiriad., *B. melanosticta* F.Y.Chong & V.S.Guanih, *B. melikopia* Kiew, *B. melinauensis* S.Julia & Kiew, *B. mendumae* M.Hughes, *B. mentewangensis* Girm., *B. meriraiensis* Kiew & S.Julia, *B. merrittii* Merr., *B. metallicolor* C.W.Lin & C.I Peng, *B. mindanaensis* Warb., *B. minutiflora* Sands, *B. monantha* Warb., *B. montis-bismarckii* Warb., *B. moszkowskii* Irmsch., *B. multidentata* Warb., *B. multijugata* M.Hughes, *B. murudensis* Merr., *B. murumensis* S.Julia & C.Y.Ling, *B. mystacina* L.B.Sm. & Wassh., *B. nagaensis* Kiew & S.Julia, *B. naumoniensis* Irmsch., *B. negrosensis* Elmer, *B. nephrophylla* Undaharta & Ardi, *B. niahensis* K.G.Pearce, *B. nix* C.W.Lin & C.I Peng, *B. nobmanniae* D.C.Thomas & Ardi, *B. nothobaramensis* Joffre, *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. ozotothrix* D.C.Thomas, *B. padangensis* Irmsch., *B. palawanensis* Merr., *B. panayensis* Merr., *B. paoana* Kiew & S.Julia, *B. papuana* Warb., *B. papulifolia* S.Julia & C.Y.Ling, *B. papyraptera* Sands, *B. paracauliflora* Rimi, C.I Peng & S.M.Ku, *B. parvilimba* Merr., *B. pediophylla* Merr. & L.M.Perry, *B. peekelii* Irmsch., *B. pellionoides* Y.M.Shui & W.H.Chen, *B. pendula* Ridl., *B. penrissenensis* Kiew & S.Julia, *B. pentaphragmifolia* Ridl., *B. peridotocolia* Rimi, C.I Peng & C.W.Lin, *B. perryae* L.B.Sm. & Wassh., *B. pinnatifida* Merr. & L.M.Perry, *B. piring* Kiew & S.Julia, *B. platyphylla* Merr., *B. pleioclada* Irmsch., *B. plieranensis* S.Julia & C.Y.Ling, *B. polilloensis* Tebbitt, *B. polyclada* C.I Peng, C.W.Lin & Rubite, *B. postarii* Kiew, *B. prasinimarginata* S.Julia, *B. prionota* D.C.Thomas & Ardi, *B. promethea* Ridl., *B. propinqua* Ridl., *B. pryeriana* Ridl., *B. pseudolateralis* Warb., *B. pubescens* Ridl., *B. punbatuensis* Kiew, *B. punchak* Kiew & S.Julia, *B. quercifolia* A.DC., *B. racemosa* Jack, *B. rachmatii* Tebbitt, *B. ramaiensis* Kiew, *B. rambutan* Rimi, *B. ramlanii* Rimi & Handry, *B. ramosii* Merr., *B. ramosissima* Kiew & S.Julia, *B. ranaiensis* Girm.,

B. randiana Merr. & L.M.Perry, *B. rantemarioensis* D.C.Thomas & Ardi, *B. renek* Rimi, *B. repanda* Blume, *B. retakensis* (Sands) Joffre, *B. rhodantha* Ridl., *B. rhodochaeta* Kiew & S.Julia, *B. rhodoneura* S.Julia, *B. rhodotricha* S.Julia & C.Y.Ling, *B. rhombipetala* S.Julia & C.Y.Ling, *B. rieckei* Warb., *B. rizalensis* Merr., *B. roseopunctata* Kiew, *B. rotundibracteata* Kiew, *B. rubida* Ridl., *B. rubrobracteolata* S.Julia & C.Y.Ling, *B. rubrosetosa* Aver., *B. ruthiae* S.Julia, *B. sageaensis* Wiriad., *B. salomonensis* Merr. & L.M.Perry, *B. samarensis* Merr., *B. sanguineopilosa* D.C.Thomas & Ardi, *B. sarangica* Kiew & S.Julia, *B. sarsinorum* Irmsch., *B. sarawakensis* Ridl., *B. sarmentosa* L.B.Sm. & Wassh., *B. saxatilis* Blume, *B. serapatensis* Kiew & S.Julia, *B. serraticauda* Merr. & L.M.Perry, *B. serratipetala* Irmsch., *B. setiamensis* S.Julia & Kiew, *B. sibutensis* Sands, *B. siccaudata* J.Door., *B. simulans* Merr. & L.M.Perry, *B. siregarii* Ardi & D.C.Thomas, *B. sirukitii* S.Julia & C.Y.Ling, *B. sogerensis* Ridl., *B. somervillei* Hemsl., *B. sphenocarpa* Irmsch., *B. spilotophylla* F.Muell., *B. stenogyna* Sands, *B. stevei* M.Hughes, *B. stichochoete* K.G.Pearce, *B. stilandra* Merr. & L.M.Perry, *B. strachwitzii* Warb. ex Irmsch., *B. strictinervis* Irmsch., *B. strictipetolaris* Irmsch., *B. subelliptica* Merr. & L.M.Perry, *B. subisensis* K.G.Pearce, *B. sublongipes* Y.M.Shui, *B. subprostrata* Merr., *B. subtruncata* Merr., *B. suffrutescens* Merr. & L.M.Perry, *B. superciliaris* C.W.Lin & C.I Peng, *B. sympodialis* Irmsch., *B. tafaensis* Merr. & L.M.Perry, *B. tania* V.S.Guanih, *B. tawaensis* Merr., *B. tebiang* S.Julia & Kiew, *B. temburongensis* Sands, *B. tenericaulis* Ridl., *B. tenuissima* S.Julia & C.Y.Ling, *B. timorensis* (Miq.) Golding & Kareg., *B. tindan* Rimi & Kimahim, *B. tinjanii* S.Julia, *B. tomaniensis* Rimi, *B. torajana* D.C.Thomas & Ardi, *B. torricellensis* Warb., *B. triangularis* Kiew & C.Y.Ling, *B. ubahribuensis* S.Julia & Kiew, *B. umbratica* S.Julia, *B. urdanetensis* Elmer, *B. urunensis* Kiew, *B. vaccinioides* Sands, *B. vanderentii* Rossiti, *B. vanderwateri* Ridl., *B. varipeltata* D.C.Thomas, *B. vermeulenii* D.C.Thomas, *B. vuijkii* Koord., *B. vulgare* S.Julia & Kiew, *B. wallacei* C.W.Lin & C.I Peng, *B. walteriana* Irmsch., *B. warburgii* K.Schum. & Lauterb., *B. wariana* Irmsch., *B. watuwilensis* Girm., *B. weberi* Merr., *B. weigallii* Hemsl., *B. wenzelii* Merr., *B. wrayi* Hemsl., *B. xiphophylla* Irmsch., *B. xiphophylloides* Kiew, *B. yiii* Kiew & S.Julia, *B. zamboangensis* Merr.

Distribution. – ASIA: Brunei, China (Hainan, Yunnan), East Timor, Indonesia (Java, Kalimantan, Lesser Sunda Islands, Maluku, Sulawesi, Sumatra, West Papua), Malaysia (Peninsular Malaysia, Sabah, Sarawak), Papua New Guinea, Philippines, Solomon Islands, Thailand, Vietnam.

Taxonomic notes. – We recognise a circumscription of *B.* sect. *Petermannia* based on Doorenbos & al. (1998) and Kiew & al. (2015) with some modifications. We recommend further research to determine which species belong in *B.* sect. *Bractebegonia*, and the relationships between the “*Begonia* amphioxus clade” and the “*Petermannia*-*Symbegonia* clade”. The range of morphology present in *B.* sect. *Petermannia* is much more apparent following recent research on Borneo by Kiew & al. (2015), and it may be that the section can be divided in more manageable units in the future. However for the time being we recognise a large and paraphyletic concept of the section.

Doorenbos & al. (1998) noted the unusual peltate, lanceolate leaves of *B. amphioxus* and its dichasial inflorescences with solitary female flowers. These characters are not shared by the other species within the “*Begonia amphioxus* clade” and we are unable to separate this group from the “*Petermannia-Symbegonia* clade” by morphology. Species in both clades share a characteristic inflorescence morphology being protandrous and with basal female flowers; and perforate anther endothecium cell wall thickening. Furthermore, species in both clades are resolved together (although with poor support) in nrDNA and mtDNA phylogenies (see review in Thomas & al., 2011). Thomas & al. (2011) discussed a scenario whereby transfer of a foreign plastid into Bornean *B. sect. Petermannia* followed by diversification within Borneo would account for the observed conflict among phylogenies and with morphology. We agree this scenario is likely, but note the presence of non-Bornean *B. cucphuongensis* (Vietnam) and *B. hainanensis* Chun & F.Chun (China: Hainan) in the “*Begonia amphioxus* clade”. These species may represent a back-colonisation from Borneo or be relatives of the plants from which chloroplast capture occurred.

Begonia saxatilis is moved here, although initially described in the genus *Diploclinium*, it has a typical *B. sect. Petermannia* inflorescence with female flowers at the base. *Begonia warburgii* was treated by Doorenbos & al. (1998) as only a tentative member of *B. sect. Petermannia*. We assign this species to the section with confidence because of the similarity between this species and *B. bipinnatifida*. The Bornean *B. piring* has paired female flowers at the base of a male-flower cyme and so fits very comfortably in *B. sect. Petermannia*, and it is moved here from *B. sect. Diploclinium*. *Begonia rubrosetosa* is also moved from *B. sect. Diploclinium*, as it lacks tubers and is likely allied to other caulescent species from Vietnam in *B. sect. Petermannia*. *Begonia beccarii* was previously unplaced (Hughes, 2008), and is moved to *B. sect. Petermannia* as it is very close to, if not synonymous with, *B. promethea* Ridl., which is in the same section.

Begonia* sect. *Pilderia (Klotzsch) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 141. 1859 ≡ *Pilderia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 127. 1854 – Type (designated by Swart, ING Card 10693. 1960): *Pilderia urticifolia* Klotzsch = *Begonia buddleiifolia* A.DC. — [Fig. 17A]

Species list. – 6 species: *B. buddleiifolia* A.DC., *B. glandulifera* Griseb., *B. humillima* L.B.Sm. & Wassh., *B. jenmanii* Tutin, *B. mariannensis* Wassh. & T.McClellan, *B. tepuiensis* Moonlight & Jara

Distribution. – AMERICAS: Colombia, Ecuador, Guyana, Peru, Trinidad-Tobago, Venezuela.

Taxonomic notes. – We refer to the description in Moonlight & Jara-Muñoz (2017) and follow the circumscription therein.

Begonia* sect. *Platycentrum (Klotzsch) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 134. 1859 ≡ *Platycentrum* Klotzsch in Abh. Königl. Akad. Wiss. Berlin 1854: 243. 1855 ≡ *Begonia* subg. *Platycentrum* (Klotzsch) C.B.Clarke in Bot. J. Linn.

- Soc. 18: 118. 1881 – Type: *Platycentrum xanthiana* (Hook.) Klotzsch ≡ *B. xanthinum* Hook. — [Fig. 14B]
 = *Begonia* sect. *Elasticae* C.B.Clarke in Bot. J. Linn. Soc. 18: 115. 1881 – **Type (designated here):** *B. episcopalis* C.B. Clarke = *Begonia griffithiana* (A.DC.) Warb.
 = *Begonia* sect. *Euplatycentrum* C.B.Clarke in Bot. J. Linn. Soc. 18: 115. 1881, nom. illeg. – Type: *Begonia xanthina* Hook.
 = *Begonia* sect. *Monolobium* T.C.Ku in Gu & al., Fl. China 13: 207. 2007 – Type: *Begonia wutaiana* C.I Peng & Y.K.Chen.
 = *Begonia* sect. *Sphenanthera* (Hassk.) Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 140. 1894 ≡ *Sphenanthera* Hassk. in Verslagen Meded. Afd. Natuurk. Kon. Akad. Wetensch. 4: 139. 1855 ≡ *Casparya* sect. *Sphenanthera* (Hassk.) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 118. 1859, **syn. nov.** – Type: *Sphenanthera robusta* (Blume) Hassk. ex Klotzsch ≡ *Begonia robusta* Blume.
 = *Casparya* sect. *Holoclinium* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 118. 1859 ≡ *Begonia* sect. *Holoclinium* (A.DC.) Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 142. 1894, **syn. nov.** – Type: *Casparya trisulcata* A.DC. = *Begonia longifolia* Blume.
 = *Casparya* sect. *Polyschisma* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 119. 1859 ≡ *Begonia* sect. *Polyschisma* (A.DC.) Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 149. 1894, **syn. nov.** – Type: *Casparya crassicaulis* A.DC. = *Begonia multangula* Blume.
 = *Meziera* sect. *Monopteron* A.DC., Prodr. 15(1): 406. 1864 ≡ *Begonia* sect. *Monopteron* (A.DC.) Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 142. 1894, **syn. nov.** – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 5. 1972): *Meziera nepalensis* A.DC. = *Begonia nelapensis* (A.DC.) Warb.

Species list. – 171 species: *B. ×chungii* C.I Peng & S.M.Ku, *B. ×taipeiensis* C.I Peng, *B. abdullahpieei* Kiew, *B. aborensis* Dunn*, *B. acetosella* Craib*, *B. adenostegia* Stapf, *B. aequilateralis* Irmsch., *B. algaia* L.B.Sm. & Wassh., *B. alpina* L.B.Sm. & Wassh., *B. altissima* Ridl., *B. annulata* K.Koch, *B. aptera* Blume*, *B. areolata* Miq., *B. augustinei* Hemsl., *B. austrotaiwanensis* Y.Chen & C.I Peng, *B. balan-sana* Gagnep.*, *B. baliensis* Girm.*, *B. baviensis* Gagnep., *B. beddomei* Hook., *B. bouffordii* C.I Peng, *B. brevipedunculata* Y.M.Shui, *B. brevisetulosa* C.Y.Wu, *B. burkillii* Dunn*, *B. caobangensis* C.I Peng & C.W.Lin, *B. cathayana* Hemsl., *B. cathartii* Hook.f., *B. ceratocarpa* S.H.Huang & Y.M.Shui*, *B. chishuiensis* T.C.Ku, *B. chitoensis* T.S.Lui & M.J.Lai, *B. chuyunshanensis* C.I Peng & Y.K.Chen, *B. chlorocarpa* Irmsch. ex Sands*, *B. circumlobata* Hance, *B. coelocentroides* Y.M.Shui & Z.D.Wei, *B. coptidifolia* H.G.Ye, F.G.Wang, Y.S.Ye & C.I Peng, *B. crocea* C.I Peng, *B. cucurbitifolia* C.Y.Wu, *B. daweishanensis* S.H.Huang & Y.M.Shui, *B. decora* Stapf, *B. deliciosa* Linden ex Fotsch, *B. diadema* Linden ex Rodigas, *B. dielseiana* E.Pritz. ex Diels, *B. difformis* (Irmsch.) W.C. Leong, C.I Peng & K-F.Chung, *B. digyna* Irmsch., *B. discrepans* Irmsch., *B. dryadis* Irmsch., *B. duclouxii* Gagnep., *B. edulis* H.Lév., *B. emeiensis* C.M.Hu ex C.Y.Wu & T.C.Ku, *B. flaviflora* H.Hara, *B. formosana* (Hayata) Masam., *B. forrestii* Irmsch., *B. foveolata* Irmsch., *B. fraseri* Kiew, *B. gagnepainiana* Irmsch., *B. goniotis* C.B.Clarke,

B. griffithiana (A.DC.) Warb., *B. gulinqingensis* S.H.Huang & Y.M.Shui, *B. hahiepiana* H.Q.Nguyen & Tebbitt*, *B. halconensis* Merr.*, *B. handelii* Irmsch.*, *B. hatacoa* Buch.-Ham. Ex D.Don, *B. hayamiana* Nob.Tanaka*, *B. hayatae* Gagnep.*, *B. hekouensis* S.H.Huang, *B. hemsleyana* Hook.f., *B. herveyana* King, *B. hongkongensis* F.W.Xing, *B. houttuynioides* T.T.Yu & W.P.Fang, *B. iridescens* Dunn, *B. jinyunensis* C.I Peng, B.Ding & Q.Wang, *B. kachinensis* Nob.Tanaka*, *B. khaophanomensis* Phutthai & M.Hughes, *B. kingdon-wardii* Tebbitt*, *B. klossii* Ridl., *B. koelzii* R.Camfield, *B. koksunii* Kiew, *B. lacerata* Irmsch., *B. laminariae* Irmsch., *B. lancangensis* S.H.Huang*, *B. lecomtei* Gagnep., *B. lempuyangensis* Girm.*, *B. leuserensis* M.Hughes, *B. limprichtii* Irmsch., *B. lipingensis* Irmsch., *B. longanensis* C.Y.Wu, *B. longialata* K.Y.Guan & D.K. Tian, *B. longicarpa* K.Y.Guan & D.K.Tian*, *B. longicaulis* Ridl., *B. longiciliata* C.Y.Wu, *B. longifolia* Blume*, *B. lukuana* Y.C.Liu & C.H.Ou*, *B. macrotoma* Irmsch., *B. maguanensis* S.H.Huang & Y.M.Shui, *B. manhaoensis* S.H.Huang & Y.M.Shui, *B. maxwelliana* King, *B. megalophyllaria* C.Y.Wu, *B. megaptera* A.DC., *B. menglianensis* Y.Y.Qian, *B. mengtzeana* Irmsch., *B. multangula* Blume*, *B. multibracteata* Girm.*, *B. myanmarica* C.I Peng & Y.D.Kim, *B. nantoensis* M.J.Lai & N.J.Chung, *B. nepalensis* (A.DC.) Warb., *B. nuwakotensis* S.Rajbhandary, *B. obovoidea* Craib*, *B. obversa* C.B.Clarke, *B. oligocarpa* A.DC. ex Koord., *B. oreodoxa* Chun & F.Chun ex C.Y.Wu & T.C.Ku, *B. oreophila* Kiew, *B. palmata* D.Don, *B. paucilobata* C.Y.Wu, *B. paupercula* King, *B. pavonina* Ridl., *B. pedatifida* H.Lév., *B. peii* C.Y.Wu, *B. perakensis* King, *B. pinglinensis* C.I Peng, *B. praetermissa* Kiew, *B. proluxa* Craib, *B. pseudoscottii* Girm.*, *B. psilophylla* Irmsch., *B. pulchrifolia* D.K.Tian & C.H.Li, *B. purpureofolia* S.H.Huang & Y.M.Shui, *B. reflexisquamata* C.Y.Wu, *B. repenticaulis* Irmsch., *B. rex* Putz., *B. rheifolia* Irmsch., *B. rhoephila* Ridl., *B. rhyacophila* Kiew, *B. robusta* Blume*, *B. rockii* Irmsch., *B. roxburghii* (Miq.) A.DC.*, *B. rubinea* H-Z.Li, *B. rubropunctata* S.H.Huang & Y.M.Shui, *B. sandalifolia* C.B.Clarke, *B. scitifolia* Irmsch., *B. scortechinii* King, *B. scottii* Tebbitt*, *B. shilendrae* Rekha Morris & P.D.Mcillan, *B. siamensis* Gagnep., *B. sikkimensis* A.DC., *B. silletensis* (A.DC.) C.B.Clarke*, *B. sizemoreae* Kiew, *B. smithiana* T.T.Yu, *B. sphenantheroides* C.I Peng, *B. subhowii* S.H.Huang, *B. taiwaniana* Hayata, *B. taligera* S.Rajbhandary, *B. tamdaoensis* C.I Peng, *B. tampinica* Burkill ex Irmsch., *B. tarokoensis* M.J.Lai, *B. tengchiana* C.I Peng & Y.K.Chen, *B. tessaricarpa* C.B.Clarke*, *B. tetralobata* Y.M.Shui, *B. teysmanniana* (Miq.) Tebbitt, *B. thomsonii* A.DC., *B. togashii* Nob.Tanaka & C.I Peng, *B. truncatiloba* Irmsch., *B. tsaii* Irmsch., *B. tsoongii* C.Y.Wu, *B. tuberculosa* Girm., *B. vallicola* Kiew, *B. venusta* King, *B. versicolor* Irmsch., *B. villifolia* Irmsch., *B. wui-senioris* C.I Peng, *B. wutaiana* C.I Peng & Y.K.Chen, *B. wyepingiana* Kiew, *B. xanthina* Hook., *B. yingjiangensis* S.H.Huang. — [*The “Sphenanthera group”]

Species whose membership is doubtful. – 6 species: *B. amabilis* Linden, *B. dux* C.B.Clarke, *B. gungshanensis* C.Y.Wu, *B. langbianensis* Baker f., *B. polytricha* C.Y.Wu, *B. setifolia* Irmsch.

Distribution. – ASIA: Bhutan, China (Chongqing, Fujian, Guangdong, Guangxi, Guizhou, Hainan, Heilongjiang, Hong

Kong, Hubei, Jiangsi, Sichuan, Tibet, Yunnan), India (Arunachal Pradesh, Assam, Darjeeling, Manipur, Meghalaya, Mizoram, Nagaland, Sikkim, Tripura), Indonesia (Bali, Java, Lesser Sunda Islands, Maluku, Sulawesi, Sumatra), Laos, Malaysia (Peninsular Malaysia, Sabah), Myanmar, Nepal, Philippines, Taiwan, Thailand, Vietnam.

Taxonomic notes. – Maintaining *B. sect. Platycentrum* separate from *B. sect. Sphenanthera* (Hughes & Girmansyah, 2011) is no longer tenable in the face of molecular data from both chloroplast and nuclear data showing the latter to be polyphyletic (Tebbutt & al., 2006; Thomas & al., 2011; this study). Although the fruit type of the vast majority of species in *B. sect. Platycentrum* (2-locular splash-cup, dehiscent, with one enlarged wing) is instantly diagnostic, the fruits of species in *B. sect. Sphenanthera* vary in locule number (3–8) and shape, being united only by having a fleshy fruit wall. The type of *B. sect. Sphenanthera*, *B. robusta* Blume, has a fruit which is intermediate between the two sections, having one wing enlarged, but with fleshy walls and three locules; Doorenbos & al. (1998) state “if it did not have a 3-locular ovary, one would not hesitate to put *B. robusta* in *Platycentrum*”. The newly enlarged *B. sect. Platycentrum* is characterised by a rhizomatous habit (with a few exceptions; e.g., *B. longifolia* Blume and allies, which are caulescent, but have a rhizomatous stem base), highly convolute stigmas, stamens on a column, and anthers dehiscing through long lateral slits with an extended connective. We distinguish the members of the section with fleshy fruit walls in the informally named “Sphenanthera group” of *B. sect. Platycentrum*.

Begonia sect. *Monopteron* shares with *B. sect. Platycentrum* its two locular ovaries with bifid placentae and we replicate Rajbhandary & al. (2011) in placing the section within the *B. sect. Platycentrum*. The two sections were differentiated by the presence or absence of two lateral wings on the fruits, which otherwise share an enlarged dorsal wing. We synonymise *B. sect. Monopteron* with *B. sect. Platycentrum* herein. *Begonia halconensis* Merr. from Mindoro in the Philippines is moved here from *B. sect. Petermannia* based on its very close resemblance to the widespread *B. longifolia*, and phylogenetic evidence in Tebbitt & al. (2006).

We refer to the descriptions in Doorenbos & al. (1998) of *B. sect. Platycentrum* (p. 155) and *B. sect. Sphenanthera* (p. 194).

Begonia sect. *Pritzelia* (Klotzsch) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 137. 1859 ≡ *Pritzelia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 126. 1854 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 6. 1972): *Pritzelia fischeri* (Otto & A.Dietr.) Klotzsch ≡ *Begonia dietrichiana* Irmsch. — [Fig. 17B] = *Ewaldia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 123. 1854 ≡ *Begonia* sect. *Ewaldia* (Klotzsch) A.DC., Prodr. 15(1): 372. 1864 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 4. 1972): *Ewaldia lobata* (Schott) Klotzsch = *Begonia rufa* Thunb. = *Gurltia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 123. 1854 – Type: *Gurltia meyeri* (Otto & A.Dietr.) Klotzsch = *Begonia tomentosa* Schott.

- = *Scheidweilera* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 123. 1854 = *Begonia* sect. *Scheidweilera* (Klotzsch) A.DC., Prodr. 15(1): 370. 1864, **syn. nov.** – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 7. 1972): *Scheidweilera muricata* (Scheidw.) Klotzsch = *Begonia pentaphylla* Walp.
- = *Saueria* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 122. 1854 = *Begonia* sect. *Saueria* A.DC., Prodr. 15(1): 288. 1864 – Type: *Saueria sulcata* (Scheidw.) Klotzsch = *Begonia dichotoma* Jacq.
- = *Trendelenburgia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 123. 1854 = *Begonia* sect. *Trendelenburgia* (Klotzsch) A.DC. in Martius, Fl. Bras. 4(1): 377. 1861, **syn. nov.** – Type: *Trendelenburgia fruticosa* Klotzsch = *Begonia fruticosa* (Klotzsch) A.DC.
- = *Steineria* Klotzsch in Abh. Königl. Akad. Wiss. Berlin 1854: 243. 1855 = *Begonia* sect. *Steineria* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 288. 1859 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 6. 1972): *Steineria ferruginea* Klotzsch = *Begonia hookeriana* Gardner.
- = *Nephromischus* Klotzsch in Braun & al., Append. Gen. Sp. Hort. Berol. 1855: 1. 1855 vel 1856 – Type: *Nephromischus rutilans* (Van Houtte) Klotzsch = *Begonia rutilans* Van Houtte.
- = *Begonia* sect. *Philippomartia* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 139. 1859 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 2. 1972): *Begonia neglecta* A.DC.
- = *Begonia* sect. *Plurilobarica* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 136. 1859 – Type: *Begonia schlumbergeriana* A.DC.
- = *Begonia* sect. *Dasystyles* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 143. 1859 – Type: *Begonia frigida* hort. ex A.DC.
- = *Begonia* sect. *Bradea* Toledo in Arq. Bot. Estado Sao Paulo 2(3): 61. 1946 – Type: *Begonia rufoserica* Toledo.
- = *Begonia* sect. *Gehrtia* Toledo in Arq. Bot. Estado Sao Paulo 2(3): 62. 1946 – Type: *Begonia adiantiformis* Toledo = *Begonia itatiensis* Irmsch. ex Brade.
- Species list.* – 147 species: *B. acetosa* Vell., *B. acida* Vell., *B. altamiroi* Brade, *B. angularis* Raddi, *B. angulata* Vell., *B. apparicioi* Brade, *B. ×antonietae* Brade, *B. arborescens* Raddi, *B. bahiensis* A.DC., *B. besleriifolia* Schott, *B. bidentata* Raddi, *B. biguassuensis* Brade, *B. bonitoensis* Brade, *B. boraceiensis* Handro, *B. boucheana* (Klotzsch) A.DC., *B. bradei* Irmsch., *B. brevilibata* Irmsch., *B. bufoderma* L.B.Sm. & Wassh., *B. callosa* L.Kollmann, *B. calvescens* (Brade ex L.B.Sm. & R.C.Sm.) E.L.Jacques & Mamede, *B. camposportoana* Brade, *B. capanemae* Brade, *B. caraguatubensis* Brade, *B. cariocana* Brade ex L.B.Sm. & Wassh., *B. catharinensis* Brade, *B. collaris* Brade, *B. concinna* Schott, *B. cordata* Vell., *B. cornitepala* Irmsch., *B. crispula* Brade, *B. curtii* L.B.Sm. & B.G.Schub., *B. declinata* Vell., *B. densifolia* Irmsch., *B. dentiloba* A.DC., *B. dichotoma* Jacq., *B. dietrichiana* Irmsch., *B. digitata* Raddi, *B. echinosepala* Regel, *B. elianae* Gregório & J.A.S. Costa, *B. epipsila* Brade, *B. fabulosa* L.B.Sm. & Wassh., *B. fernando-costae* Irmsch., *B. fiebrigii* C.DC., *B. fluminensis* Brade, *B. forgetiana* Hemsl.,

B. friburgensis Brade, *B. frigida* hort. ex A.DC., *B. fruticosa* (Klotzsch) A.DC., *B. fuscocaulis* Brade, *B. gardneri* A.DC., *B. garuvae* L.B.Sm. & R.C.Sm., *B. gehrtii* Irmsch., *B. hammoniae* Irmsch., *B. handroi* Brade, *B. heringeri* Brade, *B. hilariana* A.DC., *B. hispida* Schott, *B. hookeriana* Gardner, *B. hugelii* (Klotzsch) A.DC., *B. incisoserrata* A.DC., *B. inculta* Irmsch., *B. insularis* Brade, *B. isopterocarpa* Irmsch., *B. itaguassuensis* Brade, *B. itatiensis* Brade, *B. itatinensis* Irmsch. ex Brade, *B. itupavensis* Brade, *B. jocelinoi* Brade, *B. juliana* Loefgr. ex Irmsch., *B. larorum* L.B.Sm. & Wassh., *B. lineolata* Brade, *B. listada* L.B.Sm. & Wassh., *B. longibarbata* Brade, *B. lossiae* L.Kollmann, *B. luxurians* Scheidw., *B. magdalenensis* Brade, *B. matogrossensis* L.B.Sm. ex S.F.Smith & Wassh., *B. mattos-silvae* L.B.Sm. ex S.F.Smith & Wassh., *B. membranacea* A.DC., *B. metallica* W.G.Sm., *B. moysesii* Brade, *B. neglecta* A.DC., *B. neocomensium* A.DC., *B. nuda* Irmsch., *B. obscura* Brade, *B. occhionii* Brade, *B. odeteantha* Handro, *B. olsoniae* L.B.Sm. & B.G.Schub., *B. organensis* Brade, *B. otophylla* L.B.Sm. & B.G.Schub., *B. paganuccii* Gregório & J.A.S.Costa, *B. paleata* Schott ex A.DC., *B. paranaensis* Brade, *B. parviflora* Poepp. & Endl., *B. parvifolia* Schott, *B. parvistipulata* Irmsch., *B. paulensis* A.DC., *B. peltifolia* Schott, *B. pentaphylla* Walp., *B. peristegia* Stapf, *B. pickelii* Irmsch., *B. pilgeriana* Irmsch., *B. pinheironis* L.B.Sm. ex S.F.Smith & Wassh., *B. piresiana* Handro, *B. pluvialis* L.B.Sm. ex S.F.Smith & Wassh., *B. polyandra* Irmsch., *B. princeps* A.DC., *B. pulchella* Raddi, *B. ramentacea* Paxton, *B. reniformis* Dryand., *B. riedelii* A.DC., *B. rigida* Linden ex Regel, *B. rotunda* Vell., *B. rubropilosa* A.DC., *B. rufa* Thunb., *B. rufoserica* Toledo, *B. rupium* Irmsch., *B. russelliana* L.B.Sm. ex S.F.Smith & Wassh., *B. rutilans* hort. Van-Houtte ex A.DC., *B. salesopolensis* S.J.Gomes & Mamede, *B. sanguinea* Raddi, *B. sarmentacea* hort. ex Brilmayer, *B. saxifraga* A.DC., *B. scabrida* A.DC., *B. scabruidoidea* L.B.Sm. & Wassh., *B. scharffiana* Regel, *B. scharffii* Hook.f., *B. schlumbergeriana* Lem., *B. semidigitata* Brade, *B. serranegrae* L.B.Sm. ex S.F.Smith & Wassh., *B. solimitata* L.B.Sm. & Wassh., *B. solitudinis* Brade, *B. spinibarbis* Irmsch., *B. squamipes* Irmsch., *B. stenolepis* L.B.Sm. & R.C.Sm., *B. stenophylla* A.DC., *B. subacida* Irmsch., *B. sylvatica* Meisn. ex A.DC., *B. sylvestris* A.DC., *B. toledoana* Handro, *B. tomentosa* Schott, *B. valdensium* A.DC., *B. valida* Goebel, *B. venosa* Skan ex Hook.f., *B. verruculosa* L.B.Sm., *B. vicina* Irmsch., *B. windischii* L.B.Sm. ex S.F.Smith & Wassh.

Species whose membership is doubtful. – 1: *B. erecta* Vell.

Distribution. – AMERICAS: Argentina (Misiones), Bolivia, Brazil (Alagoas; Bahia, Espírito Santo, Minas Gerais, Mato Grosso, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo), Colombia, Costa Rica, Ecuador, Panamá, Paraguay, Peru, Venezuela.

Taxonomic notes. – We place all sampled rhizomatous species of *B.* sect. *Pritzelia* within the “core *Pritzelia* clade” (e.g., *B. olsoniae*, *B. fluminensis*, *B. moysesii*) except *B. acetosa* and *B. subacida*. We have been unable to identify morphological characters that separate these two species from *B.* sect. *Pritzelia* to our satisfaction. We retain all rhizomatous members of *B.* sect. *Pritzelia* within the section and await further study of these species.

We further resolve *B. sect. Scheidweilaria* and the monotypic *B. sect. Trendelenbergia* within this clade, both of which we reduce to synonyms of *B. sect. Pritzelia*. The latter was maintained as separate from *B. sect. Pritzelia* by Doorenbos & al. (1998) due to the types' supposed lack of cystoliths. Herbarium work (P.W. Moonlight, unpub. data) confirms the presence of cystoliths in *B. fruticosa*. The similarity between *B. sect. Scheidweilaria* and *B. sect. Pritzelia* was noted upon by Doorenbos & al. (1998), the former differing primarily in their compound leaves (except *B. parviflora*) and anthers that are shorter than the filaments.

Begonia venosa is resolved in the “core *Pritzelia* clade” as sister to the very similar *Begonia curtii* L.B.Sm. & B.G.Schub. These two species share the cystoliths and bifid placentae (Moonlight, unpublished data) characteristic of *B. sect. Pritzelia* and we reclassify *B. venosa* in this section.

Begonia matogrossensis was tentatively described by its authors in *B. sect. Ruizopavonia* on account of its superficial similarity to *B. holtonis* A.DC. (Smith & Wasshausen, 1999), and *B. besleriifolia* and *B. elianae* were both described in the same section. The female flowers of *B. matogrossensis* are unknown, but the habit and staminate flower morphology of all three species are consistent with *B. sect. Pritzelia*. The pistillate flower morphology and fruit morphology of *B. besleriifolia* and *B. elianae* are also both consistent with the section. Given their Brazilian distribution (*B. sect. Ruizopavonia* is an Andean section) and the presence of cystoliths in the leaf laminae of *B. matogrossensis* and *B. elianae* (characteristic of *B. sect. Pritzelia* but absent in *B. sect. Ruizopavonia*), we assign all three species to *B. sect. Pritzelia*. We have been unable to confirm the presence of cystoliths in *B. elianae* but they are expected to be present.

We refer to the description in Doorenbos & al. (1998: 159), which fits our new amended circumscription. Like Doorenbos & al. (1998), we treat *B. erecta* Vell as doubtfully assigned to section as it is only known from an illustration.

Begonia* sect. *Putzeysia (Klotzsch) A.DC., Prodr. 15(1): 314. 1864 ≡ *Putzeysia* Klotzsch in Abh. Königl. Akad. Wiss. Berlin 1854: 254. 1855 – Type: *Putzeysia gemmipara* (Hook.f. & Thomson) Klotzsch ≡ *Begonia gemmipara* Hook.f. & Thomson. — [Fig. 14C]

Species list. – 1 species: *B. gemmipara* Hook.f. & Thomson.

Distribution. – ASIA: Bhutan, India (Darjeeling, Sikkim), Nepal.

Taxonomic notes. – We agree with Doorenbos & al. (1998) in noting the similarity of this species to those of *B. sect. Diploclinium*, although it differs in its seeds having adpressed papillae, and in having unique clusters of axillary tubercles. We retain *B. sect. Putzeysia* as a monotypic section and refer to the description in Doorenbos & al. (1998: 164).

Begonia* sect. *Quadrilobaria A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 130. 1859 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 6. 1972): *Begonia nossibea* A.DC. — [Fig. 11K]

Species list. – 20 species: *B. anjuanensis* Humb. ex Keraudren & Bosser, *B. ankaranensis* Humb. ex Keraudren

& Bosser, *B. antsingyensis* Humb. ex Keraudren & Bosser, *B. antsiranensis* Aymonin & Bosser, *B. bagotiana* Humb. ex Keraudren & Bosser, *B. bekopakensis* Aymonin & Bosser, *B. bernieri* A.DC., *B. boiviniana* A.DC., *B. decaryana* Humb. ex Keraudren & Bosser, *B. francoisii* Guillaumin, *B. goudotii* A.DC., *B. heteropoda* Baker, *B. isalensis* Humb. ex Keraudren & Bosser, *B. leandrii* Humb. ex Keraudren & Bosser, *B. mananjebensis* Humb. ex Keraudren & Bosser, *B. neoperrieri* Humb. ex Keraudren & Bosser, *B. nossibea* A.DC., *B. sambiranensis* Humb. ex Keraudren & Bosser, *B. trullifolia* Guillaumin, *B. tsaratananensis* Aymonin & Bosser.

Distribution. – AFRICA: Comoros, Madagascar.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 165) and follow the circumscription therein with the addition of *B. trullifolia* (unassigned by Doorenbos & al., 1998) because of its similarity to *B. goudotii*.

Begonia* sect. *Quadriperigon Ziesenh. in Begonian 35: 257. 1968 – Type: *Begonia abaculoides* Ziesenh. = *Begonia boisseri* A.DC. — [Fig. 17C]

= *Begonia* (sect. *Begoniastrum*) subsect. *Euknesebeckia* Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 149. 1894 – Type: *Begonia monoptera* Link & Otto = *Begonia balmisiana* Bálmis.

Species list. – 19 species: *B. angustiloba* A.DC., *B. anodifolia* A.DC., *B. balmisiana* Bálmis, *B. biserrata* Lindl., *B. boissieri* A.DC., *B. bulbifera* Link & Otto, *B. dealbata* Liebm., *B. fusibulba* C.DC., *B. gracilior* Burt-Utley & McVaugh, *B. gracilis* Kunth, *B. macdanielsii* Standl., *B. ornithocarpa* Standl., *B. palmeri* S.Watson, *B. pedata* Liebm., *B. portillana* S.Watson, *B. rhodochlamys* L.B.Sm. & B.G.Schub., *B. sandtii* Houghton ex Ziesenh., *B. tapatia* Burt-Utley & McVaugh, *B. uruapensis* Sessé & Moc.

Species whose membership is doubtful. – 1 species: *B. racemiflora* Ortiges ex C.Chev.

Distribution. – AMERICAS: El Salvador, Guatemala, Honduras, Mexico (Aguascalientes, Baja California, Chiapas, Chihuahua, Colima, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, México Distrito Federal, México State, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Sonora, Tabasco, Tamaulipas, Yucatán, Zacatecas).

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 167) and follow the circumscription therein.

Begonia* sect. *Reichenheimia (Klotzsch) A.DC. Prodr. 15(1): 385. 1864 ≡ *Reichenheimia* Klotzsch in Abh. Königl. Akad. Wiss. Berlin 1854: 174. 1855 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 7. 1972): *Reichenheimia thwaitesii* (Hook.) Klotzsch ≡ *Begonia thwaitesii* Hook. — [Fig. 14D]

= *Mitscherlichia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 124. 1854 ≡ *Begonia* sect. *Mitscherlichia* (Klotzsch) A.DC., Prodr. 15(1): 389. 1864 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 7. 1972): *Begonia albo-coccinea* Hook.

= *Begonia* subg. *Aschisma* C.B.Clarke in Bot. J. Linn. Soc.

18: 117. 1881 – **Type (designated here):** *Begonia fibrosa* C.B.Clarke.

= *Begonia* sect. *Uniplacentales* C.B.Clarke in Hooker, Fl. Brit. India 2: 652. 1879 – **Type (designated here):** *Begonia fibrosa* C.B.Clarke.

Species list. – 20 species: *B. albococcinea* Hook., *B. cardiophora* Irmsch., *B. chingii* Irmsch., *B. fibrosa* C.B.Clarke, *B. floccifera* Bedd., *B. harmandii* Gagnep., *B. henryi* Hemsl., *B. hymenophylla* Gagnep., *B. intermixta* Irmsch., *B. morelii* Irmsch. ex Kareg., *B. nivea* Parish ex Kurz, *B. nymphaeifolia* T.T.Yu, *B. parvula* H.Lév. & Vaniot, *B. phrixophylla* Blatt. & McCann, *B. pierrei* Gagnep., *B. pumilio* Irmsch., *B. subpeltata* Wight, *B. tenera* Dryand., *B. thwaitesii* Hook., *B. trichocarpa* Dalzell.

Distribution. – ASIA: Cambodia, China (Guangxi, Guizhou, Hainan, Yunnan), India (Karnataka, Nagaland), Laos, Myanmar, Sri Lanka, Thailand, Vietnam.

Taxonomic notes. – This section is much reduced from its earlier concept, following the description of *B. sect. Jackia* which now contains many of the species hitherto included in it. It likely represents a phylogenetically disparate assemblage of species united by having a tuberous habit and entire placenta. We await further study of the affinities of individual species and anticipate further phylogenetic work may result in the continued reduction of *B. sect. Reichenheimia*.

Begonia sect. *Ridleyella* Irmsch. in Mitt. Inst. Allg. Bot. Hamburg 8: 105. 1929 – Type: *Begonia eiromischa* Ridl. — [Fig. 14E]

Description. – Acaulescent, rhizomatous herbs, perennial. Stipules persistent. Leaves alternate, peltate or basifixed (*B. padawanensis*), blade subsymmetrical, veins peltate to palmate-pinnate, raised above. Inflorescence axillary, few flowered, cymose, bracts deciduous or persistent. Male flowers: with 3 or 4 free perianth segments; androecium zygomorphic, stamens 25–35, free, anthers obovate, dehiscing via lateral slits, connective retuse. Female flowers: bracteoles absent or present at the base of the ovary, with 3 to 5 free perianth segments; ovary and fruit with 3 wings, wings equal or subequal, 3-locular, placentas axile, entire, bearing ovules on both surfaces; styles 3, free or united at the base, bifid, stigmatic papillae in a spirally twisted band. Fruit a capsule.

Species list. – 7 species: *B. burtii* Kiew & S.Julia, *B. eiromischa* Ridl., *B. kingiana* Irmsch., *B. padawanensis* C.W.Lin & C.I.Peng, *B. payung* Kiew & S.Julia, *B. serianensis* C.W.Lin & C.I.Peng, *B. speluncae* Ridl.

Distribution. – ASIA: Malaysia (Peninsular Malaysia, Sarawak).

Taxonomic notes. – In the phylogeny we resolve *B. speluncae* as sister to *B. kingiana*, and the two species share a creeping, rhizomatous habit; peltate leaves; prominent venation on the leaf upper surfaces; four tepals in the male flower and five tepals in the female flower; asymmetric androecium; and stamens with a retuse apex. These characteristics are shared by *B. burtii*, *B. padawanensis*, *B. payung* and *B. serianensis* (although *B. padawanensis* has basifixed leaves) from Sarawak. These species differ however from *B. kingiana* in

their tri- rather than bi-locular ovaries. We transfer these four species to *B. sect. Ridleyella*. The recircumscribed section is morphologically most similar to *B. sect. Jackia*, sharing the rhizomatous habit of that section, but distinguished by five tepals in the female flower; asymmetric androecium and retuse stamens. All species assigned to *B. sect. Ridleyella* share a preference for limestone habitats. We agree with Doorenbos & al. (1998) in concluding the assignment of *B. pumila* to the section is doubtful, and we move that species to *B. sect. Parvibegonia*.

Begonia sect. *Rossmannia* A.DC., Prodr. 15(1): 333. 1864 ≡ *Rossmannia* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854 – Type: *Rossmannia repens* Klotzsch = *Begonia rossmanniae* A.DC. — [Fig. 17D]

Species list. – 1 species: *B. rossmanniae* A.DC.

Distribution. – AMERICAS: Brazil (Acre), Colombia, Ecuador, Peru.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 174), follow the circumscription therein, and refer to the discussion in Moonlight & Jara-Muñoz (2017) for comparisons with the closely related *B. sect. Pilderia*.

Begonia sect. *Rostrobegonia* Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 141. 1894 – Type: *Begonia rostrata* Welw. ex Hook.f. — [Fig. 11L]

Species list. – 9 species: *B. bequaertii* Robyns & Lawalrée, *B. engleri* Gilg, *B. johnstonii* Oliv. ex Hook.f., *B. nyassensis* Irmsch., *B. rostrata* Welw. ex Hook.f., *B. rumpiensis* Kupicha, *B. schliebenii* Irmsch., *B. sonderiana* Irmsch., *B. wollastonii* Baker f.

Distribution. – AFRICA: Angola, Democratic Republic of the Congo, Ghana, Ivory Coast, Kenya, Liberia, Malawi, Mali, Mozambique, Nigeria, Sierra Leone, South Africa, Tanzania, Togo, Uganda, Zimbabwe.

Taxonomic notes. – *Begonia* sect. *Rostrobegonia* and *B. sect. Sexalaria* differ in their style morphology and chromosome number thus we retain them as separate sections herein. We refer to the description in Doorenbos & al. (1998: 176) and follow the circumscription therein.

Begonia sect. *Ruizopavonia* A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 139. 1859 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 7. 1972): *Begonia alnifolia* A.DC. — [Fig. 17E]

Species list. – 26 species: *B. alnifolia* A.DC., *B. boreoharlingii* Tebbitt & Moonlight, *B. botryoides* Moonlight & Tebbitt*, *B. carpinifolia* Liebm., *B. consobrina* Irmsch., *B. convallariodora* C.DC., *B. cooperi* C.DC., *B. cuatrecasana* L.B.Sm. & B.G.Schub., *B. cymbalifera* L.B.Sm. & B.G.Schub., *B. dugandiana* L.B.Sm. & B.G.Schub., *B. estrellensis* C.DC., *B. extensa* L.B.Sm. & B.G.Schub., *B. glauca* (Klotzsch) Ruiz & Pav. ex A.DC., *B. glaucoides* Irmsch., *B. harlingii* L.B.Sm. & Wassh.*, *B. juninensis* Irmsch., *B. lignescens* C.V.Morton, *B. peruviana* A.DC., *B. pilosella* Irmsch., *B. prionophylla* Irmsch., *B. rubiginosipes* Irmsch., *B. seemanniana* A.DC., *B. tiliifolia* C.DC.*,

B. tonduzii C.DC., *B. viridiflora* A.DC., *B. xylopoda* L.B.Sm. & B.G.Schub. — [*The “tiliifolia group”]

Species whose membership is doubtful. – 6 species: *B. bangii* Kuntze, *B. buchtienii* Irmsch., *B. chaetocarpa* Kuntze, *B. leptostyla* Irmsch., *B. oblanceolata* Rusby, *B. varistyla* Irmsch.

Distribution. – AMERICAS: Bolivia, Colombia, Costa Rica, Ecuador, Guatemala, Honduras, México (Chiapas), Nicaragua, Panama, Peru, Venezuela.

Taxonomic notes. – We recognise a much reduced circumscription of *B. sect. Ruizopavonia* relative to Doorenbos & al. (1998). We resolve a clade with species that share raised veins on the underside of the leaves, elliptic or oblong anthers longer than the filaments, and fewer than five female tepals (except *B. boreoharlingii*, *B. harlingii* and *B. tiliifolia*). These characters are shared by the type *B. alnifolia* thus we recircumscribe *B. sect. Ruizopavonia* to include these species. The remainder of species are transferred to *B. sect. Cyathocnemis*, *B. sect. Donaldia*, *B. sect. Lepsia* and *B. sect. Pritzelia* as discussed under those sections. We place *B. viridiflora* in *B. sect. Ruizopavonia* as it resolves within the section and shares the section’s characteristic scandent habit and pinnate leaves.

We only tentatively assign the Bolivian members of *B. sect. Ruizopavonia* with multifid styles to the section. We sample no species of this problematic group and note the difficulty separating these poorly-known species from *B. sect. Hydristyles* (see discussion in Doorenbos & al., 1998). We consider it more likely that their true affinity is with that section, but we are reluctant to change their section without phylogenetic data.

Begonia* sect. *Scutobegonia Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 140. 1894 – Type: *Begonia lacunosa* Warb. — [Fig. 12A]

Species list. – 25 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. lopensis* Sosef & M.Leal, *B. mbanensis* Sosef, *B. mildbraedii* Gilg, *B. monte-alenensi* Sosef, *B. montis-elephantis* J.J.de Wilde, *B. peperomioides* Hook.f., *B. puberula* Sosef, *B. scutulium* Hook.f., *B. susaniae* Sosef, *B. vankerckhovenii* De Wild., *B. vittarifolia* N.Hallé, *B. wilksii* Sosef, *B. zairensis* Sosef, *B. zenkeriana* L.B.Sm. & Wassh.

Distribution. – AFRICA: Angola, Cameroon, Democratic Republic of the Congo, Equatorial Guinea, Gabón, Ghana, Ivory Coast, Nigeria, Republic of the Congo.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 184) and follow the circumscription therein.

Begonia* sect. *Semibegoniella (C.DC.) F.A.Barkley & Baranov in Buxtonian 1 (Suppl. 1): 7. 1972 = *Semibegoniella* C.DC. in Bull. Herb. Boissier 2(7): 307. 1908 – Type: *Semibegoniella sodiroi* C.DC. = *Begonia longirostris* Benth. — [Fig. 17F] = *Begoniella* Oliv. in Trans. Linn. Soc. Bot. 28: 513. 1873 – Type: *Begonia whitei* Oliv. = *Begonia oliveri* L.B.Sm. & B.G.Schub.

Species list. – 15 species: *B. hexandra* Irmsch., *B. holmnielseniana* L.B.Sm. & Wassh., *B. irmscheri* L.B.Sm. & B.G.

Schub., *B. kalbreyeri* (Oliv.) L.B.Sm. & B.G.Schub., *B. killipiana* L.B.Sm. & B.G.Schub., *B. lehmannii* (Irmsch.) L.B.Sm. & B.G.Schub., *B. libera* (L.B.Sm. & B.G.Schub.) L.B.Sm. & B.G.Schub., *B. longirostris* Benth., *B. napoensis* L.B.Sm. & B.G.Schub., *B. oliveri* L.B.Sm. & B.G.Schub., *B. pecten-nervia* L.B.Sm. & Wassh., *B. silverstonii* Jara, *B. suaviola* Jara, *B. tetrandra* Irmsch., *B. valvata* L.B.Sm. & B.G.Schub.

Distribution. – AMERICAS: Colombia, Ecuador.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 187) and follow the circumscription therein.

Begonia* sect. *Sexalaria A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 127. 1859 – Type: *Begonia annobonensis* A.DC. — [Fig. 12B]

Species list. – 1 species: *B. annobonensis* A.DC.

Distribution. – AFRICA: Cameroon, Equatorial Guinea (Annobón), São Tomé and Príncipe (Príncipe, São Tomé).

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 189) and follow the circumscription therein.

Begonia* sect. *Solananthera A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 128. 1859 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 7. 1972): *Begonia solananthera* A.DC. — [Fig. 17G]

Species list. – 3 species: *B. integerrima* Spreng., *B. radicans* Vell., *B. solananthera* A.DC.

Distribution. – AMERICAS: Brazil (Bahia, Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo).

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 192) and follow the circumscription therein.

Begonia* sect. *Squamibegonia Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 139. 1894 – Type: *Begonia ampla* Hook.f. — [Fig. 12C]

Species list. – 3 species: *B. ampla* Hook.f., *B. bonus-henricus* J.J.de Wilde, *B. poculifera* Hook.f.

Distribution. – AFRICA: Angola, Burundi, Cameroon, Democratic Republic of the Congo, Equatorial Guinea (Annobón, Bioko), Gabón, Nigeria, Republic of the Congo, Rwanda, São Tomé and Príncipe (Príncipe, São Tomé), Tanzania, Uganda.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 197) and follow the circumscription therein.

Begonia* sect. *Stellandrae Moonlight, **sect. nov.** – Type: *Begonia hoehneana* Irmsch. — [Fig. 17H]

Description. – Caulescent, repent herbs, perennial. Stipules persistent. Leaves alternate, basifixed, blade subsymmetrical, veins palmate. Inflorescence axillary, a dichasial cyme, bracts deciduous. Male flowers: with 4 free perianth segments; stamens 4 or 8, free, spreading from the apex of the column, anthers linear, dehiscing via lateral slits, connective projecting. Female flowers: bracteoles 2 at the base of the ovary, with 5 free perianth segments; ovary and fruit with 3 wings, wings subequal, 3-locular, placentas axile, entire, bearing ovules on both surfaces; styles 3, free, bifid, stigmatic papillae in a twice-spirally twisted band. Fruit a capsule.

Species list. – 1 species: *B. hoehneana* Irmsch.

Distribution. – AMERICAS: Brazil (São Paulo).

Etymology. – The epithet is from the Latin *stella* (star) and *andro* (male), referring to the type's stamens, which point outwards in a star-like fashion from the apex of a column.

Taxonomic notes. – The position of *B. hoehneana* has been uncertain since its description. Irmscher (1953) placed it within *B. sect. Pritzelia* but noted the species' unusual habit and androecium. Doorenbos & al. (1998) did not classify the species to section. Given its phylogenetically isolated position and the large morphological differences between *B. hoehneana* and the “Wageneria clade”, we create *B. sect. Stellandrae* to encompass this species. *Begonia sect. Stellandrae* is easily distinguished from all other American sections of *Begonia* by its combination of a creeping habit and anthers spreading from the apex of a long column.

Begonia sect. Symbegonia (Warb.) L.L.Forrest & Hollingsw. in Pl. Syst. Evol 241: 208. 2003 ≡ *Symbegonia* Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 149. 1894 – Type: *Symbegonia fulvo-villosa* (Warb.) Warb. ≡ *Begonia fulvo-villosa* Warb. — [Fig. 14F]

Species list. – 13 species: *B. arfakensis* (Gibbs) L.L.Forrest & Hollingsw., *B. argenteomarginata* Tebbitt, *B. fulvo-villosa* Warb., *B. mooreana* (Irmsch.) L.L.Forrest & Hollingsw., *B. pulchra* (Ridl.) L.L.Forrest & Hollingsw., *B. strigosa* (Warb.) L.L.Forrest & Hollingsw., *B. symbracteosa* L.L.Forrest & Hollingsw., *B. symgeraniifolia* L.L.Forrest & Hollingsw., *B. symhirta* L.L.Forrest & Hollingsw., *B. sympapuana* L.L.Forrest & Hollingsw., *B. symparvifolia* L.L.Forrest & Hollingsw., *B. symsanguinea* L.L.Forrest & Hollingsw., *B. yapensis* M.Hughes

Distribution. – ASIA: Indonesia (West Papua), Papua New Guinea.

Taxonomic notes. – *Begonia sect. Symbegonia* is nested within *B. sect. Petermannia* but is highly distinctive, with all species displaying fused tepals and elongate stigmas in the female flowers and many also displaying fused tepals in the male flower and columnar androecia (Hughes & al., 2015a). Following Forrest & Hollingsworth (2003), who transferred the genus *Symbegonia* into *Begonia*, we are reluctant to sink the section into *B. sect. Petermannia* and lose the utility of such a recognisable group, despite the fact it renders *B. sect. Petermannia* paraphyletic. The position of *B. arfakensis* in the phylogeny sister to an unidentified member of *B. sect. Petermannia* from Papua also renders *B. sect. Symbegonia* polyphyletic; this is a marked incongruence between morphological and molecular data and is potentially the result of chloroplast capture.

We refer to the description in Forrest & Hollingsworth & al. (2003) and follow the circumscription therein.

Begonia sect. Tetrachia Brade in Rodriguesia 18: 21. 1945 – Type: *Begonia quadrilocularis* Brade = *Begonia egregia* N.E.Br. — [Fig. 17I]

Description. – Caulescent, erect succulent herbs, perennial. Stipules deciduous. Leaves alternate, peltate or basifixed,

blade subsymmetrical or asymmetrical, veins peltate-pinnate to palmate-pinnate. Inflorescence axillary, many flowered, cymose, bracts deciduous. Male flowers: with 2 or 4 free perianth segments; stamens 25 to numerous, free or filaments united in a column, anthers oblong or obovate, dehiscing via lateral slits, connective produced. Female flowers: bracteoles 2 at the base of the ovary, with 5 or 6 (*B. egregia*) free perianth segments; ovary and fruit with 3 wings, wings subequal, 3- or 4-locular (*B. egregia*), placentas axile, entire or bifid, bearing ovules on both surfaces; styles 3, free or united at the base, bifid, stigmatic papillae in a spirally twisted band. Fruit a capsule.

Species list. – 16 species: *B. aguiabrancensis* L.Kollmann, *B. albidula* Brade, *B. egregia* N.E.Br., *B. fellereriana* Irmsch., *B. goldingiana* L.Kollmann & A.Fontana, *B. grisea* A.DC., *B. ibitiocensis* E.L.Jacques & Mamede, *B. kuhlmannii* Brade, *B. lealii* Brade, *B. novalombardiensis* L.Kollmann, *B. obdeltata* Gregório & E.L.Jacques, *B. pernambucensis* Brade, *B. ruhlmanniana* Irmsch., *B. ruschii* L.Kollmann, *B. umbraculifera* Hook.f., *B. wasshauseniana* L.Kollmann & Peixoto

Distribution. – AMERICAS: Brazil (Alagoas, Bahia, Espírito Santo, Minas Gerais, Paraíba, Pernambuco, Rio de Janeiro)

Taxonomic notes. – *Begonia sect. Tetrachia* was previously classified as monotypic, containing only *B. egregia* (Doorenbos & al., 1998). Our analyses resolve this species as nested within a clade containing three species of Brazilian *Begonia* currently classified within *B. sect. Pritzelia* and *B. sect. Knesebeckia*. Almost all of these species have stellate or peltate, scale-like hairs (*B. umbraculifera* is glabrous); frequently peltate leaves; axile, usually simple placentation; and cymose inflorescences. These characteristics are shared with ten unsampled Brazilian dry-adapted species of *B. sect. Begonia*, *B. sect. Knesebeckia* and *B. sect. Pritzelia*. We expand *B. sect. Tetrachia* to include these species but note that *B. egregia* remains unique within the section in its female flowers with 6 tepals and four locules (rather than 5 tepals and three locules).

Begonia sect. Tetrachia A.DC., Prodr. 15(1): 517. 1864 – Type: *Begonia mannii* Hook.f. — [Fig. 12D]

= *Begonia sect. Fuscibegonia* Warb. in Engler & Prantl, Nat. Pflanzenfam. 3(6a): 141. 1894 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 8. 1972): *Begonia eminii* Warb.

= *Begonia* (sect. *Fuscibegonia*) ser. *Subaequilaterales* Engl. in Engler & Drude, Veg. Erde 9(3, 2): 618. 1921 – Type (designated by Doorenbos & al. in Wageningen Agric. Univ. Pap. 98(2): 201. 1998): *Begonia polygonoides* Hook.f.

= *Begonia* (sect. *Fuscibegonia*) ser. *Inaequilaterales* Engl. in Engler & Drude, Veg. Erde 9(3, 2): 620. 1921 – Type (designated by Doorenbos & al. in Wageningen Agric. Univ. Pap. 98(2): 201. 1998): *Begonia eminii* Warb.

= *Begonia sect. Irmschera* Ziesenh. in Begonian 38(7): 161. 1971 – Type: *Begonia mauricei* Ziesenh. = *Begonia loranthoides* Hook.f.

Species list. – 31 species: *B. afromigrata* J.J.de Wilde, *B. capillipes* Gilg, *B. cavallyensis* A.Chev., *B. ebolowensis*

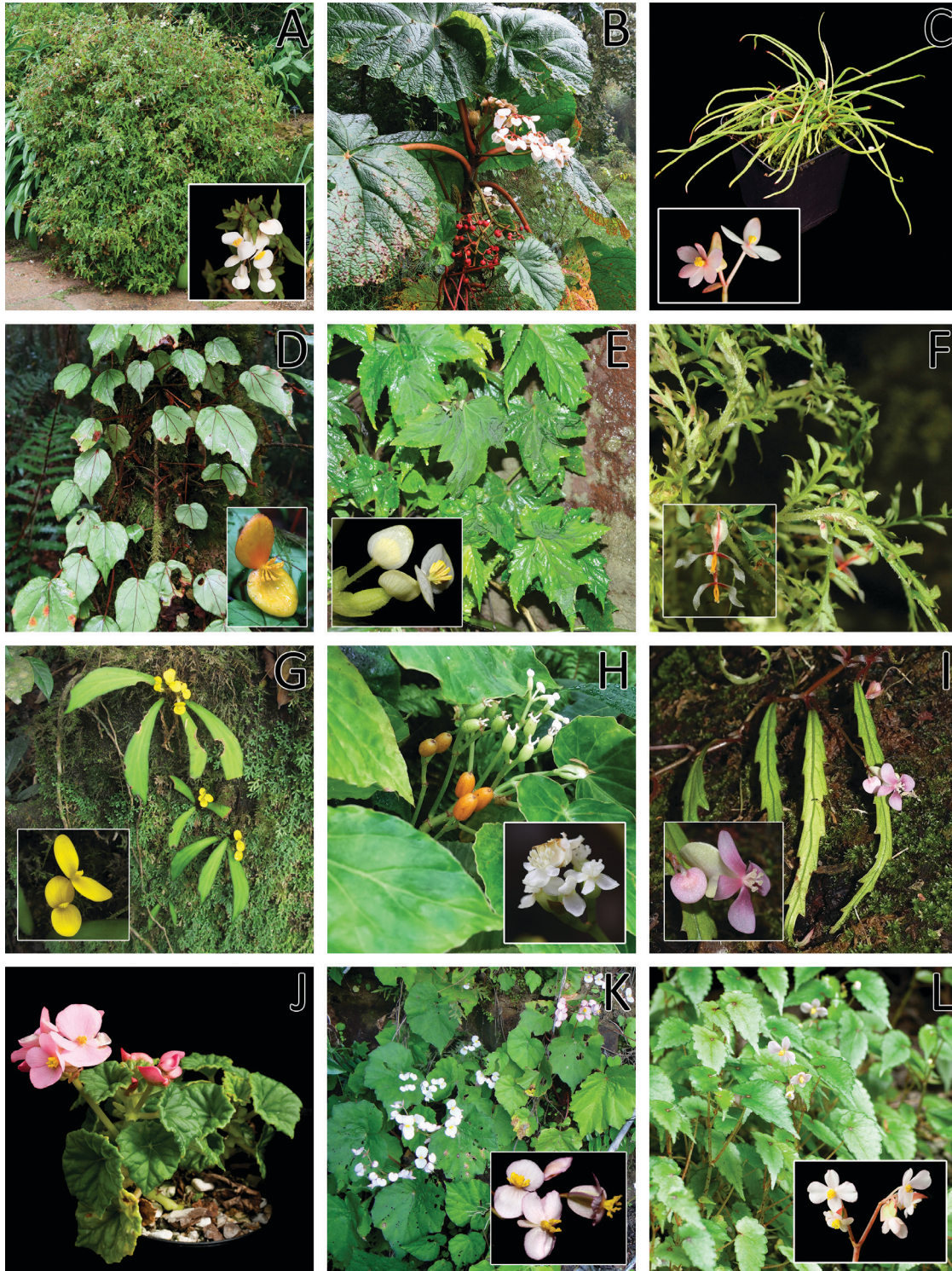


Fig. 11. Sections of African *Begonia*. **A**, *B. sect. Augustia*, *B. dregei*, RBGE living accession number 20000906, South Africa, McLellan, *T.* 223 (E); **B**, *B. sect. Baccabegonia*, *B. baccata*, Sao Tomé, Berthold, C. & Gardner, *M.F.* 5 (E); **C**, *B. sect. Erminea*, *B. bogneri*, RBGE living accession number 19860844; **D**, *B. sect. Cristasemen*, *B. thomeana*, Sao Tomé, Berthold, C. & Gardner, *M.F.* 13 (E); **E**, *B. sect. Exalabegonia*, *B. oxyloba*, Guinea, Bidault, E. & Diabaté, *M.* 665 (MO); **F**, *B. sect. Filicibegonia*, *B. asplenifolia*, Gabon, cultivated in private collection; **G**, *B. sect. Loasibegonia*, *B. scutifolia*, Cameroon, Droisart, V. & al. 1214 (MO); **H**, *B. sect. Mezierea*, *B. salaziensis*, Mauritius, cultivated in St. Andrews BG; **I**, *B. sect. Nerviplacentaria*, *B. henrilaportei*, Madagascar, Scherberich, D. 969 (LYJB); **J**, *B. sect. Peltaugustia*, *B. samhaensis*, RBGE living accession number 19990398, Socotra, Hughes, *M.* H6 (E); **K**, *B. sect. Quadrilobaria*, *B. nossibea*, Madagascar; **L**, *B. sect. Rostrobegonia*, *B. johnstonii*, RBGE living accession number 20131209, Barber, S. & al. 14 (E). — Photographs by P.W. Moonlight (A, C, J, L); M. Gardner (B, D); E. Bidault (E), J. Duruisseau (F, K), V. Droisart (G), M. Hughes (H), D. Scherberich (I, K inset).

Engl., *B. elaeagnifolia* Hook.f., *B. eminii* Warb., *B. furfuracea* Hook.f., *B. fusialata* Warb., *B. fusicarpa* Irmsch., *B. gabonensis* J.J.de Wilde, *B. horticola* Irmsch., *B. karperi* J.C.Arends, *B. kisuluana* Büttner, *B. komoensis* Irmsch., *B. letestui* J.J.de Wilde, *B. longipetiolata* Gilg, *B. loranthoides* Hook.f., *B. mannii* Hook.f., *B. molleri* (C.DC.) Warb., *B. oxyanthera* Warb., *B. pelargoniiflora* J.J.de Wilde & J.C.Arends, *B. polygonoides* Hook.f., *B. preussii* Warb., *B. rubromarginata* Gilg, *B. rubro-nervata* 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 Irmsch.

Distribution. – AFRICA: Angola, Burundi, Cameroon, Central African Republic, Democratic Republic of the Congo, Equatorial Guinea (Equatorial Guinea, Bioko), Gabón, Ghana, Guinea, Ivory Coast, Kenya, Liberia, Nigeria, Republic of the Congo, Rwanda, Sierra Leone, São Tomé and Príncipe (Príncipe, São Tomé), South Sudan, Tanzania, Uganda. ASIA: Laos; Thailand (*B. afromigrata*).

Taxonomic notes. – We resolve *B. sect. Baccabegonia* and *B. sect. Squamibegonia* as nested within *B. sect. Tetraphila*. These sections differ in a number of characters (e.g., male tepal number, fruit dehiscence, see Doorenbos & al., 1998 for more details) and are thus useful for diagnostic purposes. If *B. sect. Squamibegonia* and *B. sect. Baccabegonia* are to be retained, *B. sect. Tetraphila* will require recircumscription if it is to be a monophyletic section. This section is the largest in Africa and contains considerable morphological diversity,

and it is likely morphological characters will be found to aid recircumscription.

We refer to the description in Doorenbos & al. (1998: 207) and follow the circumscription therein.

Begonia sect. *Trachelocarpus* (Müll.Berol.) A.DC. in Martius, Fl. Bras. 4(1): 381. 1861 ≡ *Trachelocarpus* Müll.Berol. in Ann. Bot. Syst. 4: 909. 1857 – Type: *Trachelocarpus rhizocarpus* Müll.Berol. = *Begonia depauperata* Schott. — [Fig. 17J]

= *Trachelanthus* Klotzsch in Abh. Königl. Akad. Wiss. Berlin 1854: 240. 1855, non *Trachelanthus* G.Kunze – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 8. 1972): *Trachelanthus rhizocarpus* Klotzsch = *Begonia depauperata* Schott.

Species list. – 5 species: *B. depauperata* Schott, *B. fulvo-setulosa* Brade, *B. herbacea* Vell., *B. lanceolata* Vell., *B. veloziana* Walp.

Distribution. – AMERICAS: Brazil (Paraná, Rio de Janeiro, Santa Catarina, São Paulo).

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 204) and follow the circumscription therein.

Begonia sect. *Urniformia* Ziesenh. in Begonian 41: 12. 1974 – Type: *Begonia pitteri* C.DC. = *Begonia heydei* C.DC. — [Fig. 17K]

Species list. – 1 species: *B. heydei* C.DC.

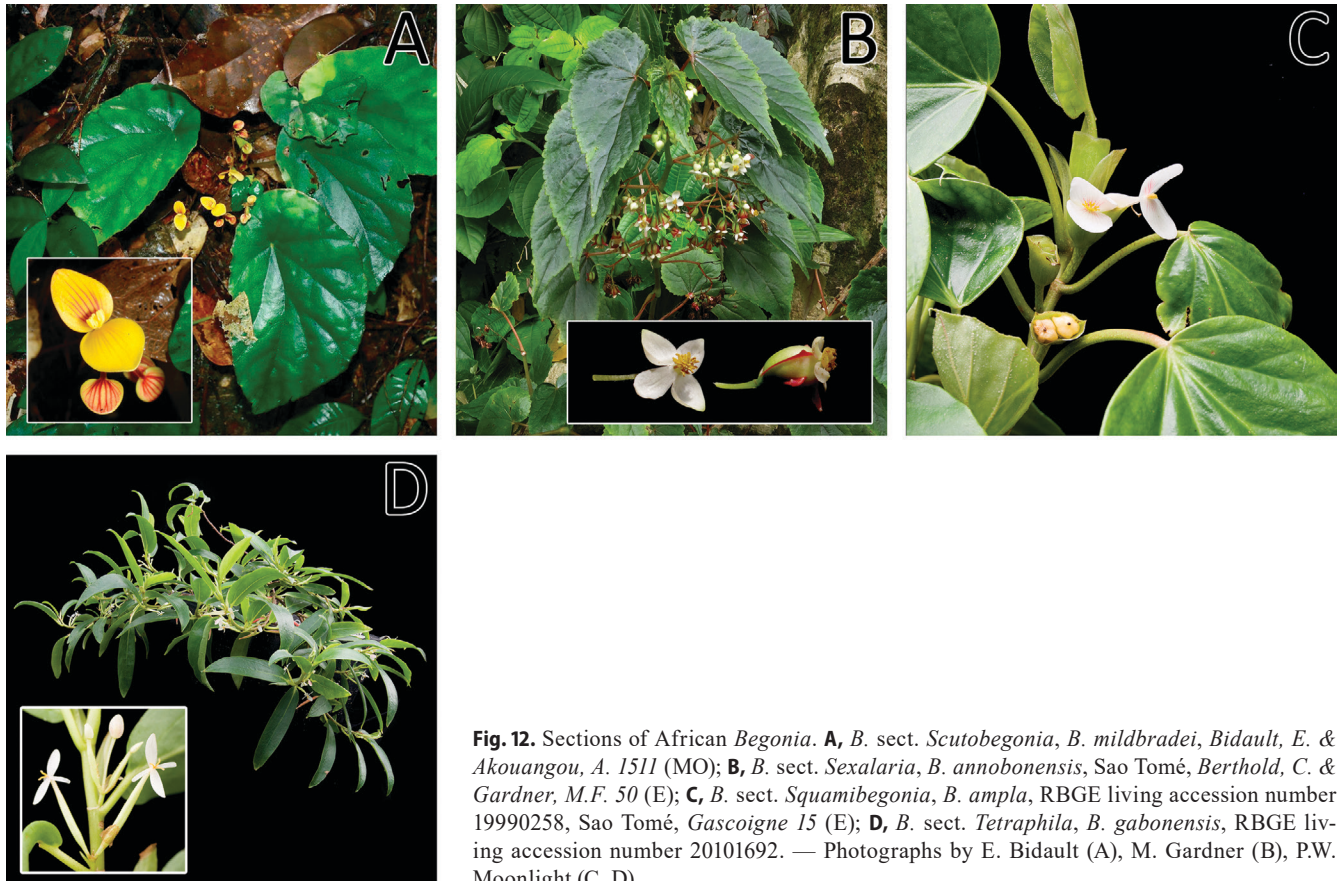


Fig. 12. Sections of African *Begonia*. **A**, *B. sect. Scutobegonia*, *B. mildbradei*, Bidault, E. & Akouangou, A. 1511 (MO); **B**, *B. sect. Sexalaria*, *B. annobonensis*, Sao Tomé, Berthold, C. & Gardner, M.F. 50 (E); **C**, *B. sect. Squamibegonia*, *B. ampla*, RBGE living accession number 19990258, Sao Tomé, Gascoigne 15 (E); **D**, *B. sect. Tetraphila*, *B. gabonensis*, RBGE living accession number 20101692. — Photographs by E. Bidault (A), M. Gardner (B), P.W. Moonlight (C, D).

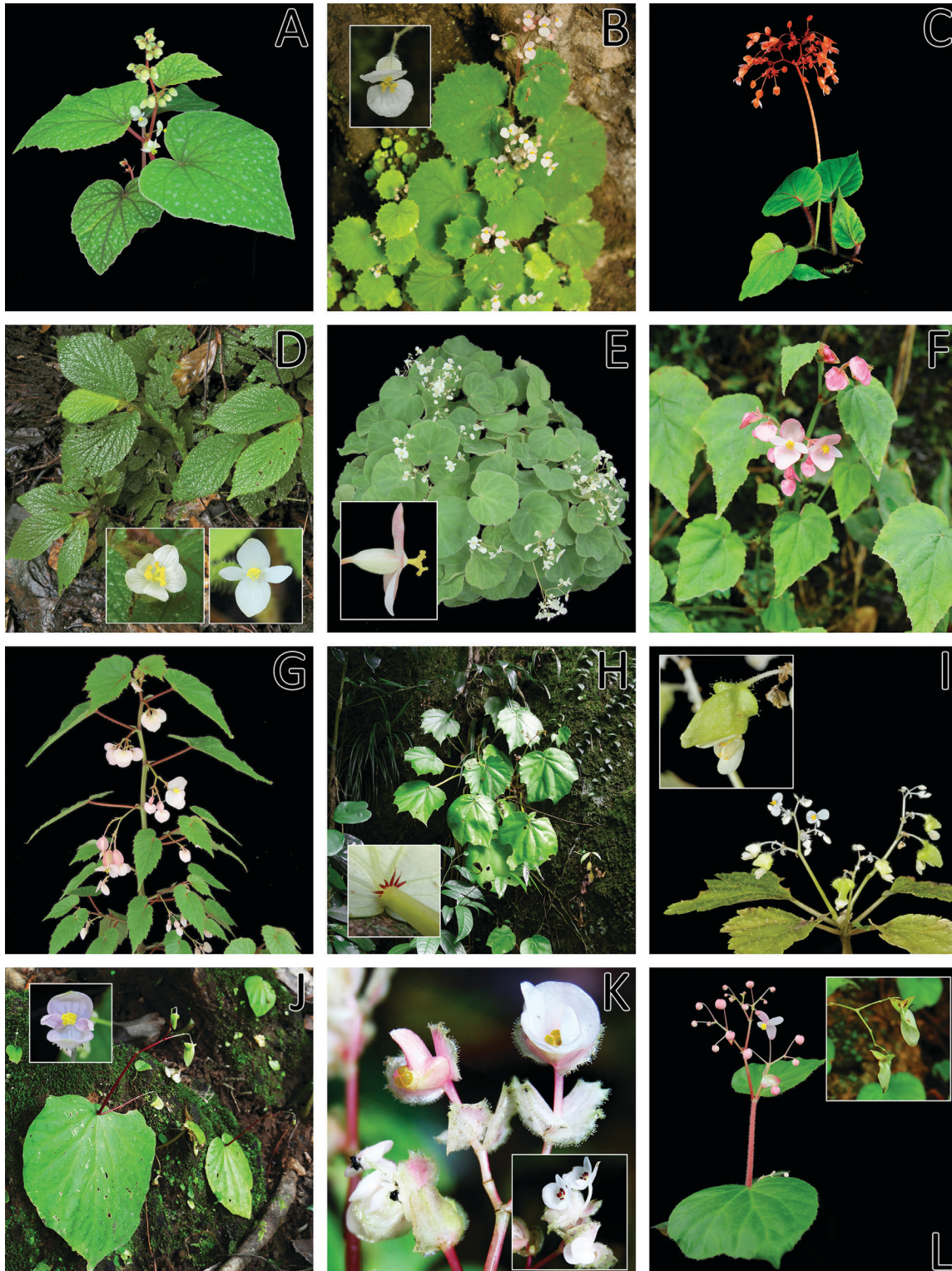


Fig. 13. Sections of Asian *Begonia*. **A**, *B.* sect. *Alicida*, *B. alicida*, Thailand; **B**, *B.* sect. *Apterobegonia*, *B. phutthaii*, Thailand, Middleton, D.J. & al. 5822, 5827 (E); **C**, *B.* sect. *Baryandra*, *B. oxysperma*, Mount Banahaw, Luzon, the Philippines; **D**, *B.* sect. *Bracteibegonia*, *B. bracteata*, Sumatra, Girmansyah, D. & Hughes, M. DEDEN1495 (E); **E**, *B.* sect. *Coelocentrum*, *B. porteri*, Guangxi, Peng, C.-I 19840 (HAST); **F**, *B.* sect. *Diploclinium*, *B. grandis*, Yunnan, China; **G**, *B.* sect. *Haagea*, *B. dipetala*, Sri Lanka, Peng, C.-I 21011 (HAST); **H**, *B.* sect. *Jackia*, *B. sublobata*, Sumatra, Girmansyah, D. DEDEN1486 (E); **I**, *B.* sect. *Lauchea*, *B. adenopoda*, Thailand, Middleton, D.J. & al. PK78473 (E); **J**, *B.* sect. *Monophyllon*, *B. prolifera*, Thailand, Peng, C.-I 24195 (HAST); **K**, *B.* sect. *Oligandrae*, *B. pentandra*, Papua New Guinea, Takeuchi, W.N. & al. 23126 (A); **L**, *B.* sect. *Parvibegonia*, *B. martabanica*, Kanchanaburi, Thailand. — Photographs by C.I Peng (A, C, D [inset], E, G, J, L), D. Middleton (B, I), M. Hughes (D, F, H), W. Takeuchi (K).

Distribution. – AMERICAS: Costa Rica, Guatemala, Panama.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 209) and follow the circumscription therein.

Begonia sect. *Wagneria* (Klotzsch) A.DC. in Ann. Sci. Nat., Bot., ser. 4, 11: 137. 1859 ≡ *Wagneria* Klotzsch in Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin 1854: 126. 1854 – Type (designated by Barkley & Baranov in Buxtonian 1(Suppl. 1): 3. 1972): *Wagneria fagifolia* (Fisch. ex Otto & A.Dietr.) Klotzsch ≡ *Begonia fagifolia* Fisch. ex Otto & A.Dietr. — [Fig. 17L]

= *Begonia* sect. *Enita* Brade in Rodriguésia 32: 160. 1957 – Type: *Wagneria convolvulacea* Klotzsch ≡ *Begonia convolvulacea* (Klotzsch) A.DC.

Species list. – 7 species: *B. convolvulacea* (Klotzsch) A.DC., *B. epibaterium* Mart. ex A.DC., *B. fagifolia* Fisch. ex Otto & A.Dietr., *B. glabra* Aubl., *B. inconspicua* Brade, *B. polygonifolia* A.DC., *B. smilacina* A.DC.

Distribution. – AMERICAS: Belize, Brazil (Acre, Alagoas, Amapá, Amazonas, Bahia, Ceará, Distrito Federal, Espírito Santo, Goiás, Minas Gerais, Paraíba, Paraná, Pernambuco,

Rio de Janeiro, Rondônia, Santa Catarina, São Paulo, Sergipe), Bolivia, Colombia, Costa Rica, Cuba, Ecuador, French Guiana, Guatemala, Guyana, Honduras, Jamaica, México (Chiapas, Guerrero, Hidalgo, Oaxaca, Puebla, Querétaro, Tabasco, Tamaulipas, Veracruz), Nicaragua, Panama, Peru, Suriname, Trinidad-Tobago, Venezuela (Venezuela, Venezuelan Antilles).

Taxonomic notes. – *Begonia* sect. *Wagneria* was separated from *B. sect. Pritzelia* by Doorenbos & al. (1998) due to its distinct scandent habit. We resolve all members of the section within a well-supported clade with a number of species of *B. sect. Pritzelia* characterised by large, palmately veined and slightly bullate leaves and lax, cymose inflorescences. These species include *B. reniformis*, which was previously placed by Klotzsch in his genus *Wagneria*. However, a number of species treated within *Wagneria* by Klotzsch are resolved in the “core *Pritzelia* clade” (e.g., *B. hispida* and *B. hugelii*) The difference between these groups remains unclear. We refer to the description in Doorenbos & al. (1998: 210), follow the circumscription therein, and informally name the wider clade the “*Wagneria* clade”. Further morphological and phylogenetic work is required to determine which other similar members of *B. sect. Pritzelia* resolve within the “*Wagneria* clade” (e.g.,

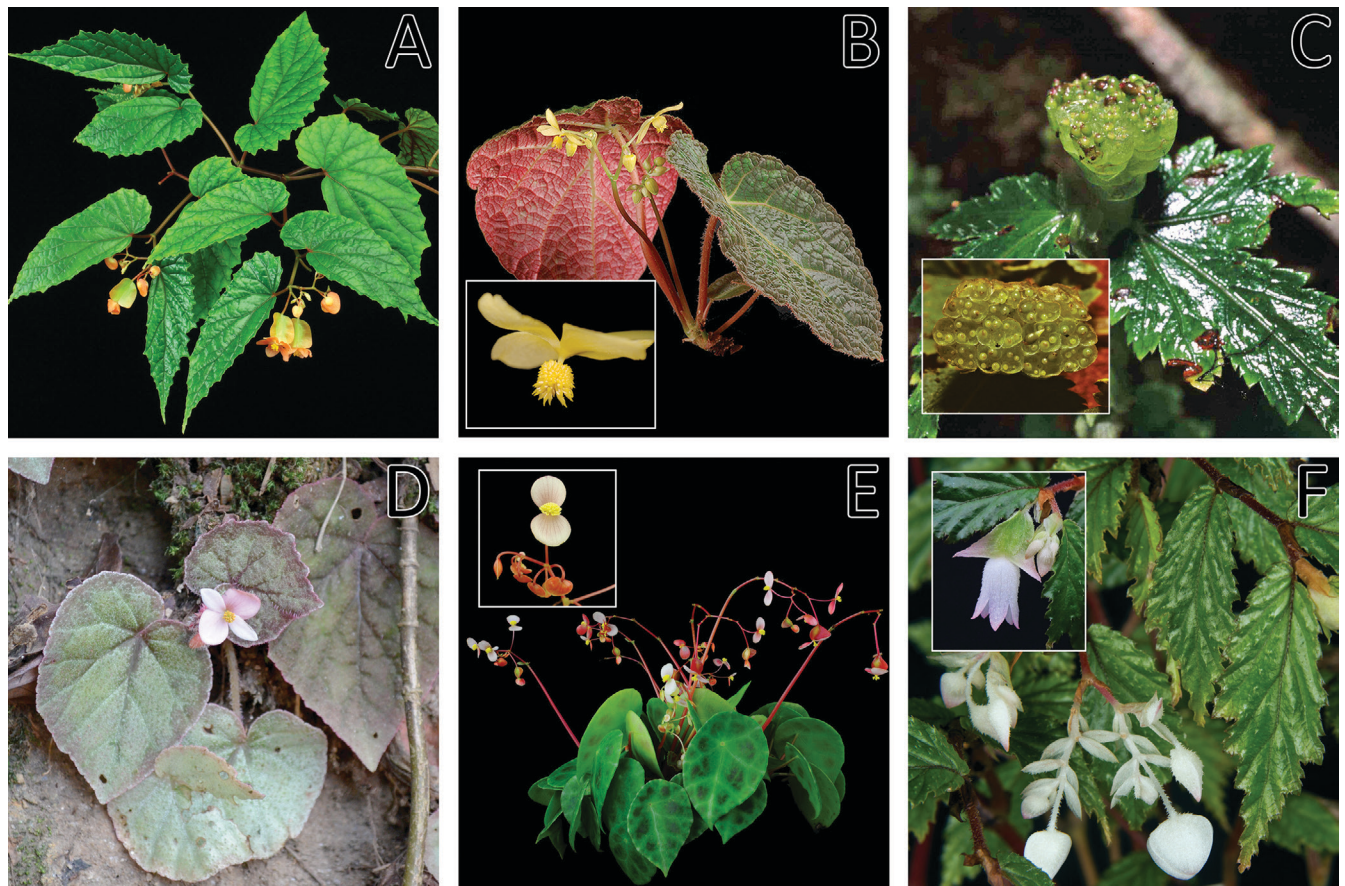


Fig. 14. Sections of Asian *Begonia*. **A**, *B. sect. Petermannia*, *B. cummingiana*, Philippines; **B**, *B. sect. Platycentrum*, *B. xanthina*, Yunnan, China; **C**, *B. sect. Putzeysia*, *B. gemmipara*, West Bengal, India; **D**, *B. sect. Reichenheimia*, *B. tenera*, Sri Lanka; **E**, *B. sect. Ridleyella*, *B. kingiana*, Peninsula Malaysia, Peng. C.-I 21226 (HAST); **F**, *B. sect. Symbegonia*, *B. arfakensis*, RBGE living accession number 20090808, West Papua, Argent, G. & al. 305. — Photographs by C.I Peng (A, B, E), P. Blanc (C), M. Hughes (D, F).

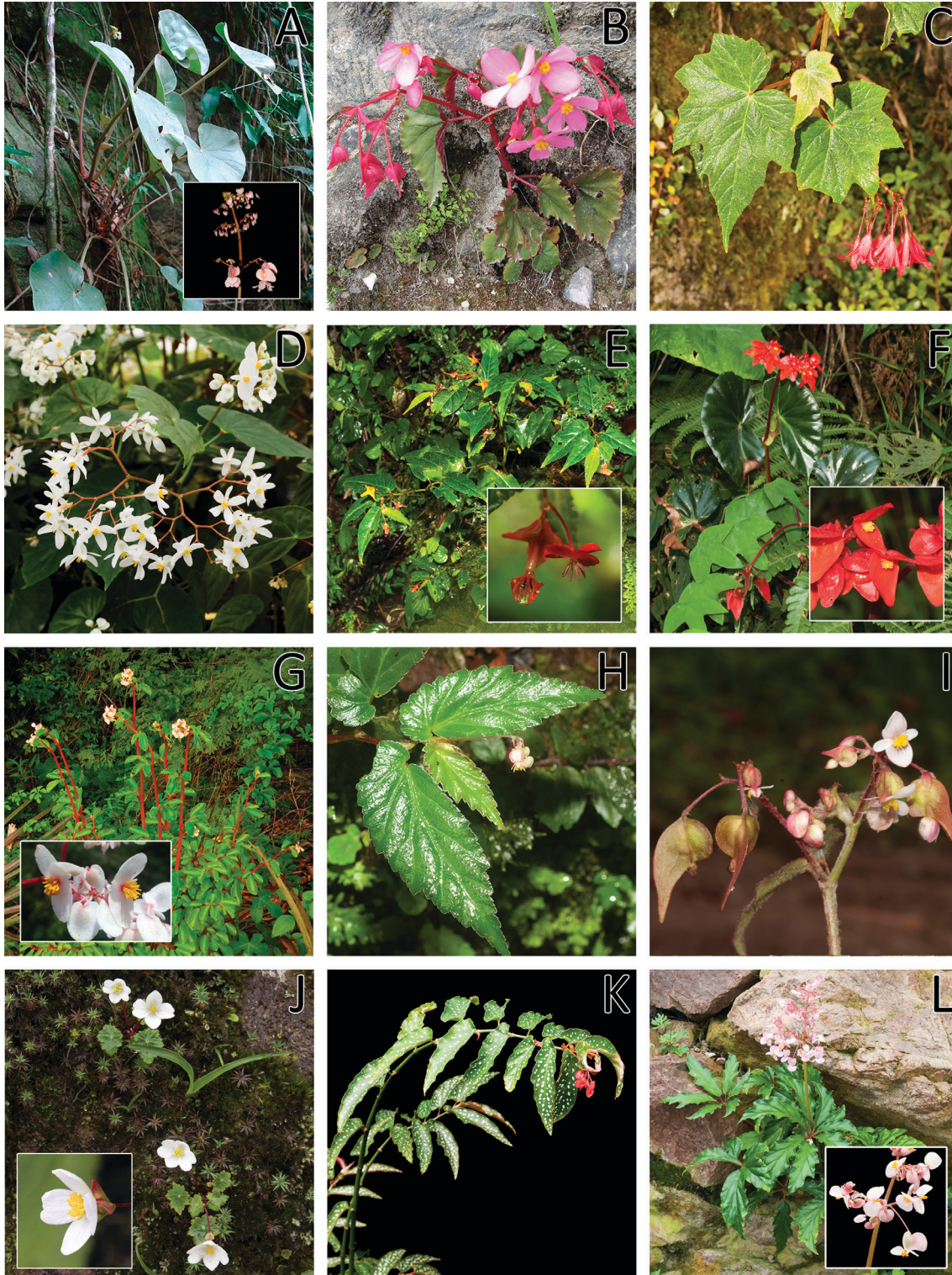


Fig. 15. Sections of American *Begonia*. **A**, *B. sect. Astrothrix*, *B. fragae*, Brasil, *Fraga* C.N. 2323 (UPCB); **B**, *B. sect. Australes*, *B. micranthera*, Bolivia, *Sarkinen & al.* 2144 (FHO); **C**, *B. sect. Barya*, *B. monadelpha*, Peru, *Moonlight, P. & Daza*, A. 148 (E); **D**, *B. sect. Begonia*, *B. odorata*, RBGE living accession number 20082086; **E**, *B. sect. Casparya*, *B. urticae*, Peru, *Moonlight, P. & Daza*, A. 154 (E); **F**, *B. sect. Cyathocnemis*, *B. altoperuviana*, Peru, *Moonlight, P. & Daza*, A. 83 (E); **G**, *B. sect. Donaldia*, *B. saxicola*, Bahia, *Cardoso, D.* 1305 (HUEFS); **H**, *B. sect. Doratometra*, *B. semiovata*, Peru, *Moonlight, P. & Daza*, A. 172 (E); **I**, *B. sect. Ephemera*, *B. fischeri*, Peru, *Moonlight, P. & Daza*, A. 124 (E); **J**, *B. sect. Eupetalum*, *B. geraniifolia*, Peru, *Moonlight, P. & Daza*, A. 116 (E); **K**, *B. sect. Gaerdtia*, *B. maculata*, RBGE living accession number 19891579; **L**, *B. sect. Gireoudia*, *B. carolineifolia*, RBGE living accession number 20100417, *Twyford*, A. 584 (E). — Photographs by L. Kollmann (A), T. Sarkinen (B), P.W. Moonlight (C–F, H–L), D. Cardoso (G).

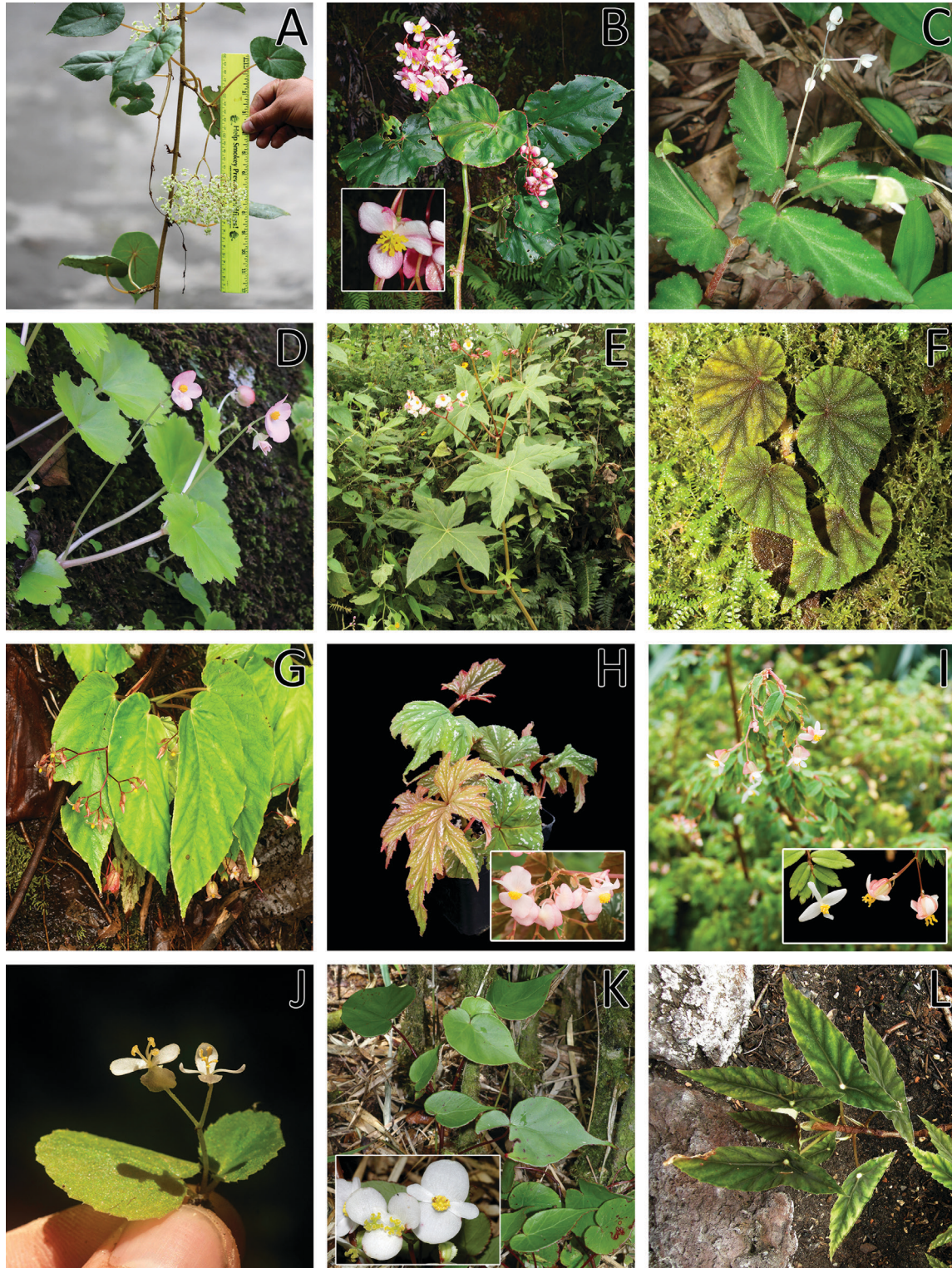


Fig. 16. Sections of American *Begonia*. **A**, *B. sect. Gobenia*, *B. tropaeolifolia*, Ecuador, Tebbitt, M. & Gutierrez, D. 850 (QCA); **B**, *B. sect. Hydristyles*, *B. fissistyla*, A. Orejuela 2830 (USM); **C**, *B. sect. Kollmannia*, *B. jaguarensis*, Espirito Santo, Kollmann, L. & Lopes, R.S. 11418 (MBML); **D**, Core *B. sect. Knesebeckia*, *B. monophylla*, Nuevo León; **E**, *B. sect. Knesebeckia* group I, *B. velata*, Peru, Tebbitt, M. & Daza, A. 838 (MOL); **F**, *B. sect. Knesebeckia* group II, *B. aff. microcarpa*, Peru, Moonlight, P. & Daza, A. 156 (E); **G**, *B. sect. Knesebeckia* group III, *B. chemillenensis*, Peru, Moonlight, P. & Daza, A. 314 (E); **H**, *B. sect. Latistigma*, *B. aconitifolia*, RBGE living accession number 20140767; **I**, *B. sect. Lepsia*, *B. foliosa*, RBGE living accession number 19480286; **J**, *B. sect. Microtuberosa*, *B. elachista*, Moonlight, P. & Daza, A. 318 (E); **K**, *B. sect. Parietoplacentalia*, *B. oaxacana*, Knapp, S. & A. Munro 9984 (BM); **L**, *B. sect. Pereira*, *B. lubbersii*, Berlin Botanic Garden. — Photographs by M.C. Tebbitt (A, E), A. Orejuela (B), L. Kollmann (C), S. Eduardo (D), P.W. Moonlight (F–J), A. Munro (K), J.-P. Bachelot Pierre (L).

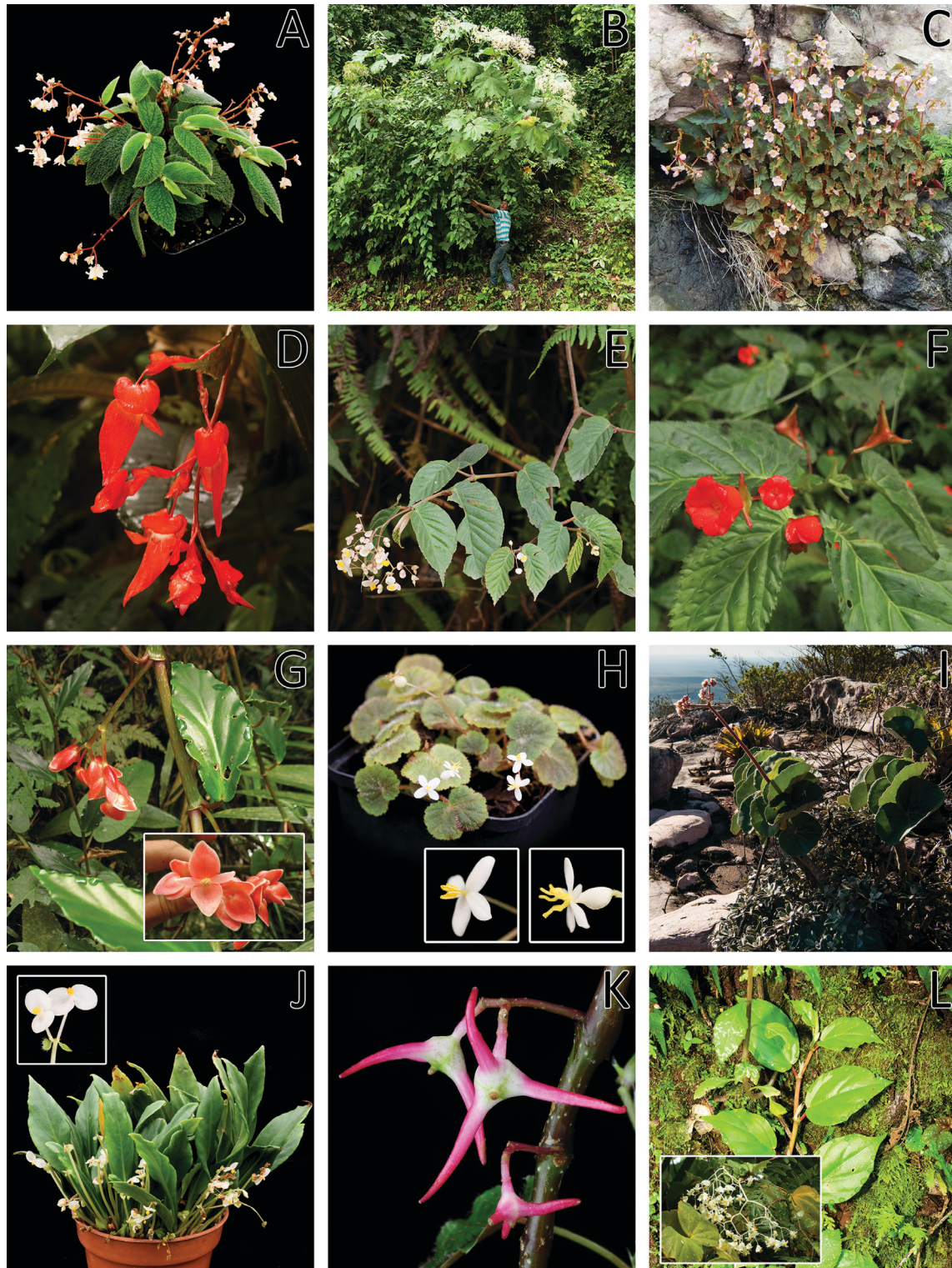


Fig. 17. Sections of American *Begonia*. **A**, *B. sect. Pilderia*, *B. buddleiifolia*, RBGE living accession number 20160126, Peru, Moonlight, P. & Daza, A. 165 (E); **B**, *B. sect. Pritzelia*, *B. parviflora*, Peru, Moonlight, P. & Daza, A. 171 (E); **C**, *B. sect. Quadriperigonia*, *B. gracilis*, Chihuahua; **D**, *B. sect. Rossmannia*, *B. rossmanniae*, Peru, Moonlight, P.W. & Daza, A. 315 (E); **E**, *B. sect. Ruizopavonia*, *B. peruviana*, Peru, Moonlight, P. & Daza, A. 82 (E); **F**, *B. sect. Semibegoniella*, *B. longirostris*, Ecuador; **G**, *B. sect. Solananthera*, *B. radicans*, São Paulo; **H**, *B. sect. Stellandraea*, *B. hoehneana*, RBGE living accession number 20141394; **I**, *B. sect. Tetrachia*, *B. grisea*, Bahia, Moonlight, P.W. & Fernandes, M. 750 (HUEFS); **J**, *B. sect. Trachelocarpus*, *B. herbacea*, RBGE living accession number 19731859; **K**, *B. sect. Urniformia*, *B. heydei*, RBGE living accession number 20131992; **L**, *B. sect. Wagneria*, *B. glabra*, Peru, P. Moonlight & A. Daza 240 (E). — Photographs by P.W. Moonlight (A, B, D, E, H–J, L), A. McDonnell (C), A. Jara-Muñoz (F), A. Benedito (G), C.I Peng (K).

B. caraguatatubensis Brade, *B. collaris* Brade). A revision of these sections is overdue, and may clarify the boundaries between *B. sect. Pritzelia* and *B. sect. Wageneria*.

Begonia* sect. *Warburgina Kuntze, Revis. Gen. Pl. 3(2): 105.

1898 – Type: *Begonia comata* Kuntze.

Species list. – 1 species: *B. comata* Kuntze.

Distribution. – AMERICAS: Bolivia.

Taxonomic notes. – We refer to the description in Doorenbos & al. (1998: 213) and follow the circumscription therein.

Species Unassigned to Section (do not match current sections): 32 species: *Begonia antaisaka* Humb. ex Keraudren & Bosser, *B. archboldiana* Merr. & L.M.Perry, *B. bataiensis* Kiew, *B. bifurcata* L.B.Sm. & B.G.Schub., *B. boisiana* Gagnep., *B. calcarea* Ridl.*, *B. crassula* Aver., *B. cremnophila* Tebbitt**, *B. erythrothrix* Tebbitt & Moonlight, *B. fractiflexa* S.Julia & Kiew, *B. froebelii* A.DC., *B. gracilicyma* Irmsch. ex M.Hughes, *B. herteri* Irmsch., *B. hohuanensis* S.S.Ying, *B. kanaensis* Kiew & C.Y.Ling*, *B. laccophora* Sands, *B. lingiae* S.Julia*, *B. lutea* L.B.Sm. & B.G.Schub., *B. malabarica* Lam., *B. masoalaensis* M.Hughes, *B. peltatifolia* H.L.Li, *B. physandra* Merr. & L.M.Perry, *B. rigidifolia* Aver., *B. rubrotepala* S.Julia*, *B. sabahensis* Kiew & J.H.Tan*, *B. sadirensis* Kiew & S.Julia*, *B. smithiae* Geddes, *B. speculum* Moonlight & Tebbitt**, *B. tanala* Humb. ex Keraudren & Bosser, *B. thyrsoides* Irmsch., *B. urubambensis* Tebbitt**, *B. viscosa* Aver. & H.Q.Nguyen. — [*The “calcarea group”; **the “cremnophila group”]

Species unassigned to section (imperfectly known): 50 species: *B. anaimalaiensis* Bedd., *B. brongniartiana* Lem., *B. brongniartii* Lem., *B. burkei* hort., *B. capensis* L.f., *B. castaneifolia* hort. ex Otto & A.Dietr., *B. cerasiphylla* L.B.Sm. & Wassh., *B. chakensis* S.Julia & C.Y.Ling, *B. complicata* (Hassk.) A.DC., *B. diptera* Dryand., *B. donkelaariana* Lem., *B. eriocaulon* Neumann, *B. gemmirhiza* H.Lév., *B. groenewegensis* hort. ex K. Koch & G.A. Fintelmann, *B. herteri* Irmsch., *B. hochbaumii* hort. ex E.Otto, *B. intermedia* Veitch ex Van Houtte, *B. khasiana* C.B.Clarke, *B. lansbergeae* Linden & Rodigas, *B. lemaoutii* hort. ex Vallerand, *B. macrotis* Vis., *B. maracuyensis* Parodi, *B. martynia* hort., *B. medusae* Linden, *B. mexera* hort., *B. meysselliana* Linden, *B. microptera* Hook., *B. muroptera* hort., *B. mutabilis* Harland, *B. nigricans* L.H.Bailey, *B. nobilis* hort., *B. northiana* hort. ex Gentil, *B. nummularifolia* Putz., *B. opulifolia* Loudon, *B. orchidiflora* Griff., *B. palmatiloba* Linden & André, *B. paniculata* D.Parodi, *B. pantherina* Putz. ex Linden, *B. papillaris* Herb. ex Cels, *B. paraguayensis* D.Parodi, *B. phyllomaniaca* Mart., *B. piperoides* Linden, *B. porteana* Van Geert, *B. preseriana* hort., *B. putzeysii* hort., *B. stipularis* Spreng., *B. strigulosa* (Hassk.) A.DC., *B. sunorchis* C.Chev., *B. tascellezii* hort., *B. villifera* Galeotti.

■ AUTHOR CONTRIBUTIONS

PWM and MH designed the research; PWM, WHA, LAP, K-FC, DG, AJ-M, RK, W-CL, YL, LDKM, C-IP, AJP, TP, SR, CR, RRR, DS, MCT, DCT, NHZ and MH collected the samples; PWM, DF, RH, AJ-M, AM, LDKM, MO’C, TP, DCT, NHZ and MH provided the molecular data; PWM and MH performed the analyses; MP provided database support; PWM, WA, K-FC, AJ-M, RK, C-IP, TP, SR, RRR, SJ, DS, Y-MS, MCT, DCT and MH interpreted the results; PWM and MH wrote the manuscript; and all authors were involved in editing the manuscript. — K-FC, <https://orcid.org/0000-0003-3628-2567>, bochung@gate.sinica.edu.tw; DG, deden_bo@yahoo.com; MH, <https://orcid.org/0000-0002-2168-0514>, mhughes@rbge.ac.uk; RK, ruth@frim.gov.my; PWM, <https://orcid.org/0000-0003-4342-2089>; C-IP, <https://orcid.org/0000-0002-9175-1146>; DCT, <https://orcid.org/0000-0002-1307-6042>, Daniel_THOMAS@nparks.gov.sg; HPW, <https://orcid.org/0000-0002-5231-3987>

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Appendix 1. GenBank accession numbers and voucher specimen information.

Taxon, collector plus collection number (herbarium code), *ndhA* intron, *ndhF-rp132* spacer, *rp132-trnL* spacer (“–” indicates missing sequence; accessions starting with “MH” are newly obtained for this study)

Begonia abdullahpieei, C.I Peng 22727 (HAST), MH207018, MH207427, MH207848; *B. aberrans*, M. Hughes 786 (E), KP712927, KP713097, KP713247; *B. aborensis*, J. Durisseau 100493 (LBG), MH207019, MH207428, MH207849; *B. acerifolia*, P.W. Moonlight & A. Daza 96 (E), –, MH207429, –, *B. acerifolia*, M. Tebbitt 768 (QCA), MH207020, MH207430, MH207850; *B. acerifolia*, M. Tebbitt 788 (QCA), MH207021, MH207431, MH207851; *B. acerifolia*, M. Tebbitt & A. Daza 797 (E), MH207022, MH207433, –, *B. acerifolia*, M. Tebbitt & A. Daza 810 (E), MH207023, MH207434, MH207852; *B. acerifolia*, M. Tebbitt & A. Daza 831 (E), MH207024, MH207435, –, *B. acerifolia*, M. Tebbitt & A. Daza 843 (E), MH207025, MH207436, MH207853; *B. acerifolia*, A. Parada 3342 (USZ), –, MH207432, –, *B. acerifolia*, P.W. Moonlight & A. Daza 120 (E), MH207026, MH207437, MH207854; *B. acerifolia*, T. Sarkinen 2058 (E), KP713031, KP713140, –, *B. acerifolia*, C.-I Peng 20869 (HAST), KP713069, KP713076, –, *B. aceroides*, T. Phutthai 243 (E), JF756385, JF756469, JF756553; *B. acetosa*, M. Tebbitt, S.M. Swensen & J. Yeadon 15 (BKL), KP712965, KP713154, KP713324; *B. acetosella*, Glasgow B.G. 003-152-95 (E), JF756367, JF756451, JF756535; *B. acida*, C.-I Peng 21294 (HAST), KP712957, KP713148, KP713330; *B. aconitifolia*, C.-I Peng 22224 (HAST), KP712925, –, –, *B. aconitifolia*, Tebbitt s.n., MH235394, MH235397, MH235432; *B. acuminatissima*, R.R. Rubite R321 (PNH), KR186445, KR186532, KR186706; *B. acutifolia*, M. Tebbitt 127 (BKL), KP713047, KP713166, KP713248; *B. acutifolia*, L.L. Forrest 160 (E), KP713055, KP713165, KP713249; *B. alabensis*, F. Lens 072 (SBG), MH207030, MH207441, MH207858; *B. alabensis*, F. Lens 078 (SBG), MH207031, MH207442, MH207859; *B. albo-coccinea*, C.-I Peng P23302 (HAST), KR186447, KR186534, KR186708; *B. albomaculata*, P.W. Moonlight & A. Daza 126 (E), MH207032, MH207443, MH207860; *B. albomaculata*, P.W. Moonlight & A. Daza 198 (E), MH207033, MH207444, MH207861; *B. albomaculata*, P.W. Moonlight & A. Daza 213 (E), MH207034, MH207445, –, *B. alicia-clarkiae*, E20110203, KP713007, KP713200, KP713233; *B. alicida*, T. Phutthai 139 (E), JF756388, JF756472, JF756556; *B. almedana*, A. Twyford 264 (E), MH207035, MH207446, MH207862; *B. altoperuviana*, P. W. Moonlight & A. Daza 84 (E), MH207036, MH207447, MH207863; *B. altoperuviana*, M. Tebbitt & A. Daza 823 (E), MH207037, MH207448, MH207864; *B. amphioxus*, D.C. Thomas 08116 (E), MH207038, MH207449, MH207865; *B. ampla*, Sukuwana 45 E00198091 (E), KP712979, –, –, *B. anemoniflora*, P.W. Moonlight & A. Daza 222 (E), MH207039, MH207450, MH207866; *B. anemoniflora*, P.W. Moonlight & A. Daza 230 (E), MH207040, MH207451, MH207867; *B. angularis*, M. Tebbitt 78 (BKL), KP712948, KP713217, KP713279; *B. angustifolia*, A. JaraMuñoz 2765 (COL), MH207041, MH207452, –, *B. anisoptera*, R.R. Rubite R479 (PNH), KR186448, KR186535, KR186709; *B. annobonensis*, M.F. Gardner, C.E. Berthold 49 (E), MH207042, –, MH207868; *B. aptera*, Smith & Galloway 67 (E), JF756369, JF756453, JF756537; *B. arborescens* var. *confertiflora*, M. Tebbitt 119 (BKL), KP712953, KP713162, KP713334; *B. areolata*, SUBOE 81 (E), MH207043, MH207454, MH207869; *B. areolata*, Gao & Hollingsworth 24141 (E), JF756366, JF756450, JF756534; *B. arfakensis*, ABEG 305 (E), MH207044, MH207454, MH207870; *B. argenteomarginata*, Glasgow B.G. 008-038-87 (E), JF756417, JF756501, JF756585; *B. arrogans*, P.W. Moonlight & A. Daza 27 (E), MH207045, MH207455, –, *B. arrogans*, P.W. Moonlight & A. Daza 285 (E), MH207046, MH207456, MH207871; *B. atricha*, SUBOE 11 (E), MH207047, MH207457, MH207872; *B. augustae*, B. Sénéchal 070409 (LBG), MH207048, MH207458, MH207873; *B. baccata*, M.E. Gardner & C.E. Berthold 5 (E), MH207049, MH207459, MH207874; *B. baik*, C.I Peng 24235 (HAST), MH207050, –, MH207875; *B. balansana*, J. Durisseau 120338 (LBG), MH207051, MH207460, MH207876; *B. baramensis*, P34 S09 (SBG), –, MH207461, MH207877; *B. barbellata*, P33 SBG s.n. (SBG), MH207052, MH207462, MH207878; *B. barkeri*, HAST RM08 304 A, KP713034, KP713138, –, *B. barkeri*, A. Twyford 530 E00668768 (E), KP713061, KP713081, KP713245; *B. barkleyana*, M. Peixoto 041650 (LBG), MH207053, MH207463, MH207879; *B. baviensis*, HNE 388 (E), MH207054, MH207464, MH207880; *B. beludruvena*, M. Hughes & Taufiq 1541 (E), –, MH207465, MH207881; *B. beryllae*, F. Lens 071 (SBG), MH207055, MH207466, MH207882; *B. cf. beryllae*, F. Lens 074 (SBG), MH207091, MH207501, MH207917; *B. bifurcata*, M. Tebbitt 782 (QCA), –, MH207467, MH207883; *B. bifurcata*, P.W. Moonlight & A. Daza 105 (E), KX756296, KX756307, MH207884; *B. bifurcata*, P.W. Moonlight & A. Daza 117 (E), KX756278, KX756308, MH207885; *B. biliranensis*, R.R. Rubite R311 (PNH), KR186449, KR186536, KR186710; *B. bipinnatifida*, Krieb s.n. (SBG), MH207058, MH207470, MH207886; *B. bissei*, W.G.C. 655 (E), MH207049, –, MH207887; *B. blancii*, C.-I Peng P22545 (HAST), KR186450, KR186537, KR186711; *B. bogneri*, L.L. Forrest 200 E00171239 (E), KP712977, KP713185, –, *B. boissiana*, no voucher, MH207060, MH207471, MH207888; *B. boliviensis*, no voucher, MH207062, MH207473, MH207890; *B. boliviensis*, M. Tebbitt 704 (USZ), MH207063, MH207474, MH207891; *B. boliviensis*, M. Tebbitt s.n. (USZ), MH207064, MH207475, MH207892; *B. boliviensis*, M. Tebbitt s.n. (USZ), MH207065, MH207476, MH207893; *B. boliviensis*, L.L. Forrest 182 (E), JF756346, JF756430, JF756514; *B. bonthainensis*, D.C. Thomas 09-63 (E), KP712932, KP713108, KP713327; *B. bonthainensis*, C.-I Peng P22531 (HAST), KR186451, KR186538, KR186712; *B. boquetensis*, B. Sénéchal 60681 (LBG), MH207066, MH207477, MH207894; *B. botryoides*, M. Tebbitt 777 (QCA), MH207067, MH207478, MH207895; *B. bracteata*, W.H. Ardi 25 (E), KP712991, KP713110, KP713323; *B. bracteosa*, M. Tebbitt & A. Daza 820 (E), MH207068, MH207479, MH207896; *B. bradei*, M. Tebbitt 121 (BKL), KP712960, KP713225, KP713287; *B. brandisiana*, Chamchamroon 3614 (E), JF756379, JF756463, JF756547; *B. bredlovei*, 08301 (HAST), KP713036, KP713109, –, *B. brevicordata*, M. Tebbitt & A. Daza 822 (E), MH207069, MH207480, MH207897; *B. breviramosa*, Reeve 142 (E), JF756414, JF756498, JF756582; *B. brossonnetifolia*, B. Sénéchal 110685 (LBG), MH207070, MH207481, MH207898; *B. bruneiana*, NHZ34 (SBG), MH207071, MH207482, MH207899; *B. bryophila ined.*, Chien-I Huang 6100 (E), MH207072, MH207483, MH207900; *B. buddleiifolia*, A. JaraMuñoz 2599 (E), KX756286, KX756327, MH207901; *B. buddleiifolia*, P.W. Moonlight & A. Daza 165 (E), MH207074, MH207485, MH207902; *B. buddleiifolia*, P.W. Moonlight & A. Daza 316 (E), MH207075, MH207486, MH207903; *B. bufoderma*, Lyon B.G. 80415 (LBG), MH207076, MH207487, MH207904; *B. bullatifolia*, C.-I Peng 21323 (HAST), KP713073, KP713128, –, *B. bullatifolia*, J. Durisseau 120348 (LBG), KX756303, –, MH207905; *B. burbridgei*, no voucher, MH207079, MH207489, MH207906; *B. burbridgei*, F. Lens 040 (SBG), MH207080, MH207490, MH207907; *B. calcicola*, C.-I Peng P20761 (HAST), KR186452, KR186539, KR186713; *B. calderonii*, A. Twyford 455 (E), MH207081, MH207491, MH207908; *B. callosa*, Lyon B.G. 90451 (LBG), MH207082, MH207492, MH207909; *B. calzadae*, A. Twyford 445 (E), MH207083, MH207493, MH207910; *B. camiguinensis*, R.R. Rubite R506 (PNH), KR186453, KR186540, KR186714; *B. capanemae*, M. Tebbitt, Swensen & Yeadon 7 (BKL), KP712949, KP713160, KP713280; *B. capensis*, Salamone, C. - LBG 20504, MH235383, MH235414, MH235434; *B. capituliformis*, Kinho & A.D. Poulson 169 (E), JN133309, JN133384, JN133413; *B. cardiocarpa*, Glasgow B.G. 006-006-92 (E), KP713018, KP713184, KP713301; *B. carolineifolia*, A. Twyford 457 (E), MH207085, MH207495, MH207912; *B. carolineifolia*, M. Tebbitt 80 (BKL), KP713033, KP713103, KP713244; *B. carrieae*, Tebbitt 151 (BKL), MH207086, MH207496, MH207913; *B. carrieae*, Lyon B.G. s.n. (LBG), MH207087, MH207497, –, *B. castilloi*, R.R. Rubite R98 (PNH), KR186454, KR186541, KR186715; *B. catharinensis*, B. Sénéchal 50723 (LBG), MH207088, MH207498, MH207914; *B. cathartii*, B. Sénéchal 130528 (LBG), MH207089, MH207499, MH207915; *B. aff. cauliflora*, F. Lens 065 (SBG), MH207027, MH207438, MH207855; *B. ceratocarpa*, Y.M. Shui & al. B2015207 (KUN), MH207090, MH207500, MH207916; *B. chemillenensis*, P.W. Moonlight & A. Daza 278 (E), MH207096, MH207505, MH207922; *B. chemillenensis*, P.W. Moonlight & A. Daza 287 (E), –, MH207506, MH207923; *B. chemillenensis*, P.W. Moonlight & A. Daza 292 (E), MH207097, MH207507, MH207924; *B. chemillenensis*, P.W. Moonlight & A. Daza 294 (E), –, MH207508, –, *B. chemillenensis*, P.W. Moonlight & A. Daza 313 (E), MH207098, MH207509, MH207925; *B. chemillenensis*, P.W. Moonlight & A. Daza 314 (E), MH207099, MH207510, MH207926; *B. chemillenensis*, P.W. Moonlight & A. Daza 317 (E), MH207100, –, –, *B. chiasmogyna*, D.C. Thomas 07-29 (E), JN133310, JN133385,

Appendix 1. Continued.

JN133414; *B. chingipengii*, C.-I Peng P23368 (HAST), KR186455, KR186542, KR186716; *B. chlorolepis*, A. JaraMuñoz 2327 (COL), MH207101, MH207511, MH207927; *B. chloroneura*, L.L. Forrest 128 (E), JF756394, JF756478, JF756562; *B. chloroneura*, P. Wilkie & al. 29015 (E), KR186456, KR186543, KR186717; *B. chlorosticta*, L.L. Forrest 41 (E), JF756402, JF756486, JF756570; *B. chrysantha*, M. Tebbitt 748 (USZ), MH207102, MH207512, MH207928; *B. cinnabarina*, M. Tebbitt 705 (USZ), MH207103, MH207513, MH207929; *B. cinnabarina*, M. Tebbitt 745 (USZ), MH207104, MH207514, MH207930; *B. clarkei*, M. Tebbitt & A. Daza 798 (E), –, MH207515, –, *B. clarkei*, M. Tebbitt & A. Daza 802 (E), MH207105, MH207516, –, *B. clarkei*, M. Tebbitt & A. Daza 804 (E), MH207106, MH207517, MH207931; *B. clarkei*, M. Tebbitt & A. Daza 806 (E), MH207107, MH207518, MH207932; *B. clarkei*, M. Tebbitt & A. Daza 811 (E), MH207108, MH207519, MH207933; *B. clarkei*, M. Tebbitt & A. Daza 815 (E), MH207109, MH207520, MH207934; *B. clarkei*, M. Tebbitt & A. Daza 818 (E), MH207110, MH207521, MH207935; *B. clarkei*, M. Tebbitt & A. Daza 819 (E), MH207111, MH207522, MH207936; *B. clarkei*, M. Tebbitt 824 (E), KX756293, KX756304, MH207937; *B. clarkei*, M. Tebbitt 738 (USZ), –, MH207524, –, *B. cleopatrae*, RBGE - Philippine National Herbarium Expedition 1998-25416 (E), JF756390, JF756474, JF756558; *B. cleopatrae*, P. Wilkie & al. 25373 (E), KR186457, KR186544, KR186718; *B. coccinea*, Glasgow B.G. 001-119-85, KP712929, KP713137, KP713275; *B. colombiana*, D.C. 43980 (COL), MH207113, MH207525, MH207938; *B. comestibilis*, D.C. Thomas & W.H. Ardi 09-62 (E), JN133311, JN133386, JN133415; *B. conchifolia*, M. Tebbitt 89 (BKL), KP713021, KP713083, KP713305; *B. aff. congesta*, D.C. Thomas 09-05 (E), JN133306, JN133381, JN133410; *B. aff. congesta*, D.C. Thomas 09-05 (E), JN133324, JN133399, JN133428; *B. consobrina*, Lyon B.G. 140666 (LBG), MH207114, MH207526, MH207939; *B. convallariodora*, B. Sénéchal CRBS/EB201117 (LBG), MH207115, MH207527, MH207940; *B. convolvulacea*, L.L. Forrest 168 E0020588 (E), KP712951, KP713146, KP713290; *B. copelandii*, R.R. Rubite R238 (PNH), KR186514, KR186601, KR186774; *B. copeyana*, B. Sénéchal CRBS/EB201139 (LBG), MH207116, MH207528, MH207941; *B. corallina*, Lyon B.G. 880164 (LBG), MH207117, –, *B. cornitepala*, B. Sénéchal 130507 (LBG), MH207118, MH207529, MH207942; *B. corredorana*, RBGE 20071055, MH207119, –, *B. corrugata*, D.C. Thomas 09-02 (E), JF756401, JF756485, JF756569; *B. coursii*, 20132227 (E), MH207120, MH207530, MH207943; *B. crassicaulis*, M. Tebbitt 84 (BKL), KP713022, KP713084, KP713300; *B. crassipes*, Faden 86/67 C.-I Peng 20867 (HAST), KP712967, KP713180, –, *B. cremnophila*, M. Tebbitt 753 (USZ), KX756282, KX756309, MH207944; *B. croatii*, D. Gould 100344 (LBG), MH207122, MH207532, MH207945; *B. cubensis*, M. Tebbitt 66 (BKL), KP713049, KP713170, KP713283; *B. cucphuongensis*, C.I Peng 20227 (HAST), MH207123, MH207533, MH207946; *B. cucphuongensis*, CK040 (KUN), MH207124, MH207534, MH207947; *B. cucullata*, J. P. Grieneray 110707 (LBG), MH207125, MH207535, MH207948; *B. culasiensis*, R.R. Rubite R234 (PNH), KR186459, KR186546, KR186719; *B. culasiensis*, C.-I Peng P23793 (HAST), KR186458, KR186545, no data; *B. curtii*, S. Follin 70392 (LBG), MH207126, MH207536, MH207949; *B. cyanescens*, S06 (SBG), MH207127, MH207537, MH207950; *B. cyathophora*, no voucher, KP713075, KP713171, KP713255; *B. decora*, S. Neale 8C (E), JF756355, JF756439, JF756523; *B. demissa*, T. Phutthai 221 (E), JF756384, JF756468, JF756552; *B. dentatiloba*, M. Tebbitt 126 (BKL), KP712983, KP713218, KP713299; *B. descoleana*, Lyon B.G. 120349 (LBG), MH207128, MH207538, MH207951; *B. diadema*, D. Permingeat 50584 (LBG), MH207129, MH207539, MH207952; *B. dichotoma*, Glasgow B.G. 03714766 (E), MH207130, MH207540, MH207953; *B. dichotoma*, Goldsmith U163 (E), MH207131, MH207541, MH207954; *B. dichotoma*, Glasgow B.G. 037-147-66 (E), KP713056, KP713177, KP713283; *B. dichroa*, Glasgow B.G. 001-096-95, KP712931, KP713192, KP713343; *B. didyma*, D.C. Thomas 08-77 (E), KP712936, KP713129, KP713226; *B. dietrichiana*, M. Tebbitt 147 (BKL), KP712976, KP713191, KP713271; *B. dioica*, Chien-I Huang 13651 (E), MH207132, MH207542, MH207955; *B. dipetala*, D.C. Thomas 100468 (E), JF756341, JF756425, JF756509; *B. dipetala*, C.-I Peng P22520 (HAST), KR186460, KR186547, KR186720; *B. dolichocarpa*, P. Wilkie 1014 (E), MH207133, MH207543, MH207956; *B. doloiisii*, PH 115 (SBG), MH207134, –, MH207957; *B. domingensis*, Lyon B.G. 140495 (LBG), MH207135, MH207544, MH207958; *B. dominicalis*, Glasgow B.G. 008-139-69 (E), KP713052, KP713169, KP713267; *B. dregei*, T. McLellan 415 (E), JF756338, JF756422, JF756506; *B. dregei*, T. McLellan 212 E00198090 (E), KP713014, KP713174, KP713309; *B. dregei*, C.-I Peng P20868 (HAST), KR186461, KR186548, KR186721; *B. dregei*, No voucher (AS balcony), MH235380, MH235408, MH235418; *B. droopiae*, C.P. Puglisi 123 (E), MH207136, MH207545, MH207959; *B. dux*, C.I Peng 23656 (HAST), MH207137, MH207546, MH207960; *B. echinosepala*, M. Tebbitt, Swensen & Yeadon 5 (BKL), KP712944, KP713220, KP713278; *B. edmundoi*, L.L. Forrest 196 (E), KP712994, KP713216, KP713261; *B. egregia*, L.L. Forrest 173 E00205197 (E), KP712969, KP713153, –, *B. elachista*, Moonlight 318 (E), KX756285, KX756324, MH207961; *B. elachista*, Moonlight 318 (E), KX756297, KX756324, MH207962; *B. elaeagnifolia*, Glasgow B.G. 010-079-97 (E), –, MH207549, MH207963; *B. elisabethae*, T. Phutthai 239 (E), JF756381, JF756465, JF756549; *B. aff. elisabethae*, D.C. Thomas 08-149 (E), KP712937, KP713123, KP713240, KP713240; *B. elmeri*, R.R. Rubite R319 (PNH), KR186462, KR186549, KR186722; *B. eminii*, C.-I Peng 22515 (HAST), KP712962, KP713193, KP713311; *B. engleri*, no voucher, KP713312, KP713313, KP713342; *B. epipsila*, C.-I Peng 21292 (HAST), KP712946, KP713187, KP713318; *B. erythrogyna*, S. Follin 90517 (LBG), MH207140, MH207550, MH207964; *B. aff. erythrogyna*, F. Lens 002 (SBG), MH207028, MH207439, MH207856; *B. exigua*, F.F. Pezzini 146 (E), MH207141, MH207551, MH207965; *B. exigua*, P.H. Alves de Melo 4993 (HRCB), MH207142, MH207552, MH207966; *B. fagifolia*, Glasgow B.G. 010-075-71 (E), KP712954, KP713142, KP713293; *B. faustinoi*, L.L. Forrest 187 (E), KP713008, KP713088, KP713228; *B. fenicis*, D.C. Thomas 08-119 (E), JF756392, JF756476, JF756560; *B. fenicis*, C.-I Peng P10794 (HAST), KR186464, KR186551, KR186724; *B. fenicis*, NK 11979 (HAST), KR186465, KR186552, KR186725; *B. ferruginea*, A. JaraMuñoz 2739 (COL), MH207143, MH207553, MH207967; *B. fischeri*, D.C. 41113 (COL), MH207146, MH207557, MH207971; *B. fischeri*, A. JaraMuñoz 2560 (COL), MH207144, MH207555, MH207969; *B. fischeri*, P.W. Moonlight & A. Daza 74 (E), –, MH207554, MH207968; *B. fischeri*, P.W. Moonlight & A. Daza 124 (E), MH207145, MH207556, MH207970; *B. fissyistyla*, L.L. Forrest 157 E00205201 (E), KP713051, KP713173, KP713250; *B. fissyistyla*, Tebbitt, Swensen & Yeadon 8 (BKL), MH235391, MH235415, MH235423; *B. cf. fissyistyla*, Lyon B.G. 890537 (LBG), MH207092, MH207502, MH207918; *B. flacca*, D.C. Thomas & W.H. Ardi 09-133 (E), JN133312, JN133387, JN133416; *B. flagellaris*, Chien-I Huang 6010 (E), MH207147, MH207558, MH207972; *B. flagellaris*, Chien-I Huang 6010 (E), MH207148, MH207559, MH207973; *B. flagellaris*, S. Rajbhandary & S. Bista S33 (E), JF756353, JF756437, JF756521; *B. floccifera*, L.L. Forrest 238 (E), JF756343, JF756427, JF756511; *B. fluminensis*, C.-I Peng 22328 (HAST), KP712939, KP713221, KP713314; *B. fluvialis*, M. Hughes 1489 (E), MH207150, MH207561, MH207975; *B. foliosa*, Unknown s.n. E19480286 (E), KP713060, KP713176, KP713310; *B. forbesii*, C.-I Peng P22685 (HAST), KR186467, KR186554, KR186727; *B. foxworthyi*, C.-I Peng P22721 (HAST), KR186468, KR186555, KR186728; *B. friburgensis*, Lyon B.G. 31318 (LBG), MH207151, MH207562, MH207976; *B. froebelii*, M. Tebbitt 786 (QCA), KX756288, KX756305, MH207977; *B. fruticosa*, Lyon B.G. 070728 (LBG), MH207153, MH207564, MH207978; *B. fruticosa*, F. Pauz 20532 (LBG), –, MH207565, –, *B. fulvovetulosula*, B. Sénéchal 70728 (LBG), KX756279, KX756331, –, *B. furfuracea*, B. Sénéchal 31610 (LBG), MH207154, MH207566, MH207979; *B. aff. fusca*, A. Twyford 677 (E), MH207029, MH207440, MH207857; *B. fuscisetosa*, 20120800 (E), MH207155, –, MH207980; *B. gabaldonensis*, C.-I Peng P23356 (HAST), KR186469, KR186556, KR186729; *B. gabonensis*, L.L. Forrest 230 E00205158 (E), KP712985, KP713215, KP713321; *B. galeolepis*, Krieb s.n. (SBG), MH207156, –, MH207981; *B. gamolepis*, A. JaraMuñoz 2616 (COL), MH207157, MH207567, MH207981; *B. garagarana*, B. Sénéchal CRBS/EB201120 (LBG), MH207158, MH207568, MH207983; *B. gardneri*, D. Permingeat 50722 (LBG), MH207159, MH207569, MH207984; *B. gehrtii*, M. Tebbitt 85 (BKL), MH207160, MH207570, MH207985; *B. gehrtii*, C.-I Peng 21202 (HAST), KP712941, KP713222, KP713313; *B. geraniifolia*, M. Tebbitt & A. Daza 840 (E), MH207162, MH207572, MH207987; *B. geraniifolia*, P.W. Moonlight & A. Daza 116 (E), KX756283, KX756311, MH207988; *B. germaniana*, M. Tebbitt 709 (USZ), MH207164, MH207574, MH207989; *B. gesnerioides*, P.W. Moonlight & A. Daza 183 (E), –, MH207575, MH207990; *B. gesnerioides*, P.W. Moonlight & A. Daza 184 (E), –, MH207576, –, *B. gigabraceata*, C.I Peng 22174 (HAST), MH207165, MH207577, MH207991; *B. gitingensis*, R.R. Rubite R255 (PNH), KR186470, KR186557, KR186730; *B. glabra*, Z. Badcock 7 (E), MH207166, –, MH207992; *B. glabra*, s.n. (HAST), KP712943, KP713145, KP713291; *B. glabra*, P.W. Moonlight & A. Daza 38 (E), MH207168, MH207579, MH207994; *B. glabra*, P.W. Moonlight & A. Daza 26 (E), MH207169, –, MH207995; *B. glabra*, P.W. Moonlight & A. Daza 153 (E), MH207170, MH207580, MH207996; *B. glabra*, No voucher, MH235379, –, *B. glandulifera*, M. Gardner 6608 (E), KX756294, KX756328, MH207997; *B. goegoensis*, D.C. Thomas 08-107 (E), JF756376, JF756460, JF756544; *B. goudotii*, V. Plana 120 (E), JF756347, JF756431, JF756515; *B. gracilis*, Z. Badcock 9 (E), KP713004, KP713078, KP713260; *B. grandis*, D.C. Thomas 08-145 (E), JF756351, JF756435, JF756519; *B. griffithiana*, C.I Peng 20851 (HAST), MH207172, MH207582, MH207998; *B. grisea*, Lyon B.G. 11433 (LBG), MH207173, MH207583, MH207999;

Appendix 1. Continued.

B. guaduensis, C.-I Peng 22518 (HAST), KP713054, KP713178, KP713294; *B. cf. guaduensis*, DC 43489 (COL), MH207093, MH207503, MH207919; *B. gueritziana*, C.-I Peng P22311 (HAST), KR186471, KR186558, KR186731; *B. gueritziana*, C.-I Peng P22342 (HAST), KR186472, KR186559, KR186732; *B. aff. gueritziana*, P22344 (HAST), MH235385, MH235401, MH235426; *B. gutierrezii*, P. Blanc s.n. (E), KR186473, KR186560, KR186733; *B. guttapila*, D.C. Thomas 08-81 (E), JF756405, JF756489, JF756573; *B. hainanensis*, C.I Peng 19543 (HAST), MH207174, MH207584, MH208000; *B. hainanensis*, Y.M. Shui & al. B2011044 (KUN), MH207175, MH207585, MH208001; *B. handelii*, J. Durisseau 130285 (LBG), MH207176, MH207586, MH208002; *B. harauensis*, D.C. Thomas 09-134 (E), JN133330, JN133405, JN133434; *B. hatacoa*, D.C. Thomas 08-110 (E), JF756354, JF756438, JF756522; *B. hekensis*, D.C. Thomas & W.H. Ardi 08-43 (E), JN133313, JN133388, JN133417; *B. heliantha*, R.T. Pennington & A. Daza 1113 (E), –, MH207587, –, *B. henrilaportei*, J. Durisseau 060667 (LBG), MH207177, MH207588, MH208003; *B. heracleifolia*, A. Twyford 597 (E), MH207178, MH207589, MH208004; *B. cf. heracleifolia*, B. Sénéchal 50849 (LBG), MH207094, –, MH207920; *B. herbacea*, L.L. Forrest 153 E00205153 (E), KP713015, KP713202, MH208005; *B. hernandioides*, D.C. Thomas 08-118 (E), JF756393, JF756477, JF756561; *B. hernandioides*, C.-I Peng P21006 (HAST), KR186474, KR186561, KR186734; *B. hernandioides*, R.R. Rubite R106 (PNH), KR186475, KR186562, KR186735; *B. heydei*, P22624 (HAST), MH207180, MH207591, –, *B. heydei*, Lyon B.G. 140136 (LBG), MH207181, MH207592, –, *B. heydei*, C.-I Peng 22624 (HAST), KP713030, KP713114, –, *B. hirtella*, P.W. Moonlight & A. Daza 163 (E), MH207182, MH207593, MH208006; *B. hirtella*, P.W. Moonlight & A. Daza 286 (E), MH207183, MH207594, MH208007; *B. hispida* var. *cucullifera*, M. Tebbitt 122 (BKL), KP713064, KP713159, KP713281; *B. hispidissima*, Kinho & A.D. Poulson 168 (E), JN133314, JN133389, JN133418; *B. hitchcockii*, A. JaraMuñoz 2758 (COL), KX756291, KX756313, MH208008; *B. hitchcockii*, EQJD04 (LBG), KX756292, KX756316, MH208009; *B. hitchcockii*, P.W. Moonlight & A. Daza 123 (E), KX756290, KX756315, MH208010; *B. hitchcockii*, P.W. Moonlight & A. Daza 151 (E), MH207187, MH207598, MH208011; *B. hoehneana*, 20131494 (E), MH207188, MH207599, MH208012; *B. holtonis*, Forrest 152 (E), KP713062, KP713175, MH208013; *B. holtonis*, Glasgow B.G. 01112984 (E), MH207190, MH207601, MH208014; *B. holtonis*, A. JaraMuñoz 2382 (COL), MH207191, MH207603, MH208015; *B. holtumii*, J. Durisseau 100498 (LBG), MH207193, MH207602, MH208017; *B. holtumii*, C.I Peng 22736 (HAST), MH207192, –, MH208016; *B. hookeriana*, Lyon B.G. 880089 (LBG), MH207194, MH207604, MH208018; *B. hugelii*, B. Sénéchal 20121 (LBG), MH207195, MH207605, MH208019; *B. hugesii*, C.-I Peng P23466 (HAST), KR186476, KR186563, KR186736; *B. hugesii*, C.-I Peng P23475 (HAST), KR186477, KR186564, KR186737; *B. humbertii*, 20132230 (E), MH207196, –, MH208020; *B. humilis*, D. Scherberich 1077 (LBG), –, MH207606, MH208021; *B. hydrocotylifolia*, M. Tebbitt 86 (BKL), KP713039, KP713085, KP713246; *B. hymenophylla*, T. Phutthai 232 (E), JF756382, JF756466, JF756550; *B. ignorata*, C.-I Peng P22725 (HAST), KR186478, KR186565, KR186738; *B. imbricata*, F. Lens 075 (SBG), MH207197, MH207607, MH208022; *B. imperialis*, Caen 8979 (E), MH207198, MH207608, MH208023; *B. imperialis*, Glasgow B.G. 0028979 (E), MH207199, MH207609, –, *B. incarnata*, A. Twyford 587 (E), KP713065, KP713090, KP713232; *B. inobangensis*, F. Lens 062 (SBG), MH207200, MH207610, MH208024; *B. inostegia*, F. Lens 021 (SBG), MH207201, MH207611, MH208025; *B. insularis*, M. Peixoto 041658 (LBG), MH207202, MH207612, MH208026; *B. integerrima*, M. Tebbitt 69 (BKL), KP713000, KP713099, KP713242; *B. involucrata*, Tebbitt, Swensen & Yeadon 23 (BKL), KP712995, KP713082, KP713332; *B. involucrata*, 20070426 (E), MH207204, MH207614, MH208028; *B. isoptera*, SUBOE 74 (E), MH207205, MH207615, MH208029; *B. itaguassuensis*, Lyon B.G. 10570 (LBG), MH207206, MH207616, MH208030; *B. itatiensis*, Lyon B.G. 140316 (LBG), MH207207, MH207617, MH208031; *B. jaguarensis*, Lyon B.G. 120352 (LBG), MH207208, MH207618, MH208032; *B. jambilhana*, NHZ14 (SBG), MH207209, MH207619, MH208033; *B. jocellinoi*, C.-I Peng 23331 (HAST), KP712982, KP713143, KP713315; *B. joffrei*, S15 (SBG), MH207210, MH207620, MH208034; *B. johnstonii*, no voucher, KP712996, KP713134, KP713339; *B. juliana*, M. Tebbitt 132 (BKL), KP712950, KP713158, KP713285; *B. karangputihensis*, C. Puglisi & al. 53 (E), MH207211, –, *B. karwinskyana*, RM-04-16/P20880 (HAST), KP713037, KP713086, KP713316; *B. kemumuensis*, D. Girmansyah & M. Hughes 1499 (E), MH207212, MH207621, MH208035; *B. kingiana*, D.C. Thomas 08-102 (E), JF756374, JF756458, JF756542; *B. kingiana*, C.-I Peng P21226 (HAST), KR186479, KR186566, KR186739; *B. kisuluana*, Forrest 215 (E), MH207213, MH207622, MH208036; *B. kisuluana*, Lyon B.G. 120318 (LBG), –, MH207623, MH208037; *B. kl-emmaei*, R.R. Rubite R182 (PNH), KR186480, KR186567, KR186740; *B. koksunii*, J. Durisseau 140138 (LBG), MH207214, MH207624, MH208038; *B. komoensis*, Tchimbélé 01/2012 (LBG), MH207215, MH207625, MH208039; *B. komoensis*, Tchimbélé 01/2012 (LBG), –, MH207626, MH208040; *B. koordersii*, D.C. Thomas & W.H. Ardi 08-62 (E), JF756407, JF756491, JF756575; *B. krystofii*, M. Tebbitt 701 (USZ), MH207216, MH207627, MH208041; *B. kudoensis*, C.P. Puglisi 67 (E), MH207217, MH207628, MH208042; *B. kuhlmannii*, Glasgow B.G. 00402907 (E), KP712942, KP713157, KP713272; *B. labiennis*, NHZ24 (SBG), MH207219, MH207630, –, *B. lanceolata*, Tebbitt MBG02 (E), KP713068, KP713101, KP713253; *B. lanceolata*, B. Sénéchal 20374 (LBG), KX756289, KX756332, MH208045; *B. laruei*, D.C. Thomas 08-138 (E), JF756403, JF756487, JF756571; *B. laruei*, Puglisi et al. CP225 (E), –, MH235412, MH235417; *B. lasioura*, D.C. Thomas & W.H. Ardi 09-110 (E), JN133315, JN133390, JN133419; *B. leprosa*, Permingeat, D. 274 (LBG), –, MH235433; *B. letouzeyi*, J. Durisseau 110677 (LBG), MH207222, –, MH208046; *B. limprichtii*, J. Durisseau 60823 (LBG), MH207223, MH207633, MH208047; *B. lindleyana*, 20051412 (E), MH207224, MH207634, MH208048; *B. listada*, C.-I Peng 21053 (HAST), KP712980, KP713155, KP713296; *B. lithophila*, Y.M. Shui & al. B2012064 (KUN), MH207225, MH207635, MH208049; *B. longifolia*, Neale 11C (E), JF756368, JF756452, JF756536; *B. longipetiolata*, C.-I Peng 22519 (HAST), KP712970, KP713181, –, *B. longiscapa*, R.R. Rubite R298 (PNH), KR186482, KR186569, KR186742; *B. longiscapa*, R.R. Rubite R309 (PNH), KR186483, KR186570, KR186743; *B. lophoptera*, M. Tebbitt & A. Daza 807 (E), MH207226, MH207636, –, *B. lophoptera*, P.W. Moonlight & A. Daza 231 (E), MH207227, MH207637, MH208050; *B. loranthoides* subsp. *loranthoides*, E00205240 (E), KP713029, KP713213, –, *B. lubbersii*, L.L. Forrest 194 (E), KP712981, KP713100, KP713237; *B. ludicra*, P22052/RM08 (HAST), KP713009, KP713092, –, *B. ludicra*, A. Twyford 680 (E), MH207229, MH207639, MH208051; *B. ludicra*, A. Twyford 687 (E), MH207230, MH207640, MH208052; *B. ludwigii*, P.W. Moonlight & A. Daza 96 (E), MH207231, MH207641, –, *B. ludwigii*, M. Tebbitt 780 (QCA), MH207232, MH207642, –, *B. ludwigii*, M. Tebbitt 791 (QCA), –, MH207643, –, *B. lugonis*, Lyon B.G. 150110 (LBG), MH207233, MH207644, MH208053; *B. lunaris*, Lyon B.G. 140256 (LBG), MH207234, –, MH208054; *B. lutea*, JaraMuñoz AMB 332 (COL), KX756287, KX756320, –, *B. luxurians*, M. Tebbitt 158 (BKL), KP712940, KP713223, KP713288; *B. luzonensis*, C.-I Peng P22344 (HAST), KR186446, KR186533, KR186707; *B. luzonensis*, R.R. Rubite R316 (PNH), KR186484, KR186571, KR186744; *B. luzonensis*, R.R. Rubite R420 (PNH), KR186485, KR186572, KR186745; *B. lyallii f. lyallii*, J. Durisseau 130264 (LBG), MH207236, –, MH208055; *B. lyallii f. masoalensis*, 20132228 (E), MH207237, –, MH208056; *B. lyman-smithii*, M. Tebbitt 116 (BKL), –, MH207646, MH208057; *B. lynciorum*, RM04-01 (HAST), KP713041, KP713197, –, *B. macduffieana*, Glasgow B.G. 002-004-86, KP712928, KP713210, KP713276; *B. macintyreana*, D.C. Thomas 07-28 (E), JN133316, JN133391, JN133420; *B. macrocarpa*, Lyon B.G. 100726 (LBG), –, MH207647, MH208058; *B. maculata*, Glasgow B.G. 008-151-95, KP712930, KP713206, KP713274; *B. madecassa*, 20132231 (E), MH207238, MH207648, MH208059; *B. madecassa*, C.-I Peng 22318 (HAST), KP712973, KP713179, –, *B. majungaensis*, 20132228 (E), MH207239, –, MH208060; *B. malabarica*, L.L. Forrest 288 (E), JF756342, JF756426, JF756510; *B. mamutensis*, F. Lens 029 (SBG), MH207240, MH207649, MH208061; *B. manicata*, A. Twyford 590 (E), MH207241, MH207650, MH208062; *B. manicata*, Z. Badcock 8 (E), KP712989, KP713131, KP713259; *B. manillensis*, R.R. Rubite R256 (PNH), KR186486, KR186573, KR186746; *B. mariannensis*, J. Durisseau 80396 (LBG), KX756299, KX756329, –, *B. mariti*, RM-08-352 (HAST), KP713035, KP713113, –, *B. martabanica*, Peng 24184 (HAST), –, MH244437, MH244440; *B. masaragensis*, D.C. Thomas 09-131 (E), JF756409, JF756493, JF756577; *B. masoniana*, L.L. Forrest s.n. (E), JF756372, JF756456, JF756540; *B. masoniana*, C.-I Peng P21411 (HAST), KR186487, KR186574, KR186747; *B. maynensis*, P.W. Moonlight & A. Daza 134 (E), MH207242, MH207651, –, *B. maynensis*, P.W. Moonlight & A. Daza 185 (E), MH207243, MH207654, MH208064; *B. maynensis*, Lyon B.G. 1050058 (LBG), MH207244, MH207655, MH208065; *B. maynensis*, P.W. Moonlight & A. Daza 162 (E), –, MH207652, MH208063; *B. maynensis*, P.W. Moonlight & A. Daza 176 (E), –, MH207653, –, *B. maynensis*, C.-I Peng s.n. (HAST), KP713063, KP713141, –, *B. mazaе*, Hollands 008 E00668725 (E), KP713002, KP713116, KP713238; *B. aff. mekongensis*, D.C. Thomas & W.H. Ardi 09-108 (E), JN133308, JN133383, JN133412; *B. mendumae*, D.C. Thomas 07-27 (E), JN133317, JN133392, JN133421; *B. meridensis*, A. JaraMuñoz 2730 (COL), –, MH207656, MH208066; *B. meridensis*, L.L. Forrest 181 E00205112 (E), KP713057, KP713132, KP713308; *B. meridensis*, Glasgow Botanic Garden 014-124-82, KP713057, KP713132, KP713308; *B. cf. meridensis*, A. JaraMuñoz 2342 (COL), MH207095, MH207504, MH207921;

Appendix 1. Continued.

B. merrilliana, C.-I Peng P23765 (HAST), KR186488, KR186575, KR186748; *B. mexicana*, J. Duruisseau 140145 (LBG), MH207245, –, MH208067; *B. meyerijohannis*, S. Barber & al. 38 (E), MH207246, MH207657, MH208068; *B. micranthera*, M. Tebbitt 702 (USZ), MH207247, MH207658, MH208069; *B. micranthera*, T. Sarkinen 2029 (E), KP713032, KP713204, –, *B. micranthera*, T. Sarkinen 2043 (E), KP713066, KP713198, –, *B. micranthera*, T. Sarkinen 2144 (E), KP713071, KP713199, –, *B. microsperma*, C.-I Peng s.n. (HAST), KP713010, KP713194, KP713325; *B. mindorensis*, R.R. Rubite R326 (PNH), KR186489, KR186576, KR186749; *B. mindorensis*, C.-I Peng P23456 (HAST), KR186490, KR186577, KR186750; *B. minor*, M. Tebbitt 74 (BKL), KP713053, KP713167, KP713265; *B. minutifolia*, J. Duruisseau 66060 (LBG), –, MH207659, –, *B. molleri*, D. Permingeat 327 (LBG), –, –, MH208070; *B. mollicaulis*, Glasgow B.G. 014-254-99 (E), KP713044, KP713212, KP713338; *B. monadelpha*, T. Sarkinen 2205 (E), KP713005, KP713117, MH208071; *B. monadelpha*, P.W. Moonlight & A. Daza 69 (E), MH207249, MH207661, MH208072; *B. monadelpha*, M. Tebbitt & A. Daza 833 (E), MH207250, MH207662, –, *B. monadelpha*, P.W. Moonlight & A. Daza 148 (E), MH207251, MH207663, MH208073; *B. morsei*, Unknown s.n. (E), JF756373, JF756457, JF756541; *B. motzintlensis*, A. Twyford 337 (E), MH207252, MH207664, MH208074; *B. moyesii*, Lyon B.G. 110675 (LBG), MH207253, MH207665, MH208075; *B. multangula*, D.C. Thomas & W.H. Ardi 08-90 (E), JF756364, JF756448, JF756532; *B. aff. multangula*, D.C. Thomas 09-85 (E), KP712963, KP713125, KP713239; *B. multijugata*, P. Wilkie 768 (E), JF756404, JF756488, JF756572; *B. multinervia*, M. Tebbitt 131 (BKL), KP713023, KP713163, KP713258; *B. multistaminea*, RBGE 20071056, MH207254, MH207666, MH208076; *B. muricata*, W.H. Ardi & D.C. Thomas W127 (E), JF756378, JF756462, JF756546; *B. murina*, C.I Peng 24137 (HAST), MH207255, MH207667, MH208077; *B. nana*, Lyon B.G. 140495 (LBG), MH207256, MH207668, –, *B. negrosensis*, P. Wilkie 76 (E), JF756411, JF756495, JF756579; *B. nelumbifolia*, R. Hollands 009 (E), KP713040, KP713077, KP713230; *B. nelumbifolia*, TNY19 (HAST), MH235378, MH235398, MH235421; *B. nelumbiifolia*, C.-I Peng P20879 (HAST), KR186491, KR186578, KR186751; *B. nepalensis*, B. Sénéchal 41155 (LBG), –, –, MH208078; *B. nepalensis*, C.I Peng 20854 (HAST), MH207257, MH207669, MH208079; *B. nigritarum*, R.R. Rubite R419 (PNH), KR186492, KR186579, KR186752; *B. nigritarum*, R.R. Rubite R406 (PNH), KR186493, KR186580, KR186753; *B. nigritarum*, C.-I Peng P23855 (HAST), KR186494, KR186581, KR186754; *B. nigritarum*, C.-I Peng P23373 (HAST), KR186495, KR186582, KR186755; *B. nigritarum*, C.-I Peng P23451 (HAST), KR186496, KR186583, KR186756; *B. nigritarum*, C.-I Peng P23372 (HAST), KR186497, KR186584, KR186757; *B. nigritarum*, C.-I Peng P23586 (HAST), KR186498, KR186585, KR186758; *B. nigritarum*, C.-I Peng P23858 (HAST), KR186499, KR186586, KR186759; *B. ningmingensis*, C.-I Peng P20322 (HAST), KR186500, KR186587, KR186760; *B. nitida*, Lyon B.G. 920013 (LBG), MH207258, MH207670, –, *B. nobmanniae*, D.C. Thomas 09-123 (E), JN133318, JN133393, JN133422; *B. nossibia*, 110200080 (HAST), KP712974, KP713183, –, *B. nosyanganensis*, J. Duruisseau & B. Senecal s.n. (LBG), MH235384, MH235413, MH235424; *B. nothobaramensis*, S08 (SBG), MH207259, MH207671, MH208080; *B. nurii*, C. Salamone 50627 (LBG), MH207260, MH207672, MH208081; *B. nurii*, FRI 824 (FRIM), MH207261, MH207673, MH208082; *B. oaxacana*, no voucher, KX756280, KX756325, –, *B. obliqua*, Lyon B.G. 80132 (LBG), MH207262, MH207674, MH208083; *B. oblongifolia*, F. Lens 028 (SBG), MH207263, MH207675, MH208084; *B. oblongifolia*, F. Lens 014 (SBG), MH207264, MH207676, MH208085; *B. obovoidea*, T. Phutthai 244 (E), JF756386, JF756470, JF756554; *B. obscura*, E20030603 (E), KP712945, KP713219, KP713282; *B. obtecticalis*, P.W. Moonlight & A. Daza 212 (E), MH207265, MH207677, MH208086; *B. obtusifolia*, C.-I Peng P23828 (HAST), KR186501, KR186588, KR186761; *B. octopetala*, P.W. Moonlight & A. Daza 67 (E), MH207266, MH207678, MH208087; *B. octopetala*, P.W. Moonlight & A. Daza 70 (E), MH207267, –, –, *B. octopetala*, M. Tebbitt 790 (QCA), MH207268, MH207679, MH208088; *B. octopetala*, M. Tebbitt & A. Daza 825 (E), MH207269, MH207680, –, *B. octopetala*, M. Tebbitt & A. Daza 842 (E), MH207270, MH207681, –, *B. octopetala*, M. Tebbitt & A. Daza 844 (E), MH207271, MH207682, MH208089; *B. octopetala*, P.W. Moonlight & A. Daza 208 (E), MH207272, –, MH208090; *B. odetiantha*, Glasgow B.G. 009-007-97 (E), KP712975, KP713190, KP713270; *B. odorata*, L.L. Forrest 158 E00205104 (E), KP713059, KP713168, KP713266; *B. olbia*, L.L. Forrest 185 E00205103 (E), KP712933, KP713186, KP713306; *B. olivacea*, C.P. Puglisi 239 (E), MH207273, MH207683, MH208091; *B. olsoniae*, J. Duruisseau 60665 (LBG), MH207274, MH207684, MH208092; *B. olsoniae*, M. Tebbitt, Swensen & Yeadon 18 (BKL), KP713001, KP713156, KP713297; *B. opuliflora*, Lyon B.G. 21735 (LBG), MH207275, MH207685, MH208093; *B. oxyanthera*, Glasgow B.G. 00411378 (E), MH207276, MH207686, MH208094; *B. oxyanthera*, Lyon B.G. 11285 (LBG), –, MH207687, –, *B. oxyloba*, L.L. Forrest 279 E00205102 (E), JF756335, JF756419, JF756503; *B. oxysperma*, R.R. Rubite R213 (PNH), KR186502, KR186589, KR186762; *B. oxysperma*, C.-I Peng P23015 (HAST), KR186503, KR186590, KR186763; *B. ozotothrix*, D.C. Thomas & W.H. Ardi 08-58 (E), JN133319, JN133394, JN133423; *B. pachypoda*, Glasgow B.G. 015-107-89, KP712926, –, KP713268; *B. palawanensis*, C.-I Peng P23453 (HAST), KR186504, KR186591, KR186764; *B. paleata*, M. Peixoto 90309 (LBG), MH207277, MH207688, MH208095; *B. palmata*, M. Moller 01-127 (E), JF756360, JF756444, JF756528; *B. papyraptera*, NZH08 (SBG), MH207278, MH207689, –, *B. paracauliflora*, C.I Peng 22309 (HAST), MH207279, MH207690, MH208096; *B. paranaensis*, M. Tebbitt, Swensen & Yeadon 25 (BKL), KP712947, KP713147, KP713298; *B. parcifolia*, M. Tebbitt 769 (QCA), MH207280, MH207691, MH208097; *B. parcifolia*, M. Tebbitt 779 (QCA), –, MH207692, MH208098; *B. parcifolia*, M. Tebbitt & A. Daza 845 (E), MH207281, MH207693, –, *B. parcifolia*, M. Tebbitt 783 (QCA), KX756277, KX756317, –, *B. parilis*, A. Mauriere 880035 (LBG), MH207282, MH207694, MH208099; *B. parviflora*, P.W. Moonlight & A. Daza 37 (E), MH207283, MH207695, MH208100; *B. parviflora*, P.W. Moonlight & A. Daza 155 (E), MH207284, MH207696, MH208101; *B. pasamanensis*, D. Girmansyah & M. Hughes 1506 (E), MH207285, MH207697, MH208102; *B. pavonina*, S. Neale 9C (E), JF756356, JF756440, JF756524; *B. pearcei*, Lyon B.G. 10128 (LBG), MH207286, MH207698, MH208103; *B. pectennervia*, A. Jara Muñoz 2621 (COL), MH207287, MH207699, MH208104; *B. pedatifida*, Lyon B.G. 21121 (LBG), MH207288, MH207700, MH208105; *B. pelata*, A. Mauriere 870118 (LBG), –, MH207701, –, *B. pelata*, 233332 (HAST), KP712988, KP713104, –, *B. pelata*, M. Tebbitt 153 (BKL), KP712992, KP713105, KP713235; *B. peltatifolia*, Y.M. Shui & al. Q031 (KUN), MH207289, MH207702, MH208106; *B. pendula*, DCT 09-03 (cult. SING), JF756395, JF756479, JF756563; *B. perakensis*, B. Sénéchal 110694 (LBG), MH207291, MH207704, MH208108; *B. perdusenii*, B. Sénéchal 130513 (LBG), MH207290, MH207703, MH208107; *B. peruviana*, P.W. Moonlight & A. Daza 173 (E), –, MH207705, –, *B. peruviana*, Moonlight 39 (E), –, –, MH208109; *B. peruviana*, M. Tebbitt & A. Daza 832 (E), –, MH207789, –, *B. petastifolia*, M. Tebbitt 83 (BKL), KP712935, KP713152, *B. phantasma*, M. Tebbitt 757 (USZ), MH207292, MH207706, MH208110; *B. phantasma*, M. Tebbitt 721 (USZ), MH207293, MH207707, MH208111; *B. picta*, Chien-I Huang 5993 (E), MH207294, MH207708, MH208112; *B. pilgeriana*, M. Peixoto 120314 (LBG), MH207295, MH207709, MH208113; *B. pinetorum*, Hollands 006 E00668796 (E), KP713067, KP713091, KP713312; *B. piurensis*, Moonlight & Daza (E), MH207296, MH207710, MH208114; *B. piurensis*, P.W. Moonlight & A. Daza 111 (E), KX756276, KX756318, –, *B. platanifolia*, Glasgow B.G. 00604504 (E), MH207297, MH207711, MH208115; *B. platanifolia*, Lyon B.G. 42262 (LBG), MH207298, MH207712, MH208116; *B. plebeja*, A. Twyford 606 (E), MH207299, MH207713, MH208117; *B. pleiopetala*, M. Tebbitt & A. Daza 813 (E), MH207300, MH207714, MH208118; *B. pleiopetala*, P.W. Moonlight & A. Daza 295 (E), MH207301, MH207715, –, *B. pleiopetala*, P.W. Moonlight & A. Daza 297 (E), MH207302, MH207716, MH208119; *B. plumieri*, Lyon B.G. 100703 (LBG), MH207303, MH207717, MH208120; *B. pluviialis*, Lyon B.G. 940319 (LBG), MH207304, MH207718, MH208121; *B. poculifera*, L.L. Forrest 234 (E), JF756348, JF756432, JF756516; *B. poilanei*, Tran Huu Dang s.n. (E), MH207305, MH207719, MH208122; *B. poliloensis*, L.L. Forrest 139 (E), JF756412, JF756496, JF756580; *B. polyandra*, Lyon B.G. 140319 (LBG), MH207306, MH207720, MH208123; *B. polygonata*, M. Tebbitt 139 (BKL), KP712987, KP713106, KP713234; *B. polygonata*, Glasgow B.G. 01712370 (E), MH207308, MH207722, MH208125; *B. polygonata*, Glasgow B.G. 01712370 (E), MH207309, MH207723, MH208126; *B. polygonoides*, van der Burg 244 (WAG), JF756336, JF756420, JF756504; *B. polypetala*, M. Tebbitt & A. Daza MT839b (E), MH207310, MH207724, –, *B. polypetala*, P.W. Moonlight & A. Daza 113 (E), MH207311, MH207725, MH208127; *B. polypetala*, P.W. Moonlight & A. Daza 119 (E), MH207312, MH207726, MH208128; *B. polypetala*, Tebbitt 787 (USZ), MH235388, MH235403, MH235429; *B. polypetala*, Tebbitt 828 (USZ), MH235389, MH235409, –, *B. popenoi*, E20110200, KP713020, KP713095, KP713302; *B. princeps*, D. Permingeat 21701 (LBG), MH207313, MH207727, MH208129; *B. pringlei*, Glasgow B.G. 01800283 (E), MH207314, MH207728, –, *B. pringlei*, M. Tebbitt 130 (BKL), KP713074, KP713119, KP713319; *B. prionota*, D.C. Thomas & W.H. Ardi 09-97 (E), JN133320, JN133395, JN133424; *B. pruniata*, Glasgow B.G. 04010383 (E), MH207315, MH207729, MH208130; *B. pseudodaedalea*, A. Twyford 1066 (E), MH207316, MH207730, MH208131; *B. pseudodryadis*, M. Moeller 121890 (E), MH207317, MH207731, –, *B. pseudolateralis*, D.C. Thomas & W.H. Ardi 08-23 (E), JF756408, JF756492, JF756576; *B. pseudolubbersii*, Glasgow B.G. 045-023-92 (E), KP713072, KP713203, KP713329;

Appendix 1. Continued.

B. pseudopleiopetala, M. Tebbitt & A. Daza 827 (E), MH207318, –, –; *B. pteridiformis*, Lyon B.G. s.n. (LBG), MH207319, MH207732, MH208132; *B. pulchella*, M. Peixoto 41666 (LBG), MH207320, MH207733, MH208133; *B. pululahuana*, A. JaraMuñoz 2659 (QCA), MH207321, MH207734, –, –; *B. pulvinifera*, J. Duruisseau 140148 (LBG), MH207322, MH207735, –, –; *B. purpusii*, M. Tebbitt 70 (BKL), KP713028, KP713087, KP713251; *B. puspitae*, C. Pugliesi & al. 134 (E), MH207323, MH207736, MH208134; *B. pustulata*, MBG 1999-01-01, KP712998, KP713093, KP713227; *B. puttii*, S. Suddee 3375 (E), KP712959, KP713201, KP713326; *B. quadrialata*, Lyon B.G. 80424 (LBG), –, –, MH207737, MH208135; *B. rabillii*, S. Suddee 3371 (E), KP712968, KP713164, KP713328; *B. racemosa*, D. Girmansyah & M. Hughes 1509 (E), MH207324, MH207738, MH208136; *B. racemosa*, D. Girmansyah & M. Hughes 1509 (E), MH207325, –, –; *B. rachmatii*, Krieb s.n. (SBG), MH207326, MH207739, MH208137; *B. radicans*, Glasgow B.G. 009-089-95 (E), JF756345, JF756429, JF756513; *B. radicans*, Glasgow B.G. 009-089-95 (E), JF756345, JF756429, JF756513; *B. rajah*, Girmansyah & al. DEDEN1497 (E), –, –, MH207740, MH208138; *B. rajah*, Lyon B.G. 880168 (LBG), MH207327, MH207741, MH208139; *B. rajah*, FRIM 47082 (FRIM), MH207328, MH207742, MH208140; *B. rantemariensis*, Krieb s.n. (SBG), MH207329, MH207743, MH208141; *B. rantemarioensis*, D.C. Thomas & W.H. Ardi 09-78 (E), JN133321, JN133396, JN133425; *B. reginula*, FRIM 82471 (FRIM), MH207330, MH207744, MH208142; *B. reniformis*, Suksuwan 26 E00198096 (E), KP712952, KP713149, KP713292; *B. rhoephila*, J. Duruisseau 130617 (LBG), MH207331, MH207745, MH208143; *B. rigida*, Lyon B.G. 22147 (LBG), MH207332, MH207746, MH208144; *B. robusta*, D.C. Thomas & W.H. Ardi 08-133 (E), JF756363, JF756447, JF756531; *B. rossmanniae*, P. W. Moonlight & A. Daza 315 (E), KX756302, MH207747, MH208145; *B. rossmanniae*, D. Scherberich 1095 (LBG), KX756300, KX756330, MH208146; *B. rotundifolia*, Lyon B.G. 10553 (LBG), MH207335, –, –, MH208147; *B. roxburghii*, D.C. Thomas 08-103 (E), JF756371, JF756455, JF756539; *B. rubella*, Chien-I Huang 6000 (E), MH207336, MH207749, MH208148; *B. rubida*, S. Follin 110183 (LBG), MH207337, MH207750, MH208149; *B. rubitea*, R.R. Rubite R356 (PNH), KR186505, KR186592, KR186765; *B. rubriflora*, M. Peixoto 41645 (LBG), MH207338, –, –, MH208150; *B. rufa*, Lyon B.G. 140648 (LBG), MH207339, MH207751, MH208151; *B. rufipila*, R.R. Rubite R265 (PNH), KR186506, KR186593, KR186766; *B. rufoserica*, M. Peixoto s.n. (LBG), MH207340, MH207752, MH208152; *B. sageensis*, Krieb s.n. (SBG), MH207341, MH207753, MH208153; *B. salaziensis*, Lyon B.G. 100629 (E), MH207342, MH207754, MH208154; *B. salesopolensis*, Lyon B.G. 140322 (LBG), –, –, MH207755, –, –; *B. salicifolia*, Lyon B.G. 910693 (LBG), MH207343, MH207756, –, –; *B. samhaensis*, D.C. Thomas 09-01 (E), JF756339, JF756423, JF756507; *B. sanguinea*, C.-I Peng 21284 (HAST), KP712978, KP713188, KP713317; *B. sanguineopilosa*, D.C. Thomas & W.H. Ardi 09-125 (E), JN133322, JN133397, JN133426; *B. santos-limae*, C.-I Peng 21320 (HAST), KP713016, KP713126, –, –; *B. sarcophylla*, M. Tebbitt 153 (BKL), KP712986, KP713079, KP713236; *B. sartorii*, M. Tebbitt 153 (BKL), MH207344, MH207757, –, –; *B. sartorii*, A. Twyford 448 (E), MH207345, MH207758, MH208156; *B. scabrida*, Brown, K. 21551 (LBG), –, –, –; *B. scharffiana*, De Lacheisserie 890443 (LBG), MH207346, MH207759, MH208157; *B. scharffii*, M. Tebbitt 124 (BKL), KP712961, KP713224, KP713286; *B. schmidtiana*, E20080890 (E), KP713058, KP713120, KP713264; *B. sciaphila*, J. Duruisseau 120357 (LBG), –, –, MH207760, MH208158; *B. scottii*, M. Hughes 1569 (E), MH207347, MH207761, MH208159; *B. scottii*, C. Pugliesi & al. 217 (E), MH207348, MH207762, MH208160; *B. scutifolia*, J. Duruisseau 60659 (LBG), –, –, MH207763, MH208161; *B. scutifolia*, C.I Peng 23324 (HAST), MH207349, MH207764, MH208162; *B. sect. Gobenia*, No voucher, MH235377, –, –, –; *B. seemanniana*, no voucher, MH207350, MH207765, MH208163; *B. segregata*, Duruisseau 140144 (LBG), KX756281, KX756314, –, –; *B. semidigitata*, Lyon B.G. 140324 (LBG), MH207351, MH207766, MH208164; *B. semiovata*, P.W. Moonlight & A. Daza 172 (E), MH207352, MH207767, –, –; *B. semiovata*, P.W. Moonlight & A. Daza 127 (E), MH207353, MH207768, MH208165; *B. sericoneura*, RBGE 20071052, MH207354, MH207769, MH208166; *B. sericoneura*, A. Twyford 854 (E), MH207355, MH207770, MH208167; *B. sericoneura*, A. Twyford 1110 (E), MH207356, MH207771, MH208168; *B. sericoneura*, M. Tebbitt 133 (BKL), KP713012, KP713089, KP713303; *B. serotina*, M. Tebbitt 773 (QCA), MH207357, MH207772, MH208169; *B. serotina*, M. Tebbitt 776 (QCA), KX756284, KX756319, MH208170; *B. serratifolia*, Woods, P.J.B. 1916 (E), JF756413, JF756497, JF756581; *B. sibthorpoides*, Tan PC 82520 (FRIM), MH207359, MH207774, MH208171; *B. sibthorpoides*, Mo. Hairul FRI 60095 (FRIM), MH207360, MH207775, MH208172; *B. sibiricus*, S11 (SBG), MH207361, –, –, MH208173; *B. siccacaudata*, D.C. Thomas 09-60 (E), JF756418, JF756502, JF756586; *B. sikkimensis*, D.C. Thomas 08-144 (E), JF756359, JF756443, JF756527; *B. silletensis*, D.C. Thomas 08-104 (E), JF756370, JF756454, JF756538; *B. silvertonii*, A. JaraMuñoz 2383 (COL), MH207362, MH207776, MH208174; *B. simolapensis*, C. Pugliesi & al. 228 (E), –, –, MH207777, MH208175; *B. sinofloribunda*, Y.M. Shui & al. B2003009 (KUN), MH207363, MH207778, MH208176; *B. sizemoreae*, D.C. Thomas 08-111 (E), JF756361, JF756445, JF756529; *B. smilacina*, Cazaux, A. 0140454R (LBG), MH207364, MH207779, –, –; *B. smithiae*, Chamchamroon 3662 (E), JF756389, JF756473, JF756557; *B. socotrana*, T. Miller 19210/10 (E), JF756340, JF756508; *B. solananthera*, Glasgow B.G. 021-070-04 (E), KP712999, KP713098, KP713243; *B. solaniflora*, A. JaraMuñoz 2564 (COL), MH207365, MH207780, MH208177; *B. solimutata*, E20110208 (E), KP713042, KP713207, KP713337; *B. sousae*, A. Twyford 20 (E), MH207366, MH207781, MH208178; *B. sp. nov. sect. Baryandra*, C.-I Peng P23859 (HAST), KR186444, KR186531, KR186705; *B. sp. nov. sect. Baryandra*, C.-I Peng P23508 (HAST), KR186463, KR186550, KR186723; *B. sp. nov. sect. Casparya*, A. JaraMuñoz 2732 (COL), MH207369, MH207783, –, –; *B. sp. nov. sect. Casparya*, A. JaraMuñoz 2740 (COL), MH207370, MH207784, MH208181; *B. sp. nov. sect. Casparya*, A. JaraMuñoz 2736 (COL), MH207371, MH207785, MH208182; *B. sp. nov. sect. Casparya*, A. JaraMuñoz 2754 (COL), MH207368, MH207782, MH208180; *B. sp. nov. sect. Casparya*, A. JaraMuñoz 2728 (COL), MH207367, –, –, MH208179; *B. sp. nov. sect. Cyathocnemis*, P.W. Moonlight & A. Daza 146 (E), MH207372, MH207786, MH208183; *B. sp. nov. sect. Cyathocnemis*, P.W. Moonlight & A. Daza 150 (E), MH207373, MH207787, –, –; *B. sp. nov. sect. Cyathocnemis*, P.W. Moonlight & A. Daza 144 (E), –, –, MH207790, –, –; *B. sp. nov. sect. Gobenia*, A. Jara-Muñoz 2622 (COL), –, –, MH207788, –, –; *B. sp. nov. sect. Knesebeckia group II*, P.W. Moonlight & A. Daza 159 (E), KX756301, KX756321, MH208193; *B. sp. nov. sect. Knesebeckia group II*, P.W. Moonlight & A. Daza 156 (E), KX756295, KX756322, MH208194; *B. sp. sect. Baryandra*, Kokubagata GK71 (HAST), KR186509, KR186596, KR186769; *B. sp. sect. Baryandra*, R.R. Rubite R136 (PNH), KR186510, KR186597, KR186770; *B. sp. sect. Baryandra*, R.R. Rubite R290 (PNH), KR186511, KR186598, KR186771; *B. sp. sect. Baryandra*, C.-I Peng P23452 (HAST), KR186512, KR186599, KR186772; *B. sp. sect. Baryandra*, C.-I Peng P23418 (HAST), KR186513, KR186600, KR186773; *B. sp. sect. Baryandra*, No voucher (AS balcony), MH235386, MH235402, MH235427; *B. sp. sect. Bracteibegonia*, D.C. Thomas & W.H. Ardi 08-132 (E), JN133328, JN133403, JN133432; *B. sp. sect. Cyathocnemis*, P.W. Moonlight & A. Daza 36 (E), MH207374, MH207791, MH208185; *B. sp. sect. Cyathocnemis*, P.W. Moonlight & A. Daza 95 (E), MH207375, –, –, MH208186; *B. sp. sect. Cyathocnemis*, P.W. Moonlight & A. Daza 86 (E), –, –, MH208184; *B. sp. sect. Cyathocnemis*, P.W. Moonlight & A. Daza 25 (E), MH235390, –, –, MH235430; *B. sp. sect. Diplocnium*, D.C. Thomas 08-145 (E), JF756352, JF756436, JF756520; *B. sp. sect. Diplocnium*, No voucher, MH235382, MH235416, MH235419; *B. sp. sect. Erminea*, Duruisseau, J. Senechal, B. LBG 100651, MH207376, MH207792, MH208187; *B. sp. sect. Gireoudia*, B. Sénéchal CRBS/EB201134 (LBG), MH207377, MH207793, MH208188; *B. sp. sect. Gireoudia*, Lyon B.G. 880193 (LBG), MH207378, MH207794, MH208189; *B. sp. sect. Gireoudia*, Glasgow B.G. 027-044-89 U195 (E), KP712993, KP713211, –, –; *B. sp. sect. Gobenia*, A. Jara-Muñoz 2620 (COL), –, –, MH207795, –, –; *B. sp. sect. Gobenia*, AJM 2623, –, –, MH235405, –, –; *B. sp. sect. Jackia*, D.C. Thomas 08-85 (E), JF756375, JF756459, JF756543; *B. sp. sect. Jackia*, MH1542 (E), MH235393, MH235399, MH235422; *B. sp. sect. Loasibegonia*, P20248 (HAST), –, –, MH235410, –, –; *B. sp. sect. Parvibegonia*, T. Phutthai 195 (E), JF756380, JF756464, JF756548; *B. sp. sect. Petermannia*, D.C. Thomas 08-135 (E), KP712934, KP713130, KP713336; *B. sp. sect. Petermannia*, DCT 07-1 (E), JN133323, JN133398, JN133427; *B. sp. sect. Petermannia*, DCT 08-146 (E), JN133327, JN133402, JN133431; *B. sp. sect. Petermannia*, DCT 09-136(E), JN133325, JN133400, JN133429; *B. sp. sect. Petermannia*, DCT 09-138 (E), JN133331, JN133406, JN133435; *B. sp. sect. Platycentrum*, L.L. Forrest 31 (E), JF756362, JF756446, JF756530; *B. sp. sect. Pritzelia*, Lyon B.G. 90450 (LBG), MH207379, MH207797, MH208190; *B. speculum*, P.W. Moonlight & A. Daza 158 (E), MH207380, MH207798, MH208191; *B. speluncae*, S. Follin 90457 (LBG), MH207381, MH207799, MH208192; *B. squamulosa*, C.-I Peng 21280 (HAST), KP712971, KP713182, –, –; *B. squarrosa*, RBGE 20071058, MH207384, MH207802, MH208195; *B. squarrosa*, J. Duruisseau 130620 (LBG), –, –, MH207803, –, –; *B. staudtii*, J. Duruisseau 120358 (LBG), –, –, MH207804, MH208196; *B. stenogyna*, S10 (SBG), MH207385, MH207805, MH208197; *B. stevei*, Scott, S. M. 04-315 (E), MH235381, MH235411, MH235420; *B. stictopoda*, M. Hughes 1409 (E), MH207387, MH207807, –, –; *B. stictopoda*, C. Pugliesi & al. 239 (E), MH207386, MH207806, MH208198; *B. stigmosa*, M. Tebbitt 134 (BKL), KP712997, KP713096, KP713331; *B. stigmosa*, Adolfo Jara AJM 2729, MH235387, MH235404, –, –; *B. aff. strigillosa*, A. Twyford 346 E00619702 (E), KP713027, KP713161, KP713333; *B. strigosa*, Glasgow B.G. 004-137-91 (E), JF756416, JF756500, JF756584; *B. suaveolens*,

Appendix 1. Continued.

Lyon B.G. 80425 (LBG), MH207388, MH207808, MH208199; **B. subacida**, *B. Sénéchal 120320* (LBG), MH207389, MH207809, MH208200; **B. subciliata**, *P.W. Moonlight & A. Daza 189* (E), MH207390, MH207810, MH208201; **B. subciliata**, *P.W. Moonlight & A. Daza 241* (E), MH207391, MH207811, MH208202; **B. sublobata**, *Girmansyah & al. DEDEN1486* (E), KR186515, KR186602, KR186775; **B. subnummarifolia**, no voucher, KR186516, KR186603, KR186776; **B. suborbiculata**, *R.R. Rubite R353* (PNH), KR186517, KR186604, KR186777; **B. subscutata**, *Glasgow B.G. 05307997* (E), MH207392, MH207812, MH208203; **B. subscutata**, *C.-I Peng s.n.* (HAST), KP712958, KP713208, –; **B. subspinulosa**, *M. Tebbitt & A. Daza 808* (E), MH207393, MH207813, MH208204; **B. subvillosa**, *C.-I Peng 21291* (HAST), KP713046, KP713122, KP713262; **B. subvillosa**, *Surin 25 E00198120* (E), KP713045, KP713121, KP713263; **B. sudjanae**, *D.C. Thomas 08-109* (E), JF756377, JF756461, JF756545; **B. susaniae**, *J. Duruisseau 060661* (LBG), –, MH207814, MH208205; **B. sutherlandii**, *D.C. Thomas 08-140* (E), JF756337, JF756421, JF756505; **B. sutherlandii**, *Jasper 1200-5* (HAST), KR186518, KR186605, KR186778; **B. sykakiengii**, *C.-I Peng P23856* (HAST), KR186519, KR186606, KR186779; **B. sykakiengii**, *C.-I Peng P23890* (HAST), KR186520, KR186607, KR186780; **B. sylvestris**, *Senechal LBG 130370*, MH235392, MH235400, MH235431; **B. symsanguinea**, *L.L. Forrest 199* (E), JF756415, JF756499, JF756583; **B. tagbanua**, *P. Blanc s.n.* (E), KR186521, KR186608, KR186781; **B. tagbanua**, *C.-I Peng P23472* (HAST), KR186522, KR186609, KR186782; **B. taraw**, *P. Blanc s.n. taraw 2* (E), KR186523, KR186610, KR186783; **B. taraw**, *P. Blanc s.n. taraw 1* (E), KR186524, KR186611, KR186784; **B. tayabensis**, *R.R. Rubite R360* (PNH), KR186525, KR186612, KR186785; **B. tenera**, *L. Kumarage 68* (E), MH207394, MH207815, MH208206; **B. tenuifolia**, *D.C. Thomas 08-86* (E), JF756349, JF756433, JF756517; **B. tetrandra**, *A. JaraMuñoz 2632* (COL), MH207395, MH207816, MH208207; **B. teuscheri**, *Lyon B.G. 20483* (LBG), MH207396, MH207817, MH208208; **B. thelmae**, *20131424* (E), MH207397, –, MH208209; **B. thiemei**, *A. Twyford 205 E00668802* (E), KP713003, KP713094, KP713229; **B. thomsonii**, *Lyon B.G. 140496* (LBG), MH207398, MH207818, MH208210; **B. thwaitesii**, *L. Kumarage 23* (E), MH207399, MH207819, MH208211; **B. thyrsoidea**, *M. Tebbitt & A. Daza 809* (E), –, MH207820, MH208212; **B. tigrina**, *C.-I Peng P22720* (HAST), KR186526, KR186613, KR186786; **B. tiliifolia**, *A. Jara-Muñoz 2650A* (COL), –, MH207821, –; **B. toledana**, *A. JaraMuñoz 2750* (COL), MH207400, MH207822, MH208213; **B. tominana**, *M. Tebbitt 719* (USZ), MH207401, MH207823, MH208214; **B. tonduzii**, *Lyon B.G. 140248* (LBG), MH207402, MH207824, MH208215; **B. torajana**, *D.C. Thomas & W.H. Ardi 09-104* (E), JN133332, JN133407, JN133436; **B. trianae**, *A. JaraMuñoz 2668* (COL), MH207403, MH207825, MH208216; **B. tribenensis**, *Chien-I Huang 6043* (E), MH207404, MH207826, MH208217; **B. trichochila**, *C.-I Peng P20764* (HAST), KR186527, KR186614, KR186787; **B. trichopoda**, *SUBOE 97* (E), MH207405, MH207827, MH208218; **B. tumbezensis**, *M. Tebbitt 770* (QCA), –, MH207828, –; **B. ulmifolia**, *E00198123*, KP713048, KP713136, KP713341; **B. ulmifolia**, *C.I Peng 22518* (HAST), MH207407, MH207830, MH208220; **B. ulmifolia**, *L.L. Forrest 169 E00183958* (E), KP713043, KP713135, KP713273; **B. ulmifolia**, *Brown, K. 21551* (LBG), MH235395, MH235406, MH235425; **B. umbellata**, *A. JaraMuñoz 2762* (COL), MH207408, MH207831, MH208221; **B. undulata**, *C.-I Peng 21275* (HAST), KP712938, KP713139, –; **B. urticae**, *P.W. Moonlight & A. Daza 73* (E), MH207409, MH207832, –; **B. urubambensis**, *M. Tebbitt & A. Daza 800* (E), MH207410, MH207833, MH208222; **B. urubambensis**, *P.W. Moonlight & A. Daza 244* (E), KX756298, KX756310, –; **B. urubambensis**, *P.W. Moonlight & A. Daza 253* (E), MH207412, MH207835, –; **B. vaccinioides**, *Sabah NP 25535* (SNP), MH207413, MH207836, MH208223; **B. valerioi**, *B. Sénéchal 60678* (LBG), MH207414, MH207837, –; **B. valida**, *Glasgow B.G. 007-066-75* (E), KP712964, KP713144, KP713289; **B. vankerckhovenii**, *J.P. Biteau 070718* (LBG), MH207415, –, MH208224; **B. variegata**, *J. Duruisseau 100652* (LBG), –, –, MH208225; **B. varipeltata**, *D.C. Thomas & W.H. Ardi 08-51* (E), JF756410, JF756494, JF756578; **B. varipeltata**, *Kreb s.n.* (SBG), MH207416, MH207838, MH208226; **B. velata**, *M. Tebbitt & A. Daza 838* (E), MH207417, MH207839, –; **B. velata**, *P.W. Moonlight & A. Daza 107* (E), MH207418, MH207840, MH208227; **B. venosa**, *20030608* (E), MH207419, –, MH208228; **B. venosa**, *Suksuwan 34 E00198104* (E), KP712966, KP713150, KP713284; **B. venusta**, *S. Neale 7* (E), JF756357, JF756441, JF756525; **B. verecunda**, *D.C. Thomas 08-137* (E), JF756399, JF756483, JF756567; **B. vermeulenii**, *Vermeulen 2301* (L), JN133333, JN133408, JN133437; **B. versicolor**, *L.L. Forrest 2* (E), JF756358, JF756442, JF756526; **B. violifolia**, *Lyon B.G. 880079* (LBG), MH207420, MH207841, –; **B. viridiflora** var. *parviflora*, *P.W. Moonlight & A. Daza 216* (E), MH207421, MH207842, MH208229; **B. viridiflora** var. *viridiflora*, *P.W. Moonlight & A. Daza 206* (E), MH207422, MH207843, MH208230; **B. wadei**, *R.R. Rubite R699* (PNH), KR186528, KR186615, KR186788; **B. watuwilensis**, *D.C. Thomas 09-55* (E), JF756406, JF756490, JF756574; **B. weberbaueri**, *T. Sarkinen 2216* (E), KP713024, KP713102, KP713340; **B. weberbaueri**, *Tebbit 829* (USZ), MH235396, MH235407, MH235428; **B. weigallii**, *Pitisopa, Gardner, Herrington 10* (E), JN133334, JN133409, JN133438; **B. wilsonii**, *Y.M. Shui & al. B2013151* (KUN), MH207423, MH207844, MH208231; **B. wollnyi**, *M. Tebbitt s.n.* (USZ), MH207424, MH207845, MH208232; **B. woodii**, *C.-I Peng P23479* (HAST), KR186529, KR186616, KR186789; **B. woodii**, *C.-I Peng P23496* (HAST), KR186530, KR186617, KR186790; **B. yapenensis**, *ABEG 211* (E), MH207425, MH207846, MH208233; **B. yunnanensis**, *C.I Peng 20941* (HAST), MH207426, MH207847, MH208234; **H. sandwicensis**, *Edutg Monn 1245-2005*, MH244433, MH244435, MH244438.