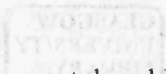


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**Systematics and Biogeography of the Afro-
Malagasy Fleshy-fruited *Begonia* (Begoniaceae)**

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

Vanessa Plana


Division of Environmental and Evolutionary Biology

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ABSTRACT

The ca. 158 African species of *Begonia* represent 16 sections and occur principally in the tropical rain forests of West and Central Africa, but are also found in the more seasonal forests of East and South Africa. Other species are island endemics found in: the Socotran Archipelago (2 spp.); Madagascar, the Mascarenes and Comores (50 spp.); and the Gulf of Guinea Islands (4 spp.). Afro-Malagasy begonias include 40 species in sections *Baccabegonia*, *Squamibegonia*, *Tetraphila* and *Mezierea*, that possess fleshy fruits, presumed to be an adaptation to bird or ant dispersal.

A phylogeny of African *Begonia* based on chloroplast *trnL* intron nucleotide sequences resolved the wingless fleshy-fruited species of African *Begonia* as monophyletic with the exception of species in section *Mezierea*. This section is polyphyletic with *B. meyeri-johannis* and *B. oxyloba* forming an unresolved clade, and *B. salaziensis* and *B. comorensis* more closely related to winged, dry-fruited Malagasy species. All endemic Malagasy and Mascarene species sampled (representing sections *Mezierea*, *Erminea*, *Quadrilobaria* and *Nervioplacentaria*) form a monophyletic group. Another clade comprises the terrestrial, hydrophytic, predominantly West and Central African, wing-fruited species in sections *Scutobegonia*, *Loasibegonia*, *Filicibegonia* and *Cristasemen* plus *Begonia iucunda*. It includes the monotypic section *Cristasemen* and *B. iucunda* that are sister to the remaining, more species-rich sections. This result is mirrored by morphological and previous ITS data, and a new section, *Chasmophila*, is established to accommodate *B. iucunda*. The predominantly East and South African species in sections *Augustia*, *Rostrobegonia*, *Sexalaria* and *Peltaugustia* are more closely related to American and Asian species of *Begonia* than they are to other African species.

A comparison of separate analyses based on the chloroplast *trnL* intron and the nuclear ribosomal internal transcribed spacer (ITS) and 26S regions show congruence in portions of the tree that depict the West and Central African and endemic Malagasy begonias, but are incongruent among the clades that include Asian, American and East and South African species. In the ITS phylogeny Asian and American species form two separate monophyletic clades which collapsed when ambiguously aligned regions in the

ITS matrix were eliminated. In the *trnL* intron phylogeny American and Asian species are interdigitated. These results weaken prior claims that American and Asian species of *Begonia* are monophyletic. A combined *trnL* intron, ITS and 26S analysis shows that fleshy fruits are apomorphic within *Begonia* and evolved at least twice in Africa.

An overview of morphological character and character state delimitations in *Begonia* found that different workers interpret morphology and delimit character states in different ways. Twenty-seven characters were identified for the fleshy-fruited begonias of sections *Baccabegonia*, *Squamibegonia* and *Tetraphila*. When combined with molecular data, morphology resolved nodes that molecular data alone did not. This combined analysis suggests non-monophyly of section *Tetraphila*, but a re-delimitation of this section is not advised. Section *Squamibegonia* (*B. poculifera*, *B. ampla*, and *B. bonus-henricus*) is monophyletic with *B. baccata* (section *Baccabegonia*) as sister. The best indicators of species relationships within *Tetraphila* are stigma and style morphology; forked styles with twisted stigmas are plesiomorphic within the section and simple styles with contracted stigmas at their apex are apomorphic. Leaf shape and habit characters also provide valuable synapomorphies.

Dates of evolutionary events in African *Begonia* were estimated assuming an age of two million years for *B. salaziensis*, equivalent to the age of Réunion, and are congruent with biogeographical hypotheses based on other plant and animal phylogenies and with geological and climatological evidence. A large proportion of the current diversity of *Begonia* in Africa is of pre-Pleistocene origin, and many of the main lineages probably arose at the end of the Miocene, reflecting the general aridification that converted large parts of central Africa into savanna or rain forest-savanna mosaic. Areas previously identified as Pleistocene rain forest refugia have probably acted as refugia repeatedly since the Miocene. São Tomé is identified as an important pre-Pleistocene refuge for the genus. Species of relatively recent Pleistocene origin are concentrated in the species-rich sections *Tetraphila*, *Loasibegonia* and *Scutobegonia*. *Begonia* diversification on Madagascar is postulated to have followed a single dispersal event at ca. 12 Ma, followed by the more recent dispersal of *B. oxyloba* from the mainland.

DECLARATION

I hereby declare that this thesis is composed of work carried out by myself unless otherwise acknowledged, and that this thesis is of my own composition. The research was carried out in the period of October 1998 to October 2001. This thesis has not in whole or in part been previously presented for any other degree.

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CHAPTER 1 Introduction: the genus *Begonia* and its African representatives

1.1 THE BEGONIACEAE C.AGARDH AND ITS FAMILY RELATIONSHIPS

The number of genera recognised in the Begoniaceae differs in recent accounts, ranging from two (Mabberley, 1993) to four (Takhtajan, 1997) or five (Heywood, 1993). However, specialists currently working on the family appear to agree that it comprises three genera: *Begonia* L.¹, *Symbegonia* Warb. and *Hillebrandia* Oliv. (van den Berg, 1983; de Wilde, 1984; Tebbitt, 1997; Badcock, 1998; Forrest, 2000). In the past, the family has been placed in the order Begoniales (Takhtajan, 1997) and the Violales (Cronquist, 1981), but it currently forms part of the Cucurbitales alongside Corynocarpaceae, Anisophyllaceae, Coriariaceae, Cucurbitaceae, Datisceae and Tetramelaceae (Chase et al., 1993; Angiosperm Phylogeny Group, 1998). In a recent phylogenetic study of the Cucurbitales, Swensen et al. (1998) found *Datisca* L. (Datisceae) to be sister to the Begoniaceae. The family Datisceae itself proved to be non-monophyletic, with the other two genera of Datisceae, *Octomeles* Miq. and *Tetrameles* R.Br., placed as sister to the Begoniaceae plus *Datisca* clade. As a result, Swensen et al. (1998) recommended the recognition of the family Tetramelaceae to accommodate *Octomeles* and *Tetrameles* following the taxonomy of Airy Shaw (1964).

In contrast to the large size of Begoniaceae, reflecting the exceptional species diversity of the genus *Begonia* (ca. 1400 spp.), families closely related to the Begoniaceae are comparatively very small. *Datisca* (Datisceae) comprises two species, while both *Tetrameles* (Tetramelaceae) and *Octomeles* (Tetramelaceae) are monotypic, and Corynocarpaceae and Coriariaceae have only five species each. In contrast, the Anisophyllaceae contain 29 species in four genera and the Cucurbitaceae

contain 760 species in 121 genera. The distributional patterns of these families and their genera are also quite disparate. The genus *Datisca* is a northern hemisphere taxon while other close relatives of the Begoniaceae (Tetramelaceae, Coriariaceae and Corynocarpaceae) are from Asian, East Asian and Pacific regions. The Begoniaceae itself is pantropical.

1.2 THE GENUS *BEGONIA*

Of the three genera currently recognised in the Begoniaceae, the pantropical genus *Begonia* is by far the largest and is among the ten most species-rich angiosperm genera (Frodin, pers. comm. 1999). It comprises approximately 1400 species currently subdivided into 63 sections (Doorenbos et al., 1998). It occurs both in tropical and subtropical regions, although is notably absent from Australia. *Begonia* shows the classical pattern of species distribution found in so many other pantropical taxa (Richards, 1973), with poor species representation in Africa compared with both Asia and the Neotropics (Doorenbos et al., 1998). Compared to the over 600 species each found in both South America and Asia, Africa (including Madagascar and the Mascarenes) supports only an estimated 158 *Begonia* species, divided into 16 sections.

The 12 species of *Symbegonia*, all endemic to New Guinea, are easily identifiable by the diagnostic campanulate corolla. Recent studies based on DNA sequence data from the chloroplast region *trnC-trnD* (Badcock, 1998) and the internal transcribed spacer regions (ITS1 and ITS2) of the 18S–26S ribosomal repeat arrays (Forrest, 2000) have shown *Symbegonia* to be nested within *Begonia*, specifically within the Asian section *Petermannia*. This suggests that *Symbegonia* is an extreme morphological variant of *Begonia*. In contrast, in molecular studies where both *Hillebrandia sandwicensis* and species of *Begonia* have been sampled, *Hillebrandia* always resolves sister to *Begonia* (Forrest, 2000; Wagstaff & Dawson, 2000). The genus *Hillebrandia* is monotypic, the single species *H. sandwicensis* being endemic to the Hawaiian archipelago.

¹ Authorities are given for generic and subgeneric taxa outside of Begoniaceae. In the Begoniaceae, section authorities are included the first time sections are mentioned in the text. Species nomenclature follows Doorenbos et al. (1998) and authors are not included here.

1.3 THE GENUS *BEGONIA* IN AFRICA

Most sections within the continental African *Begonia* are morphologically well characterised, due primarily to intensive taxonomic research carried out at the Agricultural University in Wageningen over the past 20 years. Relatively recent published taxonomic revisions cover sections *Baccabegonia* (Reitsma, 1985), *Squamibegonia* (de Wilde & Arends, 1980), *Mezierea* (Klazenga et al., 1994), *Loasibegonia* (Sosef, 1994), *Scutobegonia* (Sosef, 1994), *Rostrobegonia* (Irmscher, 1961), *Augustia* (Irmscher, 1961) and *Cristasemen* (de Wilde, 1984). Moreover, the revisions of sections *Tetraphila* (de Wilde, pers. comm., 1999) and *Filicibegonia* (Wieringa, pers. comm., 2000) are in progress. The mainland African begonias have also been treated for several floras, including the Flora of Tropical Africa (Hooker, 1871), the Flore du Congo du Rwanda et du Burundi (Wilczek, 1969) and the Flora of Southern Africa (Hilliard, 1976). The Malagasy *Begonia* species were last revised by Keraudren-Aymonin (1983) for the Flore de Madagascar, who recognised 50 species. These species were not assigned to any sections, however, as she considered it premature in the absence of a clear, widely accepted review of sectional delimitations.

Doorenbos et al. (1998), in their recent review of the sections of *Begonia*, recognised four endemic Malagasy sections (*Erminea*, *Quadrilobaria*, *Nervioplacentaria* and *Muscibegonia*). One further section, *Mezierea*, though more widespread, has species that are endemic to both Madagascar and the Mascarenes. Of the 14 sections of *Begonia* on continental Africa, three (*Peltaugustia*, *Augustia*, and *Rostrobegonia*) are concentrated in eastern and southern regions of the continent, from the Socotran Archipelago to South Africa. The remaining sections (*Loasibegonia*, *Scutobegonia*, *Filicibegonia*, *Cristasemen*, *Sexalaria*, *Tetraphila*, *Squamibegonia* and *Baccabegonia*) are predominantly West and Central African, showing highest species-diversity in lowland and sub-montane regions of western Central Africa, from southern Nigeria to Gabon (including the Gulf of Guinea islands). Among these tropical African begonias is a group of 34 species representing three sections: *Tetraphila*, *Squamibegonia* and *Baccabegonia*. These species, in addition to the six in the Afro-Malagasy section *Mezierea*, are characterised by the possession of fleshy or pulpy, berry-like fruits, showing little if any trace of the expanded wing-like appendages that characterise the remainder of the genus. The term ‘fleshy’ on its own has been used widely to refer only

to the berry-like fruits in these species and to those in the Asian section *Spenanthera* and the American section *Parietoplacentaria* (van den Berg, 1984; de Lange & Bouman 1991; Doorenbos et al. 1998). This terminology is followed in this thesis, and species in these four sections are referred to as the “fleshy-fruited begonias”. In Africa, there are a few other species, such as those in section *Erminea* from Madagascar or the African section *Scutobegonia* that have intermediate fruits that exhibit a fleshy or pulpy texture and possess fleshy wings or wing-like appendages. The fruits in these species have been termed ‘juicy’ by some authors (Sosef, 1994). There is no standard by which we can distinguish fleshy from juicy, and these terms should be considered interchangeable. Both terms refer to the fruits of some *Begonia* species that, rather than forming dry capsules at maturity, as is common in the genus, remain pulpy. In the following chapters the fruits of species like those in section *Erminea* or *Scutobegonia* are termed winged fleshy-fruited species, and it is these wings that separate them from the main subjects of this study.

1.4 AIMS OF THE PRESENT STUDY

This thesis investigates the evolution and biogeography of the wingless fleshy-fruited *Begonia* in Africa. In order to test the monophyly of this group, sampling was extended to include numerous other African representatives of the genus, in addition to several Asian and American species. The chloroplast DNA (cpDNA) *trnL* intron was chosen because during the early stages of the project, while testing different gene loci for their phylogenetic value, it was found to have an adequate degree of variation among African species of *Begonia*. It was also favoured because an extensive cpDNA phylogeny for the genus did not previously exist. The aims of the thesis are:

1) To test the phylogenetic hypothesis for *Begonia* based upon sequence data of the internal transcribed spacer (ITS) of nuclear ribosomal DNA (nrDNA).

Forrest (2000) produced a phylogeny of *Begonia* based on ITS sequence data. This study was the first to significantly sample the genus, and included approximately 10% of species in the genus. On closer inspection of the ITS data it was obvious that the levels of divergence in the locus, particularly between African lineages, were so high that aligning many sequences was an ambiguous process. As a result, it is necessary to

test the phylogenetic hypothesis proposed for *Begonia* based on ITS sequence data with a new, independent cpDNA data set, particularly among African species. This would help to answer the question whether there is congruence between the phylogenetic hypotheses of African *Begonia* based on nrDNA and cpDNA sequence data. Based on a comparison of phylogenies based on *trnC-trnD* (Badcock, 1998) and ITS sequences, there have been some indications that there may be a localised lack of congruence. This was tested by sequencing the *trnL* intron for a much broader sample of species than the *trnC-trnD* study.

2) To investigate the origin and evolution of fleshy fruits in Africa and to study character evolution in species with this fruit type.

Based on morphological evidence, fleshy-fruits have been believed to be good indicators of close evolutionary relationships. Here I aimed to test both this hypothesis and answer the following questions: Have fleshy-fruits originated once (as is implied by morphology) or on more than one occasion (as suggested by nrDNA data)? If they have arisen more than once, where and how often? Finally, what are the relationships among fleshy-fruited begonias in Africa and what are the patterns of morphological character evolution among these species.?

3) To investigate the biogeography of African begonias.

The patterns of plant distribution we see in the African tropics today have been considered to be largely attributable to climatic changes during the Pleistocene. By combining the phylogenetic information from earlier parts of this study, together with distribution information and knowledge of the climatological and geological history of Africa, this section of the project approached the following questions: Do areas of *Begonia* distribution and tree topology give insights into refugial patterns? And can a molecular clock approach be used in *Begonia* to assess how divergence patterns correlate with the physical history of Africa?

All three subjects are discussed in more than one of the following chapters. These have been designed to stand alone like papers submitted to a peer reviewed journal. As a result, there is a slight degree of repetition where an effort has been made to place these subjects into context within each chapter.

CHAPTER 2 Phylogenetic relationships of the Afro-Malagasy *Begonia* inferred from *trnL* intron sequences

2.1 INTRODUCTION

There are an estimated 158 species of *Begonia* in Africa, distributed throughout sub-Saharan Africa, Madagascar and their offshore islands (Doorenbos et al., 1998). Approximately one third of the 158 African begonias are endemic to Madagascar and associated islands (Mascarenes, Seychelles and Comoros). *Begonia* diversity in Africa is notably lower than in Asia or America, each of which maintains over 600 species. This pattern of diversity, showing a contrasting high species richness in Asia and the Neotropics with respect to a relatively species poor Africa, is recorded in numerous other angiosperm genera (Richards, 1973).

There are two ecologically distinct classes of *Begonia* on mainland Africa. The first consists of those species found in moist habitats of Tropical African lowland and sub-montane evergreen rain forest, and which rarely occur East of the Lake Kivu region. The centre of diversity for this group is in western Central Africa, in Cameroon and Gabon. These include species in sections *Baccabegonia*, *Squamibegonia*, *Tetraphila*, *Loasibegonia*, *Scutobegonia*, *Filicibegonia* and *Cristasemen*. The second group is adapted to more seasonal, sometimes arid conditions and has a general afro-montane, tropical East African distribution, ranging from the Socotran archipelago throughout the Eastern Arc mountains to South Africa, with a few outlier species in West and Central Africa; it includes 24 species in sections *Rostrobegonia*, *Peltaugustia* and *Augustia*. Section *Sexalaria*, comprised of the single species *B. annobonensis*, is endemic to west Central Africa, but is part of this group, being found in areas with increased seasonality

in areas of coastal Cameroon and the Gulf of Guinea islands.

Only one section, *Mezierea*, which belongs to the group of wet forest species, occurs on both continental Africa and Madagascar. Four species in this section are endemic to Madagascar and the Mascarenes (*B. salaziensis*, *B. humbertii*, *B. comorensis* and *B. seychellensis*); *B. meyeri-johannis* is found in East Africa whereas *B. oxyloba* is more widespread, occurring throughout tropical Africa and Madagascar (Klazenga et al. 1994).

2.1.1 Classification of African Begonia

Klotsch (1855) was the first author to place the 210 species of *Begonia* (described up to that time) into 41 genera in the Begoniaceae. Subsequent authors, however, did not follow Klotsch's subdivision of the family (Doorenbos et al, 1998). In 1859, A. de Candolle produced the second monograph of the Begoniaceae, where he reduced most of Klotsch's (1855) genera to sections, and where he recognised only three genera in the Begoniaceae: *Begonia*, *Casparya* and *Mezierea*. De Candolle's (1859) African sections, which he placed in the genus *Begonia* and which still exist today are: *Augustia* (Klotsch) A. DC., *Erminea* A. DC., *Filicibegonia* A. DC., *Loasibegonia* A. DC., *Muscibegonia* A. DC., *Nervioplacentalia* A. DC., *Quadrilobaria* A. DC., *Sexalaria* A. DC. and *Tetraphila* A. DC. In 1867, Bentham and Hooker placed 329 out of the then 330 species of Begoniaceae in the genus *Begonia*, while the single remaining species was maintained in the monotypic genus *Hillebrandia* described a year earlier by Oliver (1866). Warburg (1894) was the first systematist to classify the genus *Begonia* according to geography, highlighting the importance of physical proximity in *Begonia* classification. He was also the first worker to officially reduce the genus *Mezierea* (Gaud.) Warb. to a section of *Begonia*. To de Candolle's (1859) sections, he added sections *Rostrobegonia* Warb., *Scutobegonia* Warb. and *Squamibegonia* Warb. He did not agree, however, with de Candolle's circumscription of section *Nervioplacentalia*, which he listed under "dubious sections". He also created *Peltaugustia* (Warb.) Barkley,

a subsection of *Augustia*, to accommodate the island endemic *B. socotrana*. Irmscher's (1925) monograph of the family largely followed Warburg's classification, but reinstated the Malagasy section *Nerviplaceholders*. Baranov & Barkley (1974) elevated Warburg's subsection *Peltauugustia* to sectional rank. A new species discovered by V. Plana in 1995 on the island of Samhah, adjacent to Socotra, has also been placed in this section (Hughes & Miller, in press). In 1984, de Wilde erected the section *Cristasemen* J.J. de Wilde to accommodate *B. thomeana*, previously placed in section *Loasibegonia*. In the same year, Reitsma created section *Baccabegonia* Reitsma to accommodate *B. baccata* and *B. crateris*, two endemic species from the island of São Tomé (Gulf of Guinea islands), which were previously in section *Squamibegonia*. Thus, there are currently 16 recognised sections of *Begonia* in Africa (Doorenbos et al., 1998).

2.1.2 Sources of molecular phylogenetic data in *Begonia*

Segments of the chloroplast and nuclear genomes are those most commonly sequenced in plants. The mitochondrial genome has, in contrast, been little used in plant studies due to its slow substitution rates and extensive intramolecular recombination (Soltis & Soltis, 1998). The chloroplast genome in photosynthetic land plants is relatively small (120-200 kb) and most genes in it are viewed as effectively single-copy (Soltis & Soltis, 1998). This avoids some of the problems in estimating phylogenies for some multigene families in the nuclear genome which can be subjected to differing levels of concerted evolution (Hershkovitz et al., 1999). It is also significant that chloroplasts are predominantly uniparentally inherited (via the mother in most angiosperms), and that cpDNA molecules are not therefore subject to recombination. This recombination present in nuclear genes is what makes nuclear genes a mosaic of sequences with differing evolutionary histories. In contrast, the cpDNA genome represents an organellar rather than an organismal history and these histories may or may not be congruent. However, it is recombination, combined with incomplete concerted evolution of gene copies, which can complicate sequencing and estimating phylogenies in nuclear regions such as ITS.

Non-coding chloroplast sequences are now regularly used in isolation or in combination with other genomic regions to resolve phylogenetic relationships at the species level and above. The *trnL* intron and *trnL-trnF* spacer are some of the most commonly sequenced regions of the plastid (see Soltis & Soltis, 1998). The *trnL-F* region consists of the *trnL* intron, which commonly ranges from 350 to 600 bp, the small 3' exon and the adjacent *trnL-trnF* spacer which is relatively small ranging from 120 to 350 bp (Soltis & Soltis, 1998). Gielly & Taberlet (1994) found that on average the *trnL* region can evolve up to three times faster (including a high frequency of insertions/deletions) than *rbcL* in some groups. Although most studies using sequences from the *trnL* intron and *trnL-trnF* spacer are at the genus level and above, a few recent studies have found this region useful for resolving species relationships (e.g. Fernandez et al., 2001; Fukuda et al., 2001; Muasya et al., 2001).

Tebbitt (1997) sequenced the *trnL-trnF* region of 12 species of *Begonia*, including one African species, to investigate its utility for the resolution of phylogenetic relationships, but found the *trnL* region to be insufficiently variable to merit further work. Similar claims were made for ITS by L. Brouillet (pers. comm., 1995, in Tebbit, 1997), but subsequently ITS has been shown to have very significant levels of sequence divergence, in some instances to the extent of causing alignment difficulties (Forrest, 2000). Alignment ambiguity in Forrest's study was noted as being considerably more significant among African species, and for this reason it was thought appropriate for this study to sequence the *trnL* region in further taxa, to investigate whether suitable levels of cpDNA variation could be found among African species.

2.1.3 Previous molecular phylogenetic work on African *Begonia*

The first molecular phylogeny of *Begonia* to include African species was carried out by Tebbit (1997). He included only eight species, *B. meyeri-johannis*, *B. salaziensis*, *B. manii*, *B. sutherlandii*, *B. dregei*, *B. johnstonii*, *B. quadrialata* and *B. prismatocarpa* in a broader study examining the relationships in the Asian section

Sphenanthera based on a cladistic analysis of restriction fragment length polymorphism (RFLP) data from the *trnC-trnD* region of the plastid. In a study focusing on the American section *Knesebeckia*, Badcock (1998) also extended her sampling to perform a preliminary estimate of the phylogeny of *Begonia* based on sequence data from the chloroplast *trnC-trnD* region (Fig. 2.1). Her sample of five African species (*B. manii*, *B. salaziensis*, *B. meyeri-johannis*, *B. dregei*, *B. sutherlandii*) gave the first indications of (1) the closer links between the East and South African species to Asian and American

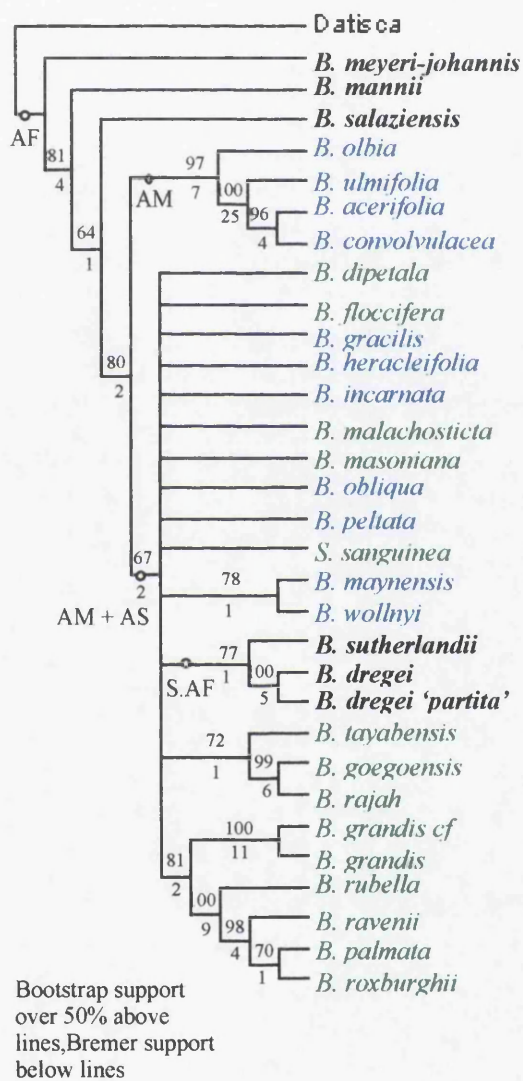
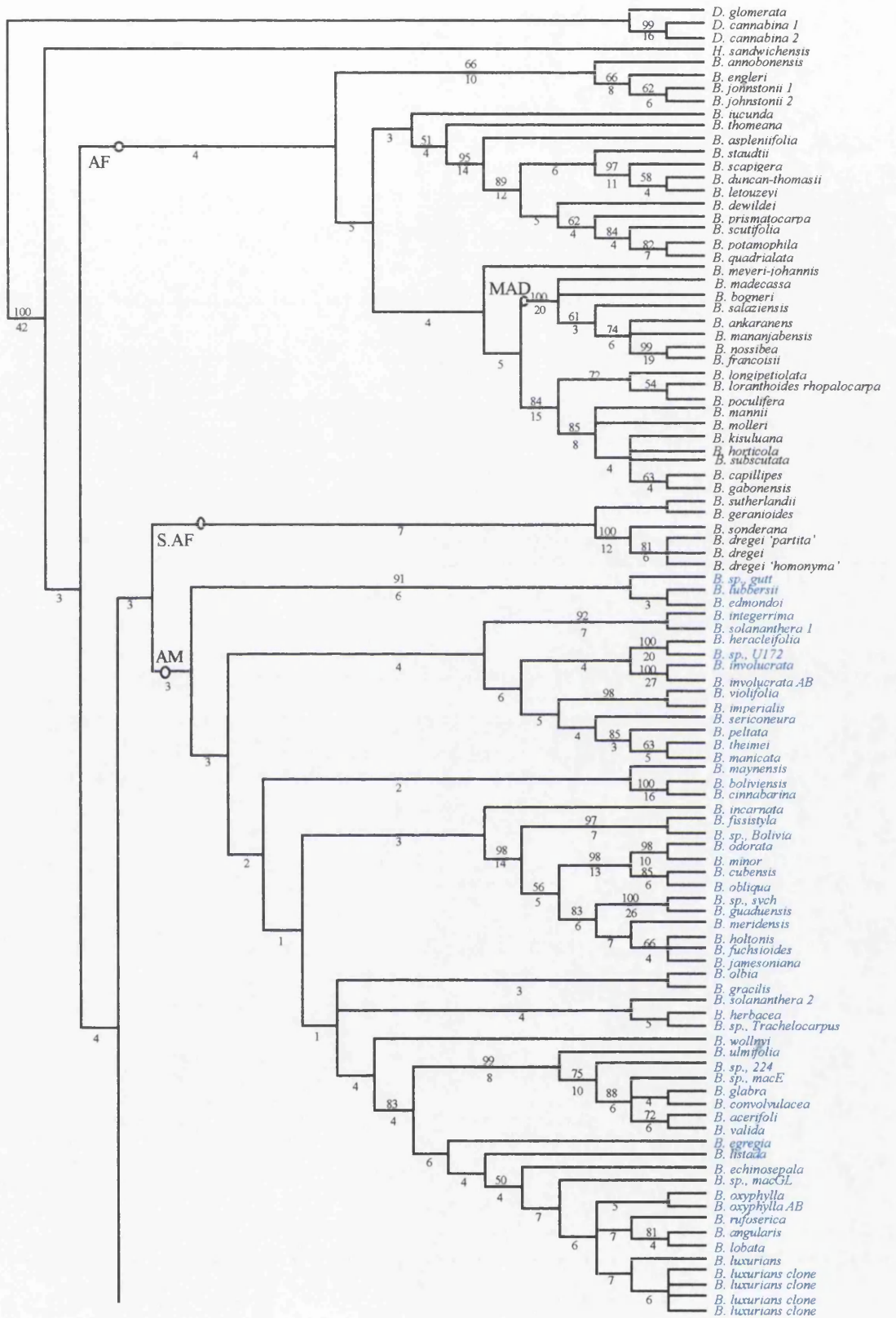


Figure 2.1 *TrnC-trnD* phylogeny of *Begonia* (from Forrest, 2000, based on Badcock, 1998). African species are denoted in black, Asian in green and American in blue.

species, and (2) the polyphyly of the African section *Mezierea*. Unfortunately, both of these studies included a very restricted number of African species. In Tebbitt's study only 33% (8/ 24 species) of the sampled species were African. In Badcock's study the number of species was even lower with only 15% (5/32 species) of species originating in Africa.

The phylogenetic analyses of *Begonia* conducted by Forrest (2000) based on sequences from the internal transcribed spacer (ITS) (Fig. 2.2) and 26S regions of nrDNA, sampled 172 species of *Begonia* (41 African) across its entire geographic range, representing 40 of the 63 sections currently recognised. The ITS data indicated that both American and Asian species are monophyletic (although weakly supported), with the New Guinea genus *Symbegonia* deeply nested within the Asian clade and showing evolutionary affinities with species in section *Petermannia* (Klotzsch) A. D. C. In addition African species were non-monophyletic, with some seasonally adapted begonias from East and South Africa (sections *Augustia* and *Peltaugustia*) holding closer links to Asian and American species than to other African species. This last discovery, together with additional evidence demonstrating the polyphyly of section *Mezierea*, are two results that were presaged by the *trnC-trnD* analyses of Badcock (1998). The results from the separate ITS and 26S analyses in Forrest's (2000) study, however, were noticeably different. The 26S results did not show the level of geographic clustering shown by the ITS data, particularly among American and Asian species. In addition, the 26S data resolved a number of African wet forest species (*B. thomeana*, *B. dewildei*, *B. scapigera* and *B. iucunda*) in a clade consisting of American, Asian and seasonally adapted African begonias rather than with other African wet forest and Malagasy begonias as did the ITS phylogeny. There are also two principal disparities between the plastid and nrDNA phylogenies. The first is a discordance between basal nodes, with the *trnC-trnD* data showing the species *B. meyeri-johannis* (presently in section *Mezierea*) as the basal branch in *Begonia*, whereas the accepted ITS phylogeny places *B. meyeri-johannis* as sister to the other fleshy-fruited and Malagasy begonias. This result is also reflected in the 26S phylogeny (Forrest, 2000).



The second discrepancy between the *trnC-trnD* and ITS phylogenies is that, like the 26S data set, the *trnC-trnD* phylogeny does not support the monophyly of Asian and American species.

The disagreements observed between existent *Begonia* phylogenies can probably be attributed to differences in levels of sequence divergence between the different genetic loci, resulting in higher levels of alignment ambiguity where sequence divergence is high. In the ITS data matrix (Forrest, 2000) large portions of ITS 1 and ITS 2 are alignment ambiguous, and in fact over half the matrix shows problems in alignment. This contrasts with the alignment of 26S or *trnC-trnD* where the alignment of only small regions in the matrix could be variously interpreted and cause problems. The effects these alignment ambiguous regions in ITS have on the final topology are discussed further in the following chapter.

A comparison of the *Begonia* phylogenies presented in two previous studies, one based on ITS sequence data (Forrest, 2000) and the other on partial *trnC-trnD* sequences (Badcock, 1998), shows a notable disparity in species sampling, particularly among the basal nodes. Whereas the ITS phylogeny includes many Africa species, there is poor sampling for this continent in the *trnC-trnD* phylogeny. This study aims to test the phylogenetic hypothesis based on ITS sequences (Forrest, 2000) (Fig. 2.2) with an independent data set comparable to the *trnC-trnD* study (Badcock, 1998) incorporating a much broader sampling of African species. This will allow further investigation of species relationships among African *Begonia*, with the aim of interpreting the evolution of fleshy fruits, sectional monophyly and species-level biogeography.

2.2 MATERIALS AND METHODS

2.2.1 *Sampling and outgroup selection*

Plant material was obtained from living collections at the Glasgow Botanic Garden and the Royal Botanic Garden Edinburgh, and from fieldwork carried out by myself in Cameroon with the support of the Royal Botanic Gardens Kew. Material from Madagascar and São Tomé was received from field workers in those regions. Fifty-seven (approximately 36%) out of 158 African species of *Begonia* were sampled, representing 15 of the 16 sections found in Africa and Madagascar (see Appendix 1). Within sections the sampling was (sampled species/total number of species in section): *Augustia* (3/12), *Baccabegonia* (1/2), *Cristasemen* (1/1), *Erminea* (4/12), *Filicibegonia* (1/8), *Loasibegonia* (6/19), *Mezierea* (4/6), *Nervioplacentaria* (2/7), *Peltaugustia* (1/2), *Quadrilobaria* (5/19), *Rostrobegonia* (3/10), *Scutobegonia* (2/21), *Sexalaria* (1/1), *Squamibegonia* (3/3) and *Tetraphila* (19/30). American and Asian species were sampled as place-holders to test the monophyly of the African sections, in light of previous studies (Badcock, 1998; Forrest, 2000). A wide sample was taken from 15 different American and Asian sections, corresponding to those American and Asian species used to generate the 26S topology by Forrest (2000), with the aim of comparing the 26S, ITS and *trnL* data sets in the following chapter. *Hillebrandia sandwicensis* and *Symbegonia sanguinea* were included in the ingroup. Evidence from the chloroplast-encoded *rbcL* gene and nuclear 18S ribosomal DNA has shown that *Begonia* is monophyletic (Swensen et al., 1994; Swensen et al. 1998; Wagstaff & Dawson, 2000) and that it is therefore a suitable ingroup (Nixon & Carpenter, 1993). However, evidence from the internal transcribed spacer region (ITS) of nuclear ribosomal DNA (Forrest, 2000) has shown *Symbegonia* to be nested within *Begonia*, and it is therefore treated as part of the ingroup. The same studies have shown *Datisca* to be sister to the Begoniaceae and therefore, a suitable outgroup for rooting a phylogenetic analysis. Both known species of *Datisca* (*D. glomerata* and *D. cannabina*) were therefore chosen as outgroups.

2.2.2 Molecular methods

Total DNA extractions were carried out from silica-dried or fresh material, using a modified Doyle & Doyle (1987) CTAB protocol with the addition of 20 μl (in 980 μl of CTAB) of 10% DTT or 2-mercaptoethanol. Including a small amount of PVPP (polyvinylpolypyrrolidone) in the initial grinding process helped to remove secondary plant products such as polyphenolics, tannins and quinones. One or two discs of plant material were obtained using the top of a 1.5 ml Eppendorf tube as a cutter. The material was ground in 1.5 ml eppendorf tubes with acid-purified sand and then incubated in the 1 ml modified CTAB buffer at 65°C for 30 minutes. The samples were then extracted twice with 200 μl of chloroform-isoamyl alcohol (24:1). After each addition of the chloroform-isoamyl alcohol the tubes were gently shaken to obtain a single phase and then centrifuged for 2 minutes at 13,000 rpm. After centrifuging, the aqueous upper phase was removed to a clean 1.5 ml Eppendorf tube. The DNA was then precipitated by adding 600 μl of ice-cold isopropanol for ca. 12 hours (overnight). The tubes were centrifuged for 2 minutes at 13,000 rpm to pellet the nucleic acid precipitate, and the pellet was washed in 1 ml of wash buffer (76% ethanol + 10 mM NH_4Ac). The final pellet was suspended in 100 μl of 1X TE buffer (10 Mm Tris-HCl + 1 Mm EDTA). DNA presence was determined by electrophoresis running 5 μl of the sample on a 0.8% agarose for 30 minutes at 80V. When yield of total genomic DNA was insufficient using this method, three mini-extractions were carried out using the above CTAB protocol. The final pellet was diluted in 100 μl of water rather than TE buffer and all three extractions were then combined into a DNEasy Plant Mini Kit extraction column (Qiagen) and the DNEasy extraction protocol was followed from step 4. DNA presence was determined as above.

PCR-amplification of the *trnL* intron and spacer used the universal primers trn-c (forward) and trn-d (reverse) and trn-e (forward) and trn-f (reverse) (Taberlet et al., 1991). Amplification reactions which were made up to 50 μl contained 33 μl dH_2O , 2.5 μl 50 mM MgCl_2 , 5 μl 10X NH_4 buffer (160 mM $(\text{NH}_4)_2 \text{SO}_4$, 670 mM tris-HCl (pH

8.8 at 25°C), 0.1% Tween-20), 1.5 µl of each primer at a concentration of 10 µM, 5 µl 2 mM dNTPs, 0.5 µl (2.5 units) of Biotaq DNA polymerase (Bioline), and 1 µl DNA. The PCR amplification program for the *trnL* intron was: a single initial cycle of 94°C for 3 minutes, followed by 30 cycles of 94°C for 1 minute (denaturation), 50°C for 30 seconds (annealing), and 72°C for 1 minute (extension). The PCR products were cleaned using the QIAquick PCR Purification Kit columns (Qiagen) following the manufacturer's protocol. Forward and reverse sequencing reactions of the purified PCR templates were made up to 10 µl and were performed with the Amersham Thermo Sequenase™ II dye terminator cycle sequencing premix kit. The reactions included 2 µl of the sequencing premix, 0.25 µl of the primer at a concentration of 10 µM, 6.75 µl of dH₂O, and 1 µl (ca. 200 ng) of the PCR template. Sequence cycling parameters were 25 cycles of 96°C for 10 seconds, 50°C for 5 seconds and 60°C for 4 minutes.

The forward and reverse sequences were obtained using an ABI (Applied Biosystems) Prism 377 automated DNA sequencer. The *trnL-F* intergenic spacer did not prove useful due to a mononucleotide (T) repeat at the 5' end affecting the reading of the rest of the sequence due to PCR slippage, and therefore only sequences from the *trnL* intron were used in this study. Sequences were checked using first Factura (Applied Biosystems) and then Sequence Navigator, and assembled using AutoAssembler 2.1 (Applied Biosystems). An initial alignment was carried out in Sequence Navigator using CLUSTAL. Further alignments were performed manually in PAUP* version 4.0b7 (Swofford, 2000). Strong sequence similarity for the *trnL* data made alignment by eye relatively straightforward (Appendix 2).

2.2.3 Phylogenetic analysis

Gaps inferred from the sequence alignment were coded according to the simple method described by Simmons & Ochoterena (2000) where gaps with shared 5' and 3' termini are coded as additional presence/absence characters. The region between base positions 374 and 434 was excluded from the analysis because of alignment ambiguity

and the presence of a mononucleotide repeat (T) at the 5' end. Gaps present in single taxa were also coded to include gap autapomorphies in the final branch lengths.

An initial heuristic search involving a first round of swapping was carried out with the following parameters: 1000 random addition sequences, followed by TBR swapping, and not invoking either multrees or steepest descent. Random addition sequences are carried out to avoid parsimony islands. Not invoking multrees results in the saving of a single optimal tree per replicate, while not invoking steepest descent limits swapping to optimal trees only. The tree output from this first round of swapping was then fed as starting topologies into a second round of swapping, invoking steepest descent and multrees and saving 10,000 trees, which is considered to be sufficient to capture all topological variation (e.g. Sanderson & Doyle, 1993). To limit the number of trees found, the “collapse branches if minimum length is 0” option was invoked, collapsing branches in which there exists at least one most-parsimonious reconstruction for every character such that no length is assigned to the branch. A heuristic search was carried out using 1000 random addition sequences, followed by TBR swapping, invoking both multrees and steepest descent. This method gave the same strict consensus tree as when the “collapse branches if maximum length is 0” option was used, but with a significant reduction in tree number (12 most parsimonious trees). Therefore, this method, which is computationally more efficient, was used in subsequent analysis which tested the effects of different gap penalties. A sensitivity analysis (Whiting et al., 1997) was carried out to test the topological effects of gaps, in which gaps were treated as (a) a fifth state, (b) as missing, or (c) coded separately.

A ratchet analysis (Nixon, 1999b) was implemented in NONA (Goloboff, 1993) with the Windows interface Winclada (Nixon, 1999a) to determine whether a shorter tree could be found using a different tree searching approach. A ratchet analysis is an efficient method of surveying a wider tree space and of breaking islands by sampling many islands with fewer trees in each island (Giribet & Wheeler, 1999; Nixon, 1999b; Quicke et al., 2001) (Fig. 2.3). The ratchet analysis works by generating an initial tree on

which some branch swapping (typically TBR) is performed. A random subset of characters is then selected and weighted (the weight is increased by 1 or more), followed by swapping on this weighted tree. One or a few optimal trees from this swap are kept. The weights are then set to the original default (generally all characters showing equal weights), followed by branch swapping on the current tree until an optimal tree is found. The modified parsimony ratchet method presented by Quicke et al. (2001) weighs characters which performed well in the initial branch swapping stage (those with high consistency and retention indices) rather than choosing random characters. The default for the parsimony ratchet in Winclada is to run 200 iterations. Commonly, this 200-iteration cycle is repeated 50-100 times (D. Bailey, pers. comm., 2001). The results

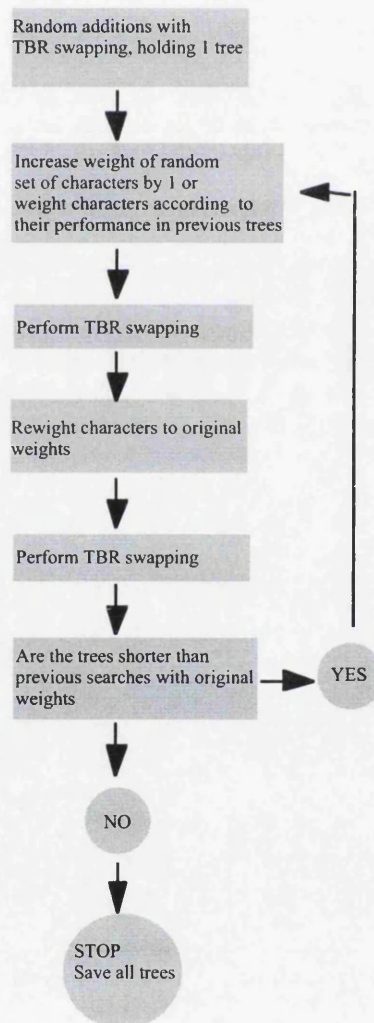


Figure 2.3 A flow chart showing the parsimony ratchet (after Quicke et al. 2001).

from all 50-100 trials are pooled, and then filtered to retain only the optimal trees. Using character weighting to move through tree space allows movement among islands without losing all the information created during the swapping exercise on the initial tree, potentially generating shorter trees.

Branch support was investigated using 10,000 bootstrap replicates, keeping only one tree per random addition sequence and swapping with TBR, with both multrees and steepest descent switched off. The following criteria are used, in the text, for bootstrap support: 50-69% weak, 70-85% medium and 86-100% strong. Decay indices (Bremer, 1988) were calculated using AutoDecay version 4.0 (Eriksson, 1998) as an alternative method to test branch support.

To investigate the effects a non-parsimony approach would have on the final topology, a maximum likelihood analysis was carried out. Parsimony reconstructs phylogeny by minimising character state changes across the entire tree. In contrast maximum likelihood is model-based and calculates the likelihood of the observed data given a particular model of evolution. The evolutionary model which best fits the given *trnL* sequence data was calculated using Modeltest 3.06 (Posada & Krandall, 1998). The Akaike information criterion (AIC), which selects the best-fit model while imposing a penalty for unnecessary parameters, was TVM+G (TVM + Γ). This model is a transversional model with the assumption that substitution rates follow a gamma (Γ or G) distribution i.e. substitution rates are not equal. In a transversional model different empirical substitution rates are assumed for different transversions, and equal rates are assumed for transitions ((Rmat) = (0.5819 1.0057 0.1689 0.7470 1.0057)). In this model equal base frequencies were not assumed and were set to (Lset Base) = (0.4092 0.1484 0.1638) and the fraction of invariable sites was (Pinvar) = 0. The gamma distribution was estimated to have a shape = 0.7960, where although most sites are invariable a few have very high rates of substitution. Searches were carried out using TBR.

2.3 RESULTS

The length of the *trnL* intron ranged from 369 bp in *B. baccata* and species in section *Squamibegonia* to 535 bp in most other species. *Begonia baccata* (section *Baccabegonia*), and all three species in section *Squamibegonia*, share a large (231 bp) deletion. Uncorrected pairwise distance measures among the *Begonia* species sampled ranged from zero between species in section *Squamibegonia* (*B. ampla*, *B. bonus-henricus*, *B. poculifera*) to 0.073 (7.3%) between the American species *B. convolvulacea* and *B. herbacea*. In Africa, the highest divergence separated *B. iucunda* and *B. annobonensis* (6%). Sequence divergence may reach 6% among American species (excluding *B. herbacea* which shows high sequence divergence and a proportionately very long branch length in the topology) and only 2% between Asian species, explaining why Tebbitt (1997) concluded that the *trnL* region was not useful for phylogeny reconstruction.

The parsimony analysis of 129 informative characters yielded 10,000 trees of length 335, consistency index (CI) of 0.776 (0.691 excluding uninformative characters) and retention index (RI) of 0.887. The strict consensus of these trees is shown in Figure 2.4. *TrnL* intron sequences were useful for resolving sectional relationships, giving in addition finer resolution within sections, particularly among African species, but they proved unable to satisfactorily resolve basal relationships.

The parsimony ratchet analysis in NONA provided trees with the same length (335 steps), and the same strict consensus topology as the maximum parsimony analysis in PAUP. In this study the ratchet analysis in NONA performed equally to the maximum parsimony analysis in PAUP, and therefore as an alternative search strategy gives greater confidence to the matching result. The ratchet analysis is particularly valuable to test whether the shortest tree has been found using standard parsimony search strategies in PAUP.

The single maximum likelihood tree was also identical to the strict consensus topologies generated by the maximum parsimony and ratchet analyses.

All trees resolve five main clades (Figs. 2.4 and 2.5). Section *Meziera* is clearly non-monophyletic. The mainland species of this section, *B. oxyloba* and *B. meyeri-johannis* (Clade III), form a separate well supported (99% bootstrap) clade. The Malagasy and Mascarene species in section *Meziera* (*B. salaziensis* and *B. comorensis*) form a well-supported clade (87%), nested within a strongly supported (86%) monophyletic Malagasy clade (Clade IV). All trees resolve section *Erminea* as monophyletic, all species of which have fleshy alate fruits, though their placement as sister to the rest of the Malagasy *Begonia* is poorly supported. Within Clade IV, there is a poorly supported (52%) clade consisting of species in sections *Quadrilobaria* and *Nerviplantaria*. Morphologically, both sections are very similar, separated only by the presence of a wood-like stem in section *Nerviplantaria* (Doorenbos et al., 1998).

All African mainland fleshy-fruited species, with the exception of the two species in section *Meziera*, are a monophyletic group (Clade I). All species in this clade are also characterised by the presence of peltate scales on the leaves, stem and inflorescence, and epiphytic habit of most species (section *Baccabegonia* is terrestrial or rupestral, as are a few species in section *Tetraphila*). This clade is poorly supported (59%), but within it there is strong support (97%) for the sister relationship of *B. baccata* to a strongly monophyletic (86% bootstrap) section *Squamibegonia*. Most species in section *Tetraphila* form a moderately supported clade (74%). *Begonia loranthoides*, *B. longipetiolata* and *B. eleagnifolia*, all currently placed in section *Tetraphila*, are not resolved with respect to the core *Tetraphila* clade or the *Squamibegonia/Baccabegonia* clade. They occur together in a well-supported clade (92%). These three species deviate notably in morphology from the typical *Tetraphila* species.

Clade V consists of the West and Central African terrestrial species of *Begonia*

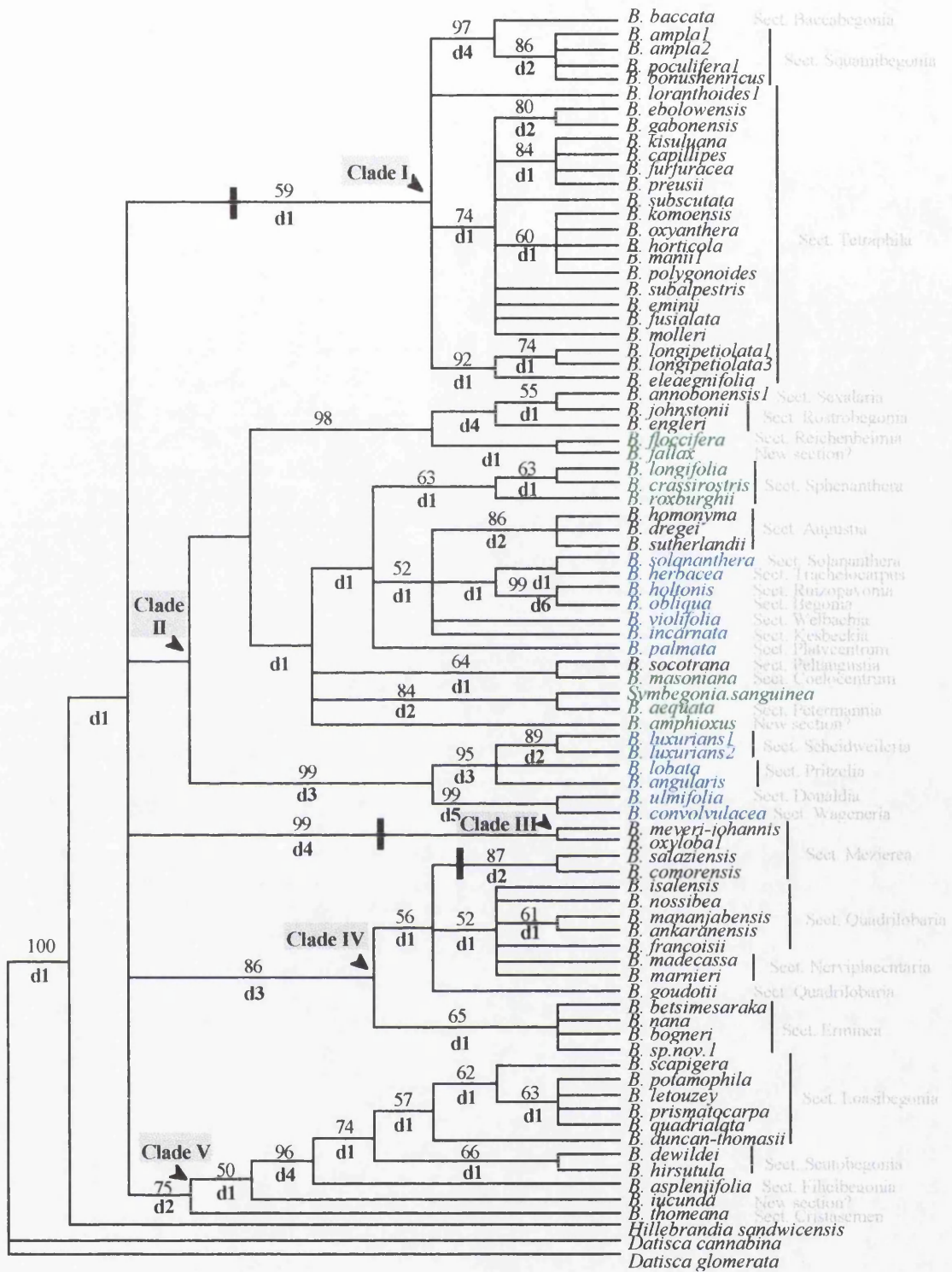


Figure 2.4 Strict consensus of a maximum of 10,000 trees generated from the heuristic search of *trnL* sequences using ACCTRAN optimisation. *Begonia* species in black are African, in green are Asian and in blue are American. Numbers above the branches are bootstrap support values, those below are decay index values. The presence of fleshy fruits is mapped onto the cladogram with a solid black bar.

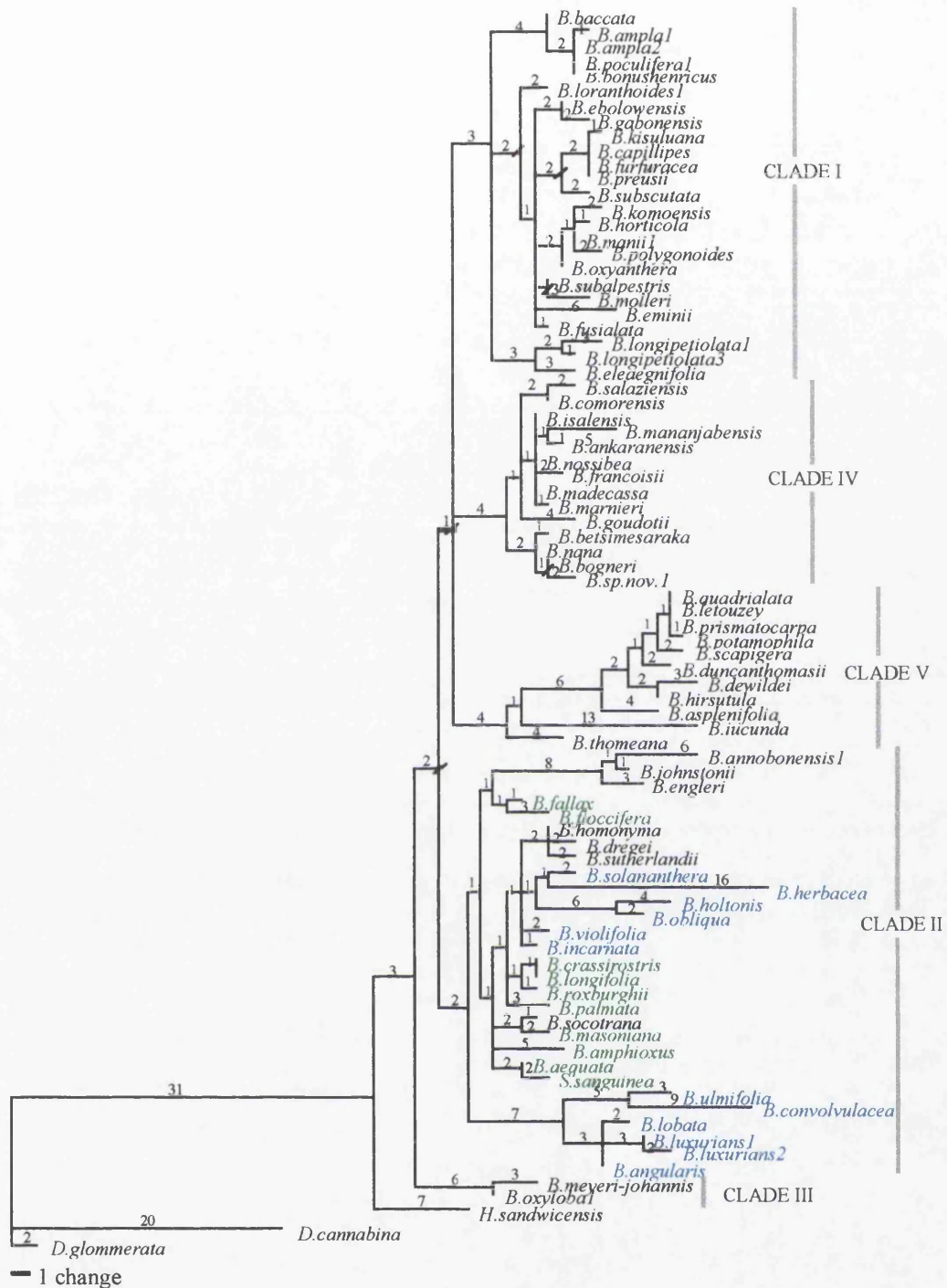


Figure 2.5 One of 10,000 most parsimonious trees based on *trnL* sequence data, using ACCTRAN optimisation. Branch lengths include autapomorphies. Nodes which are not supported in the strict consensus are indicated by a short diagonal line. *Begonia* species in black are African, in green are Asian and in blue are American. Numbers above the branches are branch lengths. Clade numbers refer to those in Fig. 2.4.

with two frequently yellow tepals in male and female flowers. Sections *Loasibegonia* and *Scutobegonia* are both monophyletic (albeit weakly supported), despite the poor sampling of section *Scutobegonia*. Sister to this core clade is *B. aspleniifolia* (96% bootstrap), one of eight species in section *Filicibegonia*. Weakly to moderately supported, but sister to this clade, are *B. iucunda*, a species from the Western Congo (Bas-Congo and Kasai regions, Democratic Republic of Congo (Zaire)) which currently has not been assigned a section (but see Chapter 5) and *B. thomeana*, the only known species in section *Cristasemen*.

Whereas Clades I, III, IV and V are comprised of uniquely African or Malagasy species, Clade II (Fig. 2.4 and Fig. 2.6) is geographically mixed, showing that African begonias do not form a monophyletic group, a result that supports previous ITS sequence data (Forrest, 2000). Basal nodes within this group lack bootstrap support. African species found here are those with a general East and South African distribution. *Begonia socotrana*, an endemic species from Socotra (an island off the Horn of Africa), also occurs in this clade. All trees resolve a paraphyletic *Rostrobegonia* with respect to the monotypic section *Sexalaria* (*B. annobonensis*), albeit with weak bootstrap support (55%). *Begonia annobonensis* is distributed from Coastal Cameroon to the Gulf of Guinea islands. The Asian species *B. fallax* and *B. floccifera* are strongly supported as part of this African clade (98% bootstrap). Section *Augustia* is strongly monophyletic (85% bootstrap), and is nested within a clade containing Asian and African species. Similarly, *B. socotrana* is sister to the Asian species *B. masoniana*.

2.3.1 Sensitivity analysis

Treating gaps as a fifth state produces aberrant results in which *Hillebrandia sandwicensis* was nested within the fleshy-fruited species, as sister to the *Baccabegonia/Squamibegonia* clade (2.7a). Treating gaps longer than one position with a fifth state for each individual character position produces errors because the algorithm assumes adjacent gap characters are independent of each other, when the entire length of

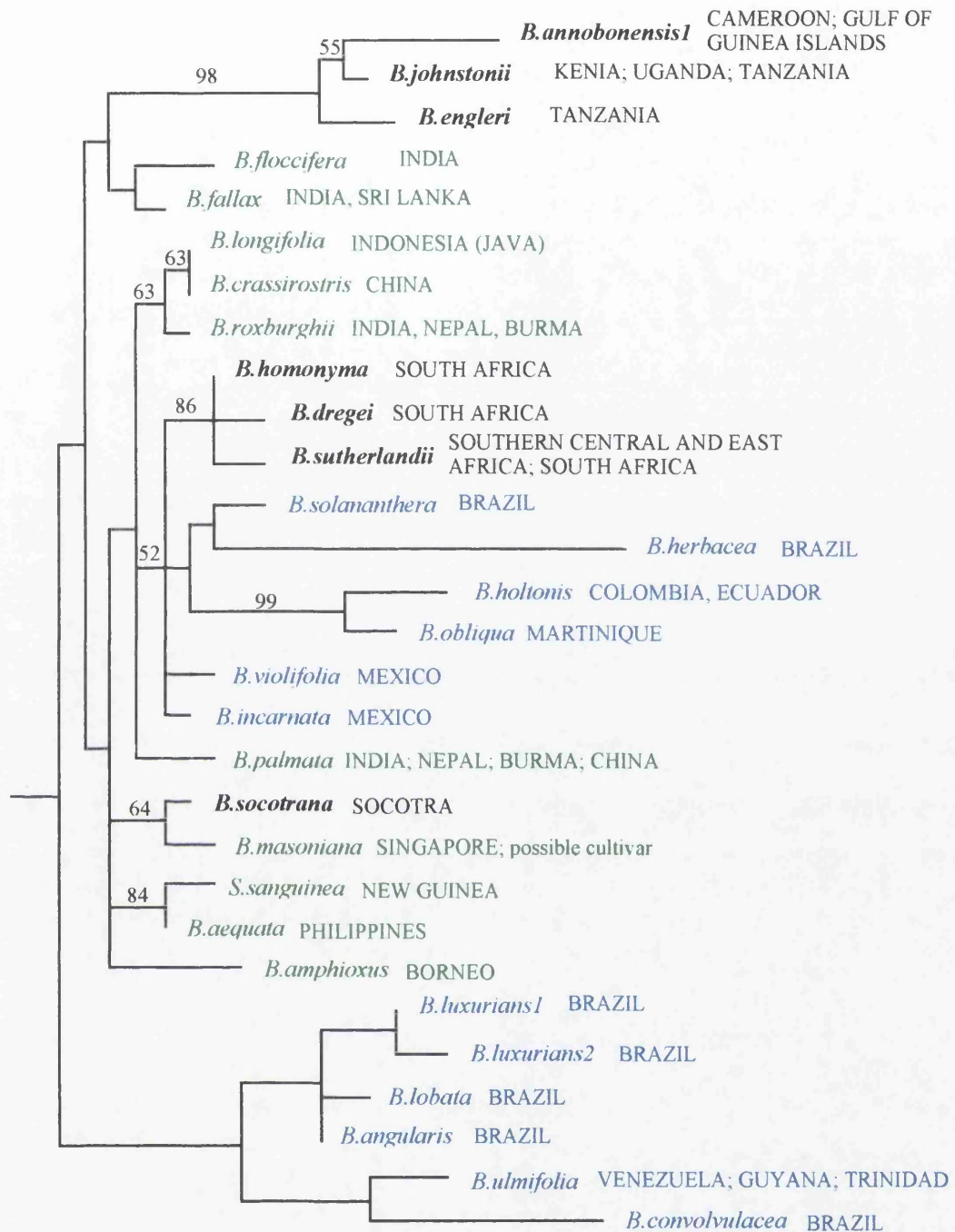


Figure 2.6 Magnified diagram of Clade II showing geographical distributions. One of 10,000 most parsimonious trees based on *trnL* sequence data, using ACCTRAN optimisation. Branch lengths include autapomorphies. All nodes are retained in the strict consensus. Numbers above the branches are bootstrap values. *Begonia* species in black are African, green are Asian and blue are American.

the gap probably represents a single insertion or deletion event (Eernisse & Kluge, 1993). Species in the *Baccabegonia/Squamibegonia* group possess a 231 bp deletion, whereas *Hillebrandia* has a 226 bp deletion in a similar, but not identical, position. In this case the overlap of their long but differently positioned gaps is assumed to represent multiple shared evolutionary events rather than two unrelated events.

Treating gaps as missing in the absence of a gap matrix produced a strict consensus topology with significant structure except among numerous Asian and American species (Fig. 2.7b). Analysis of the gap matrix alone produced an unresolved bush, except among species in sections *Tetraphila*, *Squamibegonia* and *Baccabegonia*. The differences observed by removing the gap matrix, show that most of the informative characters in the *trnL* sequence data are provided by base substitutions, but indels are important in providing grouping information, particularly among Asian and American species.

2.4 DISCUSSION

2.4.1 *The polyphyly of section Mezierea and the evolution of fleshy fruits in African Begonia*

The results from the parsimony analysis of *trnL* sequence data show section *Mezierea*, all species of which have fleshy fruits, to be polyphyletic (Figs. 2.4 and 2.5). This confirms, with far greater sampling, previous indications from other molecular studies (Badcock, 1998; Forrest, 2000), and has great significance, both with respect to the evolution of fleshy fruits in *Begonia* and the long-held idea that the presence of fleshy fruits in *Begonia* is a unique synapomorphy.

Section *Mezierea* was last revised in 1994 (Klazenga et al., 1994) and is composed of six species; *B. meyeri-johannis*, *B. oxyloba*, *B. comorensis*, *B. salaziensis*,

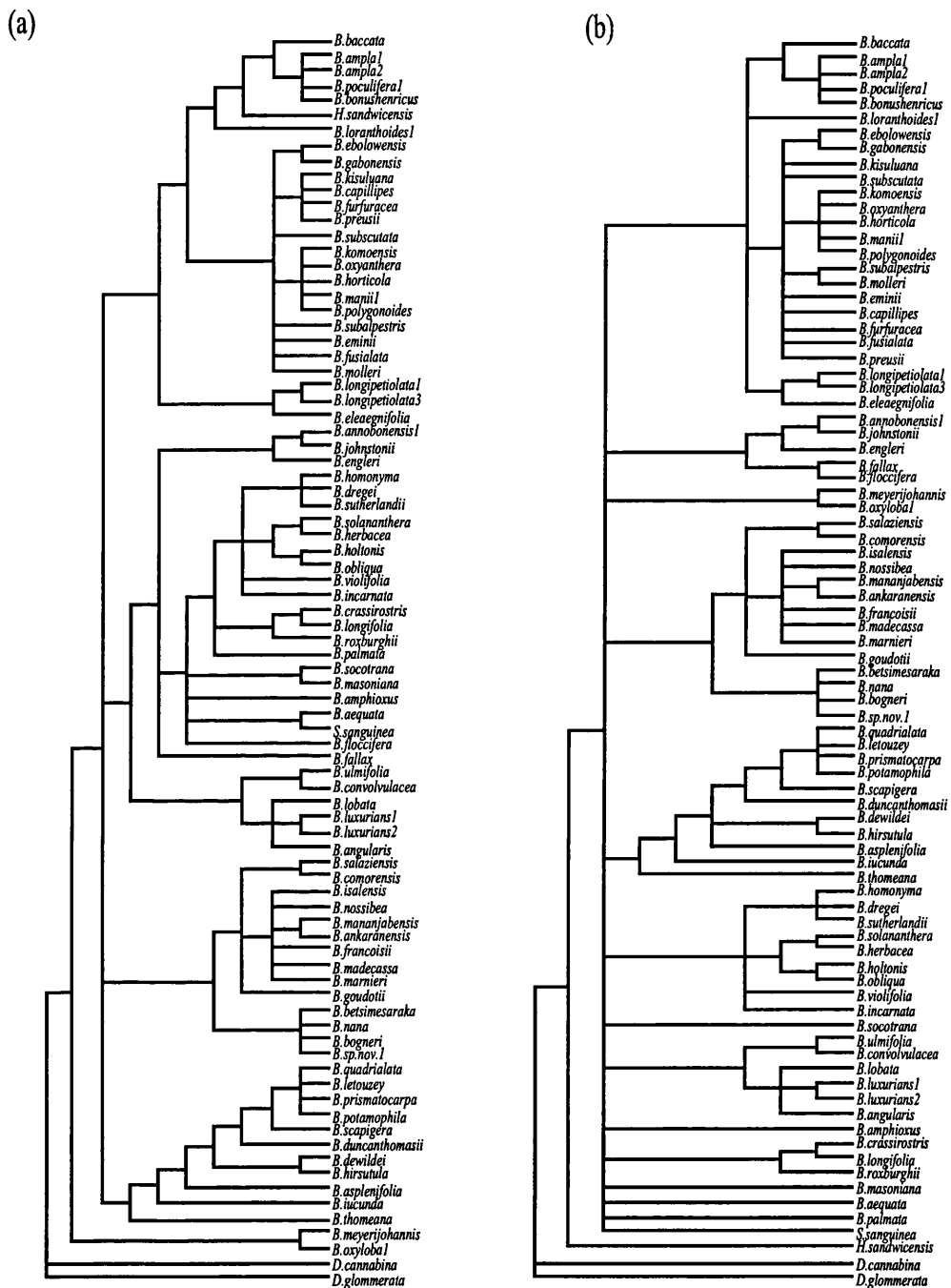


Figure 2.7 Strict consensus of a maximum of 10,000 trees generated from the heuristic search of *trnL* sequences when (a) gaps are treated as a fifth state and (b) gaps are treated as missing in the absence of a gap matrix.

B. humbertii and *B. seychellensis*. Klazenga et al. (1994: 271) described the differentiating characters of the section: "Section *Meziera* may be distinguished from all other sections by its placentation which is topographically parietal for more than 60% of the ovary. From sections *Tetraphila* and *Baccabegonia* it also differs by the indehiscence of the fruits and from section *Squamibegonia* by the absence of a perianth tube and the absence of bracts that envelop the inflorescence and persist in the infructescence." Most of its characteristics are absences of defining characters for other sections, which is often the symptom of a non-monophyletic group (Judd et al., 1999). Of all species in section *Meziera*, the species *B. meyeri-johannis* has always been regarded as aberrant or unique within the section due to its lianescent habit, unisexual inflorescences, penta-locular ovary, five styles and possible dioecy. However, as a whole, section *Meziera* is strongly heterogeneous. *Begonia salaziensis* and *B. humbertii* have female flowers with four tepals, whereas *B. comorensis*, *B. oxyloba* and *B. seychellensis* have female flowers with only two tepals, and *B. meyeri-johannis* can have two or four. In contrast, all species of section *Tetraphila* have four tepals and all members of section *Squamibegonia* have two.

Divisions observed in the section delimited using different morphological characters often conflict with each other, and none of them agree with the molecular results (Table 2.1). In the case of pollen morphology, specimens of *B. pycnocaulis* and *B. cladocarpa*, both now synonyms of *B. oxyloba*, possess different pollen types (van den Berg, 1984). It is no surprise, therefore, that although there is strong molecular evidence to separate the Malagasy and Mascarene species (*B. comorensis* and *B. salaziensis*) from the mainland and widespread African members (*B. oxyloba* and *B. meyeri-johannis*) of *Meziera*, there are no morphological characters to justify this separation. Clades like this one, which are supported by molecular evidence but not by currently recognised morphological characters, are termed cryptic. Examples of cryptic clades have been found in *Astragalus* (Wojciechowski et al., 1993), Rhamnaceae (Richardson et al., 2000) and *Andira* (Pennington & Gemeinholzer, 2000). *Begonia salaziensis* is the type species of section *Meziera*. If a new section were to be created it

Table 2.1 Relationships in section *Mezierea* hypothesised from different morphological characters.

Pollen morphology (van den Berg, 1985)	Placentation (Reitsma, 1983)	General morphology and placentation (de Wilde & Arends, 1989)	Seed morphology (de Lange & Bouman, 1992)
<u><i>B. comorensis</i>-type</u> <i>B. comorensis</i> <i>B. meyeri-johannis</i> <i>B. seychellensis</i> <i>B. cladocarpa</i> (= <i>B. oxyloba</i>) <u><i>B. oxyloba</i>-type</u> <i>B. oxyloba</i> <i>B. pycnocaulis</i> (= <i>B. oxyloba</i>)	<u>Subgroup A1</u> <i>B. oxyloba</i> <i>B. meyeri-johannis</i> <i>B. seychellensis</i>	<u>Group 1</u> <i>B. salaziensis</i> <i>B. humbertii</i> <u>Group2</u> <i>B. meyeri-johannis</i> <u>Group 3</u> <i>B. oxyloba</i> <i>B. comorensis</i> (= <i>B. comorensis</i> + <i>B. seychellensis</i>)	<u>Group 1</u> <i>B. meyeri-johannis</i> <u>Group 2</u> <i>B. salaziensis</i> <u>Group 3</u> <i>B. humbertii</i> <u>Group 4</u> <i>B. oxyloba</i> <i>B. seychellensis</i> <i>B. comorensis</i>

would have to accommodate *B. oxyloba* and *B. meyeri-johannis*. Both species are very different, one of the most obvious differences being the habit; *B. oxyloba* is an erect herb, whereas *B. meyeri-johannis* is lianescent. But *B. meyeri-johannis* also differs by its penta-locular ovaries, five styles and unisexual inflorescence (Klazenga et al., 1994). In order to create a section to accommodate these species detailed morphological studies need to be carried out to find morphological synapomorphies for this clade.

Based on pollen morphology (van den Berg, 1984) and placentation (Reitsma, 1983; de Wilde & Arends, 1989) the fleshy-fruited African sections *Mezierea*, *Tetraphila*, *Baccabegonia* and *Squamibegonia* have been considered the least derived within *Begonia*, with section *Mezierea* possessing the greatest number of primitive states. De Lange & Bouman (1991) agreed that, of the African sections possessing fleshy fruits, section *Mezierea* was the least derived, but strongly opposed the view that all fleshy-fruited African begonias represented a basal lineage within the genus. They proposed that the seed characters of these species, typically associated with zoochory,

were derived within the genus, quite distinct from those associated with the wind- or water-dispersed seeds that are more common within the genus, and that are also found in Datisceae, sister family to Begoniaceae.

In her study primarily dedicated to the phylogenetic investigation of section *Knesebeckia*, Badcock (1998: 30) attempted to answer the question "Is *Mezierea* basal within *Begonia* and does it form a clade with sections *Baccabegonia*, *Squamibegonia* and *Tetraphila*?" Using both morphological data and sequence data from the plastid region *trnC-trnD* she concluded that a clade of *B. meyeri-johannis*, *B. salaziensis* and *B. manii* (all fleshy-fruited species) formed basal dichotomies with the rest of *Begonia*. In this hypothesis, fleshy fruits would have arisen early in *Begonia*, evolving from the leathery or dry unwinged capsules characteristic not only of the genus *Hillebrandia*, but also of *Datisca*, the outgroup genus. Alternatively, and more recently, in an ITS-based phylogeny of *Begonia* created by cladistic parsimony methods, the fleshy-fruited species appear derived, nested within a wing-fruited clade (Forrest, 2000).

The *trnL* topology gives no resolution at the deeper nodes in *Begonia*, and it is therefore impossible to give a clear answer to whether the fleshy-fruited species are basal in the genus. Even though the relationships between *B. oxyloba* and *B. meyeri-johannis* are unresolved with respect to other African clades, the remaining species in the section *Mezierea* (i.e. species occurring Madagascar and the Mascarenes) are certainly not basal as they are nested within a Malagasy clade. The *trnL* phylogeny indicates clearly that fleshy-fruits evolved at least twice in Africa, once on mainland Africa and once on Madagascar, and that therefore the presence of fleshy fruits in *Begonia* does not diagnose a single group (Fig. 2.8). The convergent evolution of fleshy fruits is a common phenomenon, and has been recorded in the Melastomataceae, where fleshy fruits have evolved three times (Clausing et al., 2000), or in the Rubiaceae, where fleshy fruits are believed to have arisen 12 independent times in different genera (Bremer & Eriksson, 1992).

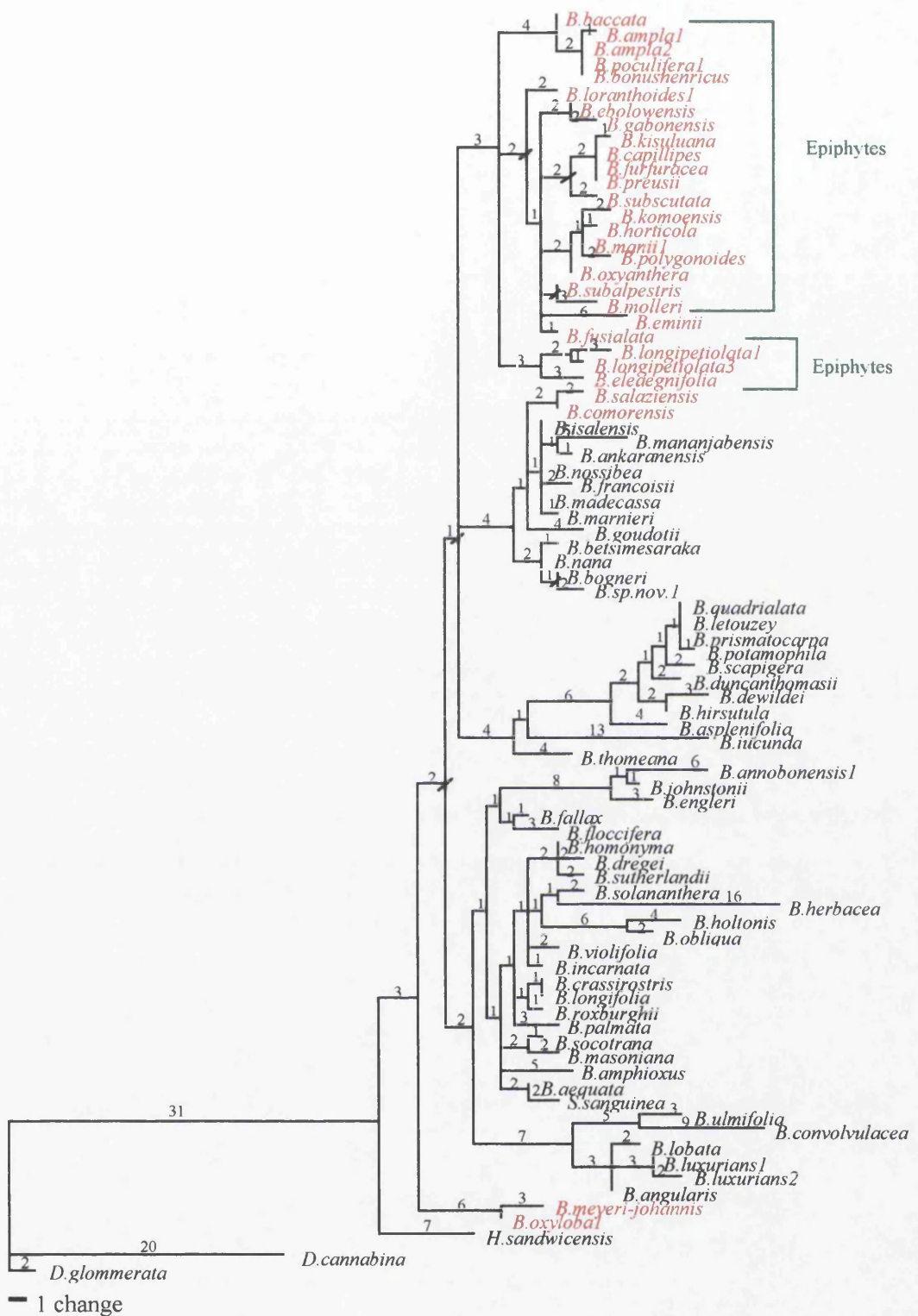


Figure 2.8 Phylogram obtained from parsimony analysis of *trnL* sequence data showing fleshy-fruited African species in red. Branch lengths include autapomorphies. Nodes which are not supported in the strict consensus are indicated by a short diagonal line. Numbers above the branches represent branch lengths.

Although a majority rule consensus shows that 74% of trees place *B. meyeri-johannis* plus *B. oxyloba* as sister to the rest of the genus, topologies showing this small clade as sister to the fleshy-fruited plus Malagasy species are present among the remaining trees. ITS data suggests that the plesiomorphic fruit-type of *Begonia* would have been winged (Forrest, 2000). Fruit-type optimisations are ambiguous for *trnL*, mirroring the conflicting evidence between ITS and *trnC-trnD* data. Unfortunately, the question as to the plesiomorphic fruit-type of *Begonia* remains unanswered.

It is significant that most fleshy-fruited species from mainland Africa are monophyletic (Clade 1, Fig. 2.4). Unlike species in section *Mezierea* which have an indumentum consisting of simple multicellular hairs, species in sections *Tetraphila*, *Squamibegonia* and *Baccabegonia* have a peltate, scale-like indumentum, and this is an important synapomorphy for the group. A more detailed assessment of this group, including a combined *trnL*, ITS and morphological phylogeny, is presented in Chapter 4.

As in the Melastomataceae, baccate fruits in *Begonia* are strongly associated with bird dispersal (Clausing et al., 2000), and in *Begonia* they are also closely associated with epiphytism (Fig. 2.8). It is possible that similar growth forms and habitats may have promoted independent origins of bird-adapted berries in African *Begonia*. It remains unclear whether epiphytism in African *Begonia* evolved subsequent to fleshy-fruits, or whether epiphytism and fleshy fruits evolved in tandem. The evolution of fleshy-fruits appears to be a good precursor of epiphytisms and it is tempting to hypothesise that if dispersed by birds the seeds of early fleshy-fruited begonias would have been deposited in the tree canopy, therefore possibly triggering an epiphytic habit.

2.4.2 Evolution of the West African yellow-flowered Begonia and related species

Clade V (Figs. 2.4 and 2.5) incorporates the hydrophilic, predominantly terrestrial, wing-fruited begonias, with two tepals in male and female flowers which are

frequently yellow. They are also frequently rhizomatous in the case of *Scutobegonia*, *Loasibegonia* and *Cristasemen*. Although weakly sampled (particularly section *Scutobegonia*) there are some indications that both sections *Scutobegonia* and *Loasibegonia* could each be monophyletic. However, this interpretation conflicts with ITS data (Forrest, 2000) that show *B. dewildei*, of section *Scutobegonia*, nested within section *Loasibegonia*. As Sosef (1994) deduced from morphological affinities, section *Filicibegonia* is sister to *Loasibegonia* plus *Scutobegonia*. *Filicibegonia* shares similarities in the inflorescences and stigmas with these two other sections, and they all possess small seeds with large collar cells (de Lange & Bouman, 1991). Levels of endemism are higher among these species than they are among the fleshy-fruited species with similar distributions, and this has been ascribed to their poor dispersal mechanism, which probably occurs by wind or rain-splash (Sosef, 1994). Assuming that sections *Loasibegonia* and *Scutobegonia* are monophyletic as currently circumscribed, there is an increase in species richness in this clade, with the basal branches consisting of single species in monotypic sections (i.e. *B. thomeana* in section *Cristasemen* and *B. iucunda*), and a more species-rich derived group (section *Filicibegonia* and sections *Loasibegonia* and *Scutobegonia*). The solitary positions held by *B. iucunda* and *B. thomeana* are supported by their unusual morphology. *Begonia thomeana* is a climber, known from São Tomé and Gabon. One of its most characteristic features, apart from its climbing habit, are its long, fusiform seeds. Similarly, *B. iucunda*, a species from the Western Congo (Bas-Congo and Kasai regions, Democratic Republic of Congo (Zaire)) has characteristic solitary flowers and a stoloniferous habit with an underground tuber, from which a rooted rhizome is produced that develops above the ground into a flowering upright stem. Whereas the branches in the more species-rich sections *Filicibegonia*, *Scutobegonia* and *Loasibegonia* are comparable to those of the fleshy-fruited or Malagasy species in Clades I and IV (Fig. 2.5), there is a substantial molecular distance between these species and *B. iucunda* and *B. thomeana*. This could reflect high extinction rates in a once widespread clade, followed by relatively recent speciation generating the diversity in *Loasibegonia* and *Scutobegonia*. Alternatively, the *B. iucunda*

and *B. thomeana* lineages may have speciated less than those leading to *Loasibegonia* or *Scutobegonia*.

2.4.3 The phylogenetic position of the East and South African begonias and questions regarding the monophyly of Asian and American species

Clade II (Figs. 2.4 and 2.5) differs strongly from the other clades by the lack of large geographically monophyletic groups; rather African, Asian and American species are interdigitated (Fig. 2.6). Section *Rostrobegonia* is most closely related to an Indian clade, section *Augustia* to American species, and *B. socotrana* (section *Peltaugustia*) is sister to *B. masoniana*, an Asian species. Similarly, neither the American nor the Asian species taxa are monophyletic. This pattern contrasts strongly with findings based on ITS sequences of 174 American, Asian and African species, which suggested geography to be the prime indicator of species relationships and showed monophyly at the continental level for South American and Asian species (Forrest, 2000; Fig. 2.2). In her study the East and South African begonias (with the exception of *B. socotrana*) emerged as sister to an American/Asian clade in the case of species in section *Augustia*, or sister to all West and Central African and Malagasy species in the case of *Rostrobegonia* and *Sexalaria*. Asian and American species were split into two clades, one for each continent. *Begonia socotrana* resolved as sister to two Indian species, a clade which itself was sister to a larger Asian clade.

Patterns resembling those found in the *trnL* intron sequence based study presented here emerged from a phylogeny based on sequence data from part of the plastid *trnC-trnD* region, where there was no clear association between phylogeny and geography (Badcock, 1998), and in a 26S nrDNA phylogeny (Forrest, 2000). The 26S phylogeny based on 35 *Begonia* species was generated to investigate deeper relationships within *Begonia* based on a slower evolving nuclear gene than ITS. Maximum parsimony analysis and maximum likelihood analyses of the 26S sequence data showed little geographic structure among the American and Asian species. Indeed,

26S appeared to give an erroneous estimate of phylogeny, since many of the relationships shown are not corroborated by any other data set. Forrest (2000) then produced an ITS phylogeny of the same species as the 26S sampling. The results of the maximum likelihood analysis showed the same geographic structure seen in the more expanded sampling. Therefore, sampling density alone cannot be the cause of section *Augustia* nesting within an American/Asian clade in the plastid DNA studies. Reasons for this discrepancy between nrDNA and cpDNA phylogenies (discussed in greater detail in the following chapter) can include non-biological reasons such as differences in sampling, or biological reasons that include sequence rate heterogeneity, lineage sorting, chloroplast capture, hybridisation and introgression. The place-holder effect (Sytsma & Baum, 1996), where topologies vary according to the choice of place-holding taxa, may also be the reason for the incongruence in this clade between the chloroplast genes and ITS.

2.4.4 Implications for the taxonomy of sections *Augustia*, *Rostrobegonia*, *Augustia* and *Sexalaria*

The general assumption that geography is a good predictor of relationships in *Begonia*, led authors such as Doorenbos et al. (1998) to assume that sections *Augustia*, *Rostrobegonia* and *Peltaugustia* were closely related, prompting comments such as “[Section *Rostrobegonia* is] closely related to section *Augustia* and possibly identical with it.” (p. 178). But as can be seen in Fig. 2.4 this is not the case, and suggests morphological heterogeneity in these sections as currently circumscribed.

Species in sections *Augustia*, *Rostrobegonia* and *Peltaugustia* constitute only about 15% of all African species, but are very characteristic in their adaptation to more seasonal conditions such as those found in present-day East and South Africa afro-montane regions. Whereas the majority of these species occur in this region, one species in section *Rostrobegonia*, *B. rostrata* (not sampled), occurs in West and Central Africa, showing a clear geographical disjunction with other species in the section. *Begonia*

annobonensis, in section *Sexalaria*, is known only from coastal Cameroon and the Gulf of Guinea islands, and is very similar to species in section *Rostrobegonia*. The *trnL* phylogeny (Fig. 2.6) shows *B. annobonensis* nested within section *Rostrobegonia*, which suggests the desirability of merging both sections. However, in the ITS phylogeny *B. annobonensis* is sister to section *Rostrobegonia* (Forrest, 2000), making a taxonomic decision without further evidence unwise.

The *trnL* sequence data give no evidence for the postulated close relationship between section *Rostrobegonia* and *Augustia*. It does, however, give evidence for a monophyletic *Augustia* and a monophyletic *Rostrobegonia*. This is not supported by studies in which broader sampling of these sections has been carried out. Forrest (2000) included *B. sonderana* (section *Rostrobegonia*) in her ITS study (there were problems amplifying the *trnL* intron for this species). This species clustered with species in section *Augustia* (*B. homonyma*, *B. dregei* and *B. sutherlandii*), indicating that neither section as currently defined is monophyletic. Partial ITS sequence data (T. McLellan, 2000, pers. comm. in Forrest, 2000) confirm the current position of *B. brevibracteata* in section *Augustia*. M. Hughes (pers. comm., 2001) believes that section *Rostrobegonia* should only include *B. engleri*, *B. johnstonii*, *B. rostrata* and possibly *B. annobonensis*, which are species characterised by being annuals or short lived-fleshy-stemmed perennials, having serrate to crenate leaf margins, a tuft of hairs at the apex of the petiole, and lacking tubers or bulbils.

2.4.5 The monophyly of Malagasy Begonia

TrnL sequence data shows a monophyletic clade (Clade IV, Figs. 2.4 and 2.5) consisting of all endemic Malagasy species. This suggests a single dispersal event to Madagascar from mainland Africa and subsequent speciation on the island. *Begonia oxyloba* which is a widespread species also found on Madagascar is excluded from this clade and probably represents a later dispersal event to Madagascar. There are approximately 50 species of *Begonia* which are endemic to Madagascar or its associated

islands (the Mascarenes, Comoros and Seychelles). In the revision of *Begonia* for the Flore de Madagascar et des Comores, Keraudren-Aymonin abstained from placing the Malagasy species into any of the sections existent at the time (1983). At present, there are four sections recognised in Madagascar: section *Nerviplaceholders* (7 species), section *Quadrilobaria* (19 species), section *Muscibegonia* (2 species) and section *Erminea* (12 species). A few species such as *B. bosseri* or *B. mangorensis* have not been ascribed to any of the existing sections (Doorenbos et al., 1998). Section *Erminea* (*B. betsimesaraka*, *B. nana*, *B. bogneri* and *B. sp. nov.* 1 in Clade IV Figs. 2.4 and 2.5) is characterised by the presence of fleshy winged fruits, and this distinction is mirrored in the monophyly of this section in the *trnL* phylogeny. In contrast, neither section *Quadrilobaria* nor *Nerviplaceholders*, both of which have dry winged fruits, are resolved as monophyletic (Clade IV, Fig. 2.4). Doorenbos et al. (1998) noted that the only probable difference between these two sections was the presence of a woody stem in section *Nerviplaceholders*. The possible lack of monophyly in these two Malagasy sections means that further work should be done to find the morphological characters, if present, that best mirror their phylogenetic relationships. This should be done in combination with broader sampling and the addition of nrDNA sequence data such as ITS. Doorenbos et al. (1998) highlighted similarities among sections *Quadrilobaria*, *Rostrobegonia* and *Augustia*, based on tepal number and caulescence, but there is no evidence from *trnL* for the close relationships between these sections.

2.4.6 Is *Begonia* the result of a rapid radiation?

The lack of resolution at the basal nodes of a molecular cladogram can be due to several reasons such as multiple substitutions at high divergence rates (Olmstead et al., 1998; Cruickshank et al., 2001), a high taxon to character ratio (Cruickshank et al., 2001), or a rapid radiation over a short period of time (Bateman, 1999; Cruickshank et al., 2001) that occurs faster than the genomic region used in phylogenetic analyses is evolving. Since both the *trnL* phylogeny presented here and phylogenies presented in other studies show either no resolution or resolution in the absence of significant

bootstrap support, there is some indication that the major lineages of *Begonia* which led to the extant species arose during a very short period of time. However, it is also true that there is character conflict among the basal nodes leading to the lack of resolution. This is indicated by the basal polytomy found in the *trnL* phylogeny being “soft” i.e. it is present in the strict consensus, but individual trees are resolved, although conflictingly at these nodes. Molecular branch lengths subtending species (or groups of species) of African *Begonia* and two American clades (one holding *B. luxurians*, *B. lobata*, *B. angularis*, *B. ulmifolia* and *B. convolvulacea*, and the other *B. solananthera*, *B. herbacea*, *B. holtonis* and *B. obliqua*; see Fig. 2.6) are particularly long, indicating faster evolutionary rates within these groups.

2.5 CONCLUSIONS

Using *trnL* sequence data to estimate phylogeny in African begonias gave well-supported and well-resolved sectional relationships, but the relationships between these clades, or basal nodes, were unresolved. Mainland fleshy-fruited species with peltate indumentum (comprising sections *Baccabegonia*, *Squamibegonia* and *Tetraphila*) are monophyletic. Species in the remaining fleshy-fruited section *Mezierea* possess an indumentum made up of simple hairs, and are not as closely related to other fleshy-fruited species as once thought. Section *Mezierea* is polyphyletic, with the Malagasy members of the section resolving within a monophyletic Malagasy clade. The terrestrial, 2-tepaled, West and Central African yellow-flowered begonias and their related species also form a monophyletic clade, with the monotypic section *Cristasemen* and *B. iucunda* (see Chapter 5) holding a solitary, basal position. The predominantly East and South African sections species in *Rostrobegonia*, *Augustia*, *Sexalaria* and *Peltaugustia* show greater affinity with Asian and American begonias and are interdigitated among them. Therefore, the *trnL* phylogeny does not support previous findings which show all American and all Asian species to be monophyletic. The molecular phylogeny agrees, on the most part, with the sectional delimitation of African species based on morphology,

although further work should be carried out to delimit boundaries between sections *Augustia*, *Rostrobegonia* and *Sexalaria*, between the Malagasy sections and within section *Mezierea*. The *trnL* topology showed high levels of similarity with the phylogeny produced from ITS sequence data in the relationships between west and central African and Malagasy species. However, there are some notable incongruences among the basal nodes and among the relationships of American and Asian species. The following chapter examines these incongruences more carefully, to investigate whether the differences reflect underlying biological processes or are a product of phylogenetic estimation procedures.

CHAPTER 3 Phylogenetic analysis of Afro-Malagasy *Begonia* based on combined nuclear ribosomal and chloroplast sequence data

3.1 INTRODUCTION

Incongruence between phylogenetic estimates from different data sets is a common occurrence and has therefore, been the topic of widespread discussion (for a recent review see Wendel & Doyle, 1998; Johnson & Soltis, 1998). As was noted in Chapter 2, analyses based on the *trnL* intron (present study) and ITS (Forrest, 2000) show some incongruence and little or no support for the basal nodes in the separate phylogenies. Determining whether this incongruence is due to "real" causes brought about by underlying biological mechanisms or "spurious" causes reflecting stochastic error in data generation and analysis can be difficult to assess, but is best achieved by studying the level of character and topological incongruence between data sets. In this chapter I investigate the root of the topological incongruence between *trnL* intron and ITS sequence data and determine whether a total evidence approach gives greater support to all clades, resolving basal relationships in *Begonia*, particularly among African clades. Since the basal relationships in the *trnL* intron phylogeny were unresolved, and those in the ITS phylogeny were poorly supported, it was hoped that a broader sampling of 26S (a relatively slowly evolving region) sequence data in combination with *trnL* and ITS data would further resolve these relationships.

3.2 CAUSES OF TOPOLOGICAL INCONGRUENCE AMONG PHYLOGENIES

There are two main causes for phylogenetic incongruence (differing topological patterns due to character conflict). Real causes which can underlie phylogenetic incongruence include convergent or rapid morphological evolution that cause

discrepancies between morphological and molecular data (Bateman, 1999), rapid diversification, lineage sorting, and hybridisation and introgression (for review see Wendel & Doyle, 1998). The main spurious reasons can be accounted for by gene choice, sequencing error (although this is now much reduced) and taxon sampling (for review see Wendel & Doyle, 1998).

There is growing evidence that true heterogeneity produced by biological or “real” processes does occur (Riesberg & Soltis, 1991), although how common this heterogeneity is remains unclear. In African *Begonia* there is evidence of natural hybridisation in some species in sections *Loasibegonia* and *Scutobegonia* (Sosef, 1994). Hybridisation has also been recorded among Asian species of the genus (Peng & Cheng, 1991; Teo & Kiew, 1999). Overall, given the number of *Begonia* species, there is little recorded evidence of hybridisation in the wild. In contrast, crossings of different species in artificial conditions, often between species from different continents, has been very successful, as is demonstrated by the vast number of hybrid cultivars in existence.

3.3 COMBINED OR SEPARATE DATA ANALYSIS?

The question of how to use different data sets in phylogenetic analyses has been the topic of heated discussion in the literature (for reviews see de Queiroz et al., 1995; Huelsenbeck et al., 1996). Three philosophies surround the topic of combining or segregating different data sets: (1) the combined or “total evidence” approach (Kluge, 1989), also termed “simultaneous analysis” (Nixon & Carpenter, 1996), (2) the consensus approach (Miyamoto & Fitch, 1995), also termed “separate analysis” (Huelsenbeck, et al., 1996) or “taxonomic congruence” (Eernisse & Kluge, 1993) and (3) the conditional combination approach (Bull et al., 1993; de Queiroz, 1993 or “prior agreement approach” (Chippindale & Wiens, 1994).

The combined “total evidence” approach states that the greater number of characters that are used in an analysis the higher the likelihood of the true tree being recovered or of increased support being found for specific relationships within the tree. It argues that data should always be combined (Hillis, 1987; Kluge, 1989; Barrett et al., 1991; Donoghue & Sanderson, 1992; Eernisse & Kluge, 1993; Kluge & Wolf, 1993).

Unlike the consensus method (see below), which considers only taxonomic congruence, the total evidence method allows characters from different partitions (i.e. different data sets within a combined analysis) to interact with each other, resolving character conflict. When large numbers of characters are all combined, even if from different sources (i.e. morphology or different genes), then the total evidence approach should provide the best estimate of phylogeny, as the true phylogenetic signal will overcome misleading effects caused by biologically induced data partition heterogeneity (Chippindale & Wiens, 1994). Results of this process may, however, recover trees which are antagonistic to one or other of the data sets, and the approach fails to recognise discrepancies in the results of separate analysis of data sets which may be due to biological (e.g. lineage sorting, chloroplast capture) rather than artificial reasons (e.g. stochastic error) (Johnson & Soltis, 1998). Therefore, combining data *a priori* leaves no space in which to explore phylogenetic signals resulting from independent data sets, and in essence denies the occurrence of natural events such as hybridisation, which can bring about this type of incongruence.

In contrast, the consensus method advocates that partitions should be analysed separately and that different phylogenetic estimates should be compared using taxonomic congruence: that is, creating a consensus of the most parsimonious trees resulting from the separate analyses (Miyamoto & Fitch, 1995). Advocates of this method were concerned that the total evidence approach, when combining a fast and a slow evolving gene, could lead to swamping of the phylogenetic signal from a slow gene by that from a faster gene because the latter provides far more characters (Miyamoto, 1985). The same scenario would occur with large and small data sets, for example the combination of molecular and morphological data, where the morphological matrix is generally comprised of a significantly smaller number of characters. However, phylogenetic signal observed in the resulting topology of a combined analysis is not necessarily correlated with the number of variable characters (as high levels of homoplasy can show), but rather to the pattern of character covariation (Gauthier et al., 1988). Eernisse & Kluge (1993:1172-3) summarised the main criticisms levelled against the consensus method; "(1) a consensus of different fundamental cladograms can be positively misleading; (2) the different data sets being analysed are equally weighted, but their constituent characters are unequally weighted when the sizes of the data sets differ; (3) there is no clear basis for achieving a

consensus of suites of equally parsimonious, fundamental cladograms; and (4) partitioning evidence into classes is artificial because there is little reason to believe such categories are mind-independent categories with discoverable boundaries."

Consensus approaches are not commonly used because the resulting consensus topologies can show considerably lower levels of resolution than trees recovered from the separate analyses, and this method does not allow independent characters to interact with each other. Advocates of the total evidence approach disagree strongly with separate analyses because the notion of partitions is artificial (Barrett et al., 1991; Eernisse & Kluge, 1993). The main criticism of consensus methods is that they, as in the total evidence approach, do not attempt to determine whether the discrepancies between different phylogenetic estimates from different partitions are the result of biological or stochastic events (Huelsenbeck et al., 1996). Furthermore, consensus methods aim to summarise congruence between different topologies irrespective of the support levels of shared clades (Chavarria & Carpenter, 1994).

The conditional combination approach is the most widespread method used to treat separate data sets (for examples of recent papers see Joy & Conn, 2001; Roalson et al., 2001; Simmons et al., 2001). This method employs statistical methods to determine whether or not phylogenetic estimates resulting from different data sets are congruent and whether data sets should be combined (Bull et al., 1993; de Queiroz, 1993; Rodrigo, 1993). This approach resembles the total evidence approach except that when the data are shown to be significantly incongruent, combining them is not advised (Huelsenbeck, 1996). This method allows for the exploration of different data sets, and room to investigate the cause of topological incongruences when present. In addition, it ensures the combination of data sets that are not significantly incongruent (Johnson & Soltis, 1998). This method, however, raises the question of measuring levels of agreement between different topologies. Numerous statistical and other methods have been proposed to measure incongruence and determine when incongruence is "significant" (reviewed by Johnson & Soltis, 1998). Dependence on a statistical value may simply give quantitative justification to something that is inherently apparent from the topologies, therefore a statistical value alone may be insufficient to determine whether or not to combine data sets (Johnson & Soltis, 1998). Fundamentally, the 5% ($P = 0.05$) threshold in congruence tests such as the incongruence length difference test (ILD,

Farris et al., 1994) at which to reject the null hypothesis is an arbitrary value and therefore should be interpreted with care, especially in borderline cases. However, if statistical tests show overwhelming support or rejection for data combination this can be useful in deciding whether or not to combine data.

Evaluating the level of incongruence by the degree of support of respective clades is a commonly used non-statistical (or qualitative) method (Seelanen et al., 1997; Eldenäs & Linder, 2000; Richardson et al., 2000). De Queiroz (1993) was the first author to suggest that bootstrap values for clades could form the basis for the combination of data partitions. Seelanen et al. (1997) used clade support as a heterogeneity test, coining the terms “soft incongruence” and “hard incongruence”. Soft incongruence reflects conflicting taxon positions or clades with low bootstrap support. In these cases data combination is recommended. Data combination should not be considered in the face of “hard incongruence”, when alternative phylogenetic hypotheses are well-supported by high bootstrap values.

The conditional combination approach was used in this study to treat multiple data sets. Levels of incongruence were examined using both Farris et al.’s (1994) incongruence length difference (ILD) test (the most commonly used statistic) and the degree of bootstrap support for particular clades. The ILD is termed the partition homogeneity test in PAUP (Swofford, 2000).

3.4 METHODS

3.4.1 *Sampling and molecular methods*

The overall aim of taxon sampling in this study was to produce an even sample of African *Begonia* species sequenced for *trnL*, ITS and 26S (Appendix 1). The *trnL* intron sequences used were the same as those in Chapter 2. The choice of non-African placeholder species in the *trnL* matrix was guided by species sequenced for 26S by Forrest (2000). A proportion of the ITS and 26S sequences were obtained from Forrest (2000). Seventeen species (mostly from Madagascar or fleshy-fruited mainland African species) which were present in the *trnL* data set but absent from Forrest's (2000) ITS

data set were sequenced for ITS. Similarly, 14 species that were present in the *trnL* data set but absent from the 26S data set were sequenced for 26S. Outgroups were selected as in Chapter 2 (*Datisca cannabina* and *D. glomerata*). *Symbegonia sanguinea* and *Hillebrandia sandwicensis* were treated as part of the ingroup.

Primers used for amplification of ITS1/ITS2 were AB101 and AB102 (Sun et al., 1994). Part of the 26S region was amplified using primers p71 and p81 (Oxelman & Liden, 1995). Sequencing methods used in this study were like those described in Chapter 2 and are not described in detail here. Amplification reactions were made up to 50 μ l: each contained 33 μ l dH₂O, 2.5 μ l 50 mM MgCl₂, 5 μ l 10X NH₄ buffer (160 mM (NH₄)₂ SO₄, 670 mM tris-HCl (pH 8.8 at 25°C), 0.1% Tween-20), 1.5 μ l of each primer at a concentration of 10 μ M, 5 μ l 2mM dNTPs, 0.5 μ l (2.5 units) of Biotaq DNA polymerase (Bioline), and 1 μ l DNA. The PCR program for ITS included an initial cycle at 94°C for 3 minutes, 30 cycles of 94°C for 1 minute, 55°C for 1 minute and 72°C for 1 minute 30 seconds, and a final single cycle at 72°C for 5 minutes. The PCR program for 26S involved an initial denaturing step at 95°C for 4 minutes followed by 30 cycles of 95°C for 30 seconds, 57°C for 1 minute and 72°C for 2 minutes, and a final extension cycle of 72°C for 7 minutes. The PCR products were cleaned using the QIAquick PCR Purification Kit columns (Qiagen) following the manufacturer's suggested protocol.

Forward and reverse sequencing reactions of the purified PCR templates were made up to 10 μ l and were performed with the Amersham Thermo SequenaseTM II dye terminator cycle sequencing premix kit. The reactions included 2 μ l of the sequencing premix, 0.25 μ l of the primer at a concentration of 10 μ M, 6.75 μ l of dH₂O, and 1 μ l (ca. 200 ng of DNA) of the PCR template. Sequence cycling parameters were 25 cycles of 96°C for 10 seconds, 50°C for 5 seconds, and 60°C for 4 minutes. The forward and reverse sequences were obtained using an ABI (Applied Biosystems) Prism 377 automated DNA sequencer. Sequences were checked using Factura (Applied Biosystems) and assembled using AutoAssembler 2.1 (Applied Biosystems).

Problems in the form of sequence polymorphism have been previously found when amplifying ITS in several *Begonia* species but when cloning was carried out and analysed all copies clustered together in the same clade (Forrest, 2000). This problem

was not widespread among the species sequenced here. Although there is high sequence divergence of this region at the section level (Forrest, 2000), divergence between closely related species is low.

3.4.2 *Phylogenetic analyses*

The same *trnL* intron alignment presented in Chapter 2 was used. ITS sequences generated in this study were added to the alignment presented by Forrest (2000). An attempt was made to realign the entire ITS matrix using CLUSTAL with subsequent manual alignment in PAUP* version 4.0b7 (Swofford, 2000). However, the CLUSTAL alignment was much worse than Forrest's (2000) alignment, and it was finally decided to use Forrest's alignment as a template to which sequences were added and small alignment readjustments made by eye. High rates of sequence divergence in parts of the ITS data set rendered large parts of the ITS1 and ITS2 alignment-ambiguous. Although alignment was straightforward among closely related species (e.g. those in section *Tetraphila*), there were alignment problems and therefore severe problems of character definition in a large part of this region between less closely related species (e.g. between species in section *Tetraphila* and species in section *Mezierea*). To investigate the effects these regions have on the topology, sensitivity analyses (Whiting et al., 1997) were carried out by both including and excluding these regions. The following characters were then excluded from the analyses: 697–856, 893–894, 902–910, 921–929, 951–997, 1174–1340, 1369–1372, 1394–1398, 1410–1415, 1436–1444, 1456–1513 and 1519–1576. The alignment-ambiguous region 374–434 of *trnL* was also excluded from all analyses as in Chapter 2. Forrest's 26S alignment was used and subsequent species added and aligned by eye. The alignment-ambiguous regions 1768–1771 and 1893–1896 were excluded from the 26S analysis.

Two matrices were created with different numbers of coded taxa: (1) ITS–*trnL* (Appendix 3); and (2) ITS–*trnL*–26S (Appendix 4). Seventy-seven ITS and *trnL* intron sequences were available for the same species (i.e. representing the same accessions). There were, however, only 48 26S sequences available, so the *trnL* and ITS matrices had to be culled, so that all matrices had identical terminal taxa, prior to a combined analysis with the 26S data.

In all analyses, an initial heuristic search involving a first round of branch swapping was carried out using the following parameters: 1000 random addition sequences (to prevent tree searches being trapped in local optima), followed by TBR swapping, and not invoking either multrees or steepest descent. Not invoking multrees results in the saving of a single optimal tree per replicate, while not invoking steepest descent limits swapping to optimal trees only. The tree output from this first round of swapping was then fed as starting topologies into a second round of swapping, invoking steepest descent and multrees and saving a total of 5000 trees.

Branch support was investigated using 10,000 bootstrap replicates, keeping only one tree per random addition sequence and swapping with TBR, with both multrees and steepest descent switched off.

To test congruence between the ITS, *trnL* and 26S data sets an ILD test was carried out, as implemented in PAUP* version 4.0b7. This test is based in random repartitioning of the combined data, where in this case the *trnL*, 26S and ITS matrices are considered as partitions of the combined data set. The null hypothesis would expect characters that give phylogenetic information to be randomly distributed between data sets. Random partitions are then carried out to test whether these provide distance values less than the distance between the original partition tests. To reject the null hypothesis (i.e. to accept incongruence between data sets) the type I error rate is commonly set at 5%, therefore when $P < 0.05$ we can reject the null hypothesis and assume that the data sets are significantly incongruent (Johnson & Soltis, 1998). Congruence was also subjectively assessed by observing congruence with respect to support values for separate clades (Seelanan et al., 1997; Eldenäs & Linder, 2000; Richardson et al., 2000).

3.5 RESULTS

Table 3.1 shows the results from both the separate and combined analyses. Over half of the ITS characters were removed from the analysis when alignment-ambiguous regions were excluded, and the number of informative characters was quartered, thus approximating the number obtained from the more readily aligned *trnL* data.

Table 3.1 Statistics from maximum parsimony analysis of separate and simultaneous analyses of *trnL*, 26S and ITS data sets.

Analysis	No. of species in matrix	Total no. of characters	No. of parsimony informative characters	No. of trees	Tree length (L)	Consistency index (CI)	Retention index (RI)
<i>TrnL</i> only	77	611	120	5000+	320	0.784	0.884
<i>TrnL</i> only	48	611	105	455	254	0.807	0.854
ITS only (ambiguous regions of ITS included)	77	935	523	9	3187	0.432	0.715
ITS only (ambiguous regions of ITS excluded)	77	401	142	5000+	740	0.478	0.713
ITS only (ambiguous regions of ITS excluded)	48	401	115	560	535	0.525	0.681
ITS+ <i>trnL</i> (ambiguous regions of ITS included)	77	1546	643	30	3537	0.461	0.725
ITS+ <i>trnL</i> (ambiguous regions of ITS excluded)	77	1012	262	5000+	1084	0.558	0.753
26S only	48	490	75	5000+	269	0.691	0.833
26S+ITS+ <i>trnL</i> (ambiguous regions of ITS excluded)	48	1502	295	150	1093	0.614	0.741

3.5.1 *trnL* intron data set

Uncorrected pairwise differences for the *trnL* intron ranged from zero between *B. bonus-henricus* and *B. poculifera*, *B. preusii* and *B. capillipes*, *B. furfuracea* and *B. capillipes*, and *B. furfuracea* and *B. preusii*, to 0.065 between *B. duncan-thomasii* and *B. herbacea*. The 77 taxon *trnL* intron matrix had a total of 611 characters, of which 120 were parsimony informative. The heuristic search produced 5000 most parsimonious trees (the maximum permitted to accumulate) with a length of 320 steps, CI of 0.784 and RI of 0.884. Figure 3.1 shows the strict consensus of all most-parsimonious trees. The analysis of the *trnL* sequence data gave the same strict consensus topology (Fig. 3.1) as that produced in the full *trnL* analysis in Chapter 2 (Figs. 2.1 and 2.2), even though fewer species were sampled (77 as opposed to 84). Although relationships among basal nodes were poorly resolved, all 5000 most parsimonious trees agreed on four major clades. Clade 1 (Fig. 3.1) comprises the mainland African fleshy-fruited species with the exclusion of *B. meyeri-johannis* (section *Mezierea*); it consists of sections *Baccabegonia*, *Squamibegonia* and *Tetraphila*. All sampled endemic Malagasy species are monophyletic in Clade 2 (Fig. 3.1). This is particularly relevant to species currently included in section *Mezierea* (*B. salaziensis*, *B. comorensis* and *B. meyeri-johannis*). As discussed in the previous chapter, there is now strong evidence that this section is not monophyletic. Clade 3 (Fig. 3.1) includes sections *Loasibegonia*, *Scutobegonia*, *Filicibegonia* and *Cristasemen*, together with *B. iucunda*; this group consists of West and Central African terrestrial, hydrophytic begonias, possessing winged fruits and (in most species) yellow flowers.

The species adapted to more seasonal habitats of eastern and southern Africa or coastal regions of West and West Central Africa (sections *Rostrobegonia*, *Augustia*, *Sexalaria* and *Peltaugustia*) are more closely related to American and Asian species than they are to other African begonias, as is demonstrated by Clade 4 (Fig. 3.1). The African *B. annobonensis*, the single species in section *Sexalaria*, is nested within section *Rostrobegonia*, suggesting the possibility of amalgamating these two sections.

For the *trnL* phylogeny, major groups with strong bootstrap support are the Malagasy clade (Clade 2) (91%), the monophyletic section *Squamibegonia* (87%), the

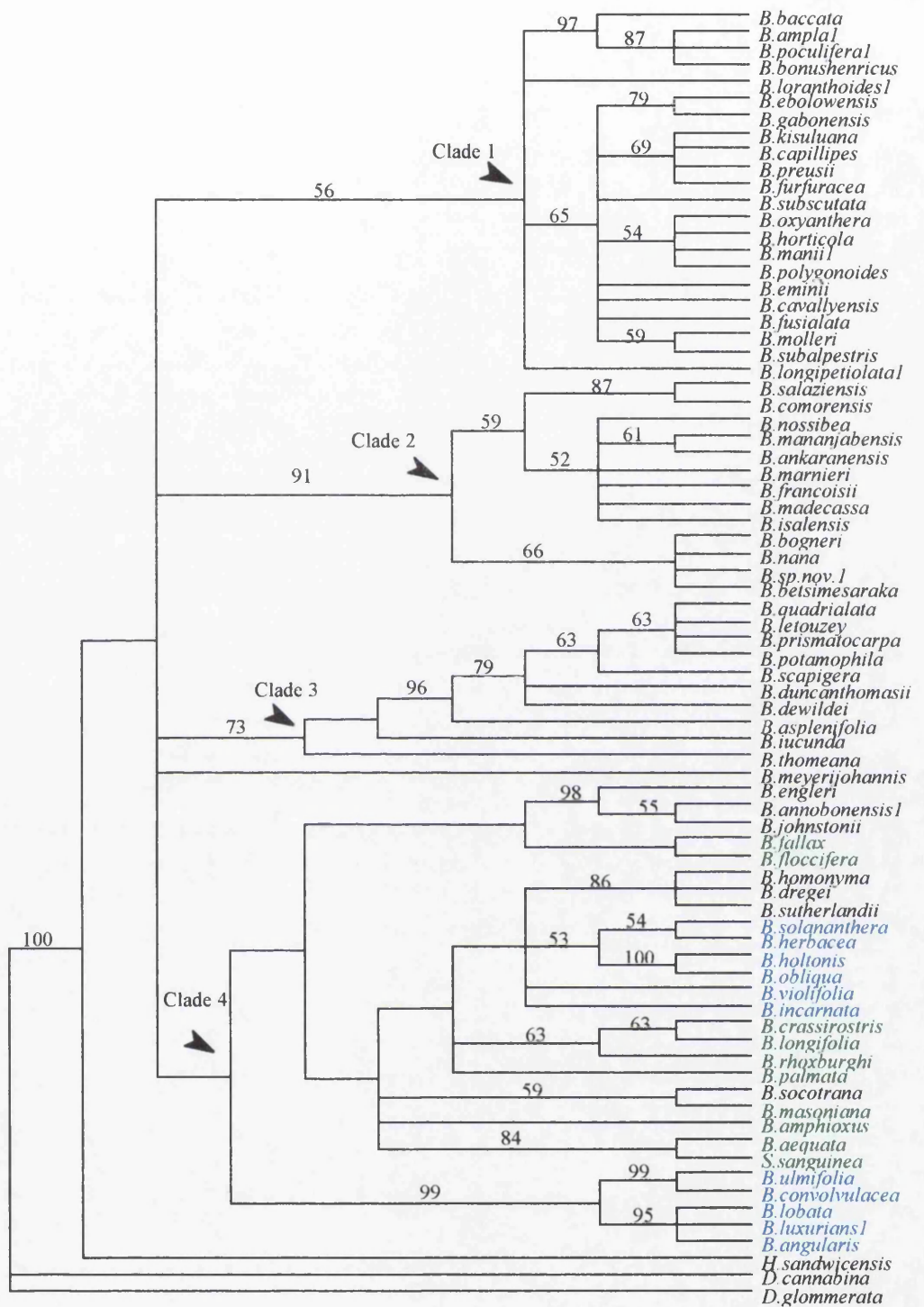


Figure 3.1 Strict consensus of 5000 most parsimonious trees of 320 steps produced by maximum parsimony analysis of *trnL* intron data (77 taxon matrix). Numbers above the branches are bootstrap values. African species are black, Asian are green and American are blue.

sister relationship of *B. baccata* to this clade (97%), the monophyly of sections *Rostrobegonia* + *Sexalaria* (98%), and several groupings within Clade 4. Overall, bootstrap values are moderate to low in many cases, due to short branch lengths and low levels of sequence divergence.

Analysis of the 48 taxon *trnL* sequence matrix gave very similar results in terms of topology and bootstrap support for particular clades (Fig. 3.3a) as the 77 taxon matrix. The analysis yielded 455 trees of length 254 steps, CI of 0.807 and RI of 0.854.

3.5.2 ITS data set

Uncorrected pairwise differences for ITS ranged from zero between *B. cavallyensis*, *B. subscutata* and *B. oxyanthera* and 0.22 between *B. floccifera* and *B. herbacea*. A heuristic search of the 77 taxon ITS data set gave variable results, depending primarily on whether or not alignment-ambiguous areas were included. When these ambiguous regions were included a heuristic search yielded only nine most parsimonious trees of length 3187 steps. The CI of 0.432 and RI 0.715 show that although characters are highly homoplasious they do give grouping information. The strict consensus of all nine trees (Fig. 3.2a) gave the same result as the ITS strict consensus topology presented by Forrest (2000) in which her alignment-ambiguous regions were removed, even though sampling in the present study was much lower (77 as opposed to 177 coded species). The similarities and differences between Forrest's ITS phylogeny and the *trnL* phylogeny were discussed in Chapter 2. However, comparison of Figs. 3.1 and 3.2a show that both trees agree on a monophyletic Malagasy clade (including all Malagasy endemics) (Clade 2) and a clade consisting of the West and Central African yellow-flowered begonias and affiliated species (Clade 3). The positions of *B. iucunda* and *B. thomeana* are reversed in Clade 3. The ITS phylogeny gives better resolution of the fleshy-fruited species in Clade 1 and much greater bootstrap support (100%). In addition, in Clade 1, *B. loranthoides* and *B. longipetiolata*, two species in section *Tetraphila*, show closer relationships to sections *Squamibegonia* and *Baccabegonia* than to other species in section *Tetraphila*. This relationship is well-supported by a bootstrap value of 98%. Although *trnL* alone could not resolve the position of *B. meyeri-johannis*, this analysis places it as sister to all Central, West African and endemic Malagasy species (Clades 1, 2 and 3 collectively). Basal nodes are

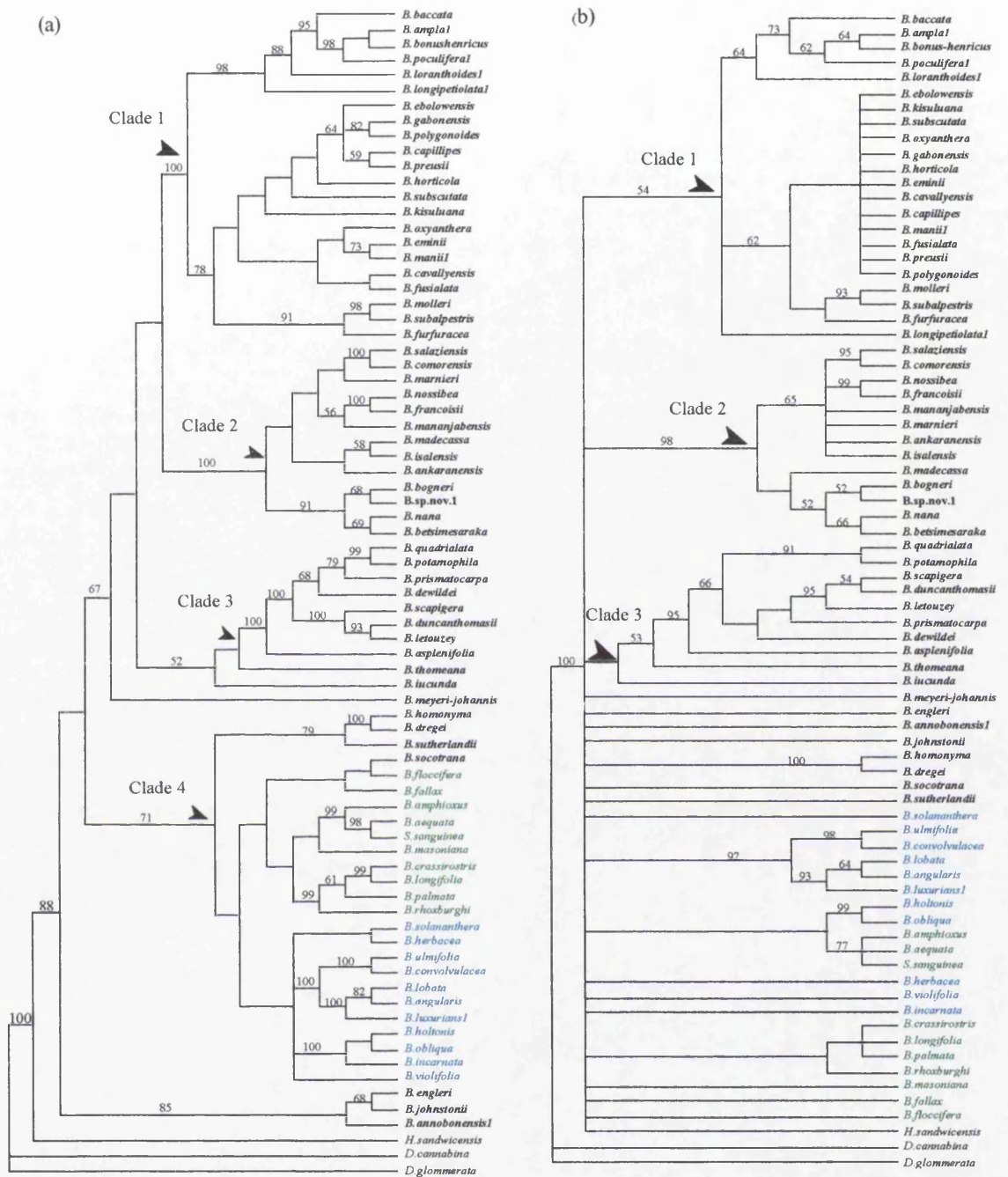


Figure 3.2 Strict consensus of trees produced from a maximum parsimony analysis of the 77 taxon ITS data in which (a) ambiguous regions were included in the analysis, and (b) ambiguous regions were excluded from the analysis. Numbers above the branches represent bootstrap support values. African species are black, Asian in green and American in blue.

poorly supported. Species in sections *Rostrbegonia* and *Sexalaria* (*B. engleri*, *B. johnstonii* and *B. annobonensis*) are shown as sister to the rest of *Begonia*, although this lacks high bootstrap support and strongly contrasts with the placement of these taxa in Clade 4 of the *trnL* tree (Fig. 3.1). Finally, there is a strong geographic element to the monophyly of the American and Asian species (Fig. 3.2a), a pattern seen in Forrest's (2000) phylogeny but not corroborated by the *trnL* phylogeny (Fig. 3.1) or the ITS phylogeny where ambiguous alignment regions were excluded (Fig. 3.2b).

Removing ambiguous regions left 401 characters, of which 142 were parsimony informative. This ITS alignment yielded 5000+ most parsimonious trees of length 740 (over four times shorter than when ambiguous regions were included). The CI for these trees was 0.478 and the RI was 0.713, showing that removing the ambiguous regions did not affect the overall CI and RI values, and therefore the overall degree of homoplasy. Figure 3.2b shows the strict consensus for these trees. Clades 1, 2 and 3 comprise the same species as in the equivalent clades in Figure 3.2a, albeit with less resolution among them. The relationships among and between American, Asian, and East and South African begonias in Clade 4 were most affected by removing ambiguous regions (Fig. 3.2a), and completely collapsed (Fig. 3.2b). Due to the uncertainty in terms of character definition, ambiguous regions were excluded from all the remaining analyses.

A heuristic search of the 48 taxon ITS matrix (in which ambiguous regions were excluded) produced a considerably different consensus topology (Fig. 3.3b), although differences with the 77 taxon analysis are among the basal nodes that have no bootstrap support. The analysis yielded 560 trees of length 535, a CI value of 0.525 and RI of 0.681. Unlike the *trnL* sequence data, the analyses showed ITS sequence data to be sensitive to taxon sampling. This may be caused by severe alignment ambiguities brought about by highly divergent sequences in ITS. Forrest's (2000) results, showed significant topological differences between strict consensus topologies from 177 taxon and 38 taxon parsimony analyses. There were also contrasting results between Forrest's (2000) parsimony and maximum likelihood analyses, with the maximum likelihood analysis showing results more comparable with the *trnL* intron results. Maximum likelihood methods are known to correct for super-imposed substitutions (Doyle & Davis, 1998), and this is probably the reason for the effects seen in the different

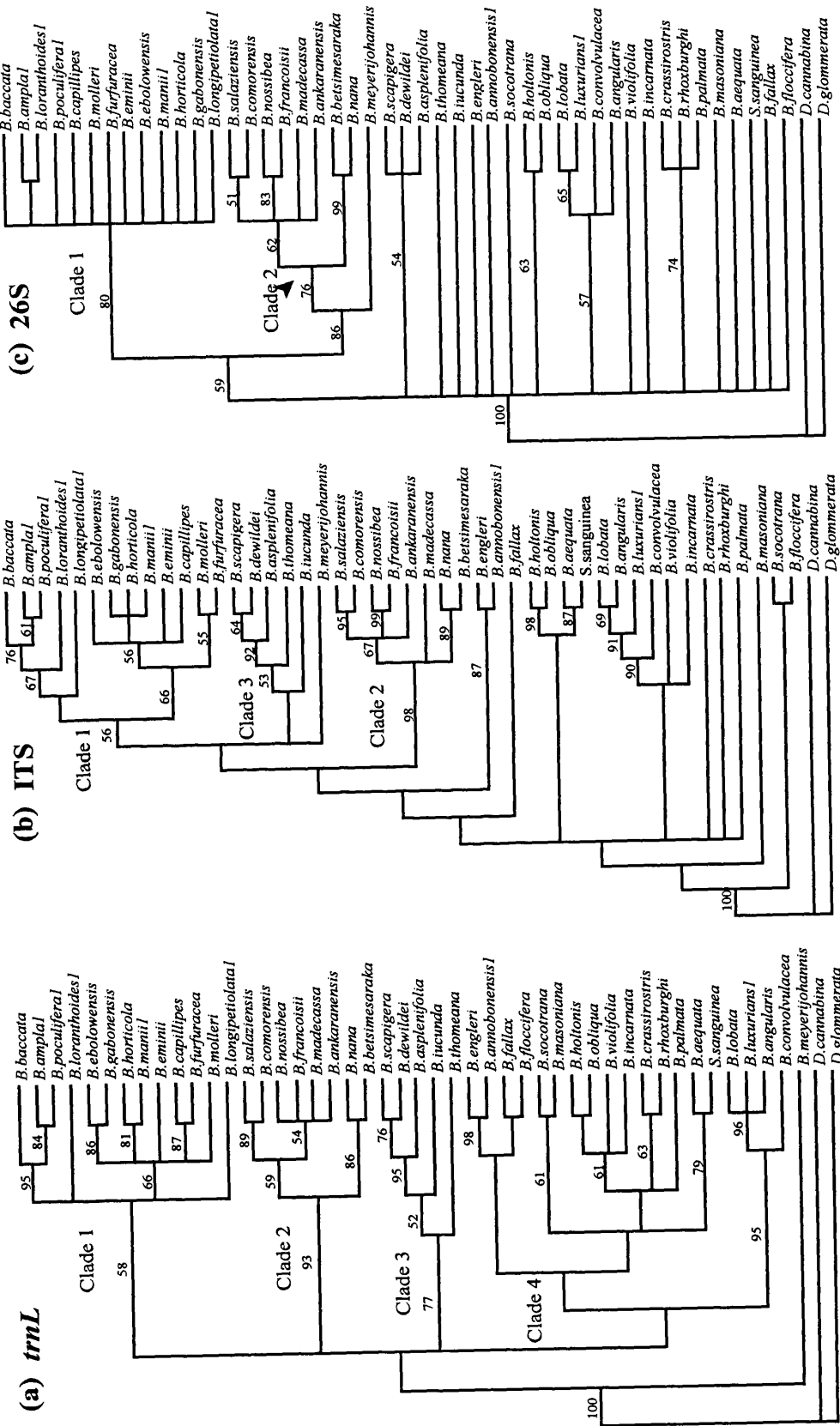


Figure 3.3 Strict consensus of the separate maximum parsimony analyses of 48-taxon matrices generated from (a) *trnL*, (b) ITS and (c) 26S.

analyses. Sequence divergence for ITS between distantly related species of *Begonia* is so high, that super-imposed substitution seems likely. Removing the ambiguous regions in conjunction with lower sampling shows serious effects on results. Whereas most of the African clades are comprised of the same species, the structure of the backbone in this culled ITS phylogeny has no equivalent or support in any other analysis. Analysis of sequences with high levels of homoplasy may be more sensitive to taxon sampling than sequences from regions with lower levels of homoplasy (as is the case for *trnL* intron in this study). Clearly, ITS is evolving so quickly that it is at the limit of its usefulness for resolving relationships across all *Begonia* species.

3.5.3 26S data set

Uncorrected pairwise differences ranged from zero between *B. molleri*, *B. capillipes* and *B. ebolowensis* to 0.17 between *D. cannabina* and *B. baccata*. The greatest difference within the ingroup was 0.15 between *B. baccata* and *B. betsimisaraka*. Of the 490 characters included, 75 were parsimony informative. A heuristic search on the 48 taxon 26S data matrix yielded 5000+ most parsimonious trees, with CI 0.691 and RI 0.833. Figure 3.3c shows the strict consensus for these trees. All trees agree on a well-supported (80%) monophyletic fleshy-fruited clade including species in sections *Squamibegonia*, *Baccabegonia* and *Tetraphila* (Clade 1, Fig. 3.3). The endemic Malagasy species form the well-supported (76%) Clade 2. *Begonia meyeri-johannis* is situated as sister to the Malagasy species in a well-supported relationship (86%) not resolved by ITS or *trnL*. In addition, the fleshy-fruited species in Clade 1 are sister to the Malagasy species plus *B. meyeri-johannis*; although the relevant bootstrap values are low, this relationship is mirrored in the ITS phylogeny when ambiguous regions are included. The rest of the tree is a polytomy with small, moderately supported groupings among the placeholder taxa. Some relationships recovered by the 26S data are in the basal nodes, which are poorly resolved by both ITS and *trnL* alone.

3.5.4 Congruence tests

ILD tests were carried out for the 77 taxon ITS and *trnL* matrices and for the 48 taxon ITS, *trnL* and 26S matrices. The partition homogeneity test between the *trnL* and

ITS 77 taxon data sets gave a value of $P = 0.107$ (not significant) when the ambiguous regions were included and $P = 0.074$ when they were removed. The partition homogeneity test results for the 48 taxon matrix including ITS, *trnL* and 26S are as follows: 26S vs. ITS, $P = 0.126$ (not significant); 26S vs. *trnL*, $P = 0.011$ (significant); and *trnL* vs. ITS, $P = 0.339$ (not significant). Whereas there is statistically no significant incongruence between the 26S and ITS and between *trnL* and ITS, there is significant incongruence between the 26S and *trnL* data sets. If there is no significant incongruence between 26S and *trnL* and between *trnL* and ITS, logically there should not be any significant incongruence between 26S and *trnL*. This inference, is not however, suggested by the P value of 0.011. The 26S region of the nrDNA is upstream from the ITS tandem repeat region, forming part of the same locus and should therefore track the same evolutionary history as ITS, as they are unlikely to be affected by recombination. Given this discrepancy between P values, and the fact that incongruences between the three different gene topologies are poorly supported, it seems reasonable to combine all three data sets.

3.5.5 Combined data sets

3.5.5.1 ITS and *trnL*

The 77 taxon matrix of combined *trnL* and ITS sequences contained 1012 characters, of which 262 were parsimony informative. Cladistic analysis excluding alignment-ambiguous regions of ITS, yielded 5000+ most parsimonious trees of length 1084, CI of 0.558 and RI of 0.753. The strict consensus tree (Fig. 3.4) shows the same topological pattern as for the *trnL* data alone, but with little resolution in Clade 4 where most of the conflict between the data sets resides. Unfortunately, data combination cannot resolve basal nodes and therefore gives little information on the relationships among the major clades. This could have occurred because there are still not enough characters to resolve these nodes, or ITS may not be useful at this taxonomic level and regularly disagrees with *trnL*. Bootstrap values are better than those from the *trnL* analysis, giving increased support values for the major clades, particularly Clade 1 (56% bootstrap in the *trnL* only topology and 93% in the combined topology) and Clade 4 (no support in the *trnL* topology and 62% in the combined topology).

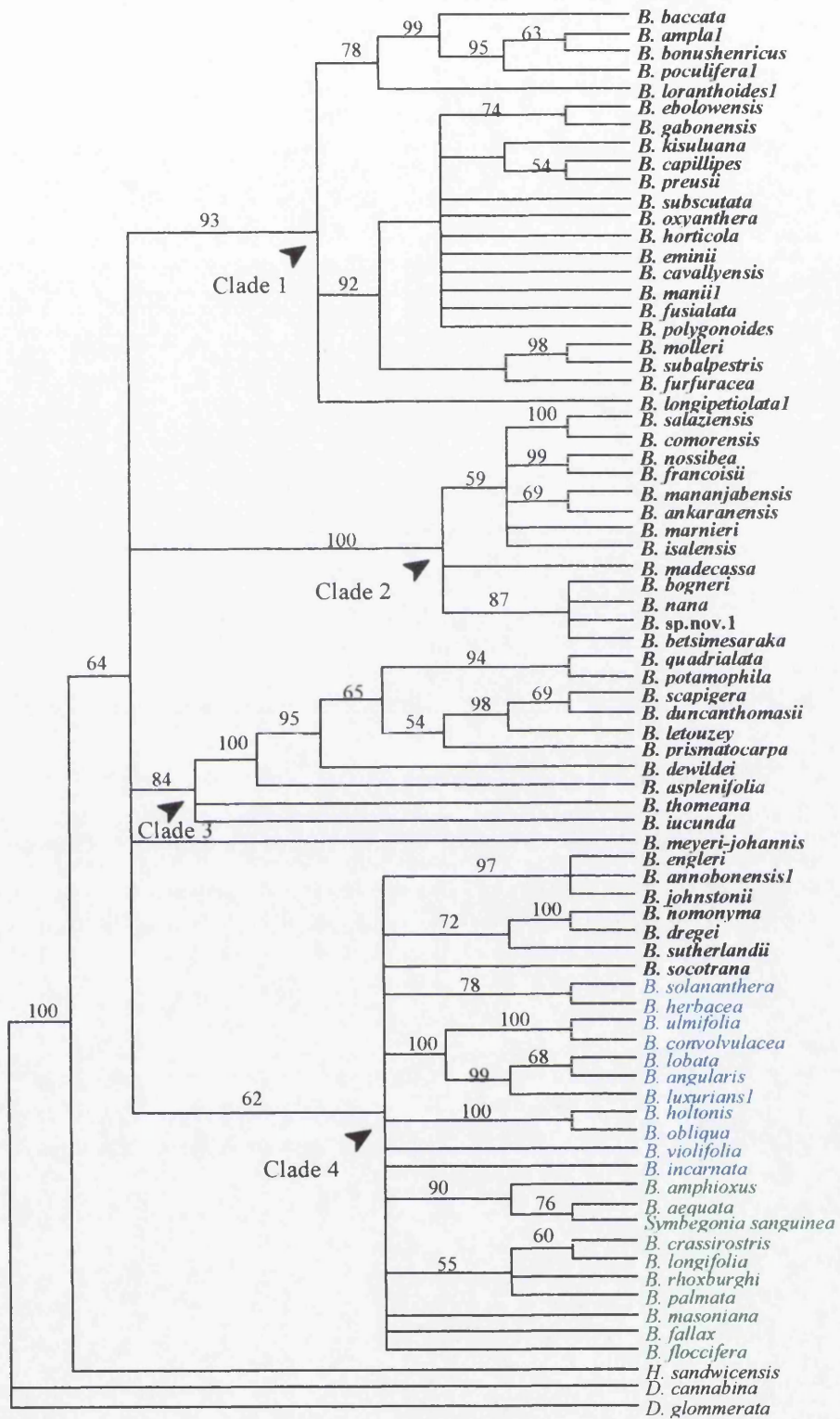


Figure 3.4 Consensus tree of 5000 most parsimonious trees produced by maximum parsimony analysis of combined *trnL* intron and ITS data where alignment-ambiguous regions have been excluded from the analysis. Values above branches represent bootstrap support. African species are in bold, Asian in green and American in blue.

Figure 3.5 shows a randomly selected most parsimonious tree. Branch lengths vary greatly in different major clades. Clades 1 and 2 (the fleshy-fruited begonias and Malagasy begonias, respectively) have uniform branch lengths from the more basal to the more derived species. Clade 3, comprising the yellow flowered begonias and their allies, shows an unbalanced topology with long branches at the base and shorter branches towards the apex. However, branch lengths are on average longer in this clade than in the other two African clades. Clade 4 is very variable in branch length which could be a reflection of sampling artefact since the greatest diversity of begonias occur in America and Asia and if entirely sampled this clade would encompass about 1200 species. Alternatively, accelerated molecular rates may have caused species to exhibit long branch lengths.

3.5.5.2 ITS, *trnL* and 26S

The 48 taxon matrix, which combined ITS, *trnL* and 26S sequences, had 1502 characters of which 295 (19.7%) were parsimony informative. The heuristic search yielded 150 most parsimonious trees of length 1093, CI of 0.62 and RI of 0.74. The combination of 26S, *trnL* intron and ITS sequences was able to resolve basal relationships within *Begonia*, particularly among the African species (Fig. 3.6). Although bootstrap support values are only moderately significant for these basal relationships, this is a significant advance from the general polytomies or entirely unsupported relationships which have resulted from the analysis of ITS and *trnL* sequences alone. In the combined analysis, *B. meyeri-johannis*, which showed an unresolved position in previous studies is sister to the endemic Malagasy taxa. As seen in the separate analyses, the endemic Malagasy taxa are monophyletic including *B. salaziensis* and *B. comorensis* (Clade 2, Fig. 3.6). Because of their fleshy fruits, these two species belonging to section *Mezierea* were never hypothesised to have close relationships with other Malagasy taxa, all of which have winged fruits. This Malagasy + *B. meyeri-johannis* clade is sister to the fleshy-fruited African *Begonia* clade (Clade 1). The mainland African, yellow-flowered *Begonia* and related taxa (sections *Loasibegonia*, *Scutobegonia*, *Cristasemen*, *Filicibegonia* and *B. iucunda*) are also monophyletic (Clade 3), as seen in previous studies and in the single-gene analyses; however, they are together sister to a fleshy-fruited plus Malagasy clade. The East and South African begonias join a poorly resolved clade with American and Asian species

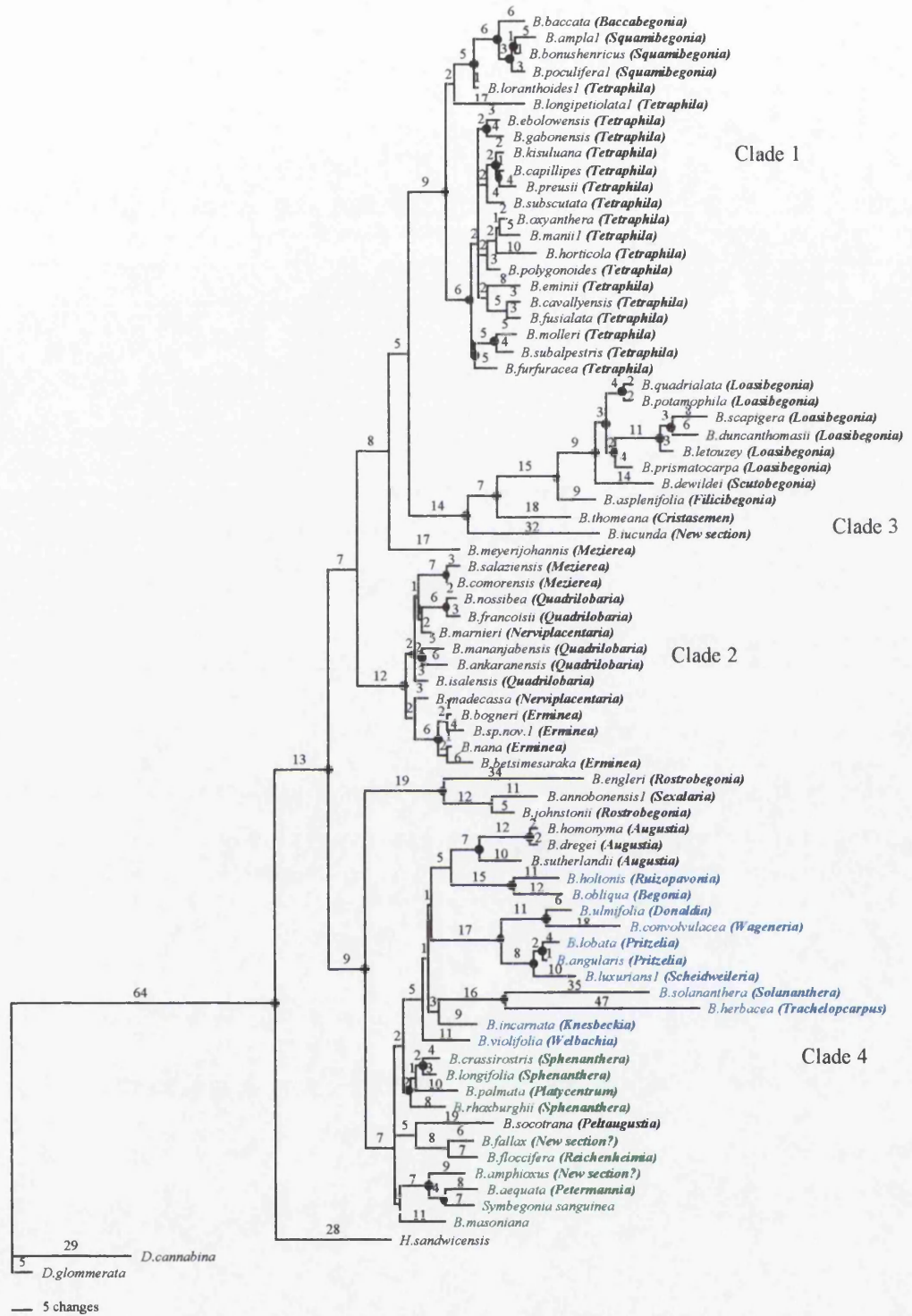


Figure 3.5 One of 5000 most parsimonious trees produced by a maximum parsimony analysis of combined *trnL* intron and ITS data. Values above the branches represent branch lengths. Black circles are the nodes that are retained in the strict consensus. Section names are in parentheses. Species which occur in Africa are in black, Asia in green and America in blue.

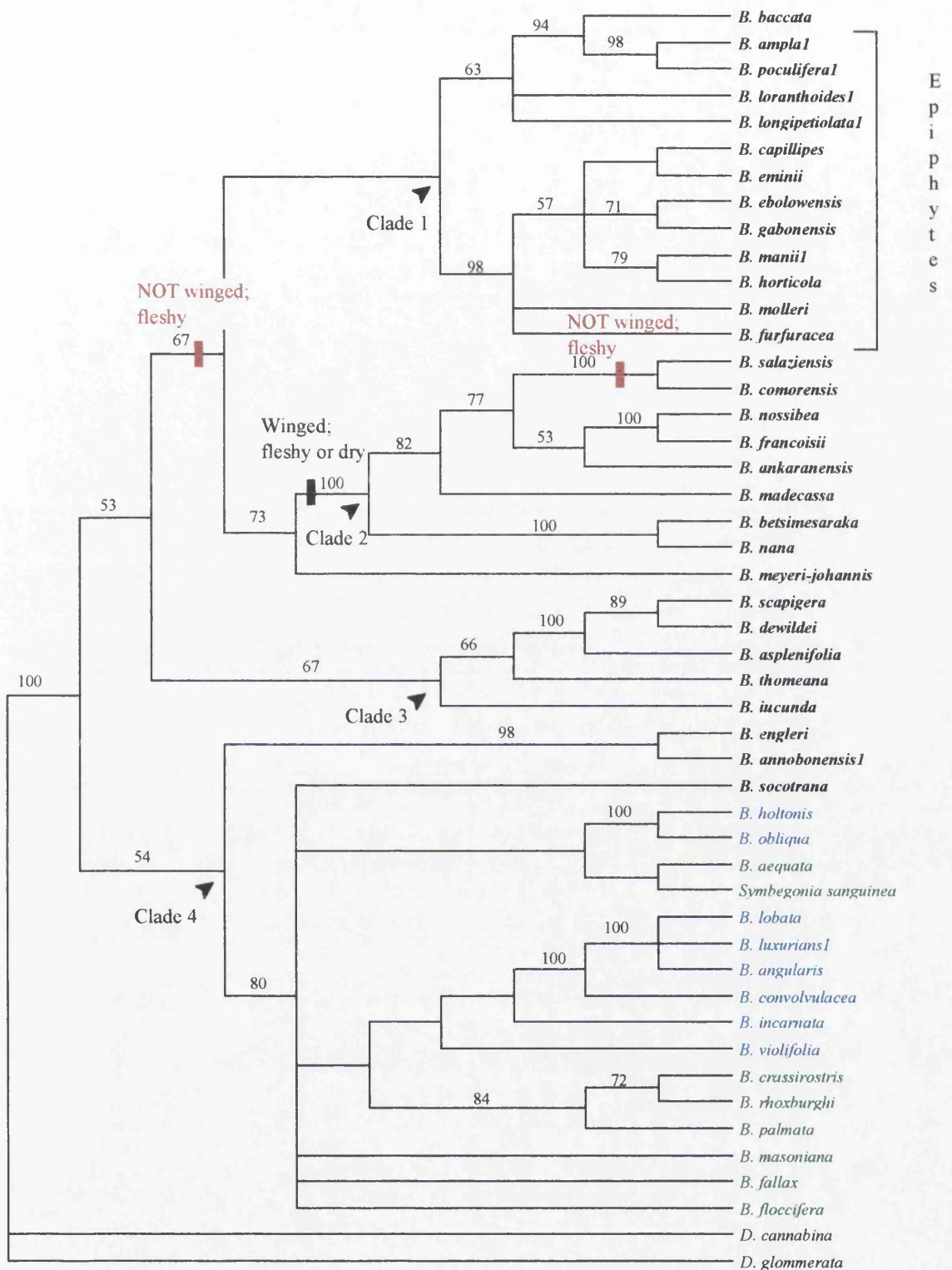


Figure 3.6 Strict consensus of 150 trees generated by the maximum parsimony analysis of the 48 taxon combined *trnL*, ITS, and 26S matrix. Values above the branches represent bootstrap support. Presence of fleshy fruits is mapped across the tree. Species which occur in Africa are in black, Asia in green and America in blue.

(Clade 4); the close relationships between this group of African begonias and American and Asian species corroborates earlier findings and the single-gene analyses.

3.5.6 Molecular evolution

Figure 3.7 charts the number of steps per character optimised on a single most parsimonious tree from the combined 26S, *trnL* and ITS analysis. The *trnL* intron has an even distribution of substitutions along its entire length with variable characters changing a maximum of six times. In contrast, ITS1 and ITS2 positions change a maximum of 14 times. This indication of high levels of homoplasy is widespread throughout the entire ITS region except in the conserved 5.8S gene. Although most characters in 26S show low levels of homoplasy, a few sites change at a similar rate to ITS, up to a maximum of 12 times. The differences in levels of homoplasy between the data sets can clearly be seen in Figure 3.8, where ITS has a greater number of characters with more steps. On average the number of changes per site (tree length divided by number of variable positions) is 2.7 for *trnL*, 5.2 for ITS, and 3.59 for 26S.

3.6 DISCUSSION

3.6.1 The value of different genes for phylogeny reconstruction in Begonia

The ITS region had a maximum divergence of 33% within ingroup taxa and 37% between ingroup and outgroup species. Removing the highly conserved 5.8S region from the calculation gives a maximum 49% divergence between ingroup and outgroup species and a maximum 47% between ingroup species. This high level of variation makes homology assessment and character definition by sequence alignment in large parts of the ITS1 and ITS2 regions virtually impossible. Homoplasy and alignment ambiguities can be the primary cause of phylogenetic noise (Lake, 1991). Therefore, the high rate of molecular evolution of ITS, compounded by a complex secondary structure, means we could expect phylogenetic signal to be obscured by homoplasy (Wendel & Doyle, 1998), with long branch attraction (Felsenstein, 1978) as one likely expression of this homoplasy. Nonetheless, ITS does provide phylogenetic signal, and many of the relationships, particularly among African species, uncovered by

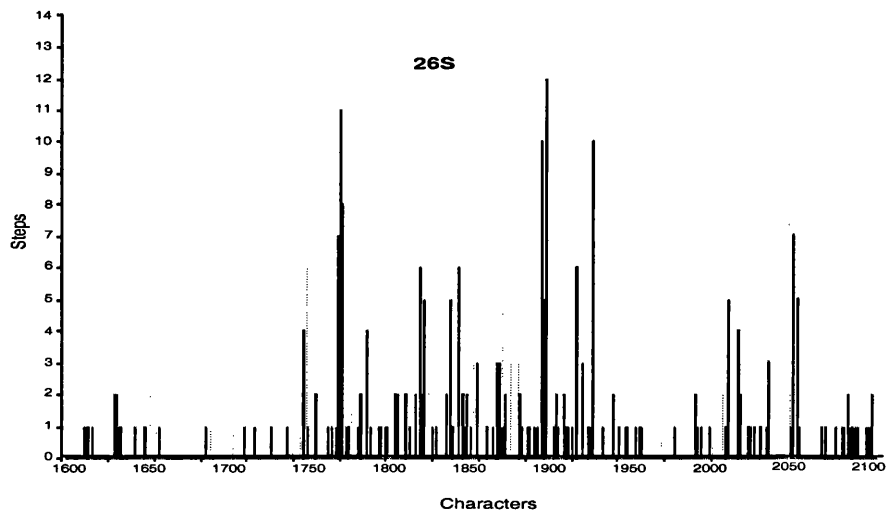
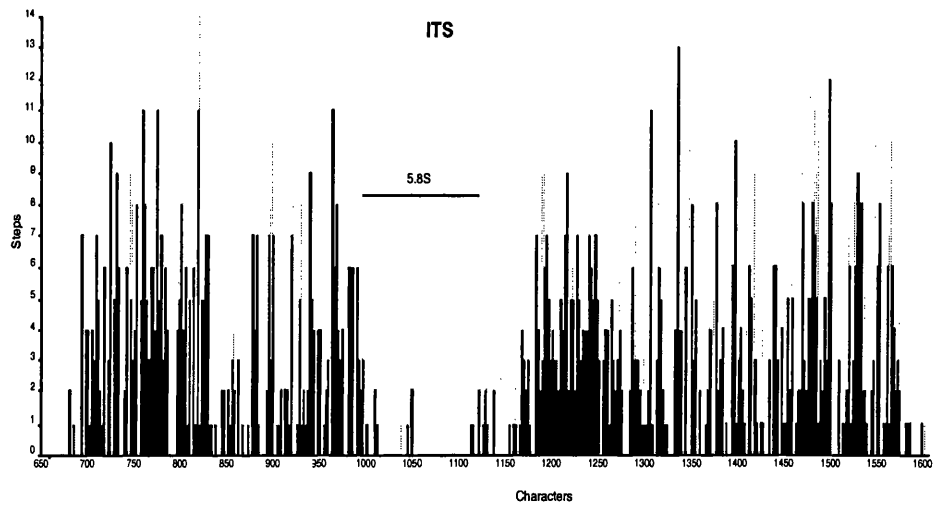
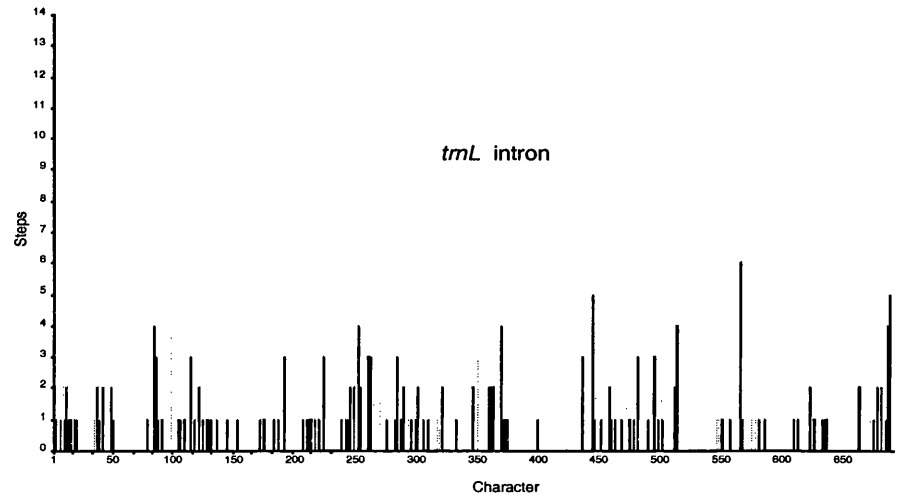


Figure 3.7 Number of steps per character optimised on a single most parsimonious tree from the combined 26S, *trnL* intron and ITS analysis.

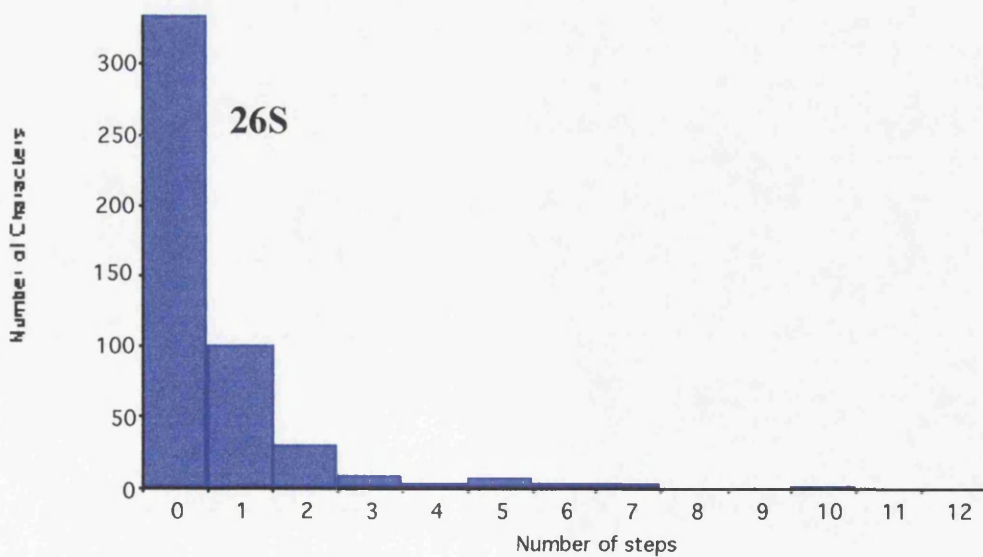
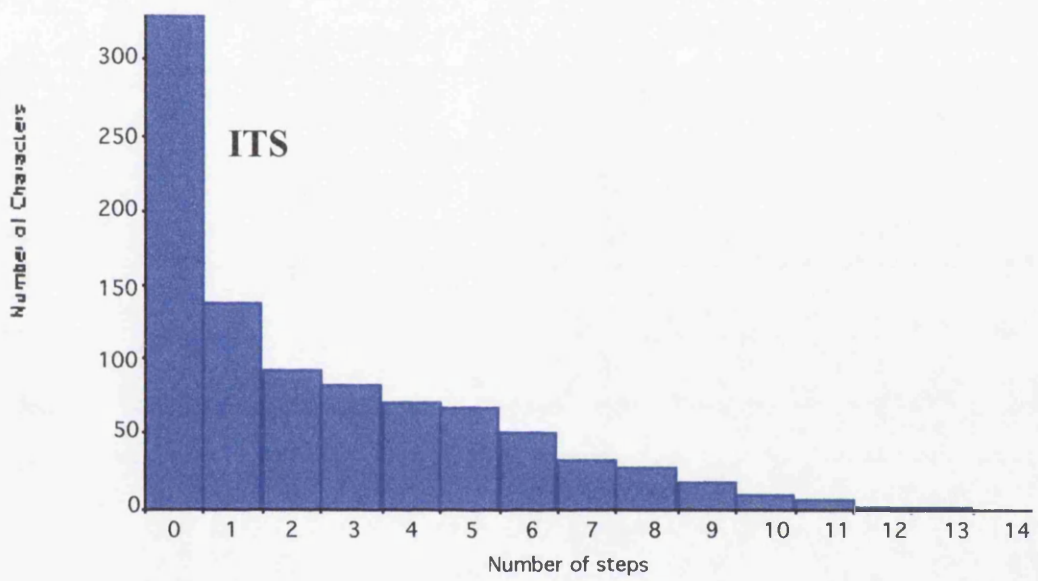
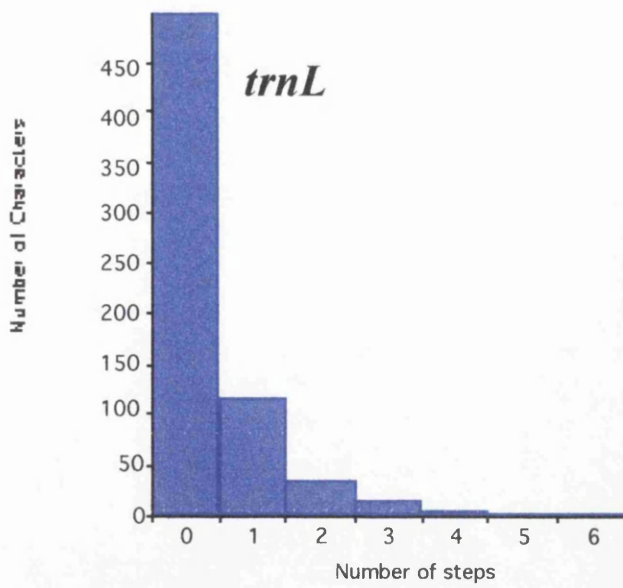


Figure 3.8 Number of steps for each of the variable sites optimised on a single most parsimonious tree.

the ITS data have been corroborated here by cpDNA (*trnL* intron) sequence data. It should, however, be emphasised that we can only be confident that some signal is emerging from ITS because it is congruent with results from sequences (*trnL*, 26S) where sequence alignment and character definition is unambiguous.

Forrest (2000) mostly excluded small gapped areas from her ITS analyses and many of the regions which were retained in her analyses were alignment-ambiguous. This had the similar effect on the resulting topology as not excluding any regions at all, as was concluded in this study, where a topology almost identical to Forrest's (2000) was recovered by including all alignment ambiguous regions in the analysis. Conflicting parts of the *trnL* intron and ITS trees are probably due to high levels of homoplasy and contrasting taxon sampling rather than to biological mechanisms. One cannot be certain whether the phylogenetic signal recovered by ITS in certain parts of the tree which is apparently correct due to its corroboration by cpDNA sequence data is also correct in areas of the tree for which there is no cpDNA evidence. This point is emphasised by the fact that most relationships found among these species in Forrest's (2000) study, or in this study when alignment-ambiguous regions are included, collapse when alignment-ambiguous areas are excluded. The greater resolution achieved by including alignment-ambiguous regions could be a useful indicator of phylogenetic relationships, but without greater corroboration from other sources these relationships will remain equivocal.

The detrimental effects of poor taxon sampling for ITS are obvious in the unusual topology, unsupported by other data sets, recovered when the 48 taxon ITS matrix was analysed excluding the alignment-ambiguous regions (Fig. 3.3b). The effects of taxon sampling and the disparity of sequences between unrelated species means that ITS sequence data are not the most optimal region with which to study *Begonia* phylogeny across the entire genus. They are, however, well-suited to resolving relationships among groups of closely related species. In these cases alignment ambiguities are substantially reduced, as can be seen by comparing the alignment of species in section *Tetraphila*, or the endemic Malagasy species, in contrast to species that are not closely related. For this reason, ITS is used in conjunction with *trnL* and morphology to explore character evolution and biogeography of the fleshy-fruited species in more detail in Chapter 4.

The maximum value of *trnL* intron sequence variation is only one third that found in ITS. Although this means it provides fewer informative characters, these characters can be reliably identified by unambiguous sequence alignment. Furthermore, problems of superimposed substitutions, which confound parsimony approaches to inferring phylogeny are minimised. This study showed that the *trnL* intron results are not significantly affected by taxon sampling, and therefore it remains a good locus with which to study the monophyly of sections and sectional relationships among African *Begonia*.

The lack of resolution provided by the 26S data set was surprising because the number of changes per site fell between those found in ITS and *trnL*, and only small regions were excluded. It suggests high levels of character conflict, which could be due to low species sampling.

3.6.2 Reliability of the ILD congruence test

The ILD (or partition homogeneity test, as it is called in PAUP) is one of the most commonly used statistical approaches to test congruence between different data sets. It is frequently used as a data set heterogeneity test in the conditional combination approach, where data sets are only combined when they have been demonstrated not to be heterogeneous (Bull et al., 1993; de Queiroz, 1993; Rodrigo, 1993). Yoder et al. (2001) recently identified an interesting side-effect of the ILD and the effective distrust it produces: “Even so, the test’s [ILD] perceived sensitivity has undergone a steady decline. When the ILD was originally developed, Farris recommended a P-value of 0.05 as the threshold for determining noncombinability. Since then, numerous investigators have applied the test to empirical data and have found that P-values < 0.05, and even as low as 0.001, should not preclude data set combination.” (p. 418). Many authors (e.g. Pennington, 1996; Chase & Albert, 1998) have questioned the use of incongruence indices in general as a tool for deciding to combine data sets, and have proceeded with simultaneous analyses in the face of adverse incongruence index values. They argue that the fundamental issue is whether individual characters in a phylogenetic analysis can be considered independent indicators of relationships, which is generally determined before cladistic analyses, and cannot be measured by any index. In this study, the ILD gave illogical results because P values between 26S and ITS, and between 26S and *trnL*

showed no significant heterogeneity ($P > 0.05$), but the P value was significant ($P < 0.05$) between 26S and *trnL*. It appears more valuable, and more simple to carry out thorough, independent analysis on separate data sets and assess discordance by comparing strict consensus topologies and bootstrap support.

3.6.3 *The evolution of fleshy fruits in Africa*

The combined topology gives insight into the evolution of fleshy fruits, which was not possible with the *trnL* data alone (Fig. 3.6). If we map the presence of fleshy fruits most parsimoniously onto this tree then it is apparent that fleshy fruits are apomorphic within African *Begonia*, and that the dry winged fruit of most species in the genus is plesiomorphic, not only for the entire genus but also for African *Begonia*. Because *B. meyeri-johannis* (section *Mezierea*), which has unwinged fleshy fruits, is sister to the endemic Malagasy species of *Begonia*, then within Madagascar there is a reversal to winged fruits which the majority of species in Clade 2 possess. In this clade there is a subsequent reversal back to unwinged fleshy fruits in the Malagasy species of section *Mezierea*, *B. comorensis* and *B. salaziensis*.

From this phylogeny (Fig. 3.6) it is possible to infer that epiphytism in African begonias evolved subsequent to fleshy fruits. Epiphytism evolved only once and was restricted to rainforest species. If bird dispersal is indeed the favoured dispersal mechanism for at least some fleshy-fruited species, then an epiphytic habit coupled with this fruit type would be the most effective combination with which to attract bird vectors. The sister relationship in the combined analysis between the terrestrial West and Central African yellow-flowered begonias and allies, and the fleshy-fruited + Malagasy species, is consistent with the idea of fleshy fruits as key innovations allowing greater dispersal power, and the potential to invade new regions (e.g. Madagascar) and exploit new niches, thereby promoting speciation.

3.6.4 *Taxonomic and phylogenetic implications*

Previous studies, based on ITS, concluded that there was a strong geographic element that defined the monophyly of Asian and American species respectively (Forrest, 2000). Results from several analyses, including multiple alignment elision

methods and maximum likelihood as well as maximum parsimony analyses, supported this conclusion. However, results from the analyses of *trnC-trnD* (Badcock, 1998) and *trnL* intron sequence data, as well as the results from the re-analysis of the ITS data, where alignment-ambiguous regions were excluded, do not show this clear geographic monophyly of American and Asian species.

This result casts into doubt previous biogeographical and evolutionary hypotheses based on ITS sequences alone. The assumption of a monophyletic Asian and a monophyletic American *Begonia*, led to postulations that *Begonia*, having originated in Africa, spread East to Asia via the rafting effect of India's split from Africa, and spread West across the Atlantic to South America via the Walvis ridge (Forrest, 2000). The cpDNA phylogenies suggest repeated exchange between America and Asia, either through long distance dispersal, migration via Tertiary boreotropical vegetation, or a combination of the two. In either case, it was the lineages of African *Begonia* more adapted to seasonal conditions, and now almost exclusively restricted to eastern and southern Africa, that were the precursors to the extensive speciation that occurred Asia and the Neotropics. In addition, the cpDNA and combined results challenge current phylogenetic studies being undertaken on American *Begonia*, where the underlying assumption is the monophyly of American species.

Congruence among topological patterns produced from independent data sets provides the best estimate of phylogeny (Penny & Hendy, 1986; Cracraft & Helm-Bychowski, 1991; Lanyon, 1993; Miyamoto & Fitch, 1995; Purvis, 1995). The separate and combined analyses, all recover the same clades for West and Central African and Malagasy species of *Begonia* (Clades 1, 2 and 3 in Fig. 3.1, 3.4 and 3.6). This provides a robust phylogenetic framework in which to pursue further work on these groups, as is done in Chapter four on the fleshy-fruited African species.

The most inclusive estimate of relationships among the basal nodes in *Begonia* can be seen in the strict consensus of the combined analysis of *trnL*, ITS and 26S (Fig. 3.6). The combined topology agrees with the *trnL* topology on the position of sections *Sexalaria* and *Rostrobegonia* (*B. annobonensis* and *B. engleri*) as sister to all American and Asian species, and to African species in section *Peltaugustia* (26S sequences were not available for species in section *Augustia*). Significantly, this relationship emerged in

a maximum likelihood analysis of ITS data, but was not supported by the maximum parsimony analysis results on the same data, which became the accepted phylogenetic hypothesis (Forrest, 2000).

3.7 CONCLUSIONS

ITS sequences show up to almost 50% divergence with ITS 1 and ITS 2 producing high levels of ambiguous sequence alignment. Although ITS may not be the optimal region with which to study species relationships across the whole of the genus *Begonia* it is useful among closely related species, where many of the problems involving sequence alignment and therefore homology assessment are minimised. The level of variation found in *trnL* intron sequences of *Begonia* is approximately one third of that found in ITS. As was discussed in Chapter 2, the *trnL* intron is an excellent mid-range marker with little alignment ambiguity and which is not markedly susceptible to taxon sampling. It gives well-supported resolution among sections, but can give insufficient variation between closely related species, or conflicting character optimisations at basal nodes, resulting in no resolution at this deeper phylogenetic level. 26S is generally conserved, though short areas of highly divergent sequence had to be removed. It is potentially useful for resolving basal relationships when combined with sequences from other gene loci, but its apparent susceptibility to taxon sampling should be further investigated.

Although there appeared to be strong incongruences in parts of the ITS and *trnL* topologies, these incongruences are not well-supported and therefore indicate that they could be due to stochastic rather than biological causes. Removing ambiguous regions from the ITS sequences in the analysis gives a topology that does not conflict with that generated from an analysis of the *trnL* data. However, the ambiguous regions of ITS do possess some phylogenetic signal, because broadly similar clade relationships among African species are uncovered by ITS, *trnL* and 26S sequence data.

Ambiguous results surround relationships between the African species in sections *Rostrobegonia*, *Augustia*, *Sexalaria* and *Peltaugustia*, as well as among Asian and American species. Results from *trnL* and combined sequence analysis show

Rostrobegonia (and *Sexalaria* in the *trnL* phylogeny) as sister to a clade consisting of American, Asian and African species in sections *Augustia* and *Peltaugustia*.

In addition, relationships uncovered by cpDNA sequences do not show the strong geographic constraint among Asian and American species that is revealed from the analysis of ITS sequences. This is very significant in view of current phylogenetic work on American species of *Begonia* (S. Swensen, pers. comm., 2001). Therefore, for the future, broad-scale sampling of American and Asian species in a *trnL* intron matrix should give interesting insights. However, because *trnL* may have limited variation within American and Asian species, sequencing these for other plastid genes such as *matK* or nuclear genes such as *adh* might provide more characters to determine whether Asian and American species of *Begonia* are truly monophyletic (as some ITS analyses postulate) or not (as cpDNA data imply).

Based on the analyses of independent data sets and the combined analyses, there is strong support for the main African clades outlined in Chapter 2: that is, 1) a monophyletic fleshy-fruited clade consisting of species with peltate, scale-like indumentum in sections *Baccabegonia*, *Squamibegonia*, and *Tetraphila*; 2) a monophyletic Malagasy clade, including all endemic Malagasy species, even those in section *Mezierea*; and 3) a monophyletic group consisting of the West and Central African yellow-flowered begonias and allies, representing sections *Loasibegonia*, *Scutobegonia*, *Filicibegonia*, *Cristasemen* and *B. iucunda*.

Chapter 4 examines in more detail the clade of mainland fleshy-fruited species with peltate indumentum (sections *Baccabegonia*, *Squamibegonia* and *Tetraphila*). Chapter 5 discusses taxonomic changes, including the establishment of a new section to accommodate *Begonia iucunda*. Biogeographic interpretation is withheld for the final chapter (Chapter 6).

CHAPTER 4 Cladistic analysis of the fleshy-fruited African sections *Baccabegonia*, *Squamibegonia* and *Tetraphila* based on combined morphological and molecular data

4.1 INTRODUCTION

4.1.1 African fleshy-fruited *Begonia*

Continental Africa and Madagascar possess ca. 158 species of *Begonia*, approximately 11% of the ca. 1400 species currently recognised in the genus. Although less numerous, the begonias of Africa are among the most morphologically diverse in the genus. *Begonia* species are generally characterised by winged capsules which, at maturity, either dehisce or disintegrate to release the seeds. However, in Africa one quarter of species have fleshy, wingless, often berry-like fruits. In Asia only species in section *Sphenanthera* (Hassk.) Warb. have fleshy fruits (26/600+ spp.) and in the Neotropics they are found only in the three species of section *Parietoplacentalia* Ziesenh. (3/600+ spp.) (Doorenbos et al., 1998). Although fleshy fruits cannot be said to be a key innovation within the genus (as is apparent by the small number of fleshy-fruited species in Asia and America), they appear to have played an important role in the diversification of *Begonia* in Africa. The fleshy-fruited African begonias are placed in four sections: *Baccabegonia* (2 spp.), *Squamibegonia* (3 spp.), *Mezierea* (6 spp.) and *Tetraphila* (30 spp.). Species in the Malagasy section *Erminea* have fleshy fruits with small wings. Studies in the placentation (Reitsma, 1983) and morphology of species in section *Erminea* have found them to have more in common with other wing-fruited species than with species possessing fleshy, non-winged fruits.

Fleshy-fruitedness in *Begonia* is interesting, not only because it is relatively rare but because it may be related to animal dispersal (van den Berg, 1984). The fruits are frequently coloured red, yellow, white or pink; they are indehiscent in sections *Squamibegonia* and *Meziera* but dehiscent in the other two sections (de Lange & Bouman, 1991). The placentae of section *Tetraphila* are also often brightly coloured (Arends, 1992; de Lange & Bouman, 1991). Other indications of an endozoochorous syndrome are larger seeds, with a loss of the cuticular ornamentation and a thick exotesta (de Lange & Bouman, 1991). De Lange & Bouman (1991) proposed that the arils found attached to seeds in section *Tetraphila* might be an adaptation to ant dispersal, with the aril acting as an eliosome: an oil-rich tissue found on the exterior of seeds which is attractive to animal dispersers. Ants are attracted to the eliosome for its nutritional value and disperse the seeds without damaging them.

Recent molecular studies (Chapters 2 and 3; Forrest, 2000) do not support the long-held view that fleshy-fruitedness amongst the African *Begonia* provides strong evidence of monophyly. Sequence data from the *trnL* intron and from the internal transcribed spacer (ITS) region of nuclear ribosomal DNA have shown section *Meziera* to be less closely related to other fleshy-fruited species than was previously thought (Chapter 2; Forrest, 2000). Moreover, the section is polyphyletic, with the Malagasy species sampled from the section (*B. salaziensis* and *B. comorensis*) sister to other Malagasy species, all of which have alate fruits (Forrest, 2000; Plana, Chapter 2). The remaining fleshy-fruited species in sections *Baccabegonia*, *Squamibegonia* and *Tetraphila* are monophyletic, and hence are the focus of this study.

Sections *Baccabegonia*, *Squamibegonia* and *Tetraphila* are distributed throughout West and Central Africa, with their centre of diversity in the western half of the Guineo-Congolian rain forest region (White, 1979). Although a small number of these species are narrow endemics, the majority have a broader Central African distribution, and a few are widespread. Most species are epiphytic, and possess almost symmetrical leaves that are often thick and fleshy. The principal synapomorphy for this

group of begonias is the presence of a peltate scale-like indumentum, which is only known in two other unrelated species, *B. stellata* and *B. prismatocarpa*, both in section *Loasibegonia* (Sosef, 1994; Doorenbos et al., 1998).

Section *Baccabegonia* consists of the two species *B. baccata* and *B. crateris*, both of which are endemic to the island of São Tome (one of the Gulf of Guinea Islands). Both species were originally placed in section *Squamibegonia* by Warburg (1894), whose classification was followed by Engler (1921) and Irmscher (1925). De Wilde & Arends (1980) placed both species in section *Mezierea*, but with some hesitation. The section *Baccabegonia* was created by Reitsma (1985) to accommodate both species, which are morphologically very similar to each other. The opinion that they could be synonymous has been expressed (Ferreira, 1965) but was rejected by Reitsma (1985), who differentiated them by the heavier indumentum of *B. crateris* and by contrasting positions of the petiole (leaves petiolate in *B. crateris*) and stamens. Together they are characterised by globose dehiscent fruits, septal placentation with four placentae per locule, and by a large number of ovules (250-300). They are by far the largest of all the fleshy-fruited *Begonia* species in Africa, reaching a height of up to 4 m and a leaf diameter of 50 cm. Studies showing that the pollen of species of section *Baccabegonia* shares characteristics with those of the supposedly primitive section *Mezierea* have been interpreted as indicating that species in section *Baccabegonia* are palaeoendemics on São Tomé (van den Berg, 1984).

Section *Squamibegonia* was last revised by de Wilde & Arends (1980), who recognised three species within this section. *Begonia ampla* and *B. bonus-henricus* occur in western Central Africa. *Begonia ampla* extends to the Gulf of Guinea Islands, while *B. poculifera* is widespread across tropical Africa. This section is very distinct due to the large, persistent, cup-shaped bracts subtending the inflorescence, the indehiscent fruits that develop within these bract and the two tepals in male and female flowers.

Section *Tetraphila* is currently under revision (J.J.F.E. de Wilde, pers. comm., 2000). It consists of 30 species and is believed to show the most advanced fruit and seed characters among the fleshy-fruited taxa (Klazenga et al., 1994). Although the majority of species are narrow range endemics, several have broad Central African distributions and one species, *B. eminii*, is widespread throughout tropical Africa. Most are epiphytic or rupestral, though *B. eminii*, *B. fusialata* and *B. tatoniana* are terrestrial. Both male and female flowers have four tepals, and the long, indehiscent, fusiform fruits are unique within the genus. *Begonia loranthoides* is the only species in the section to lack this characteristic fruit in some of its populations, and was originally placed in section *Squamibegonia* by Warburg (1894, 1895). Later studies by de Wilde & Arends (1979) concluded that this species had greater affinities with species in section *Tetraphila*, where it is now placed. The fruit in some populations is, however, rather distinct, polygonal in transverse section, and can range in shape from club-shaped to ellipsoid. The bracts subtending the inflorescence are large and enclose the young inflorescence, but are less persistent than those in species of section *Squamibegonia*, and eventually abscise.

Species complexes and pairs of morphologically similar, or geminate, species have been identified within section *Tetraphila* (Hagman & de Wilde, 1983; Arends, 1992). One aggregate consists of six species, *B. elaeagnifolia*, *B. rwandensis*, *B. karperi*, *B. longipetiolata*, *B. pelargoniiflora* and *B. squamulosa*, characterised by creeping prostrate stems, male flowers with a zygomorphic androecium and poricidal anther dehiscence (Arends, 1992). It is rare to find different kinds of anther dehiscence in the same genus, leading to the suggestion that poricidal dehiscence may be a derived state within the section (Arends, 1992). Two species subgroups were identified by Arends within this complex, although the divisions were based on an arbitrary division of a continuous character. The first, which includes *B. longipetiolata* and *B. squamulosa*, is characterised by male inflorescences with more than five flowers. The second subgroup consists of the two species, *B. karperi* and *B. elaeagnifolia*, and is characterised by a male inflorescence with up to five flowers. Arends considered the "more than five

flowered" state to be primitive. Examples of geminate species include *B. cavallyensis* and *B. fusicarpa*, which are thought to be altitudinal vicariads (i.e. sister species adapted to living at different altitudes; Hagman & de Wilde, 1983). Within this group, studies on seeds, placentation and pollen morphology show conflicting relationships (Reitsma, 1983; van den Berg, 1984; de Lange & Bouman, 1991).

Ploidy has been observed in section *Tetraphila*. Sporophytic chromosome numbers of several accessions of *B. squamulosa*, *B. elaeagnifolia* and *B. longipetiolata* range from 71-76, approximately double the 36-39 reported in other accessions of these species (Arends, 1992). The counts of 71-76 are putative tetraploids or aneuploid tetraploids postulated to have been derived from diploid progenitors as the result of autopolyploidy (Arends, 1992). In *B. squamulosa* and *B. elaeagnifolia* the tetraploids are restricted to the Crystal Mountains in northern Gabon, where they may have proliferated at the expense of the parental diploids (Arends, 1992).

In this study three separate data sets (cpDNA, nrDNA and morphology) are used to investigate species relationships and character evolution among the fleshy-fruited African *Begonia* in sections *Baccabegonia*, *Squamibegonia* and *Tetraphila*, and to assess which morphological characters provide the best estimates of phylogeny. Although there is a considerable debate on whether to combine different kinds of data or analyse them separately (for review see de Queiroz et al., 1995; Wendel & Doyle, 1998; Johnson & Soltis, 1998; Bateman, 1999; Savolainen et al., 2000), there is general agreement that one should assess congruence between data partitions and then perform a combined analysis if the data sets are not heterogeneous, show only weak incongruence, or if the causes of incongruence are believed to be spurious (Wendel & Doyle, 1998). This approach is termed the "conditional combination" approach and was discussed in more detail in Chapter 3. A morphological matrix has been constructed and previous morphological studies (Tebbutt, 1997; Badcock, 1998; Doorenbos et al., 1998; Forrest, 2000) are reviewed. Issues regarding character coding and past character and character state definitions in *Begonia* are discussed.

4.1.2 Coding morphology in cladistic analyses

Character coding of morphological variation (i.e. the representation of the variation of a group of organisms in a data matrix) is considered the “bête noire” of cladistic analyses (Pogue & Mickevich, 1990). This is because morphology often does not translate neatly into characters and character states. Furthermore, variation of individual features is quantitative and hard to divide into discrete states (Stevens, 2000). There is a growing problem of a lack of widely accepted procedures or a consensus on the best approach to deal with specific coding problems (Thiele, 1993; Stevens, 2000). The main issues concerning character coding are the treatment of continuous (or overlapping), polymorphic and inapplicable data and these are discussed in further detail below.

4.1.2.1 Continuous variation

Continuous phenotypic variation may take the form of morphometric (e.g. length) or meristic (number) data. This kind of variation is problematic because attribute values of different taxa overlap, and lines separating character states are arbitrary. For this reason, continuous data have been considered less effective in uncovering species relationships (Crisp & Weston, 1987; Pimentel and Riggins, 1987), and incur several problems such as: (1) non-repeatability and (2) questions of homology and inheritance regarding individual states (Stevens, 2000). The question of non-repeatability was addressed by Gift & Stevens (1997) in a study where 49 individuals were given a set of graphs denoting variation in 10 characters of *Kalmia* (Ericaceae), and asked to delimit states within these characters. They concluded that the way the data was presented influenced the delimitation of character states, and that states in the same data were delimited differently by different individuals. Stevens (2000) also pointed out that if continuous data is going to be used, then some type of sensitivity analyses should be carried out to test the effects of changing the boundaries between arbitrary states, like is

done with molecular data. Despite such evidence as that given by Gift & Stevens (1997), some authors claim that disregarding continuous variation eliminates a potentially important source of characters which can provide useful phylogenetic structure (Thiele, 1993; Wiens, 2000). For this reason and due to the general rarity of discrete characters in morphology, continuous data, particularly in studies based exclusively on morphology, is frequently used (for example, Sosef, 1994; Wieringa, 1999). The collection of morphometric data can be time-consuming, and adequate phylogenetic structure can also be accomplished with a small number of good discrete characters (Pennington, 1996; Carine & Scotland, in prep.). For these reasons, and others mentioned above, continuously variable data were not included in this study.

4.1.2.2 Coding missing or inapplicable data

Inapplicable data refers to those characters which are not applicable due to the absence of the feature in a subgroup of the terminal taxa. The most widespread method for treating inapplicable data is termed reductive coding (*sensu* Strong & Lipscomb (1999), after Wilkinson (1995)). It has also been termed inapplicable data coding (missing) by Hawkins et al. (1997). This method is comparable to the treatment of indels in molecular data because taxa that lack the feature are scored as missing, and is the most commonly used (for examples see Luckow & Hopkins, 1995; Cox & Williams, 2000; Michelangeli, 2000; Navarro & Liria, 2000). This method is by no means ideal but, in the absence of algorithms and computational methods that can handle this kind of information, it is the most favoured (e.g. Hawkins et al., 1997; Strong & Lipscomb, 1999) and was chosen for this study. Reductive coding avoids philosophical arguments about the coding and treatment of absence, such as whether absence can be considered a state or whether absence ends up being coded multiple times when it only occurs once, which violates the assumption of character independence. Alternative coding methods include: absence coding (*sensu* Strong & Lipscomb, 1999) where taxa lacking a structure are coded with a separate absence state; non-additive binary coding (*sensu* Strong & Lipscomb, 1999) or presence/absence coding (*sensu* Pleijel, 1995), which involves

coding each state of a character for presence/absence; and in composite coding (*sensu* Maddison, 1993; Strong & Lipscomb, 1999) inapplicable data are included as part of a single multistate character.

Coding inapplicable data as an additional absence state, as it is in composite coding, may cause the absence of a complex character to be coded multiple times, especially if there are many different characters associated with the same structure. In this case, “If absence is a synapomorphy then coding it multiple times is redundant and will give greater support to clades than actually exists” (Strong & Lipscomb, 1999: 368). Treating states as presence/absence will cause logically dependent characters (that is, characters which are actually states or transformations of the same character) to be treated independently. This will lead to (a) states being scored twice and (b) too much emphasis being placed on absence, which will repeatedly behave as a synapomorphy even though the actual types of absence are different and non-homologous (Lee & Bryant, 1999; Strong & Lipscomb, 1999). Composite coding accounts for the dependence between the presence or absence of a particular anatomical structure and the character variability of that structure. However, including absence as one of the character states suggests transformational dependence, so that inapplicable data may become informative in determining phylogenetic relationships when it should not (Lee & Bryant, 1999; Strong & Lipscomb, 1999).

4.1.2.3 Coding polymorphisms

Polymorphism, when a terminal taxon possesses more than one state for a single character, is a common reason for excluding characters from an analysis (called the fixed-only method; Nixon & Davis, 1991), but may result in data matrices containing insufficient information to reconstruct phylogeny (Kornet & Turner, 1999; Poe & Wiens, 2000). Computer algorithms cannot simultaneously optimise two or more states in a cell. PAUP can treat them as full polymorphisms (multistate taxa = ambiguous), which treats those cells as missing and chooses the state from the set of available states

that allows minimisation of the tree, or as polymorphism (multistate taxa = polymorphism). In the latter case PAUP designates one of the states in the cell as the ancestral state from which the other state(s) must be derived, and thereby optimises the derivations of the states in the cell. NONA treats polymorphisms by optimising subset polymorphisms, without considering them as full polymorphisms (i.e. does not treat polymorphism as ambiguous) (Goloboff, 1993). Numerous alternative ways of treating polymorphisms have been reviewed and tested (Nixon & Davis, 1991; Kornet & Turner, 1999; Poe & Wiens, 2000). One of the best ways to treat polymorphic data in order to circumvent limitations imposed by algorithms in phylogenetic software is to divide terminal taxa to remove them (Nixon & Davis, 1991). Splitting terminal taxa can, however, be problematic when handling large frequencies of polymorphic data in a matrix. NONA's treatment of polymorphic data, and the fact that it is fast, means it has been regarded by many as the best way of analysing morphological data, particularly if implementing reductive coding methods (Hawkins et al., 1997; Strong & Lipscomb, 1999). In addition, NONA's Windows interface, Winclada, can be excellent tool to observe character state distributions across a given tree. In this study polymorphic data are treated in a number of ways (as missing, as polymorphisms or excluded from the analysis) to investigate their effect on the topology and choose the method which best fits the data.

4.1.3 Review of character and character state definitions (primary homology assessments) in previous morphology-based phylogenies of Begonia

Hawkins (2000, citing Smith, 1994: 34) reiterated that "different interpretations of characters and coding are possible" and "different workers will perceive and define characters in different ways". Most researchers would agree that their definition of a character in a cladistic context agrees, more or less, with that given by Platnick (1979: 542): "a character consists of two or more different attributes (character states) found in two or more specimens that, despite their differences, can be considered alternate forms of the same thing (the character)". But researchers' knowledge of, or views on,

homology within their organisms commonly vary, leading to different assessments of primary homology (Pogue & Mickevich, 1990; Smith, 1994; Stevens, 2000). This is clearly evident among morphological cladistic analyses of *Begonia* (Table 4.1).

Morphology has been included in several phylogenetic studies of *Begonia* (e.g. Sosef, 1994; Tebbitt, 1997; Badcock, 1998; Doorenbos et al., 1998; Forrest, 2000). These studies have been conducted at the species level within targeted sections (Sosef, 1994: sections *Loasibegonia* and *Scutobegonia*), at the species level combining targeted (or putatively related) sections with widespread sampling of exemplar species in other sections (Tebbitt, 1997: section *Sphenanthera*; Badcock, 1998: section *Knesebeckia*), at the species level sampling across the entire genus with no targeted sections (Forrest, 2000), and at the section level (Doorenbos et al., 1998). Among these studies the morphological character list of Doorenbos et al. (1998) and Forrest (2000) should share the greatest number of characters with each other as they sample across the same taxonomic rank.

Sosef (1994) compiled the first phylogenetic matrix for a subset of *Begonia* species, based entirely on morphology. He aimed to study relationships among species in the African sections *Loasibegonia* and *Scutobegonia*, using a morphological cladistic approach. The analysis included 132 characters coded for 40 species in addition to four outgroup species. Being a study based on morphology alone, many of the characters chosen were continuously variable, and included macromorphological data as well anatomical features of the leaf, ovary and style.

Tebbitt (1997) created the first phylogeny of *Begonia*, combining both morphological and molecular data to investigate the monophyly of section *Sphenanthera*. In contrast to Sosef's (1994) work, the majority of species coded did not belong to a single section: he coded 40 morphological characters for 53 species across the entire genus (34 ingroup species represented sections other than *Sphenanthera*). Outgroups chosen were *Hillebrandia sandwicensis* and *Datisca glomerata*. Most of the

characters in his morphological analysis were multistate. Continuous data was mostly present in the form of meristic data or divisions between different shapes or degrees of fusion.

Badcock (1998) carried out a study similar to that of Tebbitt (1997) but focused on the Neotropical and Asian section *Knesebeckia* (note that Doorenbos et al., 1998, only recognise Neotropical species within *Knesebeckia*). She aimed to test the monophyly of the group with respect to other Neotropical and Asian species, and to study species relationships within *Knesebeckia* based on morphology. Her morphological analysis included 66 characters which she sampled not only for *Knesebeckia* but also for African, Neotropical and Asian species in an attempt to produce a preliminary estimate of the phylogeny of *Begonia*, based on both morphological and molecular data. She found *Knesebeckia* to be non-monophyletic. Badcock's (1998) coding strategy was very similar to Tebbitt's (1997), including mostly multistate characters and continuous characters in the form of meristic data and shape and fusion differentiation.

Badcock (1998) and Tebbitt (1997) described fewer characters than Sosef (1994), and of these few are over-lapping. Both sets of characters and states are much more comparable, the main reason being that Badcock and Tebbitt sampled many sections of *Begonia* other than their focal sections. However, working together, and presenting their theses only a year apart means they may have also significantly influenced each others work.

Doorenbos et al. (1998) listed 63 sections in a morphological study at the section level. They defined 63 characters, most of which are applicable to any study which includes species from different sections. They carried out a phenetic analysis to test the relationships between sections based on similarity. This would carry the assumption that sections are monophyletic. Although they worked under this assumption, they admitted that in a cladistic analysis many of the sections would probably be para- or

polyphyletic.

High levels of homoplasy (54/67 morphological characters gave CI values less than one) have been reported for morphology in *Begonia* in contrast to molecular data even among morphological characters traditionally used to delimit sections (Forrest, 2000). It should be noted, however, that in the same study molecular data showed even greater levels of homoplasy with a CI value of 0.2961 reported for one most parsimonious ITS tree. The more distantly related species are added to a matrix, the more likely there is to be spurious morphological relationships, where the high levels of homoplasy obscure phylogenetic signal (Givnish & Sytsma, 1997b). This is exacerbated by inapplicable data where a given morphological feature is altogether absent from some species, as was observed in the preliminary stages of this morphological study. Here, levels of inapplicable data increased as sampling moved further away from the targeted group of putatively related species, and a diminution in characters with genuinely discrete states was seen, because the addition of taxa inserted intermediate states.

In *Begonia*, it is possible to have characters that are applicable within and between sections, as can be seen in Table 4.1 if we compare the character lists from Doorenbos et al., (1998) and Badcock (1998). Sections are arbitrary ranks (i.e. different authors may rank groupings in *Begonia* as genera rather than sections. See Klotzsch, 1854) that commonly reflect natural groups, as has been seen in light of phylogenetic analysis of molecular data where many sections are found to be monophyletic. They are introduced by taxonomists to make large genera more manageable, and to reflect morphological relationships in a sea of taxa. In the case of a large genus such as *Begonia*, which is relatively homogeneous in terms of morphology, there can be as much morphological variation within sections as between them, and this can further complicate coding.

Features used for section definition in African, Neotropical and Asian *Begonia* have been growth habit, presence and type of above or below ground storage organs

(rhizomes, tubers and bulbils), caulescence, trichome morphology, tepal number in male and female flowers, gynoecium structure, and fruit structure.

Table 4.1 compares how four different researchers have chosen their characters and defined their character states. It is interesting to observe how different morphological characters in *Begonia* have been treated by different investigators. For example, there is a pronounced disagreement in the homology assessment of underground storage organs and stems. Tebbitt (1997) and Badcock (1998) considered tubers and rhizomes to be transformations of the same character, an opinion not shared by Doorenbos et al. (1998) and Forrest (2000), who treated the presence of tubers as a separate character. There are several examples of this type below. Some other characters, such as those describing the gynoecium and androecium, are somewhat more congruent.

4.1.4 Molecules and morphology in phylogeny reconstruction

Morphology can frequently display high levels of homoplasy (Givnish & Sytsma, 1997a) which can lead to erroneous estimates of relationships (Givnish & Sytsma, 1997b). However, if molecular and morphological data share the same phylogenetic history, and there is no substantial evidence for phylogenetic incongruence between molecules and morphology, then when combined they can both give resolution at different hierarchical levels (Pennington, 1996). In these conditions combining molecular and morphological data can be superior to the commonly used method of mapping characters *a posteriori* because the latter usually show different transformational patterns between given states than if these states were properly coded and included in a simultaneous analysis (Bateman & Simpson, 1998).

There are two additional arguments in favour of using both morphological and molecular data in phylogenetic analyses. Bateman (1999) discussed the kind of insight on evolutionary radiations that can be observed from these kinds of studies. Genomes are thought to evolve in a more or less clock-like fashion. Morphology, on the other

Table 4.1 Characterisation of *Begonia* morphology by four previous authors.

	Tebbitt (1997)	Badcock (1998)	Doorenbos (1998)	Forrest (2000)
Growth form	-	-	GROWTH FORM - terrestrial - epiphytic	-
Longevity	-	-	LONGEVITY - annual - perennial	LIFESTYLE - perennial - monocarpic
Habit	RHIZOMES or TUBERS - present - absent	ROOT TYPE - fibrous roots, no obvious storage organ - swollen storage roots - root tuber - stem tuber (corm) - rhizome STEM PRESENCE - acaulescent or shortly caulescent - stem not branching - stem branching BULBILS - present - absent	HABIT - rhizomatous - with an upright stem - with rhizomes from which upright stems arise - lianescent - acaulescent TUBERS - absent - present TUBERCLES (or CORMLETS) - absent - present	STEM TUBERS - absent - present ROOT TUBERS - absent - present BULBILS - absent - present TUBERCILS - absent - present
Stem	STEMS WOODY AT BASE - yes - no	-	STEM CONSISTENCY - herbaceous - woody (at least at base)	CAUDEX - absent - present
Stipules	STIPULE LONGEVITY - absent - long persisting - falling early	STIPULE PERSISTENCE - caducous - deciduous - persistent - absent STIPULE SHAPE - ovate-lanceolate/ triangular lanceolate/ linear lanceolate - oblong ellipsoid - triangular ovate - broadly ovate STIPULE MARGIN - entire - fimbriate - dentate or dentate fimbriate STIPULE NERVE EXCURRENT - excurrent	STIPULE MARGIN - entire - dentate	STIPULE PERSISTENCE - persistent - caducous STIPULE PAIR - both the same - different STIPULE KEELING - indistinct - strongly keeled STIPULE SPUR - imperceptible - distinctly spurred STIPULE EDGE - entire - fringed STIPULE BACK - glabrous

Stomata	<p>- not excurrent</p> <p>-</p> <p>STOMATA CLUSTERED</p> <ul style="list-style-type: none"> - no - yes 			<p>- hairy</p> <p>-</p>
Petiole	<p>PETIOLE PRESENCE</p> <ul style="list-style-type: none"> - cauline - petiolate <p>RING OF HAIRS OR TRICHOMES AT THE JUNCTION OF THE BLADE WITH THE PETIOLE</p> <ul style="list-style-type: none"> - present - absent 	<p>JUNCTION OF PETIOLE AND LEAF BLADE</p> <ul style="list-style-type: none"> - without a tuft of hairs - with a tuft of hairs 	<p>PELTATENESS</p> <ul style="list-style-type: none"> - basifixed - peltate <p>PETIOLE TRANSVERSE SECTION</p> <ul style="list-style-type: none"> - circular - crescent - square <p>TRICHOME RING AT TOP OF PETIOLE</p> <ul style="list-style-type: none"> - absent - present 	
Leaves	<p>LEAF TEXTURE</p> <ul style="list-style-type: none"> - leaf not leathery - leaf leathery <p>LEAF VENATION</p> <ul style="list-style-type: none"> - pinnate - palmate-pinnate <p>LEAF BASE SHAPE</p> <ul style="list-style-type: none"> - peltate - cordate with basal lobes - cordate without basal lobes 	<p>LEAF ARRANGEMENT</p> <ul style="list-style-type: none"> - close and distichous - alternate - opposite - whorled <p>LEAF NUMBER</p> <ul style="list-style-type: none"> - 1 or 2 - more than 2 <p>LEAF POSITION RELATIVE TO PETIOLE</p> <ul style="list-style-type: none"> - straight - oblique - transverse <p>LEAF SYMMETRY</p> <ul style="list-style-type: none"> - symmetric - asymmetric <p>LEAVES PELTATE OR NOT</p> <ul style="list-style-type: none"> - peltate - not peltate <p>LEAF DIVISION</p> <ul style="list-style-type: none"> - simple - palmately lobed - palmatifid - palmatisect - palmately compound - pinnatifid - bipinnatifid or further divided <p>LEAF VENATION</p> <ul style="list-style-type: none"> - palmate - palmate-pinnate - pinnate 	<p>LEAF MACULATION</p> <ul style="list-style-type: none"> - colour same all over - with patterning 	
Indumentum	<p>STELLATE TRICHOME</p> <ul style="list-style-type: none"> - present 	<p>INDUMENTUM OF SCALES</p> <ul style="list-style-type: none"> - absent 	<p>'FUZZY' HAIRS</p> <ul style="list-style-type: none"> - absent 	

<p>Inflorescence</p>	<ul style="list-style-type: none"> - absent - present - present - absent <p>FEMALE OR BISEXUAL INFLORESCENCE POSITION</p> <ul style="list-style-type: none"> - arising from leaf axils - false petiolar <p>FEMALE OR BISEXUAL INFLORESCENCE TYPE</p> <ul style="list-style-type: none"> - dichasium - condensed monochasium - raceme - flower solitary - panicle <p>FORM OF SEX SEPARATION</p> <ul style="list-style-type: none"> - monoecious plants with bisexual inflorescences - monoecious plants with unisexual inflorescences - dioecious plants with unisexual inflorescences <p>markedly protandrous unisexual inflorescences</p>	<ul style="list-style-type: none"> - absent - present - present - absent <p>STELLATE HAIRS</p> <ul style="list-style-type: none"> - axillary - terminal <p>FORM OF SEX SEPARATION</p> <ul style="list-style-type: none"> - monoecious with bisexual inflorescences - monoecious with unisexual inflorescences - dioecious or androdioecious <p>INFLORESCENCE POSITION</p> <ul style="list-style-type: none"> - axillary - terminal <p>PARTIAL INFLORESCENCE BRANCHING PATTERN</p> <ul style="list-style-type: none"> - monochasial - dichasial <p>SYMMETRY OF INFLORESCENCE BRANCHES</p> <ul style="list-style-type: none"> - more or less symmetrical - asymmetrical <p>NUMBER OF INFLORESCENCE BRANCHING POINTS</p> <ul style="list-style-type: none"> - single flower, one dichotomy - between 2-3 dichotomies - 3 dichotomies 	<ul style="list-style-type: none"> - present - absent - present - absent <p>INDUMENTUM OF STELLATE HAIRS</p> <ul style="list-style-type: none"> - axillary - terminal - at base of the leaf blade <p>INFLORESCENCE GENERAL ARRANGEMENT</p> <ul style="list-style-type: none"> - racemose - cymose <p>INFLORESCENCE SEXUALITY</p> <ul style="list-style-type: none"> - only bisexual - bisexual and male - bisexual and female - separate male and female <p>INFLORESCENCE DISTRIBUTION OF SEXES</p> <ul style="list-style-type: none"> - with male flowers basal and female flowers distal - with male flowers distal and female flowers basal <p>INFLORESCENCE PROTANDROUS OR PROTOGYNOUS</p> <ul style="list-style-type: none"> - protandrous - protogynous <p>BISEXUAL INFLORESCENCE TYPE</p> <ul style="list-style-type: none"> - dichasial - monochasial - dichasia at base, monochasial at apex <p>MALE INFLORESCENCE TYPE</p> <ul style="list-style-type: none"> - dichasial - monochasial - dichasia at base, monochasial at apex - consisting of solitary flowers <p>FEMALE INFLORESCENCE TYPE</p> <ul style="list-style-type: none"> - dichasial - monochasial - dichasia at base, monochasial at apex - consisting of solitary flowers <p>INFLORESCENCE NUMBER OF FEMALE FLOWERS</p> <ul style="list-style-type: none"> - 1 female flower - 2 female flowers - 3 female flowers 	<ul style="list-style-type: none"> - present - absent - present - present - axile - terminal - one - more - dioecious - monoecious - cyme - raceme - dichasial - monochasial - symmetric - asymmetric - without central flower - less than 70 - over 100 - male and female in same inflorescence, interspersed - male and female in same inflorescence, female basal - male and female on separate inflorescences <p>STELLATE HAIRS</p> <p>INFLORESCENCE POSITION</p> <p>INFLORESCENCES PER AXIL</p> <p>SEXUAL SEPARATION</p> <p>INFLORESCENCE TYPE</p> <p>INFLORESCENCE BRANCHING AT BASE</p> <p>INFLORESCENCE SYMMETRY</p> <p>DICHASIAL INFLORESCENCE: BASAL DICHOTOMIES</p> <p>FLOWER NUMBER PER INFLORESCENCE</p> <p>SEXUAL SEPARATION</p> <p>male and female in same inflorescence, interspersed</p> <p>male and female in same inflorescence, female basal</p> <p>male and female on separate inflorescences</p>
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			<p>- more than 3 female flowers INFLORESCENCE AXIS DEVELOPMENT</p> <p>- strongly reduced - not reduced</p>	
Peduncle	<p>FEMALE PEDUNCLE LENGTH</p> <p>- usually longer than 2cm - 1-2 cm - less than 0.5 cm - absent</p>	<p>PEDUNCLE PRESENCE</p> <p>- peduncle absent or less than 1 cm in length - present - elongated</p>		-
Inflorescence bracts	<p>YOUNG MALE FLOWERS ENCLOSED BY LARGE (>1cm) BRACTS</p> <p>- no - yes</p>	<p>BRACT LIKE STIPULE PRESENCE</p> <p>- present - absent</p> <p>BRACT PERSISTENCE</p> <p>- caducous - deciduous - persistent</p> <p>BRACT SHAPE AT FIRST BRANCHING</p> <p>- obovate - ovate to ovate lanceolate - broadly ovate or obovate</p> <p>BRACTS AT FIRST BRANCHING POINT</p> <p>- forming a cup - fused - patent</p> <p>BRACTS AT SECOND AND LATER BRANCHINGS</p> <p>- oblong obovate - ovate to ovate lanceolate - obovate</p> <p>broadly ovate or obovate BRACTS AT BASE OF OVARY</p> <p>- present - absent</p> <p>BRACTS WHERE NO OBVIOUS DICHOTOMY OCCURS</p> <p>- present - absent</p>	<p>BRACT PERSISTENCE</p> <p>- persistent (during flowering) - caducous</p> <p>BRACTEOLLES</p> <p>- absent - 1 - 2 - 3</p> <p>BRACTEOLE POSITION</p> <p>- inserted directly below the ovary - spaced from the base of the ovary - inserted on the ovary</p>	<p>BRACTEOLLES SUBTENDING OVARY</p> <p>- absent - 2 bracteoles - 3 bracteoles</p>
Perianth	<p>MALE TEPAL NUMBER</p> <p>- 10 - 6 - 4 - 2</p> <p>RELATIVE WIDTHS OF OUTER AND INNER MALE TEPALS</p> <p>- more or less equal</p>	<p>FLOWER COLOUR</p> <p>- white or pink - yellow or orange</p> <p>NUMBER OF SEPALS (OUTER WHORL)</p> <p>- 2 - 4-5</p> <p>NUMBER OF PETALS (INNER WHORL)</p>	<p>PERIANTH SEGMENT COLOUR</p> <p>- white or pink - red - orange - yellow</p> <p>OUTER PERIANTH SEGMENT SHAPE</p> <p>- rounded at apex - acute at apex</p>	<p>FLOWER SIZE</p> <p>- similar in male and female - distinctly larger female than male</p> <p>FLOWER COLOUR (MOST PREVALENT)</p> <p>- white or pink - yellow - red</p>

<ul style="list-style-type: none"> - inner much thinner than outer MALE TEPAL HAIR TYPE - multicellular - unicellular - glabrous - stellate FEMALE TEPAL NUMBER - 10 - 6 - 5 - 4 - 3 - 2 	<ul style="list-style-type: none"> - 0 - 2 - 5 SEPAL OUTER SURFACE HAIRY - hairy - glabrous SEPAL APEX - acute to acuminate - rounded SEPAL MARGIN - entire - dentate - fimbriate to dentate fimbriate FEMALE TEPAL FUSION - free - fused FEMALE TEPAL NUMBER - 2 - 3 - 4 - 5 - 6 - 10 FEMALE TEPAL APEX - acute to acuminate - rounded FEMALE TEPAL MARGIN - entire - dentate - fimbriate or dentate fimbriate 	<p>MALE FLOWER NUMBER OF PERIANTH SEGMENTS (listed but not coded for)</p> <p>MALE FLOWER PERIANTH SEGMENT FUSION</p> <ul style="list-style-type: none"> - free - partially fused <p>FEMALE FLOWER NUMBER OF PERIANTH SEGMENTS</p> <p>(listed but not coded for)</p> <p>FEMALE FLOWER PERIANTH SEGMENT FUSION</p> <ul style="list-style-type: none"> - free - partially fused 	<ul style="list-style-type: none"> - orange FLOWER PATTERN - tepals all one colour - both tepals with similar red veins or patches - red veins or patches only on one tepal SCENT - imperceptible - strong PERIANTH TUBE - absent - present MALE TEPAL NUMBER - 2 tepals - 4 tepals - absent MALE FLOWER SYMMETRY - radial symmetry of tepals - bilateral symmetry of tepals MALE TEPAL FUSION - free - partly fused MALE TEPAL HAIRINESS - glabrous - with hairs MALE TEPAL EDGE - entire - lobed MALE BUD SHAPE - flat - spherical FEMALE TEPAL NUMBER - 2 tepals - 3 tepals - 4 tepals - 5 tepals - 6 tepals - absent FEMALE TEPAL FUSION - free - two tepals partly fused - all tepals partly fused FEMALE TEPAL HAIRINESS - glabrous - hairy FEMALE TEPAL EDGE - entire
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Male receptacle	<p>MALE RECEPTACLE SHAPE</p> <ul style="list-style-type: none"> - flat or slightly raised - rounded or a torus 	<p>RECEPTACLE</p> <ul style="list-style-type: none"> - flat or slightly raised - rounded or a torus 		<ul style="list-style-type: none"> - lobed or serrate -
Androecium	<p>ENDOTHECIAL WALL PATTERN</p> <ul style="list-style-type: none"> - hoop shaped - U shaped - very thick U shaped <p>FILAMENT FUSION</p> <ul style="list-style-type: none"> - free to base - fused at base - fused to half way into a column - fused for whole length <p>ANTHER APEX HOODED</p> <ul style="list-style-type: none"> - no - yes <p>ANTHER DEHISCENCE POSITION</p> <ul style="list-style-type: none"> - on the inner surface - starting from the side of the locule and progressing onto the inner surface - via a straight line down side of locule <p>LOCULES NOTICEABLY SEPARATED BY CONNECTIVE</p> <ul style="list-style-type: none"> - no - yes <p>CONNECTIVE EXTENDED AT APEX</p> <ul style="list-style-type: none"> - no - slightly extended - markedly extended to shield like 	<p>ANDROPHORE</p> <ul style="list-style-type: none"> - symmetrical - asymmetrical <p>FILAMENT FUSION</p> <ul style="list-style-type: none"> - free to base - fused briefly at base - free to base, but some fusion in centre of androphore - fused into a column with filaments arising all the way up the column - fused at least half way into a column <p>CONNECTIVE EXTENSION</p> <ul style="list-style-type: none"> - not extended - extended to a tip - extended to a ledge <p>STAMEN DEHISCENCE</p> <ul style="list-style-type: none"> - dehiscent by long straight slits down the middle of the pollen sac - arcuate slits - very short arcuate slits in upper part of pollen sac <p>FILAMENT TO ANTHER LENGTH RATIO</p> <ul style="list-style-type: none"> - anthers shorter than filaments - anthers and filaments about same length - anthers longer than filaments 	<p>ANDROECIUM SYMMETRY</p> <ul style="list-style-type: none"> - actinomorphic - zygomorphic <p>FILAMENT LENGTH</p> <ul style="list-style-type: none"> - equal - unequal <p>FILAMENT FUSION</p> <ul style="list-style-type: none"> - free - partly fused - entirely fused <p>ANTHER SHAPE</p> <ul style="list-style-type: none"> - circular to elliptic - obovate - oblong - broadly triangular <p>ANTHER RELATIVE LENGTH</p> <ul style="list-style-type: none"> - longer than the filaments - about as long as the filaments - shorter than the filaments <p>ANTHER DEHISCENCE</p> <ul style="list-style-type: none"> - with apical pores - with short pore like slits - with longitudinal slits <p>ANTHER OPENING POSITION</p> <ul style="list-style-type: none"> - openings lateral - openings unilateral <p>ANTHER APEX HOODED OR NOT</p> <ul style="list-style-type: none"> - apex hooded - apex not hooded <p>CONNECTIVE EXTENSION</p> <ul style="list-style-type: none"> - extended - not extended <p>OVARY OR FRUIT NUMBER OF WINGS (listed but states not defined)</p> <p>WINGS EQUAL OR NOT</p> <ul style="list-style-type: none"> - equal or subequal in fruit - unequal in fruit <p>WINGS HOOK LIKE OR NOT</p> <ul style="list-style-type: none"> - developed into hooks - not hook or spine like <p>LOCULE NUMBER</p>	<p>ANDROECIUM</p> <ul style="list-style-type: none"> - anthers face all directions - anthers face upper and lower tepals - anthers face upper tepal <p>STAMEN NUMBER</p> <ul style="list-style-type: none"> - less than 10 - 10 or more <p>STAMEN COLOUR</p> <ul style="list-style-type: none"> - yellow - orange - red <p>ANTHER DEHISCENCE</p> <ul style="list-style-type: none"> - via slits - via pores <p>STAMEN FUSION</p> <ul style="list-style-type: none"> - free <ul style="list-style-type: none"> - fused only in the centre - fused only at one side - on a column (all fused) <p>ANTHER CONNECTIVE EXTENSION</p> <ul style="list-style-type: none"> - not extended - extended <p>ANTHER CONNECTIVE HOODING</p> <ul style="list-style-type: none"> - not hooded - hooded
Gynoecium	<p>STYLE NUMBER</p> <ul style="list-style-type: none"> - 2 - 3 - 4 - 5 - 6 <p>STYLE SHAPE</p> <ul style="list-style-type: none"> - bifid - shortly bifid 	<p>OVARY POSITION</p> <ul style="list-style-type: none"> - inferior - partially inferior <p>OVARY SEPTA NUMBER/LOCULE NUMBER</p> <ul style="list-style-type: none"> - 1 - 2 - 3 - 4 	<p>STYLE NUMBER</p> <ul style="list-style-type: none"> - 2 styles - 3 styles - 4 styles - (5-) 6 (-7) styles <p>STYLE COLOUR</p> <ul style="list-style-type: none"> - yellow - greenish - white 	

<ul style="list-style-type: none"> - many branched - entire STYLE FUSION - free - fused at base <1mm - fused at base >1mm STIGMA POSITION - in a band and spiralled - in a band and not spiralled - covering most of style or all over style OVARY POSITION - partially inferior - fully inferior LOCULE NUMBER - 2 - 3 - 4 - 5-7 PLACENTATION - parietal - axil PLACENTAE - free and bearing ovules on both surfaces - free and bearing ovules only on outer surfaces - fused OVARY APPENDAGES - no appendages - equal or almost equal wings - unequal wings - single wing - horn like expanded locules - ribs OVARY WING SHAPE - tongue shaped - equilateral triangle - wedge-ridge shaped - rounded - isosceles or scalene triangle 	<ul style="list-style-type: none"> - 5-7 LOCULE DEVELOPMENT - at least one locule not developing fully - all locules developing fully PLACENTATION - parietal - axile PLACENTAE PER LOCULE - 1 - 2 free placentate PLACENTAL LENGTH - almost as long as the locule - less than half the length of the locule STYLE NUMBER - 2 - 3 - 4 - 5 STYLE FUSION - free - fused at base - fused for more than half their length STYLE DIVISION - not divided - 2 lobed - 2 straight branches - 2 spiralling branches - lunate - lunate bicornute - many branched STIGMATIC TISSUE DISTRIBUTION - covering almost entire surface of style - covering entire surface, with some papillae confined to spiralling band - stigmatic tissue papillae covering one side of the style branches - stigmatic papillae forming a band which encircles the style branches - stigmatic papillae forming a band which spirals around the style branches 	<ul style="list-style-type: none"> (listed by states not defined) PLACENTATION - parietal - septal - axillary PLACENTAL BRANCHES PER LOCULE (listed but states not defined) OVULE PRESENCE BETWEEN PLACENTAL BRANCHES - present between placental branches - absent between placental branches STYLE NUMBER (listed but states not defined) STYLE FUSION - free - fused less than halfway - fused more than halfway STYLE SHAPE - simple - 2 lobed - 2 forked once - forked more than once STYLE PERSISTENCE - persistent in fruit - caducous in fruit STIGMAS KIDNEY SHAPED OR NOT - not kidney shaped - kidney shaped STIGMA POSITION ON STYLE - in a band and spiralled - in a band and not spiralled - all over the style - contracted near the style apex 	<ul style="list-style-type: none"> - pink - red STYLE FUSION - free - fused STYLE BRANCHING - unbranched - kidney-shaped - bifid - 3-fid - 4-fid STYLE PERSISTENCE IN FRUIT - persistent - caducous OVARY POSITION - inferior - semi-inferior LOCULE NUMBER - 1 locular - 2 locular - 3 locular - 4 locular - (5-) 6 (-7) locular PLACENTATION - one-fid - bifid, with ovules on inner and outer surfaces of placenta - bifid, with ovules only on outer surfaces of placenta 	<ul style="list-style-type: none"> FRUIT WING NUMBER - absent - 2 wings - 3 wings - 4 wings
<p>Fruit</p> <ul style="list-style-type: none"> - pendulous - nodding - more or less erect <p>FRUIT DEHISCENCE</p>	<p>PERSISTENCE OF FEMALE TEPALS ON FRUIT</p> <ul style="list-style-type: none"> - persisting - deciduous <p>PERSISTENCE OF STYLES ON FRUIT</p>	<p>FRUITS BERRY LIKE OR NOT</p> <ul style="list-style-type: none"> - berry like - not berry like <p>FRUIT DEHISCENT</p> <ul style="list-style-type: none"> - not dehiscent 	<p>FRUIT WING NUMBER</p> <ul style="list-style-type: none"> - absent - 2 wings - 3 wings - 4 wings 	

	<ul style="list-style-type: none"> - between styles - via distinct lines next to the wing - indehiscent FRUIT TEXTURE WHEN MATURE - dry - fleshy or leathery FRUIT BODY SHAPE - ovate elliptic - turbinate - comma shaped - coronate - flask shaped - fusiform 	<ul style="list-style-type: none"> - persisting - deciduous FRUIT COLOUR WHEN DRY - brown - capsule body dark brown, wings pale cream - evenly cream/white - green brown FRUIT CAPSULE BODY WALL - fleshy or leathery - wood or shell consistency - paper like - scarious FRUIT WING PRESENCE AND LENGTH - wings more or less equal - all wings, one longer - one long wing, the remainder ribs - ribs only - no wings or ribs present FRUIT WING UPPER MARGIN ATTITUDE - horizontal - ascending - descending FRUIT CAPSULE APEX - obtuse - acuminate acute CAPSULE PEDICEL ATTITUDE - erect - pendulous - recurved FRUIT DEHISCENCE - indehiscent - dehiscent at margins of wings - dehiscent irregularly along back of capsule - dehiscent in between styles 	<ul style="list-style-type: none"> - irregularly dehiscent - dehiscent near the back of the locules - dehiscent near the septa - dehiscent bot near the back of the locules and near the septa - at the back of the carpels FRUIT POSITION - more or less erect - pendulous - nodding - recurved towards the substrate FRUIT PRESENCE OF A BEAK - without or with an indistinct beak - with a distinct beak 	<ul style="list-style-type: none"> - c. 6 wings (coronate) - 1 wing FRUIT WING SYMMETRY - equal to subequal - one distinctly larger FRUIT DRY OR FLESHY - dry - fleshy FRUIT ORIENTATION - upright - pendant to nodding - recurved FRUIT HAIR - glabrous - with hairs BEAKED FRUIT - absent - present DEHISCENCE - not between styles - between styles

<p>Seeds</p>	<p>SEED ORNAMENTATION</p> <ul style="list-style-type: none"> - present - faint, only on some specimens or absent <p>OPERCULUM SHAPE</p> <ul style="list-style-type: none"> - nipple shaped - obtuse - almost flat - columnar <p>NUMBER OF TESTA CELLS ALONG LENGTH OF SEED</p> <ul style="list-style-type: none"> - 5 to 10 - 1 to 4 	<p>SPECIALIZED TESTA CELLS</p> <ul style="list-style-type: none"> - present - absent <p>SEED ARIL PRESENCE</p> <ul style="list-style-type: none"> - present - absent <p>SEED ORNAMENTATION PRESENCE</p> <ul style="list-style-type: none"> - present - faint or absent <p>SEED OPERCULUM SHAPE</p> <ul style="list-style-type: none"> - flat - nipple shaped - obtuse - columnar 	<p>-</p>	<p>-</p>
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hand, can remain unchanged for long periods of time due to stabilising selection, and is periodically interrupted by bursts of speciation. During these periods of speciation, where a high rate of morphological evolution is not coupled with an equivalent rate in molecular evolution, DNA sequence data may not be able to provide any information on species relationships (although in cases of recent radiations population level molecular markers, such as microsatellites, would, however, be able to pick up differences in molecular variation). In the intervening periods, under conditions of stabilising selection, although morphology may remain relatively unchanged and assuming that molecular evolution is, at least, vaguely clock-like, then molecular data can resolve relationships between different species. These speciation bursts, or radiations, can be studied by comparing the branch lengths from independent phylogenetic analysis based on molecular and morphological data sets (Bateman, 1999). By mapping characters on a phylogenetic tree, information regarding branch lengths in a morphological analysis would be lost.

An important advantage of defining morphological characters and character states is the knowledge it gives the researcher on the given taxonomic group. Formal classifications are based on the diagnosability of groups (i.e. using morphology), and it is important for researchers to understand the relationships between different morphological characters, and how these characters have been used in the past to diagnose species and sections. While the method of defining morphological characters and character states cannot substitute the deep knowledge which results from performing a full taxonomic revision, it can help to understand morphological variation within a group and the homology relationships between different organs. Further, it may give the researcher freedom to make decisions regarding a taxon's classification, particularly in view of reconciling phylogeny and taxonomy.

4.2 MATERIALS AND METHODS

4.2.1 *Sampling and outgroup selection*

All 34 species of sections *Baccabegonia*, *Squamibegonia*, *Tetraphila* and *Mezierea* were examined for the morphological analysis. Characters and character states were identified from the study of herbarium material (see Appendix 7), living collections at the Royal Botanic Garden Edinburgh and Glasgow Botanic Garden, and supplemented from the literature (Arends, 1992; Hagman & de Wilde, 1983; Klazenga et al., 1994; Reitsma, 1985; de Wilde & Arends, 1979, 1980).

ITS and combined *trnL*, ITS and 26S analyses resolved all endemic Malagasy species plus *B. meyeri-johannis* as sister-group to the fleshy-fruited taxa (Chapters 2 and 3, Figs. 2.2 and 3.6; Forrest, 2000). Cladistic outgroups should be chosen on the basis of comparability to the ingroup, and should possess character states that resolve their relationships with respect to the ingroup (in this case morphological similarity and alignability of DNA sequences) (Nixon & Carpenter, 1993). Outgroups from within section *Mezierea* (such as *B. meyeri-johannis*) which also have fleshy, wingless fruits were originally chosen but later discarded because of alignment ambiguities in ITS, and the lack of morphological synapomorphies supporting the outgroup which gave rise to rooting problems. The morphological problems are the result of section *Mezierea* being resolved as polyphyletic in large scale molecular analyses, consisting of two cryptic clades for which no obvious morphological synapomorphies could be found – see Chapter 2. *Begonia bogneri* and *B. betsimisaraka*, both in section *Erminea*, were chosen as outgroups because they have fleshy, winged fruits comparable to the fleshy fruits of the ingroup taxa and the ITS sequences did not show high levels of divergence from those of the ingroup.

4.2.2 Morphology

A morphological data matrix of 27 characters was created in Nexus Data Editor (Page, 2000) (Appendix 5). There were five vegetative characters, 17 floral characters, four fruit characters, and one seed character. Character states were coded for all 34 species in sections *Baccabegonia*, *Squamibegonia* and *Tetraphila* and the two outgroup species. Quantitative discrete characters in the form of meristic data (e.g. tepal number, style number, anther number) were included. Continuous variation in the form of morphometric data was excluded. The final 27 characters were selected from an initial 36 characters. Table 4.2 shows the nine characters which were initially included and explains why they were ultimately rejected. All characters were treated as equally weighted and unordered (Fitch parsimony: Fitch, 1971). Characters were coded as missing in circumstances where a given character was not applicable due to the absence of the feature. Polymorphisms were input into the data matrix since data editing programs such as Nexus Data Editor (Page, 2000) or MacClade (Maddison & Maddison, 1992) can accommodate polymorphic data.

4.2.2.1 List of Characters

1. Leaf arrangement on stem: leaves not perpendicular to stem (0); leaves perpendicular to stem (1).

This character in which a creeping stem gives rise to perpendicular leaves is specific to section *Tetraphila*. This is characteristic of species in what has been referred to as the *B. squamulosa* species aggregate, which also includes *B. longipetiolata*, *B. squamulosa*, *B. karperi*, *B. rwandensis*, *B. pelargoniiflora* and *B. elaeagnifolia* (Arends, 1992). In herbarium specimens this character is very obvious, as the leaves press perpendicular along one side only of the creeping stem. Doorenbos et al. (1998) included this aerial stem within their broad concept of rhizome. I would use the term rhizome more precisely to refer explicitly to an underground creeping stem, excluding aerial creeping stems. This creeping stem, although similar to a rhizome, is distinct in that it

lacks the numerous dry bracts found in truly rhizomatous plants such as many of the Malagasy species and mainland sections such as *Loasibegonia* and *Scutobegonia*.

2. Leaves peltate or sub-peltate: no (0); yes (1).

Peltate refers to the petiole attachment close to the middle of the leaf, as in species of section *Peltaugustia*. Sub-peltate refers to instances where the petiole is attached within, but close to, the margin of the leaf. Species such as *B. karperi* and *B. rwandensis* often have the petiole attached only 2-4 mm from the base of the lamina (Arends, 1992). See Doorenbos et al., (1998).

3. Red leaf margin: absent (0); present (1).

Several species have a conspicuous red border following the entire margin of adult leaves, which can be up to 4 mm wide.

4. Peltate scales: absent (0); present (1).

Peltate scales are usually associated with epiphytic species and are probably an adaptation to the drier canopy environment. Among the African *Begonia*, peltate scales occur in sections *Baccabegonia*, *Tetraphila* and *Squamibegonia*. Other species recorded as having peltate scales are *B. prismatocarpa* (although they were absent from the specimen growing in Edinburgh) and *B. stellata* (Doorenbos et al., 1998), both of which belong to section *Loasibegonia*. The scales develop from being almost stellate hairs in young leaves to scale-like, membranous, often translucent trichomes which are commonly helicoidal. This kind of developmental transformation has also been observed in the genus *Croton* (Euphorbiaceae) (Webster et al., 1996). They can be sparsely scattered throughout both vegetative and floral organs, and in some species they form a dense covering on the underside of the leaves that obscure the abaxial laminal surface (see Character 5). Sosef (1994) considered peltate scales to be plesiomorphic (what he called "a relict": p. 15) within section *Loasibegonia*. Peltate scales are unknown among Asian and American *Begonia* (Doorenbos et al., 1998).

5. **Dense underleaf indumentum:** absent (0); present (1).

A few species (e.g. *B. bonus-henricus*, *B. furfuracea* and *B. subscutata*) have very dense underleaf indumentum covering the entire abaxial surface. The indumentum of *B. bonus-henricus* is composed of overlapping peltate scales, some of which are helicoid, whereas the indumentum of *B. furfuracea* is superficially similar but is composed of densely packed helicoidal stellate hairs with some fusion in the centre, resulting in a structure that appears intermediate between a scale and a stellate hair.

6. **Bisexual inflorescence:** absent (0); present (1).

7. **Bisexual inflorescence type:** 1-3 flowered simple or reduced dichasium (0); many-flowered (4 or more) simple or reduced dichasium (umbelliform) (1); complex dichasium (2); dichasial at base, monochasial above (3).

One to three-flowered reduced dichasia occur in section *Tetraphila*, where the female inflorescence commonly consists of a small number of flowers. Simple bisexual inflorescences are occasionally found in some species, such as *B. cavallyensis*. In this case the inflorescence consists of two lateral female flowers and a central male flower. The terms 'simple,' 'reduced' or 'compound' were not adopted by Arends (1992), who believed those terms held evolutionary inferences and therefore preferred to use the terms 'few-flowered' and 'many-flowered.' Simple or reduced dichasium here refers to what looks like a reduction of the primary inflorescence axis, giving a congested inflorescence where the flowers appear to be in the correct position for a dichasium but where there are no inflorescence axes. The many-flowered simple or reduced dichasium found in *B. pelargoniflora* is a regularly branched cyme with reduced lateral axes except for the two axes of the first order (Arends, 1992), giving the inflorescence a superficially umbelliform appearance. A complex dichasium consists of an inflorescence which branches dichotomously and is a "hierarchy of three-flowered units" (Arends, 1992: 56). Some inflorescences divide dichasially at the base but are monochasial towards the upper portion of the inflorescence. The term monochasium is used here to refer to inflorescences like those of *B. bogneri* where the entire inflorescence consists of two or

more flowers, each borne in the axil of the bracteole of the preceding flower (Bell, 1991: 140).

Inflorescence types are generally invariable within species, although it has been noted that inflorescences can be more depauperate in cultivated specimens. *Begonia longipetiolata*, which in the wild commonly produces an inflorescence that is dichasial at the base and monochasial above, can appear monochasial in cultivated specimens (Arends, 1992). Here I have only included inflorescences from wild collections. This character may occasionally be difficult to interpret from herbarium specimens and in those cases has been coded as unknown. Goulet et al. (1994) examined the inflorescence symmetry of 71 species of *Begonia* and recognised nine different types of inflorescence architecture based on living material. This classification, however, has not been widely adopted, probably due to the difficulty of assessing inflorescence symmetry from dry herbarium material.

Treatment of this character has differed among authors. Tebbitt (1997) coded the bisexual and female inflorescence type as a single character and defined the following states: dichasium; condensed monochasium; raceme; flowers solitary; and panicle. Badcock (1998) separated inflorescence form into three characters: partial inflorescence branching pattern (monochasial or dichasial), symmetry of inflorescence branches (symmetrical or asymmetrical), and number of inflorescence branching points (single flower to one dichotomy or between two and three dichotomies or more than three dichotomies). Doorenbos et al. (1998) separated the three types of inflorescence (bisexual inflorescence, male inflorescence and female inflorescence) into three different characters and defined the states for each as: dichasial, monochasial, and dichasial at base monochasial at apex.

8. Male inflorescence: absent (0); present (1).

9. Male inflorescence type: 1-3 flowered simple or reduced dichasium (0); many flowered (four or more) simple or reduced dichasium (1); complex dichasium (2); dichasial at base, monochasial above (3); monochasium (4).

See Character 7.

10. Female inflorescence: absent (0); present (1).

11. Female inflorescence: 1-3 flowered simple or reduced dichasium (0); many-flowered (4 or more) simple or reduced dichasium (1); complex dichasium (2).

See Character 7. Doorenbos (1998) divided this character in two, one character constituting the number of flowers per inflorescence and the other defining the inflorescence type. However, the number of female flowers is continuously variable, and plants will produce different numbers of flowers per inflorescence according to growth conditions. Number of flowers per inflorescence is ultimately an ecophenotypic character, and plants grown in glasshouses often produce inflorescences with few flowers. Only herbarium material from specimens growing in the wild was examined. Among African species the number of female flowers per inflorescence is very variable; species in sections such as *Tetraphila* and *Scutobegonia* can range from one to many female flowers per inflorescence.

12. Inflorescence bracts: small, opposite, deciduous, not overlapping (0); large, persistent, obscuring inflorescence axis (1).

Bracts subtending the inflorescence in section *Squamibegonia* are large and cup- or boat-shaped, completely obscuring the rhachis of the inflorescence. They were interpreted as pseudo-bracts by de Wilde & Arends (1980: 30), who believed them to be modified stipules (an interpretation originally proposed by Irmscher, 1925). A compressed inflorescence develops within these bracts, followed by soft indehiscent fruits which expand while protected by the bracts. *Begonia loranthoides* also produces large bracts, but they never completely subtend the inflorescence and are deciduous, leaving the fruit to develop unprotected. Here these are coded as state 0. The possession

of large bracts, in section *Squamibegonia*, is correlated with the presence of a perianth tube in the female flower.

13. Number of perianth segments in male flowers: 2 (0); 4 (1).

Perianth segment number generally remains constant within species (Doorenbos et al., 1998). However, some species like *B. oxyloba* or *B. meyeri-johannis* are polymorphic for this character, having individuals with either two or four perianth segments, and in some instances (e.g. *B. longifolia*), flowers with a different numbers of tepals can be observed on the same inflorescence. Badcock (1998) coded separately the outer whorl of perianth segments, which she termed sepals, and the inner whorl, which she termed petals. Her coding agrees with several previous studies carried out in *Begonia* (Kalmbacker, 1971; Sporne, 1977; Barabé, 1980, 1981) which show that the perianth segments are distinguishable into petals and sepals by their contrasting vascular systems. In angiosperms, petals generally receive only one vascular trace whereas sepals are better irrigated; for example, the sepals of *B. handelii* have five to eight traces (Barabé, 1980, 1981). Gauthier & Arros (1963) regarded the outer perianth segments of *Hillebrandia* as sepals since they were well vascularised, and recognised petals alternating with the sepals which are, however, rudimentary and already shrivelled when the flowers open. Without examining the vascularisation of the perianth segments it is difficult to differentiate the elements of the calyx from those of the corolla, although in species where there appear to be two whorls, the exterior whorl is generally termed the sepals and the interior whorl the petals. In flowers of herbarium specimens, both male and female, where the number of perianth segments is more than four, it is almost impossible to determine which perianth segments constitute the outer whorl and which the inner. In the case of *Symbegonia* the perianth segments are fused into a tube. The male flowers are composed of two fused segments whereas in female flowers the perianth tube consists of five lobes. Perianth information in the literature has always been given as the total number of perianth segments rather than differentiating contrasting perianth whorls, and this treatment is followed here.

14. Stamen number: > 10 (0); ≤ 10 (1).

Most species in section *Tetraphila* have over 10 stamens. A small number of species have 10 or less. Species in section *Baccabegonia* and *Squamibegonia* have more than 10 stamens, except *B. poculifera* (section *Squamibegonia*) which occasionally has less than 10. This is essentially a continuous character but has been used to diagnose species (de Wilde, in prep.) and is therefore included in this study.

15. Androecium symmetry: zygomorphic (0); actinomorphic (1).

The symmetry of the androecium is usually determined by the length and fusion of the filaments. In several African sections the gradual and uneven (fasciculate) fusion of the filaments causes the anthers to resemble a ‘bunch of bananas’ (Doorenbos et al., 1998). This feature is conspicuous in sections *Tetraphila*, *Squamibegonia* and *Baccabegonia*, where the androecium is strongly asymmetrical. As in a bunch of bananas, asymmetrical androecia are also dorsiventrally compressed, whereas symmetrical androecia resemble a dome in the centre of a flower. This conspicuous difference in stamen arrangement could reflect different pollination syndromes, and although it is known that some flowers in the genus are bee pollinated, potential biological and ecological differences between symmetrical and asymmetrical androecia have not been explicitly studied. The genus *Begonia* does not produce any nectar so plants are pollinated by deceit (Ågren & Schemske, 1991; Schemske & Ågren, 1995). The only reward to pollinators is pollen, and studies of some species have shown that female *Begonia* flowers attract pollinators by mimicking male flowers (Ågren & Schemske, 1991). This was shown in *B. involucrata* which, like most *Begonia* species, has a yellow forked style with a spiral stigmatic band. Several species in section *Tetraphila* (e.g. *B. manii*, *B. komoensis* and *B. preusii*) have two to four straight, unforked styles that are conspicuously dark red at the base and become lighter towards a bright yellow apex. In these styles the stigma is a contracted region at the apex of the style.

16. Anther apex: truncate (0); apiculate (1).

Among the fleshy-fruited species of *Begonia*, the majority of species have a truncate or flattened anther apex, where the connective lies horizontally between the two thecae. In some species, such as *B. oxyanthera*, the connective extends to a point above the thecae.

17. Anther apex hooded: no (0); yes (1).

A hooded apex is formed by the extension and expansion of the connective, which curls over and partially covers the anther apertures (pores or slits). See Doorenbos et al. (1998).

18. Anther dehiscence: longidehiscent (0); “poricidal” (1).

The term poricidal indehiscence in *Begonia* has previously been used in a misleading way (Doorenbos et al., 1998). True pores occur in *Begonia* only in section *Solananthera*. The poricidal indehiscence described by Doorenbos et al. (1998) for the species in section *Tetraphila* (*B. longipetiolata*, *B. squamulosa*, *B. pelargoniiflora*, *B. rwandensis*, *B. elaeagnifolia* and *B. karperi*) and in both species of section *Peltaugustia* are in reality short slits which open from the apex of the anther for a short distance, giving a tear-shaped opening. These short slits start in the apex of the anther in species of section *Tetraphila*, and may often be obscured by the hooded apex. In section *Peltaugustia* these slits appear to start further down due to the presence of an expanded connective. The term “poricidal”, although strictly incorrect, will be used here to conserve terminology, and refers only to the indehiscence in some species in section *Tetraphila*.

19. Perianth cylinder in female flowers: absent (0); present (1).

The perianth cylinder in female flowers refers to the basal fusion of the perianth segments into a tube separating the ovary from the unfused, apical parts of the corolla tube. In Africa this structure occurs only in section *Squamibegonia*, though some fusion has been noted in some species of the Asian section *Semibegoniella* (C. DC.) Barkley &

Baranov (Doorenbos et al., 1998). In section *Squamibegonia* the tube may have evolved concurrently with the large bracts found in the species of this section. The bracts are large, tightly compressed, almost flat, and embrace the entire inflorescence except for the petaloid extremity of the perianth. The inflorescence rhachis is compressed and held within the bracts, from which only the flowers themselves are exerted. The ovary is well-protected at the base of the enclosure produced by the bracts.

20. Number of perianth segments in female flower: 2 (0); 4 (1); 5-6 (2).

See Character 13.

21. Number of styles: 2 (0); 3 (1); 4 (2); 5-7 (3).

Although this character is meristic and can show polymorphism it is informative because most species have a consistent number of styles. Most species (and sections) have female flowers with three styles. However, in section *Tetraphila* style number can vary from two (*B. capillipes* and *B. cavallyensis*) to four or five (*B. manii* and *B. squamulosa*), though this degree of polymorphism is exceptional.

22. Style shape: forked once (0); two-lobed (1); simple (2).

Style characters are, along with anther morphology, one of the most stable characters in *Begonia*. Although there is a great variety of style types within some sections (e.g. *Tetraphila*), it is a very good identifier of single morphological species or species complexes. In Africa only section *Cristasemen* has styles that are forked more than once, although the character also occurs in sections *Semibegoniella* and *Hydristylis* A. DC. (Doorenbos et al., 1998). The vast majority of African species have styles which are forked once, though two-lobed species occur in section *Loasibegonia*, wherein all species have either a two-lobed style or a forked style with short arms. In section *Tetraphila*, two-lobed stigmas characterise *B. cavallyensis* and *B. fusicarpa*. Simple styles are rare, occurring in sections *Tetraphila* (e.g. *B. preusii*, *B. manii*), *Parvibegonia* A. DC. and *Gireoudia* (Klotzsch) A. DC. (Doorenbos et al., 1998). Style shape has been characterised differently by different authors. Badcock (1998) recognised lunate

and lunate-bicornute as well as the states presented here, and separated two straight-branched styles from two spirally branched styles. Tebbitt (1997) coded the following states in his style shape character: bifid; shortly bifid; many branched; and entire. He suggested that the bifid condition was primitive because it is possessed by most *Begonia* species, together with *Hillebrandia* and *Datisca*, (see Doorenbos et al., 1998).

23. Stigma: in a spiral band (0); kidney- or horseshoe-shaped (1); contracted near the style apex (2).

This character shows a great diversity and is closely associated with style shape (discussed in greater detail by Tebbitt, 1997; Badcock, 1998). The common state in *Begonia* is where the stigma forms a band and spirals along the branches of the forked style. In many species, notably those in sections *Squamibegonia*, *Sexalaria* and *Lepsia* (Klotzsch) A. DC. (Panda & de Wilde, 1995; Doorenbos et al., 1998), stigmatic tissue covers the entire style but there is differentiation between longer hairs covering the stigma and short hairs covering the remainder of the style. Since there is trichome differentiation this state is essentially a hirsute version of the common stigmatic state in the genus. Stigmatic differentiation of the kind described above does not occur in Asian *Begonia*. In Africa, about half of the species in section *Tetraphila* have unforked styles, which are curved slightly outward toward the apex. The stigma, reduced to a short band, is located on the outside of the style where it curves at the apex. Species in which the stigma is confined to the end of the style are also found in sections *Casparya* (Klotzsch) Warb., *Doratometra* (Klotzsch) A. DC., *Eupetalum* (Lindl.) A. DC. and *Ruizopavonia* A. DC., but the condition is absent in Asia. The kidney- or horseshoe-shaped stigmas are not spiral but occur when the styles produce two buds or short arms, or the style is forked at the apex. The kidney shape occurs in species where the stigmatic tissue covers the two buds, whereas horseshoe-shaped stigmas are found in species with slightly longer stylar arms. Doorenbos et al. (1998) created two characters for the stigma; one was whether or not the stigma is kidney-shaped, and the other describes the position of the stigma on the style. The kidney to horseshoe-shaped uncoiled state here includes the "in a band and not spiralled" state of Doorenbos and is equivalent to the "in a band and

not spiralled" state described by Tebbitt (1997), which also included kidney-shaped and "moon-shaped" stigmas. Tebbitt (1997) included stigma covering most of style or all over style, as did Doorenbos et al. (1998).

24. Fruit dehiscence: dehiscent (0); indehiscent (1).

Almost all *Begonia* fruits are dehiscent. However, in Africa sections *Squamibegonia*, *Mezierea*, *Scutobegonia* and *Loasibegonia* have indehiscent fruits. Dehiscence in fleshy-fruited species of sections *Baccabegonia* and *Tetraphila* occurs by the presence of dehiscence slits at maturity and recurvation of the fruit wall to reveal an erect, seed-bearing placental column. In cultivated plants this column disintegrates during or shortly after dehiscence (Arends, 1992). This banana-like dehiscence has been compared to that of *Datisca* and *Hillebrandia*, where dehiscence occurs at the top of the fruit between the styles (Badcock, 1998). Indehiscent fruits are not known from the Neotropics (Doorenbos et al., 1998). This character is difficult to determine in fleshy fruits, especially because dehiscent fruits are not collected, probably because they persist on the plant for only a few hours (Arends, 1992). The most common type of dehiscence within *Begonia* is the formation of slits on or near the back of the locules, as opposed to occurring near the septa (Doorenbos et al., 1998). Badcock (1998) erroneously coded all fleshy fruits as indehiscent, although she recognised that some species, including those in section *Tetraphila*, are known to dehisce.

25. Fruit shape: ellipsoid, obovoid or ovoid (0); globose (1); fusiform (2); alate (3).

This continuous character is here included to separate the long fruits of section *Tetraphila* and the globose fruits of section *Baccabegonia* from all other fleshy-fruited species. Fruit shape is very diagnostic for sections, particularly for species in section *Tetraphila* which have unique long fusiform fruits. Non-fleshy-fruited species are coded as missing.

26. Fleshy fruit shape in transverse section: terete (0); triangular or trigonous (1); polygonal (2); triangular with elongate corners (3).

The transverse section of fleshy fruits can be very variable, especially within section *Tetraphila*. Most fruits are terete, but some Central African species (e.g. *B. fusialata*, *B. ebolowensis* and *B. gabonensis*) are triangular and almost winged in transverse section. The polygonal section is only found in some populations of *B. loranthoides*; others have a terete transverse section.

27. Aril surrounding seed: absent (0); present (1).

Arils are known only in section *Tetraphila* and are thought to act as an eliosome, thereby aiding ant dispersal (de Lange & Bouman, 1992).

4.2.2.2 List of Soft Characters

Bateman (1999) suggested that characters which may be generally too variable or which show continuous variation and hence are especially prone to non-genetic ecophenotypic modification i.e. modification by the environment (and which he termed “soft characters”), should not be included in a cladistic analysis, but rather mapped *a posteriori* on a cladogram along with ecological and geographical information. The following characters were initially listed among the principal characters to be included in the analysis, but were found to be variable or difficult to divide into states.

1. Habit: terrestrial or rupestral (0); epiphytic (1).

Epiphytism occurs in African and the Neotropical *Begonia*, but is absent from Asian species. In Africa there appears to be a strong correlation between epiphytism and possession of fleshy fruits, an association not observed in the Neotropics. Although the majority of species fall fully within one of these two categories, some generally epiphytic species have terrestrial individuals (and so are coded as polymorphic), and there is significant overlap between rupestral and the other two conditions.

2. Leaf margin: entire (0); dentate (1).

Species in sections *Baccabegonia* and *Squamibegonia* have entire leaf margins, as

do most species in section *Tetraphila*. In section *Tetraphila*, entire leaf margins are mostly correlated with a more narrowly elliptic leaf shape (except in the case of *B. molleri* and *B. subalpestris*) and with increase leaf fleshiness. Some species in *Tetraphila* have leaves that are less fleshy, are usually broadly elliptic and have dentate margins. Within *Tetraphila* this kind of leaf shape is never associated with forked styles and strongly twisted stigmas.

3. **Fruit colour:** yellowish, orange, pink or red (0); white or green (1).

The fruits in most species of section *Tetraphila* mature pink, reddish or orange. A small number of species (*B. fusialata*, *B. preusii*, *B. polygonoides* and *B. capillipes*) have fruits which mature white or green. The fruits of *B. fusialata* are almost completely white, the colour extending to the placenta. The fruits of *B. preusii* are reddish when immature but when mature are white. In contrast, the fruits of *B. capillipes* and *B. polygonoides* are very narrow and when mature are green. Nothing is known about why these species have evolved different mature fruit colour; it is tempting to speculate that they reflect different dispersal mechanisms or vectors.

4.2.2.3 Rejected characters

Eleven characters, which were provisionally included, were eventually rejected or treated as soft characters on the grounds of showing too much infraspecific variation, for being ecophenotypically rather than genetically variable, or in which it was difficult to establish a clear assessment of transformational homology (Table 4.2). In some cases these characters, although excluded from the parsimony analysis, were mapped *a posteriori* across a most parsimonious tree (MPT).

Most characters describing symmetry, such as inflorescence or leaf symmetry, were excluded. It is almost impossible to discern inflorescence symmetry from herbarium specimens, and leaf symmetry is difficult to quantify and is essentially a continuous character. For similar reasons, leaf texture, leaf venation and tepal shape

were also excluded.

Table 4.2 Table of characters which were initially included in the study but later excluded.

Character	Reason for exclusion from phylogenetic analysis
Habit: terrestrial or rupestral (0); epiphytic (1)	Very polymorphic because the two states are frequently present in one species.
Stem: herbaceous (0); thickened or wood-like (at least at base) (1)	Difficult to determine thickening from herbarium specimens.
Leaf margin: entire (0); dentate (1)	Continuous character
Indumentum scale type: <i>B. bonus-henricus</i> type (0); stellate (1); dentate (2); fimbriate (3)	Continuous character. Scales change in shape with age. Young scales tend to be stellate, becoming more peltate with age, with the margins dentate to fimbriate.
Venation: palmate (0); pinnate (1)	The two states frequently overlap.
Style fusion: free to base or fused to half way (0); styles fused more than half way (1)	Continuous character.
Leaf blade symmetry: almost symmetrical (0); asymmetrical (1)	Continuous character.
Perianth indumentum: glabrous (0); minute glandular hairs (1); stellate hairs (2); dentate or fimbriate scales (3); helicoidal peltate-stellate hairs (4); peltate-stellate, not helicoidal (5)	Continuous character.
Ovary and pedicel distinct: yes (0); no (1)	Continuous character.
Ovary indumentum: glabrous (0); glandular hairs (1); lepidote stellate hairs (2); lepidote helicoid hairs (3); dentate scales (4); fimbriate scales (5)	Continuous character.
Fruit colour: yellowish, orange, pink or red (0); white or green (1)	Continuous character.

4.2.3 Molecular data

ITS and *trnL* sequences for 23 species of sections *Baccabegonia*, *Squamibegonia* and *Tetraphila* obtained for the analyses in Chapters 2 and 3 were used in this combined analysis.

4.2.4 *Phylogenetic analysis*

Three main analyses were carried out to study the phylogenetic effectiveness of morphology and to compare the phylogenies resulting from separate and combined analyses of ITS, *trnL* intron and morphological data matrices. All characters were treated as unweighted and unordered (Fitch parsimony; Fitch, 1971). Maximum parsimony analyses were run on PAUP* version 4.0b7 (Swofford, 2000) and NONA (Goloboff, 1993).

4.2.4.1 Extended morphological data set

The influence of subset polymorphisms on the analysis was tested on a matrix in which 27 morphological characters were coded for all 36 known species in sections *Baccabegonia*, *Squamibegonia* and *Tetraphila*. Three separate analyses explored the effects of subset polymorphisms on the final topology yielded by PAUP. In these analyses polymorphic cells were treated as (a) ambiguous; (b) polymorphic, and (c) excluded from the analysis. All three analyses were run on PAUP* version 4.0b7 using the same two-step heuristic search strategy, which aimed to avoid local optima of tree length (parsimony islands). Trees were obtained running 1000 random addition sequences, holding one tree at each step during stepwise addition. Branch swapping was done with TBR (tree-bisection-reconnection). Steepest descent and multrees were not in effect, saving only one tree per replicate. This strategy was followed by a second search that swapped on the trees saved from the first round. The steepest descent and multrees options were invoked, and a maximum of 5000 trees were saved. A search was carried out in NONA to compare topologies produced by PAUP and to observe character optimisation across a single tree. In NONA, a heuristic search was carried out with Maxtrees = 10,001, replicates 1000, saving 10 trees per replicate. Branch swapping invoked TBR, followed by another round of TBR swapping on the trees saved from the initial search.

4.2.4.2 Subsets of both morphological and molecular data sets

A subset of 23 species from sections *Tetraphila*, *Squamibegonia* and *Baccabegonia* was used in all three analyses. This matrix (Appendix 6) contained the subset of species from the morphological matrix used in analysis 4.2.4.1 for which ITS and *trnL* were available. DNA sequence data for ten species was not available either due to the lack of material or because the available material failed to generate sequences. The parsimony search using PAUP was the same as that used in analysis 4.2.4.1 except that in parts ii) and iii) the search was allowed to run to completion in the final step.

(i) Morphology only— A parsimony analysis was conducted on 27 morphological characters where multistate taxa were treated as ambiguous.

(ii) *TrnL* only— A heuristic search of 524 *trnL* intron characters was carried out in PAUP. All characters had equal weight and were unordered. Gaps were coded following the simple coding methodology proposed by Simmons & Ochoterena (2000), where they are included in the analysis and treated as missing (see Chapter 2).

(iii) ITS only—The following characters were excluded due to alignment ambiguity: 570-571, 592-636, 656-657, 688-692, 714-720, 938-1028, and 1120-1126. These regions were exclusively from the ITS1 and ITS2 spacer regions. A heuristic search of 518 characters was run where gaps were treated as missing.

Support for individual nodes was assessed using bootstrap values (Felsenstein, 1985). PAUP settings for the bootstrap analysis were: 1000 replicates, 10 random sequence additions, invoking TBR swapping and multrees.

4.2.4.3 Congruence tests

To test congruence between the three data sets an incongruence length difference

(ILD) test (Farris et al., 1994) was carried out as implemented by PAUP (called the partition homogeneity test in PAUP) (described in Chapter 3) and assessed visually by observing congruence with respect to support values for separate clades. 1000 replicates were used in the partition homogeneity test. For more details on the ILD test and on methods of assessing congruence based on bootstrap support for different clades, see Chapter 3.

4.2.4.4 Combined analysis

Characters in ITS were excluded as in analysis 4.2.4.2 part (iii). Parsimony analysis was conducted on the remaining 1069 characters. Gaps in the *trnL* partition were coded following the simple coding method advocated by Simmons & Ochoterena (2000), and were included in the analysis and treated as missing. Multistate taxa were treated as ambiguous. Trees were obtained by running 1000 random addition sequences, holding one tree at each step during stepwise addition. Branch swapping was conducted with TBR, invoking steepest descent and multrees.

4.3 RESULTS

4.3.1 Extended morphological data set

Parsimony analysis of 26 informative characters (out of a total of 27) where subset polymorphisms were treated as ambiguous yielded 212 equally most parsimonious trees of length 76, CI of 0.500 (0.493 excluding autapomorphies) and RI of 0.775. The strict consensus is shown in Figure 4.1a. When multistate taxa were treated as polymorphisms this yielded 215 equally most parsimonious trees of length 132, CI of 0.712 (0.708 excluding autapomorphies) and RI of 0.775. The strict consensus is shown in Figure 4.1b. The third search, in which characters that were polymorphic for at least one taxon (13 characters in total) were removed entirely from

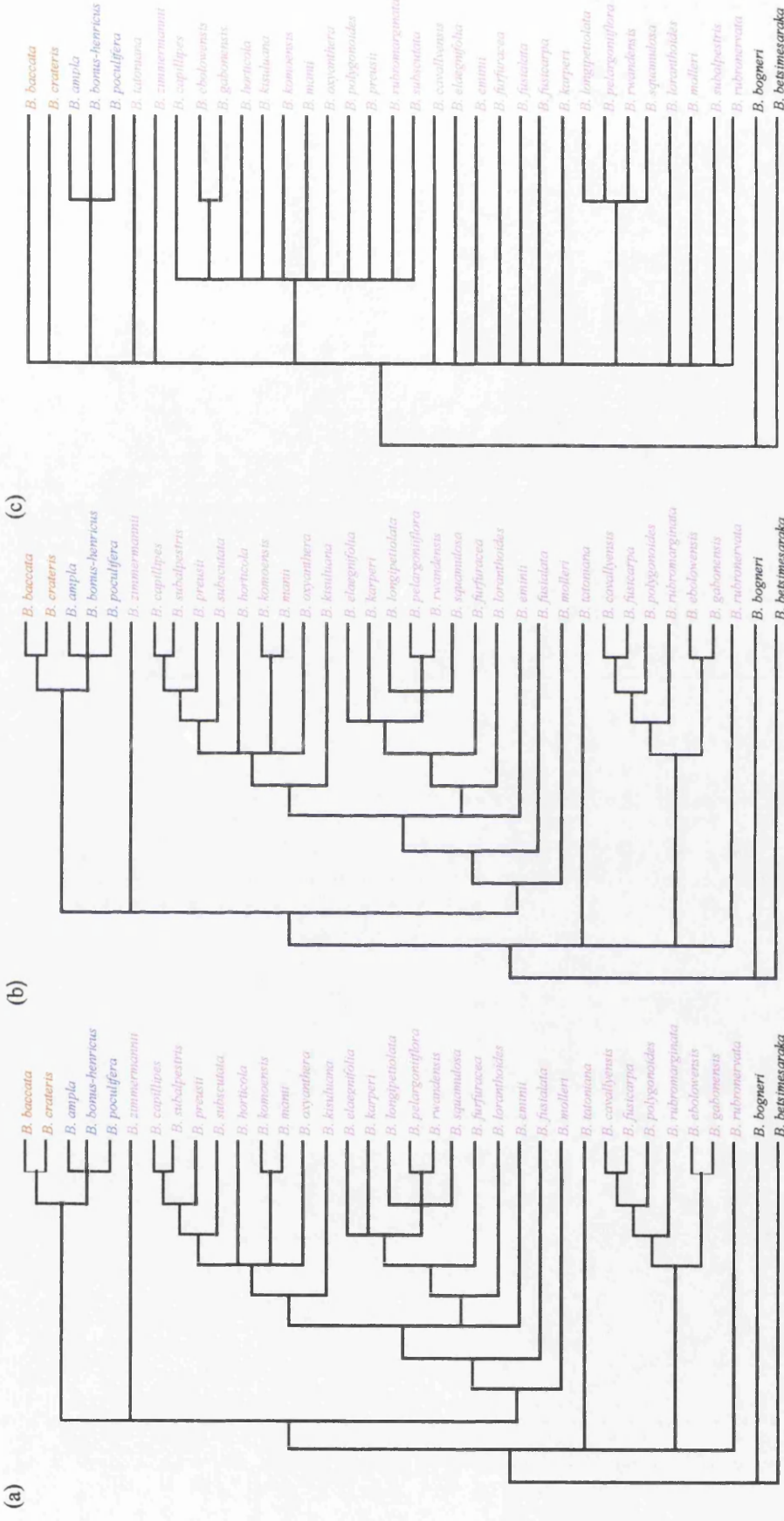


Figure 4.1 Three strict consensus trees showing the effects the different treatments of subset polymorphisms exert on the consensus topology. (a) multistate taxa as ambiguous; (b) multistate taxa as polymorphisms; and (c) multistate characters excluded. Colours denote section *Baccabegonia* (orange), section *Squamibegonia* (blue) and section *Tetraphila* (pink).

the analysis, yielded 470 trees of length 33, CI of 0.545 (0.545 excluding autapomorphies) and RI of 0.845. The strict consensus is shown in Fig. 4.1c. Treating subset polymorphisms as either ambiguous or as polymorphisms did not affect the topology of the strict consensus tree (Fig. 4.1a and 4.1b). However, tree length decreased significantly, from 132 to 76, when multistate taxa were treated as ambiguous; CI values also decreased. All most parsimonious trees in both studies showed a monophyletic *Squamibegonia* sister to both species in section *Baccabegonia* (Fig. 4.1). They also supported the monophyly of species in the *B. squamulosa* aggregate (*B. longipetiolata*, *B. squamulosa*, *B. elaeagnifolia*, *B. pelargoniiflora*, *B. karperi* and *B. rwandensis*). When subset polymorphisms were excluded from the analysis, the strict consensus tree (Fig. 4.1c) retained a monophyletic *Squamibegonia*, but did not resolve section *Baccabegonia* as sister to this clade. The *B. squamulosa* clade no longer included *B. elaeagnifolia*, leaving this species unresolved. In contrast, a clade emerged that included most species possessing straight styles (*B. capillipes* to *B. subscutata*). In this last analysis, because of a decrease in number of characters, tree length dropped dramatically to 33 steps, though the CI value was also low.

Excluding polymorphic characters from the analysis greatly decreased the number of informative characters that could be explored and gave much less resolution than when all polymorphic characters were included. The strict consensus topologies were identical regardless of whether polymorphisms were treated as ambiguous or as polymorphisms. The higher CI value when subset polymorphisms were treated as polymorphic, and the fact that only the states indicated in the cell are optimised, means that treating subset polymorphisms as such in PAUP is a superior method of treating this data, allowing the exploration of all morphological characters in the matrix. Moreover, it allows the inclusion of characters that can be phylogenetically informative, and can add resolution. Therefore, in subsequent analyses that included morphological data, subset polymorphisms were treated in this way.

The search in NONA yielded four most parsimonious trees of length 76 steps,

CI of 0.50 and RI of 0.77. The strict consensus recovered the same topology as that produced by PAUP when treating multistate taxa as polymorphic and ambiguous (Fig. 4.1b). The tree length is the same as that produced in PAUP when multistate taxa are treated as ambiguous. Figures 4.2a and 4.2b show character optimisation on the combined tree by ACCTRAN, which favours reversals, and DELTRAN, which favours parallelisms.

4.3.2 *Subset morphological and molecular data set*

(i) Morphology only—Of the 27 characters in the analysis, 23 were parsimony informative. Parsimony analysis yielded 5000+ most parsimonious trees of length 98, CI of 0.755 (0.747 excluding autapomorphies), and RI of 0.784. The strict consensus of these trees (Fig. 4.3a) shows little resolution, though all trees support a monophyletic *Squamibegonia* supported by a 96% bootstrap value. There is also good support (96%) for *B. baccata* as sister to section *Squamibegonia*. All trees agree on a monophyletic *Tetraphila*. A moderately supported clade consisting of *B. ebolowensis* and *B. gabonensis*, both of which have fruits triangular in transverse section, and an unsupported clade including comprising *B. komoensis* and *B. manii*, two species which are morphologically very similar, are also present in the strict consensus.

(ii) *TrnL* only—Of the 524 characters included in the analysis only 30 were parsimony informative. Parsimony analysis of the informative characters yielded 180 most parsimonious trees of length 105, CI of 0.952 (0.868 excluding autapomorphies) and RI of 0.917. The strict consensus is shown in Figure 4.3b. All trees resolve a monophyletic *Squamibegonia* as sister to *Baccabegonia*. All species of *Tetraphila*, excluding *B. loranthoides* and *B. longipetiolata*, form a monophyletic group. Within section *Tetraphila* there are four clades. The first, which includes *B. kisuluana*, *B. capillipes*, *B. furfuracea* and *B. preusii*, has moderate bootstrap support (66%). It consists mostly of species which have simple styles, except *B. furfuracea* which has a forked style and spiral stigma. All species have narrowly elliptic leaves with entire margins. All species

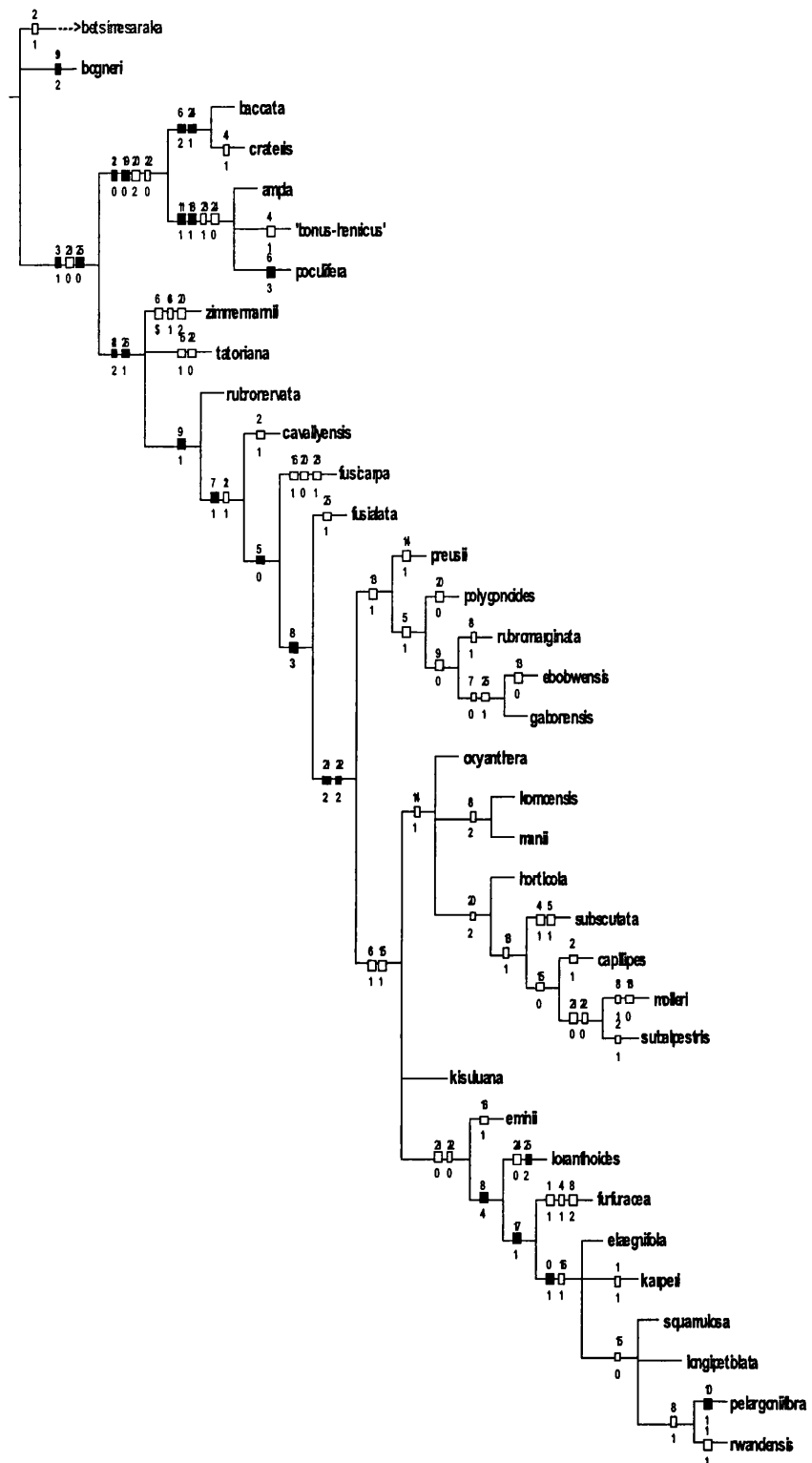


Figure 4.2a One random tree resulting from the parsimony analysis of the morphological data in NONA. Characters have been mapped using DELTRAN optimisation. The black bars represent non-homoplastic states, and the open bars homoplastic states. Numbers above the bars correspond to characters and the ones below to the states.

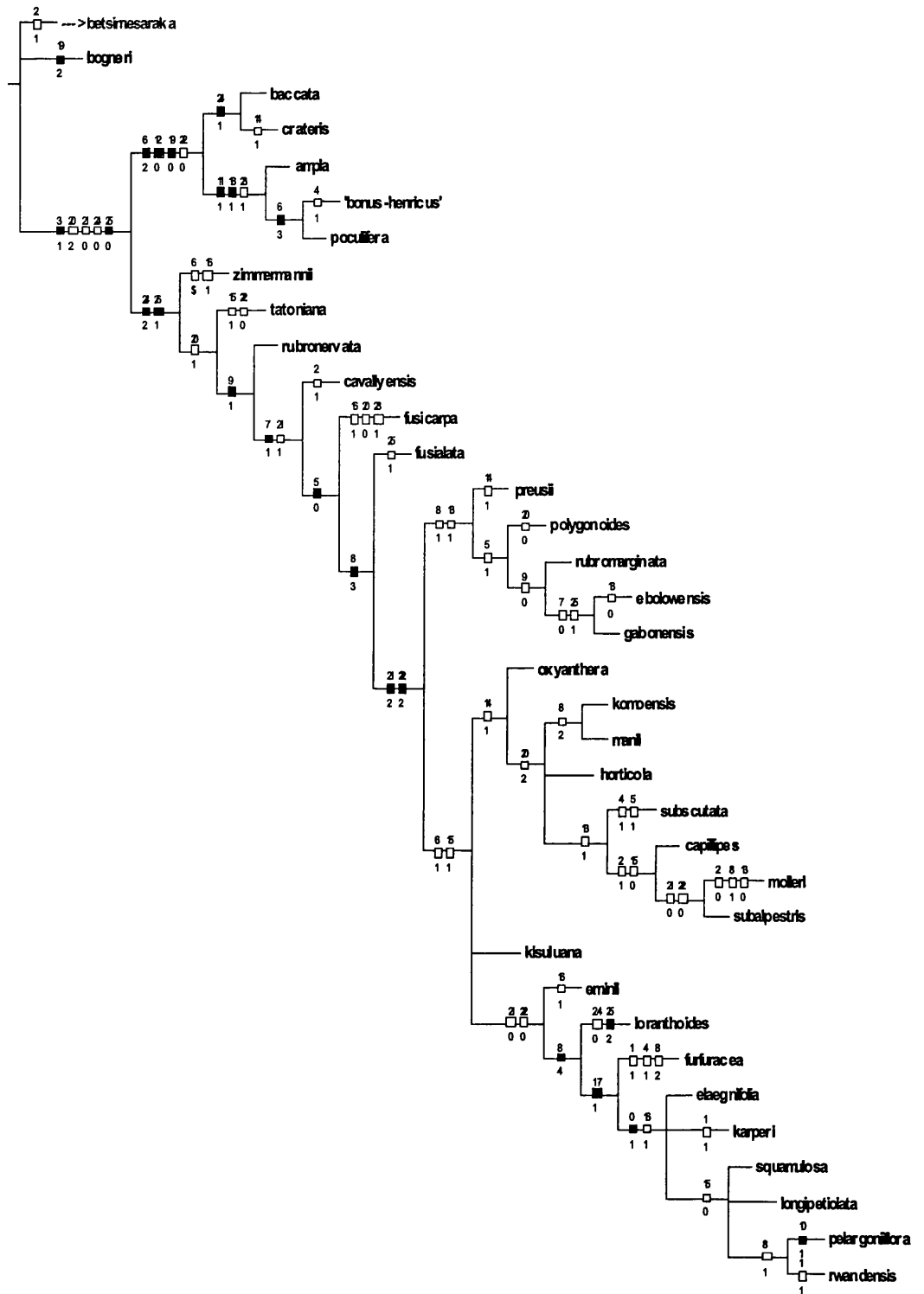


Figure 4.2b One random tree resulting from the parsimony analysis of the morphological data in NONA. Characters have been mapped using ACCTRAN optimisation. The black bars represent non-homoplastic states, and the open bars homoplastic states. Numbers above the bars correspond to characters and the ones below to the states.

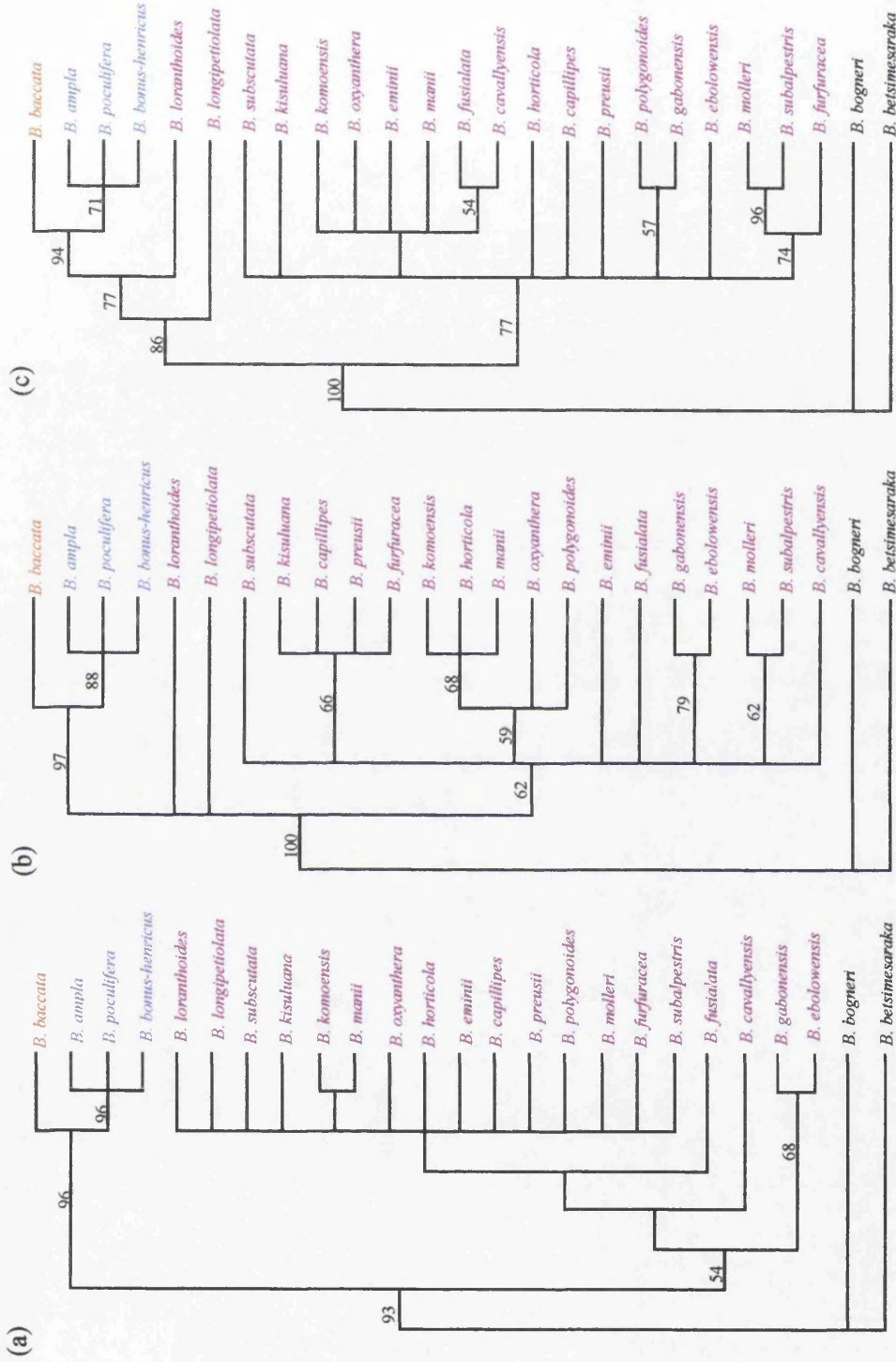


Figure 4.3 Strict consensus of the separate maximum parsimony analyses of 25-species matrices generated from a) morphology, (b) *trnL* and (c) ITS. Numbers above the branches are bootstrap values. Colours denote section *Baccabegonia* (orange), section *Squamibegonia* (blue) and section *Tetraphila* (pink).

in the second clade have straight styles (*B. komoensis*, *B. horticola*, *B. manii*, *B. polygonoides* and *B. oxyanthera*), but support for it is weak (59%). There is, however, stronger support (68%) for the sub-clade encompassing the morphologically very similar *B. komoensis*, *B. horticola* and *B. manii*. The third clade includes two species with trigonal fruits, *B. ebolowensis* and *B. gabonensis*. The last clade consists of the two São Tomé endemics, *B. subalpestris* and *B. molleri*.

(iii) ITS1— Of the 520 characters included in the analysis, 88 were parsimony informative. The heuristic search yielded 206 most parsimonious trees of length 463, CI of 0.888 (0.741 excluding autapomorphies) and RI of 0.782. The strict consensus is shown in Fig. 4.3c. The monophyly of *Squamibegonia* is well-supported, as is the position of *B. baccata* as sister to this clade. In addition, ITS sequence data resolve the position of *B. loranthoides* and *B. longipetiolata* as sisters to sections *Squamibegonia* + *Baccabegonia* with a bootstrap value of 86%, making section *Tetraphila* non-monophyletic (Fig. 4.3c). The rest of section *Tetraphila* is supported by a bootstrap value of 77%. Within *Tetraphila*, the topology is somewhat incongruent with that produced by the *trnL* data. The most striking incongruence is the position of *B. furfuracea*, which is resolved by ITS as sister to the São Tomean endemics *B. molleri* and *B. subalpestris*, with relatively strong bootstrap support of 74%. In the *trnL* consensus topology, *B. furfuracea* is similarly well-resolved within a clade that consists of *B. preusii*, *B. capillipes* and *B. kisuluana*. In this analysis, *B. gabonensis* is sister to *B. polygonoides*, although this relationship is weakly supported (57%). All most parsimonious ITS trees also agree on a weakly supported clade encompassing *B. komoensis*, *B. oxyanthera*, *B. eminii*, *B. manii* and *B. fusialata*. This clade is different in composition to the second clade in the *trnL* topology, which only includes some of the species in this clade.

Figure 4.4 shows difference in branch lengths between the molecular and morphological data sets. The morphological data showed considerably shorter branch lengths than the molecular phylogenies. This could suggest that the rates of

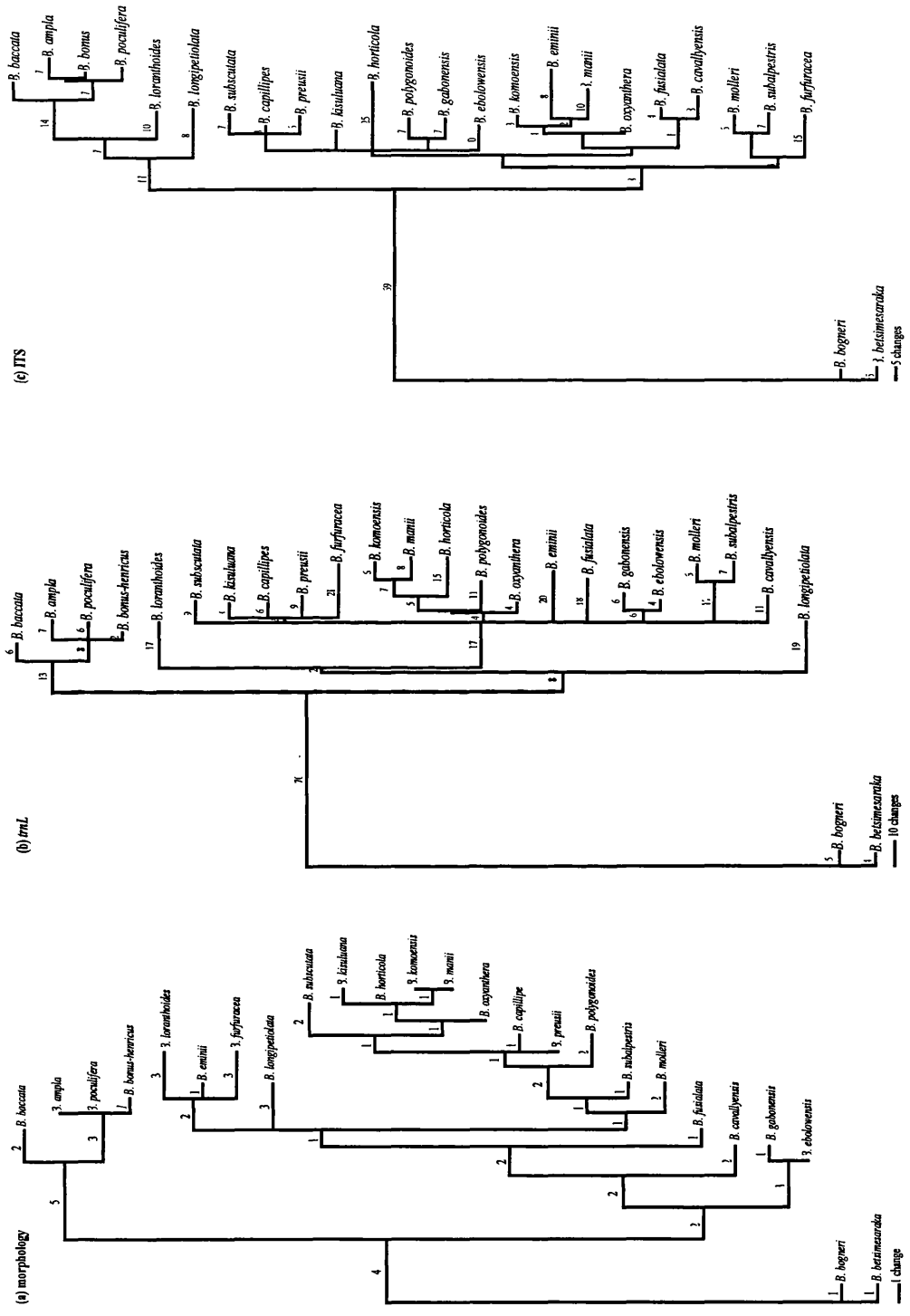


Figure 4.4 Randomly chosen most parsimonious trees generated by maximum parsimony analysis of 25-species matrices from (a) morphology, (b) *trnL* intron and (c) ITS. Numbers above the branches represent branch lengths. Note that the trees are drawn to different scales.

morphological and molecular evolution are not tandemly correlated, and that in this case morphology appears to be very conserved compared to sequence variation, especially of ITS. More probable, however, is that the differences in branch length are largely a consequence of the difference in the number of characters between the morphology and molecular data sets (27 characters vs. 520-524 characters).

(iv) Combined analysis (Figs. 4.5 and 4.6)—The results from the partition homogeneity test between the molecular partitions gave a value of $P = 0.12$, showing no significant incongruence between partitions. Incongruence between the morphological and each of the molecular data sets was strong ($P = 0.001$ (ITS)— 0.008 (*trnL*)). This high incongruence value reflects the topological incongruence between the morphology and molecular trees. However, none of this incongruence is well supported (as evidenced by high bootstrap values). Furthermore, there is no *a priori* reason to doubt that each morphological character does not provide evidence of relationships because they are genetically controlled and independent. Therefore, the morphological characters can contribute to a combined analysis. Incongruence between the two molecular partitions in the form of clade support was evident in the conflicting position of *B. furfuracea*. It was decided to retain this species in the combined analysis but to interpret its phylogenetic position with caution.

A combined parsimony analysis of 1071 ITS, *trnL* and morphological characters, of which 142 were parsimony informative, yielded 8 most parsimonious trees of length 685, CI of 0.854 (0.717 excluding autapomorphies) and RI of 0.756. Figure 4.5 shows a single most parsimonious tree with nodes retained in the strict consensus marked with a solid black circle. Section *Squamibegonia* is strongly supported by 100% bootstrap, as is the sister relationship of *B. baccata* to this clade. The inclusion of *B. longipetiolata* and *B. loranthoides* in the same clade as *Squamibegonia* and *Baccabegonia* is moderately supported (bootstrap value = 64%). *Begonia furfuracea* forms a clade with *B. molleri* and *B. subalpestris* as it did in the ITS analysis. This position seems reasonable because all species in this clade have forked styles with a coiled stigma.

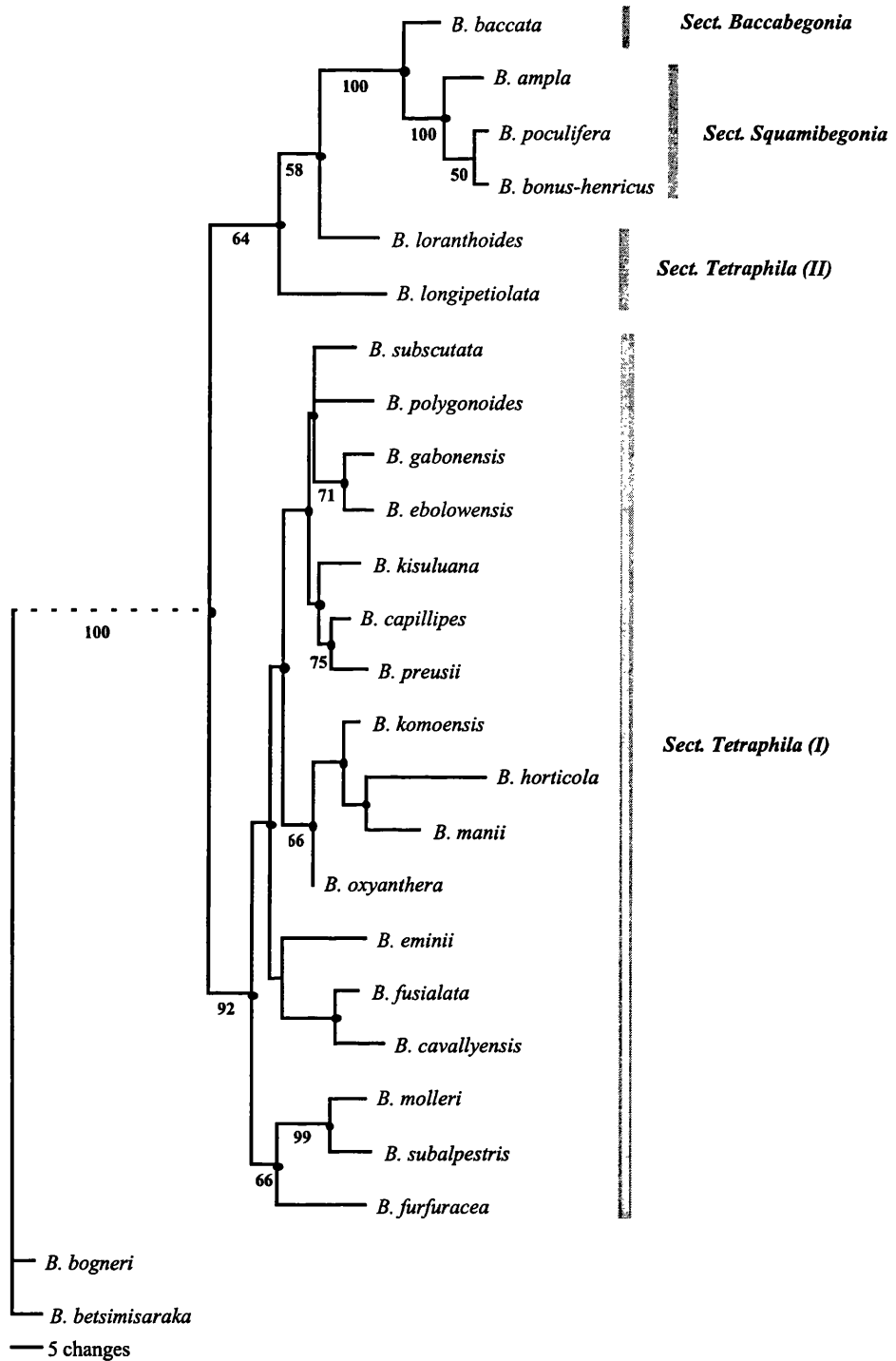


Figure 4.5 One of eight most parsimonious trees resulting from the maximum parsimony analysis of combined morphological, *trnL* and ITS data. Values beneath the branches represent bootstrap support. Branches which are retained in the strict consensus are marked with a solid black circle.

A clade consisting of species possessing broadly ovate to broadly elliptic leaves with dentate margins and prominent simple styles (*B. komoensis*, *B. horticola*, *B. manii* and *B. oxyanthera*) is poorly supported, even though morphologically this group is quite diagnostic. Unfortunately, the morphological phylogeny does not reflect this (Fig. 4.3a). Compared to other species in this clade, the styles of *B. oxyanthera* are less robust. The sister-group relationship between *B. eminii* and *B. fusialata* is not supported by all eight trees, but they are morphologically very similar. They are two of the three (the other being *B. tatoniana*) terrestrial species in section *Tetraphila*, and have leaves resembling those in the *B. komoensis* clade, and possess forked styles, but are unique in that the stigma forms a band but is not spiral. The large clade consisting of species such as *B. subscutata*, *B. gabonensis* and *B. kisuluana*, and which lacks bootstrap support, consists of species with simple styles and narrowly elliptic or obovate leaves.

Figure 4.6 shows the optimisation of morphological characters on a single most parsimonious tree, where homoplasious character states are marked in grey and non-homoplasious ones in black. Table 4.3 lists all the morphological characters and their CI and RI values. Only one character (Character 11) was not informative in the combined analysis, because some species were culled to provide a subset matrix. Nine of the 27 characters have states that show unique changes (non-homoplasious; CI = 1.00), and of these only two are autapomorphies (RI = 0) with the rest providing synapomorphies (RI = 1.00). There are no differences in levels of homoplasy between vegetative and floral character states. Many strongly homoplasious character states (showing low CI values) did give good grouping information as is denoted by the high RI values (e.g. bisexual inflorescence, androecium symmetry).

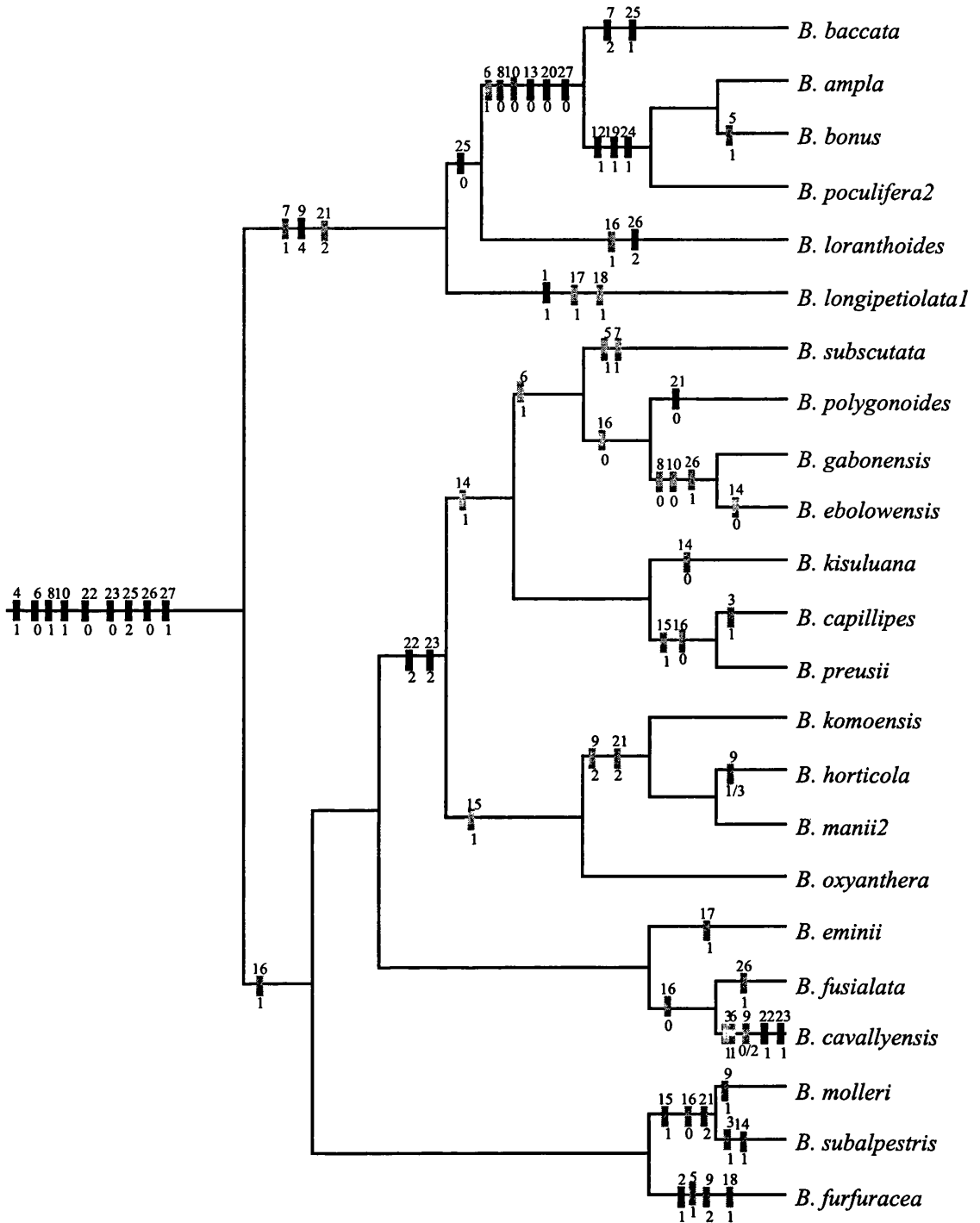


Figure 4.6 A single most parsimonious tree from the combined analysis showing morphological character optimised (ACCTRAN) on the combined topology. The black bars represent non-homoplastic states, and the grey bars homoplastic states. Polymorphisms are not marked. Numbers above and below the bars represent the characters and their states.

Table 4.3 Tabulation of morphological characters and their performance in the combined analysis (CI = consistency index; RI = retention index).

Character	No. of states	Steps	CI	RI
1. Leaf arrangement on stem	2	1	1.00	0
2. Leaves peltate or sub-peltate	2	1	1.00	0
3. Red leaf margin	2	4	0.25	0
4. Peltate scales	2	1	1.00	1.00
5. Dense underleaf indumentum	2	3	0.33	0
6. Bisexual inflorescence	2	4	0.25	0.70
7. Bisexual inflorescence type	3	3	0.67	0.67
8. Male inflorescence	2	3	0.33	0.71
9. Male inflorescence type	4	5	0.40	0
10. Female inflorescence	2	3	0.33	0.71
11. Female inflorescence type	1	0	0	0
12. Inflorescence bracts	2	1	1.00	1.00
13. Number of perianth segments in male flowers	2	1	1.00	1.00
14. Stamen number	2	4	0.25	0.40
15. Androecium symmetry	2	3	0.33	0.71
16. Anther apex	2	6	0.17	0.38
17. Anther apex hooded	2	2	0.50	0
18. Anther dehiscence	2	2	0.50	0
19. Perianth cylinder in female flowers	2	1	1.00	1.00
20. Number of perianth segments in female flowers	3	2	1.00	1.00
21. Number of styles	4	4	0.50	0.60
22. Style shape	3	3	0.67	0.92
23. Stigma	3	3	0.67	0.92
24. Fruit dehiscence	2	1	1.00	1.00
25. Fruit shape	4	3	1.00	1.00
26. Fleshy-fruit shape in transverse section	4	4	0.75	0.67
27. Aril surrounding seed	2	2	0.50	0.80

4.4 DISCUSSION

4.4.1 *Character perception in Begonia morphology*

Looking closely at the morphological cladistic studies carried out in *Begonia* to date demonstrates how different investigators do indeed perceive and define characters and their states differently. Table 4.1 shows several examples in which different authors have variously interpreted homology in *Begonia*. As was mentioned briefly in section 4.1.3 one example of this difficulty is evident in the case of underground storage organs and stems. Tebbitt (1997) assumed homology of rhizomes and tubers by defining them as states of a binary presence/absence character. Badcock (1998) also included rhizomes and tubers as alternative states of the same character, in addition to other states such as root tuber and stem tuber. Stem morphology was included as a separate character for which she differentiated several degrees of caulescence. In contrast, Doorenbos et al. (1998) included caulescence and the presence of rhizomes in the same character and treated tubers as a separate presence/absence character. Finally, Forrest (2000) coded stem tubers and root tubers as separate presence/absence characters and excluded rhizomes altogether. Another example is the differentiation between sepals and petals in *Begonia* flowers. Only Badcock (1998) made this distinction. Because both sepals and tepals in *Begonia* are petaloid, and the separate whorls are often hard to tell apart, most authors treat them as a single character with states defined as the different number of tepals.

Coding strategies are similar among all investigators (see Table 4.1). They all treat inapplicable data as missing. The vast majority of their characters have discrete states and many characters are multistate. Continuous data in the form of measurements are rare, but all use continuous meristic data such as style number. There are some instances, although rare, when descriptive continuous characters are included (e.g. degree of fusion: free; fused only at the base; fused for more than half their length). This last case evokes the difficulties that can be engendered by the variable delimitation of

arbitrary states within a continuum. Examples of this are the degree of fusion of the styles. Forrest (2000) recognised two states, whereas Doorenbos et al. (1998) and Badcock (1998) recognised three. Similarly, for filament fusion, Doorenbos et al. (1998) recognised three states, Forrest (2000) and Tebbitt (1998) four, and Badcock (1998) five.

Polymorphic characters were also treated differently by different authors. Badcock (1998) treated polymorphic data as missing unless one state was known to be 75% more prevalent than others, in which case only the common state was scored. Doorenbos et al. (1998) also coded the common state to eliminate polymorphic cells in the matrix as did Tebbitt (1997). Forrest (2000) did not encounter polymorphism because she only sampled single individuals (equivalent to her DNA vouchers) for each species. None of these approaches are acceptable, as they disregard intraspecific morphological variation.

4.4.2 How to use morphology in big genera

Studies comparing morphological and molecular data in *Begonia*, imply that morphology can be misleading in terms of defining relationships (Tebbit, 1997; Badcock, 1998; Forrest, 2000), and therefore, estimates of phylogenetic relationships within *Begonia* should not be carried out based on morphology alone. One of the primary problems is assessing homology across an entire genus the size of *Begonia* (ca. 1400 spp.). Characters such as fruit dehiscence, for example, are difficult to qualify across morphologically divergent species. In addition, the more species that are included in a morphological matrix, the greater the proportion of taxa with inapplicable or polymorphic character states. Particularly high levels of inapplicable data could lead to erroneous estimates of phylogeny due to the optimisation strategies of available phylogenetic software (see section 4.1.3.2). Finally, one of the most significant problems of coding morphology for a large genus will always be the unavoidable dilemma of finding enough morphological characters.

In view of these problems, I would recommend carrying out morphological phylogenetic studies in *Begonia* only on targeted sections; that is, either a single section or a small group of putatively related sections. This reduces problems of homology assessment, homoplasy and problems of inapplicable data, and allows morphology to provide at least some phylogenetic signal. As mentioned above, morphology alone in *Begonia* seems unlikely to give correct estimates of species relationships, so morphological data should always be used in conjunction with molecular data. Molecular data alone may not resolve all relationships, and does not satisfactorily diagnose taxa. It is interesting to observe in combined analyses the kind of phylogenetic signal that morphology can provide in a given topology, often giving greater resolution at specific nodes (see below).

4.4.3 Topological and character incongruence between ITS, morphology and trnL.

Chapter 3 discussed the pitfalls of statistical congruence tests such as the ILD. In this chapter statistical congruence tests between morphology and the individual molecular data sets all failed. This negative conclusion was not, however, supported by strong topological incongruences. Statistically significant incongruence between data sets need not preclude combining them if the source of the incongruence is local and the specific relationships involved can be determined (Baker & DeSalle, 1997). In such cases combining data is likely to improve the accuracy of the phylogeny in those sections of the tree not affected by the incongruence (Wiens, 1998).

The only supported conflicting position resulting from the separate analyses of *trnL* and ITS was for *B. furfuracea* (Fig. 4.3b and 4.3c). The reason for this conflicting position is that in the *trnL* phylogeny *B. furfuracea* shares a 10 bp gap with *B. preusii*, *B. capillipes* and *B. kisuluana*. This could be a homology for all four species. However, it is possible, based on morphological similarities (such as stigma and style morphology) *B. furfuracea* shares with *B. molleri* and *B. subalpestris*, and the overall low *trnL* intron sequence variation, that an erroneous estimate of phylogeny between these species has

been reached. In this case ITS is probably giving a more accurate estimate of relationships. The possibility of chloroplast capture between *B. furfuracea* and the other three species should not be ruled out as they do occur sympatrically.

4.4.4 Species relationships and character evolution among the fleshy-fruited African Begonia

The preferred estimate of phylogeny in this study is the combined analysis which shows almost complete resolution. Approximately 65% of the morphological characters are homoplastic in the combined analysis (Table 4.3) and among these there were no differences in levels of homoplasy between floral and vegetative characters, a result generally found for vascular plants (Bateman & Simpson, 1998). However, the characters discovered as true homologues (secondary homologies *sensu* de Pinna, 1991) in the analysis are mostly flower, fruit or inflorescence characters and coincide with characters traditionally used to define sections (e.g. numbers of perianth segments in male and female flowers, presence of perianth cylinder in female flowers, presence of inflorescence bracts, and fruit dehiscence) in *Begonia*. The apparently good choice of morphological characters by *Begonia* systematists contrasts with the poor performance of traditionally important morphological characters reported for other plant groups, such as in the Leguminosae (Lavin et al., 2001; Pennington et al., 2000). These traditional characters did not diagnose all clades, and were not able to clearly diagnose the tetraphiloid clade consisting of all species of section *Tetraphila* except *B. loranthoides* and *B. longipetiolata*. This was because section *Tetraphila* is paraphyletic with respect to sections *Squamibegonia* and *Baccabegonia* and many of the character states diagnostic to section *Tetraphila* are plesiomorphic, mapping at the very base of the tree. Macromorphological characters in fleshy-fruited African begonias, of the type used in a cladistic analysis, are therefore not able to diagnose all clades uncovered by molecular data, a problem which may be widespread in the genus. As is discussed below, characters which were not included in the analyses because of their variable nature such as habit and leaf shape are also useful for clade diagnosis, particularly within

species of section *Tetraphila*.

The *trnL* and ITS data give unequivocal support for the monophyly of section *Squamibegonia* as circumscribed by de Wilde and Arends (1980), which includes three species, *B. ampla*, *B. bonus-henricus* and *B. poculifera*. *Begonia baccata*, one of two species in section *Baccabegonia*, is sister to *Squamibegonia*. The other species in section *Baccabegonia*, *B. crateris* (not included in this study), is morphologically very similar to *B. baccata*, and suggestions have been made to merge the two species (Ferreira, 1965). Van den Berg (1984) considered *B. crateris* and *B. baccata* to be basal among the fleshy-fruited sections. However, this section is deeply nested within a predominantly epiphytic clade, suggesting a single dispersal event by an epiphytic ancestor to São Tomé. The presence of peltate scales in these two species gives further evidence for this transition, as this type of indumentum (also found in species in sections *Tetraphila* and *Squamibegonia*) is probably associated with a drier epiphytic habit, and is almost certainly a mechanism for reducing water loss. *Begonia crateris* and *B. baccata* can reach heights of 4 m, making them the largest begonias in Africa. This tendency towards gigantism is common among island species, and can reflect the colonisation of new environments followed by speciation in the presumed absence of competition (Carlquist, 1965).

The phylogenetic positions of *B. loranthoides* and *B. longipetiolata* in the combined analysis are congruent with the results based on ITS (Forrest, 2000). Forrest concluded that section *Tetraphila* was paraphyletic with respect to section *Squamibegonia*, a finding corroborated here by the combined analysis. The *trnL* sequence of *B. loranthoides* lacks the 158 bp deletion found in species of section *Squamibegonia* and *Baccabegonia*, but does possess a shorter 33 bp deletion at the end of this gap. Both in terms of morphology and *trnL* sequence structure, *B. loranthoides* is intermediate between both groups. The fruits of some populations of *B. loranthoides* differ from those typical of section *Tetraphila* by being club-shaped to ellipsoid, and polygonal in transverse section (although others possess the typical *Tetraphila* fruit

type). The bracts subtending the inflorescence are large and enclose the young inflorescence, but they are far less persistent than those in species of section *Squamibegonia*. *Begonia loranthoides* was originally placed in section *Squamibegonia* by Warburg (1895). Later studies on the species by de Wilde & Arends (1979) concluded that this species had greater affinities with species in section *Tetraphila*, and it was excluded from their subsequent re-delimitation of section *Squamibegonia* (de Wilde & Arends, 1980).

The *trnL* sequence for *B. longipetiolata* has no such gaps, lacking both the 158 bp deletion of sections *Squamibegonia* and *Baccabegonia* and the short gap found in *B. loranthoides*, and is therefore most like other species in section *Tetraphila*. However, in the sequence composition of ITS (particularly ITS1) these species show greater affinity with species in sections *Squamibegonia* and *Baccabegonia*. The results of the congruence test show high levels of congruence between the ITS and *trnL* data sets ($P = 0.12$), and while there is strong support (86%) from ITS sequence data for the inclusion of *B. loranthoides* and *B. longipetiolata* in a clade with section *Squamibegonia* and *B. baccata*, no support for this relationship exists in the *trnL* analysis, where both species are unresolved with respect to both clades. Morphologically, the close relationship between species in sections *Squamibegonia* and *Baccabegonia*, *B. loranthoides* and *B. longipetiolata* is supported by the presence of a unique monochasial male inflorescence type in all these species, and which is absent in other species of *Tetraphila*. The phylogeny given by the combined analysis suggests the derivation of sections *Baccabegonia* and *Squamibegonia* from within *Tetraphila sensu lato*. However, the tetraphiloid species associated with sections *Baccabegonia* and *Squamibegonia* are significantly different with respect to other *Tetraphila*, suggesting an early departure of that lineage from the standard *Tetraphila* form.

Within the fleshy-fruited African species, fruit morphology is not an accurate indicator of relationships as is demonstrated by the paraphyly of section *Tetraphila* (Fig. 4.7). The switch to fruit indehiscence has occurred once within the fleshy-fruited

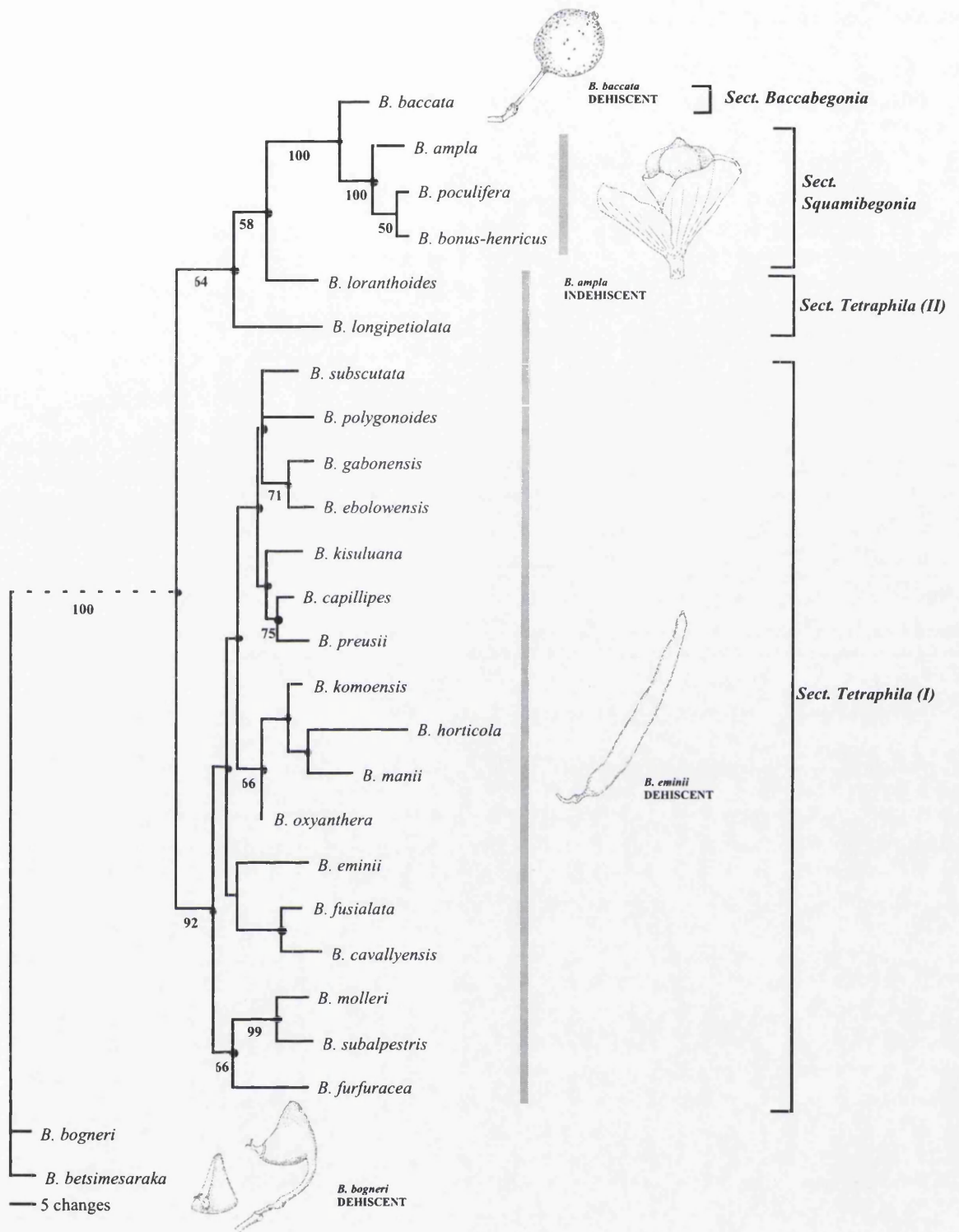


Figure 4.7 One of eight most parsimonious trees resulting from the maximum parsimony analysis of combined morphological, *trnL* and ITS data showing the distribution of fruit types. Values beneath the branches represent bootstrap support. Branches which are retained in the strict consensus are marked with a solid black circle.

African group, in section *Squamibegonia*, and a total of three times in Africa as the diphyly of section *Mezierea* has revealed (see Chapters 2 and 3). As was illustrated by Reitsma (1983), placentation in African *Begonia* is pseudo-axillary among species of section *Squamibegonia* and topographically parietal in more than 60% of the ovary in section *Mezierea*. In *Tetraphila* placentation ranges from being topographically parietal over less than 40% of the length of the ovary, with the remaining part showing septal placentation (*B. polygonoides*, *B. oxyanthera*, *B. kisuluana*, *B. molleri* and *B. subalpestris*), to entirely septal (*B. eminii*, *B. manii*, *B. komoensis*, *B. subscutata*, *B. loranthoides* and *B. fusialata*) and pseudo-axillary (*B. squamulosa*, *B. ebolowensis*, *B. poculifera*, *B. bonus-henricus* and *B. ampla*). The number of ovules per ovary in species of section *Tetraphila* (including *B. loranthoides* and *B. longipetiolata*) does not surpass 55, whereas species in section *Squamibegonia* have 80-120 ovules and those in *B. baccata* have 250-300 (Reitsma, 1983). While the number of ovules and type of placentation do not diagnose groups within *Tetraphila*, it does so for sections *Baccabegonia* and *Squamibegonia*. Similarly, the information provided by seed and pollen data (van den Berg, 1984; de Lange & Bouman, 1991) does not support relationships uncovered in the combined analysis although seeds of *Baccabegonia* are characterised by the absence of a distinct cuticular pattern and by the shallow appearance of the testa cells (de Lange and Bouman, 1991). The seeds of *Squamibegonia* have small testa cells and show a distinctive cleavage of the anticlinal walls (Bouman & de Lange, 1982). Within *Tetraphila*, the seeds of *B. ebolowensis* and *B. gabonensis* are among the largest in the section, and the seeds of *B. molleri* and *B. subalpestris* resemble each other in having faint anticlinal walls. The best morphological predictors of phylogeny in *Tetraphila* are style and stigma form, androecium characteristics, growth habit, and to a certain extent leaf shape.

Commonly, *Begonia* is characterised by homogeneous male and female flowers. In the centre of most *Begonia* female flowers are three to five yellow, forked styles around which spirals the stigma. The combined analysis resolves this style morphology as the ancestral state within this group of fleshy-fruited African species and is present

in *Baccabegonia*, *Squamibegonia*, *B. loranthoides* and the *B. squamulosa* species complex (including *B. longipetiolata*) (Fig. 4.8). Within the remaining, more narrowly delimited *Tetraphila* clade yellow, forked styles with a twisted stigma occur in *B. molleri*, *B. subalpestris* and *B. furfuracea*, and would therefore support the position of *B. furfuracea* in close association with the two São Tomean *Tetraphila* species. In addition, yellow, forked styles with a twisted stigma is the primitive state within *Tetraphila*. Therefore, all the style variation within the section which departs from the forked style and twisted stigma common to the genus is derived. There is evidence of a transformation series in stigma and style morphology. *Begonia eminii* and *B. fusialata* also possess forked styles, but the band-shaped stigma is not spiral but rather horse-shoe shaped. *Begonia eminii* and *B. fusialata* (together with *B. tatoniana*, which was not included in the study) are also the only terrestrial species in section *Tetraphila* (Fig. 4.9). *Begonia cavallyensis* has bilobed styles and is sister to *B. fusialata*, but is epiphytic. *Begonia fusicarpa* (not sampled in this study) also has bilobed styles and is a species believed to be a high altitude variant of *B. cavallyensis* (growing under 500 m altitude in contrast to at ca. 1400 m) (Hagman & de Wilde, 1983). The rest of species in section *Tetraphila* have developed simple styles where the stigma is contracted near the style apex. This is usually associated with a change in pigmentation; the style, instead of being uniformly yellow, is variously graded from yellow at the base to deep red at the apex. Begonias are pollinated by deceit (Ågren & Schemske, 1991), and there is a greater occurrence of small androecia with few anthers among the simple-styled species. Simple styles are never the only type within a section, occurring in sections *Tetraphila*, *Parvibegonia* and *Gireoudia* (Doorenbos et al., 1998), and have never therefore been used to diagnose a section.

Leaf shape and margin are good (though not infallible) indicators of relationships within section *Tetraphila* (Fig. 4.9). *Begonia eminii* and *B. fusialata*, as well as *B. komoensis*, *B. horticola*, *B. manii* and *B. oxyanthera*, have ovate to broadly elliptic leaves with dentate margins. *Begonia tatoniana* was not sampled but also has leaves of this type, and forked styles on which the stigma is a non-spiral band; it would probably

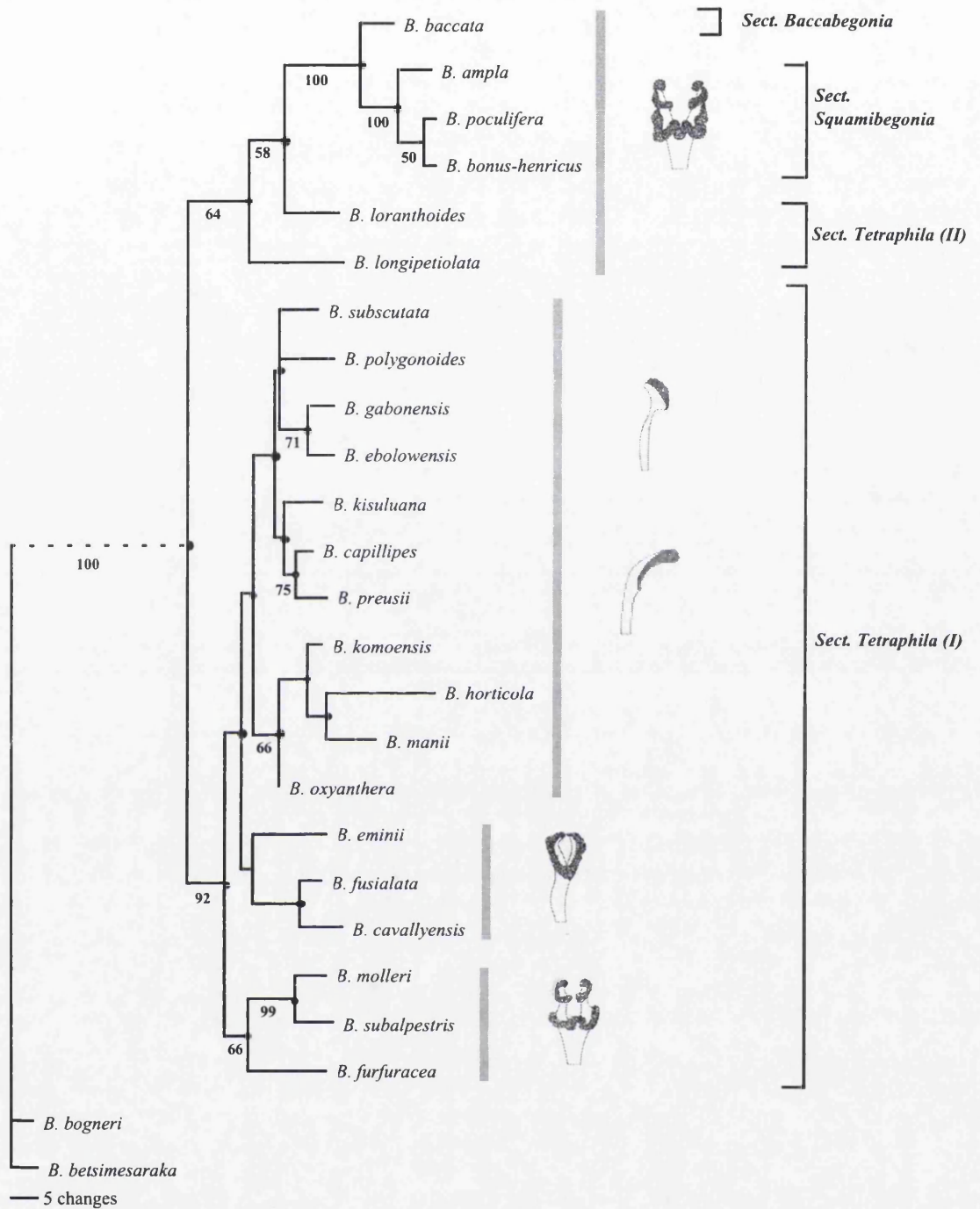


Figure 4.8 One of eight most parsimonious trees resulting from the maximum parsimony analysis of combined morphological, *trnL* and ITS data showing the distribution of style types. Values beneath the branches represent bootstrap support. Branches which are retained in the strict consensus are marked with a solid black circle.

resolve as sister to *B. fusialata* and *B. eminii*. Species in the adjacent clade (*B. preusii*, *B. capillipes*, *B. kisuluana*, *B. ebolowensis*, *B. gabonensis*, *B. polygonoides* and *B. subscutata*) rarely have dentate margins, and tend towards a more narrowly elliptic leaf shape. *Begonia komoensis*, *B. horticola* and *B. manii* are a group of closely related species that have pronounced spreading styles which can be red in colour for at least half their length. As can be seen in Figure 4.9 the possession of a terrestrial habit is only a loose indication of relationships. The possession of a red leaf margin is a homoplastic character state occurring both in the São Toméan species *B. subalpestris* and the West African species *B. cavallyensis*; two unrelated species.

4.4.5 Implications for the taxonomy of section *Tetraphila*

The delimitation and erection of sections in *Begonia* should have the ultimate purpose of aiding identification, not necessarily reflecting phylogeny, although the best scenario would reconcile the two. It would be little use to recognise groups or clades which have no obvious morphological synapomorphies. This position might, of course, be strongly criticised by proponents of the PhyloCode (de Queiroz & Gauthier, 1992, 1994). The non-monophyly of section *Tetraphila* as currently circumscribed emphasises this problem. It would be inappropriate to sink species of sections *Baccabegonia* and *Squamibegonia* into section *Tetraphila*, as they are among the most easily recognisable sections in African *Begonia* and are supported by diagnostic morphological synapomorphies. An alternative option, which would be less disruptive to existing classifications, would involve erecting two new sections, one to accommodate *B. loranthoides* and the second for species in the *B. squamulosa* species aggregate (*B. longipetiolata*, *B. squamulosa*, *B. karperi*, *B. pelargoniiflora*, *B. elaeagnifolia*, *B. rwandensis*). However, these species are characteristically tetraphiloid, possessing the long fusiform fruits characteristic to the section (although not present in all populations of *B. loranthoides*). Therefore, I do not advocate moving these species to new sections; an opinion shared with other *Begonia* specialists (e.g. J.J.F.E. de Wilde, pers. comm., 2001).

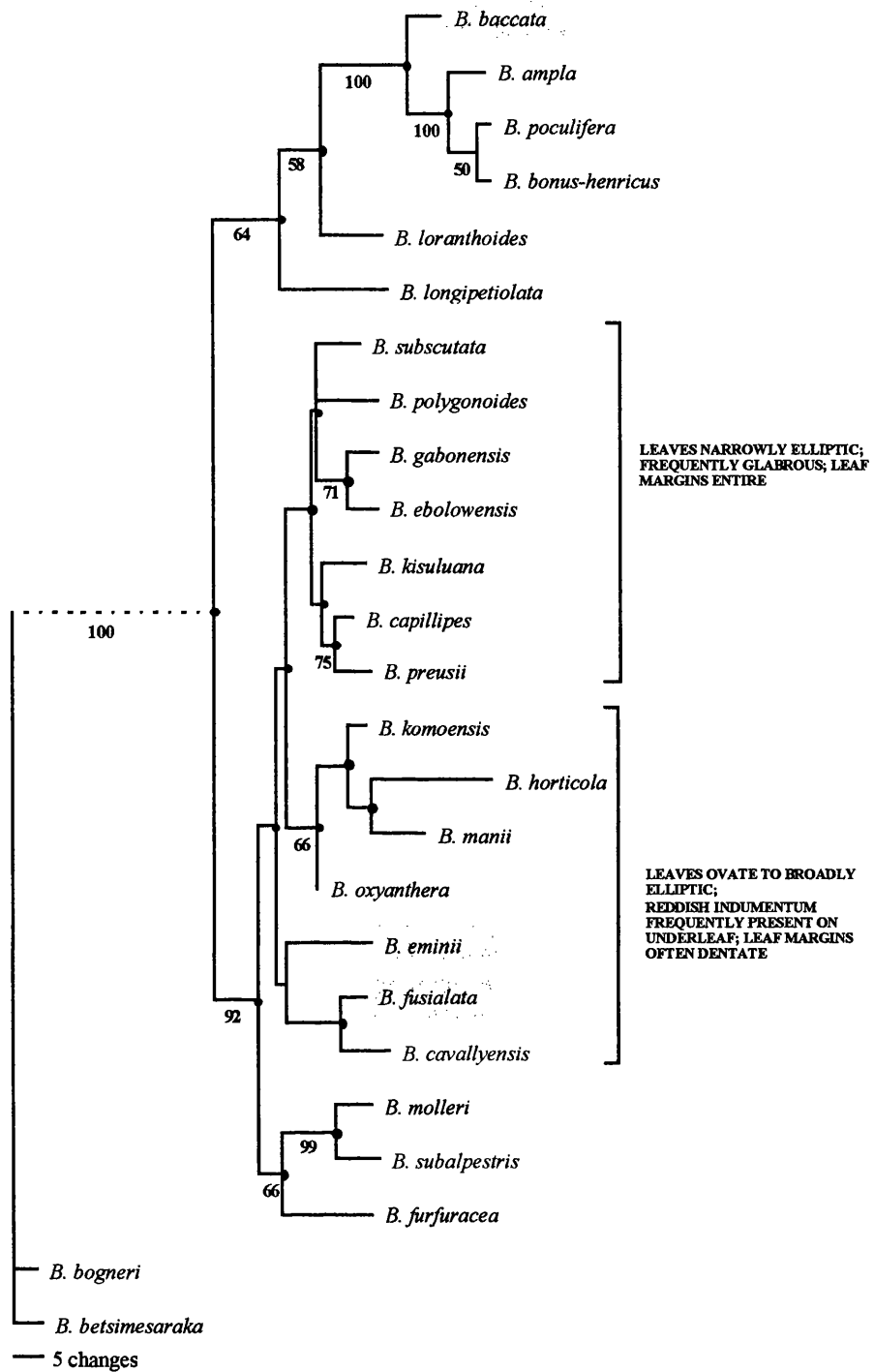


Figure 4.9 One of eight most parsimonious trees resulting from the maximum parsimony analysis of combined morphological, *trnL* and ITS data showing the distribution of terrestrial habit (grey box), red leaf margin (red), and some leaf characters. Values beneath the branches represent bootstrap support. Branches which are retained in the strict consensus are marked with a solid black circle.

4.5 CONCLUSIONS

In *Begonia*, different authors have defined characters and character states differently, demonstrating some of the problems that wholly morphological phylogenetic studies can present. Morphology alone may not give accurate estimates of phylogeny (Scotland & Olmstead, in prep.), and this has been found to be the case in *Begonia* especially in genus-wide analyses. When used in combination with molecular data, at a more restricted taxonomic level it can, however, give greater support to nodes and has the potential to resolve relationships at a phylogenetic level that molecular data cannot.

The best estimate of phylogeny for the fleshy-fruited African begonias was given by the combined analysis of morphology, *trnL* intron and ITS sequence data. Whereas the individual data sets did not resolve species relationships within *Tetraphila* effectively, the strict consensus of the combined data sets was almost entirely resolved.

The combined analysis confirmed the monophyly of section *Squamibegonia* but showed a paraphyletic *Tetraphila*. Within *Tetraphila* the best indicators of phylogeny are style shape, which shows a transformation series from the forked styles with spiral stigmas common to most species of the genus to a derived form where the styles are unforked and the stigma is contracted at the end of the style. Leaf shape is also a good indicator of species relationships within the section, showing an evolutionary trend towards smaller, narrower leaves. The terrestrial habit in *Tetraphila* arose only once, and is absent among the most derived species in the section, suggesting increasing specialisation towards an epiphytic habit.

Although section *Tetraphila* is paraphyletic, it is not useful from a morphological perspective to attempt to make it monophyletic by accommodating *B. loranthoides* and species in the *B. squamulosa* species aggregate in new sections.

CHAPTER 5 A new section of *Begonia* (section *Chasmophila*) from Africa and other taxonomic notes¹

5.1 INTRODUCTION

To date, the classification of *Begonia* has been based solely upon morphology. In some cases it has been difficult to assign species to any of the 63 sections recognised in *Begonia*, because some species do not fit clearly within the described limits of any currently recognised sections. This problem is highlighted in the recent revision of the sections of *Begonia*, where 18 species are listed under the heading "Species not attributable to any existing section" by Doorenbos et al. (1998: 217). In addition, numerous sections of *Begonia* such as *Augustia* and *Rostrobegonia* or *Diploclinium*, to name a few examples, are circumscribed with some doubts as to the exact species they encompass (Doorenbos et al., 1998). In these circumstances, molecular phylogenetics can provide useful information on the genetic relationships between species. While it is meaningless, from a taxonomic view point, to formally recognise cryptic clades (i.e. clades showing no morphological synapomorphies), phylogenies can help to identify the morphological characters which best reflect phylogeny and which may be preferable in sectional circumscriptions.

Some characters which were originally believed to be good indicators of close species relationships in *Begonia* have proved not to be because they are more homoplasious than previously thought. A prime example described in Chapters 2 and 3, is the possession of fleshy, wingless fruits in African begonias. African species with this fruit type are not monophyletic as previously assumed. Among these species the

¹ This chapter represents work performed in collaboration with J.J.F.E. de Wilde, and will form part of a co-authored paper.

presence of peltate, scale-like indumentum is a much more conservative character and therefore a more valuable indicator of relationships at the sectional level.

In the course of preparing ‘The sections of *Begonia*’, Doorenbos et al. (1998) were unable to attribute the continental African species *B. iucunda* to any existing section. The authors supplied information on the species and concluded that: “it presumably takes up an isolated position in the affinity of section *Filicibegonia* A.DC.” (pp. 218-219). The molecular research outlined in Chapters 2 and 3 on African *Begonia* species, sampling all sections recognised on the continent, supports the morphologically isolated position of *B. iucunda* and its affinity to section *Filicibegonia*, which have been suggested previously. Therefore, the new monotypic section *Chasmophila* is here described to accommodate *B. iucunda*. The phylogenetic relationships based on morphological and molecular data of this monotypic section are discussed, as are its ecology and distribution.

5.2 TAXONOMIC POSITION OF *B. IUCUNDA* AND ITS RELATION TO OTHER AFRICAN SECTIONS

Irmscher (1961) accommodated *B. iucunda* in section *Scutobegonia*. Subsequent authors, such as Barkley & Golding (1974), followed Irmscher’s sectional placement of this species, probably led by the two yellow perianth segments in both its male and female flowers. Van den Berg (1985) attributed the pollen of *B. iucunda* to a *Begonia filicifolia*-type which he considered to be characteristic for species in section *Filicibegonia*. Based on seed micromorphology, de Lange & Bouman (1991) found that species in section *Filicibegonia* formed a distinct group, but that within this group *B. iucunda* occupied an isolated position. These authors suggested that convincing evidence for the recognition of a separate section to accommodate *B. iucunda* could result from a critical re-evaluation of its morphology. Sosef (1994: 19), in a thorough monograph of sections *Loasibegonia* and *Scutobegonia*, excluded *B. iucunda*. He referred to it as “an odd species, possibly representing a distinct section, probably most closely related to the sect. *Rostrobegonia* Warb.” Later, as stated above, Doorenbos et

al. (1998) concluded that the species occupies an isolated position in the affinity of section *Filicibegonia*.

In Table 5.1, 15 morphological characters found in *B. iucunda* are compared with those of four morphologically related sections. All taxa in the table share capsular dry dehiscent fruits. The sections *Loasibegonia* and *Scutobegonia*, which include ca. 40 species, are omitted as they never show tuberous underground parts and all the species are characterised by more or less juicy indehiscent fruits which disintegrate with age. Section *Rostrobegonia* is taken in the narrow circumscription of Warburg (1895), who admitted only *B. rostrata*, *B. quintasii* (= *B. annobonensis*) and *B. johnstonii*. In Irmscher's (1961) opinion, sections *Rostrobegonia* and *Augustia* have so much in common that he supplied a description that combined the two sections into one. Recent research (Forrest, 2000; Plana, Chapters 2 and 3, M. Hughes, pers. comm., 2000), however, indicates that two and possibly even three monophyletic groups should be distinguished in this group of species. Therefore, in Table 5.1 the two sections, *Rostrobegonia* and *Augustia*, are entered separately in their original circumscription. In this concept, section *Augustia* contains most of the tuberous species, and section *Rostrobegonia* harbours annuals. The monotypic section *Cristasemen* is unique in its climbing lianescent habit and its unusual long, slender seeds (de Wilde, 1984).

From Table 5.1 it is not clear in which of the presently accepted sections *B. iucunda* could be satisfactorily placed. Among the 15 characters listed it respectively shares 10, 9, 8 and 7 with sections *Augustia*, *Cristasemen*, *Filicibegonia* and *Rostrobegonia*, respectively. Moreover, unlike section *Cristasemen*, *B. iucunda* does not show one or more unique character states which set the species distinctly apart from its congeners. Notably, de Lange & Bouman (1991) found that the size of the seed of *B. iucunda*, with a mean length of 220 μm , is the smallest among African begonias. These authors found small seeds in sections *Scutobegonia* and *Loasibegonia* and especially in section *Filicibegonia*. They discussed *B. iucunda* under section *Filicibegonia* but remarked that in its micromorphological seed characters this species deviates in several respects from the other species in the section which otherwise constitute a distinct group (de Lange & Bouman, 1991).

Table 5.1 Selected characters to discriminate *B. iucunda* and the sections *Augustia*, *Cristasemen*, *Filicibegonia* and *Rostrobegonia*.

	<i>B. iucunda</i>	<i>Augustia</i>	<i>Cristasemen</i>	<i>Filicibegonia</i>	<i>Rostrobegonia</i> (s.s.)
1. Plant longevity	perennial	perennial	perennial	perennial	annual
2. Tubers/Tubercles	present	present	absent	absent	absent
3. Tuft of hair apex petiole	absent	occasionally	absent	absent	present
4. Venation type	palmate	palmate	palmate	pinnate	palmate-pinnate
5. Inflor. sexuality	unisexual	bisexual	bisexual	usually bisexual	bisexual
6. Inflor. type	solitary	di- or monochasial	dichasial	monochasial	di- and/or monochasial
7. Inflor.: number of flowers	1	1-3	1-3	1	1-3 or more
8. Perianth segments: colour	yellow	White, pink, orange, yellow yellow	yellow	white or pink	white or pink
9. No. of perianth segments in male flowers	2	2 or 4	2	2	4
10. Androecium symmetry	zygomorphic	Actinomorphic	zygomorphic	zygomorphic	actinomorphic
11. Anthers position openings	lateral	?unilateral	unilateral	unilateral	lateral
12. No. of perianth segments in female flowers	2	(3-)5	2	2	(4)5(6)
13. Styles shape	forked once	forked once	forked twice	2-lobed	forked or lobed
14. Stigma position on style	spiralled	usually spiralled	not spiralled	not spiralled	spiralled/all over the
15. Placental branches/locule	1	1(2)	1	1	style 1 or 2

5.3 MOLECULAR PHYLOGENETIC EVIDENCE

DNA sequence data for *Begonia* from the nuclear ribosomal ITS repeat and 26S regions (Forrest, 2000; Plana, Chapter 3) and the chloroplast *trnL* intron (Plana, Chapter 2) have been obtained for 58 species of Afro-Malagasy *Begonia* (sampled from among a total of 158 species described from the region). *Begonia iucunda* was sequenced in an attempt to elucidate its phylogenetic position using different sources of data. Maximum parsimony analyses of ITS, *trnL*, 26S and combined data all resolve *B. iucunda* in an isolated position within a clade consisting of species in sections *Cristasemen*, *Filicibegonia*, *Loasibegonia* and *Scutobegonia*. The ITS (Fig. 2.2) and combined *trnL*, ITS and 26S (Fig. 3.6) phylogenies shows *B. iucunda* as sister to the rest of this clade, whereas the *trnL* intron phylogeny (Fig. 2.4) shows *B. iucunda* as sister to *Filicibegonia*, *Scutobegonia* and *Loasibegonia* only. In both topologies, however, *B. iucunda* holds a phylogenetically isolated position. Although *B. iucunda* shares morphological similarities with species in sections *Augustia* and *Rostrobegonia*, both these sections are more closely related to Asian and American species than they are to other African species (see Chapters 2 and 3).

The morphological similarities that *B. iucunda* shares with species in sections *Augustia* and *Rostrobegonia* (see Table 5.1), such as the presence of tubercles, are not a reflection of shared phylogenetic history but rather are the result of convergence (Fig. 3.6). As was seen in earlier chapters species in sections *Augustia* and *Rostrobegonia* are more closely related to American and Asian species than they are to the African rain forest species. *Begonia iucunda* is more closely related to terrestrial, hydrophilic, predominantly West and Central African species. Bearing this in mind, characters which are important in separating section *Chasmophila* and its related sections (*Cristasemen*, *Filicibegonia*, *Loasibegonia* and *Scutobegonia*) from sections *Rostrobegonia* and *Augustia* are the zygomorphic androecium (as opposed to actinomorphic), the presence of two perianth segments in female flowers (as opposed to more than two), and the presence of two tepals in male flowers (although some species in section *Augustia* have four).

5.4 A NEW AFRICAN SECTION OF *BEGONIA*

Begonia sect. *Chasmophila* J.J.de Wilde & Plana, sect. nov. Habitu plantae 6-60 cm altae stolones emittentis et e tubere usque ad 20 x 8 mm subterraneo fusiformi orientis, praesentia tuberculorum usque ad 1 cm longorum fusiformium in axillis foliorum languescentium, indumento ex pilis moniliformibus glanduliferisque constanti, floribus axillaribus solitariis luteis et seminibus minus quam 250 µm longis. Sectio nova monotypica manifeste differt a Sectionibus *Augustia*, *Cristasemen*, *Filicibegonia* et *Rostrobegonia*. Type species: *B. iucunda* Irmsch.

The stoloniferous habit of *B. iucunda*, with an underground tuber, from which a rooted rhizome is produced that develops above the ground into a flowering upright stem, is unique among African tuberous *Begonia* species. In glasshouse conditions at Wageningen the stems were observed, after flowering and fruiting, to wither and fall to the ground. At this stage the leaves are more or less dry, but still attached. Long fusiform tubercles, reaching a length of 1 cm, develop in the axils of these leaves. The tubercles are green, enveloped by longitudinally arranged rows of brown scales, and give rise to newly formed, tiny rooted plants at their apex. This formation of propagules is, in Africa, known only in section *Rostrobegonia* s.l., where it is reported for *B. wollastonii*, and in section *Augustia*, occurring in *B. sutherlandii*. The conspicuous, multicellular, uniseriate hairs, which in *B. iucunda* often show a glandular two-celled apex, are rarely encountered among African begonias. Cuerrier et al. (1990) reported comparable hairs in *B. johnstonii* and *B. engleri*, both in section *Rostrobegonia* s.s. The occurrence of this type of indumentum was also reported for *B. minutifolia* (section *Filicibegonia*) (Cuerrier et al., 1990) but has not been corroborated by recent observations (J.J.F.E. de Wilde, pers. comm., 2001).

5.5 REVISED DESCRIPTION OF *BEGONIA IUCUNDA* IRMSCH.

Irmscher in Engl. Bot. Jahrb. Syst. 81:186 (1961); Wilczek, Fl. Congo, Rwanda et Burundi, *Begoniaceae*: 42-43 (1969); van den Berg in Agric. Univ. Wageningen Papers 84(3):37 (1985); L.B. Smith et al., *Begoniaceae*, Smithsonian Contr. Bot.

60:184, 449, Fig. 21.24 (1986); de Lange & Bouman, Wageningen Agric. Univ. Papers 91(4):11, 12, 71, 73, pl. 7E & F (1992); Doorenbos et al., The sections of *Begonia*. Wageningen Agric. Univ. Papers 98(2):218 (1998).

Type: Congo (Kinshasa), Kasai, Kambangu, *Callens* 3205 (holotype K!, isotype BR!).

Plants erect or pendant, 6-60 cm tall, unbranched or with up to 7 axillary branches from the base; stem often somewhat zigzag, fleshy and wine red *in vivo*, up to 9 mm wide at the base, sparsely and patently hairy, the hairs multicellular, uniseriate, often 2-celled at the apex, glandular, very uneven in length; the stems growing from subterraneous rooted rhizomes up to 14 cm long that sprout from broadly fusiform brownish tubers up to 20 x 8 mm; rhizomes white, comparatively thin and thickening upwards from where the stem arises; newly produced tubers white. Stipules persistent, narrowly triangular to subulate, sometimes fimbriate, 1.5-7 mm long, pale green, margin ciliate. Leaves not peltate; petiole continuing into the blade at a distinct angle, 0.5-3 cm long, pink to dark wine red, puberulous; leaf blade herbaceous, membranous when dry, asymmetrical, narrowly oblong to ovate or falcately ovate, attenuate towards the apex or acuminate in the upper part, 2-12 x 0.8-4 cm, with 7-9 palmate main nerves but the midrib usually most pronounced, the nerves green but sometimes wine red on the lower surface; margin coarsely serrate-dentate, ciliate (usually with a short cilium between the teeth); cordate to more often obliquely cordate at the base, one side cuneate to rounded or slightly cordate, the other lobe cordate, the sides not overlapping, top acute; upper surface medium green, dull, puberulous; lower surface pale green; the main and larger secondary nerves not prominent on the upper surface, prominent and more or less densely covered with patent soft white multicellular hairs on the lower surface. Inflorescences highly reduced: flowers solitary, developing in the axils of the upper leaves; bracts or bracteoles absent; very rarely a male and a female flower from the same axil; flowering usually starting with 1 to 4 female flowers followed by male flowers. Male flower: buds flat, at anthesis the pedicel 5-20 mm long, slender, glandular puberulous, wine red; perianth segments 2, very broadly obovate to almost circular, 5-10 x 5-13 mm, yellow; androecium a zygomorphic fascicle, stamens 9-19, yellow; filaments fused at the base into a very short central column, those of the inner rows 0.2-1.0 mm long, those of the outer rows up to 2 mm long; anthers oblong, ca. 1 mm long,

slightly cucullate at the rounded to somewhat emarginate apex, opening by two lateral slits which run along the whole length of the anther. Female flower: similar to the male but the pedicel elongating in fruit, up to 47 mm; perianth segments 2, very broadly obovate, up to 10 x 13 mm, yellow; styles 3, yellow, up to 3 mm long, fused in the lower one third, the top divided into an elongated V-shape, the arms up to 1.5 mm long and bearing a confluent slender stigmatic band which is spirally twisted for one turn around each arm; ovary obovoid to ellipsoid, minutely glandular puberulous, ca. 4.5 x 3 mm, 3-locular, 3-winged. Wings very unequal in size, widening upwards, two wings narrow, the third wing much wider, ovate; placentation axillary, placentas 1 per locule, entire, flat, stretching deep into the locules, densely packed with ovules on both sides. Fruit borne on an extended erect pedicel, the capsule often somewhat nodding, septicidal, oblong, the locular part up to 15 x 5 mm, with 3 very unequal wings along entire length; wings distinctly enlarged in fruit, the largest wing widely extending beyond the top of the locule, triangular with rounded top, the longest side up to 21 mm, the other wings much smaller. Styles persistent in fruit.

Etymology. The specific epithet *iucunda*, coined by Irmscher (1961) for the combination *Begonia iucunda*, is derived from the Latin adjective *iucundus* meaning pleasant, agreeable or delightful.

Distribution. Known from Inoni in Congo (Brazzaville) and from the eastern part of the Bas Zaire region and southern and western areas of the Bandundu region of the Dem. Rep. of Congo (Kinshasa).

Habitat. In cracks and on ledges of steep exposed rock faces; on steep slopes near waterfalls; in shaded places among rocks.

Field notes. De Wilde visited one of the localities of *B. iucunda* at Inoni, 161 km North of Brazzaville in Congo in February 1993. This area is ca. 650 m above sea level and dominated by undulating savannah with shrubs and small trees, and scattered with forest pockets. *Begonia iucunda* grows in the cracks and ledges of local rocky outcrops. Small individuals of the species, no more than 6 cm tall, in flower and fruit occur in small cracks containing little soil. However, in a deposit of loose soil at the base of a steep slope, and in the half-shade of small trees, *B. iucunda* has been observed to form

vigorous branched plants up to 60 cm tall. The dimensions of almost all parts of these individuals largely exceed those of the occupants of the cliffs. This exceptional variation is included in the above description (de Wilde, van der Maesen & Moutsambote, 11.033, WAG).

Specimens examined. Congo (Brazzaville). Inoni, 161 km along the road N of Brazzaville, fl., fr., 6 Febr. 1993, *de Wilde et al.* 11.033 (W, WAG); *ibidem*, 8-20 May 1950, *Koechlin* 718 (IEC); *ibidem*, 10 March 1971, *Sita* 3067 (IEC, P). **Dem. Rep. Congo (Kinshasa).** Lower Congo, Kimbele, between Tumba Mani and Popokabaka, 1902, *Butaye* in *J. Gillet* 2295 (BR); S of Madimba, fl., fr. 7 Febr. 1952, *Devred* 1070 (BR, K); Kimvula, 5 Jan 1959, *Pauwels* 1042 (BR). Kasai, Kingunda, fl., fr. 16 Febr. 1950, *Callens* 2435 (BM, BR); Kambangu, fl., fr. 9 Febr. 1952, *Callens* 3205 (BR, K, iso- and holotype); Kibunda, fl., fr. 27 April 1953, *Callens* 3995 (BR).

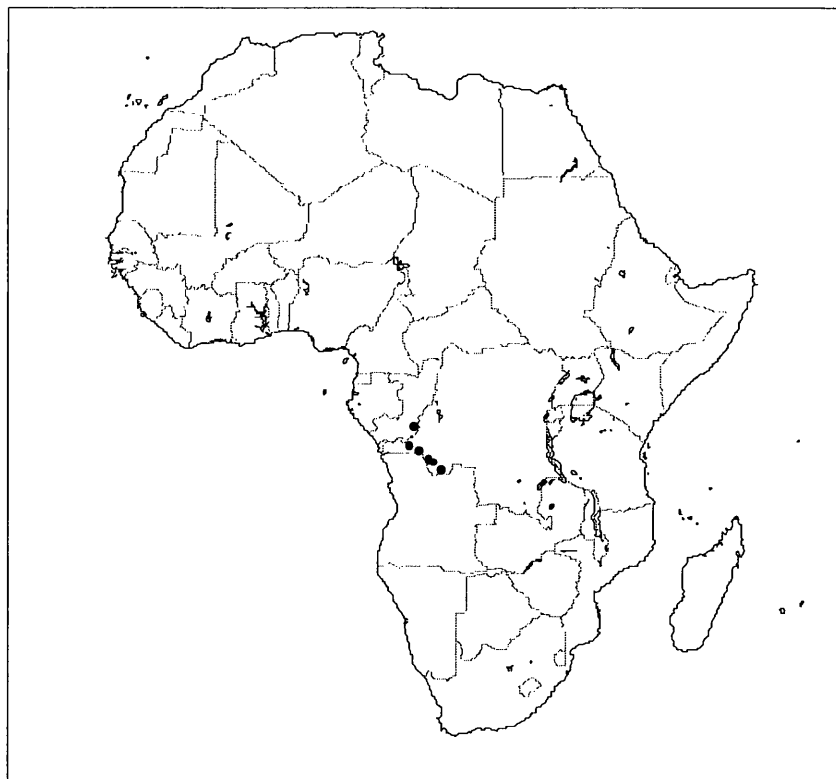


Figure 5.1 Distribution of *Begonia iucunda*.

5.6 CONCLUSION

There is overwhelming evidence, from both molecular and morphological sources, for the erection of a new monotypic section to accommodate *B. iucunda*.

CHAPTER 6 Evolutionary history and biogeography of Afro-Malagasy *Begonia*

6.1 INTRODUCTION

The African flora is characterised by a comparatively low species richness relative to the Neotropics and Asia which has been attributed to the significant climatic changes during the Tertiary and Quaternary, and which would have greatly affected the composition and distribution of the flora and fauna, shaping the biotic diversity we see today (Richards, 1973). Of the estimated 1400 species of *Begonia*, only about 158 occur in Africa and Madagascar, contrasting with the over 600 species found in Asia and a similar number in America (Doorenbos et al., 1998).

Molecular studies of biodiversity focusing on patterns of species relationships can help to understand the evolutionary processes that generate diversity in tropical ecosystems. To date, only two molecular phylogenies are known for lowland tropical African plants (Harris et al., 2000; this study). As Moritz et al. (2000) pointed out: “While progress is being made with rain forest vertebrates, comparable studies of invertebrates and plants are mostly lacking. Given the prominence of tropical arthropods and plants in accounts of global and tropical species diversity, this is clearly a major omission” (p. 554). This chapter applies a biogeographic perspective to the African *Begonia* phylogenies generated from *trnL* and ITS sequence data in previous chapters.

A two-step approach is considered. The first step tests for the presence of heterogeneity in rates of DNA sequence evolution among African lineages of *Begonia*. If

present, then a universal molecular clock cannot be assumed for the *Begonia* phylogeny, as different lineages will be acquiring mutations at different rates due to biological mechanisms such as differences in generation time (annual vs. perennial) or variations in DNA repair efficiency (Page, 1998). In this case, the second approach attempts to correct these lineage effects (Page, 1998) by calculating absolute rates of substitution. Making such corrections allows the reconstruction of divergence times, placing a time-frame on some of the cladogenic events that have produced the extant diversity in *Begonia*.

On taxon distributions, particularly of *Begonia*, and the significance these might have in uncovering the locations of former forest refuges in Africa, Sosef (1996: 609) asked “What are we looking at; what do the distribution patterns indicate?” I will now try to answer this question. Patterns of speciation and distribution can be profoundly affected by global geological and climatological events. Therefore, to aid later discussions on speciation patterns of the genus *Begonia* in Africa, the geological and climatological changes in Africa since the end of the Cretaceous are summarised.

6.2 VEGETATION AND CLIMATE HISTORY OF AFRICA

Since the break-up of Gondwana, starting in the mid-Cretaceous, Africa has moved north some 15 degrees (Axelrod & Raven, 1978), reaching its present day position in the mid-Tertiary (Maley, 1996). There are numerous reviews on the geological and climatological history of Africa (Axelrod & Raven, 1978; Coetzee, 1993; Sosef, 1994; Maley, 1996; Wieczorek et al., 2000). This synopsis is based mainly on the descriptions of Axelrod & Raven (1978) and Morley (2000), which will not be repeatedly cited; citations are given only to additional authors.

From the late Cretaceous to the early Palaeocene (77–55 Ma) Africa was isolated from other land masses and climatic conditions were stable. Because Africa was situated

approximately 15 degrees south of its present latitude a large proportion of northern Africa was covered by rain forest, which extended from east coast to west coast and from the Gulf of Guinea north to the Tethys Sea. Savannah-type woodland would have flanked the rain forest to the south, with subtropical rain forest dominating South Africa and the southern half of East Africa. Montane forests were restricted to small areas between zero and 10 degrees north. The terminal Cretaceous event brought about widespread extinctions throughout Africa, as is evidenced in the pollen record by a 50% fall in gymnosperm diversity at this time.

In the Palaeocene to early Eocene (65–46 Ma), the west African flora diversified almost without interruption. Climate was probably more seasonal, and diversification occurred during the change in lowland vegetation to a mosaic of rain forest and savannah extending over what is today the Congo Basin (Coetzee, 1993). Grass pollen was common in Cameroon, together with forest elements (Salard-Cheboldaeff, 1990). The end of the Eocene was once again marked by global cooling, most notably tracked in Africa by the extinction of many palms and an overall species diversity decrease, although this episode did not drastically alter the biotic composition of the continent.

The Miocene (23-5 Ma) was one of the most defining periods of Africa's geological and climatological history, and the biotic composition of African today was very much determined by Miocene events. The uplift of the Afro-montane region provided greater topographic diversity and rain forest species were able to begin invading higher, colder zones. Although there was a general trend throughout the Miocene towards ever greater aridification, the early Miocene was warm and more humid. Savannah woodland gradually replaced lowland forest in the central and northern Sahara and in parts of South Africa. At the same time the lowland rain forest belt shifted southwards to its almost present-day position, but probably extended continuously, from the west to the east coast of Africa (Coetzee, 1993). The mid-Miocene closure of the Tethys Sea resulted in a drier climate with significant drying effect on the rain forest of the Sahara. In Africa, uplift and accompanying warping and vulcanism started in the

late Oligocene–early Miocene, together with the opening of the Great Rift Valley. By the late Miocene (7 Ma) the Eastern Arc mountains were uplifted, uplands produced by volcanic activity in West Central Africa were present, and the Gulf of Guinea islands had emerged. Therefore, by the end of the Miocene, most of the present topology of Africa was in existence.

This new face of the African continent, coupled with a drastic cooling of global temperature that caused the formation of ice caps in Antarctica, brought about regional differences in climate, resulting in widespread impoverishment of the rain forest flora and fauna from the mid-Miocene to the early Pliocene. There is evidence in Ethiopia of dense evergreen forest occurring at altitudes of between 900 and 1000 m during the late Miocene (8 Ma), when these upland areas served as rain forest refugia (Yemane et al., 1987 in Coetzee, 1993); that is, areas of restricted rain forest distribution during periods of decreased temperature and precipitation. Importantly, few extinctions of rain forest plant species have been noted during the late Miocene (10–5 Ma) (Maley, 1996), suggesting that many present-day African lineages date from the pre-Miocene. Therefore, under the moister conditions of the middle and late Tertiary the African rain forest was probably very species rich, especially into the Miocene, but the following progressively drier climates eliminated many of them.

The early Pliocene (5–3.5 Ma) was characterised by moist climates, the expansion and diversification of rain forests and the retraction of savannah. Pollen assemblages from this time show increased species diversity; the late Miocene rain forest taxa are joined by many other species. Pollen suggesting montane elements (conifers) appear in the latest Tertiary. Diversity peaked just before the end of the Pliocene (3.5 Ma). At this time rain forest extended to 20 degrees north. At 3.48 Ma there is evidence for a change to a much drier climate. Late Tertiary–early Quaternary floras from five localities in the mountains of Cameroon show a rich environment where approximately 230 species were identified, most of them very similar or equivalent to extant species. Later this flora was affected by episodes of ice-age aridity. During the

late Pliocene (3.5–1.5 Ma) there were much more pronounced climatic changes, with marked drying and cooling cycles. The Great Rift Valley developed in the Pliocene and early Pleistocene, as did the Congo Basin (Coetzee, 1993). 2.7 Ma marks the first appearance of West African gymnosperm pollen since the Cretaceous. Major arid phases during the late Pliocene occurred at 3.2 and 3.0 Ma, resulting in a reduced expanse of grasses and numerous regional extinctions. Aridification was a general feature of the late Pliocene.

The Quaternary (1.8 Ma to present) is characterised by marked glacial variations, particularly from 800,000 BP onwards. The most arid periods, coinciding with glaciations, resulted in fragmentation of forests and formation of forest refugia. The lowering of temperatures resulted in the extension of montane floras to lower altitude, more or less replacing lowland rain forest, and allowing the migration of montane floras and faunas between mountain ranges. With subsequent warming these montane floras would then be once again isolated on mountains. Since 2.5 Ma there have been 21 glacial-cycles, nine major and 12 minor (Hamilton, 1982; Hamilton & Taylor, 1991; Sosef, 1994). The last period of maximum global warming occurred in the Holocene (last 11,000 years), while the last glacial maxima resulting in forest fragmentation occurred in the Pleistocene, from 160,000–130,000 Ma and from 24,000–12,000 Ma (Maley, 1996). Maley (1987) suggested that stratiform cloud formation across central tropical Africa during glacial maxima would have caused a decrease in temperature but not contributed to rainfall, making climatic conditions significantly more arid.

A study from Lake Barombi, located ca. 80 km from the sea in western Cameroon and at approximately 300 m altitude, showed that from 24,000 BP rain forest persisted in this area with only limited variations (Maley, 1991, 1998; Maley & Brenac, 1998). Even when there was evidence for increase in grass pollen, and a recession in forest, there were still significant forest patches. There is also evidence for a mixed forest during cooler periods where lowland species are associated with montane species (Maley, 1991). This is comparable to situations seen today in hill summits around

Yaounde, where mountain species are found in association with lowland evergreen forest species (Achoundong, 1985 in Maley, 1991). In contrast, areas such as Lake Simnda, in southern Congo, lacked the climatic and edaphic conditions found in areas like western Cameroon which allowed the maintenance of rain forest during glacial maxima (Vincens et al., 1998). Colyn et al. (1991) questioned the degree to which montane forests lowered their altitudinal range during glacial periods. They postulated that lowland forest patches would have persisted near rivers during dry climatic periods and that the effects of aridification would have been less noticeable in the Congo (Zaire) Basin than in areas such as East Africa. In addition, they postulated that rather than montane forest spreading widely, it did not perhaps reach the Congo Basin but that rather this region maintained seasonally tropical dry forest even during glacial maxima, a scenario similar to that proposed for the Amazon Basin (Pennington et al., 2000).

Pollen analysis taken at Bosumtwi (Ghana) and Barombi Mbo (W. Cameroon), both below 500 m, have demonstrated that the montane forest indicator *Olea capensis* extended into the lowlands prior to the Holocene. At around 18,000 BP there was a culmination of an arid period when mean annual temperatures are estimated to have been 3 or 4° C below the present (Maley, in press).

There are therefore, several stages in the past 77 my which mark the impoverishment of the hydrophilous African flora: the Cretaceous–Tertiary boundary, the end of the Eocene, and the end of the Miocene (Maley, 1996). Morley (2000) includes the period during the mid- and late Pliocene where the onset of glaciations in the Northern Hemisphere (and probably also the increased topographical structure of the continent) resulted in successive drying and cooling events. To these events should be added the glacial and interglacial cycles (a total of 21 events) which occurred in the Plio-Pleistocene, precipitated by glaciations in the northern hemisphere and accentuated by the increased topological structure of the African continent (Maley, 1996; Morley, 2000). Habitat-related mechanisms which could have driven speciation, such as the repeated contraction and expansion of forest and savannah, would have been most

effective during the late Pleistocene (0.9 Ma) when large amplitude cycles with large climatic shifts occurred with short intervals.

Climatic oscillations during the Quaternary would have caused lowland forests (below 1500 m) to contract and expand in response. Therefore, during periods of glacial maxima, or when conditions were markedly dryer and cooler, lowland rain forest would have persisted in restricted areas. These postulated refugia would 'trap' species until more favourable conditions (i.e. wetter and warmer) allowed them to re-expand their ranges (Sosef, 1994). This would presumably occur repeatedly in concert with the pronounced and rapid climatic oscillations during the Pleistocene. Several workers have attempted to identify or give evidence for the location of these putative Pleistocene refugia based on either high species richness or high levels of endemism (Aubréville, 1962; Diamond & Hamilton, 1980; Endler, 1982; Grubb, 1982; Mayr & O'Hara, 1986; Colyn et al., 1991; Sosef, 1994; Robbrecht, 1996) (Fig. 6.1, refugia 1-6). The postulated refugia generally coincide well with Afro-montane regions, although refugia have also been suggested in lowland regions such as the Zaire River Basin (Colyn et al., 1991) based on primate distributions. Recent evidence has shown that, contrary to expectation, high levels of endemism are not correlated with high levels of rainfall (Linder, 2001), but rather with areas of historical climatic stability (Lovett & Friis, 1996). In his study of *Begonia* sections *Loasibegonia* and *Scutobegonia*, Sosef (1994) identified ten refuges, six of which had already been postulated based on the distributions of other plant and animal species, as well as four new refuges he proposed based on the distribution of species in *Begonia* sections *Loasibegonia* and *Scutobegonia* (Fig. 6.1, a-d).

These continual cycles of climatic change had a significant impact on the diversity and distribution of the African flora and fauna. The narrowing of forest habitat ranges during glacial maxima limited forest organisms to areas with continually high degrees of humidity and shade, such as crevasses and gallery forests in lowland areas and along mid-altitude regions of Africa's montane regions. Glacial maxima would often have

meant large numbers of local extinctions, and in some cases would eliminate entire lineages, or leave a few representatives of once species-rich groups.

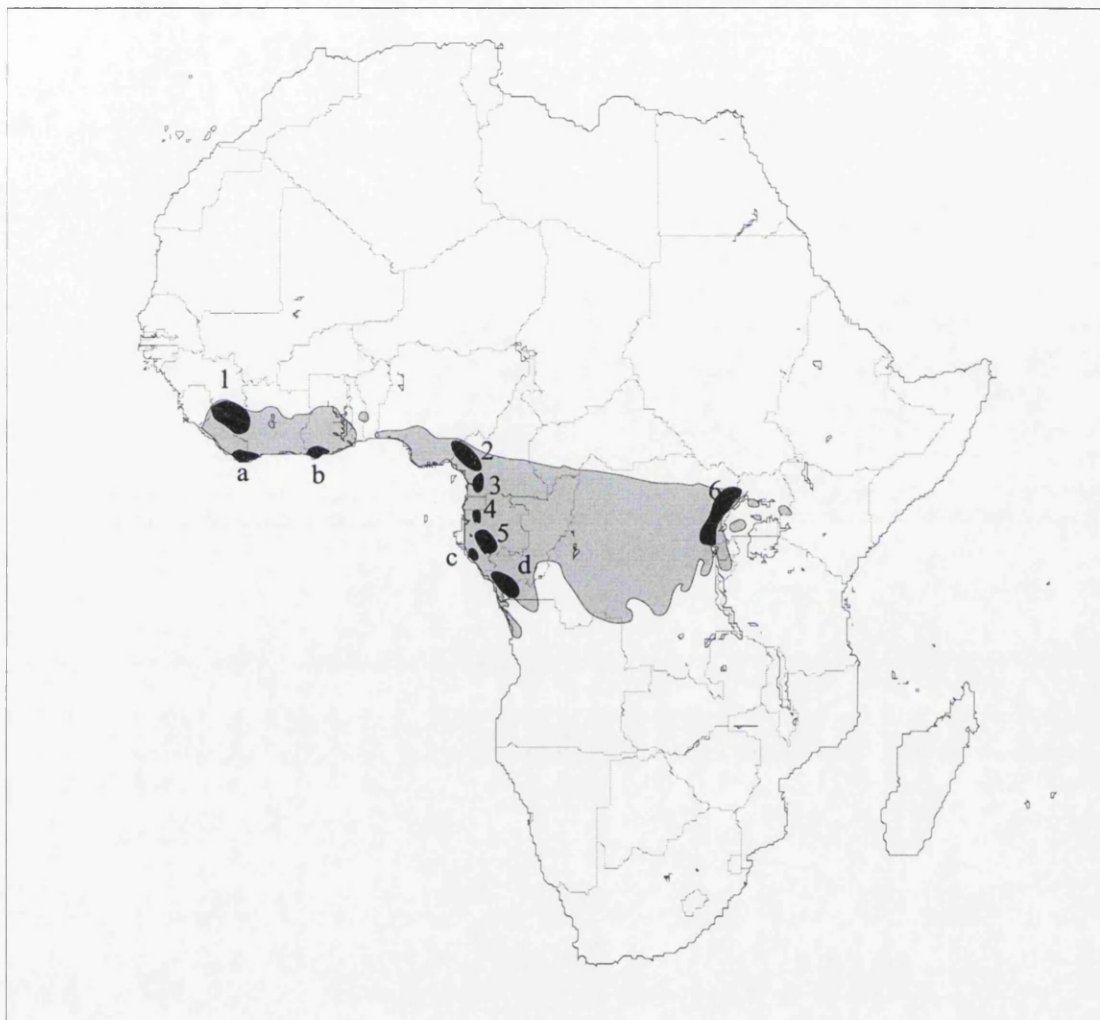


Figure 6.1 Location of postulated glacial lowland refugia in Africa proposed by Maley (1987) (1–6) and Sosef (1994) (a–d). 1) Liberia; 2) West Cameroon mountains; 3) South Cameroon Plateau; 4) Crystal Mountains; 5) Chaillu Massif; and 6) the eastern Zaire (Kivu). a) Cape Palmas; b) Cape Three Points; c) Doudou Mountains; and d) the Mayombe. Hatched area represents present-day distribution of lowland rain forest (after Sosef, 1994).

6.2.1 Geological history of Madagascar and other African offshore islands

6.2.1.1 Madagascar

Madagascar is situated ca. 300 km from the coast of Mozambique and reaches an altitude of 2867 m. Once part of Gondwana, Madagascar separated from eastern Africa during the end of the Jurassic (ca. 140 Ma) via the Davie Ridge transformation fault as a result of oceanic expansion which ended in the lower Cretaceous (110 Ma) (Fröhlich, 1996). However, it did not separate from India and the Australo-Antarctic continental bloc until the beginning of the upper Cretaceous (88 Ma) (Storey et al., 1995; Fröhlich, 1996) and as a result the Malagasy flora, particularly in the eastern humid forests, has strong affinities with the indo-australo-malesian floras (Schatz, 1996). Therefore, the flora of Madagascar consists of Gondwanan elements, and the result of continuous dispersal events across the Indian Ocean (Schatz, 1996). The latter can be divided into (a) those which occurred along “Lemurian Stepping-stones” and (b) continuous long distance dispersal events, many of them recent, resulting from ocean currents and prevailing winds (Schatz, 1996). Of the 10,000 to 12,000 plant species found on Madagascar over 80% are endemic (Rajeriarison, 1996), including the ca. 50 species of *Begonia* (except the widespread African *B. oxyloba* and a few introduced species) (Keraudren-Aymonin, 1983). Begonias on Madagascar are found predominantly in northern and eastern forests.

6.2.1.2 Mauritius and Réunion

Mauritius is volcanic in origin and situated 840 km from Madagascar and approximately 200 km from Réunion. The island is dated at about 7.8 Ma (Emerick & Duncan, 1982). Mauritius has a varied topography with ranges of peaks, plateaux and low lying plains, but only reaches a maximum altitude of 826 m and therefore is less habitat-rich than Réunion. There are 800–900 native species of plants, roughly one third of which are endemic (Strahm, 1984).

Réunion is situated 780 km from east of Madagascar and is estimated to be 2 Ma (Emerick & Duncan, 1982). Réunion has a central massif which reaches an altitude of 3069 m. There are an estimated 500 species of indigenous seed plants. As Réunion is younger than Mauritius, it presumably gained at least some of its plant species from Mauritius.

Begonia salaziensis is the only *Begonia* species endemic to these islands. Most of the populations of *B. salaziensis* occur on Réunion. In the treatment of section *Mezierea* (Klazenga et al., 1994) only four collections are recorded for Mauritius, in contrast to almost 30 in Réunion.

6.2.1.3 The Comores

The Comores are situated at the northern end of the Mozambique Channel, and consist of four main islands: Mayotte, Anjouan, Moheli and Grande Comore. These islands are mostly basalt and range in altitude from 660 m in Mayotte to 2361 m in the island of Grande Comore. The Comoro Islands exhibit a geomorphological progression of oceanic island chains from the still-active Grande Comore to the highly eroded Mayotte. Age estimates for the islands show that Grande Comore is recent (0.01 ± 0.01 Ma), followed by Anjouan (1.52 ± 0.10 Ma), Moheli (2.81 ± 0.08 Ma), and Mayotte (5.40 ± 0.01 Ma) (Emerick & Duncan, 1982). *Begonia comorensis* is the only *Begonia* species endemic to this group of islands. It is morphologically very similar to *B. seychellensis* of which it has been a synonym in the past (Keraudren-Aymonin, 1983).

6.2.1.4 São Tomé

São Tomé is one of four islands in the Gulf of Guinea. It lies 250 km off the coast of Gabon and is 47 km long and 27 km wide. São Tomé reaches a maximum altitude of 2024 m at the summit of the Pico de São Tomé. It has the greatest angiosperm diversity and highest level of endemism of the volcanic Gulf of Guinea

islands (Bioko is a continental island), with a total of 601 species of which 81 are endemic (Figuereido, 1994).

Although the ages of rocks from São Tomé reach back as far as 13 Ma, it is unclear whether the island was emergent at this time (Barfod, pers. comm., 2001). The earliest volcanic rock dated from São Tomé is approximately 13 Ma. However, the date for the earliest unequivocal above sea-level deposits of volcanic origin come from basalt flows which are up to 3 Ma (Barfod, pers. comm., 2001). However, on nearby Príncipe emergent basalt flows as old as 24 Ma have been found.

There are eight species of *Begonia* on São Tomé of which four (*B. baccata*, *B. crateris*, *B. molleri* and *B. subalpestris*) are endemic.

6.3 METHODS

6.3.1 *Taxon sampling and sequences*

The same 77 species and sequences were used for molecular clock estimates as in the combined ITS and *trnL* analysis in Chapter 3. *Datisca glomerata* and *D. cannabina* were again used as outgroups.

6.3.2 *Phylogenetic relationships*

The same random parsimonious tree resulting from the maximum parsimony analysis of 77 combined ITS and *trnL* intron sequences in Chapter 3 was used (Fig. 3.5) to carry out a molecular clock analysis and estimate node ages. To test rate heterogeneity and determine node age estimates the combined ITS and *trnL* intron topology was used onto which only the ITS data was optimised. The optimisation of ITS over that of the *trnL* intron was preferred because non-parametric rate smoothing (NPRS) is known to be inaccurate when sequence divergence is low (Sanderson, 2001).

6.3.3 *Molecular clock analyses and calibrations*

Branch lengths were fitted to one of the most parsimonious trees derived from the combined analysis onto which the ITS data analysis was optimised. Modeltest 3.06 (Posada & Krandaall, 1998) was run before carrying out the likelihood ratio test to investigate which likelihood model best fits the ITS data. The best-fit model selected by the AIC in Modeltest was TrNef+I+G. This model assumes an equal base frequency, equal rates for transversions but a different rate for transitions (Rmat = (1.0000 3.8096 1.0000 1.0000 5.0926)), a gamma distribution with shape = 0.6181 and a low level of invariable sites (Pinvar = 0.1704). A likelihood-ratio test (LRT) was used to assess whether substitution rates in ITS are clock-like (Felsenstein, 1981). The basic premise behind the LRT is that the likelihood of a tree that is constrained by clock-like change will be significantly different from one that is not constrained by a molecular clock. In this case the molecular clock is the null hypothesis. This statistic may be found by twice the difference in log likelihood of branch lengths between a rate-constrained tree and a tree that has no constraints on branches [$2\Delta = -\ln \text{constrained} - (-\ln \text{unconstrained})$]. The degrees of freedom is calculated by $n-2$, where n is the number of taxa. The resulting log likelihood is then compared to a χ^2 (chi-squared) distribution. If the log likelihood is greater than 95% percentile of the χ^2 distribution, then the null hypothesis (molecular clock) is rejected.

6.4 RESULTS

The maximum likelihood model described above was used to fit ML branch lengths to one of the most parsimonious trees in the combined analysis on which only the ITS data was optimised. The log likelihood of the constrained model was 4660.68, and that of the unconstrained model 4539.28. The chi-squared value was therefore 121.4 with 75 degrees of freedom, hence the molecular clock was rejected with $p < 0.005$. In cases where the molecular clock is rejected an ultrametric tree (i.e. a tree in which all terminal

tips are equidistant from the root) can be used to estimate divergence times on the basis of parsimony branch lengths, using a non-parametric rate smoothing (NPRS) function (Sanderson, 1997).

NPRS (Sanderson, 1997) was chosen to construct an ultrametric tree as implemented by TreeEdit version 1.0 alpha 4-61 (Rambaut & Charleston, 2000). Non-parametric rate smoothing does not assume equal substitution rates (i.e. a perfect molecular clock) across the tree like other methods such as Langley–Fitch (Sanderson, 2001), but rather attempts to minimise the ancestor-descendant rate difference for every node of the tree. It will therefore smooth local transformations in rate as it changes across a tree. It is driven by the likelihood that evolutionary rates are autocorrelated in time, and therefore that there is a degree of rate heritability, although the degree of autocorrelation is not fixed to any one value. This means that in cases where, for example, terminal species have an accelerated substitution rate, reflected as a long branch, the length of the branch will be corrected according to other branch lengths in the same clade.

To calibrate the tree in absolute time maximum dates of 7.8 Ma and 2 Ma, equivalent to the ages of Mauritius and Réunion respectively, were used to constrain the age of *B. salaziensis*; *B. salaziensis* occurs on both islands. An additional age constraint for the node leading to *B. baccata* of 13 Ma, equivalent to the maximum age of volcanic rock found on São Tomé, was used as a cross-validation point. *Begonia comorensis* was also included in the analysis, but its maximum age of 5.4 Ma (maximum age of Mayotte, the oldest of these volcanic islands) was not used because of the sister relationship between *B. salaziensis* and *B. comorensis* and the inability in TreeEdit to constrain more than one node.

The results of the NPRS are summarised in Figure 6.2 and discussed below.

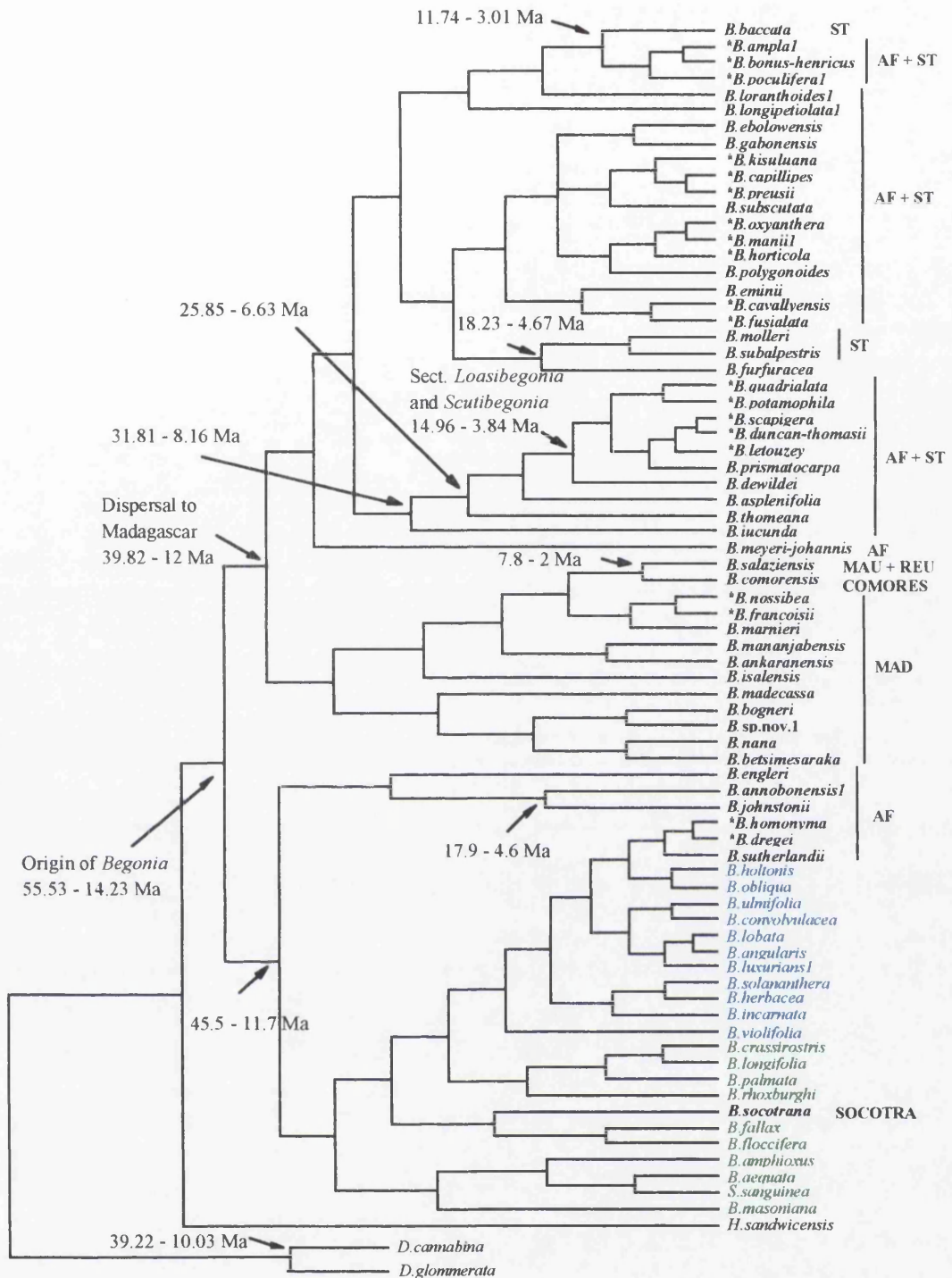


Figure 6.2 One most parsimonious tree resulting from the analysis of combined *trnL* intron and ITS sequence data. Branch lengths are proportional to the number of changes in the ITS data. Asterisks indicate African species which originated in the Pleistocene (when *B. salaziensis* is calibrated at 2 Ma). AF = mainland Africa; ST = São Tomé; MAU = Mauritius; REU = Réunion; and Mad = Madagascar. Section names are given after the African species. African species are in black, Asian in green and American in blue.

6.5 DISCUSSION

6.5.1 Dating the phylogeny

Figure 6.2 shows a topology resulting from the parsimony analysis of the combined nuclear and plastid data. Branch lengths are proportional to the changes in the ITS data. The three calibration dates for this phylogeny ranged from 2 Ma to 13 Ma. The maximum differences in ages of nodes when values of 2 and 7.8 Ma were used to date the divergence between the *B. salaziensis* and *B. comorensis* lineages, varied by as little as 1.5 my in terminal nodes to almost 38 my for basal nodes such as that defining the origin of *Begonia*. On continental Africa, it is therefore difficult to estimate which of the dates may be more accurate, especially in the absence of fossil evidence or multiple events representing multiple dates which can be used to calibrate different parts of the phylogeny. The age of São Tomé was used for this purpose. It is an old island compared to other islands like Réunion or Mauritius, and the fact that it is a volcanic island which has never been connected to the mainland (G. Fitton, pers. comm., 2001) means that it is unfit to use to calibrate the phylogeny as dispersal could have occurred at any time during the last 13 Ma. This is a significant problem when using the age of islands as calibration dates. The node in a phylogeny corresponding to a particular island is not the age of the origin of the island but the range from the origin of the island to the present, as in fact dispersal onto a volcanic island may have occurred very recently, unless there is proof to the contrary. In situations where species are endemic to an island that is part of an island chain (e.g. Hawaiian Islands), species or lineages may actually pre-date the age of the island, having dispersed there after the island arose and become extinct elsewhere. The ages of islands like São Tomé, however, can be used to check the accuracy of other calibration points in this phylogeny. For example, when the origin of *B. salaziensis* is dated at 7.8 Ma, the age of the node leading to *B. baccata* is 11.74 Ma which is well within the earliest age known for this island.

Having dates for only terminal nodes of the phylogeny can create greater standard deviation errors towards the base of the tree. Ideally, there should therefore be more than one calibration point, and at least one of these should occur close to the base of the tree. Terminal node dating is probably unable to accurately predict rate changes, which might have occurred earlier in the phylogeny. Keeping these problems with dating phylogenies in mind, the ages presented below should be considered with caution, as preliminary estimates for certain events in *Begonia* evolution.

Age estimation throughout the phylogeny using the age of Réunion (2 Ma) to calibrate the divergence between the *B. salaziensis* and *B. comorensis* lineages gives a remarkably good fit to the numerous hypotheses presented on the evolutionary history of African organisms in the last 6-10 Ma. These estimates are consistent with hypotheses based on plant distributions, plant and animal fossil finds, geological evidence, and other phylogenetic evidence, which are discussed below.

It does, however, give an estimated age for *Begonia* of 14 Ma, which seems recent for such a widespread and species-rich genus. This however, is consistent with the age of *Begonia* previously estimated at 26-9 Ma based on percent divergence between ITS sequences (Forrest, 2000). The 14 Ma estimate for *Begonia* does not seem aberrantly recent when compared to age estimates for other plants groups such the legume genus *Inga*. Consisting of ca. 300 neotropical rain forest trees, *Inga* is estimated to have speciated in the last 10 my, and therefore a product of recent speciation (Richardson, et al., 2001). Alternatively, the earlier date of 51 Ma when *B. salaziensis* is calibrated based on the age of Mauritius (7.8 Ma) puts the origin of *Begonia* in the Palaeocene, which seems remarkably early. Wagstaff & Dawson (2000) mapped fossil ages on a Cucurbitales phylogeny. Rates were not tested for homogeneity and no rate smoothing was carried out. Within the Cucurbitales, *Begonia* is significantly derived, and the taxonomically nearest fossil to *Begonia* known is one identified as belonging to the Tetramelaceae, the sister family to Begoniaceae + Datisceae. The age for this fossil is

given as 55 Ma. The given topology (p. 139) in their study does not reflect a homogeneous molecular rate and suggests a date later than 51 Ma for *Begonia*.

Using the later calibration for *B. salaziensis* (2 Ma) gives an age of 10 Ma for the split between the two known species of genus *Datisca* used as the outgroup in this study. A similar age for this division was found based on cpDNA restriction site variation, where a substitution rate of 10^{-9} nucleotides per site per year and a constant molecular rate was assumed, giving an estimate of 8.7 ± 1.7 Ma for the split between *D. cannabina* and *D. glomerata* (Liston et al., 1992).

Divergence rates in numbers of substitutions per site per year can be calculated for *Begonia* using branch lengths (number of autapomorphies) for *B. salaziensis* in the ITS phylogeny and the estimated age for this species (Réunion at 2 Ma or Mauritius at 7.8 Ma). This can be calculated as follows (the estimated of 2 Ma is used for this example): First, the number of substitutions per my is calculated (branch length (1)/age of taxon (2 Ma) = 0.5 substitutions/my); secondly, to obtain the number of substitutions per site per my the number of substitutions per year is divided by the total number of sites, in this case the length of ITS ($0.5/401 = 1.24 \times 10^{-3}$ no. of substitutions/ site/ my) and then divided by one million to give the number of substitution per site per year (1.24×10^{-9} subs/site/yr). Using this method estimates for substitution rates for *B. salaziensis* are 1.24×10^{-9} subs/site/yr (when using the age for Réunion) or 3.2×10^{-10} (when using the age for Mauritius). These results can then be compared to those compiled for other genera (Table 6.1; Richardson et al., 2001). The faster rate of 1.24×10^{-9} subs/site/yr is comparable to that found in other herbaceous genera, particularly that reported for *Saxifraga* (Table 6.1). Generation times for *Begonia* can be very short, and in some cases is less than a year (personal observation in cultivation), which could account for this accelerated rate. Estimates of substitution rates given by using the age of Mauritius (7.8 Ma) as a calibration point give rates comparable to those found in Winteraceae, a genus of trees with a slow generation time (Table 6.1). These slow rates are unlikely in a genus like *Begonia*, and are therefore

Table 6.1 Calibrated molecular rates for *Begonia* compared to other plant genera (from Richardson et al., 2001).

Rate source	Habit/Minimum generation time	Genomic region	Calibrated rate (s/s/y)
<i>Aichryson</i> , Crassulaceae	Annual or perennial herbs/1-2 yrs	ITS2	5.69×10^{-9}
<i>Astragalus</i> , Leguminosae	Annual or perennial herbs/1-2 yrs	ITS	3.5×10^{-9}
<i>Dendroseris</i> , Compositae	Shrubs/ ca. 4 yrs	ITS	3.94×10^{-9}
<i>Gossypium</i> , Malvaceae	Shrubs/2-3 yrs	ITS	5.3×10^{-9}
<i>Inga</i> , Leguminosae	Trees and shrubs/2-3 yrs	ITS	2.41×10^{-9}
<i>Lupinus</i> , Leguminosae	Annual or perennial herbs, occasionally shrubby/1-2 yrs	ITS1/ITS2	$3.6 \times 10^{-9}/3.3 \times 10^{-9}$
<i>Phytica</i> , Rhamnaceae	Trees and shrubs/2-3 yrs	ITS	2.44×10^{-9}
Silverswords, Compositae	Woody perennials/2-3 yrs	ITS	3.00×10^{-9}
<i>Saxifraga</i> , Saxifragaceae	Annual or perennial herbs/1-2 yrs	ITS	1.72×10^{-9}
<i>Begonia</i> , Begoniaceae	Annual or perennial herbs	ITS	1.24×10^{-9} or 3.2×10^{-10}
<i>Robinsonia</i> , Compositae	Woody pachycaul/2-3 yrs	ITS	7.83×10^{-9}
Winteraceae	Trees and shrubs/6-10 yrs	ITS1	3.2×10^{-10} to 5.2×10^{-10}
Winteraceae	Trees and shrubs/6-10 yrs	ITS2	3.6×10^{-10} to 5.7×10^{-10}

rejected. These results give strong and further support for hypotheses of African *Begonia* evolution based on a 2 Ma divergence estimate for *B. salaziensis*.

The argument and results presented above strongly favour a 2 Ma calibration for *B. salaziensis* and the resulting node age estimates using this calibration are discussed below.

6.5.2 *Begonias in Madagascar*

In previous chapters, evidence has been presented that shows the endemic Malagasy species of *Begonia* to be monophyletic. In evolutionary terms, this demonstrates that they are the result of a single colonisation event, followed by insular speciation and subsequent dispersal to offshore islands such as the Mascarenes, Comores or Seychelles (Fig. 6.2). This pattern of colonisation and speciation on Madagascar has been observed in other organisms such as murids (Jansa, 1999), but no explicit molecular evidence is known for other plant genera. Other groups, such as *Streptocarpus* (Gesneriaceae), show patterns indicating that the Malagasy species are the result of more than one colonisation event (Möller & Cronk, in press) from the African mainland. Similarly, although adapted to dry tropical forest rather than rain forest, the Malagasy species of the legume genus *Ormocarpum*, have been shown to be the result of two dispersal events postulated to have occurred sometime in the Tertiary (Lavin et al., 2000).

How *Begonia* could have reached Madagascar remains unclear, because the fruit type of the ancestor of these species is ambiguous. The basal Malagasy dichotomy in the *trnL* phylogeny (Fig. 2.4 in Chapter 2) leads to a clade consisting of species with fleshy winged fruits (section *Erminea*) and to another clade consisting predominantly of dry, wing-fruited species (the fleshy-fruited endemic Malagasy species are nested within this second clade). Species in section *Erminea* possess fleshy fruits, yet these fruits are also winged and all species have true axillary placentation, where the placentae

grow out of a central vertical column. This is the common placental type in *Begonia* correlated with the presence of wings. However, fleshy fruits are believed to be bird dispersed and would therefore be good candidates for trans-oceanic dispersal, so it may have been that the first begonias to arrive in Madagascar had fleshy fruits. Further evidence of this can be found in Figure 3.6 (Chapter 3) where the combined ITS, *trnL* intron and 26S phylogeny shows the fleshy fruited, mainland African species *B. meyeri-johannis* as sister to a Malagasy clade.

Although the fruit type of the ancestor of Malagasy endemic begonias remains hypothetical there is evidence for what may be a more recent dispersal to Madagascar. *Begonia oxyloba* is a widespread species that occurs widely on the African mainland and is also found on Madagascar. Its indehiscent fruits mature reddish-green and the seeds are faintly ornamented suggesting animal dispersal (de Lange & Bouman, 1991). Although nothing is known about the actual disperser, its presence on Madagascar and its occasional growth as an epiphyte suggests bird dispersal. This may be an indication of the mechanism behind the earlier dispersal event which led to the significant speciation of the endemic species on Madagascar.

Dates for the origin of *Begonia* in Madagascar range from 12–47 Ma. Madagascar split from Gondwana in the early Cretaceous, ca. 140 Ma. However, geological studies on the Davie Fracture Zone of the Mozambique channel have suggested the presence of a land-bridge between Madagascar and mainland Africa from the mid-Eocene to early Miocene (45–26 Ma), coinciding with the ages of some Malagasy mammalian groups (McCall, 1997). Choosing the earlier estimate of 47 Ma for the divergence of the endemic Malagasy group of begonias predates the presence of this land-bridge. The preferred later age of 12 Ma would make the presence of a land-bridge between these two land masses too early for it to have been instrumental in the dispersal of *Begonia* to Madagascar.

6.5.3 The São Tomé refuge: neoendemics or palaeoendemics?

Of the eight species of *Begonia* found on São Tomé, four are endemic (Table 6.2). *Begonia baccata* and *B. crateris* make up the endemic São Toméan section *Baccabegonia*, whereas *B. molleri* and *B. subalpestris* belong to section *Tetraphila*, which includes 28 additional mainland African species. Of the non-endemic species *B. thomeana* (section *Cristasemen*) has a disjunct distribution, occurring only on São Tomé and in the Massif du Chaillu in Gabon. The remaining non-endemics found on São Tomé, *B. annobonensis* (section *Sexalaria*), *B. ampla* (section *Squamibegonia*) and *B. loranthoides* (section *Tetraphila*), have populations both on São Tomé and on the mainland, and are either widespread on the mainland or have populations near the coast in Cameroon and Gabon.

On the basis of pollen morphology data, van den Berg (1984) suggested that species in section *Baccabegonia* are palaeoendemics (relicts of a group which once had a much wider distribution). The NPRS analysis gives younger ages for the endemic species of section *Baccabegonia* (*B. baccata*) than the two endemics of section

Table 6.2 Table showing distribution of *Begonia* species found on São Tomé.

Species (Section)	Presence in São Tomé
<i>Begonia baccata</i> (<i>Baccabegonia</i>)	Endemic
<i>Begonia crateris</i> (<i>Baccabegonia</i>)	Endemic (not sampled)
<i>Begonia molleri</i> (<i>Tetraphila</i>)	Endemic
<i>Begonia subalpestris</i> (<i>Tetraphila</i>)	Endemic
<i>Begonia loranthoides</i> (<i>Tetraphila</i>)	São Tomé, Príncipe, Cameroon to Congo (Kinshasa)
<i>Begonia ampla</i> (<i>Squamibegonia</i>)	São Tomé, Central Africa
<i>Begonia thomeana</i> (<i>Cristasemen</i>)	São Tomé, Gabon
<i>Begonia annobonensis</i> (<i>Sexalaria</i>)	São Tomé, Príncipe, Pagalu, Cameroon

Tetraphila (*B. molleri* and *B. subalpestris*) regardless of the calibrations used. The age difference between these two endemic lineages varies between one and two million years. The endemic São Tomé species from section *Tetraphila*, together with the mainland and Bioko species *B. furfuracea*, are sister to the rest of the section. These species have retained some primitive characters such as twisted stigmas (most common type in the genus), unlike other members of the section which have a diverse array of gynoecia types (Figs. 6.2 and 6.3). *Begonia molleri* and *B. subalpestris* are morphologically distinct from each other in flower size and leaf pigmentation, but at the same time conform to the general tetraphiloid morphology (i.e. presence of long fusiform fruits) and are morphologically comparable to their mainland sister taxon *B. furfuracea*. In contrast, the two species in section *Baccabegonia* are morphologically very similar, differing mainly in the degree of pubescence. However, unlike *B. molleri* and *B. subalpestris*, they are morphologically very distinct from their sister group, section *Squamibegonia*. Taking into account these morphological comparisons, the similar ages of the São Tomean endemics in section *Tetraphila* (4.67-18.23 Ma) and section *Baccabegonia* (3.01-11.74 Ma) is surprising since, based on morphology, one would assume section *Baccabegonia* to be considerably older. Therefore, within *Tetraphila*, *B. molleri* and *B. subalpestris* appear to be the result of an early dispersal to São Tomé from a tetraphiloid ancestor, and could therefore be considered palaeoendemics. The phylogenetic position of the giant terrestrial *B. baccata*, nested within a clade consisting of smaller epiphytes, suggests a classical island radiation scenario where a new colonising species adapts, often adapting radically different habits like gigantism, in a new environment with little competition (Carlquist, 1965, 1974). Examples of this type of innovative insular adaptations have, for example, been found in the acquisition of woodiness in *Echium* (Boraginaceae) and *Sonchus* (Compositae) in Macaronesia (Baldwin et al., 1998). However, the premise that tetraphiloid species such as *B. molleri* and *B. subalpestris* would have already been present on São Tomé at that time suggests that *B. baccata* and *B. crateris* could be palaeoendemics, and hence would have once been part of a more widespread group of taxa that became extinct on the mainland.

Baldwin (1998) interpreted island groups as palaeoendemics if they and the continental sister group are derived from a common ancestor (as opposed to island species being descendants of a most recent common ancestor, as is the case for neo-endemics). This palaeoendemics definition agrees with the sister relationship between the insular section *Baccabegonia* and its sister group, the continental section *Squamibegonia*. Age estimates for section *Baccabegonia* range from 3 to 11.7 Ma, depending on whether *B. salaziensis* is calibrated on the age of Réunion (2 Ma) or Mauritius (7.8 Ma).

The ca. 3 Ma estimate for the age of *B. baccata* coincides with the age given for the earliest known unequivocal above-seal-level deposits of volcanic origin on São Tomé. However, estimates for *B. molleri* and *B. subalpestris* are older (4.67 Ma), suggesting that São Tomé could have been above sea level before 3 Ma. The earliest submarine volcanic deposits known from São Tomé are from ca. 13 Ma, but equally there is no evidence that this rock was above sea level at that time. Dating the node between *B. baccata* and section *Squamibegonia* (*B. ampla*, *B. poculifera* and *B. bonus-henricus*) at 13 Ma gives a date for the age of *B. salaziensis* earlier than that of the island of Mauritius (7.8 Ma). This points towards some of the problems of dating phylogenies based on the ages of islands, particularly older islands such as São Tomé. If the situation for São Tomé is common among islands (i.e. that the age estimated for an island is possibly not equal to the actual age the island has been above sea level) then nodes in dated phylogenies will be estimated as being older than their actual ages.

More recent dispersal events are evident in *B. ampla*, *B. poculifera*, *B. thomeana*, *B. annobonensis* and *B. loranthoides*, which are found both on the African mainland and on São Tomé and other Gulf of Guinea islands. As noted above no species in section *Tetraphila* occur both on mainland Africa and on São Tomé.

São Tomé is not commonly highlighted as being an important historical climatic refuge. Much more attention has been paid to the postulated rain forest refuges of continental Africa. For *Begonia*, the island of São Tomé appears to be an important pre-

Pleistocene refuge. Its situation ca. 250 km from the mainland ensured that its flora and fauna would be buffered from the climatic conditions that perturbed the mainland. Even taking the latest dates estimated on the combined phylogeny, the endemic begonias of São Tomé are of pre-Pleistocene origin. *Begonia thomeana*, present in both São Tomé and the Massif de Chaillu in Gabon, dates from the late Miocene (6.6 Ma). The endemic begonias of São Tomé are therefore relicts of lineages which might have formerly been more widespread on mainland Africa.

6.5.4 *Refuge begonias on mainland Africa*

The distributions of species of *Begonia* in sections *Loasibegonia* and *Scutobegonia* have been used to indicate the position of postulated Pleistocene rain forest refugia. Sosef (1994) argued that the location of former refuges could be deduced from the present-day distribution of this group of begonias because of the high degree of endemism in this group and the inability of the seeds to disperse effectively, usually dropping to the ground below the mother plant. Species from both these sections originated relatively recently (3.8–14.96 Ma), compared to other sections in the same clade (Clade 2, Fig. 6.3). The most recent node within these sections is dated at 0.52 Ma using the latest calibration date of 2 Ma for Réunion. Therefore, many of the species in these sections would have arisen during the late Pleistocene when continuous large-scale climatic oscillations may have driven speciation (and extinction). However, not all species in sections *Loasibegonia* and *Scutobegonia* evolved at this time, and it is probable that these so-called Pleistocene refugia have served as such since the end of the Miocene. It would be of interest to sample these groups more extensively to estimate what percent of species actually originated during the Pleistocene. Significantly, using the same calibration date, many of the species in section *Tetraphila* (Fig. 6.3, Clade 1; Fig. 6.1) were already in existence at the beginning of the Pleistocene. Putative vicariant events which lead to the restricted distribution of *B. cavallyensis* in the Upper Guinea region (Ivory Coast and Sierra Leone) and *B. horticola* in Eastern Congo (Kinshasa) and

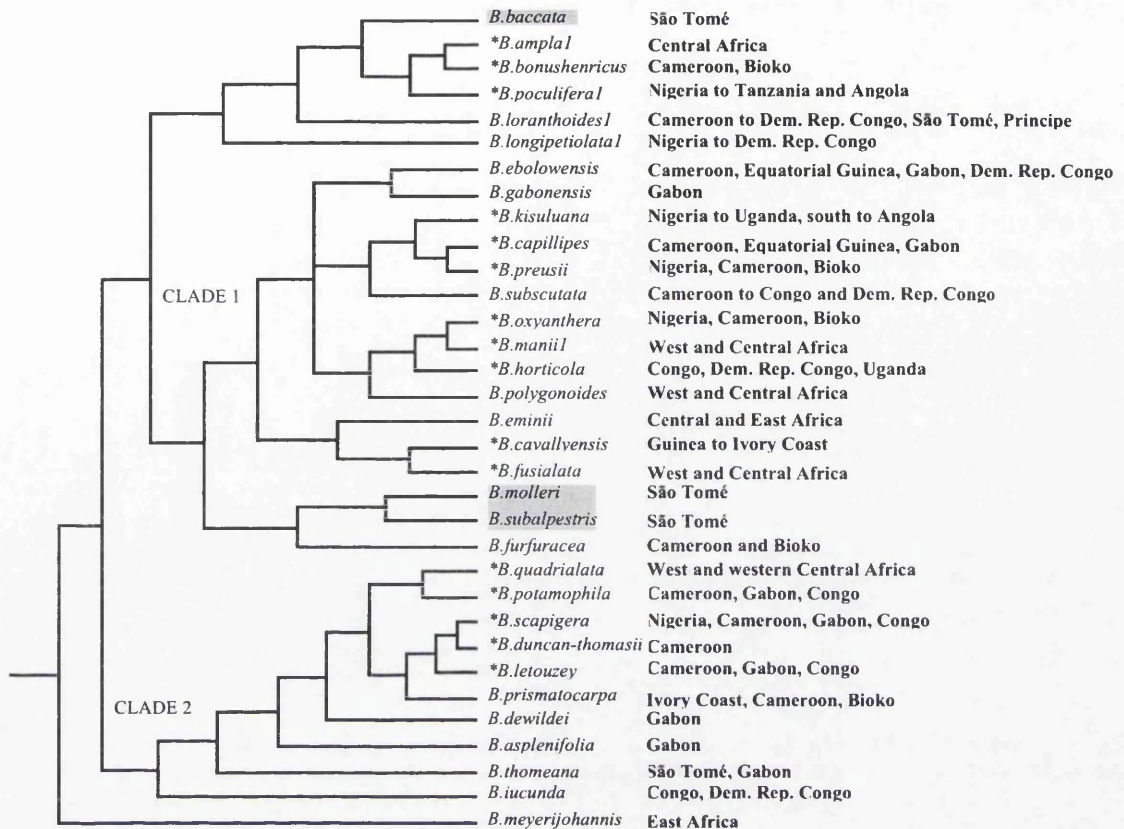


Figure 6.3 Part of one most parsimonious tree resulting from the analysis of combined *trnL* intron and ITS sequences showing the distribution of West and Central African begonias. Asterisks indicate African species which originated in the Pleistocene (when *B. salaziensis* is calibrated at 2 Ma). The grey boxes denote São Tomé endemics.

Uganda, and Mayombe in Congo (Brazzaville) occurred 1.6-1.7 Ma, as a result of widespread aridification at the end of the Pliocene.

Phylogenetically isolated or basal species of African *Begonia*, such as *B. iucunda* and *B. thomeana* occur in refuges on the periphery of the main forest refuges identified in Cameroon and Gabon. These included São Tomé, the Chaillu Massif and the western Congo (Kinshasa)/Zaire and Mayombe regions. *Begonia iucunda* is distributed in ravines in areas dominated by savannah vegetation in western Congo (Kinshasa) and in southern Congo (Brazzaville) (Chapter 5). These areas mainly fall outside the Mayombe refuge

identified by Sosef (1994) but are included in the larger western Congo/Zaire region (Maley, 1987).

The fleshy-fruited species of African *Begonia* do not have the strict pattern of endemism seen in other sections such as *Scutobegonia* or *Loasibegonia*, possibly due to the better dispersal capability conferred by bird vectors. They do show one main area of endemism in the Lower Guinea region (in Cameroon and Gabon), and two minor ones, one in the Upper Guinea region (Sierra Leone/Liberia/Ivory Coast) and the other in the Lake Kivu region. However, most species have a relatively broad central African distribution with a centre of diversity in Cameroon and Gabon. Few species occur in the other phytogeographic areas. Because afro-montane regions in Africa can be considered as ecological islands, it would be plausible that these small numbers of species in the Upper Guinea and Kivu regions could be the result of dispersal. However, dispersal probably did not account for this distribution since age estimates for both *B. horticola* (Lake Kivu region, Western Congo) and *B. cavallyensis* (Upper Guinea) are very similar suggesting they are the result of the same event. When *B. salaziensis* is dated at 2 Ma their ages are 1.65 Ma for *B. horticola* and 1.8 Ma for *B. cavallyensis*. When *B. salaziensis* is dated at 7.8 Ma their age is 6.4 Ma for *B. horticola* and 6.95 Ma for *B. cavallyensis*. This example further emphasises the difficulties in estimating correct ages for nodes. Both the later dates in the Pleistocene and the earlier dates during the late Miocene coincide with major widespread aridification in tropical Africa, which could lead to vicariance in the different regions. One would suspect that if they became isolated from other populations during the Miocene they might not be the only species occurring in this area, but that the climatic cycles during the Pleistocene may have driven speciation. The fact that they are single species within clades of morphologically similar species suggest that their split was more recent than the Miocene. All these conjectures are precarious, and unfortunately there is no fossil evidence for *Begonia* to place age estimates on deeper nodes.

Age estimates might be made more accurate in future work on *Begonia*, by combining the dates we know for African begonias based on the age of a small number of islands, with dates from geological events in other continents such as the closing of the Isthmus of Panama in the Neotropics or the age of some tropical Asian islands.

6.5.5 *Speciation patterns in wet tropical Africa*

The phylogeny of African begonias is one of only two known evolutionary studies of African rain forest plants, the other focusing on *Aframomum* (Zingiberaceae) (Harris et al., 2000). Here I compare the patterns shown by *Begonia* with other rain forest species. Molecular phylogenies of birds, mammals, lizards, frogs and salamanders from tropical regions of the Neotropics, Africa and Australia suggest that most speciation events in tropical rain forests pre-date the Pleistocene (Moritz et al., 2000). There is evidence for this in *Begonia*, where most African species seem to have originated prior to the Pleistocene. Several phylogenetic and biogeographic studies carried out on birds in Africa have found lowland rain forest faunas to be ancient, whereas species occurring in montane regions are relatively derived (Fjeldsa, 1994; Fjeldsa & Lovett, 1997; Roy, 1997; Roy et al., 2001).

Studies in African greenbuls (genus *Andropadus*) have shown the montane species to be a derived monophyletic group of Plio-Pleistocene age, whereas the lowland species are of Miocene age (Roy, 1997). A similar pattern was found among akalats (genus *Sheppardia*), a group of African forest birds (Roy et al., 2001). In the African frog genus *Hyperolius* molecular phylogenetic studies indicate that lowland rain forest is postulated to have been the ancestral habitat (as opposed to savannah), and it was hypothesised that these species originated 30–25 Ma, when lowland forests extended from coast to coast.

It has been suggested that the distribution of relatively old species in tropical rain forests may reflect a general pattern world-wide (Moritz, 2000). For plant

speciation patterns the correlation between geographical distribution, ecological distribution and age seems to be less clear. Studies on African violets (*Saintpaulia*) have revealed patterns that are the converse of those found for animals (Lindqvist & Albert, 1999, 2001). Lindqvist & Albert (2001: 39) noted “a phylogenetic trend from higher elevation to lower elevation among the major clades of *Saintpaulia*”. The basal species occur at high elevation in the Usambara Mountains. In the ginger genus *Aframomum* branch lengths resulting from the cladistic analysis of ITS sequences are very short, indicating a significant lack of molecular sequence divergence in contrast with the high levels of observed morphological variability (Harris et al., 2000). These authors postulated that the genus *Aframomum* as seen today is the result of a rapid radiation which probably took place during the Pleistocene. Similar results were found for the diverse genus legume genus *Inga* in South America; the ca. 300 species comprising the genus have very little sequence divergence and much of its diversification has been calculated to have occurred in the Pleistocene (Richardson et al., 2001).

Even with recent calibration estimations, much of the deeper variation in *Begonia* seems to have arisen at the end of the Miocene. Some clades within species-rich groups such as sections *Tetraphila*, *Loasibegonia* and *Scutobegonia*, the largest *Begonia* sections in Africa, seem to have arisen during the Pleistocene. Of the seven sampled species in sections *Loasibegonia* and *Scutobegonia* five are estimated to be of Pleistocene origin. All three species in section *Squamibegonia* are dated from the Pleistocene as are eight of the 18 species in section *Tetraphila*. The remaining species in sections *Loasibegonia*, *Scutobegonia* and *Tetraphila*, however, were probably already in existence in the Pliocene. Therefore, *Begonia* seems to show patterns similar to those found in some animals, with a significant proportion of its diversity being of pre-Pleistocene origin, but with evidence of recent Pleistocene radiations in some lineages.

Unfortunately, *trnL* intron, ITS and 26S give contradicting estimates of relationships between the East and South African species of *Begonia* in sections *Rostrubegonia* (*B. engleri* and *B. johnstonii*), *Sexalaria* (*B. annobonensis*) and *Augustia*

(*B. homonyma*, *B. dregei* and *B. sutherlandii*), so it was deemed unwise to discuss them widely here. However, the clade consisting of species in section *Rostrobegonia* (*B. engleri* and *B. johnstonii*) and section *Sexalaria* (*B. annobonensis*) diverged during the late Miocene (12 Ma) during the widespread aridification of Africa. The divergence of *B. annobonensis* from *B. johnstonii* is estimated at 4.6 Ma. Species in sections *Rostrobegonia* and *Sexalaria* are generally adapted to more seasonal conditions and while *Begonia annobonensis* is restricted to the western part of Africa, *B. engleri* and *B. johnstonii* are distributed in southern African. The divergence between *B. annobonensis* and *B. johnstonii* coincides with the early Pliocene which was characterised by moist conditions and expansion of rain forest in place of savannah. Therefore, unlike the vicariant events which formed the distributions of West and Central African species of *Begonia*, namely the expansion of savannah, those which affected species in sections *Rostrobegonia* and *Sexalaria* could have been the exact opposite: the expansion of rain forest, leaving *B. annobonensis* isolated on the west coast of Africa. In contrast to the sections just mentioned, the also southern African section *Augustia* is of relatively recent origin estimated at 1.4 Ma, with *B. homonyma* and *B. dregei* of Pleistocene origin.

Their closer relationship of these sections (*Augustia*, *Rostrobegonia*, *Sexalaria* and *Peltaugustia*) to American and Asian species rather than the African lowlands rain forest species of the genus make them particularly intriguing. Unravelling their relationships with other species in the genus should give further insights into the massive diversification of *Begonia* in the Neotropics and Asia.

6.6 CONCLUSIONS

Using the age of islands to calibrate nodes in a phylogeny can present problems because island ages will tend to give an estimate of maximum age for endemic species. Even if the range of a calibration point can be estimated to a narrow degree of accuracy, more than one calibration point is essential to cross-validate the ages of different nodes.

In this respect, even giving confidence values to nodes via methods such as bootstrapping, will give no increase in confidence, since trans-oceanic dispersal to islands can occur at any time.

Age range estimates for *Begonia* in Africa were broad when the ages of Réunion (2 Ma) and Mauritius (7.8 Ma) were used for the origin of *B. salaziensis*. Age intervals ranged from only 1.5 my for some terminal nodes to 38 my for basal nodes. However, assuming a more recent origin age for *B. salaziensis* (2 Ma) provides age estimates in other parts of the phylogeny which agree with patterns observed in other African organisms (e.g. birds). Therefore, the hypothesis presented here favours younger divergence times, but is open to discussion.

Even with the assumption that *B. salaziensis* dates from 2 Ma, a large proportion of the *Begonia* diversity seen today in Africa is of pre-Pleistocene origin. Species of Pleistocene origin are concentrated in species-rich groups such as sections *Loasibegonia*, *Scutobegonia* and *Tetraphila*, which have their centre of diversity in western Central Africa. Phylogenetically isolated taxa such as *B. longipetiolata*, *B. iucunda* and *B. thomeana* date to the late Miocene, a period of extended aridification on the African continent that had severe effects on African rain forest species. There is also a tendency for phylogenetically isolated species to occur outside the main identified rain forest refuges. All the endemic species on the island of São Tomé appear to be palaeoendemics, such as *B. thomeana*, *B. baccata*, *B. molleri* and *B. subalpestris*. Of these species, the latest age estimate is for *B. baccata* which is dated at ca. 3 Ma. Therefore, São Tomé appears to have functioned as an important (if previously unrecognised) pre-Pleistocene refuge. On the mainland, areas such as the Massif of Chaillu in Gabon, southern Congo (Brazzaville) and far western areas of Congo (Kinshasa) have played similar roles to São Tomé.

Further phylogenetic studies on other plant groups are essential to create a better picture of the historical construction of the African rain forest flora. They should be

integrated with animal phylogenies to help interpret how the geological and climatological history has prompted the diversity we see today on the continent.

CHAPTER 7 Conclusions and further work

7.1 CONCLUSIONS

Systematic research in *Begonia* is significant because it is representative of other very large angiosperm genera. Many such genera have never been the subject of thorough monographic study, and therefore their species remain hard or impossible to identify, and their evolution not understood (Mabberley, 1993). The recognition of monophyletic units within large genera like *Begonia*, which in many cases will be equivalent to currently taxonomically recognised groups (e.g. sections *Erminea*, *Squamibegonia*, *Baccabegonia*), is essential to split these genera up into manageable groups on which to perform further taxonomic and phylogenetic work. This type of broad-scale study can be very useful in answering some of the questions and doubts voiced by Doorenbos et al. (1998) with respect to sectional delimitation, relationships between sections and the taxonomic placement of some species.

The research presented in this thesis, together with a synthesis of other recent studies (Sosef, 1994; Tebbitt, 1997; Badcock, 1998; Doorenbos et al., 1998; Forrest, 2000), suggests a clear strategy to delimit monophyletic groups in *Begonia*, that could be the subject for future monographic and phylogenetic study. Furthermore, it suggests how phylogenetic relationships within such groups can be resolved.

Chapter 2 demonstrated that the chloroplast *trnL* intron provides DNA sequence data with an optimal level of variation to delimit monophyletic groups in *Begonia*. It is an ideal locus to investigate genus-wide relationships in *Begonia*. Nuclear ribosomal ITS, in contrast, presents considerable difficulties in sequence alignment across this taxonomic range, limiting its utility. In view of this, it should be a priority to carry out a more extensive plastid gene phylogeny of *Begonia*, extending sampling, in particular with respect to American and Asian species. Increased phylogenetic resolution would

also be provided if other chloroplast loci that evolve reasonably quickly, such as *matK*, were also employed.

Chapter 4 demonstrated that the faster rate of sequence evolution in ITS is an advantage when studying the relationships between closely related, and in some cases, between individual species. At this taxonomic level, sequence alignment and therefore DNA sequence character definition is less ambiguous. In combination, *trnL* and ITS provide resolution at different taxonomic levels, and in this sense are highly compatible.

Some recent authors (Scotland & Olmstead, in prep.) claimed that morphology alone does not perform well in cladistic analyses. This appears to be the case in *Begonia*, where a phylogeny based on morphological characters was not congruent with molecular estimates. However, the role of morphology in any useful classification of *Begonia* is clearly important. The molecular phylogenies can be used in conjunction with *a posteriori* character optimisation to demonstrate whether morphological characters traditionally used to define sections in *Begonia* diagnose monophyletic groups. In the case of African begonias, these morphological characters, diagnosed some, but not all clades in the molecular phylogeny. In Africa for example, the presence of a peltate scale-like indumentum reflects evolutionary relationships better than the presence of fleshy fruits (Chapter 2 and 3), and long fusiform fruits are not diagnostic of section *Tetraphila*, since this section has been found to be paraphyletic (Chapter 4). The well-resolved topology for closely related *Begonia* species resulting from simultaneous cladistic analysis of morphological and molecular data sets, demonstrates that in this restricted taxonomic context, morphology does have a role to play, and that the conclusions of Scotland & Olmstead (in prep.) are somewhat extreme. However, it appears that the difficulties in character coding and definition outlined in Chapter 4 limit the use of morphology alone in a cladistic context in *Begonia*, especially across the entire genus.

In summary, the research presented here suggests a clear research program to define phylogenetic relationships in *Begonia*, if resources for such a large task were available. The *trnL* intron and similar chloroplast loci could define wider monophyletic groups. ITS can provide resolution within these groups, and morphological characters,

in conjunction with molecular data in combined cladistic analyses can provide resolution of the relationships of closely related species.

7.2 FURTHER WORK

Recent morphological and molecular work on the genus *Begonia* has answered many questions, but in its wake created many more. Below are questions and priorities for research in the genus which have arisen from this and other recent work:

- 1) Are Asian and American begonias truly monophyletic? ITS sequence data shows Asian and American species to be monophyletic. This find is not corroborated by *trnL* intron chloroplast DNA sequence data nor by a more restricted study of the *trnC-trnD*. A wider sampling of Asian and American species for cpDNA and additional nuclear genes could give insight into this incongruence, particularly whether it is a sampling artefact because so few American and Asian species have been sampled. .
- 2) The taxonomy and evolution of Malagasy begonias. The 50 species of *Begonia* found on Madagascar, the Mascarenes and Réunion are currently divided into five sections. Some of the species on Madagascar, such *B. goudotii*, *B. bosseri* or *B. kalabenonensis* have a unique macro- and micromorphology not found on the African mainland. Using phylogenetic techniques it would be possible to investigate how these different morphologies arose, and whether the current sectional classification of Malagasy species reflects evolutionary relationships.
- 3) Phylogenetics and biogeography of refuge begonias. In 1994, Sosef investigated the relationships of species in sections *Loasibegonia* and *Scutobegonia* based on a morphological cladistic analysis. Would the phylogenetic analysis of sequence data for species in both these sections show the same patterns of relationship found on the basis of morphology? Can the presence of refugia in West Central Africa during the Pleistocene and earlier be imprinted in the genome of some of these species? How would the level of divergence between populations of a chosen species vary from regions of postulated refugia to areas outside the refugia?

- 4) A world-wide revision of the genus *Begonia*. African begonias are relatively well studied thanks to the continuing work on these species by researchers at the Agricultural University in Wageningen, and due to the manageable number of begonias present on this continent (ca. 158 species). Much less is known about both Asian and American begonias and phylogenetic work in these areas is hampered by the absence of taxonomic publications for this genus in both continents.

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APPENDIX 1 Accessions used to sequence the trnL intron, ITS and 26S in *Begonia*

Vouchers marked † represent living accessions which died before a voucher specimen was taken. "Unknown" det. indicates that unattributed label identification was accepted but not checked in detail.

SPECIES	DET. BY	SECTION	SOURCE	MATERIAL TYPE	VOUCHER
<i>Begonia aequata</i>	L. Forrest	<i>Petermannia</i>	Philippines	Living	Wilkie et al. 29140 (E)
<i>Begonia amphioxus</i>	Unknown	<i>New section?</i>	Asia	Living	L. Forrest 141 (GL 001 156 94) (E)
<i>Begonia ampla1</i>	A. Gascoigne	<i>Squamibegonia</i>	São Tomé	Silica	A. Gascoigne 015 (E)
<i>Begonia ampla2</i>	V. Plana	<i>Squamibegonia</i>	Cameroon	Silica	V. Plana 89 (E)
<i>Begonia angularis</i>	Unknown	<i>Pritzelia</i>	America	Living	L. Forrest 172 (E 1969 1797) (E)
<i>Begonia ankaranonensis2</i>	Unknown	<i>Quadrilobaria</i>	Madagascar	Living	GL 001 064-97 (no voucher†)
<i>Begonia annobonensis1</i>	A. Gascoigne	<i>Sexalaria</i>	São Tomé	Silica	A. Gascoigne 051 (E)
<i>Begonia annobonensis</i>	A. Gascoigne	<i>Sexalaria</i>	São Tomé	Silica	A. Gascoigne 052 (E)
<i>Begonia aspleniifolia</i>	Wageningen	<i>Filicibegonia</i>	Africa	Living	L. Forrest 209 (GL 001 079 97) (E)
<i>Begonia baccata</i>	A. Gascoigne	<i>Baccabegonia</i>	São Tomé	Silica	A. Gascoigne 044 (E)
<i>Begonia betsimesaraka</i>	V. Plana	<i>Erminea</i>	Madagascar	Silica	M. Moeller 9879 (E)
<i>Begonia bogneri</i>	Unknown	<i>Erminea</i>	Madagascar	Living	L. Forrest 213 (E 1986 0844) (E)
<i>Begonia bonus-henricus</i>	V. Plana	<i>Squamibegonia</i>	Cameroon	Silica	V. Plana 80 (E)
<i>Begonia capillipes</i>	Wageningen	<i>Tetraphila</i>	Africa	Living	V. Plana 65 (GL 004 079 97) (E)
<i>Begonia cavallyensis</i>	J.J.F.E. de Wilde	<i>Tetraphila</i>	Liberia	Silica	J.J.F.E. de Wilde 3397 (WAG)
<i>Begonia cf. baccata</i>	A. Gascoigne	<i>Baccabegonia</i>	São Tomé	Silica	A. Gascoigne 016 (E)
<i>Begonia cf. komoensis</i>	Wageningen	<i>Tetraphila</i>	Africa	Living	V. Plana 64 (GL 024 079 97) (E)
<i>Begonia cf. komoensis</i>	Wageningen	<i>Tetraphila</i>	Africa	Silica	V. Plana 66 (GL 003 079 97) (E)
<i>Begonia comorensis</i>	Wageningen	<i>Meziera</i>	Madagascar	Silica	P99/04 (Rochefort)
<i>Begonia convolvulacea</i>	Unknown	<i>Wagneria</i>	America	Living	L. Forrest 168 (GL 001 093 79) (E)
<i>Begonia crassirostris</i>	Unknown	<i>Sphenanthera</i>	Asia	Living	L. Forrest 109 (GL 007 079 97) (E)
<i>Begonia dewildei</i>	Unknown	<i>Scutobegonia</i>	Africa	Living	L. Forrest 208 (GL 001 041 97) (E)
<i>Begonia dregei</i>	T. McLellan	<i>Augustia</i>	South Africa	Silica	T. McLellan 415 (E)

<i>Begonia duncan-thomasii</i>	Wageningen	<i>Loasibegonia</i>	Africa	Living	L. Forrest 206 (GL 009 079 97) (E)
<i>Begonia ebolowensis</i>	Wageningen	<i>Tetraphila</i>	Africa	Silica	P99/02 (Rochefort)
<i>Begonia eleagnifolia</i>	Wageningen	<i>Tetraphila</i>	Africa	Living	V. Plana 60 (GL 010 079 97) (E)
<i>Begonia eminii</i>	Wageningen	<i>Tetraphila</i>	Africa	Living	V. Plana 70 (GL 015 079 97) (E)
<i>Begonia engleri</i>	M. Hughes	<i>Rostrobegonia</i>	Tanzania	Living	L. Forrest 236 (E 1998 2762) (E)
<i>Begonia failax</i> (<i>B. malabarica</i>)	Unknown	<i>New section?</i>	Asia	Living	L. Forrest 288 (GL 002 018 96) (E)
<i>Begonia floccifera</i>	Unknown	<i>Reichenheimia</i>	Asia	Living	L. Forrest 238 (GL 030 099 89) (E)
<i>Begonia francoisii</i>	Unknown	<i>Quadrilobaria</i>	Madagascar	Living	L. Forrest 212 (GL 002 064 97) (E)
<i>Begonia furfuracea</i>	V. Plana	<i>Tetraphila</i>	Cameroon	Silica	V. Plana 93 (E)
<i>Begonia fusialata</i>	V. Plana	<i>Tetraphila</i>	Cameroon	Silica	V. Plana 100 (E)
<i>Begonia gabonensis</i>	Wageningen	<i>Tetraphila</i>	Gabon	Living	V. Plana 58 (GL 017 079 97) (E)
<i>Begonia goudotii</i>	V. Plana	<i>Quadrilobaria</i>	Madagascar	Living	V. Plana 120 (E)
<i>Begonia herbacea</i>	M. Tebbitt	<i>Trachelocarpus</i>	America	Living	L. Forrest 163 (E 1973 1857) (E)
<i>Begonia hirsutula</i>	Wageningen	<i>Scutobegonia</i>	Africa	Living	L. Forrest 270 (GL 020 079 97) (E)
<i>Begonia holtonia</i>	Unknown	<i>Ruizopavonia</i>	America	Living	L. Forrest 152 (GL 011 129 84) (E)
<i>Begonia homonyma</i>	T. McLellan	<i>Augustia</i>	E. Cape, South Africa	Living	T. McLellan 315 (E)
<i>Begonia horicola</i>	Wageningen	<i>Tetraphila</i>	Africa	Living	V. Plana 71 (GL 021 079 97) (E)
<i>Begonia incarnata</i>	Unknown	<i>Knesbeckia</i>	America	Living	L. Forrest 162 (GL 011 089 95) (E)
<i>Begonia isalensis</i>	V. Plana	<i>Quadrilobaria</i>	Madagascar	Silica	Sieder s.n. (E)
<i>Begonia iucunda</i>	J.J.F.E. de Wilde	<i>Chasmophila</i>	Africa	Silica	De Wilde 11033 (WAG)
<i>Begonia johnstonii</i>	M. Hughes	<i>Rostrobegonia</i>	Africa	Living	L. Forrest 235 (E 1999 0653) (E)
<i>Begonia kifuluana</i>	Wageningen	<i>Tetraphila</i>	Africa	Living	V. Plana 61 (GL 023 079 97) (E)
<i>Begonia komoensis</i>	Wageningen	<i>Tetraphila</i>	Africa	Living	V. Plana 64 (GL 024 079 97) (E)
<i>Begonia letestui</i>	Wageningen	<i>Tetraphila</i>	Gabon	Silica	Arends, Louis & de Wilde 500 (WAG)
<i>Begonia letouzeyi</i>	Wageningen	<i>Loasibegonia</i>	Africa	Living	L. Forrest 207 (GL 026 079 97) (E)
<i>Begonia lobata</i>	Unknown	<i>Pritzelia</i>	America	Living	L. Forrest 174 (GL 020 167 95) (E)
<i>Begonia longifolia</i>	L. Forrest	<i>Sphenanthera</i>	China	Living	L. Forrest 28 (E)
<i>Begonia longipetiolata</i> 3	V. Plana	<i>Tetraphila</i>	Cameroon	Silica	V. Plana 105 (E)
<i>Begonia longipetiolata</i> 1	Wageningen	<i>Tetraphila</i>	Africa	Living	V. Plana 72 (GL 028 079 97) (E)
<i>Begonia longipetiolata</i> 2	Wageningen	<i>Tetraphila</i>	Africa	Silica	P99/01 (Rochefort)
<i>Begonia loranthoides</i> 1	Wageningen	<i>Tetraphila</i>	Africa	Silica	V. Plana 62 (GL 029 079 97) (E)
<i>Begonia luxurians</i>	RBGE Plant	<i>Scheidweileria</i>	America	Living	L. Forrest 179 (E 1968 5494) (E)
<i>Begonia macrocarpa</i>	Ident. Group				
<i>Begonia madecassa</i>	V. Plana	<i>Tetraphila</i>	Cameroon	Silica	V. Plana 104 (E)
<i>Begonia mananjabensis</i>	Wageningen	<i>Nerviaplacentaria</i>	Madagascar	Living	L. Forrest 211 (GL 003 064 97) (E)
	Unknown	<i>Quadrilobaria</i>	Madagascar	Living	GL 004 064 97 (no voucher†)

<i>Begonia manii</i> 1	Wageningen	<i>Tetraphila</i>	Africa	Living	V. Plana 63 (GL 032 079 97) (E)
<i>Begonia masoniana</i>	L. Forrest	<i>Coelocentrum</i>	Asia	Living	L. Forrest 123 (E 1998 0074) (E)
<i>Begonia meyeri-johannis</i>	Wageningen	<i>Meziera</i>	Africa	Living	L. Forrest 214 (GL 002 041 97) (E)
<i>Begonia molleri</i>	Wageningen	<i>Tetraphila</i>	São Tomé	Living	V. Plana 68 (GL 038 079 97) (E)
<i>Begonia nana</i>	V. Plana	<i>Erminea</i>	Madagascar	Silica	M. Moeller 9865 (E)
<i>Begonia nossibeana</i>	Unknown	<i>Quadrilobaria</i>	Madagascar	Living	GL 007 064 97 (no voucherf)
<i>Begonia obliqua</i>	Unknown	<i>Begonia</i>	America	Living	L. Forrest 160 (GL 005 105 91) (E)
<i>Begonia oxyanthera</i>	V. Plana	<i>Tetraphila</i>	Cameroon	Silica	D. Harris 6735 (Yaounde, E)
<i>Begonia oxyloba</i> 1	M. Hughes	<i>Meziera</i>	Africa	Living	M. Hughes s.n. (L. Forrest 279) (E)
<i>Begonia oxyloba</i> 2	V. Plana	<i>Meziera</i>	Cameroon	Silica	D. Harris 6734 (Yaounde, E)
<i>Begonia palmata</i>	L. Forrest	<i>Platycentrum</i>	Asia	Silica	L. Forrest 13 (E)
<i>Begonia poculifera</i> 1	V. Plana	<i>Squamibegonia</i>	Africa	Silica	D. Harris 6729 (Yaounde, E)
<i>Begonia polygonoides</i>	W. van der Burg	<i>Tetraphila</i>	Ivory Coast	Living	W.J. van der Burg 144 (WAG)
<i>Begonia potamophila</i>	Wageningen	<i>Loasibegonia</i>	Africa	Living	L. Forrest 201 (GL 042 097 97) (E)
<i>Begonia preusii</i>	V. Plana	<i>Tetraphila</i>	Cameroon	Silica	V. Plana 98 (E)
<i>Begonia prismatocarpa</i>	V. Plana	<i>Loasibegonia</i>	Africa	Living	L. Forrest 202 (E 1972 2267) (E)
<i>Begonia quadrilata</i>	Wageningen	<i>Loasibegonia</i>	Africa	Living	L. Forrest 204 (GL 055 07997) (E)
<i>Begonia loranthoides</i> 2	Wageningen	<i>Tetraphila</i>	Africa	Living	V. Plana 62 (GL 001 086 80) (E)
<i>Begonia roxburghii</i>	M. Tebbitt	<i>Sphenanthera</i>	Asia	Living	L. Forrest 103 (GL 004 093 79) (E)
<i>Begonia salaziensis</i>	Unknown	<i>Meziera</i>	Africa	Silica	K 1986 412 (E)
<i>Begonia scapigera</i>	Wageningen	<i>Loasibegonia</i>	Africa	Living	L. Forrest 287 (GL 002 057 96) (E)
<i>Begonia socotrana</i>	M. Hughes	<i>Peltaugustia</i>	Socotra	Living	M. Hughes 41 (E)
<i>Begonia solananthera</i>	Unknown	<i>Solananthera</i>	America	Living	L. Forrest 150 (GL 020 123 70) (E)
<i>Begonia</i> sp. nov.	V. Plana	<i>Erminea</i>	Madagascar	Silica	W. Baker, 1011K (E, K)
<i>Begonia squamulosa</i>	Wageningen	<i>Tetraphila</i>	Africa	Silica	P99/03 (Rocheport)
<i>Begonia squamulosa</i>	V. Plana	<i>Tetraphila</i>	Cameroon	Silica	V. Plana 79 (E)
<i>Begonia subalpestris</i>	A. Gascoigne	<i>Tetraphila</i>	São Tomé	Silica	A. Gascoigne 053 (E)
<i>Begonia subscutata</i>	Wageningen	<i>Tetraphila</i>	Africa	Living	V. Plana 69 (E)
<i>Begonia sutherlandii</i>	Unknown	<i>Augustia</i>	Africa	Living	L. Forrest 197 (E 1971 1552) (E)
<i>Begonia thomeana</i>	Wageningen	<i>Cristasemen</i>	Africa	Living	L. Forrest 199 (GL 054 079 97) (E)
<i>Begonia ulmifolia</i>	M. Sands	<i>Donaldia</i>	America	Living	L. Forrest 169 (E 1968 2869) (E)
<i>Begonia violifolia</i>	Unknown	<i>Weilbachia</i>	America	Living	L. Forrest 181 (GL 004 055 87) (E)
<i>Datisca cannabina</i>	C. Alexander	-	-	Living	L. Forrest 237 (E 1984 1126)
<i>Datisca glomerata</i>	S. Swensen	-	-	-	From Swensen
<i>Hillebrandia sandwicensis</i>	L. Brouillet	-	Hawaii	Silica	Montreal Botanic Garden 2960 57
<i>Symbegonia sanguinea</i>	Unknown	<i>Symbegonia</i>	New Guinea	Living	L. Forrest 142 (GL 003 127 93) (E)

APPENDIX 2 Aligned matrix for the *trnL* intron region (Chapter 2).

	10	20	30	40	50	60	70	80	90	100]
B. <i>baccata</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>amplai</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>amplai2</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>poculifer</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>bonushenricus</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>loranthoides1</i>	?? ? ? TGATAACTTTCAAATTCAGAGAA?C	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>ebolowensis</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>ambohonensis</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>kisuluana</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>subscutata</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>komoensis</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>oxyanthera</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>gabonensis</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>subalpestris</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>longipetiolata1</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>longipetiolata3</i>	AAGTGAT?GCTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>eleaegmifolia</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>horticola</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>emini</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>capillipes</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>manil</i>	?? ? ? TGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>furfuracea</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>fusialata</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>preusii</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>polygonoides</i>	?? ? ? TGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>molleri</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>meyeri</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>oxylobal</i>	AAGTGATAACTTTCCRRRTTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>salaziensis</i>	G?TGATAA?K?YCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>comorensis</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>betsimesaraka</i>	AAGTGAT?RCTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[87]
B. <i>nana</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[86]
B. <i>isalensis</i>	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCCTGAGCCAAATCCC						[85]


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[      10      20      30      40      50      60      70      80      90     100]
[      .      .      .      .      .      .      .      .      .      .]
H. sandwicensis AAGTGATAACTTTTCAAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCCTGAGCCAAATCCC-----GGTTTTCCGAAAAAC [86]
D. cannabina   TTC?ATTGCRGAKAAACCCAGAGAAAC-CCCAGAAGAATTAATAAAC-TGGGCAATCCTGAGCCAAATCCC-----TGTTTTCCGAAAAAC [87]
D. glomerata   AAGTGATCACTTTTCAAAATTCAGAGAAAC-CCCAGGC-AATTAATAAAC-TGGGCAATCCTGAGCCAAATCCC-----TGTTTTCCGAAAAAC [86]
Coriaria_V41*  GAGTGATAACTTTTCAAAATTCAGAGAAAC-CCCTGGC-AATTAATAAAC-TGGGCAATCCTGAGCCAAATCCC-----TGTTTTCCGAAAAAC [85]
Coriaria_jap*  GAGTGATAACTTTTCAAAATTCAGAGAAAC-CCCTGGC-AATTAATAAAC-TGGGCAATCCTGAGCCAAATCCC-----TGTTTTCCGAAAAAC [86]
Coriaria_mic*  GAGTGATAACTTTTCAAAATTCAGAGAAAC-CCCTGGC-AATTAATAAAC-TGGGCAATCCTGAGCCAAATCCC-----TGTTTTCCGAAAAAC [86]
Coriaria_ru*   GAGTGATAACTTTTCAAAATTCAGAGAAAC-CCCTGGC-AATTAATAAAC-TGGGCAATCCTGAGCCAAATCCC-----TGTTTTCCGAAAAAC [86]

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Base pair positions 374-434 were excluded from all analyses. Alignment gaps are indicated by ‘.’. Recoded indels are absence/ presence characters and are represented by base-pair positions 28, 36, 47, 71, 90, 105, 119, 129, 135, 136, 143, 196, 205, 222, 223, 228, 240, 242, 266, 268, 291, 300, 304, 319, 324, 325, 344, 345, 450, 478, 481, 483, 556, 577, 608, 613, 633, and 668 (C=0 and A=1). Species marked with an asterisk were excluded from all analyses, but left in the alignment for future work.

	110	120	130	140	150	160	170	180	190	200	
B. <i>baccata</i>	TAATC--GGTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>amplal</i>	TAATC--AGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>amplal2</i>	TAATC--AGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>poculiferal</i>	TAATC--AGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>bonushenicus</i>	TAATC--AGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>loranthoides1</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>ebolowensis</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>annobonensis1</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>subscutata</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>komoensis</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>oxyanthera</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>gabonensis</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>subalpestris</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>longipetiolata1</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[178]								
B. <i>longipetiolata3</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>eleagnifolia</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>horticola</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>emini</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>capillipes</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>manii</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>furfuracea</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>fusialata</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>preysonii</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>polygonoides</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>molleri</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>meyerijohannis</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>oxylobal</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>salaziensis</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[176]								
B. <i>comorensis</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[176]								
B. <i>betsimesaraka</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[178]								
B. <i>nana</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>isalensis</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[176]								
B. <i>nossibe</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>mananjabensis</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[179]								
B. <i>francoisii</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>madecassa</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>ankaranensis</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>marnieri</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>goudotii</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[175]								
B. <i>bogneri</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>sp.nov.1</i>	TAATC--GGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[177]								
B. <i>quadrialata</i>	TAATAGTGGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[179]								
B. <i>scapigera</i>	TAATAGTGGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[179]								
B. <i>duncanthomasii</i>	TAATAGTGGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[178]								
B. <i>letouzey</i>	TAATAGTGGTTTTCGAAAGACAAGAAACGAAAGAAAACAAAAC-----	AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAAACAATGGAGTTC--GA	[179]								

	110	120	130	140	150	160	170	180	190	200	
[
[
B. prismatocarpa	TAATAGTGGTTTCGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[179]
B. dewildei	TAATAGTGGTTTCGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[179]
B. asplenifolia	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. potamophila	TAATAGTGGTTTCGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[179]
B. iucunda	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. thomeana	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. engleri	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. johnstonii	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. homonyma	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. socotrana	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. dregei	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. sutherlandii	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. solanathera	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. hirsutula	TAATAGTGGTTTCGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[179]
B. ulmiifolia	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. holtonis	TAATC--GATTTTCGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. herbacea	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[182]
B. lobata	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[183]
B. luxurians1	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[183]
B. luxurians2	T-GTC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[181]
B. obliqua	TAATC--GATTTTCGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[176]
B. violifolia	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. incarnata	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. convolvulacea	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[178]
B. angularis	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[183]
B. amphioxus	TAA?C--GG?TTCG?AAGC?AG?ACGGAGAAAACAAAAC	-----AGG?TAGGTGCAG?GA?TCAATGGAAGCT?TTC	CAAAATGGAGTTC	--GA							[176]
B. crassirostris	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. masoniana	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. aequata	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[178]
B. longifolia	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. roxburghii	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. palmata	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
S. sanguinea	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[183]
B. fallax	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
B. floccifera	TAATC--GATTTTCGAAAGACTGAAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[177]
H. sandwicensis	TAATC--GGTTTTGAAAGACACAGAACGAAAGAAAACAAAAC	-----AGGATAGGTGCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC	--GA							[166]
D. glomerata	TAAAC--GGTTTCGAAAGC-----CGAAGAAAAC?	-----AGGGTAGGTGCAGAGACTCAATGGAAGCTGTTT	TAACAAATAGAGTTC	--GA							[165]
Coriaria_V41	TAAAC--GGTTTCGAAAGC-----CGAAGAAAAC?	-----AGGGTAGGTGCAGAGACTCAATGGAAGCTGTTT	TAACAAATGGAGTTC	--GA							[164]
Coriaria_jap	TAAAC--GGTTTCGAAAGC-----CGAAGAAAAC?	-----AGGGTAGGTGCAGAGACTCAATGGAAGCTGTTT	TAACAAATGGAGTTC	--GA							[165]
Coriaria_mic	TAAAC--GGTTTCGAAAGC-----CGAAGAAAAC	-----AAAAAGGTAGGTGCAGAGACTCAATGGAAGCTGTT	TAACAAATGGAGTTC	--GA							[170]
Coriaria_ru	TAAAC--GGTTTCGAAAGC-----CGAAGAAAAC?	-----AGGGTAGGTGCAGAGACTCAATGGAAGCTGTTT	TAACAAATGGAGTTC	--GA							[165]

	210	220	230	240	250	260	270	280	290	300
B. baccata	CTGCC	---	---	---	---	---	---	---	---	[196]
B. amplal	CTGCC	---	---	---	---	---	---	---	---	[196]
B. amplal2	CTGCC	---	---	---	---	---	---	---	---	[196]
B. poculiferal	CTGCC	---	---	---	---	---	---	---	---	[196]
B. bonushenricus	CTGCC	---	---	---	---	---	---	---	---	[196]
B. loranthoides1	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. ebolowensis	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. annobonensis1	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. kisuluana	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. subscutata	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[267]
B. kmoensis	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. oxyanthera	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. gabonensis	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. subalpestris	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. longipetiolatal	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[265]
B. longipetiolatal3	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. eleaegnifolia	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. horticola	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. eminii	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. capillipes	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. manii1	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. furfuracea	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. fusialata	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. preusii	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. polygonooides	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. molleri	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. meyerijohannis	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. oxylobal	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. salaziensis	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[263]
B. comorensis	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. betsimesaraka	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[265]
B. nana	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. isalensis	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[263]
B. nossibe	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. mananjabensis	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. francoisii	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[266]
B. madecassa	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. markaransensis	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. ankranieri	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. goudotii	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. bogneri	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[262]
B. sp. nov. 1	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[264]
B. quadrialata	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[266]
B. scapigera	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[271]
B. duncanthomasii	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[265]
B. letouzey	CTGCAGTTGCGTTAGTAAAGGCA	---	---	---	---	---	---	---	---	[266]

[210 220 230 240 250 260 270 280 290 300] .)

B.prismatocarpa [266] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAAAGAAAAAACCCTATAAATACATAGA

B.dewildei [225] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATC-----?---?-----AATACATAGA

B.asplenifolia [264] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.potamophila [266] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.iucunda [264] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.thomeana [264] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.engleri [264] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.johnstonii [264] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.homonymia [270] TTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.socotrana [270] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.dregei [270] TTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.sutherlandii [270] TTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.solananthera [270] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.hirsutula [266] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.ulmiifolia [264] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.holtonis [275] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.herbacea [275] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.lobata [270] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.luxurians1 [270] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.luxurians2 [270] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.obliqua [274] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.violifolia [270] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.incarnata [270] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.convolvulacea [265] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.angularis [269] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.amphioxus [270] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.crassirostris [270] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.masoniana [270] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.aequata [271] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.longifolia [270] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.roxburghii [270] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.palmata [270] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

S.sanguinea [278] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.fallax [264] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

B.floccifera [270] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

H.sandwicensis [256] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

D.cannabina [248] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

D.glomerata [246] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

Coriaria_V41 [246] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

Coriaria_jap [247] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

Coriaria_mic [252] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

Coriaria_ru [247] CTCGAGTTGCGTTAGTAAAGGCA---?---AATCCAAATACCTTTCTAACGAAACTCCAGAAAGAGC---ATGAAAGAGAAAAAACCCTATAAATACATAGA

[310	320	330	340	350	360	370	380	390	400]
[---	---	---	---	---	---	---	---	---	---
B. baccata	---?---	---??---	---??---	---??---	---??---	---??---	---??---	---??---	---??---	[202]
B. amplal	---?---	---??---	---??---	---??---	---??---	---??---	---??---	---??---	---??---	[202]
B. amplal2	---?---	---??---	---??---	---??---	---??---	---??---	---??---	---??---	---??---	[202]
B. poculiferal	---?---	---??---	---??---	---??---	---??---	---??---	---??---	---??---	---??---	[202]
B. bonushenricus	---?---	---??---	---??---	---??---	---??---	---??---	---??---	---??---	---??---	[202]
B. loranthoides1	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---TAGTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[325]
B. ebolowensis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[325]
B. annobonensis1	GCAATACG	---TAAFC	---AGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[320]
B. kisuluana	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GACGACTCGAAATGTTTTTTT	---	---	---	---	---	[318]
B. subscutata	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[331]
B. komoensis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[326]
B. oxyanthera	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[325]
B. gabonensis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[325]
B. subalpestris	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[325]
B. longipetiolata1	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[325]
B. longipetiolata3	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[321]
B. eleagnifolia	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[325]
B. horticola	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[326]
B. eminii	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[325]
B. capillipes	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[318]
B. manuil	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[326]
B. furfuracea	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[318]
B. fusialata	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[325]
B. preusii	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[318]
B. polygonoides	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[325]
B. molleri	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[325]
B. meyerijohannis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[325]
B. oxylobal	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[325]
B. salaziensis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[326]
B. comorensis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[326]
B. betsimesaraka	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[326]
B. nana	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[325]
B. isalensis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[325]
B. nossibe	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[326]
B. mananjabensis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[328]
B. francosisi	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[326]
B. madercassa	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[326]
B. ankaranensis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[326]
B. marnieri	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[326]
B. goudotii	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[326]
B. bogneri	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[323]
B. sp. nov. 1	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[329]
B. quadrialata	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[327]
B. scapigera	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[332]
B. duncanthomasi	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[326]
B. letouzey	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAAATGTTTTTTT	---	---	---	---	---	[327]

[410	420	430	440	450	460	470	480	490	500]
[-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
B. baccata	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTAAAAGTTGAAA [219]
B. amplal	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTAAAAGTTGAAA [219]
B. amplal2	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTAAAAGTTGAAA [219]
B. poculiferal	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTAAAAGTTGAAA [219]
B. bonushenricus	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTAAAAGTTGAAA [219]
B. loranthoidesi	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [357]
B. ebolowensis	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [388]
B. annobonensis	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [381]
B. kisuluana	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [381]
B. subscutata	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [394]
B. komoensis	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [389]
B. oxyanthera	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [388]
B. gabonensis	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [388]
B. subalpestris	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [388]
B. longipetiolatal	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [386]
B. longipetiolatal3	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [374]
B. eleaegnifolia	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [386]
B. horticola	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [389]
B. eminii	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [388]
B. capillipes	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [381]
B. manii	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [389]
B. furfuracea	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [381]
B. fusialata	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [388]
B. preusii	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [381]
B. polygonoides	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [388]
B. molleri	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [388]
B. meyerijohannis	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [391]
B. oxylobal	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [391]
B. salaziensis	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [387]
B. comorensis	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [387]
B. betsimesaraka	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [387]
B. nana	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [386]
B. isalensis	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [386]
B. nossibea	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [386]
B. mananjabensis	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [389]
B. francoisii	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [387]
B. madecassa	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [387]
B. ankaranensis	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [387]
B. marnieri	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [387]
B. goudotii	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [387]
B. bogneri	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [384]
B. sp. nov. 1	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [390]
B. quadrialata	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [388]
B. scapigera	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [393]
B. duncanthomasii	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [387]
B. letouzey	-----	-----	-----	-----	-----	-----	-----	-----	-----	CTTCAAAGTTGAAA [388]

	410	420	430	440	450	460	470	480	490	500
B. prismatocarpa	---	---	---	---	---	---	---	---	---	[388]
B. dewildei	---	---	---	---	---	---	---	---	---	[347]
B. asplenifolia	---	---	---	---	---	---	---	---	---	[386]
B. potanophila	---	---	---	---	---	---	---	---	---	[388]
B. iucunda	---	---	---	---	---	---	---	---	---	[385]
B. thomeana	---	---	---	---	---	---	---	---	---	[386]
B. engleri	---	---	---	---	---	---	---	---	---	[381]
B. johnstonii	---	---	---	---	---	---	---	---	---	[381]
B. homonyma	---	---	---	---	---	---	---	---	---	[392]
B. socotrana	---	---	---	---	---	---	---	---	---	[392]
B. dregei	---	---	---	---	---	---	---	---	---	[392]
B. sutherlandii	---	---	---	---	---	---	---	---	---	[398]
B. solananchera	---	---	---	---	---	---	---	---	---	[393]
B. hirsutula	---	---	---	---	---	---	---	---	---	[388]
B. ulmiifolia	---	---	---	---	---	---	---	---	---	[391]
B. holtonis	---	---	---	---	---	---	---	---	---	[392]
B. herbacea	---	---	---	---	---	---	---	---	---	[403]
B. lobata	---	---	---	---	---	---	---	---	---	[392]
B. luxurians1	---	---	---	---	---	---	---	---	---	[392]
B. luxurians2	---	---	---	---	---	---	---	---	---	[390]
B. obliqua	---	---	---	---	---	---	---	---	---	[396]
B. violifolia	---	---	---	---	---	---	---	---	---	[394]
B. incarnata	---	---	---	---	---	---	---	---	---	[394]
B. convolvulacea	---	---	---	---	---	---	---	---	---	[392]
B. angularis	---	---	---	---	---	---	---	---	---	[392]
B. amphioxus	---	---	---	---	---	---	---	---	---	[391]
B. crassirostris	---	---	---	---	---	---	---	---	---	[391]
B. masoniana	---	---	---	---	---	---	---	---	---	[392]
B. aequata	---	---	---	---	---	---	---	---	---	[393]
B. longifolia	---	---	---	---	---	---	---	---	---	[392]
B. roxburghii	---	---	---	---	---	---	---	---	---	[392]
B. palmata	---	---	---	---	---	---	---	---	---	[392]
S. sanguinea	---	---	---	---	---	---	---	---	---	[400]
B. fallax	---	---	---	---	---	---	---	---	---	[386]
B. floccifera	---	---	---	---	---	---	---	---	---	[392]
H. sandwicensis	---	---	---	---	---	---	---	---	---	[266]
D. cannabina	TCAAA	---	---	---	---	---	---	---	---	[379]
D. glomerata	TCAAA	---	---	---	---	---	---	---	---	[384]
Coriaria_V41	TAAAA	TTTTT	TATAGAAA	TATAGAAA	TATAGAAA	TATAGAAA	TATAGAAA	TATAGAAA	TC	[421]
Coriaria_jap	TAAAA	TTTTT	TATAGAAA	TATAGAAA	TATAGAAA	TATAGAAA	TATAGAAA	TATAGAAA	TC	[428]
Coriaria_mic	TAAAA	TTTTT	TATAGAAA	TATAGAAA	TATAGAAA	TATAGAAA	TATAGAAA	TATAGAAA	TC	[424]
Coriaria_ru	TAAAA	TTTTT	TATAGAAA	TATAGAAA	TATAGAAA	TATAGAAA	TATAGAAA	TATAGAAA	TC	[420]

	610	620	630	640	650	660	670]
B. baccata	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[358]
B. amplal	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[358]
B. amplal2	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[358]
B. pocoliferal	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[358]
B. bonushenricus	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[496]
B. loranthoides1	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[520]
B. ebolowensis	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[520]
B. annobonensis1	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[520]
B. kisuluana	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[520]
B. subscutata	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[520]
B. kemoensis	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[527]
B. oxyanthera	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[527]
B. gabonensis	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[528]
B. subalpestris	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[527]
B. longipetiolatal	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[525]
B. longipetiolata3	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[512]
B. elesegnifolia	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[525]
B. horticola	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[528]
B. emini	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[529]
B. capillipes	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[519]
B. manii	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[528]
B. furfuracea	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[520]
B. fusialata	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[528]
B. preusii	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[520]
B. polygonooides	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[528]
B. molleri	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[528]
B. meyerijohannis	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[530]
B. oxylobal	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[530]
B. salaziensis	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[526]
B. comorensis	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[526]
B. betsimesaraka	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[526]
B. nana	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[525]
B. isalensis	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[525]
B. nossibea	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[525]
B. mananjabensis	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[528]
B. francoisii	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[526]
B. madecassa	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[526]
B. ankaranensis	GATAGAGC--TCACCATTCTACATGTCAAATACC	-----	-----	-----	-----	GGACAAAAAC-T	[526]
B. marnieri	GATAGAGC--TCACCATTCTACATGTC??FC	-----	-----	-----	-----	??????????	[527]
B. goudotii	GATAGAGC--TCACCATTCTACATGTC??FC	-----	-----	-----	-----	??????????	[527]
B. bogneri	GATAGAGC--TCACCATTCTACATGTC??FC	-----	-----	-----	-----	??????????	[527]
B. sp. nov. 1	GATAGAGC--TCACCATTCTACATGTC??FC	-----	-----	-----	-----	??????????	[529]
B. quadrialata	GATAGAGC--TCACCATTCTACATGTC??FC	-----	-----	-----	-----	??????????	[527]
B. scapigera	GATAGAGC--TCACCATTCTACATGTC??FC	-----	-----	-----	-----	??????????	[532]
B. duncanthomasii	GATAGAGC--TCACCATTCTACATGTC??FC	-----	-----	-----	-----	??????????	[526]
B. letouzey	GATAGAGC--TCACCATTCTACATGTC??FC	-----	-----	-----	-----	??????????	[527]

	610	620	630	640	650	660	670
B. prismatocarpa	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[527]
B. dewildei	GATAGAGC--TCACCATTCTAC?TGCAATACC					GGACAAAAAC-T	[486]
B. asplenifolia	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[525]
B. potamophila	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[527]
B. iucunda	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[524]
B. thomeana	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[525]
B. engleri	GATAGAGC--TCACCATTCTACATGTCAAATACC					AGACAAAAAC-T	[520]
B. johnstonii	GATAGAGC--TCACCATTCTACATGTCAAATACC					AGAC??-?-T	[521]
B. homonyma	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[531]
B. dregei	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[531]
B. sutherlandii	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[531]
B. solananthera	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[537]
B. hirsutula	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[532]
B. ulmifolia	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[527]
B. holtonis	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[530]
B. herbacea	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[531]
B. lobata	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-C	[542]
B. luxurians1	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[531]
B. luxurians2	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[529]
B. obliqua	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[535]
B. violifolia	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[533]
B. incarnata	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-C	[533]
B. convolvulacea	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[556]
B. angularis	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[531]
B. amphioxus	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[530]
B. crassirostris	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[531]
B. masoniana	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[531]
B. aequata	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[532]
B. longifolia	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[531]
B. roxburghii	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[531]
B. palmata	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[531]
S. sanguinea	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[539]
B. fallax	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[525]
B. floccifera	GATAGAGC--TCACCATTCTACATGTCAAATACC					GGACAAAAAC-T	[531]
H. sandwicensis	G?TAGAGC--TCC-----?-----?-----?						[347]
D. cannabina	GATAGAGC--TCACCATTCTACATGTCAAATACC					CGACAAAAAC-T	[516]
D. glomerata	GATAGAGC--TCACCATTCTACATGTCAAATACC					CGACAAAAAC-T	[521]
Coriaria_V41	GATAGAGC--TCACCATTCTACATGTCAAATACC					TGACAAAAAC-T	[558]
Coriaria_jap	GATAGAGC--TCACCATTCTACATGTCAAATACC					TGACAAAAAC-T	[565]
Coriaria_mic	GATAGAGC--TCACCATTCTACATGTCAAATACC					TGACAAAAAC-T	[561]
Coriaria_ru	GATAGAGC--TCACCATTCTACATGTCAAATACC					TGACAAAAAC-T	[557]

APPENDIX 3 Seventy-seven taxon aligned matrix for *trnL* intron and ITS regions (Chapter 3).

	10	20	30	40	50	60	70	80	90	100	
	trnL intron										
	↑										
B. baccata	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. amplai	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	TAAA	[86]		
B. poculiferai	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. bonushenricus	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. loranthoides1	??TGATAACTTTCAAATTCAGAGAA?C	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. ebolowensis	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. kisuluana	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. subscutata	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. oxyanthera	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. gabonensis	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. longipetiolatal	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	GAAA	[87]		
B. horticola	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. eminii	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. cavallyensis	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. capillipes	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. manii1	??TGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. fusialata	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. preusii	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. polygonoides	??TGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. molleri	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. subalpestris	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. furfuracea	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATGAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. salaziensis	G?GTGATAA?K?YCAAAATTCAGAGAAC	CCCTGGC	AATAAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. comorensis	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATAAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. nossibeae	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATAAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. mananjabensis	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATAAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. marineri	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATAAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. francocassa	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATAAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. ankaranensis	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATAAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[86]		
B. isalensis	AAGTGATAACTTTCAAATTCAGAGAAC	CCCTGGC	AATAAAAAAC	TGGGCAATCTGAGCCAAATCCC	-----	GGTTTTCCGAAAAAC	-----	CAAA	[85]		

[10 20 30 40 50 60 70 80 90 100]

trnL intron

B. bogneri AAGTGATAACTTTCAAATTCAGAGAA-?-CCCTGGC-AAT-AAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [84]
B. nana AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATAAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. sp.nov.1 AAGTGAT-ACTTTCAAATTCAGAGAAAACCCCTGGC-AATAAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. betsimesaraka AAGTGAT?RCTTTCAAATTCAGAGAAAC-CCCTGGC-AATAAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [87]
B. quadrialata AAGTGATAACTTTCAAATTCAGAGAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. scapigera AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. duncanthomasi B. letouzey AAGTGATAACTTTCAAATTCAGAGAAAC-CC-TGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [85]
B. prismatocarpa AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. dewilidei AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. asplenifolia AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. potanophila AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. thomeana AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. iucunda AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. meyerijohannis AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. engleri AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. annobonensis AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. johnstonii AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. homonyma AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. socotrana AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. dregii AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. sutherlandii AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. solanathera AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. ulmifolia AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. holtonis AAGTGATAAG?GTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. herbacea AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. lobata AAGGTTAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [91]
B. luxurians1 AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [92]
B. obliqua AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [85]
B. violifolia AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. incarnata AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. convolvulacea AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [85]
B. angularis AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [92]
B. amphioxus ?AGT?TAAATTCAAATTCAGAGAAAC-CCCTGGC-GA?GAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [85]
B. crassirostris AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. longifolia AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. masoniana AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. aequata AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [87]
B. rhoxburghi AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. palmata AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
S. sanguinea AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [87]
B. fallax AAGTGATAASWKTCAAATTCAGAGAAAC-CCCTGGC-A?TAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
B. floccifera AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
D. cannabina TTC?ATTGCRGAGKAAACCCAGAGAAAC-CCAGAGAAATTAATAAC-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [87]
D. glomerata AAGTGATAACTTTCAAATTCAGAGAAAC-CCAGGC-AATTAATAAC-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]
H. sandwicensis AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAA-TGGSCAAATCTGAGCCAAATCCC-----GGTTTTCCGAAAAC-----CAA [86]

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[      10      20      30      40      50      60      70      80      90     100]
[      .      .      .      .      .      .      .      .      .      .]
trnL intron  ↑
Coriaria_V41*  GAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATTAATAAAC-TGGCAATCCTGAGCCAA-TCCC-----TGTFTTTCGAAAAC- [85]
Coriaria_jap*  GAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATTAATAAAC-TGGCAATCCTGAGCCAAATCCC-----TGTFTTTCGAAAAC- [86]
Coriaria_mic*  GAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATTAATAAAC-TGGCAATCCTGAGCCAAATCCC-----TGTFTTTCGAAAAC- [86]
Coriaria_ru*  GAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATTAATAAAC-TGGCAATCCTGAGCCAAATCCC-----TGTFTTTCGAAAAC- [86]

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TrnL intron alignment and gap coding are the same as in Appendix 1. Base pair positions of the *trnL* intron 374-434 were removed in all analyses. Base pair regions 697-856 893-894 902-910 921-929 951-997 1174-1340 1369-1372 1394-1398 1410-1415 1436-1444 1456-1513 1519-1576 of the ITS1 and ITS2 regions show alignment ambiguity and were removed from some analyses. Alignment gaps are indicated by '-'. Species marked with an asterisk were excluded from all analyses, but left in the alignment for future work.

l . 110 120 130 140 150 160 170 180 190 200] [177]
 [B. baccata TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. amplal TAATC--AGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. poculiferal TAATC--AGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. bonushenricus TAATC--AGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. loranthoides1 TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. eboluwensis TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. kisuluana TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. subscutata TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. oxyanthera TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. gabonensis TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. longipetiolatal TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [178]
 B. horticola TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. emirii TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. cavallipensis TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. capillipes TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. manii1 TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. fusialata TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. presui TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. polyonoides TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. mollieri TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. subalpestris TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. furfuracea TAATC--GGTTTCGAGAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. salaziensis TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [176]
 B. comorensis TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [176]
 B. nossibea TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. mananjabensis TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. marnieri TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. francoisi TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. madecassa TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. isalensis TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. bogneri TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [176]
 B. nana TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [175]
 B. sp. nov. 1 TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. betsimesaraka TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. quadrialata TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [178]
 B. scapigera TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [179]
 B. duncanthomasii TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [178]
 B. prismatocarpa TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [179]
 B. dewildei TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [179]
 B. asplenifolia TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. potamophila TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [179]
 B. thomeana TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. meyerijohannis TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. engleri TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]
 B. annobonensis1 TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAAAACAAC-----AGGATAGTGCAGAGACTCAATGGAAAGCTGTTCCAAACAAATGGAGTTC--GA [177]

	110	120	130	140	150	160	170	180	190	200	2001
B. johnstonii	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. homonyma	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. socotrana	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. dregei	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. sutherlandii	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. solanathera	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. ulmifolia	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. holtonis	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. herbacea	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[182]						
B. lobata	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[183]						
B. luxurians1	TAGTC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[183]						
B. obliqua	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[176]						
B. violifolia	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. incarnata	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. angularis	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. convolvulacea	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[178]						
B. amphioxus	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[183]						
B. crassirostris	TAA?C--GG?TTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGG?TAGGTCAG?GA?TCAA?TGGAAGCT?TTC?CAACAAAATGGAGTTC	--GA	[176]						
B. longifolia	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. masoniana	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. aequata	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. rhexburghi	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. palmata	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[178]						
B. fallax	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
S. sanguinea	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
B. floccifera	TAATC--GGTTTCGAAAGACAAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
D. cannabina	TAAAC--GGTTTCGAAAGC-----CGAAGAAAAC?	-----	AGGTTAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATAGAGTTC	--GA	[166]						
H. sandwicensis	TAAAC--GGTTTCGAAAGC-----CGAAGAAAAC?	-----	AGGTTAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATAGAGTTC	--GA	[166]						
D. glomerata	TAAAC--GGTTTCGAAAGC-----CGAAGAAAAC?	-----	AGGTTAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATAGAGTTC	--GA	[165]						
Coriaria_V41	TAATC--GATTTTCGAAAGACTAGAACGAAAGAAAACAAAAC	-----	AGGATAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[177]						
Coriaria_jap	TAAAC--GGTTTCGAAAGC-----AGAAGAAAAC?	-----	AGGTTAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[164]						
Coriaria_mic	TAAAC--GGTTTCGAAAGC-----CGAAGAAAAC?	-----	AGGTTAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[165]						
Coriaria_ru	TAAAC--GGTTTCGAAAGC-----CGAAGAAAAC?	-----	AGGTTAGGTCGACAGACTCAATGGAAAGCTGTTCCAAAGAAATGGAGTTC	--GA	[170]						

[110	120	130	140	150	160	170	180	190	200
[CTGCC	---	---	---	---	---	---	---	---	---
	B. baccata	---	---	---	---	---	---	---	---	---
	B. amplal	---	---	---	---	---	---	---	---	---
	B. poculifer	---	---	---	---	---	---	---	---	---
	B. bonushenricus	---	---	---	---	---	---	---	---	---
	B. loranthoides1	---	---	---	---	---	---	---	---	---
	B. ebolowensis	---	---	---	---	---	---	---	---	---
	B. kisuluana	---	---	---	---	---	---	---	---	---
	B. subscutata	---	---	---	---	---	---	---	---	---
	B. oxyanthera	---	---	---	---	---	---	---	---	---
	B. gabonensis	---	---	---	---	---	---	---	---	---
	B. longipetiolatal	---	---	---	---	---	---	---	---	---
	B. horticola	---	---	---	---	---	---	---	---	---
	B. emini	---	---	---	---	---	---	---	---	---
	B. cavallipes	---	---	---	---	---	---	---	---	---
	B. maniil	---	---	---	---	---	---	---	---	---
	B. fusialata	---	---	---	---	---	---	---	---	---
	B. preusii	---	---	---	---	---	---	---	---	---
	B. polygonoides	---	---	---	---	---	---	---	---	---
	B. molleri	---	---	---	---	---	---	---	---	---
	B. subalpestris	---	---	---	---	---	---	---	---	---
	B. furfuracea	---	---	---	---	---	---	---	---	---
	B. salaziensis	---	---	---	---	---	---	---	---	---
	B. comorensis	---	---	---	---	---	---	---	---	---
	B. nossibea	---	---	---	---	---	---	---	---	---
	B. mananjambensis	---	---	---	---	---	---	---	---	---
	B. marnieri	---	---	---	---	---	---	---	---	---
	B. francoisii	---	---	---	---	---	---	---	---	---
	B. madecassa	---	---	---	---	---	---	---	---	---
	B. ankaranensis	---	---	---	---	---	---	---	---	---
	B. isalensis	---	---	---	---	---	---	---	---	---
	B. bogneri	---	---	---	---	---	---	---	---	---
	B. nana	---	---	---	---	---	---	---	---	---
	B. sp. nov. 1	---	---	---	---	---	---	---	---	---
	B. betsimesaraka	---	---	---	---	---	---	---	---	---
	B. quadrialata	---	---	---	---	---	---	---	---	---
	B. scapigera	---	---	---	---	---	---	---	---	---
	B. duncanthomasii	---	---	---	---	---	---	---	---	---
	B. letouzey	---	---	---	---	---	---	---	---	---
	B. prismatocarpa	---	---	---	---	---	---	---	---	---
	B. dewildei	---	---	---	---	---	---	---	---	---
	B. asplenifolia	---	---	---	---	---	---	---	---	---
	B. potamophila	---	---	---	---	---	---	---	---	---
	B. thomeana	---	---	---	---	---	---	---	---	---
	B. iucunda	---	---	---	---	---	---	---	---	---
	B. meyerijohannis	---	---	---	---	---	---	---	---	---
	B. engleri	---	---	---	---	---	---	---	---	---
	B. annobonensis1	---	---	---	---	---	---	---	---	---

[210 220 230 240 250 260 270 280 290 300] .]

B. johnstonii [264] CTGCAGTTGCGTTAGTAAAGGCA----?----AATCCAAATACCTTCCATCGAAACCTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. homonyma [270] TTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. socotrana [270] CTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGAGAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. dregei [270] TTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. solanalandii [270] TTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. solanathera [270] CTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. ulmifolia [264] TTGCAGTTGCGTTAGTAAAGGCA----?----AATCCAAATACCTTCCAGCGAAACTTAGACAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. holtonis [275] CTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. herbacea [270] CTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCATCAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. lobata [275] CTGCAGTTGCGTTAGTAAAGGCA----?----AATCCAAATACCTTCCAGCGAAACTTAGACAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. luxurians1 [270] CTGCAGTTGCGTTAGTAAAGGCA----?----AATCCAAATACCTTCCAGCGAAACTTAGACAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. obliqua [274] CTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. violifolia [270] CTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. incarnata [270] CTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. convolvulacea [265] CTGCAGTTGCGTTAGTAAAGGCA----?----AATCCAAATACCTTCCAGCGAAACTTAGATAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. angularis [270] CTGCAGTTGCGTTAGTAAAGGCA----?----AATCCAAATACCTTCCAGCGAAACTTAGACAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. amphioxus [269] CTG?AGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. crassirostris [270] CTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. longifolia [270] CTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. aequata [270] CTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. rhoxburghi [271] CTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. palmata [270] CTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

S. sanguinea [278] CTGCAGTTGCGTTAGTAAAGGAAATAAAC--GGAATCCAAATACCTTCCAGCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

B. fallax [264] CTGCAGTTGCGTTAGTAAAGGCA----?----AATCCAAATACCTTCCATCGAAACTTAGAAAGAGC-----ATGAAAGAGATAAACCTTATAATACATACA

D. cannabina [248] ATGCAGTTGCGTTAGTAAAGG?C----?----AAATACCTTACAGCGAAACTCAAAAAAAGC-----ATGAAAGAGATAAACCTTATAATACATACA

D. glomerata [247] ATGCAGTTGCGTTAGTAAAGG?C----?----AAATACCTTACAGCGAAACTCAAAAAAAGC-----ATGAAAGAGATAAACCTTATAATACATACA

H. sandwicensis [256] CTGCAGTTGCGTTAGTAAAGGCA----?----AATCCAAATACCTTCCAGCGAAACTCCAGAAAGAGC-----CTGAAAGAGATAAACCTTATC-----?

Coriaria_V41 [246] CTGTAGTTGCGTTAATAAAGG?C----?----AAATACTTTCCATCGAAACTCCAGAAAGAGC-----GGGAAAGATAAACCGTATAATACATACA

Coriaria_jap [247] CTGTAGTTGCGTTAATAAAGG?C----?----AAATACTTTCCATCGAAACTCCAGAAAGAGC-----GGGAAAGATAAACCGTATAATACATACA

Coriaria_mic [252] CTGTAGTTGCGTTAATAAAGG?C----?----AAATACTTTCCATCGAAACTCCAGAAAGAGC-----GGGAAAGATAAACCGTATAATACATACA

Coriaria_ru [247] CTGTAGTTGCGTTAATAAAGG?C----?----AAATACTTTCCATCGAAACTCCAGAAAGAGC-----GGGAAAGATAAACCGTATAATACATACA

[310	320	330	340	350	360	370	380	390	400	
[---	---	---	---	---	---	---	---	---	---]
B.baccata	---	---	---	---	---	---	---	---	---	---	[202]
B.amplal	---	---	---	---	---	---	---	---	---	---	[202]
B.poculiferai	---	---	---	---	---	---	---	---	---	---	[202]
B.bonushenricus	---	---	---	---	---	---	---	---	---	---	[202]
B.loranthoides1	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	TATTAATGACGACTCGAATGTTTTTTT						[325]
B.ebololuensis	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	GATTAATGACGACTCGAATGTTTTTTT						[325]
B.kisuluwana	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[318]
B.subscutata	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[331]
B.oxyanthera	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.gabonensis	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.longipetiolatal	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.horticola	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[326]
B.eminii	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.cavallilipes	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.manii1	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[318]
B.fusialata	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[326]
B.preusii	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.polygonoides	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[318]
B.molleri	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.sublpestris	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.furfuracea	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.salaziensis	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.comorensis	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.nossibea	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[318]
B.mananjabensis	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[326]
B.marnieri	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[326]
B.francoisii	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[326]
B.madecassa	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[326]
B.ankaranensis	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[326]
B.isalensis	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.bogneri	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[323]
B.nana	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.sp.nov.1	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.betsimesaraka	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[326]
B.quadrilalata	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[327]
B.scapigera	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[326]
B.duncanthomasii	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[327]
B.letouzey	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[327]
B.primatocarpa	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[327]
B.dewildei	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[286]
B.asplenifolia	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.potamophila	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[327]
B.thomeana	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.iucunda	TAATAC	---	---	---	---	---	---	---	---	---	[324]
B.meyerijohannis	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[325]
B.engleri	GTAATACG	TACTAAAAACA	AGTATTTCAAATCA	AGTATTTCAAATCA	AGTATTTCAAATCA	---	---	---	---	---	[320]
B.annobonensis1	GCAATACG	TAATC	---	---	---	---	---	---	---	---	[320]

[310	320	330	340	350	360	370	380	390	400]
[GTAATACG	---TAATC	---?A	---AGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---
B.johnstonii	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[320]
B.homonyma	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B.socotrana	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B.dregei	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B.sutherlandii	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[337]
B.solananthera	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[332]
B.ulmiifolia	GTAATACG	---GAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[330]
B.holtonis	GTAATACG	---TAATC	---?A	---AGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	[331]
B.herbacea	ACAATACGTATACGTAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	---	[342]
B.lubata	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B.luxurians1	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B.obliqua	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[335]
B.violifolia	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[333]
B.incarnata	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[333]
B.convolvulacea	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B.angularis	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[330]
B.amphioxus	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B.crassirostris	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B.longifolia	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B.masoniana	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B.aequata	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[332]
B.rhoxburghi	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B.palmata	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
S.sanguinea	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[339]
B.fallax	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[325]
B.floccifera	GTAATACG	---TAATAAAACA	---TAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
D.cannabina	GTAC	-----CTAGAAA?C	---TATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---TTTATA	---TTT	---	[312]
D.glomerata	GTAATACG	---TACTAGAAA?C	---TATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---TTTATA	---TTT	---	[317]
H.sandwicensis	---	---?-----?-----?-----?	-----	-----	-----	-----	-----	-----	-----	[262]
Coriaria_V41	GTAATACG	---TACCATAAAAACA	---TAATATTTCAAATCA	---GATTAATACGACCCGGAATCTTTATTTTTTTTATATATATTT	---	---	---	---	---	[325]
Coriaria_jap	GTAATACG	---TACCATAAAAACA	---TAATATTTCAAATCA	---GATTAATACGACCCGGAATCTTTATTTTTTTTATATATATATTT	---	---	---	---	---	[332]
Coriaria_mic	GTAATACG	---TACCAGAAAACA	---TAATATTTCAAATCA	---GATTAATACGACCCGGAATCTTTATTTTTTTTATATATATATTT	---	---	---	---	---	[328]
Coriaria_ru	GTAATACG	---TACCAGAAAACA	---TAATATTTCAAATCA	---GATTAATACGACCCGGAATCTTTATTTTTTTTATATATATATTT	---	---	---	---	---	[324]

[410 440 450 460 470 480 490 500]

[
[
B.baccata [217] CTTAAAGTTG
B.amplal [217] CTTAAAGTTG
B.poculiferal [217] CTTAAAGTTG
B.bonushenricus [217] CTTAAAGTTG
B.loranthoides1 [355] CTTCAAGTTG
B.ebolowensis [386] AACC--GACTTCAAGTTG
B.kisuluana [379] AACC--GACTTCAAGTTG
B.subscutata [392] AACC--GACTTCAAGTTG
B.oxyanthera [386] AACC--GACTTCAAGTTG
B.gabonensis [386] AACC--GACTTCAAGTTG
B.longipetiolatal [384] CTTCAAGTTG
B.horticola [387] AACC--GACTTCAAGTTG
B.emini1 [386] AACC--GACTTCAAGTTG
B.cavalliyensis [388] AACCACCACCTTCAAGTTG
B.capillipes [379] AACC--GACTTCAAGTTG
B.mani1 [387] AACC--GACTTCAAGTTG
B.fusialata [386] AACC--GACTTCAAGTTG
B.preusii [379] AACC--GACTTCAAGTTG
B.polygonoides [386] AACC--GACTTCAAGTTG
B.molleri [386] AACC--GACTTCAAGTTG
B.subalpestris [386] AACC--GACTTCAAGTTG
B.furfuracea [379] AACC--GACTTCAAGTTG
B.salaziensis [385] CTTCAAGTTG
B.comorensis [384] TTCAAGTTG
B.nossiba [385] TTCAAGTTG
B.mananjabensis [387] CTTCAAGTTG
B.marnieri [385] CTTCAAGTTG
B.francoisii [387] CTTCAAGTTG
B.madecassa [385] CTTCAAGTTG
B.ankaranensis [385] CTTCAAGTTG
B.isalensis [384] CTTCAAGTTG
B.bogneri [382] CTTCAAGTTG
B.nana [384] CTTCAAGTTG
B.sp.nov.1 [388] CTTCAAGTTG
B.betsimesaraka [385] CTTCAAGTTG
B.quadrialata [386] CTTCAAGTTG
B.scapigera [386] CTTCAAGTTG
B.duncanthomasii [391] CTTCAAGTTT
B.letouzey [385] CTTCAAGTTT
B.prismatocarpa [386] CTTCAAGTTT
B.dewiidei [345] CTTA?AGTTT
B.asplenifolia [384] CTTCAAGTTT
B.potamophila [386] CTTCAAGTTT
B.thomeana [384] CTTCAAGTTT
B.iucunda [383] CTTCAAGTTT
B.meyerijohannis [389] AACTTCAAATTG
B.engleri [379] CTTCAAGTTT
B.annobonensis1 [379] CTTCAAGTTT

[510	520	530	540	550	560	570	580	590	600]
[AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[478]								
B. johnstonii	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[487]								
B. homonyma	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[487]								
B. socotrana	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[487]								
B. dregei	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[487]								
B. sutherlandii	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[493]								
B. solanthera	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[488]								
B. ulmi folia	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[486]								
B. holtonis	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[487]								
B. herbacea	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[498]								
B. lobata	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[487]								
B. luxurians1	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[487]								
B. obliqua	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[491]								
B. violifolia	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[489]								
B. incarnata	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[489]								
B. convolvulacea	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[487]								
B. angularis	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[487]								
B. amphioxus	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[486]								
B. crassirostris	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[487]								
B. longifolia	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[487]								
B. masoniana	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[487]								
B. aequata	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[488]								
B. rhoxburghi	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[487]								
B. palmata	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[487]								
B. sanguinea	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[495]								
B. fallax	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[481]								
B. floccifera	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[487]								
D. cannabina	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[472]								
D. glomerata	AAAAAGAAATCAAATATTTCAATGATTAAATATCAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[477]								
H. sandwicensis	-----CATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGACGAGAAATAGAAT	[332]								
Coriaria_V41	AAAAAGAAATCGAATATTTCAATTTGAT- CAA- ATAAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGATGAAAAATAGAAT	[514]								
Coriaria_jap	AAAAAGAAATCGAATATTTCAATTTGAT- CAA- ATAAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGATGAAAAATAGAAT	[521]								
Coriaria_mic	AAAAAGAAATCGAATATTTCAATTTGAT- CAA- ATAAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGATGAAAAATAGAAT	[517]								
Coriaria_ru	AAAAAGAAATCGAATATTTCAATTTGAT- CAA- ATAAATTCCTCCATCAATACTGATAGAAGATCTGTTGAAGAACTGATTC- AATCAGATGAAAAATAGAAT	[513]								

[610 . . . 620 . . . 630 . . . 640 . . . 650 . . . 660 . . . 670 . . . 680 . . . 690 . . . 700.]

ITS

B. baccata	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAACTTTCTCGTGC	[386]
B. amplai	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCTGCGAACTTTCTCGTGC	[386]
B. poculiferai	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAACTTTCTCGTGC	[386]
B. bonushenricus	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCTGCGAACTTTCTCGTGC	[386]
B. loranthoides1	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAACTTTCTCGTGC	[524]
B. ebolowensis	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--T?????????????????????GTTTGTGC	[555]
B. kisuluana	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TKCAGAAACAACCCGCGAAACCCYGTGTTGTGC	[548]
B. subscutata	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TTTCAGAAACAACCCGCGAAACCCGTTCTGTGC	[561]
B. oxyanthera	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAAACCCGTTGTGC	[554]
B. gabonensis	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAAACCCGTTGTGC	[556]
B. longipetiolatal	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAACTCTGTAGTGC	[553]
B. horticola	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCASAAACAATYCGGAAACCCGTTGTGC	[556]
B. emini	AAAGATCAGAAAGTCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAACTC-GTTTGTGC	[556]
B. cavallyensis	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--T-----	[530]
B. capillipes	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAA--?-TGCAGAAACAACCCGCGAACTCCGTTGTGC	[547]
B. manii	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAACTCTGTGTGC	[556]
B. fusialata	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAATGCAGAAACAACCCGCGAACTCCGTTGTGC	[556]
B. preusii	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAAACCCGTTGTGC	[548]
B. polygonoides	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAAACCCGTTGTGC	[556]
B. molleri	AAAGATAGAGC--TCACCATTG?CCATTGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAAACCCGTTGTGC	[556]
B. subalpestris	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAAACCCGTTGTGC	[555]
B. fufuracea	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAAACCCGTTGTGC	[548]
B. salaziensis	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAAACCCGTTGTGC	[550]
B. comorensis	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGTTGAACTAGTT-----	[550]
B. nossibe	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGTTGAACTAGTT-----	[549]
B. mananjabensis	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGTTGAACTAGTT-----	[552]
B. marnieri	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGTTGAACTAGTT-----	[551]
B. francoisii	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGTTGAACTAGTT-----	[550]
B. madeassa	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGTTGAACTAGTT-----	[550]
B. ankanensis	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGTTGAACTAGTT-----	[550]
B. isalensis	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGTTGAACTAGTT-----	[549]
B. bogneri	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAACTAGT?-----	[549]
B. nana	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAACTAGT?-----	[553]
B. sp.nov.1	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAACTAGT?-----	[550]
B. bethimesaraka	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--T-----	[528]
B. quadrialata	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--T-CAGAAACAACCCGCGAACTAGT-C	[558]
B. scapigera	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TACAGAAACAACCCGCGAACTAGT-C	[553]
B. duncanthomasi	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--T-CAGAAACAACCCGCGAACTAGT-C	[552]
B. letouzey	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--T-CAGAAACAACCCGCGAACTAGT-C	[554]
B. prismatocarpa	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TACAGAAACAACCCGCGAACTAGT-C	[552]
B. dewilidei	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAACTAGT-C	[513]
B. asplenifolia	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAACTAGT-C	[552]
B. potamophila	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAACTAGT-C	[553]
B. thomeana	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAACTAGT-C	[551]
B. iucunda	AAAGATAGAGC--TCACCATTCTACATGTCAAATACC-----GGCAAAAAAC--TGCAGAAACAACCCGCGAACTAGT-C	[549]

	610	620	630	640	650	660	670	680	690	700
B.meyerijohannis	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGTGAAC	TTGTTGA--	[556]				
B.englери	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----AGACAAAAAC--TGCAGAAAA	CAACCCCGGAAT	TGTTT---	[544]				
B.annobonensis1	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----AGACAAAAAC--TGCAGAAAA	CAACCCCGGAAT	TGTTT---	[544]				
B.johnstonii	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----AGAC????-?-?-T	-----	-----	[522]				
B.homomya	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAY	TAGTTTGGC	[559]				
B.socotrana	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[559]				
B.dregei	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[557]				
B.sutherlandii	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[563]				
B.solananthera	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[558]				
B.ulmifolia	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[557]				
B.holtonis	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[558]				
B.berbacea	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--CGCAGAAAA	CAACCCCGGAAT	TGTTT---	[568]				
B.lobata	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--CGCAGAAAA	CAACCCCGGAAT	TGTTT---	[558]				
B.luxurians1	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--T	-----	-----	[532]				
B.obliqua	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[561]				
B.violifolia	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[556]				
B.incarnata	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--CGCAGAAAA	CAACCCCGGAAT	TGTTT---	[559]				
B.convolvulacea	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[583]				
B.angularis	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[558]				
B.amphioxus	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[556]				
B.longifolia	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[557]				
B.masoniana	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[552]				
B.aequata	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[559]				
B.rhoxburghi	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[557]				
B.palmata	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[557]				
S.sanguinea	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[566]				
B.fallax	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[552]				
B.floccifera	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[532]				
D.cannabina	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[538]				
D.glommerata	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[543]				
H.sandwicensis	?AAG?TAGGC--TCC	-----?	-----GCAGAAAAAC--TGCAGAA	CAACCCCGGAAT	CGGTT--A	[373]				
Coriaria_V41	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[586]				
Coriaria_jap	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[593]				
Coriaria_mic	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[589]				
Coriaria_ru	AAAGATAGAGC--TCACCAATTCATGTC	CAATACC	-----GGACAAAAAC--TGCAGAA	CAACCCCGGAAT	TGTTT---	[585]				

	710	720	730	740	750	760	770	780	790	800	
[
[
B. baccata	AA-----C-GA-ACC-	CGCAA	GGGAA	TGGCGGGGC	GTGCTGGG	-----	CGC	-----	CGC	[427]	
B. amplal	AA-----C-GA-ACC-	CGCAA	GGGAA	TGGCGGGGC	GTGCTGGG	-----	CGC	-----	CGC	[427]	
B. poculiferal	AA-----C-GA-ACC-	CGCAA	GGGAA	TGGCGGGGC	GTGCTGGG	-----	CGC	-----	CGC	[427]	
B. bonushenricus	AA-----C-GA-ACC-	CGCAA	GGGAA	TGGCGGGGC	GTGCTGGG	-----	CGC	-----	CGC	[427]	
B. loranthoides1	AA-----C-GA-ACC-	CGCAA	GGGAA	TGGCGGGGC	TTGATGGG	-----	CGC	-----	CGC	[565]	
B. ebolowensis	AA-----C-GA-ACC-	CGCAA	GGGAG	CGCGAGGA	GTGTTGGG	-----	CGC	-----	CGC	[596]	
B. kisuluana	AA-----C-GA-ACC-	CGCAA	GGGAG	CGCGAG-A	GTGTTGGG	-----	CGC	-----	CGC	[588]	
B. subscutata	AA-----C-GA-ACC-	CGCAA	GGGAG	CGCGAGGA	GTGTTGGG	-----	CGC	-----	CGC	[602]	
B. oxyanthera	AA-----C-GA-ACC-	CGCAA	GGGAG	TGGCGAGGA	GTGTTGGG	-----	CGC	-----	CGC	[595]	
B. gabonensis	AA-----C-GA-ACC-	CGCAA	GGGAG	CGCGAGGA	GTGTTGGG	-----	CGC	-----	CGC	[597]	
B. longipetiolatal	AA-----C-GA-ACC-	CGCAA	GGGAT	GGCGAGC	GTGATGGG	-----	CGC	-----	CGC	[593]	
B. horticola	AA-----C-GA-ACC-	CGCAA	GGGAT	CGGCAAGRA	TTKTTGGG	-----	CSC	-----	CSC	[597]	
B. emini	AA-----C-GA-ACC-	CGCAA	GGGAG	TGGCGAGGA	GTGTTGGG	-----	CGC	-----	CGC	[597]	
B. cavalliensis	AA-----C-GA-ACC-	CGCAA	GGGAG	CGCGAGGA	GTGTTGGG	-----	CGC	-----	CGC	[530]	
B. capillipes	AA-----C-GA-ACC-	CGCAA	GGGAG	CGCGAGGA	GTGTTGGG	-----	CGC	-----	CGC	[588]	
B. manii	AA-----C-GA-ACC-	CGCAA	GGGAG	TGGCGAGGA	GTGTTGGG	-----	CGC	-----	CGC	[597]	
B. fusialata	AA-----C-GA-ACC-	CGCAA	GGGAG	TGGCGAGGA	GTGTTGGG	-----	CGC	-----	CGC	[597]	
B. preusii	AA-----C-GA-ACC-	CGCAA	GGGAG	CGCGAGGA	GTGTCGGG	-----	CGC	-----	CGC	[589]	
B. polygonoides	AA-----C-GA-ACC-	CGCAA	GGGAG	CGCGAGGA	GTGTTGGG	-----	CGC	-----	CGC	[597]	
B. molleri	AA-----C-GA-ACC-	CGCAA	GGGAG	CGCGAAGA	ATGTTGGG	-----	CGC	-----	CGC	[597]	
B. subalpestris	AA-----C-GA-ACC-	CGCAA	GGGAG	CGCGAGGA	GTGTTGGG	-----	C?C	-----	C?C	[595]	
B. fufuracea	AA-----C-GA-ACC-	CGCAA	GGGAG	CGCGAGGA	GTGTTGGG	-----	CGC	-----	CGC	[589]	
B. salaziensis	AA-CCAT-C-G--TCCC	CGCGC	GGGAA	TTGGCARGC	ATGTTGG	AGCTACGGCACAA	GCTT	-----	CGCGGTG	[612]	
B. comorensis	AA-CCAT-C-G--TCCC	CACGC	GGGAA	TTGGCAGGC	ATGTTGG	AGCTACGGCACAA	GCTT	-----	CGCGGTG	[612]	
B. nossibea	AA-CCAT-C-G--TCCC	CATGT	GGGAA	TTGGCAGGC	ATGTTGG	AGGTACGGCATA	GCTT	-----	TCGCGTG	[610]	
B. mananjabensis	AA-CCAT-C-G--TCCC	CATGC	GGGAA	TTGGCAGGC	ATGTTGG	AGCTAGCACAA	GCTT	-----	TCGCGTG	[613]	
B. marnieri	AA-CCAT-C-G--TCCC	CACGC	GGGAA	TTGGCAGGC	ATGTTGG	AGGTACGGCATA	GCTT	-----	TCGCGTG	[613]	
B. francoisii	AA-CCAT-C-G--TCCC	CATGT	GGGAA	TTGGCAGGC	ATGTTCA	AGGTACGGCATA	GCTT	-----	TCGCGTG	[611]	
B. madecassa	AA-CCAT-C-G--TCCC	CACGC	GGGAA	TTGGCAGGC	ATGTTGG	AGCTAGCACAA	GCTT	-----	TCGCGTG	[612]	
B. isalensis	AA-CCAT-C-G--TCCC	CACGC	GGGAA	TTGGCAGGC	ATGTTGG	AGCTAGCACAA	GCTT	-----	TCGCGTG	[612]	
B. bogneri	AA-CCAT-C-G--TCCC	CATGT	GGGAA	TTGGCAGGC	ATGTTGG	AGCTAGCACAA	GCTT	-----	TCGCGTG	[611]	
B. nana	AA-CCAT-C-G--TCCC	CATGT	GGGAA	TTGGCAGGC	ATGTTGG	AGCTAGCACAA	GCTT	-----	TCGCGTG	[612]	
B. sp. nov. 1	AA-CCAT-C-G--TCCC	CATGT	GGGAA	TTGGCAGGC	ATGTTGG	AGCTAGCACAA	GCTT	-----	TCGCGTG	[612]	
B. betsimesaraka	AA-CCAT-C-G--TCCC	CATGT	GGGAA	TTGGCAGGC	ATGTTGG	AGCTAGCACAA	GCTT	-----	TCGCGTG	[613]	
B. quadrialata	TA-CCAT-C-G--TCCC	CATGT	GGGAA	TTGTGAGGC	GTGTTGG	ASCTGC-GAC?CAA	GCTT	-----	CGCGGTG	[615]	
B. scapigera	AA-----TGC--TCCC	CCARCCAGATG	GGGAA	AGCGGGGC	GTGCTGGT-A	CGGTTAC	CGC-GCCCC	-----	CGCGGTG	[612]	
B. duncanhomasi	AA-CCACAC-GA--TTCC	CCAGCCA	GGGCT	GGGAA	AGCGGGGC	ACGCTGGT-C	CGCGTTG	CGC-GCTCC	-----	CGCGGTG	[593]
B. letouzey	AA-CCACAC-GA--TTCC	CCAGCTA	GGGCT	GGGAA	AGCGGGGC	ACGCTGGT-C	CGCATTG	CGC-GCTCC	-----	CGCGGTG	[624]
B. prismatocarpa	AA-CCACAC-GA--TTCC	CCAGCCA	GGGCT	GGGAA	AGCGGGGC	ACGCTGGT-C	CGCATTG	CGC-GCTCC	-----	CGCGGTG	[623]
B. dewildei	AA-CCAT-CTGC--TTTC	CCAGCCA	GGGAA	AGGTGGGGC	GTGCTGGT-A	CGGTTA	CGC-GCCCC	-----	CGCGGTG	[628]	
B. asplenifolia	AA-----CCC--TCTT	CCCCACT	GGGAA	AGCGGGGC	GTGCTGGT-A	CGGTTA	CGC-GCCCC	-----	CGCGGTG	[585]	
B. potamophila	AA-CCAT-CTGC--TTCC	CCAGCCA	GGGAA	AGCGGGGC	GGCTGGT-A	CGGTTA	CGC-GCCCC	-----	CGCGGTG	[606]	
B. thumanda	AA-CCAT-CTGC--TTCC	CCAGCCA	GGGAA	AGCGGGGC	GGCTGGT-A	CGGTTA	CGC-GCCCC	-----	CGCGGTG	[627]	
B. iucunda	AT-A-AT-GC-G--TCCC	CCAGCCA	GGGAA	CGCGGG	GGCACCCG-A	CGTTAC	CGC-GCCCC	-----	CGCGGTG	[593]	
B. meyerijohannis	-----CACCG-TCCC	-----	AGC	GGGAA	CGCGGG	GGCTGGT-A	CGC-GCCCC	-----	CGCGGTG	[610]	
B. engleri	-----AAACATCG-TCCC	-----	TCAC	-----	TTGG	-----	GGCTGGT-A	-----	CGCGGTG	[612]	
B. annobonensis1	-----AAACATCG-TCCC	-----	TACAA	GGGGAA	TGGTGGGT	GGCTGGT-A	CGC-GCCCC	-----	CGCGGTG	[610]	
										[603]	

[710	720	730	740	750	760	770	780	790	800]
[----	----	----	----	----	----	----	----	----	----
B.johnstonii	-----AAAG-----	-----TCCC-GCCC-----	-----CGTGC-----	-----GGAA-----	-----CGGCCCGGG-----	-----GCC- TTCGG- AGCCGTGGCT-----	-----RCR- CGT- GCAT-----	-----CGT- GCAT-----	-----GYACCVT-----	[539]
B.homonyma	-----TTGAGCG-----	-----TCCT-GCCT-----	-----CGTGC-----	-----GGAA-----	-----CTGTGCGGG-----	-----GCCG-TCGG-ATCCGGCAG-----	-----AGC- GCC-----	-----GCGCG-----	-----GCGCG-----	[622]
B.socotrana	-----CCAAAG-----	-----TCCC-GCCC-----	-----CGTGC-----	-----GGAA-----	-----CGGCCCGGG-----	-----GCC- TTCGG- AGCCGTGGCT-----	-----CGT- GCAT-----	-----GCGCG-----	-----GCGCG-----	[622]
B.dregei	-----CCCAACGATGCT-----	-----GCCA-----	-----CGCG-----	-----AGAA-----	-----GGCGT-TG-----	-----GGCGT-CTA- AATGTGGCC-----	-----CGT- GCAT-----	-----GCGCG-----	-----GCGCG-----	[633]
B.sutherlandii	-----CTAAAG-----	-----TTCC-GCTT-----	-----CGGG-----	-----GGAA-----	-----CGGTA- ATG-----	-----GGCGTT- GA- AACTCGGGCT-----	-----TGC- TTT-----	-----GTGCT-----	-----GTGCT-----	[622]
B.solananthera	-----TCAAAG-----	-----TTC- GCT-----	-----TGAC-----	-----GGAA-----	-----CAGTCTGTG-----	-----GTGTGT- GG- TGCTGTGGCT-----	-----TGC- ATAC-----	-----GTGCT-----	-----GTGCT-----	[621]
B.ulmifolia	-----RGAAT-----	-----TCCC-GCAC-----	-----TGCG-----	-----GGAA-----	-----CGTCTGGGG-----	-----GGTGA- CGG- ARGTTGGTGGC-----	-----CGC- TTT-----	-----GCGG-----	-----GCGG-----	[620]
B.holtonis	-----TCAACG-----	-----TCCC- ACT-----	-----CGAC-----	-----GGAA-----	-----TCGACGAGA-----	-----GCACGTT- GG- AGCTCGGCC-----	-----GC- CTCT-----	-----GCACST-----	-----GCACST-----	[633]
B.herbacea	-----CCAA- TG-----	-----TCCC- GTTT-----	-----CGCAC-----	-----GGAA-----	-----CGGCCCGGG-----	-----CGTGTTT- GG- TGCTGTGGCC-----	-----GC- CTCT-----	-----GTGCG-----	-----GTGCG-----	[621]
B.luxuriansl	-----CGAAT-----	-----TCCC- GCAT-----	-----TGCG-----	-----GGAA-----	-----CGCGTGG-----	-----CGGTGT- GG- AGTCTGGT-----	-----CAC- TTT-----	-----GTGCG-----	-----GTGCG-----	[614]
B.obliqua	-----CCAAACG-----	-----TCCC- GCTT-----	-----CGCG-----	-----GGAA-----	-----TGTGCGGG-----	-----GCCGT- CGG- GGACGCGCT-----	-----TGC- TTT-----	-----GCGCG-----	-----GCGCG-----	[621]
B.violifolia	-----CCAACT-----	-----TCCT- GCTT-----	-----TGCG-----	-----GGAA-----	-----GGCGT-----	-----GGCGT- CGG- AGTTGTGGCT-----	-----TGC- TTT-----	-----GCGCG-----	-----GCGCG-----	[624]
B.incarnata	-----CCAAATG-----	-----TCCC- GCTT-----	-----CGCAC-----	-----GGAA-----	-----CAGCGCGG-----	-----GCCTGT- GG- TGCTGTGGCT-----	-----TAC- CTAY-----	-----GTGTA-----	-----GTGTA-----	[647]
B.convolvulacea	-----CCAAATG-----	-----TCCC- GCTT-----	-----CGCAC-----	-----GGAA-----	-----CAGCGCGG-----	-----GCCTGT- GG- TGCTGTGGCC-----	-----GC- CTCT-----	-----GTGCG-----	-----GTGCG-----	[621]
B.amphioxus	-----CCAAACG-----	-----TCCC- GCTG-----	-----CAGT-----	-----GGAA-----	-----CGGTGTGG-----	-----GCCGT- CGG- ARCTGTGGCA-----	-----CGC- GCT-----	-----GCGCG-----	-----GCGCG-----	[621]
B.crassirostris	-----CCAAACG-----	-----TCCC- RCCC-----	-----CGTGC-----	-----GGAA-----	-----CAGYCGGA-----	-----GCACGT- CAG- AGTTGTGGAY-----	-----AGC- GCT-----	-----TCGCG-----	-----TCGCG-----	[620]
B.longifolia	-----CCAAACG-----	-----TCCC- GCCC-----	-----CGTGC-----	-----GGAA-----	-----CAGTCTGG-----	-----GCACGT- CGG- AGTTGTGGAC-----	-----AGC- GCT-----	-----TCGCG-----	-----TCGCG-----	[622]
B.masoniana	-----CTGCCTCG-----	-----TCGC- GCG-----	-----CGCG-----	-----GGAA-----	-----CGGTCTGG-----	-----GCCGT- CWG- AGTCTGCAAC-----	-----CGC- GCT-----	-----GCGCG-----	-----GCGCG-----	[620]
B.aequata	-----CCAAATG-----	-----TTC- GCTG-----	-----CAYG-----	-----GGAA-----	-----TGGCGCGG-----	-----GCCGT- CAG- AGTTGTAGCC-----	-----TGC- GTT-----	-----GCGCG-----	-----GCGCG-----	[624]
B.rhoxburghi	-----CCAAATG-----	-----TCCC- GCTT-----	-----TGTG-----	-----GGAG-----	-----CAGTCTGG-----	-----GCACGT- GG- AGCTGTGGAC-----	-----AGC- GCT-----	-----TCGCG-----	-----TCGCG-----	[622]
B.palmata	-----CCAAACG-----	-----TCCC- GCCC-----	-----CGTGC-----	-----GGAA-----	-----CGGCCGAGA-----	-----GCACGTT- GG- AACTGTGGAA-----	-----AGC- GCT-----	-----TCGCG-----	-----TCGCG-----	[622]
S.sanguinea	-----CCAAATG-----	-----TCCC- GCTG-----	-----CGCG-----	-----GGAA-----	-----TGGCGCGG-----	-----GCCGT- CGG- AGTTGTAGCT-----	-----CGC- GCT-----	-----GCTCG-----	-----GCTCG-----	[631]
B.fallax	-----CCAAACG-----	-----TCCC- GCCC-----	-----CGAG-----	-----GGAA-----	-----CGGCCCGG-----	-----GCCGT- CGG- WACTAAGGC-----	-----CGC- GCT-----	-----GCGCG-----	-----GCGCG-----	[617]
B.floccifera	-----CAAAA-----	-----TCGA- GGGG-----	-----T- GGGTCTC-----	-----GAGAG-----	-----CCCTCAGT-----	-----TCTGTGC- AG- TGAGGGGGGGTGTGGCACC-----	-----TTCCTTTACGGG-----	-----TTCCTTTACGGG-----	-----TTCCTTTACGGG-----	[532]
D.cannabina	-----CAATC-----	-----TCGG- GTGTGG-----	-----CGGGCTC-----	-----GAAAG-----	-----CCCTCGCG-----	-----TCCCGCG- GG- GGAGGGGGGGTGTAGCAC-----	-----TATCCCTTTACGGG-----	-----TATCCCTTTACGGG-----	-----TATCCCTTTACGGG-----	[621]
D.glomerata	-----AAAAAC-----	-----AC-----	-----TGTGGC-----	-----CCGTGGCAAAAAG-----	-----T- CGGGGCG-----	-----CGTCCGTG- C-----	-----CGAGCAC-----	-----CGAGCAC-----	-----CGAGCAC-----	[436]
H.sandwicensis	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	[686]
Coriaria_V41	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	[693]
Coriaria_jap	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	[689]
Coriaria_mic	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	[685]
Coriaria_ru	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	[685]

[(810 820 830 840 850 860 870 880 890 900] [599]

[687] [685] [687] [701] [687] [686] [685] [702] [688] [649] [678] [686] [689] [712] [688] [686] [684] [686] [690] [687] [696] [685] [532] [693] [699] [500] [786] [793] [789] [785]

B. johnstonii
B. homonyma
B. socotrana
B. dregei
B. sutherlandii
B. solanathera
B. ulmiifolia
B. holtonis
B. herbacea
B. lobata
B. luxurians1
B. obliqua
B. violifolia
B. incarnata
B. convolvulacea
B. angulularis
B. amphioxus
B. crassirostris
B. longifolia
B. masoniana
B. aequata
B. palmata
S. sanguinea
B. fallax
B. floccifera
D. cannabina
D. glomerata
H. sandwicensis
Coriaria_V41
Coriaria_jap
Coriaria_mic
Coriaria_ru

-----GCC--TGGC-GAGCCACGGGRRCC--CT-RACGAAGC-CT--GGCGMAGTCCGGTCAAGGAA--TCTTGA
GCCCT--GCC--TGGA-ACGCTCGGCCCC--TT-AACGAACC-CC--GACGCCAGTCCGCTCAAGGAA--TGTATA
-----GCC--GC-GGGCCGCGGCCCC--T-AACGAACC-CC--GGCGGATCAGCTCAAGGAA--CACGTA
GCCCT--GCC--TGGA-ACGCTCGGCCCC--TT-AACGAACC-CC--GACGCCAGTCCGCTCAAGGAA--TGTATA
GCCAT--GCC--TCGA-ATGCCCGCGCCCTCT--AT-AACGAACC-CC--GGCGGAGTCCGCTCAAGGAA--TATCGA
GCACCT--ACC--TCGT-ACTCCTCGTGCCCCC--T-AACAACC-GC--AACGGAGTACACCAAGGAA--TCTCAA
GCTCT--GCC--TGGC-ATGCTCGTGCCCCC--T-AACAACC-CC--GGCGGAGTCCGCTCAAGGAA--TCTCAA
GCCCA--GCC--TCGC-ACGCTCTCGGCCCC--T-AACGAACC-CC--GGCGGAGTCCGCTCAAGGAA--TGTGTA
GCCCT--GCC--TGGC-AGGCTTCGACATCCCCC--TT-AACAACC-CC--GGCGGAGTCCGCTCAAGGAA--TCTCAA
GCCCT--GCT--TTGC-AGGCTTCGCTCCCC--TT-AACAACC-CC--GGCGGAGTCCGCTCAAGGAA--TCTCAA
CCACG--GCC--GGC-ACGCTCTCGGCCCC--T-AACGAACC-CC--GGCGGAGTCCGCTCAAGGAA--TGTGTA
TCACT--GCC--TCGC-ACGCTTCGTCGCCCC--T-AACGAACC-CC--GGCGGAGTCCGCTCAAGGAA--TCTCAA
GCTCT--GCC--TGGC-ATGCTTCGTCGCCCC--T-AACAACC-CC--GGCGGAGTCCGCTCAAGGAA--TATCAA
GCCCT--GCC--TGGC-AGGCTTCGCTCCCC--CT-AACAACC-CC--GGCGGAGTCCGCTCAAGGAA--TCTCAA
GCCCT--GCC--TGGC-AGGCTTCGCTCCCC--T-AACGAACC-CC--GGCGGAGTCCGCTCAAGGAA--TGTGTA
TTCAT--GCC--CTGC-ATGCCCTCGGCCCC--T-AACRAACC-CC--GACCGAGTCCGCTCAAGGAA--TCTTGA
AGCCCA--GCC--TCGC-GGCTTCGTCGCCCC--T-AACGAACC-CC--GGCGAATTCGCTCAAGGAA--TCTAAA
CCCTT--GCC--CTGC-GTGCCCGCGGCCCC--T-AACGAACC-CC--GGCGGAGTCCGCTCAAGGAA--TCTAAA
GACCT--AAG--AGAC-ATGCTTCGTCGCCCC--T-AACGAACC-CC--GGCGAATTCGCTCAAGGAA--TCTGAA
GCCCA--GCC--TCGC-ACGCTTCGTCGCCCC--T-AACGAACC-CC--GGCGGAGTCCGCTCAAGGAA--TCTAGA
GCCCTGTGCC--CGGC-GAGCTCGGCCCCC--T-AACGAACC-CC--GGCGAATTCGCTCAAGGAA--TCC-GA

CGTGGTGGCTCGTT--CGGTTCTCTCTG--C-AAACT-AACGAACCTCC--GGCGGAGTCCGCTCAAGGAA--CAAT-A
GGGCTTGGCTCGTT--GGTTCCTCTTG--C-AAACT-AACGAACCTCC--GGCGGAGTCCGCTCAAGGAA--CAAT-A
CCCGGC-----GGGCGGCCCTCGC-----AACTCAAGGAACC-CC--GGCGAATTCGCTCAAGGAA--CAACTTT-A
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[910 920 930 940 950 960 970 980 990 1000]

[
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-CGC-YCGAGCTT---GAAAA---TCA---CAC-ACG [566]
B. baccata
A-C-TTG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-CGC-TGCGAGCTT---GAAAA---TCA---CAC-ACG [567]
B. amplal
A-C-TTG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-CGC-TGCGAGCTT---GAAAA---TCA---CAC-ACG [567]
B. poculiferal
A-C-TTG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-CGC-TGCGAGCTT---GAAAA---TCA---CAC-ACG [567]
B. bonushenricus
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [704]
B. loranthoides1
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [704]
B. boluowensis
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [728]
B. kisuluana
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [721]
B. subscutata
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [741]
B. oxyanthera
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [727]
B. gabonensis
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [730]
B. longipetiolatal
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [734]
B. horticola
W-C-T-GA---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-AMG [732]
B. emini
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [729]
B. cavalliyensis
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [554]
B. capillipes
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [722]
B. maniil
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [729]
B. fusialata
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [729]
B. preusii
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [722]
B. polyonoides
A-C-T-G---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [730]
B. molleri
A-TTG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [731]
B. subalpestris
?---TTG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [729]
B. furfuracea
A-TTG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [722]
B. salariensis
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [745]
B. nossibea
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [745]
B. mananjabensis
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [746]
B. marnieri
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [746]
B. francoisii
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [744]
B. madecassa
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [744]
B. isalensis
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [744]
B. bogneri
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [745]
B. nana
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [742]
B. sp. nov. 1
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [746]
B. betsimaraka
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [747]
B. quadrialata
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [745]
B. scapigera
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [747]
B. duncanthomasii
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [727]
B. prismatocarpa
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [762]
B. dewildei
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [719]
B. asplenifolia
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [739]
B. potamophila
A-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [761]
B. thomeana
A-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [719]
B. meyerijohannis
A-C-TG---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [747]
B. engleri
A-C-TT---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [748]
B. annobonensis1
A-C-TT---AGAAATGCGGC---TCCTCT- GCCCTCGATTCGG-GATGC---AGGGG-TGT-TGTGAGCTT---GAAAA---TCA---CAC-ACG [748]

[1010 1020 1030 1040 1050 1060 1070 1080 1090 1100]

ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [664]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [665]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [666]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [667]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [668]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [669]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [670]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [671]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [672]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [673]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [674]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [675]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [676]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [677]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [678]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [679]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [680]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [681]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [682]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [683]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [684]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [685]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [686]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [687]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [688]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [689]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [690]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [691]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [692]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [693]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [694]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [695]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [696]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [697]
ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [698]
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ACTCTCGACAACGGGATATCTCGGGCTCTCGCATCGATGAAGAACGCTAGTGAATCGGATACCTTGGTGTGAATTGCAGAAATCCC -GTGAACCATC- GAGTTTT [700]

- B. baccata
- B. amplal
- B. poculiferal
- B. bonushenricus
- B. loranthoides1
- B. eboluwensis
- B. kisuluana
- B. subscutata
- B. oxyanthera
- B. gabonensis
- B. longipetiolatal
- B. horticola
- B. emini
- B. cavalliyensis
- B. capillipes
- B. maniil
- B. fusialata
- B. preusii
- B. polygonoides
- B. mollerii
- B. sublapestris
- B. furfuracea
- B. salariensis
- B. comorensis
- B. nossibea
- B. mananjabensis
- B. marnieri
- B. francoisii
- B. madecassa
- B. ankaranensis
- B. isalensis
- B. bogneri
- B. nana
- B. sp. nov. 1
- B. betsimesaraka
- B. quadrialata
- B. scapigera
- B. duncanthomasi
- B. letouzey
- B. prismatocarpa
- B. dewilidei
- B. asplenifolia
- B. potamophila
- B. thomeana
- B. iucunda
- B. meyerijohannis
- B. engleri
- B. annobonensis1

	1010	1020	1030	1040	1050	1060	1070	1080	1090	1100	
B. johnstonii	ACTCTCGACA	AYGRATATCT	CGGCTCTCG	GATAGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[764]
B. homonyma	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[856]
B. socotrana	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[857]
B. dregei	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[856]
B. sutherlandii	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[873]
B. solanathera	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[866]
B. ulmifolia	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[853]
B. holtonis	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[855]
B. herbacea	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[875]
B. lobata	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[857]
B. luxurians1	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[818]
B. oblifolia	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[847]
B. violifolia	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[855]
B. incarnata	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[856]
B. convolvulacea	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[881]
B. angularis	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[857]
B. amphioxus	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[856]
B. crassirostris	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[856]
B. longifolia	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[853]
B. masoniana	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[853]
B. aequata	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[862]
B. rhoxburghi	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[855]
B. palmata	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[854]
B. sanguinea	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[866]
B. fallax	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[855]
B. floccifera	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[532]
D. cannabina	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[859]
D. glomerata	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[866]
H. sandwicensis	ACTCTCGACA	ACGGATATCT	CGGCTCTCG	CATCGATG	AAAGAGT	AGTGAAG	ATGCGRTA	STTGGTGTG	AAATTWCA	KAATCS	[676]
Coriaria_V41	????????	????????	????????	????????	????????	????????	????????	????????	????????	????????	[986]
Coriaria_jap	????????	????????	????????	????????	????????	????????	????????	????????	????????	????????	[993]
Coriaria_mic	????????	????????	????????	????????	????????	????????	????????	????????	????????	????????	[989]
Coriaria_ru	????????	????????	????????	????????	????????	????????	????????	????????	????????	????????	[985]

[1110 1120 1130 1140 1150 1160 1170 1180 1190 1200]

TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TGGCCCCCCCACGCTC-GCGCTATAAAAA---C-C [758]
 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TGGCCCCCCCACGCTC-CTGCCAAAAA---T-C [757]
 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TGGCCCCCCCACGCTC-CCGCCAAAAA---T-C [757]
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 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TGGCCCCCCC---GCGCCAAAAA---T [893]
 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [913]
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 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [926]
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 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [914]
 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [740]
 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [908]
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 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [916]
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 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [929]
 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [929]
 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [927]
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 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [930]
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 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [925]
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 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [930]
 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [929]
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 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [948]
 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [904]
 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [930]
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 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [933]
 TTGAACGCAAGTTGGCCCGAAGCCTTCTGGGGAGGACACGTCCTGGCTGGGCGTACCGCATCG-TAGCCCCCCC---GCSCAAAAA---TTC [935]

- B. baccata
- B. amp1al
- B. poculifer1al
- B. bonushenricus
- B. loranthoides1
- B. ebolowensis
- B. kisuluana
- B. subscutata
- B. oxyanthera
- B. gabonensis
- B. longipetiolatal
- B. horticola
- B. emini
- B. cavalliyensis
- B. capillipes
- B. manii
- B. fusialata
- B. preusii
- B. polygonoides
- B. molleri
- B. subalpestris
- B. furfuracea
- B. salaziensis
- B. comorensis
- B. nossi1
- B. mananjabensis
- B. marnieri
- B. francoisii
- B. madecassa
- B. ankaranensis
- B. isalensis
- B. bogneri
- B. nana
- B. sp. nov. 1
- B. betsimesaraka
- B. quadrialata
- B. scapigera
- B. duncanthomasii
- B. prismatocarpa
- B. dewildei
- B. asplenifolia
- B. potamophila
- B. thomeana
- B. iucunda
- B. meyeri1
- B. engleri
- B. annobonensis1

[1110	1120	1130	1140	1150	1160	1170	1180	1190	1200]
[TTGAA	-----	-----	-----	-----	-----	-----	-----	-----	-----
B. johnstonii	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATGG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[769]
B. homonyma	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATGG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[943]
B. socotrana	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATGG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[943]
B. dregei	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATAG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[943]
B. sutherlandii	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATAG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[948]
B. solanathera	TTCAACTCAAGTTGCACCCGAAAGCTTCTGGCCGAGGAAACCTTACTCTGGGCGTCATGGATGG	-TAACCCCTT-	-----	-----	-----	-----	-----	-----	-----	[958]
B. ulmifolia	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATGG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[939]
B. holtonis	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATGG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[942]
B. herbacea	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCA	-CAGCACCC-	-----	-----	-----	-----	-----	-----	-----	[959]
B. lobata	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCA	-CAGCACCC-	-----	-----	-----	-----	-----	-----	-----	[943]
B. luxurians1	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCATGATG	-GTAGCCCC-	-----	-----	-----	-----	-----	-----	-----	[903]
B. obliqua	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCG	-GAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[936]
B. violifolia	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCG	-TAGTCCCC-	-----	-----	-----	-----	-----	-----	-----	[944]
B. incarnata	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[943]
B. convolvulacea	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[968]
B. angularis	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[943]
B. amphioxus	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[947]
B. crassirostris	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[942]
B. longifolia	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[944]
B. masoniana	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[945]
B. aequata	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[950]
B. rhoxburghii	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[947]
B. palmata	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[945]
S. sanguinea	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[955]
B. fallax	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATCG	-TAGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[948]
B. floccifera	-----	-----	-----	-----	-----	-----	-----	-----	-----	[580]
D. cannabina	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATGG	-TTGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[943]
D. glomerata	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACGGATGG	-TTGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[950]
H. sandwicensis	TTGAACGCAAGTTGGCCCGAAGCTTTHGGCGAGGGCACCCTTGCCCTGGGCGTCACACATCG	-TTGCCCCC-	-----	-----	-----	-----	-----	-----	-----	[763]
Coriaria_V41	??	????????	????????	????????	????????	????????	????????	????????	????????	[1086]
Coriaria_jap	??	????????	????????	????????	????????	????????	????????	????????	????????	[1093]
Coriaria_mic	??	????????	????????	????????	????????	????????	????????	????????	????????	[1089]
Coriaria_ru	??	????????	????????	????????	????????	????????	????????	????????	????????	[1085]

	1210	1220	1230	1240	1250	1260	1270	1280	1290	1300
[
[
B.baccata	GAGTTC-AAFTCTCTG	---	---	---	---	TT	---	---	GGGGTG	[782]
B. amplal	GAGTTC-AAFTCTCTA	---	---	---	---	CT	---	---	GGGGTTG	[781]
B.poculiferai	GAGTTC-AAFTCTCTA	---	---	---	---	CT	---	---	GGGGTTT	[781]
B.bonushenicus	GA?TTC-AAFTCTCTA	---	---	---	---	TT	---	---	GGGGTTG	[781]
B.loranthoidesi	GAGTTC-AAFTCTCTC	---	---	---	---	TT	---	---	GGGGTTG	[917]
B.ebolowensis	---TC-GAFTCTCTC	---	---	---	---	TT	---	---	GGGGTCG	[933]
B.kisuluana	---TC-GAFTCTCTC	---	---	---	---	TT	---	---	GGGGTTG	[926]
B.subscutata	---TC-GAFTCTCTC	---	---	---	---	TT	---	---	GGGGTCG	[946]
B.oxyanthera	---TC-GAFTCTCTC	---	---	---	---	TT	---	---	GGGGTTG	[933]
B.gabonensis	---TC-GAFTCTCTC	---	---	---	---	TT	---	---	GGGGTCG	[935]
B.longipetiolatal	GAG-TCCAATCCYTTA	---	---	---	---	TTATAATATTT	---	---	GGGGTTG	[956]
B.horticola	---TC-GAFTCTCTC	---	---	---	---	TT	---	---	GGGGTCG	[937]
B.eminii	---TC-GAFTCTCTC	---	---	---	---	TT	---	---	GGGGTTG	[934]
B.cavalliyensis	---TC-AAFTCCCTCCC	---	---	---	---	TTCTCGGAGTTGGGTTG	---	---	GGGGTTG	[771]
B.capillipes	---TC-GAFTCTCTC	---	---	---	---	TT	---	---	GGGGTCG	[928]
B.manii	---TC-GAFTCTCTC	---	---	---	---	TT	---	---	GGGGTTG	[934]
B.fusialata	---TC-GAFTCTCTC	---	---	---	---	TT	---	---	GGGGTCG	[933]
B.preusii	---TC-GAFTCTCTC	---	---	---	---	TT	---	---	GGGGTCG	[928]
B.polygonoides	---TC-GAFTCTCTC	---	---	---	---	TT	---	---	GGGGTCG	[935]
B.molleri	---TC-AAFTCTCTCC	-GG	---	---	---	TT	---	---	GGGGTTG	[942]
B.subalpestris	---AACCTCTTC	---	---	---	---	TT	---	---	GGGGTCG	[940]
B.furfuracea	---TT-GAFTCTCTCTTTGGAG	---	---	---	---	TT	---	---	GGGGTTG	[937]
B.salaziensis	GCACGC-TCAATAATCTCGTGA	-AATAGACTTGCTATTTCTCTC	---	---	---	---	---	---	GGGGTTG	[981]
B.comorensis	GCACGC-TCAATAATCTCGTGA	-AATAGACTTGCTATTTCTCTC	---	---	---	---	---	---	GGGGTTG	[981]
B.nossibeae	GAACGC-TCAATAATCTCTTTA	-AATAGACTTGCTATTTCTCTA	---	---	---	---	---	---	GGGGTTG	[979]
B.mananjabensis	---ACGC-TCAATCTCTGGTTGA	-AATAGACCAATGCTATTTCTTA	---	---	---	---	---	---	GGGGTTG	[977]
B.marnieri	TGAACGCTCAATCTCTGGTTGA	-AATAGAACTTGCTATTTCTCTG	---	---	---	---	---	---	GGGGTTG	[987]
B.francoisii	GAACGC-TCAATCTCTGGTTTA	-AATAGACCTATGCTATTTCTTA	---	---	---	---	---	---	GGGGTTG	[980]
B.madecassa	GCACGCTCAATCTCTA	---	---	---	---	---	---	---	GGGGTTG	[950]
B.ankaranensis	GCACAGCTCAATCTCCCGTTGAGATAGACCTATGCTATMTTCTC	---	---	---	---	---	---	---	GGGGTTG	[982]
B.isalensis	GAATGCTCAATCTCTC	-GGTTGAAATAGACCT?GCTATTTGCCC	---	---	---	---	---	---	GGGGTTG	[981]
B.bogneri	SCAAGCT	---	---	---	---	---	---	---	GGGGTTG	[932]
B.nana	GCAAGCTT	---	---	---	---	---	---	---	GGGGTTG	[938]
B.sp.nov.1	GCAAGCT	---	---	---	---	---	---	---	GGGGTTG	[937]
B.betsimesaraka	GCAAGCTT	---	---	---	---	---	---	---	GGGGTTG	[936]
B.quadrialata	---	---	---	---	---	---	---	---	GGGGTTG	[963]
B.scapigera	---	---	---	---	---	---	---	---	GGGGTTG	[995]
B.duncanthomasii	---	---	---	---	---	---	---	---	GGGGTTG	[974]
B.letouzey	---	---	---	---	---	---	---	---	GGGGTTG	[973]
B.primatocarpa	---	---	---	---	---	---	---	---	GGGGTTG	[998]
B.dewildei	---	---	---	---	---	---	---	---	GGGGTTG	[952]
B.aspleniifolia	CGAGAT	---	---	---	---	---	---	---	GGGGTTG	[971]
B.potamophila	---	---	---	---	---	---	---	---	GGGGTTG	[997]
B.thomeana	---	---	---	---	---	---	---	---	GGGGTTG	[961]
B.iucunda	---	---	---	---	---	---	---	---	GGGGTTG	[976]
B.meyerijohannis	---	---	---	---	---	---	---	---	GGGGTTG	[931]
B.engleri	---	---	---	---	---	---	---	---	GGGGTTG	[935]
B.annobonensis1	GC	---	---	---	---	---	---	---	GGGGTTG	[939]
	CGGG	---	---	---	---	---	---	---	GGGGTTG	

	1210	1220	1230	1240	1250	1260	1270	1280	1290	1300	
[
[
B.johnstonii	---	CAAGCCGAGATCG	---TTCCCTC	---	GATC-ATC	---		---			[769]
B.homonyma	---	CCAACAGGACCGCTGGC	---TCCCC	---	GGAC-GAAGCA	---	GGCTC	---	GTGCC-GCTTC	---	[769]
B.socotrana	---	CAAGCCGAGATCG	---TTCCCTC	---	GATC-ATC	---		---	GCAGGGCGGG-CTG	---	[1006]
B.dregei	---		---	TTCCCTC	---	GATC-ATC	---			---	[769]
B.solanalandii	ATCGG	---	TTCCCTC	---	GATCGATC	---	GAAGTA	---	GACTC	---	[1004]
B.sulphanthera	---	AGAGGTGGTCAA	---TGTCCG	---	GATT-AAAGTA	---	GACTC	---	GTGCT-GCTTC	---	[1004]
B.ulmifolia	---	CCAC	---	GTCAGT	---	GGCGTG	---	CAAG-GAAGTA	---	GACTT	[992]
B.holtonis	---	GATGCCACCGAGG	---	CCT	---		---	GATC	---	GTGCT-ACATC	[992]
B.herbaacea	---	GAGAGGTCAA	---TGTCTC	---	GATC-GAAGCA	---	GACTC	---	CGCT-GCATC	---	[1016]
B.luxurians1	---	GAGGGGTCAA	---TGTCTC	---	GATC-GAAGCA	---	GACTC	---	CGCT-GCATC	---	[955]
B.obliqua	---	CCAA	---	GTCAGT	---	TCCGTG	---	CGTC-GAAGTA	---	GACTT	[984]
B.violifolia	---	CCAACC-TC	---	GGTC-GAAGTA	---	GACTC	---	GTGCT-GCTTC	---	GTCAGGG	[988]
B.incarnata	---	CCAACAC-CAA	---	ACTATC	---	GATC	---	GGAGTA	---	GTCTC	[994]
B.convolvulacea	---	AGAGGTGGTCAA	---GGTCCG	---	GATG-AAAGCA	---	GACTT	---	CGCT-GCAAC	---	[1021]
B.angularis	---	GAGG	---		---		---		---		[947]
B.amphioxus	---	CAAAGTA-TAA	---TCCCTC	---	GATC-AAAGTA	---	GACTT	---	GTGCT-GCTTC	---	[999]
B.grassirostris	---	CCAACAC-CAA	---	TCCATC	---	TATCC-GAAGCT	---	GACTC	---	GTGCT-GACTC	[989]
B.longifolia	---	GAA-AC-CTA	---	TGCCCTCGC	---	TGCTC-GAARTG	---	GACAC	---	TGGCTCGCCCTC	[997]
B.masoniana	---	CCAAGTA-CAA	---	TTCCCTC	---	GATC-GAAGTA	---	GACTC	---	GTGCT-GCTTC	[1007]
B.aequata	---	CCAACAA-CAA	---	TCCATC	---	GATC-GAAGCA	---	GACCG	---	CGCT-GCTTC	[1002]
B.rhoxburghi	---	CCAATAC-CAA	---	TCCATC	---	GATC-GAAGCA	---	CATC	---	GTGCT-GCTTC	[1001]
B.palmata	---	CCAAG-T-CAA	---	TCCCTC	---	GATC-GAAMYMA	---	GACTC	---	GTGCT-GCTTC	[999]
S.sanguinea	---	CAAA	---		---		---		---		[1007]
B.fallax	---		---		---		---		---		[953]
B.floccifera	---		---		---		---		---		[592]
D.cannabina	---		---		---		---		---		[967]
D.glomerata	---		---		---		---		---		[974]
H.sandwicensis	AGG	---	AAAAA-TAGTTCGAATCCC	---	GACTCCGACGGGT	---	CGGGGGATGCG	---		---	[810]
Coriaria_V41	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	[1186]
Coriaria_jap	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	[1193]
Coriaria_mic	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	[1189]
Coriaria_ru	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	[1185]

[1310 1320 1330 1340 1350 1360 1370 1380 1390 1400]

[
 [-GGCC--GGACTTT--GGTTGGAC--GAGGGGGGCAFTGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [859]
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 -GGCC--GGACTTT--GGTTGGGG-ACGAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGC [859]
 -GGCC--GGACTTT--GGTCGGGG-A?AGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGC [859]
 -GGCT--AGACTTT--GATCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [993]
 -GGCT--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1009]
 -GGCT--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1002]
 -GGCT--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1021]
 -GGCT--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1009]
 -GGCT--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1011]
 -GACC--GGACTTT--GGTTGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1033]
 -GGG--GGAMTTT--GGTTGGAM--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1013]
 -GGTT--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1010]
 -GGCT--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [847]
 -GGCT--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1003]
 -GGTT--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1010]
 -GGAT--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1009]
 -GGCT--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1011]
 -GGCC--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1018]
 -GGT--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1019]
 -TGCT--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1013]
 -GGCT--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1057]
 -GGCT--GGACTTT--GGTCGGAC--GAGGGGG-CAATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1057]
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 -GGCT--GGCAAT--GGTTCCGAT--GAGGTGG-TCATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1053]
 -GGCT--GGCAAT--GGTTCCGAT--GAGGTGG-TCATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1061]
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 -GGCT--GGCAAT--GGTTCCGAT--GAGGTGG-TCATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1057]
 -----AT--GAGGTGG-TCATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [991]
 -----AT--GAGGTGG-TCATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [997]
 -----AT--GAGGTGG-TCATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [996]
 -----AT--GAGGTGG-TCATGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [995]
 -GTTG--GGATTTGCAATC--GTTCCGA--GGGCGG-CAAGGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1044]
 -GCTT--GGATTTGCAATC--GTTCCGA--GGGCGG-CAAGGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1075]
 -GCTT--GGATTTGCAATC--GTTCCGA--GGGCGG-CAAGGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1054]
 -GCTT--GGATTTGCAATC--GTTCCGA--GGGCGG-CAAGGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1053]
 -GCTG--GGATTTGCAATC--GTTCCGA--GGGCGG-CAAGGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1079]
 -GCTG--GGATTTGCAATC--GTTCCGA--GGGCGG-CAAGGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1033]
 -GGG--GC-TGGCAATCCG--GTTTGGC--GAGGCGG-MMAGGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1050]
 -GTTG--GGATTTGCAATC--GTTCCGA--GGGCGG-CAAGGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1078]
 -GGT--GGCCTTT--GGCCTTT--GGGCGG-CAAGGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1036]
 -GGCT--GCATATT--GGGTTGGT--GGGCGG-CAAGGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1052]
 -----CAAGTTT--GGGCGG-CAAGGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1003]
 -----GGGCTTT--GGGCGG-CAAGGTTGGCCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1007]
 -----GATTTGGAT--GGTCC--GATCATGATCATCCTCCCGTCCGAGC-GATC-GGCGGFTTGGCTAAAAGTTGAGT [1005]

B. baccata
 B. amplai
 B. poculiferai
 B. bonushenicus
 B. loranthoidesi
 B. ebolowensis
 B. kisuluana
 B. subcutata
 B. oxyanthera
 B. gabonensis
 B. longipetiolatal
 B. horticola
 B. eminii
 B. cavalliensis
 B. capillipes
 B. manii
 B. fusalata
 B. polygonoides
 B. molleri
 B. subalpestris
 B. furfuracea
 B. salaziensis
 B. comorensis
 B. nossibeia
 B. mananjabensis
 B. marnieri
 B. francoisii
 B. madecassa
 B. ankaransis
 B. isalensis
 B. bogneri
 B. nana
 B. sp. nov. 1
 B. betsimesaraka
 B. quadrialata
 B. scapigera
 B. duncanthomasii
 B. letozey
 B. prismatocarpa
 B. dewildei
 B. asplenifolia
 B. potamophila
 B. thomeana
 B. iucunda
 B. meyeri johannis
 B. engleri
 B. annobonensis 1

[1410 1420 1430 1440 1450 1460 1470 1480 1490 1500]

[CCTCGGCGT--CGGCAGTGCATCGACGGTGGT---TTT---TAGCCCTCGGCGAGACAC--ATTGCACGTGGAGACGGGTATCGG--GAG--CTCC [946]
CCTCGGCGT--CGGCAGTGCATCGACGGTGGT---TTT---TAGCCCTCGGCGAGATAC--ATTGCACGTGGAGACGGGTATCGG--GAG--CTCC [946]
CCTCGGCGT--CGGCAGTGCATCGACGGTGGT---TTT---TAGCCCTCGGCGAGATAC--ATTGCACGTGGAGATCGGTATCGG--GAG--CTCC [945]
CCTCGGCGT--CGGCAGTGCATCGACGGTGGT---TTT---TAGCCCTCGGCGAGATAC--ATTGCACGTGGAGATCGGTATCGG--GAG--CTCC [945]
CCTCGGCGT--CGGCAGTGCATCGACGGTGGT---TTT---TAGCCCTCGGCGAGATAC--ATTGCACGTGGAGATCGGTATCGG--GAG--CTCC [1081]
CCTCGGCGT--CGGCAGTGCATCGACGGTGGT---TTT---TAGCCCTCGGCGAAATAC--ATTGCACGTGGAGACGGGTATCGG--GAA--CTCC [1095]
CCTCGGCGT--CGGCAGTGCATCGACGGTGGT---TTT---TAGCCCTCGGCGAAATAC--ATTGCACGTGGAGACGGGTATCGG--GAA--CTCC [1088]
CCTCGGCGT--CGGCAGTGCATCGACGGTGGT---TTT---TAGCCCTCGGCGAAATAC--ATTGCACGTGGAGACGGGTATCGG--GAA--CTCC [1108]
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CCTCGGCGT--CGGCAGTGCATCGACGGTGGT---TTT---TAGCCCTCGGCGAAATAC--ATTGCACGTGGAGACGGGTATCGG--GAA--CTCC [1099]
CCTCGGCGT--CGGCAGTGCATCGACGGTGGT---TTT---TAGCCCTCGGCGAAATAC--ATTGCACGTGGAGACGGGTATCGG--GAA--CTCC [1121]
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CCTCGGCGT--CGGCAGTGCATCGACGGTGGT---TTT---TAGCCCTCGGCGAAATAC--ATTGCACGTGGAGACGGGTATCGG--GAA--CTCC [933]
CCTCGGCGT--CGGCAGTGCATCGACGGTGGT---TTT---TAGCCCTCGGCGAAATAC--ATTGCACGTGGAGACGGGTATCGG--GAA--CTCC [1089]
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CCTCAGCGT--TGCGCAGTGCATCGACGGTGGT---GCCAT--GCCCTCGGCGAAATAC--ATTGCACGTGGAGACGGGTATCGG--GAA--CTCC [1145]
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CCTCAGCGT--TGCGCAGTGCATCGACGGTGGT---GCCAT--GCCCTCGGCGAAATAC--ATTGCACGTGGAGACGGGTATCGG--GAA--CTCC [1162]
CCTCAGCGT--TGCGCAGTGCATCGACGGTGGT---GCCAT--GCCCTCGGCGAAATAC--ATTGCACGTGGAGACGGGTATCGG--GAA--CTCC [1136]
CCTCAGCGT--TGCGCAGTGCATCGACGGTGGT---GCCAT--GCCCTCGGCGAAATAC--ATTGCACGTGGAGACGGGTATCGG--GAA--CTCC [1135]
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CCTCAGCGT--TGCGCAGTGCATCGACGGTGGT---GCCAT--GCCCTCGGCGAAATAC--ATTGCACGTGGAGACGGGTATCGG--GAA--CTCC [1137]
CCTCAGCGT--TGCGCAGTGCATCGACGGTGGT---GCCAT--GCCCTCGGCGAAATAC--ATTGCACGTGGAGACGGGTATCGG--GAA--CTCC [1164]
CCTCAGCGT--TGCGCAGTGCATCGACGGTGGT---GCCAT--GCCCTCGGCGAAATAC--ATTGCACGTGGAGACGGGTATCGG--GAA--CTCC [1121]
CCTCAGCGT--TGCGCAGTGCATCGACGGTGGT---GCCAT--GCCCTCGGCGAAATAC--ATTGCACGTGGAGACGGGTATCGG--GAA--CTCC [1139]
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- [B. baccata
- [B. ampial
- [B. poculiferai
- [B. bonushenicus
- [B. loranthoides1
- [B. ebolowensis
- [B. kisuluana
- [B. subscutata
- [B. oxyanthera
- [B. gabonensis
- [B. longipetiolatal
- [B. horticola
- [B. eminii
- [B. cavalliensis
- [B. capillipes
- [B. manii
- [B. fusialata
- [B. preusii
- [B. polygonoides
- [B. molleri
- [B. subalpestris
- [B. furfuracea
- [B. salaziensis
- [B. comorensis
- [B. nossibea
- [B. mananjabensis
- [B. marnieri
- [B. francoisii
- [B. madecassa
- [B. ankaranensis
- [B. isalensis
- [B. bogneri
- [B. nana
- [B. sp. nov. 1
- [B. betsimesaraka
- [B. quadrialata
- [B. scapigera
- [B. duncanthomasii
- [B. letouzey
- [B. prismatocarpa
- [B. dewilidei
- [B. asplenifolia
- [B. potamophila
- [B. thomeana
- [B. iucunda
- [B. meyerijohannis
- [B. engleri
- [B. annobonensis1

[1410 1420 1430 1440 1450 1460 1470 1480 1490 1500] [769]

[1133] CCTAGGCGT--CTTGGCGCGGATCGACGGTGGT---GTCAAT--GCCCTCGACGAATTAC--GTTGCGCCTCGAGACGCGCTTGG--GAA--CTCC

[1175] CCTCGGCGT--CTTCGACGCGATCGACGGTGGTA---GCCAT--GCCCTCGACGAATCG--GTCGCGCATGGGACGCGCTCGCG--GAA--CTCC

[1133] CCTAGGCGT--CTTGGCGCGGATCGACGGTGGT---GTCAAT--GCCCTCGACGAATTAC--GTTGCGCCTCGAGACGCGCTTGG--GAA--CTCC

[1151] CCTCGGCGT--CTTGGCGCGGATCGACGGTGGT---GTCAAT--GCCCTCGACGAATTAC--ATTGCGCAGCGGAGACTGCTGTCTG--GAA--CTC-

[1156] C-----T--GTGGTGAATGACGGTGGT---TGCCAT--GCCCTCAACCAATTAT--GTTGCGCTTGGAGACGCGCACTGG--GAA--ATCC

[1156] CATTTGGCGT--CTTGGCGCGGATCGACGGTGGT---TCCAT--GCCCTCGACGAATAC--ATTGCGCTTGGAGTGTGCTAGT--GGA--CTGC

[1153] CCTCGGCGT--CTCGCGCGGATCGACGGTGGT---GACAT--GCCCTCGACGAAT--AC--GTTGCGCTCGCAAGATGCGGTTTGA--GAA--CTC-

[1180] CTACAGCAT--CTTGCAGTTCGATCGACGGTGGT---KCCAT--GCCCTCGATGAATAC--GTTGYACATCMAGGCGGAGTGTGA--GAA--CTCC

[1159] CCTAGGCGT--ATTGCGGCGGATCGACGGTGGT---TCCAT--GCCCTCGACGAATAC--ATTGCGCTTGGAGATGCGTCTATT--GAA--CTCT

[1119] CCTTTGGCGT--CTTGGCGCGGATCGACGGTGGT---TCCAT--GCCCTCGACGAATAC--ATTGCGCTTGGAGATGCGTCTATT--GAA--CTCT

[1146] CCTCGGCGT--CTTGGCGGCAATCGRCGGTGGT---GACAT--GCTTTCGACGAAT--AC--ATTGCGCTTGGAAAGCGCGCTCGG--GAA--CTC-

[1151] CCTCGGCGC--CTTGTGCGGATCGACGGTGGT---TCTAT--GCCCTCGACGAATTAC--GTTGCGCTTGGAGGCGCGCTCGG--GAA--CTCC

[1157] CCTCGGCGT--CTTGGCGCGGATCGACGGTGGT---GCCAT--GCCCTCGACGAATTAC--ATTGCGCTTGGAGACGCGCTCGG--GAA--CTCC

[1185] CTTTGGCGT--CTTGCAGCGGATCGACGGTGGT---TCCAT--GCCCTCGACGAATAC--ATTGCGCTTGGAGTGTGCTAGT--GGA--CTGC

[1094] CCTTGGCGT--ATTGCGGCGGATCGACGGTGGT---TCCAT--GCCCTCGACGAATAC--ATTGCGCTTGGAGATGCGTCTATT--GAA--CTCT

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[1154] CCTCGGCGT--CTCGACGCGGATCGACGGTGGT---GCCAT--GCCCTCGACGAATTAC--ATTGCTTGGAGGTCGCTGTGG--GAA--CTCC

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[1179] CCTCGGCGT--CTTGCAGCGGATCGACGGTGGT---GCCAT--GCCCTCGACGAATTAC--GTTGCGCGGAGAGCGGATCGG--GAA--CTCC

[1164] CCTCGGCGT--CCAGCGCGGATCGACGGTGGT---GCCAT--GCCCTCGACGAATTAC--TWTGCGCTTGGAGACGCGTCTGA--GTA--CTCC

[1167] CCTCGGCGT--CTTGCAGCGGATCGACGGTGGT---GCCAT--GCTTCGACGTTTAC--ATTGTGATGCAAGGCGCGCTGGG--GAA--CTCC

[1163] CCTCGGCGT--CTTGCAGCGGATCGACGGTGGT---GCCAT--GCCCTCGACGAATTAC--ATTGCTTGGAGGCGCGCTGGG--GAA--CTCC

[1169] CCTCGGCGT--CTTGCAGCGGATCGACGGTGGT---GTCAAT--GCCCTCGACGAATTAC--TWTGCGCTTGGAGACGCGTCTGG--GTA--CTCC

[1113] CCCCAGCGT--CTTGCAGCGGATCGACGGTGGT---GCCATGTCCTCGACGACTTAC--GTTGCGCCTGCTCGACGCGCTCGG--GAG--CTCC

[754] CCTCGGCGT--ATTGCGGCGGATCGACGGTGGT---GCCAT--GCCCTCGACGAATCGC--GTTGCGCGCGGAGACGCGCGCGG--GAA--CTCC

[1104] CCTCGGC--TTCAAT--CGCGCGACAAACGGTGGT---GTCAAA--GC--CTCAGCGTCTGT-----CAGGTGTGTC--TGATGAAAACC--GAGG--TC-

[1111] CCTCGGC--TTCAAT--CGCGGTACAAACGGTGGT---GTCAAA--GC--CTCAGCGTCTGT-----CGCGTGGTT--TGATGAAAACATC--GAGG--TC-

[963] TCTCGGCGT--CGCGGCTGCGATCGACGGTGGT---GCCAT--GCCCTCGCGGCAAAACAAAGTTGCACTCGCGCGTGCATCTCCGA--GAAG--CTCC

[1386] ???

[1393] ???

[1389] ???

[1385] ???

B. johnstonii
B. homonyma
B. socotrana
B. dregei
B. sutherlandii
B. solanathera
B. ulmifolia
B. holtonis
B. herbacea
B. lobata
B. luxurians1
B. obliqua
B. violifolia
B. incarnata
B. convolvulacea
B. angularis
B. amphioxus
B. crassirostris
B. longifolia
B. masoniana
B. aequata
B. palmata
B. fallax
B. floccifera
D. camnabina
H. glomerata
H. sandwicensis
Coriaria_V41
Coriaria_jap
Coriaria_mic
Coriaria_ru

1510 1520 1530 1540 1550 1560 1570 1580 1590 1600
 [CACGC-----GACC?---TGC-TGCGCTGCCTCGTCG-GTT---CCTCGG-AGAAG---GACGAGGA-GGCGCTAT---CGAAGC-GAC [1013]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---CCTCGG-AGAAG---GACGAGGA-GGCGCTAT---CGAAGC-GAC [1013]
 [CACGT-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---CCTCGG-AGAAG---GACGAGGA-GGCGCTAT---CGAAGC-GAC [1012]
 [CACG?-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---CCTCGG-AGAAG---GACGAGGA-GGCGCTAT---CGAAGC-GAC [1012]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---CCTCGG-AGAAG---GACGAGGA-GGCGCTAT---CGAAGC-GAC [1148]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---TTC---GAAC---GACGAGGA-GGCGCTAT---CGAAGC-GAC [1158]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---TTC---GAAC---GACGAGGA-GGCGCTAT---CGAAGC-GAC [1151]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---TTC---GAAC---GACGAGGA-GGCGCTAT---CGAAGC-GAC [1171]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---TTC---GAAC---GACGAGGA-GGCGCTAT---CGAAGC-GAC [1171]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---TTC---GAAC---GACGAGGA-GGCGCTAT---CGAAGC-GAC [1163]
 [CACGC-----GACC---TAC-TGCGCTGCCTCGTCG-GTT---CTTCGG-AGAAC---GACGAGGA-GGCGCTAT---CGAAGC-GAC [1191]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---CTTC---GAAC---GACGAGGA-GGCGCTAT---CGAAGC-GAC [1164]
 [CTTTCG-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---CGT---AGAAC---GACGGGTA-?GC?CTAT---TCGAA-C-GAC [1160]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---GAGAAACGAC-----GGAGAACGAC----- [970]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---CTCC---GAAC---GACGGGA-GGCGCTAT---CGARGC-GAC [1152]
 [CTTTCG-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---CTAC---GAAC---GATGGGA-GGCGCTAT---CGAAGC-GAC [1159]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---CTCC---GAGC---GACGGGA-GGCGCTAT---CGAAGC-GAC [1159]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---CTCC---GAAC---GACGGGA-GGCGCTAT---CGAAGC-GAC [1153]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---TCTCC---GAAC---GACTGGGAGGCGCTAT---CGAA?C-GAC [1162]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---GGA-----GACGAGG-GGCGCTAT---CGAAGC-GAC [1163]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---GGA-----GACGAGG-GGCGCTAT---CGAAGC-GAC [1211]
 [CACGC-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---GGA-----GACGAGG-GGCGCTAT---CGAAGC-GAC [1158]
 [TTTGC-----GACCC---TAT-TGCGCTGCCTCGTCG-GTT---CCTTCG-AGCCG---VATGAGAA-GACGWTAT---CGAAGC-GAC [1211]
 [TTTGC-----GACCC---TAT-TGCGCTGCCTCGTCG-GTT---CCTTCG-AGAAC---AATGAGAA-GAGCTTAT---CGAAGC-GAC [1211]
 [TTTGC-----GACCC---AAT-TGCGCTGCCTCGTCG-GTT---CCTTCG-AGAAC---AATGAGAA-TAGCTTAT---CGAAGC-GAC [1209]
 [CTTGC-----GACCC---AAT-TGCGCTGCCTCGTCG-GTT---CCTTCG-AGAAC---AATGAGAA-GAGCTTAT---CGAAGC-GAC [1207]
 [-----GACCC-----TAT-TGCGCTGCCTCGTCG-GTT---CCTTCG-AGAAC---AATGAGAA-GAGCTTAT---CGAAGC-GAC [1061]
 [TTTGC-----TACCC---AAT-TGCGCTGCCTCGTCG-GTT---CCTTCG-AGAAC---AATGAGAA-GAGCTTAT---CGAAGC-GAC [1210]
 [TTTGT-----GACCC---TAT-TGCGCTGCCTCGTCG-GTT---CCTTCG-AGAAC---AATGAGAA-GAGCTTAT---CGAAGC-GAC [1180]
 [TTTGC-----GACCC---AAT-TGCGCTGCCTCGTCG-GTT---CCTTCG-AGAAC---AATGAGAA-GAGCTTAT---CGAAGC-GAC [1212]
 [TTTGC-----GACCC---AAT-TGCGCTGCCTCGTCG-GTT---CCTTCG-AGAAC---AATGAGAA-GAGCTTAT---CGAAGC-GAC [1211]
 [TTTGC-----GACCC---TAT-TGCGCTGCCTCGTCG-GTT---CCTTCG-AGAAC---AATGAGAA-GAGCTTAT---CGAAGC-GAC [1145]
 [TTTGC-----GACCC---TAT-TGCGCTGCCTCGTCG-GTT---CCTTCG-AGAAC---AATGAGAA-GAGCTTAT---CGAAGC-GAC [1151]
 [TTTGC-----GACCC---TAT-TGCGCTGCCTCGTCG-GTT---CCTTCG-AGAAC---AATGAGAA-GAGCTTAT---CGAAGC-GAC [1158]
 [TTTGC-----GACCC---TAT-TGCGCTGCCTCGTCG-GTT---CCTTCG-AGAAC---AATGAGAA-GAGCTTAT---CGAAGC-GAC [1149]
 [ATTCG-----GACCC---TGC-TGATGATGTCG-GCCT---CGCGGGT-TCCCT---GCGTG-A-GGCGCTGC---CGAAAC-GAC [1195]
 [ATAG-----GACCC---TGC-TGATGATGTCG-GCCT---CGCGGGT-TCCCT---GCGTG-A-GGCGCTGC---CGAAAC-GAC [1225]
 [ATAG-----GACCC---TGC-TGATGATGTCG-GCCT---CGCGGGT-TCCCT---GCGTG-A-GGCGCTGC---CGAAAC-GAC [1200]
 [ATACA-----GACCC---TGC-TGATGATGTCG-GCCT---CGCGGGT-TCCCT---GCGTG-A-GGCGCTGC---CGAAGC-GAC [1199]
 [ATGG-----GACCC---TGC-TGATGATGTCG-GCCT---CGCGGGT-TCCCT---GCGTG-A-GGCGCTGC---CGAAGC-GAC [1231]
 [CATGG-----GACCC---TGC-TGATGATGTCG-GCCT---CGCGGGT-TCCCT---GCGTG-A-GGCGCTGC---CGAAGC-GAC [1185]
 [ATGG-----GACCC---TGC-TGATGATGTCG-GCCT---CGCGGGT-TCCCT---GCGTG-A-GGCGCTGC---CGAAGC-GAC [1196]
 [ATTCG-----GACCC---TTCCTTACGA-TGCCTTTCCT---CGCGGGT-TCCCT---GCGTG-A-GGCGCTGC---CGAAGC-GAC [1230]
 [YTACA-----GACC---TCC-TGCGC-TGCTC-GTCGGCT---CMTTTCG-GAAC---GACGGG-A-GGCGAYGT---CGAAGC-GAC [1184]
 [-----GACCC---TTGC-GCGCTGCCTCGTCG-TGAGATTT---CATT---GAGAAC---GAGGAGAA-G-GCGCTAT---CGAAGC-GAC [1201]
 [GCCAA-----GACCC---TGC-TGCGCTGCCTCGTCG-GTT---CCTTCG-GGATC---GACGGGR-GAGCTTAT---CGAAGC-GAC [1157]
 [TTTGC-----AACCC-----TAT-TGCGCTGCCTCGTCG-GTT---CCGTTAG-GTGCA-----GCGCYTC-GACATCAT---CGAAGC-GAC [1105]
 [TTTGC-----GACCC---TAT-TGCGCTGCCTCGTCG-GTT---CCGTTAG-GTGCA-----GCGCYTC-GACATCAT---CGAAGC-GAC [1162]


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[ 1510 1520 1530 1540 1550 1560 1570 1580 1590 1600]
[  ]
B.johnstonii [769]
B.homonyma [1195]
B.socostrana [1239]
B.dregei [1195]
B.sutherlandii [1225]
B.solananthera [1217]
B.ulmifolia [1197]
B.holtonis [1215]
B.herbacea [1246]
B.lobata [1200]
B.luxurians1 [1149]
B.obliqua [1208]
B.violifolia [1213]
B.incarnata [1219]
B.convolvulacea [1226]
B.angularis [1135]
B.amphioxus [1224]
B.crassirostris [1216]
B.longifolia [1226]
B.masoniana [1241]
B.aequata [1227]
B.rhoxburghi [1229]
B.palmata [1225]
S.sanguinea [1231]
B.fallax [1177]
B.floccifera [820]
D.cannabina [1147]
D.glonmerata [1154]
H.sandwicensis [1035]
Coriaria_V41 [1486]
Coriaria_jap [1493]
Coriaria_mic [1489]
Coriaria_ru [1485]

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 B.baccata [1018] CCCA?
 B.amplal [1018] CCCAG
 B.poculiferal [1017] CCCAG
 B.bonushenicus [1017] CCCAG
 B.loranthoides1 [1153] CCCAG
 B.ebolowensis [1163] CCCAG
 B.kisuluana [1156] CCCAG
 B.subscutata [1176] CCCAG
 B.oxyanthera ----- [1126]
 B.gabonensis CCCAG [1168]
 B.longipetiolatal CCCAG [1196]
 B.horticola CCCAG [1169]
 B.eminii CCCAG [1165]
 B.cavallyensis ----- [970]
 B.capillipes CCCAG [1157]
 B.maniil CCCAG [1164]
 B.fusialata CCCAG [1164]
 B.preusii CCCAG [1158]
 B.polygonoides CC-AG [1166]
 B.molleri CCCAG [1168]
 B.subalpestris ????? [1216]
 B.furfuracea CCCAG [1163]
 B.salaziensis CCCAG [1216]
 B.comorensis CCCAG [1216]
 B.nossibea CCCAG [1214]
 B.mananjabensis CCCAG [1212]
 B.marnieri ----- [1061]
 B.francoisii CCCAG [1215]
 B.madecassa CCCAG [1185]
 B.ankaranensis CCCAG [1217]
 B.isalensis CCCAG [1216]
 B.bogneri CCCAG [1150]
 B.nana CCC?G [1156]
 B.sp.nov.1 ????? [1163]
 B.betsimesaraka CCC?G [1154]
 B.quadrialata CCCAG [1200]
 B.scapigera CCCAG [1230]
 B.duncanthomasii CCCAG [1205]
 B.letouzey CYCAG [1204]
 B.prismatocarpa CCCAG [1236]
 B.dewildei CCCAG [1190]
 B.asplenifolia CCCAG [1201]
 B.potamophila CCCAG [1235]
 B.thomeana CCCAG [1189]
 B.iucunda CCCAG [1206]
 B.meyerijohannis CCCAG [1162]
 B.engleri ----- [1105]
 B.annobonsis1 CCCAG [1167]

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[
 [
     ]
 ]
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B.johnstonii [769]
B.homonyma [1200]
B.socotrana CCCAG [1244]
B.dregei CCCAG [1200]
B.sutherlandii CCCAG [1230]
B.solananthera CCAAAG [1222]
B.ulmifolia CCCAG [1202]
B.holtonis CCCAG [1220]
B.herbacea CCCAG [1251]
B.lobata CCCAG [1205]
B.luxurians1 CCCAG [1154]
B.obliqua CCCAG [1213]
B.violifolia CCCAG [1218]
B.incarnata CCCAG [1224]
B.convolvulacea CCCAG [1231]
B.angularis CCCAG [1140]
B.amphioxus CCCAG [1229]
B.crassirostris CCCAG [1221]
B.longifolia CCCAG [1231]
B.masoniana CCCAG [1246]
B.aequata CCCAG [1232]
B.rhoxburghi CCCAG [1234]
B.palmata CCCAG [1230]
S.sanguinea CCCAG [1236]
B.fallax CCCAG [1182]
B.floccifera CCCAG [825]
D.cannabina CCCAG [1152]
D.glonmerata CCCAG [1159]
H.sandwicensis CCCAG [1040]
Coriaria_V41 ????? [1491]
Coriaria_jap ????? [1498]
Coriaria_mic ????? [1494]
Coriaria_ru ????? [1490]

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APPENDIX 4 Forty-eight taxon aligned matrix for *trnL* intron, ITS regions and 26 regions (Chapter 3).

	10	20	30	40	50	60	70	80	90	100
B. baccata	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. amplai	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. poculiferai	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. loranthoides1	??TGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. ebolowensis	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. gabonensis	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. longipetiolatal	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[87]							
B. horticola	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. eminii	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. capillipes	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. manii	??TGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. molleri	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. furfuracea	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. salaziensis	G?GTGATAA?YCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. comorensis	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. nossibeae	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. francoisii	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. madeccassa	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. ankaranensis	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. nana	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. betsimesaraka	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[87]							
B. scapigera	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. dewildei	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. spilenifolia	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. thomeana	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. liucunda	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. meyeri-johannis	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. engleri	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. annobonensis1	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. socotrana	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. holtonis	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[86]							
B. lobata	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[92]							
B. luxurians1	AAGTGATAACTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCTGAGCCAAATCCC	-----GGTTTTCCGAAAAAC	[92]							

B. obliqua AAGTGATA-CTTTCAAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCCTGAGCCAAATCCC-----GTTTTTCCGAAAAAC [85]
 B. violifolia AAGTGATAACTTTTCAAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-GGGCAATCCTGAGCCAAATCCC-----GGTTTTCCGAAAAAC [86]
 B. incarnata AAGTGATAACTTTTCAAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCCTGAGCCAAATCCC-----GGTTTTCCGAAAAAC [86]
 B. convolvulacea AAGTGATAACTTTTCAAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCCTGAGCCAAATCCC-----TAAA [85]
 B. angularis AAGTGATA?CTTTCAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCCTGAGCCAAATCCC-----GGTTTTCCGAAAAACAAAACAAA [92]
 B. crassirostris AAGTGATAACTTTTCAAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCCTGAGCCAAATCCC-----GTTTTTCCGAAAAAC [86]
 B. masoniana AAGTGATAACTTTTCAAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCCTGAGCCAAATCCC-----GGTTTTTCCGAAAAAC [86]
 B. aequata AAGTGATAACTTTTCAAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCCTGAGCCAAATCCC-----GGTTTTTCCGAAAAAC [87]
 B. rhoxburghi AAGTGATAACTTTTCAAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCCTGAGCCAAATCCC-----GGTTTTTCCGAAAAAC [86]
 B. palmata AAGTGATAACTTTTCAAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCCTGAGCCAAATCCC-----GGTTTTTCCGAAAAAC [86]
 S. sanguinea AAGTGATAACTTTTCAAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCCTGAGCCAAATCCC-----GGTTTTTCCGAAAAAC [87]
 B. fallax AAGTGATAASWKTCAAATTCAGAGAAAC-CCCTGGC-A?TGAAAAAC-TGGGCAATCCTGAGCCAAATCCC-----GGTTTTTCCGAAAAAC [86]
 B. floccifera AAGTGATAACTTTTCAAAATTCAGAGAAAC-CCCTGGC-AATGAAAAAC-TGGGCAATCCTGAGCCAAATCCC-----GGTTTTTCCGAAAAAC [86]
 D. cannabina TTC?ATTGCRGAGKAAACCCAGAGAAAC-CCAGAGAAATTA AAAAC-TGGGCAATCCTGAGCCAAATCCC-----TGTTTTTCCGAAAAAC [87]
 D. glomerata AAGTGATACTTTTCAAATTCAGAGAAAC-CCAGGC-AAATTA AAAAC-TGGGCAATCCTGAGCCAAATCCC-----TGTTTTTCCGAAAAAC [86]

TrnL intron alignment and gap coding are the same as in Appendix 1. ITS alignment is the same as in Appendix 2. Base pair positions of the *trnL* intron 374-434 were removed in all analyses. Base pair regions 697-856 893-894 902-910 921-929 951-997 1174-1340 1369-1372 1394-1398 1410-1415 1436-1444 1456-1513 1519-1576 of the ITS1 and ITS2 regions show alignment ambiguity and were removed from some analyses. Alignment gaps are indicated by '-'. *TrnL* intron = bps 1-670; ITS = bps 671-1605; bps 26S = 1606-2103.

	110	120	130	140	150	160	170	180	190	200
B. baccata	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. amplal	TAATC--AGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. poculiferal	TAATC--AGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. loranthoides1	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. ebolowensis	TAATC--GGTTTCGAGAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. gabonensis	TAATC--GGTTTCGAGAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. longipetiolatal	TAATC--GGTTTCGAGAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. horticola	TAATC--GGTTTCGAGAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. eminii	TAATC--GGTTTCGAGAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. cepillipes	TAATC--GGTTTCGAGAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. manii1	TAATC--GGTTTCGAGAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. molieri	TAATC--GGTTTCGAGAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. furfuracea	TAATC--GGTTTCGAGAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. salaziensis	TAATC--GGTTTCGAAAGACAAGAAC--AAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[176]						
B. comorensis	TAATC--GGTTTCGAAAGACAAGAAC--AAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. nossibe	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. francoisii	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. madecassa	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. ankaranensis	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. nana	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. betimesaraka	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[178]						
B. scapigera	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[179]						
B. dewildei	TAATAGTGTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[179]						
B. asplenifolia	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. thomeana	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. luconda	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. meyerijohannis	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. engleri	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. annobonensis1	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. socotrana	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. holtonis	TAATC--GATTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. lobata	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[183]						
B. luxurians1	TAGTC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[176]						
B. obliqua	TAATC--GATTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. violifolia	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. incarnata	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. convolvulacea	TAATC--GATTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[178]						
B. angulularis	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. crassirostris	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. masoniana	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[178]						
B. aequata	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. rhoxburghi	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. palmata	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[183]						
S. sanguinea	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. fallax	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[177]						
B. floccifera	TAATC--GGTTTCGAAAGACAAGAACGAAGAAAAAACAAC	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[166]						
D. cannabina	TAAC--GGTTTCGAAAGC-----CGAAGAAAC?	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[165]						
D. glommerata	TAAC--GGTTTCGAAAGC-----CGAAGAAAC?	-----AGGATAGGTCAGAGACTCAATGGAAGCTGTTCCAA	CAAAATGGAGTTC--GA	[165]						

[210	220	230	240	250	260	270	280	290	300]
[CTGCC	---	---	---	---	---	---	---	---	---
	B. baccata	---??---	---TCCAAC---	---	---	---	---	---	---	[196]
	B. amplal	---??---	---TCCAAC---	---	---	---	---	---	---	[196]
	B. poculiferal	---??---	---TCCAAC---	---	---	---	---	---	---	[196]
	B. loranthoides1	---	---	---	---	---	---	---	---	[264]
	B. ebolowensis	---	---	---	---	---	---	---	---	[264]
	B. gabonensis	---	---	---	---	---	---	---	---	[264]
	B. longipetiolatal	---	---	---	---	---	---	---	---	[265]
	B. horticola	---	---	---	---	---	---	---	---	[264]
	B. eminii	---	---	---	---	---	---	---	---	[264]
	B. capillipes	---	---	---	---	---	---	---	---	[264]
	B. manii	---	---	---	---	---	---	---	---	[264]
	B. molleri	---	---	---	---	---	---	---	---	[264]
	B. furfuracea	---	---	---	---	---	---	---	---	[264]
	B. salaziensis	---	---	---	---	---	---	---	---	[264]
	B. comorensis	---	---	---	---	---	---	---	---	[263]
	B. nossibea	---	---	---	---	---	---	---	---	[264]
	B. francoisii	---	---	---	---	---	---	---	---	[264]
	B. madecassa	---	---	---	---	---	---	---	---	[264]
	B. ankarahensis	---	---	---	---	---	---	---	---	[264]
	B. nana	---	---	---	---	---	---	---	---	[264]
	B. betsimesaraka	---	---	---	---	---	---	---	---	[265]
	B. scapigera	---	---	---	---	---	---	---	---	[271]
	B. dewildei	---	---	---	---	---	---	---	---	[225]
	B. asplenifolia	---	---	---	---	---	---	---	---	[264]
	B. thomeana	---	---	---	---	---	---	---	---	[264]
	B. iucunda	---	---	---	---	---	---	---	---	[264]
	B. meyeriJohannis	---	---	---	---	---	---	---	---	[264]
	B. engleri	---	---	---	---	---	---	---	---	[264]
	B. annobonensis1	---	---	---	---	---	---	---	---	[264]
	B. socotrana	---	---	---	---	---	---	---	---	[270]
	B. holtonis	---	---	---	---	---	---	---	---	[275]
	B. lobata	---	---	---	---	---	---	---	---	[270]
	B. luxurians1	---	---	---	---	---	---	---	---	[270]
	B. obliqua	---	---	---	---	---	---	---	---	[274]
	B. violifolia	---	---	---	---	---	---	---	---	[270]
	B. incarnata	---	---	---	---	---	---	---	---	[270]
	B. convolvulacea	---	---	---	---	---	---	---	---	[265]
	B. angularis	---	---	---	---	---	---	---	---	[270]
	B. crassirostris	---	---	---	---	---	---	---	---	[270]
	B. masoniana	---	---	---	---	---	---	---	---	[270]
	B. aequata	---	---	---	---	---	---	---	---	[271]
	B. rhoxburghi	---	---	---	---	---	---	---	---	[270]
	B. palmata	---	---	---	---	---	---	---	---	[270]
	S. sanguinea	---	---	---	---	---	---	---	---	[264]
	B. fallax	---	---	---	---	---	---	---	---	[264]
	B. floccifera	---	---	---	---	---	---	---	---	[270]
	D. cannabina	---	---	---	---	---	---	---	---	[248]
	D. glommerata	---	---	---	---	---	---	---	---	[247]

	310	320	330	340	350	360	370	380	390	400]
[---	---	---	---	---	---	---	---	---	---
[---	---	---	---	---	---	---	---	---	---
B. baccata	---	---	---	---	---	---	---	---	---	[202]
B. amplai	---	---	---	---	---	---	---	---	---	[202]
B. poculiferai	---	---	---	---	---	---	---	---	---	[202]
B. loranthoides1	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---TATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[325]
B. ebolowensis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[325]
B. gabonensis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[325]
B. longipetiotala1	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[325]
B. horticoila	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[325]
B. emini1	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[318]
B. capillipes	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[326]
B. manii1	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[326]
B. molieri	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[325]
B. furfuracea	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[318]
B. salazariensis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[326]
B. comorensis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[326]
B. nossibeae	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[326]
B. francoisii	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[326]
B. madecassa	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[326]
B. ankaranensis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[326]
B. nana	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[325]
B. betsimesaraka	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[326]
B. scapigera	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[332]
B. dewildei	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[286]
B. asplenifolia	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[325]
B. thomeana	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[325]
B. hiucunda	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[324]
B. meyerijohannis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[325]
B. engleri	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[320]
B. socotrana	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[320]
B. holtonis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B. lobata	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B. luxurians1	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B. obliqua	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[335]
B. violifolia	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[333]
B. incarnata	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[333]
B. convolvulacea	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B. angulularis	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B. crassirostris	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B. masoniana	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B. aquata	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[332]
B. rhoxburghi	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
B. palmata	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
S. sanguinea	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[339]
B. fallax	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[325]
B. floccifera	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[331]
D. cannabina	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[312]
D. glommerata	GTAATACG	TACTAAAAACA	---AAGTATTTCAAATCA	---GATTAATGACGACTCGAATGTTTTTTT	---	---	---	---	---	[317]

[410	420	430	440	450	460	470	480	490	500]
[-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
B. baccata	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----CTTAAAGTTG
B. amplal	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----CTTAAAGTTG
B. poculiferal	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----CTTAAAGTTG
B. loranthoides1	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----CTTCAAGTTG
B. ebolowensis	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. gabonensis	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. longipetiolatal	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. horticola	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. eminii	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. capillipes	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. manii1	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. molleri	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. furfuracea	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. salaziensis	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. comorensis	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. nossibea	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. francoisii	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. madecassa	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. ankaranensis	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. nana	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. betimesaraka	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. scapigera	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. dewildei	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. asplenifolia	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. thomeana	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. luconda	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. meyerijohannis	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. engleri	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. annobonensis1	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. socotrana	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. holtonis	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. lobata	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. luxurians1	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. obliqua	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. violifolia	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. incarnata	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. convolvulacea	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. angularis	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. crassirostris	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. masoniana	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. aequata	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. rhoxburghi	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. palmata	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
S. sanguinea	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. fallax	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
B. floccifera	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
D. cannabina	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG
D. glommerata	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----GACTTCAAGTTG

	510	520	530	540	550	560	570	580	590	600]	
B. baccata	AAAAAGAAATTAATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[314]									
B. amplal	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[314]									
B. polanthiferal	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[314]									
B. loranthoides1	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[452]									
B. ebolowensis	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[483]									
B. gabonensis	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[484]									
B. longipetiolatal	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[481]									
B. horticola	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[484]									
B. eminii	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[483]									
B. capillipes	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[476]									
B. manii	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[484]									
B. molleri	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[483]									
B. furfuracea	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[476]									
B. salaziensis	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[482]									
B. comorensis	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[482]									
B. nossibeae	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[481]									
B. francoisii	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[482]									
B. madecassa	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[482]									
B. ankaranensis	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[482]									
B. nana	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[481]									
B. betsimesaraka	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[482]									
B. seapigera	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[488]									
B. dewildel	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[442]									
B. asplenifolia	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[481]									
B. thomeana	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[481]									
B. iucunda	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[480]									
B. meyerijohannis	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[486]									
B. engleri	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[476]									
B. annobonensis1	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[476]									
B. socotrana	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[487]									
B. holtonis	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[487]									
B. lobata	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[487]									
B. luxurians1	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[487]									
B. obliqua	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[487]									
B. violifolia	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[489]									
B. incarnata	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[489]									
B. convolvulacea	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[489]									
B. angulularis	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[487]									
B. crassirostris	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[487]									
B. masoniana	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[487]									
B. aequata	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[488]									
B. hoxburghi	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[487]									
B. palmata	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[487]									
S. sanguinea	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[495]									
B. fallax	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[481]									
B. floccifera	AAAAAGAAATTCAAATATTCATTGATTAATAATTCATTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[487]									
D. cannabina	AAAAAGAAATTCAAATATTCATTGAT--CAA--ATCATTTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[472]									
D. glommerata	AAAAAGAAATTCAAATATTCATTGAT--CAA--ATCATTTCACATCCATCATATACTGTATAGAC--TCCGTTGAAGAAGAAATGATTC--AATCAGACGAGAAATAGAAT	[477]									

	610	620	630	640	650	660	670	680	690	700]
B. baccata	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[386]						
B. amplai	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[386]						
B. poculiferal	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[386]						
B. loranthoides1	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[524]						
B. ebolowensis	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[555]						
B. gabonensis	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[556]						
B. longipetiolatal	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[553]						
B. horticola	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[556]						
B. eminii	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[556]						
B. capillipes	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[556]						
B. manii1	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[547]						
B. mollerii	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[556]						
B. furfuracea	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[548]						
B. salaziensis	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[556]						
B. comorensis	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[550]						
B. nossibeae	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[550]						
B. francoisii	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[549]						
B. madeirana	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[550]						
B. ankaranensis	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[550]						
B. nana	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[549]						
B. betsimisaraka	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[550]						
B. scapigeri	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[550]						
B. dewildei	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[513]						
B. asplenifolia	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[552]						
B. thomeana	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[551]						
B. iucunda	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[549]						
B. meyeriJohannis	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[556]						
B. engleri	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[544]						
B. annobonensis1	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[544]						
B. socotrana	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[559]						
B. holtonis	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[558]						
B. lobata	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[558]						
B. luxurians1	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[553]						
B. obliqua	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[561]						
B. violifolia	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[556]						
B. incarnata	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[559]						
B. convolvulacea	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[583]						
B. angulularis	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[558]						
B. crassirostris	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[555]						
B. masoniana	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[552]						
B. aequata	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[559]						
B. rhoxburghi	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[557]						
B. palmata	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[557]						
S. sanguinea	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[566]						
B. fallax	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[552]						
B. floccifera	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[532]						
D. cannabina	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[538]						
D. glommerata	AAAGATAGAGC--TCACCATTTCTACATGTCAATACC	-----	GGACAATAAAC--TGCAGAACAACCCCGGAACTTGTCTGTC	[543]						

	710	720	730	740	750	760	770	780	790	800
B. baccata	AA-----C-GA-ACCC-----CGCAA--GGGAA--TGGCGGGGGC-GTGTCTGGGG--	[427]								
B. amplal	AA-----C-GA-ACCC-----CGCAA--GGGAA--TGGCGGGGGC-GTGTCTGGGG--	[427]								
B. pocaliferal	AA-----C-GA-ACCC-----CGCAA--GGGAA--TGGCGGGGGC-GTGTCTGGGG--	[427]								
B. loranthoides1	AA-----C-GA-ACCC-----CGCAA--GGGAA--TGGCGGGGGC-TTGTATGGGG--	[565]								
B. ebolowensis	AA-----C-GA-ACCC-----CGCAA--GGGGAG--CGGCGAGGA--GTGTTGGGG--	[596]								
B. gabonensis	AA-----C-GA-ACCC-----CGCAA--GGGGAT--GGCGAAGC--GTGATGGGG--	[597]								
B. longipetiolatal	AA-----C-GA-ACCC-----CGCAA--GGGGAT--GGCGAAGC--TTKTITGGGG--	[593]								
B. horticola	AA-----C-GA-ACCC-----CGCAA--GGGGAG--TGGCGAGGA--GTGTTGGGG--	[597]								
B. emini	AA-----C-GA-ACCC-----CGCAA--GGGGAG--TGGCGAGGA--GTGTTGGGG--	[597]								
B. capillilipes	AA-----C-GA-ACCC-----CGCAA--GGGGAG--TGGCGAGGA--GTGTTGGGG--	[588]								
B. manii	AA-----C-GA-ACCC-----CGCAA--GGGGAG--TGGCGAGGA--GTGTTGGGG--	[597]								
B. molleri	AA-----C-GA-ACCC-----CGCAA--GGGGAG--TGGCGAAGA--ATGTTGGGG--	[597]								
B. furfuracea	AA-----C-GA-ACCC-----CGCAA--GGGGAG--TGGCGAGGA--GTGCTGGGG--	[589]								
B. salaziensis	AA-CCAT-C-G-TCCC-----CAGC-----TTCGAGGC--ATGTTGG--AGTACGGCACAA--GCTT--GCCTG	[612]								
B. comorensis	AA-CCAT-C-G-TCCC-----CAGC-----TTCGAGGC--ATGTTGG--AGTACGGCACAA--GCTT--GCCTG	[612]								
B. nossibe	AA-CCAT-C-G-TCCC-----CAGC-----TTCGAGGC--ATGTTGG--AGTACGGCACAA--GCTT--GCCTG	[612]								
B. francoisii	AA-CCAT-C-G-TCCC-----CAGC-----TTCGAGGC--ATGTTGG--AGTACGGCACAA--GCTT--GCCTG	[611]								
B. madecassa	AA-CCAT-TG-TCCC-----CAGC-----TTCGAGGC--ATGTTGG--AGTACGGCACAA--GCTT--GCCTG	[612]								
B. ankaranensis	AA-CCAT-C-G-TCCC-----CAGC-----TTCGAGGC--ATGTTGG--AGTACGGCACAA--GCTT--GCCTG	[611]								
B. nana	AA-CCAT-CTG-TCCC-----CAITG-----GGGAA--TGTGAGGC--GTGTTGG--AGTACGGCACAA--GCTT--GCCTG	[613]								
B. betsimesaraka	AA-CCAT-C-G-TCCC-----CAGC-----TTCGAGGC--ATGTTGG--AGTACGGCACAA--GCTT--GCCTG	[612]								
B. scapigera	AA-CCACAC-GA-TTTC-CCAGCC-CGGGT-----GGGAA--TGTGAGGC--GTGTTGG--AGTACGGCACAA--GCTT--GCCTG	[631]								
B. dewildei	AA-CCACG-CGC-TTTC-CCAGCC-CGGGT-----GGGAA--TGTGAGGC--GTGTTGG--AGTACGGCACAA--GCTT--GCCTG	[585]								
B. asplenifolia	---CCC-----TCIT-CCCACT-----GGGAG--AGGCGCGG--TTCGCRGA-A-----CGC-GCCT--GCCTG	[606]								
B. thomeana	---CCAT-CT-----GTCC-----GGGAA--CGGCGG--CGCACCGG-A-----GC-CGCG--GC-CGCG	[593]								
B. iucunda	AT-A-AT-CGC-G-TTCC-CCAGCA-----GGAA--CGGCGG--TGTGCGCG--GGCTGC-GGAT--CGCC-----GCTGTGC	[610]								
B. meyerijohannis	---CACG-TCCC-----ACGC-----GGGAA--CGGCGG--GCGGTCTG--GGCTGC-GCACACKTC--KC-GTGC	[612]								
B. engleri	---AAACATCG-TCCC-TCAC-----TTGG-----GGGAA--CGGCGG--GCGGTCTG--GGCTGC-GCACACKTC--KC-GTGC	[610]								
B. annobonensis1	---AAACATCG-TCCC-----TACAA--GGGGAA--TGTGCGGT--GCGTGCCA-A-----GGCT--GT-G-TT-----GTGTGT	[603]								
B. socotrana	---TTGAGCG-----TCCT-GCCT-----CGTGC-----GGAA--TGTGCGGG--GGCG-TCCG-ATCCCGGGAC--AGC-GCCC--TGCGCGC	[627]								
B. holtonis	---RGAAT-----TCCC-GCAC-----TGCG-----GGAA--CGGTGCGG--GCGTGA-CGG-ARGTGTGGC--CGC-TTIT--GCGCGC	[620]								
B. lobata	---CCAA-TG-----TCCC-GTIT-----CGCAC-----GGAA--CGGCGCGG--GCGTGT--GG-TGCTGTGGCC--GC-CTCT--GTGCGC	[621]								
B. luxurians1	---CGAAT-----TCCC-GCAT-----TGCG-----GGAA--CGGCGG--GCGGTG--GG-AGTCTGTGGT--CAC-TTIT--GTGCGC	[614]								
B. obliqua	---CCAAAG-----TCCC-GTIT-----CGCG-----GGAA--CGGCGG--GCGGTG--GG-AGTCTGTGGT--CAC-TTIT--GTGCGC	[621]								
B. violifolia	---CCAACT-----TCCT-GCTT-----TGCG-----GGAA--TGGTGGGG--GCGGT-CGG-AGTGTGGCT--TGC-TTIT--GCGCGC	[624]								
B. incarnata	---CCAACT-----TCCT-GCTT-----TGCG-----GGAA--TGGTGGGG--GCGGT-CGG-AGTGTGGCT--TGC-TTIT--GCGCGC	[624]								
B. convolvulacea	---CCAAAG-----TCCC-GTIT-----CGCAC-----GGAA--TGTGCGGG--GCGGTG--GG-TGCTGTGGCT--TAC-CTAT--GTGTGA	[647]								
B. angularis	---CCAAAG-----TCCC-GTIT-----CGCAC-----GGAA--TGTGCGGG--GCGGTG--GG-TGCTGTGGCT--TAC-CTAT--GTGTGA	[621]								
B. crassirostris	---CCAAAG-----TCCC-RCCC-----CGTGC-----GGAA--CAGYCGGA--GCAGT-CAG-AGTGTGGAY--AGC-GCTT--TCGCGC	[620]								
B. masoniana	CTGCTTCG-----TCGC-GCG-----CGCM-----GGAA--CGGTGCGG--GCGGT-CWG-AGTGTCCAAC--CGC-GCTT--GCGCGT	[620]								
B. aequata	---CCAAAG-----TCTC-GCT-----CAYC-----GGAA--TGGCGCGG--GCGGT-CAG-AGTGTAGCC--TGC-GTIT--GCGCGC	[624]								
B. rhoxburghi	---CCAAAG-----TCCC-GCT-----TGTC-----GGAA--CAGYCGGA--GCAGT-CAG-AGTGTAGCC--TGC-GTIT--GCGCGC	[622]								
B. palmata	---CCAAAG-----TCCC-GCCC-----CGTGC-----GGAA--CGGCGCAG--GCAGT-CAG-AGTGTAGCC--TGC-GTIT--GCGCGC	[622]								
S. sanguinea	---CCAAAG-----TCCC-GCTG-----CGCG-----GGAA--TGGCGCGG--GCGGT-CGG-AGTGTGAGCT--GC-GCTT--GCTCGA	[631]								
B. fallax	---CCAAAG-----TCCC-GCG-----CGAG-----GGAA--CGGCGCGG--GCGGT-CGG-WACTAAGGC--CGC-GCTC--GCGCGC	[617]								
B. floccifera	-----CAAAA-----TCCA-----TCCC-----GGAA--CGGCGCGG--GCGGT-CGG-WACTAAGGC--CGC-GCTC--GCGCGC	[532]								
D. cannabina	---CAATC-----TCGA-GGGG-T-GGCTC-GAGAGG-CCCTCAGT-TCITGTC-AG-TGAGGCGGCGGTGTCGACCTGTCCTTTACGGG	[621]								
D. glomerata	---CAATC-----TCGG-GTGTGCG-CGGGTC-GAAAGAG-CCCTCAGG-TCGCGCGC-GG-GGAGGCGGCGGTGTCGACCTATCCTTTACGGG	[627]								

	810	820	830	840	850	860	870	880	890	900
B. baccata	-----TCGGGC-GC--TCCTCGGC-----TCCCGCGCACCTC-AACGAACC-CCC-GGCGGAGTCGCGCCAAAGGAA--TTTTTA	[496]								
B. amplal	-----TAGGCG-GC--TCCTCGGTA-----TCCC-GCGACCTT-AACGAACC-CCC-GGCGGAGTCGCGCCAAAGGAA--TCTTTA	[496]								
B. poculiferal	-----TAGGCG-GC--TCCTCGGC-----TCCCGCGCACCTT-AACGAACC-CCC-GGCGGAGTCGCGCCAAAGGAA--TCTTTA	[496]								
B. loranthoides1	-----TCGGCG-GC--TCCTTGCG-----TCCCGCGCACCTT-AACGAACC-CCC-GGCGGAGTCGCGCCAAAGGAA--TCTTTA	[634]								
B. ebolowensis	-----AAGCCCCGATT-----TCG-CGGCACCTT-AACGAACC-CCC-GGCGGAGTCGCGTCAAGGAA--TATGTA	[660]								
B. gabonensis	-----AAGCCCCGATT-----TCG-CGGCACCTT-AACGAACC-CCC-GGCGGAGTCGCGTCAAGGAA--TATTTA	[661]								
B. longipetiolata1	-----TCGCC-GC--TCCKCAGC-----TCCCGCCACCTT-AACGAACC-CCC-GGCGGAGTCGCGTCAAGGAA--TATTTA	[664]								
B. horticola	-----AASCCSCSWTT-----YCS-CSCSCACCTT-AACRAACC-CCC-SGCGGAGTCGKSTCARAGAA--TATTTA	[661]								
B. eminii	-----ACGCCCGCATT-----TCG-CGCGCACCTT-AACGAACC-CCC-GGCGGAGTCGCGTCAAGGAA--TATATA	[660]								
B. capillipes	-----AAGCCCCGATT-----TCG-CGCGCACCTT-AACGAACC-CCC-GGCGGAGTCGCGTCAAGGAA--TATTTA	[652]								
B. manii1	-----AAGCCCCGATT-----TCG-CGCGCACCTT-AACGAACC-CCC-GGCGGAGTCGCGTCAAGGAA--TATATA	[660]								
B. mollieri	-----AAGCCCCGATT-----TCG-CGCGCACCTT-AACGAACC-CCC-GGCGGAGTCGCGTCAAGGAA--TCTTTA	[661]								
B. furfuracea	-----ACGCCCCACATT-----CCA-CGCGCACCTT-AACGAACC-CCC-GGCGGAGTCGCGTCAAGGAA--TCTTTA	[653]								
B. salaziensis	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[676]								
B. comorensis	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[676]								
B. nossibe	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[674]								
B. francoisii	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[675]								
B. madecassa	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[676]								
B. ankaranensis	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[675]								
B. nana	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[677]								
B. betsimesaraka	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[676]								
B. scapigera	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[675]								
B. dewildei	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[676]								
B. asplenifolia	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[677]								
B. thomeana	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[676]								
B. luconda	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[677]								
B. meyerijohannis	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[676]								
B. engleri	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[675]								
B. annobonensis1	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[673]								
B. socotrana	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[685]								
B. holtonis	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[685]								
B. lobata	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[688]								
B. luxurians1	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[649]								
B. obliqua	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[678]								
B. violifolia	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[686]								
B. incarnata	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[689]								
B. convolvulacea	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[712]								
B. angularis	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[688]								
B. crassirostris	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[684]								
B. masoniana	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[686]								
B. aequata	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[690]								
B. thoxburghi	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[687]								
B. palmata	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[687]								
S. sanguinea	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[696]								
B. fallax	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[685]								
B. floccifera	-----GCC--TTGC-ATGCTCGGA-----ACCAT-AACGAACC-CC--GGCGGAGTCGCGTCAAGGAA--TCTTTA	[532]								
D. cannabina	-----CGTGGTCTGGCTCGTT-CCGTTCCCTCTTG-----C-AAACT-AACGAACCCTCC--GGCGGAGTCGCGCCAAAGGAA--CAAT-A	[693]								
D. glommerata	-----CGGCTTGGCTCGTT-GCGTTCCCTCTTG-----C-AAACT-AACGAACCCTCC--GGCGGAGTCGCGCCAAAGGAA--CAAT-A	[699]								

	910	920	930	940	950	960	970	980	990	1000
B. baccata	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[566]								
B. amplal	A-C-TTG--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[567]								
B. poculiferal	A-C-TTG--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[567]								
B. loranthoides1	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[704]								
B. ebolowensis	A-C-T--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[728]								
B. gabonensis	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[730]								
B. longipetiolatal	A--TTG--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[734]								
B. horticola	W-C-T-GA--AGAAACGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-AMG	[732]								
B. eminii	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[729]								
B. capillipes	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[722]								
B. manili	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[729]								
B. molleri	A--TTG--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[731]								
B. furfuracea	A--TTG--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[722]								
B. salaziensis	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[745]								
B. comorensis	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[745]								
B. nosisiba	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[743]								
B. francoisii	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[744]								
B. madecassa	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[744]								
B. ankaranensis	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[744]								
B. nana	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[746]								
B. betimesaraka	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[745]								
B. scapigera	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[745]								
B. dewildel	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[719]								
B. asplenifolia	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[739]								
B. thomeana	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[719]								
B. luconda	A-T-TG--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACA	[745]								
B. meyerijohannis	A-C-T-G--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[747]								
B. engleri	A-C-TT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[748]								
B. annobonensis1	A-C-TT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[748]								
B. socotrana	A-C-TG--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[759]								
B. holtonis	A-C-GT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[757]								
B. lobata	A-C-TT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[759]								
B. luxurians1	A-C-TT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[720]								
B. obliqua	A-C-TT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[749]								
B. violifolia	AAC-TC--ATAACGGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[757]								
B. incarnata	A-C-TT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[758]								
B. convolvulacea	A-C-TT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[783]								
B. angularis	A-C-TT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[759]								
B. crassirostris	A-C-TT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[753]								
B. masoniana	A-C-TT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[755]								
B. aequata	A-C-TT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[764]								
B. rhoxburghi	A-C-TT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[756]								
B. palmata	A-C-TT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[756]								
S. sanguinea	A-C-TT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[768]								
B. fallax	A-C-TT--AGAATCGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[757]								
B. floccifera	-----ATAACGGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[532]								
D. caennabina	A-C-A--ATAACGGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[761]								
D. glommerata	A-C-A--ATAACGGGC--TCCCTT-GCCCTCGAFTTCGG-GATGC--AGGG-CGC-YGCGAGCTT--GAAAA--TCA-CAC-ACG	[768]								

	1010	1020	1030	1040	1050	1060	1070	1080	1090	1100]
B. baccata	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[664]								
B. amplal	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[665]								
B. poculiferal	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[665]								
B. loranthoides1	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[802]								
B. ebolowensis	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[826]								
B. gabonensis	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[828]								
B. longipetiolatal	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[832]								
B. horticola	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[830]								
B. eminii	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[827]								
B. capillipes	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[820]								
B. manii1	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[826]								
B. molleri	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[829]								
B. furfuracea	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[820]								
B. salaziensis	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[843]								
B. comorensis	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[843]								
B. nossibeae	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[841]								
B. francoisii	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[842]								
B. madecassa	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[842]								
B. ankaransensis	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[842]								
B. nana	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[845]								
B. betsimesaraka	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[843]								
B. seapigera	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[862]								
B. dewildei	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[817]								
B. asplenifolia	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[837]								
B. thomeana	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[817]								
B. tiucunda	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[843]								
B. meyerijohannis	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[845]								
B. engleri	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[846]								
B. annobonensis1	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[846]								
B. socotrana	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[857]								
B. holtonis	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[855]								
B. lobata	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[857]								
B. luxurians1	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[818]								
B. obliqua	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[847]								
B. violifolia	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[855]								
B. incarnata	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[856]								
B. convolvulacea	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[881]								
B. angulolaris	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[857]								
B. crassirostris	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[851]								
B. masoniana	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[853]								
B. aequata	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[862]								
B. rhoxburghi	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[855]								
B. palmata	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[854]								
S. sanguinea	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[866]								
B. fallax	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[855]								
B. floccifera	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[532]								
D. cannabina	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[859]								
D. glommerata	ACTCTCGACAACGGGATATCTCGGCTCTCGCATCGATCGAATCGGATAGTGAATCGGATACCTTGGTGTGAAATTCGAGAAATCCC-GTGAACCATC-GAGTTT	[866]								

	1110	1120	1130	1140	1150	1160	1170	1180	1190	1200	
B. baccata	TTGAACGCAAGTTGCGCCCGAAGCCTTCTGGCGGAGGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-GCGCCTATAAAAA	[758]									
B. amplal	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CTGSCAAAAAA	[757]									
B. poculiferal	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[757]									
B. loranthoides1	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[893]									
B. ebolowensis	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[913]									
B. gabonensis	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[915]									
B. longipatiolatal	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[924]									
B. horticola	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[917]									
B. eminiil	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[914]									
B. capillilipes	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[908]									
B. maniiil	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[914]									
B. molleril	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[916]									
B. furfuracea	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[908]									
B. salaziensis	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[929]									
B. comorensis	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[929]									
B. nossibeal	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[927]									
B. francoisil	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[928]									
B. madericassa	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[927]									
B. ankaraniensis	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[928]									
B. nana	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[930]									
B. betsimesaraka	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[928]									
B. scapigera	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[951]									
B. dewildei	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[906]									
B. asplenifolia	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[929]									
B. thomeana	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[904]									
B. iucunda	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[930]									
B. meyerijohannis	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[931]									
B. engleri	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[933]									
B. annobonensis1	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[935]									
B. socotrana	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[943]									
B. holtonis	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[942]									
B. lobata	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[943]									
B. luxurians1	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[903]									
B. obliqua	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[936]									
B. violifolia	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[944]									
B. incarnata	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[943]									
B. convolvulacea	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[968]									
B. angularis	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[943]									
B. crassirostris	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[942]									
B. masoniana	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[945]									
B. aequata	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[950]									
B. rhoxburghi	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[947]									
B. palmata	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[945]									
S. sanguinea	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[955]									
B. fallax	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[948]									
B. floccifera	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[580]									
D. cannabina	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[943]									
D. glomerata	TTGAACGCAAGTTGCGCCCGAAGCCTTGGCGGAGGGACGCTGCTGCTGGGGTTCACGCAATCG-TGGCCCTCCACGCTC-CCGCCAAAAAA	[950]									

[1310	1320	1330	1340	1350	1360	1370	1380	1390	1400]
[----	----	----	----	----	----	----	----	----	----
B. baccata	--GGCC--GGACTTTT--	----	-----GGTTGGAC----	-----GAGGGGGCAGTTTGGCTCCCGTGGCAGC--GATC--GCGCGGTTGGCCCTAAAAGTTGAGT	[859]					
B. amplai	--GGCC--GGACTTTT--	----	-----GGTTGGGG--	-----GAGGGGGCAATTTGGCTCCCGTGGCAGC--GGTC--GCGCGGTTGGCCCTAAAAGTTGAGC	[860]					
B. poculiferai	--GGCC--GGACTTTT--	----	-----GGTTGGGG--	-----ACGAGGGGG--CAATTTGGCTCCCGTGGCAGC--GATC--GCGCGGTTGGCCCTAAAAGTTGAGC	[859]					
B. loranthoides1	--GGCC--AGACTTTT--	----	-----GGTCGGAC--	-----GAGGGGG--CAATTTGGCTCCCGTGGCAGC--GATC--GCGCGGTTGGCCCTAAAAGTTGAGT	[993]					
B. ebolowensis	--GGCT--GGACTTTT--	----	-----GGTVGGAC--	-----GAGGGGG--CGATTTGGCTCCCGTGGCAGC--GATC--GCGCGGTTAGCCCTAAAAGTCGAGT	[1009]					
B. abonensis	--GGCT--GGACTTTT--	----	-----GGTVGGAC--	-----GAGGGGG--CGATTTGGCTCCCGTGGCAGC--GATC--GCGCGGTTGGCCCTAAAAGTCGAGT	[1011]					
B. longipetiolatal	--GACC--GGACTTTT--	----	-----GGTVGGAC--	-----GAGGGGG--CAATTTGGCTCCCGTGGCAGC--GATC--GCGCGGTTGGCCCTAAAAGTTGAGT	[1033]					
B. horticola	--GGTA--GGACTTTT--	----	-----GGTVGGAM--	-----GAGGGGG--CAATTTGGCTCCCGTGGCAGC--GATC--GCGCGGTTGGCCCTAAAAGTTGAGT	[1013]					
B. eminii	--GGTT--GGACTTTT--	----	-----GGTCGGAC--	-----GAGGGGG--TGATTTGGCTCCCGTGGCAGC--GATC--GCGCGGTTGGCCCTAAAAGTCGAGT	[1010]					
B. capillipes	--GGTT--GGACTTTT--	----	-----GGTVGGAC--	-----GAGGGGG--CGATTTGGCTCCCGTGGCAGC--GATC--GCGCGGTTGGCCCTAAAAGTCGAGT	[1003]					
B. manii1	--GGTT--GGACTTTT--	----	-----GGTVGGAC--	-----GAGGGGG--CGATTTGGCTCCCGTGGCAGC--GATC--GCGCGGTTGGCCCTAAAAGTCGAGT	[1010]					
B. molleri	--GGCC--GGACTTTT--	----	-----GGTCGGAC--	-----GAGGGGG--CAATTTGGCTCCCGTGGCAGC--GATC--GCGCGGTTGGCCCTAAAAGTCGAGT	[1018]					
B. furfuracea	--TGCT--GGACTTTT--	----	-----GGTCGGAC--	-----GAGGGGG--TAATTTGGCTCCCGTGGCAGC--GATC--GCGCGGTTGGCCCTAAAAGTCGAGT	[1013]					
B. salazariensis	--GGCT--TGCAAT--	----	-----GGTTTCGAT--	-----GAGTTGG--TAATTTGGCTCCCGTGGCAGC--AAGT--GCACTGGTTGGTCTAAAATTTGAGT	[1057]					
B. comorensis	--GGCT--TGCAAT--	----	-----GGTTTCGAT--	-----GAGTTGG--TAATTTGGCTCCCGTGGCAGC--AAGT--GCACTGGTTGGTCTAAAATTTGAGT	[1057]					
B. nossibeae	--GGCT--GGCAAT--	----	-----GGTTTCGAT--	-----GAGTTGG--TCATTTGACTCCCTTGGCAGC--AAGT--GCATGGTTGGTCTAAAATTTGAGT	[1055]					
B. francoisii	--GGCT--GGCAAT--	----	-----GGTTTCGAT--	-----GAGTTGG--TCATTTGACTCCCTTGGCAGC--AAGT--GCATGGTTGGTCTAAAATTTGAGT	[1056]					
B. madecassa	--GGTT--GGCAAT--	----	-----GGTTTCGAT--	-----GAGTTGG--TAATTTGGCTCCCGTGGCAGC--AAGT--GCATGGTTGGTCTAAAATTTGAGT	[1026]					
B. ankaranensis	--GGCT--GGCAAT--	----	-----GGTTTCGAT--	-----GAGTTGG--TAGTTGGCTCCCGTGGCAGC--AAGT--GCGCGGTTGGTCTAAAATTTGAGT	[1058]					
B. nana	----	----	-----AT--	-----GAGTTGG--CAATTTGGCTCCCGTGGCAGC--AAGT--GCACGGTTGGTCTAAAATTTGAGT	[997]					
B. betsimesaraka	----	----	-----AT--	-----GAGTTGG--CAATTTGGCTCCCGTGGCAGC--AAGT--GCACGGTTGGTCTAAAATTTGAGT	[995]					
B. scapigera	--GCTT--GGATTTGACGCTC--	----	-----GTTTGGAC--	-----GGGGGGT--CAAGTTGGCTCCCGTGGCAGC--AAGC--ACC--TCGCGGTTGGTCTAAAAGTTGAGT	[1075]					
B. dewildei	--GCTG--GGATTTGCGTCTC--	----	-----GTTTGGAC--	-----GAGCGGG--CAAGTTGGCTCCCGTGGCAGC--AAGA--GCGCGGTTGGTCTAAAAGTTGAGT	[1033]					
B. asplenifolia	--GCGG--GC--TGSCATCCG--	----	-----GTTTGGC--	-----GAGCGGG--MMAGTTGGCTCCCGTGGCAGC--AGCC--GCGCGGTTGGTCTAAAAGTTGAGT	[1050]					
B. thomeana	--GGT--GGCCTTT--	----	-----GCTCCGGAC--	-----GGGGTGG--TAACGTTGGCTCCCGTGGCAGC--GATC--GCGCGGTTGGCCCTAAAAGTCGAGC	[1036]					
B. luocunda	--GGCTT--GCATAAT--	----	-----GCTTGGT--	-----GGGGTGG--TAACGTTGGCTCCCGTGGCAGC--GATC--GCGCGGTTGGCCCTAAAAGTCGAGC	[1052]					
B. meyerijohannis	----	----	-----GGCCAGAC--	-----GGGGGGG--TAATTTGGCTCCCGTGGCAGC--GCTC--GCACGGTTGGCCCTAAAAGTCGAGT	[1003]					
B. engleri	--GGCCTTT--	----	-----GGCTGGCC--	-----GAGTTGG--CGACATTTGATCTCCCGTGGTGG--CY--TCGCGGTTGGTCTAAAATTTGAGT	[1007]					
B. annobonensis1	----	----	-----GGCCAGAC--	-----GGGGGGG--TAATTTGGCTCCCGTGGCAGC--GCTC--GCACGGTTGGCCCTAAAAGTCGAGT	[1005]					
B. socotrana	--CGCC--GGCCTTGGCGGG--	----	-----AGGGGGTC--	-----GAGTTGG--CGACATTTGATCTCCCGTGGTGG--AGCC--TCGCGGTTGGTCTAAAATTTGAGT	[1087]					
B. holtonis	--GGCT--GGTTGGGA--	----	-----GAGTTGGTC--	-----GGGGGGC--AGACATTTGGCTCCCGTGGCAGC--GACC--TCGCGGTTGGTCTAAAAGTCGAGT	[1068]					
B. lobata	--GGCT--GGCCTT--	----	-----TGCGGTTG--	-----GTGGCGG--CGACATTTGGCTCCCGTGGCAGC--GACC--TCGCGGTTGGCCCTAAAAGTTGAGT	[1071]					
B. luxurians1	--GGCT--GGCCTT--	----	-----GGCGGTTG--	-----GTGGTGG--CGACATTTGGCTCCCGTGGCAGC--GACC--TCGCGGTTGGCCCTAAAATTTGAGT	[1031]					
B. obliqua	GGGGCA--GA--TGGGA--	----	-----GAA--TGCTC--	-----GGGGGGT--AGAAATGGCTCCCGTGGCAGC--ATCCATCGG--TTGGTCTAAAAGTCGAGT	[1061]					
B. violifolia	--GGGT--GGCCTTTC--	----	-----GTTTGGTC--	-----GGGTGG--CGACATTTGGCTCCCGTGGCAGC--AACC--TCGCGGTTGGCCCTAAAATTTGAGT	[1064]					
B. incarnata	--GGCT--GGCCTTTT--	----	-----GGGTGGTC--	-----GGGTGG--CAACATTTGGCTCCCGTGGCAGC--AACC--TCGCGGTTGGTCTAAAATTTGAGT	[1070]					
B. convolvulaceae	--GGCTT--GCTCTT--	----	-----GGGTGATG--	-----GTGGTGG--CGACATTTGGCTCCCGTGGCAGC--AATC--TCGCGGTTGGTCTAAAATTTGAGT	[1097]					
B. angularis	----	----	-----GGGCAGTC--	-----GTGGCGG--CGACATTTGGCTCCCGTGGCAGC--GACC--TCGCGGTTGGCCCTAAAATTTGAGT	[1006]					
B. crassirostris	GTGGCT--GGCCTTTT--	----	-----GGGCAGTC--	-----GGGGAGG--CGACATTTGGCTCCCGTGGCAGC--AACC--TCGCGGTTGGTCTAAAATTTGAGT	[1067]					
B. masoniana	TTTGT--GGCCTTTT--	----	-----GGGTGGTC--	-----GGGGAGG--CCACTTTGGCTCCCGTGGCAGC--AACC--TCGCGGTTGGTCTAAAATTTGAGT	[1067]					
B. aequata	----	----	-----GGTTCGTC--	-----GGGGAGG--CGTTCGCTCCCGTGGCAGC--AACC--TCGCGGTTGGTCTAAAATTTGAGT	[1089]					
B. rhoxburghii	GTGT--GGCCTTTT--	----	-----GGGCAGTC--	-----GGGGAGG--CGACATTTGGCTCCCGTGGCAGC--AACC--TCGCGGTTGGTCTAAAATTTGAGT	[1080]					
B. palmata	GTGGCT--GGTCTTTT--	----	-----GGGGTC--	-----GGGGAGG--CGACATTTGGCTCCCGTGGCAGC--AACC--TCGCGGTTGGTCTAAAATTTGAGT	[1076]					
S. sanguinea	----	----	-----GGTTCGTC--	-----GGGGAGG--CGACATTTGGCTCCCGTGGCAGC--ARCY--TCGCGGTTGGTCTAAAATTTGAGT	[1082]					
B. fallax	GGTGT--GGCCTTTT--	----	-----GGTCGGTC--	-----GGGGAGG--CGACATTTGGCTCCCGTGGCAGC--AACC--GCGCGGTTGGCCCTAAAATTTGAGT	[1024]					
B. floccifera	----	----	-----GGGTGTTT--	-----GGGGAGG--CGACATTTGGCTCCCGTGGCAGC--AGCC--TCGCGGTTGGCCCTAAAATTTGAGT	[667]					
D. cannabina	----	----	-----GG--GGCC--	-----GG--GGCC--AGATTTGGTCTCCCGTGGCAGC--TGTT--GTGTGGTTGGCCCTAAAAGTCGAGT	[1022]					
D. glommerata	----	----	-----GG--GAGC--	-----GG--GAGC--AGACATTTGGTCTCCCGTGGCAGC--TGCC--GTGTGGTTGGCCCTAAAAGTCGAGT	[1029]					

[1410 1420 1430 1440 1450 1460 1470 1480 1490 1500]

[CCTGGCGT--CGCGAGTGCATCGACGGTGGTT--TTT--TAGCCCTCGGCGAGACAC--ATTGCACGTGCGAGACGGGTATCGG--GAG--CTCC [1946]
CCTGGCGT--CGCGAGTGCATCGACGGTGGTT--TT--TAGCCCTCGGCGAGATAC--ATTGCACGTGCGAGACGGGTATCGG--GAG--CTCC [1946]
CCTGGCGT--CGCGAGTGCATCGACGGTGGTT--TT--TAGCCCTCGGCGAGATAC--ATTGCACGTGCGAGACGGGTATCGG--GAG--CTCC [1945]
CCTGGCGT--CGCGAGTGCATCGACGGTGGTT--TT--TTGCCCTCGGCGAGATAC--ATTGCACGTGCGAGACGGGTATCGG--GAGGGCTCC [1081]
CCTGGCGT--CGCGAGTGCATCGACGGTGGTT--TT--TAGCCCTCGGCGAAATAC--GTTGCACGTGCGAGACGGGTATCGG--GAA--CTCC [1095]
CCTGGCGT--CGCGAGTGCATCGACGGTGGTT--TTATTAGCCCTCGGCGAAACAC--GTTGCACGTGCGAGACGGGTATCGG--GAA--CTCC [1099]
CCTGGCGT--CGCGAGTGCATCGACGGTGGTT--TTTA--TAGCCCTCGGCGAAATAC--ATTGCACGTGCGAGACGGGTATCGG--GAG--CTCC [1121]
CCTGGCGT--CGCGAGTGCATCGACGGTGGTT--TTTA--TAGCCCTCGGCGAAATAC--ATTGCACGTGCGAGACGGGTATCGG--GAA--TTCC [1101]
CCTGGCGT--CGCGAGTGCATCGACGGTGGTT--TTTA--GCCCCTCGGCGAAATAC--GTTGCACGTGCGAGATCGGATCGG--GAA--CTCC [1096]
CCTGGCGT--CGCGAGTGCATCGACGGTGGTT--TTTA--GCCCCTCGGCGAAATAC--GTTGCACGTGCGAGATCGGATCGG--GAA--TTCC [1089]
CCTGGCGT--CGCGAGTGCATCGACGGTGGTT--TTTA--GCCCCTCGGCGAAATAC--GTTGCACGTGCGAGATCGGATCGG--GAA--TTCC [1095]
CCTGGCGT--CGCGAGTGCATCGACGGTGGTT--TTTG--GCCCCTCGGCGAAATAC--GTTGCACGTGCGAGACGGGTATCGG--GAA--CTCC [1104]
CCTGGCGT--CGCGAGTGCATCGACGGTGGTT--TTTA--GCCCCTCGGCGAAATAC--GTTGCACGTGCGAGATCGATACAG--GAA--CTCC [1099]
CCTGGCGT--TGCGAGTGCATCGGCGTGGTT--GCCAT--GCCCTCGGCGAAATAC--ATTGCACGTGCGGAGTGCATGTTCCG--GAA--CTCC [1144]
CCTGGCGT--TGCGAGTGCATCGGCGTGGTT--GCCAT--GCCCTCGGCGAAATAC--ATTGCACGTGCGGAGTGCATGTTCCG--GAA--CTCC [1144]
CCTAGCGT--TGCGAGTGCATCGACGGTGGTT--GCCAT--GCCCTCGGCGAAATAC--ATTGCACGTGCGGAGTGCATGTTGA--GAA--CTCC [1142]
CCTAGCGT--TGCGAGTGCATCGACGGTGGTT--GCCAT--GCCCTCGGCGAAATAC--ATTGCACGTGCGGAGTGCATGTTGA--GAA--CTCC [1143]
CCTGGCGT--TGCGAGTGCATCGGCGTGGTT--GTCAT--GCCCTCGGCGAAATAC--ATTGCACGTGCGGAGTGCATGTTCCG--GAA--CTCC [1113]
CCTGGCGT--TGCGAGTGCATCGGCGTGGTT--GCCAT--GCCCTCGGCGAAATAC--ATTGCACGTGCGGAGTGCATGTTCCG--GAA--CTCC [1145]
CCTGGCGT--TGCGAGTGCATCGGCGTGGTT--GCCAT--GCCCTCGGCGAAATAC--ATTGCACGTGCGGAGTGCATGTTCCG--GAA--CTCC [1084]
CCTGGCGT--TGCGAGTGCATCGGCGTGGTT--GCCAT--GCCCTCGGCGAAATAC--ATTGCACGTGCGGAGTGCATGTTCCG--GAA--CTCC [1082]
GCTGGCGT--TGCGAGTGCATCGACGGTGGTT--TTGTA--GCCCTCGGCGAAATAC--GTTGCACGTGCGGAGTGCATGTTCCG--GAG--CTCC [1162]
GATGGCGT--TGCGAGTGCATCGACGGTGGTT--TCCAT--TCCCTCGGCGAAATAC--GTTGCACGTGCGGAGTGCATGTTCCG--GAG--CTCC [1121]
ACTGGCGT--CGCGAGTGCATCGGCGTGGTT--CASTC--ACCCTCGGCGAAATAC--GRTGCACGTGCGGAGTGCATGTTCCG--GAG--CTCC [1137]
GTTGGCGT--CGCGAGTGCATCGGCGTGGTT--TCCAT--GCCCTCGGCGAAATAC--GTTGCACGTGCGGAGTGCATGTTCCG--GAG--CTCC [1121]
CCTGGCGT--CGCGAGTGCATCGGCGTGGTT--GCCAT--ACCCTCGGCGAAATAC--ATTGCACGTGCGAGTGCATGTTTG--AGTA--GTTCC [1139]
CCTGGCGT--CGCGAGTGCATCGGCGTGGTT--GCCAT--ACCCTCGGCGAAATAC--ATTGCACGTGCGAGTGCATGTTTG--GAA--CTCT [1090]
CCTCAGCAT--CGCGAACAGTGCATGTTGGTT--GGAAT--GCCCTGFTGGATAC--GTTTCCCTCACAGACGCGCCTACGAG--GAA--CTCT [1095]
CCTCAGCAT--CGCACACGATGCACGGTGGTT--GCAAT--GCCCTGFTGGATAC--ATTGGGCTGTGAGATCGGATACGAG--GAA--ATCC [1093]
CCTGGCGT--CTTCGACGCGATCGACGGTGGTT--GCCAT--GCCCTCGAGAAATAC--GTTCCGCGATGCGGAGCAGCCTCGCG--GAA--CTCC [1175]
CCTGGCGT--CTTCGCGGCGATCGACGGTGGTT--GACAT--GCCCTCGAGAAAT--AC--GTTGGGCTGCAAGATCGGTTTGA--GAA--CTC- [1153]
CCTGGCGT--ATTGGGCGGATCGACGGTGGTT--TCCAT--GCCCTCGAGAAATAC--ATTGGGCTGCGAGATGCTTAT--GAA--CTCT [1159]
CCTGGCGT--CTTGGGCGGATCGACGGTGGTT--TCCAT--GCCCTCGAGAAATAC--ATTGGGCTGCGAGATGCTTAT--GAA--CTCT [1119]
CCTGGCGT--CTTGGGCGGATCGACGGTGGTT--GACAT--GCCCTCGAGAAAT--AC--ATTGGGCTGCGAGACGGGTTCGG--GAA--CTC- [1146]
CCTGGCGT--CTTGGGCGGATCGACGGTGGTT--TCTAT--GCCCTCGAGAAATAC--GTTGGGCTGCGAGGCGCGCTCGG--GAA--CTCC [1151]
CCTGGCGT--CTTGGGCGGATCGACGGTGGTT--GCCAT--GCCCTCGAGAAATAC--ATTGGGCTGCGAGACGGGTTCGG--GAA--CTCC [1157]
CCTGGCGT--ATTGGGCGGATCGACGGTGGTT--TCCAT--GCCCTCGAGAAATAC--ATTGGGCTGCGAGATGCTTAT--GGA--CTCC [1185]
CCTGGCGT--CTCGCAGCGGATCGACGGTGGTT--TCCAT--GCCCTCGAGAAATAC--ATTGGGCTGCGAGATGCTTAT--GGA--CTCT [1094]
CCTGGCGT--CTCGCAGCGGATCGACGGTGGTT--GCCAT--GCCCTCGAGAAATAC--ATTGGGCTGCGAGATGCTTAT--GGA--CTCC [1154]
CCTGGCGT--CTTGGGCGGATCGACGGTGGTT--GCCAT--GCCCTCGAGAAATAC--GTTTGGCCCGCGAGGAGCGGATCGG--GAA--CTCC [1179]
CCTGGCGT--CCAGGCGGATCGACGGTGGTT--GCCAT--GCCCTCGAGAAATAC--GTTTGGCCCGCGAGGAGCGGATCGG--GAA--CTCC [1164]
CCTGGCGT--CTTGCAGCGGATCGACGGTGGTT--GCCAT--GCCCTCGAGCTTATAC--ATTGGGCTGCGAGACGGGTTCGA--GTA--CTCC [1167]
CCTGGCGT--CTTGGGCGGATCGACGGTGGTT--GCCAT--GCCCTCGAGAAATAC--ATTGGGCTGCGAGGCGCGCGTGGG--GAA--CTCC [1163]
CCTGGCGT--CTTGGGCGGATCGACGGTGGTT--GTCAT--GCCCTCGAGAAATAC--ATTGGGCTGCGAGACGGGTTCGA--GTA--CTCC [1169]
CCTGGCGT--CTTGGGCGGATCGACGGTGGTT--GCCAT--GCCCTCGAGAAATAC--GTTGGGCTGCGAGACGGGTTCGA--GTA--CTCC [1113]
CCTGGCGT--CTTGGGCGGATCGACGGTGGTT--GCCAT--GCCCTCGAGAAATAC--GTTGGGCTGCGAGACGGGTTCGA--GTA--CTCC [754]
CCTGGC--TTTCAAT--GCGCGGCAAAACGGTGGTT--GTCAA--GC--CTCAGGCTCTGT-----CACGTGTCT--TGATGAAAAC--GAGG--TC- [1104]
CCTGGC--TTTCAAT--GCGCGTGCACAAACGGTGGTT--GTCAA--GC--CTCAGGCTCTGT-----GCGGTGCTGT--TGATGAAAACATC--GAGG--TC- [1111]

	1510	1520	1530	1540	1550	1560	1570	1580	1590	1600
B. baccata	-CACGC	-----GACC?	-TGC-TGCCTGCCTCGTCG-GTT	-----CCTCGG-AGAAG	-----GACGAGGA-GGCCTAT	-----CGAAGC-GAC	[1013]			
B. amplal	-CACGC	-----GACC	-TGC-TGCCTGCCTCGTTG-GTT	-----CCTCGG-AGAAG	-----GACGAGGA-GGCCTAT	-----CGAAGC-GAC	[1013]			
B. poculiferal	-CACGT	-----GACC	-TGC-TGCCTGCCTCGTCG-GTT	-----CCTCGG-AGAAG	-----GACGAGGA-GGCCTAT	-----CGAAGC-GAC	[1012]			
B. loranthoides1	-CACGC	-----GACC	-TGC-TGCCTGCCTCGTTG-AAT	-----CCTCGG-AGAAG	-----GACGAGGA-GGCCTAT	-----CGAAGC-GAC	[1148]			
B. ebolowensis	-CACGC	-----GACC	-TGC-TGCCTGCC-CGATC-GTTT	-----TTC	-----GACGGGA-GGCCTAT	-----CGAAGC-GAC	[1158]			
B. gbonensis	-CACGC	-----GACC	-TGC-TGCCTGCC-CGGTC-GTT	-----CTCCG-GAAC	-----GACGGGA-GGCCTAT	-----CGAAGC-GAC	[1163]			
B. longipetiolatal	-CACGC	-----GACC	-TAC-TGCCTGCCTCGACC-CIT	-----CTTGAGGAAGGAAGA-GAA	-----GGCGCGTAT	-----CGAAGC-GAC	[1191]			
B. horticola	-CACGC	-----GACC	-TGC-TGCCTGCC-CTGYC-GTT	-----CTCC	-----GACGGGA-GGCCTAT	-----CGAAGC-GAC	[1164]			
B. eminii	CTTTGC	-----GACC	-TGC-TGCCTGCC-CCGTC-GTT	-----CGT-AGAAC	-----GACGGGA-GGCCTAT	-----TCGAA-C-GAC	[1160]			
B. capillipes	-CACGC	-----GACC	-TGC-TGCCTGCC-CGGTC-GTT	-----CTCC	-----GACGGGA-GGCCTAT	-----CGARGC-GAC	[1152]			
B. manili	-CACGC	-----GACC	-TGC-TGCCTGCC-CCGTC-GTT	-----CTAC-GAAC	-----GATGGGA-GGCCTAT	-----CGAAGC-GAC	[1159]			
B. molleri	-CACGC	-----GACC	-TGC-TGCCTGCC-CTC-GGA	-----GAAC	-----GACGAGG-GGCCTAT	-----CGAAGC-GAC	[1163]			
B. fufuracea	-CACGC	-----GACC	-TGC-TGCCTGCC-CTC-GGA	-----GAAC	-----GACGAGG-GGCCTAT	-----CGAAGC-GAC	[1158]			
B. salaziensis	-TTTGC	-----GACC	-TAT-TGCCTGCCTC-GCTTGT	-----CCTCCG-AGCC	-----VATGAGAA-GACGWTAT	-----CGAAGC-GAC	[1211]			
B. comorensis	-TTTGC	-----GACC	-TAT-TGCCTGCCTC-GTTGGTT	-----CCTCCG-AGAAC	-----AATGAGAA-GACGTTAT	-----CGAAGC-GAC	[1211]			
B. nossibea	-TTTGC	-----GACC	-AAT-TGTGCTGCCTT-GTTGGTT	-----CCTTCG-AGAAC	-----AATGAGAA-TACGTTAT	-----CGAAGC-GAC	[1209]			
B. francoisii	-TTTGC	-----GACC	-AAT-TGTGCTGCCTT-GTTGGTT	-----CCTTCG-AGAAC	-----AATGAGAA-GACGTTAT	-----CGAAGC-GAC	[1210]			
B. madecassa	-TTTGT	-----GACC	-TAT-TGCCTGCCTC-GTTGGTT	-----CCTCGA-AGAAC	-----AACGAGAA-GACGTTAT	-----CGAAGC-GAC	[1180]			
B. ankaranensis	-TTTGC	-----GACC	-AAT-TGTGCTGCCTC-GTTGGTT	-----CCTTCG-AGAAC	-----AATGAGAA-GACGTTAT	-----CGAAGC-GAC	[1212]			
B. nana	-TTTGC	-----GACC	-TAT-TGCCTGCCTC-GTTGGTT	-----CCTCCG-AGAAC	-----CATGAGAA-GACGTTAT	-----CGAAGC-GAC	[1151]			
B. betsimesaraka	-TTTGC	-----GACC	-TAT-TGCCTGCCTC-GTTGGTT	-----CCTCCG-AGAAC	-----CATGAGAA-GACGTTAT	-----CGAAGC-GAC	[1149]			
B. scapigera	-ATACG	-----GACC	-TGC-TGATGATGCC-GCT	-----CGCGGT-TCCCT	-----GCGAGAA-GGCCTG	-----CGAAGC-GAC	[1225]			
B. dewildei	CATGG	-----GACC	-TGC-TGATGA-CGCC-TTCC	-----CGCGGT-TCCCC	-----CCMGGA-GGCCTG	-----CGAAGC-GAC	[1185]			
B. asplenifolia	-ATCG	-----GACC	-TGC-TGATGCCCTGCT	-----CGCGGAG-ATCT	-----GCGAGAT-GGCCTG	-----CGAAGC-GAC	[1196]			
B. thomeana	-G	-----GACC	-TCC-TGCC-CTGCTC-GTCGGCT	-----CMTTCG-GAAC	-----GACGGG-A-GCGAYGT	-----CGAAGC-GAC	[1184]			
B. lucunda	-GCAA	-----GACC	-TGC-TGCCTGCCTC-TCGATTT	-----CATT-GAGAAC	-----GAGGAGAA-G-CGCTAT	-----CGAAGC-GAC	[1201]			
B. meyerijohannis	-TTTGC	-----GACC	-TGC-TGCCTGCCTC-GTCGGTT	-----CCTCCG-GGATC	-----GACGGGR-GACGTCAT	-----CGAAGC-GAC	[1157]			
B. engleri	-TTTGC	-----GACC	-----AACC	-----	-----	-----	[1105]			
B. annobonensis1	-TTTGC	-----GACC	-TAT-TGTGTCATTC-GTTGCTAA	-----CCGTTAG-GTGCA	-----GCGGYTC-GACATCAT	-----CGAAGC-GAC	[1162]			
B. socotrana	-TCCAG	-----GACC	-TAA-TGCCTGCCTC-GCCGG	-----ACG-AGACC	-----GGCGAGGA-GACGTCGTAT	-----CGAAGC-GAC	[1239]			
B. holtonis	-TTGAC	-----GACC	-TAG-TGCCTGCGGA-GTC	-----GGAGA-AGAAC	-----GACGAGCA-GACGTTAT	-----CGAAGC-GAC	[1215]			
B. lobata	-TGGAC	-----GACCCTCT-AAT	-----GTTCC	-----	-----TCA-AATGTTAT	-----CGAAGC-GAC	[1200]			
B. luxurians1	-TGGAC	-----GACCCTC	-----	-----	-----A-AATGTTAT	-----CGAAGC-GAC	[1149]			
B. obliqua	-TGGAG	-----GACCC	-AG-TGCCTGCGGA-GTC	-----GGACA-GGAAC	-----GATGAGCA-GACGTTAT	-----CGAAGC-GAC	[1208]			
B. violifolia	-TCGAC	-----GACC	-TAA-CGCTGCGCTG-GTTGG	-----GCA-ACACC	-----GGCGAGCA-GACGTTAT	-----CGAAGC-GAC	[1213]			
B. incarnata	-TCGAC	-----GACC	-TAA-TGCCTGCGCTA-GCCGG	-----ACA-ACACT	-----GGCGAGCA-GACGTTAT	-----AGAACG-GAC	[1219]			
B. convolvulacea	-TCAAC	-----GACCCTCA-TAA	-----CGTTA	-----	-----TGA-ACGTTAT	-----CGAAGC-GAC	[1226]			
B. angularis	-TTCAC	-----GACC	-TAA-TGCCTGACTC-GTC	-----GGAGG-ACAAC	-----GGCGAGAA-GATGTTAT	-----CGAAGC-GAC	[1135]			
B. crassirostris	-TGGTY	-----GACC	-TAA-TGCCTGACTC-GTT	-----GGACA-RCACC	-----AGCGAGGA-GACGTTAT	-----CGAAGC-GAC	[1216]			
B. masoniana	-TCAAC	-----GACC	-TAA-TGCCTGACTC-GTT	-----GGACA-ACACC	-----AGCGAGAA-GGCCTAT	-----CGAAGC-GAC	[1227]			
B. seaquata	-TCGAC	-----GACC	-TAA-TGCCTGACTC-GTC	-----GGACA-ACAAC	-----GGCGAGAA-GACGTTAT	-----CGAAGC-GAC	[1229]			
B. rhoxburghi	-TCGAC	-----GACC	-TAA-TGCCTGACTC-GTC	-----GGACA-ACACC	-----GACGAGAA-GACGTTAT	-----CGAAGC-GAC	[1225]			
B. palmeta	-TCGTC	-----GACC	-TAA-TGCCTGACTC-GTT	-----GGACR-CAAC	-----AGCGAGAA-GGCCTAT	-----CGAAGC-GAC	[1231]			
S. sanguinea	-TCGAC	-----GACCCTC	-TAA-TGCCTGACTC-GCT	-----GGACA-ATGCC	-----AGCGAGCA-GACGTTAT	-----CGAAGC-GAC	[1177]			
B. fallax	-TTTGC	-----GACC	-TCA-CGCTGCAACC-CCC	-----GGAGG-AC-TCGT	-----CCCGCGGGAA-GACGTCAT	-----CGGAGC-GAC	[820]			
B. floccifera	-GAATA	-----GACC	-TTC-TGTGTCGACTT	-----	-----CGA	-----CGACGT-GAC	[1147]			
D. cannabina	-TAATA	-----GACC	-TTC-TGCCTGCACCTT	-----	-----CGA	-----CGCTAT-GAC	[1154]			
D. glommerata	-TAATA	-----GACC	-TTC-TGCCTGCACCTT	-----	-----CGA	-----CGCTAT-GAC	[1154]			

	1610	1620	1630	1640	1650	1660	1670	1680	1690	1700]
B. baccata	CCCC?AFTTCCGTTCAAGGCTAAATA-TTAGGGAGAGACCAATAGTACAAACAAGAATCCGAGGGGAAAGATGAAAAGGACTTTGAGAAAAGAGTCAAAGAGT	[1112]								
B. amplal	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1112]								
B. pocaliferal	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1111]								
B. loranthoides1	CCCAG-----GCTAART--TTG-C--AGACGATAGCAAG--TACCYTGAGGGAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1227]								
B. ebolowensis	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1257]								
B. gabonensis	CCCAG-----TACCYTGAGGGAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1216]								
B. longipetiolatal	CCCAG-----CAAGTACCYTGAGGGAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1248]								
B. horticola	CCCAG-----AGGCTAAATA-TTGG--AGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1251]								
B. eminiil	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1259]								
B. capillipes	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1251]								
B. maniiil	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1258]								
B. molleri	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1261]								
B. furfuracea	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1257]								
B. salaziensis	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1310]								
B. comorensis	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1310]								
B. nossibe	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1308]								
B. francoisii	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1309]								
B. madecassa	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1279]								
B. ankaranensis	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1311]								
B. nana	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1250]								
B. betimesaraka	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1248]								
B. scapigera	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1324]								
B. dewilidei	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1284]								
B. asplenifolia	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1295]								
B. thomeana	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1283]								
B. lucunda	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1300]								
B. meyerijohannis	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1256]								
B. engleri	-----ATTCCGTTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1199]								
B. socotrana	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1338]								
B. holtonis	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1261]								
B. lobata	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1315]								
B. luxurians1	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1299]								
B. obliqua	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1248]								
B. violifolia	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1307]								
B. incarnata	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1312]								
B. convolvulacea	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1318]								
B. angularis	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1325]								
B. crassirostris	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1315]								
B. masoniana	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1340]								
B. aequata	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1326]								
B. rhoxburghi	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1328]								
B. palmata	CCCAG-----TCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1323]								
B. sanguinea	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1330]								
B. fallax	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1276]								
B. floccifera	CCCAGATTCCTCCAAAGGCTAAATA-TTGGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[918]								
D. cannabina	CCCAGATTCCTCCAAAGGCTAAATA-CAGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1246]								
D. glomerata	CCCAGATTCCTCCAAAGGCTAAATA-CGSGCGAGAGACCGATAGCAAAAGAATACCCGCGAGGAAAGATGAAAAGACTTTGAGAAAAGAGTCAAAGAGT	[1253]								

	1710	1720	1730	1740	1750	1760	1770	1780	1790	1800
[ACTTGAATTCGTCAGGAGGAAGT	TAGATGGGGTGGTGGTGGCC	TTCGCTTGGATGGAATGATGCC	-TAGCCCGGTCTGCTATCGACTTAGGGTGT-	[1210]					
B. baccata	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGCTTGGTCCGATGGAAC	CGCCGG -TAGCTGGTCTGCCAATCGACTCAGGGCGC-	[1210]					
B. amplai	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1209]					
B. pocaliferai	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1325]					
B. loranthoides1	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1354]					
B. bolowensis	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1314]					
B. gabonensis	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1346]					
B. longipetiolatal	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1348]					
B. horticola	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1356]					
B. capillipes	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1348]					
B. manili	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1357]					
B. molleri	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1358]					
B. furfuracea	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1354]					
B. salaziensis	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1408]					
B. comorensis	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1408]					
B. nossibeae	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1406]					
B. francoisii	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1407]					
B. madecassa	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1377]					
B. ankaranensis	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1409]					
B. nana	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1348]					
B. bethinesaraka	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1346]					
B. scapigera	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1421]					
B. dewildei	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1381]					
B. asplenifolia	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1391]					
B. thomeana	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1380]					
B. lucunda	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1397]					
B. meyeriJohannis	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1354]					
B. engleri	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1297]					
B. annobonensis1	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1359]					
B. socotrana	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1436]					
B. holtonis	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1413]					
B. lobata	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1397]					
B. luxurians1	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1346]					
B. obliqua	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1405]					
B. violifolia	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1410]					
B. incarnata	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1416]					
B. convolvulacea	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1423]					
B. angularis	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1332]					
B. crassirostris	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1413]					
B. masoniana	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1424]					
B. aequata	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1426]					
B. rhoxburghi	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1421]					
B. palmata	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1428]					
S. sanguinea	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1374]					
B. fallax	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1017]					
B. floccifera	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1344]					
D. cannabina	ACTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-	[1351]					
D. glommerata	GCTTGAATTCGTCGGAGGGAAG	CGGATGGGGCCGGTGGCCCTT	GGTCCGATGGAACGGCCGG	-TAGCCCGGTCTGCCAATCGACTCAGGGCGC-						

	1910	1920	1930	1940	1950	1960	1970	1980	1990	2000
B. baccata	GTG-CITTCAGCATCAGCGGCTAATGGCGCTCAGCCCTCGGGTTCCTTAATCAGCTTGCTTGAACAATGGACCAATGAGTCTGACATGTGCGGAGTCAA	[1409]								
B. amplal	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1409]								
B. pulchiferal	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1408]								
B. loranthoides1	GCTTTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1524]								
B. ebolowensis	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1553]								
B. gabonensis	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1513]								
B. longipetiolatal	T-TGCTTCGACATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1544]								
B. horticola	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1547]								
B. eminii	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1555]								
B. capillipes	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1547]								
B. manii	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1556]								
B. molieri	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1557]								
B. furfuracea	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1553]								
B. salazariensis	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1606]								
B. comorensis	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1606]								
B. nossibeae	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1604]								
B. francoisii	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1605]								
B. madecassa	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1575]								
B. ankararansis	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1607]								
B. nana	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1546]								
B. betimesaraka	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1544]								
B. scapigera	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1619]								
B. dewildei	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1579]								
B. asplenifolia	-----	[1457]								
B. thomeana	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1578]								
B. luconda	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1595]								
B. meyerijohannis	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1552]								
B. engleri	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1495]								
B. annobonensis1	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1557]								
B. socotrana	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1634]								
B. holtonis	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1611]								
B. lobata	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1595]								
B. luxurians1	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1544]								
B. obliqua	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1603]								
B. violifolia	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1608]								
B. incarnata	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1614]								
B. angulvulacea	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1621]								
B. angularis	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1530]								
B. crassirostris	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1611]								
B. masoniana	-----	[1443]								
B. aequata	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1622]								
B. rhoxburghi	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1624]								
B. palmata	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1619]								
S. sanguinea	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1626]								
B. fallax	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1573]								
B. floccifera	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1216]								
D. cannabina	GTG-CITTCGGCATCAGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1543]								
D. glomerata	GTG-CITTCGGCAACTCGCGGCTCCCGCGCTCGGCTCGGGTTCCTCCCAATCGGCCCGTCTTGAACAACGGACCAAGGAGTCTGACATGTGCGGAGTCAA	[1550]								

	2010	2020	2030	2040	2050	2060	2070	2080	2090	2100
[
[
B. baccata	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCA?GT-	TGCACCGCCAAATCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1507]				
B. amplal	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGG-TTCGAG	[1506]				
B. pocaliferal	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1506]				
B. loranthoides1	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	-GC-CCG	[1585]				
B. belowowensis	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1651]				
B. gabonensis	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1611]				
B. longipetiolatal	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1607]				
B. horticola	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1645]				
B. emini	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1653]				
B. capillipes	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1644]				
B. manuil	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1654]				
B. molleri	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1655]				
B. furfuracea	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1650]				
B. salazienis	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1704]				
B. comorensis	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1704]				
B. nossibeae	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1702]				
B. francoisii	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1703]				
B. medecassa	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1612]				
B. ankaranensis	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1646]				
B. nana	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1643]				
B. betsimesaraka	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1643]				
B. scapigera	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1716]				
B. dewildei	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1677]				
B. asplenifolia	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1457]				
B. thomeana	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1675]				
B. iucunda	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACMGCCGACCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1693]				
B. meyeri1	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1650]				
B. engleri	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-G-GGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1592]				
B. annobonensis1	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GCCGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1655]				
B. socotrana	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1733]				
B. holtonis	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1709]				
B. lobata	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1693]				
B. luxurians1	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1642]				
B. obliqua	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1701]				
B. violifolia	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1706]				
B. incarnata	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1712]				
B. convolvulacea	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1719]				
B. angularis	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1628]				
B. crassirostris	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1709]				
B. masoniana	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1443]				
B. aequata	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1721]				
B. rhoxburghi	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1722]				
B. palmata	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1717]				
S. sanguinea	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1724]				
B. fallax	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GAGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1671]				
B. floccifera	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-G-GGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1313]				
D. cannabina	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GTGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1641]				
D. glomerata	CGGGCCAGTAAACCCCGT	GAGGCGCAAGAAGCTAA	TGGCGGGATCCCCCTA	-GTGGGT-	TGCACCGCCAGCCGACCTTGATCTTCTGAGAAGGGTTCGAG	[1648]				

[]]

[[

B.baccata T-G [1509]

B.amplal T-G [1508]

B.poculiferal T-G [1508]

B.loranthoides1 --- [1585]

B.ebolowensis TTG [1654]

B.gabonensis T-G [1613]

B.longipetiolatal1 --- [1607]

B.horticola T-G [1647]

B.eminii T-G [1655]

B.capillipes T-G [1646]

B.manii T-G [1656]

B.molleri T-G [1657]

B.fururacea T-G [1652]

B.salaziensis T-G [1706]

B.comorensis T-G [1706]

B.nossibe T-G [1704]

B.francoisii T-G [1705]

B.madecassa --- [1612]

B.ankaranensis --- [1646]

B.nana GTG [1646]

B.betsimesaraka T-G [1644]

B.scapigera T-G [1718]

B.dewildei T-G [1679]

B.asplenifolia --- [1457]

B.thomeana T-G [1677]

B.iucunda T-G [1695]

B.meyeriJohannis T-G [1652]

B.engleri T-G [1594]

B.annobonensis1 T-G [1657]

B.socotrana T-G [1735]

B.holtonis T-G [1711]

B.lobata T-G [1695]

B.luxurians1 T-G [1644]

B.obliqua T-G [1703]

B.violifolia T-G [1708]

B.incarnata T-G [1714]

B.convolvulacea T-G [1721]

B.angularis T-G [1630]

B.crassirostris T-G [1711]

B.masoniana --- [1443]

B.aequata T-G [1723]

B.rhoxburghi T-G [1724]

B.palmata T-G [1719]

S.sanguinea T-G [1726]

B.fallax T-G [1673]

B.floccifera T-G [1315]

D.cannabina T-G [1643]

D.glommerata T-G [1650]

APPENDIX 5 Extended morphological data matrix (Chapter 4).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
<i>B. baccata</i>	0	0	0	1	0	1	2	0	-	0	-	0	0	0	0	0	0	0	0	0	2/3	0	0	0	1	0	0
<i>B. crateris</i>	0	0/1	0	1	0	1	2	0	-	0	-	0	0	0	1	0	0	0	0	0	2/3	0	0	0	1	0	0
<i>B. ampla</i>	0	0	0	1	0	1	1	0	-	0	-	1	0	0	0	0	0	0	1	0	2	0	0	1	0/1	0	0
<i>B. bonus-henricus</i>	0	0	0	1	1	1	1	0	-	0	-	1	0	0	0	0	0	0	1	0	2	0	0	1	0/1	0	0
<i>B. poculifera</i>	0	0	0	1	0	1	1	0	-	0	-	1	0	0/1	0	0	0	0	1	0	2/3	0	0	1	0	0	0
<i>B. capillipes</i>	0	0	1	1	0	0	-	1	1/3	1	0	0	1	1	1	0	0	0	0	1	0/1/2	2	2	0	2	0	1
<i>B. cavallyensis</i>	0	0	1	1	0	1	0	1	0	1	0	0	0/1	0	0	0	?	0	0	0/1	0/1	1	1	0	2	0	1
<i>B. ebolowensis</i>	0	0	0	1	0	1	0	0	-	0	-	0	1	0	0	0	0	0	0	1	1	2	2	0	2	1	1
<i>B. elaeagnifolia</i>	1	0	0	1	0	0	-	1	4	1	0	0	1	0	0	1	1	1	0	1	0/1/2	0	0	0	2	0	1
<i>B. eminii</i>	0	0	0	1	0	0	-	1	2/3	1	0	0	1	0	0	1	1	0	0	1	1	0	0	0	2	0	1
<i>B. furfuracea</i>	0	1	0	1	1	0	-	1	2	1	0	0	1	0	0	1	0	1	0	1	1	0	0	0	2	0	1
<i>B. fusialata</i>	0	0	0	1	0	0	-	1	3	1	0	0	1	0	0	0	0	0	0	1	1	0	1	0	2	1	1
<i>B. fusicarpa</i>	0	0	0	1	0	0	-	1	2	1	0/2	0	1	0	0	0	1	0	0	1	0	1	1	1	2	0	1
<i>B. gabonensis</i>	0	0	0	1	0	1	0	0	-	0	-	0	1	1	0	0	0	0	0	1	1	2	2	0	2	1	1
<i>B. horticola</i>	0	0	0	1	0	0	-	1	1/3	1	0	0	1	0	1	1	0	0	0	1	2	2	2	0	2	0	1
<i>B. karperi</i>	1	1	0	1	0	0	-	1	4	1	0	0	1	0	0	1	1	1	0	1	0/1/2	0	0	0	2	0	1
<i>B. kisuluana</i>	0	0	0/1	1	0	0	-	1	3	1	0	0	1	0	0	1	0	0	0	1	1/2	2	2	0	2	0	1
<i>B. komoensis</i>	0	0	0	1	0	0	-	1	2	1	0	0	1	0	1	1	0	0	0	1	1/2	2	2	0	2	0	1
<i>B. longipetiolata</i>	1	0	0/1	1	0	0	-	1	0/3/4	1	0	0	0/1	0	0	0	1	1	0	1	0/1/2/3	0	0	0	2	0	1

<i>B. loranthoides</i>	0	0	0	1	0	0	-	1	4	1	0	0	1	0	0	1	0	0	1	1/2	0	0	0	2	2	1
<i>B. mani</i>	0	0	0	1	0	0	-	1	2	1	0	0	1	0	1	0	0	1	1/2/3	2	2	0	2	0	1	
<i>B. molleri</i>	0	0	0	1	0	0	-	1	1	1	0	0	1	0	1	0	0	1	2	0	0	0	2	0	1	
<i>B. oxyanthera</i>	0	0	0	1	0	0	-	1	3	1	0	0	1	0	1	0	0	1	1	2	2	0	2	0	1	
<i>B. perlargoniiflora</i>	1	0	0	1	0	0/1	1	1	1	1	1	0	1	0	0	1	1	0	1/2	0	0	0	2	0	1	
<i>B. polygonoides</i>	0	0	0/1	1	0	1	0	1	1/3	1	0	0	1	1	0/1	0	0	0	1	0	2	2	0	2	0	1
<i>B. preusii</i>	0	0	0	1	0	0	-	1	1/3	1	0	0	1	1	1	0	0	1	1	2	2	0	2	0	1	
<i>B. rubromarginata</i>	0	0	0	1	0	1	0	1	1	0	-	0	1	?	0	0	0	0	1	1	2	2	0	2	0	1
<i>B. rubronervata</i>	0	0	0	1	0	1	0	0	-	1	-	0	1	?	0	0	0	0	0/1	0/1	0	1	0	2	0	1
<i>B. rwandensis</i>	0/1	1	0	1	0	0	-	1	1/3	1	0	0	1	0	0	1	1	0	1/2	0	0	0	2	0	1	
<i>B. squamulosa</i>	1	0	0	1	0	0	-	1	0/3/4	1	0	0	1	0	0	1	1	0	1/2/3	0	0	0	2	0	1	
<i>B. subalpestris</i>	0	0	1	1	0	0	-	1	3	1	0	0	1	1	1	0	0	0	1/2	0	0	0	2	0	1	
<i>B. subscutata</i>	0	0/1	0	1	1	1	1	1	3	1	0	0	1	1	0/1	1	0	0	0/1/2	2	2	0	2	0	1	
<i>B. tatoniana</i>	0	0	0	1	0	1	0	0	-	0	-	0	1	0	0	1	0	0	1	0	0	0	2	0	1	
<i>B. zimmemmannii</i>	0	0	?	1	0	1	1/3	0	-	0	-	0	1	?	0	0	1	0	2	0	1	0	2	0	1	
<i>B. bogneri (OG)</i>	0	0	0	0	0	1	?	0	-	0	-	0	1	0	0	0	0	2	1	1	1	?	3	3	0	
<i>B. betsimisaraka (OG)</i>	0	0	1	0	0	1	?	0	-	0	-	0	1	0	?	?	0	0	1/2	1	1	1	?	3	3	0

[110	120	130	140	150	160	170	180	190	200]
[AGAACGAGAAAAA	AGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----			[176]
	B. baccata									
	B. amplal	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[176]
	B. poculifera2	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[176]
	B. bonus_henricus	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[176]
	B. loranthoides1	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[176]
	B. longipetiollatal	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[199]
	B. subscutata	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. kisuluana	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. komoensis	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. oxyanthera	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. horticola	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. eminii	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. capillipes	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. manii2	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. fusialata	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. preusii	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. polygonoides	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. ebolowensis	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. ebollowensis	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. moller1	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. furfuracea	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. subalpestris	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. cavallyensis	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[198]
	B. bogneri	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[196]
	B. betsimesaraka	AGAACGAGAAAAA	CAAAAAGGATAGGTGCAGAGACT	CAATGGAAAGCTGTTCCAA	CAAAATGGAGTTGACTGCC	-----	TCCAAC	----		[199]

I	B. baccata	-----	210	220	230	240	250	260	270	280	290	300	[178]
I	B. amplal	-----	210	220	230	240	250	260	270	280	290	300	[178]
	B. poculifera2	-----	210	220	230	240	250	260	270	280	290	300	[178]
	B. bonus_henricus	-----	210	220	230	240	250	260	270	280	290	300	[178]
	B. loranthoides1	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	TATTAATGACGACTCGAA									
	B. longipetiolatal	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. subscutata	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. kisuluana	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. komoensis	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. oxyanthera	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. horticola	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. eminii	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. capillipes	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. manii2	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. fusialata	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. preusii	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. polygonoides	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. gabonensis	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. ebolowensis	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. molleri	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. furfuracea	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. subalpestris	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. cavallyensis	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. bogneri	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									
	B. betsimesaraka	TCCAGCGAAACTCCGGAAAG--	GATGAAAGATRAAACCTATATACATACGTATACGTTACTAAAAAGTATTTCAAATCA--	GATTAATGACGACTCGAA									

I	310	320	330	340	350	360	370	380	390	400	
I	----	----	----	----	----	----	----	----	----	----]
	----	----	----	----	----	----	----	----	----	----	[220]
B.baccata	----	----	----	----	----	----	----	----	----	----	[220]
B.amplal	----	----	----	----	----	----	----	----	----	----	[220]
B.poculifera2	----	----	----	----	----	----	----	----	----	----	[220]
B.bonus_henricus	----	----	----	----	----	----	----	----	----	----	[220]
B.loranthoides1	----	----	----	----	----	----	----	----	----	----	[358]
B.longipetiotal	1-TTTTTTC	AATGATATAGTGA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCC	---AACTTCAAGT	GA	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.subscutata	TGTTTTTTC	AATGATATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.kisuluana	TGTTTTTTC	AATGATATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCCAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.komoensis	TTTTTTTTT	TAATAATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.oxyanthera	TTTTTTTTT	TAATAATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.horticola	TTTTTTTTT	TAATAATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.eminii	TGTTTTTTC	AATGATATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.capillipes	TTTTTTTTT	TAATAATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.mani12	TTTTTTTTT	TAATAATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.fusialata	TGTTTTTTC	AATGATATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.preusii	TGTTTTTTC	AATGATATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.polygonoides	TGTTTTTTC	AATGATATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.gabonensis	TGTTTTTTC	AATGATATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.ebolowensis	TGTTTTTTC	AATGATATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.molleri	TGTTTTTTC	AATGATATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.furfuracea	TGTTTTTTC	AATGATATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.subalpestris	TGTTTTTTC	AATGATATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.cavalliyensis	TGTTTTTTC	AATGATATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CCACGGAC	TTCAAGT	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.bogneri	TGTTTTTTC	AATGATATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CGC	---AACTTCAAGG	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT
B.betsimesaraka	TGTTTTTTC	AATGATATAGTCA	AAATGAACGAA	TGTTGTA	AAATCAAT	---CGC	---AACTTCAAGG	TG	AAAAAGAA	TCA	AAATTTCAATTTGATTTAAAT

I	410	420	430	440	450	460	470	480	490	500	
I											.j
B. baccata	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[317]	
B. amplal	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[317]	
B. poculifera2	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[317]	
B. bonus_Henricus	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[317]	
B. l. longipetiolata1	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[455]	
B. subscutata	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[484]	
B. kisuluana	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[492]	
B. k.omoensis	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[479]	
B. oxyanthera	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[487]	
B. horticola	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[486]	
B. eminii	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[487]	
B. capillipes	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[488]	
B. manii2	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[479]	
B. fusialata	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[487]	
B. preusii	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[486]	
B. polygonoides	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[479]	
B. gabonensis	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[487]	
B. ebolowensis	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[486]	
B. molleri	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[486]	
B. furfuracea	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[479]	
B. subalpestris	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[486]	
B. cavallyensis	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[488]	
B. bogneri	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[482]	
B. betsimesaraka	ATCATTCACCTCCATCATATAA	CTGATAGATCCGGTTGAAGA	AAATTTGATTC	AA	TCAGACGAGAA	TAGAATAA	AGATAGAG	--	TCCCATTTCTACATGTCAATAC	[485]	

[510 : : 520 : : 530 : : 540 : : 550 : : 560 : : 570 : : 580 : : 590 : : 600]

ITS

B. baccata GGACAAAAA-T-GAAAATTTATAGTGCAGAACACCCCGCAACTTGTGTGCAAGCAACCCCGCAAGGGAA-TGGCGGGGGCGTGTGGGGCG- [406]
 B. amplai GGACAAAAA-T-GAAATTTATAGTGCAGAACACCCCGCAACTTGTGTGCAAGCAACCCCGCAAGGGAA-TGGCGGGGGCGTGTGGGGCG- [406]
 B. poculifera2 GGACAAAAA-T-GAAAATTTATAGTGCAGAACACCCCGCAACTTGTGTGCAAGCAACCCCGCAAGGGAA-TGGCGGGGGCGTGTGGGGCG- [406]
 B. bonus_henricus GGACAAAAA-T-GAAATTTATAGTGCAGAACACCCCGCAACTTGTGTGCAAGCAACCCCGCAAGGGAA-TGGCGGGGGCGTGTGGGGCG- [406]
 B. loranthoides1 GGACAAAAA-T-GAAAATTTATAGTGCAGAACACCCCGCAACTTGTGTGCAAGCAACCCCGCAAGGGAA-TGGCGGGGGCGTGTGGGGCG- [544]
 B. longipetiolata1 GGACAAAAA-TTGAAAATTTATAGTGCAGAACACCCCGCAACTCGTAGTGCAGAACCCCGCAAGGGAA-TGGCCGAGG-CGTGATGGGGCG- [573]
 B. subscutata GGACAAAAA-T-GAAAATTTATAGTGCAGAACACCCCGCAACTCGTGTGCAAGCAACCCCGCAAGGGAGCGCGAGGA-GTGTGGGGCG- [581]
 B. kisuluana GGACAAAAA-T-GAAATTTATAGTKCAGAACACCCCGCAACTCGTGTGCAAGCAACCCCGCAAGGGAGCGCGAG-A-GTGTGGGGCG- [567]
 B. komoensis GGACAAAAA-T-GAAAATTTATAGTGCAGAACACCCCGCAACTCGTGTGCAAGCAACCCCGCAAGGGAGTGGCGAGGA-GTGTGGGGCG- [576]
 B. oxyanthera GGACAAAAA-T-GAAATTTATAGTGCAGAACACCC- GCGAAACCCGTTGTGCAAGCAACCCCGCAAGGGAGTGGCGAGGA-GTGTGGGGCG- [574]
 B. horticola GGACAAAAA-T--AAAATTTATAGTGCASAACTYCGCAACCCGTTGTGCAAGCAACCCCGCAAGGGATCGGCAAGRA-TTKTTGGGGCG- [575]
 B. eminii GGACAAAAA-T-GAA- TTTATCC?GCAGAACACCCCGCGAA-TCGTTGTGCAAGCAACCCCGCAAGGGAGTGGCGAGGA-GTGTGGGGCG- [575]
 B. capillipes GGACAAAAA-T-GAAAATTTATAGTGCAGAACACCCCGCGAAATCCGTTGTGCAAGCAACCCCGCAAGGGAGCGCGAGGA-GTGTGGGGCG- [567]
 B. mani12 GGACAAAAA-T-GAAATTTGCGTGCAGAACACCCCGCGAACTCGTGTGCAAGCAACCCCGCAAGGGAGTGGCGAGGA-GTGTGGGGCG- [576]
 B. fusialata GGACAAAAA-T-GAAATTTATAGTGCAGAACACCCCGCAACTGTTGTGCAAGCAACCCCGCAAGGGAGTGGCGAGGA-GTGTGGGGCG- [576]
 B. preusii GGACAAAAA-T-GAAATTTATAGTGCAGAACACCCCGCAACCCGTTGTGCAAGCAACCCCGCAAGGGAGTGGCGAGGA-GTGTGGGGCG- [568]
 B. polygonooides GGACAAAAA-T-GAAAATTTATAGTGCAGAACACCCCGCAACCCGTTGTGCAAGCAACCCCGCAAGGGAGCGCGAGGA-GTGTGGGGCG- [576]
 B. gabonensis GGACAAAAA-T-GAAATTTATAGTGCAGAACACCCCGCGAAACCCGTTGTGCAAGCAACCCCGCAAGGGAGCGCGAGGA-GTGTGGGGCG- [576]
 B. ebolowensis GGACAAAAA-T-GAAAATTTATAGTGCAGAACACCCG?? [575]
 B. molleri GGACAAAAA-T-GAAATTTATAGTGCAGAACACCCGCGAAACCCGTTGTGCAAGCAACCCCGCAAGGGAGCGCGAGGA-ATGTTGGGGCG- [576]
 B. furfuracea GGACAAAAA-T-GAAAATTTATAGTGCAGAACACCCGCGAAACCCGTTGTGCAAGCAACCCCGCAAGGGAGCGCGAGGA-GTGTGGGGCG- [568]
 B. subalpestris GGACAAAAA-T-GAAATTTATAGTGCAGAACACCCGCGAAACCCGTTGTGCAAGCAACCCCGCAAGGGAGCGCGAGGA-GTGTGGGGCG- [574]
 B. cavalliensis GGACAAAAA-T-GAAAATTTATAGT----- [510]
 B. bogneri GGACAAAAA-T-GAAATTTATAGTGCAGAACACCCCGCAACTAGTTAACCATCG-TCGCCATGTGGAAATGT-GAGG-CGTGTGGAGCTGCGACACA [577]
 B. betsimesaraka GGACAAAAA-T-GAAATTTATAGTGCAGAACACCCCGCAACTAGT?AACCATCG-TCCCCATGTGGAAATGT-GAGGC-GTGTGGAGCTGCGGCACA [580]

[710	720	730	740	750	760	770	780	790	800]		
]												
B. baccata	GCTCCTGCCCCGATTT	CGG	GATGC	---	AGGGG	CGCYGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[579]	
B. amplal	GCTCCTGCCCCG	GTTGGG	GATGT	---	AGGGG	CGCTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[580]	
B. poculifera2	GCTCCTGCCCCG	GTTGGG	GATGC	---	AGGGG	CGCTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[580]	
B. bonus_henricus	GCTCCTGCCCCG	GTTGGG	GATGC	---	AGGGG	CGCTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[580]	
B. loranthoides1	GCTCCTGCCCCG	GTTGGG	GATGC	---	AGGGG	TGTTGTGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[717]	
B. longipetiolatal	GCTCCTGCCCCG	GCTGGG	GATGC	---	AGGGG	CGTTTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[748]	
B. subscutata	GCTCCTGCCCCG	G	CTTGGG	GATGCATG	CAAGGGG	CGCTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[754]	
B. kisuluana	GCTCCTGCCCCG	G	CTTGGG	GATGC	---	AGGGG	TGCTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[734]
B. komoensis	GCTCCTGCCCCG	G	CTTGGG	GATGC	---	AGGGG	CGCTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[742]
B. oxyanthera	GCTCCTGCCCCG	G	CTTGGG	GATGC	---	AGGGG	CGCTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[740]
B. horticola	GCTCCTGCCCCG	G	CTTGGG	GATGC	---	AGGGG	CGCTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[744]
B. eminii	GCTCCTGCCCCG	G	CTTGGG	GATGC	---	AGGGG	CGTTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[741]
B. capillipes	GCTCCTGCCCCG	G	CTTGGG	GATGC	---	AGGGG	CGCTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[735]
B. manii2	GTTCCCTGCCCCG	G	CTTGGG	GATGC	---	AGGGG	CGCTGTGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[742]
B. fusialata	GCTCCTGCCCCG	G	CTTGGG	GATGT	---	AGGGG	TGCTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[742]
B. preusii	GCTCCTGCCCCG	G	CTTGGG	GATGC	---	AGGGG	CGTTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[735]
B. polygonoides	GCTCCTGCCCCG	G	CTTGGG	GATGC	---	AGGGG	CGCTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[743]
B. gabonensis	GCTCCTGCCCCG	G	CTTGGG	GATGC	---	AGGGG	CGCTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[743]
B. ebolowensis	GCTCCTGCCCCG	G	CTTGGG	GATGC	---	AGGGG	CGCTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[741]
B. mollerii	GTTCCCTGCCCCG	G	CTTGGG	GATGC	---	AGGGG	CGCTGTGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[744]
B. furfuracea	GCTCCTGCCCCG	G	CTTGGG	GATGC	---	AGGGG	CGCTGGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[735]
B. subalpestris	GTTCCCTGCCCCG	G	CTTGGG	GATGC	---	AGGGG	CGCTGTGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[742]
B. cavallyensis	GTTCCCTGCCCCG	G	CTTGGG	GATGC	---	AGGGG	CGCTGTGAGCTTGA	AAATCA	--	CACACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[548]
B. bognerii	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	[755]	
B. betsimesaraka	GCTCCTGCCCCG	GACTT	CGG	GATGY	---	AGGGG	TGCTGGAACTTGG	TTATCA	--	TGAACGACTCTCG	CAACCGGATATCTCGGCTCTCGCATC	[758]

I	810	:	820	:	830	:	840	:	850	:	860	:	870	:	880	:	890	:	900	:	
I		:		:		:		:		:		:		:		:		:		:	
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[679]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[680]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[680]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[680]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[817]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[848]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[854]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[834]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[842]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[840]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[844]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[841]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[835]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[841]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[842]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[835]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[843]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[843]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[841]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[844]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[835]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[842]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[845]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[843]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[841]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[844]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[842]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[845]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[648]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[855]
	GATGAAGAACG	TAGTGA	AAATCGG	TACTTGG	TGTGAA	TTGC	AGATCC	CGGTGA	ACCAATCG	GATG	TTTTG	AAACG	CAAGT	TG	CGCC	CCG	AAAG	CCCTT	CTGG	CGGA	[858]

- B. baccata
- B. amplal
- B. poculifera2
- B. bonus_henricus
- B. loranthoides1
- B. longipetiolatal
- B. subscutata
- B. kisuluana
- B. komoensis
- B. oxyanthera
- B. horticola
- B. eminii
- B. capillipes
- B. manii2
- B. fusialata
- B. preusii
- B. polygonoides
- B. gabonensis
- B. ebolowensis
- B. molleri
- B. furfuracea
- B. subalpestris
- B. cavallyensis
- B. bogneri
- B. betsimesaraka

[910	920	930	940	950	960	970	980	990	1000]		
[B. baccata	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCAGC	CTGGCCCT	TATAAAA	---C-CGAGTTC	-AATCTCCTG	-TT	[755]	
	B. amplai	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCAGC	CTGGCCCT	TATAAAA	---T-CGAGTTC	-AATCTCCTA	-CT	[754]	
	B. poculifera2	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCAGC	CTGGCCCT	CGCCAAAAA	---T-CGAGTTC	-AATCTCCTA	-CT	[754]	
	B. bonus_henricus	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCAGC	CTGGCCCT	CGCCAAAAA	---T-CGA?TTC	-AATCTCCTA	-TT	[754]	
	B. loranthoides1	GGGCAYGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCGC	---GC	---GCCAAAAA	AAAAAAC	-TGAGTTC	-AATCTCCTA	-TT	[890]
	B. longipetiolata1	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCGC	---GC	---GCCAAAAA	AAAAAAC	CCCGAG	-TCCAATCCYTTA	-TT	[930]
	B. subscutata	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCGC	---GC	---GCCAAAAA	---TGC	---TC-GATCTCTTC	---TT	[919]	
	B. kisuluana	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCGC	---GC	---GCCAAAAA	---TGC	---TC-GATCTCTTC	---TT	[899]	
	B. komoensis	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCGC	---G?	---GCCAAAAA	---TGC	---TC-GATCTCTTC	---TT	[907]	
	B. oxyanthera	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCGC	---GC	---GCCAAAAA	---TGC	---TC-GATCTCTTC	---TT	[906]	
	B. horticola	GGGCAHGT	TGCTGGCGG	CTACRCAT	GTAGCCCCC	CGC	---GC	---GCCAAAAA	---TGC	---TC-GATCTCTTC	---TT	[909]	
	B. eminii	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCGC	---GC	---TCCAAAAA	---TGC	---TC-GATCTCTTC	---TT	[906]	
	B. capillipes	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCGC	---GC	---GCCAAAAA	---TGC	---TC-GATCTCTTC	---TT	[901]	
	B. manii2	RGGCACKT	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCGC	---GC	---ACCAAAAA	---TGC	---TC-GATCTCTTC	---TT	[907]	
	B. fusialata	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCGC	---GC	---CGCCAAAAA	---TGC	---TC-GATCTCTTC	---TT	[907]	
	B. preusii	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCGC	---GC	---GCCAAAAA	---TGC	---TC-GATCTCTTC	---TT	[901]	
	B. polygonoides	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCGC	---GC	---GCCAAAAA	---TGC	---TC-GATCTCTTC	---TT	[908]	
	B. gabonensis	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCGC	---GC	---GCCAAAAA	---TGC	---TC-GATCTCTTC	---TT	[908]	
	B. ebolowensis	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGTGGCCCC	CCCCCGC	---GC	---GCCAAAAA	---TTC	---TC-GATCTCTTC	---TT	[906]	
	B. molleri	AGGCACGTC	TGCTGGCGG	CTACGGAT	CGGCCCCC	CGC	---GC	---GCCAAAAA	---GC	---TC-AATCTCTTC	---TTCC-GG	[915]	
	B. furfuracea	GGGCACGTC	TGCTGGCGG	CTACGGAT	CGGCCCCC	CGC	---GC	---GCCAAAAA	---GT	---TT--GATCTCTTC	---TTCTTGGAG	[910]	
	B. subalpestris	GGG?A?GT	TGCTGGCGG	CTACTCAT	CTCAGCCCC	CGC	---GC	---GCCAAAAA	CCCA	---AACCTCTTC	---TTCC-GG	[913]	
	B. cavallyensis	GGGCACGTC	TGCTGGCGG	CTACGGAT	?GTAGCCCCC	CGC	---GC	---ACC?AAAA	---TGC	---TC-AATCCCTTCC	TTCTCGGAG	[725]	
	B. bogneri	GGGCACGTC	TGCTGGCGG	CTACACAT	CGCCACCCAC	---GC	---ACC	---AACAAA	---GC	---TTC-AAGC-TAT	---	[913]	
	B. betsimesaraka	GGGCACGTC	TGCTGGCGG	CTACACAT	CGCCACCCAC	---GC	---ACC	---AACAAA	---GC	---TTGCAAGCTTAT	---	[918]	

I	1010	1020	1030	1040	1050	1060	1070	1080	1090	1100]	
[.	
	GGGGTGGGCTGGACTTT-GGTT--GGACGAGAGGGGGCACTGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[852]									[852]
	GGGGTGGGCGGACTTT-GGTCGGGACGAGGGGGCAATGTTGGCCCTCCCGTCGATCGGTCGGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[853]									[853]
	GGGGTGGGCGGACTTT-GGTTGGGACGAGAGGGG-CAATGTTGGCCCTCCCGTCGAGCGATTCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[852]									[852]
	GGGGTGGGCGGACTTT-GGTCGGGGA?AGGGGG-CAATGTTGGCCCTCCCGTCGAGCGAT?GCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[852]									[852]
	GGGGTGGGCGGACTTT-GGTC--GGACGAGAGGGG-CAATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[986]									[986]
	GGGGTGGACCCGACTTTTGTT--GGACGAGAGGGG-CAATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[1027]									[1027]
	GGGGTGGGCTGGACTTT-GGTC--GGACGAGAGGGG-CAATGTTGGG-CTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[1014]									[1014]
	GGGGTGGGCTGGACTTT-GGTC--GGACGAGAGGGG-CAATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[995]									[995]
	GGGGTGGGCTGGACTTT-GGTC--GGACGAGAGGGG-CAATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[1003]									[1003]
	GGGGTGGGCTGGACTTT-GGTC--GGACGAGAGGGG-CAATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[1002]									[1002]
	GGGGTGGGAGGACTTT-GGTY--GGAMGAGAGGGG-CAATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[1005]									[1005]
	GGGGTGGGCTGGACTTT-GGTC--GGACGAGAGGGG-TGATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[1002]									[1002]
	GGGGTGGGCTGGACTTT-GGTC--GGACGAGAGGGG-CAATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[996]									[996]
	GGGGTGGGCTGGACTTT-GGTC--GGACGAGAGGGG-CAATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[1002]									[1002]
	GGAGTGGGATGGACTTT-GGTC--GGACGAGAGGGG-TGATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[1003]									[1003]
	GGGGTGGGCTGGACTTT-GGTC--GGACGAGAGGGG-CAATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[997]									[997]
	GGGGTGGGCTGGACTTT-GGTC--GGACGAGAGGGG-CAATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[1004]									[1004]
	GGGGTGGGCTGGACTTT-GGTC--GGACGAGAGGGG-CAATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[1004]									[1004]
	GGGGTGGGCTGGACTTT-GGTC--GGACGAGAGGGG-CAATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[1002]									[1002]
	GGGGTGGGCTGGACTTT-GGTC--GGACGAGAGGGG-CAATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[1011]									[1011]
	GGGGTGGGCTGGACTTT-GGTC--GGACGAGAGGGG-TAATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[1006]									[1006]
	GGGGTGGGCTGGACTTT-GGTC--GGACGAGAGGGG-?GATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[1010]									[1010]
	GGGGTGGGCTGGACTTT-GGTC--GGACGAGAGGGG-?GATGTTGGCCCTCCCGTCGAGCGATCGCGCGGTTGGCCCTAAAGTTGATGTCCTCGGCGTCCGG	[821]									[821]
	-----GAGGTGG-TAATGTTGACCTCCCGTCGAGCAAGTGCACGCGGTTGGTCTAAATTTGATGTCCTCGGCGTCCGG	[983]									[983]
	-----GAGGTGG-CAATGTTGGCCCTCCCGTCGAGCAAGTGCACGCGGTTGGTCTAAATTTGATGTCCTCGGCGTCCGG	[988]									[988]

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- B. cavallayensis
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- B. betsimesaraka

[1110	1120	1130	1140	1150	1160	1170	1180	1190	1200]		
[CAGTGGATCGACGGTGGTTTT	----TAGCCCTCGGCGAGACACAT	TGACGTGGAGACGGCGGTAT	CGGGAG	--CTCCAC	----	GCGACC	?TGC	TGCG	[1943]		
	CAGTGGATCGACGGTGGTTTT	----TAGCCCTCGGCGAGATACAT	TGACGTGGAGACGGCGGTAT	CGGGAG	--CTCCAC	----	GCGACC	?TGC	TGCG	[1943]		
	CAGTGGATCGACGGTGGTTTT	----TAGCCCTCGGCGAGATACAT	TGACGTGGAGACGGCGGTAT	CGGGAG	--CTCCAC	----	GCGACC	?TGC	TGCG	[1942]		
	CAGTGGATCGACGGTGGTTTT	----TAGCCCTCGGCGAGATACAT	TGACGTGGAGACGGCGGTAT	CGGGAG	--CTCCAC	----	GCGACC	?TGC	TGCG	[1942]		
	CAGTGGATCGACGGTGGTTTT	----TTGCCCTCGGCGAGATACAT	TGACGTGGAGACGGCGGTAT	CGGGAG	--CTCCAC	----	GCGACC	?TGC	TGCG	[1078]		
	CAGTGGATCGACGGTGGTTTT	----TTGCCCTCGGCGAGATACAT	TGACGTGGAGACGGCGGTAT	CGGGAG	--CTCCAC	----	GCGACC	?TGC	TGCG	[1118]		
	CAGTGGACCG	CGGTGGTTTT	----ATAGCCCTCGGCGAAATAC	TGTCGACGTGGAGACGGCGGTAT	CGGGAA	--CTCCAC	----	GCGACC	?TGC	TGCG	[1105]	
	CAGTGGACCGACGGTGGTTTT	----TAGCCCTCGGCGAAATAC	TGTCGACGTGGAGACGGCGGTAT	CGGGAA	--CTCCAC	----	GCGACC	?TGC	TGCG	[1085]		
	CAGTGGACCGACGGTGGTTTT	----TAGCCCTCGGCGAAATAC	TGTCGACGTGGAGACGGCGGTAT	CGGGAA	--CTCCAC	----	GCGACC	?TGC	TGCG	[1093]		
	CAGTGGACCGACGGTGGTTTT	----TAGCCCTCGGCGAAATAC	TGTCGACGTGGAGACGGCGGTAT	CGGGAA	--CTCCAC	----	GCGACC	?TGC	TGCG	[1092]		
	CAGTGGACCGACGGTGGTTTT	----ATRSCTTSGS	SGAAWACGTTGAA	CGSSS	GASGCGTWT	SGGGAA	--TTCCAC	----	GCGACC	?TGC	TGCG	[1097]
	CAGTGGACCGACGGTGGTTTT	----TAGCCCTCGGCGAAATAC	TGTCGACGTGGAGACGGCGGTAT	CGGGAA	--CTCCAC	----	TTTGG	CGAC	CCCTGC	TGCG	[1093]	
	CAGTGGACCGACGGTGGTTTT	----TAGCCCTCGGCGAAACAC	GTTGACGTGGAGACGGCGGTAT	CGGGAA	--CTCCAC	----	GCGACC	?TGC	TGCG	[1086]		
	CAGTGGACCGACGGTGGTTTT	----TAGCCCTCGGCGAAATAC	TGTCGACGTGGAGACGGCGGTAT	CGGGAA	--TTCC	----	TTTGG	CGAC	CCCTGC	TGCG	[1093]	
	CAGTGGACCGACGGTGGTTTT	----TAGCCCTCGGCGAAATAC	TGTCGACGTGGAGACGGCGGTAT	CGGGAA	--CTC	?CAC	----	GCGACC	?TGC	TGCG	[1094]	
	CAGTGGACCGACGGTGGTTTT	----TAGCCCTCGGCGAAATAC	TGTCGACGTGGAGACGGCGGTAT	CGGGAA	--CTCCAC	----	GCGACC	?TGC	TGCG	[1087]		
	CAGTGGACCGACGGTGGTTTT	----TAGCCCTCGGCGAAACAC	GTTGACGTGGAGACGGCGGTAT	CGGGAA	--CTCCAC	----	GCGACC	?TGC	TGCG	[1094]		
	CAGTGGACCGACGGTGGTTTT	----TAGCCCTCGGCGAAATAC	TGTCGACGTGGAGACGGCGGTAT	CGGGAA	--CTCCAC	----	GCGACC	?TGC	TGCG	[1096]		
	CAGTGGACCGACGGTGGTTTT	----TAGCCCTCGGCGAAATAC	TGTCGACGTGGAGACGGCGGTAT	CGGGAA	--CTCCAC	----	GCGACC	?TGC	TGCG	[1092]		
	CAGTGGACCGACGGTGGTTTT	----TGGCCCTCGGCGAAATAC	TGTCGACGTGGAGACGGCGGTAT	CGGGAA	--CTCCAC	----	GCGACC	?TGC	TGCG	[1101]		
	CAGTGGACCGACGGTGGTTTT	----TAGCCCTCGGCGAAATAC	TGTCGACGTGGAGACGGCGGTAT	CAGGAA	--CTCCAC	----	GCGACC	?TGC	TGCG	[1096]		
	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	????????????????	[1110]		
	CAGTGGACCGACGGTGGTTTT	----TAGCCCTCGGCGA	ATACGTTGACGTGGAGACGGCGGTAT	AGGGGA	--CCAC	CAC	----	GCGACC	?TGC	TGCG	[911]	
	CAGTGGATCGGCGGTGGTT	----GCCAT	----GCCCTCGGCGAAATACAT	TGACGTGGAGACGGCGGTAT	CGGGAA	--CTCC	----	TTTGG	CGAC	CCCTAT	TGCG	[1074]
	CAGTGGATCGGCGGTGGTT	----GCCAT	----GCCCTCGGCGAAATACAT	TGACGTGGAGACGGCGGTAT	CGGGAA	--CTCC	----	TTTGG	CGAC	CCCTAT	TGCG	[1079]

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- B. subscutata
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- B. cavallyensis
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[1210 : 1220 : 1230]
 [: : :]

Morphology

B.baccata CTG00010120-0 -000000000 {23}000100
 B.amplal CTG00010110-0 -100000010 2001{01}00
 B.poculifera2 CTG00010110-0 -10{01}000010 {23}001000
 B.bonus_henricus CTG0001110-0 -100000010 2001{01}00
 B.loranthoides1 TTG000100-141 0010010001 {12}000021
 B.longipetiotala CTG10{01}100-1{034}1 00{01}0001101 {0123}000201
 B.subscutata CTG0{01}01111131 0011{01}10001 {012}220201
 B.kisuluana CTG00{01}100-131 0010010001 {12}220201
 B.komoensis CTG000100-121 0010110001 {12}220201
 B.oxyanthera CTG000100-131 0010110001 1220201
 B.horticola CTG000100-1{13}1 0010110001 2220201
 B.eminii CTG000100-1{23}1 0010011001 1000201
 B.capillipes CTG000100-1{13}1 001110001 {012}220201
 B.maniid CTG000100-121 0010110001 {123}220201
 B.fusialata CTG000100-131 001000001 1010211
 B.preusii CTG000100-1{13}1 0011100001 1220201
 B.polygonoides CTG00{01}10101{113}1 0011{01}00001 0220201
 B.gabonensis CTG00010100-0 -011000001 1220211
 B.ebolowensis CTG00010100-0 -01000001 1220211
 B.molleri CTG000100-111 0010100001 2000201
 B.fururacea CTG010110-121 0010010101 1000201
 B.subalpestris ???001100-131 0011100001 {12}000201
 B.cavalliyensis CTG00110101{02}1 00{01}000?00{01} {01}110201
 B.bogneri CTG000001?0-0 -010000002 111?330
 B.betsimesaraka CTG001001?0-0 -010???00{12} 111?330

