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Systematics and floral evolution of the Dialiinae (Caesalpinioideae)

a diverse lineage of tropical legumes

par

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“A straight line may be the shortest
distance between two points,
but it is by no means the most interesting.”

-The Doctor

Résumé

Le clade Dialiinae représente l'une des premières lignées de la sous-famille Caesalpinioideae des Leguminosae. Il se compose de 17 genres (environ 90 espèces), avec des taxons qui sont répandus dans toutes les régions tropicales du monde. Morphologiquement, le groupe comprend un assemblage divers de taxons qui peut représenter une « phase expérimentale » dans l'évolution florale des légumineuses. Différents représentants du clade présentent de la poly-, mono-, et asymétrie, et semblent avoir subi un haut degré de perte d'organe, produisant, dans certains cas, des fleurs extrêmement réduites qui sont à peine reconnaissables comme appartenant à la famille des légumineuses.

Afin d'obtenir une image plus claire de l'évolution florale du clade Dialiinae, une phylogénie bien résolue et bien soutenue est nécessaire. Dans le but de créer une telle phylogénie, un total de 37 échantillons d'ADN des Dialiinae a été séquencé pour deux régions chloroplastiques, soit *rps16* et *trnL*. De plus, une étude morphologique complète a été réalisée. Un total de 135 caractères végétatifs et reproductifs a été évalué pour 79 espèces de Dialiinae et pour quatre groupes externes. Les analyses phylogénétiques ont d'abord été effectuées sur un groupe restreint de taxons pour lesquels les trois types de données étaient disponibles. Les nœuds fortement soutenus de cette phylogénie ont ensuite été utilisés comme contrainte pour une seconde analyse de parcimonie avec les données morphologiques d'un ensemble plus important de taxons. Les caractères morphologiques ont été optimisés sur l'un des arbres les plus parcimonieux de cette seconde analyse. Un certain nombre de nouvelles relations au niveau de l'espèce ont été résolues, créant une image plus claire quant à l'évolution de la forme florale dans le temps, particulièrement pour les genres *Labichea* et *Dialium*.

En plus de leur morphologie florale mature diverse, les Dialiinae sont également très variables dans leur ontogénèse florale, affichant à la fois la perte et la suppression des organes, et présentant une variété de modes d'initiation d'organes. Afin de construire une image plus complète du développement floral et de l'évolution dans ce clade, l'ontogénèse florale de plusieurs espèces non documentées à ce jour a été étudiée. La série complète du développement a été compilée pour six espèces de Dialiinae; quatre de

Dialium, ainsi que *Poeppigia procera* et *Mendoravia dumaziana*. Le mode et le moment de l'initiation des organes étaient pour la plupart uniforme pour toutes les espèces de *Dialium* étudiés. Tant pour ce qui est des gains ou des pertes d'organes chez *Dialium*, une tendance est apparente – l'absence d'organe abaxial. Que ce soit pour les sépales ou les étamines, les gains se produisent toujours en position médiane adaxiale, tandis que les étamines et les pétales perdus sont toujours les organes les plus ventraux. Les taxons étudiés ici illustrent le manque apparent de canalisation du développement observé chez les Caesalpinioideae. Cette plasticité ontogénétique est le reflet de la diversité morphologique au niveau des fleurs tel qu'observée dans l'ensemble de la sous-famille.

Une des espèces de Dialiinae, *Apuleia leiocarpa*, produit une inflorescence andromonoïque, une caractéristique qui est unique en son clade et rare dans les légumineuses dans son ensemble. La microscopie optique et électronique ont été utilisées pour entreprendre une étude détaillée de la morphologie florale de ce taxon. On a constaté que tandis que les fleurs hermaphrodites produisent un seul carpelle et deux étamines, les fleurs staminées produisent trois étamines sans toutefois montrer signe de développement du carpelle. Les inflorescences semblent produire près de quatre fois plus de fleurs staminées que de fleurs hermaphrodites, lesquelles occupent toujours la position centrale de l'inflorescence cymeuse. Ce ratio élevé mâle/bisexuel et la détermination précoce du sexe chez *Apuleia* sont rares chez les Caesalpinioideae, ce qui suggère que l'andromonoecie se développe dans ce genre comme un moyen d'accroître la dispersion du pollen plutôt qu'en réponse à des limitations de ressources.

Mots-clés: andromonoecie, *Apuleia leiocarpa*, Caesalpinoideae, Dialiinae, morphologie florale, ontogénie florale, phylogénétiques, systématiques

Abstract

The Dialiinae clade represents one of the early-diverging lineages of the legume subfamily Caesalpinioideae; it consists of 17 genera (*circa* 90 species), and is pantropically distributed. Morphologically, the group comprises a diverse assemblage of taxa that may represent a so-called "experimental phase" in legume floral evolution. Different members of the clade exhibit poly-, mono-, and asymmetry, as well as having undergone a high degree of organ loss, producing, in some cases, extremely reduced flowers which are barely recognisable as belonging to the legume family.

In order to obtain a clearer picture of floral evolution in the Dialiinae, a well resolved and well supported phylogeny is needed onto which morphological characters may be optimised. With the goal of creating such a phylogeny, a total of 37 Dialiinae DNA samples were sequenced for two plastid genes, *rpS16* and *trnL*. Additionally, a comprehensive morphological study was carried out. A total of 135 vegetative and reproductive characters were scored for 79 ingroup and four outgroup taxa. Phylogenetic analyses were carried out first on a restricted group of taxa for which all three data sets were available. The highly supported nodes of this phylogeny were then used as a constraint for a second parsimony analysis of morphological data from a much larger taxon set. Morphological characters were then mapped onto one of 20,000 most parsimonious trees from this second analysis. A number of novel species-level relationships were resolved, creating a clearer picture of changes in floral form over time, particularly in the genera *Labichea* and *Dialium*.

In addition to their diverse mature floral morphology, the Dialiinae are also widely variable in their floral ontogeny, displaying both organ loss and suppression, and exhibiting a wide variety of organ initiation modes. In order to build a more complete picture of floral development and evolution in this clade, the floral ontogeny of several previously undocumented species was investigated. Complete developmental series were compiled for six species of the Dialiinae; four from *Dialium*, as well as *Poeppigia procera* and *Mendoravia dumaziana*. Mode and timing of organ initiation were mostly consistent across the *Dialium* species studied. In the instances of both gains and losses of floral organs in *Dialium*, one trend is apparent — an absence of abaxial organs. Gains in both sepals and stamens occur in the adaxial median position, while stamens and petals that are lost are always the ventral-most organs. The taxa examined here exemplify the apparent lack of developmental canalisation seen in caesalpinioid legumes. This ontogenetic evolvability is reflective of the morphological diversity shown by flowers across the subfamily.

One of the species of the Dialiinae, *Apuleia leiocarpa*, produces an andromonoecious inflorescence, a feature that is unique in its clade and rare in the Leguminosae as a whole. Light and electron microscopy were used to undertake a detailed study of the floral morphology of this taxon. It was found that while hermaphrodite flowers produced a single carpel and two stamens, staminate flowers developed three stamens but showed no sign of carpel development. Inflorescences also appear to produce approximately four times as many staminate as hermaphrodite flowers, with hermaphroditic flowers consistently occupying the central position in cymose inflorescences. Both this high male-to-bisexual ratio and the early determination of gender seen in *Apuleia* are rare in the Caesalpinioideae and suggest that andromonoecy developed in this genus as a means to increase pollen dispersal rather than in response to resource limitations.

Keywords: andromonoecy, *Apuleia leiocarpa*, Caesalpinioideae, Dialiinae, floral morphology, floral ontogeny, phylogenetics, systematics

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For Éric… time for a new adventure.
And Morley. I wish you could have come along.

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Chapter 1 – General Introduction

1.1 A brief introduction to the Dialiinae clade

The Dialiinae *s.l.* clade (hereafter referred to simply as the Dialiinae) is a monophyletic group within the paraphyletic Cassieae tribe (Leguminosae: Caesalpinioideae). The clade is made up of 17 genera (*c.* 90 species), including the 14 genera of Dialiinae *sensu* Irwin & Barneby (1981), the nested bigeneric Australian subtribe Labicheinae, and the monospecific genus *Poeppigia*, formerly of the tribe Caesalpiniae (Herendeen et al., 2003; Lewis et al., 2005). Members of this clade are pantropically distributed, with taxa occurring in Central and South America, Africa, Madagascar, Southeast Asia, and Australia (Figure 1.1; Lewis et al., 2005). With the exceptions of the genera *Labichea* and *Petalostylis*, which are shrubs, all clade members are trees. Morphological features uniting the clade, and occurring in all or nearly all taxa, include a thyrsoid inflorescence, the absence of vestured pits in the secondary xylem, basifixed anthers, and the loss of the antepetalous stamen whorl (Herendeen et al., 2003).

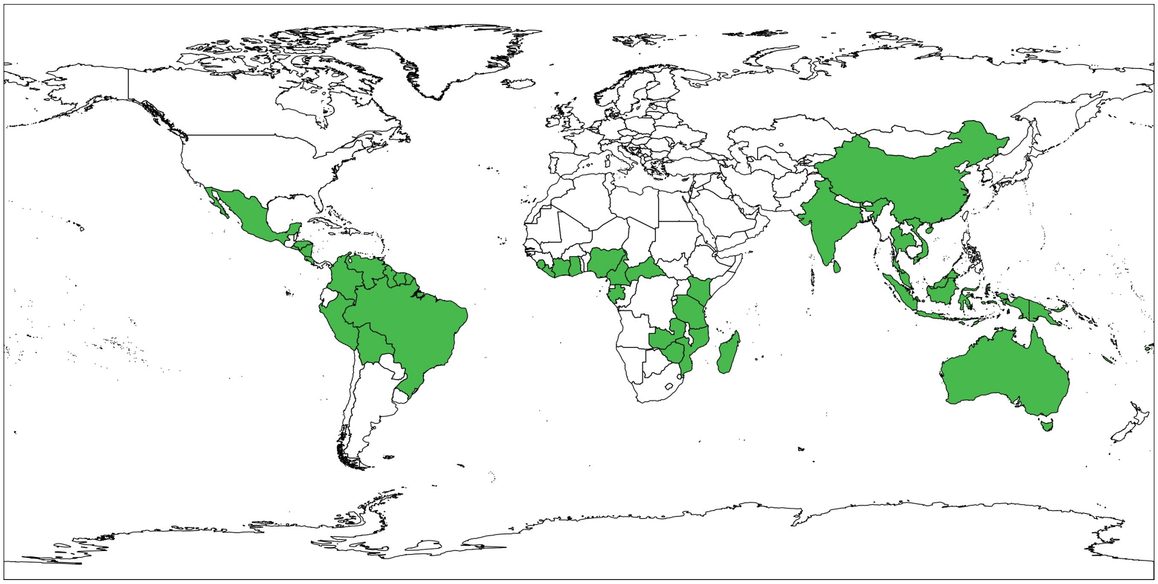

Figure 1.1. Countries in which Dialiinae species occur, based on herbarium voucher locality data.

Below are brief descriptions of each of the 17 genera of the Dialiinae, plus *Dansera*, which, along with *Uittienia*, has at times been considered either a sub-genus of *Dialium* or a separate genus. Legumes of the World (Lewis et al., 2005), following the phylogeny of Herendeen *et al.* (2003), treats *Uittienia*, but not *Dansera*, as a separate genus. Distinctive or unusual morphological features are highlighted.

Androcalymma Dwyer: 1 sp., *Androcalymma glabrifolium* Dwyer, found in upper Brazilian Amazonia (Irwin and Barneby, 1981). Only two collections are known to have been made (Krukoff 8827, 9005), and each was made from the same tree, in 1936 (Koeppen, 1963). The fruit of this species is unknown. Flowers of *A. glabrifolium* display imbricate descending aestivation and deflexed anthers resembling a cowl, suggesting the generic name (Dwyer, 1957).

Apuleia Mart.: 1 sp., *Apuleia leiocarpa* (Vogel) J.F. Macbr., found principally from northeast Peru to southeast Brazil and northern Argentina (Irwin and Barneby, 1981). Although previously considered to be comprised of up to three species, a recent morphometric evaluation of species limits has found only a single species with wide morphological variation (de Sousa et al., 2010). *Apuleia leiocarpa* possesses regularly trimerous flowers due to a reduction in floral organs (Irwin and Barneby, 1981). Inflorescences are andromonoecious and both flower types feature a sunken, tubular hypanthium (de Sousa et al., 2010; Zimmerman et al., 2013a).

Baudouinia Baill.: 4-6 spp., found in Madagascar and considered by Irwin and Barneby (1981) to be of uncertain placement in the subtribe. Species of *Baudouinia* possess simple leaves and an indehiscent, drupaceous fruit (Capuron, 1968). While Irwin & Barneby (1981) recognise only four species, Leguminosae of Madagascar (Du Puy et al., 2002) recognises the five species of Capuron's (1968) revision, plus a sixth new species, *B. capuronii*, which they name for Capuron himself.

Dansera Steenis: 1 sp., *Dansera procera* Steenis, synonym of *Dialium procerum* Steenis (Steyaert), endemic to south Sumatra. *Dansera* is sometimes considered a segregate genus of *Dialium*, at other times a subgenus (van Steenis, 1948; Steyaert, 1953). Legumes of the World (Lewis et al., 2005) does not treat *Dansera* as a separate genus. *Dansera* is set apart from the rest of *Dialium* by its combination of unifoliolate leaves and higher stamen number (van Steenis, 1948).

Dialium L.: c.40 spp., with pantropical distribution, although species diversity is concentrated in West Africa (Aubréville, 1968; Irwin and Barneby, 1981). *Dialium* species possess an indehiscent, drupaceous fruit and display greatly reduced numbers of floral organs, particularly in the corolla and androecium (Chakravarty, 1969; Irwin and Barneby, 1981; Tucker, 1998; Zimmerman et al., 2013b). Trimery of the calyx and corolla is observed only in the three species that are endemic to Madagascar (Du Puy et al., 2002).

Dicorynia Benth.: 2 spp., found in the Amazonian Hylaea and the Guianas of South America (Irwin and Barneby, 1981). Species of *Dicorynia* show imbricate descending aestivation and a reduction in floral organ numbers, as well as highly dimorphic anthers with increased numbers of locules (Koeppen, 1967).

Distemonanthus Benth.: 1 sp., *Distemonanthus benthamianus* Baill., found in tropical West Africa, particularly from Sierra Leone to Gabon (Irwin and Barneby, 1981). Flowers of *D. benthamianus* display a reduction in organ numbers in both the corolla and the androecium, the latter of which is asymmetrical (Irwin and Barneby, 1981).

Eligmocarpus Capuron: 1 sp., *Eligmocarpus cynometroides* Capuron, found in Madagascar (Irwin and Barneby, 1981). Also considered by Irwin and Barneby (1981) to be of uncertain placement, *E. cynometroides* possesses a plicate, indehiscent, drupaceous fruit, imbricate descending petal aestivation, and an androecial arrangement of five united and five free anthers (Capuron, 1968). Endemic to a very restricted region of Madagascar, this genus is highly threatened by logging activities (Du Puy et al., 2002).

Kalappia Kosterm.: 1 sp., *Kalappia celebica* Kosterm., restricted to a tiny area on the Indonesian island of Sulawesi (formerly Celebes) and potentially an endangered species (Kostermans, 1952; Irwin and Barneby, 1981; Lewis et al., 2005). The fruits of this species are dehiscent along the non-placental suture and possess a narrow flange along the placental suture (Kostermans, 1952).

Koompassia Maingay: 3 spp., found in southeast Asia, from the Malay Peninsula to Sumatra, the Philippines, and New Guinea (Irwin and Barneby, 1981). Fruits of *Koompassia* species are indehiscent and winged along both sutures (de Wit, 1947; Kostermans, 1950). Exceptionally large and towering canopy trees, *Koompassia* specimens of up to 88 metres in height and nearly 3 metres in trunk diameter have been recorded (de Wit, 1947).

Labichea Gaudichaud-Beaupre ex DC.: c.14 spp., subtribe Labicheinae, found in Queensland and western Australia (Irwin and Barneby, 1981). Species of *Labichea* possess leaves that are unifoliolate or palmately compound and a distichous, racemose inflorescence (Irwin and Barneby, 1981). Two stamens are present, of which one is usually much longer than the other (McCarthy and Orchard, 1998). The inner whorls develop in an unusual asymmetrical arrangement (Tucker, 1998).

Martiodendron Gleason: 5 spp., found in tropical South America, particularly southern Venezuela, the Guianas, and Amazonia (Irwin and Barneby, 1981). *Martiodendron* species possess a fruit similar to that of *Koompassia*, as well as modified “hooded” anthers, in which a terminal pollen cup closes over the pores when wet (Koeppen and Iltis, 1962). The subject of a century-long disagreement on naming conventions, this genus was originally dubbed *Martiusia* by Bentham, before becoming *Martia*, and finally *Martiodendron* (Koeppen and Iltis, 1962 and references therein).

Mendoravia Capuron: 1 sp., *Mendoravia dumaziana* Capuron, found in southeastern Madagascar (Irwin and Barneby, 1981). Considered by Irwin and Barneby (1981) to be anomalous in the Dialiinae, this species is one of two taxa, the other being *Poeppigia*, to have vestured pits in the secondary xylem (Herendeen, 2000). *Mendoravia* also possesses simple leaves and ligneous fruits which dehisce in a spiral fashion along both sutures, neither of which is a typical feature of this clade (Capuron, 1968; Du Puy et al., 2002).

Petalostylis R. Br.: 2 spp., subtribe Labicheinae, found in Queensland and western Australia (Irwin and Barneby, 1981). *Petalostylis* produces solitary flowers, or rarely simple cymes, and is unique in the Cassieae in the possession of a highly modified, petaloid style (Irwin and Barneby, 1981). Although they have different ranges, the two species are highly similar morphologically, and are distinguished principally by leaflet number and size (McCarthy and Orchard, 1998).

Poeppigia C. Presl: 1 sp., *Poeppigia procera* C. Presl, found throughout much of the neotropics, formerly of the tribe Caesalpiniae (Polhill and Vidal, 1981). This genus was placed within Dialiinae *s.l.* by the combined molecular-morphological study of Herendeen *et al*. (2003), and placed as sister to the rest of the clade in plastid sequence analyses (Bruneau et al., 2001; Bruneau et al., 2008). *Poeppigia* flowers have dorsifixed anthers and a calyx-tube forming a hypanthium. Fruits of *P. procera* are membranous and winged on the placental suture (Polhill and Vidal, 1981). Like *Mendoravia*, the wood of this species has vestured pits (Herendeen, 2000).

Storckiella Seem.: 5 spp., found in northeastern Australia, New Caledonia, and Fiji (Irwin and Barneby, 1981). Fruits of this genus display a single wing on the placental suture and a hypanthium in some taxa (McCarthy and Orchard, 1998; Nielsen et al., 2005). Two species have exactly four stamens, while others have unstable numbers of between nine and 14 (EZ, personal observation).

Uittienia Steenis: 1 sp., *Uittienia modesta* Steenis, synonym of *Dialium modestum* Stey., endemic to Borneo. Sometimes considered a segregate genus of *Dialium*, at other times, a sub-genus (van Steenis, 1948; Steyaert, 1953). *Uittienia* is set apart from the rest of *Dialium* by its unifoliolate leaves, uniovulate ovaries, and five-part corolla (van Steenis, 1948).

Zenia Chun: 1 sp., *Zenia insignis* Chun, found in southeast China (Irwin and Barneby, 1981). *Zenia insignis* displays imbricate descending aestivation of the corolla, a broad expanded receptacle, and an indehiscent fruit with a single wing on the placental suture;

leaves are exstipulate (Chun, 1946).

In a recent phylogeny based on *matK* and *trnL* plastid sequences, Bruneau *et al.* (2008) found the Dialiinae to be strongly supported as a sister group to the Papilionoideae, plus the clade comprised of the Mimosoideae and most of the Caesalpinieae and Cassieae lineages, a result supported by the earlier phylogeny of Herendeen *et al.* (2003), which included both *trnL* sequences and morphological characters. Estimated to be the youngest of the caesalpinioid lineages at 34 million years, the authors found that while there were several well-supported clades within the Dialiinae, relationships among these clades were only weakly supported. A detailed discussion of the genus- and species-level systematics of the clade is given in chapter two of this thesis.

1.2 Research objectives

The great diversity of floral form in the Dialiinae clade makes it an important piece of the puzzle that is legume floral evolution. The progression of forms in the group, however, cannot be fully appreciated without a well-resolved phylogeny to elucidate the relationships among its members. This is why, with this research project, I have attempted to both fully document the vegetative and reproductive morphology of the Dialiinae, and to use this and other data to clarify its systematics. By far, the greatest obstacle to this goal was a dearth of recently collected, or, in the case of ontogenetic work, spirit-preserved, material. This will be apparent both in the relatively sparse coverage of the molecular data, and in the very few species for which I was able to document a floral developmental series. Prior to the last twenty years, herbarium specimens were not prepared with DNA preservation in mind, and as such were commonly treated with ethanol or formalin, both of which severely degrade DNA (Staats et al., 2011). For rarely-collected taxa, this can easily exclude all herbarium specimens from use in molecular studies. Similarly, samples for ontogenetic work must be collected at a specific stage of flowering and immediately fixed loose in a preservative, rather than being pressed. Samples meeting these requirements are available, sadly, for only a small fraction of Dialiinae species. Conversely, samples for morphological study, if well-pressed and kept, may be of any age, and even sterile branches can yield some amount of data. Thus, for this section of my study, I have nearly complete species coverage, and have carried out the most exhaustive morphological study of the Dialiinae to date.

The research portion of this thesis is divided into three chapters, each detailing a different aspect of my doctoral project. The first (chapter two), explores the results of combined and separate phylogenetic analyses using molecular and morphological datasets. Here, we have been able to discover new, well-supported relationships within the Dialiinae at the species and generic levels, and to create a picture of the path of floral evolution within the clade.

This study focussed on the mature morphology of the flower, which represents only the endpoint of a dynamic process of floral development. As such, we were unable to evaluate whether putatively homologous characters were produced via a common developmental pathway, or whether dissimilar appearances at maturity masked essentially similar ontogenetic processes (Tucker et al., 1993; Buzgo et al., 2004). Shedding new light on these questions was the motivation for the next part of this project, a study of the floral ontogeny of the Dialiinae.

Chapter three documents the complete floral development of six Dialiinae species from three different genera, adding to previous work in this area by Shirley Tucker (1998). We found a lack of developmental canalisation which is reflective of the morphological diversity seen throughout much of the caesalpinioid subfamily, and which is supportive of the claim that these lineages represent an experimental phase in legume evolution (Prenner and Klitgaard, 2008).

While conducting electron microscope observations of samples for our ontogenetic study, we also examined several collections of species for which only mature flowers were available. One of these in particular, *Apuleia leiocarpa*, had an unusual floral morphology, displaying several traits which are quite rare in legumes and which had not been previously noted in the literature. Given that caesalpinioid floral morphological diversity has, at least at the generic level, been surveyed extensively in the past (see Lewis *et al*., 2005 and references therein), the novelty of our observations led us to carry out an in-depth morphological study of this taxon, which appears as chapter four of this thesis. Based on the atypical appearance and distribution of staminate flowers in this andromonoecious species, we were able to speculate on their ecological function and to contrast them with other cases of andromonoecy in the legumes. Our work emphasises the role that highly detailed microscopic study can play when considering the ecological advantage behind the production of unisexual flowers.

The three chapters comprising my research projects are followed by a general discussion on what has been achieved by this body of work and what the next steps down this path should be.

Systematics and floral evolution of the Dialiinae (Caesalpinioideae), a diverse lineage of tropical legumes

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Chapter 2 – Systematics and floral evolution of the Dialiinae (Caesalpinioideae), a diverse lineage of tropical legumes

2.0 Abstract

The Dialiinae clade is an early-diverging lineage of caesalpinioid legumes containing approximately 90 species in 17 genera. Dialiinae floral morphology is highly variable and may provide clues to caesalpinioid evolution, but a well-resolved phylogeny is needed. Here, we have carried out a comprehensive morphological study of 79 Dialiinae species and four outgroups. For all available Dialiinae DNA samples, two plastid genes, *rpS16* and *trnL*, were sequenced. A combined phylogenetic analysis using the parsimony criterion was completed on a reduced taxon set for which all three datasets were available. Highly supported nodes from the strict consensus tree of this analysis were then used to constrain the nodes of a second analysis using only morphological data with an expanded taxon set. Several new, highly supported relationships have been discovered at the species level, particularly within the genera *Labichea* and *Dialium*. A high degree of organ loss is common in the Dialiinae and often results in a bilaterally symmetrical flower. The loss of the antepetalous stamen whorl was found to be a synapomorphy for most of the clade. The absence of consistent morphological features in the Dialiinae, coupled with the small size of each genus, suggests the clade may be evidence of a hypothesized "experimental phase" in early legume evolution.

Keywords: Dialiinae, Caesalpinioideae, phylogeny, morphology, floral symmetry, organ loss

2.1 Introduction

The Dialiinae clade is one of the early-diverging lineages of the paraphyletic legume subfamily Caesalpinioideae (Irwin and Barneby, 1981). Composed of 17 genera (*circa* 90 species), the clade is pantropically distributed and, with the exception of two shrubby genera, *Labichea* and *Petalostylis*, is made up entirely of trees. At an estimated age of 34 million years (Bruneau et al., 2008), it may be the youngest of the caesalpinioid lineages, although no fossil evidence is available with which to calibrate this estimate.

Morphologically, the Dialiinae clade is highly diverse, displaying multiple symmetries and widely varied numbers of floral organs. Several key morphological features seen in all or nearly all of the Dialiinae distinguish this group from other caesalpinioid taxa. The first is the presence of thyrsoid inflorescences, a rare condition in the primarily racemose Leguminosae (Irwin and Barneby, 1981; Tucker, 1998). The second is an indehiscent drupaceous or samaroid pod (Irwin and Barneby, 1981). Third is the absence of vestured pits in the xylem, a condition seen elsewhere in Caesalpinioideae only in Cercideae and *Duparquetia* (Herendeen, 2000). Studies examining floral development in the clade have shown that, in addition to a highly variable mature morphology, Dialiinae flowers show an unusual amount of variability in their ontogeny (Tucker, 1998; Zimmerman et al., 2013b). In contrast to the highly canalised development of papilionoid legumes, these basal caesalpinioids display nearly every combination of helical, unidirectional, bidirectional, and synchronous organ initiation across their four whorls (Tucker, 1998, 2003; Zimmerman et al., 2013b; Bruneau et al., 2014). There is also a greater incidence of outright organ loss, as opposed to mid-stage suppression, than is typically seen in legumes (Tucker, 1998). Tucker (1988b) has suggested that organ loss in a given whorl may disrupt the next successive whorl, as in the case of *Dialium guineense*, where the loss of four petals is followed by the initiation of only two members of an expected five-part stamen whorl, and these in unusual positions (Tucker, 1998). If Tucker's hypothesis is correct, uncanalised development and frequent incidences of organ loss in this clade are not independent characteristics. This erratic development, combined with highly variable adult forms, may be evidence of an "experimental phase" in legume floral evolution prior to the appearance of the highly successful papilionoid lineage, as proposed by Prenner and Klitgaard (2008). Another hypothesis put forward in response to the decreasing floral organ numbers observed in the tribe Cassieae, which included Dialiinae until recently, is that it represents a trend of increasing sterility, based on gradually diminishing numbers of functional stamens (Thompson, 1925). When applied solely to the Dialiinae, this hypothesis is attractive, since the genus sister to the other Dialiinae genera possesses the full legume complement of 10 functional stamens, while the most deeply nested genera frequently have only two (Irwin and Barneby, 1981; Bruneau et al., 2001; Bruneau et al., 2008). To make more definitive statements regarding trends, however, will require a better resolution of the species- and genus-level relationships in this clade.

Three recent phylogenetic analyses have attempted to clarify the systematics of the Dialiinae clade (Bruneau et al., 2001; Herendeen et al., 2003; Bruneau et al., 2008) using plastid sequences and morphological characters. These have succeeded in resolving some, but not all, generic level relationships, leaving many unknowns. Taxon sampling has also precluded species-level resolution. The aforementioned studies have included between 15 and 17 of the approximately 90 Dialiinae species (11-14 of the 17 genera) each, using single representative members of most genera, in a largely overlapping taxon set, and have focused on determining genus-level relationships rather than resolving the tree at the species level.

Here, we improve upon previous taxon sampling by carrying out a comprehensive morphological study for the clade and combining this with molecular data where possible. The morphological analysis was carried out on 79 ingroup and four outgroup taxa, including all 17 genera of the Dialiinae. In addition, phylogenetic analyses were completed on a reduced set of taxa for which both molecular (*trnL* and *rpS16* introns) and morphological data had been obtained. Our overall objective has been to produce a Dialiinae phylogeny with greater species level resolution and a clearer picture of the clade's floral evolution in order to better understand its place within the Caesalpinioideae.

2.2 Materials and Methods

2.2.1 Taxon Sampling & Morphological Methods

A total of 79 ingroup species are included in the morphological analysis (Table 2.2, all species authorities given therein), as well as four outgroup species (*Cercis canadensis*, *Barnebydendron riedelii*, *Delonix regia,* and *Duparquetia orchidacea*). Approximately ten species are not included because material could not be obtained, but all genera are included, and for each genus, a majority of species were scored. Outgroup species were selected from other early-diverging lineages of the Caesalpinioideae, including Cercideae, Detarieae and Duparquetiinae, and also from the *Peltophorum* clade, as described in the most recent work by the Legume Phylogeny Working Group (LPWG, 2013). Morphology was studied primarily from herbarium specimens from K, MO, US, F, A, WAG, and NY, with alcohol-preserved flowers used when available. When dried flowers from vouchers were used, they were rehydrated with boiling water and a small amount of detergent, then moved through an ethanol series and dissected in 80% EtOH. In nearly all cases, late pre-anthesis buds were dissected to ensure proper counts of organ numbers. Leaf clearings and epidermal peels were made following the method of Herendeen & Dilcher (1990) to allow the study of venation and epidermal anatomy, respectively. Observations were made using a Nikon Eclipse TE2000-U compound microscope and a Wild Heerbrugg dissecting microscope.

The character list used was modified from that of the Caesalpinioid Legume Working Group (Herendeen et al., 2003) and is comprised of 135 characters (Table 2.3); 29 vegetative, 76 floral, one pollen, six fruit, nine venation, and 14 epidermal. Of these characters, 78 are binary, while 57 are multistate. This list was originally developed for use with all caesalpinioid legumes, and as such, some characters (*eg*. those involving detarioid leaf glands) are constant in the Dialiinae (these characters are noted with an asterisk in Table 2.3). These characters were left in the matrix (Table 2.4) in order to facilitate its easy assimilation into future studies. A number of character states were added where necessary to capture the full spectrum of variation in the Dialiinae. Pollen characters were primarily scored from the literature, specifically from the work of Hannah Banks and coworkers (Banks et al., 2003; Banks et al., 2006), and from Graham *et al*. (1980). An average of four specimens per species was scored. Data was coded in Mesquite v.2.75 (Maddison and Maddison, 2011).

2.2.2 Molecular Methods

A total of 37 ingroup species are included in the combined molecular analysis (Appendix I). This group comprises 15 of the 17 genera in the Dialiinae clade. The monospecific genus *Androcalymma* could not be included due to the fact that material was collected only once, as a type specimen, during the 1930s, and viable DNA has never been successfully extracted. Another rarely-collected monospecific genus, *Uittienia*, was also not included due to a lack of viable DNA. The two plastid regions sequenced were the *rpS16* intron and the *trnL* (UAA) intron. These were selected due to their relative ease of amplification and phylogenetic resolution appropriate to the group being studied. Of the 45 sequences included in the *trnL* analysis, 22 were downloaded from Genbank (see Appendix I), while the remaining 23 were newly generated in this study. All 36 *rpS16* sequences are original to this study.

For most taxa studied, DNA was extracted using the method of Ky *et al*. (2000), modified for use with 5mL centrifuge tubes. PCR amplifications were carried out in reaction volumes of 50µL, including 0.5µL Phusion High-Fidelity DNA polymerase (New England Biolabs, Ipswich, MA, USA), 10µL 5x Phusion HF buffer (New England Biolabs, Ipswich, MA, USA), 0.5µL bovine serum albumin at 10mg/mL (New England Biolabs, Ipswich, MA, USA), 1µL 10µM dNTPs (Fermentas, Burlington, ON, Canada), 2µL each forward and reverse primers at 10µM, and 2.5µL template DNA. For *trnL* amplifications, primers were the "c" and "d" primers described in Taberlet *et al.* (1991), while *rpS16* amplifications used the rpsF and rpsR2 primers of Oxelman *et al.* (1997). In the case of *trnL*, amplifications were carried out for 35 cycles of 10s at 98°C, 45s at 60°C, and 60s at 72°C. The 35 cycles were preceded by an initial 60s phase at 98°C and followed by 120s at 72°C. For *rpS16* amplifications, the following program was used: 10s at 98°C, 25s at 65°C, and 35s at 72°C. Here, the 35 cycles were preceded by an initial 30s phase at 98°C and followed by 120s at 72°C. Purification and sequencing of PCR products was carried out at the Genome Quebec Sequencing Platform (Montreal, Quebec) using Big Dye Terminator 3.1 chemistry on an ABI 3730xl DNA Analyzer (Applied Biosystems, Carlsbad, CA, USA).

2.2.3 Phylogenetic Analyses

Sequences were initially checked for quality using FinchTV v.1.5.0 (Geospiza Inc.) before contigs were assembled using Sequencher sequence analysis software v.4.8 (Gene Codes Corporation, Ann Arbor, MI, USA). Alignments were made in MEGA v.5.2.2 (Tamura et al., 2011) using default parameters and then corrected by eye. Finished alignments were exported in nexus format and gap-coded using modified complex indel coding, implemented in SeqState v.1.4.1 (Muller, 2005). Matrices were created for each individual data set, for the combined *trnL+rpS16* molecular data, and for all three data sets (molecular + morphological) combined, both without missing data (reduced taxon set) and with substantial missing data allowed (full taxon set).

All matrices were analysed using the parsimony criterion, with calculations performed in PAUP* v.4.0b10 (Swofford, 2002). A first series of trees was generated by retaining a maximum of five most parsimonious trees per replicate from 1000 random addition replicates using the tree bisection-reconnection (TBR) branch-swapping option. This first series of most parsimonious trees was then used as the starting point for a heuristic analysis using TBR branch swapping, retaining a maximum of 20,000 trees. Strict consensus trees were constructed for each analysis, and support values were obtained using a bootstrap procedure. Bootstrapping was done using a heuristic search with TBR branch swapping, retaining a maximum of two trees for each sub-replicate for a total of 5000 replicates. An analysis was also carried out using only the morphological data set, with nodes constrained using the highly supported nodes (bootstrap values of greater than 85) obtained from the analysis of all three data sets without missing data. This was implemented using PAUP*'s "AsBackbone" constraint option, with all other settings as described above. This last procedure was conducted in order to use well-supported relationships obtained from an analysis with a much smaller taxon set to give resolution to a much larger, but less well-supported analysis.

A Bayesian analysis was run on the combined molecular data. The matrix was divided into two partitions, one for nucleotide sequences and the other for the coded gaps. Simple gap coding (Simmons and Ochoterena, 2000) was used, once again implemented in SeqState v.1.4.1 (Muller, 2005). Using ModelTest v.2.3 (Nylander, 2004), the best model for the DNA partition was estimated to be GTR+G according to both the Akaike Information Criterion (Akaike, 1974) and the hierarchical likelihood ratio test (Posada and Crandall, 2001). The model for the gap partition was set to restriction data. Bayesian analysis was performed using MrBayes 3.2.2 (Ronquist and Huelsenbeck, 2003), implemented using the CIPRES Science Gateway (Miller et al, 2010), with ten million generations, two parallel runs of four Markov Chain Monte Carlo each, and one swap per swapping cycle. Trees were sampled every 1000 generations, and the first 2.5 million generations were discarded as "burn-in."

Trees were visualised using FigTree v.1.4.0 (Andrew Rambaut, http://tree.bio.ed.ac.uk/software/figtree/). For the constrained analysis described above, a single most-parsimonious tree was chosen at random from the set of 20,000 equally parsimonious trees. Using Winclada v.1.00.08 (Nixon, 2002), all morphological character changes were mapped onto the branches of the tree.

2.3 Results

2.3.1 Sequence characteristics

The *rpS16* gene was between 693 and 825 bp in length, with an aligned length of 882 bp. The *trnL* intron aligned with a length of 658 bp, with individual sequences of between 579 and 743 bp. The morphological data was composed of 135 characters, of which 99 (73%) were parsimony informative. The combined molecular-morphological analysis produced a total of 277 (16%) parsimony informative characters, with 35%, 41% and 24% coming from the morphology, *rpS16*, and *trnL* regions, respectively. The combined analysis with reduced taxon sampling contained 5.87% missing data, whereas the combined analysis with the full taxon sampling contained 51.28% missing data. Further summary statistics are given in Table 2.1.

Table 2.1. Summary statistics based on individual analyses of each data set.

Data Type	Aligned Length	Indels	Variable Sites	Parsimony Informative characters	GC%	CI	RI	Ingroup Taxa
rpS16	882	62	318	115	31.6	0.85	0.83	35
trnL	658	39	145	70	35.2	0.83	0.85	44
morphology	135	n/a	107	99	n/a	0.24	0.58	79

2.3.2 Phylogenetic analyses

The combined analysis with full taxon sampling resulted in 7968 most parsimonious trees of length 1609 (C.I.=0.46; R.I.=0.69). This analysis was negatively affected by the quantity of missing data and produced results which were not in accordance with any previous analysis, nor with the other results of this study. The resulting trees are therefore not presented here (but see Appendix II).

The reduced taxon combined analysis resulted in only four most parsimonious trees of length 1163 (C.I.=0.62; R.I.=0.65); the strict consensus of these trees, with bootstrap values above 50% noted, is presented here as Figure 2.1. This analysis, which was comprised of 37 ingroup taxa, strongly supports a monophyletic Dialiinae with *Poeppigia procera* as sister to the rest of the clade. Very strong support is also found for a lineage of two Malagasy genera, within which *Eligmocarpus* is sister to a monophyletic *Baudouinia*. *Zenia insignis* is found to be sister to a highly supported polytomy consisting of (*Mendoravia* + *Koompassia*), ((*Apuleia* + *Distemonanthus*) + (*Dicorynia* + *Dialium*)), *Martiodendron*, and (*Kalappia* + (*Storckiella* + (*Labichea* + *Petalostylis*))). Other highly supported inter-generic relationships are *Dialium* and *Dicorynia*, *Apuleia* and *Distemonanthus*, and an Australasian clade consisting of *Storckiell*a, *Labichea,* and *Petalostylis*.

At the species level, several new and well supported groups are resolved. For example, relationships among the four *Labichea* species are well resolved with *L. buettneriana* as sister to the other three species sampled (*L. punctata, L. lanceolata,* and *L. nitida*). Within *Dialium*, which has proven difficult to resolve even with three data sets, *D. guianense* is well supported as sister to *D. dinklagei, D. holtzii,* and *D. schlechteri*. This clade, in turn, is highly supported as sister to the remaining *Dialium* species.

The constrained morphological analysis resulted in 20,000 most parsimonious trees (maximum number saved) of length 794 (C.I.=0.23; R.I.=0.58); the strict consensus of these trees, with bootstrap values above 50% noted, is presented here as Figure 2.2. This tree has lower support values and a much lower consistency index than the tree described above, yet contains several moderately to highly supported nodes which do not appear in the smaller, combined tree. The Malagasy clade of (*Baudouinia* + *Eligmocarpus*) is here highly supported as sister to the rest of the Dialiinae clade. Oddly, *Poeppigia* was not found to be part of the clade in this analysis, but grouped as part of a polytomy with *Barnebydendron* and *Delonix*. Within the genus *Storckiella*, *S. vitiensis* is highly supported as sister to (*S. comptonii* + *S. pancheri* + *S. neocaledonica*), while *S.*

australiensis is moderately supported as sister to all other *Storckiella* species. Within *Koompassia*, *K. malaccensis* has moderate support as sister to (*K. excelsa* + *K. parvifolia*). While the smaller analysis produced a polytomy for all species of *Martiodendron*, this tree gives moderate support for *M. elatum* as sister to (*M. excelsum* + *M. parviflorum* + *M. mediterraneum*), as well as strong support for *M. fluminense* as sister to the remainder of the genus. Resolution for *Dialium* was quite low in this analysis, although moderate support was found for a clade of two Malagasy species, *D. occidentale* + *D. unifoliolatum*, which were not included in the combined analysis due to lack of viable DNA.

In both the constrained morphology and reduced combined analyses, several monotypic genera, including *Zenia, Kalappia,* and *Mendoravia* (as well as *Uittienia* and *Androcalymma*, which appear only in the morphological analysis), occupy weakly-supported positions in the phylogeny.

The Bayesian analysis of molecular data (Appendix II) produced a tree with a generally similar topology to that of the combined parsimony analysis (Figure 2.1). Compared to the parsimony analysis, there is a slightly different arrangement of the species-level relationships within *Baudouinia*, although these were not highly supported in the parsimony tree. The *Apuleia* + *Distemonanthus* clade is more basal in the Bayesian tree compared to the parsimony tree, although equally well-supported. Both *Storckiella* and *Martiodendron* are polyphyletic in the Bayesian phylogeny, an issue encountered in the molecular parsimony phylogeny as well (Appendix II). The Australo-Melanesian clade, resolved in the combined parsimony tree as *Storckiella* + *(Labichea* + *Petalostylis)*, is found in the Bayesian analysis to be *Petalostylis* + *(Storckiella* + *Labichea)*. There is also no species-level resolution within *Labichea* in the Bayesian phylogeny. The *Dialium* clade shows only minor species-level differences between the combined parsimony and molecular Bayesian analyses.

2.3.3 Morphological Characters

One of the most parsimonious trees from the constrained morphological analysis was chosen at random to illustrate character distribution (Figure 2.3). In the following paragraphs, numbers given in square brackets correspond to character numbers in the morphological matrix (Table 2.3). Four characters are shown to support a Dialiinae clade which does not include *Poeppigia*. These include the absence of clawed petals [93], anthers which are glabrous [112] and widest basally [108], and a drupaceous fruit [134]. The first-branching lineage of *Eligmocarpus* + *Baudouinia* has three synapomorphies; leaves widest at the middle [17], linear anthers [109], and anthers which dehisce via short slits or terminal pores [115]. The highly supported *Apuleia* + *Distemonanthus* clade is also based on three synapomorphies; the presence of a hypanthium [69], sepals which are glabrous on their interior surface [84], and a peltate stigma [124]. A suite of characters distinguishes the Australian clade *Labichea* + *Petalostylis*. These include a shrubby habit [7], a rachis which is grooved adaxially [14], anomocytic stomata [41], simple inflorescences [55], the presence of a basal central spot on the corolla [87], linear anthers [109], and a stipitate ovary [118]. The clade consisting of *Dialium, Dicorynia*, and *Androcalymma* has only two synapomorphies at its base: a dimerous androecium [97] and the presence of acuminate leaf tips [22]. The latter character is reversed numerous times within the clade. Synapomorphies corresponding to highly supported clades in the constrained analysis are summarised in Table 2.5.

2.4 Discussion

2.4.1 Comparison of phylogenies

Originally circumscribed as two subtribes by Irwin and Barneby (1981), the Dialiinae *sensu lato* clade consists of the 14 genera initially included, as well as the monospecific genus *Poeppigia*, formerly part of the Caesalpiniae, and the two nested genera of the Australian Labicheinae clade (Lewis et al., 2005). Three of the original 14 genera, *Mendoravia*, *Eligmocarpus*, and *Baudouinia*, were considered anomalous due to various morphological traits, and in need of possible reassignment, although subsequent molecular phylogenies have borne out the authors' initial placement (Irwin and Barneby, 1981).

The recent phylogenetic analyses of Bruneau et al. (2001; 2008), using *trnL* and *mat/3'-trnK* plastid sequences, have found the Dialiinae *sensu* Irwin and Barneby (1981) to be monophyletic only with the inclusion of the Labicheinae (*Labichea* + *Petalostylis*), which were formerly given subtribe rank. The genus *Poeppigia* was found to be sister to the Dialiinae/Labicheinae clade. Within the clade, *Dicorynia* was strongly supported as being sister to a monophyletic *Dialium*. Two groupings in these phylogenies which produced very high bootstrap values were a Malagasy clade, *Baudouinia* + *Eligmocarpus*, and the two monotypic genera, *Apuleia* + *Distemonanthus*, from the New World and West Africa, respectively. The remaining genera were not highly resolved.

A contemporary analysis combining the *trnL* sequence data with morphological characters (Herendeen et al., 2003) again found the Labicheinae to be nested within Dialiinae. Here, *Labichea, Petalostylis*, and the Australasian *Storckiella* formed a monophyletic group. Also in this analysis, *Poeppigia* was found to nest within Dialiinae, sister to the Malagasy genus *Baudouinia*. Interestingly, this phylogeny placed the New World genus *Dicorynia* within *Dialium*, perhaps in part based on its similarly reduced number of floral organs.

The phylogenies presented here represent a greater level of support and resolution, as well as a greater breadth of taxon coverage, than has previously been obtained for the Dialiinae clade, allowing for a better understanding of interspecific relationships and floral evolution in this group. Overall, intergeneric relationships are consistent with what has been found in previous studies (Bruneau et al., 2001; Herendeen et al., 2003; Bruneau et al., 2008), but a number of new lower-level groupings have been uncovered. The only significant topological difference at the intergeneric level between the combined analysis of this study and that of the most recently published phylogeny, Bruneau *et al*. (2008), is in our highly supported placement of *Storckiella* as sister to *Labichea* + *Petalostylis*, where the previous study found a topology of *Labichea* + (*Storckiella* + *Petalostylis*). It is worth noting that Bruneau *et al.* (2008) also uncovered a *Mendoravia* + *Koompassia* clade, although, as in our study, it did not have good bootstrap support.

Our present findings mirror several aspects of the combined morphology+molecular phylogeny of Herendeen *et al*. (2003), although low bootstrap support has been similarly problematic in our morphological analysis. These authors found the same grouping of the Australasian genera, with *Storckiella* sister to *Labichea* + *Petalostylis*. Our maximum parsimony tree, based on the constrained morphological analysis (Figure 2.3) also shows the genus *Dicorynia* as being nested within *Dialium*. This nesting does not appear in the reduced taxon combined analysis, however.

2.4.2 Biogeography

While the Dialiinae clade as a whole is pantropically distributed, individual clades within it tend to be more geographically restricted. The *Baudouinia* + *Eligmocarpus* clade, for example, is endemic to Madagascar, while the *Storckiella* + *(Labichea* + *Petalostylis)* clade is found only in Australia and the nearby islands of New Caledonia and Fiji. Conversely, the *Apuleia* + *Distemonanthus* clade has a South America-West Africa distribution. The uncertainty in the clade age estimate of 34 million years due to the lack of a fossil record does not eliminate the possibility of dispersal via the North Atlantic land bridge (Doyle and Luckow, 2003; Bruneau et al., 2008), although marine dispersal could also explain this pattern. Similarly, *Dialium* has its centre of species diversity in equatorial West Africa, but members of the genus can be found in South America, Madagascar, India, Southeast Asia, and elsewhere in Africa. The sister group of *Dialium*, *Dicorynia*, is found exclusively in South America. Here, marine dispersal seems the most likely scenario. Interclade relationships in the Dialiinae are not well-supported through much of the tree, although *Poeppigia* has been found to be sister to the rest of the clade both in our combined analysis and in that of Bruneau *et al*. (2008), which may point toward a Central American origin for the clade. Overall, the phylogeny of the Dialiinae clade does not tell an easily interpreted biogeographical story, and further research will be needed in order to create a coherent reconstruction.

2.4.3 Roaming monotypic genera

One aspect of Diallinae phylogeny which has failed to be resolved with this study is the placement of several monotypic genera. Specifically, *Kalappia celebica, Mendoravia dumaziana, Zenia insignis*, *Androcalymma glabrifolium*, and *Uittienia modesta*. While the affinities of some of these genera have echoed those of previous phylogenies, none of the above are well-supported in the topology of any of our analyses.

Occurring only in a very restricted area on the Indonesian island of Sulawesi (formerly Celebes) (Kostermans, 1952), *Kalappia celebica* has not been included in previous phylogenetic studies. The flowers of this species have a pentamerous calyx and corolla, and a seven to nine part androecium, of which only four or five are fertile. In our reduced combined analysis, *Kalappia* is sister to the Australasian clade containing *Storckiella, Labichea*, and *Petalostylis*. Morphologically, the species shares several similarities with *Storckiella*, including leaflet shape and number, higher stamen numbers, and ventrally winged fruits. Biogeographically, these similarities make sense, given their distribution in neighbouring regions of southeast Asia, Australia, and Melanesia.

Mendoravia is one of three Dialiinae genera endemic to Madagascar, the others being *Eligmocarpus* and *Baudouinia*. Together with *Poeppigia procera*, *M. dumaziana* is also one of only two Dialiinae species to have wood containing vestured pits in the xylem (Herendeen, 2000; Herendeen et al., 2003). These two occurrences would seem to be due to two independent gains, however, since neither our analyses nor that of Bruneau *et al*. (2008) find the two genera to be closely allied. Both the phylogeny of Bruneau *et al*. (2008) and our own reduced combined analysis have found *Mendoravia* to be sister to the southeast Asian genus *Koompassia*, albeit with low support. Morphological affinities between these two genera are not obvious; leaves, flowers, and fruit are all quite dissimilar, both structurally and in terms of organ numbers. Furthermore, the geographic distribution of the two genera make their affiliation unlikely.

Zenia is a southeast Asian genus that was first described in the mid-twentieth century (Chun, 1946). It appears to be one of the more problematic Dialiinae taxa, having different affinities in Herendeen *et al*. (2003), Bruneau *et al*. (2008), and in the present study. Herendeen *et al*. (2003) found *Zenia* to be sister to *Dialium* + *Dicorynia*, while Bruneau *et al*. (2008) found it to be sister to *Martiodendron*. Our reduced combined analysis found *Zenia* to be sister to a polytomy containing most other Dialiinae genera (Figure 2.1), while our constrained morphology analysis found it to be sister to *Uittienia*. In none of these cases was the position of the genus well-supported. Herendeen (2000) suggests a possible affinity with *Dicorynia, Koompassia, Martiodendron,* and *Storckiella* due to their shared trait of membranous fruits with vascularised wings on one or both sutures.

Androcalymma is a South American genus that is not well known because it has only been collected once, from a single tree in Brazil, in 1936 (Dwyer, 1957; Koeppen, 1963). The fruit is not known and the species has never been successfully sequenced. Koeppen and Iltis (1962) suggested an affinity to *Martiodendron* based on the presence of sclerotic parenchyma cells in the wood, which they state is very unusual among legumes. An affinity to *Zenia* is also possible, based on their similar floral structure of a pentamerous calyx and corolla paired with a tetramerous androecium, a pattern also seen in certain species of *Martiodendron*. Unlike *Zenia* and *Martiodendron*, however, *Androcalymma* does not produce staminodes. The position of the genus is unresolved in our analyses, being part of a large polytomy in the strict consensus of the constrained morphological analysis.

Uittienia modesta is an Indonesian species that has at times been considered a subgenus of *Dialium*, with the synonym *Dialium modestum* (Van Steenis) Steyaert used for the species (Steyaert, 1953). The morphological basis for this grouping is the similar drupaceous fruit, thyrsoid inflorescence, and small, unshowy flowers with a pentamerous calyx and expanded receptacle. The strict consensus of our constrained morphological analysis found *Uittienia* to be sister to *Zenia*, while a lack of viable DNA prevented *Uittienia*'s inclusion in the reduced combined analysis. Synapomorphies linking *Uittienia* with *Zenia* are the presence of staminodes, an expanded receptacle, and trichomes on the style. These few traits aside, *Uittienia* is much more similar in appearance to *Dialium*, and is probably best considered allied to it until molecular evidence can support or refute this assumption. However, as *Zenia* was found to be sister to *Dialium* + *Dicorynia* in the analyses of Herendeen *et al*. (2003), this apparent contradiction may disappear in a resolved tree.

2.4.4 Labichea

While only four species of *Labichea* could be successfully sequenced for inclusion in the reduced combined analysis, they have yielded several novel and well-supported relationships. We found *L. lanceolata* and *L. nitida* to be most closely related, and sister to *L. punctata*. *Labichea buettneriana* was found to be sister to all of the above. Morphologically, *L. buettneriana* can be distinguished from the other three species through the presence of long, white trichomes densely covering all above-ground surfaces of the plant save the inner three floral whorls and the adaxial leaf surfaces. It is also the only species of the four with multifoliolate pinnate leaves; *L. punctata* is unifoliolate, while *L. lanceolata* and *L. nitida* have palmate leaves. Leaves in *L. buettneriana* are also obtuse at both the base and the tip, while the others have lanceolate leaves. *Labichea teretifolia*, which is not included in the reduced combined analysis, has leaves which are so narrowed as to be digitate, with recurved margins that give leaflets a needle-like appearance. The evolutionary movement from wide, rounded leaflets spaced out along a multifoliolate leaf to narrow leaflets crowded into a palmate arrangement, thereby simulating a highly divided simple leaf, or reduced to a unifoliolate state would seem to be one of several adaptations to a hot, arid Australian environment (Givnish, 1987; Xu et al., 2009). All *Labichea* species are trichome-covered to varying extents, and it follows that the species with the greatest exposed leaflet area, *L. buettneriana*, would have the greatest density of these. The species occurs only in north-eastern Queensland, which experiences very hot summers (McCarthy and Orchard, 1998). Leaflets in this genus are also very tough and leathery, further reducing water loss. This toughness is, in fact, related to the low number of species included in our combined analyses; the leaflets are very difficult to both extract DNA from and to clear for use in venation scoring.

2.4.5 Dialium clades

In the morphological analysis strict consensus (Figure 2.2), only a single clade is resolved within *Dialium*, the rest being part of a large polytomy. This clade, made up of *Dansera procera* (syn. *Dialium procerum* (Van Steenis) Steyaert), *Dialium kunstleri* (syn. *Dialium trifoliolatum* de Wit & Dirk), *D. madagascariense, D. occidentale*, and *D. unifoliolatum*, presents an interesting suite of traits relative to the rest of the genus. The clade is differentiated from other *Dialium* species by its trimerous calyx; all other members of the genus have five sepals, with the exception of *D. hexasepalum*, which has six. This group also presents leaflet arrangements not seen elsewhere in *Dialium*. *Dansera procera*, *Dialium occidentale*, and *D. unifoliolatum* are all unifoliolate, while *D. kunstleri* and *D. madagascariense* are both trifoliolate. All other *Dialium* species have at least five leaflets. Three of these species, *D. madagascariense, D. occidentale*, and *D. unifoliolatum*, are the only members of *Dialium* that are endemic to Madagascar. These Malagasy species also share the trait, unique in *Dialium*, of a trimerous corolla; most other congenerics have either no corolla or a single petal. That all three Malagasy species have a reduced leaflet number is interesting in view of the fact that the only two simple-leaved genera of the Dialiinae, *Baudouinia* and *Mendoravia*, are also endemic to Madagascar. These genera are not closely allied to *Dialium*, so it is interesting to speculate on whether there exists some aspect of their native environment which makes monophyllous leaves advantageous, as we suggest above for *Labichea*.

In the combined analysis (Figure 2.1), there is a single highly supported clade resolved within *Dialium*; this clade consists of *D. dinklagei, D. holtzii, D. schlechteri,* and *D. guianense*. The princinpal morphological character distinguishing these taxa from others in this tree is the absence of the corolla. The other *Dialium* species in the combined analysis, with the exception of *D. excelsum* (which also lacks petals), have a single adaxial median petal. Outside of the Malagasy species described above, and *Dialium englerianum*, which has five petals, all *Dialium* species either have a single petal or lack a corolla. In those which do produce petals, they are typically very short and stunted, as though vestigial. Again, the Malagasy species are the exception; in these taxa, petals are longer than the stamens and curve over them in the late bud. In terms of stamen numbers, *D. schlechteri* is an unusual specimen, being the only member of its genus to develop a full ten-part androecium. Given the position of *Dialium* in this and other analyses (Bruneau et al., 2001; Herendeen et al., 2003; Bruneau et al., 2008), this is clearly a secondary gain; with only a couple of exceptions, the rest of the genus has a two-part androecium. This feature of the genus lead to speculation that *Dialium* was part of a trend of decreasing stamen numbers in the (former) Cassieae tribe as a whole (Thompson, 1925).

2.4.6 Stamen loss and suppression

With a better-resolved phylogeny for this clade, we are now able to evaluate whether, as suggested by Thompson (1925), members of the Dialiinae represent part of a drift toward increasing sterility he described for Cassieae. Within the clade, we see not so much a trend toward fertile stamen loss, as a precipitous drop after the divergence of the two first-diverging clades, *Poeppigia* and *Eligmocarpus*+*Baudouinia*. In these genera, all ten, or rarely seven to eight, as in the case of *Baudouinia fluggeiformis* and *B. rouxevillei*, of the fertile stamens expected in the legume floral groundplan (Tucker, 2003) are retained. Outside of these lineages, however, the number drops to a mode of 2-4 fertile stamens as the antepetalous whorl is lost in the vast majority of species, making decreased stamen numbers a synapomorphy for this group. Several species do retain higher organ numbers, such as *Mendoravia dumaziana*, with 10-12 stamens, and two *Storckiella* species, *S. neocaledonica* and *S. vitiensis*, which produce 10-14 stamens; but these appear to be secondary gains, at least in the case of *Storckiella*. In *Mendoravia*, it is difficult to say whether or not the high stamen number represents a secondary gain, as the position of the genus is not well-supported in either this or previous phylogenies of the clade (Bruneau et al., 2001; Herendeen et al., 2003; Bruneau et al., 2008). Nevertheless, it seems clear, based on our current phylogeny of this clade, that increasing sterility, as measured by decreasing fertile stamen numbers, is not a trend in the Dialiinae. That is to say, stamen numbers do not gradually diminish in increasingly nested clades.

Incidences of drastic reduction in stamen number within the caesalpinioid grade are not confined to the Dialiinae. Species of the large cercidioid genus *Bauhinia* undergo the loss or suppression of one to nine stamens as part of a transition series from fertile stamens to staminodes to complete stamen loss (Tucker, 1988b; Walker-Larsen and Harder, 2000). Most often, this reduction takes the form of suppression, and staminodes of varying shapes are present (Tucker, 1988b). While no function is known for these staminodes, Tucker (1988a) speculates that they may aid in attracting pollinators. Decreased stamen numbers in Dialiinae are most often due to complete loss than to reduction to a visible staminode, but these do occur in several genera, including *Distemonanthus, Martiodendron, Kalappia, Petalostylis*, and *Zenia*. As noted above, the most commonly lost stamens in the Dialiinae are those of the inner, or antepetalous, stamen whorl, which is often lost in its entirety. Walker-Larsen and Harder (2000), in their survey of patterns of stamen reduction in angiosperms, note that the reduction of one of the two ancestral stamen whorls is common in animal-pollinated families of the Rosidae. This type of loss is linked to the reallocation of resources to produce a greater number of smaller flowers or to adaptations that increase the efficiency of pollen dispersal, thereby lessening the amount of pollen required per flower. While pollinators of the Dialiinae have not been studied, the genus with the greatest reduction in stamen numbers, *Dialium*, does produce large numbers of very small flowers.

2.4.7 Characters of interest

A number of the 135 morphological characters scored for this study present interesting states or patterns of variation within the Dialiinae, but are not linked to a discussion of any particular clade (for a visual comparison of clades and key morphological features, see Figure 2.4). We will review several of them here.

Sepal number is surprisingly stable in the Dialiinae, given the variable organ numbers observed in the corolla and androecium; the majority of genera have a pentamerous calyx. In *Apuleia* and the Malagasy *Dialium* clade, a shift to a trimerous calyx is seen, and is accompanied by trimery in the corolla as well (Zimmerman et al., 2013a). Tetramerous calices are present in certain species of *Labichea* and *Storckiella*, and are in each case paired with a tetramerous corolla. In the case of *Labichea* species, Tucker (1998) attributed calyx tetramery to sepal fusion, but given that the fifth sepal in pentamerous species is always much smaller and under-developed compared to the remaining four, we feel this is likely a case of outright loss. Similarly, in *Mendoravia*, the calyx may be pentamerous or hexamerous from one flower to the next, but the number of sepals and petals is always found to be equal for a given flower (Zimmerman et al., 2013b). This trend points to a link between the calyx and corolla merosity, perhaps relating to available space on the floral meristem during development (Zimmerman et al., 2013b). Of course, there are numerous species with a reduced corolla that have not lost sepals, notably in *Dialium*, which may have a full calyx and no corolla at all, suggesting multiple causes of petal loss in the clade.

Symmetry was not treated as a single character in this analysis, but is the overall effect of numerous individual characters, including organ number, arrangement, and level of differentiation in each of the four floral whorls. The Dialiinae clade exhibits polysymmetry, asymmetry, and, most commonly, bilateral symmetry. What we see in this group, however, is not the highly organised and canalised zygomorphy of the papilionoid legumes (Endress' "constitutional monosymmetry"; Endress, 1999), but one brought about by either bilateral organ loss, as in the androecium of most *Dialium* species, in which only the two adaxial lateral organs remain; or by a late-stage modification, as in the petaloid style of *Petalostylis* ("positional monosymmetry"; Endress, 1999). Asymmetry in the Dialiinae takes three forms. In *Distemonanthus*, the loss of all but one adaxial lateral and one abaxial lateral stamen produces an asymmetrical androecium in an otherwise zygomorphic flower. In *Dicorynia*, asymmetry is based not on organ placement, but form. The two stamens are symmetrically arranged, but highly dimorphic, owing to a stout "club" stamen. Finally, in *Labichea*, asymmetry is much more fundamental, occurring early in ontogeny, likely due to an irregularly shaped floral meristem following the late initiation of a vestigial fifth sepal (Tucker, 1998). This leaves the remaining three whorls to develop at odd angles and degrees of rotation to one another, with no possible line of symmetry. While Tucker (1998) found this type of development, resulting in a highly asymmetrical flower, to be unique among studied legumes, she notes that *Chamaecrista fasciculata* has a similarly irregular floral meristem during ontogeny, yet produces a regularly arranged flower at anthesis (Tucker, 1996).

In the course of the morphological study, several discrepancies were found between the literature and the specimens which were being studied. Whether or not these represent errors on the part of earlier investigators, or merely natural variation, we would like to note those discrepancies here. Firstly, the original description of *Dansera procera* (van Steenis, 1948) refers to the species as being uniovulate, one of the characters distinguishing it from *Dialium*. The later revision by Steyaert (1953), which lumps *Dansera* into *Dialium*, describes it as 2-ovuled, as in *Dialium*. After numerous floral dissections on several different collections, we find that the flowers are consistently 2-ovuled, as described by Steyaert (1953). Secondly, the floral ontogenetic study of several Dialiinae species by Tucker (1998; see Table 1 therein) describes *Petalostylis labicheoides* as producing five sepals, the two adaxial members of which fuse to create a single broad, adaxial median sepal. After many floral dissections from numerous collections, we found only flowers with five free sepals. Our finding agrees with the description in Flora of Australia (McCarthy and Orchard, 1998). This suggests that the flowers studied by Tucker, which were collected in a single locality, may not have been the norm. It is interesting to note that one of the *Petalostylis labicheoides* vouchers examined for the current analysis also displayed a trait not noted in the literature; the presence of simple cymes, where all other specimens had only solitary flowers. However, Flora of Australia (McCarthy and Orchard, 1998) describes this genus as producing solitary flowers or short racemes. The occasional presence of cymes in this genus suggests that the genetic basis still exists for a reversion to the ancestral state. We did not observe racemes in any *Petalostylis* voucher examined.

Despite numerous exceptions in this clade with varying morphology, the typical member of the Dialiinae can be characterised as a tropical tree or shrub lacking vestured pits in the secondary xylem and producing imparipinnately compound, or occasionally simple, leaves. Stomata are abaxial only, with paracytic or anomocytic guard cells. Highly branched, thyrsoid inflorescences are borne in both terminal and axillary positions. Flowers are bisexual, with five free, equal to sub-equal sepals that are frequently tomentose on the exterior surface. A hypanthium is rarely present, although the receptacle may be broad and flattened, bearing nectary-like bodies. Petals are five or fewer, free, equal to sub-equal, and glabrous, with highly variable aestivation in bud. Stamen number is highly variable, but usually five or fewer, with only members of the antesepalous whorl present. Filaments are short, free, and uniform, bearing basifixed anthers that are rectangular to lanceolate and dehisce via short or long latrorse slits. Anther bases may be sagittate. The single carpel is pubescent, may be stipitate or sessile, and bears a truncate or rarely peltate stigma atop a slender, glabrous style. Ovules may be one to many, but are frequently two. Fruits are either indehiscent drupes, or coriaceous or membraneous pods, which may be dehiscent or not.

2.4.8 Lack of canalisation in the Dialiinae

A recurring theme in the Dialiinae, both in terms of floral development (Zimmerman et al., 2013b) and floral morphology, is the many exceptions to any general description of pattern or process. The clade lacks a consistent mode of organ initiation, organ number, symmetry, fruit type, sexuality, and wood anatomy, to name but a few instances. Yet it has been repeatedly determined, with high confidence, to be a monophyletic group based on molecular phylogenetic analyses (Bruneau et al., 2001; Bruneau et al., 2008). In their discussion of the floral development of *Duparquetia orchidacea*, another early-branching caesalpinioid lineage, Prenner and Klitgaard (2008) note that among early legumes, there may have been a distinct experimental phase of evolution, in which different developmental pathways eventually resulted in the highly canalised – and highly successful – papilionoid flower. Polhill *et al*. (1981) have suggested that the key innovation of the zygomorphic papilionoid flower is the ability to simultaneously produce a greater radial display via the flag and protect the inner floral whorls via the keel. Other legume lineages, they note, have tended to favour one function over the other. Throughout the caesalpinioid grade, there are repeated shifts toward a zygomorphic flower (Polhill et al., 1981), sometimes with clear convergence on the papilionoid model, albeit through a series of late-stage modifications, rather than a fundamental change in the developmental programme (Tucker, 2002). Even at the ontogenetic level, the extreme diversity seen in the mode and timing of organ initiation among caesalpinioids (Tucker, 2003; Prenner and Klitgaard, 2008; Zimmerman et al., 2013; Bruneau et al., 2014) suggests that no innovation had yet conferred a sufficient advantage to become canalised. The Dialiinae, being composed of relatively small, and often monotypic, genera with significant morphological and ontogenetic differences among them, may provide further evidence for Prenner and Klitgaard's (2008) hypothesis of "experimental" adaptations in floral morphology among basal legumes.

Table 2.2. Specimens used in this study for the construction of the morphological character matrix.

Taxon	Voucher	Locality	Herb.
Androcalymma glabrifolium Dwyer	B.A. Krukoff 9005	Brazil	US
	B.A. Krukoff 8827	Brazil	US
Apuleia leiocarpa (Vogel) JF Macbr.	B. Klitgaard & F.C.P. Garcia 66	Brazil	MO
	A.G. Ruiz 217	Peru	MO
	G.C.G. Argent 6657	Brazil	MO
	P. Fragomemi 11642	Brazil	MO
	Harley & Souza 10720	Brazil	K
	Heringer *et al*. 5426	Brazil	K
	Pennington & Rowe 172	Bolivia	MO
	W. Ganev 1231	Brazil	K
	R. Vasquez *et al*. 14369	Peru	MO
	Sant'Ana *et al*. 361	Brazil	MO
	Zarucchi & Barbosa 3739	Colombia	MO
	F.C. Hoehne 13-IX-1945	Brazil	F
Baudouinia fluggeiformis Baill.	DuPuy M703	Madagascar	MO
	Qamamoufisoa 2037	Madagascar	MO
	Rakotoniaina 6244	Madagascar	MO
	H. Humbert 19241	Madagascar	K
	H. Humbert 11554	Madagascar	K
	L.J. Razafitsalama *et al.* 696	Madagascar	MO
Baudouinia louvelii R. Vig.	Vigvier 45	Madagascar	MO
	Ludovic & Rakotoarivony 215	Madagascar	K
	R. Razakamalala 268	Madagascar	K
	Rabevohitra *et al*. 4417	Madagascar	MO
	Razakamalala & Rabehevitra 641	Madagascar	MO
Baudouinia rouxevillei H. Perrier	L.J. Dorr 4145	Madagascar	MO
Baudouinia sollyaeformis Baill.	R. Capuron 22984_SF	Madagascar	K
	R. Ramananjanahary *et al*. 306	Madagascar	MO
	R. Rabevohitra 4511	Madagascar	MO
	F. Ratovoson 962	Madagascar	MO
Dansera procera Van Steenis	M. Jacobs 5221	Borneo	K
	Van Steenis 31989	Sumatra	K
	J.S. Burley 1579	Sumatra	MO
	J.S. Burley & B. Lee 265	Sumatra	A
Dialium angolense Welw. ex Oliver	G. McPherson 16193	Gabon	MO
	Van Meer 1505	Nigeria	MO
	G. McPherson 16246	Gabon	MO
Dialium aubrevillei Pellegr.	de Wilde & Voorhoeve 3663	Liberia	A
	Versteegh & der Outer 748	Ivory Coast	MO
	L. Aké Assi 10929	Ivory Coast	MO
	A.A. Enti 1357	Ghana	MO
	J. Deaw 321	Ghana	F
Dialium bipindense Harms	M.S. Pierre 222	Gabon	K
	J. Stone *et al.* 5019	Gabon	MO
	J.M. & B. Reitsma 1451	Gabon	MO
Dialium cochinchinense Pierre	M. King 5612	Thailand	US
	D.D. Soejarto & K. Sydara 10850	Laos	K
	L. Pierre 814	China	MO
	Herendeen & Pooma 1-v-1999-6	China	US

Dialium corbisieri Staner	J. Stone *et al*. 5015	Gabon	MO
	Amsini 314	Zaire	MO
	J. Louis 3868	Congo	MO
Dialium densiflorum Harms	G. Walters *et al*. 490	Gabon	MO
	Le Testu 1619	Gabon	MO
Dialium dinklagei Harms	Linder 68	Liberia	A
	C. Vigne 972/194	Gold Coast	K
	C. Versteegh 110	Ivory Coast	MO
	Merello *et al*. 1219	Ghana	MO
Dialium englerianum Henriques	R. Devred 715	Congo	K
	D.J. Harris *et al*. 3065	Congo	MO
	L. Pauwels 604	Zaire	MO
	B. Masens 578	Congo	MO
	Mshasha 210	Rhodesia	MO
Dialium eurysepalum Harms	J.M. & B. Reitsma 1456	Gabon	MO
Dialium excelsum J. Louis ex Stey	J. Louis 2887	Congo	K
	T.B. Hart 1411	Zaire	MO
	T.B. Hart 280	Zaire	MO
	P. Gerard 4166	Zaire	MO
Dialium guianense (Aubl.) Sandwith	Palacias 1364	Mexico	MO
	O. Valverde *et al*. 81	Costa Rica	MO
	M. Groppo Jr. 896	Brazil	F
	G.I. Manriquez 2649	Mexico	MO
	B.A. Krukoff 6262	Brazil	MO
	Rabelo *et al.* 3118	Brazil	US
Dialium guineense Willd.	G. McPherson 16217	Gabon	MO
	Fox 156	Sierra Leone	K
	G. McPherson 16288	Gabon	MO
	Corbisier-Bolond 1689	Congo	F
	Zenker 2360	Cameroon	MO
	Geerling & Bokdam 987	*illegible*	MO
Dialium hexasepalum Harms	Ewango 2302	Congo	MO
	T.B. Hart 978	Zaire	MO
Dialium holtzii Harms	S.R. Semsei 2412	Kenya	K
	O.A. Kibure 333	Tanzania	MO
	Mwangoka & Saidi 2179	Tanzania	MO
	S.R. Semsei S694	Kenya	MO
Dialium hydnocarpoides de Wit	Talip 65854	Indonesia	MO
	Kessler *et al*. 78	Indonesia	K
	D. Sundaling 97318	Malaysia	MO
Dialium indum L.	O. Ismawi s.37817	Malaysia	MO
	G.D. Haviland 2281	Borneo	K
	Kostermans 6562	Borneo	MO
	Ambri *et al*. AA341	Indonesia	MO
Dialium kunstleri Prain	K. Sidiyasa 422	Indonesia	K
	Meijer 141468	Indonesia	F
	I. Pa'ie S25286	Indonesia	K
	Meijer & Audey 122361	Indonesia	F
Dialium lopense Breteler	G. McPherson 16244	Gabon	MO
Dialium madagascariense Baill.	Randrianaivo 701	Madagascar	MO
	G.E. Schatz *et al*. 3839	Madagascar	MO
	G.E. Schatz *et al*. 3632	Madagascar	MO
Dialium occidentale (Capuron) DuPuy&Rabev.	Ranirison *et al*. PR217	Madagascar	MO

	Gautier *et al*. LG4242	Madagascar	MO
	R. Capuron 24526_SF	Madagascar	MO
	R. Capuron 8444_SF	Madagascar	MO
	Ranirison 917	Madagascar	MO
Dialium orientale Baker f.	J.B. Gillett 20357	Kenya	MO
	S.A. Robertson 3716	Kenya	MO
Dialium ovoideum Thwaites	T.B. Worthington 4748	Ceylon	K
	Kostermans 25240	Ceylon	US
	W. Meijer 1284	Ceylon	K
Dialium pachyphyllum Harms	Olorunfemi *et al*. 76394	Nigeria	K
	H. Breyne 2205	Zaire	MO
	van der Burgt *et al*. 937	Cameroon	MO
	Le Testu 9566	Gabon	MO
Dialium patens Baker	C. Niyomdham *et al*. 1170	Thailand	K
	C. Niyondham 1184	Thailand	A
Dialium pentandrum Louis ex Steyaert	G. Troupin 4712	Zaire	MO
	T.B. Hart 1366	Zaire	MO
	J. Louis 3948	Congo	MO
Dialium platysepalum Baker	M. Kasim 236	Malaysia	K
	P.F. Cockburn 66222	Malaysia	A
	J.W. Smith 70361	Malaya	K
	Ngadiman 36908	Malaysia	MO
Dialium pobeguinii Pellegr.	F.C. Deighton 1752	Sierra Leone	K
Dialium polyanthum Harms	G. McPherson 16192	Gabon	MO
	G. Walters *et al*. 1077	Gabon	MO
	T.B. Hart 853	Zaire	MO
	G. Walters *et al*. 946	Gabon	MO
	G. McPherson 16656	Gabon	MO
Dialium reygaerti de Wild.	J. Louis 8505	Congo	K
Dialium schlechteri Harms	L.A. Grandvaux 7962	Mozambique	K
	Groenendijk & de Koning 189	Mozambique	MO
Dialium soyauxii Harms	G. McPherson 15430	Gabon	MO
	Floret & Louis 1505	Gabon	MO
Dialium tessmannii Harms	Corbisier 1642	Congo	K
	G. Le Testu 608	Gabon	MO
Dialium travancoricum Bourd.	J.L. Bourdillon 1005	India	K
Dialium unifoliolatum (Capuron) DuPuy&Rabev	S.G. Razafimandimbison 169	Madagascar	MO
	J. Randrianasolo *et al*. 173	Madagascar	MO
	D. Meyers 48	Madagascar	MO
	J. Randrianasolo *et al*. 232	Madagascar	MO
Dialium zenkeri Harms	Harris & Fay 1308	Centr.Afr.Rep.	MO
	Harris & Fay 1205	Centr.Afr.Rep.	MO
	Kenfack 833	Cameroon	MO
	Harris & Fay 961	Centr.Afr.Rep.	MO
	Léonard 178	Congo	MO
Dicorynia guianensis Amshoff	S. Mori & de Granville 8801	French Guiana	MO
	Hammel & Koemar 21377	Surinam	MO
	S. Mori 8885	French Guiana	K
Dicorynia paraensis Benth.	C.A. Cid & J. Lima 3564	Brazil	MO
	Ducke 23322	Brazil	K
	Amaral *et al*. 618	Brazil	MO
	J. Velazco 1005	Venezuela	MO
	C.A. Cid & J. Lima 3753	Brazil	MO

	Amaral *et al*. 401	Brazil	K
	Ducke 23319	Brazil	K
	Ducke 24184	Brazil	K
Distemonanthus benthamianus Baill.	de Wilde 7969	Cameroon	MO
	Le Testu 1161	Gabon	MO
	C. Vigne 4265	Ghana	MO
	L. White 1490	Gabon	MO
	Versteegh & Jansen 811	Liberia	MO
	J.D. Kennedy 1615	Nigeria	F
	Zenker 360	Cameroon	F
Eligmocarpus cynometroides Capuron	Dumetz & G. McPherson 1102	Madagascar	MO
	J. Rabenantoandro *et al*. 1610	Madagascar	MO
	J.H. McWhirter 204	Madagascar	K
Kalappia celebica Kosterm.	Keppil 389	Indonesia	MO
	E.A.Widjaja 9102	Indonesia	US
Koompassia excelsa (Becc.) Taub.	*s.n.* A2	Malaysia	K
	Herendeen 1-v-1999-7	Thailand	US
	Enggah 7269	Borneo	K
	Fedilis 88184	unknown	MO
	Cundra A2404	unknown	MO
Koompassia malaccensis Maing.	Y. Laumonier TFB2005	Sumatra	MO
	K. Ogata KEP105037	Malaya	K
	F.C. Yong 94673	Malaya	K
	Sundaling 93185	Malaysia	MO
	Ridley *s.n.*	India	US
Koompassia parvifolia Prain	Lorzing 13095	Indonesia	K
Labichea brassii C.T. White & Francis	J.R. Clarkson 10544	Queensland	K
	J.R. Clarkson 5302	Queensland	MO
	J.R. Clarkson 5255	Queensland	MO
Labichea buettneriana F. Muell.	L. Pedley 2625	Queensland	K
	J.R. Clarkson 3294	Queensland	MO
Labichea cassioides Gaudichaud-Beaupre ex DC	A.S. George 9173	W. Australia	K
Labichea digitata Benth.	Bidwell 25	Australia	K
Labichea diversifolia Meisn.	L. Preiss 1027	W. Australia	MO
Labichea eremaea C.A. Gardner	P.S. Short 1547	W. Australia	K
Labichea lanceolata Benth.	Archer 2009955	W. Australia	NY
	Went & Went A-17	W. Australia	US
	Eames & Hotchkiss *s.n.*	Australia	MO
	Clarke *s.n.*	Australia	US
	A. Strid 20640	W. Australia	MO
	N.N. Donner 2810	W. Australia	K
	Kospien 1332	Australia	MO
Labichea nitida Benth.	J.R. Clarkson 2774B	Queensland	MO
Labichea punctata Benth.	A. Morrison 321	W. Australia	K
	Nordenstam 703	W. Australia	MO
Labichea rupestris Benth.	Coveny & Hind 6805	Queensland	K
	Jackes *s.n.*	Queensland	MO
	S.T. Blake 9931	Queensland	K
Labichea stellata J.H. Ross	P.S. Short 1724C	Australia	K
Labichea teretifolia C.A. Gardner	A.M. Ashby 276	W. Australia	MO
Martiodendron elatum (Ducke) Gleason	Stergios & Velazco 14132	Venezuela	MO
	Ducke 16853	Brazil	US
	G.E. Schatz 728	Brazil	MO

	Prance & Silva 58613	Brazil	NY
	B.A. Krukoff 4950	Brazil	MO
Martiodendron excelsum (Benth.) Gleason	Mutchnick 543	Guyana	MO
	Mutchnick 834	Guyana	K
	B. Hoffman 1233	Guyana	K
	Redden *et al*. 1169	Guyana	MO
	Ducke 1389	Brazil	US
Martiodendron fluminense Lombardi	P.P.Oliveira 354A	unknown	MO
Martiodendron mediterraneum Koeppen	de Lima 632	Brazil	NY
	de Lima 5009	Barbados	MO
	de Pardo *et al*. 85	Brazil	MO
	Hatschback 38335	Brazil	MO
	P.R. Farag 20	Brazil	MO
Martiodendron parviflorum (Amshoff) Koeppen	Harley *s.n.*	French Guiana	US
	Fernandez 8470	unknown	MO
	Bridgewater *et al*. S710	Brazil	K
	Ratter *et al*. 6766	Brazil	MO
	S.J. Filho	Brazil	F
	Stahel 145	Surinam	MO
	H.S. Irwin *et al*. 21125	Brazil	K
Mendoravia dumaziana Capuron	Capuron 28341_SF	Madagascar	MO
	Capuron 28343_SF	Madagascar	MO
	McWhirter 212	Madagascar	K
	McWhirter 213	Madagascar	K
Petalostylis cassioides E. Pritzel	P.E. Conrick 1152	N. Australia	MO
	M.G. Corrick 9313	W. Australia	K
	Gardner 7901	W. Australia	K
	Latz 12175	Australia	MO
Petalostylis labicheoides R. Br.	K. Newby 10532	W. Australia	K
	D.B. Symon 3004	S. Australia	K
	E.F. Constable 4654	New S. Wales	MO
	A.D. Chapman 1289	Queensland	US
	A.E. Orme & R. Johnstone 534	New S. Wales	K
	D.J.E. Whibley 2122	S. Australia	MO
	Coveny 12062	Australia	MO
	Grimes 3208	Australia	MO
Poeppigia procera C. Presl.	Hughes 1484	unknown	MO
	L.O. Williams 14320	El Salvador	US
	R.M. King 2741	Mexico	US
	Lewis *et al*. 1125	Brazil	K
	Esteban & Martinez 23879	Mexico	MO
	B.A. Krukoff 5708	Brazil	US
Storckiella australiensis J.H. Ross & B. Hyland	K. Hill *et al*. 2096	Queensland	K
Storckiella comptonii Baker f.	G. McPherson 3471	NewCaledonia	MO
	M.P. Simmons 1875	NewCaledonia	MO
Storckiella neocaledonica Nielsen, Labat, Munz.	J.N. Labat 3520	NewCaledonia	MO
	MacKee 46431	NewCaledonia	K
Storckiella pancheri Baill.	H.S. MacKee 16161	NewCaledonia	MO
	G. McPherson 2648	NewCaledonia	MO
	P. Bamps 5719	NewCaledonia	K
	G. McPherson 5604	NewCaledonia	MO

	G. McPherson 2830	NewCaledonia	MO
	H.S. MacKee 34504	NewCaledonia	K
	H.S. MacKee 6584	NewCaledonia	US
Storckiella vitiensis Seem.	Angus 11887	Fiji	US
	W.J. Howard H395	Fiji	K
Uittienia modesta Van Steenis	A. Kostermans 5386	Borneo	K
	A. Kostermans 13709B	Borneo	K
	A. Kostermans 13231	Borneo	A
	A. Kostermans 5885	Borneo	A
	A. Kostermans 21422	Borneo	A
Zenia insignis Chun	Chen 147	China	US
	US3464689	China	US
	Lu & Chen 2090	China	K
	Averyanov *et al*. 5748	Vietnam	MO
	Le *et al*. HN385	Vietnam	MO
	Arnold Arboretum *s.n.*	China	A
Outgroups			
Barnebydendron riedelii Tul.	R.B. Foster 11963	Peru	F
	J. Lissot *s.n.*	Venezuela	US
	G.P. Lewis *et al*. 1615	Brazil	K
Cercis canadensis L.	N.B. Jacobs 87	U.S.A.	MO
	Jardin Botanique de Montréal	Canada	MT
Delonix regia (Bojer ex Hook) Raf.	T.J. Killeen 1135	Bolivia	F
	T. Bradley 31902	unknown	MO
	B. Emmons 30	unknown	US
Duparquetia orchidacea Baill.	G. McPherson 16287	Gabon	MO
	A.A. Enti 334	Gabon	MO
	Thomas & Mambo 4221	Cameroon	US
	Deaw 334	unknown	MO

Table 2.3. Morphological characters used in the phylogenetic analysis

All multistate characters are treated as unordered. Asterisks indicate characters which are invariant for this taxon set. They have been included here in order to facilitate the integration of this data with that of past and future studies by the Caesalpinioid Legume Working Group (Herendeen *et al*. 2003), from whom this character list was modified. Similarly, some states in otherwise variable characters may not appear in the matrix. Comments (in grey) below on the distribution of noteworthy individual characters refer only to ingroup taxa.

1. Vestured pits: absent [0], present [1]. Present only in *Mendoravia dumaziana* and *Poeppigia procera*.

2. Fruit wings: absent [0], placental vascularized wing [1], placental nonvascularized wing [2], vascularized wing on both sutures [3], distal wings [4], proximal wings [5], woody, nonvascularized wings [6].

3*. Woody vertical flange in median plane on placental suture: absent [0], present [1].

4. Woody lip on placental suture on each valve: absent [0], present [1]. Present only in *Eligmocarpus*.

5*. Carpel number: five [0], one [1].

6*. Pulvinus on petiole and petiolule: absent [0], present [1]. A pulvinus is a swelling at the base of the petiole or petiolule, near the point of attachment.

7. Habit: tree [0], shrub [1], herb [2], liana [3]. A shrub is here defined as having multiple stems and a height of less than three metres. All Dialiinae species are trees, with the exception of *Labichea* and *Petalostylis*, which are shrubs.

8. Leaf form: simple [0], pinnate (including unifoliolate) [1], bipinnate [2], palmate [3]. Unifoliolate leaves are distinguished from simple leaves by the presence of a second pulvinus, defining both a petiole and a petiolule. Simple leaves are found in *Baudouinia* and *Mendoravia*. Palmate leaves are found in some *Labichea* species. All others are pinnate.

9. Leaflet number per leaf, or pinna of bipinnate leaves: multifoliolate [0], bifoliolate [1], unifoliolate [2], trifoliolate [3]. Unifoliolate and/or trifoliolate leaves occur in a few species of *Dialium* and *Labichea*. All other pinnate leaves are multifoliolate.

10. Pinnation type: imparipinnate [0], paripinnate [1], variable within specimen [2]. Most leaves are imparipinnate. The only entirely paripinnate genus is *Poeppigia*.

11. Leaflet insertion: opposite to sub-opposite [0], alternate [1], mixed [2].

12. Leaflet primary vein: straight [0], curved [1].

13. Primary vein position: central [0], near distal margin [1], near proximal margin [2].

14. Rachis grooved adaxially: absent [0], present [1]. This character can be difficult to interpret in dried samples, but is somewhat more easily seen in the basal portion of the rachis, when present. Consistently present in both *Petalostylis* and *Poeppigia*.

15. Rachis (and petiole) winged between leaflet pairs: absent [0], lateral wing present [1], vertical wing or ridge present [2].

16. Appendages on rachis at leaflet insertion: absent [0], present [1].

17. Leaflet shape: widest basally [0], widest at middle [1], widest distally [2]. As with other leaf shape measurements, highly variable species are scored as missing data.

18*. Leaflet margin: entire [0], toothed [1].

19. Leaflet base: acute [0], obtuse to truncate [1], cordate [2].

20. Leaflet base: equal [0], unequal, one margin of the lamina attached below the other on the petiolule [1].

21. Leaflet apex: obtuse [0], acute [1].

22. Leaflet apex acuminate: absent [0], present [1].

23. Leaflet apex emarginate or retuse: absent [0], present [1].

24. Leaflet apex aristate or mucronate: absent [0], present [1].

25*. Gland on primary vein near or at apex of leaflet: absent [0], present [1].

26. Secondary venation: brochidodromous [0], craspedodromous [1], secondaries connecting to intramarginal vein [2], clado-semicraspedodromous [3], cladodromous [4], eucamptodromous [5]. For further explanation, see the Manual of Leaf Architecture [Leaf Architecture Working Group, 1999]. The majority of species have brochidodromous venation.

27. Crater-like gland on leaflet lamina: absent [0], present [1].

28. Crater-like gland position: scattered [0], paired at base of leaf and scattered [1].

29. Leaflets petiolulate: petiolulate [0], sessile to sub-sessile (<1mm) [1].

30. Twisted petiolules: absent [0], present [1].

31*. Stipules: absent [0], present [1]. Due to most species in this group having very early caducous stipules, characters 31, 35, and 36 were primarily scored from stipule scars.

32. Stipule form: scale-like [0], foliose (having a leaf-like lamina) [1], spinescent [2], thread-like [3]. *Poeppigia* and *Petalostylis* have foliose stipules. Most others, in cases where they could be observed, were scale-like.

33. Stipules branched or pinnate: absent [0], present [1].

34. Stipule base auriculate: absent [0], present [1].

35*. Stipule insertion: lateral [0], oblique (intrapetiolar) [1].

36*. Stipule connate basally: absent [0], present [1].

37. Primary venation: pinnate [0], actinodromous (several veins of equal size radiating from the base of the lamina) [1]. Always pinnate in ingroup taxa.

38. Acrodromous basal veins: absent [0], present [1]. An acrodromous vein is a secondary vein diverging at or above the base of the lamina and running in convergent arches toward the apex over some or all of the blade length.

39. Primary vein continuous to apex: present [0], absent [1].

40. Stomatal location: abaxial [0], abaxial and adaxial [1].

41. Stomata form: paracytic [0], anomocytic [1], cyclocytic [2], brachyparacytic [3]. Brachyparacytic in several *Dialium* taxa and *Uittienia*; otherwise all taxa either paracytic or anomocytic.

42. Giant stomata: absent [0], present [1]. Conspicuously large stomata, present together with typically sized stomata. Present only in *Baudouinia*.

43. Inner stomatal ledges: inconspicuous [0], large and heavily cutinized [1].

44*. Papillae overarching stomata: absent [0], round papillae present [1], elongate ridges present [2].

45. Cutinization of abaxial anticlinal walls: anticlinal walls of all cells cutinized and visible [0], anticlinal walls of cells near stomata not cutinized [1], anticlinal walls of all cells not cutinized [2].

46. Epidermal cells surrounding subsidiary cells: stain like ground cells [0], stain like subsidiary cells [1].

47. Ornamentation on abaxial/adaxial surface of cells: absent [0], present [1]. Present in several *Dialium* species only.

48. Papillae on ground cells: absent [0], present and low [1], pronounced [2].

49. Abaxial trichomes: absent [0], present [1].

50. Adaxial trichomes: absent [0], present [1].

51. Marginal trichomes: absent [0], present [1].

52. Trichome base: simple [0], subdermally buttressed and often heavily cutinized [1].

53. Trichome base diameter: as wide as trichome, not enlarged [0], large diameter [1].

54. Inflorescence structure: indeterminate (ie- raceme, spike, panicle) [0], determinate (ie- cyme) [1], solitary [2], cyme and solitary both present [3]. Both cymes and solitary flowers were observed in the genus *Petalostylis*. *Labichea* species produce a raceme. All other species produce a cymose (thyrsoid) inflorescence.

55. Inflorescence structure: simple [0], compound [1].

56. Flower arrangement in inflorescence: spiral [0], distichous [1]. Scored as inapplicable for cymose inflorescences, which are distichous by definition.

57*. Pedicel: present [0], absent [1].

58. Pedicel jointed: absent [0], present [1].

59*. Bracteoles: present [0], absent [1].

60. Bracteole persistence: caducous [0], persistent to anthesis [1].

61*. Bracteoles enclosing flower bud (late-stage buds): not enclosing bud [0], enclosing bud [1].

62. Bracteole aestivation: distant [0], valvate [1], imbricate [2], adaxial surfaces touching [3]. Due to the small size and early caducous nature of bracteoles in this group, this character was difficult to score accurately.

63*. Bracteole position on pedicel: low to middle [0], high [1].

64. Bracteole position: opposite to sub-opposite [0], alternate [1].

65*. Bracteole connation: free [0], connate [1].

66*. Gland-tipped bracteole: absent [0], present [1].

67*. Pedicel twisted: absent [0], present [1].

68. Sexuality: perfect [0], monoecious [1], andromonoecious [2], dioecious [3], dioecious and perfect [4]. All flowers were perfect, with the exception of the andromonoecious *Apuleia leiocarpa*.

69. Hypanthium: absent [0], present [1]. Present in *Apuleia, Distemonanthus, Poeppigia*, and most *Storckiella* species.

70. Hypanthium shape: open [0], tubular [1]. With the exception of *Poeppigia*, and hypanthia were tubular.

71. Hypanthium pubescence (interior): absent [0], present [1].

72*. Calyx and corolla differentiated: present [0], absent [1]. Scored as present for petal-less species if taxa with a differentiated calyx and corolla occur elsewhere in the same genus.

73. Sepal number: five [0], four [1], three [2], two [3], one [4], unstable [5], six [6]. See Chapter 2 discussion.

74*. Adaxial lateral sepal pair connate to yield a single broad adaxial sepal: absent [0], present [1].

75. Sepal connation: free to base or rim of hypanthium [0], connate above base or above hypanthium [1]. Connation present only in *Poeppigia*.

76. Sepal lobes reflexed at anthesis: absent [0], present [1].

77. Median sepal position: abaxial [0], adaxial [1], both [2]. State [2] applies to tetramerous species in which a sepal develops in both median positions.

78. Calyx aestivation: imbricate [0], very narrowly imbricate to valvate [1], distant [2]. Narrowly imbricate to valvate in *Koompassia, Martiodendron*, and most *Storckiella* species. Imbricate in all others.

79. Sepal lobe width: width of sepal bases uniform [0], abaxial median sepal broader than others [1], adaxial median sepal broader than others [2], two median sepals which are broader than any lateral sepals [3], lower lateral sepals broader than other sepals [4], abaxial median sepal narrower than all others [5], lower lateral sepals narrower than all others [6], adaxial lateral sepals broader than remaining equal sepals [7].

80. Sepal thickness: uniform [0], sepal margins very thin and hyaline, often lighter in colour [1].

81. Calyx base symmetry: symmetrical [0], slightly asymmetrical [1], strongly gibbous [2].

82. Simple trichomes on margin of sepals: absent [0], present [1].

83. Indument of sepal lobes, outer surface (simple trichomes): absent [0], present [1].

84. Indument of sepal lobes, inner surface (simple trichomes): absent [0], present [1].

85. Petal number at anthesis (including vestigial petals): five [0], four [1], three [2], two [3], one [4], absent [5], unstable [6]. See Chapter 2 discussion.

86. Vestigial petal at anthesis: absent [0], all petals reduced [1], four lateral petals reduced, median petal fully formed [2], one abaxial petal reduced [3], two adaxial petals reduced [4], two abaxial petals reduced [5]. Scored as inapplicable for species with only one petal, since there is no basis for size comparison, as well as for species with no petals (to keep the character independent from #85). A single reduced abaxial petal was seen in several species of *Labichea*.

87. Petal colouration pattern: uniformly coloured [0], guide lines present [1], splotches [2], basal central spot [3]. This character is sometimes difficult to determine from herbarium specimens, and was scored from the literature whenever possible. Non-uniform colouration seen in *Labichea* and *Petalostylis*.

88. Differentiation of median petal: not differentiated, all petals uniform [0], adaxial petal larger than remaining equal petals [1], adaxial petal smaller than remaining equal petals [2], adaxial and upper lateral petals uniform and different from smaller lower lateral petals [3], median petal, upper laterals, and lower laterals all different sizes [4]. Scored as inapplicable in taxa with tetramerous corollas.

89. Differentiation of lateral petals: upper and lower lateral petals uniform, not differentiated [0], upper lateral petals and lower lateral petals differentiated [1]. Scored as state [0] for tetramerous *Labichea* species, to indicate that petals are all of the same size.

90. Median petal clasping ovary in bud: absent [0], present [1].

91. Petal connation at anthesis: free [0], all connate, at least proximally [1], some petals connate [2]. Petal connation does not occur in Dialiinae.

92. Petal aestivation in bud: imbricate ascending (standard innermost) [0], imbricate descending (standard outermost) [1], valvate [2], contort [3], imbricate descending, but with one margin of upper petal in and other distant [4], distant [5].

93. Petals clawed: absent [0], upper petals clawed [1], four lateral petals clawed [2], all petals clawed [3], only two lateral petals, both clawed [4], median petal clawed [5].

94. Trichomes on inner surface of petals: absent [0], present [1].

95. Trichomes on outer surface of petals: absent [0], present [1].

96. Trichomes on margin of petals: absent [0], present [1].

97. Androecium, total organ number: ten [0], five [1], three [2], two [3], one [4], nine [5], more than twice the petal number [6], four [7], seven [8], unstable [9], six [A]. See Chapter 2 discussion.

98. Fertile stamen number (morphologically appearing fertile; does not recognize cryptic sterile anthers): ten [0], five [1], three [2], two [3], one [4], variable [5], nine [6], four [7], more than ten [8], seven [9], six [A].

99. Staminodes in bisexual flowers: absent [0], present [1]. See Chapter 2 discussion.

100. Staminode structure: consisting of filament only [0], consisting of filament and sterile anther [1].

101. Stamen connation: free [0], all filaments connate, at least proximally, to form a tube [1], all filaments connate, at least proximally, to form a sheath (open on one side) [2], some connate and some free [3], all connate except at junction at adaxial petal [4], filaments free, anthers connate [5]. Partial connation (state 3) occurs in *Martiodendron elatum, Eligmocarpus cynometroides,* and *Baudouinia rouxevillei*.

102. Filament exsertion: filaments short, stamens included within corolla at anthesis [0], filaments long, stamens longer than corolla (exserted) [1].

103. Filament length: equal [0], two whorls of different lengths [1], one stamen shorter than others [2], several lengths unrelated to stamen whorls [3], one or more stamens larger than others [4], two stamens of different lengths [5].

104. Stamen presentation: uniform distribution around carpel [0], clustered abaxially (declinate) [1]. Scored as inapplicable for species with only two stamens.

105. Filament apex: uniform or gradually tapering; not abruptly narrowed [0], abruptly narrowed thin at anther attachment [1].

106. Indument of filament (simple trichomes): absent [0], present at base only [1], present to apex [2].

107. Anther attachment: basifixed [0], dorsifixed [1], basifixed and dorsifixed in different stamen cycles [2]. In *Poeppigia*, anthers are dorsifixed. All others are basifixed.

108. Anther diameter: widest about the middle [0], widest basally [1], widest apically [2].

109. Anther shape: oblong to rectangular [0], square to circular [1], linear [2].

110. Indument of staminode filaments (simple trichomes): absent [0], present [1].

111. Fertile anther size: uniform [0], dimorphic [1], polymorphic [2]. Dimorphic anthers seen in *Dicorynia, Labichea*, and *Martiodendron*. Polymorphic anthers seen in *Baudouinia* and *Martiodendron*. In *Baudouinia*, abaxial anthers are longer, and gradually shorten toward the adaxial side. In *Martiodendron*, some species have three different anther sizes, with the largest morphs in the abaxial lateral positions, and the smallest in either the abaxial median or adaxial lateral positions, depending on the species.

112. Indument of anther (simple trichomes): absent [0], present [1], dimorphic (present on some anthers, but not others) [2].

113. Anther base markedly sagittate: absent [0], present [1].

114. Anther locule number: four [0], two [1], eight or more [2]. "Club" stamens in *Dicorynia* have between eight and ten anther locules.

115. Anther dehiscence: longitudinal slits [0], short slits or terminal pores [1]. In most genera, dehiscence is via short slits. True pores less common (*cf. Mendoravia*).

116. Anther dehiscence orientation: introrse (open toward gynoecium) [0], latrorse (open laterally) [1], extrorse (open toward flower exterior) [2].

117. Ovary insertion position: at base of calyx [0], on hypanthium adaxial wall [1], on hypanthium abaxial wall [2], on rim of hypanthium [3]. State 2 seen in *Apuleia* and *Poeppigia*. All others have ovary insertion at base of calyx.

118. Ovary stipe: absent [0], present [1].

119. Ovary indument (simple trichomes): absent [0], present [1].

120. Gynoecium surface papilose: absent [0], present [1].

121. Style form: slender (substantially longer than width) [0], short and stout [1], absent (stigma sessile on ovary) [2], petaloid [3]. Flowers of genus *Petalostylis* produce a petaloid style.

122. Style curvature: straight [0], abruptly bent adaxially [1], coiled [2], bent abaxially [3].

123*. Stigma position: terminal [0], sublateral [1], lateral [2].

124. Stigma shape: terete (truncate) [0], peltate [1], crateriform [2], hollow and tubular [3], hollow and funnel-shaped [4], capitate [5]. *Petalostylis* and *Mendoravia* have a capitate stigma. All others are terete or peltate.

125. Ovule number: one [0], two [1], more than two [2].

126. Pollen ornamentation type: striate [0], perforate to reticulate [1], rugulate [2], verrucate [3], striate [4], gemmate [5]. *Dialium guianense* pollen is striate. All others for which information was available were perforate to reticulate (state 1).

127. Tertiary veins: alternate percurrent [0], opposite percurrent [1], mixed parallel and opposite [2], random reticulate [3].

128. Quaternary veins: alternate percurrent [0], opposite percurrent [1], polygonal reticulate [2].

129. Free-ending veinlets: absent [0], unbranched [1], one branch [2], two or more branches [3].

130. Broad expanded receptacle: absent [0], present [1]. An expanded receptacle is a broad, flat or slightly curved surface across which floral organs are spaciously distributed; may be associated with nectaries. Present in many *Dialium* species, as well as *Uittienia* and *Zenia*.

131. Hooded anthers: absent [0], present [1]. Subterminal pores are covered by a hygroscopic, hood-like, terminal pollen cup, which closes over the pores when moistened (Koeppen & Iltis, 1962). Present only in *Martiodendron*.

132. Style indument: glabrous [0], hairy [1].

133. Widest point of fruit: apex [0], middle [1], base [2].

134. Fruit texture: coriaceous (leathery) [0], ligneous (woody) [1], drupaceous (fleshy covering over hard "stone") [2], membraneous (papery) [3]. Drupes in *Dialium, Uittienia*, and *Baudouinia*. Ligneous fruits only in *Eligmocarpus*. All others coriaceous or membraneous; sometimes variable within a genus.

135. Fruit dehiscence: indehiscent [0], dehiscent along ventral suture [1], dehiscent along dorsal suture [2], dehiscent along both sutures [3]. *Dicorynia* fruits dehiscent along the dorsal suture. Those of *Kalappia, Labichea, Mendoravia, Petalostylis*, and *Storckiella* dehisce along both sutures. All others are indehiscent.

Table 2.4. Morphological matrix.

	001	002	003	004	005	006	007	008	009	010	011	012	013	014	015	016	017	018	019	020	021	022	023	024	025	026	027	028	029	030	031	032	033	034	035	036	037	038	039	040	041	042	043	044	045	046
Androcalymma_glabrifolium	0	?	?	?	1	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Apuleia_molaris	0	2	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	1	0	0	0	0	-
Apuleia_leiocarpa	0	2	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	1	0	0	0	0	-
Baudouinia_fluggeiformis	0	0	0	0	1	1	0	0	-	-	-	0	0	-	-	-	1	0	0	0	1	0	0	0	0	0	0	-	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	-
Baudouinia_louvelii	0	0	0	0	1	1	0	0	-	-	-	0	0	-	-	-	2	0	0	0	0	0	1	0	0	0	0	-	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	-
Baudouinia_rouxevillei	0	0	0	0	1	1	0	0	-	-	-	0	0	-	-	-	2	0	0	0	0	0	0	0	0	4	0	-	-	-	1	0	0	0	0	0	0	0	1	0	1	1	1	0	0	-
Baudouinia_sollyaeformis	0	0	0	0	1	1	0	0	-	-	-	0	0	-	-	-	2	0	0	0	0	0	0	0	0	0	0	-	0	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0	0	-
Dansera_procera	0	0	0	0	1	1	0	1	2	0	-	0	0	-	-	-	1	0	1	0	1	1	0	0	0	5	0	-	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dialium_angolense	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	1	0	0	0
Dialium_aubrevillei	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	1	0	0	0
Dialium_bipindense	0	0	0	0	1	1	0	1	0	0	2	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	2	0
Dialium_cochinchinense	0	0	0	0	1	1	0	1	0	0	2	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Dialium_corbisieri	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Dialium_densiflorum	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	-	0	0	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0
Dialium_dinklagei	0	0	0	0	1	1	0	1	0	0	0	0	2	0	0	0	1	0	1	0	1	0	0	0	0	0	0	-	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Dialium_englerianum	0	0	0	0	1	1	0	1	0	0	2	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	-	0	0	?	?	?	?	?	?	0	0	0	0	0	0	0	0	2	?
Dialium_eurysepalum	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	-	0	0	?	?	?	?	?	?	0	0	0	0	0	0	0	0	1	0
Dialium_excelsum	0	0	0	0	1	1	0	1	0	0	1	0	2	0	0	0	1	0	?	1	1	1	1	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	1	0
Dialium_guianense	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	-	0	0	1	0	0	0	0	0	0	0	0	0	3	0	0	0	0	-
Dialium_guineense	0	0	0	0	1	1	0	1	0	0	2	0	0	0	0	0	1	0	1	0	?	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	3	0	0	0	0	0
Dialium_hexasepalum	0	0	0	0	1	1	0	1	0	0	0	0	2	0	0	0	1	0	1	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	1	0
Dialium_holtzii	0	0	0	0	1	1	0	1	0	0	2	0	2	0	0	0	0	0	1	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	1	0
Dialium_hydnocarpoides	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Dialium_indum	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Dialium_kunstleri	0	0	0	0	1	1	0	1	3	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Dialium_lopense	0	0	0	0	1	1	0	1	0	0	2	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Dialium_madagascariense	0	0	0	0	1	1	0	1	3	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	-	0	0	1	?	?	?	?	?	0	0	1	0	0	0	0	0	0	0
Dialium_occidentale	0	0	0	0	1	1	0	1	2	0	-	0	0	-	-	-	1	0	0	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0
Dialium_orientale	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	?	0	1	0	?	0	1	0	0	0	0	-	0	0	1	?	?	?	0	?	0	0	0	0	0	0	0	0	0	0
Dialium_ovoideum	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	3	0	0	0	0	0
Dialium_pachyphyllum	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Dialium_patens	0	0	0	0	1	1	0	1	0	0	2	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Dialium_pentandrum	0	0	0	0	1	1	0	1	0	2	2	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Dialium_platysepalum	0	0	0	0	1	1	0	1	0	0	2	0	0	0	0	0	1	0	1	0	1	1	0	1	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Dialium_pobeguini	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	4	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	2	0
Dialium_polyanthum	0	0	0	0	1	1	0	1	0	0	2	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Dialium_reygaerti	0	0	0	0	1	1	0	1	0	0	2	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	1	0	0	0
Dialium_schlechteri	0	0	0	0	1	1	0	1	0	0	2	0	2	0	0	0	1	0	1	0	1	0	1	0	0	0	0	-	0	0	1	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0
Dialium_soyauxii	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	-	0	0	1	?	?	?	?	?	0	0	0	0	0	0	0	0	2	0
Dialium_tessmannii	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	1	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Dialium_travancoricum	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	?	?	0	0	0	0	0	0	1	0	0	0
Dialium_unifoliolatum	0	0	0	0	1	1	0	1	2	0	-	0	0	-	-	-	1	0	0	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	0	?	0	0	0	0	0	0	0	0	0	0
Dialium_zenkeri	0	0	0	0	1	1	0	1	0	2	2	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	?	?	0	0	0	0	0	0	0	0	2	0
Dicorynia_guianensis	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	2	0

	001	002	003	004	005	006	007	008	009	010	011	012	013	014	015	016	017	018	019	020	021	022	023	024	025	026	027	028	029	030	031	032	033	034	035	036	037	038	039	040	041	042	043	044	045	046
Dicorynia_paraensis	0	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Distemonanthus_benthamianus	0	1	0	0	1	1	0	1	0	0	2	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	?	0	0	0	2	?
Eligmocarpus_cynometroides	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	2	0	0	1	0	0	1	0	0	0	0	-	1	-	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	-
Kalappia_celebica	0	2	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	-	0	0	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0
Koompassia_excelsa	0	3	0	0	1	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	1	1	0	1	0	0	0	-	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Koompassia_malaccensis	0	3	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	-	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Koompassia_parvifolia	0	?	?	?	1	1	0	1	0	2	1	0	0	1	0	0	1	0	0	0	1	1	1	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	2	0
Labichea_brassii	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	1	0	0	0	0	-
Labichea_buettneriana	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	1	0	0	0	0	-
Labichea_cassioides	0	?	?	?	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	-	1	-	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-
Labichea_digitata	0	?	?	?	1	1	1	3	0	-	-	0	0	-	-	-	1	0	0	0	1	0	0	1	0	0	0	-	1	-	1	?	?	?	0	0	0	0	0	0	1	0	0	0	0	-
Labichea_diversifolia	0	?	?	?	1	1	1	3	0	-	-	0	0	-	-	-	1	0	0	0	1	0	0	1	0	0	0	-	1	-	?	?	?	?	?	?	0	?	0	0	1	0	0	0	0	-
Labichea_cremaea	0	?	?	?	1	1	1	3	0	-	-	0	0	-	-	-	1	0	0	0	1	0	0	1	0	0	0	-	1	-	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	-
Labichea_lanceolata	0	0	0	0	1	1	1	3	0	-	-	0	0	-	-	-	1	0	0	0	1	0	0	1	0	0	0	-	1	-	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-
Labichea_nitida	0	0	0	0	1	1	1	3	0	-	-	0	0	-	-	-	2	0	0	0	?	0	0	1	0	0	0	-	1	-	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-
Labichea_punctata	0	0	0	0	1	1	1	1	2	-	-	0	0	-	-	-	1	0	0	0	1	0	0	1	0	0	0	-	1	-	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-
Labichea_rupestris	0	?	?	?	1	1	1	3	0	-	-	0	0	-	-	-	1	0	0	0	1	0	0	1	0	0	0	-	1	-	1	?	?	?	0	0	0	0	0	0	1	0	0	0	0	-
Labichea_stellata	0	?	?	?	1	1	1	3	0	-	-	0	0	-	-	-	1	0	0	1	0	0	0	1	0	0	0	-	1	-	1	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?
Labichea_teretifolia	0	?	?	?	1	?	1	3	0	-	-	0	0	-	-	-	1	0	0	0	1	0	0	1	0	-	0	-	1	-	1	1	0	0	0	0	0	?	0	0	1	0	0	0	0	-
Martiodendron_elatum	0	3	0	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Martiodendron_excelsum	0	3	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	2	0	1	0	0	1	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Martiodendron_fluminense	0	3	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	1	0	3	0	-	0	0	1	?	?	?	0	0	0	0	0	0	?	?	?	?	?	?
Martiodendron_mediterraneum	0	3	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	2	0	1	0	1	0	0	0	0	-	0	0	1	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0
Martiodendron_parviflorum	0	3	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	2	0	1	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Mendoravia_dumaziana	1	2	0	0	1	1	0	0	-	-	-	0	0	-	-	-	0	0	1	0	1	0	0	0	0	0	0	-	-	-	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Petalostylis_cassioides	0	0	0	0	1	1	1	1	0	0	2	0	0	1	0	0	2	0	1	0	0	0	1	1	0	0	0	-	0	0	1	1	0	1	0	0	0	?	0	1	1	0	0	0	0	-
Petalostylis_labicheoides	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	0	2	0	0	0	0	1	0	1	0	0	0	-	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	2	0
Poeppigia_procera	1	2	0	0	1	1	0	1	0	1	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	-	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	-
Storckiella_australiensis	0	2	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	-	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Storckiella_comptonii	0	2	0	0	1	1	0	1	0	2	2	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	1	0	0	0
Storckiella_neocaledonica	0	2	0	0	1	1	0	1	0	2	2	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	-	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Storckiella_pancheri	0	2	0	0	1	1	0	1	0	0	2	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Storckiella_vitiensis	0	2	0	0	1	1	0	1	0	0	2	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	-	0	0	1	?	?	?	0	0	0	0	0	0	0	0	1	0	0	0
Uittienia_modesta	0	0	0	0	1	1	0	1	2	0	-	0	0	-	-	-	1	0	0	0	1	1	0	0	0	5	0	-	0	0	1	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Zenia_insignis	0	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	-	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-
Duparquetia_orchidacea	0	0	0	1	1	1	3	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	-	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Barnebydendron_riedelii	1	1	0	0	1	1	0	1	0	1	0	0	0	1	0	0	1	0	1	1	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	-
Cercis_canadensis	0	2	0	0	1	1	0	1	2	0	-	-	-	-	-	-	1	0	2	0	0	0	0	0	0	0	0	-	-	0	1	1	0	0	0	0	1	-	0	0	1	0	0	0	2	-
Delonix_regia	1	0	0	0	1	1	0	2	0	1	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	-	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	-

	047	048	049	050	051	052	053	054	055	056	057	058	059	060	061	062	063	064	065	066	067	068	069	070	071	072	073	074	075	076	077	078	079	080	081	082	083	084	085	086	087	088	089	090	091	092
Androcalymma_glabrifolium	0	0	1	0	0	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	?	1	0	1	0	1
Apuleia_molaris	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	?	0	0	0	0	0	2	1	1	1	0	2	0	0	1	0	0	0	0	0	1	1	0	2	0	0	0	-	0	0	5
Apuleia_leiocarpa	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	?	0	0	0	0	0	2	1	1	1	0	2	0	0	1	0	0	0	0	0	1	1	0	2	0	?	0	-	0	0	5
Baudouinia_fluggeiformis	0	0	1	0	0	0	0	1	1	-	0	0	0	0	0	?	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	4	1	1	0	1	1	0	0	0	0	0	0	0	0
Baudouinia_louvelii	0	0	0	0	0	-	-	1	1	-	0	0	0	1	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	4	1	0	0	0	1	0	0	0	3	1	1	0	0
Baudouinia_rouxevillei	0	0	1	1	0	0	0	1	0	-	0	0	0	1	0	?	0	?	0	0	0	0	0	-	-	0	0	0	0	?	0	0	4	1	1	0	0	1	0	0	0	0	0	0	0	0
Baudouinia_sollyaeformis	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	5	1	1	0	1	1	0	0	0	0	0	0	0	0
Dansera_procera	0	0	1	0	0	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	2	0	0	1	0	0	5	0	1	1	1	1	5	-	-	-	-	-	-	-
Dialium_angolense	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	?	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	6	0	0	1	1	1	4	-	0	-	-	0	-	-
Dialium_aubrevillei	0	0	1	0	1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	6	0	0	1	1	1	4	-	0	-	-	0	-	-
Dialium_bipindense	0	2	1	0	1	0	0	1	1	-	0	0	0	1	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	6	0	0	1	1	1	4	-	0	-	-	0	-	-
Dialium_cochinchinense	0	0	1	1	1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	1	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_corbisieri	1	0	1	1	1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	1	1	1	4	-	0	-	-	0	-	-
Dialium_densiflorum	0	2	0	0	0	-	-	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	6	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_dinklagei	0	2	1	1	1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	6	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_englerianum	0	2	1	1	1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	?	2	0	-	0	-
Dialium_eurysepalum	0	0	0	0	1	0	0	1	1	-	0	0	0	1	0	1	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_excelsum	0	0	0	0	0	-	-	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_guianense	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	1	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_guineense	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	0	0	1	0	0	0	0	0	-	-	0	0	0	0	0	0	0	6	0	0	1	1	1	4	-	0	-	-	0	-	-
Dialium_hexasepalum	0	0	0	0	1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	6	0	0	1	2	0	?	0	0	1	1	1	?	?	?	?	?	?	?	?
Dialium_holtzii	0	0	1	1	1	0	0	1	1	-	0	0	0	0	0	3	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_hydnocarpoides	0	2	1	1	1	0	0	1	1	-	0	0	0	0	0	3	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	1	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_indum	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	?	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	6	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_kunstleri	1	0	0	0	0	-	-	1	1	-	0	0	0	0	0	?	0	0	0	0	0	0	0	-	-	0	?	?	?	?	?	?	?	?	?	1	1	1	?	?	?	?	?	?	?	?
Dialium_lopense	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	?	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	6	0	0	1	1	1	4	-	0	-	-	0	-	-
Dialium_madagascariense	1	0	0	0	0	-	-	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	2	0	0	1	0	0	0	0	0	0	1	1	2	0	0	0	-	1	0	1
Dialium_occidentale	0	0	0	0	0	-	-	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	2	0	0	1	0	0	0	1	0	0	0	0	2	0	0	0	-	0	0	0
Dialium_orientale	0	0	1	1	1	0	0	1	1	-	0	0	0	0	0	0	0	1	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_ovoideum	0	0	1	0	0	0	0	1	1	-	0	0	0	0	0	?	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_pachyphyllum	0	0	1	0	1	0	0	1	1	-	0	0	0	1	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	6	0	0	1	1	1	4	-	0	-	-	0	-	-
Dialium_patens	0	0	1	0	0	0	0	1	1	-	0	0	0	1	0	3	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_pentandrum	0	0	1	0	1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	1	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_platysepalum	0	2	1	1	1	0	0	1	1	-	0	0	0	0	0	3	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	0	1	1	1	1	5	-	-	-	-	-	-	-
Dialium_pobeguini	0	0	1	1	1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	0	0	1	1	0	4	-	?	-	-	-	-	-
Dialium_polyanthum	0	0	1	0	1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	6	0	0	1	1	1	4	-	0	-	-	0	-	-
Dialium_reygaerti	0	0	1	1	1	0	0	1	1	-	0	0	0	0	0	?	0	1	0	0	0	0	0	-	-	0	0	0	0	?	0	0	1	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_schlechteri	0	0	1	1	1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_soyauxii	0	2	1	0	1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	0	0	0	1	1	1	5	-	-	-	-	-	-	-
Dialium_tessmannii	0	0	1	0	0	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	5	0	0	1	1	1	4	-	0	-	-	0	-	-
Dialium_travancoricum	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	?	0	0	0	0	0	1	1	1	4	-	?	-	-	-	-	-
Dialium_unifoliolatum	1	0	0	0	0	-	-	1	1	-	0	0	0	0	0	?	0	0	0	0	0	0	0	-	-	0	2	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	-	0	0	0
Dialium_zenkeri	0	2	1	0	0	1	1	1	1	-	0	0	0	0	0	?	0	0	?	0	0	0	0	-	-	0	0	0	0	?	0	0	0	0	0	1	1	1	5	-	-	-	-	-	-	-
Dicorynia_guianensis	0	2	1	1	0	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	1	0	0	1	1	0	2	0	0	0	-	1	0	1

	047	048	049	050	051	052	053	054	055	056	057	058	059	060	061	062	063	064	065	066	067	068	069	070	071	072	073	074	075	076	077	078	079	080	081	082	083	084	085	086	087	088	089	090	091	092
Dicorynia_paraensis	0	2	1	1	1	0	0	1	1	-	0	0	0	1	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	1	0	0	1	1	0	2	0	0	0	-	0	0	1
Distemonanthus_benthamianus	0	2	1	1	1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	7	0	1	1	1	0	2	0	0	1	-	0	0	5
Eligmocarpus_cynometroides	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	5	0	0	1	1	1	0	0	0	3	1	1	0	1
Kalappia_celebica	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	2	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	7	0	1	1	1	1	0	0	0	1	1	?	0	0
Koompassia_excelsa	0	0	1	0	1	0	0	1	1	-	0	0	0	0	0	0	0	1	0	0	0	0	0	-	-	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	5
Koompassia_malaccensis	0	0	1	0	1	0	0	1	1	-	0	0	0	1	0	0	0	1	0	0	0	0	0	-	-	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	2
Koompassia_parvifolia	0	0	1	0	0	0	0	1	1	-	0	0	0	0	0	0	0	1	0	0	0	0	0	-	-	0	0	0	0	1	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	5
Labichea_brassii	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	?	0	0	0	?	0	0	0	-	-	0	0	0	0	1	2	0	3	1	2	1	1	0	1	0	?	-	0	1	0	3
Labichea_buettneriana	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	?	0	0	0	0	0	0	0	-	-	0	0	0	0	?	2	0	3	1	2	1	1	1	1	0	?	-	0	?	0	?
Labichea_cassioides	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	?	0	0	0	0	0	0	0	-	-	0	0	0	0	?	2	0	3	1	1	0	1	1	0	3	2	-	0	1	0	3
Labichea_digitata	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	?	0	0	0	?	0	0	0	-	-	0	1	0	0	1	2	0	3	1	2	1	1	1	1	0	?	-	0	1	0	3
Labichea_diversifolia	0	0	1	0	1	0	0	0	?	?	0	0	0	0	0	?	0	?	0	0	0	0	0	-	-	0	0	0	0	?	2	0	3	1	0	0	1	1	1	0	?	-	0	1	0	0
Labichea_eremaea	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	3	0	0	0	0	0	0	0	-	-	0	0	0	0	1	2	0	3	1	?	0	1	0	0	3	?	-	0	1	0	3
Labichea_lanceolata	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	-	-	0	1	0	0	1	2	0	3	1	2	0	1	0	1	0	3	-	0	1	0	3
Labichea_nitida	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	?	0	0	0	0	0	0	0	-	-	0	0	0	0	?	2	0	3	1	2	0	1	0	1	0	?	-	0	1	0	3
Labichea_punctata	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	?	0	0	0	0	0	0	0	-	-	0	0	0	0	1	2	0	3	1	1	0	1	0	1	0	2	-	0	1	0	3
Labichea_rupestris	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	3	0	0	0	0	0	0	0	-	-	0	1	0	0	?	2	0	3	1	1	0	1	0	1	0	?	-	0	1	0	3
Labichea_stellata	?	?	1	1	1	?	?	0	0	1	0	0	?	?	?	?	?	?	?	?	?	0	0	-	-	0	0	0	0	1	2	0	3	0	1	?	1	?	1	0	?	-	0	?	0	?
Labichea_teretifolia	0	0	1	1	0	1	0	0	0	1	0	0	0	0	?	?	?	?	?	?	0	0	0	-	-	0	0	0	0	?	2	0	0	1	1	0	1	0	1	0	?	-	0	1	0	3
Martiodendron_elatum	0	0	1	0	1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	1	5	0	1	0	1	1	0	0	?	1	0	0	0	0
Martiodendron_excelsum	0	0	1	1	1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	1	5	0	1	1	1	1	0	0	0	1	0	1	0	0
Martiodendron_fluminense	?	?	?	?	?	?	?	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	1	5	1	1	0	1	1	0	0	?	0	0	0	0	0
Martiodendron_mediterraneum	0	0	1	0	0	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	1	5	0	1	1	1	1	0	0	0	1	0	0	0	0
Martiodendron_parviflorum	0	0	1	1	1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	1	5	0	1	0	1	1	0	0	0	1	0	1	0	0
Mendoravia_dumaziana	0	0	0	0	0	-	-	1	0	-	0	0	0	1	0	?	0	?	0	0	0	0	0	-	-	0	5	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	?	0	?
Petalostylis_cassioides	0	1	1	0	0	0	0	3	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	1	0	1	1	1	1	0	0	3	0	0	1	0	0
Petalostylis_labicheoides	0	2	1	1	1	0	0	3	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	1	0	1	1	1	1	0	0	3	0	0	1	0	0
Poeppigia_procera	0	0	0	1	0	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	0	0
Storckiella_australiensis	0	0	1	0	0	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	1	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	1
Storckiella_comptonii	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	0	0	1	2	1	0	1	0	1	1	1	1	0	0	-	0	-	0	5
Storckiella_neocaledonica	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1	2	1	0	0	0	0	1	1	1	0	0	-	0	-	0	5
Storckiella_pancheri	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1	-	1	0	0	0	0	1	0	1	0	0	0	-	0	0	2
Storckiella_vitiensis	0	0	1	0	0	0	0	1	1	-	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	0	0	0	-	1	0	1	0	0	1	0	1	0	0	-	0	-	0	?
Uittienia_modesta	0	0	1	0	0	0	0	1	1	-	0	0	0	1	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	?	0	0	0	1	0	0	0	?	0	0	?	0	?
Zenia_insignis	0	0	1	1	0	0	0	1	1	-	0	0	0	0	0	?	0	1	0	0	0	0	0	-	-	0	0	0	0	0	0	0	4	0	0	1	1	1	0	0	0	0	0	0	0	1
Duparquetia_orchidacea	0	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	-	-	0	1	0	0	0	2	0	1	0	2	0	1	0	0	5	1	3	1	0	0	1
Barnebydendron_riedelii	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	1	0	0	0	-	0	0	1	1	1	0	0	0	5	0	4	1	0	0	0
Cercis_canadensis	0	0	0	0	0	-	-	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	1	1	0	0	0
Delonix_regia	0	0	1	1	1	0	0	0	1	0	0	1	?	?	?	?	?	?	?	?	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	2	1	0	0	0	?

	093	094	095	096	097	098	099	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135
Androcalymma_glabrifolium	0	0	1	0	7	7	0	-	0	0	0	0	1	0	0	1	0	-	0	1	1	0	1	0	0	0	1	0	1	0	0	0	1	1	0	2	3	0	0	0	?	?	?
Apuleia_molaris	3	0	0	0	2	2	0	-	0	0	0	-	1	2	0	1	0	-	0	0	0	0	1	0	2	1	1	0	0	0	0	1	2	?	0	2	2	0	0	1	1	0	0
Apuleia_leiocarpa	0	0	0	0	2	2	0	-	0	0	0	-	1	2	0	1	0	-	0	0	1	0	1	0	2	1	1	0	1	0	0	1	2	1	0	2	3	0	0	1	1	0	0
Baudouinia_fluggeiformis	0	0	0	0	9	5	0	-	0	0	0	0	0	0	0	0	2	-	2	0	0	0	1	0	0	1	1	0	0	0	0	0	2	?	0	2	3	0	0	0	1	2	0
Baudouinia_louvelii	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	1	2	-	0	1	0	0	1	0	0	0	0	0	1	0	0	0	2	?	3	2	3	0	0	0	1	2	0
Baudouinia_rouxevillei	0	0	0	0	9	5	0	-	3	0	0	0	0	0	0	0	2	-	2	0	0	0	1	0	0	1	0	0	0	0	0	0	2	?	3	-	3	0	0	0	1	2	0
Baudouinia_sollyaeformis	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	1	2	-	2	1	0	0	1	0	0	1	1	0	0	0	0	0	2	?	0	0	3	0	0	0	1	2	0
Dansera_procera	-	-	-	-	A	A	0	-	0	0	4	0	0	0	0	1	2	-	0	1	1	0	0	1	0	1	1	0	0	0	0	0	1	1	0	2	3	0	0	0	1	2	0
Dialium_angolense	0	0	0	0	3	3	0	-	0	0	0	-	0	0	0	1	0	-	0	1	1	0	0	1	0	0	1	0	0	0	0	0	1	?	0	2	3	1	0	0	1	2	0
Dialium_aubrevillei	0	1	1	0	3	3	0	-	0	0	0	-	0	0	0	0	0	-	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	?	0	2	3	1	0	0	1	2	0
Dialium_bipindense	0	1	1	0	3	3	0	-	0	0	0	-	0	0	0	0	0	-	0	1	1	0	0	1	0	0	1	0	0	0	0	0	1	?	0	2	3	1	0	0	1	2	0
Dialium_cochinchinense	-	-	-	-	3	3	0	-	0	0	0	-	0	0	0	1	0	-	0	1	1	0	0	1	0	0	1	0	0	0	0	0	1	1	0	2	3	0	0	0	1	2	0
Dialium_corbisieri	0	1	0	0	3	3	0	-	0	0	0	-	0	0	0	1	0	-	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	?	0	0	3	1	0	0	1	2	0
Dialium_densiflorum	-	-	-	-	3	3	0	-	0	0	0	-	0	0	0	0	1	-	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	?	0	0	3	1	0	0	1	2	0
Dialium_dinklagei	-	-	-	-	3	3	0	-	0	0	0	-	0	0	0	1	0	-	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	?	0	2	3	1	0	0	1	2	0
Dialium_englerianum	-	1	1	0	1	1	0	-	0	0	0	0	0	0	0	1	0	-	0	1	1	0	0	1	0	0	1	0	0	0	0	0	1	?	0	0	3	1	0	0	1	2	0
Dialium_eurysepalum	-	-	-	-	3	3	0	-	0	0	0	-	0	0	0	1	1	-	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	?	0	2	3	1	0	0	1	2	0
Dialium_excelsum	-	-	-	-	3	3	0	-	0	0	0	-	0	0	0	1	0	-	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	?	0	0	3	1	0	0	1	2	0
Dialium_guianense	-	-	-	-	3	3	0	-	0	0	0	-	0	0	0	0	1	-	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	0	0	2	3	1	0	1	1	2	0
Dialium_guineense	0	1	1	0	3	3	0	-	0	0	0	-	0	0	0	1	0	-	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	?	0	2	2	1	0	1	1	2	0
Dialium_hexasepalum	?	?	?	?	?	?	?	?	0	0	?	?	0	0	0	1	0	?	0	0	0	0	0	1	0	0	1	1	0	0	0	0	2	?	0	2	3	1	0	1	1	2	0
Dialium_holtzii	-	-	-	-	3	3	0	-	0	0	0	-	0	0	0	1	0	-	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	?	0	2	3	1	0	0	1	2	0
Dialium_hydnocarpoides	-	-	-	-	3	3	0	-	0	0	0	-	0	0	0	0	0	-	0	1	1	0	0	1	0	0	1	0	0	0	0	0	1	?	0	2	3	0	0	0	1	2	0
Dialium_indum	-	-	-	-	3	3	0	-	0	0	0	-	1	0	0	1	0	-	0	1	1	0	0	2	0	0	1	0	0	0	0	0	1	?	0	2	3	0	0	1	1	2	0
Dialium_kunstleri	?	?	?	?	?	?	?	?	?	0	0	?	?	?	0	?	?	?	?	?	?	0	0	1	0	1	1	0	0	0	0	0	1	?	?	?	?	?	0	1	1	2	0
Dialium_lopense	0	1	1	0	3	3	0	-	0	0	0	-	0	0	0	1	0	-	0	1	1	0	0	1	0	0	1	0	0	1	0	0	1	?	0	0	3	1	0	0	1	2	0
Dialium_madagascariense	3	1	0	0	3	3	0	-	0	0	0	-	1	0	0	0	0	-	0	1	0	0	0	1	0	1	1	0	0	0	0	0	1	?	0	2	3	0	0	0	1	2	0
Dialium_occidentale	3	0	0	0	3	3	0	-	0	0	0	-	0	0	0	1	0	-	0	1	0	0	0	1	0	1	1	0	0	0	0	0	1	?	0	2	3	0	0	0	1	2	0
Dialium_orientale	-	-	-	-	3	3	0	-	0	0	0	-	0	0	0	1	0	-	0	1	0	0	0	1	0	1	1	0	0	1	0	0	1	?	0	2	3	1	0	0	1	2	0
Dialium_ovoideum	-	-	-	-	2	3	1	1	0	0	0	-	0	0	0	1	2	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	1	?	0	2	3	0	0	0	1	2	0
Dialium_pachyphyllum	0	0	0	0	3	3	0	-	0	0	0	-	0	0	0	1	0	-	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	?	0	2	3	1	0	0	1	2	0
Dialium_patens	-	-	-	-	3	3	0	-	0	0	0	-	0	0	0	0	0	-	0	1	1	0	0	1	0	0	1	0	0	0	0	0	1	?	0	2	3	0	0	0	1	2	0
Dialium_pentandrum	-	-	-	-	1	1	0	-	0	0	0	0	0	0	0	0	1	-	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	?	0	0	3	1	0	0	1	2	0
Dialium_platysepalum	-	-	-	-	3	3	0	-	0	0	0	-	0	0	0	1	0	-	0	1	0	0	0	2	0	0	1	0	0	1	0	0	1	?	0	2	3	1	0	0	1	2	0
Dialium_pobeguini	-	1	1	0	1	1	0	-	0	0	0	0	0	0	0	1	0	-	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	?	0	0	3	1	0	1	1	2	0
Dialium_polyanthum	0	1	1	0	3	3	0	-	0	0	0	-	0	0	0	1	0	-	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	?	0	0	3	1	0	0	1	2	0
Dialium_reygaerti	-	-	-	-	3	3	0	-	0	0	0	-	0	0	0	1	0	-	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1	?	0	0	3	1	0	1	1	2	0
Dialium_schlechteri	-	-	-	-	0	0	0	-	0	0	0	0	0	0	0	1	0	-	0	0	1	0	0	0	0	1	1	0	0	0	0	5	0	?	0	0	3	1	0	0	1	2	0
Dialium_soyauxii	-	-	-	-	3	3	0	-	0	0	0	-	0	0	0	0	1	-	0	1	1	0	0	1	0	0	1	0	0	0	0	1	1	?	0	0	3	1	0	0	1	2	0
Dialium_tessmannii	0	0	0	0	3	3	0	-	0	1	0	-	0	0	0	1	0	-	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	?	0	0	3	1	0	0	1	2	0
Dialium_travancoricum	-	1	1	0	3	3	0	-	0	0	0	-	0	0	0	0	0	-	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	?	0	0	3	0	0	0	1	2	0
Dialium_unifoliolatum	3	0	0	0	3	3	0	-	0	0	0	-	0	0	0	1	2	-	0	1	0	0	0	1	0	1	1	0	0	0	0	0	1	?	0	0	3	0	0	0	1	2	0
Dialium_zenkeri	-	-	-	-	3	3	0	-	0	0	0	-	0	0	0	0	0	-	0	1	0	0	0	1	0	1	1	0	0	0	0	0	1	?	0	0	3	1	0	0	1	2	0
Dicorynia_guianensis	4	0	1	0	3	3	0	-	0	0	5	-	0	2	0	2	0	-	1	1	0	2	1	1	0	0	1	0	0	2	0	0	1	?	0	0	3	0	0	0	1	0	2

	093	094	095	096	097	098	099	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135
Dicorynia_paraensis	0	0	1	0	3	3	0	-	0	0	5	-	0	0	0	0	0	-	1	0	0	2	1	1	0	0	1	0	0	0	0	0	2	1	0	0	3	0	0	1	1	0	2
Distemonanthus_benthamianus	0	0	0	0	1	3	1	0	0	1	0	0	0	0	0	1	2	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	2	1	0	2	3	0	0	0	1	0	0
Eligmocarpus_cynometroides	0	0	0	0	0	0	0	-	3	0	0	0	0	0	0	1	2	-	0	2	0	0	1	1	0	0	0	0	0	1	0	0	2	1	3	2	3	0	0	0	1	1	0
Kalappia_celebica	3	0	0	0	5	1	1	1	0	0	3	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	2	?	0	2	2	0	0	0	1	0	3
Koompassia_excelsa	0	0	0	0	1	1	0	-	0	0	0	0	1	0	0	0	0	-	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	?	0	0	3	0	0	0	0	0	0
Koompassia_malaccensis	0	0	0	0	1	1	0	-	0	0	0	0	0	0	0	1	0	-	0	0	1	0	1	1	0	0	1	0	1	1	0	0	0	?	0	0	3	0	0	0	0	3	0
Koompassia_parvifolia	0	0	0	0	1	1	0	-	0	0	0	0	0	0	0	0	0	-	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	?	3	2	2	0	0	0	0	?	?
Labichea_brassii	0	0	0	0	3	3	0	-	0	0	0	-	0	0	0	1	2	-	1	1	0	0	1	2	0	1	1	0	0	0	0	0	1	?	0	2	1	0	0	0	1	0	3
Labichea_buettneriana	0	?	?	?	3	3	0	-	0	0	0	-	0	?	0	1	2	-	1	?	0	0	1	0	0	1	1	0	0	0	0	0	1	1	0	2	3	0	0	0	1	0	3
Labichea_cassioides	0	0	0	0	3	3	0	-	0	0	0	-	0	0	0	1	2	-	1	0	0	0	0	1	0	1	1	0	0	0	0	0	1	?	0	2	3	0	0	0	?	?	3
Labichea_digitata	0	1	1	0	3	3	0	-	0	0	0	-	0	0	0	1	0	-	1	0	0	0	1	1	0	1	1	0	0	0	0	0	1	?	0	2	0	0	0	0	?	?	3
Labichea_diversifolia	0	0	0	0	3	3	0	-	0	0	0	-	0	0	0	1	2	-	1	0	0	0	1	2	0	1	1	0	0	0	0	0	1	?	0	2	3	0	0	0	?	?	3
Labichea_eremaea	0	0	0	0	3	3	0	-	0	0	0	-	0	0	0	1	2	-	1	0	0	0	1	2	0	1	1	0	0	0	0	0	1	?	-	-	-	0	0	0	?	?	3
Labichea_lanceolata	3	0	0	0	3	3	0	-	0	0	0	-	0	0	0	1	2	-	1	0	0	0	1	2	0	1	1	0	0	1	0	0	1	?	0	2	3	0	0	0	1	0	3
Labichea_nitida	0	1	0	0	3	3	0	-	0	0	0	-	0	0	0	1	2	-	1	1	0	0	1	2	0	1	1	0	0	0	0	1	1	?	0	2	3	0	0	0	1	0	3
Labichea_punctata	0	0	0	0	3	3	0	-	0	0	0	-	0	0	0	1	2	-	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	1	0	2	3	0	0	0	0	0	3
Labichea_rupestris	0	0	0	0	3	3	0	-	0	0	0	-	0	0	0	1	2	-	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	?	0	2	3	0	0	0	?	?	3
Labichea_stellata	0	?	?	?	3	3	0	-	0	0	0	-	0	?	0	1	2	-	0	?	0	0	0	0	0	1	1	0	0	0	0	?	?	?	?	?	?	0	0	0	?	?	?
Labichea_teretifolia	0	0	0	0	3	3	0	-	0	0	0	-	0	0	0	1	2	-	1	0	0	0	1	2	0	1	1	0	0	0	0	0	1	?	-	-	-	0	0	0	?	?	3
Martiodendron_elatum	3	0	0	0	0	9	1	0	3	0	0	0	0	0	0	1	2	0	2	0	1	0	1	0	0	0	1	0	0	0	0	0	0	?	0	2	1	0	1	0	1	0	0
Martiodendron_excelsum	3	0	0	0	7	7	0	-	0	0	0	0	0	0	0	1	2	-	1	1	1	0	1	0	0	0	1	0	0	1	0	0	0	?	0	0	1	0	1	0	1	0	0
Martiodendron_fluminense	0	0	0	0	1	1	0	-	0	?	0	0	0	0	0	1	2	-	2	0	0	0	1	0	0	0	1	0	0	0	0	0	0	?	?	?	?	0	1	0	1	0	0
Martiodendron_mediterraneum	3	0	1	0	1	1	0	-	0	0	4	0	0	0	0	1	2	-	2	1	1	0	1	0	0	0	1	0	0	0	0	0	1	1	0	2	1	0	1	0	1	0	0
Martiodendron_parviflorum	3	0	0	0	1	7	1	0	0	0	0	0	0	0	0	1	2	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	?	0	2	0	0	1	0	1	0	0
Mendoravia_dumaziana	0	0	0	0	6	8	0	-	0	0	0	0	0	0	0	1	0	-	0	0	0	0	1	0	0	0	0	0	1	0	0	5	2	1	3	2	3	0	0	0	1	0	3
Petalostylis_cassioides	0	0	0	0	1	2	1	1	0	0	0	0	0	0	0	1	2	0	0	0	0	0	1	0	0	1	1	0	3	1	0	5	2	?	3	-	3	0	0	0	1	3	3
Petalostylis_labicheoides	0	0	0	0	1	2	1	1	0	0	0	0	0	0	0	1	2	0	0	0	1	0	1	0	0	1	1	0	3	1	0	5	2	?	3	-	3	0	0	0	1	0	3
Poeppigia_procera	2	1	0	0	0	0	0	-	0	0	0	0	0	0	1	0	1	-	0	0	0	0	0	0	2	1	1	0	1	0	0	0	2	1	3	-	3	0	0	0	1	3	0
Storckiella_australiensis	0	0	0	0	1	1	0	-	0	0	0	0	1	0	0	0	0	-	0	0	0	0	1	1	0	0	1	0	0	1	0	0	2	1	0	0	1	0	0	0	1	0	3
Storckiella_comptonii	0	1	1	0	7	7	0	-	0	0	0	0	0	2	0	1	2	-	0	1	0	0	1	0	0	1	1	0	0	0	0	0	2	?	0	0	1	0	0	0	1	0	3
Storckiella_neocaledonica	0	1	1	0	6	8	0	-	0	0	0	0	0	0	0	1	2	-	0	0	0	0	1	0	0	1	1	0	0	0	0	0	2	?	0	0	1	0	0	0	1	3	3
Storckiella_pancheri	0	1	1	0	7	7	0	-	0	0	0	0	0	2	0	1	2	-	0	0	0	0	1	0	0	0	1	0	0	0	0	0	2	?	0	0	1	0	0	0	1	0	3
Storckiella_vitiensis	0	0	0	0	6	8	0	-	0	0	0	0	0	0	0	1	2	-	0	0	0	0	1	0	0	1	1	0	0	0	0	0	2	?	0	0	1	0	0	0	1	0	3
Uittienia_modesta	0	?	?	?	1	2	1	0	0	0	0	0	0	?	0	1	0	?	0	?	1	0	0	1	0	1	1	0	0	0	0	0	0	?	2	0	3	1	0	1	1	2	0
Zenia_insignis	0	0	1	0	1	7	1	0	0	0	0	0	0	2	0	1	2	1	0	1	0	0	0	1	0	1	1	0	1	3	0	0	2	1	0	2	3	1	0	1	1	3	0
Duparquetia_orchidacea	2	0	0	1	7	7	0	-	5	0	0	0	0	0	0	0	2	-	0	0	0	0	1	0	0	1	1	0	0	0	0	0	2	1	1	0	2	0	0	0	1	1	0
Barnebydendron_riedelii	5	0	0	0	0	0	0	-	3	1	1	0	0	0	1	0	0	-	0	1	0	0	0	1	0	1	0	0	0	0	0	5	2	?	0	-	3	0	0	0	1	3	0
Cercis_canadensis	3	0	0	0	0	0	0	-	0	0	1	0	0	1	1	0	0	-	0	0	0	0	0	0	0	1	0	0	0	1	0	5	2	?	3	2	1	0	0	0	1	3	0
Delonix_regia	3	0	0	0	0	0	0	-	0	1	0	0	0	1	1	0	0	-	0	0	0	0	0	1	0	0	1	0	0	0	0	3	2	1	3	-	3	0	0	0	1	1	3

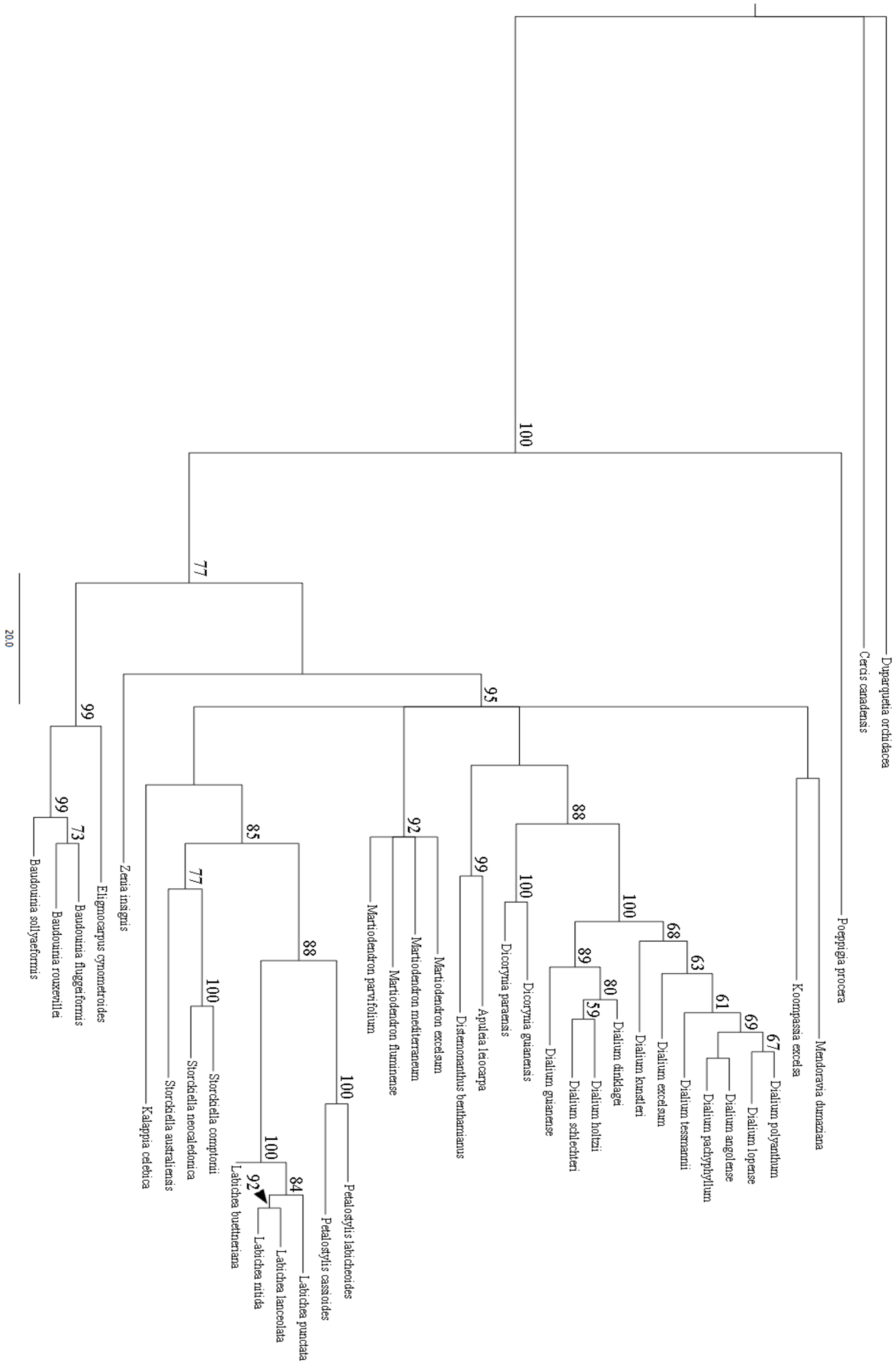

Fig. 2.1. Strict consensus tree based on the combined molecular and morphological maximum parsimony analysis of the reduced taxon set without missing molecular data. Bootstrap values above 50 are given above the supported node.

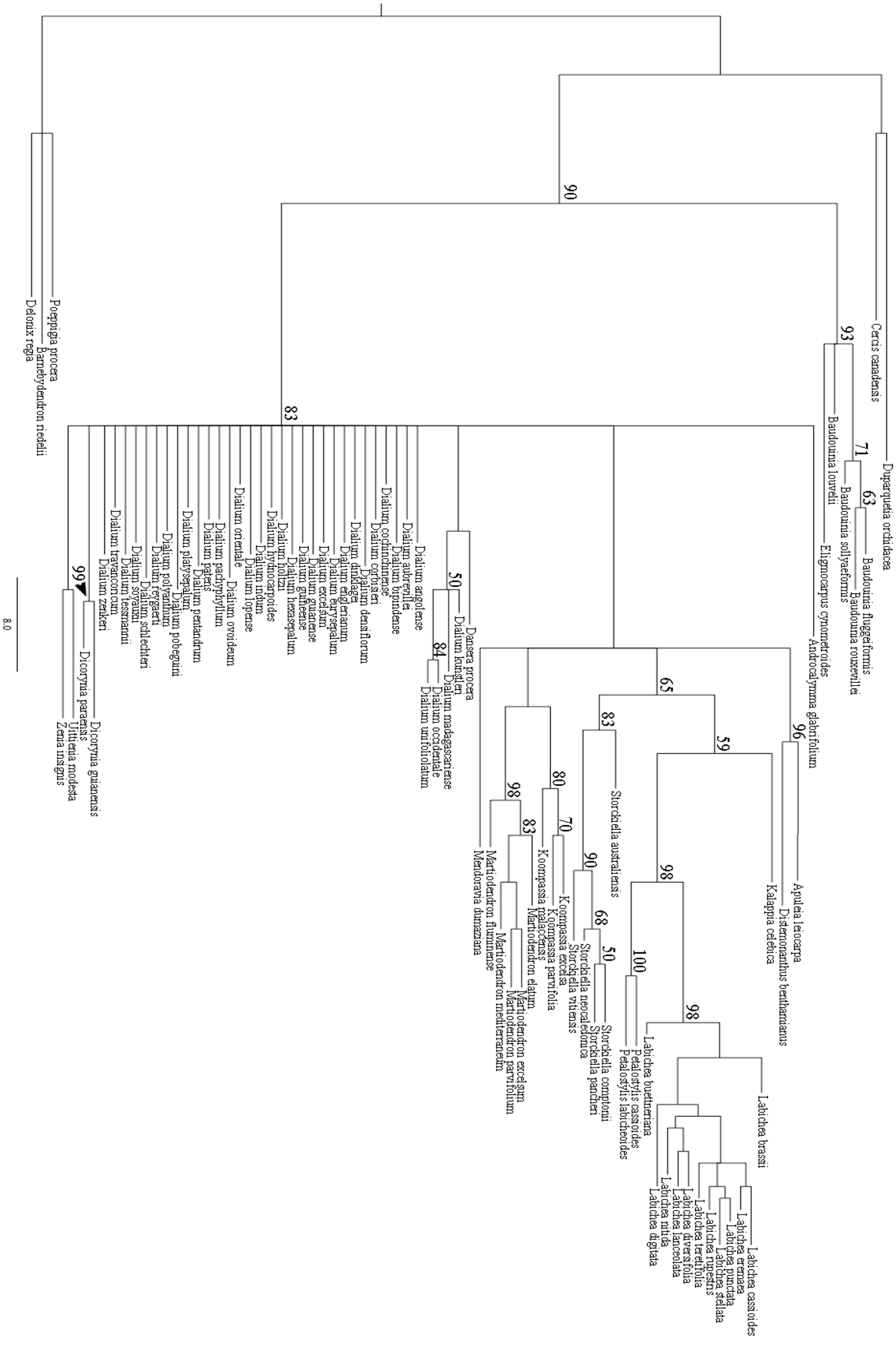

Fig. 2.2. Strict consensus tree based on a maximum parsimony analysis of morphological data constrained using the highly supported nodes in Figure 2.1. Bootstrap values above 50 are given above the supported node.

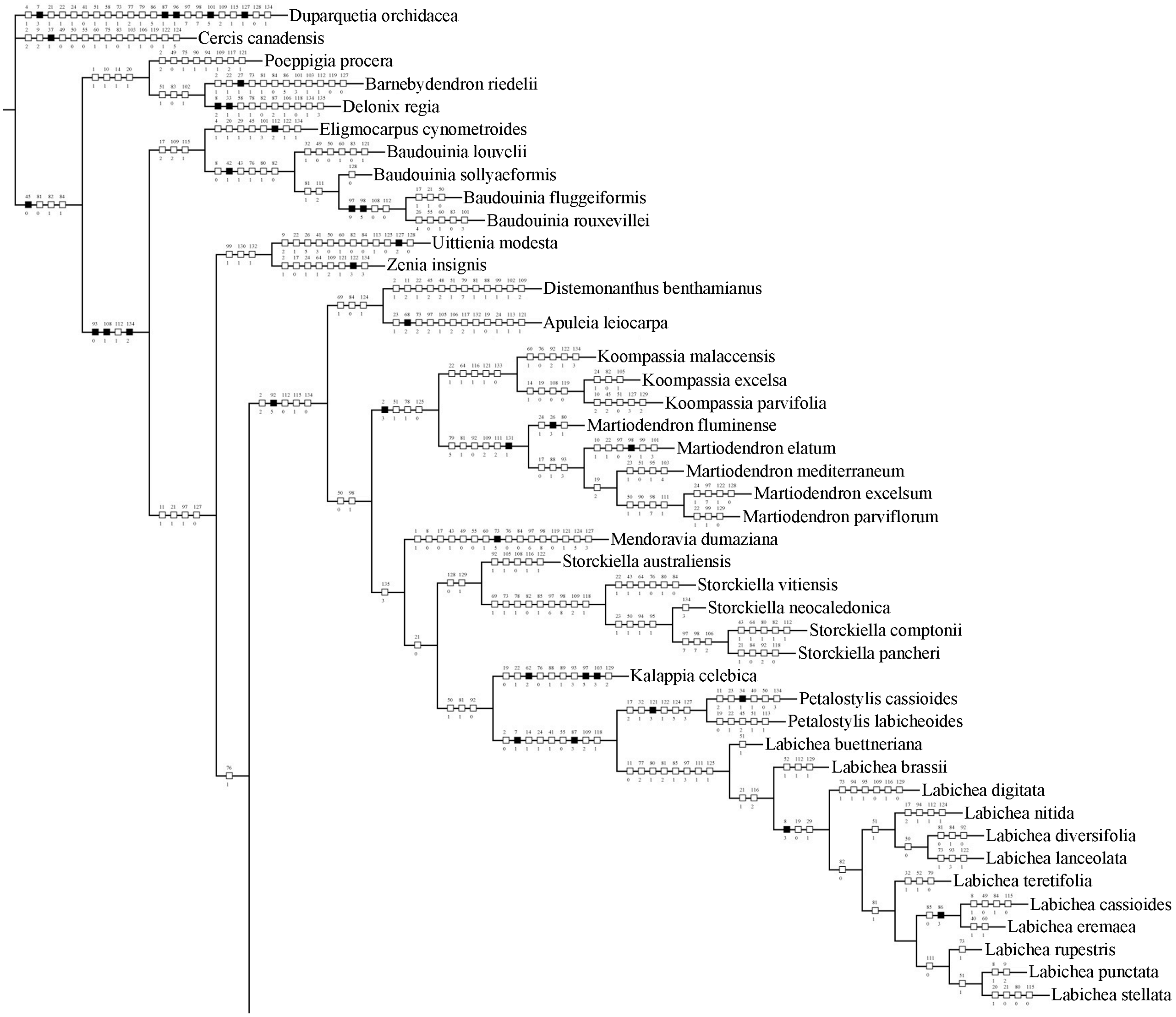

Fig. 2.3a. One of 20,000 most parsimonious trees from the constrained morphological analysis, with morphological characters optimised on the branches. Character numbers are above branches and character state numbers below. (Upper portion.)

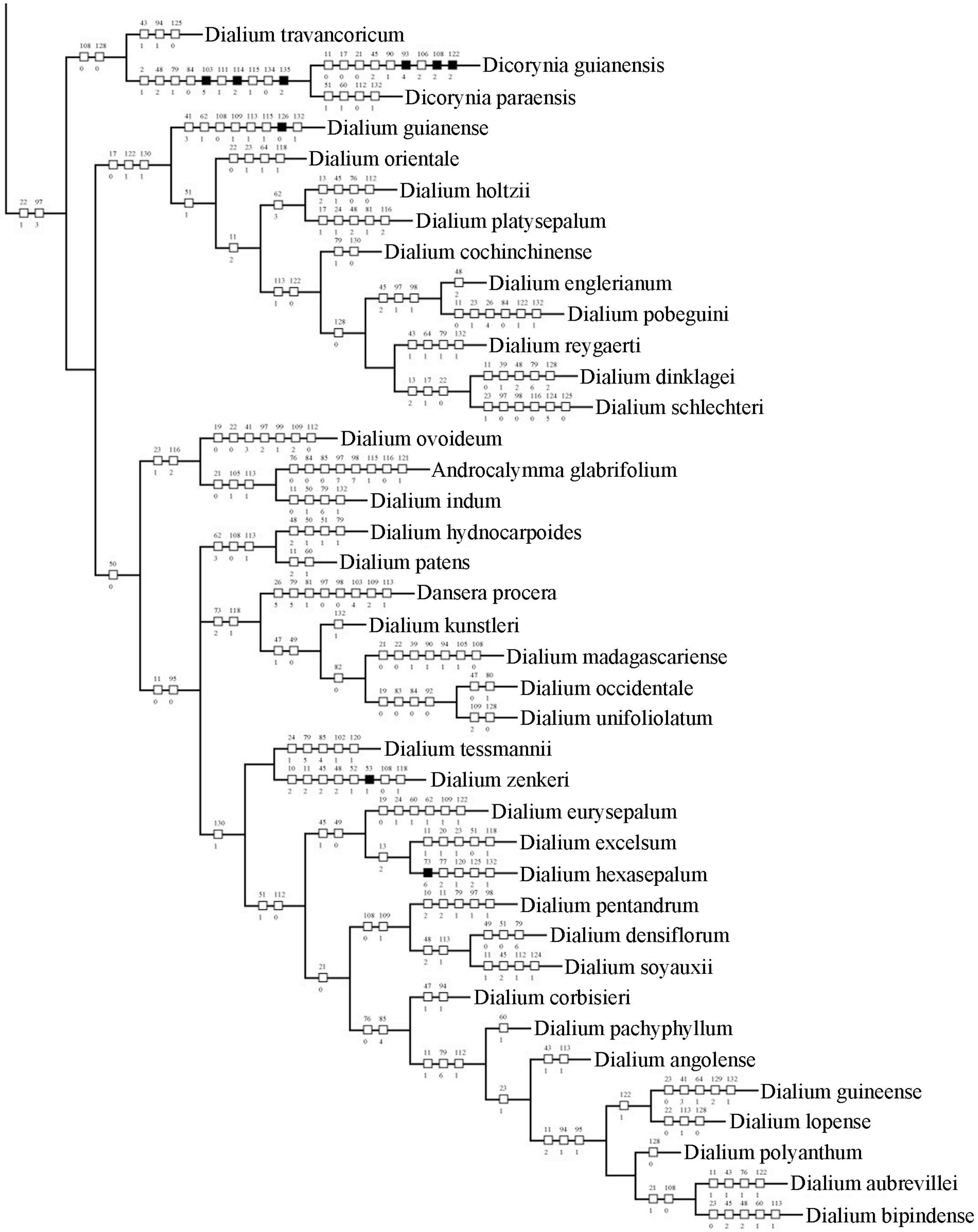

Fig. 2.3b. One of 20,000 most parsimonious trees from the constrained morphological analysis, with morphological characters optimised on the branches. Character numbers are above branches and character state numbers below. (Lower portion.)

Table 2.5. Floral and fruit synapomorphies supporting clades with >75% bootstrap support in the strict consensus of the constrained analysis. (NB: *Poeppigia* did not resolve as part of a monophyletic Dialiinae in this analysis, and so is not considered to be a part of it here.)

Clade	**Synapomorphies**
Dialiinae	Petals not clawed, anthers widest basally, simple trichomes on anthers, drupaceous fruits
Dialiinae (not including *Baudouinia+Eligmocarpus*)	Five stamens
Baudouinia + Eligmocarpus	Linear anthers, anthers opening via short slits
Storckiella	Not supported by any floral or fruit characters
Storckiella (not including *S. australiensis*)	Hypanthium present, tetramerous calyx, calyx narrowly imbricate to valvate, sepal margins glabrous, tetramerous corolla, total stamens more than twice the number of petals, more than ten fertile stamens, linear anthers, gynoecium stipitate
Labichea + Petalostylis	Simple inflorescences, basal central spot on petal, linear anthers, gynoecium stipitate, fruit wings absent
Labichea	Median sepals in both abaxial and adaxial positions, sepal margins thin and hyaline, calyx base strongly gibbous, tetramerous corolla, two stamens, fertile anthers dimorphic, two ovules
Petalostylis	Petaloid style, style bent adaxially, stigma capitate
Koompassia	Bracteoles alternate, latrorse anther dehiscence, style stout, fruit widest at apex
Martiodendron	Abaxial median sepal narrower than all others, calyx base slightly asymmetrical, imbricate ascending petal aestivation, linear anthers, fertile anthers polymorphic, anthers hooded
Martiodendron (not including *M. fluminense*)	Adaxial petal larger than remaining equal petals, all petals clawed
Apuleia + Distemonanthus	Hypanthium present, inner surface of sepal lobes glabrous, peltate stigma
Dicorynia	Abaxial median sepal broader than others, inner surface of sepals glabrous, two stamens of different lengths, anthers dimorphic, anther locule number eight or more, anthers dehiscing via short slits, fruits coriaceous and dehiscent along dorsal suture, with a nonvascularised placental wing
Dialium occidentale + D. unifoliolatum	Inner and outer surfaces of sepals glabrous, imbricate ascending petal aestivation

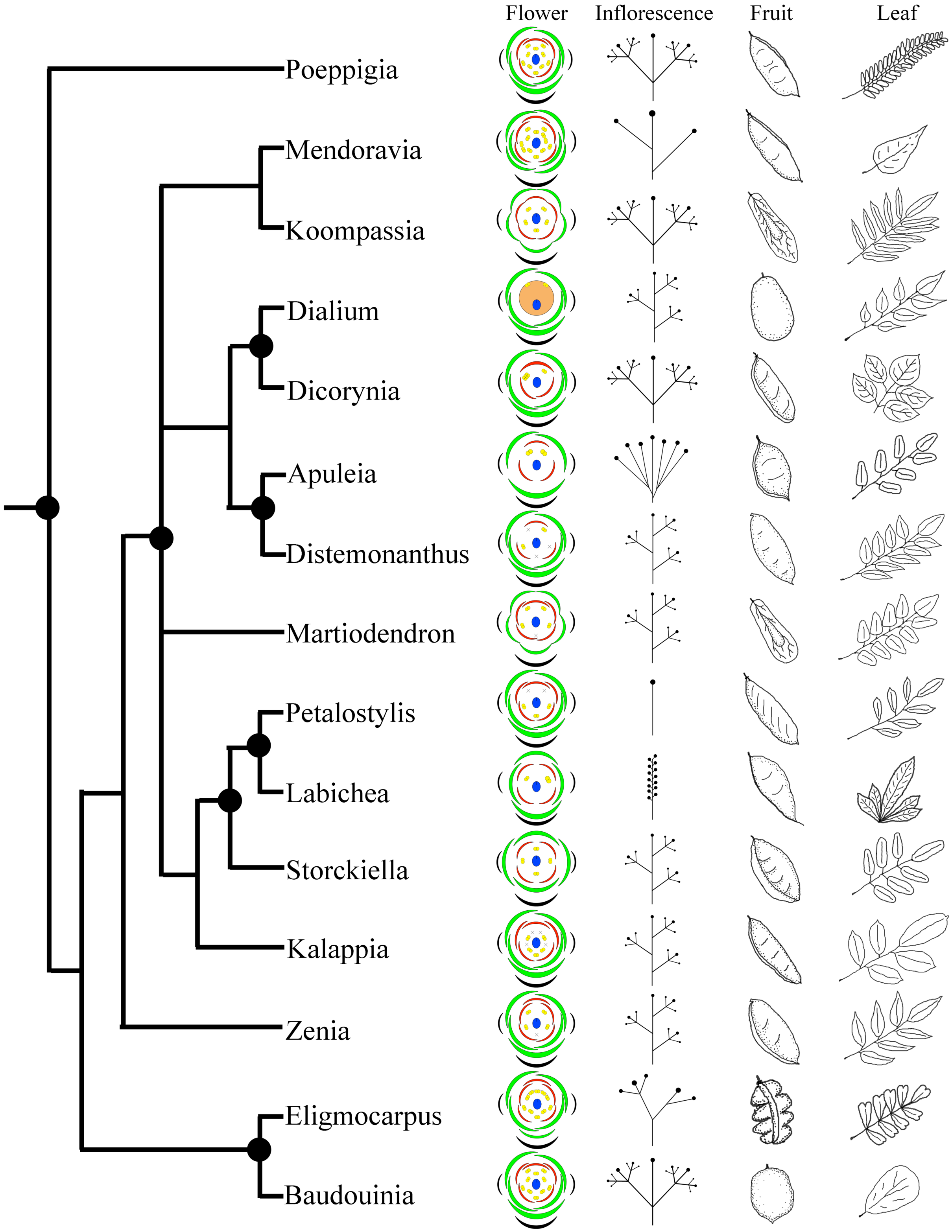

Fig. 2.4. Key morphological features by genus compared to the strict consensus topology of the combined analysis. Black circles indicate nodes with 85% bootstrap support or greater. Some features vary within a genus; in these cases, representative examples have been chosen.

Floral ontogeny in Dialiinae (Caesalpinioideae: Cassieae), a study in organ loss and instability

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Chapter 3 – Floral ontogeny in Dialiinae (Caesalpinioideae: Cassieae), a study in organ loss and instability

3.0 Abstract

The Caesalpinioideae are widely variable in their floral ontogeny, and among caesalpinioids, members of the polyphyletic tribe Cassieae are particularly diverse. Within the Cassieae, the monophyletic Dialiinae clade is marked by a high degree of organ loss, particularly in the largest genus, *Dialium*. The purpose of this work is to explore the ontogeny of several previously undocumented species of the diverse Dialiinae clade, with the goal of building a more complete picture of floral development and evolution in this group, particularly within *Dialium*. We have documented the floral ontogeny of six species of the Dialiinae; four from *Dialium*, as well as *Poeppigia procera* and *Mendoravia dumaziana*. Mode and timing of organ initiation were mostly consistent across the *Dialium* species studied. With the exception of *Dialium dinklagei*, which undergoes helical calyx initiation, all flowers initiated sepals bidirectionally. In the instances of both gains and losses of floral organs in *Dialium*, one trend is apparent — an absence of abaxial organs. Gains in both sepals and stamens occur in the adaxial median position, while stamens and petals which are lost are always the ventral-most organs. Organ initiation in *Poeppigia* and *Mendoravia* is unlike that seen in *Dialium*. *Poeppigia* shows a ventral to dorsal unidirectional sepal initiation, while both *Poeppigia* and *Mendoravia* display near-synchronous initiation of the corolla and staminal whorls. The taxa examined here exemplify the apparent lack of developmental canalisation seen in caesalpinioid legumes. This ontogenetic plasticity is reflective of the morphological diversity shown by flowers across the subfamily, representing what has been described as an “experimental” phase in legume floral evolution.

Keywords: Dialiinae, Cassieae, Floral morphology, Ontogeny

3.1 Introduction

Subfamily Caesalpinioideae, a basal grade of the legume family from which the other two subfamilies, Mimosoideae and Papilionoideae, are derived (Wojciechowski et al., 2004; LPWG, 2013), represents a diverse assembly of floral forms, ranging from large, showy flowers to tiny, highly reduced ones bearing little resemblance to the popular image of a legume flower (Polhill et al., 1981; Lewis et al., 2005). The varied shapes, sizes, and symmetries found in this group are the products of differing developmental pathways (Takhtajan, 1972). Convergent mature morphologies may be arrived at via dissimilar ontogenies, as in the case of the papilionaceous flowers found in *Cercis* (Tucker, 2002), while seemingly drastic differences may arise at the end of an otherwise identical ontogeny, as in the late developing asymmetry of *Lathyrus latifolius* compared to congenerics (Prenner, 2003). As a source of additional information on putative homologies and evolutionary processes, the study of floral development is a useful tool in helping to elucidate phylogenetic relationships among plants (Tucker et al., 1993; Buzgo et al., 2004).

Unlike the Papilionoideae, which display a relatively high degree of consistency in their floral development, the Caesalpinioideae are widely variable in their ontogeny (Tucker, 2003). Among caesalpinioids, members of the polyphyletic tribe Cassieae (Bruneau et al., 2008) are particularly diverse, displaying numerous modes and combinations of organogenesis among whorls, and frequent suppression or loss of floral organs (Tucker, 2003). Within the Cassieae, the monophyletic Dialiinae clade consists of circa 90 tree and shrub species, distributed pantropically (Irwin and Barneby, 1981; Lewis et al., 2005). The clade is united by the presence of cymose inflorescences and the absence of vestured pits in the xylem (Herendeen et al., 2003). It is also marked by a high degree of organ loss, particularly in the largest genus, *Dialium*, and floral symmetries which include polysymmetry, bilateral symmetry, and asymmetry. Despite their varied mature morphologies, very few of these flowers have ever been studied developmentally, a task which may help to clarify their yet unresolved phylogeny and aid in understanding floral evolution in the clade. To our knowledge, the only published research on the floral ontogeny of the Dialiinae was completed by Tucker (1998), who examined detailed developmental series of three species, *Dialium guineense*, *Labichea lanceolata*, and *Petalostylis labicheoides*, with partial observations of a fourth, *Dialium guianense*. She found that the four species shared among them several aspects of development, including organ loss and abaxial, nonmedian initiation of the first sepal. More pronounced, however, were the numerous differences, such as varied modes of sepal, petal, and stamen initiation; organ suppression versus loss; and bilateral symmetry versus asymmetry. The only intrageneric comparisons which could be made were between the two *Dialium* species, one of which was not fully presented, so it is yet unknown whether the variability seen among genera is also present at lower taxonomic levels.

The purpose of this work is to explore the ontogeny of several previously undocumented species of the diverse Dialiinae clade, with the goal of building a more complete picture of floral development and evolution in this group and within its largest genus, *Dialium*. Do these very different mature forms have any common element in their ontogenies, or are the developmental pathways as variable as the flowers they produce?

The taxa examined here represent both basal and highly derived members of the Dialiinae clade. We have documented the floral ontogeny of six species of the Dialiinae; four from *Dialium*, as well as *Poeppigia procera* and *Mendoravia dumaziana*, which have been found in recent phylogenies (Bruneau et al., 2001, 2008; Herendeen et al., 2003) to occupy basal positions in the clade. *Dialium dinklagei*, *Dialium orientale* (both from Africa), and *D. guianense*, from South America, represent the typical morphology of the genus: a pentamerous calyx, absent corolla, two stamens, and a unicarpellate gynoecium set atop a broad, flat receptacle. *Dialium pentandrum*, another African taxon, is one of a small number of Dialium species with an androecium of five or more stamens. It differs from the three species above in both its five-part androecium and the presence of a single petal. *Poeppigia procera*, which has been found in molecular phylogenetic analyses to be sister to the rest of the Dialiinae clade (Bruneau et al., 2001, 2008), is a New World species whose floral morphology corresponds to the typical legume groundplan of a pentamerous calyx and corolla, and diplostemonous androecium. *Mendoravia dumaziana*, an anomalous species in the clade due to its simple leaves and vestured pits, the latter being a trait shared with *Poeppigia*, is unstable with respect to floral organ number; both the calyx and corolla may be five- or six-parted, while the androecium ranges from 10 to 13 stamens. An exploration of morphological and developmental trends in these species will give clues to the evolutionary processes at work in a diverse and poorly understood, but representative, group of early diverging legumes.

3.2 Materials and Methods

For scanning electron microscopy (SEM), 20–30 flowers per species were dissected in 70% ethanol and critical-point-dried using an Autosamdri-815B critical-point dryer (Tousimis Research, Rockville, Maryland, USA). Dried material was then mounted onto specimen stubs using clear nail polish, coated with platinum using an Emitech K550 sputter coater (Emitech, Ashford, UK), and examined using a Hitachi cold field emission SEM S-4700-II (Hitachi High Technologies, Tokyo, Japan). All SEM work was carried out at the Royal Botanic Gardens, Kew. SEM images were edited using Adobe Photoshop CS5. Floral diagrams and formulae were developed following recommendations by Prenner *et al.* (2010). SEM images show abaxial side at bottom unless otherwise noted. The following abbreviations have been used: B = bract; Bl = bracteole; S = sepal; P = petal; A = antesepalous stamen; a = antepetalous; C = carpel; St = style; F = floral meristem, o = ovule; oi = outer integument; ii = inner integument; nu = nucellus.

Specimens examined under the stereo microscope were removed from herbarium vouchers and rehydrated in boiling water with a small amount of surfactant, then dehydrated through an ethanol series to 80% ethanol, in which they were dissected and observed using a binocular dissecting microscope (Wild Heerbrugg, Switzerland). Approximately 25 flowers per species were examined. These dissections were then used to produce the illustrations used in Figs. 3.1, 3.4, 3.7, 3.10, 3.14, and 3.17.

Specimens examined were as follows: *D. pentandrum*: G. Troupin 4712, Irangi, Zaire, 1957 (MO); T.B. Hart 1366, Haute Zaire, Lenda, Zaire, 1992 (MO); Troupin 4645, Kivu, Congo, 1954 (K). *D. guianense*: Krukoff 6262, State of Amazonas, Humayta Municipality, Brazil, 1934 (MO); Rabelo *et al.* 3118, Amapá, Macapá, Brazil, 1984 (NY); G.I. Manriquez 2649, Veracruz, Mexico, 1985 (MO); Coronado *et al.* 2026, Jinotega, Nicaragua, 2005 (MO); W. Palacios 1364, Napo, Ecuador, 1986 (MO). *D. dinklagei*: M. Morello *et al.* 1219, Eastern Ghana, 1995 (MO); Versteegh & der Outer

258, Bingerville, Ivory Coast, 1969 (MO); Linder 68, Firestone Plantation #3, Liberia, 1926 (A); de Koning 6774, Abidjan, Ivory Coast, 1976 (MO). *D. orientale*: J.B. Gillett 20357, Lamu District, Kenya, 1973 (MO); S.A. Robertson 3716, Kilifi, Kenya, 1983 (MO); ILC6-13, Lowveld Botanical Garden, Nelspruit, South Africa, 2013 (JRAU). *P. procera:* C.G. Hernández & E.A. Pérez-Garcia 2358, Oaxaca, Mexico, 1998 (MO); Molina & Molina 12572, Santa Ana, Honduras, 1963 (US); G. Davidse *et al*. 18383, Zulia, Distrito Perija, Venezuela, 1980 (MO); G.P. Lewis & H.P.N. Pearson 1125, Piauí São Raimundo Nonato, Brazil, 1982 (K). *M. dumaziana*: Capuron SF28343, Eastern Madagascar, 1968 (MO); McWhirter 212, Ebakika, Madagascar, 1968 (K).

3.3 Results

3.3.1. *D. pentandrum*

3.3.1.1. Mature morphology (Fig. 3.1)

This African tree species produces a thyrsoid inflorescence (*sensu* Prenner et al., 2009; Endress, 2010; Fig. 3.1d). Flowers are pedicellate and preceded by opposite, early-caducous bracteoles on the lower portion of the pedicel. The calyx consists of five rounded sepals which are imbricate in bud and become reflexed at anthesis (Fig. 3.1b, f). The median sepal is abaxial and slightly broader than the others. Sepals are tomentose on the margins and outer surface, and puberulent on the inner surface. The corolla may be absent or, more often, it consists of a single narrowly ovate petal in the adaxial median position (Fig. 3.1a). The androecium consists of five (rarely six) antesepalous stamens of equal size. Anthers are basifixed, ovate, and display latrorse dehiscence along longitudinal slits, opening fully at the distal end (Fig. 3.1f). The sessile single carpel is densely velutinous and sits at the centre of an expanded, nearly flat receptacle. Two ovules are typically present. The slender style is glabrous and bends sharply toward the adaxial side, ending in a small, capitate stigma (Fig. 3.1e). The fruit is a one- to two-seeded indehiscent drupe. Leaves are imparipinnately compound with sub-opposite to alternate leaflet insertion (Fig. 3.1c).

3.3.1.2. Floral ontogeny (Figs. 3.2, 3.3)

Paired bracteoles develop successively in the adaxial lateral positions relative to the floral meristem (Fig. 3.2a, c). In opposite lateral flowers, bracteole development is mirror-image; one initiates the right-hand bracteole first, while the other begins with the left (Fig. 3.2a, b). Five sepals follow, the first in the median abaxial position, and develop bidirectionally (Fig. 3.2d, e). The second sepal is formed either to the left (Fig. 3.2d) or to the right (3.2e) of the median plane. This indicates a directionality in sepal formation even though initiation is not helical, but bidirectional. Trichomes form on the outer surface of the first-initiated sepals relatively early in development (Fig. 3.2e). Calyx differentiation occurs well before the initiation of the inner whorls, closing over the floral meristem before any interior organ primordia have formed (Fig. 3.2f). While the order of initiation of the inner three whorls was not directly observed, based on relative organ sizes, the domelike carpel primordium develops next, followed by a single whorl of five antesepalous stamens, then a single petal in the adaxial median position (Fig. 3.3a). There is no sign (*i.e.* primordia) of the remaining four petals, which are apparently completely lost. Androecium initiation seems to begin with the abaxial median and adaxial lateral organs, followed by the abaxial laterals (Fig. 3.3a). As the anthers differentiate and grooves form delimiting the four microsporangia, an upturned style develops, which is terminated by a small stigmatic area (Fig. 3.3b). Concurrently, the petal expands into a lamina, lagging well behind the stamens in size. At this point, numerous trichomes have formed on the receptacle and the surface of the ovary. As the bud reaches maturity, a small, capitate stigma is apparent on the sharply upturned style (Fig. 3.3c–f). The surface of the ovary is densely covered in linear trichomes, while the anthers and inner petal surface bear short, hooked trichomes (Fig. 3.3c, d). Rarely, a sixth stamen is present in the adaxial median position (Fig. 3.3c, d). Although a distinct anther is formed, the stamen remains much smaller than those of the antesepalous whorl. The mature ovary contains two (rarely one) tightly packed ovules (Fig. 3.3e).

3.3.2. *D. guianense*

3.3.2.1. Mature morphology (Fig. 3.4)

This South American species produces thyrsoid inflorescences (Fig. 3.4g). Pedicellate flowers are subtended by bracts and preceded by opposite, early-caducous bracteoles situated on the lower half of the pedicel (Fig. 3.4c). The pentamerous calyx is imbricate in bud (Fig. 3.4d), becoming reflexed at anthesis. Sepals are uniform at the base and tomentose on all surfaces. The corolla is absent (Fig. 3.4a). The androecium consists of two stamens in the adaxial lateral positions, situated along the rim of a broad receptacular disc. Anthers are basifixed, widely ovate, and have sagittate bases (Fig. 3.4b). Dehiscence is latrorse, along longitudinal slits, opening completely at the tip. The sessile carpel contains two ovules. It is densely velutinous and sits toward the abaxial side of the expanded receptacle (Fig. 3.4a, c). The slender, distally glabrous style curves adaxially, ending in a small, terete stigma (Fig. 3.4e). The fruit is a one- to two-seeded, indehiscent drupe. Leaves are imparipinnately compound with alternate leaflet insertion (Fig. 3.4f).

3.3.2.2. Floral ontogeny (Figs. 3.5, 3.6)

As in *D. pentandrum*, paired bracteoles develop successively within the enclosing bract, and occur in a slightly adaxial position relative to the floral meristem (Fig. 3.5a, b). The pentamerous calyx is initiated bidirectionally, beginning with the abaxial sepal, which occurs at or near the median plane (Fig. 3.5b, c). Also similar to *D. pentandrum*, trichomes are seen on the outer surface of the first-initiated sepals early in their development (Fig. 3.5c). A dome-like carpel primordium is initiated next, followed by two synchronous stamen primordia (Fig. 3.5d). We could not find any sign of petal primordia or further stamen primordia. Therefore these organs must be regarded as completely lost. As the carpel enlarges, the cleft becomes visible on the adaxial side, rotated somewhat off the median, and trichomes start to grow from the narrow strip of receptacle between the calyx and the abaxial side of the carpel (Fig. 3.5e). The receptacle is closely packed at this point in ontogeny, but by anthesis, it will have expanded greatly. Trichomes continue to grow around and on the surface of the ovary until it is densely covered (Fig. 3.5f). Anthers have now developed grooves separating four microsporangia, and a terete stigmatic surface is apparent at the tip of the short, glabrous style (Fig. 3.5f). At maturity, the style has lengthened and curved adaxially between the oblong, sagittate anthers (Fig. 3.6a). The stamens now sit at the edge of an expanded receptacle. The receptacle is concave to quite flat and is covered with stomata and short, hooked trichomes similar to those on the petal and anthers of *D. pentandrum* (Fig. 3.6b, c). The mature ovary contains two (rarely one) tightly packed ovules (Fig. 3.6d).

3.3.3. *D. dinklagei*

3.3.3.1. Mature morphology (Fig. 3.7)

This African tree produces thyrsoid inflorescences (Fig. 3.7d). Early caducous bracteoles precede the flower on the lower half of the pedicel (Fig. 3.7e). The calyx consists of five sepals, imbricate in bud, which reflex at anthesis (Fig. 3.7a, c). The abaxial lateral sepals are slightly narrower at the base than the remaining equal members. All surfaces of the calyx are puberulent to tomentose. The corolla is absent. The two stamens are located in the adaxial lateral positions at the edge of a broad receptacle (Fig. 3.7a). The basifixed anthers are ovate with slightly sagittate bases (Fig. 3.7f). Dehiscence is latrorse via longitudinal slits. The sessile ovary sits on a broad receptacle and is densely velutinous (Fig. 3.7c). It bears two ovules. A slender, glabrous style ends in a small, terete stigma (Fig. 3.7b). The fruit is an indehiscent drupe. Leaves are imparipinnate with sub-opposite leaflet insertion (Fig. 3.7g).

3.3.3.2. Floral ontogeny (Figs. 3.8, 3.9)

Bracteoles in this species are somewhat smaller than in the two previous species, and are more skewed to the adaxial side of the flower (Fig. 3.8a). Unlike the other *Dialium* species examined, the pentamerous calyx is initiated helically, rather than bidirectionally, in either clockwise or anti-clockwise direction (Fig. 3.8b, c). A slightly modified form of helical initiation is sometimes seen (Fig. 3.8b). The first sepal is initiated abaxially, on or near the median plane, and may develop trichome initials on its outer surface even before other sepal primordia are apparent (Fig. 3.8a). The inner whorls do not initiate until after longer plastochron, during which the calyx has closed over (Fig. 3.8d). Inner whorl development begins with a dome-like carpel primordium which sits toward the abaxial side of the pentagonal meristem (Fig. 3.8d, e). Lagging slightly behind the carpel are two stamen primordia, which initiate in rapid succession in the adaxial lateral positions (Fig. 3.8f). Aside from these two stamens, no further promordia (either petals or stamens) could be observed, and these organs are therefore considered as completely lost. The carpel cleft forms on the adaxial side, aligned with a distinct gap between the two developing stamens (Fig. 3.9a). As in the other *Dialium* species, trichomes can be seen forming around the abaxial and lateral edges of the carpel at this point. While the organs are tightly packed in bud, at anthesis, the stamens will be situated at the edge of a wide receptacle (Fig. 3.9b–d). The glabrous style curves adaxially and is terminated by a small, terete stigma (Fig. 3.9c, d). The mature ovary holds two (rarely one) tightly packed ovules (Fig. 3.9e).

3.3.4. *D. orientale*

3.3.4.1. Mature morphology (Fig. 3.10)

As with the *Dialium* species described above, *D. orientale* is an African tree which produces thyrsoid inflorescences (Fig. 3.10e). Bracteoles are early caducous, occurring on the lower to mid-portion of the pedicel. The calyx consists of five (rarely six) equal sepals which are imbricate in bud and reflexed at anthesis (Fig. 3.10a, c, g). All surfaces of the sepals are puberulent to densely tomentose. The corolla is absent. Two (rarely three) stamens with basifixed anthers are located in the adaxial lateral and (if three) adaxial median positions (Fig. 3.10a, g). The anthers are ovate with sagittate bases, opening in a latrorse fashion via longitudinal slits (Fig. 3.10b). A shortly stipitate ovary sits on a broad, nearly flat receptacle and is densely velutinous (Fig. 3.10g). It contains two ovules. A long, glabrous style ends in a small, terete stigma (Fig. 3.10d). The fruit is an indehiscent drupe. Leaves are imparipinnate with sub-opposite leaflet insertion (Fig. 3.10f).

3.3.4.2. Floral ontogeny (Figs. 3.11–3.13)

Paired bracteoles develop successively within an enclosing bract, occurring in a slightly adaxial position relative to the floral meristem (Fig. 3.11a). The pentamerous calyx is initiated bidirectionally, beginning with the abaxial sepal, which occurs at or near the median plane (Fig. 3.11b). The next sepal to initiate is one of the adaxial laterals; which one depends on the position of the bud relative to the central flower of the cyme. The second initiated sepal will be the one nearest to the adaxial side of that central flower (Fig. 3.11c). The third sepal initiated is the other adaxial lateral organ, followed by the abaxial laterals in close succession to one another (Fig. 3.11d, e). Following the initiation of all sepals, distinct primordia can be seen for both the carpel and the androecium (Fig. 3.11f). Two stamens initiate in rapid succession, lagging slightly behind the carpel. At later stages, the developing stamens are pressed closely to the carpel and have a slightly flattened appearance, but usually sit at a distance from one another, with a distinct gap between them and above the carpel cleft (Fig. 3.12a, b). In some flowers, the carpel cleft is off-median and faces one of the stamens (Fig. 3.12c). The cleft remains open during the mid-stage of development (Fig. 3.12d). Near maturity, the ovary contains two tightly-packed ovules (Fig. 3.12e, f). Occasionally, a sixth sepal initiates later than the others in the adaxial median position (Fig. 3.13a, b). While the organ begins development completely overlapped by the two adaxial lateral sepals, by maturity, it sits between them (Fig. 3.13c, d, e). Flowers with six sepals seem to always develop an accompanying third stamen, which develops just adjacent to the extra sepal in the adaxial median position (Fig. 3.13c, d). In some cases, however, the additional stamen fails to develop fully and remains a staminode, with both anther and filament present (Fig. 3.13e). Rarely, an extra, apparently functional, carpel is also formed alongside the first (Fig. 3.13f).

3.3.5. *P. procera*

3.3.5.1. Mature morphology (Fig. 3.14)

This monospecific South American tree genus produces terminal and axillary thyrsoid inflorescences (Fig. 3.14b). Flowers are pedicellate with oppositely arranged bracteoles persisting through late development on the mid-portion of the pedicel (Fig. 3.14b). The pentamerous calyx is distant in bud and connate above a shallow, open hypanthium (Fig. 3.14e). The sepals are equal in size and puberulent over all surfaces. Five petals are undifferentiated and uniform in colour, with imbricate ascending aestivation in bud (Fig. 3.14a, e, g). The androecium is arranged in two whorls of five stamens each. Anthers are dorsifixed, elliptic, and dehisce via introrse longitudinal slits; filaments are many times longer than anthers (Fig. 3.14a, c). The stipitate gynoecium attaches to the base of the hypanthium. The abaxial suture is covered in long trichomes (Fig. 3.14d). The small stigmatic area is sub-sessile, the style being only a slight extension of the ovary. As many as eight ovules are present. The fruit is membraneous and indehiscent, bearing one to two seeds (Fig. 3.14f). Leaves are paripinnately compound with opposite insertion of sessile leaflets (Fig. 3.14f).

3.3.5.2. Floral ontogeny (Figs. 3.15, 3.16)

Two bracteoles develop successively, in a more lateral – as opposed to adaxial – position than seen in *Dialium* (Fig. 3.15a, b). The pentamerous calyx develops unidirectionally, beginning with an off-median abaxial sepal and proceeding adaxially (Fig. 3.15b). Five petals initiate simultaneously and at the same time as the carpel primordium, followed closely by the antesepalous stamen whorl (Fig. 3.15c, d). Once initiated, the adaxial lateral petals enlarge more quickly than the rest of the whorl (Figs. 3.15d, e, 16a). The antepetalous stamen whorl is the last to develop, initiating in rapid succession, in an apparently variable order (Figs. 3.15e, 16a). In one case, as the upper antepetalous stamens begin to enlarge, the abaxial lateral organs have not yet been initiated (Fig. 3.15f), while in another, the opposite order seems to occur (Fig. 3.16a). At this point, the adaxial surface of the carpel begins to infold (Fig. 3.15e). The cleft continues to deepen as the stamens enlarge, tilting inward toward the carpel as they grow (Fig. 3.16b, c). In some flowers, the carpel cleft does not occur on the median, but tilts slightly toward one side or the other (Fig. 3.16b). As anthers differentiate in the late stages of ontogeny, the antesepalous stamen whorl remains tilted inward toward the carpel. The antepetalous stamens are much smaller and have shorter filaments even late in ontogeny, but equalize by anthesis (Fig. 3.16d). A small stigmatic patch develops atop a short extension of the ovary, remaining sub-sessile at maturity (Fig. 3.16d–f). The stipitate ovary contains up to eight ovules attached by marginal placentation (Fig. 3.16e). Long trichomes cover the upper portion of the stipe as well as the nonplacental suture of the ovary.

3.3.6. *M. dumaziana*

3.3.6.1. Mature morphology (Fig. 3.17)

The monospecific Malagasy genus *Mendoravia* produces axillary inflorescences with relatively few flowers (Fig. 3.17d). A detailed classification of the inflorescence type is not possible based on the available specimens (but see Capuron, 1968). Bracteoles in this species are small and persistent, occurring on the lower portion of the pedicel. The calyx consists of five or six narrowly imbricate, triangular sepals which do not reflex at anthesis (Fig. 3.17a, b). Sepals are puberulent on the margins and outer surface. The corolla is made up of five to six sub-equal, glabrous petals of unknown aestivation (Fig. 3.17a, b). Stamen number ranges from 10 to 13 (rarely more or less), arranged in two whorls of at least five organs each (Fig. 3.17a, b). Anthers are basifixed and narrowly oblong, opening via slightly introrse terminal pores (Fig. 3.17e). The sub-sessile ovary is sparsely puberulent, with a short style ending in a large, peltate stigma (Fig. 3.17c). It bears 2–3 ovules. The fruit is coriaceous and dehiscent along both sutures. Leaves are simple (Fig. 3.17f).

3.3.6.2. Floral ontogeny (Figs. 3.18, 3.19)

The narrowly imbricate calyx develops and closes over very early in this species, and as such, we were unable to find buds young enough to allow the study of calyx initiation. The lag in the initiation of the inner whorls is long; removal of the closed calyx exposes an irregularly five-sided meristem with no obvious organ initiation yet taking place (Fig. 3.18a). Number and arrangement of organs are very unstable in *Mendoravia*. Fig. 3.18b shows the rapid sequence initiation of the corolla, beginning with a petal in the abaxial, rather than adaxial, median position. In some flowers, petal and stamen initiation follows no obvious pattern in terms of either sequence or location; neither is it uncommon for a pair of stamens to form where only a single organ is expected (Fig. 3.18d, e). In more regularly arranged flowers, the antesepalous stamen whorl initiates simultaneously, with the abaxial organ located in the median position (Fig. 3.18e, f). The antepetalous stamen whorl follows in quick succession, also initiating simultaneously, with the adaxial stamen in the median position. It was found that even in regularly arranged flowers, doubled stamens were common (Fig. 3.18d, e). The carpel develops slightly ahead of the androecium, with a cleft forming on or near the adaxial median after all stamens have differentiated (Fig. 3.18e, f). As the corolla closes over the inner two whorls, trichomes grow both from the tips of the outer surfaces of the petals and from the spaces between organs on the receptacle (Figs. 3.18e, f, 3.19a). A sixth petal may form in either the abaxial median (Fig. 3.19a) or one of the lateral positions (Fig. 3.19b), and may develop adjacent to an additional stamen (Fig. 3.19b). Mature anthers are narrowly oblong, with sagittate bases and poricidal dehiscence (Fig. 3.19c, d). The stigma is large and peltate (Fig. 3.19e). The mature ovary contains two ovules attached by marginal placentation (Fig. 3.19f). While only a single mature ovary was available here for examination, Irwin and Barneby (1981) state that 2–3 ovules are characteristic.

3.4 Discussion

3.4.1. Floral ontogeny of genus Dialium

The most striking feature of *Dialium* flowers is their extreme organ loss, which in most cases results in flowers with only two to three stamens and a single petal or a corolla which is completely absent (Irwin and Barneby, 1981). Tucker (1998) described them as being so reduced that they are "barely recognisable as members of Leguminosae." Of the four *Dialium* species studied here, three species produce a bi-staminate androecium and no corolla, while the fourth retains all five antesepalous stamens and one petal.

Another unusual feature of the genus, and of Dialiinae as a whole, is its thyrsoid inflorescences; the central flower produces buds in the axils of both bracteoles, which themselves become central flowers in the next iteration of the pattern (see Prenner et al., 2009; Endress, 2010). In *Dialium*, this was found to be associated with a mirror symmetry in the development of the bracteoles and calyx across the plane of the central inflorescence axis. It has been noted that in *Polygala myrtifolia*, the direction of helical sepal initiation is predetermined by the order in which two sequential bracteoles are formed (Prenner, 2004b). This also seems to be the case in *Dialium*, although bracteole order may itself be predetermined by the relative position of the flower on the inflorescence. In asymmetrical flowers of *Labichea*, a genus which, exceptionally for the Dialiinae, produces racemes, the phenomenon of 'pendulum symmetry,' an alternation of right- and left-handed enantiomorphs, is observed along the length of the inflorescence (Goebel, 1928; Tucker, 1998). A similar phenomenon of symmetry at the level of the inflorescence was recently described for the papilionoid *Swainsona formosa* (Prenner, 2013b), and an analogous condition may be occurring in *Dialium*.

Mode and timing of organ initiation were mostly consistent across the *Dialium* species studied. With the exception of *D. dinklagei*, which undergoes helical or modified-helical calyx initiation, all flowers initiated sepals bidirectionally, beginning with the median sepal. Bidirectional organogeny of this type was described by Tucker (1998) in the calyces of *D. guineense* and *P. labicheoides* (Dialiinae). It is seen only rarely elsewhere in Caesalpinioideae, such as in *Haematoxylum* (Tucker and Kantz, 1997), while Prenner (2004e) found a similar mode in a few papilionoid species. Bidirectional calyx development in *Martiodendron excelsum* (E. Zimmerman, personal observation), another member of the Dialiinae, suggests that it is not confined to these two genera, but that it may be the dominant mode of initiation in the clade. Organs also appear to arise bidirectionally in the androecium of *D. pentandrum*. If we assume that the paired stamens of the other *Dialium* species represent remnants of a once pentamerous whorl, their rapid, successive initiation may be the remaining, abbreviated form of earlier bidirectionality.

As noted by previous authors (Chakravarty, 1969; Tucker, 1998) and by ourselves with respect to *Apuleia* (Zimmerman et al., 2013), it is not uncommon in Dialiinae for flowers to develop extra organs in any of their whorls. Here, we have found extra sepals and carpels in *D. orientale*, as well as extra stamens in *D. orientale* and *D. pentandrum*. In *D. orientale*, the appearance of an additional stamen in the adaxial median position is always found to correspond to an additional sepal in the same position. Unlike the adaxial median stamen which occurs in *D. pentandrum* and appears, due to position and relative size, to be part of the lost inner stamen whorl, the extra stamen in *D. orientale* is the same size as the other stamens and is located immediately opposite the sixth sepal, suggesting that the two cases are not analogous. In *D. orientale*, the extra stamen may develop due to the additional space opened up on the floral meristem as the sixth sepal expands. A third stamen in the adaxial median position is also present in the six-sepaled species, *Dialium hexasepalum* (E. Zimmerman, pers. obs.).

In the instances of both gains and losses of floral organs in *Dialium*, one trend is apparent — an absence of abaxial organs. Gains in both sepals and stamens occur in the adaxial median position, while stamens and petals which are lost are always the ventral-most organs. This may suggest a gradient in the expression of certain floral development genes acting vertically across the meristem. Interestingly, the calyx appears not to be affected by this phenomenon. With the exception of several Malagasy species which exhibit trimery of both the calyx and corolla, and the monospecific segregate genus *Dansera*, sepals are never lost in *Dialium* (E. Zimmerman, pers. obs.). Organ loss or suppression localised to the abaxial side of the flower is rare in legumes, but has been noted in both the androecium of *Duparquetia* (Prenner and Klitgaard, 2008) and in the corolla of certain members of the resin-producing Detarieae (Fougere-Danezan et al., 2010). In the Detarieae, this results in the absence or reduction of either the abaxial lateral or all four lateral petals. The authors suggest that abaxial petals are more labile, and are suppressed as part of repeated shifts toward zygomorphy within the tribe. Abaxial suppression may be related to the action of a gene with differential expression across a dorsal–ventral axis, such as that of the *CYCLOIDEA*-like genes, which have a dorsalizing effect in *Lotus japonicus* petals (Feng et al., 2006) and have also been found to control floral organ number in *Antirrhinum majus* (Cubas, 2004). The related *CYCLOIDEA*-like gene, *LegCYC*, has been found to be present in a single copy in *D. guianense*, but expression studies have not yet been carried out in caesalpinioid legumes (Citerne et al., 2003).

3.4.2. Floral ontogeny of genera Mendoravia & Poeppigia

As noted above, instability of organ numbers is a recurring theme in the Dialiinae, and the monospecific Malagasy genus *Mendoravia* is a striking example of this. Rather than developing the occasional extra organ, as seen in *Dialium*, *Mendoravia* regularly has variable numbers of sepals (5–6), petals (5–6), and stamens (10–12) (Capuron, 1968). In specimens we studied, sepal and petal numbers appeared to be equal within each flower. As with *D. orientale*, it is possible that the addition of an extra sepal created a space on the meristem in which an extra organ, in this instance a petal, could form. However, the vast majority of our samples possessed only five of each organ, making it difficult to say that this is always the case. A number of buds with a pentamerous calyx and corolla developed 11 stamens, while others had only the standard ten, suggesting variation in the androecium is not linked to the two outer whorls. While no conclusions can be made based on SEM images, additional stamens appear to be duplicates, initiating immediately adjacent to one another and developing at the same rate.

Organ initiation in *Poeppigia* and *Mendoravia* is unlike that seen in *Dialium*. *Poeppigia*, the monospecific New World genus hypothesized to be sister to the rest of the Dialiinae clade, shows a ventral to dorsal unidirectional sepal initiation which has not been seen elsewhere in the clade, but is the standard form in papilionoids (Tucker, 2003). Mode of initiation in the calyx could not be determined in *Mendoravia* due to its very early development relative to the rest of the flower; specimens at a sufficiently early stage could not be obtained. This long pause between the development of the calyx and that of the inner whorls is also seen in *Martiodendron*. Both *Poeppigia* and *Mendoravia* display near-synchronous initiation of the corolla and staminal whorls. Among Dialiinae, synchronous petal formation was also reported for *P. labicheoides* (Tucker, 1998). Outside the clade, synchronous organ formation is frequently seen in mimosoids (Ramirez-Domenech and Tucker, 1990) and was also found in the sepals (Prenner, 2004d) and in the petal whorl of some papilionoids such as *Daviesia cordata* (Prenner, 2004a) and *Lespedeza thunbergii* (Prenner, 2004d; for more examples, see also Table 1 in Prenner, 2013b). This shows that synchronous organ formation is a recurring theme among legumes which is found more frequently in some groups than in others. The addition of more data will help to better understand this character and to evaluate potential systematic implications.

Several *Poeppigia* flowers in this study displayed what has been referred to as an "asymmetric androecium" (Prenner, 2004f), in which the adaxial antepetalous stamen does not lie on the median plane. Prenner (2004f) describes this phenomenon in a number of papilionoid legumes, noting that it is often accompanied by an off-median carpel cleft, which seems to be the case in *Poeppigia* as well. *Mendoravia* flowers frequently form an off-median carpel cleft, although in these instances the androecium deviates more extensively from the common groundplan of ten stamens in two whorls of five, both in terms of stamen number and position. In both of these species, however, asymmetry during early development does not occur in all flowers; it is not canalised, as it would seem to be in the cases discussed by Prenner (2004f), perhaps indicating a greater developmental plasticity in the studied taxa.

3.4.3. Ontogenetic trends in the Dialiinae

The taxa examined here exemplify the apparent lack of developmental canalisation seen in caesalpinioid legumes. Compared to a group such as the papilionoids, which display similar timing and mode of development across much of the subfamily, considerable variation can be seen in as restricted a subset as the Dialiinae clade (Tucker, 1998, 2003). This ontogenetic plasticity is reflective of the morphological diversity shown by flowers across the Caesalpinioideae, representing what has been described as an "experimental" phase in legume floral evolution (Prenner and Klitgaard, 2008).

Taken together with the Dialiinae taxa studied by Tucker (1998), we observed differing combinations of bidirectional, helical, unidirectional, and synchronous initiation; differing plastochrons between whorls; and both losses and gains of organs relative to the legume floral groundplan. In the case of Dialium, we see variation in organogeny even at an intrageneric level.

Recent molecular and morphological phylogenetic analyses have suggested that the basalmost groups in the Dialiinae are the genus *Poeppigia* and the Malagasy clade containing *Baudouinia*, *Eligmocarpus*, and in some cases, *Mendoravia* (Herendeen et al., 2003; Bruneau et al., 2008). Interestingly, these are also the genera least affected by organ loss. With the exception of up to four lost stamens in certain species of *Baudouinia*, all of these taxa possess at least the typical legume complement of 21 organs (Irwin and Barneby, 1981; Polhill and Vidal, 1981; Herendeen, 2000). Located as they are at the opposite end of the phylogeny from the highly reduced *Dialium*, a trend of increasing organ loss is suggested. Thompson (1925) described a phenomenon of increasing sterility in the Cassieae, based in part on the stamen loss common in the Dialiinae. Pollinators have not been well-documented in the clade, although certain morphological features in the group, such as putative nectaries on the expanded receptacle in *Dialium* and poricidal anthers in *Mendoravia*, suggest possible specialisations geared toward a particular type of pollination. We are in the process of generating a more highly resolved and well-supported phylogeny of the clade to explore these hypotheses of floral evolution.

Finally, the floral organ reductions found in the Dialiinae observed here are dissimilar to those seen in most other legume taxa because reductions are due to a complete loss of the organs in question, rather than a post-initiation suppression, which is common in legumes (Tucker, 1988b). Tucker (1988b) notes that cases of outright loss are most prevalent in caesalpinioids, and in particular in various Cassieae groups and in tribe Detarieae. Among papilionoid legumes, organ loss can also be found in *Dalea candida* (Amorpheae), in which the inner stamen whorl is lost (McMahon and Hufford, 2002) and in *Abrus precatorius*, in which the adaxial stamen of the inner whorl is lost (Prenner, 2013a). These anomalous cases show that while ontogenetic themes such as organ loss seem to occur more frequently in caesalpinioids, they also occur sporadically in the other two subfamilies. This demonstrates that on one hand, borders between legume subfamilies are relatively well established and defined, but on the other hand, recurring themes still point toward them all belonging to a single family.

3.5 Acknowledgements

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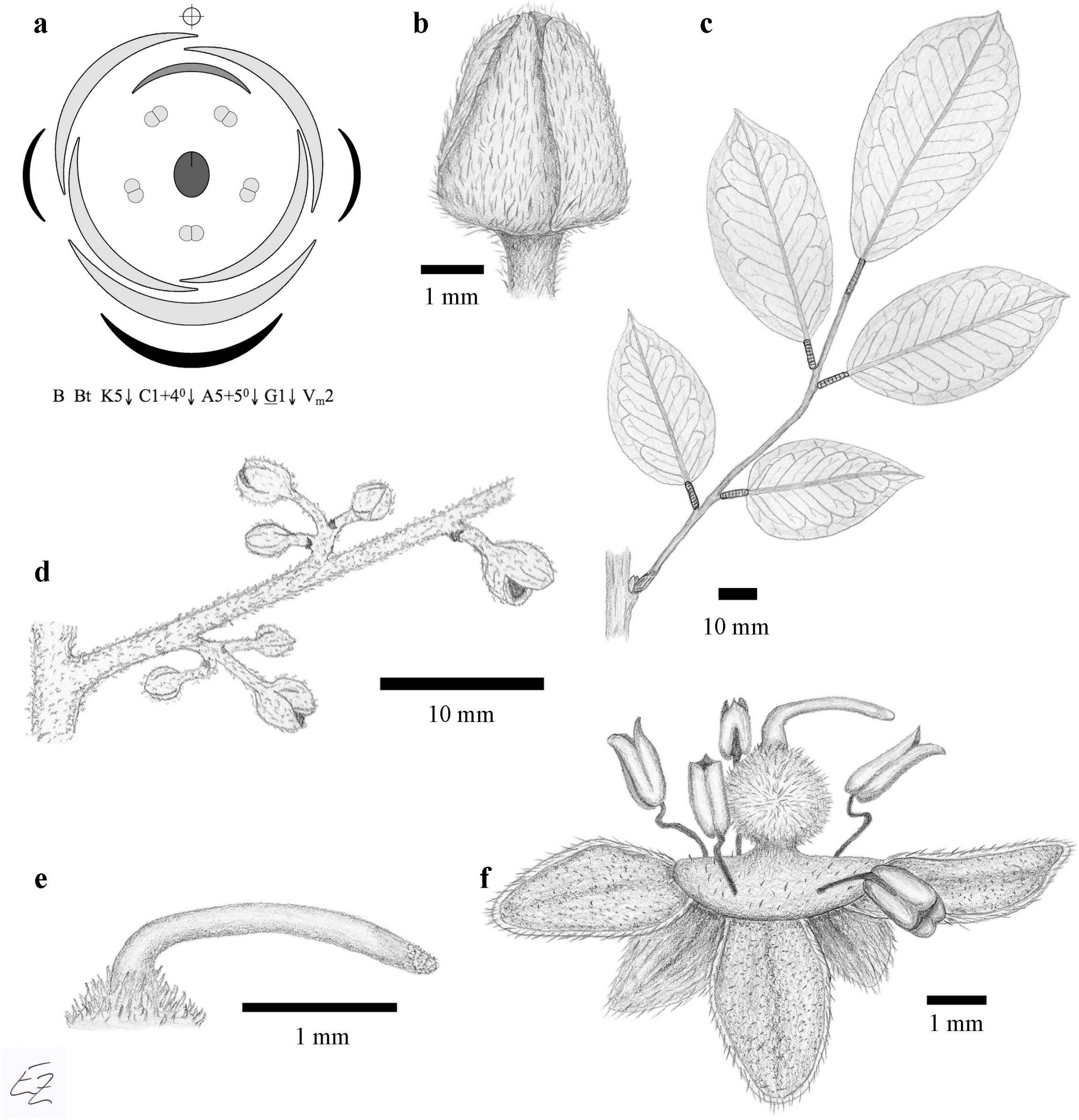

Fig. 3.1. Drawings and floral diagram of *Dialium pentandrum*. a. Floral diagram and formula. b. Flower bud prior to anthesis. c. Compound leaf. d. Section of inflorescence showing cymose units. e. Detail of style and stigma. f. Post-anthesis flower; single petal has dehisced. Vouchers: b, d–f, Troupin 4712 (MO); c, Hart 1366 (MO).

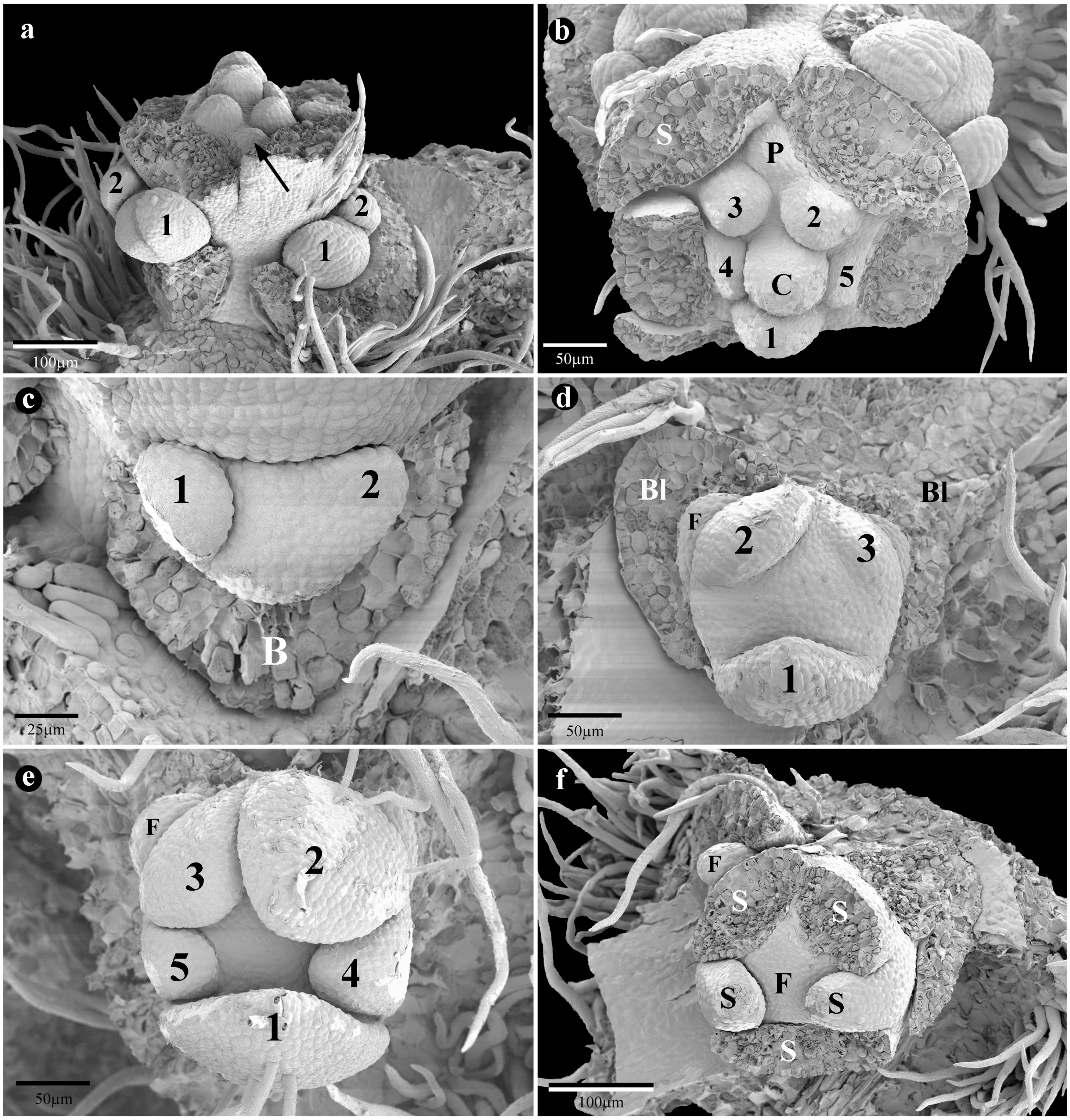

Fig. 3.2. SEM micrographs of *Dialium pentandrum*. a. Adaxial view of developing flower (sepals removed) with two lateral flowers initiated toward the adaxial side of the central flower. Arrow indicates single petal. Numbers indicate order of bracteole initiation. b. Frontal view of (a), showing bidirectional development of antesepalous stamen whorl (sepals removed), with gynoecium development more advanced, and petal lagging behind. Numbers indicate order of stamen initiation. c. Detail of lateral flower initial showing sequential initiation of bracteoles. d. Early bidirectional initiation of first three sepals, beginning with the abaxial median organ. e. Bidirectional calyx development, with trichomes already present on the outer surface of the oldest sepals. Numbers indicate order of sepal initiation. f. Bud with three first-initiated sepals removed, showing lack of organ initiation with- in the inner whorls at this stage of development. Voucher: Troupin 4645 (K).

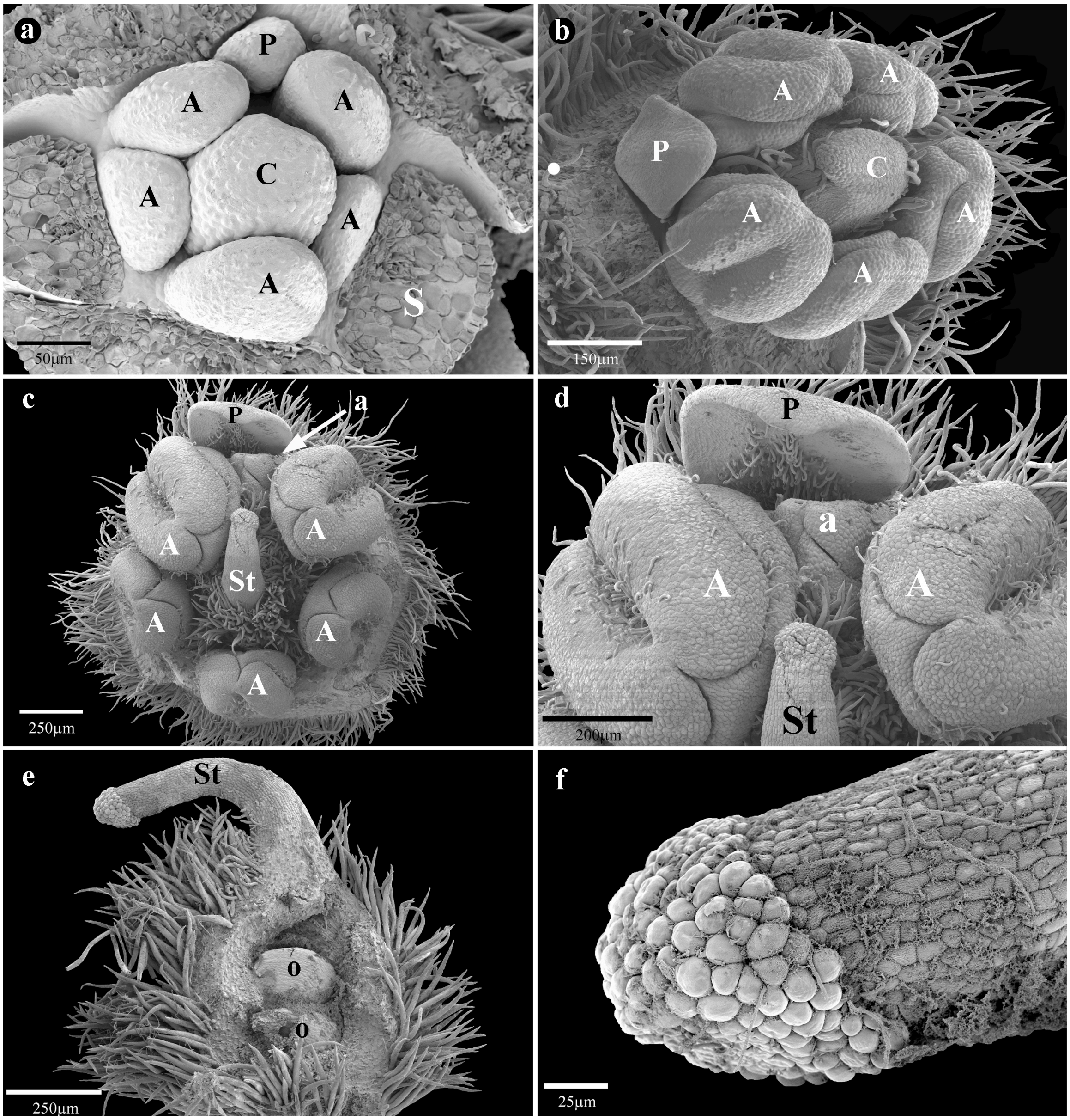

Fig. 3.3. SEM micrographs of *Dialium pentandrum*. a. Putative bidirectional development of antesepalous stamen whorl and growth of young carpel. Single petal in adaxial median position lags slightly behind development of inner whorls. b. Differentiation of anthers and upcurved style. Trichomes proliferate among the inner organs at this stage. Carpel starts to bend in the adaxial direction. White dot indicates the adaxial side of the flower. c. Flower with late-developing additional stamen (arrow) opposite single petal. Differentiation of stigma and dense trichome cover on ovary. d. Detail of (c) showing sixth stamen. Dense, hooked trichomes are visible along the inner midrib of the single petal and on the surface of mature anthers. e. Opened mature ovary, showing two ovules. f. Detail of papillate stigma. Voucher: Troupin 4645 (K).

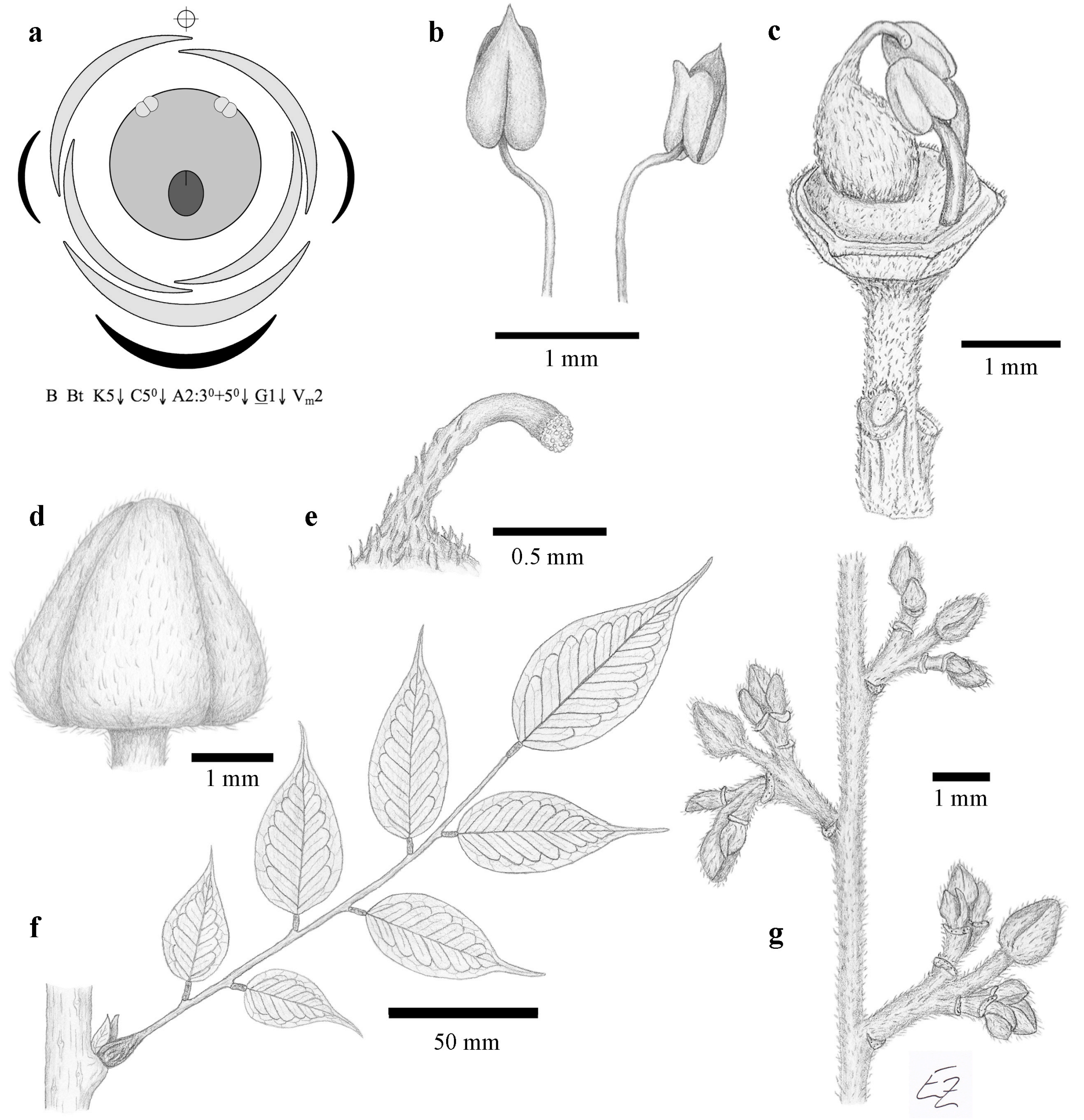

Fig. 3.4. Drawings and floral diagram of *Dialium guianense*. a. Floral diagram and formula. b. Mature stamens showing reflexed filaments and longitudinal anther dehiscence. c. Flower bud just prior to anthesis, sepals removed. d. Flower bud prior to anthesis. e. Detail of style and stigma. f. Compound leaf. g. Section of inflorescence showing cymose units. Vouchers: b, G.I. Manriquez 2649 (MO); c–e, Rabelo 3118 (NY); f, Coronado *et al*. 2026 (MO); g, Krukoff 6262 (MO).

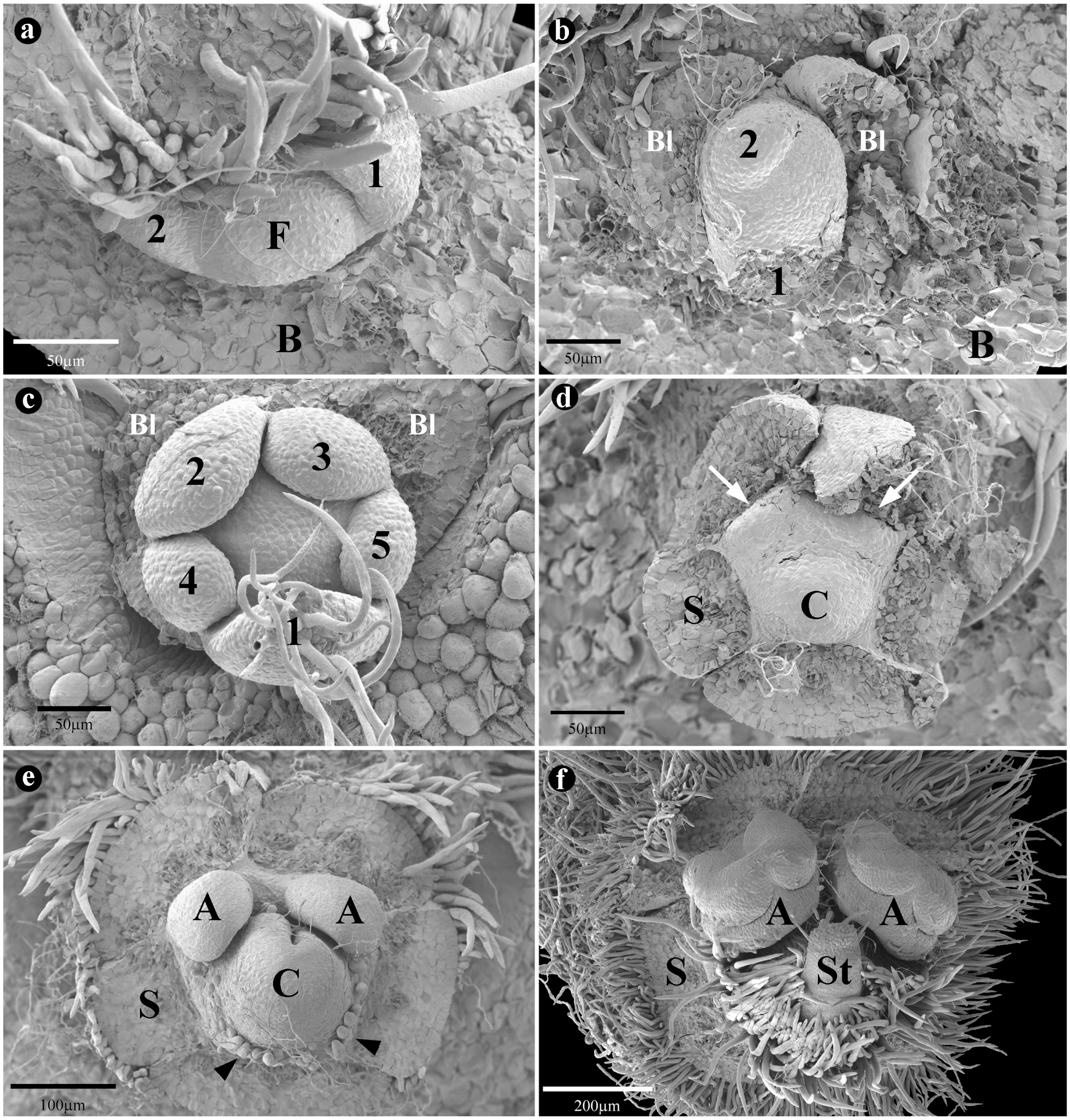

Fig. 3.5. SEM micrographs of *Dialium guianense*. a. Sequential initiation of bracteoles in a lateral flower (bract removed). b. Initiation of first (damaged) and second sepals in abaxial median and adaxial lateral positions, respectively. c. Bidirectional sepal development with first sepal in ± median abaxial position. Early trichome growth on sepal outer surface and bracteoles in adaxial lateral, somewhat asymmetrical positions. d. Initiation of domelike carpel primordium followed by two stamen primordia (arrows; sepals removed). e. Off-centre cleft formation in the carpel and trichome development around its base (arrowheads; sepals removed). f. Anther and stigma differentiation. The carpel is now densely covered in trichomes and the style bends in the adaxial direction. Voucher: Palacios 1364 (MO).

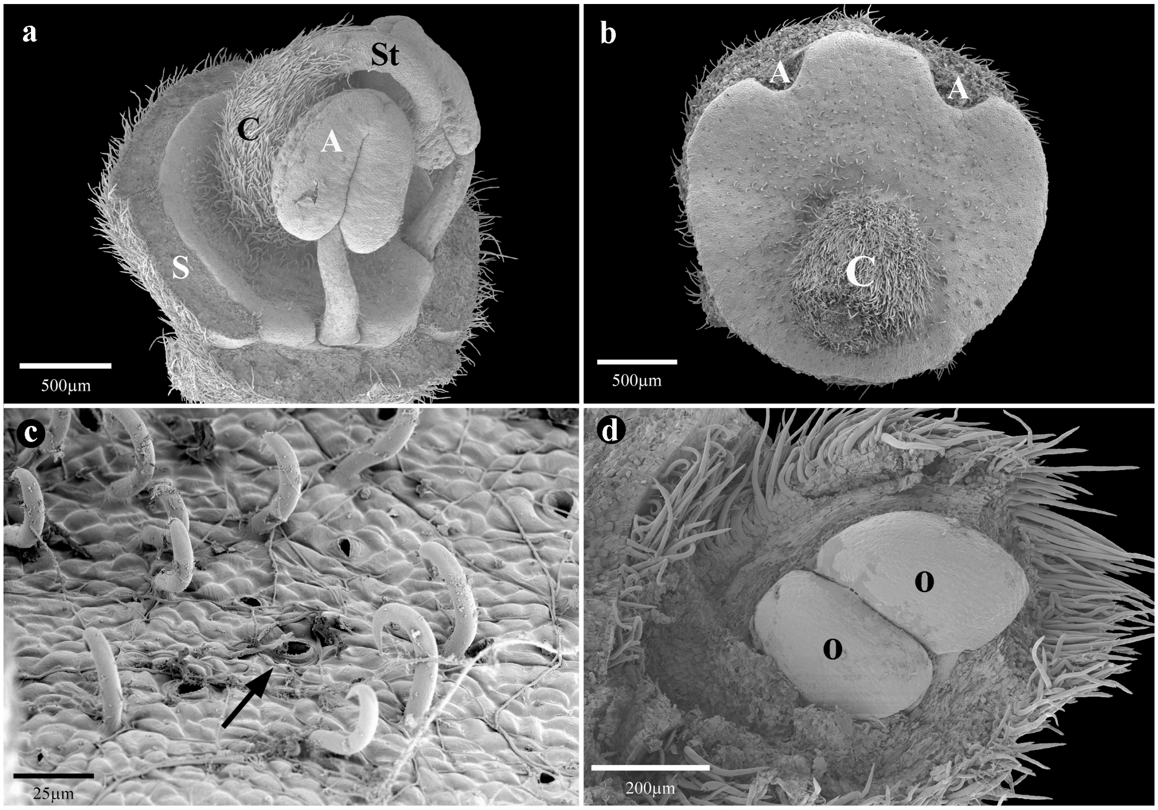

Fig. 3.6. SEM micrographs of *Dialium guianense*. a. Mature flower showing expanded, pubescent receptacle and sharp style curvature within the bud (sepals removed). b. Flat surface of the expanded receptacle (mature flower with calyx, androecium, and style removed). c. Detail of receptacle showing stomata (arrow) and hooked trichomes. d. Mature ovary opened to reveal two ovules. Voucher: Palacios 1364 (MO).

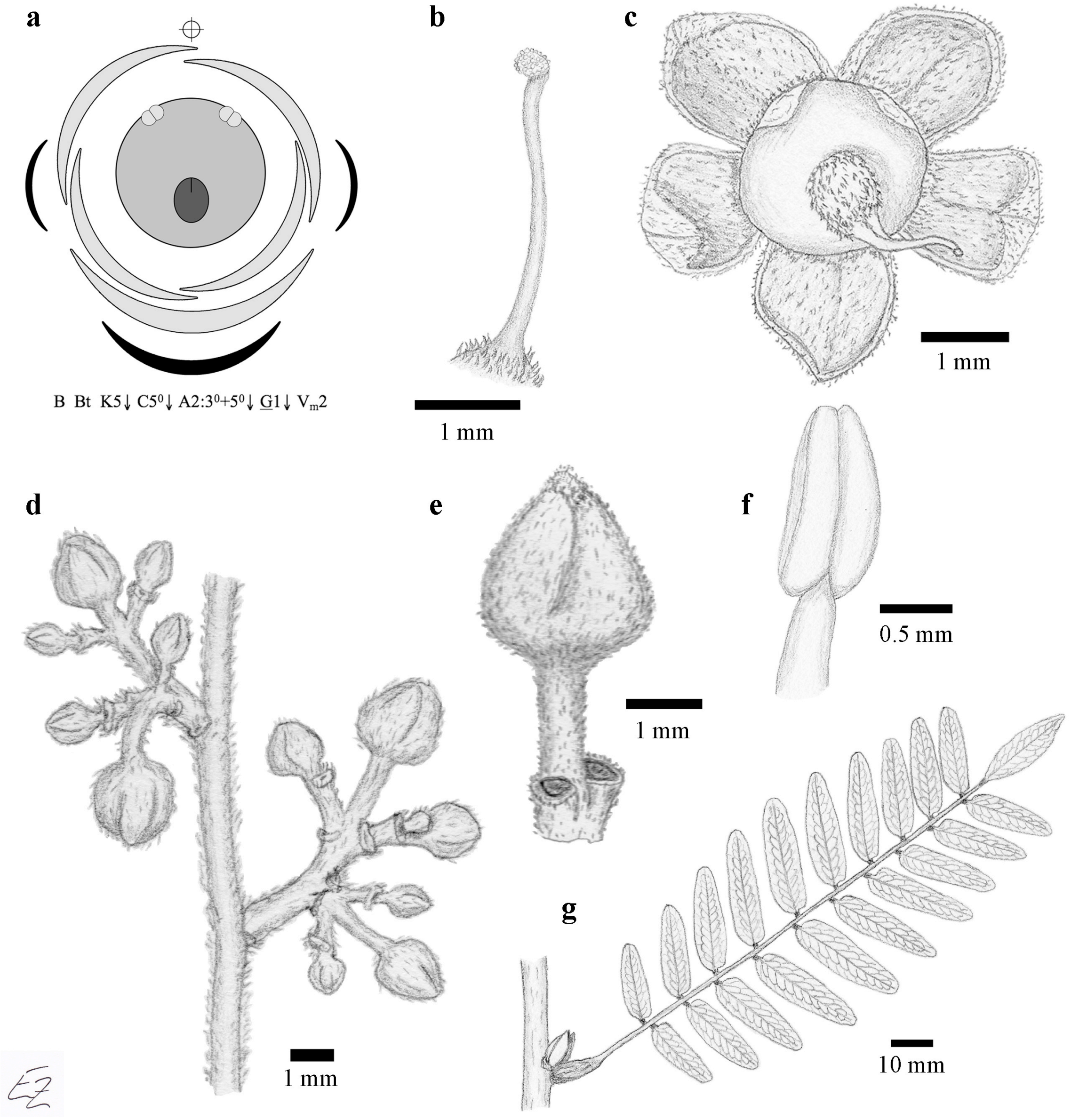

Fig. 3.7. Drawings and floral diagram of *Dialium dinklagei*. a. Floral diagram and formula. b. Detail of style and stigma. c. Post-anthesis flower; stamens have dehisced, leaving distinct scars. d. Section of inflorescence showing cymose units. e. Flower bud prior to anthesis. f. Detail of stamen. g. Compound leaf. Vouchers: b–c,e–f, Linder 68 (A); d, Morello *et al*. 1219 (MO); g, Versteegh & der Outer 258 (MO).

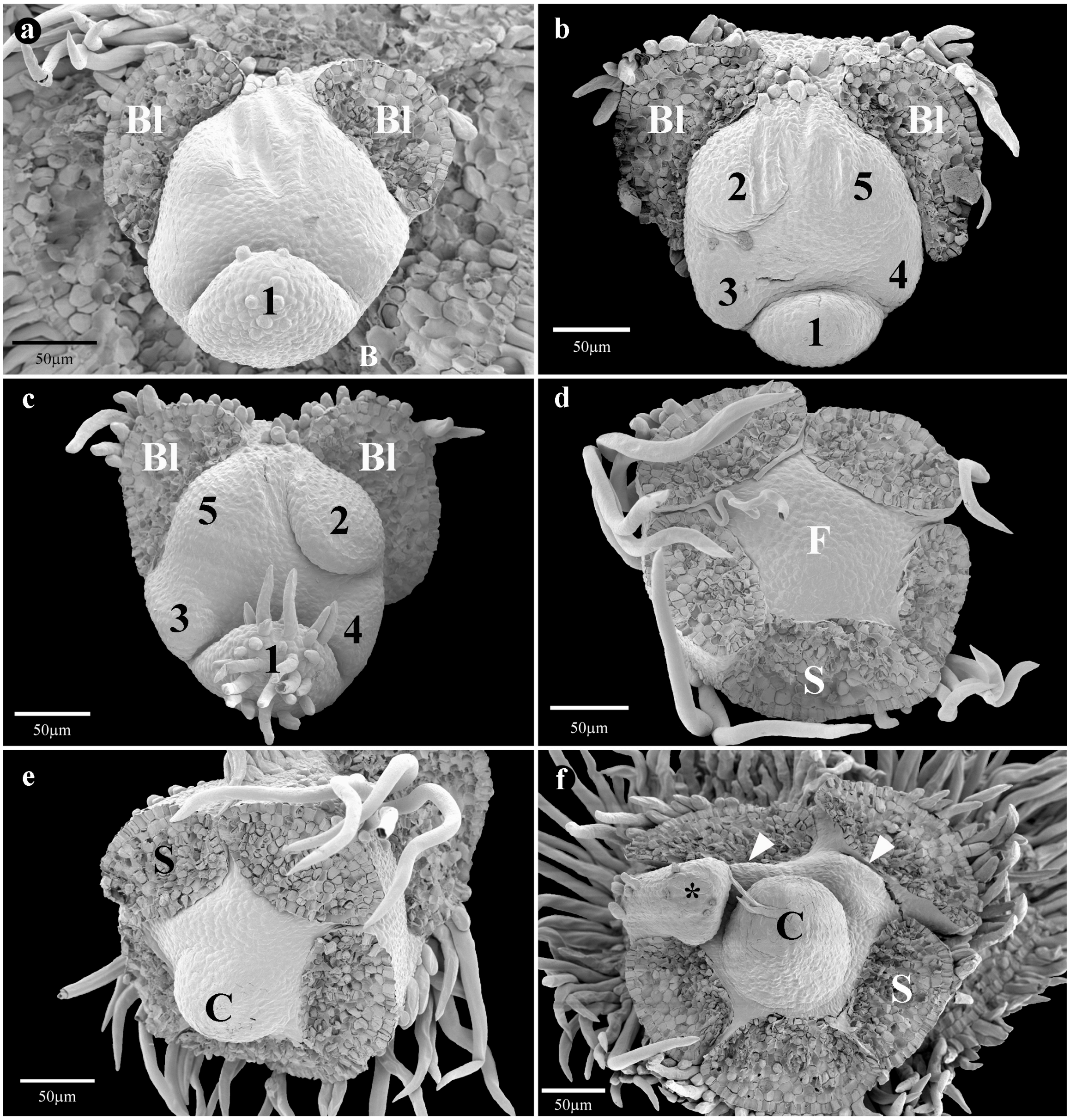

Fig. 3.8. SEM micrographs of *Dialium dinklagei*. a. Initiation of first sepal in abaxial median position. Trichome initials already apparent on outer surface of sepal. Bracteoles (removed) in adaxial lateral positions. b. Subsequent calyx development showing clockwise modified-helical initiation. Numbers indicate order of sepal initiation. c. Later calyx development showing elongation of trichomes on the first-initiated sepal. Here, sepal initiation is in an anticlockwise helix. Numbers indicate order of sepal initiation. d. Large, well-differentiated sepals removed to show the long lag prior to initiation of the inner whorls. e. A domelike carpel primordium is evident before stamens are initiated (calyx removed). f. Synchronous initiation of stamens in the adaxial lateral positions (arrowheads). It also shows an uncharacteristic sixth sepal in an adaxial lateral position (asterisk). Voucher: de Koning 6774 (MO).

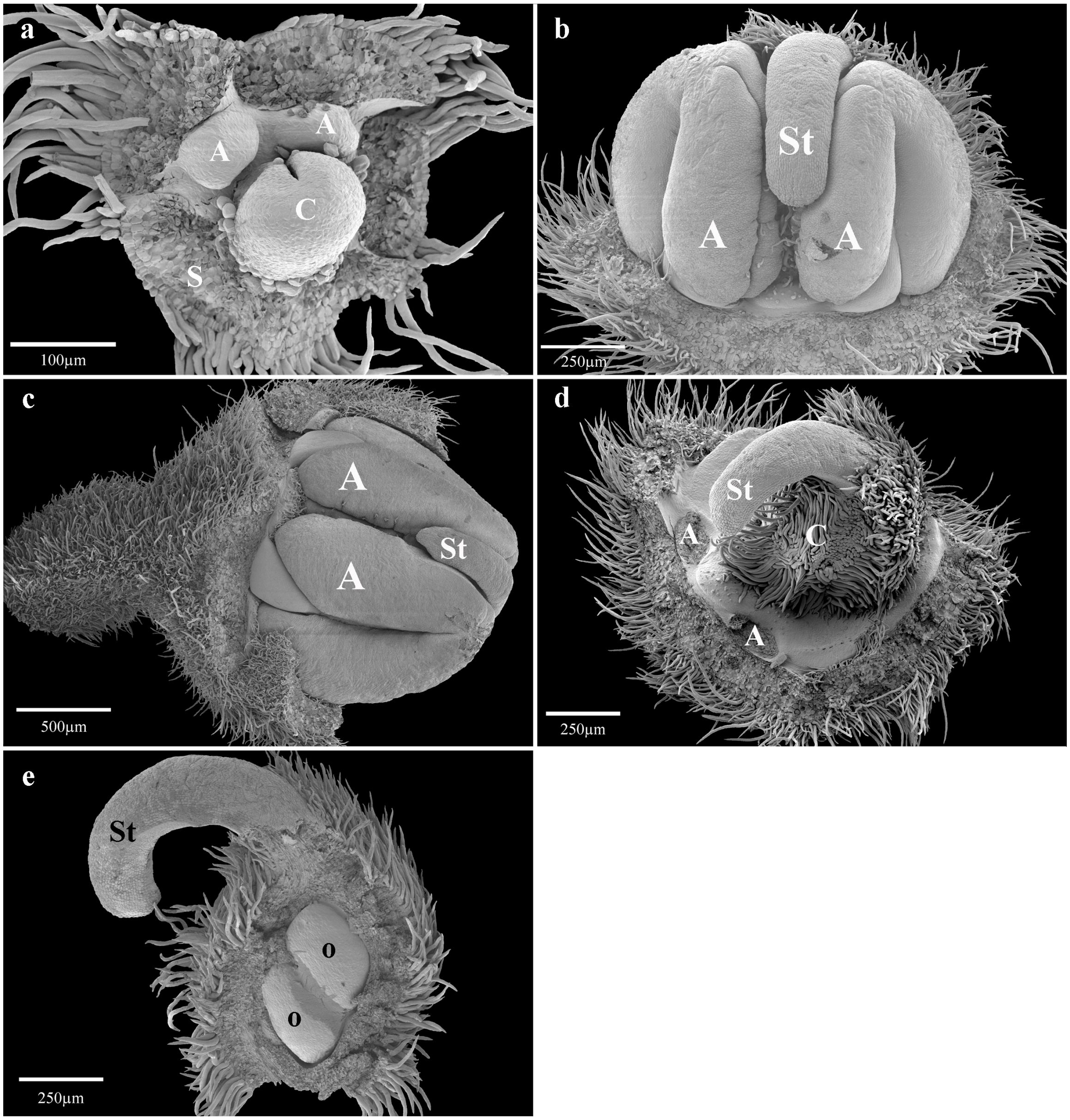

Fig. 3.9. SEM micrographs of *Dialium dinklagei*. a. Near-synchronous initiation of stamens in adaxial lateral positions. Carpel cleft is visible, as are trichomes at gynoecium base. b. Adaxial view on late stage showing sub-sessile anthers and sharply incurved style. c. Lateral view of the tightly packed stamens and gynoecium. d. Mature gynoecium with stamens removed to show the dense growth of trichomes covering the entire surface of the ovary. e. Mature ovary, opened to show two ovules. Voucher: de Koning 6774 (MO).

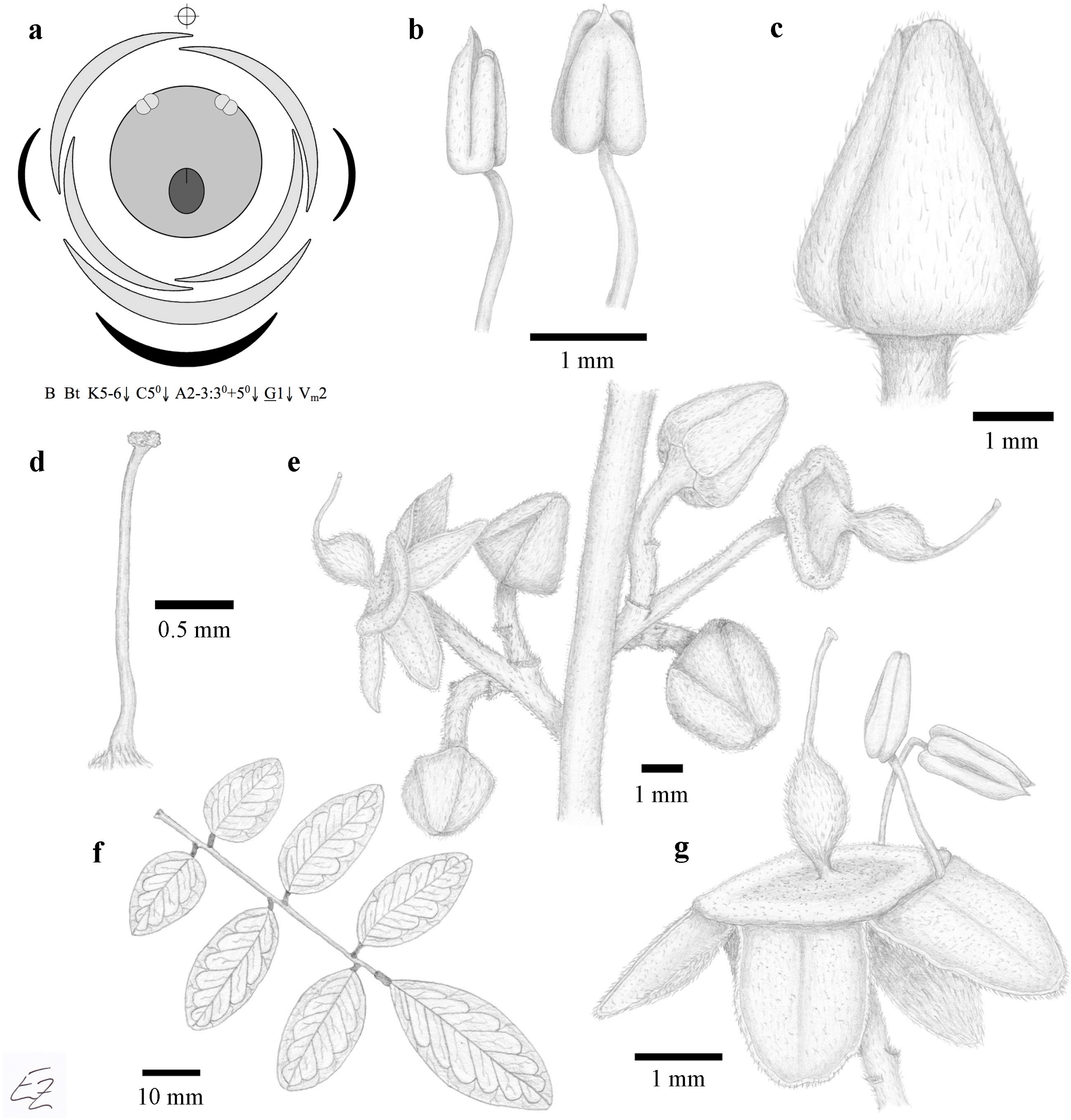

Fig. 3.10. Drawings and floral diagram of *Dialium orientale*. a. Floral diagram and formula. b. Detail of stamens. c. Flower bud prior to anthesis. d. Detail of style and stigma. e. Section of inflorescence showing cymose units. f. Compound leaf. g. Post-anthesis flower. Vouchers: b, Robertson 3716 (MO); c–g, Gillett 20357 (MO).

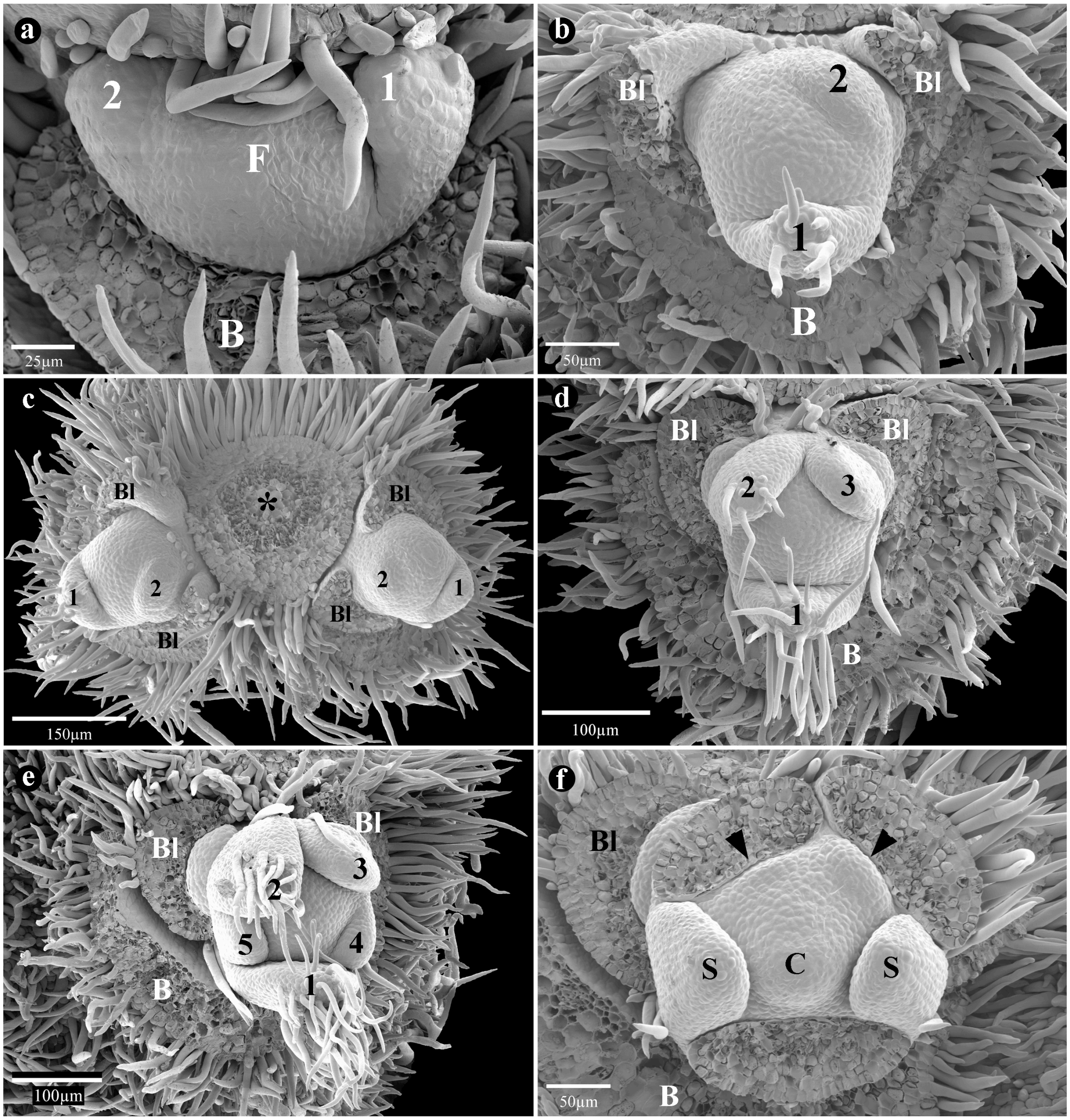

Fig. 3.11. SEM micrographs of *Dialium orientale*. a. Sequential initiation of bracteoles in a lateral flower (bract removed). b. Numbered initiation of first and second sepals in abaxial median and adaxial lateral positions, respectively. c. Adaxial view of cymose unit with central flower removed (asterisk). Initiation of first two sepals in lateral flowers (numbered) shows mirror symmetry across the central axis. d. Bidirectional initiation of first three sepals. e. Later bidirectional initiation of sepals showing all five organs. Dense trichome growth evident on abaxial sepal. f. Domelike carpel primordium and near-synchronous initiation of two stamen primordia (arrowheads). First three sepals removed. Voucher: ILC6-13 (JRAU).

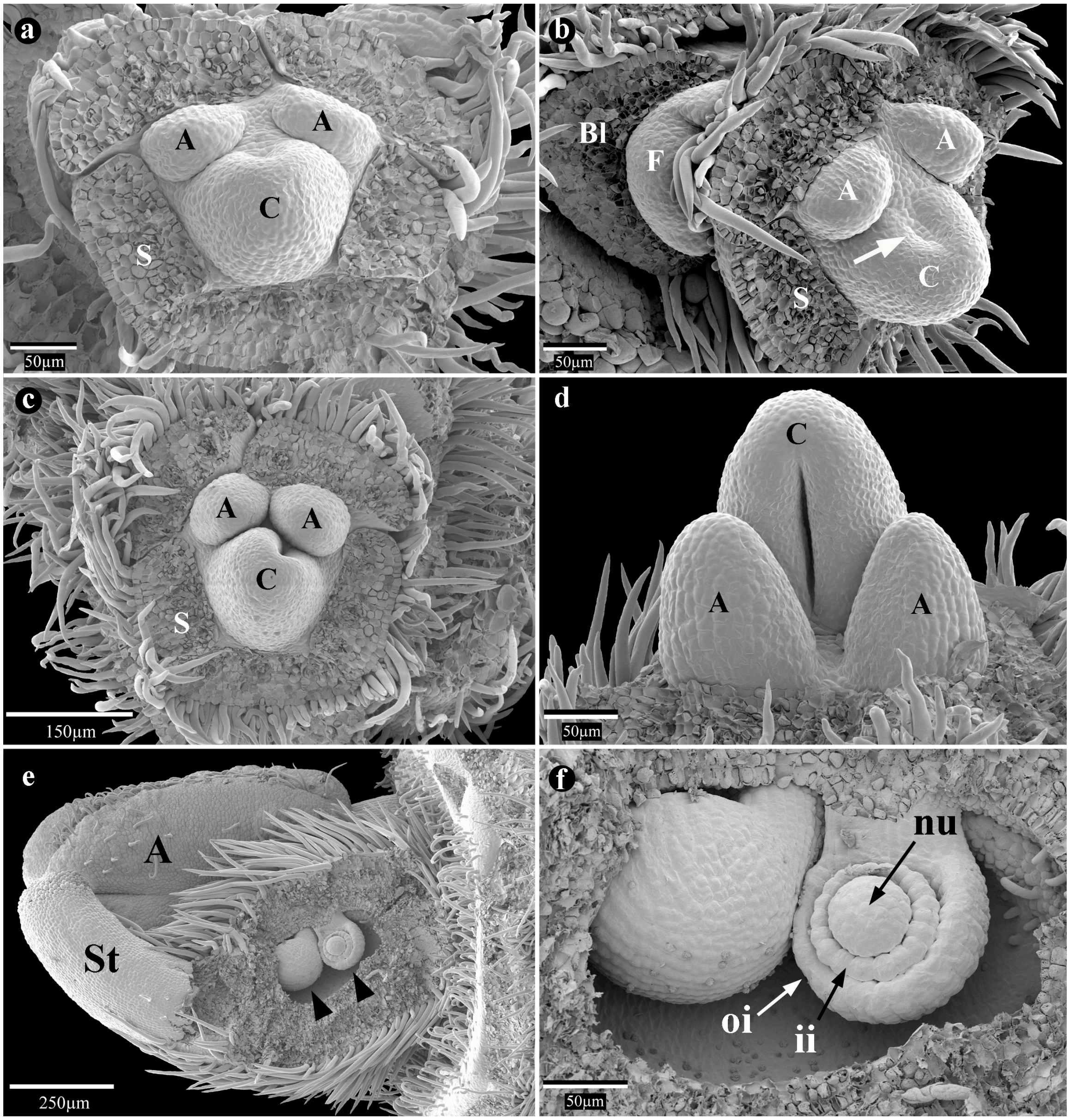

Fig. 3.12. SEM micrographs of *Dialium orientale*. a. Developing carpel and stamens showing carpel cleft aligned with median plane. Stamens are appressed to carpel prior to receptacle expansion. b. Adaxial view of (a) showing early infolding of carpel cleft (arrow). c. Flower in which carpel cleft has developed off-median, pointing directly at one of the stamens. d. Adaxial view of later, infolded carpel cleft, ± aligned with median plane. One stamen lags slightly behind the other in size. e. Opened ovary showing two ovules (arrowheads). f. Detail of developing ovules. Ovule on right with outer and inner integuments, not yet enclosing the central nucellus. Voucher: ILC6-13 (JRAU).

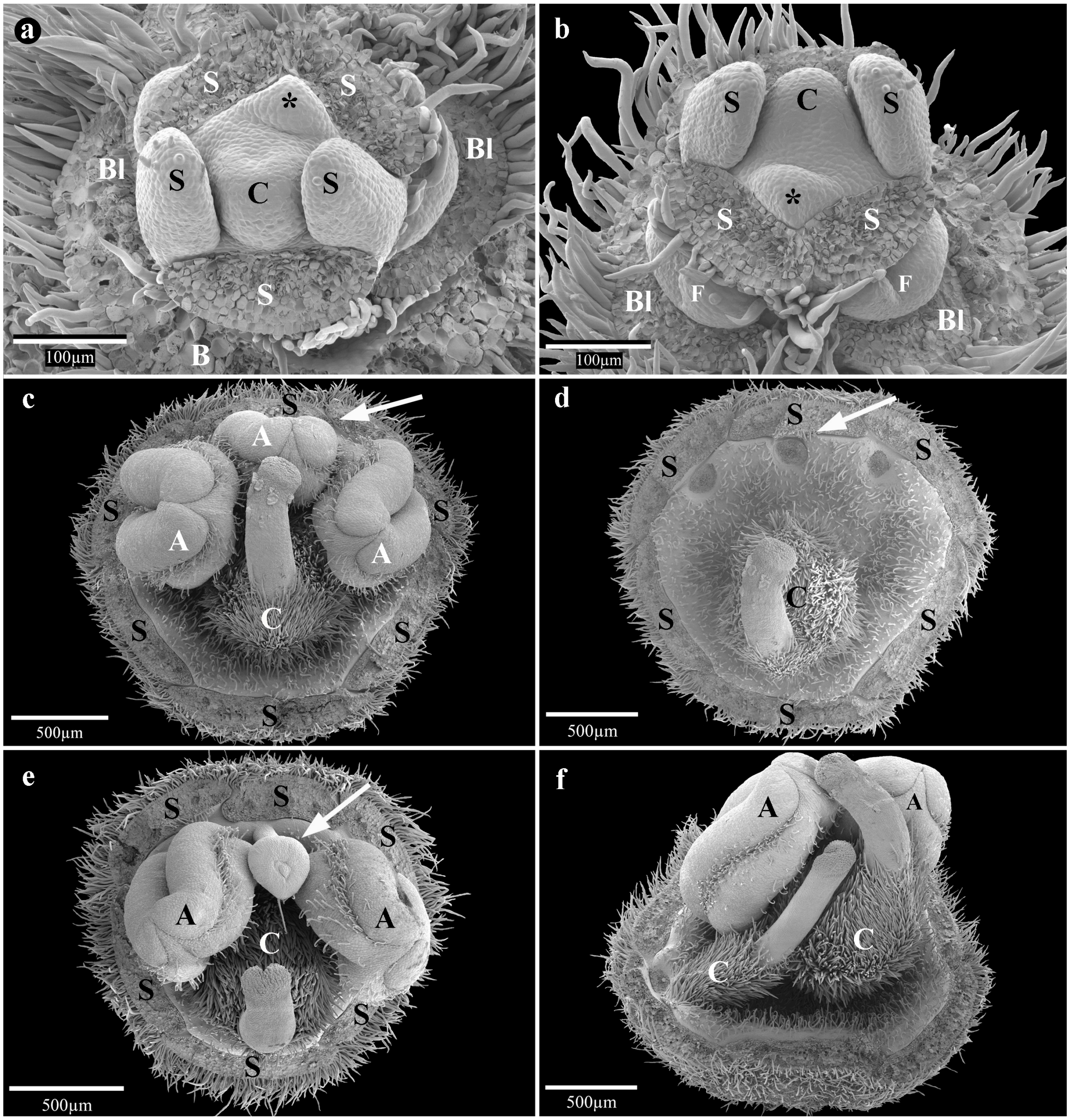

Fig. 3.13. SEM micrographs of *Dialium orientale*. a. Flower with late-developing sixth sepal in the adaxial median position (asterisk). Androecium has not yet begun to initiate. b. Adaxial view of (a). Sixth sepal is in close contact with the margins of the adaxial lateral sepals as it enlarges. c. Late stage bud with an additional stamen in the adaxial median position, equal in size to the lateral stamens. This flower also has a sixth sepal in the adaxial position (arrow). d. Flower from (c) with stamens removed, showing that the base of the third stamen (arrow) develops directly adjacent to the sixth sepal. e. Another flower with six sepals. A staminode has developed adjacent to the adaxial sepal (arrow). f. A flower which has developed an additional, smaller carpel in a lateral position. Voucher: ILC6-13 (JRAU).

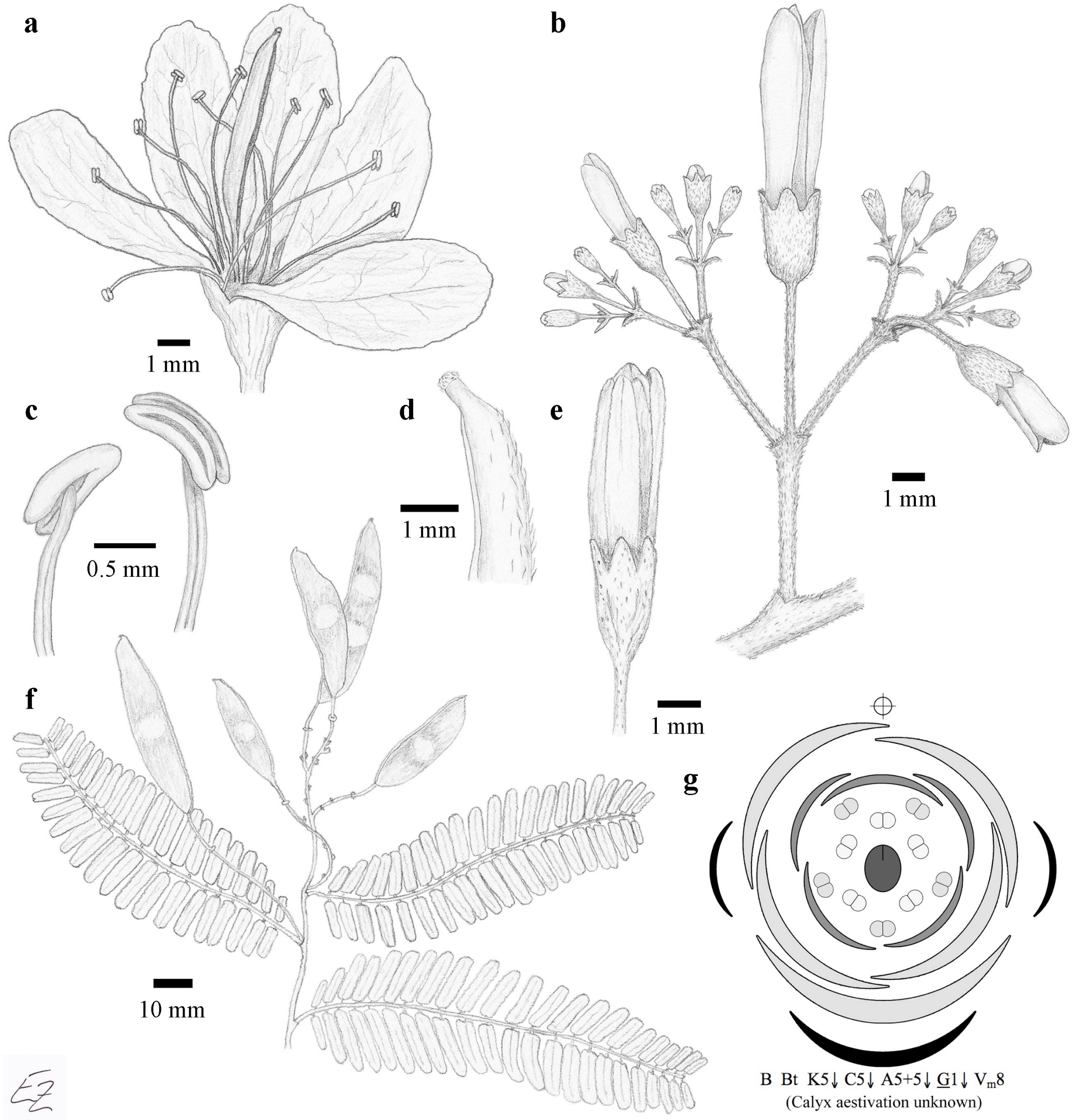

Fig. 3.14. Drawings and floral diagram of *Poeppigia procera*. a. Flower at anthesis. b. Section of inflorescence showing cymose units. c. Detail of stamens showing dorsifixed anthers and longitudinal dehiscence. d. Detail of sub-sessile stigma. e. Detail of flower just prior to anthesis. f. Compound leaves with axillary and terminal infructescences. g. Floral diagram and formula. Vouchers: a, c–e, Molina & Molina 12572 (US); b, G. Davidse et al. 18383 (MO); f, Hernández 2358 (MO).

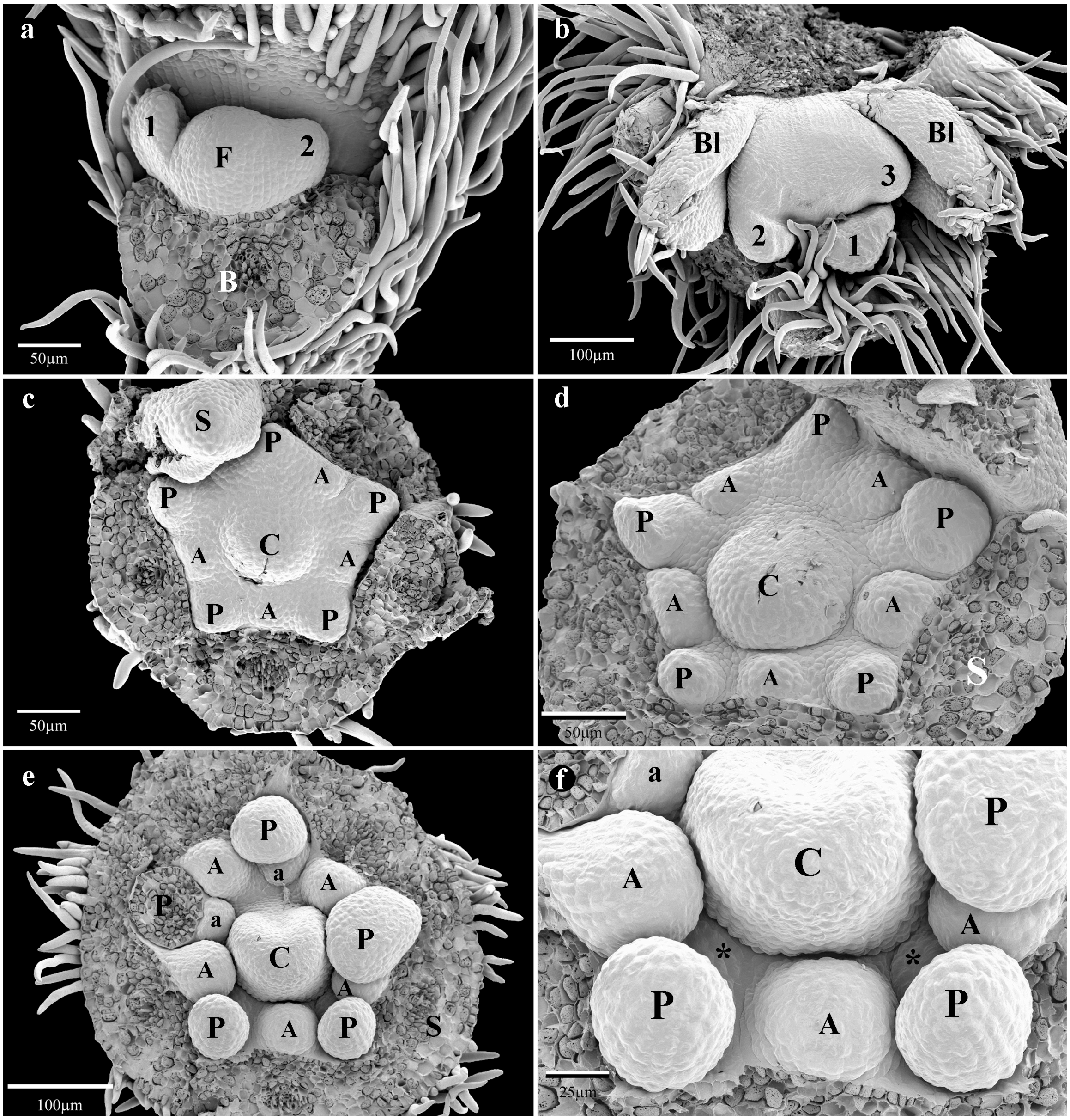

Fig. 3.15. SEM micrographs of *Poeppigia procera*. a. Early lateral flower primordium in the axil of a bract (removed) with successive developing bracteoles. b. Unidirectional sepal development beginning abaxially. The first sepal is slightly displaced from the median. Numbers indicate order of sepal initiation. c. Synchronous petal development (calyx removed). A dome-shaped carpel primordium is evident. Antesepalous stamen primordia are just becoming visible. d. Near-synchronous development of the corolla and antesepalous stamens. Adaxial lateral petals are slightly larger than the rest of their whorl, as are abaxial lateral stamens. Stamens lag behind petals and carpel. e. Antepetalous stamen development, showing a tendency to delay abaxial development in this whorl. Adaxial antepetalous stamen is slightly off the median plane. f. Detail of (e), showing delayed initiation of abaxial lateral stamens in the antepetalous whorl (asterisks). Voucher: Lewis & Pearson 1125 (K).

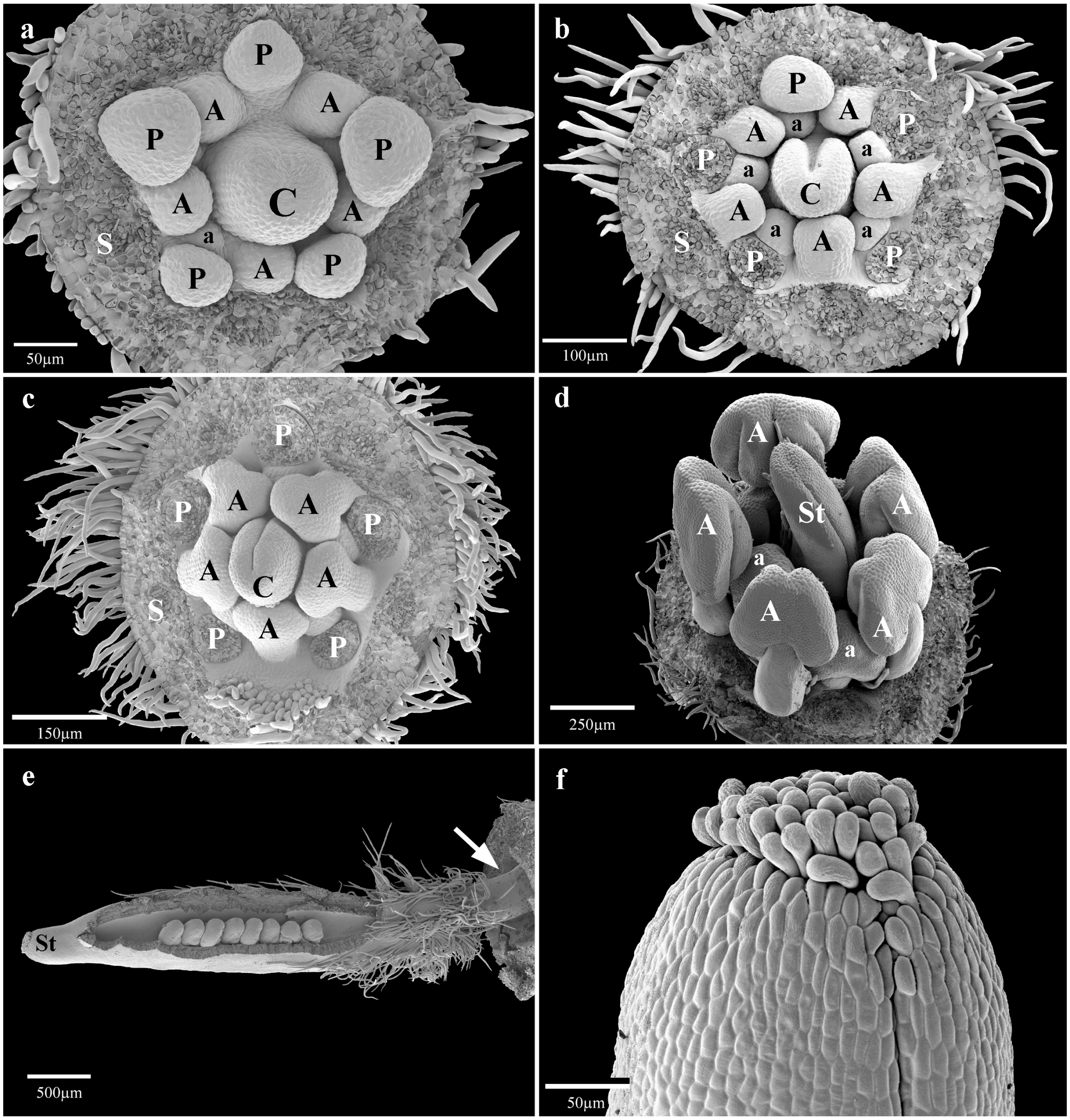

Fig. 3.16. SEM micrographs of *Poeppigia procera*. a. Development of inner whorls, showing adaxial lateral petals which are larger than the rest of the corolla (calyx removed). Carpel cleft is barely visible on adaxial side. b. Synchronous development of antepetalous stamen whorl, lagging slightly behind outer stamens. Adaxial stamen of inner whorl slightly off median plane. Carpel cleft open and evident, also pointing slightly to the right of the median plane. c. Anther differentiation in the outer stamen whorl and a closing of the carpel cleft. Inner stamen whorl (not visible) remains relatively small. d. Later anther differentiation and development of the sub-sessile stigma as the carpel lengthens. e. Mature ovary opened to show eight ovules with marginal placentation. The small size of the stigmatic area is apparent, as is a distinct stipe (arrow) at the base of the ovary. f. Detail of stigmatic surface. Voucher: Lewis & Pearson 1125 (K).

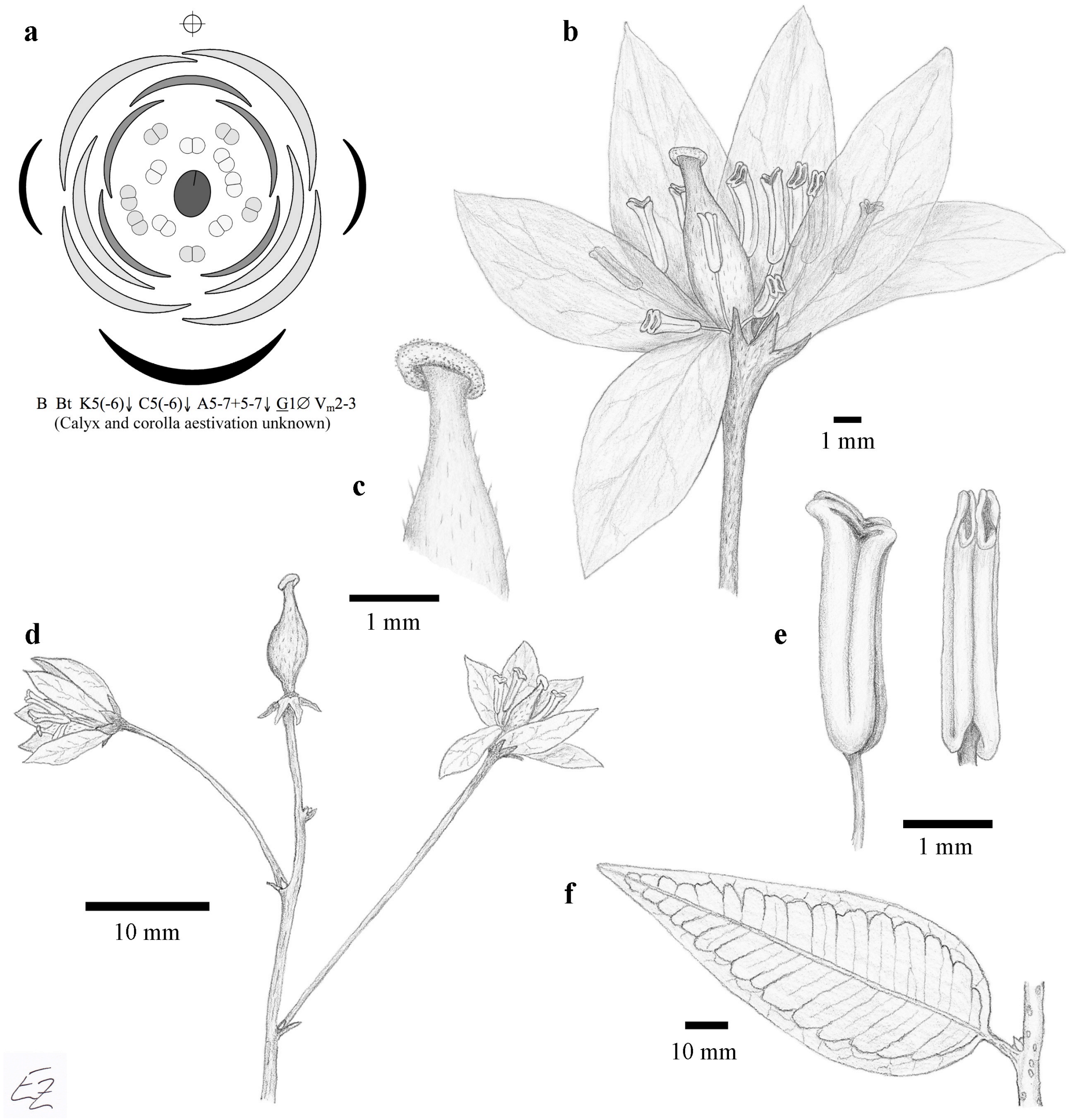

Fig. 3.17. Drawings and floral diagram of *Mendoravia dumaziana*. a. Floral diagram and formula. b. Flower at anthesis. c. Detail of stigma and short style. d. Whole inflorescence. e. Detail of stamens showing poricidal dehiscence. f. Simple leaf. Voucher: Capuron SF28343 (MO).

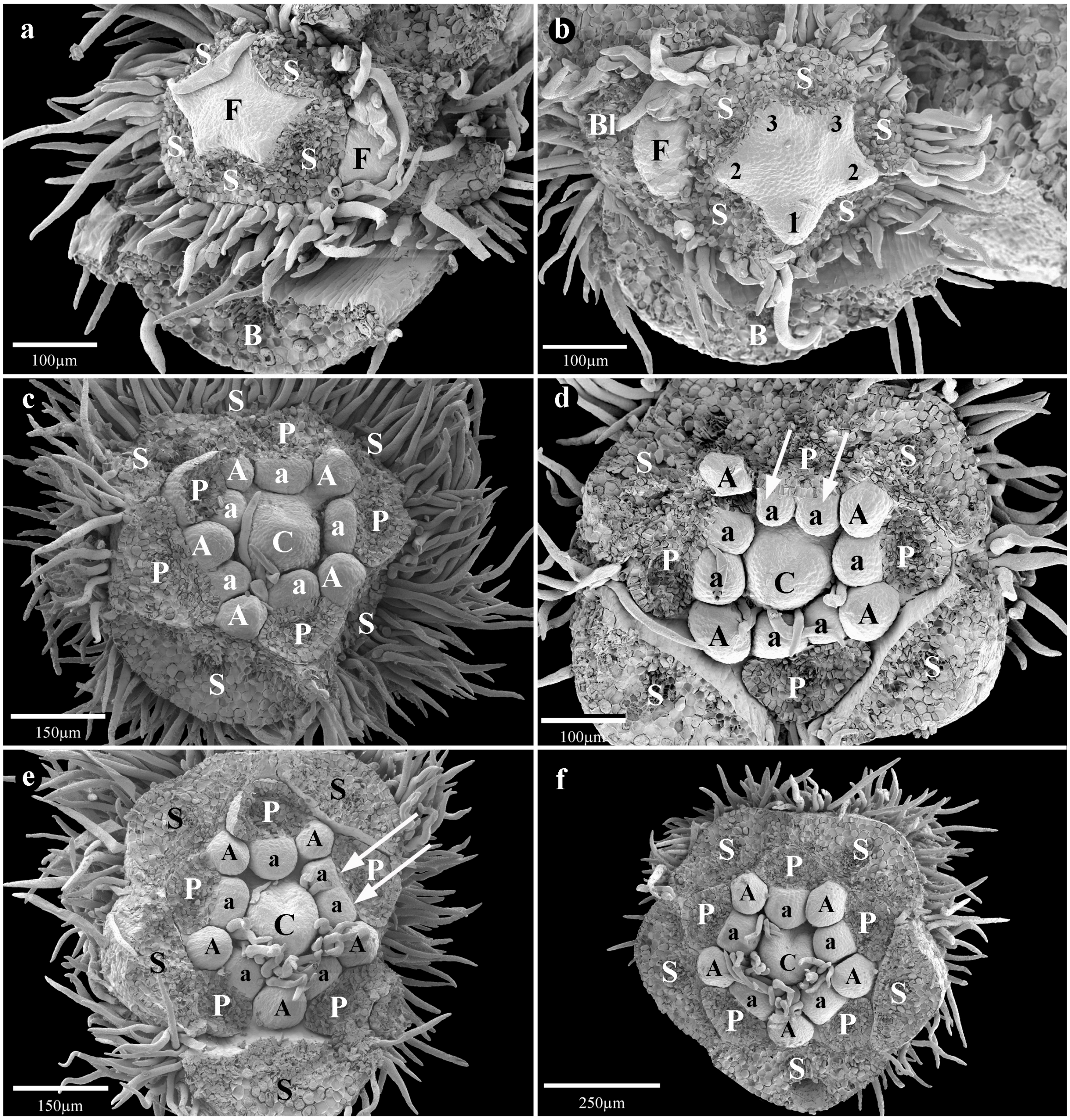

Fig. 3.18. SEM micrographs of *Mendoravia dumaziana*. a. Five-sided, undifferentiated floral apex with the already closed calyx removed, demonstrating very early sepal development relative to the inner whorls. b. Unidirectional corolla initiation (numbered), showing a five-sided meristem with, the first petal in the abaxial median position ("upside-down", *c.f.* orientation in (a)). c. Developing stamen primordia, showing the somewhat disordered arrangement of organs (calyx and corolla removed). Dome-like carpel primordium visible at centre. d. Disordered arrangement of the developing androecium, with an apparent duplication of one of the inner, adaxial stamens (arrows; calyx and corolla removed). e. Androecium development, showing an apparent duplication of the adaxial lateral stamen of the antepetalous whorl (arrows) for a total of 11 stamens (calyx and corolla removed). Early cleft formation visible on the adaxial surface of the gynoecium. f. Synchronous development of outer stamen whorl, followed by inner stamen whorl, with trichome growth among primordia (calyx and corolla removed). Carpel cleft is visible and slightly off median, pointing to the right. Voucher: McWhirter 212 (K).

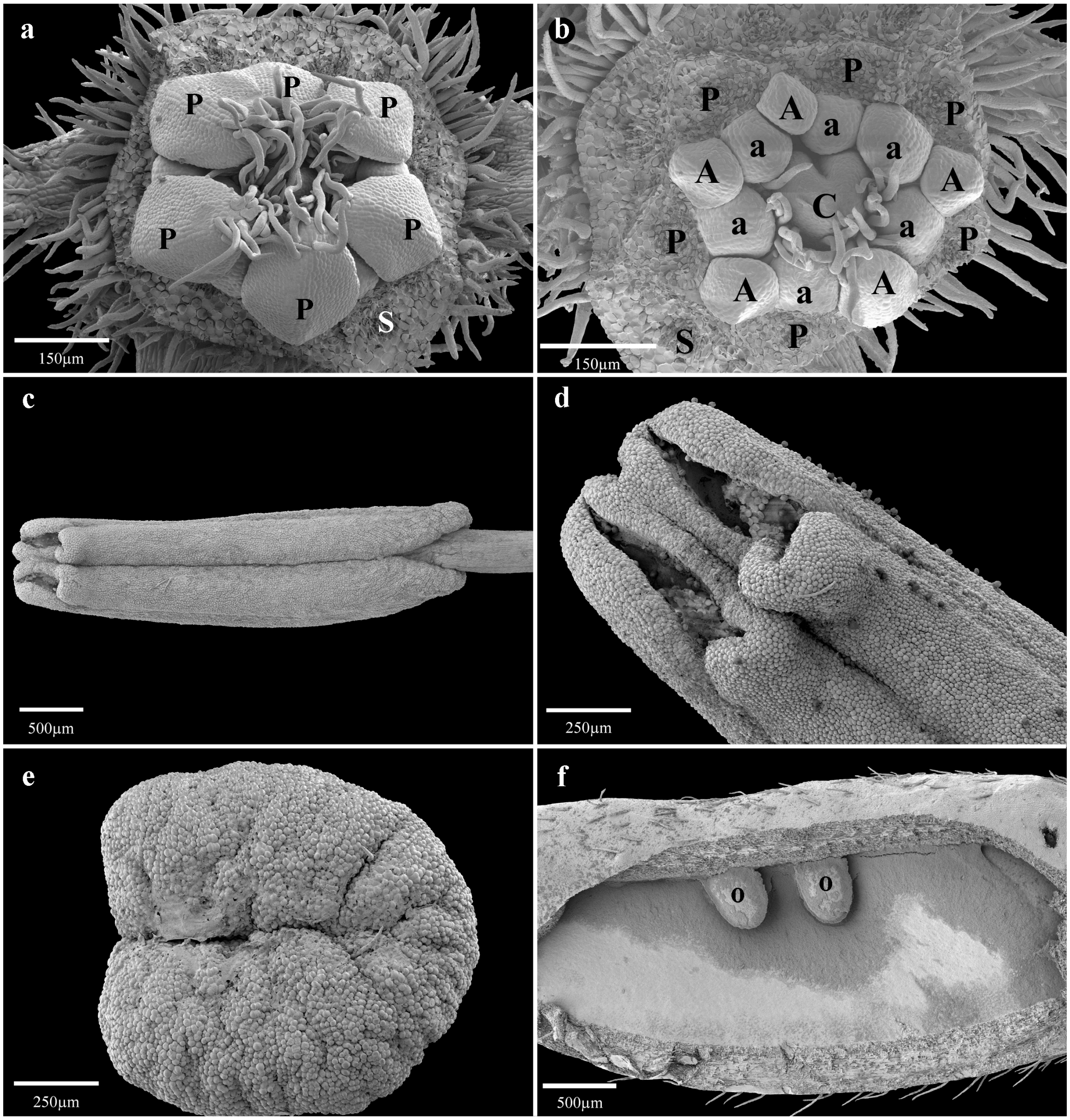

Fig. 3.19. SEM micrographs of *Mendoravia dumaziana*. a. Six-part corolla closing over inner whorls as trichomes grow from their outer surfaces near the apices, as well as from within the interior (calyx removed). b. Androecium development, showing an additional antepetalous stamen in the adaxial lateral position, as well as an additional petal located adjacent to it. Carpel cleft is shifted off the median plane, toward these additional organs. c. Mature stamen, showing sagittate anther base and slightly introrse poricidal dehiscence. d. Detail of anther opening and emerging pollen grains. e. Surface detail of peltate stigma. f. Opened mature ovary showing two ovules with marginal placentation. Voucher: McWhirter 212 (K).

Floral morphology of *Apuleia leiocarpa* (Dialiinae: Leguminosae), an unusual andromonoecious legume

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Chapter 4 – Floral morphology of *Apuleia leiocarpa* (Dialiinae: Leguminosae), an unusual andromonoecious legume

4.0 Abstract

Apuleia leiocarpa (Vogel) J. F. Macbr. is a South American tree species belonging to the caesalpinioid subfamily of the Leguminosae. Phylogenetic analyses have placed *Apuleia* into the Dialiinae *s.l.* clade, with which it shares numerous morphological similarities, including dichasial cymose inflorescences. The genus has also been reported to be andromonoecious, a trait not seen elsewhere in its clade and only infrequently in the Caesalpinioideae. Scanning electron microscopy and stereomicroscopy were used to investigate the floral morphology of *A. leiocarpa*. It was found that while hermaphrodite flowers produced a single carpel and two stamens, staminate flowers developed three stamens but showed no signs of any carpel development. The third stamen fills the volume of the missing carpel within the bud as it grows. Inflorescences also appear to produce approximately four times as many staminate as hermaphrodite flowers. Both this high male-to-bisexual ratio and the early determination of gender seen in *Apuleia* are rare in the Caesalpinioideae and suggest that andromonoecy developed in this genus as a means to increase pollen dispersal rather than in response to resource limitations.

Keywords: Apuleia, Dialiinae, Caesalpinioideae, Leguminosae, floral morphology, andromonoecy, trimery

4.1 Introduction

Apuleia leiocarpa (Vogel) J. F. Macbr. is an andromonoecious South American tree species belonging to the caesalpinioid subfamily of the Leguminosae. Caesalpinioideae possesses the greatest floral morphological diversity of the three legume subfamilies (Lewis et al., 2000), comprising taxa with both actinomorphic and zygomorphic flowers, as well as, particularly within tribe Cassieae, drastic reductions in floral organ number (Tucker 1988b, 1998). This subfamily, which has been described as the most ‘‘taxonomically problematic’’ of the three (Gasson et al., 2003), contains numerous taxa that have not yet been studied in detail but that may provide clues to floral evolution in the Leguminosae. *Apuleia leiocarpa* is one such taxon.

The only member of its genus according to a recent revision (de Sousa et al., 2010), *A. leiocarpa* has been placed by phylogenetic analyses into the Dialiinae *s.l.* clade (Doyle et al., 1997; Kajita et al., 2001; Lewis, 2005; Bruneau et al., 2008). Dialiinae *s.l.* is made up of the Cassieae subtribes Dialiinae and Labicheinae, the latter comprising the Australian genera *Labichea* Gaud. ex DC and *Petalostylis* R. Br. The clade is united by its cymose inflorescences (except in Labicheinae), wood lacking in vestured pits, and greatly decreased floral organ numbers—all uncommon features in the Caesalpinioideae as a whole.

The precise position of *Apuleia* within Dialiinae *s.l.* remains uncertain (Bruneau et al. 2008), but the phylogenetic analysis of Bruneau et al. (2008), based on *matK* exon plus *39-trnK* and *trnL* intron sequences, placed *Apuleia* and *Distemonanthus* as sister groups with a high degree of confidence. Koeppen (1978) also suggested a close relationship between *Apuleia* and the monospecific West African genus *Distemonanthus* Benth. based on similarities in wood anatomy, specifically, in the presence and deposition of silica bodies. Indeed, Koeppen (1978) goes on to note that there are morphological similarities in the leaves, flowers, and fruits of the two species but does not expand on this observation.

Andromonoecy, the form of sex expression seen in the genus *Apuleia* (Kalin Arroyo, 1981), which produces both staminate and hermaphrodite flowers, is otherwise unknown in the Dialiinae and rare among legumes. It has been found in *circa* 4000 species of flowering plants belonging to at least 33 families and appears to have evolved independently numerous times (Miller and Diggle, 2003). In some species, andromonoecy is brought about by a late-stage suppression of the gynoecium; the organ is formed but ceases growth prior to maturity and appears stunted or underdeveloped at anthesis (Beavon and Chapman, 2011). In other species, however, the female organs are simply not initiated (Tucker, 1991). No mention is made in the literature as to which of these staminate flower morphologies is seen in *Apuleia*.

Here, flowers were dissected and observed using a stereomicroscope and scanning electron microscopy (SEM) to examine in detail the floral morphology of *A. leiocarpa*. A comparison is made with other andromonoecious caesalpinioid legumes, and some of the functional implications of sex expression in the genus are discussed. Similarities and differences with the Dialiinae clade as a whole are also explored.

4.2 Materials and Methods

For SEM, flowers were dissected in 70% ethanol and critical-point dried using an Autosamdri-815B critical-point dryer (Tousimis Research, Rockville, MD). Dried material was then mounted onto specimen stubs using clear nail polish, coated with platinum using an Emitech K550 sputter-coater (Emitech, Ashford, UK), and examined using a Hitachi cold-field emission SEM S-4700-II (Hitachi High Technologies, Tokyo). All SEM work was carried out at the Royal Botanic Gardens, Kew. SEM images were edited using Adobe Photoshop CS5. Floral diagrams and formulas were developed following recommendations by Prenner et al. (2010).

Specimens examined under the stereomicroscope were removed from herbarium vouchers and rehydrated in boiling water with a small amount of surfactant and then dehydrated through an ethanol series to 80% ethanol, in which they were dissected and observed using a binocular dissecting microscope (Wild Heerbrugg). These dissections were then used to produce the illustrations used in figure 4.1.

Specimens examined were as follows: G.C.G. Argent 6657, State of Mato Grosso, Amarelao, Brazil, 1968 (MO); P. Fragomemi 11642, Rio Grande do Sul, Brazil, 1968 (MO); R.M. Harley & R. Souza 10720, State of Mato Grosso, Brazil, 1969 (K); Heringer et al. 5426, Bacia do Rio Sao Bartolmeu, fr., Brazil, 1980 (K); B.B. Klitgaard & F.C.P. Garcia 66, State of Bahia, Brazil, 1994 (MO); Pennington and Rowe 172, Pando, Puerto Oro, Bolivia, 1988 (MO); A.G. Ruiz 217-AGR, Loreto, Maynas Province, Peru, 1965 (MO); Sant'Ana *et al*. 361, State of Bahia, Brazil, 1993 (MO); R. Vasquez, R. Ortiz and N. Jaramillo 14369, Loreto, Maynas Province, Peru, 1990 (MO); J.L. Zarucchi & C.E. Barbosa 3739, Vichada, Colombia, 1985 (MO).

4.3 Results

The bisexual flowers of *Apuleia leiocarpa* tend to occupy the central (terminal) position in a compound dichasium, as well as some of the central positions in higher-order cymes, while the younger lateral flowers are staminate (fig. 4.1a). The more flowers present on an inflorescence, the more likely the occurrence of multiple bisexual flowers. Figure 4.1a represents a smaller but common inflorescence size.

Phyllomes subtending the central flower are early caducous, leaving visible scars (fig. 4.1a), while those occurring on lateral flowers are minute and ephemeral. On mature inflorescences, the scars, which occur on the lower portion of the pedicel, are very difficult to discern and are therefore not illustrated in figure 4.1a but are shown in the floral diagram (fig. 4.1b).

4.3.1 Bisexual Flowers (Figs. 4.1, 4.2)

Both floral morphs possess a trimerous calyx and corolla (fig. 4.1b, 4.1c). In bisexual flowers, the inner whorls consist of a single pistil and two stamens in the adaxial lateral positions, opposite the adaxial lateral sepals, although additional pistils and stamens are occasionally present (figs. 4.1c, 4.1d, 4.2a). A longitudinal section of a hermaphrodite flower shows that the gynoecium, which consists of a single carpel, is stipitate and arises from the base of a narrow, tubular hypanthium (fig. 4.2b–4.2d), while the perianth and androecium arise from the rim of the hypanthium (fig. 4.3c). The carpel encloses up to four narrow, elongated ovules (fig. 4.2b), which are attached with a short funicle to the ovary wall (fig. 4.2e). The stigma is peltate and covered with short papillae (fig. 4.2f).

4.3.2 Staminate Flowers (Figs. 4.1, 4.3)

Staminate flowers of *A. leiocarpa* do not appear to develop either a functional or a vestigial gynoecium. Three stamens (rarely four) develop on the rim of the hypanthium, with the third stamen occupying the volume taken up by the gynoecium in the hermaphrodite flower (fig. 4.1b, 4.3a, 4.3c, 4.3d). At the center of the floral surface, a trichome-filled triangular opening leads to the sunken hypanthium (fig. 4.3c, 4.3e), although in some flowers, this develops merely as a three-pointed slit (fig. 4.2d). In cross section, the hypanthium appears to be compressed into three nearly separate chambers (fig. 4.3e); no tissue resembling a suppressed gynoecium is apparent. Anthers dehisce with longitudinal slits (fig. 4.3b) and release tricolporate pollen grains with microreticulate surfaces (fig. 4.3f). The adaxial surface of the anthers is covered with characteristic hooked trichomes (fig. 4.3g).

4.4 Discussion

4.4.1 Morphology in relation to the Dialiinae Clade

The basic legume flower is thought to be built on a ground plan of a pentamerous calyx and corolla, two pentamerous whorls of stamens, and a unicarpellate gynoecium, for a total of 21 floral organs (Tucker 2003). The subfamily Caesalpinioideae, which forms a basal grade in the Leguminosae, and in particular the tribe Cassieae, shows the greatest and most frequent deviation from this ground plan, both via organ suppression and, less frequently, complete loss (Tucker 2003; Prenner and Klitgaard 2008). The Dialiinae *s.l.* clade (Bruneau et al. 2001), which is composed of the two Cassieae subtribes Dialiinae and Labicheinae of Irwin and Barneby (1981) plus the genus *Poeppigia* C. Presl., displays high levels of organ loss, particularly in the androecium. Several species of the genus *Dialium* L., e.g., possess only eight organs: five sepals, two stamens, and a carpel. While *Dialium* represents an extreme, very few species in the clade retain a full set of antepetalous stamens, the vast majority having lost this whorl entirely.

Apuleia leiocarpa, with its nine remaining organs, seems to share this characteristic of the clade. Occasionally, a second carpel, with or without additional stamens, is present (fig. 4.1d), a phenomenon noted in certain other caesalpinioid genera, such as *Bauhinia* L. (Tucker 1988a), *Ceratonia* L. (Tucker, 1992), and *Dialium* (Chakravarty 1969). While a unicarpellate bisexual flower bearing three stamens has been illustrated in Irwin and Barneby's (1981) revision of Cassieae, this state has not been observed in the many flowers dissected for the purposes of this study and may have represented an atypical individual.

In addition to the extensive organ loss of *A. leiocarpa*, several other aspects of its floral morphology link it to the Dialiinae *s.l.* (E. Zimmerman, unpublished data). The small, nonshowy flowers have erect, basifixed anthers, traits seen consistently in this group. Like most of the clade, the outer calyx surface and the carpel of *A. leiocarpa* are densely covered in trichomes (fig. 4.3a). The adaxial surfaces of the stamen filaments are also covered in the distinctive hooked trichomes typical of *Dialium* and several other genera of the Dialiinae (fig. 4.3g).

Apuleia is unique within the Dialiinae *s.l.* in that it is the only taxon within the clade displaying trimery of the calyx, corolla, and androecium (E. Zimmerman, unpublished data). While several species of the genus *Dialium* possess trimerous outer whorls, none are entirely three parted; the majority of *Dialium* species maintain a typically leguminous five-parted calyx. The genus *Distemonanthus*, to which *Apuleia* has been linked based on molecular data (Bruneau et al. 2008), shares its three-part corolla and tubular hypanthium but has a five-parted calyx and androecium (including three staminodes). In fact, only one other genus in the Caesalpinioideae, *Gleditsia* L., produces flowers trimerous in all three of the outer whorls (Endress, 1996). Interestingly, in *Gleditsia*, as in *Apuleia*, this arrangement is seen only in the staminate flowers of an andromonoecious species, *Gleditsia triacanthos* L. (Tucker, 1991). This curious link between trimery and andromonoecy is unlikely to be more than coincidence, however, as *Gleditsia* belongs to the Umtiza clade of tribe Caesalpinieae and is not closely related to the Dialiinae (Bruneau et al. 2008). In addition, *G. triacanthos* is known to produce tetramerous and pentamerous flowers (Tucker 1991), which does not occur in *Apuleia*.

4.4.2 Andromonoecy in Apuleia

The second unusual aspect of floral morphology in *A. leiocarpa* is its andromonoecious inflorescence. Although this phenomenon occurs in a small number of species within the Caesalpinioideae, notably, in the genera *Caesalpinia* L., *Anthonotha* P. Beauv., and *Bauhinia* (Ramirez et al., 1984; Bullock, 1985; Tucker, 1988a; Hokche and Ramirez, 1990; Lewis and Gibbs, 1999), it is not seen elsewhere in the Dialiinae. The form of andromonoecy would seem to differ as well; in other caesalpinioids, unisexual flowers typically begin development uniformly bisexual, only later becoming functionally male as gynoecial development is suppressed just before anthesis, often in response to fruit set elsewhere on the inflorescence (Tucker, 1988a, 1992; Gibbs et al., 1999). This phenomenon has also been noted in the andromonoecious mimosoid taxon *Calliandra angustifolia*, which produces staminate flowers containing reduced carpels as a result of suppression late in ontogeny (Prenner, 2004c).

In an ontogenetic study of the dioecious caesalpinioid tree *Ceratonia siliqua* L., which had previously been reported to be the only legume forming unisexual flowers at inception (Thompson, 1925, 1944), Tucker (1992) found that early development in all floral morphs (staminate, pistillate, and hermaphrodite) was identical. Only after both stamens and carpel had been initiated and the carpel had formed a full-length cleft did gynoecial development cease. However, Tucker (1991) noted, for example, that in some staminate flowers of *G. triacanthos*—specifically, the trimerous ones—the gynoecium sometimes completely fails to initiate. In male flowers of *Apuleia*, the gynoecium does not appear to develop at all, and its volume within the bud is occupied by another organ, the third stamen. This suggests that unlike most other andromonoecious caesalpinioids, gender is determined very early in development and *Apuleia* does not possess a labile sexual response. That is, gender determination is unlikely to be affected by environmental factors or nearby fruit set. The consistent localization of the hermaphrodite flower at the center of the cyme supports this theory.

The occurrence of a characteristic total floral organ number coupled with variability within whorls was discussed by Tian *et al*. (2007) in their study of *Circaeaster agrestis* Maxim (Ranunculales). The authors proposed two possible explanations for the phenomenon. The first is that the various floral morphs all represented reductions from a higher possible total organ number. In *Apuleia*, this would imply a floral formula of K3C3A3G1, from which either a stamen or the carpel is always lost in an individual flower. The second explanation suggested by the authors is the homeotic transformation of one organ into the other. In this case, homeosis would lead to the carpel of the hermaphrodite developing instead as a third stamen, forming a staminate flower. Both explanations have merit, but further investigation, particularly of juvenile specimens, is needed to determine which may be occurring in *Apuleia*.

Another anomaly of the *Apuleia* inflorescence is the ratio of the two floral morphs. Other andromonoecious caesalpinioids have been reported as having relatively high numbers of hermaphroditic flowers compared to staminate flowers: 2.1:1 in *Anthonotha noldeae* (Rossberg) Exell et Hillc. (Beavon and Chapman 2011), 3:1 in *Bauhinia ungulata* L. (Ramirez et al. 1984), and 15:1 in *Bauhinia aculeata* L. (Hokche and Ramirez 1990). While formal counts could not be made for this study because of a lack of material, we found that hermaphroditic flowers were outnumbered by male flowers by at least four to one in the inflorescences we examined—a reversal of the ratio seen in the species above. A few inflorescences were found in which all flowers were staminate. In the case of *A. noldeae*, Beavon and Chapman (2011) note that approximately 80% of visits to the flowers are made by nectar and/or pollen thieves, as opposed to legitimate pollinators, and that this may lead to a high number of non-fruit-setting hermaphrodite flowers.

Several theories have been advanced regarding the evolutionary utility of andromonoecy. Resource allocation modeling by Spalik (1991) suggests that the production of nonfruiting flowers may increase the pollen dispersal within a population at a relatively low energy cost compared to the production of further ovules. Other authors describe the selective suppression of gynoecial development as a response to such external factors as resource availability, abiotic stress, and predation (Gibbs et al. 1999; Beavon and Chapman 2011). A principal difference between these explanations is that the latter results in gender expression being determined relatively late in floral development via carpel suppression (Diggle, 1991), while the former may be genetically ''pre-programmed'' and insensitive to environmental factors. This suggests that the nonlabile form of andromonoecy seen in *Apuleia* may have occurred less as a response to external stresses than as a means to increase pollen availability.

Because of the current lack of juvenile material of this species, the work presented here is based on the examination of mature flowers. Should specimens become available for ontogenetic study in the future, these findings should be verified using earlier developmental stages.

4.5 Acknowledgments

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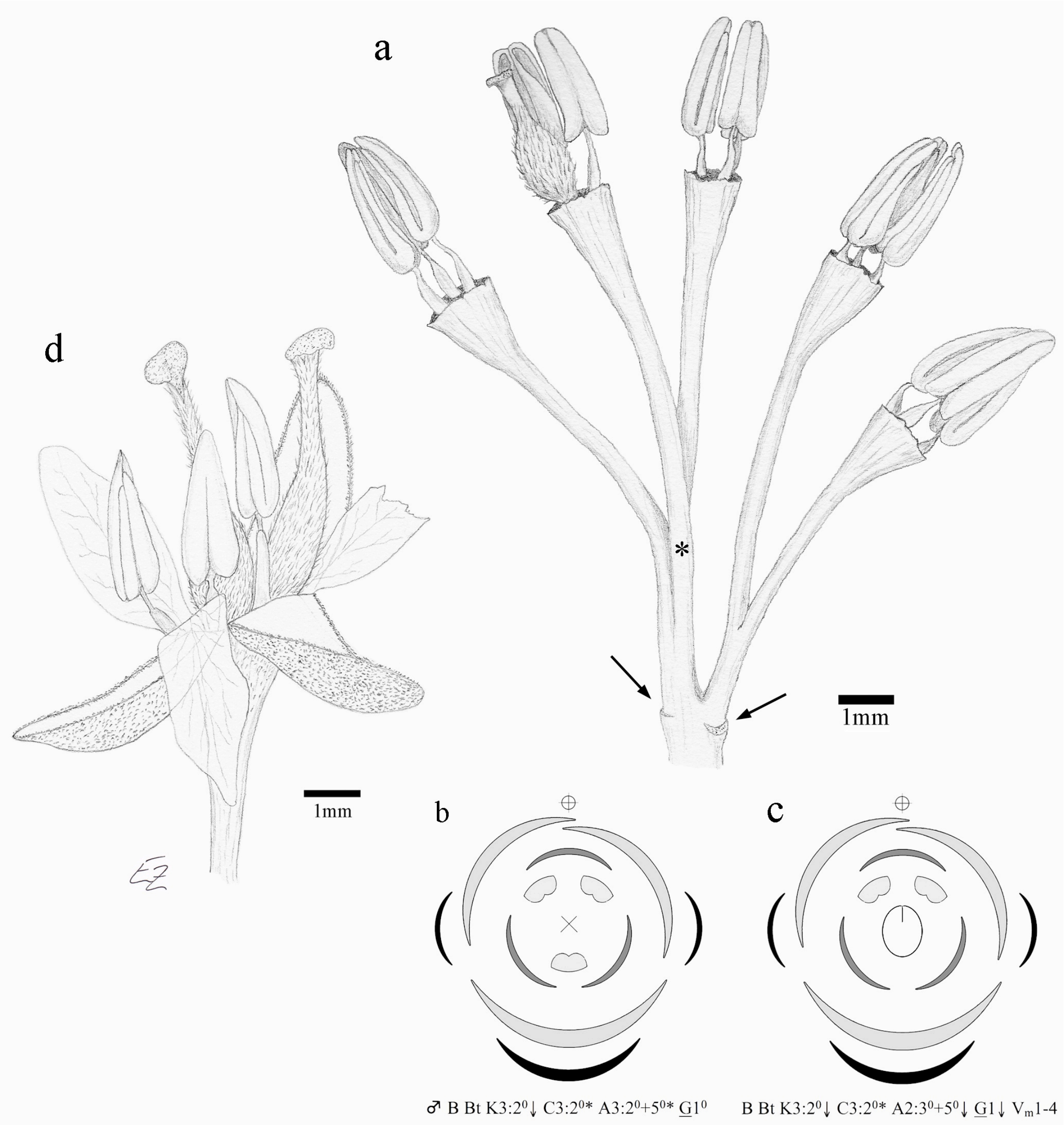

Fig. 4.1 Drawings and floral diagrams of *Apuleia leiocarpa*. Drawings from specimen Heringer *et al*. 5426. a, Cymose inflorescence with calyx and corolla removed from each flower to show arrangement of floral morphs. Central flower (indicated by an asterisk) is hermaphroditic, while younger lateral flowers are staminate. Arrows indicate scars left by flower-subtending phyllomes. b, Floral diagram and formula of staminate flower (format follows Prenner et al. 2010). c, Floral diagram and formula of hermaphrodite flower. d, Flower that has developed an additional carpel and stamen.

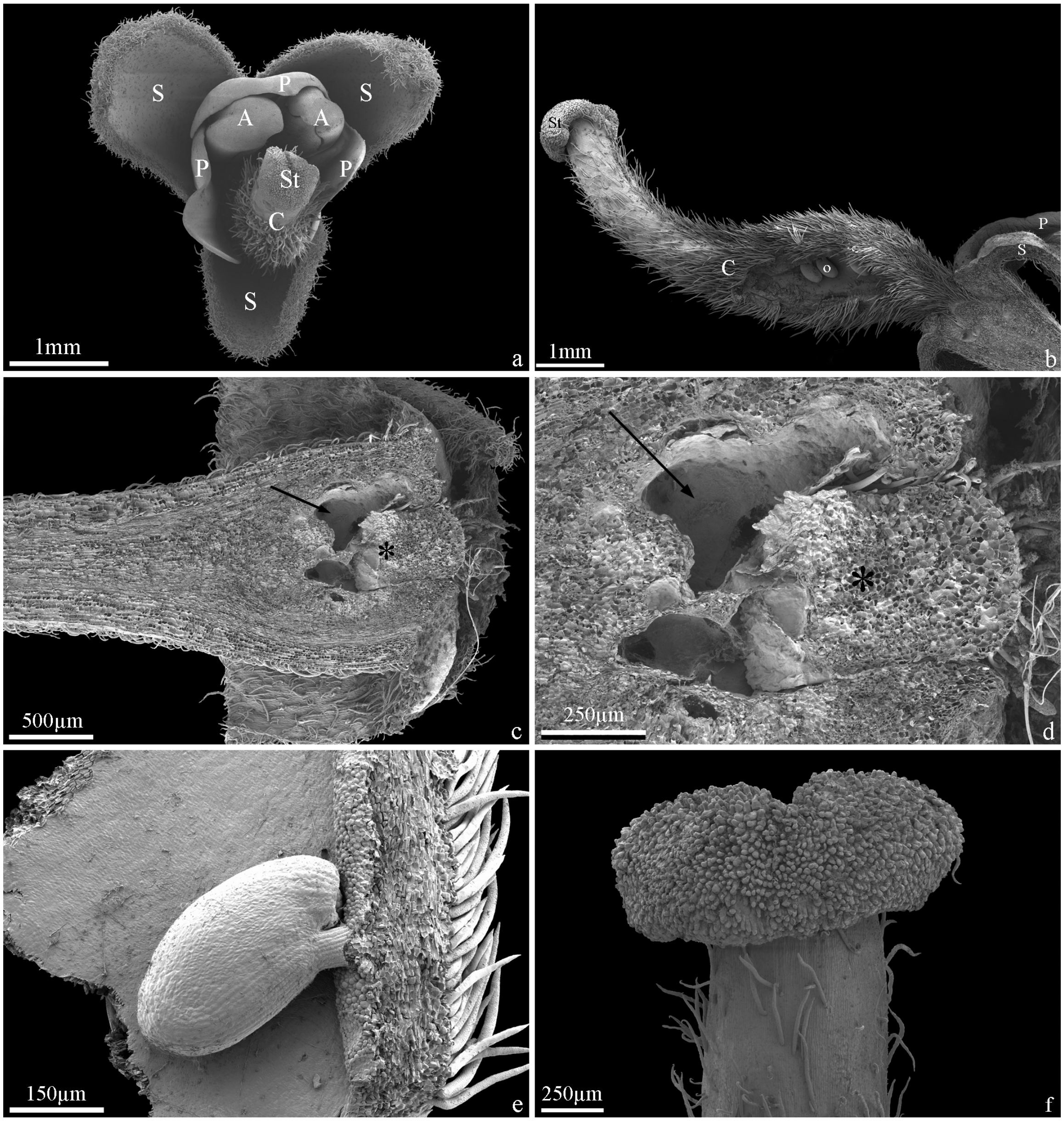

Fig. 4.2 SEM micrographs of a hermaphrodite flower of *Apuleia leiocarpa*, specimen Pennington and Rowe 172. Abaxial side is at base unless otherwise noted. a, Frontal view of flower at anthesis with gynoecium in the abaxial median position and two adaxial lateral stamens. b, Gynoecium with ovary wall removed to show ovules. c, d, Longitudinal section of flower base. Asterisk shows the placement of the stipe within the tubular hypanthium. Arrow indicates cavity formed by hypanthium walls. d, Detail of stipe attachment. e, Ovule attached to ovary wall. f, Detail of peltate stigma, abaxial side. A=stamen; C=carpel; o=ovule; P=petal; S=sepal; St=stigma.

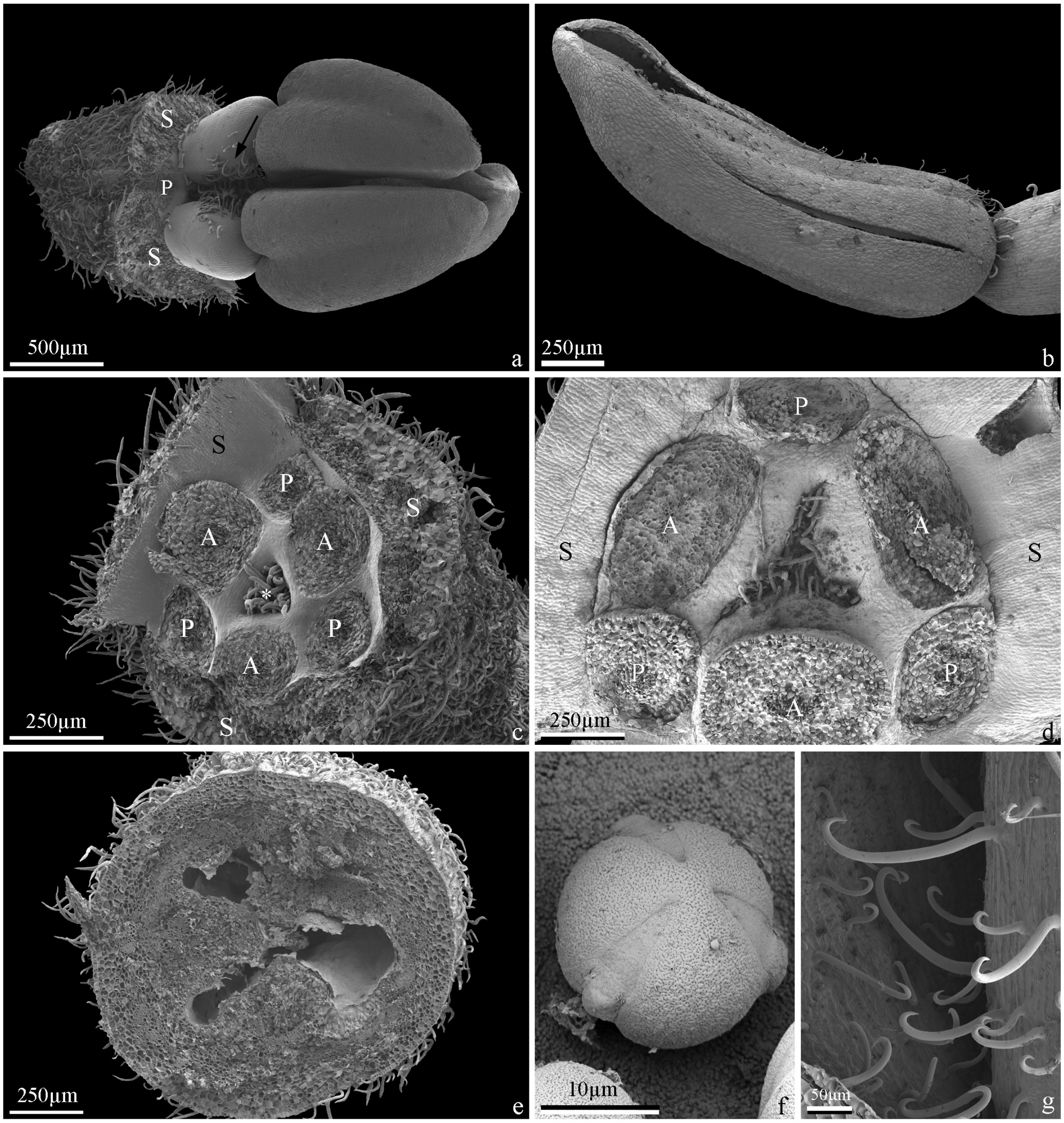

Fig. 4.3 SEM micrographs of a staminate flower of *Apuleia leiocarpa*, specimen Pennington and Rowe 172. Abaxial side is at base unless otherwise noted. a, Lateral view of staminate flower with calyx and corolla removed. Hooked trichomes are visible on the adaxial surfaces of the filaments (arrow). b, Adaxial surface of anther with longitudinal, introrse dehiscence. c, d, Receptacle of flower with calyx, corolla, and stamens removed. Hooked trichomes are visible through the triangular opening of the sunken hypanthium at the center of the floral surface (asterisk). In d, the opening has been compressed to a three-pointed slit. e, Cross section just above the base of the hypanthium. The space takes on a three-chambered form and shows no sign of gynoecial development. f, Tricolporate pollen grain. g, Detail of the adaxial surface of the filament with hooked trichomes. A=stamen; P=petal; S=sepal.

Chapter 5 – General Discussion and Conclusion

The Dialiinae were chosen as the subject of study for this thesis because they are a highly diverse group of legumes for which neither the species-level taxonomic relationships, nor the full range of morphological variation was known (Herendeen et al., 2003; Bruneau et al., 2008). As one of the basal lineages of the caesalpinioid grade, their history and form provide a window into early legume evolution.

With this thesis, a great deal more is now known about Dialiinae morphology and the breadth of its variation. For nearly every species, a comprehensive record of vegetative and floral traits is now available, and clade-wide trends, such as positional zygomorphy via organ loss and an apparent link between organ losses in the calyx and corolla, have been identified for further investigation. While ontogenetic study of the Dialiinae has only scratched the surface in terms of surveyed taxa, we now know that floral development in this clade is even less canalized then might be expected (Tucker, 1997), with differences in early-stage organ initiation even between congeneric species, and no consistent developmental pattern from one genus to the next (Zimmerman et al., 2013).

In terms of Dialiinae systematics, a fully resolved and well-supported phylogeny is still far from being realized. The genus *Dialium*, in particular, lacks resolution, and the position of several monotypic genera is still unknown. That being said, advances have been made. Better resolution within *Labichea*, for example, shows an evolutionary progression from pinnate leaves with broad leaflets to palmate or unifoliolate leaves with leathery, lanceolate leaflets, perhaps as an adaptation to an arid climate. A newly resolved Malagasy clade within *Dialium* shows a tendency toward trimery not seen elsewhere in the genus.

The major limiting factor in the scope of this project was the availability of suitable material. As alluded to in the introductory chapter, both ontogenetic samples and viable DNA were in short supply. To a much lesser extent, the morphological scoring was also affected, as specimens for several species could not be obtained, or did not have sufficiently well-preserved flowers for dissection. In these cases, scoring was done from the literature whenever possible, but these descriptions were never as comprehensive as the scoring attempted here, resulting in a few species with significant missing data. Of course, the only solution for this lack of material is for further field work to be done, with an eye to caesalpinioid taxa, in some of the "hot spots" of rarely-collected Dialiinae species; namely, western Africa, Madagascar, and southeast Asia (Malaysia and Indonesia in particular). Ideally, this field work should be carried out at staggered times throughout the year, as the non-synchronised flowering periods of tropical trees makes individual species difficult to spot during different months (K. Redden, pers. comm.).

Despite the lack of recent collections, better results might have been obtained in the molecular aspect of the project through more effective DNA extraction techniques. Many samples, even those from collections made within the last twenty years, failed at this point in the workflow. While several extraction methods, including commercial kits, were tested, and the protocol settled upon (Ky et al., 2000) was optimised for larger volumes of difficult material, there may exist new and better protocols of which we were not aware. Sequencing of contaminant angiosperm DNA was also a frequent problem during this project, particularly with *rpS16* amplicons. While this was very probably a further result of extracting poor quality DNA from old and degraded samples, the use of more intensive measures to reduce contamination in the lab, such as the use of laminar flow hoods, may improve this situation.

A further survey of genes which may resolve species-level relationships is also needed. For this study, the nuclear floral development gene *legume-cycloidea* (*LegCYC*) was cloned and sequenced in 45 ingroup taxa for the purpose of determining lower-level relationships. A parsimony analysis of these sequences can be found in Appendix III; analysis methodology was as described in chapter two. Despite its reportedly low copy number (Citerne et al., 2003) – only a single copy was isolated from non-papilionoid taxa, including *Dialium guianense* – we found as many as six distinct sequences per species. The number may in fact be higher; only six clones per species were sequenced. These copies often did not group with one another in a phylogeny, but had to be separated into smaller and smaller sub-groups, making any single sub-group impractically small for use in further analyses. Five principal sub-groups were found, and when the sequences were translated, three were putative pseudogenes, with stop codons in all three reading frames. Even assuming the limit of variation in this gene had been captured in our sample of six clones per individual, a good deal more sequencing would have to be done in order to sequence one of the two non-pseudogene haplotypes for each species. It is possible that more specific primers could be designed to amplify only the desired variants, but as this is already a short amplicon (*circa* 330 bp) and polymorphic sites were not necessarily near the ends, significant information could be lost in so doing. If a single- or very low-copy nuclear gene can be found for use in a future Dialiinae phylogeny, it may give resolution in areas where the plastid genes used in this research did not.

One area in which data from this thesis might be put to good use is the revision of the genus *Dialium*. Various publications and online databases currently contain a contradictory array of accepted and non-accepted synonyms for species in this genus, and there does not seem to be a consensus on the number of species it contains, making complete and systematic study of the group difficult. A revision based on morphology, anatomy, cytology, and phytochemistry was completed by Rojo (1982) as a doctoral thesis, but was never published. The observations made in this thesis are largely complementary to those made by Rojo (1982), and could add depth and further diagnostic features to a much-needed future revision.

The Dialiinae are a highly morphologically and developmentally diverse clade, as is shown by their variable floral symmetry, sexuality, organogeny, and organ numbers. The uncanalized nature of their flowers mirrors a similar trend seen elsewhere in the basal legumes (Tucker, 1998, 2003; Endress, 1999). The improved picture of phylogenetic relationships in the Dialiinae and the progression of floral forms produced over the course of their evolution put forth in this thesis will allow us to better understand the adaptive range and constraints of the caesalpinioid subfamily.

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Appendix I

Specimens used in the molecular analysis. Superscripts on Genbank accession numbers not generated for this study indicate original publication (listed below table).

Taxon	**Voucher**	**Herb.**	**Genbank No.** ***trnL***	**Genbank No.** ***rpS16***
Apuleia leiocarpa (Vogel) JF Macbr.	B. Klitgaard & F.C.P. Garcia 66	K	[1]EU361737	KJ620926
Baudouinia fluggeiformis Baill.	SNGF 794	K	n/a	KJ620908
Baudouinia fluggeiformis Baill.	DuPuy M703	K	[2]AF365082	n/a
Baudouinia rouxevillei H. Perrier	Bruneau 1379	MO	KJ620939	KJ620910
Baudouinia sollyaeformis Baill.	F. Ratovoson 962	MO	KJ620940	KJ620909
Dialium angolense Welw. ex Oliver	Wieringa 2395	WAG	KJ620952	KJ620916
Dialium cochinchinense Pierre	Herendeen 1-v-1999-6	US	[2]AF365025	n/a
Dialium dinklagei Harms	Breteler 13349	WAG	[2]AF365032	KJ620914
Dialium excelsum J. Louis ex Stey	T.B. Hart 1411	MO	KJ620953	KJ620919
Dialium guianense (Aubl.) Sandwith	D. Cardoso 3382	HUEFS	KJ620961	KJ620922
Dialium guineense Willd.	Breteler 14748	WAG	[2]AF365081	n/a
Dialium holtzii Harms	Herendeen 9-XII-97-1	US	KJ620954	KJ620920
Dialium kunstleri Prain	Sidiyasa 422	K	KJ620959	KJ620918
Dialium lopense Breteler	de Wilde 11770	WAG	[2]AF365026	KJ620915
Dialium pachyphyllum Harms	van der Burgt *et al.* 937	MO	KJ620955	KJ620917
Dialium pentandrum Louis ex Steyaert	G. Troupin 4712	MO	KJ620957	n/a
Dialium platysepalum Baker	Ambri 1250	K	n/a	KJ620911
Dialium polyanthum Harms	G. Walters 946	MO	KJ620956	KJ620912
Dialium schlechteri Harms	ILC6-12	JRAU	KJ620960	KJ620921
Dialium tessmannii Harms	Breteler 15470	WAG	[2]AF365027	KJ620913
Dialium unifoliolatum (Capuron) Du Puy & Rabev	Mada 109	n/a	[3]KC479263	n/a
Dialium zenkeri Harms	Kenfack 833	MO	KJ620958	n/a
Dicorynia guianensis Amshoff	Barabé 7	MT	[2]AF365083	KJ620923
Dicorynia paraensis Benth.	D. Cardoso 3397	HUEFS	KJ620941	KJ620924
Distemonanthus benthamianus Baill.	Wieringa 3235	WAG	[2]AF365084	KJ620928
Eligmocarpus cynometroides Capuron	McWhirter 204	K	[1]EU361801	n/a
Eligmocarpus cynometroides Capuron	Dumetz 1102	MO	n/a	KJ620907
Kalappia celebica Kosterm.	E.A.Widjaja 9102	US	KJ620950	KJ620938
Koompassia excelsa (Becc.) Taub.	Herendeen 1-V-99-7	US	[1]EU361816	KJ620929
Labichea buettneriana F. Muell.	Gray 07649	MO	KJ620944	n/a
Labichea lanceolata Benth.	D. Seigler 14719	MO	KJ620945	n/a
Labichea nitida Benth.	J.R. Clarkson 2774B	MO	KJ620946	n/a
Labichea punctata Benth.	Nordetam 703	US	[2]AF365076	n/a
Martiodendron excelsum (Benth.) Gleason	Pennington 397	K	KJ620942	KJ620925
Martiodendron fluminense Lombardi	Oliveira 354A	MO	KJ620943	KJ620930
Martiodendron mediterraneum Koeppen	Queiroz 10162	HUEFS	[4]FJ009870	n/a
Martiodendron mediterraneum Koeppen	deLima 5009	MO	n/a	KJ620927
Martiodendron parviflorum (Amshoff) Koeppen	Bridgewater *et al.* 710	E	[2]AF365086	KJ620931
Mendoravia dumaziana Capuron	McWhirter 212	K	[1]EU361823	n/a
Mendoravia dumaziana Capuron	Capuron 28343_SF	MO	n/a	KJ620906
Petalostylis cassioides E. Pritzel	P.K. Latz 12175	MO	KJ620947	KJ620934
Petalostylis labicheoides R. Br.	Coveny 12062	MO	[2]AF365077	KJ620933
Poeppigia procera C. Presl.	Klitgaard 65	K	[5]AY899682	n/a

Poeppigia procera C. Presl.	Marulanda 2020	MO	n/a	KJ620905
Storckiella australiensis J.H. Ross & B. Hyland	K. Hill *et al.* 2096	K	[2]AF365078	KJ620936
Storckiella comptonii Baker f.	Simmons 1875	MO	KJ620948	KJ620935
Storckiella neocaledonica Nielsen, Labat, Munz.	J.N. Labat 3520	K	KJ620949	KJ620937
Zenia insignis Chun	Averyanov 5748	MO	KJ620951	KJ620932
Cercis canadensis L.	Bruneau 802	MT	[6]FJ801162	KJ620904
Duparquetia orchidacea Baill.	Bruneau 1098	K	[1]EU361800	n/a
Duparquetia orchidacea Baill.	G. McPherson 16287	MO	n/a	KJ620903

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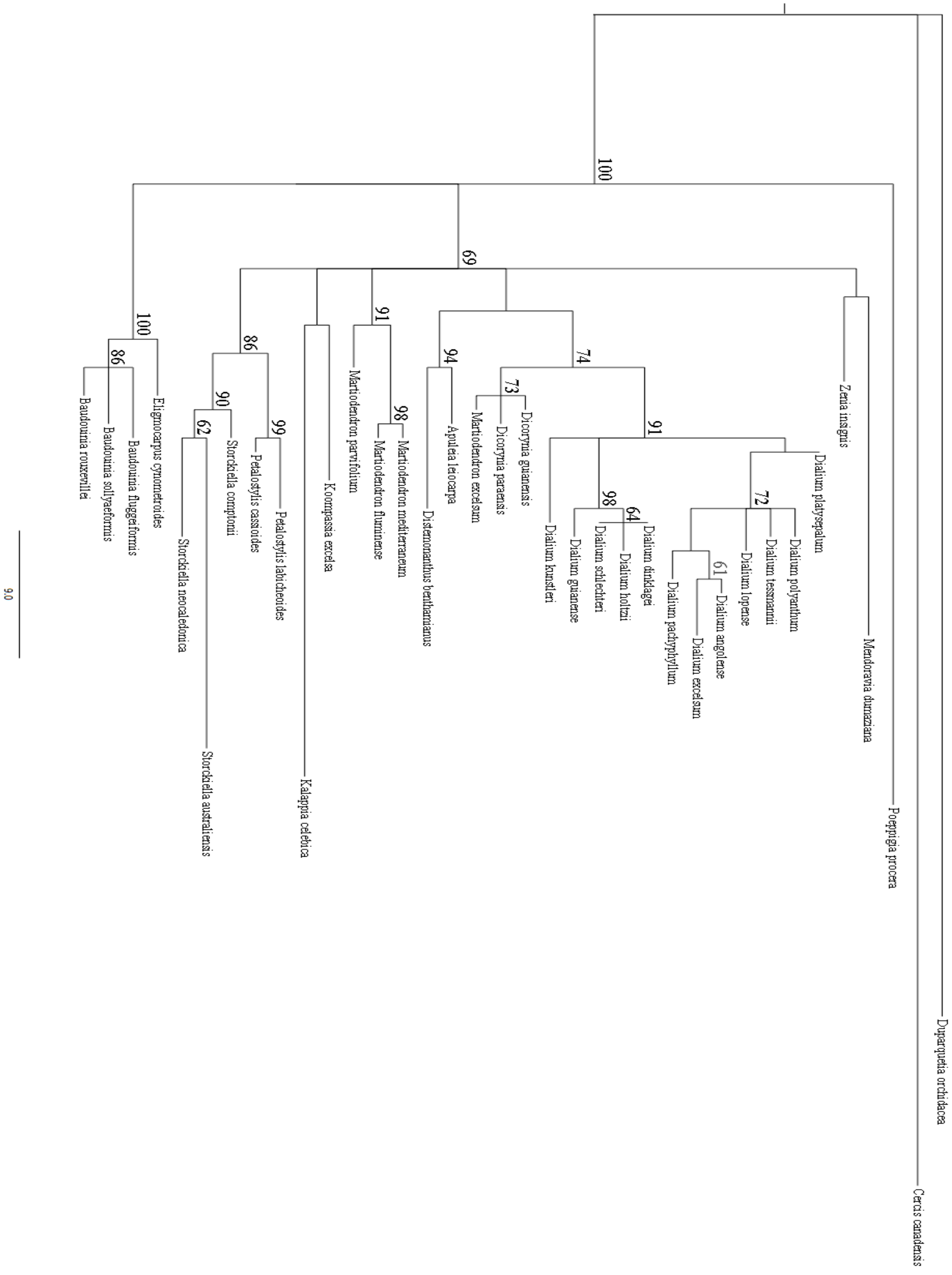
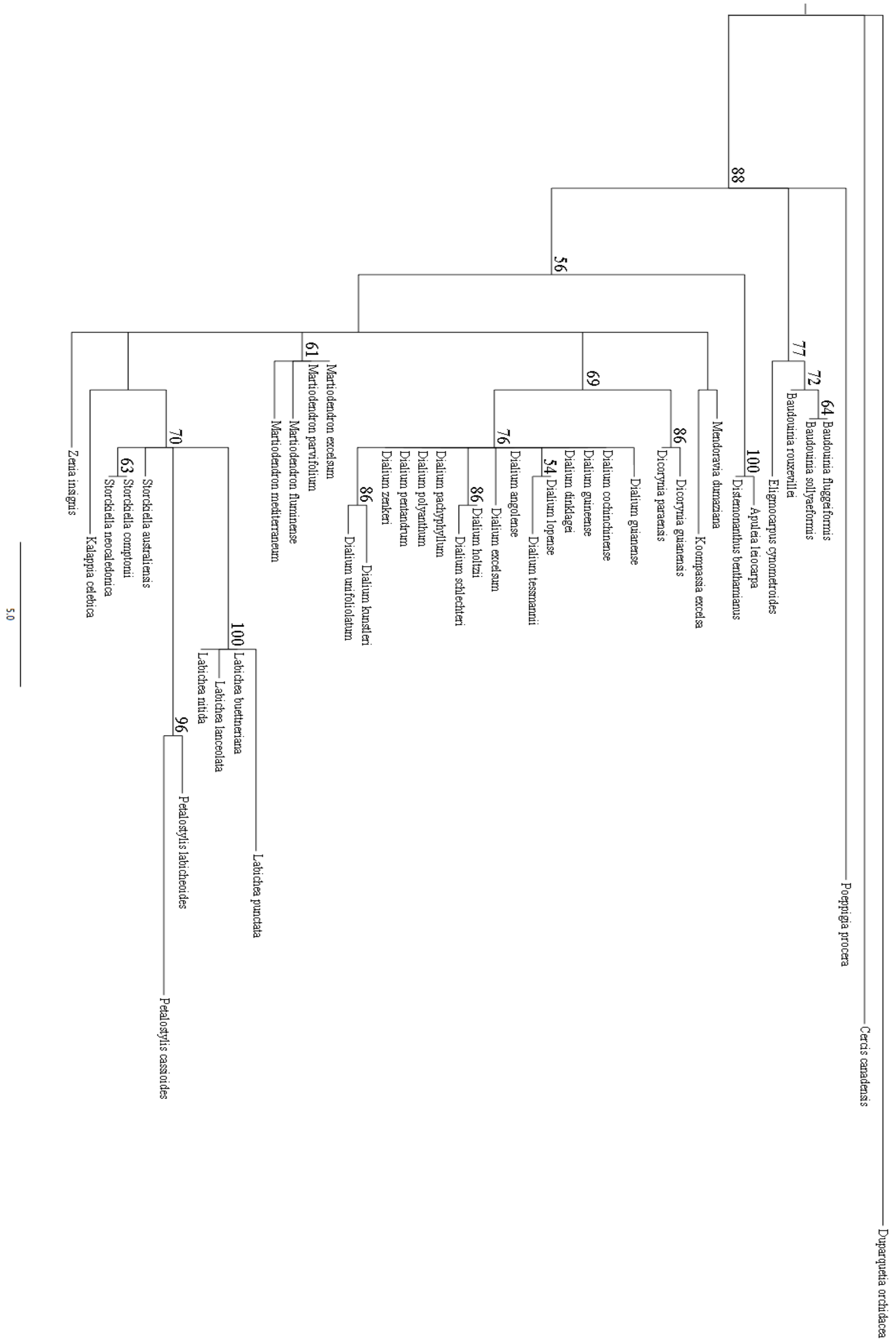
Appendix II

Additional phylogenetic trees.

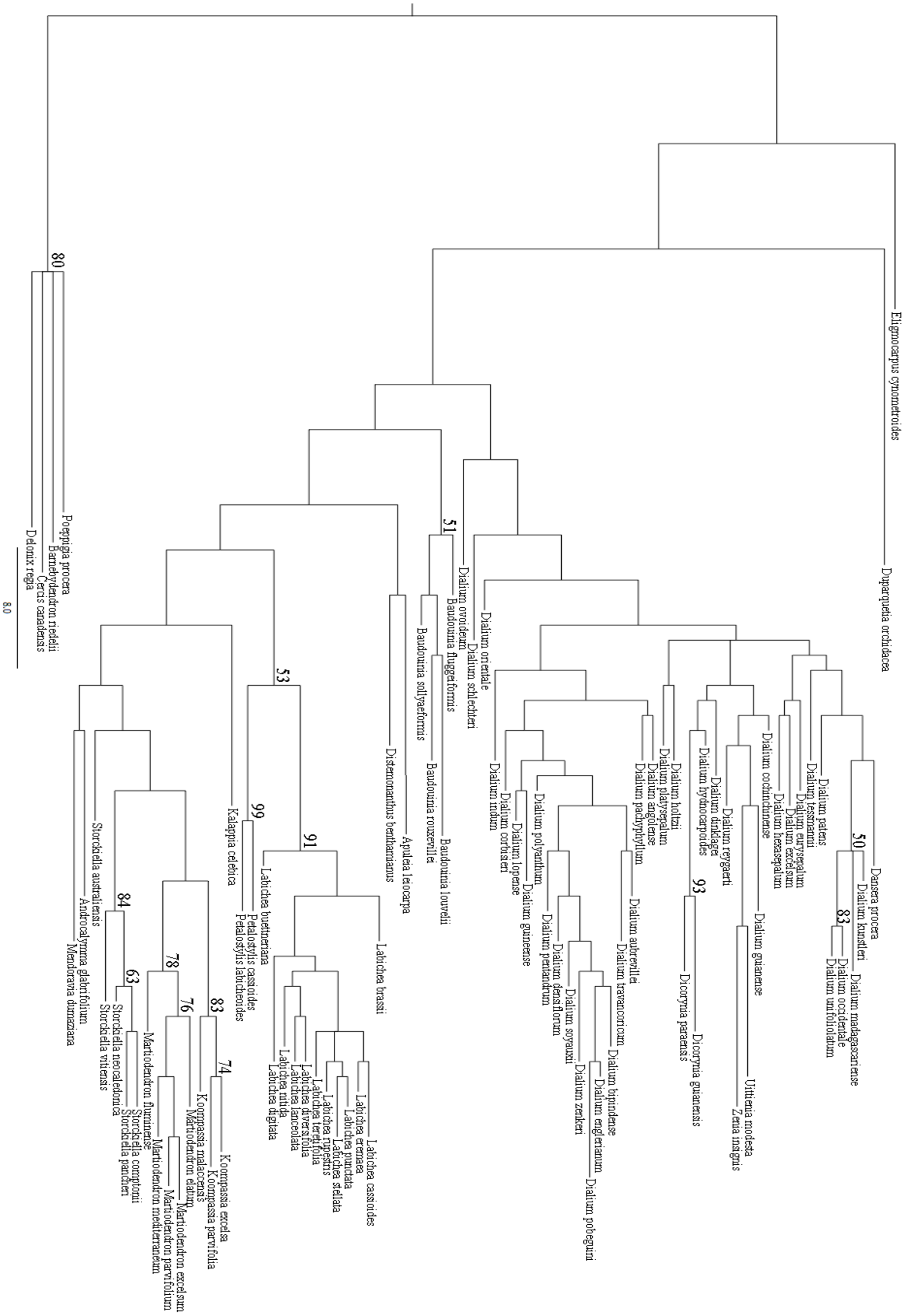
a) Strict consensus of parsimony analysis based on *rpS16* intron. Bootstrap values greater than 50% given above nodes.



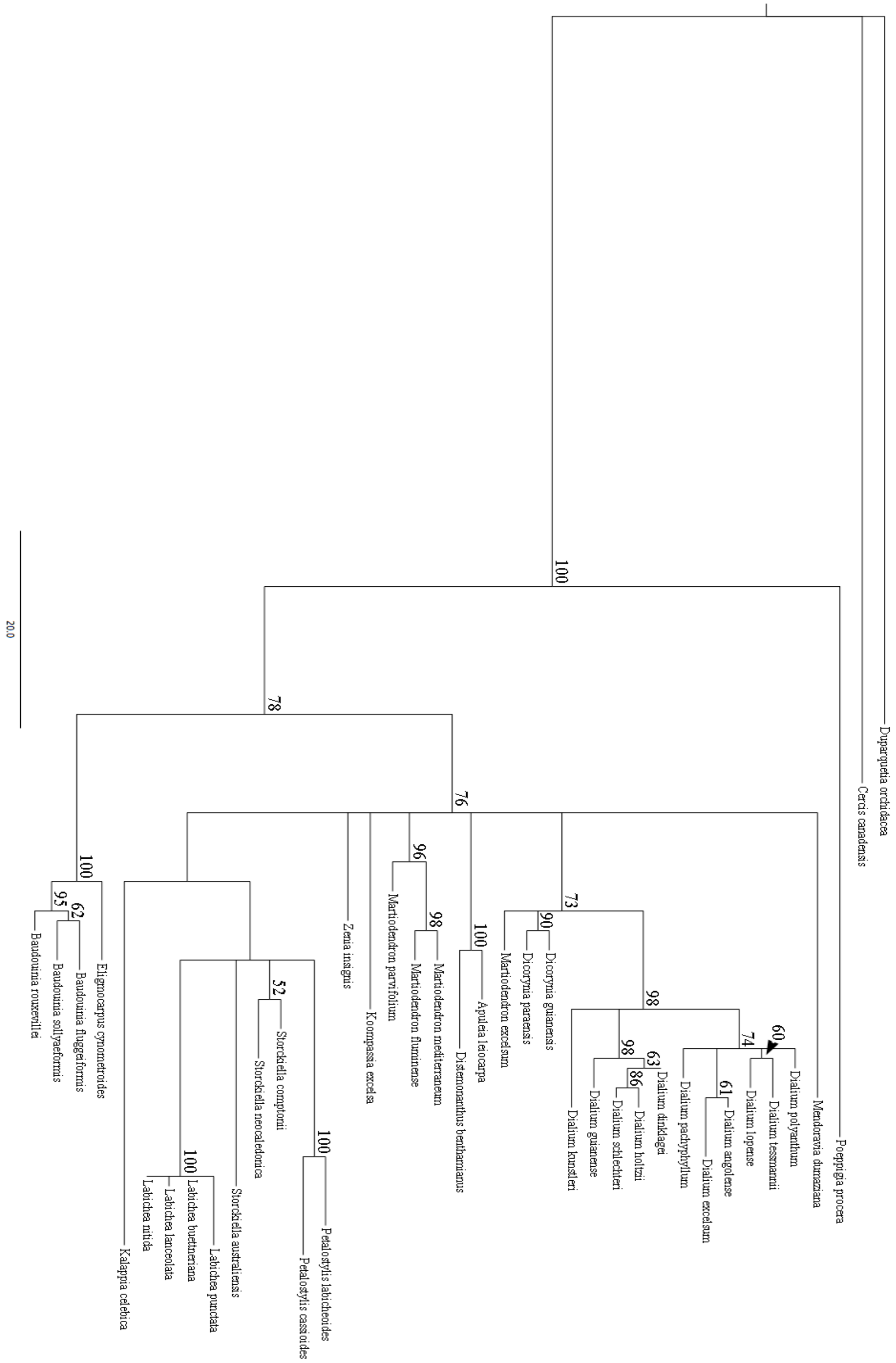
b) Strict consensus of parsimony analysis based on *trnL* intron. Bootstrap values greater than 50% given above nodes.



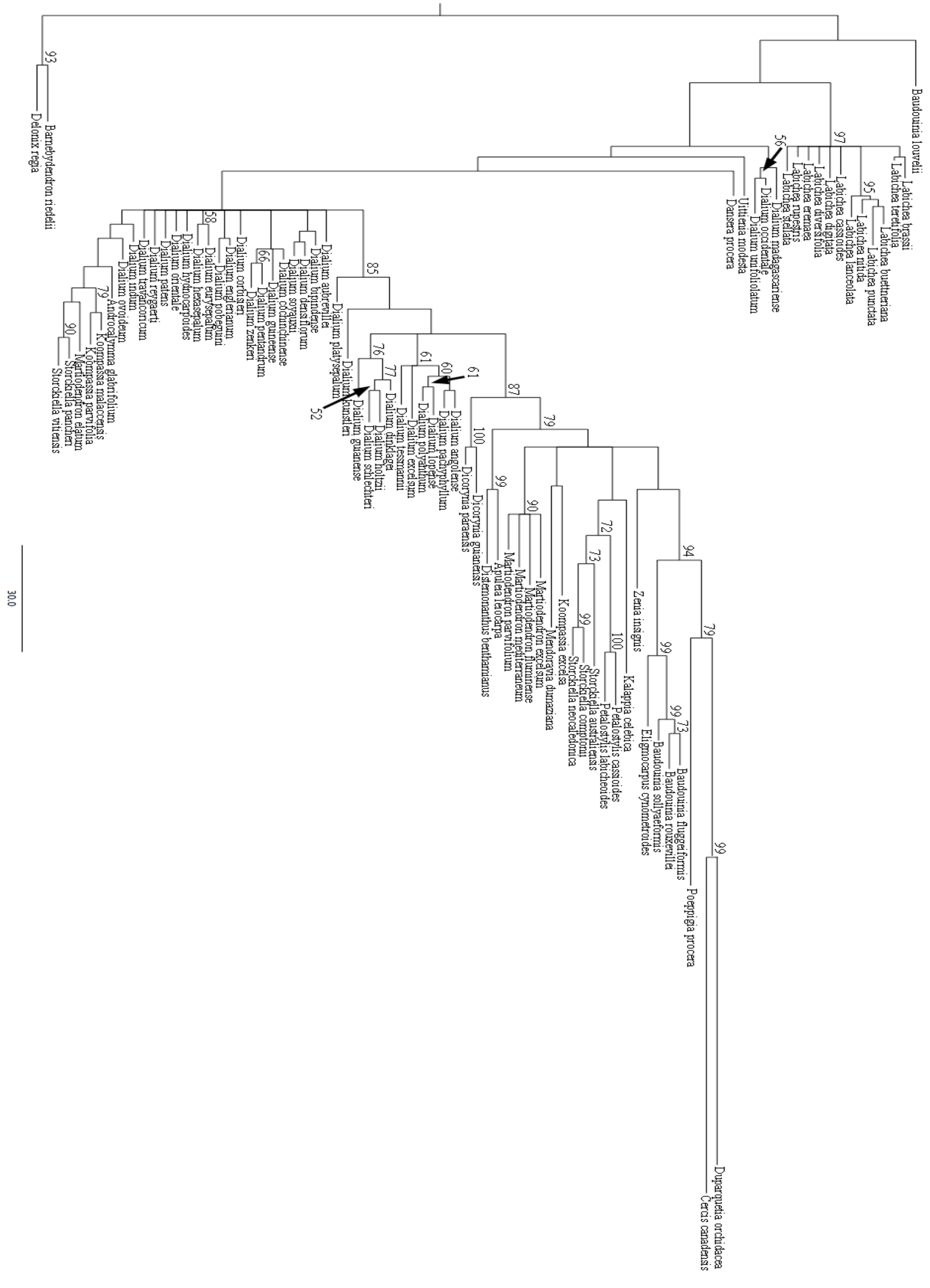
c) Strict consensus of parsimony analysis based on morphological characters. Bootstrap values greater than 50% given above nodes.



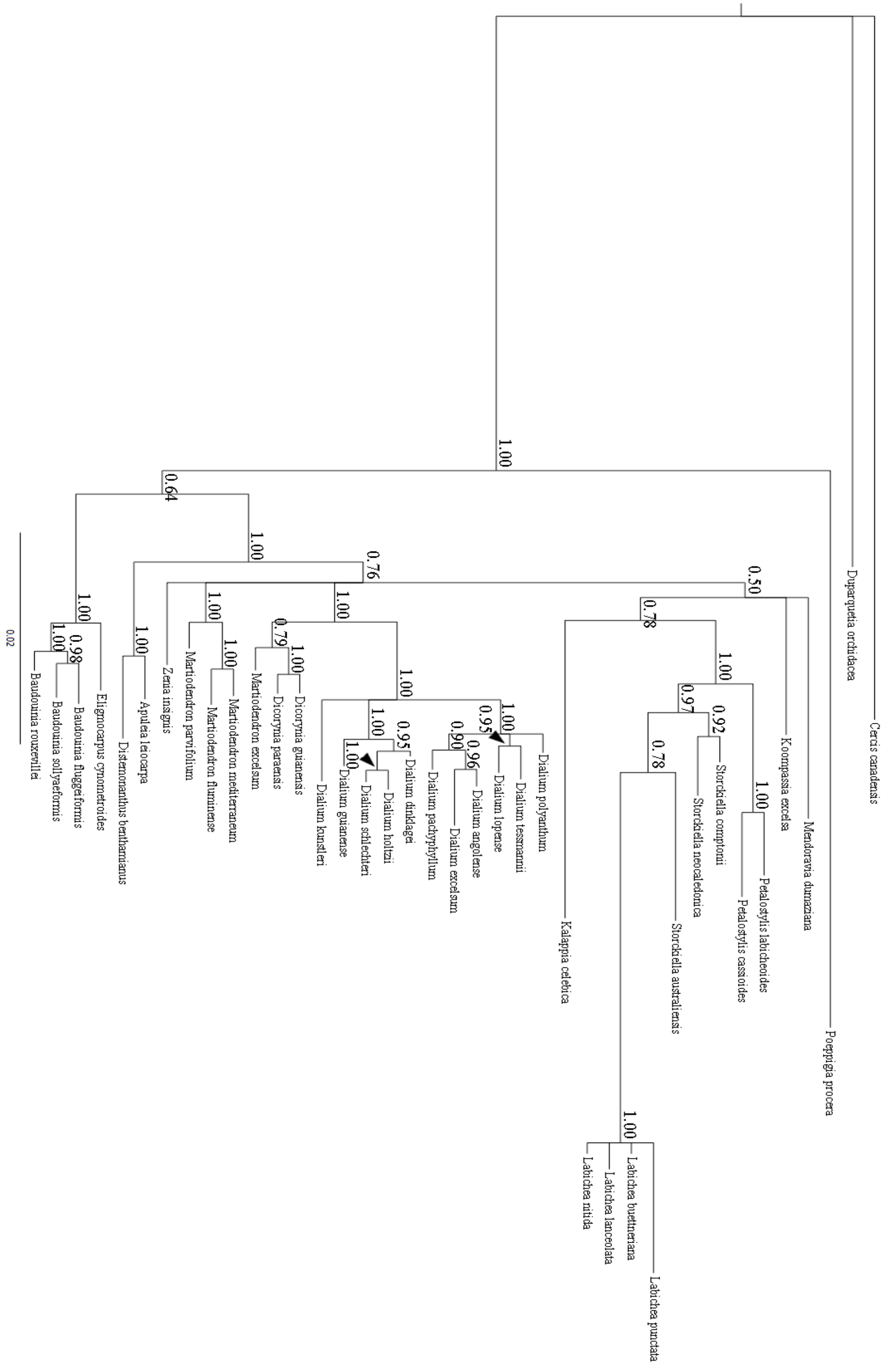
d) Strict consensus of parsimony analysis based on combined *rpS16* and *trnL* introns. Bootstrap values greater than 50% given above nodes.



e) Strict consensus of parsimony analysis based on combined molecular and morphological data with expanded taxon set (missing data allowed). Bootstrap values greater than 50% given above nodes.



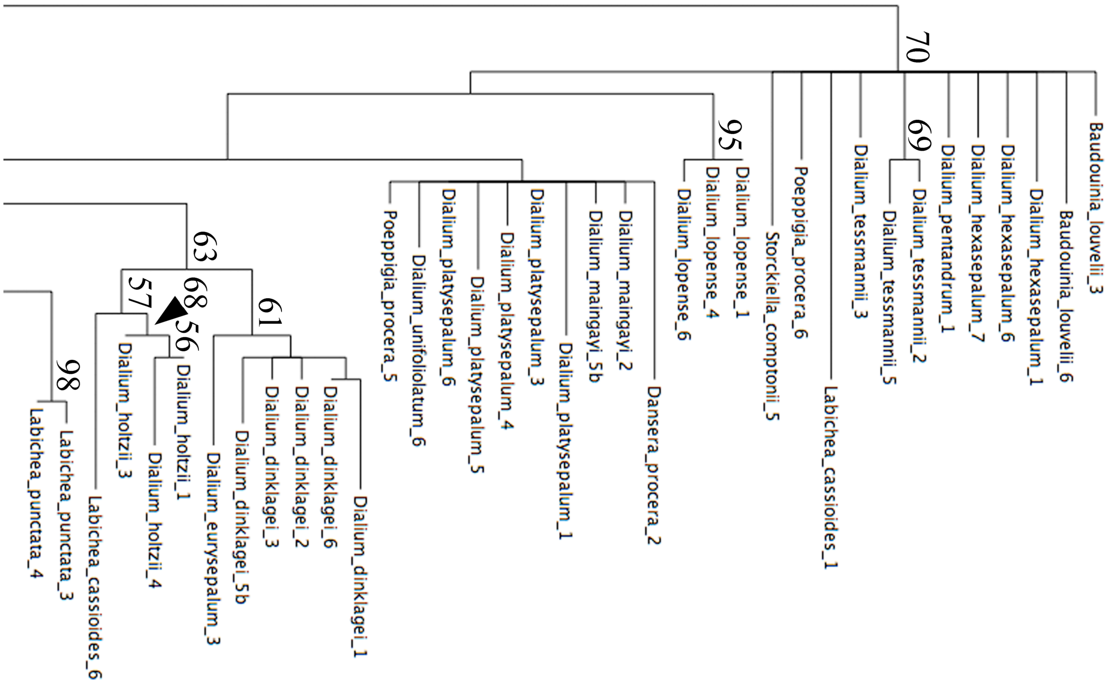
f) Bayesian majority rule consensus based on combined *rpS16* and *trnL* introns. Posterior probabilities greater than 0.5 given above nodes.

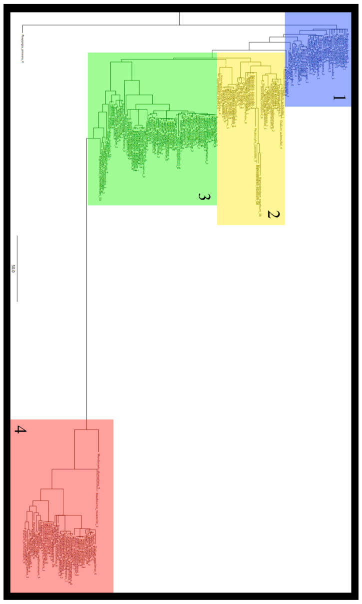


Appendix III

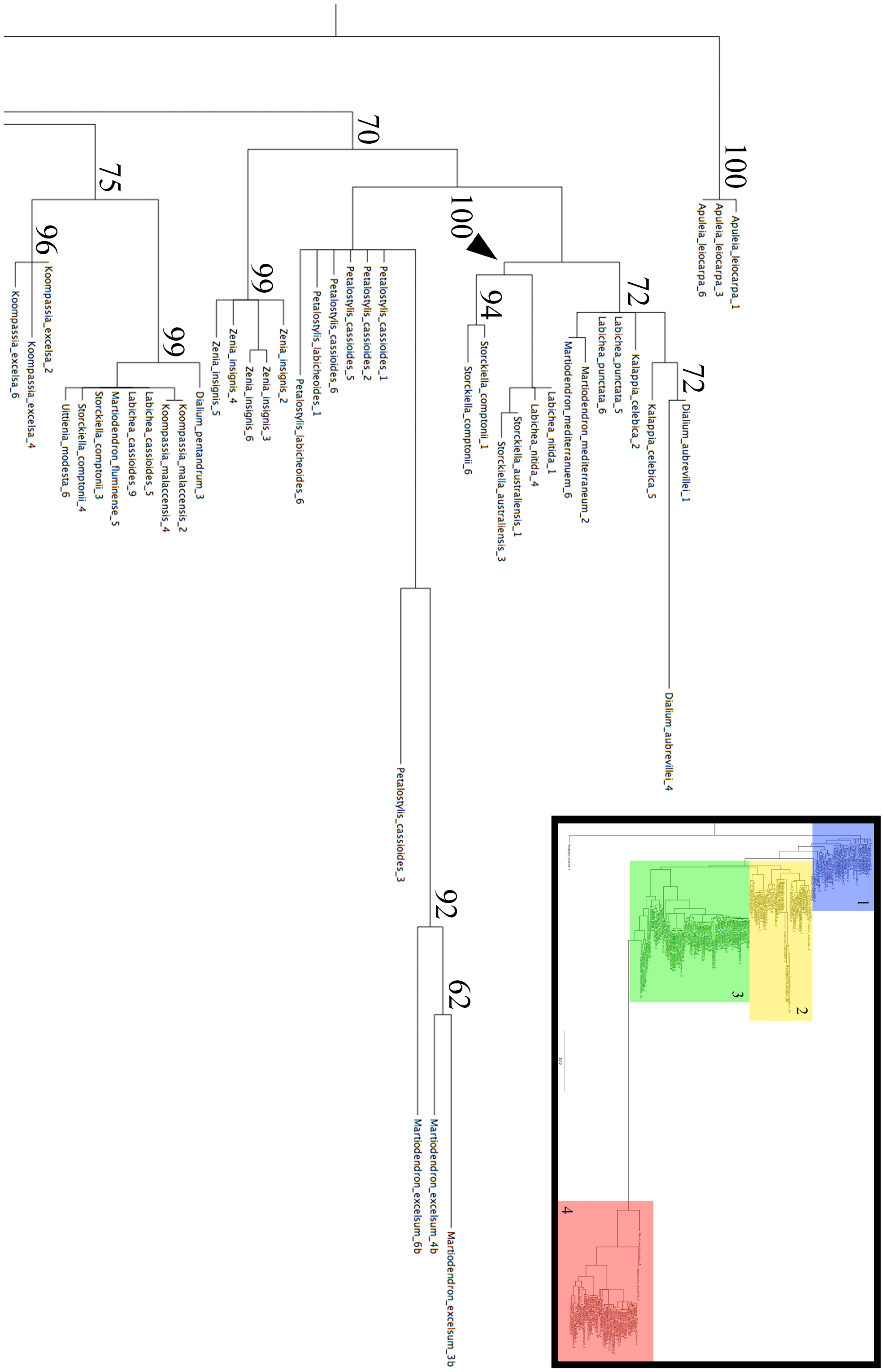
Parsimony analysis of *LegumeCYCLOIDEA* data. Strict consensus tree is presented. Bootstrap values above 50% are given above nodes.

a) *LegCYC* strict consensus tree; quadrant one.

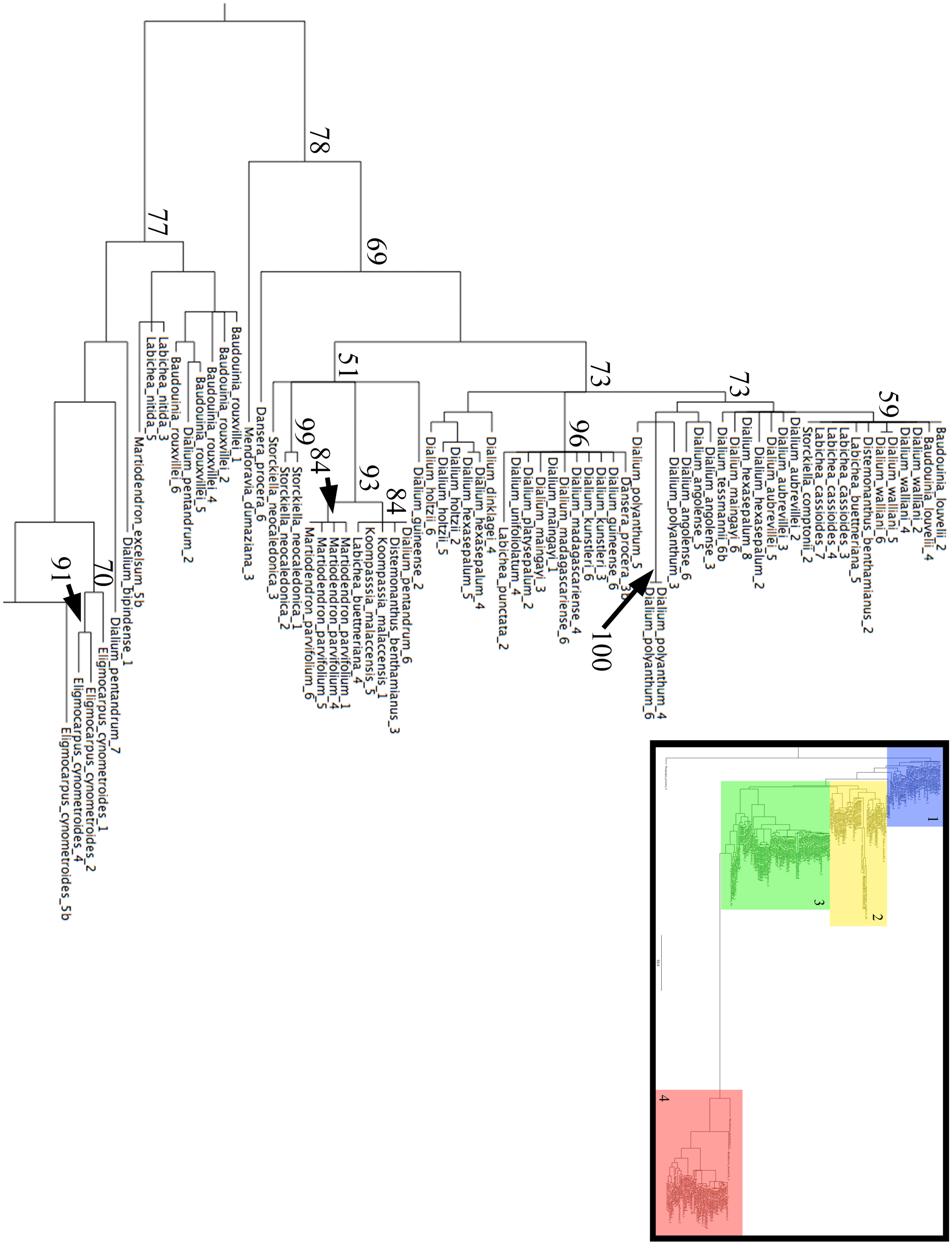




b) *LegCYC* strict consensus tree; quadrant two.



c) *LegCYC* strict consensus tree; quadrant three.



d) *LegCYC* strict consensus tree; quadrant four.