

Research Article

Perianth evolution and implications for generic delimitation in the eucalypts (Myrtaceae), including the description of the new genus, *Blakella*

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Received 30 March 2023; Accepted 30 October 2023

Abstract Eucalypts (Myrtaceae tribe Eucalypteae) are currently placed in seven genera. Traditionally, *Eucalyptus* was defined by its operculum, but when phylogenies placed *Angophora*, with free sepals and petals, as sister to the operculate bloodwood eucalypts, the latter were segregated into a new genus, *Corymbia*. Yet, generic delimitation in the tribe Eucalypteae remains uncertain. Here, we address these problems using phylogenetic analysis with the largest molecular data set to date. We captured 101 low-copy nuclear exons from 392 samples representing 266 species. Our phylogenetic analysis used maximum likelihood (IQtree) and multispecies coalescent (Astral). At two nodes critical to generic delimitation, we tested alternative relationships among *Arillastrum*, *Angophora*, *Eucalyptus*, and *Corymbia* using Shimodaira's approximately unbiased test. Phylogenetic mapping was used to explore the evolution of perianth traits. Monophyly of *Corymbia* relative to *Angophora* was decisively rejected. All alternative relationships among the seven currently recognized Eucalypteae genera imply homoplasy in the evolutionary origins of the operculum. Inferred evolutionary transitions in perianth traits are congruent with divergences between major clades, except that the expression of separate sepals and petals in *Angophora*, which is nested within the operculate genus *Corymbia*, appears to be a reversal to the plesiomorphic perianth structure. Here, we formally raise *Corymbia* subg. *Blakella* to genus rank and make the relevant new combinations. We also define and name three sections within *Blakella* (*Blakella* sect. *Blakella*, *Blakella* sect. *Naviculares*, and *Blakella* sect. *Maculatae*), and two series within *Blakella* sect. *Maculatae* (*Blakella* ser. *Maculatae* and *Blakella* ser. *Torellianae*). *Corymbia* is reduced to the red bloodwoods.

Key words: *Angophora*, *Blakella*, classification, *Corymbia*, *Eucalyptus*, homoplasy, low-copy nuclear loci, perianth evolution, phylogeny, targeted capture.

1 Introduction

Eucalypts are an exceptional group of trees and shrubs because they dominate the forests and woodlands of much of the Australian continent. They are even scattered

throughout most of the central arid zone, which generally lacks tree-dominated communities. Recent overviews estimate the number of species between 796 (Slee et al., 2020) and about 855 (Nicolle, 2022). Eucalypts are globally significant in commerce and industry, with worldwide

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plantations for timber, paper pulp, essential oils, and firewood.

Myrtaceae tribe Eucalypteae currently has seven genera in total (Wilson, 2011). The focus of this study is eucalypts in the strict sense, which currently comprise a clade of three genera (Schuster et al., 2018; Thornhill et al., 2019): *Angophora*, *Corymbia*, and *Eucalyptus*. When we use the common name “eucalypt(s),” we refer collectively to just these three genera and a fourth genus described here.

The existing eucalypt classification has been developed mostly from morphology, which has remained the dominant line of evidence for classification until recently (Brooker, 2000). Understanding perianth homology and evolution has long been considered key to the generic classification of the eucalypts (Brown, 1814; Pryor & Knox, 1971; Johnson, 1972; Drinnan & Ladiges, 1988, 1989a, 1989b, 1989c, 1991a, 1991b; Hill & Johnson, 1995; Bohte & Drinnan, 2005; Slee et al., 2020). Traditionally, most species were placed in *Eucalyptus*, based on the perianth being fused into an operculum (hence the name of the genus), whereas *Angophora* was distinguished by its conspicuous, free petals, and sepals (Pryor & Knox, 1971; Brooker & Kleinig, 1983). Although it was generally accepted that the operculum is formed from different perianth parts in different groups of eucalypts, interpretations have differed between studies. For example, the monocalypts (then classified as *Eucalyptus* sect. *Eucalyptus*) have a single uniformly structured operculum of uncertain homology—whether sepaline (Pryor & Knox, 1971), petaline (Drinnan & Ladiges, 1989b), or a composite of both (Hill & Johnson, 1995).

Interpreting perianth evolution became more problematic when it was found that *Angophora*, with free petals and sepals, appeared to be more closely related to bloodwoods than to *Eucalyptus* s.s. (Johnson, 1972; Hill & Johnson, 1995; Ladiges et al., 1995), even though both bloodwoods and *Eucalyptus* have the perianth modified into opercula. To explain this conundrum, it has been generally assumed that opercula originated independently in bloodwoods and *Eucalyptus*, perhaps multiple times (e.g., Hill & Johnson, 1995). Congruent with this hypothesis, some taxa within both bloodwoods and *Eucalyptus* have separate sepaline and petaline opercula, whereas others (e.g., in *Eucalyptus* subg. *Eudesmia*) combine distinct sepals with a petaline operculum (Drinnan & Ladiges, 1988, 1989a, 1989b, 1989c, 1991a, 1991b; Slee et al., 2020). However, the alternative hypothesis that the free sepals and petals of *Angophora* have re-evolved from an operculate ancestor has not been seriously considered. For example, Carr & Carr (1987) treated bloodwoods as section *Corymbosae* of *Eucalyptus* and described some novel traits characteristic of bloodwoods, particularly the rubber cuticle. They noted that this and some other traits were also found in *Angophora* but did not consider the taxonomic implications.

In a monograph based on a cladistic analysis of morphology, Hill & Johnson (1995) segregated the bloodwood *Eucalyptus* species into a new genus *Corymbia*, diagnosed by characters of the hairs, bristle glands, and xylem vessels, among others. *Angophora* was the monophyletic sister group to *Corymbia* in their cladistic analysis, and these authors maintained it as a distinct genus with close affinity to *Corymbia*. They noted that, while *Angophora* has

conspicuous free petals, some *Corymbia* species also have free petals, albeit enclosed within a calycine calyptra, with which they are shed simultaneously at anthesis. In the same year, Udovicic et al. (1995) published a molecular phylogenetic analysis of the eucalypt genera *Angophora* and *Eucalyptus* s.l. (including the bloodwoods), using sequences of 5S ribosomal DNA. The results were inconclusive, with none of the three genera recognized by Hill & Johnson (*Angophora*, *Corymbia*, and *Eucalyptus* sens. str.) being consistently monophyletic. Brooker (2000) considered the evidence from both the previous studies unconvincing and formally sank *Angophora* and *Corymbia* into *Eucalyptus*. However, *Angophora* had never been synonymized previously, and Brooker's work was not accepted by the wider taxonomic community (e.g., Ladiges & Udovicic, 2000). Acceptance of three genera of eucalypts (*Angophora*, *Corymbia*, and *Eucalyptus*) has continued to the present.

Subsequent research on higher-level classification of eucalypts has mainly used molecular data, including DNA from both the chloroplast and nuclear genomes, especially 5.8S nuclear ribosomal DNA and its flanking internal transcribed spacers (ITS). Molecular studies using ribosomal DNA (rDNA) have consistently found support for the monophyly of *Eucalyptus* (e.g., Steane et al., 1999, 2002; Schuster et al., 2018; Thornhill et al., 2019). However, incomplete lineage sorting and chloroplast capture have led to phylogenetic estimates using chloroplast data failing to accurately reflect evolutionary history. For example, within *Eucalyptus* subg. *Eucalyptus* (monocalypts), McKinnon et al. (1999) found that chloroplast DNA (cpDNA) reflected geography rather than taxonomic relationships established by morphology and nuclear DNA, suggesting introgression between co-located taxa. Similarly, using a large sample from across the taxonomic breadth of eucalypts with sequences of most of the chloroplast genome, Schuster et al. (2018) found strongly supported resolution of higher-level relationships that was strikingly incongruent with the phylogeny using nuclear ITS (internal transcribed spacer) sequences from the same taxa. Monophyly was strongly contradicted for *Corymbia*, its two subgenera *Corymbia* and *Blakella*, and most sections within these groups. This incongruence was also attributed by the authors to the geographic sharing of chloroplast DNA across taxa. Within *Corymbia* subg. *Blakella*, Healey et al. (2018) sequenced whole chloroplast genomes and nuclear external transcribed spacers (ETS) from within two sections (*Torellianae* and *Maculatae*) and found chloroplast capture across sections. Similar examples include Udovicic & Ladiges (2000), McKinnon et al. (2001, 2004), and Bayly et al. (2013). Overall, in the studies showing chloroplast capture, nuclear data (if included in the analysis) accurately reflected taxonomic relationships based originally on morphology.

Even when using nuclear markers alone, the relationships of the small genus *Angophora* (nine spp.) to *Corymbia* have proved difficult to resolve with confidence. Multiple previous studies using nuclear ribosomal DNA found *Angophora* to be nested within the bloodwood clade. For example, Thornhill et al. (2019) found *Angophora* was either sister to or within *Corymbia*, with poor support in either place, and both Steane et al. (1999) and Schuster et al. (2018) found *Corymbia* to be paraphyletic by the inclusion of *Angophora*. However, taxonomists did not act to resolve the problem, perhaps

because this relationship was unexpected and did not receive good or consistent statistical support from their data.

In contrast, Parra-O et al. (2006) used nuclear ribosomal DNA (nrDNA) (ETS and ITS) sequences alone and in combination with morphological data (Parra-O et al., 2009). They found *Angophora* and *Corymbia* to be reciprocally monophyletic, with *Eucalyptus* and other Eucalypteae genera as the sister groups. Although bootstrap support for the *Corymbia* clade (excluding *Angophora*) was not strong (67–78), these authors (Parra-O et al., 2009) presented a new infrageneric classification of *Corymbia*, comprising two subgenera (*Corymbia* subg. *Corymbia* and *Corymbia* subg. *Blakella*), which were the two monophyletic sister groups comprising the genus. They also recognized sections within the subgenera, partly based on Hill & Johnson (1995) and Brooker (2000). However, resolution and branch support among the lower-level taxa (sections) in the tree were not good.

Two serial publications synthesize the taxonomic classification of eucalypts based on evidence published in the primary literature. EUCLID edition 4 (Slee et al., 2020) is the most comprehensive taxonomic treatment of eucalypts at the species level, including descriptions, illustrations, and an interactive key to all recognized species, and is based on morphology. Additionally, Nicolle (2022) publishes an annually updated classification of the eucalypts stated to be based on all available evidence.

There is still uncertainty in eucalypt relationships at deeper levels, particularly in *Corymbia*, the delimitation of its subgenera, and their relationship to *Angophora*. All previous molecular studies have used a very limited number of nuclear genes, focussing on ribosomal DNA. Here, we present and analyze the largest eucalypt data set to date (combining 392 terminal species with 101 nuclear genes) with the aim of testing the monophyly of higher taxa within Eucalypteae at multiple ranks, especially the currently recognized genera *Angophora*, *Corymbia*, and *Eucalyptus*. We also reconstruct perianth traits on the phylogeny to test previous interpretations of perianth evolution and their use to define genera in the group. Finally, we reclassify the *Corymbia*–*Angophora* clade and some taxa within *Eucalyptus*, where necessary, to achieve monophyly of higher taxa within the Eucalypteae, particularly genera.

2 Material and Methods

2.1 Sampling

Hereafter, the term “eucalypts s.l.” refers to the clade comprising *Angophora*, *Corymbia*, and *Eucalyptus*. “*Corymbia* s.l.” refers to the *Corymbia* clade, comprising *Corymbia* subg. *Corymbia*, *Corymbia* subg. *Blakella* and *Angophora* (Fig. 2). Sampling represented all genera within Myrtaceae tribe Eucalypteae *sensu* Wilson et al. (2005) except *Allosyncarpia*, *Eucalyptopsis*, and *Stockwellia*. Within the eucalypts, both subgenera of *Corymbia* (Parra-O et al., 2009) and six of eight subgenera of *Eucalyptus*—except *Acerosae* (*Eucalyptus curtisii*) and *Alveolata* (*Eucalyptus microcorys*), both of which are monotypic—were sampled. There were 392 species-level taxa, including eleven outgroups, which were selected based on whole-of-family phylogenies by Wilson et al. (2005) and

Thornhill & Crisp (2012), Thornhill et al. (2015), and included species of *Osbornia* and *Melaleuca* (tribe Melaleuceae), *Backhousia* (tribe Backhousieae), *Tristaniopsis* (tribe Kaniaceae), *Syncarpia* (tribe Syncarpieae), and *Arillastrum* (tribe Eucalypteae). The tree was rooted between Melaleuceae and the rest, based on earlier studies (Wilson et al., 2005; Thornhill et al., 2015).

Most samples were field-collected leaf tissue with vouchers lodged in the Australian National Herbarium (CANB), where the identifications were verified by Andrew Slee. These were supplemented by leaf samples taken directly from CANB herbarium sheets with permission. Samples from Currency Creek Arboretum (Currency Creek, South Australia) and the Australian National Botanic Gardens (Canberra) were taken with permission from vouchered living trees (details in Thornhill et al., 2015). All taxa and accessions sampled are listed in Suppinfo S1, and the nomenclature follows Slee et al. (2020), which largely follows Brooker (2000) for *Eucalyptus* and Hill & Johnson (1995) for *Corymbia*. In case of conflicts between authorities, we follow the Australian Plant Census (APC, <https://biodiversity.org.au/nsi/services/search/taxonomy>).

2.2 Target capture and sequencing

As data for this study were acquired prior to the angiosperm 353 capture set (Johnson et al., 2019) becoming available, we used a target-capture approach aimed at identifying and sequencing up to 200 orthologous low-copy loci from the nuclear genome with the potential to resolve species-level relationships across the large family Myrtaceae, as per Choi et al. (2019).

In plates of 48 samples, the pooled DNA library for each specimen was hybridized to the target probes using the SeqCap EZ Developer Library (NimbleGen, Madison, WI, USA) following the manufacturer's instructions with minor modifications detailed in Choi et al. (2019). Recovery and wash of hybridized samples were carried out using the SeqCap Hybridisation and Wash Kit (NimbleGen, Mannheim, Germany) following the manufacturer's instructions. After indexing-PCR and purification, the captured libraries were sequenced on the Illumina MiSeq platform (one pool of 48 samples) and the HiSeq. 2000 (all other pools) platform (100 bp paired-end read protocol) at the Bio-molecular Research Facilities at The Australian National University.

2.3 Data handling and mapping of reads

The quality of the raw reads was investigated using FastQC (Andrews, 2010) (<http://www.bioinformatics.babraham.ac.uk/projects/fastqc/>). BBduk within BBTools was used to remove Illumina adaptors, low-quality reads and sequences using standard parameters (trimq = 30, minlen = 40, ktrim = r, hdist = 1, tpe tbo; <http://jgi.gov/data-and-tools/bb-tools/>). The cleaned reads were re-checked using FastQC. After read cleaning, axe demultiplexer was used to sort reads by barcode using standard parameters (<https://manpages.debian.org/testing/axe-demultiplexer/axe-demux.1.en.html>). The reads were mapped against the *Eucalyptus grandis* targets using bwa-mem (Li & Durbin, 2009). Sam files were converted to bam, sorted, and indexed using samtools v1.3.1 (Li et al., 2009). Picard was used to remove duplicates

(<http://broadinstitute.github.io/picard/>). Finally, Platypus was used to call variants with standard parameters (Rimmer et al., 2014).

2.4 Sequence alignment and editing

Sequences were imported into Geneious Prime ver. 2020.1.2 (Biomatters Ltd.) for assembly, alignment, and editing. Initially, each locus was aligned separately across all samples using MAFFT ver. 1.4.0 (Biomatters Ltd.). After trimming, alignments were adjusted by eye. This included deleting sites with >95% missing data. A Neighbour Joining tree was generated for each locus and inspected for anomalies, such as likely chimeric sequences indicated by long, often misplaced branches. Every locus was assessed for paralogy (multiple gene copies) as indicated by concerted sharing of polymorphisms among distantly related taxa, and such loci were excluded. Randomly scattered polymorphic base calls were assumed to indicate allelic variation, and such loci were retained. Ninety-nine of the 200 targeted genes were discarded, leaving 101 putatively single-copy genes. These were concatenated using Geneious. All samples with >60% of concatenated sequence missing were culled, leaving 392 of 521 of the original eucalypt + outgroup sequences in the final alignment, which totalled 129 354 base pairs, comprising 27 100 parsimony-informative sites, 14 807 singleton sites, and 87 447 constant sites. The final set of 101 loci are listed in Suppinfo S2, identified by their labels in the annotated *E. grandis* genome (Myburg et al., 2014).

2.5 Phylogenetic analysis

Phylogenies were first estimated from the concatenated sequences of all 101 nuclear loci, initially treated as a single partition, using maximum likelihood (ML) as implemented in RAxML ver. 8.2.12 (Stamatakis, 2014) on the CIPRES Science Gateway (Miller et al., 2010) with a GTR + G model. Additionally, ML analyses were run using IQtree ver. 1.6.10 (Nguyen et al., 2015), first with a single partition and then with the DNA divided into 101 partitions (loci: Suppinfo S2), each with its own model (Chernomor et al., 2016), estimated using ModelFinder (Kalyanamoorthy et al., 2017). Node support was estimated using ultrafast bootstrap (UFB) with 1000 replicates (Minh et al., 2013; Hoang et al., 2018), as well as site (sites concordance factor [sCF]) and gene (genes concordance factor [gCF]) concordance factors (Minh et al., 2020). Site concordance is measured using 100 randomly resampled quartets: for an internal branch in a rooted tree, there are three possible quartets, so the null expectation is 33% of sites. Gene concordance measures the proportion (%) of genes supporting the branch. In a different approach, we estimated the species tree using the 101 individual gene trees from IQtree with the multispecies coalescent model implemented in Astral-II (Mirarab & Warnow, 2015). In an Astral tree, internal branch lengths are in coalescent units and branch support is estimated by local posterior probability (LPP), which is the probability that this is the true branch given the set of gene trees (computed based on the quartet score and assuming incomplete lineage sorting).

2.6 Approximately unbiased (AU) tests of alternative topologies

Using each IQtree (single- and multipartition), in turn, we tested the alternative relationships among *Arillastrum* and the eucalypt genera (*Angophora*, *Corymbia*, and *Eucalyptus*) with the AU test of Shimodaira (2002) using 1000 replicates. The first question was whether some of the eucalypt genera are more closely related to *Arillastrum* than to the rest of the eucalypts; in other words, could we rule out that *Arillastrum* is nested within the eucalypt clade? The second question asked whether *Corymbia* is monophyletic, particularly in relation to *Angophora*, given the contrasting findings in earlier studies, reviewed above.

2.7 Mapping of perianth traits

The IQtrees with branch lengths were imported to Mesquite ver. 3.61 (Maddison & Maddison, 2019) for trait mapping and hypothesis testing. Relevant trait data from Euclid edition 4 (Slee et al., 2020) were also imported to Mesquite. We defined the following three characters for testing hypotheses about perianth evolution.

2.7.1 Character 1, compound petals (Drinnan & Ladiges, 1988)

1.1: Petals simple (Fig. 1A). 1.2: Petals compound with keel and limb differentiation (Fig. 1B). The developmental studies by Drinnan and Ladiges led to their recognition of a homologous keel-and-limb petal structure throughout *Angophora* and *Corymbia*. However, the interpretation of this character is unclear in *Eucalyptus*. Drinnan & Ladiges (1989a, 1989c) considered the four adaxial buttresses of the petals in *Eucalyptus* subg. *Eudesmia*, on which the stamens develop to be homologous with the keel component of the compound petals in *Angophora* and *Corymbia*. In other subgenera of *Eucalyptus* (Drinnan & Ladiges, 1989b, 1989c, 1991b), these authors described the circumfloral buttress that bears the stamens ("stemonophore") as arising between the corolla and gynoecium. Later (Ladiges et al., 1995), they coded the stamen-bearing buttress as a separate (nonhomologous) character in eudesmids (*E. subg. Eudesmia*) in contrast to the stemonophore of *Eucalyptus* subg. *Eucalyptus* and *Eucalyptus* subg. *Symphyomyrtus*. Hill & Johnson (1995) demurred, suggesting a single origin of the stemonophore, followed by losses (reversals) in some eucalypt lineages. Given these differing interpretations, we scored this character as uncertain (?) in all species of *Eucalyptus* except eudesmids.

2.7.2 Character 2, corolla type

2.1: Free petals (Figs. 1A, 1B). 2.2: Single operculum lacking discernable petaline parts. 2.3: Single operculum of connate, discernable petals with sutures and/or free tips (Figs. 1D, 1F). 2.4: Forming a double operculum with the calyx (Figs. 1E, 1G). 2.5: Petals are discernable inside and shed with the sepaline operculum.

In some species of *Corymbia sensu stricto* (= *Corymbia* B, *sensu* Steane et al. 2002), separate petals are reported to be discernable to varying degrees in early development of the bud, for example, *Corymbia arnhemensis*, *Corymbia calophylla*, *Corymbia ficifolia*, *Corymbia gummifera*, *Corymbia intermedia*, *Corymbia jacobsoniana*, *Corymbia ptychocarpa*, and *Corymbia trachyphloia* (Willis, 1951; Drinnan & Ladiges, 1988; Hill & Johnson, 1995) but are retained inside and adherent to the

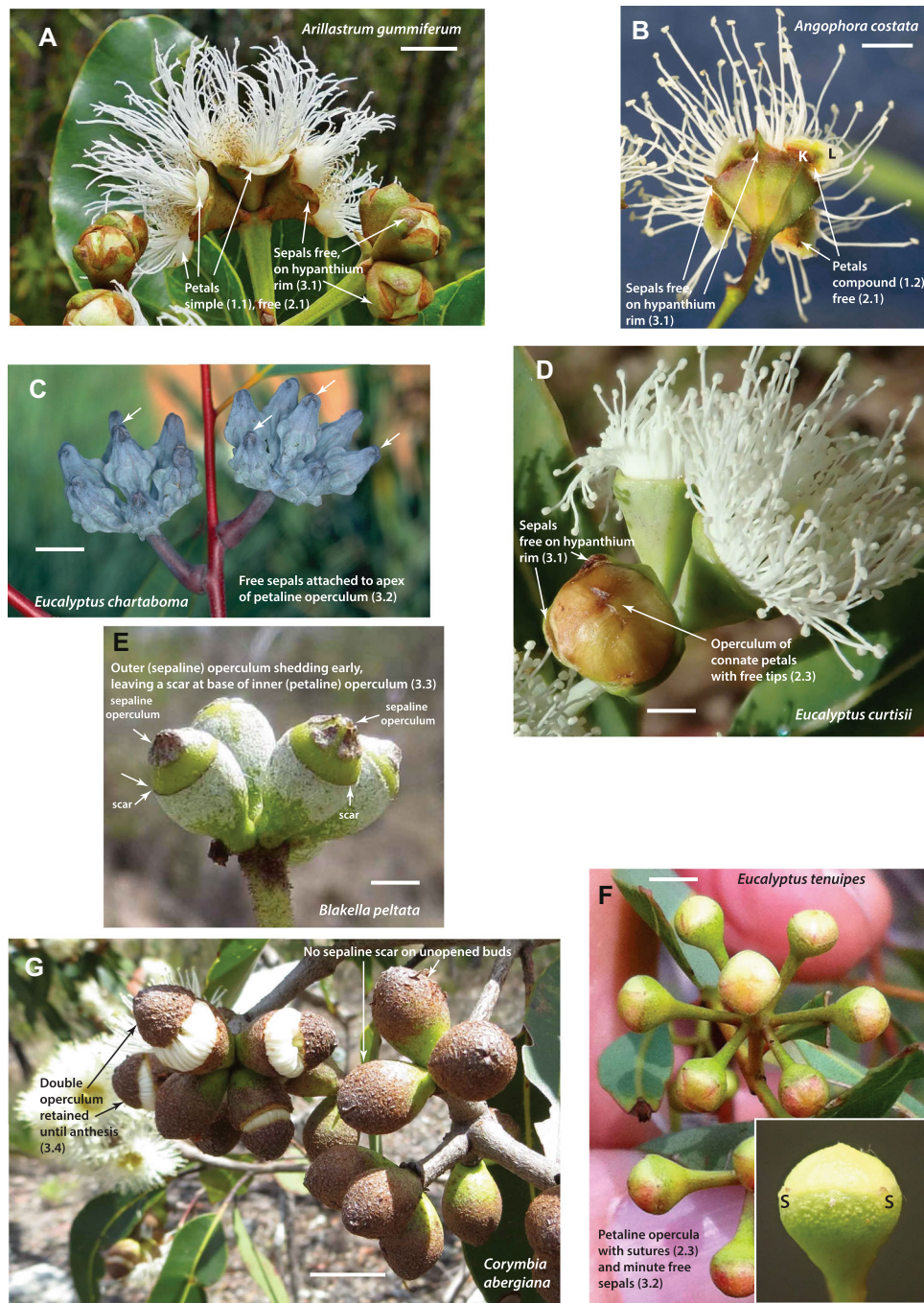


Fig. 1. (next page) Perianth characters used for mapping on the phylogeny. **A**, *Arillastrum gummiferum*: Petals simple (1.1) and free (2.1); sepals free, inserted on hypanthium rim (3.1) (Photo: Benoît Henry). **B**, *Angophora costata*: Petals compound (1.2), each with a limb (L) and keel (K), and free (2.1); sepals free and acuminate, inserted on hypanthium rim (3.1) (Photo: Benoît Henry). **C**, *Eucalyptus chartaboma*: Sepals (arrowed) free, attached to the tip of petaline operculum (3.2) (Photo: © M. Fagg 1977). **D**, *Eucalyptus curtisii*: Operculum of discernable, connate petals with free tips (2.3); sepals free, inserted on hypanthium rim (3.1) (Photo: M. Crisp). **E**, *Blakella peltata*: Outer (sepaline) operculum fragmenting and shedding early, leaving a scar at the base of the inner (petaline) operculum (3.3) (Photo: M. Crisp). **F**, *Eucalyptus tenuipes*: Operculum of marginally connate petals with visible sutures (2.3) and minute-free sepals (S in inset) attached to hypanthium rim, alternating with petals (3.2) (Photo: M. Crisp). **G**, *Corymbia abergiana*: Double operculum, shed as a whole at anthesis (3.4), hence showing no scar such as seen in taxa in which the outer (sepaline) operculum is shed early (Photo: M. Crisp). Decimal numbers refer to characters and states defined in Section 2. Scale bars: A = 15 mm; B = 5 mm; C = 10 mm; D = 2 mm; E = 5 mm; F = 2.5 mm (main) and 1 mm (inset); G = 10 mm.

underside of the sepaline operculum until anthesis (Hill & Johnson, 1995). We examined buds at anthesis of four of these species, and it was clear that the separate petals had fused fully with the sepaline operculum. Nevertheless, these species are scored here as having a separate character state (2.5) for this trait.

All eudesmids (*E. subg. Eudesmia*) have a single (petaline) operculum (character state 2.2), but in some species, the sepals are attached to the apex of the operculum (character state 3.2, Fig. 1C). However, the sepals remain separate from each other, and no eudesmid forms a sepaline operculum as such (Gibbs et al., 2009).

2.7.3 Character 3, calyx type

3.1: Free sepals, attached to hypanthium rim (Figs. 1A, 1B, 1D, 1F). 3.2: Free sepals, attached to the apex of petaline operculum (Fig. 1C). 3.3: Sepaline operculum, shed before petaline operculum or as a separate structure from petaline (inner) operculum at anthesis (Fig. 1E). 3.4: Sepals fused with petals into a double operculum, which is evident from the absence of a scar prior to anthesis, when both opercula are shed as a unit (Fig. 1G). 3.5: Calyx nil at any stage of floral development (*E. subg. Eucalyptus* only).

The calyx was assumed to be absent in *E. subg. Eucalyptus* based on a comparative developmental study of species from this subgenus and *Eucalyptus cloeziana* (*Eucalyptus subg. Idiogenes*), which was considered closely related (Drinnan & Ladiges, 1989b). Hill & Johnson (1995) disagreed, suggesting, on the basis of their unpublished observations of operculum development in these taxa, that the operculum in *E. subg. Eucalyptus* is a composite of calyx and corolla, similar to that of *Eucalyptus* sect. *Miniatae*. In these eudesmids, separate sepals are visible at the apex of the mature petaline operculum (Fig. 1C). However, the operculum of *E. subg. Eucalyptus* shows no evidence of sepals at any stage of development (Drinnan & Ladiges, 1989b). Therefore, we scored the corolla type of *E. subg. Eucalyptus* as a single petaline operculum (character state 2.2) and the calyx type as nil (character state 3.5).

The following manipulations were made to the trees to explore the effects of alternative topologies on the inferred evolution of perianth traits: (i) alternative placement of *Arillastrum* as sister to *Corymbia* + *Angophora*, which was not rejected by the AU test; and (ii) alternative placement of *Angophora* as sister to *Corymbia subg. Blakella*, which was not decisively ruled out by the AU test. Models used for trait reconstruction were parsimony (unordered coding) and Mk1 (Asymmetrical Markov k-state 2 parameter model: Lewis, 2001; Maddison & Maddison, 2019).

3 Results

3.1 Phylogeny

The entire single-partition IQtree is shown in Figs. 2–4. Branch support values are omitted from this figure due to insufficient room and instead are shown for all nodes in Suppinfo S3. Additionally, support for important nodes (only) is shown in Tables 1 (molecular), 2 (morphology), and Suppinfo S4 and referenced by numbered nodes in Figs. 2–4 and the circle tree in Suppinfo S5. In this (single-partition)

IQtree, *Angophora* is nested within *Corymbia* s.l., as these genera are currently defined (Hill & Johnson, 1995; Slee et al., 2020) (Fig. 2). *Corymbia* s.l. is split into two clades (Fig. 2; Tables 1), being *Corymbia subg. Blakella* and *Corymbia subg. Corymbia*, with *Angophora* sister to *C. subg. Corymbia* (red bloodwoods). *Angophora* + *Corymbia* is sister to *Eucalyptus*, with *Arillastrum* sister to these (Fig. 2). This same result was obtained from all analytical methods: IQtree with one (Fig. 2; Suppinfo S3) and 101 partitions (Suppinfo S6), Astral (Suppinfo S7) (Tables 1 and 2), and RAXML.

In the single-partition IQtree, branch support (Table 1) for all the above relationships was very high (99–100) as measured by UFB. Similarly, LPP in the Astral tree was 1.0 at all these nodes. Concordance factors varied among these nodes: they were high for the most recent common ancestor (MRCA) of *Corymbia* s.l., which included *Angophora* (gCF = 86, sCF = 88), and for *Eucalyptus* as currently defined (gCF = 91, sCF = 86). Concordance factors were lower for *C. subg. Blakella* (gCF = 45, sCF = 67–68), for *C. subg. Corymbia* (gCF = 22, sCF = 64–66), and also for two other clades relevant to the generic definition: (i) the eucalypts s.l. clade (i.e., *Angophora* + *C. subg. Blakella* + *C. subg. Corymbia* + *Eucalyptus*) (gCF = 45, sCF = 34–35), which is sister to *Arillastrum*; and (ii) the sister-group relationship between *C. subg. Corymbia* and *Angophora* (gCF = 17, sCF = 43–44).

We used AU tests to compare relationships (i) and (ii) above with their alternatives (Fig. 5). A sister-group relationship between *Arillastrum* and *Eucalyptus* was rejected ($P = 0.017$), but a sister relationship between *Arillastrum* and *Corymbia* + *Angophora* to the exclusion of *Eucalyptus* was not ($P = 0.187$). Monophyly of *Corymbia* with respect to the exclusion of *Angophora* was strongly rejected ($P < 0.0007$), and a sister-group relationship between *Angophora* and *C. subg. Blakella* to the exclusion of *C. subg. Corymbia* was also rejected but with marginal significance ($P = 0.040$).

Concordance factors for all nodes in the single-partition IQtree were plotted to show the relationship between sCF and gCF (Suppinfo S8). The plot was skewed, with gCF scores consistently lower than corresponding sCF values for the same nodes. This perhaps resulted from our targeting of highly conserved exons. We observed little variation within many exons, especially the short ones (Suppinfo S2 and S9) —in nearly all loci, <20% of sites were variable. Such loci might have zero information relative to the existence of particular nodes. In contrast, sCF considers the whole alignment for each node, so lack of variation within individual exons has less influence on this statistic.

Putative recognition traits for the major clades within Eucalypteae, including genera and above, are shown in Table 2 with references, and a key to eucalypt genera using morphology is provided in the Taxonomy section. Some phenotypic traits appear to be unique and unreversed (synapomorphic), for example, bristle glands in clade 2 (*Corymbia* s.l., incl. *Angophora*); sepal and petal morphology in *Angophora*; stemonophore and ovule arrangement in *Eucalyptus*. Other traits are homoplastic, being found elsewhere in the eucalypts or Myrtaceae, or are absent in a few species of the clade. The latter have been included because they are macroscopic and useful for diagnosis from closely related clades. For example, *C. subg. Blakella* and *C. subg. Corymbia* both have double opercula in all species, but

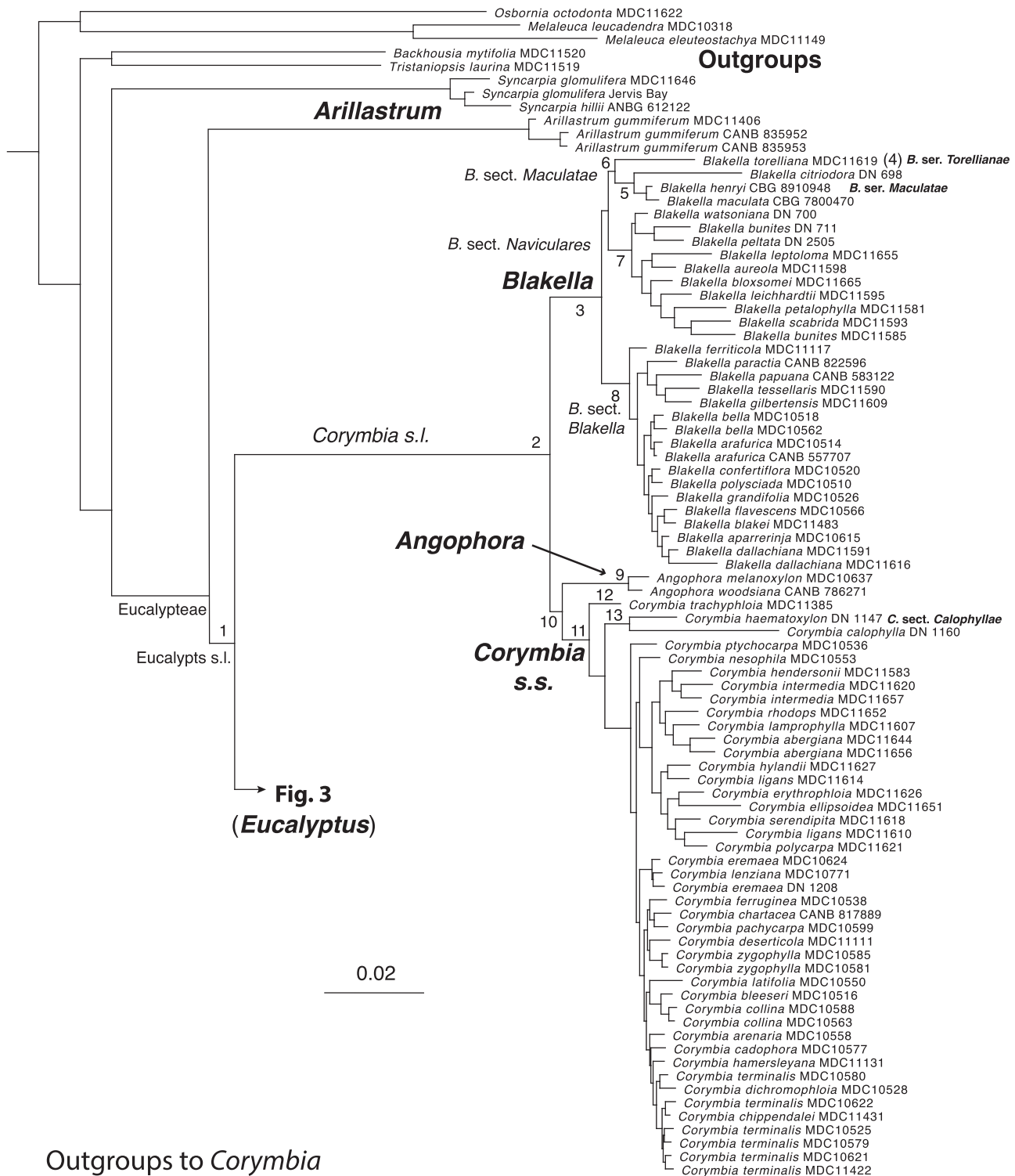
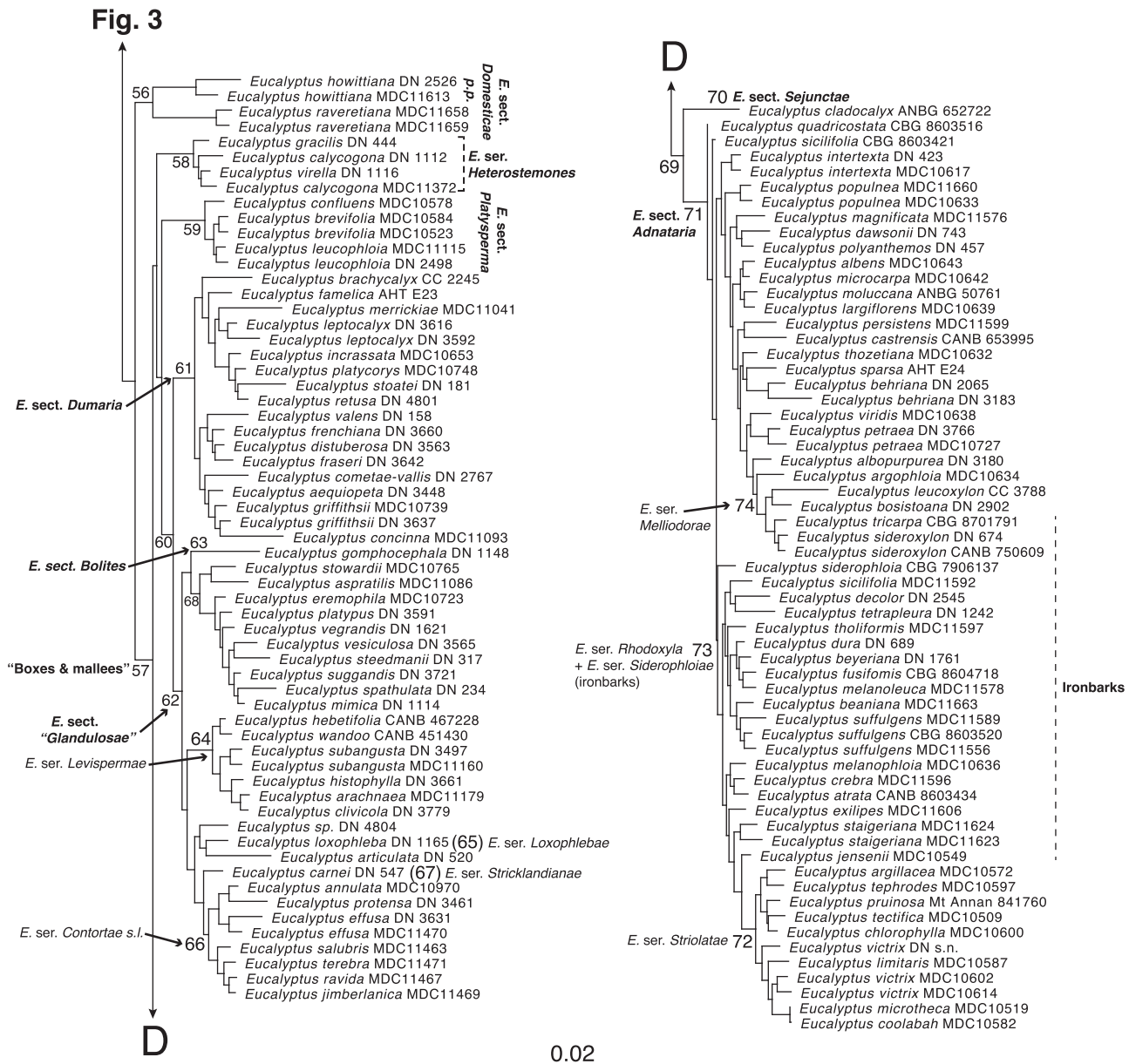


Fig. 2. The single-partition maximum likelihood phylogeny: outgroups to *Corymbia*. Tree estimated from concatenated sequences of 101 nuclear loci using IQtree ver. 1.6.10 (Nguyen et al. 2015) with a model estimated using ModelFinder (Kalyaanamoorthy et al., 2017). Support values are not shown due to lack of space. Most numbers at nodes refer to notes, including support statistics, in the text, Tables 1 and 2 and/or Suppinfo S3–S4. Some numbers refer to terminal branches. Scale bar represents substitutions per site.



Fig. 3. The single-partition maximum likelihood phylogeny: *Eucalyptus* part 1. Tree estimated from concatenated sequences of 101 nuclear loci using IQtree with ModelFinder. Support values are not shown due to lack of space. Most numbers at nodes refer to notes, including support statistics, in the text, Tables 1 and 2 and/or Suppinfo S3–S4. Some numbers refer to terminal branches. Scale bar represents substitutions per site.



Eucalyptus subg. *Symphyomyrtus* (part 2)

Fig. 4. The single-partition maximum likelihood phylogeny: *Eucalyptus* subg. *Symphyomyrtus*, part 2. Tree estimated from concatenated sequences of 101 nuclear loci using IQtree with ModelFinder. Support values are not shown due to lack of space. Most numbers at nodes refer to notes, including support statistics, in the text, Tables 1 and 2 and/or Suppinfo S3–S4. Some numbers refer to terminal branches. Scale bar represents substitutions per site.

in *C.* subg. *Blakella*, the outer (sepaline) operculum is usually shed before anthesis, whereas in *C.* subg. *Corymbia*, both opercula are shed together at anthesis. Double opercula also occur in *Eucalyptus* subg. *Symphyomyrtus*, apparently an independent origin within the genus (Suppinfo S10). It is worth noting that although the sister-group relationship between *Angophora* and *C.* subg. *Corymbia* is not strongly supported by the DNA (gCF 17 and sCF 43–44); two phenotypic traits support this clade (Table 2). One is that

both taxa are hosts to the galling scale insect genus *Ascelis*, and the other is stigmas mop-like with long papillae (Boland & Sedgley, 1986).

Currently recognized infrageneric taxa within *Eucalyptus* were assessed by comparing the nDNA topologies with the classification of Nicolle (2022). Many are supported as monophyletic, while others are not. Seventy-four current taxa from subgenus to series rank are numbered in Figs. 2–4 and Suppinfo S5–S6 (though some of these are represented

Table 1 Main eucalypt clades: molecular support

Clade name	Node number	Sister	One partn			101 partns		
			One partn IQtree UFB	One partn IQtree gCF	One partn IQtree sCF	Astral LPP	101 partns IQtree UFB	101 partns IQtree sCF
Eucalypts s.l. (Angophora + Corymbia s.l. + Eucalyptus)	1	Arillastrum	99	45	35	1.0	99	34
Corymbia s.l. including Angophora	2	Eucalyptus	100	86	88	1.0	100	87.7
Corymbia subg. Blakella	3	Angophora + Corymbia subg. Corymbia	100	45	66.7	1.0	100	68
Angophora	9	Corymbia subg. Corymbia	100	67	90.8	1.0	100	91.4
Angophora + Corymbia subg. Corymbia	10	Corymbia subg. Blakella	100	17	44	1.0	100	43.2
Corymbia subg. Corymbia	11	Angophora	100	21.6	65.7	1.0	100	64
Eucalyptus	14	Corymbia s.l. including Angophora	100	91	86	1.0	100	86

Clade (node) numbering corresponds with Figs. 2–4 and Suppinfo S4; gCF, genes concordance factor; LPP, local posterior probability; partn, partition; sCF, sites concordance factor; UFB, ultrafast bootstrap.

by a single terminal branch). These taxa are also listed in Tables 1 and 2 and Suppinfo S4, showing branch support (where applicable) by the indices used above, plus diagnostic morphological characters and taxonomic comments. Results within the *Angophora–Blakella–Corymbia* clade are described above. Within *Eucalyptus*, *Eucalyptus* subg. *Eudesmia* (node 15) is strongly supported, but the three trees (IQtree 1 partition, IQtree 101 partitions, and Astral) each show a different relationship of *E. similis* to the other two clades (*Eucalyptus* sect. *Limbatae* and *Eucalyptus* ser. *Miniatae*).

Eucalyptus subg. *Eucalyptus* (22, monocalypts) is a supported clade with the monotypic subgenera *Eucalyptus* subg. *Cuboidea* (20, *Eucalyptus tenuipes*) and *E. subg. Idiogenes* (21, *Eucalyptus cloeziana*) as its successive sisters. Within the monocalypts, taxa supported as clades include the jarrah/tingle group (25, *Eucalyptus* sect. *Longistylus*), white mahoganies (26, *Eucalyptus* sect. *Amentum*), stringybarks (31, *Eucalyptus* sect. *Pachyphloiae*). Clade 32, comprising the ashes, snow gums, and peppermints, is unnamed. The mainly Western Australian *Eucalyptus* sect. *Frutices* (28) is monophyletic, but contra Nicolle (2022) does not include *Eucalyptus suberea* (23), which is sister to the rest of *E. subg. Eucalyptus* (24). Finally, the rare and distinctive woolly-barked *Eucalyptus rubiginosa* (27, *Eucalyptus* subg. *Primitiva* Brooker) from SE Qld is placed as a sister to *E. sect. Amentum* (26, white mahoganies) and should be reduced to sectional rank like its sister group to correct the nesting of one subgenus within another (*E. subg. Eucalyptus*).

Eucalyptus subg. *Symphyomyrtus* (Figs. 3–4) is the largest subgenus with ca. 470 species (Nicolle & Jones, 2018). Our data support the monophyly of several of its sections: *Eucalyptus* sect. *Curviptera* (40), including spectacular flowering mallees such as *Eucalyptus macrocarpa* and *Eucalyptus youngiana*; *Eucalyptus* sect. *Pumilio* (48, grey gums); *Eucalyptus* sect. *Exsertaria* (49, red gums including the iconic *Eucalyptus camaldulensis*); *Eucalyptus* sect. *Platysperma* (59, tropical snappy gums); *Eucalyptus* sect. *Dumaria* (61, mainly southern mallees and mallets). Sister to *Eucalyptus* sect. *Sejunctae* (70, the monotypic sugar gum) is *Eucalyptus* sect. *Adnataria* (71), the species-rich boxes and ironbarks. This clade is poorly resolved internally, although the included *Eucalyptus* ser. *Melliodorae* (74) is monophyletic and has several morphological synapomorphies, for example, a broad deciduous stemonophore, five or more fruit valves, sterile outer stamens and axillary inflorescences. Our trees support *Eucalyptus* sect. *Maidenaria* *sensu stricto* (55, a diverse group of eastern forest trees including the Tasmanian blue gum, *Eucalyptus globulus*). However, *Eucalyptus* sect. *Latoangulatae sensu Nicolle & Jones* (2018) and Nicolle (2022) is paraphyletic because it includes *E. sect. Maidenaria*. This problem could be resolved by formally merging *Latoangulatae* and *E. sect. Maidenaria* s.l. (54), but the relationships between the species in these two sections warrant a more thorough investigation of alternatives before formalizing any taxonomic change.

The four species of “tropical boxes,” comprising *Eucalyptus deglupta* (35, *Eucalyptus* sect. *Equatoria*), and *Eucalyptus brachyandra*, *Eucalyptus howittiana*, and *Eucalyptus raveretiana* (*Eucalyptus* sect. *Domesticae*, 35 and 56),

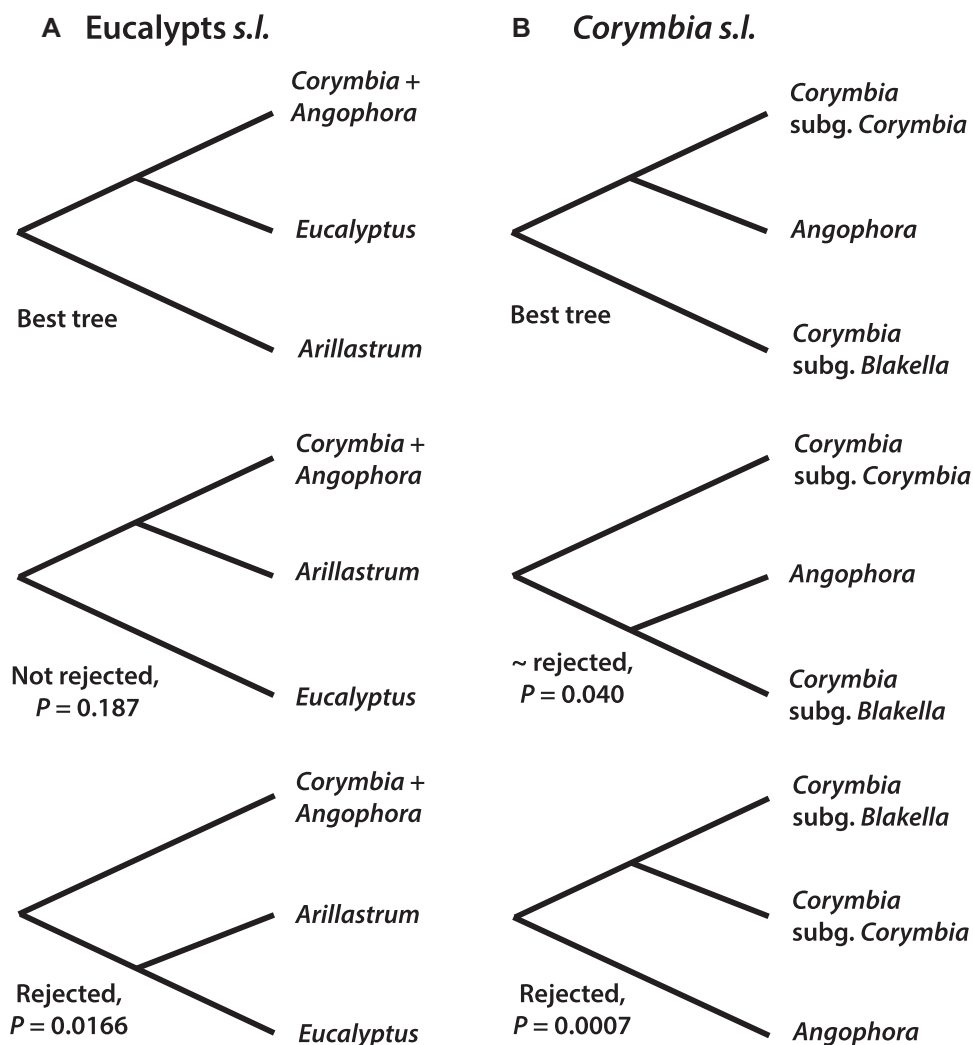


Fig. 5. Approximately unbiased (AU) tests (Shimodaira, 2002) of alternative resolutions of clades relevant to the definition of genera. **A**, *Eucalypts* s.l., comprising *Arillastrum*, *Eucalyptus*, and *Corymbia* + *Angophora*. **B**, *Corymbia* s.l., comprising *Corymbia* subg. *Blakella*, *Corymbia* subg. *Corymbia*, and *Angophora*. Each column shows the three alternative topologies under test for that clade. Note that *Corymbia* s.l. (B) is nested within *eucalypts* s.l. (A) but each of these relationships was tested separately. The “best tree” at the top of each column is from the single-partition IQtree (Figs. 2–4).

are problematic because they do not find a stable position in the different analyses, but are placed as sister to either of two major clades (37 and 57) within *E.* subg. *Symphyomyrtus* (Figs. 3–4, Suppinfo S5–S7). Moreover, in different analyses, different combinations of the four species are placed at each node, and there is weak support for any relationship. These species should remain as currently classified at sectional rank pending further investigation.

The previously recognized *Eucalyptus* sect. *Bisectae* was found to be nonmonophyletic, splitting into two separate supported clades: *E.* sect. *Bisectae* s.s. (38) and *Eucalyptus* sect. “*Glandulosae*” Nicolle *ined.* (62). These correspond, respectively, to the *Bisectae* I and *Bisectae* II clades of Steane et al. (2002). *Eucalyptus* sect. “*Glandulosae*” is sister to *E.* sect. *Dumaria* (61) in a moderately supported clade (60) and comprises *Eucalyptus* ser. *Elongatae*, *Clinatae*, *Erectae*, *Lehmannianae*, *Levispermae*, and *Dundasianae* (Nicolle, 2022). *Glandulosae* could be merged with a single, expanded *E.* sect.

Dumaria (D. Nicolle, pers. comm., 2023), but a complicating factor is that the monotypic *Eucalyptus* sect. *Bolites* (*Eucalyptus gomphocephala*), which is inside (Fig. 3) or sister to (62a in 101 partn tree) *Glandulosae*, has equal priority with *E.* sect. *Bolites*.

3.2 Perianth evolution on the phylogeny

Trait maps on the single-partition tree and on alternative topologies imply homoplasy in the perianth evolution of the eucalypts, specifically with respect to the origins of the bud cap (operculum or calyptra), which was traditionally used to define *Eucalyptus*, including the bloodwoods (currently in *Corymbia*).

3.2.1 Compound petals (keel & limb) (Character 1: Suppinfo S11)

Compound petals are absent in the outgroups, and petals are reconstructed as likely to have been simple in the MRCA of Eucalypteae (parsimony unequivocally so; Mk1 proportional

Table 2 Main eucalypt clades: morphological support

Clade name	Node number	Sister	Characters
Eucalypts s.l. (<i>Angophora</i> + <i>Corymbia</i> s.l. + <i>Eucalyptus</i>)	1	<i>Arillastrum</i>	Adult leaves with many (>10) lateral veins (LH, 1983; HJ, 1995).
<i>Corymbia</i> s.l. including <i>Angophora</i>	2	<i>Eucalyptus</i>	Seedlings have bristle glands (raised multicellular oil glands with four micropapillate cap cells) (L, 1984; HJ, 1995). Xylem vessels solitary (JB, 1984; HJ, 1995).
<i>Corymbia</i> subg. <i>Blakella</i>	3	<i>Angophora</i> + <i>Corymbia</i> subg. <i>Corymbia</i>	Sepaline operculum shed early (scar present, except sometimes in <i>Maculatae</i>) (Fig. 1E). Also occurs in <i>Eucalyptus</i> subg. <i>Symphyomyrtus</i> .
<i>Angophora</i>	9	<i>Corymbia</i> subg. <i>Corymbia</i>	Sepals free on hypanthium rim, rigid, and subulate (Fig. 1B). Mature petals free and clearly compound, with keel and limb of contrasting texture and colour (Fig. 1B). Petal keels resembling and functioning like sepals, protecting unopened bud (Fig. 1B). Host-specific galling scale insects (<i>Ascelis</i>). Stigmas mop-like with long papillae (Boland & Sedgley, 1986).
<i>Angophora</i> + <i>Corymbia</i> subg. <i>Corymbia</i>	10	<i>Corymbia</i> subg. <i>Blakella</i>	Operculum double, shed intact at anthesis (HJ, 1995). (Fig. 1G)
<i>Corymbia</i> subg. <i>Corymbia</i>	11	<i>Angophora</i>	Seeds winged (absent in <i>C. sect. Calophyllae</i>). Operculum petaline (Figs. 1C, 1D, 1F); double by the inclusion of calyx in <i>E. subg. Symphyomyrtus</i> .
<i>Eucalyptus</i>	14	<i>Corymbia</i> s.l. including <i>Angophora</i>	Stemonophore develops from basal buttress of petals (DL, 1989; HJ, 1995; onwards). Placental elongation unidirectional, resulting in a regular, even number of ovule columns (BD, 2005).

Clade (node) numbering corresponds with Figs. 2–4 and Suppinfo S4.; B&D, Bohte & Drinnan (2005); BS, Boland & Sedgley (1986); DL, Drinnan & Ladiges (1988, 1989a, 1989b, 1989c, 1991a, 1991b); JB, Johnson & Briggs (1984); HJ, Hill & Johnson (1995); L, Ladiges (1984); LH, Ladiges & Humphries (1983).

likelihood = 0.808). Thereafter, petals transition to compound in the MRCA of *Eucalyptus* s.s. (parsimony unequivocal; Mk1 proportional likelihood 0.901). Compound petals reconstruct as uniformly present throughout *Angophora* and *Corymbia* s.l., including their MRCA, under both models (e.g., Mk1 proportional likelihood = 0.9999). Compound petals also map as present throughout the eudesmids and their MRCA and, according to parsimony, the MRCA of *Eucalyptus*; however, Mk1 indicated an equivocal reconstruction in the MRCA of *Eucalyptus*, presumably due to the “unknown” score for all included species.

3.2.2 Corolla type (Character 2: Suppinfo S10)

In all extant species of *Corymbia* and *Eucalyptus*, the mature corolla forms a petaline or double operculum, whereas both *Angophora* and the outgroups have free petals. According to both likelihood and parsimony reconstructions, the MRCA of eucalypts s.l. most likely had free petals (Mk1 proportional likelihood = 0.935). Parsimony inferred free petals in the MRCA

of *Angophora* + *Corymbia* s.l., as well as in the MRCA of *Angophora* (which has free petals) + *C. subg. Corymbia* (in which the petals are incorporated into a double operculum in the mature bud). The Mk1 reconstruction of the corolla type in the *Angophora*–*Corymbia* clade is more equivocal with free petals, most likely in the MRCA of *Angophora* + *Corymbia* s.l. (proportional likelihood = 0.677), while discernable petals inside a double operculum (0.128) or petals and sepals forming a double operculum (0.191) were much less likely. In the MRCA of *Angophora* + *Corymbia* s.s., the Mk1 reconstruction of this character is similarly equivocal (free petals = 0.687; separately discernable = 0.165; part of a double operculum = 0.146).

A transition from free petals to a single petaline operculum was reconstructed in the MRCA of *Eucalyptus* (Mk1 proportional likelihood = 0.874). Within this genus, there was a transition to a double operculum (comprising fused sepals as well as petals) in *E. subg. Symphyomyrtus*, but the other subgenera retained a petaline-only operculum, in some cases with visible sutures between the fused petals.

3.2.3 Calyx type (Character 3: Suppinfo S12)

Free sepals attached to the hypanthium rim, the outgroup state, are reconstructed by Mk1 as likely retained in the MRCAs of *Angophora* + *Corymbia* s.l. (0.739), through the MRCA of *Angophora* + *C. subg. Corymbia* (0.757) to that of *Angophora* (1.000). Parsimony unequivocally reconstructs the retention of free sepals through all these successive MRCAs to *Angophora*. Independent transitions to a sepaline operculum in the MRCA of *Corymbia* subg. *Blakella* and that of *C. subg. Corymbia* is inferred by Mk1 (proportional likelihoods, respectively, 0.999 and 0.997). That the sepaline opercula in these genera had independent origins is supported by their subsequent development: in *C. subg. Blakella*, the sepaline operculum is shed early, or at least is separable from the petaline operculum at anthesis. By contrast, in *C. subg. Corymbia*, the sepaline operculum is retained and shed as a single unit combined with the petaline (inner) operculum at anthesis. Alternatively, we redefined the calyx character to three simple states: (i) sepals developed and free; (ii) sepals united into an operculum; (iii) sepals nil. When traced on the tree (not shown), there is a transition from free sepals to the operculate state in the MRCA of *Angophora*, *C. subg. Blakella* and *Corymbia*. This is followed by a reversal to free sepals in *Angophora*. The third state is present only in monocalypts, originating from the loss of free sepals in its immediate ancestor.

Free sepals reconstruct as retained in the MRCA of *Eucalyptus* (proportional likelihood = 0.995) and into some of its main clades, including subgenera *Cuboidea* (*E. tenuipes*), *Idiogenes* (*E. cloeziana*), *Cruciformes* (*Eucalyptus guilfoylei*), and sporadically as reversals within *E. subg. Symphyomyrtus* (e.g., *Eucalyptus mimica* and *Eucalyptus steedmanii*). The MRCA of *E. subg. Eudesmia* likely retained free sepals (0.793), which were subsequently retained through *E. sect. Limbatae*. However, in the remaining eudesmid lineages (*Eucalyptus* sect. *Miniatae* and *Eucalyptus* ser. *Similes*), there were one (or more) transitions to free sepals attached to the tip of the petaline operculum rather than to the hypanthium rim. This uncertainty in the number of transitions within eudesmids was also indicated by parsimony. The monocalypts all have a single, apparently noncomposite operculum, which we scored as petaline after Drinnan & Ladiges (1989b). It is worth noting here that the successive sister taxa to this subgenus (*E. subgenera Cuboidea* and *Idiogenes*) have minute-free, caducous sepals on the hypanthium rim. Therefore, the operculum of these taxa, including *E. subg. Eucalyptus*, appears to be entirely petaline in origin.

4 Discussion

A strong finding of this study is that *Angophora* is nested inside *Corymbia* s.l., in contrast to previous work that either found equivocal support for this relationship (Steane et al., 1999, 2002; Whittock et al., 2003; Thornhill et al., 2019) or found instead that *Angophora* and *Corymbia* s.l. were sister groups (Hill & Johnson, 1995; Ladiges et al., 1995; Udovicic & Ladiges, 2000; Parra-O et al., 2006; Ochieng et al., 2007a, 2007b). Some previous cpDNA phylogenies found *Corymbia* to be paraphyletic, with *Angophora* sister to

Corymbia subg. *Blakella* (Bayly et al., 2013; Schuster et al., 2018). In contrast, the latter study alternatively used nrDNA and found *Angophora* to be sister to *Corymbia* subg. *Corymbia*. In the present study, we found strong support for a sister-group relationship between *Angophora* and *C. subg. Corymbia*, relative to *C. subg. Blakella* (Tables 1 and 2). Also, in the present study, an AU test strongly rejected the monophyly of *Corymbia*, relative to *Angophora*, and also rejected a sister group relationship between *Angophora* and *C. subg. Blakella* (Fig. 5). The taxonomic implications of this are discussed below, where we conclude that *C. subg. Blakella* should be raised to generic rank, and we formalise the implied taxonomic changes in Section 5. Hereafter, we refer to this clade simply as “*Blakella*.”

Given this result and that *Blakella* and *Corymbia* s.s. both have petals united into opercula, are the free petals of *Angophora* a reversal of the condition in the outgroups? This seems unlikely, first, because the trait maps of corolla type in Suppinfo S10a,b suggest that *Angophora* has retained the outgroup state of free petals and that operculum originated independently in *Blakella* and *Corymbia* s.s. Supporting this inference, the petaline opercula of *Blakella* and *Corymbia* s.s. differ in ontogeny. *Blakella* has a double operculum, with the outer (sepaline) component being shed separately and early, while the inner (petaline) component is retained until anthesis (Fig. 1E; Suppinfo S12a, S12b). Note, however, that in the spotted gums (*Blakella* sect. *Maculatae*: *Blakella citriodora*, *Blakella henryi*, and *Blakella maculata*), the outer operculum can be retained late, even up to anthesis, and shed together with the inner operculum. *Corymbia* s.s. also has a double operculum, but it is retained intact as a single unit until anthesis (Fig. 1G; Suppinfo S12a, S12b). Admittedly, the Mk1 reconstruction of sepal evolution is somewhat equivocal (Suppinfo S12a), allowing with a low proportional likelihood (0.26) that the outer operculum might be retained until anthesis in the MRCA of *Angophora*, *Blakella*, and *Corymbia* s.s. Nevertheless, the proportional likelihood is much higher (0.74) that ancestrally free sepals were retained in the MRCA of that clade. Moreover, parsimony unequivocally supports the retention of ancestrally free sepals through to *Angophora* (Suppinfo S12b). We experimentally simplified the calyx character to three states: (i) sepals developed and free; (ii) sepals united into an operculum; (iii) sepals nil. When traced on the tree (not shown), there is a transition from free sepals to the operculate state in the MRCA of *Angophora*, *Blakella*, and *Corymbia*. This is followed by a reversal to free sepals in *Angophora*. Against this alternative hypothesis, the opercula in *Blakella* and *Corymbia* develop differently and are likely to have originated independently, with *Angophora* retaining the outgroup state (free sepals). The third state of the simplified character—sepals nil—is present only in monocalypts [*Eucalyptus* subg. *Eucalyptus*] and irrelevant to sepal evolution in *Angophora*, *Blakella*, and *Corymbia*.

4.1 *Eucalyptus*: one operculum or many?

Homoplasy in the opercula of eucalypts is not a new suggestion (e.g., Hill & Johnson, 1995; Ladiges et al., 1995). The MRCA of eucalypts s.l. reconstructs as most likely having free petals and sepals, as in the outgroups (Suppinfo S10, S12). From this common ancestor, opercula originated at least three times and more if subsequent parallel changes are

counted (Suppinfo S10, S12). As discussed above, double opercula likely arose independently in the MRCAs of *Blakella* and *Corymbia* s.s. In the MRCA of *Eucalyptus*, a petaline-only operculum likely originated from an ancestor with free petals, retaining sutures at the fused petal margins (proportional likelihood = 0.105; Suppinfo S10). Sutures are visible in the extant species of *Eucalyptus* subgenera *Cruciformes*, *Cuboidea*, and *Acerosae* (Figs. 1D, 1F). Also, free sepals have been retained as vestigial structures in multiple *Eucalyptus* subgenera, including *Acerosae* (Fig. 1D), *Cuboidea* (Fig. 1F), *Eudesmia* (Fig. 1C), *Idiogenes* (Slee et al., 2020), and *Symphyomyrtus* (*Eucalyptus mimica* and *Eucalyptus steedmanii*, Slee et al., 2020). Within *Eucalyptus* subg. *Eudesmia* sepals remain free from each other and are either attached to the rim of the hypanthium (group A: Gibbs et al., 2009) or attached to the petaline operculum (Fig. 1C) and still discernable (group B), at least in early development (Drinnan & Ladiges, 1989a, 1989c). The single, petaline operculum persisted into the main *Eucalyptus* lineages, then became double by the inclusion of the sepals in the MRCA of *Eucalyptus* subg. *Symphyomyrtus* s.l. (Suppinfo S10, S12). Within this subgenus, the sepaline (outer) operculum is shed prior to anthesis, leaving a circular scar, except in some species within *Eucalyptus* sect. *Adnataria* that are considered to retain both opercula until anthesis (Slee et al., 2020).

4.2 The enigmatic operculum of the monocalypts

There has been a longstanding controversy about the operculum of *E. subg. Eucalyptus*. In all species, its composition is uniform, with no evidence of sepals, petals, or two opercula fused together. Hill & Johnson (1995, 480) stated that petaline opercula had arisen repeatedly and that the operculum of *E. subg. Eucalyptus* had been hitherto misinterpreted. They cited “unpublished” observations that in young buds of *Eucalyptus rubiginosa*, *Eucalyptus cloeziana*, and *Eucalyptus acmenoides*, the operculum (“calyptra”) is a unified structure produced by intercalary growth of a ring meristem at the base of both whorls. This is essentially what Drinnan & Ladiges (1989b) had observed in their study of bud development but drew a different conclusion, favoring a petaline-only interpretation of the operculum by comparison with *E. cloeziana* and other eucalypt groups. *Eucalyptus cloeziana* (= *Eucalyptus* subg. *Idiogenes*) is sister to *E. subg. Eucalyptus* (Fig. 3) and has vestigial deciduous sepals (Slee et al., 2020), so its operculum is strictly petaline. By including this evidence, our trait mapping supports the interpretation of Drinnan & Ladiges (1989b) rather than that of Hill & Johnson (1995) (Suppinfo S10, S12).

We mapped sepaline characters on the phylogeny (Suppinfo S12), scoring species of *E. subg. Eucalyptus* s.s., as having no sepals because neither free sepals nor a sepaline operculum is discernable in species of this clade. The successive sister groups of *E. subg. Eucalyptus* (*Eucalyptus* subg. *Cuboidea* and *Eucalyptus* subg. *Idiogenes*) were scored as having vestigial free sepals attached to the rim of the hypanthium. (The eudesmid group *Eucalyptus* sect. *Limbatae* was also scored as having free sepals on the hypanthium rim.) In the result of the mapping, the operculum of the shared MRCA of the clade, including *E. subg. Cuboidea*, *E. subg. Idiogenes* and *E. subg. Eucalyptus* was decisively reconstructed as having free sepals attached to the

hypanthium rim, as were the MRCAs of *Eucalyptus*, eucalypts s.l., and Eucalypteae (Suppinfo S12). That is the operculum of *E. subg. Eucalyptus* is inferred to be strictly petaline. Drinnan & Ladiges (1989b) argued that a petaline homology of the operculum in *E. subg. Eucalyptus* could only be inferred indirectly since no primordia identifiable as sepaline were observed. Here, we make such an inference indirectly via the reconstruction of sepal evolution on the phylogeny. In support of the inferred sister-group relationship between *E. subg. Idiogenes* and *E. subg. Eucalyptus* (Fig. 2), both subgenera uniquely share the gall-inducing scale insect *Apiomorpha variabilis* (unpubl. obs., L.G. Cook & M.D. Crisp). Additionally, verified hybrids occur between these two subgenera (Stokoe et al., 2001).

4.3 Taxonomic implications

The molecular phylogeny shows support for much of the existing morphology-based classification down to sectional level and below in some cases (Suppinfo S4). Some of these long-recognized taxa have no unequivocal phenotypic synapomorphies. Examples include the eucalypts as a whole, that is, the clade here termed “eucalypts s.l.” (Fig. 2), comprising *Angophora*, *Blakella*, *Corymbia*, and *Eucalyptus* s.s., for which the only credible “synapomorphy” is a quantitative trait—the number of lateral veins per leaf (Tables 1 and 2). Defining traits used for other taxa are found in closely related clades, for example, a sepaline operculum that is shed separately, usually before anthesis, leaving a scar (*Blakella* and most species of *E. subg. Symphyomyrtus*) (Tables 1 and 2). Many such taxa are supported by molecular data despite having been defined previously using combinations of phenotypic characters that are separately homoplastic across the eucalypts. Comments are made in Suppinfo S4 about clades, numbered in Suppinfo S5 and S6, that have no evident phenotypic synapomorphy. Some changes foreshadowed by this analysis are discussed as follows and formalized in the Taxonomy section below.

Angophora, *Blakella*, and *Corymbia*

The molecular phylogenies of Ochieng et al. (2007a) and Parra-O et al. (2009) placed *Angophora* as sister to all bloodwoods, but this hypothesis was decisively rejected by AU tests applied to our data ($P = 0.0007$, Fig. 5 part 2). This result is not actually new: *Angophora* falls within *Corymbia* in several published analyses (Steane et al., 2002; Bayly et al., 2013; Schuster et al., 2018; Thornhill et al., 2019). However, the last two studies included cpDNA sequence data showing strong evidence of introgression and chloroplast capture within *Corymbia*. Consequently, the chloroplast-only data provides incomplete and partially misleading evidence of bloodwood phylogeny. By contrast, the nuclear data in those studies is congruent with morphology-based classification, as is our nuclear data. However, the nuclear data used in the cited studies was limited, being ribosomal sequences totaling a few thousand base pairs. In contrast, our study used sequences of many (101) nuclear genes totaling 129 kb in length, so our nuclear data set is a much larger and broader sample of the genome than in previous studies. Thereby we provide a strong test that confirms the earlier findings that *Corymbia* is paraphyletic. Independent support of this result comes from

Ascelis + *Cystococcus*, a host-specific clade of gall-inducing scale insect, which feeds only on *Angophora* and red bloodwoods (sister taxa in our trees) and not on the rest of *Corymbia* (Semple et al., 2015).

We recommend the elevation of *Corymbia* subg. *Blakella* (L.D.Pryor & L.A.S.Johnson ex Brooker) Parra-O et al. (2009) to generic rank because this would rectify the paraphyly of *Corymbia*. *Blakella* includes all the species previously placed in *Corymbia* except the red bloodwoods (*Corymbia* subg. *Corymbia*) and is strongly supported as monophyletic in our analyses (clade 3 in Suppinfo S4). An alternative solution would be to unite *Angophora* and *Corymbia* into a single genus, although this was deemed unacceptable when considered by Hill & Johnson (1995). Brooker (2000) went even further and sank both *Angophora* and *Corymbia* into *Eucalyptus*. Notably, *Angophora* had never been synonymized before. However, Brooker's revised generic taxonomy was not adopted widely. Hill & Johnson suggested that the monophyly of the non-*Arillastrum* eucalypts (i.e. "eucalypts s.l." as defined above) was not certain; this suggestion has merit because our AU tests did not reject a sister-group relationship between *Arillastrum* and the *Angophora*–*Corymbia* clade, relative to *Eucalyptus* (Fig. 5). This leaves open the possibility that Brooker's solution of sinking all the non-*Arillastrum* eucalypts into *Eucalyptus* might render *Eucalyptus* paraphyletic, which seems a riskier solution to the likely paraphyly of *Corymbia* than defining the new genus *Blakella*.

Blakella has a single morphological synapomorphy within the *Angophora*–*Corymbia* clade: the development of separate sepaline and petaline opercula (Tables 1 and 2). In *Corymbia sensu stricto*, these are usually shed separately, with the sepaline operculum falling off early, leaving a visible scar until anthesis. However, in *B. sect. Maculatae*, the outer (sepaline) operculum scar is often retained and both opercula shed as a unit at anthesis—but in this case, they can be separated manually. The early shedding of the sepaline operculum distinguishes *Blakella* from *Corymbia* subg. *Corymbia* (red bloodwoods), which has a double operculum that is retained intact until anthesis. However, as noted above, an operculum scar originated independently within *E. subg. Symphyomyrtus*. Phenotypic traits distinguishing *Eucalyptus* (including *Symphyomyrtus*) from *Blakella* include the following: the absence of bristle glands, xylem vessels grouped, a stemophore that develops from the basal buttress of the petal primordia and unidirectional placental elongation, resulting in two to six regular ovule columns (Tables 1 and 2). Within *Blakella*, three supported clades in all trees (Fig. 2; Suppinfo S4) correspond with infrageneric taxa previously recognized within *Corymbia* (Nicolle, 2022), namely: clade 6, *Corymbia* sect. *Maculatae* (spotted gums); clade 7, *Corymbia* sect. *Naviculares* (yellow bloodwoods); and clade 8, *Corymbia* sect. *Blakella* (ghost gums). Here, we propose to recognize all three clades at sectional rank within *Blakella*.

Within *Blakella* sect. *Maculatae*, we recognize two series: a monotypic branch (4), *Blakella* ser. *Torellianae* (*B. torelliana*) and its sister clade (5), *B. ser. Maculatae*. *Blakella torelliana* (Cadaghi) has a history of placement as a monotypic taxon with uncertain affinity within the bloodwoods (Hill & Johnson, 1995; Slee et al., 2020). However, recent genetic analysis reveals introgression between populations of *B. torelliana* and at least two species of *B. subg. Maculatae*

(Healey et al., 2018), indicating a close relationship between these taxa, which are sister groups in our phylogeny. Therefore, the reduction of the last two taxa to series seems appropriate. In a review, Griffin et al. (1988) reported multiple instances of natural hybrids between eucalypt sections but none between subgenera, except manipulated crosses.

The red bloodwoods (*Corymbia* subg. *Corymbia sensu* Parra-O et al., 2009; Nicolle, 2022) are here treated as a genus in a new, restricted circumscription (clade 11). They share a synapomorphy, being the retention of the outer (sepaline) operculum until anthesis, leaving no scar (a trait occurring independently in a group within *E. sect. Adnataria* and sometimes in the spotted gums). Another red-bloodwood synapomorphy is that they are hosts to the galling scale insects of *Cystococcus* (Semple et al., 2015). *Corymbia trachyphloia* (brown bloodwood) is host to a recently described species of *Cystococcus* (loc. cit.) and is sister to the red bloodwoods. It also shares petaline-operculum retention with the red bloodwoods.

5 Taxonomy

Key to genera of Eucalypteae, modified from Wilson (2011) to include *Blakella*

- 1a. Ovary 2-locular.....2
- 1b. Ovary usually 3–5-locular (eucalypts s.l.).....5
- 2a. Leaves opposite.....3
- 2b. Leaves whorled.....*Allosyncarpia*
- 3a. Calyx lobes free.....*Arillastrum*
- 3b. Calyx calyptrate (operculate).....4
- 4a. Inflorescences three-flowered; hypanthium splitting into four segments at anthesis.....*Stockwellia*
- 4b. Inflorescences seven-flowered; hypanthium not splitting at anthesis.....*Eucalyptopsis*
- 5a. Petals free in open flowers, compound, consisting of a membranous white limb and a firm-textured, calyx-like keel (Fig. 1B).....*Angophora*
- 5b. Corolla or whole perianth calyptrate (operculate).....6
- 6a. Ovules within each locule arranged in an even number of columns (two, four, or six), rarely five to six; xylem vessels grouped in transection of wood; operculum single (petaline only) or double (petaline and sepaline)*Eucalyptus*
- 6b. Ovules arranged irregularly with columns absent or indistinct; xylem vessels solitary in wood transection; operculum double.....7
- 7a. Double operculum remaining intact, lacking a scar and shed as a unit at anthesis (Fig. 1G).....*Corymbia*
- 7b. Outer (sepaline) operculum shed separately and usually early, leaving a scar, or if both opercula shed together, then easily separable (Fig. 1E).....*Blakella*

6 Formal taxonomic changes

We are following the taxonomy of Euclid (Slee et al., 2020) with respect to the species and subspecies we are

recognising in *Blakella*. Full nomenclatural details of names, synonyms, and types may be found in the Australian Plant Name Index (APNI) <<https://biodiversity.org.au/nsl/services/search/names>>. Numbers in square brackets refer to clades or terminal branches in Figs. 2–4, Suppinfo S3–S4.

Transfer of species from *Corymbia* sect. *Naviculares*, *Corymbia* sect. *Abbreviatae*, *Corymbia* sect. *Maculatae* and *Corymbia* sect. *Torellianae* into *Blakella*, gen. nov.

Our results strongly support the conclusion that *Corymbia* in the current circumscription (Hill & Johnson, 1995; Parra-O et al., 2009; Slee et al., 2020; Nicolle, 2022) is paraphyletic by the exclusion of *Angophora*. The latter genus is most likely the sister to the red bloodwoods *Corymbia sensu stricto*, given the outcome of the AU tests (Fig. 5). Here, we formally raise *Corymbia* subg. *Blakella* to a genus and expand it to include the species of these four sections of *Corymbia*, while reducing *Corymbia* to just the red bloodwoods, including *Corymbia trachyphloia*, the brown bloodwood. This seems the most sensible taxonomic solution because it preserves *Angophora*, which is a name with a long history of recognition, whether it is the sister of *Blakella* or *Corymbia* s.s. It also minimizes the number of taxonomic changes to the currently accepted taxonomy. For species-level taxonomy (and below), we follow Euclid (Slee et al., 2020) and the APC (<https://biodiversity.org.au/nsl/services/search/taxonomy>), which are currently in agreement.

Blakella (L.D.Pryor & L.A.S.Johnson ex Brooker) Crisp & L.G.Cook, **gen. et stat. nov.** [3]

Basionym: *Eucalyptus* subg. *Blakella* L.D.Pryor & L.A.S.-Johnson ex Brooker, Aust. Syst. Bot. 13: 89 (2000).

Replaced synonym: *Eucalyptus* subser. *Clavigerae* Maiden, Crit. Rev. Gen. *Eucalyptus* 6: 536 (1924).

Eucalyptus ser. *Clavigerae* (Maiden) S.T.Blake, Aust. J. Bot. 1: 209 (1953)

Corymbia subg. *Blakella* (L.D.Pryor & L.A.S.Johnson) Parra-Os. & Ladiges, Aust. Syst. Bot. 22: 397 (2009).

Type: *E. clavigera* A.Cunn. ex Schauer

Blakella* sect. *Blakella [8]

Eucalyptus sect. *Abbreviatae* Brooker, Aust. Syst. Bot. 13: 90 (2000).

Corymbia sect. *Abbreviatae* (Brooker) Parra-Os. & Ladiges, Aust. Syst. Bot. 22: 397 (2009).

Type: *E. polysciada* F.Muell.

Eucalyptus sect. *Extensae* Brooker, Aust. Syst. Bot. 13: 90 (2000).

Replaced synonym: *E.* subser. *Tessellatae* Blakely, Key *Eucalypts* 15, 74 (1934).

Type: *E. tessellaris* F.Muell.

Eucalyptus ser. *Scutiformes* Maiden, Crit. Rev. Gen. *Eucalyptus* 7: 113 (1929)

Type: *E. grandifolia* R.Br. ex Benth., lecto, fide G.M.Chippendale, Fl. Australia 19: 505 (1988).

Blakella aparrerinja (K.D.Hill & L.A.S.Johnson) Crisp & L.G.Cook, **comb. nov.**

Basionym: *Corymbia aparrerinja* K.D.Hill & L.A.S.Johnson, *Telopea* 6: 453 (1995).

Eucalyptus aparrerinja (K.D.Hill & L.A.S.Johnson) Brooker, Aust. Syst. Bot. 13: 137 (2000).

Blakella arafurica (K.D.Hill & L.A.S.Johnson) Crisp & L.G.Cook, **comb. nov.**

Basionym: *Corymbia arafurica* K.D.Hill & L.A.S.Johnson, *Telopea* 6: 409 (1995).

Blakella aspera (F.Muell.) Crisp & L.G.Cook, **comb. nov.**

Basionym: *Eucalyptus aspera* F.Muell., J. Proc. Linn. Soc., Bot. 3: 95 (1859).

Corymbia aspera (F.Muell.) K.D.Hill & L.A.S.Johnson, *Telopea* 6: 448 (1995).

Blakella bella (K.D.Hill & L.A.S.Johnson) Crisp & L.G.Cook, **comb. nov.**

Basionym: *Corymbia bella* K.D.Hill & L.A.S.Johnson, *Telopea* 6: 411 (1995).

Eucalyptus bella (K.D.Hill & L.A.S.Johnson) Brooker, Aust. Syst. Bot. 13: 137 (2000).

Blakella blakei (K.D.Hill & L.A.S.Johnson) Crisp & L.G.Cook, **comb. nov.**

Basionym: *Corymbia blakei* K.D.Hill & L.A.S.Johnson, *Telopea* 6: 437 (1995).

Eucalyptus blakei (K.D.Hill & L.A.S.Johnson) Brooker, Aust. Syst. Bot. 13: 137 (2000).

Blakella candida (K.D.Hill & L.A.S.Johnson) Crisp & L.G.Cook, **comb. nov.**

Basionym: *Corymbia candida* K.D.Hill & L.A.S.Johnson, *Telopea* 6: 440 (1995).

Eucalyptus candida (K.D.Hill & L.A.S.Johnson) Brooker, Aust. Syst. Bot. 13: 138 (2000).

Blakella clavigera (A.Cunn. ex Schauer) Crisp & L.G.Cook, **comb. nov.**

Basionym: *Eucalyptus clavigera* A.Cunn. ex Schauer in Walpers, W.G., *Repertorium Botanices Systematicae* 2: 926 (1843).

Corymbia clavigera (A.Cunn. ex Schauer) K.D.Hill & L.A.S.Johnson, *Telopea* 6: 413 (1995).

Blakella confertiflora (Kippist) Crisp & L.G.Cook, **comb. nov.**

Basionym: *Eucalyptus confertiflora* Kippist in Mueller, J. Proc. Linn. Soc., Bot. 3: 96 (1859).

Corymbia confertiflora (Kippist) K.D.Hill & L.A.S.Johnson, *Telopea* 6: 428 (1995).

Blakella dallachiana (Benth.) Crisp & L.G.Cook, **comb. et stat. nov.**

Basionym: *Eucalyptus tessellaris* F.Muell. var. *dallachiana* Benth., Fl. Austral. 3: 251 (1867).

Eucalyptus clavigera var. *dallachiana* (Benth.) Maiden, J. Proc. Roy. Soc. New South Wales 47: 77 (1913).

Corymbia dallachiana (Benth.) K.D.Hill & L.A.S.Johnson, *Telopea* 6: 451 (1995).

Blakella dendromerinx (K.D.Hill & L.A.S.Johnson) Crisp & L.G.Cook, **comb. nov.**

Basionym: *Corymbia dendromerinx* K.D.Hill & L.A.S.-Johnson, *Telopea* 6: 431 (1995).

Blakella disjuncta (K.D.Hill & L.A.S.Johnson) Crisp & L.G.Cook, **comb. nov.**

Basionym: *Corymbia disjuncta* K.D.Hill & L.A.S.Johnson, *Telopea* 6: 423 (1995).

Blakella ferritcola (Brooker & Edgecombe) Crisp & L.G.Cook, **comb. nov.**

Basionym: *Eucalyptus ferritcola* Brooker & Edgecombe, *Nuytsia* 5: 373 (1986).

Corymbia ferritcola (Brooker & Edgecombe) K.D.Hill & L.A.S.Johnson, *Telopea* 6: 446 (1995).

Blakella flavescens (K.D.Hill & L.A.S.Johnson) Crisp & L.G.Cook, **comb. nov.**

Basionym: *Corymbia flavescens* K.D.Hill & L.A.S.Johnson, *Telopea* 6: 455 (1995).

Eucalyptus flavescens (K.D.Hill & L.A.S.Johnson) Brooker, *Aust. Syst. Bot.* 13: 138 (2000).

Blakella gilbertensis (Maiden & Blakely) Crisp & L.G.Cook, *comb. et stat. nov.*

Basionym: *Eucalyptus clavigera* var. *gilbertensis* Maiden & Blakely in Maiden, *Crit. Rev. Gen. Eucalyptus* 7: 432 (1928).

Eucalyptus gilbertensis (Maiden & Blakely) S.T.Blake, *Aust. J. Bot.* 1: 220 (1953).

Corymbia gilbertensis (Maiden & Blakely) K.D.Hill & L.A.S.Johnson, *Telopea* 6: 435 (1995).

Blakella grandifolia (R.Br. ex Benth.) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus grandifolia* R.Br. ex Benth., *Fl. Austral.* 3: 250 (1867).

Corymbia grandifolia (R.Br. ex Benth.) K.D.Hill & L.A.S.Johnson, *Telopea* 6: 457 (1995).

Blakella grandifolia subsp. *lamprocardia* (L.A.S.Johnson) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Corymbia grandifolia* subsp. *lamprocardia* L.A.S.Johnson in K.D.Hill & L.A.S.Johnson, *Telopea* 6: 461 (1995).

Blakella grandifolia subsp. *longa* (L.A.S.Johnson) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Corymbia grandifolia* subsp. *longa* L.A.S.Johnson in K.D.Hill & L.A.S.Johnson, *Telopea* 6: 460 (1995).

Blakella kombolgiensis (Brooker & Dunlop) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus kombolgiensis* Brooker & Dunlop, *Aust. Forest Res.* 8: 212 (1978).

Corymbia kombolgiensis (Brooker & Dunlop) K.D.Hill & L.A.S.Johnson, *Telopea* 6: 414 (1995).

Blakella papuana (F.Muell.) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus papuana* F.Muell., *Descr. Notes Papuan Pl.* 1: 8 (1875).

Corymbia papuana (F.Muell.) K.D.Hill & L.A.S.Johnson, *Telopea* 6: 405 (1995).

Blakella paractia (K.D.Hill & L.A.S.Johnson) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Corymbia paractia* K.D.Hill & L.A.S.Johnson, *Telopea* 6: 462 (1995).

Blakella pauciseta (K.D.Hill & L.A.S.Johnson) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Corymbia pauciseta* K.D.Hill & L.A.S.Johnson, *Telopea* 6: 426 (1995).

Blakella polysciada (F.Muell.) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus polysciada* F.Muell., *J. Linn. Soc., Bot.* 3: 98 (1859).

Corymbia polysciada (F.Muell.) K.D.Hill & L.A.S.Johnson, *Telopea* 6: 413 (1995).

Blakella tessellaris (F.Muell.) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus tessellaris* F.Muell., *J. Proc. Linn. Soc., Bot.* 3: 88 (1859).

Corymbia tessellaris (F.Muell.) K.D.Hill & L.A.S.Johnson, *Telopea* 6: 402 (1995).

Blakella torta (K.D.Hill & L.A.S.Johnson) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Corymbia torta* K.D.Hill & L.A.S.Johnson, *Telopea* 6: 418 (1995).

Blakella sect. *Naviculares* (Maiden) Crisp & L.G.Cook, *comb. et stat. nov.* [7]

Basionym: *Eucalyptus* ser. *Naviculares* Maiden, *Crit. Rev. Gen. Eucalyptus* 7: 109 (1925).

Corymbia sect. *Naviculares* (Maiden) Parra-Os. & Ladiges, *Aust. Syst. Bot.* 22: 397 (2009).

Type: *Eucalyptus eximia* Schauer, lecto, fide G.M.Chippendale, *Fl. Australia* 19: 502 (1988).

Eucalyptus subser. *Ochrophloiae* Blakely, *Key Eucalypts* 18, 94 (1934).

Type: *E. eximia* Schauer, lecto, fide G.M.Chippendale, *Fl. Australia* 19: 502 (1988).

Blakella aureola (Brooker & A.R.Bean) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus aureola* Brooker & A.R.Bean, *Austrobaileya* 3: 430 (1991).

Corymbia aureola (Brooker & A.R.Bean) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 374 (1995).

Blakella bloxsomei (Maiden) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus bloxsomei* Maiden, *J. Proc. Roy. Soc. New South Wales* 59: 156 (1925).

Corymbia bloxsomei (Maiden) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 372 (1995).

Blakella bunites (Brooker & A.R.Bean) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus bunites* Brooker & A.R.Bean, *Austrobaileya* 3: 423 (1991).

Corymbia bunites (Brooker & A.R.Bean) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 373 (1995).

Blakella eximia (Schauer) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus eximia* Schauer in Walpers, *W.G., Repertorium Botanices Systematicae* 2: 925 (1843).

Corymbia eximia (Schauer) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 383 (1995).

Blakella leichhardtii (F.M.Bailey) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus leichhardtii* F.M.Bailey, *Queensland Agric. J.* 16: 493 (1906).

Eucalyptus peltata subsp. *leichhardtii* (F.M.Bailey) L.A.S. Johnson & Blaxell, *Contrib. New South Wales Natl. Herb.* 4: 453 (1973).

Corymbia leichhardtii (F.M.Bailey) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 370 (1995).

Blakella leptoloma (Brooker & A.R.Bean) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus leptoloma* Brooker & A.R.Bean, *Austrobaileya* 3: 432 (1991).

Corymbia leptoloma (Brooker & A.R.Bean) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 369 (1995).

Blakella peltata (Benth.) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus peltata* Benth., *Fl. Austr.* 3: 254 (1867).

Corymbia peltata (Benth.) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 381 (1995).

Blakella petalophylla (Brooker & A.R.Bean) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus petalophylla* Brooker & A.R.Bean, *Austrobaileya* 3: 428 (1991).

Corymbia petalophylla (Brooker & A.R.Bean) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 375 (1995).

Blakella scabrida (Brooker & A.R.Bean) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus scabrida* Brooker & A.R.Bean, *Austrobaileya* 3: 420 (1991).

Corymbia scabrida (Brooker & A.R.Bean) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 382 (1995).

Blakella watsoniana (F.Muell.) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus watsoniana* F.Muell., *Fragm. Phytogr. Austral.* 10: 98 (1877).

Corymbia watsoniana (F.Muell.) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 378 (1995).

Blakella watsoniana subsp. *capillata* (Brooker & A.R.Bean) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus watsoniana* subsp. *capillata* Brooker & A.R.Bean, *Austrobaileya* 3: 428 (1991).

Corymbia watsoniana subsp. *capillata* (Brooker & A.R.Bean) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 379 (1995).

Corymbia catenaria K.D.Hill & L.A.S.Johnson, *Telopea* 6: 376 (1995).

Blakella* sect. *Maculatae (Blakely) Crisp & L.G. Cook, *comb. et stat. nov.* [6]

Basionym: *Eucalyptus* subser. *Maculatae* Blakely, *Key Eucalypts* 18, 96 (1934).

E. ser. *Maculatae* (Blakely) Chippend., *Fl. Australia* 19: 500 (1988).

Corymbia sect. *Maculatae* (Blakely) Parra-Os. & Ladiges, *Aust. Syst. Bot.* 22: 397 (2009).

Type: *E. maculata* Hook.

Blakella* ser. *Maculatae (Blakely) Crisp & L.G. Cook, *comb. et stat. nov.* [5]

Blakella citriodora (Hook.) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus citriodora* Hook. in T.L.Mitchell, *J. Exped. Tropical Australia* 235 (1848).

Corymbia citriodora (Hook.) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 388 (1995).

Eucalyptus variegata F.Muell., *J. Linn. Soc., Bot.* 3: 88 (1859).

Corymbia variegata (F.Muell.) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 389 (1995).

Corymbia citriodora subsp. *variegata* (F.Muell.) A.R.Bean & M.W.McDonald, *Austrobaileya* 5: 735 (2000).

Blakella henryi (S.T.Blake) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus henryi* S.T.Blake, *Austrobaileya* 1: 4 (1977).

Corymbia henryi (S.T.Blake) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 396 (1995).

Blakella maculata (Hook.) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus maculata* Hook., *Icon. Pl.* 7: t. 619 (1844).

Corymbia maculata (Hook.) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 393 (1995).

Blakella* ser. *Torellianae (Chippend.) Crisp & L.G.Cook, *comb. nov.* [4]

Basionym: *Eucalyptus* ser. *Torellianae* Chippend., *Fl. Australia* 19: 506 (1988).

Corymbia sect. *Torellianae* (Chippend.) Parra-Os. & Ladiges, *Aust. Syst. Bot.* 22: 397 (2009).

Type: *E. torelliana* F.Muell.

Blakella torelliana (F.Muell.) Crisp & L.G.Cook, *comb. nov.*

Basionym: *Eucalyptus torelliana* F.Muell., *Fragm.* 10: 106 (1877).

Corymbia torelliana (F.Muell.) K.D. Hill & L.A.S. Johnson, *Telopea* 6: 385 (1995).

Corymbia K.D. Hill & L.A.S. Johnson, *Telopea* 6: 214 (1995). [11]

Type: *C. gummifera* (Gaertner) K.D. Hill & L.A.S. Johnson.

Corymbia* subg. *Corymbia

The autonym subgenus, comprising all the red bloodwoods, was established when Parra-O et al. (2009) published *C. subg. Blakella* but becomes superfluous with the elevation of *C. subg. Blakella* to generic rank. In our phylogeny, *Corymbia trachyphloia*, the brown bloodwood, is sister to the rest of the red bloodwoods and is here included in *Corymbia sensu stricto*.

Acknowledgements

The authors thank Andrew Slee (sadly deceased) for providing expertise on the taxonomy of the study group and checking species identifications. We also thank Monica Ruibal for a significant contribution to the laboratory work. We are grateful to Lindsay Popple for his assistance with the fieldwork. We thank Mike Bayly and Dean Nicolle for their insightful and useful comments on the manuscript. The following institutes are thanked for allowing the collection of leaves from their vouchered trees: Australian National Botanic Gardens and Currency Creek Arboretum. This work was supported by an Australian Research Council Discovery grant DP130101141 to M.D.C. and L.G.C., an ARC Discovery grant DP200103151 to B.Q.M., and a Chan-Zuckerberg Initiative grant EOSS4-0000000312 to B.Q.M. for open-source software for science. Open access publishing facilitated by Australian National University, as part of the Wiley-Australian National University agreement via the Council of Australian University Librarians.

Author Contributions

Michael D. Crisp and Lyn G. Cook conceived, planned, and oversaw the project, obtained funding, conducted the fieldwork, and drafted the manuscript. Michael D. Crisp managed the project. Andrew H. Thornhill provided samples from fieldwork, herbarium specimens, and cultivation. Carsten Kulheim oversaw the lab work, Bokyung Choi and Yen Po Lin performed the lab work, and Bokyung Choi, Robert D. Edwards, and Alicia Toon helped design the baits. Karen Meusemann, James Hereward, and Alicia Toon developed and implemented pipelines for extracting the sequence data. Bui Q. Minh carried out the phylogenetic analyses. All authors contributed to the drafting.

Data Availability Statement

Voucher specimens for the DNA samples are held in the Australian National Herbarium, CSIRO, Canberra. The following data files are available in the Dryad Digital Repository (Crisp et al., 2023, <https://doi.org/10.5061/dryad.gb5mkkwww>): aligned and concatenated partitioned DNA sequences <concatenated_sequences_dataset_101_loci.phy>; a nexus file of the partition boundaries and model for each partition <101concat

29May.nex.run1.best_scheme.nex>; perianth morphology data mapped on the phylogeny <Traits_dataset_Mesquite.nex> and the treefiles, respectively, resulting from the run1 <101concat-29May.nex.run1.treefile.tre> and run2 <101concat-29May.phy.gz.run2.treefile.tre> IQtree analyses.

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Supplementary Material

The following supplementary material is available online for this article at <http://onlinelibrary.wiley.com/doi/10.1111/jse.13047/supinfo>:

Suppinfo S1. List of samples and their associated labels in the phylogenetic tree.

Suppinfo S2. A table with details of the 101 loci targeted in the annotated reference genome of *Eucalyptus grandis*.

Suppinfo S3. IQtree from concatenated (single partition) analysis, showing support at nodes from concordance analyses (SH-aLRT/ultrafast bootstrap/genes concordance factor/site concordance factor).

Suppinfo S4. A tabulation of recognized and informal higher eucalypt taxa with support values from IQtree, diagnostic morphology, and comparison with classification by Nicolle (2022).

Suppinfo S5. Circular IQtree from concatenated (single partition) analysis with clades coloured by previous taxonomy.

Suppinfo S6. Circular IQtree from 101-partition IQtree analysis, with support at main nodes numbered according to the table in Suppinfo S4 and nodes colored by previous taxonomy.

Suppinfo S7. Circular tree from Astral analysis of the 101-partition data, showing local posterior probabilities at nodes.

Suppinfo S8. Concordance factors for all nodes in the single-partition IQtree in a scatter plot showing the relationship between site concordance factor (sCF) and gene concordance factor. Points below the red line (sCF = 33.3) represent unsupported nodes.

Suppinfo S9. Ranked plot of % informative sites per locus (across targeted loci).

Suppinfo S10. Corolla type mapped on the single-partition IQtree using Mk1 (a) and parsimony (b) models.

Suppinfo S11. Compound petals mapped on the single-partition IQtree using Mk1 (a) and parsimony (b) models.

Suppinfo S12. Calyx types mapped onto the single-partition IQtree using Mk1 (a) and parsimony (b) models.