

# Evolutionary relationships in *Eucalyptus* sens. lat. – a synopsis

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This article complements the introductory essay about eucalypts included in the "Learn about Eucalypts" section. Its aim is to provide an up-to-date account of the outcomes of research derived from different groups during the past 5 years relating to relationships within *Eucalyptus* s.s. As such it includes only those publications and hypotheses relating to higher level relationships of major groupings within the eucalypts. Some of the research reported below also provides insights into biogeographic relationships of the eucalypt group – in large part these are not the focus of this article and are not discussed in detail.

## Introduction

The first comprehensive classification of the eucalypts was published by Blakely in 1934, in which he treated more than 600 taxa, building on earlier work of Maiden and Mueller. Blakely's classification remained the critical reference for *Eucalyptus* taxonomists for the next 37 years when a new but informal classification was published by Pryor and Johnson (1971). In this work the authors divided the genus into seven subgenera, and although of an informal nature, presented a system of great advance on Blakely's treatment. The small genus *Angophora* was retained.

The next 20 years saw much debate about the naturalness of *Eucalyptus* and whether other genera should be recognized (e.g., Johnson 1987). Based on morphological data, Hill and Johnson in 1995 proposed a split in the genus and recognition of the genus *Corymbia*. This new genus of c. 113 species, comprised the ghost gums and the bloodwoods, and Hill and Johnson concluded that *Corymbia* is the sister group to *Angophora*, with the synapomorphy of the distinctive cap cells on bristle glands (Ladiges 1984) being unambiguous. The remaining taxa in *Eucalyptus* were not treated by Hill and Johnson in a formal taxonomic sense.

In 2000, Brooker published a formal classification of the eucalypts, which was a synthesis in the form of an updated taxonomy to accommodate the numerous taxa published since Chippendale's 1988 treatment. This work recognized one genus, *Eucalyptus* and included *Angophora* and *Corymbia* as two of a total of 13 subgenera. The treatment assigned all species accepted by Brooker and published prior to 1999 to a hierarchical system of subgenera, sections, subsections, series, subseries and supraspecies (Brooker 2000). The approx. 800 species of *Eucalyptus* were divided into 13 subgenera, two of which were the ghost gums (subgenus *Blakella*) and bloodwoods (subgenus *Corymbia*), which constitute Hill and Johnson's single genus *Corymbia*.

This new classification of the eucalypts by Brooker (2000) based on comparative morphology, stimulated further debate as to whether *Angophora* and *Corymbia* should be included within *Eucalyptus* s.s., and also whether the bloodwood group *Corymbia* is monophyletic.

In the second edition of EUCLID (Brooker *et al.* 2002), while considerable discussion was still running in the botanical community about the acceptance of *Corymbia* as a monophyletic group, a conservative approach was adopted in which both genera *Eucalyptus* and *Angophora* were recognized in a traditional sense.

## The eucalypt group

To place the discussion of relationships across the eucalypts in context it is worth reiterating here the seven genera for which there is general agreement of what constitutes 'the eucalypt group'. *Eucalyptus* L'Hér. is the largest genus with more than 660 species occurring primarily in Australia, and with a few species in Indonesia, the Philippines, Timor and New Guinea. The sister group to *Eucalyptus* is the lineage containing *Corymbia* Hill & Johnson (c. 90 species) widespread in northern Australia, extending to New Guinea, and *Angophora* Cav. (9 taxa) restricted to eastern Australia.

Four other smaller genera make up the eucalypt group. *Arillastrum* Pancher & Baill. is a monotypic genus (*A. gummiferum*) endemic to New Caledonia; *Allosyncarpia* S.T.Blake from Arnhem Land in northern Australia is also monotypic (*A. ternata*); a third monotypic genus *Stockwellia* D.J.Carr, S.G.M.Carr & B.Hyland is restricted to the Atherton Tableland of north Queensland (*S. quadrifida*). The genus *Eucalyptopsis* C.T.White comprises two species, *E. papuana* and *E. alauda* and is found in New Guinea and the Moluccan Archipelago.

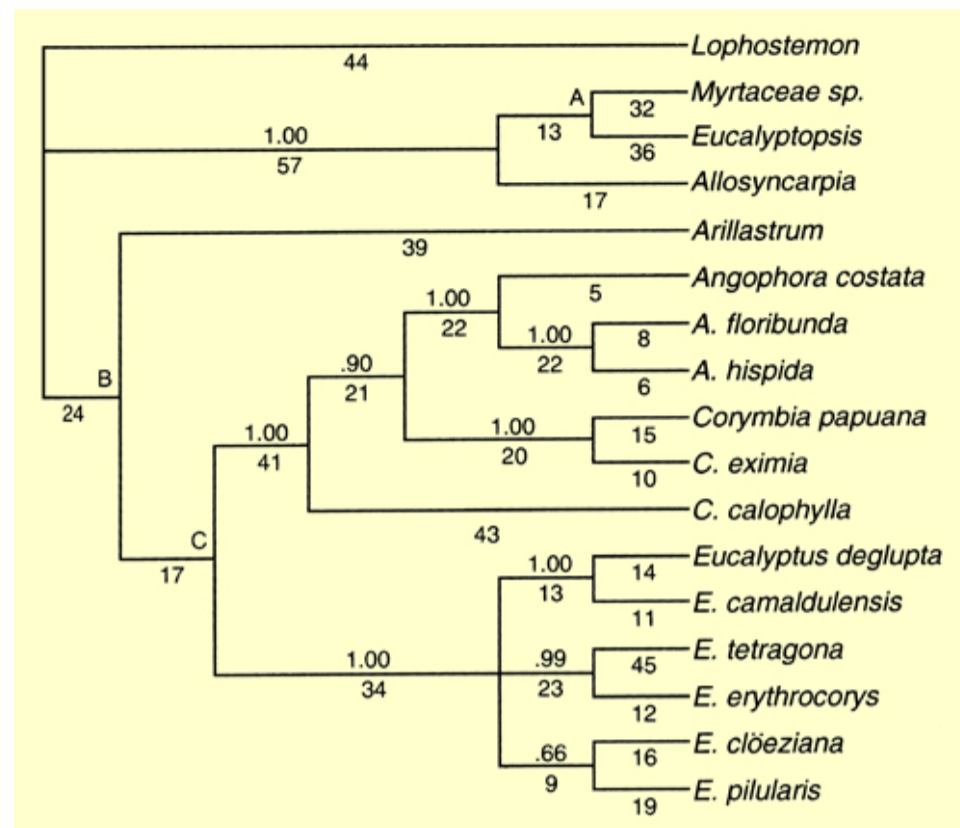
## Phylogenetic hypotheses

Despite the considerable debate surrounding the classification of the eucalypts based on differing interpretations of morphological features and their significance in evolutionary history, cladistic analyses of morphological and molecular datasets show a high degree of agreement on the higher level phylogeny of the group. Summaries and accounts of major pieces of work contributing to our understanding of eucalypt relationships follow.

**Udovicic & Ladiges (2000)** used a number of different nuclear and chloroplast DNA regions to examine their informativeness in understanding the phylogeny of the genera in the eucalypt group. Parsimony analyses of this sequence data from all the DNA regions revealed three major clades in all cases – the basal *Stockwellia* (the undescribed "Myrtaceae sp." at that time), *Eucalyptopsis* and *Allosyncarpia* clade, the *Angophora* and *Corymbia* clade and the *Eucalyptus* clade. The position of the seventh genus of the eucalypt group, *Arillastrum*, was not well resolved and showed different relationships to the other clades depending on the DNA region

analysed. The combined (total evidence) dataset (Figure 1- from Udovicic & Ladiges 2000) depicts a resolved relationship of *Arillastrum* as sister to the *Angophora-Corymbia* and *Eucalyptus* clades, but these basal nodes were not well supported. The authors concluded that there was not enough sequence variation present to resolve the exact position of *Arillastrum*.

All of the analyses in Udovicic & Ladiges (2000) indicated *Angophora* and *Corymbia* to be a monophyletic group separate from *Eucalyptus*. These relationships were congruent with those of earlier studies based on morphology and molecular data (Hill & Johnson 1995; Ladiges *et al.* 1995; Udovicic *et al.* 1995; Steane *et al.* 1999).

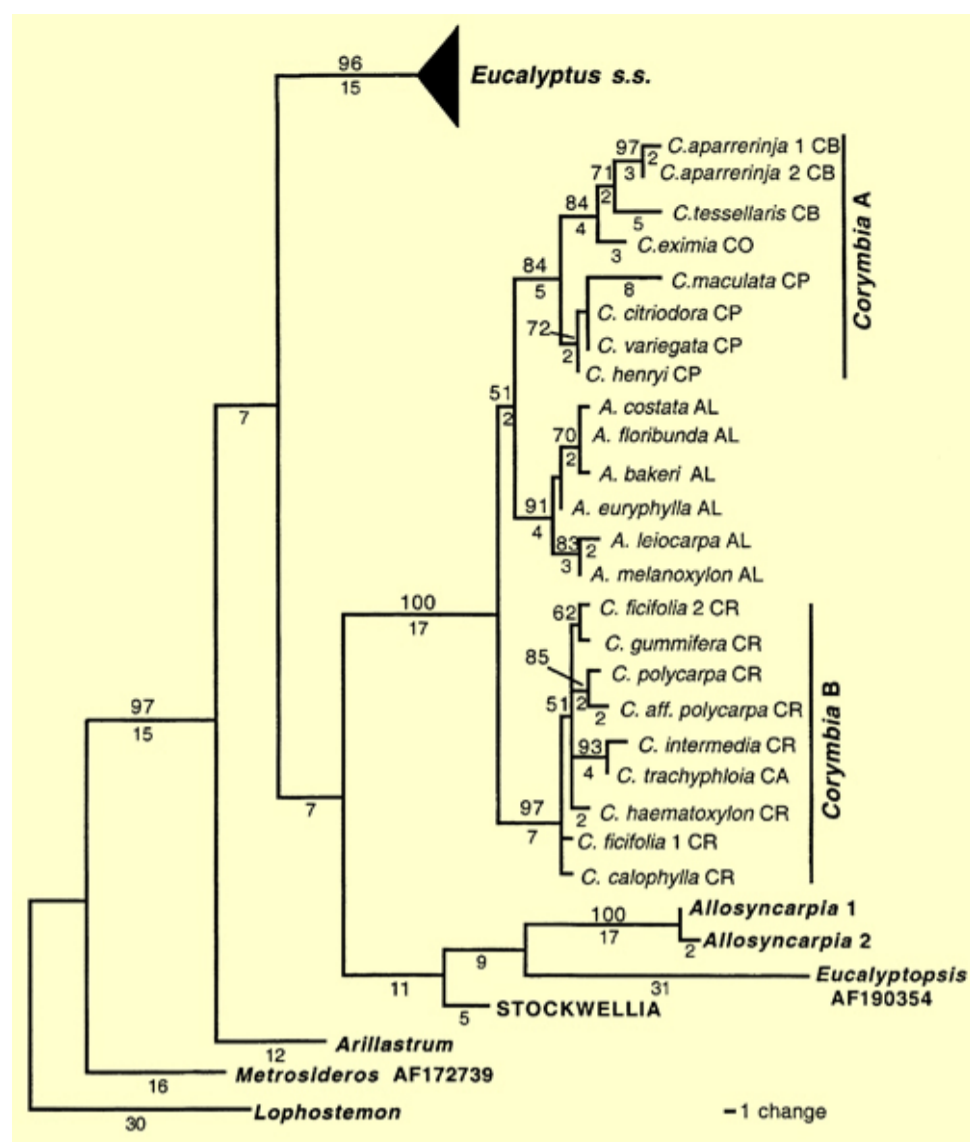


**Figure 1.** Strict consensus tree, based on a combined data set for 16 ingroup taxa and the outgroup, *Lophostemon confertus*. Including 13 indels, there were 313 informative characters yielding three equally parsimonious trees of length 693, CI = 0.60, RI = 0.69. Jackknife values greater than 0.50 are shown above branches and letters A, B & C denote nodes with a jackknife value less than 0.50 that could be collapsed. Numbers of characters supporting a node are shown below branches. (Source: Udovicic & Ladiges 2000, Fig.5)

**Steane *et al.* (2002)** undertook an expanded survey, following their earlier study (Steane *et al.* 1999), using ITS sequences for 90 species of *Eucalyptus s.s.* and 28 species of related eucalypt genera and outgroups. Their study revealed phylogenetic information for higher level relationships among the eucalypts and also between sections and subgenera.

Their results indicated that *Angophora* and *Corymbia* form a well supported clade differentiated from *Eucalyptus s.s.* and they argued that the ITS results provided evidence that the two genera should not be regarded as subgenera of *Eucalyptus* without clear indication of the relationships between *Eucalyptus s.s.* and the other eucalypt genera. They suggested that if the genus *Eucalyptus* is to be expanded to include *Angophora* and *Corymbia* (*sensu* Brooker 2000), the ITS data implied that *Allosyncarpia*, *Eucalyptopsis* and *Stockwellia*, and potentially *Arillastrum* should also be included in *Eucalyptus*.

Their study showed *Allosyncarpia*, *Eucalyptopsis*, *Stockwellia* and *Arillastrum* were also separated from *Eucalyptus* (Figure 2 – from Steane *et al.* 2002). The long branch lengths in this analysis, however, point to the divergent nature of the relationships distinguishing *Angophora* + *Corymbia*, *Allosyncarpia*, *Eucalyptopsis*, *Stockwellia* and *Arillastrum* from each other and from *Eucalyptus s.s.*



**Figure 2.** Phylogram of one of the 18695 FDS cladograms, detailing relative positions of *Allosyncarpia*, *Arillastrum*, *Angophora*, *Corymbia*, *Eucalyptopsis* and 'Stockwellia' relative to *Eucalyptus s.s.*, when rooted on *Lophostemon* (see text). Clades representing 'Corymbia A' (Clade A) and 'Corymbia B' (Clade B) are indicated. Branch lengths are shown below branches; numbers are not shown when branch length = 1. Bootstrap percentages greater than 50% are shown above branches. Letters following species names represent taxon codes (Table 1). The triangle leading to *Eucalyptus s.s.* represents multiple terminal taxa within that clade. STOCKWELLIA—two samples of 'Stockwellia' had identical ITS sequences and were reduced to a single operational taxonomic unit. Tree topology, branch lengths and bootstrap support from the AFOG analysis are very similar to those in this figure. (Source: Steane *et al.* 2002, Fig.2)

In contrast, the branch lengths within *Eucalyptus* itself are relatively short and the authors support a case for maintaining *Angophora* + *Corymbia*, *Allosyncarpia*, *Eucalyptopsis*, *Stockwellia*, *Arillastrum* and *Eucalyptus* as separate genera.

The analysis of the full data set places *Arillastrum* near the base of the cladogram, as sister to all other eucalypts.

Increased sampling using ITS data did not resolve the relationship between *Angophora* and *Corymbia*, but showed *Corymbia* to be paraphyletic with *Angophora* nested within. Here *Angophora* is sister to *Corymbia* 'A' the yellow bloodwoods (informal sect. *Ochraria*), the paper-fruited bloodwoods or ghost gums (informal sect. *Blakearia*) and the spotted gums (informal sect. *Politaria*). This is congruent with results of earlier studies based on cpDNA data (Udovicic and Ladiges 2000).

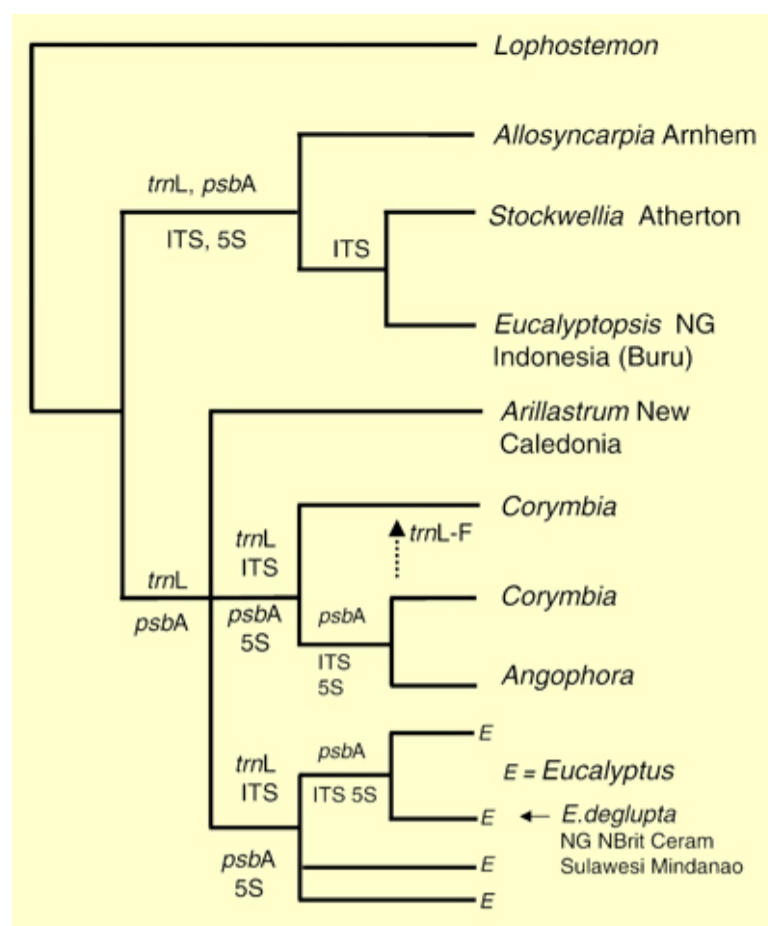
**Whitlock *et al.* (2003)** mainly relates to the tropical box species (subgenus *Minutifructus*), but chloroplast data provide further evidence for the genetic differentiation of *Angophora* and *Corymbia* (together with *Arillastrum*) from *Eucalyptus*. It also showed *Corymbia* to be paraphyletic. This study indicated that the chloroplast DNA data may be potentially informative in revealing relationships within the eucalypts, and will be better tested with more complete taxon sampling.

**Ladiges *et al.* (2003)** used the current state of phylogenetic analysis of the eucalypts (and the 'melaleuca group'), together with geological events and fossil evidence to explore further Australian biogeographical patterns and to test historical connections of biotas.

These authors presented the current knowledge of phylogenetic relationships of the seven genera (Figure 3 – from Ladiges *et al.* 2003) based on both nuclear and chloroplast DNA as reported by Udovicic & Ladiges (2000). This strict consensus tree revealed two major lineages within the eucalypt group, corresponding to earlier recognised *Eucalyptopsis* and *Eucalyptus* alliances of Briggs & Johnson (1979).

The position of *Arillastrum* and its relationship with the *Angophora-Corymbia* and *Eucalyptus* groups led Ladiges *et al.* (2003) to propose that the divergence of *Arillastrum* from *Angophora*, *Corymbia* and *Eucalyptus* corresponded to the geological vicariance event when the Lord Howe Rise and Norfolk Ridge (including New Caledonia) detached from the Australia-Antarctic land mass. They concluded that this split of ancestral taxa began in the late Cretaceous, about 65-70 million years ago. In applying molecular dating techniques to a study of southern hemisphere Myrtales Sytsma *et al.* (2004) also showed the eucalypt lineage to date back to the late Cretaceous.

Ladiges *et al.* (2003) discuss the differentiation of clades and phylogenetic patterns in relation to major geological and climatic events.



**Figure 3.** Summary molecular phylogeny of the eucalypt group based on both nuclear (ITS and 5 S rDNA spacer regions) and chloroplast DNA sequence data (psbA–trnH intergenic spacer, trnL intron and trnL–F spacer regions; *Lophostemon* is an outgroup taxon. The data sets that support particular nodes are shown (based on Udovicic & Ladiges, 2000, strict consensus tree, Fig. 5, p. 643, Fig. 1 this document) (Source: Ladiges *et al.* 2003, Fig. 2)

**Crisp *et al.* (2004)** included the eucalypts among other groups of community-dominant Australian plants, such as Casuarinaceae, pea-flowered legumes and *Banksia*, in their analysis combining fossil evidence with molecular phylogenies to provide insights on the history of radiation and extinction of the flora of Australia.

The study used the approach of molecular dating to allocate dates to nodes of a eucalypt phylogenetic tree based on ITS sequence data from Steane *et al.* (2002). The eucalypt chronogram (Crisp *et al.* 2004, Fig. 3) was calibrated using the assumption of Ladiges *et al.* (2003) that a vicariance event c. 70 million years ago isolated *Arillastrum* in New Caledonia from the rest of the eucalypts in Australia.

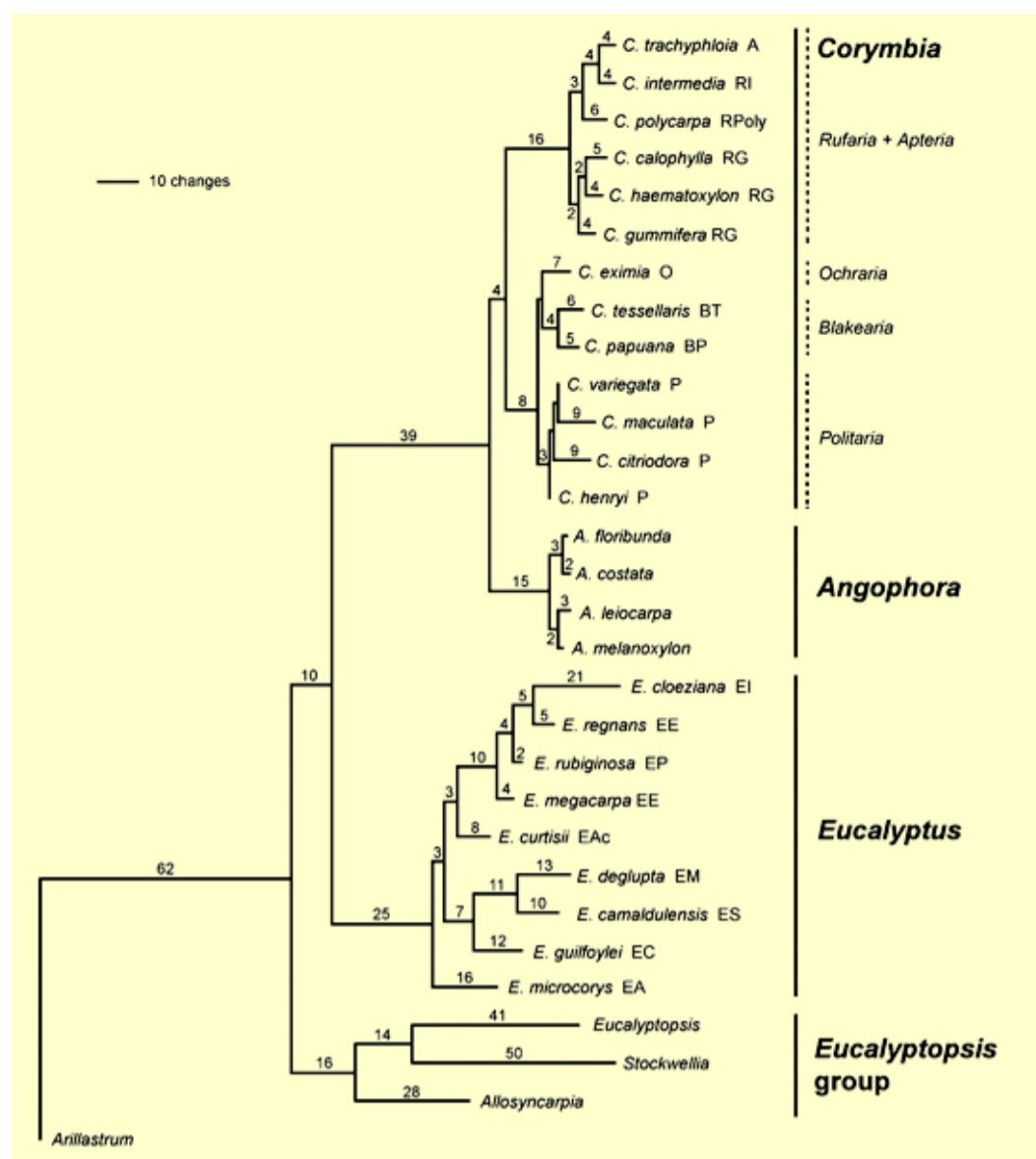
The molecular dating approach does throw some insight on the radiation of the group within Australia. Using the calibration of 70 million years ago for the divergence of the eucalypts from *Arillastrum*, Crisp *et al.*'s molecular dating suggests the diversification of eucalypts proceeded steadily for at least 30 million years before Australia became isolated from Antarctica, and continued through the mid-Cenozoic.

While Crisp *et al.* (2004) do not provide any new evidence contributing to the understanding of the relationships within the eucalypts, the chronogram (their Fig. 3) that they present (one of several equally parsimonious solutions) reflects some slightly different topology from previous analyses. For instance, the positions of *Arillastrum* and that of the *Corymbia* + *Angophora* clade is different from other cladograms based on chloroplast DNA (Whittock *et al.* 2003), and molecules and morphology (Udovicic and Ladiges 2000; Ladiges *et al.* 2003).

In raising concerns about deriving dates from sequence data, **Ladiges and Udovicic (2005)** make comparisons between some of the hypotheses proposed by Crisp *et al.* (2004) and those of Ladiges *et al.* (2003). In particular they discuss the conclusions drawn from molecular dating and biogeographic approaches with respect to the *Eucalyptopsis*-*Allosyncarpia*-*Stockwellia* clade and relationships between these three genera.

In the most recent work on the eucalypts, **Parra-O *et al.* (2006)** sequenced the ETS region of nuclear ribosomal DNA for an extensive range of taxa to specifically address the question of monophyly of *Corymbia* and to clarify relationships within the eucalypt group. The ETS dataset was combined with ITS sequences from previous studies of Steane *et al.* (2002) and Udovicic and Ladiges (2000).

The analyses of the combined ETS and ITS sequences resulted in three well supported clades – the *Corymbia* + *Angophora* clade, *Eucalyptus* and the *Eucalyptopsis* group (Figure 4 – from Parra-O *et al.* 2006). *Corymbia* is shown to be monophyletic, and *Eucalyptus* is sister to the combined *Corymbia* + *Angophora* clade. This research provides evidence for the recognition of *Corymbia* and *Angophora* as separate genera.



**Figure 4.** One of the six most parsimonious trees obtained from analysis of the combined dataset (ETS + ITS), showing branch lengths. Letters following species and group names represent taxon codes. *Corymbia*: A = Sect. *Apteria*; B = Sect. *Blakearia* (BP, ser. *Papuanae*; BT, ser. *Tessellares*); O = Sect. *Ochraria*; P = Sect. *Politaria*; R = Sect. *Rufaria* (RG, ser. *Gummiferae*; RI, ser. *Intermediae*; RPoly, ser. *Polycarpae*). *Eucalyptus*: EA, subg. *Alveolata*; Eac, subg. *Acerosa*; EC, subg. *Cruciformes*; EE, subg. *Eucalyptus*; EI, subg. *Idiogenes*; EM, subg. *Minutifructus*; EP, subg. *Primitiva*; ES, subg. *Symphomyrtus*. (Source: Parra-O *et al.* 2006, Fig. 4)

There is strong support for the *Corymbia* + *Angophora* clade and the authors emphasise that this grouping is recovered in all molecular phylogenetic studies to date, including the use of two other nuclear and seven chloroplast regions (as discussed above). The ETS and ITS analyses again reveal the long branch to the *Corymbia* + *Angophora* clade with the implication that this is a deep divergence from *Eucalyptus*.

This combined analysis of ETS and ITS does not resolve unequivocally the relationships at the basal nodes of the eucalypts. The *Eucalyptopsis* group is shown to be outside the *Corymbia* + *Angophora* and *Eucalyptus* clade.

The analyses of Parra-O *et al.* (2006) reveal the monophyly of the *Eucalyptopsis* group, consistent with the results of earlier molecular studies, and supported by morphological characters (Bohte and Drinnan 2005). Within the *Eucalyptopsis* group there is strong support for *Allosyncarpia* as sister to the clade of *Stockwellia* + *Eucalyptopsis*. The latter sister relationship has been identified in some molecular analyses and is supported with morphology data, with *Stockwellia* and *Eucalyptopsis* sharing undifferentiated perianth parts and elongated fusiform buds as discussed by Bohte and Drinnan (2005).

## Summary

It is likely that the current level of activities surrounding the eucalypts will result in further hypotheses being proposed, and potentially, additional changes in eucalypt classification. One implication of this increased knowledge is that some researchers may recommend additional changes in eucalypt nomenclature.

The taxonomic and nomenclatural situation in *Eucalyptus sens lat.* is common to many large economically and environmentally important plant groups, *i.e.*, there is a dynamic tension between presenting a natural classification reflecting phylogenetic relationships and the pragmatic treatment that maintains nomenclatural stability.

We have adopted here in *EUCLID - Eucalypts of Australia* some of the recent proposed changes, namely recognising the current wide acceptance of *Angophora* and *Corymbia* as genera distinct from *Eucalyptus*. Over time and with new information and different interpretations it is possible that the prevailing consensus may shift in different directions. We note that there is no universally accepted circumscription for these icons of the Australian flora, but, to the best of our ability we believe that EUCLID reflects the most widely accepted nomenclatural concepts.

Judy West

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