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# The evolution and phylogenetic placement of invasive Australian *Acacia* species

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## ABSTRACT

**Aim** *Acacia* is the largest genus of plants in Australia with over 1000 species. A subset of these species is invasive in many parts of the world including Africa, the Americas, Europe, the Middle East, Asia and the Pacific region. We investigate the phylogenetic relationships of the invasive species in relation to the genus as a whole. This will provide a framework for studying the evolution of traits that make *Acacia* species such successful invaders and could assist in screening other species for invasive potential.

**Location** Australia and global.

**Methods** We sequenced four plastid and two nuclear DNA regions for 110 Australian *Acacia* species, including 16 species that have large invasive ranges outside Australia. A Bayesian phylogenetic tree was generated to define the major lineages of *Acacia* and to determine the phylogenetic placement of the invasive species.

**Results** Invasive *Acacia* species do not form a monophyletic group but do form small clusters throughout the phylogeny. There are no taxonomic characters that uniquely describe the invasive *Acacia* species.

**Main conclusions** The legume subfamily Mimosoideae has a high percentage of invasive species and the Australian *Acacia* species have the highest rate of all the legumes. There is some evidence of phylogenetic clumping of invasive species of *Acacia* in the limited sampling presented here. This phylogeny provides a framework for further testing of the evolution of traits associated with invasiveness in *Acacia*.

## Keywords

*Acacia*, biological invasions, invasive species, legumes, Mimosoideae, phylogeny.

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## INTRODUCTION

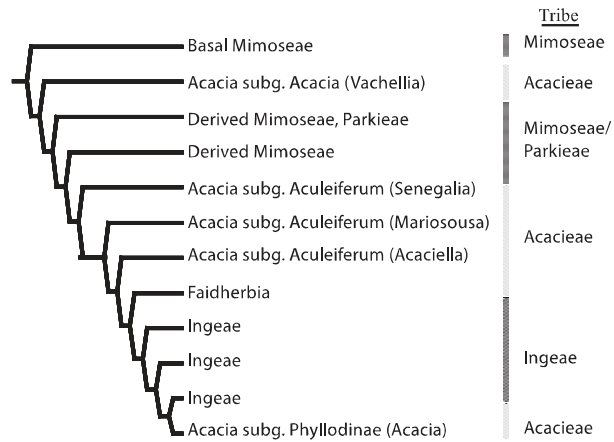
*Acacia* Mill. was first described by Miller (1754), and the genus has gone through much iteration with *Acacia s.l.* as we currently understand it largely framed by Bentham (1875). The distributional range of *Acacia s.l.* is broad, covering much of the world's subtropical arid areas (Lewis *et al.*, 2005) including the Americas, Africa, Asia and Australia. Through extensive morphological and molecular systematic studies (Chappill & Maslin, 1995; Brain & Maslin, 1996; Miller & Bayer, 2000, 2001; Luckow *et al.*, 2003; Brown *et al.*, 2008), it is now agreed that *Acacia s.l.* comprises three large lineages, roughly equivalent to subgenera *Acacia*, *Aculiferum* Vassal and *Phyllodineae* (DC.) Seringe, and three newly segregated smaller genera

(Box 1). See Maslin *et al.* (2003) for a detailed overview of the generic history of *Acacia s.l.*

In 2005, a retypification of the genus from the African species *Acacia nilotica* (L.) Willd. Ex Delile, now *Vachellia nilotica* (L.) P.J.H. Hurter & Mabb. (Mabberley, 2008), to the Australian species *Acacia penninervis* Sieber ex DC. was approved at the XVII International Botanical Congress in Vienna (McNeill *et al.*, 2005). Under this change, most Australian species belong to the genus *Acacia*. Acceptance of this retypification still remains controversial (Luckow *et al.*, 2005; Rijckevorsel, 2006; Smith *et al.*, 2006; Moore, 2007, 2008).

There are 1028 species of *Acacia s.l.* in Australia, of which 1012 (Council of Heads of Australasian Herbaria, 2010); Table 1) belong to a single clade, formerly known as *Acacia* subg.

## Box 1 Mimosoideae: phylogenetic overview and weedy taxa



The Leguminosae, is one of the largest plant families with over 700 genera and 19,000 species (Lewis *et al.*, 2005). The family has three subfamilies two of which are monophyletic (Papilionoideae and the Mimosoideae) and each is derived from a paraphyletic Caesalpinoideae.

The legume subfamily, Mimosoideae, is predominantly comprised of three large tribes: Mimosaeae, Acacieae and the Ingeae. Molecular phylogenetic research over the last 10 years has tested these tribal boundaries and in turn the relationships of individual genera within the tribes. These results clearly indicate that the three large tribes are not natural lineages (Bukhari *et al.*, 1999; Miller & Bayer, 2000, 2001; Luckow *et al.*, 2003, Brown *et al.*, 2008). The Mimosaeae is basal with the smaller tribe Parkieae and part of the Acacieae embedded within it. The tribe Ingeae is paraphyletic in relation to the Acacieae, which is polyphyletic. It appears that a meaningful monophyletic tribal classification for the subfamily will be difficult to circumscribe.

Also these results clearly demonstrate that *Acacia s.l.* is not monophyletic and that the three main lineages are not closely related. *Acacia* subg. *Acacia* is a well-supported clade placed within in the Tribe Mimosaeae. It is closely related to the basal Mimosaeae such as *Prosopis*, *Neptunia*, *Desmanthus* and *Leucaena* and to the more derived Mimosaeae clade which contains the genera *Parkia*, *Piptadenia*, *Anadenanthera*, *Mimosa* and *Microlobius*. Many of these genera contain invasive species.

The largest subgenus, *Acacia* subg. *Phyllodineae*, is more closely related to the species of the Tribe Ingeae than to other *Acacia s.l.* species. (See Box 2 for more phylogenetic information on the Ingeae.)

*Acacia* subg. *Acueiferum* was determined to be non-monophyletic and three genera have been named or proposed for the segregate lineages (Rico Arce, 2006; Seigler *et al.*, 2006). The core of *Acacia* subg. *Aculeiferum* is monophyletic and consists of over 200 species with a range similar to that of *Acacia* subg. *Acacia*: ranging from the America, Africa, Asia and into northern Australia.

Invasive species are common in the family with 122 species known to be invasive. The phylogenetic distribution of the invasive species is skewed both due to historical and biological reasons (Richardson *et al.*, 2011).

*Phyllodineae* (synonymous with *Racosperma* Mart.), now *Acacia s.s.* in the new taxonomy. The remaining 16 species found in Australia, which include some naturalized taxa, comprise taxa of *Acaciella* Britton & Rose (3), *Senegalia* Rafinesque (2) and *Vachellia* (11) (Council of Heads of Australasian Herbaria, 2010). Eighteen species of *Acacia s.s.* occur naturally outside continental Australia, ten of which are not found in Australia. This paper and the others in this special issue of *Diversity and Distributions* focus on the 1012 species, a group which are often referred to as the Australian acacias (Richardson *et al.*, 2011).

Recent phylogenetic analysis of *Acacia s.s.* has identified well-supported clades that do not closely resemble the traditional classification of taxa by Pedley (1978) or Bentham (1875). These groups were informally named by Murphy *et al.* (2010) as comprising five clades. Two of these clades were resolved at basal nodes and consisted mostly of uninerved phyllodinous taxa. One clade was named the '*Acacia victoriae* and *Acacia pyrifolia* clade', and the second the '*Acacia murrayana* clade', with these two groups occurring predominantly in

Table 1 Invasive legume species based on taxonomic category.

Taxonomic group	Number of invasive species	Total number of species	Percentage invasive
Leguminosae (Fabaceae)	121	19,320	0.63
Subfamily Caesalpinioideae	22	2250	0.98
Subfamily Mimosoideae	56	3270	1.71
Tribe Acacieae	31	1450	2.14
Australian <i>Acacia</i>	23	1020	2.25
Tribe Ingeae	11	951	1.16
Tribe Mimosaeae	14	869	1.61

Species totals are from Lewis *et al.* (2005) and Council of Heads of Australasian Herbaria (2010). The number of woody trees and shrubs that are invasive species is from Richardson & Rejmánek (2011). Many taxa of subfamily Papilionoideae are not woody and therefore not included in the included in the Richardson & Rejmánek (2011) list or in this table.

semi-arid and arid regions of Australia. A ‘Pulchelloidea clade’ was named to comprise members of the sections *Pulchellae*, *Alatae*, *Lycopodiifoliae* and some members of sect. *Phyllodineae* of Pedley (1978). The fourth named clade, the ‘p.u.b. clade’, was a large assemblage of plurinerved and uninerved phyllodinous taxa and also bi-pinnate taxa from section *Botrycephalae* (members of which were placed in a fifth named informal ‘Botrycephalae subclade’).

Dispersal of Australian acacias has happened several times with presumed long-distance dispersal events to Madagascar, Hawaii and South East Asia (Pedley, 1975, 1986). These dispersal events are hypothesized to predate human intervention in species distribution boundaries, although occurring relatively recently in geological time. However, such hypotheses remain to be tested. Owing to the consequences of human intervention (Griffin *et al.*, 2011; Le Roux *et al.*, 2011; Richardson *et al.*, 2011), the ranges of some Australian acacias have changed dramatically. Many legumes and species of *Acacia* in particular have been moved around the world by humans for various purposes ranging from sand dune stabilization and forestry as well as for the tannin and perfume industries (Maslin, 2001; Marchante *et al.*, 2008; Kull *et al.*, 2011; Richardson *et al.*, 2011). In many cases, an unforeseen consequence of the cultivation of *Acacia* species has allowed their establishment and invasion in many parts of the world. Twenty-three species of Australian acacias are now considered invasive outside Australia. Some species such as *Acacia mearnsii*, *Acacia longifolia* and *Acacia cyclops* are invasive in many areas of the world from Africa, Europe, the Middle East, the Americas to Asia. Others such as *A. victoriae* were only recently recognized as invasive (Richardson & Rejmánek, 2011). The high level of *Acacia* use worldwide is expected to provide an opportunity for other species to become invasive in the future (Wilson *et al.*, 2011).

The goal of this paper is to explore the molecular phylogenetic relationships of selected invasive species of *Acacia* within a broader phylogenetic framework of the *Acacia s.s.* clade using plastid and nuclear ribosomal DNA sequence data. We then use the resulting phylogeny to answer questions regarding invasive species of *Acacia* such as: (1) Do the invasive species form a monophyletic group(s)? (2) What are the sister taxon relationships to invasive species? (3) Are there key morphological or spatial traits that correlate with the invasive species?

## METHODS

### Taxon sampling

The sampling consisted of 121 OTUs representing 110 *Acacia* species (Appendix 1). The species were selected based on the main lineages of *Acacia* (Murphy *et al.*, 2010) and the list of invasive and non-invasive taxa present in South Africa (Richardson *et al.*, 2011). Sixteen sampled species are invasive. Three separate data alignments and phylogenetic analyses were conducted. First, a dataset consisting of 60 species of *Acacia* was developed which represents all the main lineages of *Acacia*

so far identified (Murphy *et al.*, 2010). This will be referred to as the ‘overall’ dataset and analysis. Owing to high levels of variation, portions of the DNA sequences were not able to be aligned; therefore, two subset analyses were also performed. The subset analyses allowed better sequence alignment and homology assessment, and resulted in more sites included in the phylogenetic analyses. The first subset consisted of 43 OTUs and 40 species and will be referred to as the ‘mearnsii’ dataset because of the presence of this representative invasive species. The second comprised 46 OTUs and 44 species and will be referred to as the ‘melanoxyton’ dataset because of the presence of this representative invasive species.

Invasive species of *Acacia* are represented in all three datasets. Placeholder species from the mearnsii and melanoxyton datasets were included in the overall dataset. Outgroup taxa, *Parachidendron pruinosum* and *Paraserianthes lophantha* subsp. *lophantha*, were chosen based on results of previous studies (Miller & Bayer, 2000, 2001; Luckow *et al.*, 2003; Brown *et al.*, 2008). Fresh leaf samples were collected either in the field or from cultivated plants of known provenance, and where no other material was available, from herbarium specimens.

### DNA isolation, amplification and sequencing

Genomic DNA was extracted from 10 to 100 mg of fresh or silica gel-dried leaf tissue, or from herbarium material, using the DNeasy Plant Mini kit (Qiagen, Valencia, CA) either individually or in the 96-well plate format. Six regions were amplified and sequenced of which four were plastid loci and two nuclear. The four plastid loci sequenced were *psbA-trnH* intergenic spacer, *trnL-F* intron and intergenic spacer, *rpl32-trnL* intergenic spacer and a portion of the *matK* region. All amplifications were performed using the PCR profile outlined by Shaw *et al.* (2005). The primers used were as follows: *psbA-trnH* [Sang *et al.* (1997)], *trnL-F* [Taberlet *et al.* (1991)], *rpl32-trnL* [Shaw *et al.* (2007)] and *matK* 59R/6 [Johnson & Soltis (1994)]. The complete sequences of nuclear ribosomal DNA internal (ITS) and external (ETS) transcribed spacers were amplified and sequenced using the primers and protocols described by Murphy *et al.* (2010). All sequences are lodged in Genbank (JF419907–JF420546).

### Phylogenetic analyses

Contiguous sequences were edited using Sequencher™ v.3.0 (Gene Codes Corporation, Ann Arbor, MI) and manually aligned in BioEdit sequence alignment editor v.4.8.6 (Hall, 1999). Sequence alignments and PAUP/Nexus formatted files are available from the authors upon request, and all sequences are lodged in Genbank (see Appendix 1).

Any uncertain base positions, generally located close to priming sites, and highly variable regions with uncertain sequence homology, were excluded from phylogenetic analysis. Individual base positions were coded as unordered multistates, and potentially informative insertions/deletions (indels) were coded as additional binary characters.

Bayesian analyses were performed using MrBayes version 3.1.2 (Ronquist & Huelsenbeck, 2003). Posada & Crandall (1998) (Modeltest v.1.1) determined that the GTR + I + gamma model was the best-fit model for both the plastid and nuclear partitions, and it was applied to each DNA sequence partition. Indel characters were included as a separate partition, and a standard (morphology) discrete state model with a gamma shape parameter was applied to this partition (Lewis, 2001). The Markov chain Monte Carlo search was run for 5 million generations with trees sampled every 1000 generations. MrBayes performed two simultaneous analyses starting from different random trees (Nruns = 2), each with four Markov chains (Nchains = 4). The first 2000 trees were discarded from each run. A Bayesian consensus phylogram with posterior probability values plotted was calculated in MrBayes. Maximum parsimony analyses were performed with the heuristic search option (excluding uninformative characters) in PAUP\* 4.02 (Swofford, 1999). A four-step search method for multiple islands was performed with 10,000 random replicates (Olmstead & Palmer, 1994). Support for internal branches was evaluated by the fast bootstrap method with 10,000 replicates (Felsenstein, 1985). A partition homogeneity test was conducted in PAUP\* 4.02 (Swofford, 1999) using 100 random replications to test whether the plastid and nuclear data partitions are congruent.

## RESULTS

### Phylogenetic analyses

In the overall dataset that contained the broadest sampling of species of *Acacia*, the four concatenated plastid sequences aligned to 3337 nucleotides, while the nuclear ribosomal DNA aligned to 1263 nucleotides, and for this dataset, 29 indel characters were scored. The two subset analyses had shorter alignments, because of fewer indels than found in the overall dataset.

For each dataset, the nuclear and plastid sequence partitions were analyzed separately. The partition homogeneity test indicated that the two partitions were congruent and the resulting phylogenies (not shown) were broadly concordant. The minor discrepancies between the nuclear and plastid phylogenies are only at the branch tips where the posterior probabilities and bootstrap values are low.

The main clades resolved are broadly congruent in the three trees presented here (Figs 1–3: overall, melanoxyton and mearnsii). Two invasive taxa, namely *Acacia saligna* and *A. victoriae*, were only included in the overall analysis and not in the subset analyses because these taxa are not members of the two subset clades.

In the overall tree (Fig. 1), the major lineages shown, similar to Murphy *et al.* (2010), are supported with maximal posterior probability values (PP = 1.00). These are (A) The *A. victoriae* and *A. pyrifolia* clade, (B) The Pulchelloidea clade, (C) The *A. murrayana* clade, (D) The melanoxyton clade and (E) The mearnsii clade. The latter two are equivalent to the p.u.b. clade

of Murphy *et al.* (2010). As previously found and based on the current sampling, none of the sections of Pedley (1978) are resolved as monophyletic. However, additional resolution was found for taxa within the melanoxyton and mearnsii clades than previously discovered. It is notable that the current phylogenetic analysis has identified new taxa that should be placed within the lineages found by Murphy *et al.* (2010).

Clades that include invasive taxa (Figs 1–3) have been identified as follows:

**A.** Resolved at the earliest diverging node of the overall tree (Fig. 1, clade A) is *A. victoriae*, placed in a clade with *A. pyrifolia* and *Acacia dempsteri* (the *A. victoriae* and *A. pyrifolia* clade, PP = 1.00).

**B.** In the Pulchelloidea clade (Fig. 1, clade B, PP = 1.00), *A. saligna*, with *A. alata*, is the sister group (PP = 0.98) to the remaining eleven sampled Pulchelloidea taxa. *Acacia saligna* is the sole invasive taxon so far identified in the Pulchelloidea clade.

**C.** There are no invasive species within the *A. murrayana* clade (Fig. 1, clade C).

The melanoxyton (Fig. 1, clade D) and mearnsii (Fig. 1, clade E) clades together (Fig. 1, PP: 1.00) are equivalent to the largely unresolved p.u.b. clade of Murphy *et al.* (2010). Additional taxa were included in the present subset analyses for the melanoxyton clade (Fig. 2) and the mearnsii clade (Fig. 3), and most of the invasive taxa are found in these clades.

**D.** The melanoxyton clade contains six recognized invasive species in four broad groups:

(i) In the *Acacia cognata* subclade (Fig. 2, top), a notable group of invasive species occurs. These are *A. implexa* and *A. melanoxyton* as sister taxa (PP = 1.00), related to a clade, with very low PP support (PP = 0.51), that include *A. verticillata*, *A. genistifolia*, *A. baeuerlenii*, and *A. elongata*.

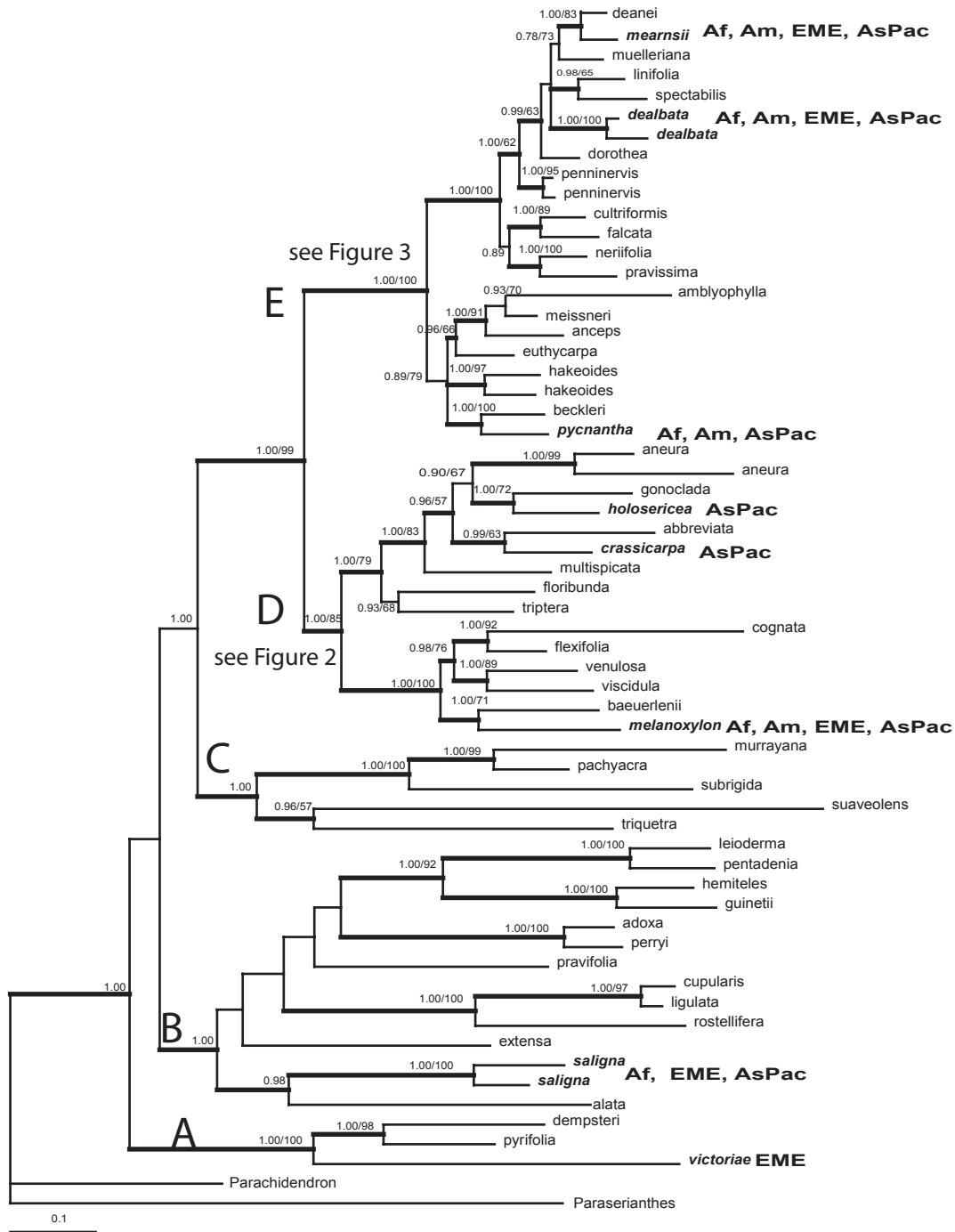
(ii) *Acacia cyclops* and *A. ixiophylla* (PP = 0.61) are the sister clades to the remaining taxa in the *A. cognata* clade of which *A. cyclops* is invasive.

(iii) An *A. longifolia* clade, as identified by Brown *et al.* (2010), is resolved (with PP = 0.99) to include *Acacia longissima*, *Acacia mucronata* and the invasive *A. longifolia*.

(iv) In the *Acacia aneura* subclade (Fig. 2, bottom), only a single invasive lineage is identified; *A. crasscarpa* and *A. holosericea* are sister clades (PP: 0.65) to *A. aulacocarpa*, an apparently non-invasive species.

**E.** The large mearnsii clade (Fig. 3), which includes uninerved phyllodinous and bipinnate taxa also includes *A. penninervis*, the newly designated type species of *Acacia* (Orchard & Maslin, 2003). This clade includes seven invasive species and therefore has the largest number of invasive taxa within it.

Some grouping of invasive species is noted within the mearnsii clade. Five invasive species (*Acacia baileyana*, *A. dealbata*, *A. decurrens*, *A. mearnsii* and *A. podalyriifolia*) occur in this clade along with 10 non-invasive species (PP = 1.00). This clade represents taxa with both bipinnate and phyllodinous mature vegetative leaves. The other invasive



**Figure 1** Bayesian phylogenetic tree of the 'overall' dataset. Number above node is the Bayesian posterior probability (PP) followed by the bootstrap value. Bold branches indicate PP > 0.90. Taxa in bold italic are invasive with the following codes indicating areas of invasiveness. Af, Africa; Am, North and South America and Caribbean Islands; EME, Europe, Middle East and Atlantic Islands; AsPac, Asia, Australia, New Zealand, Indian and Pacific Islands.

taxa in the *mearnsii* clade, *A. pycnantha* and *A. elata* do not group closely together.

Of the 23 known invasive *Acacia* species, seven are not sampled in this phylogeny. Based on previous knowledge, we can estimate that *A. mangium* and *A. auriculiformis* would group in the *aneura* subclade of the *melanoxyton* clade,

possibly near the invasive species *A. crassicarpa* and *A. holosericea*. No confident prediction can be undertaken as yet for the phylogenetic placement of the other invasive species *A. iteaphylla*, *A. paradoxa*, *A. retinodes*, *A. salicina* and *A. stricta*. These species await future molecular phylogenetic research.



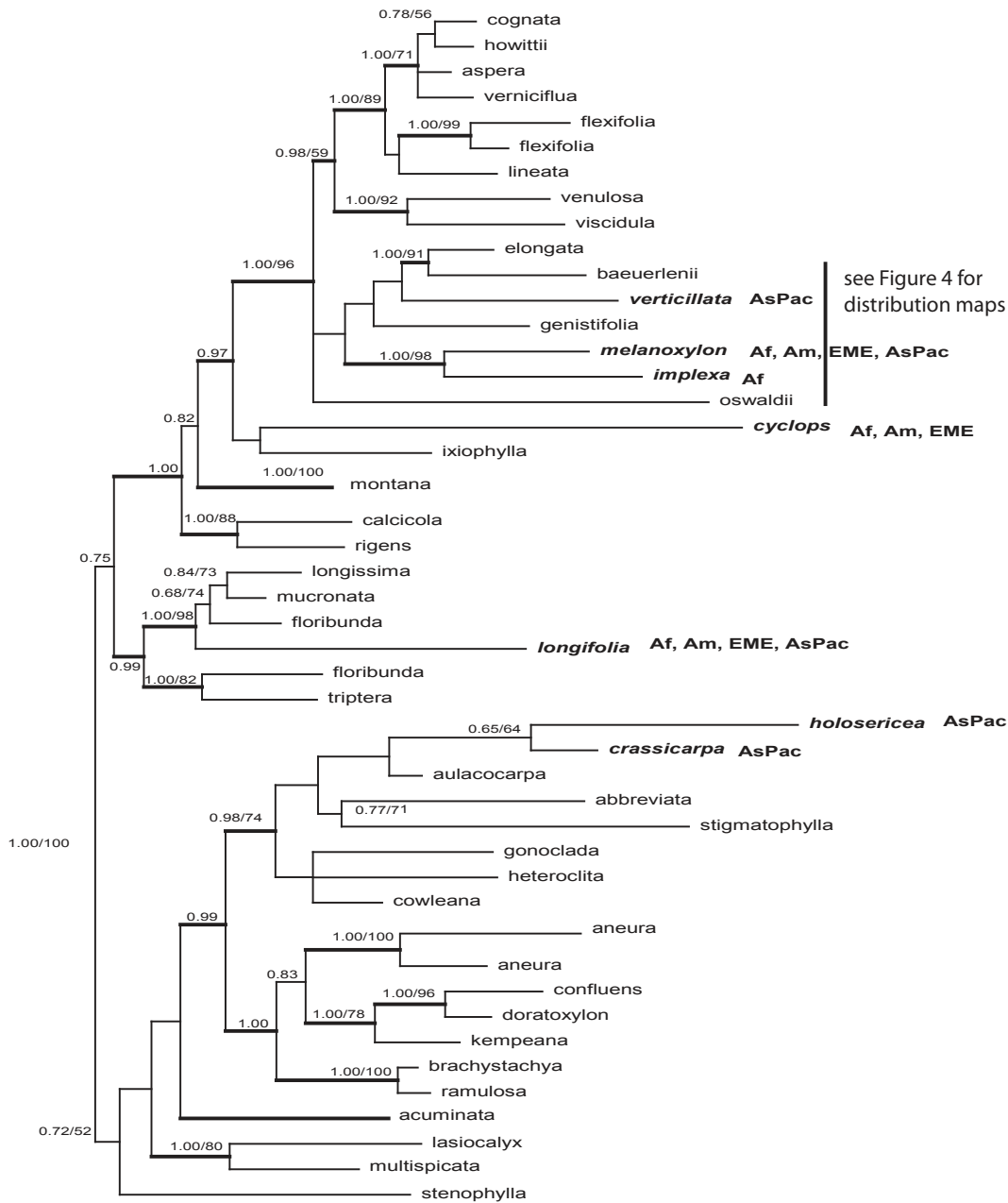


Figure 2 Bayesian phylogenetic tree of the 'melanoxyton' dataset. Notes as in Fig. 1.

## DISCUSSION

With over 19,000 species, the legumes are one of the largest families of flowering plants (Lewis *et al.*, 2005). The family comprises a paraphyletic subfamily, the Caesalpinioideae and two monophyletic subfamilies, the Papilionoideae and the Mimosoideae. The largest subfamily, Papilionoideae, contains over 13,800 species, many of which are important as food crops such as *Glycine*, *Pisum* and *Vigna*.

Richardson & Rejmánek (2011) identified 121 woody legume species that are clearly invasive (*sensu* Pyšek *et al.*, 2004) somewhere in the world. However, weed species are apparently not evenly spread in a phylogenetic sense across

subfamilies or within them. For example, 56 of the 3270 recognized species in subfamily Mimosoideae are considered invasive, whereas only 22 of 2250 Caesalpinioideae species are invasive, a rate is 5.5 times higher (Table 1). The Australian acacias have the highest rate of invasiveness of any large lineage of the legume family with 2.16% (22 of 1020) of the species known to be invasive. This percentage of invasive species is higher than other large woody plant families such as the Diptocarpaceae (0.3%) and the Fagaceae (0.7%). The percentage of invasive species in *Acacia* is higher than in the Myrtaceae, but much lower than in *Pinus* (12%), both of which have been planted worldwide (Richardson & Rejmánek, 2004).

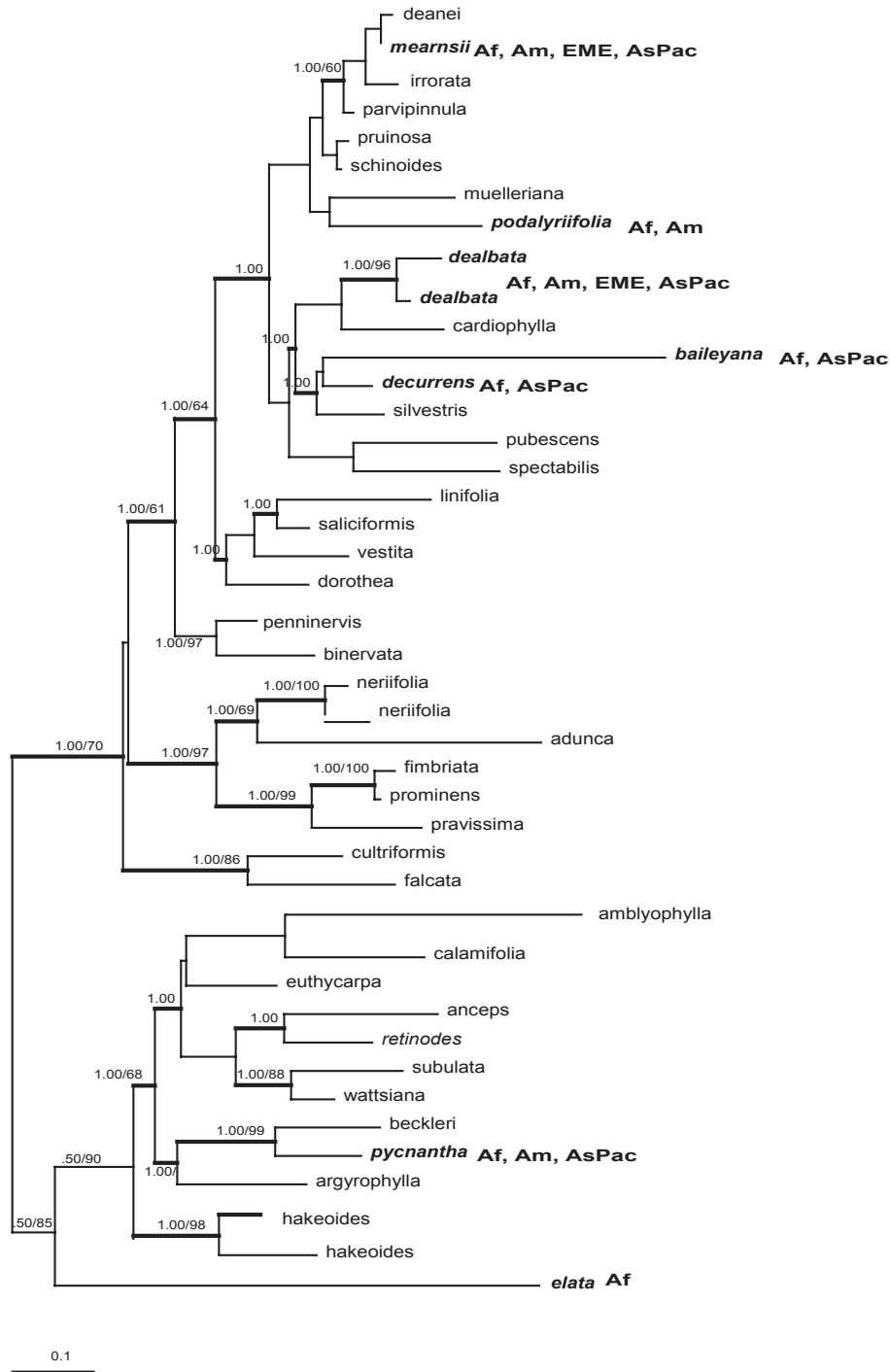


Figure 3 Bayesian phylogenetic tree of the ‘mearnsii’ dataset. Notes as in Fig. 1.

There does not appear to be a high correlation between a legume species being used as a food and its invasiveness. The subfamily Papilionoideae contains most of the human cultivated food species including soybean, pea, cowpea and dry beans but has fewer invasive species than the less species-rich subfamily Mimosoideae. The Mimosoideae has more woody perennial species than the Papilionoideae, and perhaps it is this life history that drives the higher rate of invasiveness. These data suggest

that there are particular affinities towards invasiveness in some plant lineages but fewer in others.

Other than the Australian *Acacia* species that are the main subject of this special issue, there are several other weedy mimosoid legumes with large invasive ranges. Several genera with invasive species cluster together near the base of the phylogenetic tree depicted in Box 1. These include *Prosopis* spp. (mesquite), *Acacia* (*Vachellia*) *nilotica* (prickly acacia),



*Leucaena leucocephala* and *Mimosa pigra*. All these species are highly invasive and can be found in Africa, the Americas and the Asian Pacific region (Richardson & Rejmánek, 2011).

In Australia, the Commonwealth Government has identified the 20 worst weeds: the Weeds of National Significance (WONS) list (<http://www.weeds.org.au/natsig.htm>). These were determined based on invasiveness, impact, potential for spread and other social and environmental impacts. Of these 20 species, five are legumes, including three mimosoid legumes mesquite, prickly acacia and *M. pigra*.

The level of invasiveness of different Australian acacias seems to have more to do with human-mediated events than with biological features of the species (Carruthers *et al.*, 2011; Gibson *et al.*, 2011; Griffin *et al.*, 2011). However the woody, arborescent habit of Mimosoid legumes appears to make it more receptive to invasiveness. The widespread use of Mimosoid legumes as forage species and in various types of forestry and agroforestry programmes worldwide has radically enhanced their invasiveness potential (Griffin *et al.*, 2011; Richardson *et al.*, 2011).

#### AUSTRALIAN ACACIAS AND INVASIVE RELATIONSHIPS

This study has built on previous phylogenetic analyses of *Acacia* s.s. by increasing taxon sampling and particularly by increasing the amount of DNA sequence data sampled to provide a more comprehensive phylogeny with greater phylogenetic resolution than previously available. The overall aim and focus of this study was to place in a broad phylogenetic context some of the known invasive species of *Acacia* and to provide some general insights into the evolution of invasiveness in the *Acacia* s.s. clade. The current study also provides some insights that should be useful for predicting future invasions in the group.

Overall, an important discovery from the phylogenetic analysis in the current study is that invasive taxa do not form a single clade. Rather, invasiveness is spread across the phylogeny of *Acacia*. However, given this, there are some clades in which several invasive taxa occur; probably, the most notable of these is the subclade that contains *A. melanoxylon* (Fig. 2) which contains six species: *A. melanoxylon*, *A. implexa*, *A. verticillata*, *A. genistifolia*, *A. baeuerlenii* and *A. elongata*. The first three of these are known to be invasive (Richardson & Rejmánek, 2011). *A. genistifolia*, currently not known as invasive in its introduced range, may well become invasive and should be carefully monitored. The range of the species in this grouping is in southeastern Australia (Fig. 4). In all cases, the distribution of the invasive species is much larger than the non-invasive sister species (see Hui *et al.*, 2011).

Another group of taxa found in the aneura subclade of the melanoxylon clade contains *A. holosericea* and *A. crassicaarpa*. This clade is also the likely place for two other invasive species that were not sampled: *A. mangium* and *A. auriculiformis*. All are northern Australian species and have been used, with the exception of *A. holosericea*, in South East Asian forestry

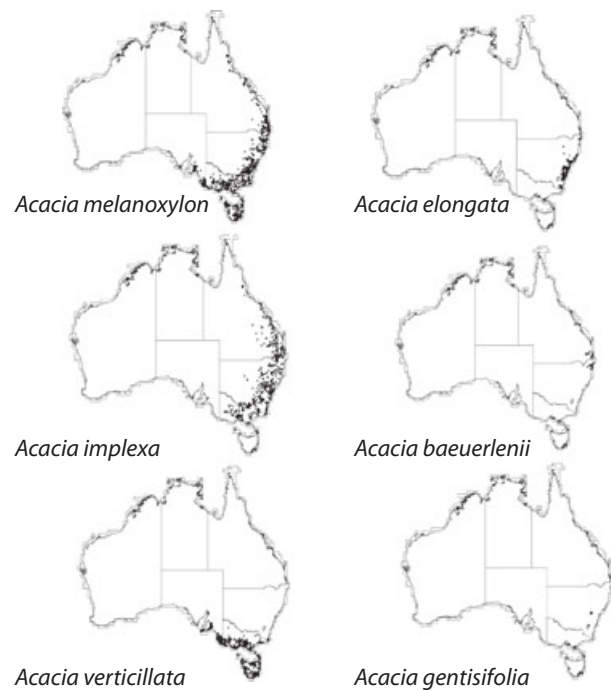


Figure 4 Distribution map of selected species of the melanoxylon clade (see Fig. 2). Data derived from an edited version of the Australian Virtual Herbarium Council of Heads of Australasian Herbaria (2010).

projects (Griffin *et al.*, 2011). Interestingly, as in the melanoxylon clade, the ecological tolerances and distribution of *A. crassicaarpa* are broader than its closest relatives, *A. peregrina* and *A. midgleyi* (McDonald & Maslin, 2000).

Furthermore, the mearnsii clade (Fig. 3), which while being the target of increased taxon sampling for the current analysis, also has a large number of invasive species within it: *A. dealbata*, *A. baileyana* and *A. decurrens*. These species group with *A. cardiopylla*, *A. silvestris*, *A. pubescens* and *A. spectabilis*. With the exception of *A. spectabilis*, the invasive species have larger natural ranges.

The species range distribution should be interpreted with caution as the Australian ranges shown may include range expansion because of the species' invasiveness (Hui *et al.*, 2011). In general, the native distribution of invasive species is smaller than the current distribution in Australia. For example, the native distribution *A. baileyana* is restricted to a small area of NSW, but it is naturalized in much of SE Australia (Orchard *et al.*, 2001). However, for most species, the circumscription of native and naturalized boundaries is unclear. Therefore, when compared to their sister species, it appears that the characteristics that allow a species to be invasive may also have an effect in the native range distribution.

The phylogenetic clustering of invasive species may have less to do with them possessing traits associated with invasiveness per se than with them having traits that make them more important in forestry and other industries that gave the species a foothold in many areas of the world.

**Box 2** Tribe Ingeae: phylogenetic overview and weedy taxa

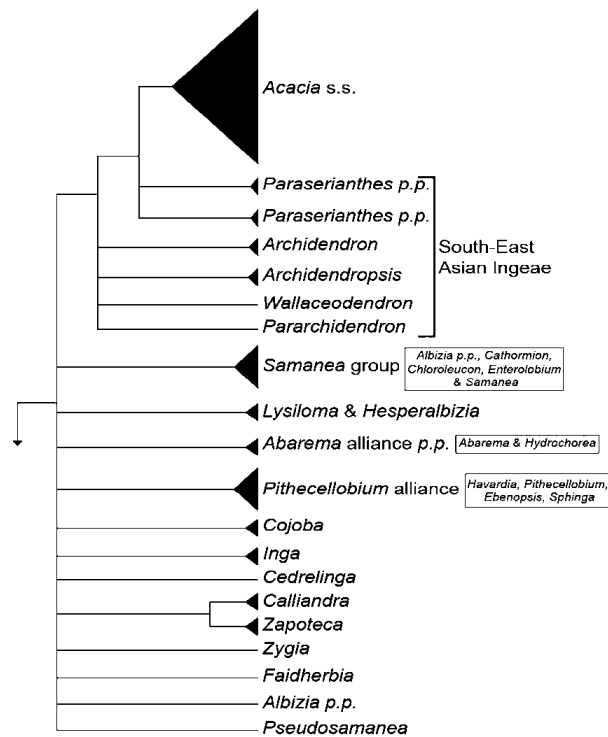
Tribe Ingeae is pantropical with 36 genera and *c.* 1000 species. It is differentiated from tribe Acacieae by one character: fusion of stamens into a tube in Ingeae and free stamens in Acacieae (Elias, 1981; Nielsen, 1981). Tribe Ingeae has repeatedly been shown to be paraphyletic, with *Acacia sensu stricto* nested within it (Brown *et al.*, 2008; Dayanandan *et al.*, 1997; Lavin *et al.*, 2005; Luckow *et al.*, 2003, 2000; Miller *et al.*, 2003a, 2003b; Miller & Bayer, 2000, 2001, 2003; Wojciechowski *et al.*, 2004). An intra-tribal classification was proposed by Barneby & Grimes (1996), which described five alliances based on developmental and macro-morphological characteristics. Some modifications have since been suggested (see Brown, 2008) and several alliances have been disputed by a molecular phylogenetic analysis (Brown *et al.*, 2008). Phylogenetic relationships within tribe Ingeae are not well understood with many terminal clades resolved but the deeper relationships within the tribe not yet determined (Figure a).

Like many acacias, numerous Ingeae taxa are significant weeds world-wide, including species of *Albizia* Durazz., *Lysiloma* Benth., *Paraserianthes sensu lato* I.C. Nielsen, *Pithecellobium* Martius and *Samanea* Merr. The placement of these weedy taxa, if known, are scattered across the phylogeny (see Figure a). However, several weedy taxa — *Albizia lebeck* (L.) Benth, *Albizia saponaria* Blume ex. Miq. and *Samanea saman* (Jacq.) Merr. — are united in the *Samanea* group of Brown *et al.* (2008); Figure a).

Relationships of some taxa are well supported, for example *Paraserianthes* and *Pithecellobium*. *Pithecellobium dulce* is related to *Ebenopsis*, *Havardia*, *Sphinga* and *Painteria*, in the *Pithecellobium*-alliance (Barneby & Grimes, 1996; Brown *et al.*, 2008). *Paraserianthes sensu lato* is the closest relative to *Acacia sensu stricto*. It includes four species, two of which are widely planted and invasive taxa: *Paraserianthes lophantha* and *Paraserianthes falcataria* (= *Falcataria moluccana*).

Relationships of other weedy Ingeae taxa, however, are not understood. For example, *Lysiloma*, which includes several weed species (*L. acapulcense*, *L. bahamensis* and *L. latisiliqua*). *Lysiloma* was placed in the *Chloroleucon*-alliance of Barneby & Grimes (1996), however, Lewis & Rico (2005) did not think it belonged there and left it unplaced within the alliances. Molecular phylogenies suggest that *Lysiloma* is monophyletic and related to *Hesperalbizia*, of the *Samanea*-alliance (Barneby & Grimes, 1996), but these studies include less than a quarter of known species of *Lysiloma* (Luckow *et al.*, 2003; Miller *et al.*, 2003b; Brown *et al.*, 2008).

Limited data is available on the intraspecific variation of weedy Ingeae, e.g. *A. lebeck* (Aparajita & Rout, 2009). However, work is underway on some taxa (e.g. *P. lophantha*).



(a) Summary molecular phylogeny of Tribe Ingeae based on nrDNA sequences of the ITS and ETS (Brown *et al.*, 2008).

Additionally, the sampling in this study is not random. With over 1000 species in the genus, it is unlikely that we have sampled all the sister species of the known invasive species. The ‘clustering’ of invasive species may therefore be an artefact of the limited species sampled. This can only be overcome by highly intensive phylogenetic sampling.

Gallagher *et al.* (2011) investigated difference in several functional traits between invasive and non-invasive *Acacia* species. They found invasive species to be taller, more prone to seed dispersal by vertebrates, have a larger native range including adapted to a broader range of annual precipitation than non-invasive *Acacia* species. No differences were found in

seed mass, specific leaf area, relative growth rate and genome size (Gallagher *et al.*, 2011). Data are needed for other functional traits, and full testing of these hypotheses will require a fully sampled and more resolved phylogeny.

Plant morphological characters, especially leaf and inflorescences traits, have been used to classify *Acacia* species into sections (Pedley, 1978). These groupings have allowed convenient discussion of the variation within *Acacia* but are not considered to be natural groups (Maslin *et al.*, 2003). The most important taxonomic character is leaf type. Two sections contain only taxa with bipinnate leaves. The other sections are phyllodinous and were divided based on the number of prominent nerves in the phyllode. There is no correlation of leaf type with invasiveness. Some invasive species have bipinnate leaves, while others have phyllodes with either single or multiple nerves.

The major taxonomically important characters of the inflorescence are their shape and arrangement. The inflorescences are either globose or spicate and can be arranged in racemes or along the stem. Again there is no correlation of invasiveness and inflorescence form.

In conclusion, the legume subfamily Mimosoideae and in particular the Australian species of *Acacia* have a high percentage of invasive species compared to other legumes. It is becoming clear that invasiveness is closely associated with human-mediated introduction and dissemination, so it is very likely that the percentage of invasive *Acacia* species will rise in the future. There is some evidence of phylogenetic clumping of invasive species of *Acacia* in the limited sampling presented here with invasive species tending to have a larger native distribution than their non-invasive sister species. While no major taxonomic character is shared among the invasive species, this phylogenetic framework provides a structure for further testing the evolution of traits associated with invasiveness.

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## BIOSKETCHES

**Joseph T. Miller** is a molecular systematist and focuses his research on the plant genus *Acacia*. **Daniel J. Murphy** and **Gillian K. Brown** are also molecular systematists with major interests in the evolution and classification of *Acacia* and other Mimosoid legumes. **Carlos E. González-Orozco** is a GIS scientist with broad interests in the Australian flora. **David M. Richardson** is an invasion ecologist with an interest in legumes as invasive species.

Author contributions: J.T.M., D.J.M. and D.M.R. conceived the ideas, J.T.M. and C.E.G.-O. collected the data, J.T.M., D.J.M. and G.K.B. analysed the data and J.T.M. led the writing.

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Editor: Andrew Lowe

## APPENDIX 1 MATERIAL USED IN THIS STUDY

Taxon	Herbarium voucher specimen or collector number
<i>Acacia abbreviata</i> Maslin	CANB 793276
<i>Acacia acuminata</i> Benth.	Mt Annan BG 866885
<i>Acacia adoxa</i> Pedley	ANBG 8212874
<i>Acacia adunca</i> A.Cunn. ex Don.	ANBG 8502778
<i>Acacia alata</i> R.Br.	CANB 00579597
<i>Acacia anceps</i> DC.	CANB 793283
<i>Acacia aneura</i> F.Muell. ex Benth.	CANB 635377
<i>Acacia aneura</i> F.Muell. ex Benth.	Clarke12a
<i>Acacia argyrophylla</i> Hook.	CANB 793288
<i>Acacia aspera</i> Lindl.	CANB 793290
<i>Acacia aulacocarpa</i> A.Cunn. ex Benth.	ClarkeB
<i>Acacia auriculiformis</i> A.Cunn. ex Benth.	ATSC 15688
<i>Acacia baeuerlenii</i> Maiden & R.T.Baker	Clarke22b
<i>Acacia baileyana</i> F.Muell.	CANB 00693196
<i>Acacia beckleri</i> Tindale	ANBG 9707897
<i>Acacia binervata</i> DC.	ATSC 16245
<i>Acacia brachystachya</i> Benth.	CANB 793304
<i>Acacia calamifolia</i> Lodd.	CANB 793310
<i>Acacia calcicola</i> Forde & Ising	CANB 793311
<i>Acacia cardiophylla</i> A.Cunn. ex Benth.	CANB 492118
<i>Acacia cognata</i> Domin	ANBG 9101965
<i>Acacia cognata</i> Domin	CANB 615708
<i>Acacia confluens</i> Maiden & Blakely	CANB 793329
<i>Acacia crassicarpa</i> A.Cunn. ex Benth.	ATSC 15698
<i>Acacia cultriformis</i> A.Cunn. ex G.Don	CANB 793341
<i>Acacia cupularis</i> Domin	CANB 633912
<i>Acacia cyclops</i> A.Cunn. ex G.Don	CANB 793345
<i>Acacia dealbata</i> Link	ANBG 9101960
<i>Acacia dealbata</i> Link	CANB 738126.1
<i>Acacia dealbata</i> Link	Clarke3d
<i>Acacia deanei</i> (R.T.Baker) M.B.Welch, Coombs & McGlynn	Clarke20d
<i>Acacia decurrens</i> Willd.	CANB 793354
<i>Acacia dempsteri</i> F.Muell.	ANBG 680141
<i>Acacia doratoxylon</i> A.Cunn.	Clarke33d
<i>Acacia dorothea</i> Maiden	Clarke40d
<i>Acacia elata</i> A.Cunn. ex Benth.	ANBG 632927
<i>Acacia elongata</i> Sieber ex DC.	Clarke27e
<i>Acacia epacantha</i> (Maslin) Maslin	CANB 623291
<i>Acacia euthycarpa</i> (J.M.Black) J.M.Black	CANB 793378
<i>Acacia extensa</i> Lindl.	CANB 793382
<i>Acacia falcata</i> Willd.	Clarke4f
<i>Acacia fimbriata</i> A.Cunn. ex G.Don	Clarke26f
<i>Acacia flexifolia</i> Benth.	CANB 793390
<i>Acacia flexifolia</i> Benth.	Clarke6f
<i>Acacia floribunda</i> (Vent.) Willd.	ANBG 9611057
<i>Acacia floribunda</i> (Vent.) Willd.	Clarke7f
<i>Acacia genistifolia</i> Link	CANB 793395
<i>Acacia gonoclada</i> F.Muell.	ATSC 14721
<i>Acacia guinetii</i> Maslin	CANB 793406
<i>Acacia hakeoides</i> A.Cunn. ex Benth.	CANB 793281
<i>Acacia hakeoides</i> A.Cunn. ex Benth.	Clarke19h
<i>Acacia hakeoides</i> A.Cunn. ex Benth.	Mt Annan BG 842668
<i>Acacia hakeoides</i> A.Cunn. ex Benth.	CANB 793407
<i>Acacia hammondii</i> Maiden	CANB 793410
<i>Acacia hemiteles</i> Benth.	CANB 633963
<i>Acacia heteroclita</i> Meisn.	CANB 793415
<i>Acacia holosericea</i> A.Cunn. ex G.Don	ATSC 15669
<i>Acacia howittii</i> F.Muell.	CANB 793419
<i>Acacia implexa</i> Benth.	Clarke11i
<i>Acacia irrorata</i> Sieber ex Spreng.	CANB 793423

## APPENDIX 1 Continued.

Taxon	Herbarium voucher specimen or collector number
<i>Acacia ixiophylla</i> Benth.	CANB 793426
<i>Acacia jonesii</i> F.Muell. & Maiden	Mt Annan BG 20051433
<i>Acacia kempeana</i> F.Muell.	CANB 793435
<i>Acacia lasiocalyx</i> C.R.P.Andrews	CANB 793438
<i>Acacia leioderma</i> Maslin	CANB 793443
<i>Acacia ligulata</i> A.Cunn. ex Benth.	ANBG 8210071
<i>Acacia lineata</i> A.Cunn. ex G.Don	Mt Annan BG 842542
<i>Acacia limifolia</i> (Vent.) Willd.	ANBG 9409682
<i>Acacia longifolia</i> (Andrews) Willd.	JN782
<i>Acacia longissima</i> Hort. ex H.L.Wendl.	CANB 793457
<i>Acacia mearnsii</i> De Wild.	ANBG 12
<i>Acacia mearnsii</i> De Wild.	CANB 793467
<i>Acacia mearnsii</i> De Wild.	Clarke37m
<i>Acacia meisneri</i> Lehm. ex Meisn.	CANB 793468
<i>Acacia melanoxylon</i> R.Br.	Mt Annan BG 860538
<i>Acacia montana</i> Benth.	Clarke32m
<i>Acacia mucronata</i> Willd. ex H.L.Wendl.	CANB 615743
<i>Acacia muelleriana</i> Maiden & R.T.Baker	CANB 634004
<i>Acacia multispicata</i> Benth.	ANBG 9710019
<i>Acacia murrayana</i> F.Muell. ex Benth.	CANB 793477
<i>Acacia nerifolia</i> A.Cunn. ex Benth.	Clarke8n
<i>Acacia oswaldii</i> F.Muell.	CANB 793495
<i>Acacia pachyacra</i> Maiden & Blakely	MELU- SRA 239
<i>Acacia parvipinnula</i> Tindale	MELU- SRA 31
<i>Acacia penninervis</i> Sieber ex DC.	CANB 793506
<i>Acacia pentadenia</i> Lindl.	CANB 793507
<i>Acacia perryi</i> Pedley	CANB 793511
<i>Acacia podalyriifolia</i> A.Cunn. ex G.Don	ANBG 9406554
<i>Acacia pravifolia</i> F.Muell.	Clarke39p
<i>Acacia pravissima</i> F.Muell. ex Benth.	CANB 793515
<i>Acacia prominens</i> A.Cunn. ex G.Don	Mt Annan BG 981404
<i>Acacia pruinosa</i> A.Cunn. ex Benth.	CANB 793518
<i>Acacia pubescens</i> (Vent.) R.Br.	MEL 2111926
<i>Acacia pycnantha</i> Benth.	CANB 793526
<i>Acacia pyrifolia</i> DC.	CANB 793527
<i>Acacia ramulosa</i> W.Fitzg.	CANB 793528
<i>Acacia retinodes</i> Schltld.	CANB 587946
<i>Acacia rigens</i> A.Cunn. ex G.Don	CANB 634045
<i>Acacia rostellifera</i> Benth.	CANB 793537
<i>Acacia saliciformis</i> Tindale	Mt Annan BG 884112
<i>Acacia saligna</i> (Labill.) H.L.Wendl.	CANB 634053
<i>Acacia saligna</i> (Labill.) H.L.Wendl.	CANB 793541
<i>Acacia schinoides</i> Benth.	CANB 793542
<i>Acacia silvestris</i> Tindale	CANB 793549
<i>Acacia spectabilis</i> A.Cunn. ex Benth.	CANB 793553
<i>Acacia stenophylla</i> A.Cunn. ex Benth.	CANB 793555
<i>Acacia stigmatophylla</i> A.Cunn. ex Benth.	CANB 793556
<i>Acacia suaveolens</i> (Sm.) Willd.	ANBG 643849
<i>Acacia subrigida</i> Maslin	MELU- SRA 106
<i>Acacia subulata</i> Bonpl.	ANBG 657697
<i>Acacia triptera</i> Benth.	Clarke18t
<i>Acacia triquetra</i> Benth.	CANB 793573
<i>Acacia venulosa</i> Benth.	ANBG 9705373
<i>Acacia verniciflua</i> A.Cunn.	Mt Annan BG 13007
<i>Acacia verticillata</i> (L'Her.) Willd.	CANB 793581
<i>Acacia vestita</i> Ker Gawl.	CANB 793583
<i>Acacia victoriae</i> Benth.	AD 99835210 s51
<i>Acacia viscidula</i> Benth.	Clarke1v
<i>Acacia wattiana</i> F.Muell. ex Benth.	CANB 793588
<i>Pararchidendron pruinsum</i> (Benth.) I.C.Nielsen	ANBG 820099
<i>Paraserianthes lophantha</i> (Willd.) I.C.Nielsen	MEL 2057862