

Evolutionary and taxonomic relationships of *Acacia s.l.* (Leguminosae: Mimosoideae)

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Abstract. The species of *Acacia s.l.* are currently undergoing a taxonomic upheaval. This is due, in large part, to recent molecular work that has confirmed previous morphological studies and concluded that the genus is not monophyletic. At least five monophyletic lineages have been defined within the genus and, largely on the basis of molecular data, these are distributed throughout the tribes Acacieae, Ingeae and Mimosae of the Mimosoideae. We provide new and review previous molecular data used to redefine the generic classification of the genus into five segregate genera. The present study doubles the number of plastid base pairs compared with previous studies, to over 7 kb of aligned sequence. These data confirm previous clades and the present is the first to identify robust support for relationships among clades on the backbone of the phylogeny. The support for *Vachellia* is stronger than for any subclade within it. However, the support for *Senegalia s.s.* is weaker than it is for each of two subclades within it. There is no support for the former tribal classification with the enlarged dataset. The nomenclatural implications of which clades are recognised at a generic level are discussed.

Additional keywords: molecular phylogeny, systematics.

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Introduction

Although several species of *Acacia s.l.* were first described by Linnaeus (1753) under the broadly defined genus *Mimosa* L., the genus *Acacia* Mill., comprising 24 diverse species, mainly from the Americas, but with the pre-Linnaean ‘ACACIA vera. *J. B.*’ said to be ‘The true Egyptian *Acacia*’, was published by Miller (1754). As Miller had not by then adopted Linnaean binary nomenclature, none of his species was provided with a binomial. Subsequently, Miller (1757) identified his ACACIA vera. *J. B.* species with a species that Linnaeus (1753) had named *Mimosa scorpioides*, later selected as the type of *Acacia* (Abrams 1944). Numerous new species were subsequently described, notably by Willdenow (1806), but the genus *Acacia* remained at best a loosely coherent group. Beginning in the 1830s and culminating in 1875, George Bentham (Bentham 1842, 1875) revised *Acacia*, narrowing the limits of the genus and transferring numerous species to other genera. Ultimately, he recognised six series in a widespread, pantropical–subtropical genus *Acacia s.l.*, with centres of diversity in the Americas, Africa and Australia (Bentham 1842). Few other changes appeared, until, in 1928, Britton and Rose (Britton and Rose 1928) subdivided the genus *Acacia* into several new genera, largely on the basis of fruit characters. However, most of these genera were not accepted by later systematists, and Bentham’s 1875 (Bentham 1875) treatment remained the basis for classification until late in the

20th century. At that time, ~1450 species had been ascribed to the genus, making it one of the largest of all plant genera (Maslin *et al.* 2003; Lewis *et al.* 2005). As more information accumulated, Vassal (1972) segregated *Acacia s.l.* into three subgenera. The distribution of the largest of these, *Acacia* subg. *Phyllodineae* (DC.) Ser., with ~960 described species, was centred in Australia (Maslin *et al.* 2003), with a smaller number in Madagascar, Asia and various Pacific Islands. The other two subgenera, *Acacia* subg. *Acacia* and *Acacia* subg. *Aculeiferum* Vassal (Lewis *et al.* 2005), shared a similar distributional pattern in Africa and the Americas, with fewer species in Asia, Australia and the Pacific region (Table 1).

Later, Pedley (1989) proposed recognition of these subgenera as genera *Racosperma* (DC.) Mart., *Acacia s.s.*, and *Senegalia* Raf. respectively. Although it was by then well established that *Acacia s.l.* comprised several divergent groups, the relationship of these groups to each other and to members of tribes Ingeae and Mimosae remained uncertain, owing to a lack of a robust and well sampled phylogeny. Maslin (1987, 1989) urged caution before implementation of such major taxonomic changes with insufficient supporting data (see Pedley’s responses: Pedley 1987, 1989).

The taxonomy of *Acacia* became more contentious in 2005, when a proposal (Orchard and Maslin 2003) to retypify the generic name *Acacia s.l.* from *A. scorpioides* L., a synonym

Table 1. Current status of generic names applied to higher-level monophyletic units of *Acacia s.l.*

New combinations have been published for the American and Australian species, whereas only a few new combinations have been proposed for the African and Asian species (Banfi and Galasso 2008; Mabberley 2008; Seigler and Ebinger 2010). No species have naturally occurring ranges in both Africa and the Americas

Pedley 1978	Pedley 1986	Generalised distribution	Genus, post retypification (2005)
<i>Acacia</i> subg. <i>Phyllodineae</i>	<i>Racosperma</i>	Australia, Pacific region	<i>Acacia s.s.</i> (type <i>A. penninervis</i>)
<i>Acacia</i> subg. <i>Acacia</i> (type <i>A. nilotica</i>)	<i>Acacia</i>	Americas, Africa, Asia	<i>Vachellia</i>
<i>Acacia</i> subg. <i>Aculeiferum</i>	<i>Senegalia</i> sect. <i>Senegalia</i>	Americas, Africa, Asia	<i>Senegalia</i>
<i>Acacia</i> subg. <i>Aculeiferum</i> sect. <i>Filicinae</i>	<i>Senegalia</i> sect. <i>Filicinae</i>	Americas	<i>Acaciella</i>
<i>Acacia</i> subg. <i>Aculeiferum</i> 'coulteri group'	<i>Senegalia</i> sect. <i>Senegalia</i>	Americas	<i>Mariosousa</i>
<i>Acacia</i> subg. <i>Aculeiferum</i> 'skleroxyla' group	<i>Senegalia</i> sect. <i>Senegalia</i>	Americas	Not presently recognised

of *A. nilotica*, an African species, to an Australian species, *A. penninervis*, was approved at the XVII International Botanical Congress at Vienna (McNeill *et al.* 2005). Acceptance of this retypification remains controversial (Luckow *et al.* 2005; van Rijckevorsel 2006; Moore 2007, 2008; Smith *et al.* 2010, 2006; Brummitt 2011; Linder and Crisp 2011; Moore and Cotterill 2011; Moore *et al.* 2011a, 2011b; Smith and Figueiredo 2011; Thiele *et al.* 2011). However, the retypification was upheld recently at the XVIII International Botanical Congress in Melbourne in July 2011 (McNeill and Turland 2011; Smith and Figueiredo 2011).

Early molecular phylogenetic data generated to resolve these questions (Clarke *et al.* 2000; Robinson and Harris 2000) consisted largely of chloroplast restriction fragment length polymorphism data for a limited sample of either American or African taxa. Although these studies largely supported previous subgeneric and generic groupings, interpretations were limited by inadequate geographic and taxon sampling. Subsequent studies of chloroplast and nuclear DNA in which critical taxa of tribes Ingeae and Mimoseae, as well as taxa from *Acacia s.l.*, have been sampled more broadly (Miller and Bayer 2000; Miller and Bayer 2001; Luckow *et al.* 2003; Miller *et al.* 2003; Bouchenak-Khelladi *et al.* 2010; Brown *et al.* 2011), established that (1) *Acacia s.l.* is non-monophyletic, (2) two of the three major groups within *Acacia s.l.* are monophyletic and the third is non-monophyletic, (3) some *Acacia s.l.* species are more closely related to species of tribe Mimoseae than to other *Acacia s.l.* lineages and (4) the predominantly Australian clade is more closely related to species of tribe Ingeae than to other *Acacia s.l.* lineages. On the basis of both morphological and molecular data, it is widely accepted that the non-monophyletic genus *Acacia s.l.* should be subdivided.

Taxonomic changes to reflect this non-monophyly have proceeded apace over the past 5 years. Most American (Seigler *et al.* 2006b; de Queiroz 2008; Seigler and Ebinger 2009) and a smaller number of African and Asian species (Banfi and Galasso 2008; Mabberley 2008; Seigler and Ebinger 2010) of *Acacia* subg. *Aculeiferum* Vassal have been transferred to the genus *Senegalia*. A smaller number of species has been moved to the American genera *Mariosousa* (Seigler *et al.* 2006a) and *Acaciella* (Rico Arce and Bachman 2006).

In a similar manner, but considering the retypification of *Acacia* (Seigler and Ebinger 2005), most American (Seigler and Ebinger 2005) and Australian (Kodala and Wilson 2007) species of Vassal's former *Acacia* subg. *Acacia* have been transferred to the genus *Vachellia*. New combinations in

Vachellia have been published for a smaller number of African and Asian species (Banfi and Galasso 2008; Mabberley 2008; Seigler and Ebinger 2010).

Current phylogenies provide robust support for the recognition of *Senegalia*, *Mariosousa*, *Acaciella*, *Vachellia* and *Acacia s.s.* However, our knowledge of the species relationships and infrageneric groups within these genera is not well established. Furthermore, only modest amounts of molecular data relevant to resolving relationships of these genera to tribes Ingeae and Mimoseae are available. Increased sampling of critical species and geographic regions will probably lead to recognition of additional segregates. Because former tribal relationships within subfamily Mimosoideae are now in disarray, new phylogenetic data will be vital for establishing an acceptable tribal and generic system of classification.

Previous molecular studies agree on the monophyly of major clades such as *Vachellia*, *Senegalia s.s.*, *Mariosousa*, *Acaciella* and *Acacia s.s.* Although previous plastid studies have shown similar backbone topologies, none have demonstrated bootstrap support greater than 90% for phylogenetic relationships among these clades. The present study aimed to recover, with robust support, these relationships by analysing a dataset comprising double the number of plastid base pairs of that in previous work: six plastid loci and 7 kb of aligned sequence. A second aim was to investigate relationships within *Senegalia s.s.* and *Vachellia*. For both aims, exemplars were used to represent well supported clades.

Materials and methods

Species were selected to sample at least eight species each of *Senegalia* and *Vachellia* and at least three species of each lineage of *Acacia s.l.* (Appendix 1). Ingroup taxa were selected from those available on the basis of previous results (Luckow *et al.* 2003; Miller *et al.* 2003; Brown *et al.* 2008). These included species of *Mimosa*, *Anadenanthera* Speg. and *Piptadenia* Benth. of tribe Mimoseae. Seventeen samples of 10 Ingeae genera were included along with two samples of the monotypic genus *Faidherbia* A.Chev., being the only other genus previously included in tribe Acacieae. Outgroups were selected on the basis of the results of Luckow *et al.* (2003) and included species of *Desmanthus* Willd., *Leucaena* Benth., *Neptunia* Lour. and *Prosopis* L., also of tribe Mimoseae.

Material used in the present study was collected in the field and stored in silica gel or grown from seeds from various seed banks. When seeds were used, they were germinated and young leaves

harvested. DNA was extracted using a Qiagen DNeasy Plant Mini Kit (Qiagen Inc., Valencia, CA).

Sequences of the following six plastid loci were obtained: (1) *matK* gene and flanking *trnK* introns; (2) *psbA-trnH* intergenic spacer; (3) *trnL* intron; (4) *trnL-trnF* intergenic spacer region; (5) *ndhF* and (6) *atpB-rbcL* intergenic spacer. The *matK* gene and flanking *trnK* introns, the *psbA-trnH* intergenic spacer and *trnL-trnF*, intron and intergenic spacer regions were sequenced following methods outlined in Miller and Bayer (2001). For 31 sampled specimens, these three regions were previously sequenced. Thirty specimens were originally sequenced for the study. The *ndhF* region was amplified and sequenced using the 1318F and 2110R (Olmstead and Sweere 1994) primers. The *atpB-rbcL* intergenic spacer was amplified and sequenced using the *atpB-F* and *atpB-spacerR* primers of Manen *et al.* (1994). All *ndhF* and *atpB-rbcL* intergenic spacer sequences were newly generated for the study.

Data were generated by using the purified DNA as a template for direct sequencing, using the one-eighth reactions of the BIG Dye v 3.1 Terminator Cycle Sequencing Ready Reaction Kits (Applied Biosystems, Carlsbad, CA) electrophoresed on a 3730-capillary sequencer.

Chromatographic traces and contiguous alignments were edited using Sequencher (Gene Codes Corporation, Ann Arbor, MI, USA). Sequences were aligned manually with minimal gaps and base substitutions. Uncertain base positions, generally located close to the priming sites, and regions of uncertain alignment were excluded from the phylogenetic analysis. Informative insertion–deletion events (indels) were identified and coded as binary characters and gaps were treated as missing data.

Data analysis

Bayesian analysis was performed using MrBayes version 3.1.2. (Ronquist and Huelsenbeck 2003). Sequence data were divided into six partitions, one for each locus. A separate GTR+I+gamma model was applied to each of these partitions. Indel characters were included as a separate partition and a standard discrete state model with a gamma-shape parameter was applied to this partition. A Markov chain Monte Carlo search was run for 50 million generations, with trees sampled every 50 000 generations. MrBayes performed two simultaneous analyses starting from different random trees (Nruns=2), each with four Markov chains (Nchains=6). A total of 25% of the trees were discarded and the run ended with an average standard deviation of split frequencies of <0.004

Maximum parsimony analyses were performed with the heuristic search option (excluding uninformative characters) in PAUP* 4.02 (Swofford 2003). A four-step search method for multiple islands was performed with 10 000 random replicates (Olmstead and Sweere 1994). Support for internal branches was evaluated by the heuristic bootstrap method, with 10 000 bootstrap replicates each with 10 random sequence-addition replicates with TBR (Felsenstein 1985).

Results

As expected, the results of the present study support previous studies concerning the non-monophyly of *Acacia s.l.* (Fig. 1).

Clades A (*Vachellia*) and F (*Acacia s.s.*) are each monophyletic and have strong support (1.0 Bayesian posterior probability and >90% bootstrap support).

On the basis of analysis with the four outgroup taxa suggested by a previous study (Luckow *et al.* 2003), the *Vachellia* clade (Clade A) is nested within a paraphyletic tribe Mimoseae. It comprises two subclades, one containing African species and the other American species (Fig. 2A). Although the number of species included in the present analysis is small, these geographically based clades are strongly supported. The type of the generic name, *V. farnesiana*, applies to a species belonging to the American clade (Miller and Bayer 2003). The branch leading to the *Vachellia* clade (Fig. 2A) is longer than any branch within the clade, suggesting that a large number of characters are shared by all species of *Vachellia*. The two subclades are less strongly supported than the clade as a whole.

The node that contains Clades B–F and the Ingeae (Fig. 1, marked by #) is well supported (Bayesian posterior probability of 1.0 and bootstrap value of 97%). Previous plastid datasets reported lower bootstrap values for this node (71%, Bouchenak-Khelladi *et al.* 2010; 82%, Miller *et al.* 2003; and 83% Luckow *et al.* 2003). Brown *et al.* (2008) reported 80% bootstrap support with nuclear rDNA sequence; however, they did not sample Mimoseae taxa.

The clade representing the core of the genus *Senegalia* (Clade B), denoted with an asterisk in Fig. 2B, is moderately supported (Bayesian posterior probability of 1.0, 72% bootstrap value) and consists of two sister clades (each with Bayesian posterior probability of 1 and bootstrap value of 100%). One clade (B1, Fig. 2B) consists of African–Asian species (*Acacia* subgenus *Aculeiferum* sect. *Aculeiferum*) (Vassal 1972). The second clade (B2, Fig. 2B) comprises species with a pantropical distribution (*Acacia* subgenus *Aculeiferum* sect. *Monacantha*) (Vassal 1972). The longest branches and most strongly supported groups are these two subclades (B1 and B2) rather than the larger clade of B1 + B2 (i.e. the genus *Senegalia*, apart from species related to *S. skleroxyla*). Phylogenetic relationships within Clade B are poorly understood; this group is in particular need of further study.

Each of Clades B–E represents a segregate group of *Acacia* subg. *Aculeiferum*. These clades collectively form a paraphyletic grade (Fig. 1, marked by #) with respect to the Ingeae and the Australian acacias (Clade F). Two of these, Clades D and E, correspond directly to the previously described genera *Acaciella* (16 species) and *Mariosousa* (13 species), both of which have centres of diversity in Mexico. Clade C consists of a group of species related to *S. skleroxyla*. In the present analysis, two species (*S. vogeliana* and *S. visco*) are supported as members of this clade, with only low Bayesian posterior probabilities (0.82 and 0.67; Fig. 2). This presently undescribed group may contain as many as 10 mostly poorly known species and requires additional study; most of the probable species are currently recognised in *Senegalia*. Clade D (*Mariosousa*) caps a short branch with moderately strong support. The segregate genus *Acaciella* and its sister clade *Calliandra* each have many unique indels (Clade E, Fig. 2A).

These plastid data support three nodes in the Ingeae: *Acacia s.s.* that have bootstrap values above 90%. None of the previous plastid studies has shown bootstrap support above

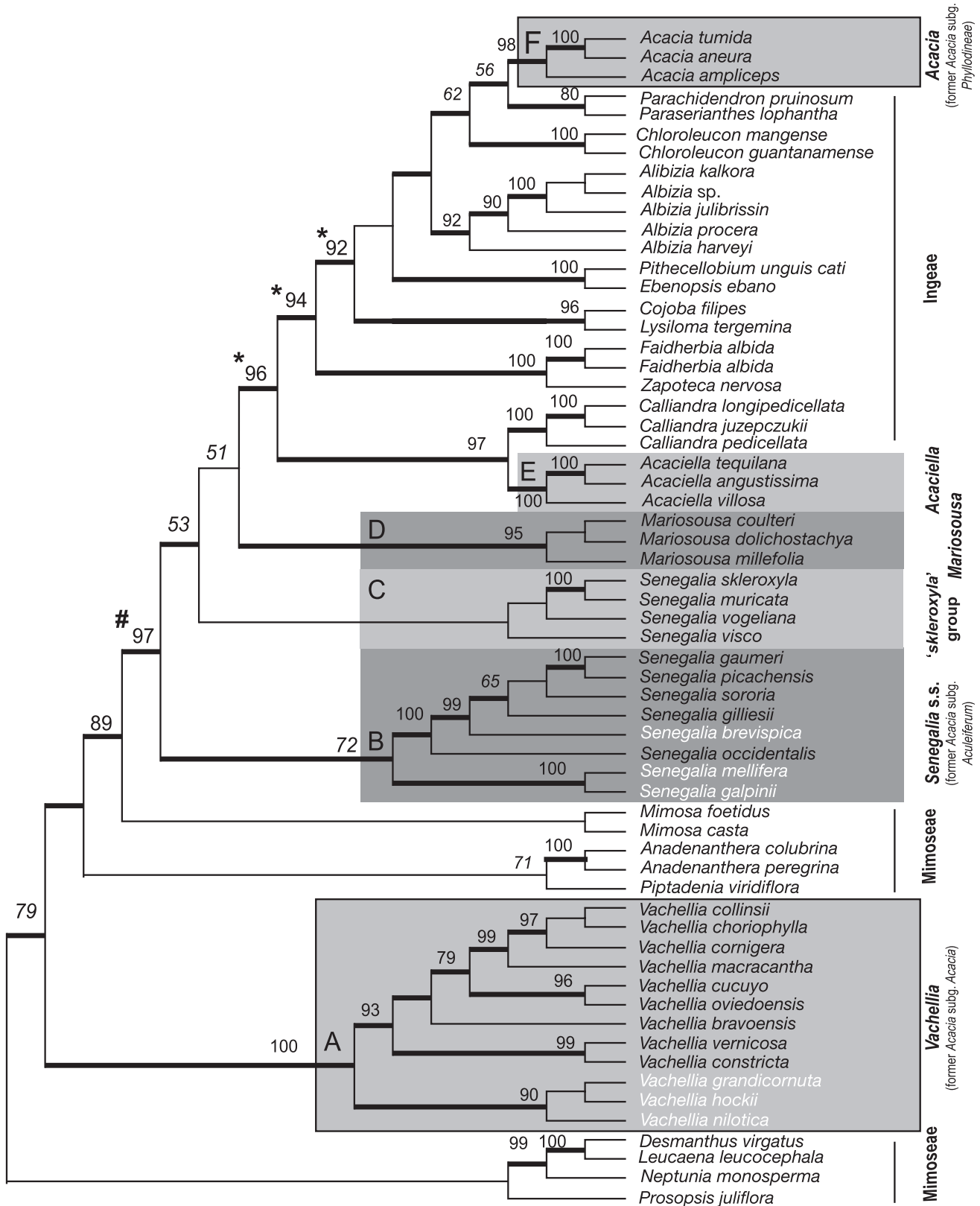


Fig. 1. Topologies of the Bayesian trees without branch lengths. The three boxes indicate the three subgenera of *Acacia* s.l. Shaded groupings indicate segregate and suggested segregate groupings. Bold lines indicate Bayesian posterior probability above 95%. African *Vachellia* and *Senegalia* are indicated in white text. Bootstrap values are given above nodes and bootstrap values below 80% are in italic.

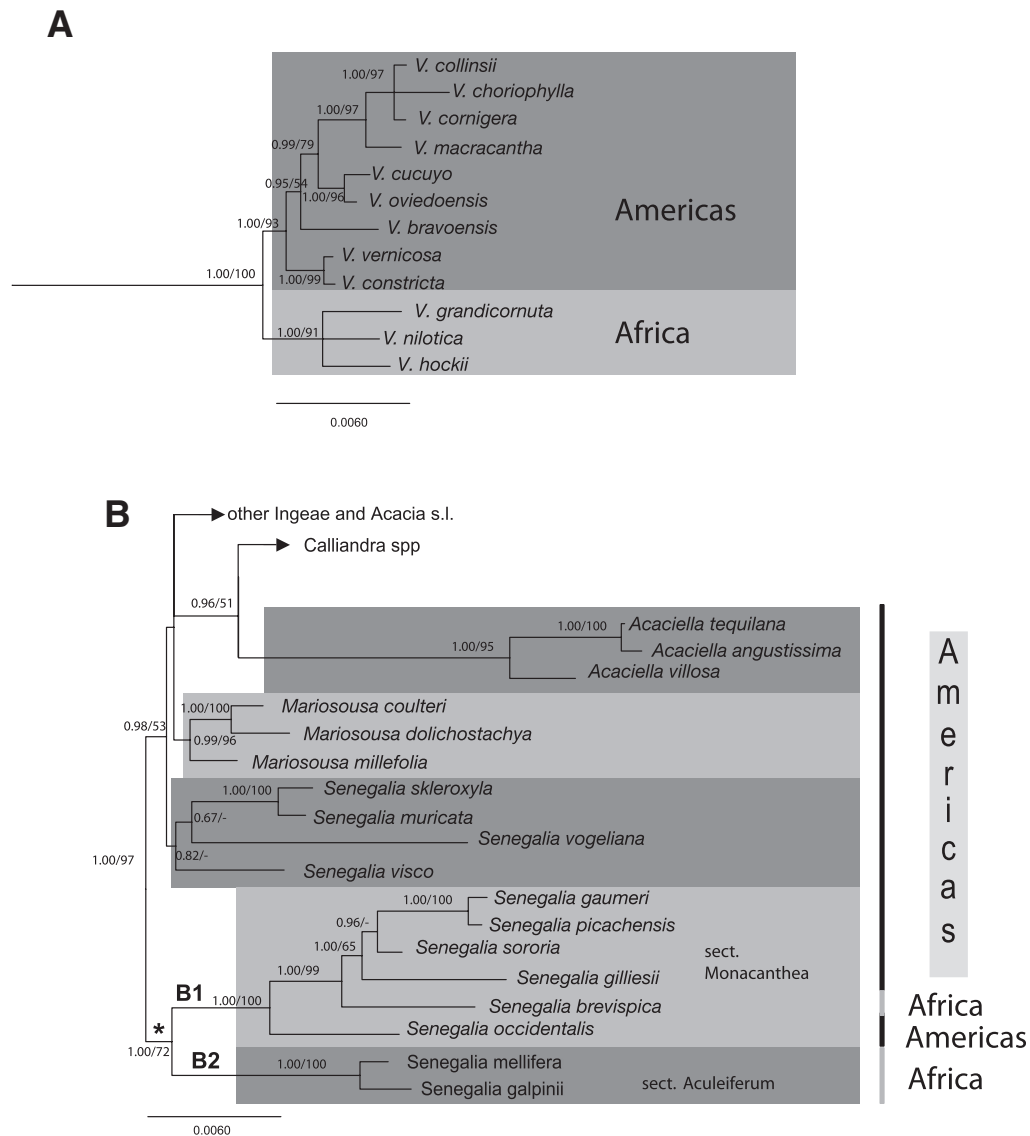


Fig. 2. Topologies of the Bayesian trees with branch lengths. Posterior probability and bootstrap support values are given. A. *Vachellia* and B. *Senegalia* s.l.

80% for node supporting two genera within the Ingeae. Brown *et al.* (2008) used nuclear-DNA sequences and detailed sampling of the Ingeae genera to provide high bootstrap support (97%) for the Ingeae : *Acacia* s.s. node. The Ingeae has been sampled more intensively in a recent study (Brown *et al.* 2008); there, *Calliandra* was not related to the single *Acaciella* species sampled. These findings suggest that the apparent *Calliandra*–*Acaciella* sister-group relationship in the present study could be an artefact caused by long-branch attraction.

Discussion

Despite considerable evidence to the contrary (see above), one proposed taxonomic solution of the *Acacia* dilemma is to maintain *Acacia* s.l. as a single entity (Smith and Figueiredo 2011). However, it should be noted that under this concept, the

only acceptable interpretation of phylogenetic studies based on molecular data is to maintain most of subfamily Mimosoideae in a single genus, *Mimosa*, with more than 4000 species; the results of both morphological and molecular phylogenetic analyses suggest better alternatives. *Vachellia* species (Clade A, both African and American) and *Acacia* s.s. species (Clade F, primarily Australian) both form strongly supported clades and should be maintained as distinct genera. As noted above, the genera *Acaciella* and *Mariosousa* (Clades D and E) have previously been segregated from within *Acacia* subg. *Aculeiferum* and also form robustly supported monophyletic groups. Pending additional morphological and molecular study and expanded sampling, the group of species related to *S. skleroxyla* (Clade C) may represent yet another group worthy of segregation from *Acacia* subg. *Aculeiferum*. If the placement of *S. visco* within this clade is supported by additional data, then

these taxa must be placed into the genus *Manganaroa* Spag. (Spegazzini 1921).

Clade A (*Vachellia*) contains two distinct groups of species, namely, one American and the other from Africa and Asia. There is stronger support for *Vachellia* as a whole than for either of the two subclades. The molecular phylogeny by Bouchenak-Khelladi *et al.* (2010) also found these two clades. That work, which has the best representation of African species of this clade, found two well supported subclades within the African *Vachellia* species. Five species, including *V. nilotica*, were sister to these main clades. There was moderate support for the African clade (0.78 posterior probability).

The type of *Vachellia* is *V. farnesiana*, applicable to an American species. Although many Asian and Australian species of this genus have not been studied in detail, both our data and those of Bouchenak-Khelladi *et al.* (2010) support maintenance of a single genus *Vachellia*. If *Vachellia* were to be subdivided, all Old World species would probably require a new generic name.

The remaining taxa of *Acacia* subg. *Aculeiferum* (Clade B, here referred to as *Senegalia*) constitute a monophyletic group. Two sections of the subgenus, *Monacantha* and *Aculeiferum*, described by Vassal (1972) correspond to the two sister subclades of Clade A. However, the genus *Senegalia* remains very poorly studied. On the basis of morphological characters and a paucity of molecular data, most, if not all, American species and some African and Asian species belong to section *Monacantha*, whereas many African and Asian species belong to section *Aculeiferum*. The type of the genus is *Senegalia senegal*, an African species classified by Vassal as a member of section *Aculeiferum*. On the basis of previous work (Miller and Bayer 2003), this species groups in a clade with other species of section *Aculeiferum*, here represented by *S. mellifera* and *S. galpinii*. Nonetheless, on the basis of molecular data and regardless of the *Acacia* type designation, *Senegalia* is a genus distinct from *Acacia s.l.* At present, the phylogeny of *Senegalia* is not well understood and there are insufficient data to clarify relationships within the genus. In particular, the relationships of the approximately fifty Brazilian species as well as several species in South-east Asia and northern Australia belonging to genus *Senegalia* have not been sufficiently studied.

The traditional tribal classification has been shown to be unnatural by DNA-sequence analyses but these have so far failed to provide sufficient support to underpin an alternative phylogenetic tribal classification. The present study, however, provides bootstrap support above 90% for several nodes on the backbone of the phylogeny. More robust sampling, with large sequence datasets, are needed, particularly in the Mimosaceae and Ingeae, to further establish support for the deep nodes. These data are critical if an alternative to the tribal classification is to be developed.

Because of the iconic nature of many of these species in different countries (e.g. the ant-acacia trees of Africa and the Americas, the characteristic umbrella-topped African savannah trees, as well as the floral emblem of Australia), it is clear that changes in our understanding of the relationships and subsequent changes in names have had a direct effect on many people. Many of the common and scientific names are found in taxonomic, ecological, conservation and horticultural literature. Although

acacia may well be used as a common name for various members of *Acacia s.l.*, future use of the name *Acacia s.s.* should be restricted to a clade of primarily Australian plants. The data presented not only support segregation of generic groups from *Acacia s.l.*, but point to a future necessary reorganisation of the tribal and subgeneric classification of the Mimosoideae.

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References

- Abrams L (1944) 'An illustrated flora of the Pacific States: Washington, Oregon, and California. Vol. 2.' (Stanford University Press: Stanford, CA)
- Banfi E, Galasso G (2008) New combinations in *Vachellia* Wight & Arn., formerly *Acacia* Mill. s.s. (Fabaceae). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* **149**, 149–150.
- Bentham G (1842) Notes on Mimosaceae, with a synopsis of species. *London Journal of Botany* **1**, 319–392.
- Bentham G (1875) Revision of the suborder Mimosaceae. *Transactions of the Linnean Society of London* **30**, 335–664.
doi:10.1111/j.1096-3642.1875.tb00005.x
- Bouchenak-Khelladi Y, Maurin O, Hurter J, van der Bank M (2010) The evolutionary history and biogeography of Mimosoideae (Leguminosae): an emphasis on African acacias. *Molecular Phylogenetics and Evolution* **57**, 495–508. doi:10.1016/j.ympev.2010.07.019
- Britton NL, Rose JN (1928) Mimosaceae. *North American Flora* **23**, 1–194.
- Brown GK, Murphy DJ, Miller JT, Ladiges PY (2008) *Acacia s.s.* and its relationship among tropical legumes, tribe Ingeae (Leguminosae: Mimosoideae). *Systematic Botany* **33**, 739–751.
doi:10.1600/036364408786500136
- Brown GK, Murphy DJ, Ladiges PY (2011) Relationships of the Australo-Malesian genus *Paraserianthes* (Mimosoideae: Leguminosae) identifies the sister group of *Acacia* sensu stricto and two biogeographical tracks. *Cladistics* **27**, 380–390. doi:10.1111/j.1096-0031.2011.00349.x
- Brummitt RK (2011) (292) *Acacia*: a solution that should be acceptable to everybody. *Taxon* **59**, 1925–1926.
- Clarke HD, Downie SR, Seigler DS (2000) Implications of chloroplast DNA restriction site variation for systematics of *Acacia* (Fabaceae: Mimosoideae). *Systematic Botany* **25**, 618–632. doi:10.2307/2666724
- de Queiroz LP 2008. 'Leguminosae da Caatinga.' (Universidade Estadual de Feira de Santana: Feira de Santana, Brazil)
- Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783–791. doi:10.2307/2408678
- Kodala PG, Wilson PG (2007) New combinations in the genus *Vachellia* (Fabaceae: Mimosoideae) from Australia. *Telopea* **11**, 233–244.
- Lewis GP, Schrire B, Mackinder B, Lock M (2005) 'Legumes of the World.' (Royal Botanic Gardens, Kew: London)
- Linnaeus C (Ed.) (1753) 'Species Plantarum'. (Imprintis Laurentii Salvii: Stockholm)
- Linder HP, Crisp M (2011) The fate of *Acacia*. *Taxon* **60**, 570–571.
- Luckow M, Miller JT, Murphy DJ, Livshultz T (2003) A phylogenetic analysis of the Mimosoideae (Leguminosae) based on chloroplast DNA sequence data. In 'Advances in legume systematics, part 10'. (Eds BB Klitgaard, A Bruneau) pp. 197–220. (Royal Botanic Gardens, Kew: London)

- Luckow M, Hughes C, Schrire B, Winter P, Fagg C, Fortunato R, Hurter J, Rico L, Breteler FJ, Bruneau A, Caccavari M, Craven L, Crisp M, Delgado AS, Demissew S, Doyle JJ, Grether R, Harris S, Herendeen PS, Hernández H, Hirsch M, Jobson AM, Klitgaard R, Labat BB, Lock J-N, Mac M, Kinder B, Pfeil B, Simpson BB, Smith GF, Sousa MS, Timberlake J, van der Maesen JG, Van Wyk AE, Vorster P, Willis CK, Wieringa JJ, Wojciechowski MF (2005) *Acacia*: the case against moving the type to Australia. *Taxon* **54**, 513–519. doi:10.2307/25065385
- Mabberley D (2008) 'Mabberley's Plant Book.' (Cambridge University Press: Cambridge, UK)
- Manen J-F, Natali A, Ehrendorfer F (1994) Phylogeny of Rubiaceae–Rubiaceae inferred from the sequence of a cpDNA intergene region. *Plant Systematics and Evolution* **190**, 195–211. doi:10.1007/BF00986193
- Maslin BR (1987) Report of discussions at IGSM meeting no. 6 on the proposal to split *Acacia*. *Bulletin of the International Group for the Study of Mimosoideae* **15**, 108–118.
- Maslin BR (1989) Wattle become of *Acacia*? *Australian Systematic Botany Society Newsletter* **58**, 1–13.
- Maslin BR, Miller JT, Seigler DS (2003) Overview of the generic status of *Acacia* (Leguminosae: Mimosoideae). *Australian Systematic Botany* **16**, 1–18. doi:10.1071/SB02008
- McNeill JS, Turland NJ (2011) Major changes to the Code of Nomenclature – Melbourne, July 2011. *Taxon* **60**, 1495–1497.
- McNeill JS, Stuessy TF, Turland NJ, Hörandl E (2005) XVII International Botanical Congress: Preliminary mail vote and report of Congress action on nomenclature proposals. *Taxon* **54**, 1057–1064.
- Miller P (1754) 'The gardeners dictionary.' Abridged edn 4. (John and James Rivington: London)
- Miller P (1757) 'The gardeners dictionary.' edn 7. (John and James Rivington: London)
- Miller JT, Bayer RJ (2000) Molecular phylogenetics of *Acacia* (Fabaceae: Mimosoideae) based on chloroplast *TrnK/MatK* and nuclear histone H3-D sequences. In 'Advances in legume systematics 9'. (Eds PS Herendeen, A Bruneau) (Royal Botanic Gardens, Kew: London)
- Miller JT, Bayer RJ (2001) Molecular phylogenetics of *Acacia* (Fabaceae: Mimosoideae) based on the chloroplast *matK* coding sequence and flanking *trnK* intron spacer regions. *American Journal of Botany* **88**, 697–705. doi:10.2307/2657071
- Miller JT, Bayer RJ (2003) Molecular phylogenetics of *Acacia* subgenera *Acacia* and *Aculeiferum* (Fabaceae: Mimosoideae), based on the chloroplast *matK* coding sequence and flanking *trnK* intron spacer regions. *Australian Systematic Botany* **16**, 27–33. doi:10.1071/SB01035
- Miller JT, Grimes JW, Murphy DJ, Bayer RJ, Ladiges PY (2003) A phylogenetic analysis of the Acacieae and Ingeae (Mimosoideae: Fabaceae) based on *trnK*, *matK*, *psbA-trnH*, and *trnL/trnF* sequence data. *Systematic Botany* **28**, 558–566.
- Moore G (2007) The handling of the proposal to conserve the name *Acacia* at the 17th international botanical congress – an attempt at minority rule. *Bothalia* **37**, 109–118.
- Moore G (2008) Action on the proposal to conserve the name *Acacia* at the nomenclature section of the XVII international botanical congress in Vienna: did the ayes have it? *The Linnean* **24**, 16–20.
- Moore A, Cotterill FPD (2011) The *Acacia* retypification debate: perspectives of African amateur botanists. *Taxon* **60**, 858–859.
- Moore G, Smith GF, Figueiredo E, Demissew S, Lewis G, Schrire B, Rico L, van Wyk AE (2011a) *Acacia*, the 2011 nomenclature section in Melbourne, and beyond. *Taxon* **59**, 1188–1195.
- Moore G, Smith GF, Figueiredo E, Demissew S, Lewis G, Schrire B, Rico L, van Wyk AE, Luckow M, Kiesling R, Sousa SM (2011b) The *Acacia* controversy resulting from minority rule at the Vienna nomenclature section: much more than arcane arguments and complex technicalities. *Taxon* **3**, 852–857.
- Olmstead RG, Sweere JA (1994) Combining data in phylogenetic systematics: an empirical approach using three molecular data sets in the Solanaceae. *Systematic Biology* **43**, 467–481. doi:10.1093/sysbio/43.4.467
- Orchard AE, Maslin BR (2003) (1584) Proposal to conserve the name *Acacia* (Leguminosae: Mimosoideae) with a conserved type. *Taxon* **52**, 362–363. doi:10.2307/3647418
- Pedley L (1987) In defence of *Racosperma*. *Bulletin of the International Group for the Study of Mimosoideae* **15**, 123–129.
- Pedley L (1989) *Racosperma* again. *Australian Systematic Botany Newsletter* **59**, 1–2.
- Rico Arce L, Bachman S (2006) A taxonomic revision of *Acaciella* (Leguminosae, Mimosoideae). *Anales del Jardín Botánico de Madrid* **63**, 189–244.
- Robinson J, Harris SA (2000) A plastid DNA phylogeny of the genus *Acacia* Miller (Acacieae, Leguminosae). *Botanical Journal of the Linnean Society* **132**, 195–222. doi:10.1111/j.1095-8339.2000.tb01527.x
- Ronquist F, Huelsenbeck JP (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**, 1572–1574. doi:10.1093/bioinformatics/btg180
- Seigler DS, Ebinger JE (2005) New combinations in the genus *Vachellia* (Fabaceae: Mimosoideae) from the New World. *Phytologia* **87**, 139–178.
- Seigler DS, Ebinger JE (2009) New combinations in the genus *Senegalia* (Fabaceae: Mimosoideae). *Phytologia* **91**, 25–29.
- Seigler DS, Ebinger JE (2010) New combinations in *Senegalia* and *Vachellia* (Fabaceae: Mimosoideae). *Phytologia* **92**, 90–93.
- Seigler DS, Ebinger JE, Miller JT (2006a) *Mariosousa*, a new segregate genus from *Acacia s.l.* (Fabaceae, Mimosoideae) from Central and North America. *Novon* **16**, 413–420. doi:10.3417/1055-3177(2006)16[413:MANSGF]2.0.CO;2
- Seigler DS, Ebinger JE, Miller JT (2006b) The genus *Senegalia* (Fabaceae: Mimosoideae) from the New World. *Phytologia* **88**, 38–93.
- Smith GF, Figueiredo E (2011) Conserving *Acacia* Mill. with a conserved type: what happened in Melbourne? *Taxon* **60**, 1504–1506.
- Smith GF, van Wyk AE, Luckow M, Schrire B (2006) Conserving *Acacia* Mill. with a conserved type. What happened in Vienna? *Taxon* **55**, 223–225. doi:10.2307/25065547
- Smith GF, Figueiredo E, Moore G (2010) Who amends the international code of botanical nomenclature? A response to Applequist *et al.* (2010). *Taxon* **60**, 213–215.
- Spegazzini CL (1921) Acacieas Argentinas. *Boletín de la Academia Nacional de Ciencias* **26**, 161–334.
- Swofford DL (2003) 'PAUP*. Phylogenetic analysis using parsimony (* and other methods). Version 4.' (Sinauer Associates: Sunderland, MA)
- Thiele KR, Funk VA, Iwatsuki K, Morat P, Peng C-I, Raven PH, Sarukh NJ, Seberg O (2011) The controversy over the retypification of *Acacia* Mill. with an Australian type: a pragmatic view. *Taxon* **60**, 194–198.
- van Rijckevorsel VP (2006) *Acacia*: what did happen at Vienna? *Anales del Jardín Botánico de Madrid* **61**, 107–110.
- Vassal J (1972) Apport des recherches ontogéniques et séminologiques à l'étude morphologique, taxonomique et phylogénique de genre *Acacia*. *Bulletin de la Société d'Histoire de Toulouse* **108**, 125–247.
- Willdenow CL (1806) 'Caroli a Linne Species Plantarum', 4th edn, vol. 4. (Imprintis G. C. Nauk: Berlin)

Appendix 1. Taxa, voucher specimens and Genbank numbers of taxa sampled in the present study

All Seigler collections are lodged at ILL. All collections new to the present study are italicised

- Acacia ampliceps* Maslin, CANB 615617, EU439993, EU811844, EU811961
Acacia aneura F.Muell. ex Benth., CANB 615661, EU440012, EU811865, EU812036
Acacia tumida F.Muell. ex Benth., CANB 615614, AF195692, AF195673, EU811863, AF195724, AF523100
Acaciella angustissima (Mill.) Britton & Rose var. *angustissima*, D. Seigler 15993, EU440019, EU811872, EU811979, EU812043
Acaciella tequilana Britton & Rose, AR1206, EU440020, EU811873, EU811980, EU812044, EU811919
Acaciella villosa (Sw.) Britton & Rose, DLEG 96-02580, EU440018, EU811871, EU812042
Albizia harveyi Fourn., DLEG 91-0136, EU439977, EU811828, EU811945, EU812003, EU811900
Albizia julibrissin Durazz., DLEG 92-0266, EU439984, EU811835, EU811952, EU812010, EU811907
Albizia kalkora Prain, CANB 615621, EU440040, EU811895, EU811999, EU812063, EU811940
Albizia procera Benth., D. Seigler 14502, EU440009, EU811861, EU811975, EU812033
Albizia spp., DLEG 92-0265, EU439975, EU811826, EU811943, EU812001, EU811898
Anadenanthera colubrina (Vell.) Brenan, L. Coradin, 5915 Kew, EU440037, EU811892, EU811996, EU812060, EU811937
Anadenanthera peregrina Speg., D. Seigler 14543, EU440022, EU811875, EU811982, EU812046, EU811921
Calliandra juzepczukii Standl., CANB 615620, EU440039, EU811894, EU811998, EU812062, EU811939
Calliandra longipedicella (McVaugh) Macqueen & H. M.Hern., CANB 615621, EU439978, EU811829, EU811946, EU812004, EU811901
Calliandra sp., D. Seigler 14513, EU440004, EU811856, EU812028, EU811971
Chloroleucon guantanamoense (Britton) Britton & Rose, D. Seigler 14537, EU439989, EU811840, EU811957, EU812015, EU811912
Chloroleucon mangense Britton & Rose, CANB 615623, EU439982, EU811832, EU811949, EU812007, EU811904
Cojoba filipis (Vent.) Barneby & J.W.Grimes, D. Seigler 14541, EU440007, EU811859, EU811973, EU812031
Desmanthus virgatus (L.) Willd., D. Seigler 14494, EU440011, EU811864, EU811976, EU812035
Ebenopsis ebano (Berland.) Barneby & J.W.Grimes, D. Seigler 15957, EU439986, EU811837, EU811954, EU812012, EU811909
Faidherbia albida (Delile) A.Chev., CANB 615551, AF522943, EU811854, AF524963, AF274120
Faidherbia albida (Delile) A.Chev., CANB 632235, EU440024, EU811877, AF523189, EU811923
Leucaena leucocephala (Lam.) de Wit, D. Seigler 15944, EU439990, EU811841, EU811958, EU812016, EU811913
Lysiloma terginum Benth., CANB 615625, EU439981, EU811833, EU811950, EU812008, EU811905
Mariosousa coulteri (Benth.) Seigler & Ebinger, D. Seigler 15953, EU440034, EU811889, EU811993, EU812057, EU811934
Mariosousa dolichostachya (S.F.Blake) Seigler & Ebinger, D. Seigler 16040, EU440033, EU811888, EU811992, EU812056, EU811933
Mariosousa millefolia (S.Watson) Seigler & Ebinger, DLEG, EU440035, EU811890, EU811994, EU812058, EU811935
Mimosa casta L., D. Seigler 14545, EU439999, EU811850, EU811967, EU812023
Mimosa foetida Jacq., CANB 615630, EU439994, EU811845, EU811962, EU811916
Neptunia monosperma F.Muell. ex Benth., CANB 9102794, EU439979, EU811830, EU811947, EU812005, EU811902
Pararchidendron pruinum (Benth.) I.C.Nielsen, ANBG 8200992, EU439985, EU811836, EU811953, EU812011, EU811908
Paraserthianthes lophantha (Willd.) I.C.Nielsen, ANBG 7901474, EU440016, EU811869, EU812040
Piptadenia viridiflora Benth., C. Hughes 1681 OFI, EU439980, EU811831, EU811948, EU812006, EU811903
Pithecellobium unguis-cati Benth., D. Seigler, 14477, EU439988, EU811839
Prosopis juliflora (Sw.) DC, D. Seigler 14481, EU439987, EU811838, EU811955, EU812013, EU811910
Senegalia brevispica (Harms) Seigler & Ebinger, T. Young 3151, Mpala, EU440013, EU811866, EU811977, EU812037, EU811918
Senegalia galpinii (Burt Davy) Seigler & Ebinger, C. W. Fagg 574 FHO, EU440000, EU811851, EU811968, EU812024
Senegalia gaumeri Britton & Rose, D. Seigler 16030, EU440038, EU811893, EU811997, EU812061, EU811938
Senegalia gilliesii (Steud.) Seigler & Ebinger, DLEG94-0167, EU439992, EU811843, EU811960, EU812018, EU811915
Senegalia mellifera (Vahl) (Seigler & Ebinger), T. Young 3168, Mpala, EU440029, EU811883, EU811988, EU812052, EU811929
Senegalia muricata (L.) Britton & Rose, D. Seigler 14548, EU440008, EU811860, EU811974, EU812032, EU440008
Senegalia occidentalis (Rose) Britton & Rose, D. Seigler 16158, EU440032, EU811886, EU811991, EU812055, EU811931
Senegalia picachensis (Brandege) Britton & Rose, D. Seigler 15981, EU439983, EU811834, EU811951, EU812009, EU811906
Senegalia skleroxyla (Tussac) Seigler & Ebinger, D. Seigler 14503, EU440006, EU811858, EU811972, EU812030
Senegalia sororia (Standl.) Britton & Rose, D. Seigler 16067, EU439991, EU811842, EU811959, EU812017, EU811914
Senegalia visco (Lorentz ex Griseb.) Seigler & Ebinger, CANB 615607, EU440036, EU811891, EU811995, EU812059, EU811936
Senegalia vogeliana (Steud.) Britton & Rose, D. Seigler 14501, EU440001, EU811852, EU811969, EU812025
Vachellia choriophylla (Benth.) Seigler & Ebinger, UI Ghse s.n., EU440017, EU811870, EU812041
Vachellia collinsii (Safford) Seigler & Ebinger, D. Seigler 16038, EU440031, EU811885, EU811990, EU812054, EU811930
Vachellia constricta (Benth.) Seigler & Ebinger, D. Seigler 16061, EU440028, EU811881, EU811987, EU812051, EU811927
Vachellia cornigera (L.) Seigler & Ebinger, D. Seigler 16049, EU440021, EU811874, EU811981, EU812045, EU811920
Vachellia cucuyo (Barneby & Zanoni) Seigler & Ebinger, D. Seigler 14534, EU440010, EU811862, EU812034
Vachellia grandicornuta (Gerstner) Seigler & Ebinger, CANB 632220, EU440026, EU811879, EU811985, EU812049, EU81192
Vachellia hockii (De Wild.) Seigler & Ebinger, T. Young 3199 Mpala, EU440014, EU811867, EU811978, EU812038
Vachellia macracantha (Humboldt & Bonpland ex Willdenow) Seigler & Ebinger, D. Seigler 16052, EU440030, EU811884, EU811989, EU812053
Vachellia nitolica (L.) P.J.Hurter & Mabb., CANB 615592, AF522979, EU811827, AF524999, AF523183, EU811899
Vachellia oviedoensis (R.García & M.Mejía) Seigler & Ebinger, D. Seigler 14529, EU440005, EU811857, EU812029
Vachellia schaffneri (S.Watson) Seigler & Ebinger, D. Seigler 15931
Vachellia vernicosa (Britton & Rose) Seigler & Ebinger, D. Seigler 16062, EU440025, EU811878, EU811984, EU812048, EU811924
Zapoteca nervosa (Urb.) H.M.Hern., D. Seigler 14535, EU439997, EU811848, EU811965, EU812021