Systematics of the tribe Ingeae (Leguminosae-Mimosoideae) over the past 25 years

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Abstract

The large tropical tribe Ingeae (Leguminosae–Mimosoideae) is one of the most poorly studied groups of legumes, with a complex and unstable taxonomic history. In the first volume of 'Advances in Legume Systematics' in 1981, Nielsen presented a revision of the tribe Ingeae, which compared all previous systems and presented a new classification for the tribe. In subsequent years, numerous taxonomic changes were proposed as a result of monographs and revisions of genera and regional groups. During this time, two somewhat incongruent classification schemes arose, creating much taxonomic confusion. These two schemes were merged in a recent classification; however, many taxonomic problems and questions remain to be answered. This paper summarises the changes and conflict in the taxonomy of the tribe over the past 25 years, based primarily on the two major regional revisions: the Neotropics by Barneby and Grimes, and SE Asia, Australia and the Pacific Islands by Nielsen, Guinet and Baretta–Kuipers. Current understanding of phylogenetic relationships of the tribe is also reviewed.

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What are the Ingeae?

The tribe Ingeae is a large group of legumes in the subfamily Mimosoideae, with close to 1000 species, in 36 genera (Lewis & Rico Arce 2005). It is distributed pantropically (Fig. 1) and only one macromorphological character differentiates it from tribe Acacieae: stamens united into a tube (Ingeae) rather than being free (Acacieae; Elias 1981). There are some exceptions to this rule, however, with several species of the Acacieae (*Acacia sens. lat.*) having stamens fused at the base, although not always forming a tube as in the Ingeae, e.g. *Acacia adengonia* (Pedley) R.S.Cowan & Maslin (Australia: WA), *Ac. eriocarpa* Brenan (Africa), *Ac. ogadensis* Chiov. (Africa), *Ac. stipulata* DC. (Australia: NT and WA), and species of the '*Vachellia* group' (Vassal 1981; Cowan & Maslin 1990). In addition, some ingioid taxa, including several species of *Havardia* Small and at least one species of *Lysiloma* Benth., have stamens that are virtually free to the base (Barneby and Grimes 1996). The main centre of diversity of tribe Ingeae is in Southern and Central America, with a secondary centre in Asia–Australia (SE Asia–Pacific Islands–Australia).

Bentham established the tribe Ingeae in 1865, recognising nine genera, primarily on characters of the legume (Bentham 1865): *Affonsea* A.St.-Hil., *Albizia* Durazz., *Archidendron* F.Muell., *Calliandra* Benth., *Enterolobium* Mart., *Inga* Mill., *Lysiloma*, *Pithecellobium* Martius and *Serianthes* Benth. In 1875 Bentham revised the suborder Mimosaceae, at that time recognising the Ingeae as being made up of 15 genera/subgenera. This revision has been the basis of all others since, despite the fact that "no firm concepts of genera were established" because of a lack of material with fruits (Nielsen 1981a: 173). Since Bentham (1875), many taxa have been described and the generic concepts of the Ingeae have changed frequently (see Nielsen 1981a for a summary table of generic changes). This nomenclatural instability within tribe Ingeae, a group of economic importance that is widely used in the Americas and Asia for agro-forestry, shade trees for crops, fuel wood, land reclamation and stock feed, has resulted in much confusion for foresters, ecologists and conservationists (Hughes 1997).

The most recent classification scheme for the Ingeae was presented in the 'Legumes of the World' (Lewis & Rico Arce 2005). This was an

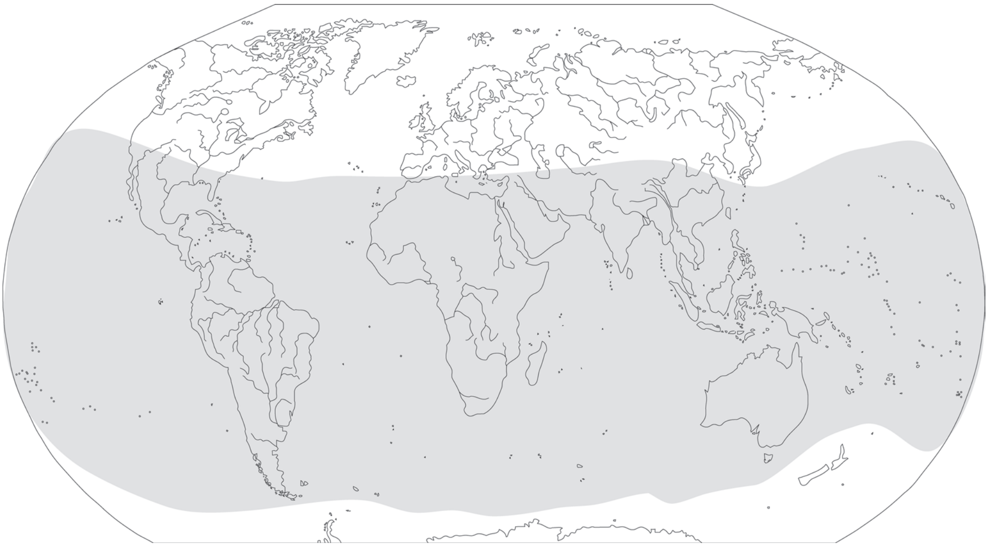

Figure 1. Distribution of tribe Ingeae. The general area that the Ingeae are distributed in is shaded in grey.

amalgamation of the two, sometimes contradictory, regional classifications (see below) that emerged after the revision of the tribe by Ivan Nielsen in 1981. Numerous taxonomic changes were proposed in regional revisions and generic monographs after Nielsen's 1981 classification. This paper aims to summarise these changes, highlighting areas where current classification systems are incongruent, and presents current phylogenetic knowledge of this large, diverse group of legumes.

Taxonomy of the Ingeae

Nielsen's 1981 classification

Nielsen (1981a) briefly described and compared the previous classifications of the Ingeae, from Bentham (1875) through to Hutchinson (1964), and concluded that only eight genera from these systems were universally accepted — *Albizia*, *Calliandra*, *Cedrelinga* Ducke, *Enterolobium*, *Inga*, *Lysiloma*, *Serianthes* and *Wallaceodendron* Koord. — with the remaining taxa being placed in the genus *Pithecellobium*. Prior to Nielsen's (1981a) classification, which was based on vegetative, floral, as well as carpological characters, classifications primarily reflected pod characteristics, resulting in what have been called 'pod-genera'. Therefore, the redefinition of many genera and the transfer of many species were necessary.

Nielsen (1981a) listed twenty-one genera in the tribe (Table 1): *Abarema* Pittier, *Affonsea*, *Albizia*, *Archidendron*, *Calliandra*, *Cedrelinga*, *Cojoba* Britton & Rose, Genus A, Genus B, Genus C, Genus D, *Havardia*, *Enterolobium*, *Inga*, *Klugiodendron* Britton & Killip, *Lysiloma*, *Marmaroxylon* Killip, *Pithecellobium*, *Punjuba* Britton & Rose, *Serianthes*, *Wallaceodendron*, and *Zygia* P.Browne. However, in the abstract he noted there were only "about 17 genera". This discrepancy can be explained by the exclusion of the four unnamed genera (Gen. A, B, C, D) and *Punjuba*, which was listed with unknown affinity. Nielsen (1981a) also presented a key to the 21 genera.

Many of the taxonomic changes proposed by Nielsen (1981a) relate to his treatment of two genera, *Albizia* and *Pithecellobium*, which had long been dumping grounds for difficult taxa. He chose to recognise *Pithecellobium* in the strict sense, recognising 20 species in the genus, in addition to several segregate genera formerly placed in *Pithecellobium* (see Nielsen 1981a), for example, *Cojoba*, *Klugiodendron*, Genus D, and *Zygia*. One species of *Pithecellobium sens. lat.* was left with unknown affinity: *Pithecellobium incuriale* (Vell.) Benth. (=*Leucochloron* Barneby & J.W.Grimes). Bentham placed *Pithecellobium incuriale* in *Pithecellobium* sect. *Samanea* ser. *Coriaceae*, however, Nielsen (1981a) did not include it with the other species formerly in this section ('Genus D' sensu Nielsen 1981a) because of its differing floral morphology.

Albizia, on the other hand, was treated by Nielsen (1981a) in a broad sense (the broadest concept of *Albizia* in the history of the tribe), including many genera that were previously segregated from *Pithecellobium*, such as *Cathormion* Hassk., *Chloroleucon* (Benth.) Britton & Rose, *Macrosamanea* Britton & Rose, *Pseudosamanea* Harms and *Samanea* Merr. This decision was primarily based on pod characteristics; however, characteristics of the seed and wood were also discussed in relation to some of the inclusions. As well as transferring a number of taxa into *Albizia*, Nielsen (1981a) segregated two former sections of *Albizia*, sect. *Lophantha* ser. *Pachyspermae* Benth. and sect. *Spiciflora* Benth. as distinct genera: Genus A and Genus B, respectively.

Cathormion and *Samanea* were included in *Albizia* by Nielsen (1981a) because he noted that it was impossible to distinguish boundaries between these taxa and *Albizia* sect. *Albizia*, with intermediate pod forms found between the dehiscent, membranous, and unsegmented pods of *Albizia lebbeck* (L.) Benth. and the segmented and indehiscent pods of *Cathormion umbellatum* (Vahl) Kosterm. Intermediate forms were also found between the pods of *Cat. umbellatum* and those of *Samanea saman* (Jacq.) Merr., which break away in 1-seeded segments. Despite the pollen characteristics of *Chloroleucon* being more similar to *Enterolobium*, and Nielsen's view that "perhaps it might be best regarded as a genus", it was included in *Albizia* because that is where it will "key out" (Nielsen 1981a: 182).

The inclusion of *Macrosamanea* and *Pseudosamanea* in Nielsen's *Albizia* is puzzling, especially because the "wood anatomy of *Pseudosamanea guachapele* differs greatly from that of *Albizia*" (Nielsen 1981a: 182). In addition, these two genera were considered by Nielsen (1981a: 182) to be "in the same alliance" as *Enterolobium*, however, he kept *Enterolobium* as a separate genus even though the boundary between it and *Albizia* was noted to be "not too sharp" (Nielsen 1981a: 182).

Nielsen (1981a) also considered *Abarema*, *Lysiloma* and *Enterolobium* to be closely related to the broadly circumscribed *Albizia*. *Abarema*, the only other genus identified in the '*Albizia* group' was distinguished from *Albizia* by red colouration on the inside of the pods, bird pollination, contorted to straight pods, and the funicle often slightly dilated. *Lysiloma* and *Enterolobium* were not included in the '*Albizia* group', although both were considered almost identical to *Albizia* by Nielsen (1981a). It appears that *Enterolobium* was only retained as a distinct genus, as it was by authors before him, because it is well known and widely cultivated in the tropics (Nielsen 1981a).

Since Nielsen's 1981 classification, taxonomic revisions of the Ingeae have generally focused on two broad geographical regions: the Neotropics (Barneby & Grimes 1996; Barneby & Grimes 1997; Barneby 1998) and SE Asia, Australia and the Pacific Islands (Nielsen *et al.* 1983; Nielsen *et al.* 1984a,b; Nielsen 1985; Nielsen 1992; Cowan 1998). Classifications of the tribe have also been presented in several new family-wide systems since 1981 (Polhill 1994; Lewis & Rico Arce 2005). A comparison of how genera have been treated in these various regional and familial classifications is presented in Table 1.

Regional revisions since 1981

Numerous generic monographs of the Ingeae were completed through the 1980s and 1990s. Nielsen continued his work on Ingeae focusing on taxa in SE Asia, the Pacific Islands and Australia (Nielsen *et al.* 1983; Nielsen *et al.* 1984a,b; Nielsen 1985). Barneby and Grimes (1996; 1997) and Barneby (1998) revised all of the Neotropical taxa except *Enterolobium* and *Lysiloma*, which were only briefly described as these had been monographed in two PhD dissertations (see Mesquita 1990 & Thompson 1980 in Barneby & Grimes 1996), and *Inga* (including *Affonsea*) and *Zapoteca* H.M.Hern. because these taxa were being treated by Pennington (1997) and Hernández (1986; 1989), respectively.

SE Asia, the Pacific Islands and Australia

The genera found in SE Asia, the Pacific Islands and Australia are: *Albizia*, *Archidendron*, *Archidendropsis* I.C.Nielsen, *Cathormion*, *Pararchidendron* I.C.Nielsen, *Paraserianthes* I. C. Nielsen, *Pithecellobium*, *Samanea*, *Serianthes*, *Thailentadopsis* Kosterm. and *Wallaceodendron*. Revisions of these Ingioid taxa in the region were predominantly completed by Nielsen, many in collaboration with Guinet and Baretta-Kuipers (Nielsen *et al.* 1983; 1984a,b; Nielsen 1985), culminating in an account of the Mimosaceae for the Flora Malesiana (Nielsen 1992). Genera recognised in Flora Malesiana, which incorporates information from the precursory

Table 1. Generic comparison between classification schemes from 1981 until present. For earlier generic classifications see Nielsen (1981). Square parentheses are used, where necessary, to highlight the different generic concepts of different authors. —, taxa not treated in that publication. Regional revisions: Nielsen (1992), SE Asia, Australia and the Pacific Islands; Barneby & Grimes (1996-1997), the Neotropics. Familial classifications: Polhill (1994); Lewis & Rico (2005).

Ingeae genera[A]	**Nielsen (1981)**	**Nielsen (1992)**[B]	**Polhill (1994)**	**Barneby & Grimes (1996–98)**	**Lewis & Rico (2005)**
Abarema	*Abarema*	—	*Abarema*	*Abarema*	*Abarema*
Affonsea	*Affonsea*	—	*Inga*	*Inga*	*Inga*
Albizia	*Albizia*	*Albizia*	*Albizia*	*Albizia*	*Albizia*
Archidendron	*Archidendron*	*Archidendron*	*Archidendron*	—	*Archidendron*
Archidendropsis	Genus B	*Archidendropsis*	*Archidendropsis*	—	*Archidendropsis*
Balizia	*Albizia*	—	—	*Balizia*	*Albizia*
Blanchetiodendron	*Albizia* or *Pithecellobium*?	—	—	*Blanchetiodendron*	*Blanchetiodendron*
Calliandra	*Calliandra*	—	*Calliandra*	*Calliandra*	*Calliandra*
Cathormion	*Albizia*	*Cathormion*	*Cathormion*	*Cathormion*	*Cathormion*
Cedrelinga	*Cedrelinga*	—	*Cedrelinga*	*Cedrelinga*	*Cedrelinga*
Chloroleucon	*Albizia*	—	*Chloroleucon*	*Chloroleucon*	*Chloroleucon*
Cojoba	*Cojoba*	—	*Cojoba*	*Cojoba*	*Cojoba*
Ebenopsis	*Havardia*	—	*Havardia*	*Ebenopsis*	*Ebenopsis*
Enterolobium	*Enterolobium*	—	*Enterolobium*	*Enterolobium*	*Enterolobium*
Faidherbia	—	—	*Faidherbia*	—	*Faidherbia*
Falcataria	Genus A p.p.	*Paraserianthes* p.p.	*Paraserianthes* p.p.	*Falcataria*	*Falcataria*
Guinetia	—	—	—	—	*Guinetia*
Havardia	*Havardia*	—	*Havardia*	*Havardia*	*Havardia*
Hesperalbizia	*Albizia*	—	*Albizia*	*Hesperalbizia*	*Hesperalbizia*
Hydrochorea	*Albizia*	—	*Albizia*	*Hydrochorea*	*Hydrochorea*
Inga	*Inga*	—	*Inga*	*Inga*	*Inga*

Ingeae genera[A]	**Nielsen (1981)**	**Nielsen (1992)**[B]	**Polhill (1994)**	**Barneby & Grimes (1996–98)**	**Lewis & Rico (2005)**
Leucochloron	*Pithecellobium incuriale*[C]	—	—	*Leucochloron*	*Leucochloron*
Klugiodendron	*Klugiodendron*	—	*Abarema*	*Abarema laeta*	*Abarema*
Lysiloma	*Lysiloma* [c.35 spp.]	—	*Lysiloma* [# not listed]	*Lysiloma* [8 spp.]	*Lysiloma* [8–9 spp.]
Macrosamanea	Genus D and *Albizia*	—	*Macrosamanea*	*Macrosamanea*	*Macrosamanea*
Marmaroxylon	*Marmaroxylon*	—	*Marmaroxylon*	*Zygia*	*Marmaroxylon*
Obolinga	—	—	*Obolinga*[D]	*Cojoba*	*Cojoba*
Painteria	*Havardia*	—	*Havardia*	*Painteria*	*Painteria*
Pararchidendron	Genus C	*Pararchidendron*	*Parachidendron*		*Pararchidendron*
Paraserianthes	Genus A	*Paraserianthes* [4 spp.]	*Paraserianthes*	*Paraserianthes* [1sp. with 4 var.]	*Paraserianthes* [1sp.]
Pithecellobium	*Pithecellobium*	*Pithecellobium*	*Pithecellobium*	*Pithecellobium*	*Pithecellobium*
Punjuba	*Punjuba*	—	*Abarema*	*Abarema*	*Abarema*
Pseudosamanea	*Albizia*	—	*Albizia*	*Pseudosamanea*	*Pseudosamanea*
Samanea	*Albizia*	*Samanea*	*Samanea*	*Samanea*	*Samanea*
Serianthes	*Serianthes*	*Serianthes*	*Serianthes*		*Serianthes*
Sphinga	*Havardia*	—	*Havardia*	*Sphinga*	*Sphinga*
Thailentadopsis	*Havardia*	—	*Havardia*	unplaced: noted to be from albizioid stock	*Thailentadopsis*
Viguieranthus	*Calliandra*	—	*Calliandra*		*Viguieranthus*
Wallaceodendron	*Wallaceodendron*	*Wallaceodendron*	*Wallaceodendron*	—	*Wallaceodendron*
Zapoteca	*Calliandra*	—	*Zapoteca*	*Zapoteca*	*Zapoteca*
Zygia	*Zygia*	—	*Zygia*	*Zygia*	*Zygia*

[A] The Ingeae genera column includes all genera that have been recognised in the Ingeae from 1981 to 2006

[B] Data in this column is based on the Flora Malesiana but also reflects the precursory work done in Malesia by Nielsen *et al.* (see text for references)

[C] Placed with unknown affinity within the genus *Pithecellobium*

[D] *Obolinga* was described by Barneby (1989) but after morphological phylogenetic analyses it was sunk into *Cojoba* (as *Co. zanonii*) papers (Nielsen *et al.* 1983; 1984a,b; Nielsen 1985), are listed in Table 1. The Ingeae were also revised for a number of local floras: e.g., Flora of Australia (Cowan 1998), Flora of New Caledonia (Nielsen 1983) and Flora of Cambodia, Laos and Vietnam (Nielsen 1981b). As a result of these works, many taxonomic changes were made from Nielsen's 1981 Ingeae classification. The only genus in the region that has not changed taxonomically since the last revision is *Wallaceodendron* (Nielsen *et al.* 1983; Nielsen *et al.* 1984b; Nielsen 1992).

The 37 species of *Albizia* recognised in SE Asia, the Pacific Islands and Australia were revised in two papers; the first (Nielsen 1979) concentrated on the mainland Asian species, while the second focused on those found in Malesia (Nielsen 1985). In both revisions, and in the Flora Malesiana (Nielsen 1992), a key to the flowering specimens as well as a key to the fruiting specimens were provided. Nielsen (1979; 1985) did not produce an infrageneric classification for the genus *Albizia* because he believed it "would be premature" (Nielsen 1985: 27) without the formal transfers and regional revisions of the American and African species he proposed belonged in *Albizia* in 1981. Nielsen (1985) did, however, employ two informal groups in the Malesian region: '*Albizia corniculata* group' and '*Serialbizia* group'.

One alteration to Nielsen's broad concept of *Albizia* of 1981 was the recognition of *Cathormion* as a distinct genus. At first, Nielsen (1992: 143) noted, of *Cathormion*, that there were "about 12 species in tropical and subtropical South America and Africa, and 1 species in the SE Asia/Australia region". But based on aberrant pollen morphology, he later decided it was preferable to consider *Cathormion* a monotypic genus of SE Asia–Australia (Nielsen 1992: 143).

Archidendron is the largest genus endemic to the SE Asian, Pacific Island and Australian region, with 94 species (Nielsen *et al.* 1984a), and the fourth largest genus in the tribe behind *Inga* (c. 300 spp.), *Calliandra* (135 spp.), and *Albizia* (c. 120-140 spp.; Lewis & Rico Arce 2005). An additional 22 species of *Archidendron* have also been listed as imperfectly known because of a lack of (good) collections or the destruction of types in Berlin (Nielsen *et al.* 1984a). Taxa, in Malesia, that were formerly referred to as *Abarema*, *Zygia* and *Morolobium* Kosterm. have been transferred to *Archidendron* with new combinations made by Nielsen *et al*. (1984a).

An infrageneric classification of the genus *Archidendron* was proposed (Nielsen *et al.* 1984a), recognising eight series based on morphology: *Archidendron* (c. 15 spp.), *Bellae* I.C.Nielsen (4 spp.), *Calycinae* I.C.Nielsen (3 spp.), *Clypeariae* (Benth.) I.C.Nielsen (c. 51 spp.), *Morolobiae* (Kosterm.) I.C.Nielsen (c. 4 spp.), *Pendulosae* (Mohl.) I.C.Nielsen (3–4 spp.), *Ptenopae* I.C.Nielsen (2 spp.) and *Stipulatae* (Mohl.) I.C.Nielsen (c. 12 spp.). A key to these series was presented in the Flora Malesiana treatment (Nielsen 1992: 88), while three identification keys to species were provided in the generic revision (Nielsen *et al.* 1984a): one for all species based on all morphological characters, and two separate keys for the flowering and fruiting specimens of series *Clypeariae*, *Archidendron* and *Bellae*.

Four new genera of Ingeae were described for the SE Asian, Pacific Islands and Australian region (Nielsen 1983; Nielsen *et al.* 1983; 1984b; Barneby & Grimes 1996) — *Archidendropsis*, *Falcataria* (I.C.Nielsen) Barneby & J.W.Grimes, *Pararchidendron* and *Paraserianthes* — and another, *Thailentadopsis*, was resurrected by Lewis and Schrire (2003). Three of the newly described genera had been identified informally in Nielsen's 1981 classification, but were not formalised until the thorough regional revision of Nielsen *et al*. (1983; 1984b). *Archidendropsis* ('Genus B', Nielsen 1981a) was described in the Flora of New Caledonia (Nielsen 1983) for the taxa with winged, thin walled seeds without pleurogram, formerly *Albizia* sect. *Spiciflorae* Benth. ser. *Platyspermae* Benth. The genus is composed of 14 species and has been divided into two subgenera (Nielsen *et al.* 1983): *Archidendropsis* (11 spp.) found in New Caledonia, New Guinea, and New Britain-Solomon Islands; and subgenus *Basaltica* I.C.Nielsen (3 spp.) found only in Australia (Queensland). Nielsen *et al*. (1983) questioned whether subg. *Basaltica* should in fact be a separate genus but based on the uniformity of flowers they decided to retain the group until further data became available.

Pararchidendron ('Genus C', Nielsen 1981a) was originally described by Nielsen (part I; Nielsen *et al*. 1983), with detailed discussion on the taxonomy and morphology presented in part III of those studies (Nielsen *et al.* 1984b). It is a monotypic genus, with four varieties, found in Indonesia (Java, Lesser Sunda Islands, Irian Jaya), Papua New Guinea and Australia (Queensland and NSW). Originally identified as including two species

(*Abarema sumbawaensis* Kosterm. and *Parar. pruinosum* (Benth.) I.C.Nielsen), *Ab. sumbawaensis* was later synonymised as a variety of *Parar. pruinosum* (Nielsen *et al.* 1984b). *Pararchidendron* has affinities to the genus *Archidendron*, differentiated by having alternate leaflets and areolate seeds (Nielsen *et al.* 1984b; Nielsen 1992).

The third new genus, segregated as 'Genus A' by Nielsen (1981a), was *Paraserianthes*. It was described as having four species, one with two subspecies and another with two varieties, and divided into two sections: *Paraserianthes* and *Falcataria* I.C.Nielsen (Nielsen *et al.* 1983). It is native to Australia, Indonesia (Sumatra, Java, Lesser Sunda Islands, Irian Jaya), Papua New Guinea and the Solomon Islands, and is considered related to *Serianthes*, but with opposite leaflets and dehiscent pods (Nielsen 1992). Members of *Paraserianthes* were formerly recognised in a section of *Albizia* (sect. *Lophantha* ser. *Pachyspermae*), however, because of their uniform flowers arranged in ± elongate spikes, they were removed and considered as a distinct genus (Nielsen 1981a).

Barneby and Grimes (1996), in their revision of neotropical Ingeae, promoted Nielsen's *Paraserianthes* section *Falcataria* to generic rank as their genus *Falcataria* and leaving *Paraserianthes* as monotypic. *Paraserianthes falcataria* (L.) I.C.Nielsen is widely planted in the neotropics and this is presumably why the only combination made was *Paras. falcataria* to *Falcataria molucanna* (Miq.) Barneby & J.W.Grimes; no combinations were made for the other two taxa of Nielsen's section *Falcataria*, which are endemic to Papua New Guinea (*Paras. pullenii* (Verdc.) I.C.Nielsen) and Australia (*Paras. toona* (Bailey) I.C.Nielsen). The decision to raise *Falcataria* to generic rank was based on cladistic morphological analyses (Grimes 1995; Barneby & Grimes 1996), which placed *Paras. falcataria* (=*Falcataria molucanna*) in an unresolved polytomy near the base of the Ingeae, while *Paras. lophantha* (Willd.) I.C.Nielsen was the sister group to other SE Asian–Pacific Island–Australian taxa. The generic concept of *Paraserianthes* remains open at this time, however, research into this problem is underway.

The last new genus recognised in the region since 1981 is *Thailentadopsis*, which was resurrected from the genus *Havardia* by Lewis and Schrire (2003). *Thailentadopsis* was originally described as a genus by Kostermans in 1977, and is currently composed of three species — *T. nitida* (Vahl) G.P.Lewis & Schrire, *T. tenuis* (Craib) Kosterm. and *T. vietnamensis* (I.C.Nielsen) G.P.Lewis & Schrire — that "cannot be confidently placed in any other currently accepted ingioid genera" (Lewis & Schrire 2003: 492). Nielsen (1981a) recognised these three species in a broadly defined *Havardia*, while Barneby and Grimes (1996) provisionally excluded them from *Havardia*, leaving them with the generic name *Pithecellobium* but later hypothesising "that they form a phylogenetically distinct group derived from a primitive albizioid stock" (Barneby & Grimes 1997: 3). The relationship of *Thailentadopsis* to other ingioid genera remains unknown, although, Lewis and Schrire (2003) note that the monotypic *Cathormion* is morphologically the most similar. They also indicate that the relationship to the three Asian species of *Calliandra* (see 'Other regions' for discussion of these Asian species of *Calliandra*) should be investigated.

The last native SE Asian, Pacific Island and Australian genus to discuss is *Serianthes*. A detailed revision of the genus was conducted after the 1981 tribal revision (Nielsen *et al.* 1983; 1984b), and *Serianthes* is now recognised as comprising about 18 species, with several other insufficiently known taxa identified but not formally described (Nielsen *et al.* 1983; 1984b; Nielsen 1992). An infrageneric classification based on the structure of the inflorescence and pods (Nielsen 1992) has also been proposed, with the genus divided into two subgenera (Nielsen *et al.* 1983), *Minahassae* I.C. Nielsen and *Serianthes*, the latter further divided into two sections, *Serianthes* and *Calycina* I.C.Nielsen.

Species of *Pithecellobium* and *Samanea* are found in the SE Asian, Pacific Islands and Australian region, however, they are either cultivated, weedy or naturalised. All species referred to the genus *Pithecellobium* in the region have now been moved to *Archidendron* and *Albizia* (Nielsen *et al.* 1984a; Nielsen 1992), with the exception of *Pi. dulce* (Roxb.) Benth., which was introduced to the Philippines from Mexico, and later introduced to India where it was first described (Nielsen 1992). *Samanea saman* is widely planted throughout the region and is now "appearing spontaneous all over the tropics" (Nielsen 1992: 156).

The Neotropics

Extensive revisions of taxa from the Neotropics have also been undertaken since Nielsen's 1981 tribal classification, predominantly by Barneby and Grimes (1996; 1997) and Barneby (1998) but with generic revisions by others (see Mesquita 1990 & Thompson 1980 in Barneby & Grimes 1996; Pennington 1997; Rico Arce *et al.* 1999). The revisions of Barneby and Grimes (1996; 1997) and Barneby (1998) primarily focused on the taxa that had been referred to the genus *Pithecellobium* at one time or other; keys are presented for all genera. After all generic revisions, 25 genera were recognised in the neotropics, including two newly described genera and the resurrection of two genera from *Pithecellobium*: *Abarema*, *Albizia*, *Balizia* Barneby & J.W.Grimes, *Blanchetiodendron* Barneby & J.W.Grimes, *Calliandra*, *Cedrelinga*, *Chloroleucon*, *Cojoba*, *Ebenopsis* Britton & Rose, *Enterolobium*, *Guinetia* L.Rico & M.Sousa, *Havardia*, *Hesperalbizia* Barneby & J.W.Grimes, *Hydrochorea* Barneby & J.W.Grimes, *Inga*, *Leucochloron* Barneby & J.W.Grimes, *Lysiloma*, *Macrosamanea*, *Painteria* Britton & Rose, *Pithecellobium*, *Pseudosamanea*, *Samanea*, *Sphinga* Barneby & J.W.Grimes, *Zapoteca*, and *Zygia*.

The taxonomy of *Cedrelinga*, *Enterolobium* and *Lysiloma* has remained almost the same since Nielsen's tribal revision (1981a). The affinities of the monotypic *Cedrelinga* remain unknown, although it has been suggested to be closely related to *Albizia*, *Enterolobium* section *Enterolobium* and the *Zygia* group (Barneby & Grimes 1996). *Enterolobium* remains a distinct genus, as it was in Nielsen (1981a), and was revised by Mesquita (1990 in Barneby & Grimes 1996) who recognised nine species. Barneby and Grimes (1996) generally agreed with Mesquita's treatment but in addition described one new species (*En. oldemanii* Barneby & J.W.Grimes) and a new section (sect. *Robrichia* Barneby & J.W.Grimes). The generic concept of *Lysiloma* remains as it did in Nielsen (1981a), however, Nielsen recognised about 35 species, while Barneby and Grimes (1996) only recognised eight species (Table 1). This difference is a result of strikingly different species delimitation of these authors, particularly in relation to a number of characters that are relatively plastic, such as, leaf–formula, pubescence, and width of pod (Barneby & Grimes 1996).

The taxonomic concepts of *Abarema*, *Cojoba*, *Inga* and *Zygia* have all been expanded in the past 25 years (Barneby & Grimes 1996; 1997; Pennington 1997). *Klugiodendron* and *Punjuba* were transferred to *Abarema* based on cladistic morphological analysis (Barneby & Grimes 1996). However, *Abarema* is now defined by a combination of homoplasious characters and "can no longer be easily defined in exact terms" (Barneby & Grimes 1996: 43). *Cojoba* has been expanded to include the monotypic genus *Obolinga* Barneby based on cladistic morphological analysis (Barneby & Grimes 1997). When *Obolinga* was described by Barneby (1989) the carpological syndromes of it and *Cojoba* were considered too different to be congeneric. However, the unique fruit type of *Obolinga* has since been found in a species of *Cojoba*, *Co. bahorucensis* J.W.Grimes & R.G.Garciá, and based on the phylogeny in Barneby and Grimes (1997), both species are nested well within the latter genus.

Species of *Inga* are found throughout the wet Neotropics and the genus contains about 300 species, including up to 50 that are imperfectly known and also taxa formerly placed in the genus *Affonsea* (Pennington 1997). *Affonsea*, which was recognised as a distinct genus by Nielsen (1981a), was originally excluded from *Inga* because of its multicarpellate ovary, however, in all other respects *Affonsea* and *Inga* are the same. Since 1981, a multicarpellate ovary has also been found in several species of *Inga* (Pennington 1997), hence the incorporation of *Affonsea* into *Inga*.

The inclusion of *Marmaroxylon* into a more broadly defined *Zygia* by Barneby and Grimes (1997) was not unexpected, as Nielsen (1981a) noted they may be congeneric. While a cladistic analysis of *Zygia* (including *Marmaroxylon*) was not undertaken, because more than one third of the species are still unknown in fruit, Barneby and Grimes (1997) did divide the genus into nine sections.

The neotropical element of *Albizia* sensu Nielsen is the generic concept in the region that has changed the most since the 1981 classification because Barneby and Grimes (1996) adopted a generic concept of *Albizia* that is considerably narrower that that of Nielsen (1981a). The American species of *Albizia* were revised by Barneby and Grimes (1996) and they developed an infrageneric classification of these species. Based on cladistic morphological analyses they reinstated *Pseudosamanea*, *Samanea* and *Chloroleucon*, which

Nielsen (1981a) synonymised under *Albizia*, and described three new genera from *Albizia* sensu Nielsen (Barneby & Grimes 1996): *Balizia*, *Hesperalbizia*, and *Hydrochorea*. However, Rico Arce did not agree with *Balizia*, sinking it back into *Albizia*, and noting that "it seems wiser to adopt a broader concept of the genus *Albizia* until the genus has been monographed across its range" (Rico Arce 1999: 555). *Albizia* is still in need of a worldwide revision.

Macrosamanea was recognised as a South American genus of zygioid affinity composed of 11 species by Barneby and Grimes (1996), while Nielsen (1981a) synonymised it under *Albizia*. The genus was originally described by Britton and Killip in 1936 based on taxa from *Pithecellobium* ser. *Coriacea* (Barneby & Grimes 1996). The generic concept of *Macrosamanea* was expanded in 1940 by Kleinhoonte to include an albizioid taxon, *Mac. pedicellaris* (DC.) Kleinh. (=*Balizia pedicellaris* (DC.) Barneby & J.W.Grimes). It was in relation to this taxon that *Macrosamanea* was synonymised under *Albizia* by Nielsen (Barneby & Grimes 1996). *Macrosamanea* sensu Barneby and Grimes (1996) is therefore equivalent in generic concept to 'Genus D' of Nielsen (1981a), with minor adjustments.

The large predominantly neotropical genus *Calliandra* has shrunk since Nielsen's 1981 classification, with two new genera being erected from it: *Viguieranthus* Villiers, primarily found in Madagascar (see 'Other regions' below); and *Zapoteca* from the Neotropics. Palynological studies of *Calliandra* indicated that two clear groups of taxa existed: one with 16-grained polyads (as found in the majority of the Ingeae) and the other with 8-grained polyads. A number of other characters can also be used to distinguish between these two groups including, characteristics of the leaflets, inflorescence, stigmas, legume, seedlings and number of chromosomes (Hernández 1986). As a result, the taxa that were formerly placed in *Calliandra* ser. *Laetevirntes*, with 16-grained polyads, were transferred to the new genus *Zapoteca* (Hernández 1986). The other major development was the subdivision of *Calliandra* into five sections and 14 series by Barneby (1998).

Three new genera have been described from *Havardia* sensu Nielsen (Barneby & Grimes 1996), each comprising three species: *Ebenopsis*, *Painteria* and *Sphinga*. *Ebenopsis* was defined by its unique pod, which is massive, ligneous, and internally septate with "obese reddish seeds". *Painteria* was "feebly distinguished from *Havardia* by tougher-walled, falcately or further recurved pods, and by straight or sinuous but not distally sigmoid seed funicles" (Barneby & Grimes 1996: 179). Members of the third genus, *Sphinga*, have been considered closely related since Bentham (1875) and were distinguished from *Havardia* because of their "greatly elongated perianth, with long, silky corolla expanding at nightfall" (Barneby & Grimes 1996). Phylogenetic analysis of these four genera — *Ebenopsis*, *Havardia*, *Painteria*, and *Sphinga* — and *Pithecellobium*, which appear to form a natural morphological group, revealed that *Sphinga* and *Havardia* are sister taxa and the three other genera form a clade, with *Painteria* and *Pithecellobium* sister taxa, and *Ebenopsis* related to them (Barneby & Grimes 1996).

Barneby and Grimes' (1997) concept of *Pithecellobium sens. str.* does not appear to differ greatly from that of Nielsen (1981a). However, they established a new genus, *Leucochloron*, for *Pithecellobium incuriale*, which Nielsen (1981a) left as affinity unknown, and three related species (Barneby & Grimes 1996). *Leucochloron* is hypothesised to be closely related to *Chloroleucon* but differs in characteristics of the axillary branchlets, pod and seed.

Blanchetiodendron is another newly described neotropical genus; it has previously been placed in *Pithecellobium*, as well as *Enterolobium* and *Albizia* (Barneby & Grimes 1996). The genus was defined by characteristics of the inflorescence, pod and seed, and is clearly related to two groups of taxa: *Leucochloron* and *Chloroleucon*, and *Albizia* sect. *Arthrosamanea*. However, it is morphologically isolated from both (Barneby & Grimes 1996).

The last new genus of Ingeae that was described from the neotropics post Nielsen 1981 is *Guinetia*; it was discovered in Mexico in 1968 but not described until 30 years later (Rico Arce *et al.* 1999). It is a monotypic genus and has characteristics of both the *Chloroleucon* and *Inga* alliances (see below), but does not match any taxon within those groups.

The phylogenetic relationships, of tribe Ingeae, resolved by Grimes (1995) was the basis of the informal grouping of genera into alliances by Barneby and Grimes (1996). For the neotropical taxa, five alliances were identified and four genera were left as affinity unknown until they can be comprehensively analysed: *Albizia*, *Enterolobium*, *Cedrelinga* and *Lysiloma*. The genera from other geographic regions, with the exception of *Archidendron*, were not placed into alliances. The alliances identified by Barneby and Grimes (1996), shown in Table 2, were: the *Abarema*–alliance including, *Abarema*, *Hydrochorea* and *Balizia*; the *Chloroleucon*–alliance including, *Blanchetiodendron*, *Chloroleucon* and *Leucochloron*; the *Inga*–alliance including, *Archidendron*, *Calliandra*, *Cojoba*, *Inga*, *Macrosamanea*, *Zapoteca* and *Zygia* (including *Marmaroxylon*); the *Samanea*–alliance

Table 2. Alliance composition comparison table. The genera of each alliance are listed as per the system of Barneby and Grimes (1996), with changes from Grimes (1999) incorporated[B], and compared to the system suggested by Lewis and Rico (2005).

Alliance	Barneby & Grimes (1996)	Lewis & Rico (2005)
Abarema–alliance	*Abarema*	*Abarema*
	Hydrochorea	*Hydrochorea*
	Balizia[A]	*Pararchidendron*
Chloroleucon–alliance	*Blanchetiodendron*	*Blanchetiodendron*
	Chloroleucon	*Cathormion*
	Leucochloron	*Chloroleucon*
	Lysiloma[B]	*Leucochloron*
		Thailentadopsis[C]
Inga–alliance	*Archidendron*	*Archidendron*
	Calliandra	*Calliandra*
	Cathormion[B]	*Cedrelinga*
	Cojoba	*Guinetia*[C]
	Inga	*Cojoba*
	Macrosamanea	*Inga*
	Zapoteca	*Macrosamanea*
	Zygia (incl. Marmaroxylon)	*Marmaroxylon*
		Viguieranthus[C]
		Zygia
Samanea–alliance	*Albizia lebbeck*[B]	
	Hesperalbizia	*Hesperalbizia*
	Samanea	*Samanea*
	Pseudosamanea	*Pseudosamanea*
Pithecellobium–alliance	*Ebenopsis*	*Ebenopsis*
	Havardia	*Havardia*
	Sphinga	*Sphinga*
	Painteria	*Painteria*
	Pithecellobium	*Pithecellobium*
Unplaced genera	*Albizia*	*Albizia*
	Cedrelinga	*Enterolobium*
	Enterolobium	*Lysiloma*

[A] *Balizia* was not recognised as a genus by Lewis and Rico (2005).

[B] taxa were placed into alliance after the analysis of Grimes (1999).

[C] taxa were described/reinstated after the revision of Barneby and Grimes (1996).

including, *Hesperalbizia*, *Samanea* and *Pseudosamanea*; and the *Pithecellobium*–alliance including, *Ebenopsis*, *Havardia*, *Sphinga*, *Painteria*, and *Pithecellobium*.

Grimes (1999) later published an updated phylogeny of the Ingeae, with revised morphological characters and previously missing data included. Some Old World taxa were represented in this phylogeny, however, no comprehensive cladistic analysis of the Old World genera was presented. The revisions resulted in several changes to the alliances (Table 2): *Cathormion* was placed in the *Inga*–alliance; the relationships between genera of the *Abarema*–alliance were now considered unresolved (previously *Abarema* was considered the derived genus of this alliance); *Albizia lebbeck* was included in the *Samanea*–alliance because of its similarity to *Samanea saman*; and the *Chloroleucon*–alliance now includes *Lysiloma*, which was previously unplaced and poorly studied in 1995.

Other regions

Genera of the Ingeae are also native to Africa, Madagascar and the Middle East and extend into Mainland Asia (Lewis & Rico Arce 2005). Ingeae in these regions have not been as extensively revised as for the Neotropics and SE Asia, the Pacific Islands and Australia, however, some important taxonomic changes have occurred in the past 25 years. The two main changes have been the transfer of *Faidherbia* A.Chev. to the tribe Ingeae from Acacieae, and the description of a new genus *Viguieranthus*.

In the first volume of 'Advances in Legume Systematics', when Nielsen reviewed the Ingeae, Vassal (1981) provided a revision of the related tribe Acacieae, recognising two genera in the tribe: *Acacia* and the monotypic *Faidherbia*. These genera were differentiated by a character of pollen tectum, and the tribe was distinguished from the Ingeae by stamens being free and not united into a tube, although, exceptions were known (see 'What are the Ingeae?' above). *Faidherbia* is one of these exceptions with "stamen filaments shortly connate basally" (Vassal 1981: 170). Vassal (1981) considered it more appropriate to include *Faidherbia* in tribe Acacieae, while Polhill (1994) later transferred it to the Ingeae. Recent phylogenetic analyses of the Ingeae (Luckow *et al.* 2003; Miller *et al.* 2003), support the transfer suggested by Polhill with *Faidherbia* placed as the sister taxon to *Zapoteca* (Ingeae).

The second major change to Ingioid taxa outside SE Asia–Pacific Islands–Australia and the Neotropics has been the segregation of *Viguieranthus* from *Calliandra* (Villiers 2002). *Viguieranthus* includes 23 species from Asia and Madagascar, differentiated from *Calliandra* by the possession of leaves with only a single pair of pinnae and inflorescences with homomorphic flowers (Villiers 2002). Hernández (1986) also noted that species of *Calliandra* from Madagascar and India were palynologically dissimilar to the remainder of the genus. However, Villiers only made combinations for the 18 Madagascan taxa when describing the genus, despite noting that it is also found in Asia. Only three taxa have been ascribed to *Calliandra* in Asia, so presumably these are the Asian *Viguieranthus* mentioned by Villiers (2002); formal nomenclatural combinations have yet to be made. The other two species ascribed to *Viguieranthus* have been suggested to be the "two rejected African calliandras", "highlighting the poor state of knowledge of generic limits within the Old World calliandras" (Lewis & Rico Arce 2005: 199).

This poor state of knowledge is not just limited to the genus *Calliandra*. The African taxa that have been ascribed to *Cathormion*, but currently recognised as *Albizia* (Nielsen 1981a) require revision. Barneby and Grimes (1996: 247) questioned whether the African *Cathormion* is congeneric with the Asiatic *Cathormion*, however, this has yet to be tested.

The Ingeae from Madagascar have recently been revised by Villiers (2002) for 'The Leguminosae of Madagascar'. In addition to the description of *Viguieranthus* (see above), it is interesting to note that Villiers' adopted the broad concept of *Albizia* sensu Nielsen, with *Albizia saman* (= *Samanea saman*) recognised as one of the 30 species of *Albizia* (Villiers 2002).

Ingeae in familial classifications

These regional revisions have provided the taxonomic framework for the Ingeae in recent familial classifications (Polhill 1994; Lewis & Rico Arce 2005). In Polhill's 1994 classification of the family Leguminosae, most of the discussion related to the subfamily Papilionoideae, however, the synopsis of legume genera included information on all subfamilies. The classification of the tribe Ingeae incorporated the work by Nielsen and

Nielsen *et al*. (1981a,b; 1983; 1983; 1984a,b; 1985; 1992) but Polhill (1994) has doubts over the characterisation of some New World genera, which have since been revised by Barneby and Grimes (see 'The Neotropics' above). Polhill (1994) recognised 25 genera in the Ingeae (Table 1), including *Faidherbia*.

The next, and most recent, classification of the family Leguminosae was published in 2005 ('Legumes of the World', edited by Lewis *et al.* 2005). The Ingeae treatment was compiled by Lewis and Rico, which brought together information from all of the regional revisions (above), presenting a synopsis of each genus with photos and descriptions. Most of the generic changes from the regional revisions were adopted, however, some were not: *Marmaroxylon* was recognised as a separate genus, although Barneby and Grimes (1996) had treated it as part of *Zygia*; and *Balizia* was not considered a separate genus from *Albizia* (Rico Arce 1999).

A diagram of hypothesised relationships of genera in the Ingeae was also included. This largely corresponded to the alliances of Barneby and Grimes (1996) but included some changes based on the molecular phylogenetic study of Luckow *et al*. (2003; Table 2). Lewis and Rico (2005) also created an Old World group to accommodate most taxa restricted to the SE Asian, Pacific Island and Australian region, excluding *Archidendron* and *Pararchidendron*. The *Pithecellobium*– and *Samanea*–alliances remain as described in Barneby and Grimes (1996) but Lewis and Rico (2005) did not mention the incorporation of *Albizia lebbeck* into *Samanea*–alliance suggested by Grimes (1999). There have been some alterations to the other three alliances (Table 2).

As *Balizia* was not recognised by Lewis and Rico (2005), it was not acknowledged in the *Abarema*–alliance. The other change to the *Abarema*–alliance was the inclusion of the Old World genus *Pararchidendron* (Table 2). No justification for its inclusion was provided and this relationship was not suggested in Barneby and Grimes (1996) nor the phylogeny of Luckow *et al*. (2003).

The genera *Cathormion* and *Thailentadopsis* were included in the *Chloroleucon*–alliance by Lewis and Rico (2005), although again, it is not clear why. Presumably *Thailentadopsis* was added because of its suggested relationship to *Cathormion* (Lewis & Schrire 2003), but Grimes (1999) placed *Cathormion* in the *Inga*–alliance, not the *Chloroleucon*–alliance. In the molecular phylogeny of Luckow *et al*. (2003) *Cathormion* is placed next to *Chloroleucon* on the tree, however, they are both in an unresolved polytomy, with numerous other taxa, and therefore not necessarily closely related.

The *Inga*–alliance of Lewis and Rico (2005) has changed the most from its original concept (Table 2). Based on results of Luckow *et al*. (2003), Lewis and Rico removed *Zapoteca* from the *Inga*–alliance and placed it, with *Faidherbia*, as sister to the rest of the tribe. Four genera have been added to the *Inga*–alliance. *Marmaroxylon* and *Viguieranthus* were recognised from genera already included in the *Inga*–alliance and the affinities of the newly described taxon, *Guinetia*, also came from within the *Inga*–alliance. The inclusion of *Cedrelinga*, however, is not well justified. Presumably it was placed in the *Inga*–alliance because it was the sister to *Calliandra* in the phylogeny of Luckow *et al*. (2003); however, the support for this relationship is extremely weak (35% bootstrap support).

Phylogenetic relationships of the Ingeae

Morphological phylogenies

Three papers attempting to resolve the relationships of the genera of the Ingeae, based on morphological data, were published in the 1990s (Chappill & Maslin 1995; Grimes 1995; Grimes 1999). The relationships of the ingioid genera in each of the analyses are not especially congruent, but this may be due to different generic sampling and the use of different characters. All of these phylogenies, however, are in agreement that the Ingeae is not monophyletic, with the different clades of Acacieae nested within the tribe Ingeae (Chappill & Maslin 1995; Grimes 1995; Grimes 1999).

Chappill and Maslin (1995) focused on the relationships within the Acacieae yet also investigated its relationships to the other tribes of the subfamily, based on characters of morphology, pollen, chemistry and anatomy. All infra-generic groups of the Acacieae were represented along with at least one exemplar from each other tribe; 24 genera of the Ingeae were sampled. As a result, some relationships between genera of the Ingeae were hypothesised but not discussed in detail.

The phylogeny of Grimes (1995) primarily focused on the New World *Pithecellobium*–complex using macromorphological, developmental, anatomical and pollen characters; this analysis formed the basis of the alliances described in the Barneby and Grimes (1996; 1997) and Barneby (1998) revisions. Four years later Grimes (1999) published another phylogeny of the Ingeae based on a modified data set. The results were generally congruent with his 1995 analysis but some modifications to the originally proposed alliances of the Ingeae were required (discussed above).

Molecular phylogenies

Members of the tribe Ingeae have also been included in various molecular phylogenetic studies; all of these have been based on sequences of chloroplast DNA (cpDNA) regions. However, two studies utilised a region of nuclear DNA (nDNA) in conjunction with a cpDNA region (H3-D, Miller & Bayer 2000; ITS, Richardson *et al.* 2001). With a few exceptions, these molecular phylogenetic studies included too few representatives (genera or species) to make meaningful inferences about the relationships within the tribe Ingeae (Dayanandan *et al.* 1997; Clarke

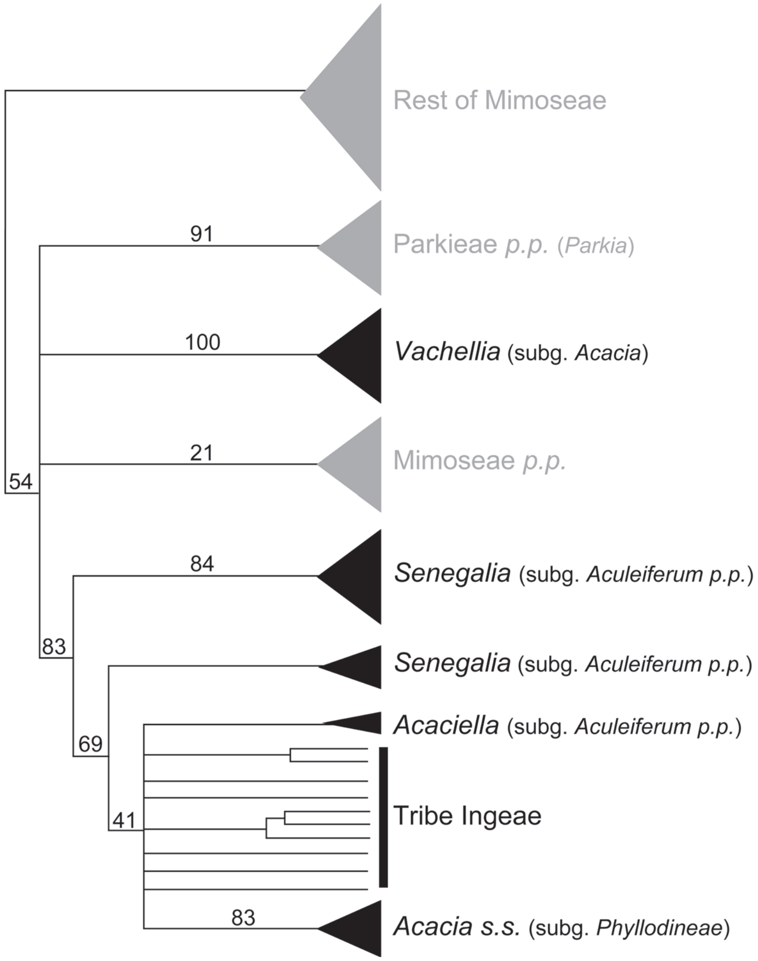

Figure 2. Relationships between members of the tribe Acacieae and Ingeae (adapted from Luckow *et al.* 2003). This is a summary phylogeny of the Mimosoideae, based on cpDNA data, of Luckow et al. (2003). Triangles represent a clade, while numbers above the node represent bootstrap values for that clade node. Clades of tribes Mimoseae and Parkieae are in grey; tribe Acacieae in black and tribe Ingeae.

et al. 2000; Luckow *et al.* 2000; Miller & Bayer 2000; Robinson & Harris 2000; Kajita *et al.* 2001; Miller & Bayer 2003; Wojciechowski *et al.* 2004; Lavin *et al.* 2005). More detailed and densely sampled molecular phylogenetic studies of the Ingeae are currently underway (Brown *et al.*, submitted).

The studies that have sampled the most Ingeae were focused on the phylogenetic relationships of the subfamily Mimosoideae (32 species/16 genera, Luckow *et al.* 2003) and the tribes Acacieae and Ingeae (21 species/15 genera, Miller *et al.* 2003). The results of these two studies were congruent, which is to be expected as they sequenced the same regions of cpDNA (*trn*K, *mat*K, *trn*L intron and *trn*L-*trn*F spacer; Miller *et al*. (2003) also sequenced the *psb*A-*trn*H spacer). The tribe Ingeae was placed in an unresolved polytomy, along with a monophyletic *Acacia sens. str.* (formerly *Acacia* subg. *Phyllodineae*) and two species of *Acaciella* (Fig. 2; Luckow *et al.* 2003; Miller *et al.* 2003): *Ac. boliviana* and *Ac. visco*. This polytomy may be a result of limited sampling or alternatively there may be insufficient informative characters in these DNA loci to resolve these relationships.

Relationships between members of the Ingeae were generally unresolved, however, some inferences can be made. Six genera were found to be monophyletic: *Calliandra*, *Ebenopsis*, *Enterolobium*, *Havardia*, *Lysiloma* and *Zapoteca*. The sampling of each genus was very limited, with most including only two species, although, three species (c. 38% of the genus) were included for *Lysiloma* and five species (c. 4% of the genus) for *Calliandra*. *Albizia* was the only genus, sampled for more than one species that was identified as polyphyletic. *Inga* was confirmed as monophyletic (Richardson *et al.* 2001), with 44 species (c. 15% of the genus) sampled for two regions of DNA (ITS and *trn*L–*trn*F).

In both analyses, *Ebenopsis* and *Havardia* formed a clade, as did *Faidherbia* and *Zapoteca*. An additional node was supported in the analysis of Miller *et al*. (2003), although the bootstrap value was low (56%): grouping *Albizia kalkora* and *Cat. umbellatum* with the monophyletic *Enterolobium*. A similar relationship was found with the H3-D nDNA region (Miller & Bayer 2000).

What is next for the Ingeae?

Although there have been considerable advances in the systematics of the Ingeae over the past 25 years, we have only just started to scratch the surface of this large, diverse and important group of legumes. Many of the difficulties and challenges that impede on the taxonomy and classification of the Ingeae, such as, getting to know large numbers of taxa over a broad geographical area and the resultant reliance on geographically focused studies which often lack monographic synthesis, also hinder the systematics of other large pantropical groups.

There are still many questions unanswered in relation to the systematics of the Ingeae, including defining the tribal limits. Should the tribe Ingeae be merged with the tribe Acacieae or should it be split up into several supergeneric taxa? With a revision of tribal classification of the Mimosoideae imminent (Luckow 2005), it is vital that we have a better understanding of the phylogenetic relationships within the currently circumscribed Ingeae. Despite an increase in phylogenetic analyses including taxa of tribe Ingeae in recent years, much remains to be done. The most comprehensive morphological analyses of the tribe to date (Grimes 1995; 1999), present only a preliminary and partially resolved hypothesis of sister group relationships for the tribe with many of the Old World taxa not well sampled (Grimes 1995; Hughes 1997). While in molecular phylogenetic studies, which can provide statistical support for the monophyly of genera and higher level grouping, sampling of the Ingeae have included only half of the 36 currently recognised genera and less than 5% of all Ingeae species.

Current data, based on limited taxon and character sampling, indicate *Acacia sens. str.* (formerly *Acacia* subgenus *Phyllodineae*) is nested within a paraphyletic Ingeae (Fig. 2) and is distantly related to other groups of tribe Acacieae. By advancing our knowledge of the Ingeae, we will also improve understanding of the evolutionary history of related genera, including *Acacia sens. str*., which is the largest genus of woody, flowering plants in Australia and an ecologically significant group, being the dominant tree or shrub in many ecosystems. Uncovering the phylogeny of the Ingeae will assist in identifying the closest relative of *Acacia sens. str.*, therefore improving the classification of *Acacia sens. str.* for all end-users. However, as well as molecular phylogenies, diagnostic morphological characters need to be identified that can be used for defining taxa that are meaningful for the broader community and end-users of taxonomic information. Many potential morphological characters in the Ingeae have been identified through monographic work, and careful interpretation of these will enhance molecular studies currently under way and in the future.

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