Generic and infrageneric classification in Acacia (Leguminosae: Mimosoideae): a list of critical species on which to build a comparative data set

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SUMMARY

Some recent proposals argue for the subdivision of the large pantropical genus Acacia. As a basis for making informed decisions on this important matter it is considered necessary that further broad-based, comparative studies be conducted. In order to assist researchers wishing to undertake such studies a list of "critical species", representative of many of the currently recognized major subgroups within the genus, is presented. Also, synoptic taxonomic notes are given for many of the currently recognized formal and informal infrageneric groups within Acacia.

INTRODUCTION

A number of recent papers have discussed or proposed the possible subdivision of Acacia (see Maslin 1988, 1989; Chappill and Maslin 1995; Pedley 1986, 1987a, 1987b). As currently conceived the genus comprises three large subgenera, Acacia, Aculeiferum and Phyllodineae, the first two pantropical in distribution and the third largely confined to the Australian region. A consensus now appears to be emerging that Acacia should be divided, but no agreement has been reached on where the dividing lines should be drawn. As discussed by Chappill and Maslin (1995) much of the problem appears to lie with the status of subgenus Aculeiferum and its relationship to subgenus Phyllodineae. What has become clear is that in many instances taxonomically relevant data are available for only a few species, for species in a restricted geographical area, or not at all. To fill these gaps in our knowledge, corroborative data should be obtained from as many representative species-groups and via as many disciplines as possible.

The genus Acacia comprises over 1200 species. Therefore, in undertaking comparative studies within a reasonable time it is not possible to examine all species. A practical solution is to choose representative species from each of the currently recognized major subgroups, bearing in mind that even the delineation of many of these subgroups is still uncertain. Multidisciplinary studies of these "critical species" will assist in devising a more meaningful classification of Acacia sensu lato and/or of the three subgenera which comprise it. Additionally, the data will be valuable in assessing the relationship of these taxa to other genera within the Mimosoideae (especially tribes Mimoseae and Ingeae) which, hopefully, will lead to a resolution of the taxonomic status of the tribe Acaciinae.

We therefore propose a list of "critical species" (Appendix 1 and 2), based on an evaluation by various experts on Acacia (see Acknowledgements) and urge those working on the genus to include as many of these taxa as possible in their studies. The "classification" used in Appendix
is in many ways a very pragmatic one (an overview of the more commonly used formal classifications of *Acacia* is given in Table 1 of Maslin 1988 and Table 1 of Chappill and Maslin 1995). At the higher levels we adopt a combination of the schemes proposed by Vassal (1972) and Pedley (1978). Because of their high species numbers the Australian sections Plurinerves plus Juliflorae, and Phyllodinae, have been divided into informal sub-groups, namely, "microneurous" vs. "oligoneurous" (Cowan and Maslin 1990) and racemos vs. non-racemos respectively. Within each higher-order taxon the species are grouped according to their presumed taxonomic affinities.

The selection of species for inclusion on the "critical list" was based on the following criteria.

- The species in total should represent, as far as possible, the taxonomic variation within the genus.
- It should be possible to acquire experimental material of the nominated species with minimal cost and effort.
- Other things being equal, preference is given to taxa that have already been studied intensively using chemistry, pollen, ontogeny, etc.

It has not been possible, however, to include only species that meet all these criteria. Some taxa have been included on their scientific merit or because of their anomalous taxonomic placement. Other species have been included simply because collections have already been made and distributed to specialists for detailed study. Species not on the list are not precluded from study; if authors contact us, we will attempt to assign the taxa to their appropriate taxonomic subgroup. This is important because some researchers may already have material which could substitute for taxa we have listed. We emphasise that this is a preliminary list of species and undoubtedly other taxa will need to be added in due course. We hope that the proposal presented in this article will both stimulate further research and facilitate a more unified approach to *Acacia* systematics. We would therefore urge workers to consider the species included on our preliminary list of "critical species" and either contact us to effect changes or to publish modifications themselves in subsequent issues of this Bulletin.

Within *Acacia* a number of broad-based comparative research programs are currently being carried out on chemistry (protease inhibitors, DNA-sequencing, gums, and immunology), morphology and anatomy (spinescence, foliar anatomy, seed morphology, seedling anatomy, pollen) and systematics. However, there is a general consensus among workers that new comparative studies are needed (Maslin 1987) and the following have been suggested as desirable topics for research:

- molecular systematics (DNA markers and allozyme markers)
- inflorescence structure
- floral organogenesis
- lipid chemistry
- phylloclade anatomy/morphogenesis
- legume anatomy
- legume morphology
- wood anatomy
TAXONOMIC NOTES ON ACACIA AND FAIDHERBIA

The following taxonomic notes are presented as an aid to researchers intending to work on Acacia and in order to provide a centennial framework for the list of "critical species" (Appendix I). This is not an exhaustive discussion of the classification of Acacia but rather synoptic notes designed to introduce researchers to some of the more important recent taxonomic literature on Acacia and Faidherbia and to provide some insights into current taxonomic thinking, especially with respect to the main species-groups that are currently recognized within Acacia. Additional relevant information will be found in the references that we cite.

1. Genus Faidherbia

Until recently this monotypic African genus was treated as a species of Acacia, namely, A. albida. However, as summarized by Ross (1979) this taxon is not closely related to the other African species of Acacia. Also, the results of recent immunological studies by Brain (1987 and 1990) and cladistic analyses of Chappill and Maslin (1995) clearly indicate that this taxon should be removed from Acacia. Although Faidherbia was placed in tribe Acacieae by Vassal (1981) it has shorted united filaments and pollen characters similar to the Enterolobium - Albizia complex (Samanea group) within Ingeae (Guinet and Lugardon 1976, Guinet 1981 and 1990).

2. Genus Acacia

In recent years there have been many studies of the phylogeny and classification of Acacia (e.g. Brain 1987 and 1990, Conn et al. 1989, Evans et al. 1977, Guinet 1969, 1979 and 1990, Guinet and Vassal 1978, Maslin et al. 1988, Chappill and Maslin (1995), Pedley 1978, 1986 and 1987, Pettigrew and Watson 1975, Ross 1973, 1979 and 1981, Tindale and Roux 1969 and 1974, Vassal 1972, Vassal and Rouane 1987 and 1991). As currently circumscribed the genus includes more than 1200 species contained in three subgenera, namely, subgenus Acacia, subgenus Aculeiferum and subgenus Phyllodineae (syn. subgenus Heterophyllum). Although Pedley (1986) attributed generic rank to these taxa, namely, Acacia, Senegalia and Racopserma respectively, these have not been widely adopted. Pedley's proposal has widespread nomenclatural implications which is one of the reasons why it is not generally accepted. Another reason is that his assessment of Acacia did not include a comparative study of allied genera in tribes Ingeae and Mimoseae. This latter deficiency was addressed in a preliminary broad-based cladistic analysis of tribe Acacieae by Chappill and Maslin (1995) where it was shown that Faidherbia and subgenus Acacia were very different from subgenus Aculeiferum and subgenus Phyllodineae.

Global distributions for the three subgenera of Acacia are given in Ross (1981).

A. Acacia subgenus Acacia

This pan-tropical group includes approximately 120-130 species (Madsen 1990). Recent studies have shown that subgenus Acacia is distinct from the other two subgenera of Acacia and that it probably evolved independently of them, (e.g. Guinet and Vassal 1978), Pedley (1986), Vassal (1988), Brain (1987 and 1990) and Chappill and Maslin (1995). However, for reasons
discussed in Maslin (1988) and Chappill and Maslin (1995) separate generic status for this taxon is not advocated at present.

Bentham (1875) divided subgenus *Acacia* into three groups based on the position of the involucre on the peduncle; however, this has proven an extremely variable character and is no longer considered suitable for discriminating infra-generic groups (Ross 1979). Although Britton and Rose (1928) divided the subgenus into 12 genera, primarily on the basis of fruit characteristics, most modern classifications do not recognize formal subordinate categories within subgenus *Acacia*. Vassal (1972), however, did divide subgenus *Acacia* section *Acacia* into two subsections, namely, Pluriserie and Uniserie, but his classification has not been generally adopted. Most African species of subgenus *Acacia* occur in the Uniserie and, as discussed by Ross (1979), no ways have yet been found to meaningfully subdivide this group. In the New World, however, where the subgenus *Acacia* is represented by about 50 species (Lee *et al.*, 1989), seven reasonably distinct, albeit small, species-groups can be recognized, while in Asia another two groups occur. (NB. These nine groups do not account for all species of subgenus *Acacia* which occur in these two regions.)

**New World Groups**

(a) *Acacia rigidula* group (comprising *A. bitimeki*, *A. brandegeana*, *A. californica*, *A. pringlei* and *A. rigidula*, fide Lee *et al.* 1989 and Clarke 1995). These species are very distinct on account of their spicate inflorescences with 4-merous, white flowers; they also have a distinctive flavonoid chemistry (Seigler, pers. comm.) This group, together with the *A. constricta* group (see below) comprised *Acaciopsis* Britton and Rose, a "genus" recognized by a strip of papery endocarp on the inner surface of each legume valve. There is a superficial resemblance of several members of the *A. rigidula* group to species of *Pithecellobium*, especially *P. dulce*.

(b) *Acacia constricta* group (comprising *A. baciculata*, *A. constricta*, *A. neovernicosa* and *A. schotii*, fide Clarke *et al.* 1990); *A. glandulifera*, a species included by Britton and Rose in the genus *Poponax* Raf. is included in the *Acacia constricta* group by Clarke (1995). *Acacia pacensis* appears to be intermediate between the *A. constricta* and *A. farnesiana* groups (Seigler, pers. comm.) although it was placed in the *A. farnesiana* group by Clarke (1995). Unlike other species of subgenus *Acacia* with globular heads, members of the *A. constricta* group sometimes have a single or scattered bracts on their peduncle instead of the usual multibracteate, whorled involucel; they also show distinctive flavonoid patterns (Seigler, pers. comm.).

(c) *Acacia farnesiana* group (comprising the New World species *A. albicorticata*, *A. atroventaria*, *A. caven*, *A. espeyensis*, *A. farnesiana*, *A. pinetorum*, *A. polyphylligenes*, *A. schaffneri*, *A. setifrons*, *A. smallii* and *A. torvula*, fide Clarke *et al.* 1989 and Clarke 1995; also the African species *A. erioloba* and *A. haematoxylon*, fide Guinet 1990). In the past a number of these species were sometimes referred to the genus *Vachellia* Wight and Arn. or *Poponax* Raf. Guinet (loc. cit.) alluded to unusual pollen characters found in members of the *A. farnesiana* group; he also noted that most of these species have stamen filaments irregularly connate at the base (no stamen tube though), a floral involucel and +/- indehiscent pods.
(d) Acacia acuifera group (comprising A. acuifera, A. anegadensis, A. barahonensis, A. belairoides, A. bucheri, A. caurina, A. cucuyo, A. daemon, A. roigii and A. zapatenis, fide Clarke and Seigler 1991 and Clarke 1995). These species are restricted to the Caribbean and are characterized by low stamen number, fruit structure and a ramified stipular spine systems.

(e) Acacia choriophylla group (comprising only A. choriophylla, fide Clarke 1995). This species is restricted to the Caribbean. It was placed in the group containing A. acuifera by Clarke and Seigler (1991) but is now known not to be related to that group; perhaps related to the Ant Acacia group (Seigler, pers. comm.)


(g) Acacia macracantha group. The three Central American non-Ant Acacias, A. macracantha, A. pinnatula and A. cochlisacantha are closely related to the Ant Acacia group, fide Ebinger and Seigler (1990) and Clarke (1995) and were among the 12 species included by Britton and Rose (1928) in the genus Poponax. The southern South American species, A. aroma, A. huarango, A. roridiana and an undescribed species are also included in the A. macracantha group by Clarke (1995).

Asian Groups

Members of the following two groups differ most obviously from other Asian species of subgenus Acacia by their paniculate inflorescences, and, in the case of the A. harmandeana group at least, their low number of stamens per flower (10-15).

(a) A. harmandeana group (comprising A. harmandeana, A. leucophloeos and A. myaimgi). Inflorescences paniculate; involucres present; stipules spiny; stamens 10-15 per flower. The genus Delopoteria Gagnepain, which was segregated from Acacia on the basis of a small gland present at the top of the anther, is treated by Nielsen (1980) as a synonym of A. harmandeana (see also Guinet 1981). Nielsen noted that gland-bearing anthers occur in most other Asian acacias.

(b) A. inopinata group (comprising A. craibii and A. inopinata). Inflorescences paniculate; involucres present; stipules spiny. Acacia inopinata was originally described as Nimtria inopinata.

B. Acacia subgenus Aculeiferum

Subgenus Aculeiferum was established by Vassal (1972) and currently includes about 180-190 species (Madsen 1990) contained in three sections, namely, Aculeiferum, Monocanthea and Filicinace. As shown in Table 1 of Maasin (1988) and Chappill and Maasin (1995) the subgenus corresponds to the combined series Vulgares and Filicinace of Bentham (1875). Species of this pantropical subgenus are widespread in both North and South America and in Africa; a small number of species are found in Asia and only one in Australia. As already noted, Pedley (1986) treated subgenus Aculeiferum as a distinct genus, Senegalia, but this change has not been widely adopted.
A number of recent studies have shown that subgenus Aculeiferum is more closely related to subgenus Phyllodineae than it is to subgenus *Acacia* with which it shares a common geographical area. Data from studies of pollen (Guinet 1990) and free amino acids (Evans et al. 1977) suggest that the differences between the two subgenera are relatively minor and this is supported by the results of a preliminary cladistic analysis by Chappill and Maslin (1995). This latter study, however, did not support the monophyly of subgenus Aculeiferum.

(a) Section Aculeiferum

Species of section Aculeiferum, which are confined to Africa and Asia, form a natural group, distinct from section Monocanthea (Evans et al. 1977, Brain 1990, Chappill and Maslin 1995). These studies also showed *A. ataxacantha* (an African species which Vassal placed in section Monocanthea) as having close affinities with species of this section; the sectional placement of this species should therefore be re-assessed. According to Ross (1979) all the African species of section Aculeiferum have spicate inflorescences and it is desirable to divide them into two groups, namely, those with prickles in pairs near the nodes and those with prickles in threes or solitary near the nodes.


(ii) Prickles solitary or in threes. *Acacia ankokoii*, *A. asak*, *A. caraniana*, *A. cheilanthifolia*, *A. condylocadra*, *A. dudgeoni*, *A. hamulosa*, *A. ogadensis*, *A. olivieri*, *A. senegal*, *A. somalensis*, *A. thomasi* and *A. zizyphispina*.

(b) Section Monocanthea

Species of section Monocanthea occur in the Americas and from Africa through Asia to Australia. No species is common to both Africa and the Americas, however, some show close similarities (Ross 1981). All non-American species of section Monocanthea which have globular heads of flowers belong to the "*Acacia pennata* group" (Brennan and Excell 1957); this group seemingly also occurs in the New World (see the *A. riparia* group below).

New World Groups

According to Seigler (pers. comm.) subgenus Aculeiferum in the New World has three main centres of diversity: (1) Mexico and adjacent southwestern U.S. and Central America; (2) southern Brazil, northern Argentina, Paraguay and Bolivia; (3) northeastern Brazil. Preliminary studies by Seigler suggest that the 50 or so taxa from area (1) can be divided into five major species-groups:

(i) Acacia acaciensis group (comprising *Acacia acaciensis*, *A. centralis*, *A. compacta*, *A. coulteri*, *A. dolichostachya*, *A. millefolia*, *A. sericea*, *A. usmanintensis*, *A. willardiana* and *Senegalia durangensis*). Members this group lack prickles but the stipules (when present) may occur as small subulate spines (e.g. *A. millefolia*, *A. centralis*) or as spinose horn-like projections (e.g. *A. coulteri*). Spinose stipules are a constant feature of species in subgenus *Acacia* but are otherwise rare (?) or absent) elsewhere in subgenus Aculeiferum. *Acacia*
willardiana differs from all other members of subgenus Aculeiferum in having leaves reduced to phylloide-like structures (see Vassal and Guinet 1972). Evans et al. (1977) showed that free amino acids of A. coultieri are the same as in species of section Aculeiferum (this section is seemingly not represented in the New World).

(ii) **Acacia berlandieri** group (comprising *Acacia anisophylla*, *A. berlandieri*, *A. crasifolia*, *A. omoriana*, *A. greggii*, *A. occidentalis*, *A. parviflora* (syn. *A. micrantha*), *peninsularis*, *A. reniformis*, *A. roemeriana*, *A. sororia*, *A. subangulata*, *A. wrightii* and *Senegalia painteri*). This is a somewhat diverse group of species; *A. berlandieri* hybridizes with a number of the taxa listed here (Seigler, pers. comm.). *Acacia greggii* was placed in the monotypic subsection Cryptocotylae by Vassal (although *A. roemeriana* was also referred to this subsection by Conn et al. 1989, its seedling ontogeny is unknown). The only other species of this group studied by Vassal was *A. berlandieri* which he placed in subsection Phanerocotylae (along with one or two species from the *A. acutensis* and *A. glomerosa* groups).

(iii) **Acacia riparia** group (comprising *Acacia hayesii*, *A. macilenta*, *A. riparia*, *A. tenuifolia* and *Senegalia acapulcensis*). These species have either globular heads (e.g. *A. riparia*, *A. tenuifolia*) or cylindrical spikes (e.g. *A. macilenta*, *A. hayesii*; *A. bonariensis* from Argentina seems close to these species). Members of the *A. riparia* group have prickles arranged in rows like members of the "*A. pennata* group" from Africa and Asia. Evans et al. (1977) showed that *A. riparia* accumulated the same unknown free amino acid as members of the "*A. pennata* group".

(iv) **Acacia glomerosa** group (comprising *Acacia gaumeri*, *A. glomerosa*, *A. interior*, *A. marnifera*, *A. mirandae*, *A. picachensis* and *A. purpursii*). Closely related to the *A. riparia* group.

(v) **Acacia amazonica** group (comprising *Acacia amazonica*, *A. kuehlmannii*, *A. lacerans*, *A. velutina*, and probably *A. serrata*).

**African Groups**

According to Ross (1979: 9) the African species of section Monocanthes share the following characters: pule yellowish-white flowers, stipitate ovaries, most are climbers or scandent shrubs, all lack secondary leaves, and all have pods which are +/- umbonate over the seeds and have a fairly conspicuous transverse venation. Ross considered it desirable to divide the African Monocanthes into those species with capitulate inflorescences and those with spicate inflorescences (Vassal 1972 did not make this distinction).

(i) **Spicate inflorescences** (*Acacia ataxacantha*, *A. chariessa*, *A. eriocarpa* and *A. macrostachya*). Ross (1979: 10) noted that these four species differed from those of group (ii) below in pollen, seedling and seed characters characters. Serological studies by Brain (1990) showed *A. ataxacantha* as being close to (spicate) members of section Aculeiferum and distinct from the capitulate species of section Monocanthes. Furthermore, Evans et al. (1977) included *A. ataxacantha* in their free amino acid Group 3 (which otherwise included species of section Aculeiferum). This species is therefore anomalous within section Monocanthes.

(ii) **Capitate inflorescences** (*Acacia adenocalyx*, *A. brevispica*, *A. ciliolata*, *A. erythrocalyx*, *A. kamerunensis*, *A. kraussiana*, *A. laistipulata*, *A. luiae*, *A. montigemo*, *A. pentagona*, *A.
Acacia baumannii, A. taylorii and A. tephridermis). Brain (1990) showed that A. brevispica and A. schweinfurthii were quite distinct serologically from the African spicate members of both section Monocaenitea and section Aculeiferum. *Acacia miyajima* on the other hand was, serologically, like a spicate species.

(c) Section Filicincae

According to Pedley (1987a) the morphological and chemical attributes of this endemic New World group suggest that it could well be treated as a distinct genus; a similar view was expressed by Guinet (in Maslin 1987) and by Seigler (pers. comm.). Guinet and Vassal (1978) were of the opinion that section Filiciniae preserves the morphological characters closest to those postulated as being ancestral in the genus. This idea was supported by the cladistic analysis of Chappill and Maslin (1995). According to Guinet (1990) section Filiciniae is closely related to the *Piptadenia* group in tribe Mimosae; however, Chappill and Maslin suggest that these similarities may be interpreted as plesiomorphics.

C. Acacia subgenus Phyllodineae

This subgenus, with in excess of 900 species is largely confined to Australia. In a recent cladistic analysis of tribe Acacieae by Chappill and Maslin (1995) subgenus Phyllodineae was supported as monophyletic with subgenus Aculeiferum section Aculeiferum the sister group. As already noted Pedley's (1986) proposal that subgenus Phyllodineae be treated as a distinct genus, *Racosperma*, has not been widely adopted.

The geographic patterns of species richness for subgenus Phyllodineae and its seven sections are mapped and discussed by Hnatiuk and Maslin (1988) and Maslin and Pedley (1988). Individual species distributions are given in Maslin and Pedley (1982) but this work is now considerably dated, especially because of the large numbers of new species which have been described (or are in preparation) since 1982. The species numbers given below follow those of Maslin (1995) and updates those given by Maslin and Pedley (1988). Most of the 20 extra-Australian species of subgenus Phyllodineae are discussed by (Pedley 1975). Coulaud et al. (1995) recently published the results of a cytogenetic investigation on *A. heterophylla* (La Reunion Island) and its close relative, *A. melanoxylon* (Australia).

As will become evident from the brief discussion which follow there is a critical need to reassess the classification of subgenus Phyllodineae in order to devise a system of meaningful categories which reflect the evolutionary history of this very large and important group.

Currently the most generally used classification is that of Pedley (1978) which represents a good, pragmatic attempt to rationalize earlier schemes by Bentham (1842, 1864, 1875) and Vassal (1972). The seven sections recognized by Pedley correspond fairly well to groupings of series or subspecies defined earlier by Bentham (see Table 1 of Maslin 1988 and Table 1 of Chappill and Maslin 1995). Although we have adopted Pedley's scheme here it does not follow that we consider all these groups to be "good" taxonomic entities. Indeed, as has been demonstrated in the recent cladistic and immunology studies by Chappill and Maslin (1995) and Brain and Maslin (in press) respectively, considerable work is still needed to elucidate the classification of subgenus Phyllodineae. Brain and Maslin in particular challenge many of the conventional beliefs concerning the classification of subgenus Phyllodineae (see discussions below).
Additional to the species-groups that are noted below there are a number from the Arid Zone which are listed in Maslin and Hopper (1982).

(a) Section Botrycephala (42 species). Species of this section are confined to eastern Australia and recent studies have suggested that it is most closely related to certain racemose species of section Phyllodineae from eastern Australia (Tindale and Roux 1969 and 1974, Vassal 1972 and Pettigrew and Watson 1975, Brain and Maslin in press).

Based on chemical data a number of subgroups have been recognized within section Botrycephala. For example, studies by Tindale and Roux (1969) of flavanoid and condensed-tannin contents of the heartwood and bark from 18 species recognized the following species-groups: (1) A. constabili, A. decaurus, A. irrorata subsp. velutinella, A. mezzii, A. paramattensis and A. trachypilosa; (2) A. filicifolia, A. irrorata and A. silvestris; (3) A. botrycephala, A. cardiophylla, A. chrysotricha, A. leucocladu subsp. argentifolia and A. oshunensis; (4) A. baileyana and A. dealbata. Also, from detailed analyses of gum from 10 species Anderson (1978) and Anderson et al. (1971 and 1984) proposed that section Botrycephala be divided into two distinct groups. Group A included six taxa (A. deanei and A. deanei subsp. paucijuga, A. irrorata subsp. irrorata, A. paramattensis, A. parvipinnula and A. trachypilosa) which differed greatly in their gum composition from the phyllodineous species of Bentham's (1864) "Division" Phyllodineae; Group B also contained six taxa (A. dealbata subsp. dealbata and subsp. subalpina, A. filicifolia, A. leucocladu, A. silvestris and A. terminalis) but these showed a strong chemical resemblance to the phyllodineous taxa examined.

Pedley (1986) suggested that perhaps A. leucoxela and A. mitchelli might constitute a third group. Acacia mitchelli, which differs from all other species of Botrycephala in having non-racemose inflorescences, was excluded from section Pulchellae by Guinet et al. (1980).

(b) Section Pulchellae (27 species). This group is endemic in south-western Western Australia (Maslin 1975 and 1979) and as discussed by Guinet et al. (1980) comprises a "core" of interrelated species centered around A. pulchella, A. browniana and A. drummondu. The affinities of the few additional species included in section Pulchellae are unclear although some seem related to species of section Phyllodineae, e.g. A. gilbertii (with A. myrtfolia) and A. insolita (with A. squamata). The relationships of the "core" species to the rest of the genus is unknown. Vassal (1972) included some in his section Pulchelloidae, however, this section was not supported by Pettigrew and Watson (1975). Acacia mitchelli, the only eastern Australian species referred by Bentham to section Pulchellae, is better placed in section Botrycephala.

(c) Section Alateae (21 species). Although this section was recognized in Pedley's (1978) classification he correctly relegated it to synonymy under section Phyllodineae (as Racosperma section Racosperma) in his 1986 scheme. For convenience this section is retained in the "critical list" below. Some of the species of this section were included in Vassal's section Pulchelloidae (see above).

(d) Section Lycopodiiformae (17 species). The tropical/ardic zone species of section Lycopodiiformae probably constitute a natural group. It is not clear how this section relates to the rest of the subgenus Phyllodineae, however, as noted by Pedley (1987c) and Cowan and Maslin (1990a) there are certain floral details which suggest some affinities to the A. deltoidea group (see under section Juliflorae below). Although A. baumii (central east coast of
Australia) was included in the section by Pedley (1978) this species is probably better placed in section Phyllocladeae somewhere near A. brumoides. Relationships between species of section Lycopodiophytae are shown in Pedley (1972). A detailed, elegant study by Rutishauser and Sattler (1986) examined phylloide architecture and development in one member of section Lycopodiophytae, namely, A. longipedunculata.

(c) Section Phyllodinae (387 species). This is the largest group within subgenus Phyllodinae. It is widespread in Australia with most species-rich areas occurring south of the Tropic of Capricorn in the temperate and adjacent semiarid areas of eastern, southeastern and southwestern Australia; the section is poorly represented in the tropical/sub-tropical north of the continent. There are no indigenous species of section Phyllodinae occurring outside Australia.

Although Bentham (1864) recognized six subseries within his series Uninerves (= section Phyllodinae) these are largely artificial groups and are generally not adopted by modern workers. Furthermore, certain species traditionally referred to this section are clearly related to species currently placed in section Plurinerves. Excluding these taxa (some of which are discussed below) most published evidence suggests that there is a major difference within subgenus Phyllodinae between species with so-called "1-nerved" phylloides (i.e. section Phyllodinae) and those with plurinerved phylloides (i.e. the combined sections Plurinerves and Juliflorae). Pedley (1986) recognized this division but refrained from attributing subgeneric rank to the two groups. Unpublished data on hybridity in Acacia (Kentick, Knox, Guinet and Maslin) show no natural or artificial hybrids recorded between species of these two groups. Although this division was evident in the cladistic analysis by Chappill and Maslin (1995) it was not able to be substantiated in the immunology study by Brain and Maslin (in press).

While inflorescence structure seems fundamentally important in defining natural groups within section Phyllodinae the traditional method of dividing species into racemose vs. non-racemose subgroups is a somewhat over-simplified approach. Indeed, the immunology study by Brain and Maslin (in press) suggests that these two subgroups are far more distinct from one another than hitherto recognized. Bentham (1864) included species with elongated racemes in subseries Racemoseae, while species with simple inflorescences or extremely reduced racemes were distributed among five other subseries. However, recent studies show examples where members of closely related species-pairs may have different inflorescence types, or where a single species may possess two different inflorescence types, e.g. A. victoriae (elongated racemes) - A. synochronica (simple inflorescences), fide Maslin (1992), A. calamifolia (very reduced racemes) - A. nematophylla (simple inflorescences), fide Maslin and Whitley (1987), A. bivenosa (both racemes and simple inflorescences), fide Chapman and Maslin (1992).

Based on a study of flavonoid patterns in Acacia Tindale and Roux (1974) showed that subseries Racemoseae could be divided into at least two basic groups. Although not all species referable to this subseries were included in their study they demonstrated that arid semi-arid species such as A. blakelyi, A. marneyana (syn. A. frumentaceae), A. prainicarpa, A. sclerosperma, A. victoriae, etc. contained pyrogallol-type compounds (which also occurred extensively in species of sections Juliflorae and Plurinerves), on the other hand species predominantly from eastern Australia, e.g. A. falcata, A. falciformis, A. fimbriata, A. kettledelliae, A. pycnantha, A. remotae, etc. contained resorcinol-type compounds (which also occurred in species of section Borystheaceae). Based on seed characters it is possible to divide this latter group into species with long funicles which encircle the seeds, e.g. A. falcata, A.
retinodes, A. rubida (there are over 40 species Australia-wide with this sort of furcile, most of these are referable to the "A. microbotrya group", fide Maslin 1995a) and those with short, non-encircling furciles, e.g. A. aduncu. A. pycnantha, A. williamsonii, etc. (Maslin, unpublished data). The Brain and Maslin immunology study showed the racemose group as comprising three subgroups (centered on A. ligulata, A. pyrifolia and A. podalyriifolia).

The non-racemose members of section Phyllodineae are generally not well-studied. However, the work by Brain and Maslin (in press) has provided some surprising insights on possible affinities for this group. In this study Brain and Maslin were unable to confirm the traditional view that the racemose and non-racemose members of section Phyllodineae are closely related; indeed, based on their serological evidence at least some non-racemose taxa were shown to be related to species currently placed in sections Plurinerves and Juliflorae. Clearly, much work is still needed to be done on the "non-racemose" in order to clarify the classification and phylogeny of the complex. To date, a few discrete groups have been recognized within this assemblage, e.g., the Triangulares group which Maslin (1978a) showed as comprising two distinct sub-groups centered around A. bisflora and A. horridula, and the A. ulicifolia group which Pedley (1969) recognized (we would add the following three non-Queensland species to those listed by Pedley: A. asparagoides, A. brownii and A. guarni).

As noted above there are some instances where the traditional division of species of subgenus Phyllodineae into unincerved vs. plurinerved groups does not result in a natural clustering of taxa. Examples of this can be found in taxonomically distant groups, e.g. the "A. wilhelmiana group" (Maslin 1990), A. marayana (1-nerved phyllodes) - A. praelongata (plurinerved phyllodes) and the "A. paradusa group" (where A. aspera, A. ausfeldii, A. dodoniifolia, A. leprosa, A. paradusa and A. rheiinocarpa all have 1-nerved phylldodes whereas A. cognata, A. glandulicarpa, A. howittii, A. montana, A. subporosa and A. verniciflua all have more than 1-nerved phyllodes). Also, diaphyllodinous species such as A. basedowii, A. diaphyllodinea, A. leptospermoideis, etc. (fide Maslin 1978 and Vassal and Maslin 1979) are anomalous in having horizontally flattened phyllodes that are 1-nerved adaxially and 3-nerved abaxially.

(f) Section Plurinerves (212 species) is discussed under section Juliflorae below.

(g) Section Juliflorae (235 species). A number of recent studies have suggested that this section is closely related to section Plurinerves, fide Tindale and Roux 1969 and 1974, Vassal 1972, Pettigrew and Watson 1975 and Tindale 1980. Indeed, in his most recent classification Pedley (1986) combined the two groups under Racusperma section Plurinerves (see Table 1 of Maslin 1988 and Chappill and Maslin 1995). However, the immunology study by Brain and Maslin (in press) in part at least challenges this view. Their results suggest that while section Plurinerves seems to be very coherent, doubt is cast on section Juliflorae as a natural group. One subgroup of species within section Juliflorae showed strong affinities with species of section Plurinerves the other subgroup (surprisingly) showed affinities with certain non-racemose species of section Phyllodineae.

These two sections are widespread in Australia and show similar geographic patterns; however, there are differences, the most important being that section Plurinerves has fewer species north of the Tropic of Capricorn and more species in inland areas of south-eastern Australia. About 20 species from these two sections occur outside Australian – see Pedley 1973 for review. Note. Subsequent to Pedley's work another two extra-Australian species referable to section Juliflorae have come to light, namely, A. pubirachis (occurs in northern Australia and in
Papua New Guinea) and a seemingly new species (allied to *A. cowleana*) endemic to the Indonesian Island of Wetar and which was noted by Nielsen (1992) under *A. leptocarpa*.

Future classifications will need to determine appropriate infrasectional categories for species encompassed by the combined sections Juliflorae and Plurinerves, and it appears that phylloide nervation will prove important in this work. In general terms these plurinerved species can be conveniently grouped according to the number and relative spacing of nerves on their phylloides. This method was adopted by Pedley (1987a), Maslin and Pedley (1988) and Cowan and Maslin (1990) where the following main trends were recognized:

1. **Microneurous phylloides.** Phylloides with numerous, very fine, closely approximating longitudinal nerves without anastomoses between them, e.g. *A. aneura*, *A. lastocaulys*, *A. tumida*, etc. (section Juliflorae), *A. calcicola*, *A. coriacea*, *A. pendula*, etc. (section Plurinerves).

2. **Oligoneurous phylloides.** Phylloides with only a few, distant longitudinal nerves. Within this pattern of nervation two subgroups can be recognized:

   (i) anastomoses absent or few between the main longitudinal nerves, e.g. *A. encinophylla*, *A. jibberdingensis* (section Juliflorae, there are relatively few species of this section with this pattern), *A. cochlearis*, *A. confusa*, *A. complanata*, *A. elongata*, etc. (section Plurinerves).

   (ii) anastomoses numerous between the main longitudinal nerves, e.g. *A. crassita*, *A. dimidiata*, *A. holosericea* (section Juliflorae), *A. tiophylla*, *A. koa* (from Hawaii), *A. melanoxylon*, *A. platycarpa*, etc. (section Plurinerves).

This system is primarily a mnemonic device for informally arranging species within this large group, nevertheless recent studies have recognized a number of species-groups within these broad categorizations, e.g. the *A. holosericea* group (Maslin and Thomson 1992: Group 2ii), the "*A. cunninghamii*" group (Pedley 1974: Group 2ii), the *A. verrucula* and *A. flavipila* groups (Cowan and Maslin 1990: Group 2ii), the *A. aneura* group (Randell 1992: Group 1) and the *A. multilineata* group (Cowan and Maslin 1990b: Group 1). However, there are some taxa that cannot be readily ascribed to any of the above groups, e.g. the *A. deltoidea* group (from Pedley 1987c and Cowan and Maslin 1990a).

Apart from phylloide nervation some groups are defined primarily by their carpological and/or inflorescence characters. For example species of the *A. stigmaphylla* group (Tindale 1980) have very distinctive pods (not unlike those of *Callistemon* spp.) while those of the *A. longifolia* group (i.e. Bentham's series Juliflorae subspecies Tetramerae and series Pungentes subspecies Spicae pro parte) are united by their 4-merous flowers (see Pedley 1964). Species from the latter group possess phylloides that fall into a number of the categories outlined above (or they may even have l-nerved phylloides as in species of section Phylloideae, e.g. *A. verticillata*).

**CONCLUSION**

This synoptic survey has indicated a number of critical problem areas in *Acacia* taxonomy. By a careful resolution across a wide range of critical species it will be possible to come to a more meaningful natural classification of this large important genus.
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REFERENCES


**Appendix 1** List of "critical species" recommended for use in comparative studies on the generic status of *Acacia*. See Appendix 2 for alphabetic listing of the species given here.

**FAIDHERBIA**

*F. albida* (Africa)

**ACACIA**

1. SUBGENUS ACACIA

   (GROUP I)

   a. *A. anegadensis* or *A.daemon* (New World)
   b. *A. bisulcata* or *A. pringleii* or *A. rigidula* (New World)
   c. *A. bidwillii* (Australia)
   d. *A. caven* or *A. farnesianna* or *A. schaffnerii* (New World) and/or *A. erioloba* or *A. haematoxylon* (Africa).
   e. *A. choriophylla*
f. A. cochlicantha or A. macracantha or A. pennatula and A. collinsii or A. cookii or A. cornigera (New World)
g. A. constricta or A. glandulifera or A. neovernicosa or A. schottii (New World)
h. A. craibii or A. inopinata (Asia)
i. A. dolichocephala (Africa)
j. A. drepanolobium (Africa)
k. A. harmandiana or A. leucopholea (Asia)
l. A. karroo or A. seyal (Africa)
m. A. nilotica (Africa, Asia)
n. A. pacensis (New World)
o. A. sphaerocephala (New World)
p. A. tortilis (Africa)

2. SUBGENUS ACULEIFERUM

A. Section Aculeiferum

(a) A. caffra or A. goezei or A. nigrescent (Africa)
b. A. catechu (India)
c. A. melifera (Africa)
d. A. modesta (India)
e. A. senegal (Africa, India)

B. Section Monacanthea

(a) A. acapulcensis or A. bonariensis or A. hayesii or A. riparia and/or A. tenufolia (New World)
b. A. acathensis or A. centralis or A. coulteri or A. mammifera or A. usumacintensis (New World)
c. A. amazonica or A. kuhlmannii or A. lacerans or A. velutina (New World)
d. A. anisophylla or A. roemeriana (New World)
e. A. articulata or A. bahiensis (New World)
f. A. berlandieri and/or A. subangulata (New World)
g. brevipica (Africa) or A. megaladena (Asia) or A. pennata (Asia) or A. schweinfurthii (Africa)
h. A. donnaiensis (New World)
i. A. eriocarpa (Africa)
j. A. glomerosa or A. purpursii (New World)
k. A. Greggii and/or A. wrighitii (New World)
l. A. thailandica (Asia)
m. A. willardiana (New World)

C. Section Filicinace

(a) A. angustissima or A. boliviana (New World)
b. A. sosae or A. tequiliana (New World)
c. A. villosa (New World)
d. A. velue (New World)

D. Section ?

(a) A. ataxacantha (Africa)
b. A. furcata (New World)
c. *A. muricata* (New World)
d. *A. visco* (New World)

3. **Subgenus Phylloideae** (Australian species unless otherwise indicated)

A. **Section Botrycephalae** *(GROUP 6)*
   a. *A. baileyana* or *A. dealbata*
   b. *A. chrysotheca*
   c. *A. cardiphylla* or *A. leucocladia*
   d. *A. decurrens* or *A. irrorata* or *A. mearnsi* or *A. parramattensis*
   e. *A. leptocladia* and/or *A. mitchelii*
   f. *A. silvestris* or *A. filicifolia*
   g. *A. schinoides* or *A. pruinosus* or *A. spectabilis*
   h. *A. elata*

B. **Section Pulchellae** *(GROUP 7)*
   a. *A. browniana* or *A. lateriticolus* or *A. pentadenia*
   b. *A. drummondii*
   c. *A. gilbertii*
   d. *A. lasiocarpa* or *A. pulchella*

C. **Section Alatae** *(an un-natural assemblage)* *(GROUP 8)*
   a. *A. alata* or *A. wilddenowiana*
   b. *A. aphylla*

D. **Section Lycopodifolii** *(GROUP 9)*
   a. *A. adoza* or *A. hippuridites* or *A. spondylophylla*

E. **Section Phylloideae** *(GROUP 10)*
   a. "Racemose species"
   a. *A. ampliceps* or *A. bivenosa* or *A. ligulata* or *A. rostellifera* or *A. sclerosperma*
   b. *A. calaminifolia* or *A. falcata* or *A. microbotrya* or *A. notabilis* or *A. retinodes* or *A. rubida* or *A. steedmanii*
   c. *A. bancroftii*
   d. *A. binervata*
   e. *A. blakelyi* or *A. scirpifolia*
   f. *A. buxifolia* or *A. cutiriformis*
   g. *A. celastriifolia* or *A. myrsifolia*
   h. *A. extensa* and/or *A. urophylla*
   i. *A. flabriata* or *A. limifolia* or *A. podalyriifolia* or *A. prominens* or *A. pyxantha* or *A. vestita*
   j. *A. fasciculata*
   k. *A. murrayana* or *A. praelongata* (phyllodes plurinerved)
   l. *A. inaequalilatis* or *A. pyrifolia*
   m. *A. synchronica* or *A. victoriae*
   n. *A. penninervis* or *A. felceformis*
   o. *A. pruinoscarpa* or *A. rafaelia*
   p. *A. suaveolens* and/or *A. hemieles* or *A. ileaphylla* or *A. praemii*
(b) "Non-racemose species" (or racemes very short)  
\begin{enumerate}[a.]  
\item A. acanthoncola or A. bidentata  
\item A. acinacea or A. flexisolia or A. lineata  
\item A. alleniana or A. junjifolia  
\item A. amblygona or A. praevisula  
\item A. andrewsi or A. barninervis  
\item A. baueri  
\item A. biflora or A. divergens  
\item A. brachyphylla or A. nitidula or A. sulcata  
\item A. brownii or A. gunni or A. ulcicifolia  
\item A. brunoioides or A. confusa or A. tindaleae  
\item A. burbridgeae or A. gniidum or A. islana or A. johnsonii  
\item A. densifera  
\item A. dictyophleba  
\item A. genistifolia and A. verticillata (sect. Juliflora)  
\item A. harniensis and/or A. rossei or A. sedifolia  
\item A. horridula or A. pyrnocephala  
\item A. insulata  
\item A. leptospermoidea  
\item A. litorea or A. truncata  
\item A. mainlandii or A. siculisformis  
\item A. merrallii or A. sericocarpa  
\item A. paradoxo (syn. A. armata) and/or A. stricta  
\item A. leprosa or A. verniciflua  
\item A. peuce  
\item A. tetragonophylla  
\item A. viscidipula or A. wilhelmiana  
\end{enumerate}  

F. Section Plurinerves  

(a) "Microneurous species"  
\begin{enumerate}[a.]  
\item A. assimilis or A. lineolata or A. rigens  
\item A. calcicola or A. cambagei or A. melvillei or A. omalophylla or A. papyrocarpa or A. pendula  
\item A. colletorioides or A. NYSSOXYLLA  
\item A. corticata  
\item A. densiflora or A. eremophila or A. Mackeyana  
\item A. owalidii  
\item A. stenophylla  
\item A. transulcens or A. naperrima  
\end{enumerate}  

(b) "Oligoneurous species"  
\begin{enumerate}[a.]  
\item A. anaticeps  
\item A. ademonogonia or A. deltoidea  
\item A. cochlearis or A. comans or A. latipes  
\item A. cognuta or A. sulporosa or A. veronica  
\item A. complanata or A. estropholiata or A. excelsa  
\item A. confusa (Taiwan, Philippines)  
\item A. consobrina or A. flavipila or A. xiiophylla  
\end{enumerate}  

\textbf{GROUP 11}
h. *A. cyclops*

i. *A. dunni* or *A. latecens* or *A. platycarpa*

j. *A. elongata*

k. *A. melanoxylon* (Australia) and *A. heterophylla* (Mascarene Islands) and/or *A. koa* (Hawaii); see Coulaud et al. (1995).

l. *A. multisiliqua* or *A. simsi*

m. *A. redolens* or *A. trineura*

n. *A. reticulata*

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**G. Section Juliflorae**

(a) **"Microneurous species"**

(GROUP 14)

a. *A. acuminata* or *A. burkittii* or *A. multispicata*

b. *A. ammobia* or *A. doratoxyylon* or *A. lastiocalyx*

c. *A. aneura* or *A. brachystachya* or *A. ramulosa* or *A. coolgardiensis*

d. *A. blaketi* or *A. burrowii* or *A. cheeli*

e. *A. cirrinoviridis* or *A. oigana* or *A. yarkrakinensis*

f. *A. cyperophylla* or *A. rhodophylla*

g. *A. ephedroides* or *A. faunaderayi* or *A. inophloia*

h. *A. eriopoda* or *A. tamida*

i. *A. gaymeri* or *A. hyaloneura* or *A. jakesiana*

j. *A. plecostarpena*

k. *A. sibberdingensis*

l. *A. kampeana* or *A. stowardii*

m. *A. zephyrophylla*

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(b) "Oligoneurous species"

(GROUP 15)

a. *A. anistocarpos* or *A. stigmatophylla*

b. *A. chisholmi* or *A. lysiophloia* or *A. monicola* (sect. Pluralvetices) or *A. trachycarpos*

c. *A. coelei* or *A. coeleana* or *A. holosericea* or *A. mangium*

d. *A. concurrens* or *A. crassa* or *A. leiocalyx* or *A. longispicata*

e. *A. demiculosa*

f. *A. longifolia* or *A. soporae*

g. *A. neurophylla*

h. *A. pachycarpa*

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**Appendix 2** An alphabetic list of taxa included in Appendix 1. The alpha-numeric designations in parentheses following species names refer to the *Acacia* subgeneric GROUP that is given in Appendix 1.

- *A. acanthoclada* (11a)
- *A. acutifolium* (3a)
- *A. aculeata* (3b)
- *A. acuminata* (11b)
- *A. acutifolia* (14a)
- *A. adenogonia* (13b)
- *A. adoxa* (9a)
- *A. alata* (8a)
- *A. alleniana* (11e)

- *A. amazonica* (3c)
- *A. amblygona* (11d)
- *A. ammobia* (14b)
- *A. amplus* (10a)
- *A. anacallinata* (14a)
- *A. anariceps* (13a)
- *A. anastrepha* (15a)
- *A. andrewsii* (11e)
- *A. anegadensis* (1a)
- *A. aneura* (14c)

- *A. angustissima* (4a)
- *A. anisephylla* (3d)
- *A. aphylloides* (8b)
- *A. amplus* (10a)
- *A. anariceps* (13a)
- *A. assimilis* (12a)
- *A. ataxacantha* (5a)
- *A. baileyana* (6a)
- *A. bancroftii* (10c)
A. barbinervis (11e)  A. consobrina (13g)  A. furcata (5b)
A. baueri (11f)  A. constricta (1g)  A. genistifolia (11n)
A. berlandieri (3f)  A. cookii (1f)  A. gigasperma (7c)
A. bidensata (11a)  A. coolgardiiens (14c)  A. glandulifera (1g)
A. bidwillii (1c)  A. coryacea (12d)  A. glomerosa (5j)
A. biflora (11g)  A. cornigera (1f)  A. gnidium (11k)
A. billerbeckii (1b)  A. couteri (3b)  A. goetzei (2a)
A. binervata (10d)  A. cowleane (15c)  A. greggii (3k)
A. bifrons (10a)  A. croa (1b)  A. gymmeri (14f)
A. blakei (14d)  A. cressa (15d)  A. haematoxylon (1d)
A. blakey (10e)  A. cultriformis (10f)  A. handonis (11b)
A. boliviana (4a)  A. cyclops (13b)  A. harmandiana (1k)
A. bonariensis (3a)  A. cyperophylla (14f)  A. hayesi (3a)
A. brachyphylla (13b)  A. daemon (1a)  A. hemiletes (10p)
A. brachystachya (11c)  A. dealbata (6a)  A. heterophylla (13k)
A. brevispica (3g)  A. decurrens (6d)  A. hippurosides (9a)
A. browniana (7a)  A. deltoidea (13b)  A. holosericea (15c)
A. brownii (11i)  A. densiflora (12e)  A. horridula (11p)
A. brunioides (11j)  A. denticulosa (15e)  A. hyaloneura (14j)
A. burhidaeae (11k)  A. dentifera (11i)  A. inaequilateralis (10l)
A. burkittii (14a)  A. dictyophleba (11m)  A. ineptifolia (14f)
A. buettelioides (10f)  A. divergens (11g)  A. ineptinata (1b)
A. burrowii (14d)  A. dolichocephala (1i)  A. insolle (11g)
A. caffra (2a)  A. dornainensis (3b)  A. irrorata (6d)
A. calafolios (10b)  A. doratosylon (14b)  A. isleana (11k)
A. calcicola (12b)  A. drepanolobium (1j)  A. iteaphylla (10p)
A. cambagei (12b)  A. drummondii (7b)  A. iteaphylla (13g)
A. cardiophylla (6c)  A. dunnii (13i)  A. jakesiana (14f)
A. catechu (2b)  A. elata (6b)  A. jibberdingensis (14k)
A. cavern (1d)  A. elongata (13j)  A. johnsonii (31k)
A. celastroides (10g)  A. estifolia (10a)  A. juncefolia (11c)
A. centralis (3b)  A. ephedroides (14g)  A. karroo (1l)
A. cheelli (14d)  A. eremophila (12e)  A. kempeana (14l)
A. chisholmii (15b)  A. eriocarpa (3i)  A. koo (13k)
A. ciliaris (1e)  A. etioloba (1d)  A. kahalmani (3e)
A. chrysanthea (6b)  A. eriopoda (14b)  A. laceras (3c)
A. citrinoviridis (14e)  A. estrophiolata (13e)  A. lasiocarpa (14b)
A. cockleartis (13e)  A. excelsa (13e)  A. lasiocarpa (7d)
A. cochlacanthus (1f)  A. extensa (10h)  A. lateriticaula (7a)
A. cognata (13d)  A. falcata (10b)  A. lateccus (13i)
A. cophi (15c)  A. fulcispora (10n)  A. latipes (13c)
A. collinsii (1f)  A. farnesiense (1d)  A. leioclados (1sh)
A. comans (13c)  A. fasciculifera (10j)  A. leprous (11w)
A. complanata (13e)  A. fauntleroyi (14g)  A. leptocladia (16d)
A. concurrens (15d)  A. filicifolia (6f)  A. leptospermoides (11t)
A. conifera (11j)  A. fimbrifera (10i)  A. leucochlorida (6c)
A. confusa (13f)  A. flaviflora (13g)  A. leucophaeoides (1k)
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