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Classification and phylogeny of *Acacia*: a synopsis

Generic classification

Acacia is a member of tribe Acacieae within subfamily Mimosoideae of the family Leguminosae (the Pea Family). The Mimosoideae (which is sometimes treated as a distinct family, the Mimosaceae) contains about 50-60 genera that are distributed throughout tropical, subtropical and warm-temperate regions of the world (Elias 1981 and Cowan 1998). Tribe Acacieae contains just two genera, the large cosmopolitan genus Acacia (containing about 1380 species, rendering it the largest genus within the Mimosoideae) and the monotypic genus Faidherbia that occurs in Africa and the Middle East. (Note: Faidherbia is sometimes classified as a member of the closely related tribe Ingeae, see Polhill 1994; additional information on the classification and phylogeny of Faidherbia is given in Maslin & Stirton 1997 and Maslin et al. 2003). As summarized by Maslin et al. (2003) many uncertainties exist not only with the status of tribe Acacieae, especially in relation to tribe Ingeae and to a lesser extent tribe Mimoseae, but also with the definition, classification and phylogeny of Acacia itself. A cladistic analysis of the Mimosoideae based on characters of morphology, pollen, chemistry and anatomy is provided in Chappill & Maslin (1995) and cladistic analyses based on a synthesis of chloroplast DNA sequence data is provided by Luckow et al. (in press).

Recent studies of the phylogeny and generic status of Acacia using cladistic analyses of morphological and chloroplast DNA sequence data have been especially informative in developing a better understanding of the group. Of particular relevance are papers by Chappill & Maslin (1995), Grimes (1999), Robinson & Harris (2000), Miller & Bayer (2000, 2001 and 2003) and Luckow et al. (in press). These new data clearly show that the genus as presently defined (i.e. Acacia sens. lat.) is not monophyletic and most likely will be split into a number of separate genera at some future date (see Maslin et al. 2003 for summary). However, it is not entirely certain at present how many genera will be recognized, or indeed, what names will be applied to at least some of them.

The <u>classification history of Acacia and nomenclatural implications</u> associated with splitting the genus is given elsewhere on WorldWideWattle; a simplified version of these issues, and in particular, the nomenclatural impacts, is also given.

The following synopsis outlines the current higher-order classification of the Acacia.

The circumscription of Acacia has been relatively stable since about the mid-19th century, following a series of papers between 1842 and 1875 by the British botanist, George Bentham. The genus was first described by Philip Miller in 1754 and until 1842, when Bentham clearly defined it's limits (by restricting the name Acacia to Mimosoid plants having numerous free stamens), a number of species which are now referable to genera within tribes Ingeae and Mimoseae, had been referred to it. In 1875 Bentham published his final (worldwide) classification of Acacia and this remained in place for about 100 years. The first major rearrangement of Bentham's scheme was undertaken by the French botanist, Jacques Vassal in 1972. Vassal divided Acacia into three subgenera, Acacia, Aculeiferum and Heterophyllum (=Phyllodineae), and this work assisted in providing the conceptual framework for Pedley's (1986) formal split of the genus into three genera. Initially Pedley (1978) viewed Acacia as comprising three large subgenera, as Vassal had done previously. However, in 1986 Pedley raised the rank of these groups to that of genus, Acacia, Senegalia and Racosperma respectively. Although it was generally accepted at the time that Acacia

comprised a number of disparate groups, Pedley's proposal was not widely adopted by the botanical community. Of primary concern was the widespread nomenclatural disruption that would ensue from splitting this enormous cosmopolitan genus. It was considered that more comprehensive information was needed in order to make informed decisions, and in particular, the need for broad-based comparative studies of *Acacia* that included genera from tribes *Ingeae* and *Mimoseae* was identified. Discussion of the reasons for not accepting Pedley's generic classification are outlined in Maslin (1987 and 1988, the latter paper was reproduced in 1989). Pedley published a defence of his scheme in 1987 and 1989.

Since 1986 there has been an accumulation of much new data derived from both morphological and molecular genetic studies, and this has led to a better understanding of the classification and phylogeny of *Acacia*. A summary of these new data is given in Maslin et al. (2003). This new work has confirmed that subg. *Acacia* and subg. *Phyllodineae* are monophyletic, however, subg. *Aculeiferum* is not monophyletic. Maslin et al. (2003) recognize three monophyletic assemblages within this last subgenus and suggest that at least five genera can be recoginzed within *Acacia sens. lat.* (species included in each of these genera are shown elsewhere on WorldWideWattle):

- 1. Acacia^A (based on Acacia subgenus Acacia; a pantropical group containing about 163 species).
- 2. Senegalia sens. str. (based on Acacia subgenus Aculeiferum; a pantropical group containing 203 species).
- 3. Acaciella (based on Acacia subg. Aculeiferum section Filicinae; a group of 15 species confined to the Americas).
- 4. *Genus x* (an undescribed genus based on a group of 13 species related to *Acacia coulteri*; confined to the Americas).
- 5. Racosperma^A (based on Acacia subgenus Phyllodineae; a group largely confined to Australia and containing 987 species).

AThe names Acacia and Racosperma as used here (and in Table 1) are those that would apply under the provisions of the International Code of Botanical Nomenclatrue by the application of currently designated types for these two genera. However, a proposal to retypify Acacia is currently in progress (Maslin & Orchard 2003) and if successful the following name changes would occur: Racosperma would be called Acacia and Acacia would be called Vachellia.

The classifications of Bentham (1875), Vassal (1972), Pedley (1978 and 1986) and Maslin et al. (2003) are shown in Table 1.

Table 1. Main classifications of Acacia from Bentham (1875) to Maslin et al. (2003).

Bentham (1875)	Vassal (1972)	Pedley (1978)	Pedley (1986)	Maslin <i>et al.</i> (2003)
ACACIA	ACACIA	ACACIA	ACACIA	ACACIA
Ser Gummiferae	Subg Acacia	Subg Acacia		
Ser Vulgares	Subg Aculeiferum	Subg	SENEGALIA	
Ser Filicinae	Sec Monacanthea	Aculeiferum	Sec Senegalia	SENEGALIA
	Sec Aculeiferum	Sec Spiciflorae	Sec Filicinae	ACACIELLA
	Sec Filicinae ¹	Sec Filicinae		GENUS X ⁴

Bentham (1875)	Vassal (1972)	Pedley (1978)	Pedley (1986)	Maslin e <i>t al.</i> (2003)
Ser Botrycephalae Ser Phyllodineae Subser Uninerves Subser Continuae Subser Alatae Subser Pungentes	Subg Phyllodineae (syn. Subg Heterophyllum) Sec Uninervea	Subg Phyllodineae Sec Botrycephalae Sec Phyllodineae Sec Alatae	RACOSPERMA Sec Racosperma	RACOSPERMA
Subser Calamiformes Subser Plurinerves	Sec Heterophyllum	Sec Plurinerves Sec Juliflorae	Sec Plurinervia	
Subser Juliflorae Subser Brunioideae ² Ser Pulchellae	Sec Pulchelloidea ³	Sec Lycopodiifoliae Sec Pulchellae	Sec Lycopodiifolia Sec Pulchella	

Note: Sec = Section, Ser = Series, Sser = Subseries, Sg = Subgenus

Classification of Australian Acacias of subgenus Phyllodineae

Acacia is the largest genus of vascular plants in Australia and a majority of the 975 described, accepted species are contained in subgenus *Phyllodineae*. There are only 19 species of the subgenus (contained in sections *Juliflorae* and *Plurinerves*) that occur outside the continent and these are found in Pacific region (east to Hawaii), Asia (north to the Phillipines) and on Madagascar and the Mascarene Islands in the Indian Ocean off the east coast of Africa. Except for *A. pubirhachis* which occurs in New Guinea these extra-Australian species are discussed in Pedley (1975).

All recent cladistic studies based on both molecular and morphological data support subgenus *Phyllodineae* as monophyletic (Chappill & Maslin 1995, Miller & Bayer 2000 and 2001 and Robinson & Harris 2000). Although the phylogenetic relationships of the subordinate groups within the subgenus have not yet been satisfactorily resolved (see <u>Maslin et al. 2003</u> for discussion) it is expected that on-going nuclear and chloroplast DNA studies will ultimately provide data to enable the construction of a meaningful classification

¹Formalized in Guinet and Vassal (1978)

²The type of subseries *Brunioideae* is referable to sec *Phyllodineae*, however, most taxa that Bentham included in this group are referable to sec *Lycopodiifoliae*; none of these species was included in Vassal's classification.

³Section *Pulchelloidea* included species from Bentham Subseries *Pulchellae*, *Alatae*, *Continuae*, *Calamiformes*, *Plurinerves* and *Uninerves*.

⁴An undescribed genus based on the species of the Acacia coulteri group (see Jawad et al. 2000).

of this group, one which is phylogetically based and which will accommodate the species in a hierarchial system containing an appropriate number of lower-order categories.

Currently the most generally used classification of subgenus *Phyllodineae* is that of Pedley (1978) in which seven sections are recognized, namely, section *Alatae*, *Botrycephalae*, *Juliflorae*, *Lycopodiifoliae*, *Phyllodineae*, *Plurinerves* and *Pulchellae* (<u>Table 1</u>). As discussed by Maslin (2001) this scheme represents a pragmatic attempt at rationalizing earlier classifications by Bentham (1842, 1864, 1875) and Vassal (1972), and offers a reasonably convenient way of arranging species into higher-order groups, but not all species are well-accommodated by these sections. Nevertheless, this scheme is a useful framework for the present discussions.

Recent cladistic, molecular and morphological studies suggest that, with the possible exception of the relatively small sections *Lycopodiifoliae* and *Pulchellae*, the sections of subgenus *Phyllodineae* (which contain about 95% of the species) are either paraphyletic or polyphyletic. Nevertheless, these studies and a range of other investigations conducted over the past few decades do reveal that some general phylogenetic trends are beginning to emerge (see <u>Maslin et al. 2003</u> for discussion). The more significant of these are noted in the following paragraphs (further details are given in the sectional discussions below).

- 1. The general trend in the recent morphological and DNA studies is for certain 'uninerved' phyllode-bearing species with elongated racemose inflorescences from section *Phyllodineae* (together with the bipinnate-leaved species of section *Botrycephalae*) to form a terminal monophyletic group, with the plurinerved species of sections *Plurinerves* and *Juliflorae* forming a series of basal paraphyletic groups. The close relationship between these racemose species of section *Phyllodineae* and species of section *Botrycephalae* has been noted by several authors (e.g. Tindale & Roux 1969 and 1974, Vassal 1972 and Pettigrew & Watson 1975, Chappill & Maslin 1995, Brain & Maslin 1996, Miller & Bayer 2001).
- 2. Among the phyllode-bearing species there appears to be some sort of taxonomic discontinuity between at least certain 'uninerved' species of section Phyllodineae and the 'plurinerved' species of sections Plurinerves and Juliflorae. The classifications of Vassal (1972) and Pedley (1986) embody these affinities and there is some support for them in the results of recent studies involving morphology (Chappill & Maslin 1995) and DNA sequence data (Murphy et al. 2000, Miller & Bayer 2001, Miller et al. in press). Interestingly, however, the serological evidence of Brain & Maslin (1996) not only failed to support this 'uninerved' vs 'plurinerved' distinction but also suggested a positive relationship between certain non-racemose species of section Phyllodineae and species from sections Plurinerves and Juliflorae (see below). Clearly, much more study is needed to elucidate relationships between these higher-order groups within subgenus Phyllodineae. There are, for example, some "natural" groups which contain both uninerved and plurinerved species, e.g. the "A. wilhelmiana group" (Maslin 1990), A. murrayana (1-nerved phyllodes) - A. praelongata (plurinerved phyllodes) and the "A. paradoxa group" (where A. aspera, A. ausfeldii, A. dodonaeifolia, A. leprosa, A. paradoxa and A. rhetinocarpa have 1-nerved phyllodes whereas A. cognata, A. glandulicarpa, A. howittii, A. montanta, A. subporosa and A. verniciflua have plurinerved phyllodes). Also, diaphyllodinous species such as A. basedowii, A. diaphyllodinea, A. leptospermoides, etc. (see Maslin 1978 and Vassal & Maslin 1979) are anomalous in having phyllodes that are 1-nerved adaxially and 3-nerved abaxially.
- 3. Among the plurinerved species there are examples of close relationships between species currently placed in section *Juliflorae* (inflorescences spicate) and section *Plurinerves* (inflorescences globular), for example, members of the *A. stigmatophylla* group (Tindale 1980); see also below under section *Plurinerves*. Additionally there are a number of species where the inflorescence shape is intermediate between a globular head and a cylindrical spike, e.g. species allied to *A. filifolia* (Chapman & Maslin 1999). This is not surprising because, as noted by Chappill & Maslin (1995), head shape is a plesiomorphic character in *Acacia*.

The serological investigation of subgenus *Phyllodineae* by Brain & Maslin (1996) revealed some higher-order patterns of relationships which were unexpected and which are at variance with established classifications. As already noted this study was not able to demonstrate a clear division between the uninerved species of section *Phyllodineae* and the plurinerved species of sections *Juliflorae* and *Plurinerves*. Furthermore, the serological evidence suggested that section *Phyllodineae* comprises two

reasonably coherent subgroups, namely, species with elongated racemose inflorescences and those with non-racemose (or rudimentary racemose) inflorescences, and surprisingly there was no sign of a close relationship between the two subgroups. The non-racemose species of section *Phyllodineae* unexpectedly showed affinities with certain species currently included in sections *Plurinerves* and *Juliflorae*. If these relationships as indicated by the serological data are valid, then a major re-appraisal of the classification of subgenus *Phyllodineae* is needed.

Sections of Subgenus Phyllodineae

Section Plurinerves (216 described, accepted species). This large and diverse group contains species characterized by having plurinerved phyllodes and globular flower heads that are arranged in either simple or racemose inflorescences. Species of section *Plurinerves* are <u>widespread in Australia</u> with the main centres of richness located in the inland areas of the southwest and southeast of the continent (Hnatiuk & Maslin 1988, Maslin & Pedley 1988).

A number of studies have suggested that section *Plurinerves* is related to section *Juliflorae* (see Tindale & Roux 1969 and 1974, Vassal 1972, Pettigrew & Watson 1975 and Tindale 1980) and indeed, in his most recent classification Pedley (1986) combined the two groups under *Racosperma* section *Plurinerves*. However, the cladistic analysis of Chappill & Maslin (1995) found that this group (i.e. the combined sections *Plurinerves* and *Juliflorae*) to be paraphyletic and that inflorescence shape, which has traditionally been used to separate the sections, was highly homoplastic. The results of recent molecular analyses by Miller & Bayer (2000, 2001), Murphy *et al.* (2000) and Miller *et al.* (in press) also show this group as paraphyletic. None of the above studies support section *Plurinerves* or section *Juliflorae* as monophyletic. The serological data of Brain & Maslin (1996) suggest a similar conclusion except that these authors did find some support for recognizing at least part of section *Plurinerves* as a 'natural' group. To resolve phylogenetic relationships involving these two sections more species need to be included in the on-going genetic investigations. Furthermore, elucidation of the complex variation patterns will be facilitated by developing a better understanding of phyllode nervature patterns.

In the absence of an effective infra-sectional classification of section *Plurinerves* a convenient (and somewhat natural) way of arranging the species is to group them according to their inflorescence structure (i.e. simple or racemose) and phyllode nervature (i.e. the number of longitudinal nerves, their spacing and whether or not intervening anastomosing secondary nerves are developed). Using these phyllode attributes, Pedley (1987a), Maslin & Pedley (1988) and Cowan & Maslin (1990a) recognized the following main nervation trends that apply to both section *Plurinerves* and section *Juliflorae* (however, not all species of the two sections can be conveniently accommodated within the groups that were defined):

- A. Phyllodes with numerous, very fine, close, longitudinal nerves without anastomoses between them (i.e. microneurous nervation).
- B. Phyllodes with few, widely-spaced longitudinal nerves (usually 3 nerves per face when phyllodes are flat, or 8-nerved in all when not flat); within this pattern two subgroups can be recognized.
 - $i. \ An astomoses \ absent \ or \ few \ between \ the \ main \ longitudinal \ nerves.$
 - ii. Anastomoses numerous between the main longitudinal (i.e. phyllodes reticulately veined).

The phyllode shape is moderately conservative, however they do vary from flat to terete/quadrangular. Notes on species groups within section *Plurinerves* are provided by <u>Maslin & Stirton</u> (1997).

View some examples of section Plurinerves taxa: <u>A. dunnii</u>, <u>A. resinistipulea</u>, <u>A. resinosa</u>.

Section Juliflorae (255 described, accepted species). This large and diverse group contains species characterized by having plurinerved phyllodes and cylindrical flower heads that are arranged in either

simple or racemose inflorescences. Species of section *Juliflorae* are <u>widespread in Australia</u> with the main centres of species richness occurring in the north, northwest and southwest of the continent and secondary centres of richness located along the Great Dividing Range in eastern Australia; although plants of this group often form a conspicuous element of the Arid Zone flora, species numbers in these areas are generally not great (Hnatiuk & Maslin 1988, Maslin & Pedley 1988). This geographic pattern is similar to that of section *Plurinerves*, however, there are differences between the two group. The most important of these being that section *Plurinerves* has fewer species north of the Tropic of Capricorn and more species in inland areas of south-eastern Australia (see Hnatiuk & Maslin 1988); a few species of both sections occur outside Australia (Pedley 1975).

As already noted above section *Plurinerves* is more closely related to section *Juliflorae* than either is to section *Phyllodineae*. The precise nature of this relationship is as yet unresolved, however, it is not likely that either section, or the two sections combined, are monophyletic. Traditionally section *Juliflorae* and *Plurinerves* are separated on the basis of the shape of their inflorescences, cylindrical in the former and globular the latter section, however, Chappill & Maslin (1995) found this to be a highly homoplastic character.

Currently there is no effective classification of species included in section *Juliflorae*. However, as with section *Plurinerves* phyllode nervature is helpful arranging species into groups. Inflorescence structure is less important for grouping the species than it is in section *Plurinerves*, however, details of the flower (especially the degree of calyx division) and pod morphology are useful attributes. The phyllode shape is moderately conservative, however they do vary from flat to terete/quadrangular. Notes on species groups within section *Juliflorae* are provided by Maslin & Stirton (1997).

View some examples of section Juliflorae taxa: <u>A. cowleana</u>, <u>A. elachantha</u>, <u>A. neurophylla subsp. erugata</u>, <u>A. stereophylla subsp. stereophylla</u>, <u>A. hilliana</u>.

Section Phyllodineae(397 described, accepted species). This is the largest group within subgenus *Phyllodineae*. The species are recognized by their '1-nerved' phyllodes and their normally globular flower heads arranged in either simple or racemose inflorescences. The section is <u>widespread in Australia</u> with the most species-rich areas occurring in southwest Western Australia and south of the Tropic of Capricorn in the temperate and adjacent semiarid areas of eastern and south-eastern Australia; the section is poorly represented in the Arid Zone and virtually absent from the tropical north of the continent (Hnatiuk & Maslin 1988, Maslin & Pedley 1988). There are no indigenous species of section *Phyllodineae* that occur outside Australia.

In the absence of an effective classification of species within section *Phyllodineae* a convenient (albeit somewhat oversimplified) way to arrange them is to divide them into two groups based on inflorescence structure, namely, racemose vs non-racemose. Serological evidence presented by Brain & Maslin (1996) suggest that fundamental differences exist not only between these two groups, but also between species-complexes within each group. These results are supported by recent molecular evidence by Miller & Bayer (2000, 2001), Murphy et al. (2000) and Miller *et al.* (in press). These studies tend to negate the assertion of Chappill & Maslin (1995) that section *Phyllodineae* is monophyletic. Furthermore, the results of the Brain & Maslin (1996) study (surprisingly) suggested that that some of the non-racemose species of section *Phyllodineae* have their greatest affinities with plurinerved species of sections *Juliflorae* and *Plurinerves*.

Although Bentham (1864) recognized six subseries within his series Uninerves (= section Phyllodineae) these are largely artifical groups and are generally not adopted by modern workers. The phyllodes on species of section *Phyllodineae* are more variable than those of sections *Juliflorae* and *Plurinerves*; they vary from flat to terete/quadrangular and sometimes display rather bizarre shapes (especially in southwest

Western Australia). Notes on species groups within section *Phyllodineae* are provided by <u>Maslin & Stirton</u> (1997).

View some examples of section Phyllodineae taxa: A. delphina, A. inaequilatera, A. suaveolens.

Section Botrycephalae (40 described, accepted species). This group comprises mostly arborescent species that are characterized by having bipinnate adult foliage and normally elongated racemose inflorescences; it predominates in temperate areas of <u>eastern and southeastern Australia</u> (Hnatiuk & Maslin 1988, Maslin & Pedley 1988). As discussed above there is a considerable body of evidence that shows a close relationship exists between section *Botrycephalae* and certain phyllodinous species (possessing racemose inflorescences) from section *Phyllodineae*.

Relationships between species currently ascribed to section Botrycephalae have not yet been fully elucidated, however, based on chemical data a number of subgroups have been recognized. Studies by Tindale and Roux (1969) of flavonoid and condensed-tannin contents of the heartwood and bark from I8 species recognized the following species-groups: (1) A. constablei, A. decurrens, A. irrorata subsp. velutinella, A. mearnsii, A. parramattensis and A. trachyphloia; (2) A. filicifolia, A. irrorata and A. silvestris; (3) A. botrycephala, A. cardiophylla, A. chrysotricha, A. leucoclada subsp. argentifolia and A. oshanesii; (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 Botrycephalae be divided into two distinct groups. Group A included six taxa (A. deanei and A. deanei subsp. paucijuga, A. irrorata subsp. irrorata, A. parramattensis, A. parvipinnula and A. trachyphloia) which differed greatly in their gum composition from the phyllodinous species of Bentham's (1864) "Division" Phyllodineae; Group B also contained six taxa (A. dealbata subsp. dealbata and subsp. subalpina, A. filicifolia, A. leucoclada, A. silvestris and A. terminalis) but these showed a strong chemical resemblance to the phyllodinous taxa examined. Pedley (1986) suggested that perhaps A. leptoclada and A. mitchellii might constitute a third group. Acacia mitchellii, which differs from all other species of Botrycephalae in having non-racemose inflorescences, was excluded from section Pulchellae by Guinet et al. (1980).

View some examples of section Botrycephalae taxa: A. parramattensis, A. mearnsii.

Section Alatae (c. 23 described, accepted species). Although Pedley (1978) recognized this section, it is a polyphyletic assemblage (Chappill & Maslin 1995, Murphy *et al.* 2000) and is unlikely to be recognized in future classifications. The decurrent phyllodes which define this group were interpreted by Chappill & Maslin (1995) as a highly homoplastic feature.

View some examples of section Alatae taxa: A. alata var. alata, A. continua.

Section Lycopodiifoliae (18 described, accepted species). This distinctive group is characterized by having whorled phyllodes and is found in the <u>Arid Zone and in northern areas</u> of the continent (see Hnatiuk & Maslin 1988 and Maslin & Pedley 1988).

Section *Lycopodiifoliae* probably constitutes a monophyletic group (Murphy *et al.* 2000) but its relationship to the rest of subgenus *Phyllodineae* is not clear. Pedley (1987a) and Cowan & Maslin (1990) suggested affinities *A. deltoidea* and its allies (section *Plurinerves*) and this relationship warrants further investigation. The monophyletic group recognized by Murphy *et al.* (2000) containing species of section *Lycopodiifoliae* and section *Pulchelloidea* (Vassal 1972) is difficult to reconcile based on morphological criteria. The character of verticillate phyllodes which characterizes this section has arisen independently in a number of unrelated groups of *Acacia*, e.g. *A. cedroides* and *A. verticillata*.

View some examples of section Lycopodiifoliae taxa: A. adoxa var. adoxa, A. spondylophylla.

Section Pulchellae (26 described, accepted species). This group of bipinnate-leaved species is endemic in south-west Western Australia (see Hnatiuk & Maslin 1988 and Maslin & Pedley 1988). This section is reviewed by Maslin (1975, 1979) and as discussed by Guinet et al. (1980) it comprises a "core" of interrelated species centered around A. pulchella, A. browniana and A. drummondii. Some of these species, together with certain phyllodinous taxa, were included by Vassal (1972) in his section Pulchelloidea. Although section Pulchelloidea was not supported by Pettigrew & Watson (1975) there is recent molecular evidence by Murphy et al. (2000) which suggests that it warrants further investigation. As already noted, however, the inclusion by Murphy et al. (2000) of species referable to section Pulchelloidea and section Lycopodiifoliae in the one monophyletic group is difficult to reconcile by morphological criteria.

View some examples of section Pulchellae taxa: A. drummondii subsp. drummondii, A. pulchella var. reflexa.

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