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ANALYSIS OF GENERIC RELATIONSHIPS IN ANACARDIACEAE

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SUMMARY

Cladistic analyses were undertaken of Anacardiaceae using non-sequence data (30 genera and 81 characters from morphology, anatomy, palynology and chemotaxonomy), sequence data (26 genera – *rbc*L) and a combined dataset of 16 genera. All analyses supported a group of genera which can be recognised at the subfamily level: Anacardioideae. Sequence data and combined datasets supported the recognition of a second subfamily: Spondiadioideae Kunth emend. Wannan. Both datasets also suggested that *Buchanania* lies outside both subfamily groups.

Key words: Anacardiaceae, cladistics, phylogeny, *rbc*L sequence data.

INTRODUCTION

The Anacardiaceae is a well recognised world-wide family of mostly tropical trees which has historically been placed in the Sapindales or Rutales (Bentham & Hooker, 1862; Takhtajan, 1980; Dahlgren 1980, 1983, 1989; Cronquist, 1981; Angiosperm Phylogeny Group, 1998; Judd et al., 1999). Cronquist (1981) placed it with the Julianiaceae and Burseraceae, the three being the only families in the Sapindales with biflavonyls and vertical intercellular secretory canals in the primary and secondary phloem. The close relationships of the Anacardiaceae and Burseraceae have been recently reiterated by analysis of *rbc*L and *atpB* sequence data (Gadek et al., 1996; Savolainen et al., 2000a). The Burseraceae are distinguished by having two epitropous ovules per locule, in contrast to the one apotropous ovule in the Anacardiaceae. The Burseraceae also frequently possess lobed cotyledons in contrast to entire cotyledons in the Anacardiaceae. *Amphipterygium* and *Orthopterygium*, once a separate family (Julianiaceae), are now considered part of the Anacardiaceae based on molecular and non-molecular data (Peterson & Fairbrothers, 1983; Wannan & Quinn, 1988, 1990, 1991; Angiosperm Phylogeny Group, 1998; Judd et al., 1999, Savolainen et al., 2000b).

The Anacardiaceae is generally considered to constitute about 70 genera and 600 species which are concentrated in the tropics of Africa, Asia and America with a smaller number of species occurring in subtropical and temperate areas. A number of infrafamilial classifications have been proposed in the Anacardiaceae (Bentham & Hooker, 1862; Marchand, 1869, 1874; Engler, 1883, 1892), but the most widely used for the last 100 years has been the five tribes of Engler (1883, 1892, 1897) which are based on floral characters and leaf dissection. A recent division of the family into five subfamilies by Takhtajan (1987) appears not to have been well accepted.

A range of systematic studies have tested the applicability of Engler's tribal classification, the most comprehensive having used stem anatomy (Jadin, 1894) or wood anatomy (Heimsch, 1942; Dadswell & Ingle, 1948; Kryn, 1953). These found support, with some reservations, for Engler's tribes. Young (1976) looked at the wood flavonoids of 16 genera of the Anacardiaceae (including Julianiaceae), in the tribes Anacardieae, Rhoeae and Spondiadeae, as well as representatives of the Burseraceae, Rutaceae, Simaroubaceae, Cneoraceae, Meliaceae, Sapindaceae, Aceraceae, Hippocastanaceae and Juglandaceae. He found that there was a range of 5-deoxyflavonoids which was restricted to the Anacardiaceae (including Julianiaceae), but there were no clear patterns at a tribal level.

More recently, Wannan & Quinn (1990, 1991) described the pericarp and floral morphology in 30 genera sampling all tribes in the family. They found that the distribution of reproductive, vegetative and secondary product character states did not closely reflect the subfamily taxonomies of either Engler (1883, 1892) or Takhtajan (1987). Rather, they found support for two informal groups, but suggested that these required further study to confirm their status. The first (Group A) included Engler's tribes Anacardieae (without *Buchanania*), Rhoeae (without *Pentaspadon* and *Campnosperma*), Dobineeae and Semecarpeae, and the second (Group B) included the Spondiadeae but with the addition of *Buchanania, Pentaspadon* and *Campnosperma*. Work by Von Teichman and associates has confirmed the importance of pericarp structure for illucidating generic affinities in the family (Von Teichman & Robbertse, 1986a, b; Von Teichman, 1987, 1990, 1991, 1992, 1993; Von Teichman & Van Wyck, 1988, 1994). Recent studies of seed anatomy (Pienaar & Von Teichman, 1998) and wood anatomy (Dong & Baas, 1993) have also provided support for Wannan & Quinn's (1991) groups.

Support for Wannan & Quinn's (1991) two informal groups has also been provided by an unpublished analysis of anatomical, morphological and *rbc*L sequence data across 17 genera (Terrazas & Chase, 1996). Their conference abstract reported two clades, broadly corresponding to Wannan & Quinn's groups. Some of their sequence data were included in a molecular analysis of the Sapindales (Gadek et al., 1996) which used 7 genera from the Anacardiaceae and three from the Burseraceae. This analysis showed the Anacardiaceae and Burseraceae as sister groups, and two main clades in the Anacardiaceae corresponding to Group A and B but with *Buchanania* diverging prior to both. Other sequence data (*rbc*L: Chayamarit, 1997) from an analysis of 16 Thai genera has also provided some support for the informal groups of Wannan & Quinn (1991), but the absence of bootstrap or decay analysis made it impossible to assess the strength of support for their clades. Recent sequence data from the internal transcribed spacer region from the ribosomal DNA has provided an indication of relationships amongst genera referred to Engler's Rhoeae or Wannan & Quinn's (1991) subgroup A2 (ITS: Miller et al., 2001). American species of *Rhus* s.s. (subgenera: *Lobadium* and *Rhus*) were shown to be closely related and more distant from other genera of the Rhoeae including *Actinocheita, Cotinus, Malosma*, *Schinus*, *Searsia* and *Toxicodendron*.

The relationships of some genera of the Rhoeae were also investigated by Aguilar-Ortigoza et al. (2004) using non-sequence data. Their main focus was on the 6 species of *Pseudosmodingium* from Mexico which were shown to be most closely related to *Bonetiella,* also from Mexico. However, the larger clade, corresponding to genera of the Rhoeae, included *Smodingium* (Africa) and Mexican representatives of *Cardenasiodendron*, *Cotinus*, *Rhus* and *Toxicodendron*. A subsequent paper by a similar team (Aguilar-Ortigoza & Sosa, 2004) combined sequence (*rbc*L) and non-sequence data for 22 genera of Anacardiaceae. Both separate datasets show good support for Wannan & Quinn's Group A (18 genera, including *Anacardium* and *Mangifera* from Engler's tribe Anacardieae) but less support for Group B (3 genera). In both analyses *Buchanania* is placed as a sister taxon to genera in Group A, but outside the clade with Group B genera. Interestingly, the paper compares the Anacardiaceae clade with a clade of hemipteran insects (*Calophya* spp.) which feed on the family; the later shows closely related species feeding on *Spondias* and *Buchanania*. A conference abstract (Pell & Urbatsch, 2001) describing analyses of sequence data from the chloroplast genome (*mat*K, *trn*L and the intergenic spacer between the *trn*L exon and *trn*F) has strongly supported the two groups of Wannan & Quinn (1991). Pell & Urbatsch (2001) reported two major clades in the family: one with members of the tribes Rhoeae, Semecarpeae, Dobineeae and Anacardieae, and the other with members of the Spondiadeae and a few members of the Rhoeae. They also reported that the Anacardiaceae proved to be monophyletic. Thus, there are some data which support the proposed infrageneric classification of Wannan & Quinn (1991). As yet, however, there has not been any broad analysis of generic relationships using the range characters which are known for the family. This paper analyses the available morphological, anatomical, chemotaxonomical, cytological, palynological characters and the available sequence data (*rbc*L) and aims to test support for the two informal subfamily groups proposed by Wannan & Quinn (1991) and identify key data gaps in the family.

METHODS

Non-sequence data

The terminal taxa used in this analysis are genera (Table 1) with characters scored from usually more than one species. The characters used are listed in Table 2 and Table 3a, b is the data matrix. A list of the autapomorphies is provided in Table 4. Many descriptions of character states were reviewed for each taxon. In a few cases where differing character states were argued in the literature, these were scored as multiple states with each source cited. In most cases, however, a single reliable authority has been cited in Table 3a, b following a critical analysis of the literature. Some unpublished data are included and are supported by vouchers in Appendices A and B.

Sequence data

Sequences for the chloroplast encoded *rbc*L gene were obtained for a subset of taxa either from GenBank or from the sources cited in Table 5. Sequences were aligned in PAUP* (Version 4.0b10; Swofford, 2002).

Analyses

Heuristic parsimony analyses were performed in PAUP* set for tree bisection reconnection branch swapping on the best trees. Multistate characters were treated as polymorphisms. Multiple replicates of random taxon addition were employed to search for multiple islands of trees, and the CONDENSE option was employed to delete duplicate trees. Support for clades was inferred using the bootstrap option in PAUP* (Felsenstein, 1985) with 500 replicates, and also by decay values (Bremer, 1988; Donoghue et al., 1992). Decay command files were created in MacClade version 4.05 (Maddison & Maddison, 2002) and executed in PAUP* using 10 replicates of random taxon addition on each constraint tree. Output trees from PAUP* were transferred to MacClade and manipulated to test other topologies and explore character state evolution.

Table 1. Genera included in analysis.

Taxon	No. of species	Natural distribution	Subfamily Group	
			Tribe[1]	Group[2]
ANACARDIACEAE				
Amphipterygium	4	Mexico	Unplaced[3]	A
Anacardium	11	Tropical America	Anacardieae	A
Astronium	13	Tropical America	Rhoeae	A
Blepharocarya	2	Australia	Rhoeae	A
Buchanania	25	Asia-Pacific, Australia	Anacardieae	B
Campnosperma	10	Tropical America, Madagascar, Seychelles, S.E. Asia, Malesia	Rhoeae	B
Cotinus	4	Temperate northern hemisphere	Rhoeae	A
Cyrtocarpa	4	Tropical America	Spondiadeae	B
Dobinea	2	Himalaya, China	Dobineeae	A
Dracontomelon	8	China, Malesia, Pacific	Spondiadeae	B
Euroschinus	6	New Caledonia, Papua New Guinea, Australia	Rhoeae	A
Harpephyllum	1	Southern Africa	Spondiadeae	B
Lannea	40	Africa, Arabia, Tropical Asia	Spondiadeae	B
Lithraea	4	South America	Rhoeae	A
Loxopterygium	4	South America	Rhoeae	A
Mangifera	35	Tropical Asia, Malesia	Anacardieae	A
Pentaspadon	6	Tropical Asia, Malesia, Pacific	Rhoeae	B
Pistacia	14	Eurasia, Malesia, Mexico, Africa	Rhoeae	A
Pleiogynium	2	Malesia, Pacific, Australia	Spondiadeae	B
Rhodosphaera	1	Australia	Rhoeae	A
Schinopsis	8	South America	Rhoeae	A
Schinus	27	South America	Rhoeae	A
Semecarpus	60	Indo-Malesia, Australia	Semecarpeae	A
Spondias[4]	8	Tropical America, Asia[4]	Spondiadeae	B
Swintonia	12	Burma, Malesia	Anacardieae	A
Tapirira	15	Tropical America	Spondiadeae	B
Toxicodendron	30	America, Indo-Malesia	Rhoeae	A
BURSERACEAE				
Bursera	c. 100	Tropical America	Bursereae[5]	
Canarium	c. 100	Africa, Malesia, Pacific, Australia	Canarieae[5]	
Garuga	4	Asia, Malesia, Pacific, Australia	Protieae[5]	

1) Engler, 1892, 1897.
2) Wannan & Quinn, 1991.
3) Not placed in any family by Engler, 1883, 1897.
4) Does not include *Solenocarpus* with representatives in Tropical Asia.
5) Leenhouts, 1955; Forman et al., 1994.

Character polarities were determined by outgroup analysis (Maddison, Donoghue & Maddison, 1984). Branch lengths were calculated using the ACCTRAN optimisation. Only unambiguous character state changes were recorded on the branches in the final figures.

Choice of taxa

Ideally terminal taxa should be species, so that both generic concepts and intergeneric relationships could be tested in the cladistic analyses. Unfortunately, nonmolecular data are not available for most of the species in the family. In fact, the full range of characters has yet to be scored for a single species. The limited data that are available have been assembled piecemeal by many workers as suitable material serendipitously has come to hand. Hence, in order to obtain a preliminary estimate of the phylogenetic signal in the available data, genera are used as the terminal taxa in the nonmolecular analysis, with the data drawn from one or more species. Genera were chosen primarily on availability of data, preferably from a number of authors. Thirty genera of Anacardiaceae are included representing all five tribes (Engler, 1892) and both informal subfamily groups (Wannan & Quinn, 1991). The outgroup for the analysis comprised three genera from the Burseraceae (*Bursera, Canarium* and *Garuga*) representing the three tribes (Leenhouts, 1955; Forman et al., 1994). The details of the genera used are provided in Table 1. Sequence data were available for representative species of only 16 of the genera included in the nonmolecular analysis (Table 5). Exemplars of three outgroups, Burseraceae, Rutaceae and Sapindaceae, were included, with trees being rooted on the last two.

Additional information is provided below for some characters (Table 2)

(5) *Leaves* – The outgroup and most Anacardiaceae have imparipinnate leaves (b). Fewer genera have simple leaves (a), though in some genera there are species with both. Paripinnate leaves (c) are very uncommon, occurring in some species of genera that possess mostly imparipinnate leaves. Bipinnate leaves occur only as polymorphic character states in *Spondias* (*S. bipinnata*; Airy Shaw & Forman, 1967) and *Bursera* (*B. bipinnata*; Porter, 1970) and have not been scored.

(9) *Inflorescence structure* – Few Anacardiaceae and Burseraceae have had their inflorescence structure analysed (sensu Briggs & Johnson, 1979; Barfod, 1988). Most descriptions do not accurately describe this character.

(10) *Flower sex* – Most genera of the Anacardiaceae, and probably Burseraceae, have unisexual flowers (b), though frequently with the aborted remnants of the other sex present. Fewer have bisexual (a) or polygamous (coded a & b) flowers. Botanists have frequently confused the sex of flowers and it is likely that the flowers of some genera which have been recorded as polygamous, and which have not been closely studied, will be found to be unisexual. In many cases the male flowers are clearly unisexual (with an aborted smaller ovary) while the female flowers appear to be bisexual but the stamens have aborted anthers which are apparent only after sectioning (Wannan & Quinn, 1992).

Table 2. Description of characters and their states.

Character number	Character	Character states
1	Habit	a = tree; b = shrub
2	Leaf duration	a = evergreen; b = deciduous
3	Leaf phyllotaxis	a = alternate; b = opposite
4	Rachis wings	a = not winged; b = winged
5	Leaves	a = simple; b = imparipinnate; c = paripinnate
6	Leaflet phyllotaxis	– = simple; a = opposite or subopposite; b = alternate
7	Leaf margin dissection	a = entire; b = dentate
8	Inflorescence position	a = terminal; b = axillary
9	Inflorescence structure	a = thyrsoid; b = panicle
10	Flower sex	a = bisexual; b = unisexual
11	Calyx number	a = 6; b = 5; c = 4; d = 3; – = absent
12	Corolla number	a = 6; b = 5; c = 4; d = 3; – = absent
13	Calyx aestivation	a = valvate; b = imbricate; – = absent
14	Corolla aestivation	a = valvate; b = imbricate; – = absent
15	Stamen number	a = 2 whorls; b = 2 whorls with antepetalous whorl reduced to staminodes; c = 1 antesepalous whorl
16	Anther orientation	a = introrse; b = extrorse
17	Nectariferous disc	a = intrastaminal; b = extrastaminal; c = absent
18	Floral axis	a = hypogynous; b = part perigynous; – = no perianth
19	Androgynophore	a = absent; b = present
20	Carpellode number	a = 5; b = 4; c = 3; d = 2; e = 1; – = bisexual flower/absent
21	Carpellode position	a = antepetalous; b = 3 arrangement; c = antesepalous; – = bisexual flower/absent
22	Carpel number (fertile or infertile)	a = 5; b = 4; c = 3; d = 2; e = 1
23	Position of fertile carpel	a = antepetalous; b = antesepalous
24	Number of locules at anthesis (fertile or infertile)	a = 5; b = 4; c = 3; d = 2; e = 1
25	Level to which carpels are connate	a = base of ovary; b = top of ovary; c = mid style; d = stigma; – = n.a. ie 1 carpel
26	Carpel definition (e.g. *Dracontomelon*)	a = present; b = absent; – = 1 carpel
27	Stylar insertion	a = ventral; b = apical; c = dorsal
28	Stigma morphology	a = *Dracontomelon*-type; b = capitate; c = spathulate; – = not as previous
29	Ovule orientation	a = apotropous; b = epitropous
30	Number of ovules per locule	a = 1; b = 2
31	Ovule insertion	a = apical; b = apico-lateral; c = latero-basal; d = basal
32	Number of ovule integuments	a = 2; b = 1
33	Microphyle orientation	a = superior; b = inferior
34	Winged fruit	a = absent; b = present
35	Postanthetic growth of hypocarp	a = absent; b = present
36	Number of seeds in fruit	a = 5; b = 4; c = 3; d = 2; e = 1
37	Operculum in fruit	a = absent; b = present
38	Thickness of fruit exocarp – no. of cells	a = 0–15; b = 16+
39	Epidermis of fruit	a = unlignified; b = lignified

40	Hypodermis of fruit	a = absent; b = parenchymatous; c = lignified
41	Mesocarp – sclereid bands associated with resin canals	a = absent; b = present
42	Mesocarp – inner parts lignified	a = absent; b = present
43	Endocarp – discrete 4th layer (outermost)	a = absent; b = parenchyma; c = sclereids
44	Endocarp – crystals in 4th layer (outermost)	a = absent; b = present
45	Endocarp – discrete 3rd layer	a = absent; b = palisade sclereids; c = sclereids; d = parenchyma
46	Endocarp – discrete 2nd layer	a = absent; b = palisade sclereids; c = sclereids; d = parenchyma
47	Endocarp – discrete 1st layer (innermost)	a = parenchyma; b = sclereids; c = palisade sclereids
48	Endocarp – 1st layer radially elongated (innermost)	a = cells not radially elongated compared to adjacent layers; b = cells $\geq$ 2 times as long
49	Embryo shape	a = straight; b = curved
50	Testa consistency	a = membranous; b = not membranous
51	Testa connection to endocarp	a = free; b = adherent; c = labyrinthine
52	Cotyledons	a = plano-convex or flat; b = lobed
53	Radicle	a = superior; b = inferior
54	Germination	a = epigeal; b = hypogeal
55	Seedling phyllotaxis	a = opposite; b = alternate
56	Seedling leaf dissection	a = imparipinnate; b = simple; c = trifoliolate
57	Seedling leaf margin	a = entire; b = serrate
58	Resin canals in phloem	a = present; b = absent
59	Resin canals in pith	a = present; b = absent
60	Resin canals in cortex	a = present; b = absent
61	Wood parenchyma-apotracheal	a = present; b = absent
62	Wood parenchyma-paratracheal	a = vasicentric and alliform/banded; b = vasicentric; c = absent
63	Wood ray width	a = 1–6 cells; b = 1–10 cells
64	Wood ray type	a = heterogeneous type IIB; b = heterogeneous type IIA; c = heterogeneous type III
65	Septate wood fibres	a = present; b = absent
66	Resin canals in wood rays	a = present; b = absent
67	Xylem vessels spirally thickened	a = present; b = absent
68	Pollen	a = *Rhus* type; b = *Pistacia* type; c = *Dobinea* type
69	Chromosome number (2n)	a = 24; b = 26; c = 28; d = 30; e = 32; f = 36; g = 40; h = 42; i = 78; j = 104; k = 22; l = 14; m = 58; n = 60
70	Butein glucoside in heartwood	a = present; b = absent
71	Sulphuretin in heartwood	a = present; b = absent
72	Sulphur glucoside in heartwood	a = present; b = absent
73	Fisetin in heartwood	a = present; b = absent
74	Fis 7-0-B glucoside in heartwood	a = present; b = absent
75	Fustin in heartwood	a = present; b = absent
76	7,3,4'trihydroxyflavone in heartwood	a = present; b = absent
77	Rengasin in heartwood	a = present; b = absent
78	Agathisflavone in leaves	a = present; b = absent
79	Amentoflavone in leaves	a = present; b = absent
80	Cupressusflavone in leaves	a = present; b = absent
81	Hinokiflavone in leaves	a = present; b = absent

(11) *Calyx number* — Most genera of the Anacardiaceae have a 5-partite calyx (b), with very few having a 6-partite (a), 4-partite (c) or 3-partite (d) calyx. Many genera are polymorphic. Only the flowers of *Amphipterygium* and female flowers of *Dobinea* and *Campylopetalum* (not in this analysis) have been interpreted as having no calyx (–). In genera with very strongly dimorphic unisexual flowers (i.e. parts absent in one sex) the number of parts has been scored from the sex in which they are present (e.g. *Dobinea*). In *Amphipterygium* the female flowers have no perianth. The male flowers are recorded as apetalous with a 5–8-partite calyx and a similar number of alternisepalous stamens (Hemsley, 1908; Hutchinson, 1959; Cronquist, 1981). Given the absence of alternisepalous stamens, and the frequent occurrence of antesepalous stamens elsewhere in the family, the perianth of the male flowers of *Amphipterygium* is here interpreted as representing a corolla. The Burseraceae are recorded with 3-, 4- or 5-partite calyces.

(12) *Corolla number* — Most genera of the Anacardiaceae have a 5-partite corolla (b), but in a few it is 6-partite (a), 4-partite (c) or 3-partite (d). Many genera are polymorphic. The Burseraceae are recorded as 3-, 4- or 5-partite. *Pistacia* has been recorded as having no corolla (–). In male flowers of *Pistacia* there is a single perianth whorl of mostly 4 (rarely 5) segments (pers. obs. on *P. chinensis*). The stamens are equal in number to, and stand opposite, the perianth segments suggesting that, as in other genera of the Anacardiaceae (e.g. *Cotinus, Semecarpus*), there is a single antesepalous whorl of stamens (and hence no corolla). This conclusion is supported by Bentham & Hooker (1862), Baillon (1878), Standley & Steyermark (1949), Rechinger (1969) and Siddiqi (1978). Payer (1857) and Eichler (1878) also considered that only the calyx is present in female flowers. The reporting of alternitepalous stamens in *P. malayana* (Hou, 1978) suggests that this character needs examination across all species attributed to this genus. In genera with strongly dimorphic unisexual flowers (i.e. parts absent in one sex) the number of parts has been scored from the flower in which parts are present (e.g. *Dobinea*).

(17) *Nectariferous disc* — Most of the outgroup and Anacardiaceae have an intrastaminal disc (a). A small number of genera have an extrastaminal disc (b) or no sign of any disc at all (c). This character can be difficult to interpret in unisexual male flowers where there are no carpellodes. However, in most cases the disc is still apparent, or the character can be scored from assessment of the sterile stamens in the female flower.

(18) *Floral axis* — The outgroup and most Anacardiaceae have an undeveloped floral axis with an hypogynous flower (a). In these, the nectariferous disc encircles the ovary with the stamens inserted on its outer edge (i.e. intrastaminal). Some genera in both families show a tendency towards perigyny (b), where the lower parts of the perianth are fused and the stamens are connate, or adnate to the fused perianth or to the disc, forming a circular column around the ovary (e.g. *Canarium, Garuga, Melanochyla, Thyrsodium*). In the Anacardiaceae, true epigyny (inferior ovary) is restricted to *Drimycarpus* and *Holigarna*, which are not included in this analysis.

(19) *Occurrence of androgynophore* — These are absent (a) from most Anacardiaceae and Burseraceae. An androgynophore (b) occurs in some species of *Mangifera, Swin-*

tonia and *Dobinea* (and also *Gluta* which is not included in this analysis). The occurrence of a gynophore has not been scored as it occurs only in *Garuga*.

(20) *Carpellode number* — Evidence of carpellodes varies considerably from well-developed carpellodes (with small locules) through to very small bulges of remnant carpellode tissue (Wannan & Quinn, 1991). Common states are those which reflect the number of carpels in the female flowers, i.e. 5 (a), 3 (c) or 1 carpellode (e). In some cases there appears to have been reduction of the vestigial carpels so much that none are evident (*Amphipterygium, Astronium, Pistacia, Rhodosphaera, Semecarpus*); this condition is scored as inapplicable (–). The character is also not applicable in bisexual flowers. This character has not been widely scored in the outgroup.

(21) *Carpellode position* — The outgroup and most Anacardiaceae often have their carpellodes reflecting the position of carpels in the female flowers: either standing opposite the petals (a), three carpellodes in a flower with a 5-partite perianth (b), or standing opposite the sepals (c). This character is not applicable (–) in bisexual flowers and in those where none are evident (as above).

(22) *Carpel number* — Ranges in the Anacardiaceae from 13 in *Pleiogynium* (an autapomorphy not coded for in this analysis) to a single carpel (e). Abortion of carpels leading to pseudomonomery is widespread in the families. This character has been inferred from the number of styles or stigmas, often with anatomical support from vascular bundles in the ovary wall and/or abortive locules (Wannan & Quinn, 1991).

(23) *Position of fertile carpel* — One of the features of the outgroup and many Anacardiaceae is that, even in multicarpellary flowers, there is only one fertile seed produced. The remaining carpels abort following anthesis or were never properly formed (Wannan & Quinn, 1991). In the outgroup and many Anacardiaceae the fertile carpel is antepetalous (a). In other Anacardiaceae the fertile carpel is antesepalous (b).

(24) *Number of locules at anthesis* — This character scores locules whether or not they are fertile and provides some indication of the degree of carpel abortion occurring during development. The greatest number of locules is in *Pleiogynium*, i.e. up to 12 (an autapomorphy not coded in this analysis); other genera have 1–5 locules.

(25) *Carpel connation* — There is a varying degree of carpel connation across the Anacardiaceae from apocarpus gynoecia in *Buchanania* (a), to genera in which the ovaries and parts of the styles are fused (c). Most genera in the Anacardiaceae have gynoecia in which the ovaries are connate and the styles free (b). The Burseraceae have almost complete connation with even the stigmas partly fused (d).

(26) *Carpel definition* — This character refers to the furrows between the individual carpels in the ovary (a) and is a feature of *Buchanania*, *Dracontomelon* and *Spondias*. Although not present (b) in most Anacardiaceae or Burseraceae it does occur widely in more distant outgroups such as the Rutaceae and Sapindaceae.

(28) *Stigma morphology* — There is a wide variety of stigma morphologies in the family but capitate or clavate stigmas (b) are the most common condition in the Anacardiaceae.

More restricted morphologies include:

- an oval opening at the top of each carpel as in *Dracontomelon* (a), which is generally characteristic of those genera in which there is good carpel definition but where the style gradually merges with the ovary, and
- spathulate (c), which appears to be a development of the capitate condition (e.g. *Amphipterygium*, *Pistacia*).

There are a number of autapomorphs which have been coded as inapplicable (–, see Table 4). The stigma morphologies of the Burseraceae are not well known. *Garuga* has a *Dracontomelon*-type of stigma (a). There has been no anatomical investigation of the crown-like angular stigma in *Canarium* that appears to be derived from the *Dracontomelon*-type. It may occur more widely in the Burseraceae.

(31) *Ovule insertion* — Robbertse et al. (1986) have suggested that the differing positions of funicle insertion on the locule wall may be related to the abortion of carpels alongside the fertile carpel (they cite *Mangifera*). While this may be true in some genera, it appears not to be the case in *Pistacia,* where on occasions there are two fertile carpels produced both with basally attached ovules (fig. 6d in Grundwag, 1976), nor in *Astronium,* where there is only a single fertile carpel (and two sterile carpels as evidenced from two other styles and stigmas) with an apically attached ovule.

(32) *Number of ovule integuments* — This character has not been widely scored. The outgroup and most Anacardiaceae have two ovule integuments (a). Much less common is one (b), and very rarely two on the outside and one on the inside (*Pistacia*). There are suggestions that a single integument has been derived from the bitegmic condition, but there is little agreement on how this may have occurred. Robbertse et al. (1986), working on *Mangifera,* have suggested that the single integument condition may be a neotonic form, but Copeland (1962) indicated that the single integument in *Anacardium* exhibited features that indicated it was the fusion product of two integuments, and Von Teichman (1990) suggested that in *Tapirira* there has been reduction of the inner integument. Hence, the single integument state may not be homologous in all taxa.

(33) *Micropyle orientation* — Micropyle orientation is upwards or superior (a) in the outgroup and most Anacardiaceae, but an inferior micropyle (b) occurs in some genera with a basally attached funicle. In *Pistacia* the micropyle is initially inferior but becomes superior during development (Marchand, 1869; Copeland, 1955). Both states were coded in this genus.

(34) *Winged fruit* — In the analysis winged fruit (b) occur only in *Loxopterygium* and *Schinopsis*. The ciliate margins in the fruit of *Blepharocarya* and the membranous margin in *Dobinea* have been interpreted as unwinged.

(35) *Postanthetic growth of hypocarp* — Occurs only in *Anacardium* and *Semecarpus* (b). The outgroup and most Anacardiaceae have no significant postanthetic growth of the perianth or floral axis (a). Postanthetic growth of the calyx occurs in *Astronium* (and also *Parishia*, not in this dataset). Postanthetic growth of the corolla occurs in *Swintonia* (and also *Gluta,* not in this dataset). These latter two conditions (calyx and corolla) were not coded as they are autapomorphs (see Table 4).

(36) *Number of seeds in fruit* — Most Anacardiaceae have a 1-seeded fruit (e). Fewer genera have 5 (a), 4 (b), 3 (c) or 2 (d) seeds. *Pleiogynium* sometimes has 12 seeds, which is double the number of parts in either perianth whorl. This autapomorphy has not been coded in this analysis.

(37) *Operculum* — This character refers to the small cap or lid which covers an opening to the locule in some of the larger heavily lignified fruits of the Anacardiaceae and Burseraceae, and which is usually dislodged during germination (Hill, 1933, 1937). Most Anacardiaceae have no operculum (a). The outgroup and some Anacardiaceae have an operculum (b) consisting of either a single piece (*Canarium, Cyrtocarpa*, *Dracontomelon, Lannea* p.p., *Pleiogynium, Spondias*) or two pieces (*Harpephyllum, Lannea* p.p.). This feature requires further study, to establish homologies especially in the Burseraceae, where there appear to be differences in splitting of the fruit at germination (Ng, 1975).

(50) *Testa consistency* — The outgroup and most Anacardiaceae have a membranous testa (a). Only some species of *Semecarpus* have a coriaceous testa that is scored as non-membranous (b). This character is uninformative for the genera in this analysis, but was scored to cite its occurrence across the family.

(51) *Testa connection to endocarp* — The outgroup and most Anacardiaceae have a testa which is free from the endocarp (a), but *Swintonia* (and species of *Bouea, Drimycarpus, Melanochyla*, *Parishia*, *Rhus* which are not in this study) have an adherent testa (b) and some *Mangifera* species have a labrynthine testa (c). This character is uninformative for the genera in this analysis, but was scored to cite its occurrence across the family.

(58) *Resin canals in the phloem* — Vertical intercellular secretory canals occur in the primary and secondary phloem (a) of all Anacardiaceae and Burseraceae. They are apparently absent (b) from all other members of the Sapindales/Rutales. This character was scored in Table 3 to confirm its occurrence across all of the genera.

(69) *Chromosome number* — There is a wide variety of chromosome number (2n) in both the Anacardiaceae and Burseraceae. The diploid numbers are scored as there has been very little analysis of base numbers in the family.

(70–81) *Occurrence of flavonoids and biflavonoids* — These have been recorded across both Anacardiaceae and Burseraceae. A range of 5-deoxyflavonoids occur in the heartwood of some Anacardiaceae and Burseraceae (Young, 1976). Biflavonoids have also been reported from the leaves of some Anacardiaceae and Burseraceae (Wannan & Quinn, 1991; Graham, unpubl.).

Autapomorphies

Table 4 lists autapomorphies that were not included in the analysis. Some of these autapomorphies may be synapomorphies in the broader context of the family.

(*text continued on p. 181*)

Table 3a. Character matrix. Character states as in Table 2; – inapplicable; ? unknown; polymorphisms within parentheses. For references to the genera see Table 3b. (This table, with references for each character state, is available from the author.)

Genera	**1–10**	**11–20**	**21–30**	**31–40**	**41–50**	**51–60**	**61–70**	**71–81**
Amphipterygium	(ab)baa bab??b	–(ab)–bc ?c??–	–c?ec ??caa	dbb?? e?a??	b?cb(ac) (ac)baa?	?a?a? ??a(ab)a	bbaaa abb?(ab)	a(ab)(ab)(ab)(ab) aaaa??
Anacardium	(ab)(ab)aaa –a(ab)a(ab)	bbbb(ac) acaae	cebe– –(ab)baa	(cd)bba(ab) eaaba	aaaa(ad) bcbba	aa(ab)aa baaaa	baa(ac)(ab) bba(adgh)b	ababb aaabbb
Astronium	abaab a(ab)(ab)ab	bbbbc aaaa–	–c?eb bbbaa	a?aaa eaaba	aa(bc)bb bcb(ab)a	?aa?? ??aa?	bbaaa abadb	bbabb ab????
Blepharocarya	a(ab)ba(bc) aa(ab)ab	(bcd)(bcd)b(ab)a aaaae	cebe– –c–aa	c?aaa eaaa(ac)	aacb(ac) (ac)baba	?a?ab baab?	bbaa(ab) bba??	????? ??(ab)bbb
Buchanania	a(ab)aaa –a(ab)?a	(abc)(abc)bba aaaa–	–(ab)aea abaaa	d?aaa eaaaa	aaaaa aba??	aaaaa baaa?	b(ab)a(ac)(ab) abak?	????? ??(ab)(ab)bb
Bursera	(ab)ba(ab)(ab) a(ab)b?(ab)	(bcd)(bcd)aaa aaaa?	?(cd)a(cd)d ?b?bb	(ab)?aaa (cd)????	????? ???(ab)a	?baa? c?ab?	bba(ac)a (ab)baab	bbbbb bbbbbb
Campnosperma	(ab)aaaa –ab?b	(bcd)(bcd)(ab)ba aaaae	ae?e– –b–aa	(ab)?aaa e?aaa	aaaaa ababa	aaa?? ??aaa	b(bc)ab(ab) aba??	????? ??bbbb
Canarium	(ab)(ab)aa(ab) a(ab)(ab)ab	dda(ab)a aa(ab)a(c)	acacd bb?bb	(ab)(ab)aaa (cde)baaa	aaaaa dba?a	?baa(ab) b(ab)aa?	bba(ac)a aba(bij)?	????? ??babb
Cotinus	bbaaa –aaab	bbbbc aaaa?	?cbeb bbbaa	dabaa eaaba	bacbb bcbb?	?a??? ??abb	bbaab baadb	aaaaa b?bbbb
Cyrtocarpa	aba?(ab) aab?(ab)	bbbba aaaa(abc)	a(abc)?(abcde)b bbbaa	a??aa eb???	????? ???(ab)?	?aa?? ??aa?	????? ?????	????? ??????
Dobinea	b?(ab)aa –b(ab)?b	(bc)(bc)aba aa(a–)ae	?e?e– –b–aa	d?aaa e?aaa	aa(ab)ad bcbba	?a??? ??aaa	(b)(bc)a?a b?cl?	????? ??????
Dracontomelon	a(ab)aab (ab)a(ab)?a	bbb(ab)a aaaa–	–(ab)a(ab)b abaaa	aaaaa (abcde)bbaa	aaaaa abaaa	aaaaa cbaa?	baa(ac)a bb?fb	abbbb bbbabb
Euroschinus	(ab)(ab)aa(bc) (ab)a(ab)?(ab)	(bc)(bc)bba aaaac	bc?ec bbbaa	b??aa eaaba	aacbb bca(ab)?	aaaab baaa?	bbaa(ab) aba??	????? ??baba
Garuga	(ab)baab abb?a	bbaaa aaba–	–aaad bbabb	(ab)?aaa (abcde)????	????? ????a	?baa(ab) (bc)baba	bba(ac)a abab?	????? ???a??
Harpephyllum	aaaab aab?b	(bc)(bc)bba ?aaa(ab)	a(ab)a(ab)b bbbaa	aaaaa (de)bbaa	abaaa abaaa	?a??? ??aa?	bbaaa ab???	????? ??bbbb

Table 3a (cont.).

Genera	**1–10**	**11–20**	**21–30**	**31–40**	**41–50**	**51–60**	**61–70**	**71–81**
Lannea	(ab)(ab)aa(ab) aa(ab)?b	(bc)(bc)bba aaaab	a(abc)abb bbbaa	aaaaa (de)b(ab)aa	abaaa aba(ab)?	aaaaa bbaa?	bbb(ac)a aba(cdg)?	????? ??bbbb
Lithraea	(ab)aa(ab)(ab) aa(ab)?(ab)	bbbaa ?aaa?	bc?e(bc) bbbaa	da?aa e??b(bc)	aa(bc)bb bcb?a	?aa?? ??ab?	bbaa(ab) baa(cd)?	????? ??baba
Loxopterygium	abaab (ab)(ab)(ab)ab	bbbbc aaaac	bc?ec b(ac)baa	d?bba eaaaa	?abbb bcbba	?aa?? ??aa?	bbaaa ab??b	ababb aa????
Mangifera	aaaaa –a(ab)a(ab)	(bc)(bc)bb(abc) a(abc)a(ab)e	?ebe– –a–aa	dbbaa eaaaa	ab(abc)b(ac) cb(ab)aa	(ac)(ab)bb(ab) baaab	aaa(ac)b bbagb	aaabb abbabb
Pentaspadon	abaab aab?(ab)	bbbb(bc) aaaaa	ae?e– –b–aa	(bc)??aa e?baa	baaaa aaa?a	aaa?? ??aa?	bba(ab)a a(ab)???	????? ??????
Pistacia	(ab)(ab)a(ab)(abc) (ab)a(ab)ab	(bcd)–b–c acaa–	–cbec bb(bc)aa	d(ab)(ab)aa eaaab	bacba abaaa	aaa(ab)a (ab)?abb	bba(ac)(ab) aab(acd)b	abaab aabbbb
Pleiogynium	aaaab aab?b	(abc)(abc)bba aaaaa	aa?ab bcbaa	b?aaa abbaa	abaaa aba(ab)?	aaaaa c(ab)aa?	b(ab)aaa ab???	????? ??b(ab)(ab)b
Rhodosphaera	a?aab aa(ab)?b	bbbba aaaa–	–c?eb bbbaa	d??aa ea(ab)aa	ab(bc)bb bcbba	?aa?? ??ab?	b(bc)ab(ab) aba??	????? ??bbbb
Schinopsis	(ab)(ab)aa(ab) (ab)a(ab)?(ab)	bbbbc ?aaa?	?c?eb b(ac)baa	b??ba e?aba	abcbb bcbba	?aa?? ??aa?	b(ab)aaa aba??	????? ??bbbb
Schinus	(ab)aa(ab)(abc) a(ab)(ab)ab	(bc)(bc)bba aaaac	bcbeb bbbaa	(ab)a(ab)aa e?abc	aacbb bcbba	?aaaa (bc)ba(ab)?	bbaaa a(ab)a(cd)?	????? ??(ab)(ab)bb
Semecarpus	(ab)aaaa –a(ab)?(ab)	(bc)(bc)b(ab)c aaaa–	–c?eb bbbaa	(abc)?bab e?aba	baaa(acd) (cd)cb(ab)(ab)	a(ab)ab(ab) baaa?	baa(ab)b bba(mn)?	????? ??(ab)(ab)bb
Spondias	abaab (ab)(ab)(ab)ba	bbbaa aaaa–	–(ab)a(ab)b abaaa	aaaaa (abcde)bbaa	baaaa abaaa	aaaaa cbaa?	b(ab)baa abaeb	aaabb abbbbb
Swintonia	a?aaa –a(ab)?(ab)	bbbbc aba(ab)e	cebe– –bbaa	(cd)??aa e?(ab)aa	aaaa(ad) dabaa	baaaa b?aa?	a(ab)a(ac)b ab??b	ababb aa????
Tapirira	(ab)aaa(bc) (ab)a(ab)b(ab)	bbbba aaaa(ab)	a(abc)a(de)b bbbaa	aaaaa (de)abac	??aaa ababa	?aaaa baaa?	bbaaa ab??b	bbabb bb????
Toxicodendron	(abc)baab aabbb	bbbbc aaaac	bc?ec bbbaa	dabaa eaaba	bacb(bc) bcba?	(ab)a?ab b?a(ab)?	b(ab)a(ac)a b(ab)adb	aaaaa bab(ab)b(ab)

Table 3b. Genera of Table 3a with references.

Amphipterygium: Baillon, 1878; Bentham & Hooker, 1862; Cronquist, 1981; Engler, 1883; Erdtman, 1952; Fritsch, 1908; Heimsch, 1942; Hemsley, 1908; Kramer, 1939; Metcalfe & Chalk, 1965; Standley, 1923; Stern, 1952; Stone, 1973; Wannan & Quinn, 1988; Young, 1976.

Anacardium: Baillon, 1878; Barfod, 1987, 1988; Copeland, 1962; Dong & Baas, 1993; Duke, 1965; Eichler, 1878; Engler, 1883; Erdtman, 1952; Goldblatt, 1981, 1984; Graham, unpubl.; Heimsch, 1942; Hou, 1978; Jadin, 1894; Kamilya & Paria, 1995; Machado, 1944; Marchand, 1869; Metcalfe & Chalk, 1965; Mitchell, 1995; Mitchell & Mori, 1987; Record, 1939; Van der Veken, 1960; Wannan, unpubl.[1]; Wannan & Quinn, 1990, 1991; Young, 1976; Young & Aist, 1987.

Astronium: Anzotegui, 1971; Baillon, 1878; Barfod, 1987; Barkley, 1968; Blackwell & Dodson, 1967; Darlington & Wylie, 1955; Engler, 1883; Heimsch, 1942; Jadin, 1894; Mitchell, 1990, 1995; Record, 1939; Standley & Steyermark, 1949; Wannan & Quinn, 1990; Young, 1976.

Blepharocarya: Airy Shaw, 1965; Bailey, 1899, 1913; Dadswell & Ingle, 1948; Engler, 1897; Graham, unpubl.; Hyland & Whiffin, 1993; Jadin, 1894; Jessup, 1985; Kryn, 1953; Mueller, 1878; Specht, 1958: 253; Wannan, unpubl.[1]; Wannan & Quinn, 1990, 1991; Wannan et al., 1985, 1987.

Buchanania: Baillon, 1878; Dadswell & Ingle, 1948; Dong & Baas, 1993; Engler, 1883; Goldblatt, 1984; Graham, unpubl.; Heimsch, 1942; Hou, 1978; Huang, 1972; Hyland & Whiffin, 1993; Jadin, 1894; Jessup, 1985; Kryn, 1953; Liao, 1973; Wannan, unpubl.[1]; Wannan & Quinn, 1990, 1991; Wannan et al., 1985; Waterhouse, unpubl.[2].

Bursera: Baillon, 1878; Bawa, 1973; Brizicky, 1962; Engler, 1883, 1892; Fedorov, 1969; Forman et al., 1994; Gillet, 1980; Graham, unpubl.; Jadin, 1894; Marchand, 1868; Metcalfe & Chalk, 1965; Porter, 1970; Record & Hess, 1943; Segaar & Van der Ham, 1993; Standley & Steyermark, 1949; Stevenson, 1979; Webber, 1941; Young, 1976.

Campnosperma: Barfod, 1987; Blackwell & Dodson, 1967; Corner, 1976; Dadswell & Ingle, 1948; Engler, 1883; Graham, unpubl.; Heimsch, 1942; Hou, 1978; Jadin, 1894; Juliano & Cuevas, 1932; Kryn, 1953; Marchand, 1869; Mitchell, 1995; Randrianasolo & Miller, 1998; Record, 1939; Wannan, 1981; Wannan & Quinn, 1990, 1991.

Canarium: Baillon, 1878; Corner, 1976; Engler, 1883; Forman et al., 1994; Goldblatt, 1981; Hewson, 1985; Hill, 1933; Hyland & Whiffin, 1993; Jadin, 1894; Leenhouts, 1955; Marchand, 1868; Metcalfe & Chalk, 1965; Ng, 1975; Perrier de la Bathie, 1946; Segaar & Van der Ham, 1993; Wannan, unpubl.[1]; Wannan, 1981; Wannan & Quinn, 1990, 1992; Wannan et al., 1985; Webber, 1941.

Cotinus: Baillon, 1878; Dong & Baas, 1993; Eichler, 1878; Engler, 1883; Goldblatt, 1981; Graham, unpubl.; Heimsch, 1942; Ibe & Leis, 1979; Kryn, 1953; Linczevski, 1949; Metcalfe & Chalk, 1965; Mitchell, 1990; Payer, 1857; Penzes, 1958; Record, 1939; Wannan & Quinn, 1990; Young, 1976.

Cyrtocarpa: Bentham & Hooker, 1862; Engler, 1883; Jadin, 1894; Metcalfe & Chalk, 1965; Mitchell, 1995; Mitchell & Daly, 1991.

Dobinea: Baillon, 1878, 1889; Bentham & Hooker, 1862; Engler, 1883, 1892; Erdtman, 1952; Forman, 1954; Franchet, 1889; Goldblatt, 1981; Heimsch, 1942; Jadin, 1894; Metcalfe & Chalk, 1965; Radlkofer, 1888; Wannan & Quinn, 1990, 1991; Willis, 1973.

Dracontomelon: Dadswell & Ingle, 1948; Dong & Baas, 1993; Engler, 1883; Goldblatt, 1981; Graham, unpubl.; Hou, 1978; Jadin, 1894; Kryn, 1953; Metcalfe & Chalk, 1965; Wannan, 1986; Wannan & Quinn, 1990, 1991; Wilkinson, 1967, 1968; Young, 1976.

Euroschinus: Bentham & Hooker, 1862; Dadswell & Ingle, 1948; Engler, 1883; Graham, unpubl.; Heimsch, 1942; Hou, 1978; Hyland & Whiffin, 1993; Jadin, 1894; Jessup, 1985; Kryn, 1953; Metcalfe & Chalk, 1965; Wannan, unpubl.[1]; Wannan, 1981; Wannan & Quinn, 1990, 1991.

Garuga: Ansari et al., 1978; Baillon, 1878; Bentham & Hooker, 1862; Cronquist, 1981; Engler, 1883; Fedorov, 1969; Forman et al., 1994; Goldblatt, 1981; Hewson, 1985; Hyland & Whiffin, 1993; Jadin, 1894; Lam, 1932; Leenhouts, 1955; Marchand, 1868; Metcalfe & Chalk, 1965; Segaar & Van der Ham, 1993; Wannan, unpubl.[1]; Webber, 1941.

Harpephyllum: Engler, 1883; Fernandes & Fernandes, 1966; Graham, unpubl.; Jadin, 1894; Kryn, 1953; Metcalfe & Chalk, 1965; Phillips, 1951; Von Teichman & Van Wyck, 1988; Wannan & Quinn, 1990, 1991; Wannan et al., 1985.

Lannea: Dong & Baas, 1993; Engler, 1883; Fedorov, 1969; Fernandes & Fernandes, 1966; Goldblatt, 1981; Graham, unpubl.; Heimsch, 1942; Hou, 1978; Kamilya & Paria, 1995; Kelkar, 1958; Kryn, 1953; Marchand, 1869; Van der Veken, 1960; Venkaiah & Shah, 1984; Von Teichman, 1987, 1988; Wannan & Quinn, 1990.

Lithraea: Anzotegui, 1971; Arrillaga-Maffei et al., 1973; Barkley, 1962c; Cabrera, 1939; Engler, 1883; Goldblatt, 1985; Graham, unpubl.; Heimsch, 1942; Jadin, 1894; Marchand, 1874; Marticorena, 1968; Metcalfe & Chalk, 1965; Moore, 1973; Pienaar & Von Teichman, 1998; Record, 1939.

Loxopterygium: Baillon, 1878; Barfod, 1987, 1988; Barkley, 1962a; Engler, 1883; Heimsch, 1942; Jadin, 1894; Macbride, 1951; Metcalfe & Chalk, 1965; Mitchell, 1995; Record, 1939; Wannan, unpubl.[1]; Young, 1976.

Mangifera: Baillon, 1878; Barfod, 1987, 1988; Copeland, 1955; Dadswell & Ingle, 1948; Dong & Baas, 1993; Duke, 1965; Engler, 1883; Erdtman, 1952; Goldblatt, 1981; Graham, unpubl.; Heimsch, 1942; Hou, 1978; Hyland & Whiffin, 1993; Jadin, 1894; Juliano & Cuevas, 1932; Kamilya & Paria, 1995; Kryn, 1953; Marchand, 1869; Metcalfe & Chalk, 1965; Von Teichman et al., 1988; Wannan & Quinn, 1990, 1991; Young, 1976.

Pentaspadon: Baillon, 1878; Dadswell & Ingle, 1948; Engler, 1883; Heimsch, 1942; Hooker, 1860, 1876; Hou, 1978; Jadin, 1894; Kryn, 1953; Marchand, 1869; Metcalfe & Chalk, 1965; Tardieu-Blot, 1962; Wannan & Quinn, 1990, 1991.

Pistacia: Baillon, 1878; Copeland, 1955; Dadswell & Ingle, 1948; Darlington & Wylie, 1955; Dong & Baas, 1993; Engler, 1883; Erdtman, 1952; Graham, unpubl.; Grundwag & Fahn, 1969; Hou, 1978; Huang, 1972; Jadin, 1894; Kryn, 1953; Metcalfe & Chalk, 1965; Payer, 1857; Siddiqi, 1978; Standley & Steyermark, 1949; Wannan, unpubl.[1]; Wannan & Quinn, 1990, 1991; Wannan et al., 1985; Young, 1976; Zohary, 1952.

Pleiogynium: Dadswell & Ingle, 1948; Engler, 1883; Graham, unpubl.; Heimsch, 1942; Hill, 1933; Hou, 1978; Hyland & Whiffin, 1993; Jadin, 1894; Jessup, 1985; Kryn, 1953; Metcalfe & Chalk, 1965; Wannan, unpubl.[1]; Wannan & Quinn, 1990, 1991.

Rhodosphaera: Bailey, 1899; Dadswell & Ingle, 1948; Engler, 1883; Floyd, 1989; Graham, unpubl.; Heimsch, 1942; Jadin, 1894; Jessup, 1985; Kryn, 1953; Wannan, 1981, 1986; Wannan & Quinn, 1990, 1991; Wannan et al., 1985.

Schinopsis: Anzotegui, 1971; Barkley, 1962b; Cabrera, 1939; Engler, 1883; Graham, unpubl.; Heimsch, 1942; Jadin, 1894; Macbride, 1951; Metcalfe & Chalk, 1965; Meyer & Barkley, 1973; Mitchell, 1990; Ragonese & Catiglioni, 1947; Record, 1939; Wannan & Quinn, 1990.

Schinus: Baillon, 1878; Barfod, 1988; Barkley, 1944; Blackwell & Dodson, 1967; Cabrera, 1939; Copeland, 1959; Darlington & Wylie, 1955; Eichler, 1878; Engler, 1883; Erdtman, 1952; Fedorov, 1969; Graham, unpubl.; Heimsch, 1942; Jadin, 1894; Jessup, 1985; Macbride, 1951; Marchand, 1869; Metcalfe & Chalk, 1965; Record, 1939; Wannan, unpubl.[1]; Wannan & Quinn, 1990, 1991; Wannan et al., 1985.

Semecarpus: Baillon, 1878; Bentham & Hooker, 1862; Dadswell & Ingle, 1948; Engler, 1883; Erdtman, 1952; Fedorov, 1969; Goldblatt, 1984; Graham, unpubl.; Heimsch, 1942; Hou, 1978; Huang, 1972; Hyland & Whiffin, 1993; Ishratullah et al., 1977; Jadin, 1894; Jessup, 1985; Kamilya & Paria, 1995; Kryn, 1953; Liao, 1973; Marchand, 1869; Ridley, 1933; Tardieu-Blot, 1962; Wannan, unpubl.[1]; Wannan & Quinn, 1990, 1991.

Spondias: Airy Shaw & Forman, 1967; Baillon, 1878; Barfod, 1987, 1988; Dong & Baas, 1993; Duke, 1965; Engler, 1883; Erdtman, 1952; Graham, unpubl.; Heimsch, 1942; Hladik & Halle, 1979; Hou, 1978; Jadin, 1894; Juliano, 1932; Kryn, 1953; Metcalfe & Chalk, 1965; Mitchell, 1995; Mitchell & Daly, 1998; Tardieu-Blot, 1962; Van der Veken, 1960; Wannan, unpubl.[1]; Wannan & Quinn, 1990; Young, 1976.

Swintonia: Dadswell & Ingle, 1948; Engler, 1883; Heimsch, 1942; Hou, 1978; Jadin, 1894; Kryn, 1953; Marchand, 1869; Metcalfe & Chalk, 1965; Tardieu-Blot, 1962; Wannan, unpubl.[1]; Wannan & Quinn, 1990; Young, 1976.

Tapirira: Baillon, 1878; Barfod, 1987, 1988; Blackwell & Dodson, 1967; Engler, 1883; Heimsch, 1942; Jadin, 1894; Macbride, 1951; Metcalfe & Chalk, 1965; Mitchell, 1995; Mori & Mitchell, 1990; Nannenga, 1936; Record, 1939; Terrazas & Wendt, 1995; Von Teichman, 1990; Wendt & Mitchell, 1995.

Toxicodendron: Barfod, 1987, 1988; Barkley, 1937; Blackwell & Dodson, 1967 ; Copeland & Doyel, 1940; Dong & Baas, 1993; Engler, 1883; Fedorov, 1969; Goldblatt, 1985; Graham, unpubl.; Harada, 1937; Heimsch, 1942; Hou, 1978; Kryn, 1953; McNair, 1918; Metcalfe & Chalk, 1965; Moore, 1973; Wannan & Quinn, 1990, 1991; Wannan et al., 1985; Young, 1974, 1976.

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1) Wannan unpublished observations (see Appendix A for cited specimens).
2) J.T. Waterhouse unpublished observations (see Appendix B for cited specimen).

Table 4. Autapomorphies for genera.

Genera	Autapomorphies
Amphipterygium	– no perianth in female flowers – female flowers and fruits enclosed in an involucre (dissimilar to *Blepharocarya*)
Astronium	– postanthetic growth of calyx
Blepharocarya	– small stigmatic area on ventral side of the stylar apex – ciliate margins of fruit – female flowers and fruits enclosed in an involucral inflorescence (dissimilar to *Amphipterygium*)
Buchanania	– fertile carpel in *Buchanania* has no stigma, therefore the number of stigmas is equal to one less than the number of carpels/styles.
Campnosperma	– discoidal stigma with irregular lobes – formed seedless second locule in fruit which is not evident in the ovary at anthesis
Canarium	– diffuse parenchyma (presumably apotracheal) in wood of some species
Cotinus	– postanthetic pedicel development of aborted flowers (giving rise to smokey appearance)
Dobinea	– no perianth in female flowers – stigma is small area on the ventral surface of the style extending downwards from the tip – membranous margin on the fruit
Garuga	– gynophore
Mangifera	– stigma is a reduced area at the tip of the style – labyrinthine testa in some species
Pentaspadon	– globose stigma
Pleiogynium	– carpel number twice the number of corolla segments (i.e. up to 12 locules)
Semecarpus	– postanthetic growth of hypocarp
Swintonia	– postanthetic growth of corolla – adherent testa

RESULTS AND DISCUSSION

Non-sequence data

A heuristic analysis with 500 replicates of random taxon addition gave a single island of 24 equally parsimonious trees of 510 steps with a rescaled consistency index of 0.53 and a retention index of 0.64. The majority rule consensus is shown in Fig. 1 together with the results of a decay analysis. Character evolution was investigated in MacClade and is shown in Fig. 2.

There is strong character support for the Anacardiaceae (decay +5) for which the following are synapomorphies: 13b (calyx aestivation imbricate), 25b (carpels connate to top of ovary), 29a (apotropous ovules), 30a (one ovule per locule), and 52a (plano-convex or flat cotyledons). One of these subsequently shows reversal (13).

Within the ingroup, taxa belonging to Group A of Wannan & Quinn (1991) constitute a monophyletic group with subgroups, A1 and A2, also retrieved as subclades. There is some character support for some elements within the subgroup A2: *Amphipterygium* and *Pistacia* (+3), *Cotinus* and *Toxicodendron* (+2), and *Loxopterygium* and *Schinopsis* (+2).

Group A is defined by a unique synapomorphy (Fig. 2: 23b, antesepalous fertile carpel). Within this clade there are two groups of genera. One clade contains 12 genera belonging to subgroup A2 of Wannan & Quinn (1991) or Engler's tribe Rhoeae. The other clade contains genera referred to subgroup A1 plus *Dobinea* from A2, or to Engler's tribes Anacardieae (*Anacardium, Mangifera, Swintonia*), Semecarpeae (*Semecarpus*) and Dobineeae (*Dobinea*). Subgroup A2 (+2) is defined by four unambiguous changes: two homoplasies (43c, 44b), a synapomorphy (59b) that undergoes two subsequent reversals, and one reversal (5b). *Blepharocarya* is sister to all other members of A2, which are arranged in two subclades: *Amphipterygium* + *Pistacia* (+3), defined by a unique synapomorphy (68b), four homoplasies and a reversal; all other members of A2 (+2), defined by a unique synapomorphy (45b) and three other changes (Fig. 2).

Subgroup A1 plus *Dobinea* (+1; *Anacardium, Dobinea, Mangifera, Semecarpus, Swintonia*) is supported by two homoplasies (46b, 48b) each also occurring amongst A2 taxa. It contains a nested clade that receives stronger support (+2) and comprises *Anacardium, Mangifera, Semecarpus* and *Swintonia*, but is not defined by any unequivocal change.

Towards the base of the tree there are 10 genera (*Buchanania, Campnosperma, Cyrtocarpa, Dracontomelon, Harpephyllum, Lannea, Pentaspadon, Pleiogynium, Spondias, Tapirira*) referred by Wannan & Quinn (1991) to Group B which corresponds to Engler's Spondiadeae with the addition of *Campnosperma, Buchanania* and *Pentaspadon*. Relationships between them are not fully resolved and there is no clustering of the lineages.

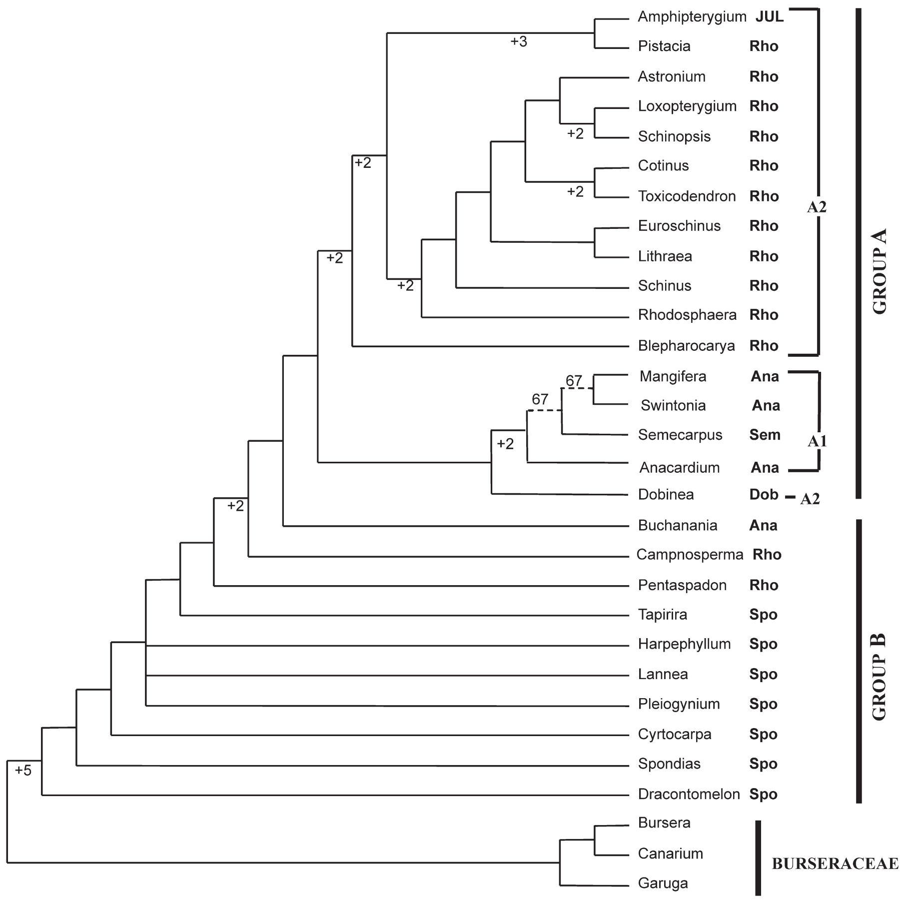

Fig. 1. Majority rule consensus tree of 24 trees (non-sequence data) showing Wannan & Quinn's (1991) subfamily groups, Engler's tribes (Rho = Rhoeae; Ana = Anacardieae; Sem = Semecarpeae; Dob = Dobineeae; Spo = Spondiadeae), and JUL = Julianiaceae. Unbroken branches present in 100% of trees; lower values above branches. Decay values > +1 shown below branches.

Characters

Of the 81 characters used, 2 were constant (16, 58), 15 were non-informative (3, 4, 6, 8, 11, 12, 18, 19, 27, 35, 50, 51, 53, 70, 80) and the remaining 64 were informative. Indications from the remaining unscored genera in the family suggest that a number of the uninformative characters will be informative in a larger dataset or when the character is scored for all 30 taxa in the dataset. Overall, the breadth of the analysis was limited by absence of data for many genera. Although taxa for the analysis were chosen on the basis of their characters being known, there were still gaps in certain characters. In other cases, there were disagreements in the scoring of character states between authors, which have been generally coded as polymorphisms. There is little doubt that the scoring of currently absent states and the checking of apparently poly-

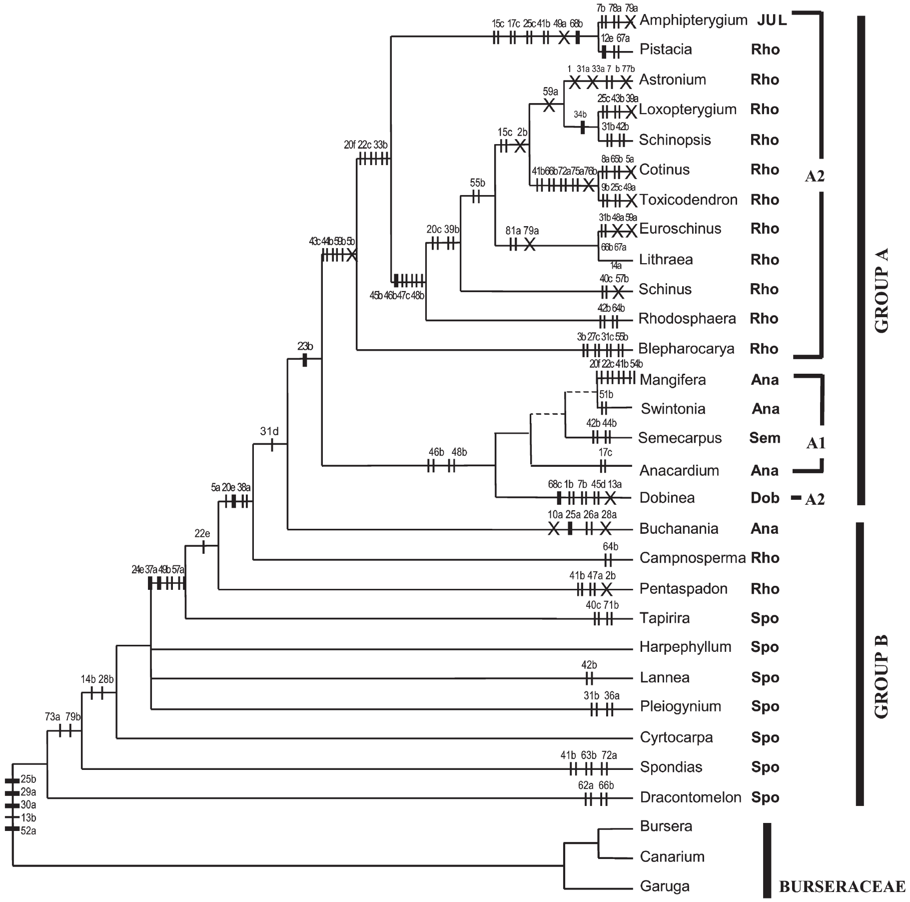

Fig. 2. Majority rule consensus tree of 24 trees (non-sequence data) showing Wannan & Quinn's (1991) subfamily groups, Engler's tribes. Abbreviations as in Fig.1. Key: **I** – unique synapomorphies within the ingroup; I – unique synapomorphies with reversals; II – synapomorphies showing homoplasy; X – reversals. Characters and states numbered as in Table 2.

morphic taxa will improve the phylogenetic signal. Two other problems related to character scoring may be assisted by a wider analysis of species or genera. The first was the need to code polymorphisms for pericarp characters where a discrete cell layer was sometimes variably present or variably lignified (e.g. character 45). The second was the occurrence of character states which were apparently unique synapomorphies for clades except for a polymorphic occurrence in a genus outside the clade. Most of these isolated polymorphic occurrences were checked as closely as possible, but the following could not be checked and appear questionable based on the overall phylogenetic signal for these taxa: 3 carpellodes (20c) and 1 locule at anthesis (24e) in *Cyrtocarpa,* and presence of Fustin in heartwood (75a) in *Amphipterygium.*

Sequence data

The 27 taxa for which *rbc*L sequences were available (Table 5) include species of 16 genera of Anacardiaceae, representing both Group A and B, and three of the five tribes, three genera of Burseraceae, and seven outgroup genera from Sapindaceae and Rutaceae.

Table 5. Taxa included in the molecular analysis.

Species	Genebank accession number	Voucher or reference	Subfamily Group	
			Tribe[1]	Group[2]
ANACARDIACEAE				
Amphipterygium adstringens (Schltdl.) Standl.	AJ402921	*Manzanero 1150* (NY) (Savolainen et al., 2000a)	Unplaced[3]	A
Anacardium occidentale L.	AY462008	*Chase s.n.*	Anacardieae	A
Astronium graveolens Jacq.	AY462009	Aguilar-Ortigoza & Sosa, 2004	Rhoeae	A
Blepharocarya depauperata Specht	U38928	*Fisher UNSW 21582*	Rhoeae	A
Buchanania latifolia Roxb.	U39275	*Terrazas 206* (CHAPA)	Anacardieae	B
Cotinus coggygria Scop.	AY510148	Lee et al., 2004	Rhoeae	A
Cyrtocarpa procera Kunth	U39272	*Wendt 6152-A* (CHAPA)	Spondiadeae	B
Mangifera indica L.	U39269	*Terrazas s.n.* (CHAPA)	Anacardieae	A
Orthopyerygium huaucui Hemsl.		*Chase s.n.*	Unplaced[3]	A
Pistacia vera L.	AJ235786	Savolainen et al., 2000a	Rhoeae	A
Rhus copallina L.	U00440	Gunter et al., 1994	Rhoeae	A
Schinopsis balansae Engl.	AY462015	Aguilar-Ortigoza & Sosa, 2004	Rhoeae	A
Schinus molle L.	U39270	*W.R. Anderson 13601* (MICH)	Rhoeae	A
Spondias cytherea Sonn.	U39274	*Terrazas s.n.* (CHAPA)	Spondiadeae	B
Tapirira mexicana Marchand	U39273	*Wendt 6142* (CHAPA)	Spondiadeae	B
Toxicodendron radicans (L.) Kuntze	U39271	*Terrazas s.n.* (CHAPA)	Rhoeae	A
BURSERACEAE				
Bursera fagaroides Engl.		*Chase s.n.*	Bursereae[4]	
Bursera inaguensis Britton	L01890	Albert et al., 1992	Bursereae[4]	
Canarium ovatum Engl.	U38856	*Fernando 1387* (LBC)	Canarieae[4]	
Commiphora habessinica (O. Berg) Engl.	U39276	*M.W. Chase 526* (K)	Bursereae[4]	
SAPINDACEAE				
Dipteronia sinensis Oliv.	U39268	*M.W. Chase 502* (K)		
Aesculus pavia Castigl.	U39277	*M.W. Chase 503* (K)		
Ganophyllum falcatum Blume		BH 9269 (CSIRO)		
Alectryon connatus (F. Muell.) Radlk.		9903089 (CBG)		
RUTACEAE				
Murraya paniculata (L.) Jack	U38860	*Quinn s.n.* (UNSW)		
Flindersia australis R.Br.	U38861	UNSW 21728		
Acronychia acidula F. Muell.	U38862	RBG 862744		

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1) Engler, 1892, 1897.
2) Wannan & Quinn, 1991.
3) Not placed in any family by Engler, 1883, 1897.
4) Leenhouts, 1955; Forman et al., 1994.

The first 28 base pairs (bp) of the aligned database were excluded from the analysis because they included one of the primer sites or were missing in many taxa. Of the remaining 1400 bp, 313 (22.4%) were variable and 141 (10%) were informative. A heuristic analysis using representatives of the Sapindaceae and Rutaceae as outgroups produced 8 trees of 541 steps with a RC = 0.48 and RI = 0.69. The Sapindaceae and Rutaceae were recognised as strongly supported individual clades (BS 100%, decay +11) that together are well separated (82%, +4) from the ingroup (Anacardiaceae and Burseraceae). The ingroup consists of two poorly supported Anacardiaceae clades and a stronger clade (90%, +4) of Burseraceae. The relationships between Burseraceae and Groups A and B of the Anacardiaceae are not resolved. The larger Anacardiaceae clade (56%, +1) contains 12 genera from Wannan & Quinn's (1991) Group A (Fig. 3) with *Buchanania* (Group B) as a weakly supported sister taxon. The strong clade (98%, +7) of Group A genera are from Engler's tribes Rhoeae and Anacardieae, and former Julianiaceae (*Amphipterygium*, *Orthopterygium*). Relationships within this clade are poorly resolved except for grouping *Astronium* with *Schinopsis* (100%, +12) and *Anacardium* with *Mangifera* (88%, +4). The weakly supported third ingroup clade (76%, +2) contains three genera from Group B or Engler's Spondiadeae (76%, +2). Within this clade *Spondias* is a sister taxon to *Cyrtocarpa* and *Tapirira*.

Combined data

An analysis of combined sequence and non-sequence data was undertaken for 16 taxa using *Bursera* and *Canarium* as outgroups. A heuristic analysis of 500 replicates of random taxon addition gave a single tree of 593 steps (CI = 0.71 excluding uninformative characters, RI = 0.64 and RC = 0.53) as shown in Fig. 4, together with the results of bootstrap and decay analyses. This combined tree shows a strong clade (BS 100%, decay +11) recognising the family Anacardiaceae. The ingroup comprises two weakly supported clades, one with 10 genera of Group A and *Buchanania* (Group B), and another with the remaining three genera of Group B. The larger clade contains a well-supported subclade (100%, +10) of Group A genera with *Buchanania* as sister taxon. Within this Group A clade there are subclades comprising *Astronium* and *Schinopsis* (100%, +12), *Amphipterygium* and *Pistacia*, (93%, +3), *Cotinus* and *Toxicodendron* (75%, +3), and *Anacardium* and *Mangifera* (94%, +4). The second Anacardiaceae clade is a weakly supported clade (67%, +2) comprising three Group B genera from Engler's Spondiadeae. In this clade, *Spondias* is again a sister group to a weakly supported subclade (65%, +2) with *Tapirira* and *Cyrtocarpa*.

Taxonomic implications

The *rbc*L data indicates that Burseraceae is closely related to the Anacardiaceae, suggesting that it lies within the ingroup which includes genera of Anacardiaceae. However, the combined data suggest that Burseraceae is well differentiated from the Anacardiaceae. Sequence data from other regions of the chloroplast genome (Pell & Urbatsch, 2001) also support a monophyletic Anacardiaceae, distinct from its sister group the Burseraceae.

Non-sequence and sequence data provide some support for the subfamily groups of Wannan & Quinn (1991) and Engler's tribes. Both datasets support placement of most genera from Engler's tribes Anacardieae and Rhoeae in a single group recognised as

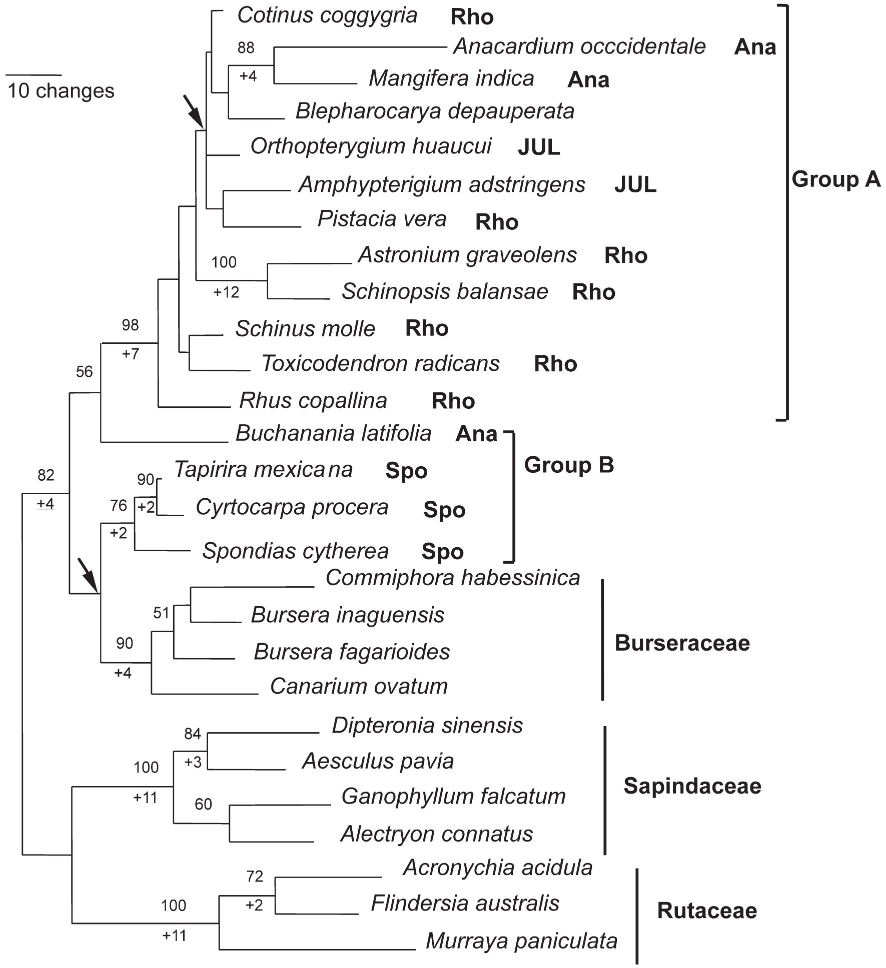

Fig. 3. One of the eight equally parsimonious trees of 541 steps in a single island found from a heuristic search of the *rbc*L database with branch lengths proportional to the amount of change; consistency index = 0.54 excluding uninformative characters; retention index = 0.69; rescaled consistency index = 0.48. Arrows indicate branches collapsing in the strict consensus. Bootstrap percentages > 50% shown above the branches; decay values > 1 shown below shown below branches. Also showing Wannan & Quinn's (1991) subfamily groups, Engler's tribes. Abbreviations as in Fig.1.

Group A by Wannan & Quinn (1991). This clade includes *Blepharocarya* as well as genera previously referred to the Julianiaceae. Both datasets suggest that *Buchanania* is a weakly linked sister taxon to Group A rather than to Group B (Wannan & Quinn, 1991). In the non-sequence data the Group A clade also includes genera from the tribes Dobineeae and Semecarpeae, which were not sampled by the sequence data. The non-sequence data suggested that there are some closer relationships amongst Group A genera, some of which are supported by *rbc*L data (*Astronium* and *Schinop-*

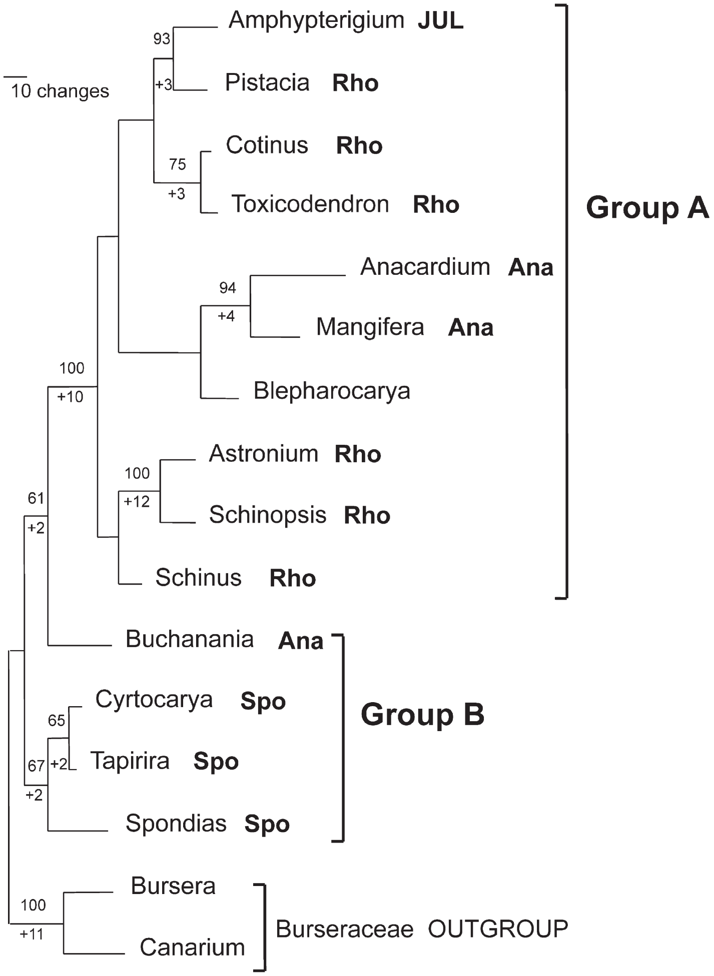

Fig. 4. Single most parsimonious tree of 593 steps found from heuristic searching of the combined database with branch lengths proportional to the amount of change; consistency index = 0.71 excluding uninformative characters; retention index = 0.64; rescaled consistency index = 0.53. Bootstrap percentages > 50% shown above the branches; decay values > 1 shown below shown below branches. Also showing Wannan & Quinn's (1991) subfamily groups and Engler's tribes. Abbreviations as in Fig.1.

sis, Amphipterygium and *Pistacia*, *Anacardium* and *Mangifera*). Closer relationships within Group A may be further resolved by sequence data from other areas (e.g. internal transcribed spacer region; Miller et al., 2001). Neither dataset provides strong support for the recognition of a clade comprising taxa from Wannan & Quinn's (1991) Group B (Fig. 3, 4). In the non-sequence data these genera occur as a basal polyotomy and in the sequence and combined data there is a weakly supported clade with *Cyrtocarpa*, *Spondias* and *Tapirira,* from Group B. However, support for Group B is provided by sequence data from other areas of the chloroplast genome (Pell & Urbatsch, 2001). Sequence and non-sequence data do not support *Buchanania* within Group B as suggested by Wannan & Quinn (1991). Rather, *Buchanania* appears as a sister taxon weakly clustered with Group A in all datasets. However, there is no strong suggestion from any dataset that *Buchanania* has any close affinities with genera of the Anacardieae where it was placed by Engler. The recognition of subclades amongst the genera of Wannan & Quinn's (1991) subgroup A1 will require a more widespread survey of the three tribes Anacardieae, Dobineeae and Semecarpeae. Initial indications, however, that *Gluta* and *Bouea*, with apotracheal wood parenchyma (Dadswell & Ingle, 1948; Kryn, 1953) and similar pericarp anatomy and floral anatomy (Wannan & Quinn, 1990, 1991) may be close to *Mangifera* and *Swintonia*. This suggestion is supported by the analysis of *rbc*L data by Chayamarit (1997), whose sequences were not made available for inclusion in this analysis.

Both data sources support the recognition of a large clade which can be recognised at the subfamily level and includes genera from Group A (or Engler's Anacardieae, Dobineeae, Rhoeae and Semecarpeae). This subfamily, here designated Anacardioideae, appears to be defined by the possession of a single unique synapomorphy (23b antesepalous fertile carpel), although this character is yet to be scored in some genera. Many members of this subfamily also possess a stratified endocarp. The combined data show weak support for the recognition of a second subfamily group based on Group B (without *Buchanania*) or on Engler's Spondiadeae that is here designated as Spondiadioideae Kunth emend. Wannan. This subfamily is also supported by sequence data from other regions of the chloroplast genome (Pell & Urbatsch, 2001). In this analysis however, there are no non-sequence synapomorphies that would define this second subfamily; instead the subfamily appears paraphyletic. The subfamily can be recognised, however, by the retention of the plesiomorphic (non-stratified) pericarp condition in the family. There are suggestions that the study of the operculae in the Anacardiaceae and Burseraceae may provide some synapomorphic support for Group B. Initial observations suggest that the operculae in the Anacardiaceae and Burseraceae may not be homologous, but hard data in this area are lacking. Some of Engler's tribes may be recognisable in modified form within the subfamily taxonomy proposed above. The non-sequence data appear to support Engler's tribes Rhoeae (without *Campnosperma* and *Pentaspadon*) and Anacardieae (without *Buchanania*). However, the absence of support for these from *rbc*L data, and from the combined dataset, suggests that any tribal boundaries will need to be determined from a wider survey of taxa and characters. There are as yet no indications of tribes within the subfamily Spondiadioideae. There remain several genera (*Buchanania, Campnosperma, Pentaspadon*) whose subfamily position remains unclear. Placed as a sister taxon to the Anacardioideae in all analyses, *Buchanania* may constitute a separate subfamily. Further sequence data for all three genera would appear to be crucially important as all three possess morphological and anatomical characters which appear intermediate between the two subfamilies. An analysis of *rbc*L data by Chayamarit (1997) showed *Buchanania* in a clade with *Pentaspadon* and *Rhus*, but the degree of support for this clade was not shown.

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APPENDICES

Appendix A. Specimens examined by B.S. Wannan for unpublished observations.

Observations of characters used in Table 2 were made on the material listed below. The locations of voucher specimens are given by the appropriate herbarium acronym.

Anacardium occidentale L.: *Zanoni 26418* (UNSW)
Blepharocarya involucrigera F. Muell.: *Hyland 10957, 13779* (QRS)
Blepharocarya involucrigera F. Muell. (male): *UNSW 12500* (UNSW)
Buchanania arborescens (Blume) Blume: *Le Cussan 615* (QRS), *Hyland 13781* (QRS)
Canarium australianum F. Muell. (female): *B.S. Wannan 1157* (NSW, UNE)
Euroschinus falcata Hook.f. var. *falcata*: *Hyland 13336* (QRS), *13385* (QRS)
Euroschinus falcata Hook.f. var. *falcata* (male): *B.S. Wannan & Jago 970* (NSW, CANB, BRI)
Euroschinus falcata Hook.f. var. *angustifolia* Benth. (female): *B.S. Wannan + 966* (NSW)
Garuga floribunda Decne.: *B.S. Wannan 1414* (NSW), *1488* (BRI, CANB)
Loxopterygium huasango Spruce ex Engl.: *Gentry 10012* (AAU, MO)
Pistacia chinensis Bunge: *UNSW 20388a* (UNSW)
Pleiogynium timorense (DC.) Leenh.: *Fitzsimmon s.n.* QRS 083601 (QRS), *Connors 131* (QRS)
Schinus terebinthifolia Raddi: *B.S. Wannan 1040* (NSW)
Semecarpus australiensis Engl.: *Hyland 11525* (QRS), *11660* (QRS), *13406* (QRS)
Spondias cytherea Sonn. (female): *B.S. Wannan 511* (NSW, BRI)
Swintonia glauca Engl. (male): *SAN 17485* (BRI)
Swintonia schwenckii (Teijsm. & Binn.) Teijsm. & Binn. ex Hook.f.: *Kostermans 5890* (CANB)

Appendix B. Specimen examined by J.T. Waterhouse for unpublished observations.

In 1980, John T. Waterhouse recorded observations (held at UNSW) on the plants of Magela Creek, Northern Territory (now Kakadu National Park). Observations were based on the voucher specimens held at UNSW. Some of these observations were used in Table 3.

Buchanania obovata Engl.: *UNSW 10554* (UNSW).