American Journal of Botany 88(11): 2013–2025. 2001.

MYRTACEAE REVISITED: A REASSESSMENT OF INFRAFAMILIAL GROUPS[1]

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Cladistic analyses are presented of *matK* sequence data as well as a nonmolecular database for an identical set of exemplar species chosen to represent the core genera or groups of genera in Myrtaceae. Eleven robust clades are recognized on the molecular data. Polyphyly of the previously recognized *Metrosideros* and *Leptospermum* alliances is confirmed, and several smaller informal taxonomic groupings are recognized from among the members of the former alliance, i.e., the *Tristania*, *Tristaniopsis*, *Metrosideros,* and *Lophostemon* groups. The nonmolecular analysis provides only limited resolution of relationships. A degree of congruence exists between the two analyses in that two separate fleshy-fruited clades, the *Acmena* and Myrtoid groups, are identified, as are the Eucalypt and *Tristania* groups, and *Psiloxylon* and *Heteropyxis* are the first lineages to diverge in both analyses. A combined analysis recognized all 11 clades that received strong support from the molecular data. A high level of homoplasy is revealed in many of the nonmolecular characters when they are examined against the combined estimate of phylogeny.

Key words: *matK;* molecular phylogeny; morphology; Myrtaceae.

The Myrtaceae is a family of at least 133 genera and >3800 species. It has centers of diversity in Australia, southeast Asia, and tropical to southern temperate America, but has little representation in Africa. The family is distinguished by a combination of the following features: entire leaves containing oil glands, ovary half inferior to inferior, stamens usually numerous, internal phloem, and vestured pits on the xylem vessels. Until relatively recently, the family has been considered to be naturally divisible into two subfamilies, the fleshy-fruited Myrtoideae and the capsular-fruited Leptospermoideae. The first serious challenge to this came from Johnson and Briggs (1984) who concluded, from a cladistic analysis based on morphological and anatomical characters, that these subfamilies must be abandoned. In their initial analysis of Myrtales, they identified a clade containing Myrtaceae plus *Heteropyxis* and *Psiloxylon,* the last two of which are often placed in monogeneric families. Using *Heteropyxis* and *Psiloxylon* as outgroups, they then analyzed the Myrtaceae, exemplified by 14 terminal taxa. One particularly interesting conclusion emerged from this analysis: *Acmena, Syzygium,* and related genera constituted a group of fleshy-fruited genera that was separate from the other genera usually assigned to the Myrtoideae. This distinction had already been flagged by strong evidence from wood and bark anatomy (Ingle and Dadswell, 1953; Chattaway, 1959).

[1] Manuscript received 5 January 2001; revision accepted 8 May 2001.

The authors thank Pauline Ladiges, Lyn Craven, Leslie Landrum, Barbara Briggs, the late Lawrie Johnson, and particularly Amy Litt for discussions on various aspects of morphology; Nikolas Lam for field assistance; Margaret Heslewood for assistance in the lab and with manuscript preparation; Dorothy Steane (*Corymbia*), Ken Sytsma (*Calyptranthes*, *Eucalyptus*, *Tepualia*), Shane Wright (*Xanthomyrtus*), and Frank Udovicic (*Eucalyptopsis*) for DNA extracts; and Stephen Teo (*Whiteodendron*), Bernie Hyland (*Thaleropia*), and Frank Zich (*Kjellbergiodendron*) for supply of plant material. This work was supported by Australian Research Council small and large (A19602649) grants to CJQ and PGW.

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However, one limitation of this analysis was the marked disparity in the size of their terminal taxa: four were monotypic genera and the remainder were groups of from two to more than ten, often large, genera. The authors were aware that their emphasis on problematic taxa led to their 14 terminal taxa being ''of unequal status'' (Johnson and Briggs, 1984, p. 733). The most notable example of this was the lumping of a heterogeneous collection of taxa into a single terminal taxon, the *Metrosideros* group, which they themselves admitted would be better treated as smaller units.

The present study began as an attempt to score a wider range of genera from this assemblage. In the process, we reviewed the characters used by Johnson and Briggs (1984), removing autapomorphies and the weighted scoring. However, the cladogram produced by analyzing the revised data showed little resolution due to extensive homoplasy (Wilson et al., 1994).

Conti, Litt, and Sytsma (1996) used *rbcL* sequence data to study relationships in the order Myrtales. Because of the breadth of the study, only five genera of Myrtaceae were included plus *Heteropyxis* and *Psiloxylon.* One of the surprising results was that a strongly supported clade of representatives of the family Vochysiaceae appeared to be the sister-group of Myrtaceae sensu stricto (s.s.). However, in a more detailed analysis of the same data, Conti et al. (1997) showed that this relationship was not strong and their maximum likelihood analysis showed Vochysiaceae to be sister to Myrtaceae sensu lato (s.l.), including *Heteropyxis* and *Psiloxylon.* The more recent *rbcL* analysis of the eudicots by Savolainen et al. (2000) also supported the latter topology.

Gadek, Wilson, and Quinn (1996) presented a preliminary molecular analysis of Myrtaceae and its near relatives based on partial sequences of the chloroplast gene *matK.* This study, which concentrated on the position of *Heteropyxis* and *Psiloxylon,* included 13 genera of Myrtaceae s.s. as well as various outgroups. Their analysis led to a number of conclusions with taxonomic implications: (1) there is a lack of support for separate family status for *Heteropyxis* and *Psiloxylon*; (2) there is

TABLE 1. Taxon and voucher details.

Species name	Voucher details	GenBank accession number[a]
Acmena graveolens (F.M. Bailey) L. S. Sm.	Gadek s.n., UNSW	GBAN-AF368194
Agonis flexuosa (Willd.) Sweet	UNSW23029	GBAN-AF184711
Anetholea anisata (Vickery) Peter G. Wilson	UNSW23516	GBAN-AF368195
Angophora hispida (Sm.) Blaxell	UNSW22897	GBAN-AF368196
Arabidopsis thaliana (L.) Heynh.		GBAN-AP000423
Archirhodomyrtus beckleri (F. Muell.) A.J. Scott	UNSW23517	GBAN-AF368197
Arillastrum gummiferum Panch. ex Baillon	Weston 1635, NSW	GBAN-AF368198
Babingtonia tozerensis A. R. Bean	PGW 1338, NSW	GBAN-AF368199
Backhousia myrtifolia Hook.	UNSW22391	GBAN-AF368200
Callistemon polandii F. M. Bailey	Jacobs 5362 & Clarkson, NSW	GBAN-AF184705
Calyptranthes pallens Griseb.	Sytsma s.n., WIS	GBAN-AF368201
Choricarpia subargentea (C.T. White) L.A.S. Johnson	UNSW22896	GBAN-AF368202
Corymbia variegata (F. Muell.) K.D. Hill & L.A.S. Johnson	RBG892048	GBAN-AF368203
Darwinia fascicularis Rudge	Conti s.n., WIS	GBAN-AF368204
Eucalyptopsis papuana C. T. White	Udovicic 191, MEL	GBAN-AF368205
Eucalyptus curtisii Blakely & C. T. White	Conti s.n., WIS	GBAN-AF368206
Eugenia uniflora L.	PGW 1335, NSW	GBAN-AF368207
Heteropyxis natalensis Harv.	PGW 1475, NSW	GBAN-AF368208
Kjellbergiodendron celebicium (Koord.) Merrill	F. Zich s.n., NSW	GBAN-AF368209
Kunzea ericoides (A. Rich.) Joy Thomps.	UNSW23512	GBAN-AF184724
Lindsayomyrtus racemoides (Greves) Craven	Hill 2039, NSW	GBAN-AF184706
Lophostemon confertus (R.Br.) Peter G. Wilson & J.T. Waterh.	UNSW23606	GBAN-AF184707
Lysicarpus angustifolius (Hook.) Druce	Conti s.n., WIS	GBAN-AF368210
Melaleuca viridiflora Gaertn.	Hind 616, NSW	GBAN-AF184708
Memecylon elaeagni Blume	Hay 8014, NSW	GBAN-AF368211
Metrosideros macropus Hook. & Arn.	Sytsma s.n., WIS	GBAN-AF368212
Osbornia octodonta F. Muell.	UNSW23593	GBAN-AF368213
Pilidiostigma sp.	Hill 2061, NSW	GBAN-AF368214
Psiloxylon mauritianium (Hook. f.) Baill.	Briggs 7233, NSW	GBAN-AF368215
Qualea grandiflora Mart.	Gadek s.n., UNSW	GBAN-AF368216
Rhodamnia argentea Benth.	UNSW22389	GBAN-AF368217
Rhynchocalyx lawsonioides Oliver	RBG822825	GBAN-AF368218
Ristantia gouldii Peter G. Wilson & B. Hyland	PGW 1350, NSW	GBAN-AF368219
Saxifraga integrifolia Hook.		GBAN-L20131
Sinapis alba L.		GBAN-X04826
Syncarpia glomulifera (Sm.) Nied.	UNSW23246	GBAN-AF368220
Syzygium australe (Link) B. Hyland	UNSW21775	GBAN-AF368221
Tepualia stipularis Griseb.	Sytsma s.n., WIS	GBAN-AF368222
Thaleropia queenslandica (L.S. Sm.) Peter G. Wilson	UNSW23045	GBAN-AF368223
Tristania neriifolia (Sims) R.Br.	UNSW23243	GBAN-AF368224
Tristaniopsis laurina (Sm.) Peter G. Wilson & J.T. Waterh.	UNSW22390	GBAN-AF184710
Whiteodendron moultonianum (W. W. Sm.) van Steenis	Teo S75422, NSW	GBAN-AF368225
Xanthomyrtus papuana Merrill & Perry	M. Heads 6601, AK	GBAN-AF368226
Xanthostemon chrysanthus (F. Muell.) Benth.	Weston 524, NSW	GBAN-AF368227

[a] The prefix GBAN-has been added to each GenBank accession number to link the online version of *American Journal of Botany* to GenBank but is not part of the actual accession number.

strong support for the monophyly of the myrtoid group, excluding *Syzygium*; (3) there is strong support for Johnson and Briggs' (1984) *Chamelaucium* alliance, including elements formerly referred to the separate subfamily Chamelaucioideae (e.g., by Schmid, 1980); and (4) the *Metrosideros* alliance is probably polyphyletic. The study by Gadek, Wilson, and Quinn (1996) also led to conclusions relating to the evolution of the ovary and the fruit within the family, i.e., that the superior, or almost superior, ovary is plesiomorphic and that fleshy fruits have arisen more than once.

This paper critically examines the morphological characters that have been used in defining relationships of genera and tribes (alliances) in Myrtaceae and integrates these with an analysis of a complementary taxon matrix comprising molecular sequences of *matK*. This is not intended to be a comprehensive molecular analysis, rather an attempt to examine critically the morphological characters commonly used in identifying affinities in the family.

MATERIALS AND METHODS

Taxa for which sequence data were obtained and details of vouchers are listed in Table 1. Taxa were chosen either to represent the core genera/groups of Johnson and Briggs (1984) or because they had a substantial literature of nonmolecular characters, particularly wood anatomy. Once the morphological data set was fixed, a matching molecular data set was compiled for the same exemplar species.

Nonmolecular database—The nonmolecular database was developed from that of Johnson and Briggs (1984). All data were checked against the original sources cited in that paper. Autapomorphies (e.g., their characters 17, 18, 19, 20, 34, 43, 46, 47, and 53) have been excluded, and the scoring of other characters has been modified. Where more than one character scored the same information, which amounted to character weighting, these have been combined (e.g., their characters 2, 3, and 4 have been combined in our character 2; 59 and 60 are combined in 43). In all, 45 characters are retained (Table 2). Four new characters are added: 4, 11, 25, and 40. The standard scoring employed here is ''unordered multistate'' without any of the weighting used

TABLE 2. Description of nonmolecular characters and their states.

Character number	Description
1	Vessel aggregation: mostly solitary (0); mostly grouped (1).
2	Vessel to ray pitting: small and tracheidal (0); small, but nontracheidal (1); large, tending to scalariform (2); large and isodiametric (3).
3	Bordered pits in fibers: present (0); absent (1).
4	Wood fibers: nonseptate (0); septate (1).
5	Vasicentric tracheids: absent (0); present (1).
6	Wood rays: weakly heterogeneous (0); strongly heterogeneous (1).
7	Silica in wood rays: absent (0); small and sparse (1); abundant (2).
8	Apotracheal vertical parenchyma: absent (0); diffuse, not banded (1); diffuse and banded (2).
9	Paratracheal vertical parenchyma: absent (0); present, neither confluent nor banded (1); present and either confluent or banded (2).
10	Crystalliferous strands in the vertical parenchyma: absent (0); present (1).
11	Oil ducts: absent (0); small ducts in the pith and cortex (1); a few large ducts in the pith (2).
12	Indumentum: absent (0); only unicellular trichomes of the ''standard'' type present (1); multicellular trichomes present (2).
13	Bristle-glands: absent (0); incipient (papillate condition) (1); present (2).
14	Stipules: absent (0); small (1); hair-like (2).
15	Vegetative phyllotaxy: initially more or less opposite, switching to helical (0); opposite throughout (1); helical throughout (2).
16	Well-defined intramarginal vein in the leaf: absent (0); present (1).
17	Inflorescence phyllotaxy: indefinite (0); opposite (1); helical (2).
18	Inflorescence branching: panicles only (0); panicles plus thyrsoids, metabotryoids, etc. (1); thyrsoids, botryoids, etc., sometimes monads (2); monads predominating (3).
19	Recaulescence in inflorescence: present (0); absent (1).
20	Anthopodium: present and stalk-like (0); reduced or absent (1).
21	Androecium: diplostemonous (0); partial loss of the antesepalous whorl (1); obhaplostemonous (2); further reduced (3).
22	Stamen proliferation: absent (0); stamens in a single whorl (1); stamens in multiple whorls (2); stamens in phalanges (3).
23	Aestivation of stamens in the mature bud: inflexed (0); straight (1).
24	Staminal connective gland: absent (0); poorly developed (1); well developed (2).
25	Anther dehiscence: poricidal (0); dehiscing by common slits (bilocular) (1); respective slits (tetralocular) (2).
26	Pollen form: longicolpate (0); syncolpate or parasyncolpate (1); brevicolpate to porate (2).
27	Carpel number relative to the mery of the flower: isomerous (0); 1 or 2 less (1); more than 2 less (2).
28	Epigyny: gynoecium free (0); partially adnate to hypanthium (1); completely adnate to hypanthium, or very nearly so (2).
29	Exaggerated growth of the free part of the ovary: absent (0); present (1).
30	Vascularization of the ovary: axile vascularization only (0); mixed (axile and transeptal) vascularization present (1); transeptal vascular traces present (2).
31	Style base: sunken (0); not sunken (1).
32	Ovule orientation: anatropous (0); hemitropous or campylotropous (1).
33	Fruit dehiscence: dehiscent (0); tardily dehiscent (1); indehiscent (2).
34	Nature of hypanthium in fruiting stage: dry (0); fleshy (1).
35	Nature of pericarp in fruit: dry (0); fleshy (1).
36	Well-organized crystalliferous layer in testa: absent (0); present (1).
37	Form of embryo: straight (0); folded or coiled (1).
38	Form of cotyledons in mature seed: flat (0); folded (1).
39	Embryo sac: monosporic (0); bisporic (1).
40	Development of hypanthium at fruiting state: hypanthium overtopping fruit (0); hypanthium partly surrounding the fruit (1); absent or below the fruit (2).
41	Perianth mery: 5(0); 5 and 4, or 4 (1).
42	Ovulodes: absent (0); present (1).
43	Number of seeds relative to the number of ovules per locule: seeds numerous and potentially equal to ovule number (0); seeds few per fruit (1); only one seed developed per fruit (2).
44	Essential oils in glands in the leaf: absent (0); present (1).
45	Base chromosome number: 11 (0); 12 (1); <11 (2).

in the Johnson and Briggs approach. *Qualea* was used as a representative of the outgroup, Vochysiaceae, this being the exemplar taxon used by Chase et al. (1993), Conti, Litt, and Sytsma (1996), and Conti et al. (1997). Morphological data for this family are derived from Flores (1993a, b), Kawasaki (1998), A. Litt (Yale University, personal communication), and P. G. Wilson (personal observations).

Following Johnson and Briggs (1984), we have taken data from Ingle and Dadswell (1953) and augmented it with data for *Psiloxylon* (Schmid, 1980), *Heteropyxis* (Stern and Brizicky, 1958; Schmid, 1980), *Kunzea* (Patel, 1994), *Calyptranthes* (Dias-Leme, Gasson, and Nic Lughada, 1995), *Anetholea* (Wilson, O'Brien, and Quinn, 2000), and the Vochysiaceae (Quirk, 1980). The terminology of Ingle and Dadswell (1953) is adopted for wood anatomy. Wood characters for some American taxa were inferred from the general descriptions provided by Record and Hess (1943).

Myrtaceae generally have fibers with distinctly bordered pits, i.e., fibertracheids (character 3); this is usually interpreted as the plesiomorphic condition. These were recorded for most myrtaceous genera in this study, plus *Heteropyxis.* A smaller number of myrtaceous genera have fibers with simple to minutely bordered pits, i.e., libriform fibers. This condition also occurs in *Psiloxylon* and in many genera of the Vochysiaceae, all of which have septate fibers (character 4), these being crystalliferous in *Psiloxylon.*

Rays (character 6) of Myrtaceae are never homogeneous; they have been scored as either weakly or strongly heterogeneous, following the distinctions used by Ingle and Dadswell (1953). In their discussion, they define these two

conditions as (1) strongly heterogeneous, uniseriate rays or uniseriate margins of multicellular rays consisting of few to many rows of upright cells; or (2) weakly heterogeneous, multiseriate rays with a single row of square to upright marginal cells. In genera with the second type, there is no tendency for the rays to be of two distinct widths, a phenomenon found frequently in the first type.

Johnson and Briggs' (1984) character 12 (presence or absence of crystalliferous fibers) appears to be an error in terminology. As far as we are aware, and as we have noted above, *Psiloxylon* is the only genus included here that has crystalliferous fibers; these were cited by Baas and Zweypfenning (1979) as a possible basis for postulating an affinity with Lythraceae. The character is excluded here as an autapomorphy. Johnson and Briggs presumably had the character ''presence or absence of crystal strands in the axial parenchyma'' in mind; these are relatively common and have been scored here as character 10.

Oil ducts (character 11) are a feature of a small number of genera but are quite variable in form. We have scored two basic types, as seen in transverse section (TS) of the petiole: small ducts both inside and outside the vascular strand (Welch, 1923), as in *Lophostemon* (state 1); and ducts (usually relatively large) occurring only within the vascular strand, as in *Corymbia* (state 2). We have scored *Arillastrum* as positive for the latter state but ducts do not occur in the petioles of all individuals (P. G. Wilson, personal observation); however, ''oil tubes'' are reported to occur in other tissues (Dawson, 1970). In *Arillastrum*, these may be a characteristic of juvenile plants as they are in some other members of the eucalypt group (Carr and Carr, 1969). Johnson and Briggs (1984) scored oil ducts as three different characters, distinguishing between stem ducts and petiole ducts; this needs further investigation, but the study by Carr and Carr demonstrated that they were not independent of each other, at least in eucalypts. Various members of Vochysiaceae, including *Qualea*, are reported to have ''traumatic axial gum ducts'' in their stems (Quirk, 1980). Although Ingle and Dadswell (1953, p. 397) noted that these are similar to those that occur in some members of the eucalypt group, we do not consider these gum ducts to be homologous with the oil ducts in Myrtaceae, and they are not scored as such.

For indumentum (character 12), we have scored three states: glabrous, ''standard,'' and multicellular hairs. ''Standard'' hairs are defined by Briggs and Johnson (1979) as ''acute, rather thick-walled, and unicellular (with no basal cell),'' but they list a number of variants, including hairs that are curled, bent, basally saccate, and two-armed. In Johnson and Briggs (1984), five different hair types are scored but four of these are autapomorphies and have no value in terms of phylogenetic reconstruction; for the purposes of this study, these four are considered variants of the standard hair type. It is possible that the thin walled, blunt-ended hair type has phylogenetic significance, but probably only within the eucalypt clade (Ladiges and Humphries, 1983). Multicellular hairs occur in *Angophora* (Johnson, 1972; Ladiges, 1984) and have been recorded for *Allosyncarpia* (Blake, 1977), a taxon not included in the present analysis. They are also found very rarely in *Syzygium* but they are not typical of the genus and have not been scored here. *Arillastrum* has short, branched hairs on the hypanthium (one of the autapomorphic characters in the Johnson and Briggs analysis), and Dawson (1970) reported short, multicellular hairs on the epicotyl. The latter, however, could not be independently confirmed, so multicellular hairs are not scored for this taxon in the present analysis. On present knowledge, *Eucalyptopsis* is glabrous.

''Bristle-glands'' (character 13) are distinctive structures characteristic of some members of the eucalypt group (Johnson, 1972; Ladiges, 1984). We have followed Johnson and Briggs (1984) in scoring these as present (state 2) in *Angophora* (and *Corymbia*) and incipient in other eucalypts (state 1). Ladiges (1984) has shown that emergent glands are present on juvenile foliage of the ''Monocalyptus'' group of eucalypts and absent in the ''Symphiomyrtus'' group. No member of the latter group is scored in the present analysis but, in this case, the absence of bristle glands appears to be the result of secondary loss rather than absence, as in the rest of the family.

Stipules (character 14) have been scored as absent, small, or hair-like. Small stipules (state 1) are paired but mostly inconspicuous and visible only on new growth near the apex of the shoot; only rarely, for example in *Calytrix*, are they readily discernible. Hair-like, or rudimentary, stipules (state 2) are often more numerous and have been documented and illustrated in Myrtaceae by Weberling (1956, 1966, 2000); these are not particularly easy to observe where herbarium material is limited and, in these cases, we have scored the character as unknown (?).

Vegetative phyllotaxy (character 15) was scored as two characters by Johnson and Briggs (1984) but we have treated it as one character with three states. Whereas the exemplar species of *Xanthostemon* (*X. chrysanthus*) has spiral phyllotaxis throughout (state 2), there are a few species that show an additional state, i.e., spiral seedling phyllotaxis that changes to opposite (Wilson, 1990); this state may have arisen more than once in this genus. The only other genus of Myrtaceae known to show this state is *Barongia* (Wilson and Hyland, 1988).

In the case of the intramarginal vein (character 16), Johnson and Briggs (1984) consider brochidodromy to be the plesiomorphic state, with strengthening of the vein arches leading to apomorphic states in which an intramarginal vein and/or various degrees of acrodromy are apparent. Examples of the wide variation that occurs in the family can be seen in Klucking (1988) and Christophel and Hyland (1993). Although Johnson and Briggs (1984) considered that this tendency had occurred along several separate lineages, we have been unable to distinguish separate states of acrodromy; all the derived forms are scored as a single apomorphic state.

Inflorescence characters follow Briggs and Johnson (1979) but scoring differs from Johnson and Briggs (1984); inflorescence phyllotaxy (character 17), for example, combines two of their characters. For ''inflorescence branching'' (character 18) we have redefined their scoring in terms of the actual inflorescence types (as scored in Briggs and Johnson, 1979), with two levels of reduction between panicle (state 0) and monad (state 3). It should be noted that indeterminate (blastotelic) raceme-like aggregations of monads are scored according to the unit inflorescence, i.e., the monad. In the monad and triad, in particular, the distinction between the pedicel and the anthopodium (character 20) has not been widely recognized, even after Briggs and Johnson (1979) pointed out its significance.

The androecium (character 21) is rather complex and difficult to score. The outgroup, Vochysiaceae, is basically obhaplostemonous (A. Litt, personal communication) but the androecium is consistently reduced to a single fertile stamen (see Fig. 6 in Kawasaki, 1998) and up to four staminodes; we have scored this as an autapomorphy (state 3). The diplostemonous condition (state 0) is found in *Psiloxylon* (Schmid, 1980), and a partial loss of the antesepalous whorl (state 1) seems to have occurred in *Heteropyxis* (Stern and Brizicky, 1958; Fernandes, 1971). In Myrtaceae s.s., Johnson and Briggs (1984, pp. 739–741) conclude that the basic condition is obdiplostemony with frequent suppression of the antesepalous whorl. They drew their conclusions from published observations of small groups of antesepalous stamens in some specimens of *Arillastrum* (Dawson, 1970) and from the observation by Bunniger (1972) of antesepalous staminal primordia developing after the antepetalous primordia in one species of *Luma* (as *Myrceugenella*). In fact, in their Table 5, Johnson and Briggs scored the myrtoids as a whole as showing this state, even though Bunniger did not observe antesepalous primordia in the other myrtoid taxa he studied (*Psidium* and *Eugenia*) and Payer (1857) did not record them in *Myrtus.* We interpret the situation in *Luma* as either a vestige of the plesiomorphic condition or a reversion towards obdiplostemony.

The work of Orlovich, Drinnan, and Ladiges (1996, 1999) has provided confirmation that, in most genera in the family, staminal primordia arise at, or adjacent to, the bases of the developing petals. In the genera they have studied, stamen initiation has occurred either within a prestaminal bulge or directly on the floral apex. They have argued (1996) that the view of Myrtaceae being basically obhaplostemonous with subsequent proliferation is not supported by their observations, since the prestaminal bulge cannot be interpreted as a single stamen primordium. The basal position of *Psiloxylon* in the Myrtaceae s.l. has been supported by molecular data (Gadek, Wilson, and Quinn, 1996), and this gives some support to Schmid's (1980) suggestion that the plesiomorphic condition in the family was likely to be diplostemony. Thus, the usual situation in the Myrtaceae s.s., although apparently a de novo development, is no doubt derived from this plesiomorphic state, perhaps via some form of obdiplostemony, and we continue use of the classical terminology as a shorthand.

Many groups, however, have yet to be investigated and, in the absence of firm data, taxa have mainly been scored as obhaplostemonous (state 2). We have not scored obdiplostemony, as it has not definitely been recorded for any of the taxa included here. For reasons stated above, *Arillastrum* has been scored as showing partial loss of the antesepalous whorl (state 1); its near relative, *Eucalyptopsis*, has been scored similarly, following Johnson and Briggs (1984). *Thaleropia* and *Tristania* occasionally have stamens that appear to be initiated in an antesepalous position (Orlovich, Drinnan, and Ladiges, 1996), and these taxa also have been scored as showing partial loss of the antesepalous whorl.

Stamen proliferation (character 22) proceeds in various ways from the staminal primordia. Stamens appear in a single row (state 1) but in some taxa further rows arise centripetally so that the mature androecium has two to many rows (state 2). Alternatively, development of the group of stamens without any lateral spreading can result in a staminal fascicle (state 3). The final form of the androecium depends on whether the stamens expand radially to occupy the available space on the rim of the hypanthium or remain clustered in front of the petals, with or without fusion. As noted by Orlovich, Drinnan, and Ladiges (1996, 1999), staminal clustering is usually the result of stamen initiation on a distinct antepetalous prestaminal bulge, whereas a more-or-less continuous ring of stamens often results from the staminal initials arising directly on the hypanthial wall in front of the developing petal primordium. The aestivation of the stamens in the mature bud (character 23) may be a significant character; they are erect in *Heteropyxis* and *Psiloxylon* (Schmid, 1980) and Vochysiaceae, but inflexed in Lythraceae, Melastomataceae, and most Myrtaceae.

Character 25, ''anther dehiscence,'' has been added. Anthers are uniformly tetralocular in the family, but Tobe and Raven (1987, 1990) have shown that *Heteropyxis* and *Psiloxylon* have anthers in which each locule opens by a separate slit (state 2). This is in contrast to most other genera in which the pair of locules in each anther cell open by a common slit (state 1). The latter state is clearly plesiomorphic, and the only other genus in Myrtales that has the former type of anther dehiscence is *Rhynchocalyx* (Rhynchocalycaceae).

Pollen form (character 26) is scored following the categories used by Patel, Skvarla, and Raven (1984), augmented by data from Pike (1956) and Gadek and Martin (1981). Pollen of Vochysiaceae is longicolpate (which we have scored as plesiomorphic) but grains are oblate spheroidal rather than oblate (Erdtman, 1952, p. 452). For pollen, Johnson and Briggs (1984) scored two separate characters, i.e., ''loss of syncolporate condition'' (which was scored as an autapomorphy for *Kjellbergiodendron*) and ''pollen with very large polar islands'' (which was scored as an autapomorphy for *Psiloxylon*). We have scored a single character with three states.

Ovary vascularization (character 30) could not be determined with any certainty in taxa with a single locule (e.g., *Darwinia*) or with basal placentation (e.g., *Lysicarpus*). Scoring of ''mixed'' vascularization follows Johnson and Briggs (1984, character 45).

With character 38, ''form of the cotyledons,'' the folded state is very diverse, ranging from cotyledons individually folded as in *Arillastrum*, to the obvolute/convolute type seen in *Tristaniopsis* and *Lophostemon*. The complex ruminate cotyledons of *Acmena* and the variable, thick cotyledons of *Lindsayomyrtus* (Hyland and van Steenis, 1973) are scored as uncertain (?) but the thick cotyledons of *Syzygium australe* are partly interlocking and are scored as folded (state 1).

The mode of embryo sac formation (character 39) is considered by Tobe and Raven (1987) to be quite significant. The vast majority of Myrtalean taxa (including all Myrtaceae) that have been examined have the *Polygonum* type of development but *Heteropyxis* and *Psiloxylon* have the *Allium* type. As Tobe and Raven (1987, 1990) point out, the *Allium* type of development is rare, being recorded elsewhere in Myrtales only in *Alzatea* (Alzateaceae).

The number of seeds relative to the number of ovules per locule (character 43) combines characters 59 and 60 of Johnson and Briggs (1984). Seed number is related to reproductive strategy, which is itself partly correlated with fruit type. Most genera in the present analysis are scored as plesiomorphic even though fertile seeds are frequently only a small percentage of seed-like objects (seed + ''chaff'') in the fruit; this is because there is no fixed pattern of seed set and all ovules appear to have the potential to become seeds. The second character state (seeds few per fruit) has been scored for two groups of genera: those with ovulodes that never become seeds and those with a more-or-less fixed pattern of seed set. The third character state (single seed per fruit) is mostly found in indehiscent fruits, the exception, in this data set, being *Whiteodendron*.

The presence of oil glands (character 44) that produce essential oils is one of the fundamental features of the family Myrtaceae s.s. *Heteropyxis* also has oil-bearing glands in the leaves, and these produce an oil that contains >90% monoterpenes (Weyerstahl et al., 1992), a rather simple complement of oils. *Psiloxylon* has leaf glands (Scott, 1980) but these do not produce any essential oils (J. J. Brophy, University of New South Wales, personal communication); glands have long been known to occur in this genus but were not considered different from similar glands that occur in Bixaceae and Flacourtiaceae (de Cordemoy, 1895).

Base chromosome number (character 45) is a potentially useful character in some parts of the family. There is considerable dysploid reduction within the *Chamelaucium* suballiance, with considerable variation in haploid number within genera. This trend is scored under state 2; in this database there is only one example, $n = 6$ in *Darwinia fascicularis*, although within the genus it varies from $n = 5$ to 11 (Smith-White, 1954; Briggs, 1962; Rye, 1979). There are two records for Vochysiaceae, both in *Vochysia* ($n = 11$, Goldblatt, 1979; $n = 12$, Berry, 1987), and these data are extrapolated to provide the ambiguity scored for *Qualea* in this analysis.

These characters have been scored (Table 3) for the same set of exemplar taxa for which sequence data are available, so as to score some of the variation within the groups that were the terminal taxa in the Johnson and Briggs (1984) analysis. Hence, the number of taxa has been considerably expanded. The nomenclature used has also been updated.

Characters were polarized by the outgroup method. Since there are problems in establishing homologies among the more distant outgroups included in the molecular analysis, the morphological analysis was rooted using *Qualea*, a representative of Vochysiaceae. As noted earlier, there is strong support from the molecular data for this being the sister family to Myrtaceae s.l.

Molecular database—DNA was extracted either by the hot CTAB (hexadecyltrimethyl ammonium bromide) method of Doyle and Doyle (1990) or using the plant DNeasy Minikit (Qiagen, Clifton Hill, Victoria, Australia) following a liquid nitrogen grind. Double-stranded templates were amplified in a Thermocycler (Perkin Elmer, Norwalk, Connecticut, USA) and purified in Wizard Preps PCR (polymerase chain reaction) columns (Promega, Annandale, New South Wales, Australia). Sequences were obtained by manual sequencing using radionucleotide labelling (Gadek, Wilson, and Quinn, 1996) or automated sequencing on an ABI Prism 377 DNA Sequencer (Perkin Elmer, Norwalk, Connecticut, USA) using fluorescent dye-labelled terminators. Electropherograms were processed using ABI software, Factura and Autoassembler. Sequences were aligned using DNA and Protein Sequence Alignment software (DAPSA; Dr. E. Harley, University of Cape Town, Cape Town, South Africa). Primers used were as per O'Brien, Quinn, and Wilson (2000).

At present, neither morphological nor DNA data provide robust evidence of any taxon within Myrtales being the unambiguous sister to Myrtaceae s.l. *Memecylon* and *Qualea* were included as representatives of possible sister families, Memecylaceae and Vochysiaceae, as indicated by Conti, Litt, and Sytsma (1996) and Conti et al. (1997). *Rhynchocalyx* was included as a more distant Myrtalean representative, *Arabidopsis* and *Sinapis* were included to represent the closely related order Brassicales [Capparales] (Chase et al., 1993; Angiosperm Phylogeny Group, 1998), and an unambiguously distant taxon, *Saxifraga*, was used to root the analysis.

Analyses—Heuristic searches were conducted in PAUP* version 4.0b8 (Swofford, 2001) using TBR (tree bisection reconnection) branch-swapping to recover the most-parsimonious trees. In all analyses, 100 replicates of random taxon addition were conducted with the heuristic search option, in order to establish whether there was more than one island of trees. To assess the impact of homoplasy in the molecular data, the trees generated were then used as starting trees in heuristic searches employing successive approximations weighting (SAW) according to the mean rescaled consistency index (RC)

TABLE 3. Nonmolecular database. Full taxon details given in Table 1. Characters and states are as in Table 2. Inapplicable character = -, state unknown = ?; polymorphisms are within parentheses.

	Character numbers										
						11111111	1	1222222	2	222333333333344444	4
Taxon	1	2345	6	7	8	9	01234567	8	9012345	6	789012345678901234	5
Acmena	1	2100	1	0	0	2	00002101	0	1022021	1	220010211 0?001021	0
Agonis	1	0001	0	0	1	1	00102210	3	1121021	1	110001000000000001	0
Anetholea	1	2100	0	0	0	1	00001101	1	0022011	1	220010200?01001021	0
Angophora	1	3001	0	0	1	2	10220101	2	1022021	1	110111000100001111	0
Archirhodomyrtus	0	0001	1	0	1	0	00102101	2	1122021	0	120210211010000001	0
Arillastrum	0	3001	0	0	1	2	02000100	2	1112021	1	110111000101000111	0
Babingtonia	0	0001	0	0	1	0	00002111	2	1121020	1	110001000010000001	0
Backhousia	0	0001	0	0	2	(01)	00102101	1	1022021	1	210011200011000021	0
Callistemon	0	1001	0	2	1	0	00100010	3	1122021	1	110001000100000001	0
Calyptranthes	0	000?	1	0	2	1	?0102101	0	1122021	0	120210211011000001	0
Choricarpa	0	0001	0	0	2	0	00102101	1	1122021	1	210002000011000021	0
Corymbia	(01)	3001	0	0	1	2	12020000	1	1022021	1	110111000100000111	0
Darwinia	0	????	?	?	?	?	?0000100	3	1121?20	2	220-10200?10000021	2
Eucalyptopsis	1	3100	0	0	1	2	0000?100	1	1112021	1	210111000101000111	0
Eucalyptus	0	3001	0	0	1	1	10010011	1	1022021	1	010111000101001101	0
Eugenia	0	0001	1	0	2	0	10102101	3	1122021	(01)	220210211010000021	0
Heteropyxis	(01)	?000	1	0	0	0	00101200	0	0010122	(01)	101001000100110001	1
Kjellbergiodendron	0	2001	0	0	1	2	12101?00	1	0122021	0	210200211001000021	0
Kunzea	0	0001	(01)	0	1	(12)	10102?20	3	1021021	1	110000000000000001	0
Lindsayomyrtus	0	??01	0	2	2	0	1200??00	1	1022021	?	111010100 00?020011	0
Lophostemon	0	1001	0	2	1	1	01102000	2	0023021	1	110210000001000001	0
Lysicarpus	0	1001	0	2	1	0	0010?101	2	1022021	1	111010000000010001	0
Melaleuca	0	1001	0	2	1	1	00100012	2	1123021	1	110000000101000001	0
Metrosideros	0	1001	1	1	1	0	00102101	2	1022021	1	111000000000000001	0
Osbornia	0	100?	1	2	2	1	0010?101	2	11?2021	1	220011200000001021	0
Pilidiostigma	0	0001	1	0	1	0	00102101	2	1122021	(01)	120210211010000001	0
Psiloxylon	1	?110	1	?	0	1	00101212	1	0000112	1	10-0112-1100120000	1
Qualea	0	0110	0	1	(12)	(12)	10101110	2	1030101	0	101011000101?20?10	(01)
Rhodamnia	0	0001	1	0	2	1	00102101	2	1122021	0	120210211010000001	0
Ristantia	0	1001	0	2	1	?	00100200	0	0022021	1	111010000001020011	0
Syncarpia	0	1001	0	2	1	1	01102101	2	0122021	1	110??0000001000001	0
Syzygium	1	2100	1	0	0	2	10002101	2	1022021	1	220010211001001021	0
Tepualia	?	1???	?	?	?	?	?0?02101	3	1021021	1	110000000000000001	0
Thaleropia	0	1001	1	2	1	0	00102101	0	0011021	2	110000000000000001	0
Tristania	0	1001	0	2	1	0	00102101	1	0011021	2	110000000000000001	0
Tristaniopsis	0	1001	0	2	1	?	00102201	2	0023021	1	111011000101010001	0
Whiteodendron	0	??0?	?	?	?	?	0200??10	1	0023021	1	111210000001020021	0
Xanthomyrtus	?	1101	1	0	2	0	00102101	2	1122021	0	120210211010000001	0
Xanthostemon	0	1001	0	2	2	0	00102201	(12)	0022021	1	111011000110020001	0

with the base weight set at 1 (Farris, 1969). This was repeated until tree length reached a constant value. In the combined analysis, all data were given the same weight. Relative support for the clades identified by parsimony analysis was estimated using the bootstrap option in PAUP. On the separate analyses of the nonmolecular and molecular data, the numbers of trees found in some replicates exhausted available computer memory. For this reason the number of trees saved in each replicate was limited to 10, and the number of replicates was set at 5000. No such limit was necessary in the analysis of the combined data; in this case the number of replicates was 500. Decay values were determined using AutoDecay (version 4.0.2'; Eriksson, 1999) and heuristic searches in PAUP* with 30 replicates of random taxon addition. Hypotheses of character evolution were examined by using MacClade (version 3.08a; Maddison and Maddison, 1999) to plot the morphological data onto trees generated from the combined data. Constraint trees were constructed in MacClade and imported into PAUP in order to conduct constraint analyses to test alternative hypotheses of evolution of nonmolecular characters.

RESULTS

Nonmolecular analysis—A heuristic search of the nonmolecular database retrieved 144 equally parsimonious trees of 234 steps in two islands (consistency index [CI] = 0.36 excluding uninformative characters, retention index [RI] = 0.62, and rescaled consistency index [RC] = 0.22). The strict consensus of these trees is shown in Fig. 1; bootstrap values >50% and decay values >1 are shown on the branches. *Psiloxylon* and *Heteropyxis* are the first lineages to diverge, but the sister relationship (cf. Fig. 1 in Gadek, Wilson, and Quinn, 1996) between them is not resolved. Monophyly of Myrtaceae s.s. is supported by 77% bootstrap (bs), and +3 decay. Several subclades receive support: the *Acmena* group (79% bs, +4 decay), the Eucalypt group (67% bs, +3 decay), and the *Tristania* group (89% bs, +3 decay). The Myrtoideae s.s. (the Myrtoid group) is also identified, but both the group and its internal topology collapse at +1 step. Relationships between the remaining taxa are unresolved.

Molecular analysis—The *matK* database consisted of sequences for the same taxon set as above, as well as the additional outgroup representatives specified earlier. Sequences extend from 20 base pairs (bp) before the start codon in *Saxifraga*, which is 67 bp downstream from that indicated for *Sinapis* (Johnson and Soltis, 1994). The first 103–107 bp were

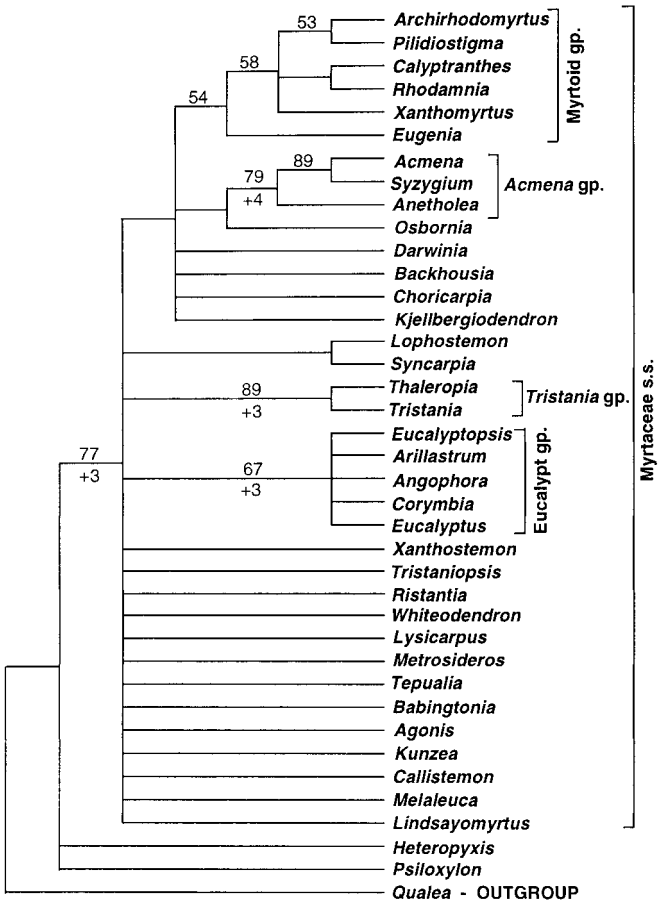

Fig. 1. Strict consensus of 144 equally parsimonious trees of 234 steps in two islands found from heuristic search of the nonmolecular database; CI = 0.36, RI = 0.62, RC = 0.22. Bootstrap percentage values >50% are shown above the branches (5000 replicates with 10 trees saved in each replicate); decay values >1 are shown below the branches.

Figure Abbreviations: CI = consistency index excluding uninformative characters; gp = group; RI = retention index; RC = rescaled consistency index.

missing from the sequences of *Corymbia*, *Ristantia*, and *Tristania*, and sequences for *Eucalyptopsis*, *Rhynchocalyx*, and *Xanthomyrtus* had 238, 434, and 188 bases, respectively, undetermined near the middle of the gene. All sequences were complete at the 3′ end except *Psiloxylon*, which lacked 19 bases.

Alignment required 21 indels, each involving up to 12 complete codons. The aligned database consisted of 1601 bp and included 496 potentially informative characters. Ten indels were potentially informative (Table 4); these were scored as additional characters and added to the database. Uncorrected pairwise sequence divergences ranged up to 7.2% (*Rhodamnia* to *Babingtonia*) within the ingroup.

Heuristic search retrieved a single island of 12 equally parsimonious trees of 1696 steps (CI = 0.59 excluding uninformative characters, RI = 0.63, and RC = 0.43). Figure 2 shows the strict consensus. There is strong support for the monophyly of the Myrtales (100% bs) and for Myrtaceae s.l. including Psiloxylaceae and Heteropyxidaceae, (100% bs). The sister relationship of *Qualea* (Vochysiaceae) to Myrtaceae s.l. and the affinity between Psiloxylaceae and Heteropyxidaceae also receive strong support (94% and 99%, respectively). Support for Myrtaceae s.s. is also strong (95%). A number of robust clades labelled A–M are recognized within Myrtaceae s.s. (Fig. 2), but relationships between them are mostly unresolved or unsupported. The first diverging lineage comprises a highly robust *Lophostemon* group (100%; clade M), together with *Xanthostemon.* Support for the entire group is only moderate (75%). The next lineage comprises the *Melaleuca* group (99%; clade L) together with *Osbornia*, but the entire clade is unsupported. Above this, clades A–D are grouped as sister to clades E–K. There is, however, no substantial bootstrap support for any of this basal topology within Myrtaceae s.s. Support for the grouping of *Lindsayomyrtus* with the *Leptospermum* group (64%; clade G) and *Xanthomyrtus* with the *Tristania* group (72%; clade B) is weak, and there is no support for the clustering of *Syncarpia* with the Eucalypt group (clade K).

TABLE 4. Informative indels scored.

Indel	Positions affected
1	132–140
2	138–140
3	147–152
4	240–275
5	288–293
6	555–557
7	612–617
8	649–654
9	660–671
10	843–845

The distribution of informative indels provides support for some of the topology. Indel 10 supports the monophyly of Myrtales, and Myrtaceae s.s. is supported by indel 7, a 6-bp deletion relative to the outgroups. The Myrtoid group is characterized by a 3-bp insertion (indel 2) that overlaps indel 1, a 9-bp insertion that occurs in *Memecylon*, *Rhynchocalyx*, and Brassicaceae. The 9-bp insertion has not been found in any of the other Myrtalean outgroups examined; under this circumstance it is more parsimonious to postulate separate origins for this indel inside and outside the Myrtales. Wider sampling reveals that indel 2 occurs in all members of the Myrtoid group that we have examined so far (P. G. Wilson and M. M. O'Brien, unpublished data). Within the Myrtoids, a 36-bp deletion (indel 4) supports the grouping of the three predominately Australian genera, *Rhodamnia*, *Pilidiostigma*, and *Archirhodomyrtus.* A 6-bp insertion (indel 5) supports the grouping of *Corymbia* with *Angophora.* Indel 6 is a 3-bp insertion that occurs in *Callistemon* and *Rhodamnia*; there is a single base difference between the inserted sequences (GGA cf. AGA, respectively), which may be seen as evidence supporting two origins of this length variant.

The successive approximations weighting analysis produced three equally parsimonious trees of 859.7 steps (CI = 0.80, RI = 0.84, RC = 0.75), but the strict consensus of these showed only one change (cf. Fig. 2) affecting an unsupported part of the tree: clade H became the sister group to clade D. All the well-supported clades were still present, and there was an increase in bootstrap support for some of the weakly supported clades.

An analysis of the combined data (all characters unweighted) yielded two equally parsimonious trees of 1217 steps (Fig.

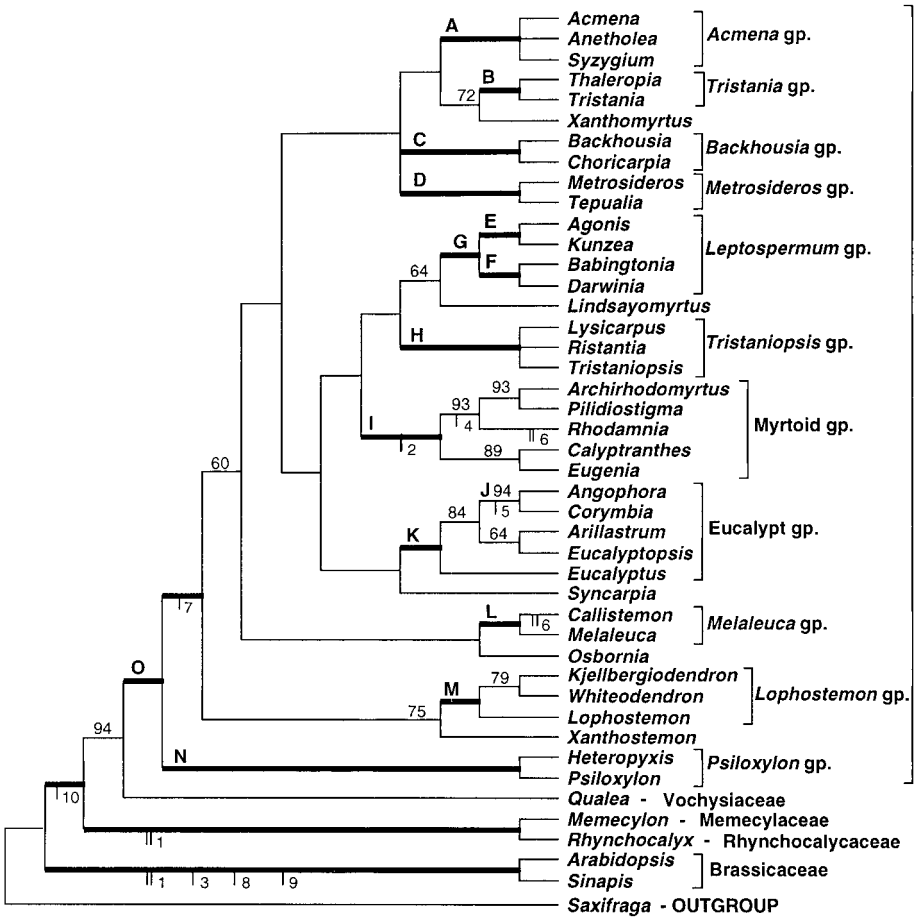

Fig. 2. Strict consensus of 12 equally parsimonious trees of 1696 steps in a single island found from heuristic search of the *matK* data; CI = 0.59, RI = 0.63, RC = 0.43. Clades marked by thick stem branches received at least 95% bootstrap support; lower values >50% are shown on the branches. Indels 1–10 (see Table 4) are mapped on the tree; single bar indicates unique indel; double bar indicates homoplastic indel.

3; CI = 0.51, RI = 0.62, RC = 0.39). Again, all the labelled clades identified in Fig. 2 were retrieved. The differences between these trees involve only clades that are unsupported or weakly supported in Fig. 2. The *Melaleuca* group (clade L) is now sister to the *Eucalypt group* (clade K). Several of the individual taxa that were placed in less well-supported positions have also moved. *Osbornia* and *Xanthomyrtus* are now the respective sister taxa of the *Acmena* group (clade A) and Myrtoid group (clade I); in the latter case there is some support for the association (75% bs, +3 decay). *Xanthostemon* is now the first lineage to diverge within Myrtaceae s.s., and the relationships of *Syncarpia* are incompletely resolved.

DISCUSSION

The molecular analysis indicates a number of relationships that are in line with recent thinking on the family, as well as a number that have not been suggested.

The *Lophostemon* group (clade M, Fig. 2) represents an early diverging lineage within Myrtaceae s.s. Johnson and Briggs (1984) scored *Kjellbergiodendron* and *Whiteodendron* separately, and their analysis placed these genera together as sister to a clade comprising *Lindsayomyrtus* and the *Acmena* group. The molecular analysis confirms the sister relationship of the first two genera but neither *Lindsayomyrtus* nor the *Acmena* group appear to be closely related to them; instead *Kjellbergiodendron* and *Whiteodendron* are robustly grouped with *Lophostemon.*

Although there is some support (75% bs) for the link between *Xanthostemon* and clade M in the molecular data, the remainder of the *Metrosideros* group of Johnson and Briggs (1984, their Table 3) are scattered through the cladogram. *Metrosideros* clusters robustly with *Tepualia* (clade D, 100% bs), *Thaleropia* (formerly *Metrosideros* sect. *Adnatae* J.W. Dawson) is sister to *Tristania* (clade B, 100%), as suggested by Wilson (1993), and *Tristaniopsis*, *Ristantia*, and *Lysicarpus* are grouped (99%) in clade H. None of these clades shows any affinity with another in this group.

There is a very strongly defined Eucalypt group, and within it there is 94% bs support for *Corymbia* as sister to *Angophora* rather than to *Eucalyptus* s.s.; this is supported by the distribution of indel 5 (see above and Fig. 2). This pattern of relationship is in agreement with other molecular studies (Udovicic, McFadden, and Ladiges, 1995; Ladiges and Udovicic, 2000), is supported by morphological evidence (Ladiges, 1984), and lends credence to the segregation of *Corymbia* from *Eucalyptus* s.l. (Hill and Johnson, 1995).

The *Leptospermum* group of Johnson and Briggs (1984), which included both the *Leptospermum* and *Calothamnus* suballiances, is not retrieved. On the sample represented here, the

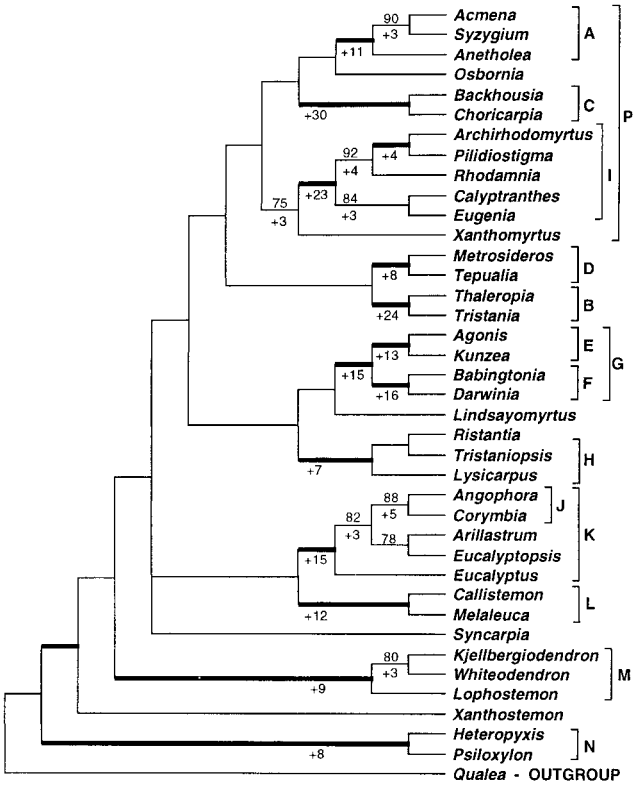

Fig. 3. Strict consensus of two trees of 1217 steps found from heuristic search of the combined molecular and nonmolecular data (all unweighted) with 100 replicates of random taxon addition; CI = 0.51, RI = 0.62, RC = 0.39. Clades marked by thick stem branches received at least 95% bootstrap support (500 replicates, full heuristic search); other values >50% are shown above branches; decay values >2 are shown below.

Chamelaucium group (clade F) is strongly indicated as sister to the *Leptospermum* suballiance (Briggs and Johnson, 1979; clade E), while the *Calothamnus* suballiance (= *Beaufortia* suballiance of Johnson and Briggs, 1983) are placed at a distance in clade L.

Fleshy-fruited taxa do not form a monophyletic group. The *matK* analysis confirms that the *Acmena* group has arisen independently of the Myrtoid group and that *Anetholea* (Wilson, O'Brien, and Quinn, 2000) is a member of it. An interesting result is that *Xanthomyrtus* does not cluster with the Myrtoid group but is loosely associated with the *Tristania* group; this is in agreement with the assertion, based on seed and embryo morphology, that the genus does not belong in the Myrtoideae s.s. (Landrum and Stevenson, 1986). It is clear from the analyses presented here that, based on its position in the phylogeny, the group of genera identified here as the Myrtoid group do not form a taxon of subfamilial rank; they would be more appropriately placed in a tribe, i.e., Myrteae.

Although there is good character support for most of the major clades in the family, the relationships between them are mostly unsupported (<50% bs). This may be the result of rapid evolutionary diversification within the family in response to the strongly selective environmental changes that occurred at the time of increasing aridity in the Oligocene/Miocene, resulting in the widespread appearance of sclerophyllous vegetation. Alternatively, it could be the result of early genetic isolation of the progenitors of the major clades in the family followed by ''gradualistic'' change. The fact that the successive approximations weighting analysis did not produce any increase in resolution or character support for clades is interpreted as evidence that the lack of a well-supported resolution of basal relationships in the family is due to insufficient characters rather than excessive homoplasy. This tends to favor the first alternative described above. Hence, additional sequence data from a region of similar variability is needed to address this situation, rather than data from a more conservative region.

Virtually all clades in the family have representatives in Australia, which suggests that these progenitors of the family as we know it were located in east Gondwana in the late Cretaceous, although the sister taxa to the Myrtaceae s.s., *Psiloxylon* and *Heteropyxis*, appear to be of west Gondwanan origin. Recent reassessment of the fossil evidence suggests the family may have been present by the middle Eocene (Manchester, Dilcher, and Wing, 1998).

The estimate of phylogeny derived from the analysis of the morphological data (Fig. 1) is poorly resolved and mostly very weakly supported, despite the reevaluation of the characters. Two separate clades of fleshy-fruited taxa are recognized (the Myrtoid and *Acmena* groups), but *Kjellbergiodendron* and *Xanthomyrtus* are ungrouped. Johnson and Briggs (1984) recognized *Acmena* and *Syzygium* as members of a lineage separate from the remaining fleshy-fruited taxa, and this group, together with *Anetholea* (Wilson, O'Brien, and Quinn, 2000), is one of the most strongly supported clades in the morphological analysis (79% bs, +4 decay).

The combination of the nonmolecular and molecular data did not affect the recognition of any of the labelled clades (cf. Figs. 2 and 3). It did, however, result in some degree of support (75% bs, +3 decay) for a link between *Xanthomyrtus* and the Myrtoid group. The different placements of *Xanthomyrtus* in the molecular and combined analyses indicates the need for caution in drawing firm conclusions on the relationships of this genus. Further data are needed to test the alternative hypotheses. Otherwise, changes between Figs. 2 and 3 are unsupported in either case. *Osbornia*, which is weakly associated with the *Melaleuca* group in Fig. 2, is the unsupported sister to the *Acmena* group in Fig. 3. There is now a sister relationship (<50% bs) between the Eucalypt and *Melaleuca* groups (clades K and L). The two fleshy-fruited groups (clades A and I) are now included, along with the *Backhousia* group, *Osbornia* and *Xanthomyrtus*, in an unsupported monophyletic assemblage (clade P).

There is marked homoplasy in many of the nonmolecular characters. Two 2-state characters (6 and 10) require 6 steps each on Fig. 1. Almost every morphological character displays some degree of homoplasy on the molecular and combined estimates of phylogeny. In some cases there is extreme homoplasy: e.g., characters 20 (presence/absence of an anthopodium) and 38 (flat/folded cotyledons) each require 9 steps on Fig. 3, while the four-state character 18 (inflorescence branching) requires a total of 20 steps on Fig. 3. Nevertheless, there are some characters that do correlate with strongly supported features of the molecular-based topology.

The separation of *Psiloxylon* and *Heteropyxis* from Myrtaceae s.s. is confirmed by (1) the stamens in the mature bud being straight rather than inflexed (character 23/state 0, Fig. 4; this state also occurs in the greatly reduced androecium of *Qualea*), (2) the anther cells dehiscing by separate slits (25/2, Fig. 4), and (3) the bisporic embryo sac (39/1, Fig. 5). Vasi-

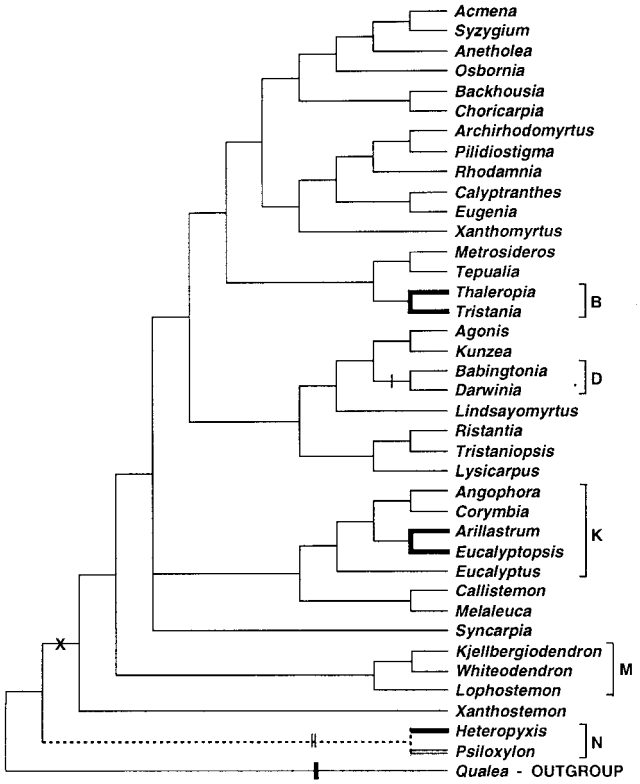

Fig. 4. Distribution of some androecial characters shown on the strict consensus of the two trees obtained from the combined analysis; clades labelled as in Fig. 3. Androecium (character 21): double branch indicates diplostemony; thick branch indicates partial loss of antesepalous whorl; thin branch indicates obhaplostemony; thick bar indicates further loss. Anther dehiscence: thin single bar indicates change to poricidal locules (25/0); double bar indicates change to locules opening by separate slits (25/2). Aestivation of stamens: X indicates change to stamens inflexed (23/0).

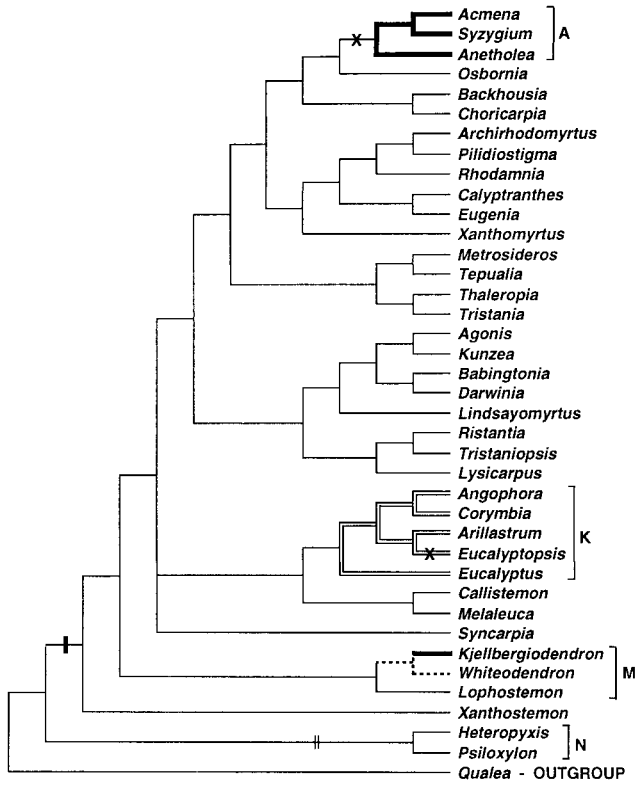

Fig. 5. Distribution of states of some nonmolecular characters on the strict consensus of the two trees obtained from the combined analysis; clades labelled as in Fig. 3. Vessel-ray pits: thick continuous branch indicates scalariform (2/2); double branch indicates large isodiametric (2/3); dashed branches are equivocal. Vasicentric tracheids present (5/1): single bar indicates gain of state; X indicates loss of state. Embryo sac formation: double bar indicates change to bisporic state (39/1).

centric tracheids (5/1, Fig. 5) also distinguish Myrtaceae s.s., but with secondary losses in the *Acmena* group and *Eucalyptopsis.* The base chromosome number for Myrtaceae s.l. is probably $x = 12$, (45/1), but the distinctiveness of this state is reduced by the equivocal records (11 and 12) from the Vochysiaceae. *Psiloxylon* and *Heteropyxis*, on the other hand, are linked to Myrtaceae by the presence of secretory cavities in the leaves and of glands in the anther connective (character 24, states 1 or 2). The most parsimonious explanation for the lack of essential oils in the leaves of *Psiloxylon* (44/0) is that the pathway for their production has been lost in that lineage.

Babingtonia and *Darwinia* share poricidal anther dehiscence (25/0, Fig. 4), a character state widespread in the *Chamelaucium* alliance. A very small, almost featureless pollen grain is a defining character for the *Tristania* group (Wilson, 1993). The eucalypt clade is distinguished by the presence of ovulodes (42/1) and by the low numbers of seeds relative to ovules (43/1), but the latter character is somewhat difficult to measure quantitatively.

Vessel-ray pitting provides some support for both the *Acmena* and Eucalypt groups, although in each case the defining state appears homoplastic (Fig. 5). Large isodiametric pits (2/3) characterize the Eucalypt group but have been recorded in *Melaleuca leucadendra* (Ingle and Dadswell, 1953). Other species of *Melaleuca*, including the one used in the present study, *M. viridiflora*, have small, nontracheidal pitting (2/1). Large, somewhat scalariform pits (2/2) are a synapomorphy for the *Acmena* group but are also found in *Kjellbergiodendron* within the *Lophostemon* group. Constraint analysis on the combined data set shows that a single origin for this state requires an additional 18 steps.

Fruit characters show an interesting distribution on the combined estimate of phylogeny (Fig. 6). The plesiomorphic state in the family is a dehiscent fruit, but indehiscence arises in four lineages: *Darwinia, Kjellbergiodendron, Psiloxylon,* and in clade P. The combined data provide strong evidence for multiple origins of indehiscence, a single origin requiring an additional 85 steps on the tree (51 steps excluding *Psiloxylon*). Fleshiness of the fruit is also shown to be homoplastic: three origins are indicated. A single origin requires an additional 66 steps on the tree. In all taxa with fleshy fruit, except *Psiloxylon,* there is the development of a fleshy hypanthium (34/1). In *Psiloxylon*, however, the fruit develops from a superior ovary, and this condition of a fleshy ovary wall devoid of a hypanthium is unique to this taxon. Even excluding *Psiloxylon*, a single origin of fleshy-fruitedness within Myrtaceae s.s. requires an additional 33 steps. We reiterate that the leathery fruits of *Lindsayomyrtus* (developed mostly from the ovary wall) and *Osbornia* (from the hypanthium) have not been scored as fleshy, nor are the indehiscent fruits of *Darwinia*, from the *Chamelaucium* alliance, in any sense fleshy. Hence there is very strong evidence for separate origins of fleshy fruit within the Myrtoid and Acmena groups, as proposed by John-

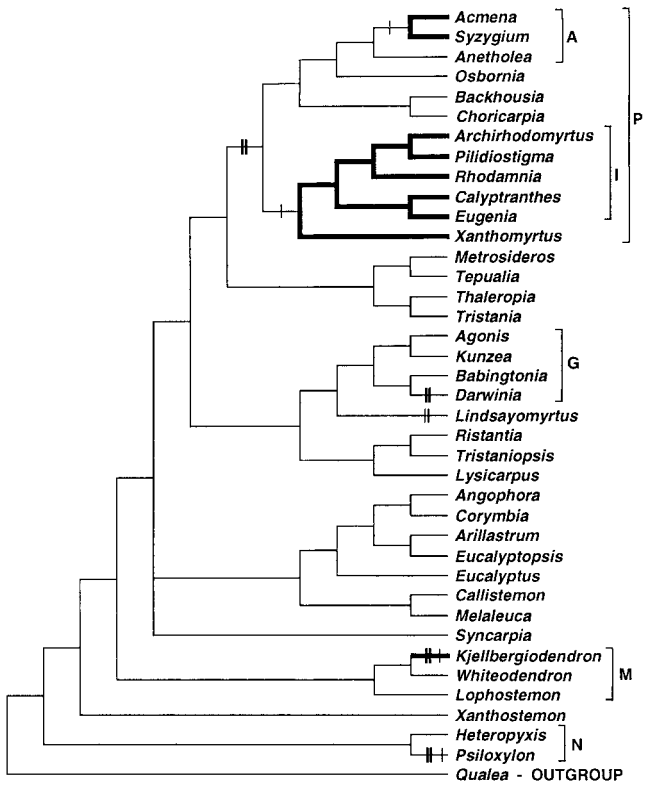

Fig. 6. Distributions of the states of three fruit characters shown on the strict consensus of the two trees obtained from the combined analysis; clades labelled as in Fig. 3. Thick double bar indicates change to indehiscent fruit (33/2); thin double bar indicates change to tardily dehiscent fruit (33/1); thick branch indicates hypanthium fleshy (34/1); single bar indicates change to fleshy ovary wall (35/1).

son and Briggs (1984). It should be noted, however, that these two groups are placed within clade P and that they therefore appear to have been derived from a common ancestor with indehiscent fruit (Fig. 6). Note, too, that *Kunzea*, which overwhelmingly has dry dehiscent fruits, also contains some species with dry indehiscent fruits (e.g., *K. cambagei*) and at least one with fleshy indehiscent fruits (*K. pomifera*).

The ''standard'' Myrtaceous unicellular hair is shown to be plesiomorphic for the family. The indumentum has been lost in clades A, F, K, and in *Lindsayomyrtus* and *Whiteodendron.* The absence of ''standard'' hairs provides one of the distinctions between the *Acmena* and Myrtoid groups (Briggs and Johnson, 1979). The eucalypts are also well known for their lack of these simple hairs, although various groups within this clade do have distinctive hair types (bristle glands and thin-walled, blunt-ended hairs) as discussed above. In the topology presented here, however, indumentum has been lost on a number of occasions, so that it is a relatively weak indicator of affinity.

There are additional characters that appear to be potentially informative but require further investigation. The *Backhousia* clade (C) seems to be characterized by a particular embryo type, having a curved hypocotyl with the cotyledons bent to one side, so that they are incumbent with respect to it; both genera are confined to Australia. The *Metrosideros* clade (D) is apparently characterized by having only five vascular traces in the hypanthium, a significant feature pointed out by Wilson (1993). From the limited data available, it seems likely that the plesiomorphic state is ten major veins but this needs to be confirmed. It is clear that *Psiloxylon* has ten veins (Fig. 3 in Schmid, 1980), and it seems likely that *Heteropyxis* does, too (Fig. 1 in Stern and Brizicky, 1958).

The *Leptospermum* clade (G) is made up of two robust subclades (E and F). The *Leptospermum* subclade (E) is discussed more fully in O'Brien, Quinn, and Wilson (2000), and the topology is similar to that found by Johnson and Briggs (1984), except that the *Melaleuca* group is excluded. The *Chamelaucium* subclade (F) may be distinguished by the distinctive embryo, which has two small cotyledons on a slender neck folded down against a relatively massive hypocotyl. By contrast, the embryos of members of the *Leptospermum* subclade are relatively unspecialized: they are straight, with the cotyledons usually longer than the hypocotyl.

There are no clear synapomorphies for the *Tristaniopsis* clade (H). Most taxa have staminal bundles of some sort, sometimes indistinct, and sterile anthers occur in *Lysicarpus* and *Ristantia.* The Myrtoid group (clade I) is defined morphologically by the combination of the fleshy fruit, the presence of indumentum of ''standard'' hairs, and the multiple whorls of stamens, although there are notable exceptions to this last feature. Traditionally, this group has been divided into three subtribes based on embryo morphology: the Myrtinae (curved/coiled embryos with small cotyledons), Myrciinae (embryos with foliaceous cotyledons), and Eugeniinae (fleshy embryo with plano-convex cotyledons). This seems to have some support here, with three taxa of Myrtinae (*Archirhodomyrtus*, *Pilidiostigma*, and *Rhodamnia*) forming a single clade (Figs. 2 and 3) but this distinction is not sustained in a wider molecular analysis (P. G. Wilson and M. M. O'Brien, unpublished data). This wider analysis indicates that most Australian Myrtinae form a clade distinct from other Myrtinae and marked by a 36-bp indel, but relatively few taxa have been sampled. Further work is needed, particularly to establish if the New Zealand and New Caledonian Myrtinae are sister to the Australian or southern South American taxa. Preliminary data show that two genera from New Zealand do not have the large indel but New Caledonian genera are yet to be sampled. It is perhaps significant that chromones, uncommon components of essential oils, have been found in some species of both New Zealand and southern South American taxa (Weyerstahl, Marschall, and Landrum, 1992).

For the *Eucalyptus* clade (K) the only additional character that may be informative, apart from the indumentum and wood anatomical characters mentioned above, is the lack of rudimentary stipules (Weberling, 1956). The *Corymbia* + *Angophora* clade (J) seems to have one clear synapomorphy, i.e., the presence of bristle glands bearing four cap cells with micropapillae (Ladiges and Humphries, 1983; Ladiges, 1984). Other possible characters, such as stem oil ducts and seed morphology, require more detailed analysis.

The members of the *Melaleuca* clade (L) seem typically to have spicate inflorescences and thickly woody fruits with inconspicuous or deciduous sepals. However, variants, such as capitate inflorescences, do occur. A similar inflorescence type is found in *Kunzea baxteri* but that species has conspicuous, persistent sepals and does not have thickly woody fruits. Ladiges et al. (1999), in a much broader study of the *Melaleuca* group, suggest that the presence of staminal bundles is the plesiomorphic condition in this clade. Staminal bundles are of widespread occurrence in the family s.s. and are found in five

of the clades in Fig. 2. Embryo type does not seem significant because embryos with flat cotyledons and embryos with obvolute cotyledons both occur in genera in the group.

Taxa in clade M share some potentially informative character states. All three genera have oil ducts: *Kjellbergiodendron* and *Whiteodendron* have relatively wide oil ducts in the pith of their petioles but in *Lophostemon* they are smaller in diameter and also occur in the cortex. A virtually identical arrangement is found in *Syncarpia,* which is reflected in the nonmolecular tree, but there is no support for a close relationship of *Syncarpia* and *Lophostemon* in the molecular analysis. *Kjellbergiodendron* and *Whiteodendron* also appear to have a similar embryo type with a larger, outer cotyledon that encloses a smaller, inner one.

Available information from bark anatomy is limited, but also corroborates some groupings of genera. Bamber (1962) presents data that support the *Melaleuca* group (clade L) and the *Leptospermum* subgroup (clade E) and strongly affirm certain genera, like *Choricarpia, Syncarpia,* and *Metrosideros.* A broader survey might provide evidence for other groups as well.

Conclusions—The *matK* sequence data allowed the identification of 11 robust groupings within the Myrtaceae s.l. However, apart from the placement of the *Psiloxylon* group as the first diverging lineage, relationships between the groups are either unresolved or weakly supported by the data. Clearly further sequence data are required before a reliable estimate can be made of the deeper relationships within the family. An increase in taxon sampling is also needed to define the limits of the infrafamilial taxonomic groups recognized here. There is strong support in the molecular data for a number of the alliances and suballiances defined by Briggs and Johnson (1979), i.e., the *Acmena*, *Backhousia*, and *Eucalyptus* alliances, the Myrtoideae s.s., and the *Calothamnus* and *Chamelaucium* suballiances. On the other hand, the *Metrosideros* and *Leptospermum* alliances are shown to be polyphyletic; neither was retrieved in analyses of either database. Several smaller informal taxonomic groupings are defined from among the members of the *Metrosideros* alliance: the *Tristania*, *Tristaniopsis*, *Metrosideros*, and *Lophostemon* groups. Despite the very limited sampling within groups in this analysis, there is robust support in the molecular data for the generic distinction between *Eucalyptus* and *Corymbia.*

Analysis of a revised and updated database of nonmolecular characters yielded only limited resolution of relationships. Despite this, there was some congruence between the morphological and molecular estimates of relationships. Two separate fleshy-fruited clades, the *Acmena* and Myrtoid groups, were identified in both analyses, as were the Eucalypt and *Tristania* groups. An analysis of the combined databases retrieved all clades identified as strongly supported on the molecular data. Estimates of the phylogeny based on the molecular data and also the combined data reveal extensive homoplasy within the family in a range of nonmolecular characters, including wood, fruit, and floral characters, which is in line with the limited resolution obtained from the nonmolecular analysis.

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