

Radiation of the Australian flora: what can comparisons of molecular phylogenies across multiple taxa tell us about the evolution of diversity in present-day communities?

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The Australian fossil record shows that from *ca.* 25 Myr ago, the aseasonal-wet biome (rainforest and wet heath) gave way to the unique Australian sclerophyll biomes dominated by eucalypts, acacias and casuarinas. This transition coincided with tectonic isolation of Australia, leading to cooler, drier, more seasonal climates. From 3 Myr ago, aridification caused rapid opening of the central Australian arid zone. Molecular phylogenies with dated nodes have provided new perspectives on how these events could have affected the evolution of the Australian flora. During the Mid-Cenozoic (25–10 Myr ago) period of climatic change, there were rapid radiations in sclerophyll taxa, such as *Banksia*, eucalypts, pea-flowered legumes and *Allocasuarina*. At the same time, taxa restricted to the aseasonal-wet biome (*Nothofagus*, Podocarpaceae and Araucariaceae) did not radiate or were depleted by extinction. During the Pliocene aridification, two Eremean biome taxa (*Lepidium* and Chenopodiaceae) radiated rapidly after dispersing into Australia from overseas. It is clear that the biomes have different histories. Lineages in the aseasonal-wet biome are species poor, with sister taxa that are species rich, either outside Australia or in the sclerophyll biomes. In conjunction with the fossil record, this indicates depletion of the Australian aseasonal-wet biome from the Mid-Cenozoic. In the sclerophyll biomes, there have been multiple exchanges between the southwest and southeast, rather than single large endemic radiations after a vicariance event. There is need for rigorous molecular phylogenetic studies so that additional questions can be addressed, such as how interactions between biomes may have driven the speciation process during radiations. New studies should include the hitherto neglected monsoonal tropics.

Keywords: Australia; molecular dating; climate change; Cenozoic; rapid radiation; extinction

1. INTRODUCTION

Biomes are broad biogeographic regions that are defined using a combination of climate, vegetation structure and ecophysiology (Brown & Lomolino 1998; Woodward *et al.* 2004). When ecological criteria such as these are emphasized, biomes usually span multiple hemispheres and continents (Cox & Moore 1993; Brown & Lomolino 1998). If taxonomic or phylogenetic criteria, such as endemism, are also included, then biomes become regional, e.g. Takhtajan's (1986) floristic regions. Here, we recognize five major biomes within Australia (table 1; figure 1) based on previous maps that used climate, vegetation structure and endemism as criteria (Burbidge 1960; Schodde 1989; Crisp *et al.* 2001). Although regional, these correspond broadly to biomes mapped worldwide.

Biomes, in general, are not fixed in space or time but evolve continuously as landscapes and climates change (Hill 1994b; Hill *et al.* 1999). There is fossil evidence of past biomes that have no modern counterpart on the planet in terms of climate or vegetation. For example, there was a unique biome in southeastern Australia during the Palaeocene as a result of a combination of high latitude and mild climate (Hill *et al.* 1999). By contrast, the Eremean biome probably did not originate until severe aridity first developed during the Pliocene (Bowler 1982; Hill *et al.* 1999). The fossil record indicates that the locations of present-day biomes differ from those of the past too. Eocene fossil floras from southern Australia bear a striking similarity in community structure and taxonomic composition to the present-day wet tropics of north Queensland (aseasonal-wet biome) (Christophel & Greenwood 1988). While this biome has persisted through time, it seems to have been displaced or contracted northwards.

In this paper we focus on Australian biomes through the Cenozoic, a period of change in Australia as a result of three major occurrences.

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Table 1. Biomes of Australia.

southeastern temperate	sclerophyll (eucalypt) forest, woodland and heath, seasonally dry
southwestern temperate	sclerophyll (eucalypt) forest, woodland and heath, Mediterranean climate
monsoonal tropics	savannah, mostly sclerophyll (eucalypt and acacia) seasonally dry
Eremean	arid shrubland, low woodland and grassland
aseasonal-wet	year-round high rainfall, tropical to temperate or subalpine, closed-canopy rainforest (volcanic soils) to heath (oligotrophic soils)

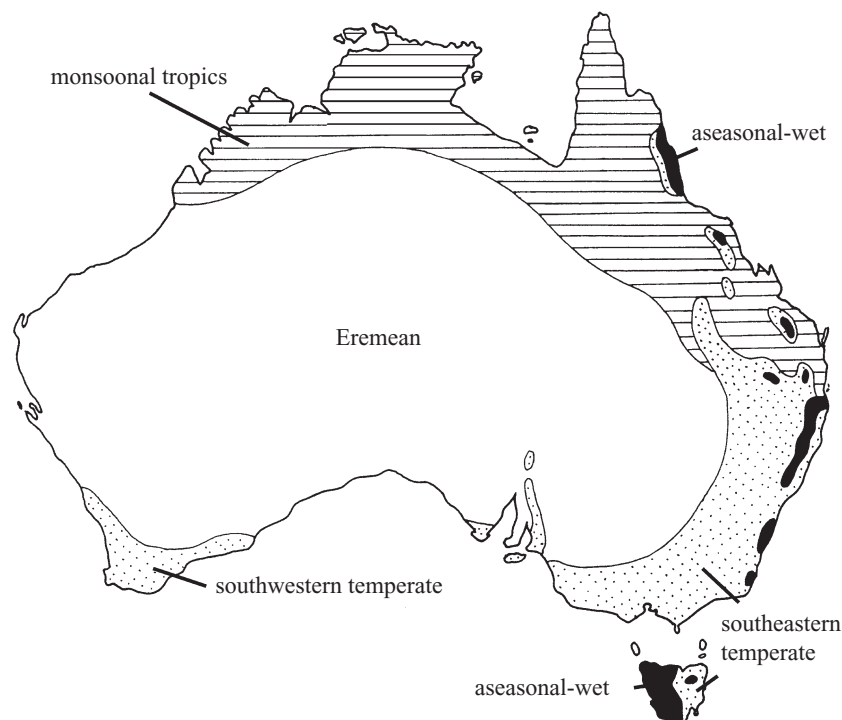


Figure 1. Map of Australian biomes (modified from Burbidge 1960; Schodde 1989). See table 1 for descriptions.

- (i) Rifting of Australia from Antarctica. Rifting started from the west during the Cretaceous but was initially very slow (5 mm per year; Quilty 1994) and was not completed until *ca.* 32 Myr ago, after which Australia and New Guinea rafted rapidly northwards at 7 cm per year (Florindo *et al.* 2003; Lawver & Gahagan 2003). Although a deep (more than 2 km) ocean passage between Tasmania and Antarctica did not exist until 32 Myr ago, a shallow sea gap was probably established over the South Tasman Rise several million years earlier (Woodburne & Case 1996). From this time, the Australian flora evolved in isolation, except for taxa that were able to disperse and establish across oceanic gaps. In the period leading up to isolation, the dominant vegetation of the southeast was similar to that of the present-day aseasonal-wet biome (Martin 1994; Hill *et al.* 1999). It was rainforest dominated by *Nothofagus*, and included many taxa occurring in the north Queensland wet tropics today, e.g. *Gymnostoma*, Banksieae, Cunoniaceae, Podocarpaceae and Myrtaceae (Hill *et al.* 1999). In central Australia, there were floras resembling the present-day sclerophyll and monsoonal tropics biomes (Greenwood 1994: fig. 4.3). Sclerophyll flora had probably existed on swampy oligotrophic soils at forest fringes from the Late Cretaceous onwards (Hill *et al.* 1999).
- (ii) Advent of the ACC. This was initiated by the oceanic isolation of Antarctica, after South America and Australia rifted northwards at about the same time (Florindo *et al.* 2003). The ACC led to global climate change by steepening the latitudinal temperature gradient, leading to the onset of glaciation in Antarctica (Lawver & Gahagan 2003) and significant cooling in the Australian Oligocene (Hill *et al.* 1999; Dodson & Macphail 2004). Between 25 and 10 Myr ago, the Australian climate became drier and more seasonal (Martin 1994), as the continent moved north into the subtropical high-pressure ridge, which blocks rain-bearing lows (currently *ca.* 30° S) (Bowler 1982; Colls & Whitaker 2001; Frakes 1999). The fossil pollen record from this period shows a steep decline in dominance of *Nothofagus*, and its replacement by sclerophyll flora dominated by Myrtaceae and Casuarinaceae (Kershaw *et al.* 1994; Martin 1994).
- (iii) Severe aridity set in during the Pliocene (5–2 Myr ago), resulting from further steepening of the latitudinal temperature gradient, intensification of the Antarctic ice cap (Bowler 1982; Frakes 1999). It now appears that the extreme wet–dry glacial cycles of the present climatic system set in around the Mid-Pliocene (2.9 Myr ago), replacing a mild wet climate that

prevailed early in the Pliocene (Dodson & Macphail 2004). In the pollen record, there was a disappearance from southern latitudes of *Nothofagus*, *Araucariaceae* and podocarps, and a rapid increase in shrubby and herbaceous taxa that dominate today's arid zone (*Chenopodiaceae*, *Asteraceae* and *Poaceae*) during the arid periods, and sclerophyll flora (eucalypts, *Acacia* and *Casuarinaceae*) during the wetter periods (Kershaw *et al.* 1994; Martin 1994; Gallagher *et al.* 2003; Dodson & Macphail 2004).

Since acceptance of continental drift theory, biota known or suspected to have been present in Australia before it rifted away from Antarctica have been considered 'Gondwanan' (Barlow 1981; Linder & Crisp 1995; McLoughlin 2001; Ericson *et al.* 2002; Sanmartín & Ronquist 2004), especially if these taxa have close relatives in other landmasses that once formed part of Gondwana. Implicit in this view is the assumption that the ancestors of such taxa were widespread in the former supercontinent and speciated by vicariance as it broke up. It is likely that many 'Gondwanan' taxa were restricted to only a portion of the supercontinent (Nelson & Ladiges 2001). Therefore, we avoid the potentially misleading term 'Gondwanan' to refer to pre-isolation flora in Australia.

The geological record suggests that the present-day flora of Australia comprises a mix of taxa with different histories: (i) lineages that were present in Australia before its isolation (more than 35 Myr ago) that have been depleted by extinction or reduced in abundance (e.g. *Araucariaceae*, *Cunoniaceae*, *Nothofagaceae* and *Podocarpaceae*); (ii) lineages that were probably present in Australia before its isolation that increased in abundance and radiated with increasing aridity (legumes, *Myrtaceae*, *Proteaceae* and *Casuarinaceae*); and (iii) taxa that arrived in Australia only after isolation and then became abundant and radiated during the onset of severe aridity (e.g. *Chenopodiaceae*, *Asteraceae* and *Poaceae*).

A key question addressed here is how accurately the fossil record reflects the evolutionary history of the Australian biota in the timing and rates of radiation and extinction. Most of the fossil record consists of pollen and spores, which often show trends in abundance of taxa that are consistent among sites, e.g. in the neogene of southeastern Australia (Kershaw *et al.* 1994). The occurrence of macrofossils is much more patchy, and there are sites where a taxon is represented by abundant pollen but no macrofossils, e.g. in *Cunoniaceae* (Barnes *et al.* 2001). However, pollen is seldom identifiable to species level and often provides little resolution within very species-diverse groups, such as eucalypts (Hill 1994a; Rozefelds 1996) or *Amaranthaceae* + *Chenopodiaceae* (Jordan & Macphail 2003). The relationship between pollen taxa and species-level diversity is unclear, even in well-studied taxa that have a good record of both pollen and macrofossils, e.g. *Nothofagus* (Hill 2001). Therefore, additional information is needed to try to measure the diversity of the Australian biota through time. Here, we use molecular phylogenies of community-dominant taxa to complement

fossil data and enhance our understanding of the evolution of the Australian flora.

From the fossil record, it has been hypothesized that a major feature of evolutionary history has been a series of punctuated radiations in which lineages diversified by rapid speciation and rose to ecological dominance, interspersed with periods of slow diversification or extinction (Bateman & DiMichelle 1994; Fortey *et al.* 1996; Kenrick & Crane 1997; Conway Morris 1998). Molecular phylogenies can be used to assess the patterns of radiation and to test hypotheses such as punctuated evolution. The rate of radiation can be tested by comparing species richness in sister taxa which are, by definition, of the same age (Sanderson & Donoghue 1996; Sanderson 1998; Schluter 2000). However, a disparity between sister taxa is inconclusive: it may indicate either an increase in speciation rate in the species-rich lineage or a decrease in its species-poor sister. Therefore, this criterion requires comparison between these sister taxa and their next more distant sister taxon. If, for example, the latter is similar in species richness with the species-poor lineage, this indicates a rate increase in the species-rich lineage (or vice versa).

Another criterion for recognizing change in the rate of radiation requires phylogenies in which branch lengths are proportional either to evolutionary change (phylograms) or, preferably, to time (chronograms). In an exponential radiation, new species appear randomly over time (figure 2a). A punctuated radiation appears as a broom-shaped molecular tree: a time-extended lineage (the handle) abruptly branching into many new lineages (the broom-head), which themselves may be little branched towards the present. During the period of rapid speciation, internal branches of a tree appear very short, or with zero length (a 'hard polytomy'). The critical criterion for a punctuated radiation is the sudden increase in speciation rate, as measured by a near-simultaneous appearance of many new lineages (figure 2b). Extinction too may be non-random over time and could contribute to a punctuated pattern of evolution. A long broom-handle preceding a rapid radiation may indicate a single long-lived ancestral species but it may, alternatively, indicate the sole survivor of a near-complete extinction of the stem-group taxa. Examination of a molecular phylogeny alone cannot distinguish between these alternative interpretations of a broom-handle. However, the fossil record may do so, by indicating whether many or few stem-group taxa existed during the time period of the broom-handle.

If independent calibration data are available, such as fossils of known age, then the absolute ages of nodes in phylogenies also can be estimated (Donoghue & Moore 2003). This allows the comparison of trees for different taxa, e.g. for congruence in the pattern and timing of radiation or extinction events (see also Linder & Hardy 2004). It also allows comparison of dated nodes in phylogenies with hypothesized causal factors, such as climatic change or vicariance events.

Here, we address several specific questions.

- (i) Are the differing macro-evolutionary histories predicted from the fossil record reflected in molecular phylogenies of those lineages?

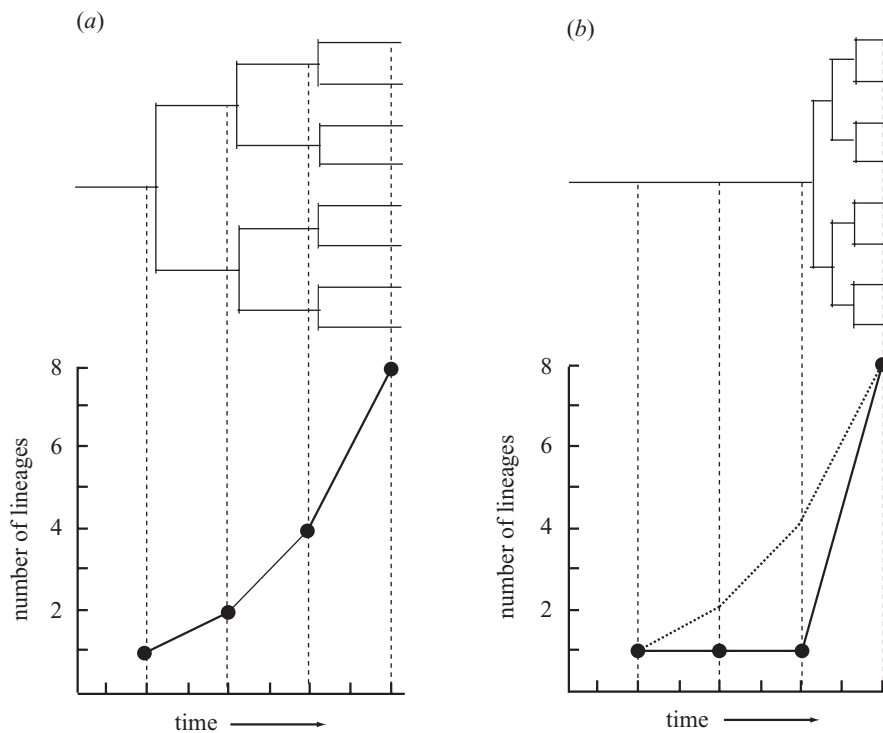


Figure 2. Chronograms of two radiations (above) and plots of the cumulative number of species over time in each (below). (a) An exponential or steady-rate radiation, (b) an explosive radiation giving a broom-shaped tree. The dotted line shows the ideal exponential curve.

- (ii) Are the major events of the Cenozoic reflected in phylogenies of lineages present during the changes? It would be expected that if major events were playing a role in radiation of the flora, then congruent patterns would be detected across multiple taxa.
- (iii) Do taxa within the same biome exhibit similar macroevolutionary patterns? For example, do Myrtaceae, Casuarinaceae, Proteaceae and legumes show a rapid increase in speciation rate during the cooling and drying of the climate between 25 and 10 Myr ago?
- (iv) Did major radiations occur within biomes or is there a reticulate pattern, with individual lineages having taxa distributed across multiple biomes? A single monophyletic radiation within each biome would suggest that the radiations were triggered by an initial adaptation, with geographical or ecological barriers between biomes. Reticulation would indicate a lack of barriers among biomes.

2. MATERIAL AND METHODS

(a) *Survey of literature*

We surveyed recent literature for published molecular datasets and trees for Australian vascular flora. The ISI Web of Science database (see <http://www.isinet.com/products/citation/wos/>) was searched for authors known to be active in plant systematics, and for plant families and genera known to be diverse in the Australian flora. Searches usually included the topic qualifier 'and phylogen*'. We did not include studies that sampled only one or a few Australian taxa, unless this was a good representation of the Australian taxa. For each study, we recorded: (i) whether trees were presented as phylograms or chronograms, which would allow an assessment of the history of radiation in the study group;

- (ii) the DNA region(s) sampled and whether these data were available, for example in GenBank, so that a molecular dating analysis could be done; (iii) the pattern of radiation, if determinable from the tree(s); (iv) the first Australian fossil record of the group; (v) the adequacy of taxon sampling (see below); and (vi) the authors' assessment (if any) of the radiation and biogeographic history of the Australian taxa in the group.

(b) *Exemplar selection*

The analysis of molecular phylogenies can be biased by artefacts. First, uneven sampling across the tree can distort the apparent trend in speciation through time (Pybus & Harvey 2000). It is necessary to comprehensively represent lineages that pass through the time period of interest. Sampling outside this period is less important. For example, as we were concerned with radiation of the eucalypts during the Oligocene and Miocene, it was unnecessary to comprehensively sample taxa from species-groups that probably diversified in the Pliocene. Second, a polytomy (broom-head) suggesting a rapid radiation can be generated artificially, either by poor quality sequences that have multiple polymorphic sites, or by saturation of the signal from the DNA region used, thus collapsing the crown of a tree. Third, comparisons among taxa of the same named rank may be invalidated by inconsistent ranking criteria or non-monophyly of taxa (Scotland & Sanderson 2004). Therefore, it is preferable to ignore rank and compare clades directly.

We chose numerically and geographically dominant taxa for which suitable molecular data were available: Leguminosae (Fabaceae) tribes Mirbelieae + Bossiaceae (Crisp & Cook 2003b), *Eucalyptus* (Myrtaceae) (Steane *et al.* 2002), Casuarinaceae (Steane *et al.* 2003) and Proteaceae genera *Banksia* + *Dryandra* (Mast & Givnish 2002).

(c) *Molecular dating*

Molecular dating was performed by using our own data for Mirbelieae + Bossiaeeae (*ndhF*), *Eucalyptus* (ITS) and Casuarinaceae (*matK*), and that obtained from GenBank for *Banksia* (*rpl16* intron). For each dataset we obtained a phylogram by tree searching in PAUP* (Swofford 2002) using the minimum evolution criterion with maximum likelihood parameters estimated using MODELTEST (Posada & Crandall 1998). We used multiple starting trees obtained by neighbour-joining and MP for the heuristic searches. For the eucalypt dataset, we also used the consensus tree from a Bayesian analysis (MRBAYES, v. 3 (Ronquist & Huelsenbeck 2003) with branch lengths estimated using maximum likelihood and a general time reversible + γ model (PAUP*). One of the best MP trees for each dataset was also used for dating nodes.

We determined likelihood scores for trees derived with and without a molecular clock enforced, using PAUP*, and conducted likelihood ratio tests. We repeated the analyses with taxa having extreme relative rates removed. In all cases, an assumption of a molecular clock was rejected and therefore rate smoothing was applied before estimating the ages of nodes. We used both non-parametric (Sanderson 1997) and penalized likelihood (truncated Newton algorithm) (Sanderson 2002) rate smoothing as implemented in 'r8s' (Sanderson 2003) to obtain chronograms for each taxon, and for each phylogeny estimation method. Calibration points for input to r8s, including fixed, maximum and minimum age constraints, were selected as described below. For each dataset, analyses were run independently with each fixed calibration point and for varying combinations of fixed and maximum and/or minimum constraints. Sources of error in estimating dates of nodes include estimation of tree topology and branch lengths, date of calibration points and their placement on the tree. Therefore we used different trees, different rate smoothing algorithms and multiple combinations of calibrations to obtain a set of estimated ages for nodes of interest. These do not correspond to statistical confidence intervals but provide an indication of the variance as a result of topology and choice of method and calibration point.

(d) *Calibration of chronograms*

(i) *Eucalypts*

Published fossil dates for eucalypts were considered unsuitable for calibration because the fossils are poorly dated and/or difficult to assign to extant taxa (Hill 1994a; Rozefelds 1996). Therefore, the eucalypt chronogram (figure 3) was calibrated using the assumption of Ladiges *et al.* (2003) that a vicariance event *ca.* 70 Myr ago isolated *Arillastrum* in New Caledonia from the rest of the eucalypts in Australia. This allowed a direct comparison of the molecular dates for nodes with the scenario of eucalypt biogeography proposed by Ladiges *et al.* (2003), because the same assumption is made about the age of the basal node in both analyses. Tectonic rifting of New Caledonia from Australia started *ca.* 85 Myr ago but there was little separation until after 74 Myr ago (Kroenke 1996). We used both the most recent (70 Myr ago) and the earliest (85 Myr ago) dates for this vicariance event to fix the *Arillastrum* + eucalypt node, and compared the respective ages estimated for other nodes from each of these calibration points.

(ii) *Casuarinaceae*

This family was widespread in Gondwana well before separation of Australia from Antarctica (Hill 1994a), but today 69 out

of the 96 species are restricted to Australia and the remainder to Malesia. Casuarinaceae and their Fagalean relatives have an excellent fossil record (Hill 1994a; Scriven & Hill 1995). *Nothofagus* is a sister group to the rest of Fagales (Manos & Steele 1997) and has abundant and unique pollen, which first appeared *ca.* 83 Myr ago (Dettman 1994; Hill 2001). Therefore we constrained the crown group of Fagales to this date. We used a fixed age for the node common to Casuarinaceae and Betulaceae (70 Myr ago) based on *Endressianthus* (Campanian–Maastrichtian age; Friis *et al.* 2003), which has affinity to Betulaceae and Casuarinaceae. We applied an internal constraint (alternatively minimum and maximum) for the *Gymnostoma* crown group of 34 Myr ago based on *Gymnostoma tasmanianum*. This fossil is from the Early Oligocene and has much detail preserved. It is stated to be clearly *Gymnostoma* (Guerin & Hill 2003).

(iii) *Banksia*

We constrained the base of the stem of the tribe Banksieae to the first appearance of its distinctive pollen *ca.* 62 Myr ago (Macphail *et al.* 1994; Martin 1994). The macrofossil *Banksiaephyllum taylorii*, from the Late Palaeocene (Carpenter *et al.* 1994), is unequivocally *Banksia*, having leaf margins and trichomes unique to that genus and absent in the sister group (G. J. Jordan, personal communication). Therefore we constrained the base of the stem of *Banksia* to either 58 Myr ago or 54 Myr ago to represent the range of uncertainty for the age of this fossil.

(iv) *Mirbelieae and Bossiaeeae*

No unequivocal fossil from this group is older than *Oxylobium pungens*, which is less than 2 Myr old (Jordan 1997). We used an age of 40 Myr for the crown group of Mirbelieae + Bossiaeeae (a near-polytomy in our analyses). This date is based on an age for the group estimated by Wojciechowski (2002) using molecular dating across the whole of Fabaceae calibrated with fossils for other taxa.

3. RESULTS

(a) *Survey of published molecular phylogenies*

We found 89 published molecular phylogenetic studies of Australian vascular flora, of which 50 presented chronograms or phylograms allowing an assessment of radiation, history (table 2). Just over half of all studies have adequate sampling at species level to allow modelling of radiation, and all but eight indicate that their data are available. Some taxonomic groups are well studied (by the criteria above) but some important Australian taxa are missing from table 2. These include many monocot taxa (including large genera of Gramineae (Poaceae), Cyperaceae and Orchidaceae), Campanulaceae, Lamiales, Proteaceae, Rutaceae and most of Asteraceae. Taxa that are diverse in the monsoonal tropics are neglected unless they are also diverse in southern biomes (e.g. eucalypts and acacias). In the aseasonal-wet biome, studies have been biased towards taxa seen as relictual (e.g. *Nothofagus*, several studies), whereas some very diverse groups, e.g. Lauraceae, Euphorbiaceae and non-eucalypt Myrtaceae, have been neglected.

The following is a brief summary of the major findings of studies of phylogenies of major groups in table 2, not including the exemplar taxa subject to molecular dating (below).

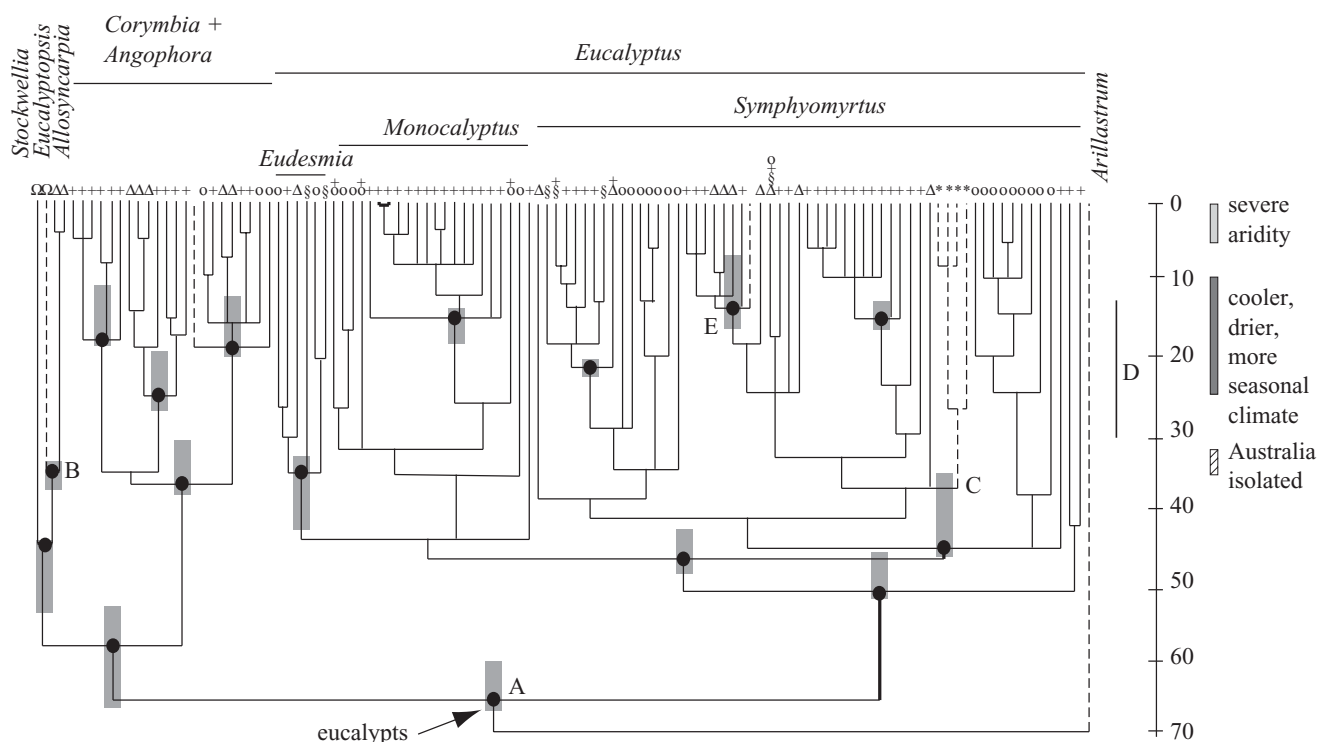


Figure 3. Chronogram of eucalypts, assuming the basal divergence between the eucalypts *sensu lato* (arrowed) and *Arillastrum* at 70 Myr ago. The scale at the right indicates age in millions of years. Major environmental changes indicated along this scale are described in the text. The dotted lineages are extra-Australian. The grey bars over the nodes indicate range of age estimates as a result of variation in topology and choice of method and calibration points. Symbols indicate the biome in which each terminal taxon occurs (Ω , aseasonal-wet; triangles, monsoonal; circles, southwest temperate; +, southeast temperate; §, eremean; *, other). Named taxa are discussed in the text. Nodes labeled A–E refer to table 4.

(i) *Taxa restricted to the aseasonal-wet biome*

Molecular phylogenies are published for several Australian taxa that are mainly restricted to the aseasonal-wet biome: *Nothofagus* (Linder & Crisp 1995; Manos 1997; Jordan & Hill 1999), Cunoniaceae (Bradford & Barnes 2001), Podocarpaceae (Conran *et al.* 2000; Kelch 2002) and Araucariaceae (Gilmore & Hill 1997; Setoguchi *et al.* 1998). These taxa have a good fossil record (Hill & Brodribb 1999; Barnes *et al.* 2001; Hill 2001), allowing a comparison of their extinct and extant diversity.

The fossil record suggests that *Nothofagus*, Araucariaceae and Podocarpaceae radiated in the Late Cretaceous and Early Cenozoic but were depleted by extinction in Australia from the Mid-Cenozoic onwards (table 3). Extinctions include *Nothofagus* subgenera *Brassospora* and *Nothofagus*, 10 genera of Podocarpaceae and two genera of Araucariaceae. Extant species-level diversity of these taxa is low in Australia (table 3).

Molecular phylogenies indicate that extant taxa within the Australian aseasonal-wet biome (*Nothofagus*, Araucariaceae, Cunoniaceae and Podocarpaceae) comprise multiple species-poor lineages having sister groups outside Australia. Specifically:

- (i) the three extant Australian species of *Nothofagus* comprise two lineages in separate subgenera (Linder & Crisp 1995; Manos 1997; Jordan & Hill 1999);
- (ii) the 14 extant Australian species of Podocarpaceae fall into 10 separate lineages (Conran *et al.* 2000);
- (iii) in Araucariaceae, *Wollemia nobilis* and both extant Australian *Araucaria* species comprise three separate

lineages (Gilmore & Hill 1997; Setoguchi *et al.* 1998). Monophyly of the three extant Australian *Agathis* has not been tested;

- (iv) although sampling of extant Australian Cunoniaceae is not comprehensive at species level, it is clear that this family comprises several species-poor lineages having sister taxa outside Australia (Bradford & Barnes 2001).

(ii) *Sclerophyll biomes*

Several taxa that are mainly represented in the southeastern and southwestern biomes have broom lineages indicating punctuated radiations, e.g. *Callitris* (Pye *et al.* 2003), *Drosera* (Rivadavia *et al.* 2003), Ericaceae tribe Styphelieae (Quinn *et al.* 2003), Fabaceae tribes Galegeae + Carmichaelinae (Wagstaff *et al.* 1999) and Mirbelieae + Bossiaeeae (Crisp & Cook 2003b), *Scaevola* (Howarth *et al.* 2003), *Banksia* + *Dryandra* (Mast 1998; Mast & Givnish 2002) and Solanaceae tribe Anthocercideae (Garcia & Olmstead 2003). Other taxa have undergone rapid radiations with a broom-head but no broom-handle, e.g. *Allocasuarina* (Steane *et al.* 2003) and eucalypts (Steane *et al.* 2002). *Acacia* is also inferred to have radiated rapidly but the data and trees presented so far do not allow a definitive assessment (Miller *et al.* 2003a; Murphy *et al.* 2003). Except for the exemplars that are dated in this study, it is unknown whether these punctuated and rapid radiations are contemporary. Those that are nested are clearly not, for example the Carmichaelinae radiation in New Zealand is nested within, and younger than, the *Swainsona* radiation

Table 2. Phylogenetic studies of vascular plant families in Australia and their applicability to analysis of radiation. (Afr, Africa; Amer, America; Aust, Australia; NCal, New Caledonia; NG, New Guinea; NZ, New Zealand; SAfr, South Africa; SAmer, South America. First Australian fossil records are taken either from the source cited here or from Martin (1994).)

family or order	taxon intrafamilial	reference	chronogram (C), phylogram (P), or data (D)	DNA regions	radiation type	first Australian record (Myr ago)	sampled well (W) or poorly (P)	original authors' notes
Alseuosmiaceae, Argophyllaceae and Phellinaceae Amaranthaceae		Karehed <i>et al.</i> (1999); Sanmartin & Ronquist (2004) Kadereit <i>et al.</i> (2003)	D PD	<i>ndhF</i> , <i>rbcl</i> <i>rbcl</i>	— rapid in late Cenozoic	— 30	W P	— recent dispersals likely
Amaryllidaceae Apocynaceae incl. Asclepiadaceae Apiaceae	<i>Crinum</i>	Meerow <i>et al.</i> (2003) Potgieter & Albert (2001)	D D	<i>tmLF</i> , ITS <i>tmLF</i>	— —	— —	P P	two dispersals into Aust Gondwanan origin of family inferred
Araucariaceae		Chandler & Plunkett (2004) Setoguchi <i>et al.</i> (1998)	D PD	26S, <i>matK</i> , <i>rbcl</i> <i>rbcl</i>	— —	26 > 130	P W	<i>Azorella</i> clade (and others) suggests ancient Gondwanan distribution Gondwanan origin inferred for <i>Araucaria</i> , recent in NCal
Araucariaceae Asphodelaceae Asteraceae Asteraceae		Gilmore & Hill (1997) Chase <i>et al.</i> (2000) Denda <i>et al.</i> (1999) Breitwieser <i>et al.</i> (1999)	D PD PD PD	<i>rbcl</i> <i>rbcl</i> , <i>tmLF</i> <i>matK</i> ITS	— — — —	> 130 15 (family) 15 (family)	P P W P	— — — multiple dispersals from Aust to NZ (mainly NZ)
Asteraceae	Gnaphalieae	Bayer <i>et al.</i> (2002)	D	<i>tmLF</i> , <i>matK</i> , ETS	—	15 (family)	W	dispersal from SAfr to Aust, followed by radiation into arid zone
Asteraceae Asteraceae Asteraceae	<i>Olearia</i> <i>Vittadinia</i>	Cross <i>et al.</i> (2002) Lowrey <i>et al.</i> (2001)	D PD	ITS ITS	— rapid and recent	15 (family) 15 (family)	W W	— dispersal from NG into the Pacific
Asteraceae	<i>Microseris</i>	Vijverberg <i>et al.</i> (1999)	rflp only	<i>tmLF</i>	—	15 (family)	?	infer colonization of Aust from Nth America
Asterales/ Rousseaceae Bombacaceae	<i>Roussaea</i> <i>Adansonia</i>	Lundberg (2001) Baum <i>et al.</i> (1998)	D CPD	<i>ndhF</i> , <i>rbcl</i> <i>rpl16 intron</i> , ITS	— broom	— —	P W	dispersal from Aust to Madagascar before Pliocene dispersal from Afr to Aust: radiation too recent for vicariance explanation
Brassicaceae	<i>Cardamine</i>	Bleeker <i>et al.</i> (2002a)	D	<i>tmLF</i> , ITS	—	ca. 0.014 kyr	W	Sth Hemisphere dispersals less than 425 kyr
Brassicaceae	<i>Rorippa</i>	Bleeker <i>et al.</i> (2002b)	D	<i>tmLF</i>	—	—	W?	Pliocene/Pleistocene origin (via dispersal) of Aust/NZ/NG spp.
Brassicaceae	<i>Lepidium</i>	Mummenhoff <i>et al.</i> (2001, 2004)	D	<i>tmTL</i> , <i>tmLF</i> , ITS	rapid	—	W	Pliocene/Pleistocene origin (via dispersal) of Aust/NZ spp.
Caryophyllaceae	<i>Scleranthus</i>	Smitsen <i>et al.</i> (2003)	PD	ITS	—	—	W	trans-Tasman dispersal

(Continued.)

Table 2. (Continued.)

Casuarinaceae	Stearns <i>et al.</i> (2003)	PD	<i>matK</i>	rapid in Allocasuarina	63	W	ancient vicariance and/or long-distance dispersal between Aust, NZ and NCal in <i>Gymnostoma</i> and <i>Casuarina</i> ; recent reticulation between southwest and southeast Aust in <i>Allocasuarina</i> multiple recent dispersals likely Gondwanan ancestry inferred multiple east-west splits Gondwanan ancestry inferred
Chenopodiaceae	Kaderleit <i>et al.</i> (2003)	PD	<i>rbcL</i>	—	30	P	Miocene speciation: Aust/SAfr distribution result of dispersal biogeography requires dispersal scenario
Cunoniaceae	Bradford & Barnes (2001)	PD	<i>rbcL</i> , <i>trnL/F</i>	—	56	P	—
Cupressaceae	Pye <i>et al.</i> (2003)	P	ITS	one broom	—	W	—
Cupressaceae	Gadek <i>et al.</i> (2000)	PD	<i>rbcL</i> , <i>matK</i>	exponential (only deep levels sampled)	100	W	—
Cycadales	Treutlein & Wink (2002)	PD	<i>rbcL</i>	—	—	P	—
Cycadales	Hill <i>et al.</i> (2003)	D	<i>rbcL</i> , <i>trnL/F</i> , ITS, 26S	—	—	P	—
Cyperaceae	Muasya <i>et al.</i> (2002)	D	<i>rps16</i> , <i>trnL/F</i> , <i>rbcL</i>	—	—	P	—
Cyperaceae	Muasya <i>et al.</i> (2001)	D	<i>rbcL</i> , <i>trnL/F</i>	—	—	P	—
Droseraceae	Rivadavia <i>et al.</i> (2003)	PD	<i>rbcL</i> , 18S	some brooms, others not	30	W	Aust or Afr origin, dispersal from Aust to SAmer and Afr
Dryopteridaceae	Perrie <i>et al.</i> (2003)	PD	<i>rps4-trnS</i>	—	—	W	Aust/NZ relationship because of dispersal, not vicariance
Ericaceae	Quinn <i>et al.</i> (2003)	P	<i>matK</i> , <i>atpB/rbcL</i> spacer	some brooms	—	W	—
Fabaceae	Miller <i>et al.</i> (2003b)	D	<i>trnK</i> , <i>matK</i> , <i>ps7bA-trnH</i> , <i>trnL/F</i>	—	24	P	—
Fabaceae	Miller <i>et al.</i> (2003a)	D	<i>trnK</i>	rapid	24	W	rapid radiation during Pleistocene
Fabaceae	Murphy <i>et al.</i> (2003)	D	ITS	rapid	24	W	—
Fabaceae	Wojciechowski <i>et al.</i> (2000)	P	multiple (supertree)	—	—	P	—
Fabaceae	Wagstaff <i>et al.</i> (1999)	C/PD	ITS	NZ broom nested within Australian broom	—	W	two dispersals from Aust to NZ
Fabaceae	Chandler <i>et al.</i> (2001)	PD	<i>psbA-trnH</i> , <i>trnK</i> intron, ETS	rapid	—	W	possible adaptive radiation of bird pollinated species
Fabaceae	Brown <i>et al.</i> (2002); Doyle <i>et al.</i> (2004)	PD	ITS, <i>H3-D</i>	—	—	W	multiple origins of allopolyploid taxa throughout the history of the genus
Fabaceae	Barker <i>et al.</i> (2000)	PD	<i>trnL</i> , <i>trnK</i> , ITS	—	—	P	—
Fabaceae	Crisp & Cook (2003b)	PD	<i>trnL/F</i> , ITS	multiple rapid radiations	—	W	endemic Aust radiation
Gentianaceae	von Hagen & Kaderleit (2001)	CD	<i>matK</i> , ITS	speciation rate calculated but sample poor	—	P	infer single dispersal into Aust + NZ from SAmer less than 2.7 Myr ago
Goodeniaceae	Gustaffson <i>et al.</i> (1996)	D	<i>rbcL</i>	—	—	P	—
Goodeniaceae	Howarth <i>et al.</i> (2003)	PD	ITS	some brooms	—	W	Aust origin with six or more dispersals out of Aust.

(Continued.)

Table 2. (Continued.)

Gunneraceae	<i>Gunnera</i>	Wanntorp & Wanntorp (2003)	D	<i>rbcl</i> , <i>rps16</i> intron, ITS	—	> 130	only 1 sp extant	dispersal from NZ to Aust
Haemodoraceae		Hopper <i>et al.</i> (1999)	D	<i>trnL/F</i>	—		P	divergence of main clades predates Gondwana break-up; extinction has been significant
Iridaceae		Reeves <i>et al.</i> (2001)	D	<i>rbcl</i> , <i>rps4</i> , <i>trnL/F</i>	—		P	—
Lauraceae		Chanderbali <i>et al.</i> (2001)	CPD	<i>trnL/F</i> , <i>psbA-trnH</i> , <i>trnT-trnL</i> , <i>rpl16</i> , 26S, ITS	exponential		W (deep nodes); P (Australia)	origin Laurasian; Cryptocareae Gondwanan incl. Aust
Lycopodiaceae		Wikstrom (2001); Wikstrom & Kenrick (2001)	PD	<i>rbcl</i>	—		P	vicariance; Aust taxa nested within Permian origin genera
Malvaceae	Gossypieae	Seelanan <i>et al.</i> (1997)	PD	ITS, <i>ndhF</i>	rapid	38–45 (family)	W	multiple recent dispersals; reticulation obscures biogeography
Malvaceae	<i>Gossypium</i> sect <i>Grandicalyx</i>	Seelanan <i>et al.</i> (1999)	PD	<i>rpl16</i> intron, ITS, <i>adhD</i>	rapid	38–45 (family)	W	Miocene origin, Pliocene–Pleistocene radiation via range fragmentation
Malvaceae	<i>Gossypium</i>	Liu <i>et al.</i> (2001)	PD	<i>FAD2-1</i>	multiple radiations	38–45 (family)	W	coastal clade sister to arid clade
Malvaceae	Hibisceae	Pfeil <i>et al.</i> (2002)	PD	<i>ndhF</i> , <i>rpl16</i>	rapid at base of <i>Hibiscus</i>	38–45 (family)	W	Gondwanan (Australian) origin, radiated in tropics
Moraceae	<i>Ficus</i>	Jousselin <i>et al.</i> (2003)	P	ITS, ETS	—		P	cospeciation with wasp pollinators
Myrtaceae		Gadek <i>et al.</i> (1996); Wilson <i>et al.</i> (2001)	PD	<i>matK</i>	—	59	P	—
Myrtaceae	<i>Beaufortia</i> suballiance	Ladiges <i>et al.</i> (1999); Brown <i>et al.</i> (2001)	D	5S, ITS-1	—		W	Gondwanan with vicariance, Early Cenozoic radiations
Myrtaceae	<i>Chamelaucium</i> suballiance	Lam <i>et al.</i> (2002)	D	<i>matK</i>	—		W	—
Myrtaceae	<i>Corymbia</i> + <i>Angophora</i> + <i>Eucalyptus</i>	Stearns <i>et al.</i> (2002)	PD	ITS	multiple radiations	56	W	—
Myrtaceae	eucalypt group	Ladiges <i>et al.</i> (2003)	D	ITS	multiple radiations	56	W	Late Cretaceous origin, radiations with climatic and geological events
Myrtaceae	<i>Leptospermum</i> suballiance	O'Brien <i>et al.</i> (2000)	D	<i>matK</i> , <i>atpB/rbcL</i> spacer	—		P	—
Myrtaceae	<i>Acmena</i> alliance	Harrington & Gadek (2004)	D	ITS, ETS	—		W, but non-Aust poor	multiple dispersals into and out of Aust.
Nothofagaceae	<i>Nothofagus</i>	Linder & Crisp (1995)	D	<i>rbcl</i>	—	80	W	deep lineages Gondwanan but Aust–NZ incongruent with vicariance model
Nothofagaceae	<i>Nothofagus</i>	Manos (1997)	D	<i>rbcl</i> , ITS	—		W	Gondwanan, vicariant
Nothofagaceae	<i>Nothofagus</i>	Setoguchi <i>et al.</i> (1997)	D	<i>atpB-rbcL</i> spacer	—	80	W	pre-Gondwanan radiation; NG and NCal recent radiations
Orchidaceae	Diurideae	Kores <i>et al.</i> (2000, 2001)	D	<i>matK</i> , <i>trnL/F</i>	—		P	—
Orchidaceae	<i>Dendrobium</i>	Yukawa & Uehara (1996); Yukawa <i>et al.</i> (1996)	PD	<i>rbcl</i>	two rapid radiations		P	dispersal into Aust
Osmundaceae		Yatabe <i>et al.</i> (1999)	PD	<i>rbcl</i>	—	250	P	—

(Continued.)

Table 2. (Continued.)

Phylogeny	Author(s)	PD	Markers	Notes	P	Biogeography
Phrymaceae	Beardsley & Olmstead (2002)	PD	<i>trnL/F</i> , ITS, <i>ETS</i>	—	P	two geographically distinct radiations; one in W Nth Amer <i>ca.</i> 130 spp.) and one in Australia (30 spp.); ancient divergence between these two
Poaceae	Barker <i>et al.</i> (2003)	D	<i>rpoC2</i> , ITS	—	W	—
Poaceae	Barker <i>et al.</i> (1998)	PD	<i>rpoC2</i>	rapid among genera?	W (deep nodes)	—
Poaceae	Soreng (1990)	rflp only	—	—	P	two dispersals into Australasia, from Asia and Amer
Poaceae	Hsiao <i>et al.</i> (1998)	D	ITS	—	P	—
Poaceae	Mant <i>et al.</i> (2000)	D (partial)	ITS	—	P	southwestern taxa more closely related to southeastern than to monsoonal
Podocarpaceae	Kelch (1998, 2002)	PD	18S	—	P	—
Podocarpaceae	Conran <i>et al.</i> (2000)	D	<i>rbcl</i>	—	W	—
Portulacaceae	Applequist & Wallace (2001)	D	<i>ndhF</i>	—	P	Amer origin, two dispersals into Aust
Proteaceae	<i>Banksia</i> + Mast (1998); Mast & Givnish (2002)	PD	<i>rp116</i> intron, <i>psbA</i> , <i>trnH</i> , <i>trnT/L</i>	two rapid radiations	W	origin and extensive radiations in the South-west; three southwest/southeast vicariance events; multiple origins of xeromorphy
Proteaceae	Hoot & Douglas (1998)	D	<i>atpB</i> , <i>atpB/rbcL</i>	—	P	Gondwanan; Mid-Cretaceous divergence between major groups; rapid radiation in Grevilleoideae.
Ranunculaceae	Schuettpelz & Hoot (2004)	PD	<i>trnL/F</i> , <i>atpB/rbcL</i> , ITS	—	P	infer China origin but southern distribution from Gondwana vicariance; tree looks too recent!
Ranunculaceae	Lockhart <i>et al.</i> (2001)	PD	J(SA), ITS	—	W	Pliocene radiation; multiple dispersals to Aust from NZ
Restionaceae	Linder <i>et al.</i> (2003)	PD	<i>rbcl</i> , <i>trnL/F</i>	Y	W (deep nodes)	diverged from Afr lineages <i>ca.</i> 70 Myr ago; early radiation exponential
Rhamnaceae	Richardson <i>et al.</i> (2000)	D	<i>rbcl</i> , <i>trnL/F</i>	—	P	<i>Discaria</i> a Gondwanan relict; Pomaderrae post-Gondwanan
Rutaceae	Scott <i>et al.</i> (2000)	D	<i>trnL/F</i>	—	W	northwards
Sapindaceae	Edwards & Gadek (2001)	D	<i>matK</i> , <i>rps16</i> intron, ITS-1	—	W	multiple radiations into Monsoonal tropics, possibly from temperate origin; dispersal into NG, NZ
Selaginellaceae	Korall <i>et al.</i> (1999); Korall & Kenrick (2002)	P	<i>rbcl</i>	Aust radiation slow, or depleted multiple radiations	W	—
Solanaceae	Garcia & Olmstead (2003)	PD	<i>ndhF</i> , <i>trnL/F</i>	—	W	two dispersals into Aust from S Amer, one Early Cenozoic, one recent
Sterculiaceae	Whitlock <i>et al.</i> (2001)	PD	<i>ndhF</i>	—	P	two dispersals out of Aust
Schizaeaceae	Wilksstrom <i>et al.</i> (2002)	PD	<i>rbcl</i>	—	P	—
Winteraceae	Karol <i>et al.</i> (2000)	PD	<i>trnL/F</i> , ITS	—	P	Mid-Cretaceous migration from Madagascar to Aust via Antarctica

Table 3. Comparison of extant and extinct diversity (number of taxa) in some Australian families that are characteristic of the aseasonal-wet biome.

	fossil		extant	
	genera	species	genera	species
Araucariaceae	4	36 (12 ^a)	3	6
Cunoniaceae	11	26	15	26
Nothofagaceae	1	10 ^b	1	3
Podocarpaceae	16	67 (34 ^a)	6	14

^a Oligocene macrofossil species.

^b Late Oligocene–Early Miocene pollen species.

in Australia (Wagstaff *et al.* 1999). In contrast to these rapid radiations, the Restionaceae, which are an important component of heathlands in the southwest and southeast, radiated steadily and exponentially throughout the Cenozoic (Linder *et al.* 2003). However, the African clade, which is a sister group to the Australian clade, radiated rapidly from the Miocene.

(iii) Monsoonal biome

The few informative studies on taxa that predominantly occur in this biome also indicate rapid radiations. The single Australian species of *Adansonia* is nested within a broom lineage of African and Madagascan taxa (Baum *et al.* 1998). It is presumed to have dispersed to Australia (Baum *et al.* 1998), because its divergence is too recent to have been the result of Gondwanan vicariance. *Gossypium* is inferred to have radiated rapidly and recently (post-Miocene), and to have undergone multiple dispersals, e.g. into the arid zone from the coast (Seelanan *et al.* 1997, 1999; Liu *et al.* 2001). *Alectryon* (Sapindaceae) is considered to have undergone multiple radiations into the monsoonal tropics, possibly from a temperate origin, and later dispersed into New Guinea and into the Pacific (Edwards & Gadek 2001).

(iv) Recent immigrants

Several studies infer recent (Late Cenozoic) arrival of taxa in Australia, followed by rapid radiation (Pliocene–Pleistocene), e.g. the Brassicaceae genera *Cardamine* (Bleeker *et al.* 2002a), *Rorippa* (Bleeker *et al.* 2002b) and *Lepidium* (Mummenhoff *et al.* 2001, 2004), *Gentianella* (von Hagen & Kadereit 2001), *Scleranthus* (Smitsen *et al.* 2003), *Ranunculus* (Lockhart *et al.* 2001) and Chenopodiaceae (Kadereit *et al.* 2003). Multiple dispersals are inferred in most of these, both into and out of Australia. These are predominantly herbs and small shrubs that have radiated in two environments that have expanded in the Pliocene and Pleistocene: the Eremean biome and cooler regions of the southeastern temperate biome.

Chenopodiaceae appears to have radiated in the Eremean biome with Pliocene aridification. Of the ca. 1500 extant species, 300 species, mostly endemic, occur in Australia (Wilson 1984). This family is not well supported as monophyletic and is either nested within Amaranthaceae or forms a polytomy with the basal nodes of Amaranthaceae (Kadereit *et al.* 2003). Unsurprisingly, pollen ascribed to chenopods is indistinguishable from that of Amaranthaceae *sensu lato* (Martin 1994; Jordan &

Macphail 2003). Such pollen first appeared in the Palaeocene (65–56 Myr ago (Kadereit *et al.* 2003)) and in Australia, ca. 30 Myr ago (Martin 1994). Molecular phylogenetic analysis suggests that chenopods in Australia comprise several separate lineages (Kadereit *et al.* 2003), and all probably originated as post-isolation immigrants, given the absence of fossils before that time. These lineages probably radiated within the past 3 Myr, i.e. from the Pliocene onset of aridity.

Lepidium is one of the few groups for which post-Pliocene radiations have been assessed by molecular dating. In Australia there are 35 endemic species, mostly occurring in the Eremean biome (Hewson 1982). All native species in Australia and New Zealand form a single chloroplast DNA clade, but two separate ITS clades (Mummenhoff *et al.* 2004). A single origin of the genus in Australasia is inferred, as a result of hybridization between two long-distance immigrants, one from North America and the other from South Africa (Mummenhoff *et al.* 2004). This event occurred no more than 1.3 Myr ago and therefore the entire radiation occurred during the Pleistocene (Mummenhoff *et al.* 2004). This genus appears to be readily dispersible, as several species are shared between Australian and New Zealand, and multiple dispersals between these areas are hypothesized (Mummenhoff *et al.* 2001).

(b) Molecular dating

(i) *Eucalypts*

Using a calibration of 70 Myr ago for the divergence of eucalypts from *Arillastrum*, the molecular dating suggests that the diversification of eucalypts proceeded steadily for at least 30 Myr before Australia became isolated from Antarctica and continued through the Mid-Cenozoic without showing evidence of a change in rate (figure 3). However, the sampling of terminal taxa for eucalypts is not yet dense enough to determine whether there has been an increase in speciation rate since the Pliocene (less than 5 Myr ago).

The molecular-dated divergence times of eucalypt lineages through the Cenozoic are older, some by a large margin, than those suggested by Ladiges *et al.* (2003) (table 4). Ladiges *et al.* estimated divergence times differently from us by linking them to climatic and tectonic events, although there is no direct evidence for causal links between any of these events. For example, they linked divergence of *Allosyncarpia* from *Eucalyptopsis* to contraction of rainforest and development of monsoonal climate in northern Australia, ca. 30–25 Myr ago, whereas molecular dating places this divergence ca. 37–35 Myr ago. The latter dates are

Table 4. Comparison of estimates of divergence times (million years ago) among eucalypt lineages, based on climatic and tectonic events (Ladiges *et al.* 2003) and molecular dating (this study). (Nodes are labelled in figure 3. Most recent and earliest divergence times are derived from different estimates of the age of the New Caledonia–Australia vicariance event at node A.)

node	event	Ladiges <i>et al.</i> (2003)	this study	
			most recent	earliest
A	<i>Arillastrum</i> (New Caledonia) versus eucalypts <i>sensu lato</i> (Australia): assumed vicariance event used for calibration	70	70	85
B	<i>Allosyncarpia</i> (monsoonal) versus <i>Eucalyptopsis</i> (wet tropics)	30–25	37–35	43–35
C	<i>Eucalyptus deglupta</i> (Southeast Asia) diverges from Australian sister taxon	10–5	38–26	45–26
D	radiation of sections in <i>Eucalyptus</i> subgenus <i>Symphyomyrtus</i>	10–5	30–13	36–13
E	divergence of <i>E. urophylla</i> (Timor) clade from Australian sister taxon	5–2	17–7	20–7

consistent with evidence for monsoonal forests in the Eocene in central Australia (Greenwood 1996). Fixing the base of the stem of eucalypts at 85 Myr ago (the earliest date for rifting between New Caledonia and Australia) makes the disparity in dates even greater (table 4). Given the uncertainty of any eucalypt fossil before the Miocene (Hill 1994a), it would be reasonable to conclude that a Cretaceous date for the basal node is too old.

Despite the discrepancy between this study and that of Ladiges *et al.* (2003), the dates inferred from the chronogram (figure 3) for some nodes have some support from fossil data. The first putative record of eucalypts is pollen of the *Angophora/Corymbia* type (*Myrtaceidites eucalyptoides*; Martin 1994) (55 Myr ago). Although there is doubt over the correct assignment of this fossil (Rozeffelds 1996), our estimates suggest an age for the base of the stem of the *Angophora + Corymbia* clade of 53–66 Myr ago, which encompasses the age of the fossil. *Eucalyptus patagonica*, consisting of fossil fruits from South America, has been tentatively assigned to subgenus *Symphyomyrtus* (Hill 1994a), and its probable Eocene age (55–34 Myr ago) includes our estimates of the age of the stem of this subgenus (41–46 Myr ago).

The only lineage occurring in the aseasonal-wet biome (*Eucalyptopsis* clade; figure 3) is very species poor (four species) by comparison with its sister group (the *Angophora + Corymbia* clade, 130 species). The radiations in these sister groups occurred at different times, with extant Australian taxa within the *Eucalyptopsis* clade appearing to have diverged *ca.* 35–40 Myr ago, whereas many of the taxa in the crown of *Angophora + Corymbia* diverged *ca.* 25 Myr ago. There is no indication from the fossil record of extinction of major lineages among the eucalypts.

Eucalyptus and *Angophora + Corymbia* each show multiple radiations in the southeast and southwest temperate, monsoonal and, to a lesser degree, the Eremean biomes. There is no clear pattern of lineages having radiated in only one biome.

(ii) *Casuarinaceae*

Fixing the age of the Fagalean crown group at 83 Myr gave an estimated age of 70 Myr for the Betulaceae–Casuarinaceae divergence, which is the same as for the fossil *Endressianthus* (above). Thus, estimates of node ages from fossils and molecular modelling are consistent. The chronogram of Casuarinaceae (figure 4) suggests that the radiation of the family has been exponential from *ca.* 48 Myr ago until *ca.* 25 Myr ago, when speciation appears

to have accelerated (or extinction decreased) in *Allocasuarina* relative to *Casuarina* and *Gymnostoma* (figure 4).

Gymnostoma is restricted to aseasonal-wet habitats and in Australia is represented by only one extant species (*Gymnostoma australianum*) whose divergence from other extant *Gymnostoma* is here estimated to have occurred almost 30 Myr ago. *Gymnostoma* was diverse in Australia during the Early Cenozoic, with up to 10 species known from the Eocene and six from the Oligocene (Scriven & Hill 1995; Guerin & Hill 2003), indicating that the genus has since been depleted by extinction.

Casuarina and *Allocasuarina* show a mixed pattern of radiation in the sclerophyll biomes (figure 4). In *Allocasuarina* there appear to have been multiple radiations in both the southeast and the southwest temperate biomes, and/or movement between biomes. Neither genus is currently speciose in the Eremean biome, with each having only two species there. The family is poorly represented in the monsoonal tropics, with only two species of *Casuarina* and three of *Allocasuarina*. All these also occur in the southeast temperate biome.

(iii) *Banksia/Dryandra*

The chronogram (figure 5) indicates that the two major lineages of the crown group diverged *ca.* 41 Myr ago and radiated rapidly from *ca.* 30 Myr ago through the Mid-Cenozoic drying period (figure 5). The representatives of *Dryandra*, a species-rich clade nested within *Banksia* (Mast & Givnish 2002), radiated rapidly from *ca.* 20 Myr ago (figure 5).

Most of the species diversity in *Banksia* occurs in the southwest temperate biome and there have been multiple radiations within this biome. After *ca.* 25 to 30 Myr ago, radiations have occurred within biomes with virtually no exchange between the southwest and southeast. Neither *Banksia* nor *Dryandra* currently occurs within the Eremean biome, except at the margins.

The sister taxon of *Banksia* (*Musgravea + Austromuelleria*) comprises only four species that are restricted to the wet tropics. This lineage is estimated to have diverged from *Banksia + Dryandra ca.* 60 Myr ago (figure 5).

(iv) *Mirbelieae and Bossiaeeae*

The chronogram of Mirbelieae and Bossiaeeae suggests that these tribes radiated in the Mid-Cenozoic period of climatic cooling and drying (figure 6). Radiation appears to have been rapid in all three major lineages (*Bossiaea*, 70

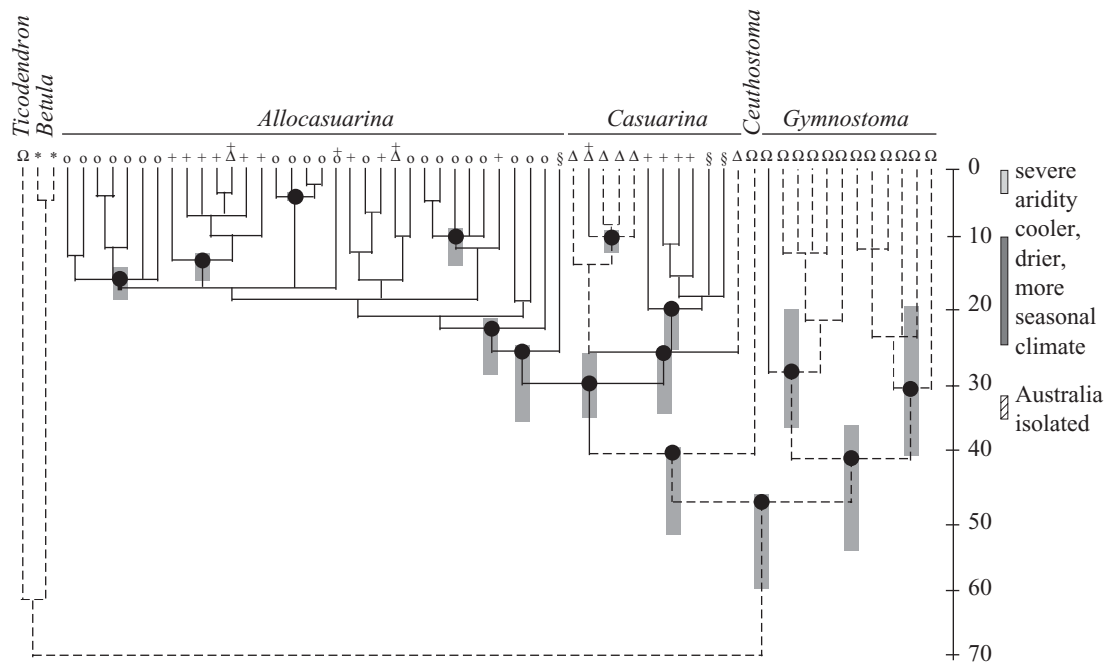


Figure 4. Chronogram of Casuarinaceae, assuming the basal divergence between this family and *Betula* + *Ticodendron* at 70 Myr ago. Symbols and labelling as in figure 3.

species; *Daviesia*, 140 species; and *Pultenaea sensu lato*, 470 species). Additionally, the radiations of all three lineages began within the same short space of time. That is, each lineage has a long stem (20+ Myr) followed by a radiation with short internal basal internodes. These short internal internodes do not appear to be the result of collapsed nodes as a result of conflict within the data. Additionally, the broom topology is found in phylogenies derived from both the chloroplast (non-recombining) and nuclear genomes (Crisp & Cook 2003a,c).

This group has its greatest species diversity in the southwest and southeast temperate biomes, poor representation in the monsoonal biome and is unknown from the aseasonal-wet biome. Most radiations within *Daviesia* appear to have been within biomes (primarily southeast and southwest), but there have been multiple movements between biomes (Crisp & Cook 2003c).

4. DISCUSSION

Molecular phylogenies and DNA sequence data are available for many Australian plant taxa (table 2) but few have been analysed or presented in a form that sheds light on the type of radiation that has occurred, or its timing. Most studies have been focused narrowly on taxonomic outcomes rather than broader evolutionary questions. The availability of the data, however, means that we can now begin to analyse the evolution of the Australian flora during the Cenozoic using time-scales derived both from fossils and molecular dating.

(a) Radiations

The taxa analysed here using chronograms show varying patterns of radiation since the isolation of Australia. The phylogenies of *Banksieae* and *Mirbelieae* + *Bossiaeeae* each show a markedly punctuated pattern whereas those of eucalypts and most of Casuarinaceae do not. Despite these

broad differences, phylogenetic patterns within these groups exhibit considerable congruence.

Irrespective of their earlier evolutionary history, our molecular-dated phylogenies indicate that taxa that now characterise the sclerophyll communities of Australia radiated rapidly during the period of climatic change, ca. 25–10 Myr ago (figures 3–6). Rapid radiations apparently occurred in each of *Bossiaea*, *Daviesia* and *Pultenaea sensu lato* (*Mirbelieae* + *Bossiaeeae*), *Allocasuarina* (Casuarinaceae), and the two major *Banksia* lineages between ca. 25–15 Myr ago. Therefore, the increase in pollen of eucalypts, Casuarinaceae and *Banksia* in the palynological record during this period (Kershaw *et al.* 1994; Martin 1994) probably reflects evolutionary radiation, in addition to ecological or geographical expansion of the group. However, the history of these taxa before the Mid-Cenozoic appears to differ. Eucalypts and banksias appear to have started radiating ca. 60 Myr ago, Casuarinaceae ca. 47 Myr ago, and *Mirbelieae* + *Bossiaeeae* in two episodes: ca. 40 Myr ago (giving rise to present-day genera), and from 20 Myr ago (giving rise to species). Some sclerophyll taxa show evidence of extinction before the Mid-Cenozoic radiation. The pollen and macrofossil record indicates a major radiation of the Proteaceae, including *Banksia*, in the Palaeocene and Eocene (Hill 1994a; Hill *et al.* 1995); however, the chronogram of *Banksia* (figure 5) indicates that only two lineages have survived from that time. In the *Mirbelieae* + *Bossiaeeae*, the long stems on lineages between 40 and 20 Myr ago also may indicate extinction. Several other taxa in table 2 show evidence of rapid radiation in the sclerophyll biomes (*Acacia*, *Callitris*, *Drosera*, Ericaceae tribe *Styphelieae*, Fabaceae tribe *Galegeae* (including *Carmichaelinae*), *Scaevola* and Solanaceae tribe *Anthocercideae*) but in the absence of molecular dating, it is unknown how many of these radiations

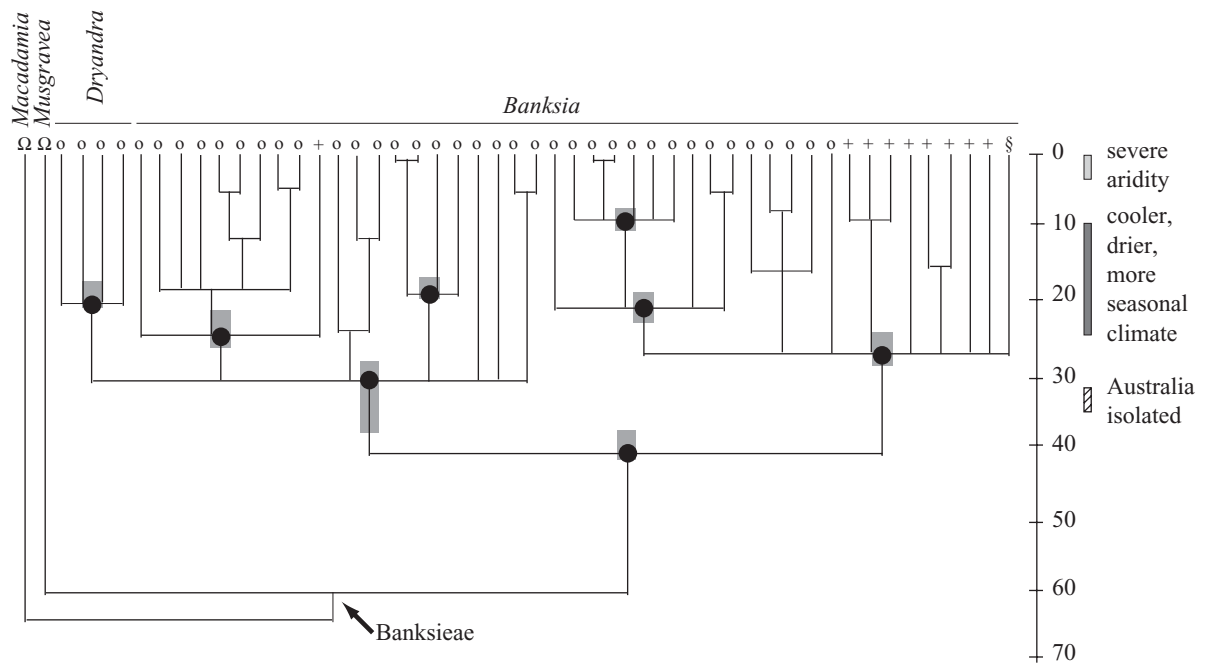


Figure 5. Chronogram of *Banksia* and *Dryandra* (Proteaceae), assuming the basal divergence between Banksieae and *Macadamia* at 62 Myr ago. Symbols and labelling as in figure 3.

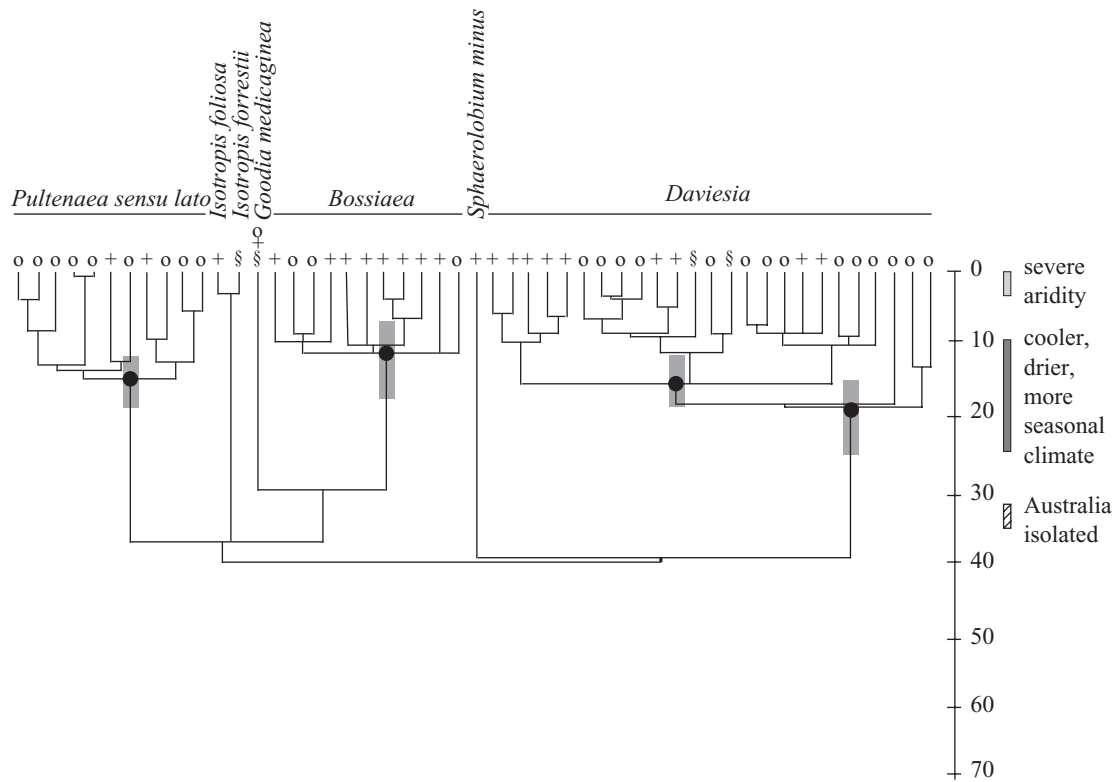


Figure 6. Chronogram of Mirbelieae + Bossiaceae (Leguminosae), assuming the basal divergence between the tribes at 40 Myr ago. Symbols and labelling as in figure 3.

occurred during the period of climatic change *ca.* 25–10 Myr ago.

Terminals of the above mentioned groups are not sampled well enough to assess radiations in the Pliocene.

(b) Biomes

It is well established from the fossil record that the present-day biomes have different histories (Hill 1994b;

Hill *et al.* 1999). The aseasonal-wet biome has its origins in the Cretaceous, was widespread but is now reduced to small refugia along the east coast. The sclerophyll biomes probably also have their origins in the Cretaceous, and rose to dominance from 25 Myr ago. There is evidence of a Monsoonal biome in central Australia in the Eocene (Greenwood 1996) and it was extensive in northern Australia by 25 Myr ago (Ladiges *et al.* 2003). The

Eremean biome perhaps originated in dry pockets during the Mid-Cenozoic but only became extensive during Pliocene aridification (Hill 2004).

Taxa mainly restricted to the aseasonal-wet biome (*Nothofagus*, Araucariaceae, Cunoniaceae and Podocarpaceae) are today represented by species-poor lineages, as are the aseasonal-wet biome taxa within eucalypts, Banksieae, and Casuarinaceae. In these last three groups, chronograms suggest that the divergence of lineages restricted to the aseasonal-wet biome from their sisters occurred more than 40 Myr ago. Thus, the molecular phylogenies analysed here indicate that there is no evidence of large radiations in the aseasonal-wet biome since the Oligocene or, alternatively, if there were radiations in this biome during this period, the evidence has been erased by extinction. Moreover, there is little evidence of multiple movements between the aseasonal-wet biome and others: aseasonal-wet lineages are not scattered throughout chronograms nor are multiple lineages from other biomes nested within multiple aseasonal-wet biome lineages. The few available molecular phylogenies of taxa restricted to this biome (Araucariaceae, Nothofagaceae, Podocarpaceae and *Gymnostoma*) support findings derived from the Australian fossil record of the Late Cretaceous and Early Cenozoic that diversity has declined. There are too few fossil data for eucalypts, Cunoniaceae and Banksieae to determine whether there has been extensive extinction, or whether there was never high diversity, of these groups in the aseasonal-wet biome. However, it is clear that there have been major regional extinctions (in central and southern Australia) of Cunoniaceae (Barnes *et al.* 2001).

There is a long-standing question as to whether there was an early vicariance event between the southeastern and southwestern temperate biomes followed by endemic radiations in each biome (Nelson 1974; Ladiges *et al.* 1987; Crisp *et al.* 1995; Mast & Givnish 2002; Hopper & Gioa 2004). Marine intrusion from the Great Australian Bight *ca.* 30 Myr ago, and perhaps aridification inland, isolated the southwest (Frakes 1999; Hopper & Gioa 2004). Subsequently, uplift of the Nullarbor limestone plateau replaced the marine barrier with an edaphic barrier and more recently, an aridity barrier. The chronograms examined here indicate that there have been multiple divergences between the southeastern and southwestern temperate biomes throughout the period of radiation of taxa that are well represented in both biomes (eucalypts, Casuarinaceae, *Banksia*, *Callitris* and Mirbelieae + Bossiaceae), although there has been no exchange in *Banksia* since *ca.* 30–25 Myr ago. Perhaps the barriers have prevented expansion of *Banksia* across the Nullarbor. This is not true of the other taxa above, all of which currently occur, albeit in low diversity, in the desert immediately north of the Nullarbor.

Taxa that now characterize arid communities (Eremean biome) appeared progressively in the Australian fossil record during the Cenozoic: Gramineae at 50 Myr ago, Amaranthaceae + Chenopodiaceae at 30 Myr ago, *Acacia* at 24 Myr ago and Asteraceae at 18 Myr ago (Martin 1994). Pockets of relatively dry, open habitat potentially suitable for these taxa have existed since the Cretaceous but they did not become abundant in the fossil record until the onset of severe aridity after 5 Myr ago (Hill *et al.* 1999: fig. 70). It appears that this onset may have triggered rapid radiation in taxa that were pre-adapted to arid environ-

ments, such as the Chenopodiaceae (Kadereit *et al.* 2003), Brassicaceae (Mummenhoff *et al.* 2004) and *Gossypium* (Seelanan *et al.* 1999; Liu *et al.* 2001). Consistent with the late opening up of the arid zone, molecular phylogenies indicate that these radiations commenced much more recently than the Mid-Cenozoic radiations in the sclerophyll biomes.

It has been hypothesized that the arid-zone flora radiated from ancestors with cosmopolitan coastal distributions, e.g. Aizoaceae *sensu lato*, Amaranthaceae + Chenopodiaceae, Asteraceae, Brassicaceae, Convolvulaceae, Frankeniaceae and Portulacaceae (Burbidge 1960). These families are a significant component of the extant flora on coastal dunes and saline tidal flats and Burbidge considered that their adaptation to salinity pre-adapted them to an arid climate. A similar suggestion has been made with respect to the entry of *Lepidium* (Brassicaceae) into the Australian environment (Mummenhoff *et al.* 2004). Both drought- and salinity-tolerance require mechanisms for managing osmotic stress, and although the mechanisms can be different (Kefu *et al.* 2003), tolerance of both stresses is widespread in the chenopods. Therefore, the possibility that one mechanism may be an exaptation for the other in this family seems worth investigating. Phylogeographic studies on species and complexes that occur both on the coast and inland in the arid zone may reveal pathways between these habitats, perhaps along riverine floodplains, e.g. *Atriplex holocarpa* + *spongiosa*, *A. australasica*, *A. suberecta*, *Dysphania glomulifera*, *Rhagodia candolleana/crassifolia*, *Enchylaena tomentosa*, *Threlkeldia diffusa* and samphires.

Representation of the monsoonal tropics biome in molecular studies so far is insufficient to allow assessment of its history. Taxa that have already been studied, such as eucalypts and acacias, are well represented in this region, and could be informative if sampled better. Tropical grass and legume groups (e.g. tribes Phaseoleae, Millettieae and Indigofereae) also need study. This biome is interesting because its radiation should be linked with that of monsoonal regions to the north of Australia (Crisp 1996).

5. CONCLUSION

In combination with the fossil record, molecular phylogenies are providing new insights about the history of radiation and extinction in the flora of Australia since its isolation from Antarctica *ca.* 30 Myr ago. The macro-evolutionary histories inferred from phylogenies differ among taxa and many of these are consistent with predictions from the fossil record. Phylogenies of taxa such as *Nothofagus* and conifers that abruptly declined in fossil abundance after 25 Myr ago have species-poor lineages through that period that have either have been decimated by extinction or failed to radiate since then. Species-rich groups that rose in fossil abundance since 25 Myr ago, such as the eucalypts, radiated extensively during that period, according to molecular phylogenies. Major environmental changes during the Cenozoic are reflected in correlated patterns among phylogenies of different taxa. Between 25 and 10 Myr ago, as the climate became drier and more seasonal, there was stasis or decline in diversity in multiple lineages occurring in rainforest habitats (e.g. *Nothofagus*, conifers, *Gymnostoma*) while an increase in speciation rate occurred in lineages characteristic of sclerophyll habitats (e.g.

Banksia, *Allocasuarina*, pea-flowered legumes). The onset of severe aridity from 3 Myr ago is probably reflected in rapid radiation of pre-adapted immigrant taxa such as Chenopodiaceae and Brassicaceae, but more phylogenies are needed to test this hypothesis. Therefore, taxa occurring in the same biomes appear to have exhibited similar macro-evolutionary patterns, and these have differed among biomes. However, this commonality of response may have been limited to the periods of major climatic change. For example, dominant sclerophyll biome taxa (eucalypts, *Banksia*, Casuarinaceae and pea-flowered legumes) appear to have differing patterns of radiation and extinction before the Mid-Cenozoic climate changes. Some radiations appear to have occurred within biomes (e.g. there were separate radiations of *Banksia* in the southwest and southeast after 25 Myr ago) but more typically there appear to have been multiple exchanges of taxa among the sclerophyll biomes throughout the Cenozoic. However, there is little evidence of multiple movements between the aseasonal wet biome and the others through its period of decline.

6. PROSPECTS

Molecular phylogenies with dated nodes provide new perspectives on the evolutionary history of the Australian flora. However, challenging questions are yet to be adequately addressed. Was rapid speciation during the radiation of the sclerophyll flora driven by expansion into newly opened habitat following an extinction event (e.g. the loss of rainforest between 20 and 12 Myr ago), or by fragmentation of contracting ranges (e.g. during the brief resurgence of rainforest ca. 5 Myr ago)? What were the timing and nature (vicariance or dispersal) of divergences between sister taxa in the southeast and southwest? To what extent does Burbidge's hypothesis explain the origins, and perhaps very rapid radiation, of the arid zone flora? Did the evolution of C4 photosynthesis have a major role in this, for example in grasses and chenopods (Kadereit *et al.* 2003; Sage 2004)?

The well-documented decline in rainforest-type communities from 25 Myr ago (Kershaw *et al.* 1994; Hill *et al.* 1999) was inferred from the decreasing abundance of pollen of higher taxa (genera and families), and did not necessarily indicate a rapid loss of species. Provided that the fossil record of a taxon is relatively detailed and continuous, comparison between it and a chronogram may discriminate between these hypotheses. For example, diversity of *Nothofagus* in southeastern Australia peaked in the Late Oligocene and Early Miocene, with four subgenera and 10 pollen species (Hill 2001).

These questions require well-sampled taxa for inferring chronograms. However, despite many (at least 89: table 2) molecular phylogenetic studies on Australian taxa, most give attention mainly to taxonomic implications. Few studies present phylograms that would allow an assessment of the nature of radiation (punctuated versus exponential). There is a need for more studies using maximum likelihood with an appropriate model, and published as a phylogram or chronogram. Dense and balanced sampling of lineages is needed. More sampling is required from arid zone and monsoonal tropical taxa to enable comparisons between these and the other biomes.

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GLOSSARY

- ACC: Antarctic Circumpolar Current
ITS: internal transcribed spacer
MP: maximum parsimony