

**A Re-evaluation of Queensland's Wet Tropics based on 'Primitive' Plants**

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The diversity of angiosperms in primitive families, which occur in the Wet Tropics of Queensland, is frequently cited as evidence of the ancient nature of the Australian rain forests, but appears to be based on flawed taxonomic assumptions. We point out the error of identifying species as being primitive rather than representing families with ancient origins, list the families from near-basal lineages using a current molecular phylogeny, and compare their diversity with other areas of rain forest in Australia, and with other tropical areas in the Pacific. Twenty-eight dicot families below the eudicot clade may be regarded as near-basal; 16 of these are present in rain forest habitat in the Wet Tropics. The diversity of near-basal families, and of the species and endemics within these families, is similar in New Caledonia, and the family diversity similar to Costa Rica. We suggest that these data are consistent with other evidence that rain forest has persisted on the Australian continent for a long time, and that the role of Australian rain forests in harbouring a significant near-basal component has been underestimated. We also suggest that ongoing management might be focussed at conserving the evolutionary history present in the near-basal lineages, especially in the face of changing climatic patterns.

**Key words:** near-basal lineages, primitive angiosperms, Gondwana, rain forest, Australia

## INTRODUCTION

The World Heritage-listed rain forests of the Wet Tropics Bioregion of north-east Queensland (15° 40'S - 19° 15'S; Fig. 1) are often lauded for the high concentration of primitive angiosperm species that they support, reflecting the Gondwanan origins of the region. Since the publication of a report by the Rainforest Conservation Society of Queensland (1986) the region has frequently been described as a home to 12 or 13 of the 'world's 19 most primitive plant families' (for example, by the Wet Tropics Management Authority 2002, and the Australian Government's Department of the Environment & Heritage 2006). Similar accounting in other rain forest areas of Australia would show 4/19 families in the temperate rain forests of south-eastern Australia in Tasmania and Victoria, 6/19 families in the monsoonal vine thickets of northern Australia between Queensland's Wet Tropics and the Kimberley region of Western Australia, and 12/19 in the subtropical rain forests between southern New South Wales and central Queensland, though with far fewer species than in the Wet Tropics.

The Rainforest Conservation Society of Queensland's (1986) report considered the orders Magnoliales and Laurales to contain the most primitive families, and arrived at its total of 13 out of 19 through use of a pollen-based phylogeny (Walker 1976). The report included the Winteraceae (but not the Lactoridaceae) in the Magnoliales *sensu* Cronquist (1981), and classified *Sphenostemon* in the Trimeniaceae (*sensu* Hutchinson 1959). Extensive collecting activities, enormous advances in phylogenetics and considerable taxonomic change since 1986 has led to a need for a reappraisal of the 'primitive plant flora' of the rain forests in the Wet Tropics Bioregion (*sensu* Environmental Australia 2005). We suggest that a single, internationally recognised, molecular phylogeny be used to address the diversity of

the group of angiosperms which may be regarded as arising from near-basal lineages (*sensu* Stevens 2006).

The identification of the extant descendants of the most primitive angiosperms is fraught with difficulties and misunderstandings, for example, the recent disagreement over how to determine the most basal angiosperm lineage (i.e., the group closest to the first angiosperm), reviewed by Lockhart & Penny (2005). Various methods have been used to try and reconstruct the angiosperm family tree, both using molecular techniques for extant plants and morphological techniques for extinct and extant plants. Bateman *et al.* (2006) provide separate composite morphological and sequence-based phylogenies drawing on a number of other published studies to draw attention to the contrasting hypotheses that these approaches are generating. However, the group of angiosperm orders which are considered to be near-basal and which in an evolutionary context precede the relatively recently evolved and more derived angiosperms, the eudicots (*sensu* Angiosperm Phylogeny Group II 2003), are consistent between the two approaches with the main exception being the placement of the monocots (Bateman *et al.* 2006). These groups of near-basal angiosperms are also broadly similar to those adopted by Stevens (2006), on which subsequent analyses in this paper are based, and by Heywood *et al.* (2007).

While the grouping of families or orders as near-basal is thus fairly well agreed upon, it is incorrect to claim that species within these taxa are primitive. A 'primitive plant flora' would refer to a group of primitive plants. We have scant evidence to show that individual species are hundreds of millions of years old and individual species may themselves be of recent evolutionary origin, or contain a suite of advanced characteristics, even though their familial affiliations may be with the near-basal angiosperms. For example, the absence of xylem vessels in *Bubbia* in the Winteraceae is hypothesised to be a derived condition, species in the family having secondarily lost their vessels to better cope with freeze-thaw conditions, rather than having failed to evolve them at all (Field *et al.* 2002). What we are actually concerned with are those lineages that appear to have branched off the main evolutionary trunk of the angiosperm family tree at a very early stage, which are referred to as near-basal lineages, and with speciation in them. To do this we assess what proportion the near-basal lineages represent of the entire angiosperm family representation within the Wet Tropics Bioregion, and how that proportion compares with other tropical floras. Thus, we can assess the contribution that taxa from near-basal lineages play in the Wet Tropics flora and have some indication of the global role that the Wet Tropics plays in supporting taxa from these lineages.

## **Methods**

We reviewed the 2145 species and 852 genera of the rain forest flora of the Wet Tropics (Metcalf & Ford *in press*) with reference to the Angiosperm Phylogeny Website (Stevens 2006), which is largely based on the groupings agreed by the Angiosperm Phylogeny Group II (2003). Nomenclature follows Bostock & Holland (2007), but familial assignment follows Stevens (2006). We consider near-basal angiosperm groups to be those branching below the eudicot clade, a definition which demarcates 28 near-basal dicot families (Table 1), and the monocots families, which we do not consider here. To make the necessary comparisons we also considered the

non-rain forest species within the Wet Tropics Bioregion, which takes the species total to 4035 and the number of genera to 1369.

We conducted similar analyses for other rain forest areas in Australia (Fig. 1), namely Cape York Peninsula (7,500 km<sup>2</sup>), incorporating rain forest types to the north of the Wet Tropics; northern tropical Australia (364,000km<sup>2</sup>), incorporating rain forest patches west of the Wet Tropics including those of western Queensland, the Northern Territory and northern Western Australia; the east-coast subtropical rain forests (1,700,000 km<sup>2</sup>) incorporating Queensland south of the Wet Tropics and the whole of New South Wales, and the *Nothofagus*-dominated temperate rain forests of Victoria and Tasmania (1,000,000 km<sup>2</sup>; Groves 1994, Neldner & Clarkson 1995, Accad *et al.* 2008, Australian Rainforest Foundation 2009). We also considered the basal lineages of New Caledonia and Costa Rica, which have similarly well researched floras and which, with the Wet Tropics, straddle the Pacific. New Caledonia (2422 dicot species; 19° - 23° S; c. 1, 200 km east of Australia) is another Gondwanan fragment and we included taxa from both the wet and dry forests and the maquis. New Caledonia is a similar size to the Wet Tropics (19, 000 km<sup>2</sup> versus the Wet Tropic's 20,000 km<sup>2</sup>) and its diversity and levels of endemism are “truly outstanding in global terms” (Lowry *et al.* 2004). Taxonomic data for New Caledonia were sourced from Jaffré *et al.* (2001).

Costa Rica (5250 dicot spp.; c. 8° - 11° N, 84° W; 51, 100 km<sup>2</sup>) is much younger, c. 50 million years old, being a product of the movement of the continental Caribbean plate over the oceanic (Pacific) Cocos plate. Positioned in Central America, the flora of Costa Rica is relict of the meeting of North and South American c. 3 million years ago, and as such “Mesoamerica has ... some of the highest levels of diversity and endemism on Earth” (Mittermeier *et al.* 2004). We used data for the entire Costa Rican flora, from all community types, taken from Instituto Nacional de Biodiversidad (2001), Hammel *et al.* (2004) and Hammel & Zamora (2005).

## Results

The Wet Tropics Bioregion can claim 16 near-basal families, all of which are found in rain forest habitats, including the Wet Tropics-endemic Austrobaileyaceae. These 16 families (7% of the Wet Tropics' families) contain 46 genera and 175 spp. (Table 2), respectively 3% and 4% of those which comprise the region's rain forest flora. A further 636 Wet Tropics species are endemic to Australia; 52 of these are from near-basal lineages (bringing the total of near-basal endemics to nearly 6% of the flora). Nearly half of the species diversity in near-basal families is attributable to extensive speciation in the Lauraceae (Table 2). Approximately 13% (93/701) of the Wet Tropics endemic species come from families with near-basal origins (42 from the Lauraceae; Metcalfe & Ford 2008). All of the Wet Tropics endemics from near-basal families are rain forest species; 96% (674/701) of the Bioregional endemics are found in rain forest habitats.

Other rain forest regions in Australia support a range of families and species from near-basal lineages, but none have the richness of the Wet Tropics in terms of species, and only the sub-tropical rain forests of eastern Australia contain a near-basal family (Trimeniaceae) not also found in the Wet Tropics (Table 3).

New Caledonia's floristic statistics look remarkably similar to those of the Wet Tropics (Table 4), with 11 near-basal families containing 111 species; approximately 5% (99/2033) of the New Caledonian endemic species come from families with near-basal origins (46 from the Lauraceae).

Costa Rica has 15 near-basal families and 569 spp; the large number of species in these families is due to tremendous speciation in the Piperaceae (*Piper* 138 spp. and *Peperomia* 134 spp.), and to a lesser extent in the Lauraceae (147 spp.) and Annonaceae (73 spp.).

## DISCUSSION

This reanalysis of the contribution that near-basal lineages make to the Wet Tropics flora achieves three aims. Firstly, through using Stevens (2006), it provides an assessment of the flora using a single contemporary phylogeny, bringing the analysis up to date and establishing a clear grouping of families from which to ascertain their presence or absence. This raises the potential number of near-basal families from 19 to 28 through the inclusion of the Nymphaeales (two families), Ceratophyllales and Chloranthales (one family each) and the Piperales (five families); in the case of the Wet Tropics this results in the addition of five new families (Table 1). Secondly, this approach provides a clear baseline from which to assess the relative importance of the Wet Tropics in an Australian context; the tropical and subtropical rain forests of eastern Australia are clearly important for the range of near-basal lineages they support (Table 3), though the Wet Tropics is considerably richer in species and density. Thirdly, the role of the Wet Tropics as a repository for near-basal lineages in a global context can be determined through comparison with other well-known floras. In this case we have considered New Caledonia and Costa Rica, both regarded as botanically rich, and found that the Wet Tropics holds equivalent diversity in its near-basal lineages.

An explanation for the high diversity of near-basal lineages in the Wet Tropics must be found in the persistence of rain forests in the region over millions of years. Pollen records show that the current extent of Australian rain forests is greater than it was on several occasions during the Tertiary and Quaternary (Kershaw 1994; Haberle 2005), although refugia existed during each contraction (Hilbert *et al.* 2007). There is debate about the extent to which Indomalayan elements migrated south into northern Australia after each drying cycle, but macrofossils from the Tertiary suggest that key families in the extant rain forest were present long before the Quaternary glaciations (Christophel 1989). Whatever the impact of migration of Indomalayan species into northern Australia was, the fact remains that the rain forests of the Wet Tropics and New Caledonia are significant strongholds of the near-basal families, and the levels of diversity and endemism within these families make them a significant repository of species from near-basal lineages.

The shared East-Gondwanan origins of the Wet Tropics and New Caledonia (and New Guinea) and the significance of the near-basal lineages in their floras suggests the longevity of rain forest habitats and their long isolation from developing floras in other parts of the tropics. South America and Africa separated from Gondwana much

earlier (167 million years ago) than the separation of Australia from New Zealand and New Caledonia (70 mya). Costa Rica, however, is less than 50 million years old, yet it has amassed a huge flora which is rich in near-basal lineages. Connections to the floras of North and South America, a central spine which rises to nearly 4000 m above sea level separating the Pacific and Caribbean coasts with their respective influences, and a huge range of habitats may explain the diversity, but not its subtleties. Why, for example, did the Piperaceae become so speciose (274 spp.) while remaining so constrained in the Wet Tropics (14 spp.) and New Caledonia (16 spp.), when the Lauraceae and Annonaceae, which are significant families in both the Wet Tropics and New Caledonia, also claim significance in Mesoamerica?

In conclusion, though the Rainforest Conservation Society of Queensland's listing (1986) of primitive families provides an under estimate of the numbers of species with near-basal lineages, our re-evaluation is unlikely to change general perceptions or only strengthen them in relation to valuing specific parts of the Wet Tropics biota. While it is misguided to talk about a primitive plant *flora*, the rain forests of the Wet Tropics Bioregion demonstrably do support a great number of families which can be described as originating from lineages that branched near the base of the angiosperm family tree. These families, genera and species contribute considerable phyletic diversity (*sensu* Sachs 1978) to the Wet Tropics, encapsulating in a genetic sense a great deal of evolutionary history. Considerable biodiversity and endemism exists within these families, making the Wet Tropics as significant as the justly famed floras of New Caledonia and Costa Rica as a rich repository for near-basal lineages. Future research will inevitably include a focus on how to preserve communities threatened by climate change occurring at an unprecedented rate. Rain forest taxa have retreated into climatic refugia in the past, but now face the challenge of moving faster than ever before and within a contested and more fragmented landscape. The traits which have allowed ancient lineages to persist through previous cycles of change may be less adaptive for future rates of change. Consequently, as conservation effort will inevitably be focussed on some species at the expense of others, we suggest that particular consideration be given to the diverse representatives of the near-basal lineages, and the communities which they inhabit.

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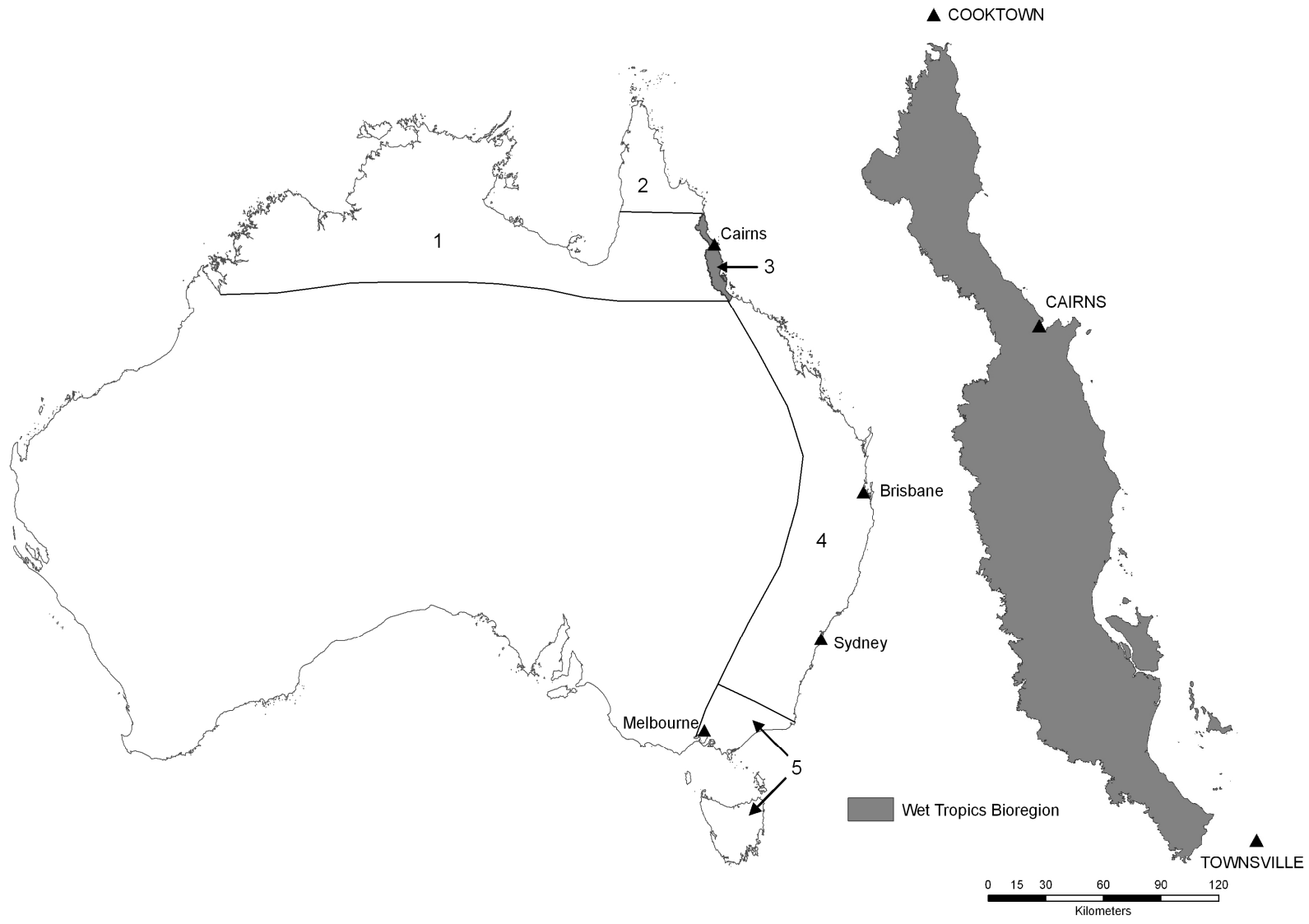
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## Figure Legend

**Fig. 1.** The location of the Wet Tropics bioregion in Australia, and the relationship of the five Australian study regions; 1 – northern tropical Australia, 2 – Cape York Peninsula, 3 – Wet Tropics, 4 – east coast subtropical rain forest, 5 – *Nothofagus* – dominated temperate rain forest.



**Table 1.** Orders and families of primitive angiosperms, showing the 19 families considered by the Rainforest Conservation Society of Queensland (RCSQ, 1986) and the ‘missing’ families revealed by modern phylogenetic classification (Stevens 2006). Families with representation in the rain forests (including aquatics adjacent to rainforest communities) of the Wet Tropics Bioregion are in bold text, with the number of genera/species present in parentheses.

<b>Order</b>	<b>RCSQ 1986</b>	<b>Stevens 2006</b>
Amborellales	Amborellaceae	Amborellaceae
Nymphaeales		<b>Cabombaceae (1/1)</b> <b>Nymphaeaceae (1/2)</b>
Austrobaileyales	<b>Austrobaileyaceae</b>	<b>Austrobaileyaceae (1/1)</b>
	Trimeniaceae*	Schisandraceae Trimeniaceae
Ceratophyllales		<b>Ceratophyllaceae (1/1)</b>
Chloranthales		Chloranthaceae
Magnoliales	<b>Myristicaceae</b> Magnoliaceae Degeneraceae	<b>Myristicaceae (1/2)</b> Magnoliaceae Degeneraceae
	<b>Himantandraceae</b>	<b>Himantandraceae (1/1)</b>
	<b>Eupomatiaceae</b>	<b>Eupomatiaceae (1/2)</b>
	<b>Annonaceae</b>	<b>Annonaceae (12/30)</b>
Lurales	<b>Atherospermataceae</b>	<b>Atherospermataceae (3/3)</b>
	Calycanthaceae + <b>Idiospermaceae</b>	<b>Calycanthaceae (1/1)</b>
	Gomortegaceae	Gomortegaceae
	<b>Hernandiaceae +</b>	<b>Hernandiaceae (1/2)</b>
	<b>Gyrocarpaceae</b>	
	<b>Lauraceae</b>	<b>Lauraceae (8/82)</b>
	<b>Monimiaceae</b>	<b>Monimiaceae (8/23)</b>
		Siparunaceae
Canellales	Canellaceae	Canellaceae
	<b>Winteraceae</b>	<b>Winteraceae (2/7)</b>
Piperales		<b>Aristolochiaceae (2/6)</b>
		Hydnoraceae Lactoridaceae
		<b>Piperaceae (2/14)</b>
		Saururaceae

\* in RCSQ (1986) *Sphenostemon*, which is present in the Wet Tropics, was included in Trimeniaceae, though neither Walker (1976) nor Cronquist (1981) regarded *Sphenostemon* as occurring in a recognised primitive family. *Sphenostemon* has been placed in Aquifoliaceae by many authors but is now regarded as being in its own family, the Sphenostemonaceae, which is not closely related to Aquifoliaceae. Stevens (2006) places Aquifoliaceae in the Aquifoliales whereas Sphenostemonaceae is unplaced near the Apiales.

**Table 2.** Genera present in primitive families (*sensu* Stevens 2006; Monimiaceae *sensu* Whiffin & Foreman 2007) in the rain forests of the Wet Tropics Bioregion. Genera in bold are endemic, and numbers in parentheses indicate the number of native species present in the Wet Tropics.

<b>Family</b>	<b>Genera</b>
Annonaceae	<i>Cananga</i> (1), <i>Desmos</i> (2), <i>Fitzalania</i> (1), <i>Goniothalamus</i> (1), <i>Haplostichanthus</i> (5), <i>Meiogyne</i> (3), <i>Melodorum</i> (4), <i>Miliusa</i> (2), <i>Polyalthia</i> (4), <i>Pseuduvaria</i> (5), <i>Uvaria</i> (1), <i>Xylopi</i> (1)
Aristolochiaceae	<i>Aristolochia</i> (2), <i>Pararistolochia</i> (4)
Atherospermataceae	<i>Daphnandra</i> (1), <i>Doryphora</i> (1), <i>Dryadodaphne</i> (1)
Austrobaileyaceae	<b><i>Austrobaileya</i></b> (1)
Cabombaceae	<i>Brasenia</i> (1)
Calycanthaceae	<b><i>Idiospermum</i></b> (1)
Ceratophyllaceae	<i>Ceratophyllum</i> (1)
Eupomatiaceae	<i>Eupomatia</i> (2)
Hernandiaceae	<i>Hernandia</i> (2)
Himantandraceae	<i>Galbulimima</i> (1)
Lauraceae	<i>Beilschmiedia</i> (9), <i>Cassytha</i> (1), <i>Cinnamomum</i> (4), <i>Cryptocarya</i> (28), <i>Endiandra</i> (29), <i>Lindera</i> (1), <i>Litsea</i> (8), <i>Neolitsea</i> (2)
Monimiaceae	<b><i>Austromatthaea</i></b> (1), <b><i>Endressia</i></b> (1), <b><i>Hemmantia</i></b> (1), <i>Hedycarya</i> (1), <i>Levieria</i> (1), <i>Palmeria</i> (2), <i>Steganthera</i> (6), <i>Wilkiea</i> (10)
Myristicaceae	<i>Myristica</i> (2)
Nymphaeaceae	<i>Nymphaea</i> (2)
Piperaceae	<i>Peperomia</i> (5), <i>Piper</i> (9)
Winteraceae	<i>Bubbia</i> (4), <i>Tasmannia</i> (3)

**Table 3.** Number of terrestrial rain forest genera/species (i.e. excluding aquatics) from near-basal lineages from each of five biogeographically distinct regions in Australia: Queensland's Wet Tropics, Cape York Peninsula, northern tropical Australia including western Queensland, Northern Territory and Western Australia, the eastern subtropical rainforests from Mackay to New South Wales, and the temperate *Nothofagus*-dominated rain forests of Victoria and Tasmania. Families (*sensu* Stevens 2006) in bold type are present in Australian rain forest formations.

<b>Family</b>	<b>Wet Tropics</b>	<b>Cape York</b>	<b>northern tropics</b>	<b>subtropics</b>	<b>temperate</b>
Amborellaceae					
Cabombaceae					
Nymphaeaceae					
<b>Austrobaileyaceae</b>	<b>1/1</b>				
Schisandraceae					
<b>Trimeniaceae</b>				<b>1/1</b>	
Ceratophyllaceae					
Chloranthaceae					
<b>Myristicaceae</b>	<b>1/2</b>	<b>2/4</b>	<b>2/3</b>	<b>1/1</b>	
Magnoliaceae					
Degeneraceae					
<b>Himantandraceae</b>	<b>1/1</b>	<b>1/1</b>		<b>1/1</b>	
<b>Eupomatiaceae</b>	<b>1/2</b>	<b>1/1</b>		<b>1/2</b>	<b>1/1</b>
<b>Annonaceae</b>	<b>12/30</b>	<b>13/20</b>	<b>8/12</b>	<b>5/7</b>	
<b>Atherospermataceae</b>	<b>3/3</b>			<b>3/8</b>	<b>1/1</b>
<b>Calycanthaceae</b>	<b>1/1</b>				
Gomortegaceae					
<b>Hernandiaceae</b>	<b>1/2</b>	<b>1/1</b>	<b>2/4</b>	<b>2/2</b>	
<b>Lauraceae</b>	<b>8/82</b>	<b>8/34</b>	<b>5/7</b>	<b>7/61</b>	
<b>Monimiaceae</b>	<b>8/23</b>	<b>3/5</b>		<b>4/8</b>	<b>1/1</b>
Siparunaceae					
Canellaceae					
<b>Winteraceae</b>	<b>2/7</b>	<b>1/1</b>		<b>2/6</b>	<b>1/4</b>
<b>Aristolochiaceae</b>	<b>2/6</b>	<b>2/3</b>	<b>1/3</b>	<b>2/5</b>	
Hydnoraceae					
Lactoridaceae					
<b>Piperaceae</b>	<b>2/14</b>	<b>2/6</b>	<b>1/1</b>	<b>2/6</b>	
Saururaceae					

**Table 4.** Numbers (and the percentage of the relevant flora that they represent) of near-basal families and the genera and species they contain from the Wet Tropics bioregion, dry and wet forest types and maquis of New Caledonia, and the national flora of Costa Rica.

	Regional flora species (endemic)	Near basal lineages (% flora)		
		families	genera	species
Wet Tropics	4,035 (701)	16 (7%)	46 (3%)	175 (4%)
New Caledonia	2,422 (2033)	11 (8%)	23 (5%)	111 (5%)
Costa Rica	5,250 (1000)	15 (9%)	56 (4%)	569 (11%)