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SUMMARY STATEMENT

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ABSTRACT

Thorne, Robert F. (Rancho Santa Ana Botanic Garden, Claremont, California 91711, U.S.A.) 1986. Summary Statement. Telopea 2(6): 697–704 — The three major floristic elements of Australasian rainforests — Australasian autochthonous, Indo-Malesian, and Antarctic — are examined by way of summarizing the various contributions to the symposium. One must bear in mind, however, our colossal ignorance of the past history of angiosperms, our limited knowledge of their past and present vagility, and the dangers of labelling too loosely plant groups as 'Gondwanic' or 'Laurasian'. The Australasian rainforests and their components are much more nearly autochthonous and Gondwanic than previously believed. There is a high percentage of generic endemism, especially in the Australian and New Caledonian rainforests, less in those of New Guinea and New Zealand. Indo-Malesian elements are strongest in the New Guinea, tropical Australian, and New Caledonian rainforests, much weaker in the Gondwanic temperate rainforests of New Zealand and southern Australia. In fact, they predominate to such an extent in New Guinea that the Papuan (or Papuasian) Region should not biogeographically be considered part of Australasia. The Antarctic elements of the temperate rainforests and tropical montane forests are largely ancient Gondwanic elements and probably most of them autochthonous in Australasia, though some originated in South Ameria and perhaps others even in Antarctica. Australasia is a much more important centre of angiosperm evolution than most biogeographers have considered it in the past. The Malesian influence on the tropical Australasian rainforests must not be minimized nor should the importance of long-distance dispersal be disregarded in seed-plant distribution.

INTRODUCTION

As should be expected from the archipelagic nature of the Australasian land masses, the relationships of their rainforests floras are diverse. As demonstrated by the participants in this symposium, the distribution patterns of the rainforest genera indicate that the floras consist primarily of three major, often overlapping, and sometimes rather poorly defined elements: the usually much underestimated autochthonous; the largely tropical Indo-Malesian; and the mostly temperate Antarctic elements. The palaeotropical, pantropical, and cosmopolitan elements, as defined by their distribution patterns, are numerous. They are, however, probably not separable in any practical way from the Indo-Malesian elements in their effect on Australasian rainforests because they presumably entered the region through the same Malesian dispersion portals along with the Indo-Malesian elements. Several less important elements, like the north-temperate montane, African, Pacific and American, seem to be rather insignificant, having little impact on the Australasian rainforest flora.

We can examine these various geographic plant elements by way of summarizing the contributions made in this symposium. We should keep in mind throughout, however, several caveats. Foremost is the awesome ignorance we have of the fossil history of most flowering plants. To describe the fossil record of the angiosperms as 'incomplete' is to make a grievous understatement. The recent discoveries made by palaeobotanists about the world have made obvious that the time of appearance of most angiospermous families has been greatly underestimated, as has the early wide dispersal of many angiospermous groups. A few of many possible examples can make the point: fruits and pollen of presently palaeotropical *Alangium* from the Oligocene Brandon lignites of Vermont (Eyde et al. 1969); a fossil leaf of the Australian endemic *Akania* from Argentine Palaeocene beds (Romero & Hickey 1976); pantropical *Diospyros* flowers, pollen, and associated ebenaceous leaves in Upper Eocene deposits in Victoria (Christophel & Basinger 1982); 'Gondwanic' *Gunnera* pollen from early Upper Cretaceous of North America and Eurasia (Jarzen 1980); and pollen of 'Gondwanic' Winteraceae from early Cretaceous deposits in Israel (Walker et al. 1983).

Secondly, we have tended to underestimate the speed and distance over which some angiosperm disseminules travel, including some not obviously adapted for long-distance dispersal. One need merely study the rich, though disharmonic, floras of distant volcanic, oceanic, high islands in the Pacific or Indian oceans to be impressed with angiospermous vagility. We have no way of estimating the dispersal capacities of the Cretaceous prototypes of our modern angiosperms beyond noting that some apparently swarmed rapidly over the terrestrial world soon after their recognized appearance in the fossil record. Of course, during the Cretaceous the present continents were contiguous or in much closer proximity than they are today. On the other hand, I must agree with Webb, Tracey & Jessup that most rainforest trees are extraordinarily lacking in vagility. That may be why so few of them get to oceanic islands.

Finally, some of us have been overly facile in labelling angiospermous groups as either 'Gondwanic' or 'Laurasian' on the basis of present and known fossil distribution patterns. The recent fossil discoveries briefly touched upon above and some of the recent phytogeographic contributions, as the discovery of fagaceous *Trigonobalanus* in Colombia (Lozano-C. et al. 1979) and the new dipterocarp subfamily Pakaraimaeoideae from the Guayana Highlands (Maguire & Ashton 1977), are shocking reminders to us of our ignorance in these matters. Also, some of us have carelessly labelled certain areas of the world, like south-eastern Asia or West Gondwanaland, as the area of origin of the angiosperms on much less than convincing evidence. We might better label such areas as regions of preservation or, better, as merely areas of high concentration of archaic angiosperms.

AUSTRALASIAN AUTOCHTHONOUS ELEMENTS

Webb, Tracey & Jessup have emphasized the autochthonous nature of Australian rainforests and their plants; have de-emphasized the intrusive elements in those rainforests; and have stressed the low vagility of many rainforest taxa. These are healthy developments if not carried too far. Some Australian authors have already gone to the extreme of describing all Australian and Indo-Malesian rainforest plants as Gondwanic, possibly because Australia and India were once part of Gondwanaland and because it would be convenient to believe that Laurasian south-eastern Asia and Malesia were likewise. This interpretation must be surprising to both geologists and phytogeographers with some knowledge of the plate tectonics and flora of south-eastern Asia and Malesia.

Australia

The rainforests of Australia, New Caledonia and New Zealand, and many of their component genera, are certainly autochthonous in that they have been present in these areas for a very long time (Christophel 1981, Christophel & Basinger 1982, Dettmann 1981, Kemp 1981, Martin 1981, 1982, Mildenhall 1980, Walker & Hope 1982). Webb & Tracey (1981) found 103 of 545 Australian rainforest genera, or 19% of the total, to be endemic to Australia. Several families, such as Akaniaceae, Austrobaileyaceae and Davidsoniaceae, and a number of subfamilies, such as Idiospermoideae of Calycanthaceae, are now restricted to Australian rainforests. Thirteen other families, especially Proteaceae with 15 endemic rainforest genera (Johnson & Briggs 1981), have three or more endemic genera in Australian rainforests, and can reasonably be accepted as old residents of Australia. Other families, like Aquifoliaceae, Ebenaceae, Fagaceae, Olacaceae, Santalaceae and Winteraceae, some monogeneric in tropical Australian forests and considered cosmopolitan or pantropical, have a long fossil record in Australia, at least before the Miocene collision with the Sunda plate, and can hardly be regarded as recent intrusives. Australian rainforests indeed do form an 'archipelago of relicts and refugia', as they have been described by Webb & Tracey (1981).

New Caledonia

The relatively small isolated island of New Caledonia has long been regarded by many of us as a treasure-house of archaic seed plants. Hence, Morat, Veillon & MacKee have performed a valuable service for us in listing and analyzing the rainforest flora of the island and adjacent smaller Loyalty Islands and Isle of Pines. Of a total indigenous flora of 3256 species, with 2476 of them endemic (76%), nearly half (1499) are listed by them as rainforest plants, with 1345 of these (nearly 90%) endemic to New Caledonia. The total indigenous flora consists of 787 genera, 108 (13.7%) of which are endemic, and 182 families, with five endemic. Of these, 365 genera, nearly half of the total, with 82 (22.4%) endemic, and 108 families, including all five of those endemic, are considered rainforest components. These high percentages of generic and family as well as specific endemism, the heavy speciation and radiation in many of the families, the large number of gymnosperms and archaic angiosperms, and the paucity of representatives of 'modern' angiospermous families certainly mark an ancient rainforest formation. These rainforests and many of their components can be regarded as autochthonous and Gondwanic in distribution. By their floristic analysis, Morat, Veillon & MacKee have cast doubt on the idea that the peridotites and other ultrabasic rocks play any considerable part in the conservation of archaic ancestral forms, at least in the rainforest flora.

New Guinea

Hartley has compiled for New Guinea a list of 716 seed-plant genera comprising the primary ever-wet forests from sea level to above 3000 m. In his analysis he found 38 genera restricted to New Guinea (including the Bismarck Archipelago), 27 nearly restricted to New Guinea or centring on the island, and 74 occurring in Australasia to the south of New Guinea, for a total of 19.4% of the rainforest genera. If these Australasian–Papuan genera can be regarded as the autochthonous Australasian element, it is considerably smaller for New Guinea than for Australia or New Caledonia. New Guinea has no endemic angiosperm families though it does share the Eupomatiaceae with Australia, Himantandraceae with Queensland and eastern Malesia, Sphenostemonaceae with New

Caledonia, Queensland and eastern Malesia, and Corynocarpaceae with Queensland, New Caledonia, New Zealand and New Hebrides.

Hartley and Whiffin & Hyland have analyzed three rainforest groups — non-aurantioid Rutaceae of New Guinea, and the Australian species of the myrtaceous *Syzygium* and allied genera and lauraceous *Cryptocarya.* The special value of these analyses lies in the deep knowledge the authors have of these large and complex groups; the Rutaceae, Myrtaceae and Lauraceae all having long histories in Australia and New Guinea. Eight of the 11 non-aurantioid Rutaceae of New Guinea appear to have reached New Guinea from Australia, two from western Malesia, and one from both western Malesia and Australia. The Whiffin & Hyland analyses have allowed them to determine floristic regions and floristic elements in the Australian rainforests, also to determine centres of diversity and endemism and relationships between these and the evolutionary history of the two myrtaceous and lauraceous groups. Centres of isolation and long-term refugia for rainforest floras were also identified.

New Zealand

Because of its long history of isolation from Australia and other Gondwanic lands for some 80 million years (Crook 1981), its south temperate location, and the disastrous effects of recurrent Pleistocene glaciations (Mildenhall 1980), one expects a greatly attenuated rainforest flora in New Zealand. Dawson's description and analysis, therefore, is quite educational for us off-islanders. It would appear that the lowland rainforests of New Zealand and the component genera have a rather long, largely austral history. According to Dawson, a few angiosperm genera, like the winteraceous *Pseudowintera* and proteaceous *Knightia* and *Toronia,* and the conifers may have reached Greater New Zealand while it was still attached to, or lying near, Gondwanic Australia. The rest of the non-endemic genera must have reached the islands by long-distance dispersal during the Cenozoic from Australia or from the north. About half the non-endemic rainforest genera do have oceanic representation. Some of the few endemic rainforest genera may have evolved in Greater New Zealand or on Greater New Caledonia, for several of the endemic genera, such as *Alseuosmia, Dactylanthus, Knightia, Nestegis* and *Rhabdothamnus,* have related genera there. The Antarctic element is expectedly quite strong in New Zealand rainforests.

INDO-MALESIAN ELEMENTS

New Guinea

Because of its proximity to Malesia, New Guinea might be expected to have the greatest impact from Indo-Malesia on its rainforest flora. Hartley's analysis proves that to be true. Aside from the 65 genera endemic to or probably originating in New Guinea, 74 centred in Australasia to the south, and 13 Antarctic genera shared with temperate South America, the great majority of the 716 New Guinea rainforest genera, or 78.8%, centre in their distributions in tropical regions to the west and north of New Guinea, though a few might have entered the big island from the east, as did *Heliconia* and *Spathiphyllum.* About 80% of the genera (571) occur in western Malesia, which can be considered the main dispersal portal for, if not the chief source of, the New Guinea rainforest flora. A few of these are Australasian genera that have reached Wallacea, a very few even as far as south-eastern Asia.

Likewise, according to Gressitt (1982), the New Guinea fauna is predominantly from oriental sources. Aside from the terrestrial mammals (other than murid rodents) and some other terrestrial vertebrates and freshwater animals, Gressitt estimates that in most cases 60–95% of the Papuan land fauna appears to be derived from south-eastern Asia, the Sunda Islands, the Philippines and Wallacea. He explains this as due to the semi-arid climatic and climate-dependent vegetative barriers to the south, particularly in the Cape York Peninsula, which have greatly reduced Australian influence and exchange with New Guinea. The wet tropical conditions of New Guinea, on the other hand, are ideal for the tropical oriental biota to the west and north that can pass the narrow water barriers of Wallacea, which have permitted invasion of New Guinea since the mid-Miocene by all but the least vagile organisms.

Because New Guinea is part of the Australian tectonic plate and because of the Australo-Papuan marsupial and bird fauna and the strong austral floristic element in the New Guinea highlands, I included New Guinea in the Australasian region for purposes of this symposium. However, I have elsewhere (Thorne 1963) for biogeographic purposes treated New Guinea, as well as the Moluccas, Bismarcks, Admiralties and Solomons as the Papuan Subregion of the Oriental Region. I still so regard it or treat it independently as New Guinea.

Australia

Although most of us seem agreed that the rainforests of Australia are basically an autochthonous phenomenon with a long history since Cretaceous time, I think the downgrading of Indo-Malesia impact has perhaps gone too far. Even Webb & Tracey (1981) admit that 81%, or 442, of their 545 Australian rainforest genera are found also outside Australia, with 28%, or 153, being shared between Australasia and Indo-Malesia. Specht (1981), in his analysis of 1285 Australian genera surveyed, found 31% to be endemic in Australia but rated 182 as Indo-Malayan prominent in the tropical/subtropical closed–forests. Beadle (1981) cites Blesser as stating that 620 of the 2220 species occurring in Northern Territory north of lat. 15°S occur outside Australia, mainly in Malaysia and India mostly in monsoon forests or littoral communities. In analyzing the rainforest flora of eastern Australia, Beadle found 120 dicotyledon genera represented in Australia by one species and in Asia by several to many. These, and another 100 genera represented in Australia by a few species each but in Asia by several to many, he thinks have probably migrated from Asia, with transportation of the disseminules across salt water. Possibly, some of these, however, are actually Gondwanic remnants hanging on as solitary or few relicts in rainforest refugia.

New Caledonia

In their analysis of the New Caledonian rainforest flora, Morat, Veillon & MacKee attributed 201, or 55%, of the 365 genera to Malesian or broader categories (pantropical, palaeotropical, etc.), and found 235 genera to be represented both in New Caledonia and Malesia. Some of these wide-ranging plants undoubtedly are ancient members of the neocaledonian flora, and some may have reached Malesia from the east or south. Nonetheless, the Indo-Malesian element seems to be strong in New Caledonia despite its long isolation from other lands. The more modern elements can have reached the island only by long-distance dispersal over salt water.

New Zealand

For New Zealand, Dawson in his maps indicated that 38 of 59 genera mapped for the New Zealand rainforest flora are found both in New Zealand and Malaysia/Asia or Indonesia/Asia. These are mostly wide-ranging genera, and can hardly be considered recent Indo-Malesian immigrants to New Zealand. There has obviously been much long-distance dispersal to New Zealand since its Cretaceous separation from Antarctica–Australia, but much of it has come from the south, west or north probably from or through New Caledonia. Many of the genera have a rather long Cenozoic fossil record in New Zealand.

ANTARCTIC ELEMENTS

Like the autochthonous Australian element, the Antarctic element of Australasian rainforests is primarily Gondwanic in distribution, and much of it probably authochthonous in Australasia as well. As described in my paper, this element predominates in the temperate rainforests and some tropical montane rainforests of the Australasian archipelago. It is strongest in the temperate rainforests of northern Queensland and New Guinea.

Dawson regards the conifer genera represented in New Zealand as being of southern origin and perhaps also half the genera of the lowland to montane tropical angiosperm genera and most of the montane tropical and temperate angiosperm genera. He did not include the *Nothofagus* temperate rainforests in his study, but surely these are largely Antarctic in origin.

Morat, Veillon & MacKee list 3.9%, or 12 genera, of their 365 New Caledonian rainforest genera as Subantarctic Pacific or Subantarctic. Most of these are what I have defined as Antarctic elements, especially the numerous conifers. These conifers, about 40 in number, and the five species of *Nothofagus* are far more prominent in the montane rainforests of New Caledonia than the low percentage of Antarctic genera would indicate.

In New Guinea, Hartley considers that 13 (only 1.8%) of the 716 rainforest genera are South Temperate Amphipacific genera, being found both in Australasia and South America outside New Guinea. Again, as in New Caledonia, these elements, though numerically small, are often dominant or at least very conspicuous in the montane forests, those mostly above 900 m. Among these are *Araucaria, Nothofagus, Papuacedrus, Phyllocladus, Podocarpus, Dacrycarpus, Falcatifolium, Tasmannia, Weinmannia, Coprosma* and *Gunnera.*

CONCLUSION

Hooker's (1860) division of the Australian flora into three major elements — the xeromorphic Australian, tropical Indo-Malayan, and temperate Antarctic — still has merit if we use these terms to describe the distributions of the Australasian rainforest elements. However, we now know that far more of the rainforest elements are autochthonous, or at least Gondwanic, than earlier workers realized. Surely Gondwanic are probably most of the Antarctic elements and many of those previously described as Indo-Malayan. The wide extent and great age of rainforests and their component genera in Australasia is attested to by the fossil record, the relict nature of Australian rainforests, and the present low vagility of rainforest angiosperms.

Biogeographers have given inadequate credit to Australasia as an important centre of evolution for many austral groups of angiosperms. Among the more important groups that had their important development, if not their origin, in Australasia are the Balanopaceae, Casuarinaceae, Centrolepidaceae, Chloanthaceae, Corynocarpaceae, Cunoniaceae (along with *Bauera* and *Davidsonia*), Epacridaceae, Goodeniaceae, Gyrostemonaceae, Haloragaceae, lamiaceous Prostantheroideae, liliaceous Xanthorrhoideae, leptospermoid Myrtaceae, Monimiaceae, Pittosporineae, poaceous Micrairoideae, Proteaceae, Restionaceae, sapindaceous Dodonaeoideae and Stylobasioideae, Alseuosmiaceae and Escalloniaceae, Stackhousiaceae, Stylidiaceae and Winteraceae.

On the other hand, we need much more fossil evidence before we give Australasia credit for some of its most famous and archaic annonalean and hamamelidalean genera like *Amborella, Austrobaileya, Degeneria, Eupomatia, Galbulimima, Idiospermum, Ostrearia* and *Neostrearia.* These relicts may have been in Australasia since Gondwanic time or the early Cenozoic but there is as yet no fossil record to prove that. Or, also plausible, they may have immigrated to Australasia in Miocene time like some of their Laurasian relatives when the Australian plate approached the Sunda plate 20–15 m. y. ago (Powell, Johnson & Veevers 1981). As with the Winteraceae, their closest relatives today are found in south-eastern Asia. Protected from more aggressive Laurasian competitors they may have survived only in the isolation of the Australasian rainforests.

Finally, we must not go too far in playing down the Malesian–south-eastern Asian influence on the flora of Australasia (Papuasia still seems safe from attack). Although perhaps not so pervasive in Australia and New Caledonia as we originally thought, the Asian–Malesian element still forms a large percentage of the generic components of the tropical rainforests of those areas. Nor should we buy the new dogma peddled by the vicariantists that long-distance dispersal is unimportant in the understanding of seed-plant distribution.

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