ANTARCTIC ELEMENTS IN AUSTRALASIAN RAINFORESTS

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ABSTRACT

Thorne, Robert F. (Rancho Santa Ana Botanic Garden, Claremont, California 91711, U.S.A.). 1986. Antarctic elements in Australasian rainforests. Telopea 2(6): 611–617 — Our interpretation of the three major Hookerian elements in the flora of Australia has changed significantly with the acceptance of plate tectonics. Like the xeromorphic Australian and tropical Indo-Malayan elements, the Antarctic elements are still recognizable in Australia, especially in temperate and montane rainforests. Also like many of the former, the Antarctic elements are actually Gondwanic and many even of autochthonous Australasian origin. The Antarctic elements of Australasian rainforests are identified, and their spectacular disjunction explained in part on a vicariance, plate-tectonic basis. Various Australasian animal groups with similar trans-Antarctic connections with South America are briefly listed. The probability that some of the more vagile plant disjuncts have achieved their disjunctions via long-distance dispersal is considered; and a limited attempt is made to identify the Gondwanic origins of various Antarctic rainforest elements as either East or West Gondwanic.

INTRODUCTION

In a very perceptive introduction to his *Flora of Tasmania*, Hooker (1860) recognized three principal elements in the flora of Australia: (1) an Australian (autochthonous) element, mostly of open plant communities; (2) an Indo-Malayan element of the tropical monsoon forests and rainforests; and (3) an Antarctic element in alpine communities and temperate rainforests. He was also aware of other, smaller elements, as the cosmopolitan element. During the following century the 'invasion' theory (Beadle 1981, Barlow 1981) was developed by authors who explained these various elements as invasions of the island continent by different floras from different directions at different times. However, our new knowledge of plate tectonics has had a vast impact upon our interpretation of the Australian flora as well as of the rest of the world (Raven & Axelrod 1972, 1974, Schuster 1976, Thorne 1978). Also our knowledge of Australian palaeobotany has greatly increased (Christophel 1981, Christophel & Basinger 1982, Dettmann 1981, Martin 1981, 1982). As a result, the 'invasion' theory has largely been discredited through a growing consensus that most of Australia's flora is indeed autochthonous and retained, though presumably much evolved, from early Cretaceous time when Australia was part of the vast southern supercontinent of Gondwanaland. The 'invading' elements are now downgraded to 'intrusive' elements, though no well informed field botanist doubts the heavy impact of these 'intruders' from abroad upon the rainforest, monsoon and littoral plant communities of eastern Australia (Burbidge 1960, Beadle 1981) and the other Australasian islands.

ANTARCTIC ELEMENTS

The Antarctic elements in Australasian rainforests are usually defined as those genera that are or were represented in both temperate Australasia and temperate South America, at least some of them also with a fossil record in Antarctica. They are most strongly represented in the temperate rainforests of New Zealand, Tasmania and south-eastern mainland Australia and in the montane or subalpine closed forests and mossy thickets of northern Queensland, New Caledonia and New Guinea. Like the autochthonous 'Australian' elements, they are mostly of Gondwanic distribution and have been in Australia for a long time, some since the Cretaceous (Dettmann 1981, Martin 1981, 1982). Many probably evolved in that part of East Gondwanaland that is now Australasia. Since the track through a warmer, moister, forested Antarctica from Australasia to southern South America must have been a broad two-way passage, some of the Antarctic elements were surely of South American (West Gondwanaland) origin. Others possibly evolved in Antarctica itself.

Elsewhere (Thorne 1972, 1978) I have listed at least 48 genera and seven families of seed plants that are essentially restricted to temperate South America and Australasia and mentioned that 28 more widely distributed genera and two families are linked in the two areas by common or closely related species. *Heterozostera* has since been recognized and must be added to the above 48. In addition, I listed the three Pacific genera (*Coprosma, Haloragis* and *Santalum*) that have representatives on the Juan Fernandez Islands but are unreported from mainland South America. Beadle (1981) stated that 52 herbaceous genera occur in temperate South America, the southern oceanic islands, New Zealand and Australia. Many of these would be included in my Circum-Antarctic or Circum-South Temperate Disjunct groups (Thorne 1972). These figures do not include those Australasian plants known to be represented now only by fossils in South America, such as *Acmopyle, Athrotaxis* and *Dacrycarpus* (Florin 1963), *Akania* (Romero & Hickey 1976), *Aponogeton, Gymnostoma* (L. A. S. Johnson pers. comm.), and the 'brassii' group of *Nothofagus*, and such closely related generic pairs or groups as *Austrotaxus–Pilgerodendron–Libocedrus–Papuacedrus, Drimys–Tasmannia, Fitzroya–Diselma, Lebetanthus–Prionotes* and *Saxe–Gothaea–Microcachrys*.

Among these Antarctic elements the following genera at least are considered by various authors, e.g. Specht (1981), Webb & Tracey (1981) and those participating in this symposium, to be represented in Australasian rainforests — *Acaena, Acmopyle, Akania, Araucaria, Aristotelia, Astelia, Athrotaxis, Beilschmiedia, Caldcluvia* (s. lat.), *Citronella, Coprosma, Coriaria, Cryptocarya, Dacryridium, Dacrycarpus, Decussocarpus, Eucryphia, Fuchsia, Gaultheria, Gevuina* (s. lat.), *Griselinia, Gunnera, Laurelia, Libertia, Libocedrus, Lomatia, Muehlenbeckia, Myrsine, Nertera, Nothofagus, Oreocallis, Orites, Papuacedrus, Passiflora, Peperomia, Podocarpus, Prionotes, Prumnopitys, Pseudopanax, Rubus, Santalum, Stachycarpus, Tasmannia, Uncinia* and *Weinmannia* (s. lat.). Other rainforest genera listed usually as cosmopolitan may well belong to this group. Additional genera, though not yet reported from temperate South America, are scattered in temperate or montane areas of Australasia and perhaps likewise should be considered Antarctic elements, especially *Agathis, Cordyline, Pennantia* and *Phyllocladus*.

Some of these Antarctic elements are dominant or remarkably conspicuous in some Australasian rainforests, especially the species of *Nothofagus, Araucaria, Agathis, Libocedrus* and Podocarpaceae. Also abundant or otherwise conspicuous are *Eucryphia, Fuchsia, Laurelia, Pseudopanax, Tasmannia* and *Weinmannia*.

EXPLANATIONS FOR ANTARCTIC DISJUNCTIONS

The spectacular disjunction between Australasia and South America, separated by wide and deep oceans or, over the pole, by a continental archipelago now deeply buried under a thick ice cap, demands explanation. Before plate tectonics revolutionized geomorphology, some of us explained the disjunction by speculating about an Antarctica much warmer and much more extensive in Cretaceous and Tertiary times (Thorne 1963), along with long-distance dispersal for some of the genera with more readily dispersible disseminules.

The now widely accepted theory of plate tectonics offers a much more plausible explanation for plant and animal groups of limited vagility. The geologists have informed us that Australia was linked to South America by Antarctica until about 55 million years ago, with close links possible through the South Tasman Rise and a narrow connection between Antarctica and South America until possibly 30 m.y. ago in Middle Oligocene time (Coleman 1980, Crook 1981, Barlow 1981). By then Antarctica had cleared the South Tasman Rise and the Drake Passage had opened between Antarctica and South America, allowing the Antarctic Circumpolar Current to develop when oceanic depths had been achieved about 23.5 m.y. ago (Crook 1981, Kemp 1981). Even until Late Oligocene (26 m.y. ago), coastal portions of Antarctica, at least near the Ross Sea, apparently supported a cool-temperate, southern-beech rainforest dominated by species of all three major groups of *Nothofagus* with two genera of Podocarpaceae and species of Myrtaceae, Proteaceae, Cyatheaceae, Gleicheniaceae, Polypodiaceae, Lycopodiaceae and Sphagnaceae also present (Kemp & Barrett 1975). By Late Miocene an extensive ice sheet covered most or all of Antarctica (Kemp 1981).

New Caledonia, New Zealand and the Lord Howe Rise were once much closer to each other and to Australia and Antarctica until the opening of the New Caledonia Trough and Tasman Sea in Late Cretaceous to late Palaeocene time, 80–60 m.y. ago (Crook 1981). The Coral Sea Basin formed 60–53 m.y. ago in Late Palaeocene time (Crook 1981), further isolating New Caledonia. Presumably *Nothofagus*, the conifers, Winteraceae, Proteaceae and other ancient seed plants with low vagility could, before these major splits occurred, have moved readily onto Greater New Caledonia and Greater New Zealand up to 80 m.y. ago and between South America and Australia via Antarctica up to 55–30 m.y. ago.

It has been suggested that the rich marsupial fauna of Australia (Archer 1981) is possibly derived from a single didelphoid stock that passed through Antarctica from South America before the terrestrial link was broken 55 m.y. ago (Jardine & McKenzie 1972). The recent discovery of fossils of the extinct South American marsupial family Polydolopidae from rocks c. 40 m.y. old on Seymour Island of the North Antarctic Peninsula (Woodburne & Zinsmeister 1982) lends much credence to this idea and to the probability of terrestrial passage through Antarctica of plant groups of limited dispersibility.

Other Australian animal groups are known to have austral, presumably trans-Antarctic connections with South America: chelid turtles (Cogger & Heatwole 1981); hylid and leptodactylid frogs (Tyler et al. 1981); ratite birds (Keast 1981); galaxiid fishes (McDowall 1981); anaspidacean shrimps, scorpion-flies, alder-flies, caddis-flies and mayflies (Williams 1981a, b); chironomids and other dipterans (Brundin 1966, Williams 1981b); spiders and pseudoscorpions

(Main 1981a, b) scarabaeoid beetles (Howden 1981); lepidoptera and mole crickets (Tindale 1981); stone-flies (Zwick 1981); dragonflies (Watson 1981); land snails (Bishop 1981); scorpions (Koch 1981); and oligochaetes (Jamieson 1981), among others.

The probability that some of the Antarctic plant elements crossed wide expanses of water by long-distance dispersal cannot be ignored. *Aristotelia, Astelia, Coprosma, Coriaria, Dianella, Fuchsia, Gaultheria, Griselinia, Myrsine, Nertera, Pernettya, Pseudopanax, Rubus* and Podocarpaceae all have fleshy fruits or seeds that must be especially attractive to birds. Furthermore, *Astelia, Coprosma, Coriaria, Dianella, Fuchsia, Myrsine, Nertera, Podocarpus* and *Rubus* have reached and become established on such oceanic islands as Samoa, Tonga and the Society and Hawaiian islands. The presence also of representatives of *Acaena, Gunnera, Peperomia, Pseudopanax, Santalum, Uncinia* and *Weinmannia* on oceanic islands indicates considerable dispersibility for species of these genera.

Although long-distance dispersal is currently unpopular due to the infatuation of many biologists with the 'new' vicariance approach to biogeography, no vicarianist has yet cared to explain how the volcanic islands, produced over hot-spots in the ocean floor, have achieved their indigenous, often rich, though disharmonic, island biotas. It is instructive that Mildenhall (1980) and Martin (1982), in discussing the similarities of the Australian and New Zealand palaeobotanical record during the Tertiary when the two lands were some 2000 km apart, concluded that long-distance dispersal had occurred. Raven (1973) and Smith (1982) apparently agreed that the Australasian and Papuan alpine floras are probably of Quaternary origin through long-distance dispersal from south-eastern Asia and Malesia.

ORIGINS OF ANTARCTIC ELEMENTS

The Gondwanic place of origin of some of the Antarctic elements is probably impossible to determine until we get much more information from the fossil record. However, the origin of some of them can be reasonably determined because of their diversity and abundance, primitive features and large number of relatives in one of the areas. It would seem rather likely that the Antarctic genera of Akaniaceae, Araliaceae, Casuarinaceae, Coriariaceae, Cunoniaceae, Elaeocarpaceae, Epacridaceae, Escalloniaceae, Monimiaceae, Proteaceae and Winteraceae are of East Gondwanic, possibly even Australasian origin. Genera like *Fuchsia, Nicotiana* and *Passiflora*, on the other hand, are surely of South American (West Gondwanic) origin. The archaic and probably ancient genera *Gunnera, Griselinia* and *Eucryphia* are rather equally distributed between Australasia and South America, though the heavy development of the escalloniaceous relatives of *Griselinia* and cunoniaceous relatives of *Eucryphia* cause me to favour an East Gondwanic origin for the latter two genera. *Nothofagus* is the biggest enigma of all (Humphries 1981). The heavy concentration of fagaceous genera in south-eastern Asia and Malesia would seem to favour an East Gondwanic if not Laurasian origin. There is, however, greater diversity (including the fossil record) of *Nothofagus* in southern South America, and the appearance of the 'brassii' group (sole representatives of the genus in New Guinea and New Caledonia) of *Nothofagus* in New Guinea is relatively recent in the fossil record (Walker & Hope 1982). *Nothofagus* is not reliably reported, even as fossil pollen, from any Laurasian area. The recent discovery of *Trigonobalanus* in Colombia (Lozano-C. et al. 1979), the presence of *Fagus* in Mexico and its fossil pollen in Puerto Rico (Graham & Jarzen 1969), and the abundant representation of *Quercus* in middle America and north-eastern South America, make the possibility of a West Gondwanic origin for *Nothofagus* somewhat more plausible. At any rate, the presence of *Nothofagus* in Australasian rainforests is very ancient, for pollen referable to the 'brassii' group has been reported from near the base of the Senonian of the Cretaceous about 82 m.y. ago (Dettmann 1981). If an 'intrusive' element in Australia, it certainly is not a recent one.

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