

THE SOUTHERN CONIFER FAMILY

ARAUCARIACEAE: History, Status, and Value for Paleoenvironmental Reconstruction

Peter Kershaw and Barbara Wagstaff

*Centre for Palynology and Palaeoecology, School of Geography and Environmental Science, PO Box 11a, Monash University, Victoria 3800, Australia;
e-mail: peter.kershaw@arts.monash.edu.au, barbara.wagstaff@arts.monash.edu.au*

Key Words biogeography, vegetation history, climate change, environmental variability

■ **Abstract** The Araucariaceae are important to biogeography because they have an ancient origin and are a distinctive and sometimes dominant component of southern hemisphere forest communities. This paper examines recent information on ecology and phylogeny and on pollen and microfossil assemblages to assess the history and present-day status of the family and its potential for refinement of past environmental, particularly climatic, conditions. From an origin in the Triassic, the family expanded and diversified in both hemispheres in the Jurassic and Early Cretaceous and remained a significant component of Gondwanan vegetation until the latter part of the Cenozoic. The development of angiosperms in the Middle Cretaceous probably assisted in the demise of some araucarian components but there was also evolution of new genera. Recorded diversity in the early Cenozoic of Australia is as high as it was in the Early Cretaceous. Continental separation and associated climatic drying, cooling, and increased variability progressively reduced the ranges of conifers to moist, predominantly mesothermal climates on continents. However, tectonic and volcanic activity, partially associated with Australia's collision with Southeast Asia, provided new opportunities for some araucarian components on Asia-Pacific islands. Araucarians provide information on climatic conditions suitable for rainforest vegetation throughout their recorded period, even prior to the recognition or even existence of these forests in the fossil record. High pollen abundance is also indicative of marginal rainforest environments where these canopy emergents can compete effectively with angiosperm forest taxa. Despite their apparent relictual status in many areas, they provide precise paleoclimatic estimates in late Quaternary pollen records and have particular value in providing evidence of climatic variability that has otherwise been difficult to detect.

INTRODUCTION

van Steenis (1971) established *Nothofagus* as the focus of study of southern hemisphere biogeography and paleoenvironments at a time when continental drift, revitalized as plate tectonics, was becoming rapidly accepted as a basic theory in the earth sciences (Le Grand 1988). Since then, a plethora of papers has appeared, not only on the ecology and biogeography of the genus, but also on its role in cool temperate rainforest dynamics, in quantitative paleoclimatic reconstructions, and in the development of methods in biogeographic study. Much of this research is presented in the recent compilation of Veblin et al. (1996). However, there is still no consensus over the place and time of origin of the genus, its ancestral source, or the subsequent biogeographic histories of its subgenera. These uncertainties, combined with its restricted climatic range and relatively recent history in geological terms means that *Nothofagus* has limited scope for elucidation of past climates and changing biogeographies over much of the hemisphere.

Araucariaceae has potential to rival or at least complement *Nothofagus* in elucidating patterns of vegetation, climate, and tectonic change in the southern hemisphere. Araucariaceae, together with Podocarpaceae and some genera of Cupressaceae, make up the southern conifers that have a history extending back to the middle or early Mesozoic Period. Both Araucariaceae and Podocarpaceae have good fossil records. Although the latter has a broader geographic range and a greater number of genera with often distinctive morphological characters that preserve in fossil material, Araucariaceae possesses a variety of features that make it an appealing subject for study.

Most members of the family have an impressive emergent habit or distinctive form that ensures their distribution is relatively well known. The family also has a fossil record composed of both macrofossils and pollen, with pollen being abundant in association with parent plants but, unlike many podocarp and *Nothofagus* species, generally not widely dispersed beyond source vegetation, except perhaps by water.

Like *Nothofagus*, araucarians are almost entirely restricted to rainforest, apart from occurrences in the unique sclerophyllous maquis vegetation on ultramafic substrates in New Caledonia (Jaffré 1995), and tend to be most common at the margins of more complex forest types. Consequently, they indicate the presence or extent of rainforest vegetation in fossil records where a majority of taxa, being angiosperms, have limited pollen representation or uncertain affinities. Being ancient, there is also the possibility that they can be useful in the identification of environments suitable for rainforest before rainforests, broadly recognized today as communities with a continuous tree canopy generally dominated by angiosperms, evolved.

Although distributed in association with rainforest, their emergent habit sets araucarians apart from the rainforest canopy to the extent that some vegetation classifications (e.g., Webb 1959) have typed communities with common araucarian emergents as woodlands rather than forests. The distinction between some

araucarian emergent species and associated rainforest has also been recognized in studies on forest basal area, where it has been found that the forest canopy trees have a constant basal area regardless of the presence or absence of araucarian emergents (Enright 1982, Ogden 1985). This "additive basal area" phenomenon (Enright & Ogden 1995) could suggest that some araucarians are distributed independently of general forest composition or structure and provide different or additional information on environmental change. Consequently, this attribute, combined with their exposure to the atmosphere above the forest canopy, may make araucarians ideal indicators of regional climatic conditions. On the other hand, their frequent inability to regenerate under a dense canopy, in the absence of disturbance, means they may not reflect their full potential climate range (Enright & Ogden 1995).

More general concern about the status of Araucariaceae, along with other conifers, has been expressed from a consideration of both present-day age class distributions and fossil studies. A number of studies have revealed that many southern conifers do not tend to conform to the reverse J-curve characteristic of continuous population recruitment but have an over-representation of larger size classes. This feature suggests a general demise that has variously been attributed to disequilibrium with the present-day climate, alteration of angiosperm/conifer balance with the extinction of major herbivores (New Zealand), and the continuation of a long-term trend towards angiosperm dominance (Enright & Ogden 1995). However, recent research (much of it summarized in Enright & Hill 1995) has shown that the predominant regeneration strategy of southern conifers is intermittent recruitment resulting from occasional disturbances, a strategy consistent with the general shade tolerance and longevity of araucarians. Consequently, fossil or tree ring records, extending beyond the time-span of ecological studies, are required to test the stability and viability of many present-day conifer populations.

The long-term fossil record shows that there has been a relative decrease in conifers generally since the angiosperms evolved (e.g., Lidgard & Crane 1990). Regal (1977) provided a comprehensive and convincing explanation for this decline based on the greater flexibility of angiosperms with respect to reproductive strategies, including the use of animals for pollination and seed dispersal, and on their high growth rates and chemical defenses against herbivory. Populations of conifers are seen as progressively isolated, a situation common in the Araucariaceae. However, the fossil record also indicates that the decline in abundance does not seem to be matched by a decrease in diversity (Lidgard & Crane 1990).

Despite the uncertainty about the degree to which araucarian distributions relate to their potential climate ranges, component taxa have been used to reconstruct or refine paleoclimatic estimates from pollen data, especially for the late Quaternary. We examine the present-day distributions and fossil history of the Araucariaceae in relation to aspects of their ecology and phylogeny to assess the validity of climatic estimates made and to examine the value of these conifers for paleoenvironmental, particularly paleoclimatic, reconstruction.

PRESENT-DAY DISTRIBUTIONS

Members of the Araucariaceae are now restricted to the South American and Southwest Asia–Western Pacific region (Figure 1) despite their extensive distribution in both hemispheres during the Mesozoic (Stockey 1990). A relictual status is also suggested by generally low species diversity and disjunct distributions on continental masses. However, relatively high diversity is recorded on islands in the Pacific and the Southeast Asian region, indicating conditions suitable for survival and continuous evolution through a long period of geological time or more recent dispersal and rapid evolution from continental sources. A long residence time may be inferred for New Caledonia and New Guinea, which were part of the southern megacontinent Gondwana during the Mesozoic Period. Recent dispersal is more likely on some relatively recently formed Southeast Asian and Western Pacific islands.

Greater insights into present distributions can be gleaned from inferred taxonomic relationships within the Araucariaceae (Setoguchi et al. 1998) (Figure 2). The family contains two major genera, *Araucaria* and *Agathis*, together with the recently discovered monotypic *Wollemia*, recorded only from a few small patches in protected gorges in southeastern Australia (Jones et al. 1995). *Wollemia nobilis* is clearly relictual and, phylogenetically, may be considered the most basal extant taxon in the family. *Araucaria* and *Agathis* are sister taxa on the basis of phylogenies derived from *rbcL* data, but extant representatives of the former show

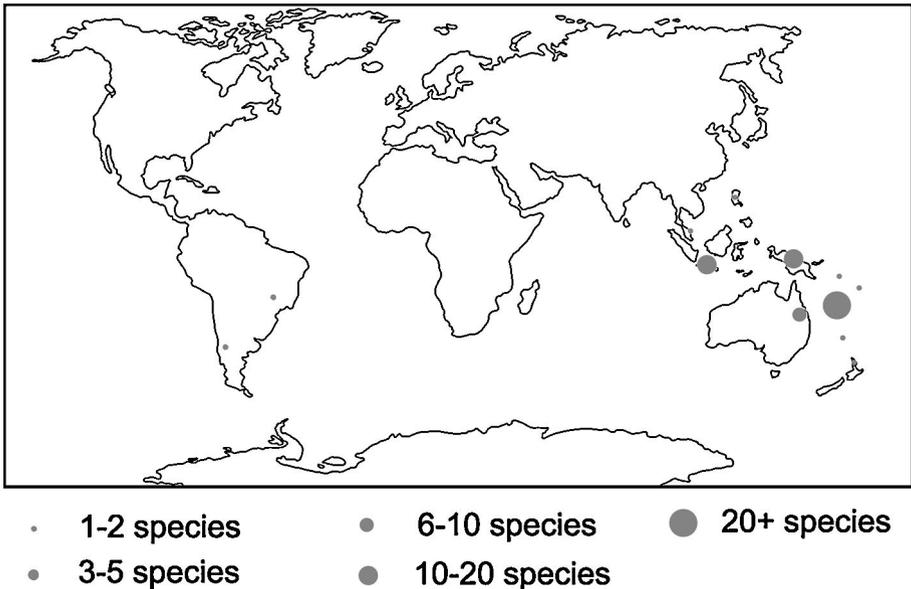


Figure 1 A generalized, global representation of species of Araucariaceae (data from Enright & Hill 1995).

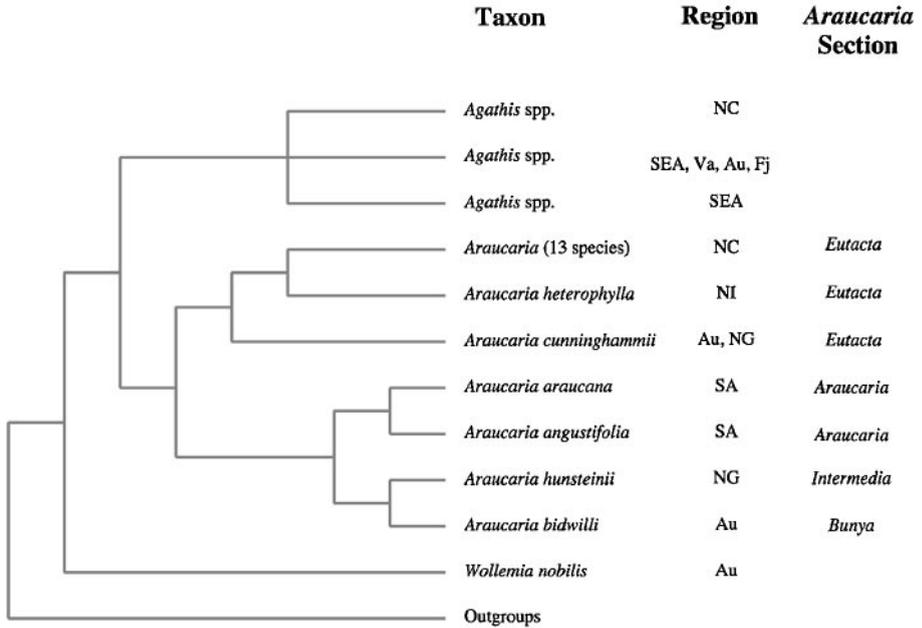


Figure 2 Phylogenetic relationships within the Araucariaceae inferred from *rbcl* gene sequences (adapted from Setoguchi et al. 1998). Geographical region abbreviations: NC, New Caledonia; SEA, Southeast Asia; Va, Vanuatu; Au, Australia; Fj, Fiji; NI, Norfolk Island; NG, New Guinea; SA, South America).

greater genetic and morphological differentiation at the species and section levels and greater geographic spread.

Within *Araucaria*, *Eutacta* has a broad distribution on Gondwanan terranes, including Australia, New Guinea, Norfolk Island, and New Caledonia, suggesting considerable geological antiquity for this section. The high diversity of species on New Caledonia has been presumed to be the result of diversification from ancestral Gondwanan stock during the Eocene Period when much of the island was covered in ultramafic rocks (Jaffré 1995). However, there is some geological evidence that the island was below sea level in the early Cenozoic (R. Hall, personal communication), and long-distance transport from Australia following re-emergence, uplift, and emplacement of ultramafic rocks during the Eocene (Aitchison et al. 1995) may have to be invoked to explain its presence. The isolation of the section *Araucaria* in South America may indicate divergence at this level since the effective environmental and physical separation of the South American and Australasian regions, probably in the early Cenozoic. The monotypic sections *Bunya* and *Intermedia* represented in Australia and New Guinea, respectively, are considered to have diverged relatively recently, perhaps in the later Cenozoic, when the development of a dry corridor effectively separated the two islands.

Agathis, unlike *Araucaria*, extends into the Southeast Asian islands and Malay Peninsula, leaving open the possibility that it had a Laurasian source, or was recycled into Gondwanan territory by India as it collided with this region in the Eocene Period (Morley 1998). However, the confinement of *Agathis* to the southwest Pacific region, combined with small morphological and genetic differentiation compared with *Araucaria*, strongly favors an Australasian source. Dispersal and diversification may have taken place since the Eocene in the case of New Caledonia, and perhaps also New Zealand if Pole's (1994) hypothesis is correct (i.e., that New Zealand became submerged in the Cenozoic and all extant taxa are derived from long-distance dispersal). Dispersal into Southeast Asia would most likely have occurred since the Early Miocene as the northward-moving Australian continent came into contact with this region.

Overall, the evidence is not consistent with a gradual decline in Araucariaceae as a result of competition with evolving angiosperms. Most taxa appear to have origins postdating the Mesozoic and early Cenozoic Period of continental drift, with long-distance dispersal and some probable evolutionary radiations in the middle to late Cenozoic. The islands, rather than the major continental masses, demonstrate this latest phase of activity, presumably because of the ability of Araucariaceae to colonize new substrates and to compete effectively under conditions of regular disturbance. Such disturbances characterize islands, especially those that experience volcanism and tectonism. The islands may also have been buffered against climatic variability that affected the continents.

Despite the unusual present-day distribution pattern of the Araucariaceae, there is some consistency in representation in relation to climatic conditions, with a concentration in lower mid-latitudes. On the continental masses of South America and Australia, *Araucaria* occurs predominantly in the subtropics, extending into the marginal tropics (Figure 1). *Agathis australis*, the only extant araucarian in New Zealand, is restricted to the "subtropical" tip of the North Island. The majority of taxa, occurring on New Caledonia, are within the tropics. A mesothermal climate is also indicated for many taxa within the equatorial region of New Guinea and Southeast Asia, because these are distributed in the lower montane zone. Major exceptions to this distribution are the *Agathis* species that occur in equatorial peat swamps, where perhaps substrates with low nutrients and poor drainage allow them to be competitive with angiosperms, and *Araucaria araucana* in Chile that extends to the treeline. However, *A. araucana* does not extend into the cool temperate forests of South America that support the majority of southern conifers on this continent.

THE FOSSIL RECORD

Overview

The representation of fossil data is patchy and sparse for most parts of the world. Only in Australia is there a substantial record of both macrofossils and pollen; as this is the only landmass to have extant representatives of all three genera,

discussion focuses on this continent. Figure 3 summarizes the evidence from Australia, in the form of stratigraphic ranges, macrofossil species records from the Cretaceous and Cenozoic periods, and averaged pollen percentages, shown against major environmental variables and events. Figure 4 shows more detailed pollen site records.

The early part of the record is characterized by uncertainty, both in what constitutes a species or even an araucarian. The earliest unequivocal Araucariaceae date from the Jurassic (Stockey 1982), and macrofossils include *Araucaria* sections *Eutacta* and *Bunya* as well as indeterminate *Araucaria* types (Hill & Brodribb 1999) and possibly other genera, although pollen grains putatively attributable to the family are recorded from the Early Triassic in Australia (De Jersey 1968).

During the Jurassic and Cretaceous *Araucaria* sections *Eutacta* and *Bunya* appear to have been widespread in both hemispheres. *Araucaria* section *Araucaria* has been recorded occasionally from the Early Cretaceous of southeastern Australia as well as from southern South America, where it currently lives (Hill & Brodribb 1999), whereas section *Intermedia* has been recorded from the Early Cenozoic of New Zealand (Pole 1994). Macrofossils attributed to *Agathis* have been recorded from the Jurassic and Cretaceous periods, although these lack sufficient diagnostic characters to allow confident identification (Hill & Brodribb 1999), and the oldest substantiated *Agathis* fossils date only from the Middle Eocene of southeastern Australia (Carpenter & Pole 1995). Unfortunately, the pollen record does not assist in determination of the history of *Agathis*, as the grains are morphologically similar to those of *Araucaria* and it has proved impossible, at least with older taxa, to separate the two genera. By contrast, *Wollemia* has distinctive pollen that is first recorded in the Turonian of southeastern Australia and subsequently in Antarctica and perhaps New Zealand (Macphail et al. 1995). However, Chambers et al. (1998) have suggested that some Early to Middle Cretaceous macrofossils may also be related to *Wollemia*.

The Araucariaceae appear to be one group of plants that evolved after the major extinction phase at the end of the Permian, prompted by arid conditions throughout much of Gondwana (Hill et al. 2000). The earliest pollen records of Araucariaceae, in the Triassic, are found in coastal Queensland, perhaps only coincidentally within the present limited geographical range of the family in Australia. They increased in abundance and diversity during the Jurassic, with high pollen values in both eastern and particularly western Australia peaking in the Late Jurassic. It is likely that rising sea levels through the Jurassic corresponded to both increased precipitation and temperature that facilitated the development of forest vegetation. However, throughout the period of evolution of the bulk of Gondwanan vegetation (the Jurassic and particularly the Cretaceous and early Cenozoic), Australia was at much higher latitudes than it is today. Consequently, light would have been a major limiting factor, placing constraints on forest development. The emergent habit could have imparted a great advantage on conifers through interception of high angle solar radiation. Another pertinent feature of Australia during the Jurassic and Early Cretaceous was that the continent was rotated with the west at lowest latitudes. The high araucarian pollen percentages through this period within the

western part of the continent may indicate an early preference of the family for these lower latitudes where independent evidence suggests climates were relatively warm and dry (McLoughlin & Hill 1996).

The initiation of continental rifting toward the end of the Jurassic resulted in the exclusion of India and southern Africa from subsequent changes in Gondwanan vegetation that included a major phase of modernization. The beginning of the Cretaceous saw perhaps the first appearance of *Wollemia*-related taxa and at least four times the number of *Araucaria* species currently represented on the continent. By contrast, there are few araucarian macrofossils recorded from the Middle to Late Cretaceous, and there is a corresponding fall in araucarian pollen abundance. However, Dettmann (1994) suggested that both Araucariaceae and Podocarpaceae were major canopy dominants through most of the Cretaceous, with a reduction in Araucariaceae toward the very end of this period. Owing to the emergence of most of the continent above sea level, fossil evidence is largely restricted to southeastern Australia. It is possible that araucarians flourished through the Middle-Late Cretaceous in the northern part of Australia, as there are high pollen percentages in the Albian and Cenomanian when fossils are preserved.

Relatively low pollen percentages for Araucariaceae in the southern part of Australia may have been a result of competition with evolving angiosperms. However, high precipitation may have been the critical factor, at least until the end of the Cretaceous when *Nothofagus*, which produces copious pollen, would have had an additional effect on reducing araucarian pollen representation. It is unfortunate that there is little quantitative information from sites in southeastern Australia within the unstable area of continental rifting, for it is considered to have been a major center of evolution of the extant Australian flora (Dettmann 1989). This period of angiosperm development appears to have included the evolution of *Wollemia* species closely related to *W. nobilis* and also to many extant podocarp genera, questioning the idea that the conifers were outcompeted by angiosperms. However, there were extinctions within the Araucariaceae, as indicated on Figure 3, that would have contributed to reduced pollen percentages.

There is some increase in Araucariaceae pollen percentages in the Palaeocene and early Eocene, with the relatively high percentage in the latter epoch derived from *Wollemia* (Macphail et al. 1994). However, macrofossil evidence is slight. There is then an increase in macrofossil records, demonstrating high diversity in the Middle Eocene and Early Oligocene. These peaks in diversity are perhaps surprising, as diversity of angiosperms was also high, with complex rainforest covering much of the continent. Pollen percentages remain low. It is likely that many Araucariaceae were restricted to unstable environments such as river margins suitable for macrofossil preservation. In addition, much of the diversity was contained within *Agathis*, which seldom achieves high population densities and the pollen of which is seldom recorded in abundance. Conditions were clearly unsuitable for the development of *Araucaria* forests.

Diversity, initially in *Agathis* spp., decreased from the Late Oligocene and especially the Early Miocene owing, according to Hill & Brodribb (1999), to the onset

of continental drying. However, from studies of pollen and lithotype variation in coal deposits of southeastern Australia, increased climatic variability may have been the critical factor (Kershaw et al. 1991). There was also a global trend toward cooler conditions at high latitudes that may have contributed to the elimination of *Agathis* from southeastern Australia, where all macrofossil records are located, and its contraction to the northeastern part of the continent. Although the movement of Australia northward into lower latitudes moderated this temperature decrease, as illustrated by temperature estimates derived from fossil assemblage data (Figure 3), *Agathis* figures prominently in determination of the lower limit of a number of temperature parameter estimates derived for the Latrobe Valley in southeastern Australia during the Early Miocene period. Consequently, any subsequent reduction in temperature is likely to have eliminated the genus. By contrast, there is an increase in representation of Araucariaceae pollen. This increase is consistent with drier or more variable climates, as regeneration in some species of *Araucaria* is facilitated by a more open rainforest canopy that is promoted by such conditions. In fact, it is *Araucaria* that defines the upper limit of the estimates of annual, wettest month and driest month rainfall in the Latrobe Valley during the Early Miocene, consistent with both a reduction in rainfall and an increase in seasonal rainfall distribution from the Cenozoic climatic "optimum." We propose that a widespread emergent *Araucaria* layer, analogous to that in the Middle Jurassic to Early Cretaceous, re-formed, perhaps suggesting a return to similar climatic conditions.

The macrofossil record ends in the Late Miocene. It is likely that expansion of the Antarctic ice sheet to close to present dimensions around the end of the Miocene and the intensification of oceanic and atmospheric circulation patterns (Bowler 1982) produced cooler and drier conditions over southeastern Australia that caused a decline in conifer diversity. However, the lack of macrofossil records is as much related to unfavorable conditions for preservation as it is to conifer representation, as the Araucariaceae achieve their highest Cenozoic pollen percentages in the Early Pliocene, although these high percentages are virtually restricted to coastal and subcoastal locations along the eastern seaboard. In southeastern Australia the distributional change in high pollen percentages from more inland to more coastal locations from the Miocene to the Early Pliocene plots the drier margin of rainforest as it contracted to present high rainfall areas along the highland coastal fringe.

The subsequent contraction of the Araucariaceae to the northeastern part of the continent in the Late Pliocene to Pleistocene could be a result of the intensification of the westerly wind system that extended over southeastern Australia (Bowler 1982). This system subjected the conifers, possibly for the first time, to a winter rainfall regime, or to the onset of Quaternary glacial/interglacial scale climatic oscillations (Shackleton et al. 1995). Increased global climatic variability in itself was probably not the major factor, as high araucarian pollen abundance values are maintained in the northeastern part of the continent.

The ability of species of Araucariaceae to survive for long periods under adverse climatic conditions in southeastern Australia is demonstrated by continued low

percentages of *Araucaria* pollen in a record from the western plains of Victoria through the whole of the Early Pleistocene (Wagstaff et al. 2001) and by the extant small stands of *Wollemia* within protected gorges in New South Wales 2 million years after the last appearance of pollen in fossil records (Macphail et al. 1995). However, it is likely that the increased amplitude of climatic oscillations that became established around the Early-Middle Pleistocene boundary (Shackleton et al. 1995) resulted in the final demise of *Araucaria* within southeastern Australia.

In general terms, this Late Cenozoic pattern of decline in Araucariaceae is also registered in New Zealand and South America (Kershaw & McGlone 1995), but there is little evidence for changing abundance or distribution in other areas that support members of the family.

Late Quaternary patterns

It is primarily within the later part of the Quaternary that araucarian fossils have been used as an indicator of environmental change. There have been substantial changes in both distribution and abundance, especially in *Araucaria*. In north-eastern Queensland the record from Lynch's Crater (Figure 5) illustrates alternation of high levels of complex rainforest, dominated by angiosperm taxa, during high rainfall interglacials, with araucarian forest and open sclerophyll forest during drier glacial stages. This pattern changed during the latter part of the last glacial period (isotope stages 4–2) when *Araucaria*, together with other southern conifers, were largely eliminated from the region and sclerophyll vegetation dominated the pollen record until complex rainforest returned under the high rainfall conditions of the Holocene. As there was no evidence for any change in the pattern of global climate cyclicality, the destruction of araucarian forest was most likely caused by burning activities of people, who, from archaeological evidence, arrived in Australia by around 40,000 years BP (Kershaw 1986). The sharp and sustained increase in charcoal abundance at this time adds support to this hypothesis.

However, this interpretation of araucarian forest decline has been questioned by evidence from a similar long pollen record constructed from marine core ODP 820 taken off the coast of northeastern Australia adjacent to the Atherton Tableland (Moss 1999, Moss & Kershaw 2000) (Figures 5 & 6). The record demonstrates that the regional decline in *Araucaria* commenced much earlier than around Lynch's Crater and well before any archaeological evidence of people, whose arrival is now considered to have been between around 50,000 to 60,000 years ago (Roberts et al. 1993). It is also apparent from the charcoal curve that fire has been a continuous feature of the region through at least the past 250,000 years. The first substantial decline in araucarian forest occurred around 130,000 years ago, at the height of the penultimate glacial period, and was associated with a peak in fire activity and an initial increase in eucalypt-dominated sclerophyll vegetation. A further sustained decline occurred about 35,000 years ago; it was also associated with a major peak in burning and a further increase

in abundance of *Eucalyptus*. This decline can be correlated with that at Lynch's Crater.

It could be argued that the earlier change was climatically induced, the fires promoted by dry glacial conditions, whereas the second *Araucaria* decline was the result of increased burning owing to human activity. However, this would not explain why araucarian forests remained intact through earlier, dry glacial periods. The key to understanding this geologically late vegetation transformation may lie in evidence provided by the extended oxygen isotope record from the ODP 820 core (Peerdeman et al. 1993). A systematic shift in isotope values, superimposed on those attributed to glacial-interglacial cyclicality, between about 350,000 and 250,000 years BP (Figure 5) has been interpreted as evidence of an increase in sea surface temperatures of some 4°C. Such an increase, not recorded beyond this region, could relate to the development of the West Pacific Warm Pool, which is centered off eastern New Guinea, to the north of this area (Isern et al. 1996).

Although a temperature increase may be expected to have led to an increase in precipitation within the region, and consequently to an expansion of rainforest vegetation, the West Pacific Warm Pool is part of a temperature gradient across the Pacific that is a prerequisite for El Niño-Southern Oscillation (ENSO) climatic variability. Consequently, the decline in araucarian forest might have been a result of increased burning during dry El Niño events, regardless of mean precipitation values. ENSO is noted for its activity on scales of a few years, but it is predicted that activity may have varied on scales of thousands of years (Clement et al. 1999). Spectral analysis has identified a preferred frequency of occurrence of 30,000 years in both the charcoal and southern conifer curves from the ODP record (Moss & Kershaw 1999). This is not a frequency of orbital solar variation that controls glacial-interglacial cyclicality, but could be an ENSO frequency that, over the past 250,000 years, has been the major influence on the dynamics of the araucarian forests. Its major impacts were around 130,000 years ago, when high ENSO activity corresponded with a dry glacial period, and between 40,000 and 35,000 years ago, when high ENSO activity coincided with the presence of people on the continent.

Sea surface temperatures could have increased within the Middle Pleistocene owing to the continued movement of Australia into the Southeast Asian region and consequent alteration of land-sea configurations. Any blockage of the major ocean current that transports warm water from the Pacific to the Indian Ocean through the Indonsian region as a component of the global oceanic circulation system would have caused the build-up of warm water in the equatorial west Pacific and influenced climate in this region and perhaps also over other parts of the globe.

The continued movement of Australia northward might also have had a direct influence on the decline in *Araucaria* through the attainment of critical temperature levels, as this movement brought northern Australia into tropical latitudes for the first time in the history of *Araucaria* on the continent. There is also evidence

for a recent decline of *Araucaria* in the subtropics (Longmore 1997), although araucarian forests have remained much more abundant in these latitudes (Figure 6).

Although climatic variability may have had a significant influence on the decline of araucarian forest, it may also have had a positive influence on conifers within wetter forest systems. At Lake Euramoo, increased representation of *Agathis* in the more complex rainforests of the Atherton Tableland over the past 5000 years may have been due to increased levels of instability associated with the onset of the latest phase of high ENSO activity (McGlone et al. 1992). This activity may have led to a similar expansion of *Agathis* in the warm-temperate to subtropical forests of New Zealand (Ogden et al. 1992).

A clearer indication of distributional changes in *Araucaria* within the late Quaternary is provided by southeastern South America (Figure 6). Limited data suggest that *A. angustifolia* may have been widely distributed during the last glacial period (prior to 20,000 years BP) but was restricted to small, moist, isolated patches during the latest Pleistocene and early Holocene. Recently analyzed records do not support a substantial shift northward of araucarian forest during cooler conditions of the last glacial period, as suggested by Colinvaux et al. (1996).

However, some northern locations may have experienced local expansion of *Araucaria* during the Pleistocene-Holocene transition. This expansion could be explained by increased precipitation and reduced temperatures from frequent southerly incursions of polar air masses facilitated by the location of the intertropical convergence zone much further north than it is today (Ledru et al. 1998). After about 8000 years BP, the frequency of polar incursions decreased within this region, and araucarian forest was replaced by semi-deciduous forest. Seasonal conditions in the early to mid-Holocene restricted the distribution of rainforest generally, although rainforest expanded gradually with a subsequent increase in effective rainfall. Araucarian forests expanded only within the past 4000 years or so, owing to the wettest and least seasonal conditions in the Holocene period. Ledru et al. (1998) suggested that the spread of *Araucaria* was also facilitated by a return to a high frequency of polar incursions, as there was no response in *Araucaria* forests north of 25°S, where the southern boundary of the intertropical convergence zone is presently located. Ledru et al. (1998) did not address the issue of ENSO variability, except to note that southern Brazil is influenced by this phenomenon. However, high Holocene levels of burning, determined from one site with a charcoal record (Behling 1997), are related to the late Holocene *Araucaria* expansion, and it is possible that this was a result of the global increase in ENSO at this time.

The pattern of increased burning through the Holocene may also relate to increased human activity within the past few thousand years. Intensification of occupation is certainly a feature of the late Holocene of Australia (Lourandos & David 2001) and may confound interpretation of late Holocene vegetation changes there. No such explanation is valid for New Zealand, though, where people did not arrive until within the past 1000 years (Anderson & McGlone 1992).

Synthesis

The Arauciaceae possibly evolved in response to ameliorating climatic conditions during or after the Permian-Triassic extinction event and Early Triassic global dry phase, and have been an important component of forest vegetation, especially in the southern hemisphere, since the Jurassic. *Araucaria* is identified in the fossil record as the oldest genus, dating back to the Jurassic, although the recently discovered genus *Wollemia* is considered, on the basis of phylogenetic relationships, to have derived prior to differentiation of *Araucaria* and *Agathis*. However, macrofossils comparable to *Wollemia* date back only to the Early Cretaceous, and the distinctive pollen is recorded from only the Late Cretaceous. From the limited range of *Wollemia* pollen in southern Australia, Antarctica, and perhaps New Zealand at its maximum during the Late Cretaceous and early Cenozoic, it is unlikely that this genus was ever extensively distributed over the southern hemisphere (Dettmann & Jarzen 1999). However, the discovery of this new genus is leading to a re-examination of taxonomic relationships of early Araucariaceae.

Within the genus *Araucaria*, sections *Eutacta* and *Bunya* have the oldest fossil records, both dating back to the Jurassic, where they were widely distributed in both hemispheres (Hill & Brodribb 1999). However, their subsequent history has been very different, with *Eutacta* still broadly distributed and diverse, apparently having been able to take advantage of mid- to late-Cenozoic opportunities for colonization, whereas *Bunya* is reduced to one species restricted to northeastern Australia and without a clear macrofossil record during the Cenozoic. Setoguchi et al. (1998) suggested, from genetic analysis, that older and younger populations attributed to *Bunya* may not be related. The other two sections of *Araucaria* (*Araucaria* and *Intermedia*) indicate wider distributions in the past, and the fossil record demonstrates their greater connection with South America. All extant sections of *Araucaria* appear to have evolved well before the final break-up of Gondwana. The extant representatives of *Agathis* show relatively minor genetic and morphological differences compared with the variation evident in *Araucaria*, and it is likely that species of the former represent the products of a relatively recent phase of evolutionary radiation in the southwestern Pacific region.

The Araucariaceae declined in abundance and range from the Early Cretaceous. Although the evolution of angiosperms is likely to have been influential in this decline, many araucarians may have been disadvantaged by the Middle Cretaceous peak in temperatures and humidity. However, *Agathis* and *Wollemia* may have evolved in association with early angiosperms and been part of the proposed center of biotic radiation within the unstable rift valley between southern Australia and Antarctica.

The more substantial fossil record for the Cenozoic illustrates marked differences between pollen and macrofossil representation. High macrofossil diversity is recorded within the period of peak temperature and rainfall conditions of the Eocene period. Many of these araucarian taxa are attributable to *Agathis*, which is able to survive in more complex rainforest than *Araucaria*. The decline in

macrofossil diversity and representation is accompanied by higher pollen relative abundances, suggesting the development of dense, species-poor araucarian forests under drier and more variable climatic conditions of the later Cenozoic. The gradual restriction of rainforest toward the eastern coastal margins of Australia that accompanied continental drying, and subsequent contraction of complex rainforest to the northeastern part of the continent under temperature decline and changing atmospheric circulation patterns are well tracked by *Araucaria* pollen.

The final restriction of *Araucaria* to small, isolated pockets, at least in northeastern Australia, was, we suggest, caused by increased climatic variability and biomass burning resulting from atmospheric and oceanic circulation changes associated with Australia's continued movement into the Southeast Asian region. However, this ENSO variability may have simultaneously facilitated the regeneration of *Agathis* in northeastern Australia and also araucarian species in angiosperm-dominated rainforests of other ENSO-affected areas such as New Zealand and southeastern South America during the late-Holocene phase of high ENSO activity.

The potential of the araucarians for palaeoenvironmental reconstruction is demonstrated by both past and present distributions, in combination with a knowledge of their ecology. In general terms, the expansion and subsequent contraction of the Araucariaceae, at least on the southern hemisphere continents, corresponds with a major climatic cycle from the Triassic to Late Quaternary. Both the development and contraction phases show high pollen abundances that suggest a dense emergent cover of *Araucaria*, regardless of the understorey, under relatively dry climatic conditions. Optimal conditions for plant growth through much of the middle of this period are characterized by high macrofossil diversity but relatively low pollen abundance of araucarians, consistent with dense understorey or canopy coverage.

The araucarians also appear to have maintained a preference for subtropical or mesothermal conditions. This is well illustrated by the present latitudinal distributions of the major continental *Araucaria* species (*A. angustifolia* in southeastern South America and *A. cunninghamii* and *A. bidwillii* in Australia) that are remarkably similar, despite an obviously long period of continental separation and representation in different sections of the genus (Figure 6, color insert). Mean annual precipitation is not a significant factor, as *A. angustifolia* requires a minimum of 1400 mm per annum, greater than the mean of either Australian species. All species have a minimum requirement of about 10°C in winter months that, perhaps together with a requirement for significant summer rainfall, could explain the southern extent of the species.

The lower latitude limit of the *Araucaria* species in Australia may relate to a sensitivity to high temperatures that made the taxon vulnerable in the tropics to increased climatic variability. The length of record in South America is insufficient to determine whether there is a trend toward reduced araucarian representation. However, this is unlikely considering that the continent has not moved northward to the same degree as Australia, and *Araucaria* appears to have been advantaged by

increased climatic variability and burning in the late Holocene. Perhaps the position of the intertropical convergence zone, and hence disturbances resulting from polar air incursions, have been critical to the survival of the species at low latitudes. This example illustrates that, although patterns of representation of many araucarians on Gondwanic land masses appear relictual and current ranges may not reflect the full potential climatic range, araucarians can be useful for refinement and probably quantification of climate from high-resolution pollen records in particular areas. Their response to climatic variability also suggests that they can provide data in addition to mean values that characterize most climate reconstructions from pollen records.

In contrast to a general decline in representation of Araucariaceae on major continental masses, there have been major expansions and evolution of *Agathis* and *Araucaria* section *Eutacta* in Southeast Asia–Pacific islands. This proliferation illustrates significant dispersal ability, an attribute not expected from the groups' continental history or current distributions. Colonization and establishment appear to have commenced by the Eocene and have been facilitated by a number of factors. These factors include emergence of islands and increased proximity to the Australian continent (via tectonic convergence and development of island arc corridors); the production of environments within humid climates not conducive to the development of a dense rainforest cover, such as extensive peat swamps, ultramafic soils, and steep slopes; and frequent disturbances resulting from tectonic and volcanic activity. There are insufficient data on the history of these island conifers derived from recent radiations to determine their response to past climate change.

ACKNOWLEDGMENTS

We thank Simon Haberle and Stephen McLoughlin for their very helpful comments on a draft of this paper; Daphne Fautin for substantial improvement of English expression; Hermann Behling, Mary Dettmann, Neil Enright, Bob Hill, Marie-Pierre Ledru, Mike Macphail, Helene Martin, John Ogden, and Liz Truswell for valuable discussion and information on this topic; and Jonathan Brown and Gary Swinton for drafting the text figures.

Visit the Annual Reviews home page at www.AnnualReviews.org

LITERATURE CITED

- Aitchison J, Clarke GL, Meffre S, Cluzel D. 1995. Eocene arc-continent collision in New Caledonia and implications for regional Southwest Pacific tectonic evolution. *Geology* 23:161–64
- Anderson A, McGlone M. 1992. Living on the edge—prehistoric land and people in New Zealand. In *The Naive Lands: Prehistory and Environmental Change in Australia and the Southwest Pacific*, ed. J. Dodson, pp. 199–241. Melbourne, Aust.: Longman Cheshire
- Behling H. 1997. Late Quaternary vegetation,

- climate and fire history of the *Araucaria* forest and campos region from Serra Campos Gerais, Paraná State (South Brazil). *Rev. Palaeobot. Palynol.* 97:109–21
- Behling H. 1998. Late Quaternary vegetational and climate changes in Brazil. *Rev. Palaeobot. Palynol.* 99:143–56
- Bowler JM. 1982. Aridity in the Tertiary and Quaternary of Australia. In *Evolution of the Flora and Fauna of Arid Australia*, ed. WR Barker, PJM Greenslade, pp. 35–45. Frewville, S. Aust.: Peacock
- Carpenter RJ, Pole MS. 1995. Eocene plant fossil from the Lefroy and Cowan palaeo-drainages, Western Australia. *Aust. Syst. Bot.* 8:1107–54
- Chambers TC, Drinnan AN, McLoughlin S. 1998. Some morphological features of Wollemi pine (*Wollemia nobilis*: Araucariaceae) and their comparison to Cretaceous plant fossils. *Int. J. Plant Sci.* 159:160–71
- Clement AC, Seager R, Cane MA. 1999. Orbital controls on the El Niño/Southern Oscillation and the tropical climate. *Paleoceanography* 14:441–56
- Colinvaux PA, Liu K-B, De Oliveira P, Bush MB, Miller MC, Kamman MS. 1996. Temperature depression in the lowland tropics in glacial times. *Clim. Change* 32:19–33
- De Jersey N. 1968. *Triassic spores and pollen grains from the Clematis Sandstone*. *Geol. Surv. Queensland Publ. No. 338, Palaeontol. Pap. No. 14*. Brisbane, Aust.: Geol. Surv. Queensland. 44 pp.
- Dettmann ME. 1989. Antarctica: Cretaceous cradle of austral temperate rainforests? In *Origins and Evolution of the Antarctic Biota*, ed. JA Crane, pp. 89–105. London: Geol. Soc. Spec. Publ. No. 47
- Dettmann ME. 1994. Cretaceous vegetation: the microfossil record. See Hill 1994, pp. 143–70
- Dettmann ME, Jarzen DM. 2000. Pollen of extant *Wollemia* (Wollemi pine) and comparisons with pollen of other extant and fossil Araucariaceae. In *Pollen and Spores Morphology and Biology*, ed. MM Harley, CM Morton, S Blackmore, pp. 187–203. Kew: R. Bot. Gard.
- Enright NJ. 1982. Does *Araucaria hunsteinii* compete with its neighbours? *Aust. J. Ecol.* 7:97–99
- Enright NJ, Hill RS. 1995. *Ecology of the Southern Conifers*. Melbourne, Aust.: Melbourne Univ. Press. 342 pp.
- Enright NJ, Ogden J. 1995. The southern conifers—a synthesis. See Enright & Hill 1995, pp. 271–87
- Greenwood DR. 1994. Palaeobotanical evidence for Tertiary climates. See Hill 1994, pp. 44–59
- Hill RS, ed. 1994. *History of the Australian Vegetation: Cretaceous to Recent*. Cambridge: Cambridge Univ. Press
- Hill RS, Brodribb TJ. 1999. Southern conifers in time and space. *Aust. J. Bot.* 47:639–96
- Hill RS, Truswell EM, McLoughlin S, Dettmann ME. 2000. Evolution of the Australian flora: fossil evidence. In *Flora of Australia, Vol. 1 (Introduction)*, ed. AE Orchard, pp. 251–320. Melbourne, Aust.: CSIRO. 2nd ed.
- Huber BT. 1998. Enhanced: tropical paradise at the Cretaceous poles. *Science* 282:2199–200
- Isern AR, McKenzie JA, Feary DA. 1996. The role of sea-surface temperature as a control on carbonate platform development in the western Coral Sea. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 124:247–72
- Jaffré T. 1995. Distribution and ecology of the conifers of New Caledonia. See Enright & Hill 1995, pp. 171–96
- Jones WG, Hill KD, Allen JM. 1995. *Wollemia nobilis*, a new living Australian genus and species in the Araucariaceae. *Telopea* 6:173–76
- Kershaw AP. 1986. Climate change and Aboriginal burning through the last two glacial-interglacial cycles from northeastern Queensland. *Nature* 322:47–49
- Kershaw AP. 1997. A bioclimatic analysis of Early to Middle Miocene brown coal floras, Latrobe Valley, southeastern Australia. *Aust. J. Bot.* 45:373–87
- Kershaw AP. 1998. Estimates of regional climatic variation within southeastern mainland

- Australia since the Last Glacial Maximum from pollen data. *Palaeoclimates* 3:107–34
- Kershaw AP, Bolger P, Sluiter IRK, Baird J, Whitelaw M. 1991. The origin and evolution of brown coal lithotypes in the Latrobe Valley, Victoria, Australia. *Int. J. Coal Geol.* 18:233–49
- Kershaw AP, McGlone MS. 1995. The Quaternary history of the southern conifers. See Enright & Hill 1995, pp. 30–63
- Ledru M-P, Salgado-Labouriau ML, Lorscheitter ML. 1998. Vegetation dynamics in southern and central Brazil during the last 10,000 yr B.P. *Rev. Palaeobot. Palynol.* 99:131–42
- Le Grand HE. 1988. *Drifting Continents and Shifting Theories*. Cambridge: Cambridge Univ. Press. 313 pp.
- Lidgard S, Crane PR. 1990. Angiosperm diversification and Cretaceous floristic trends: a comparison of palynofloras and leaf macrofloras. *Palaeobiol.* 16:77–93
- Lloyd PJ, Kershaw AP. 1997. Late Quaternary vegetation and early Holocene quantitative climatic estimates from Morwell Swamp, Latrobe Valley, south-eastern Australia. *Aust. J. Bot.* 45:549–63
- Longmore ME. 1997. Quaternary palynological records from the perched lake sediments of Fraser Island, Queensland, Australia: rainforest, forest history and climatic control. *Aust. J. Bot.* 45:507–26
- Lourandos H, David B. 2001. Long-term archaeological and environmental trends: a comparison from late Pleistocene-Holocene Australia. In *The Environmental and Cultural History and Dynamics of the Australian-Southeast Asian Region*, ed. AP Kershaw, B David, NJ Tapper, D Penny, J. Brown. Reiskirchen, Ger.: Catena. In press
- Macphail M, Alley NF, Truswell EM, Sluiter IRK. 1994. Early Tertiary vegetation: evidence from pollen and spores. See Hill 1994, pp. 189–261
- Macphail M, Hill K, Partridge A, Truswell E, Foster C. 1995. Australia: Wollemi pine: old pollen records for a newly discovered genus of gymnosperm. *Geol. Today* March–April:42–44
- McGlone MS, Kershaw AP, Markgraf V. 1992. El Niño/Southern Oscillation climatic variability in Australasian and South American palaeoenvironmental records. In *El Niño: Historical and Palaeoclimatic Aspects of the Southern Oscillation*, ed. HF Diaz, V Markgraf, pp. 435–62. Cambridge: Cambridge Univ. Press
- McLoughlin S, Hill RS. 1996. The succession of Western Australian Phanerozoic terrestrial floras. In *Gondwana Heritage: Past, Present and Future of the Western Australian Biota*, ed. SD Hopper, JA Chappell, MS Harvey, AS George, pp. 61–80. Chipping-Norton, UK: Beatty & Sons
- Miller KG, Fairbanks RG, Mountain GS. 1987. Tertiary oxygen isotope synthesis, sea level history and continental margin erosion. *Paleoceanography* 2:1–19
- Morley RJ. 1998. Palynological evidence for Tertiary plant dispersals in the SE Asian region in relation to plate tectonics and climate. In *Biogeography and Geological Evolution of SE Asia*, ed. R Hall, JD Holloway, pp. 211–34. Leiden, The Netherlands: Backbuys
- Moss PT. 1999. *Late Quaternary environments of the humid tropics of northeastern Australia*. PhD thesis. Monash Univ., Melbourne. Aust. 269 pp.
- Moss PT, Kershaw AP. 1999. Evidence from marine ODP Site 820 of fire/vegetation/climate patterns in the humid tropics of Australia over the last 250,000 years. In *Bushfire 99, Proc. Aust. Bushfire Conf., Albury, Aust., July*, pp. 269–79. Albury: Charles Sturt Univ.
- Moss PT, Kershaw AP. 2000. The last glacial cycle from the humid tropics of northeastern Australia: comparison of a terrestrial and a marine record. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 155:155–76
- Nix HA. 1991. An environmental analysis of Australian rainforests. In *The Rainforest Legacy: Australian National Rainforests Study. Vol. 2, Flora and Fauna of the Rainforests*, ed. G Werren, AP Kershaw, pp. 1–26.

- Canberra: Aust. Heritage Comm. Publ. Ser. No. 7 (2)
- Ogden J. 1985. An introduction to plant demography with special reference to New Zealand trees. *NZ J. Bot.* 23:751–72
- Ogden J, Wilson A, Hendy C, Newnham RM. 1992. The late Quaternary history of kauri (*Agathis australis*) in New Zealand and its climatic significance. *J. Biogeogr.* 19:611–22
- Peerdeman FM, Davies PJ, Chivas AR. 1993. The stable oxygen isotope signal in shallow-water, upper-slope sediments off the Great Barrier Reef (Hole 820A). *Proc. Ocean Drilling Program Sci. Res.* 133:163–73
- Pole MS. 1994. The New Zealand flora—entirely long-distance dispersal? *J. Biogeogr.* 21:625–35
- Quilty PG. 1994. The background: 144 million years of Australian palaeoclimate and palaeogeography. See Hill 1994, pp. 14–43
- Regal P. 1977. Ecology and the evolution of flowering plant dominance. *Science* 196:622–29
- Roberts R, Jones R, Smith MA. 1993. Optical dating of Deaf Adder Gorge, Northern Territory indicates human occupation between 53,000 and 60,000 years ago. *Aust. Arch.* 37:58–59
- Setoguchi H, Osawa TA, Oinaud J-C, Jaffré T, Veillon J-M. 1998. Phylogenetic relationships within Araucariaceae based on *rbcL* gene sequences. *Am. J. Bot.* 85:1507–16
- Shackleton NJ, Crowhurst S, Hagemberg T, Pisias N, Schnieder DA. 1995. A new late Neogene timescale: applications to leg 138 sites. *Proc. Ocean Drilling Program Sci. Res.* 138:73–101
- Stockey RA. 1982. The Araucariaceae: an evolutionary perspective. *Rev. Palaeobot. Palynol.* 37:133–54
- Stockey RA. 1990. Antarctic and Gondwana conifers. In *Antarctic Paleobiology*, ed. TN Taylor, EL Taylor, pp. 179–91. New York: Springer-Verlag
- van Steenis CGGJ. 1971. *Nothofagus*, a key genus to plant geography, in time and space, living and fossil, ecology and phylogeny. *Blumea* 19:65–98
- Veblin TT, Burns BR, Kitzberger T, Lara A, Villalba R. 1995. The ecology of the conifers of southern South America. See Enright & Hill 1995, pp. 120–70
- Veblin TT, Hill RS, Read J. 1996. *The Ecology and Biogeography of Nothofagus Forests*. New Haven, CT: Yale Univ. Press. 403 pp.
- Wagstaff BE, Kershaw AP, O'Sullivan P, Harle KJ, Edwards J. 2001. An Early to Middle Pleistocene palynological record from Pejark Marsh, Western Plains of Victoria, southeastern Australia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* In press
- Webb LJ. 1959. A physiognomic classification of Australian rainforests. *J. Ecol.* 8:118–29

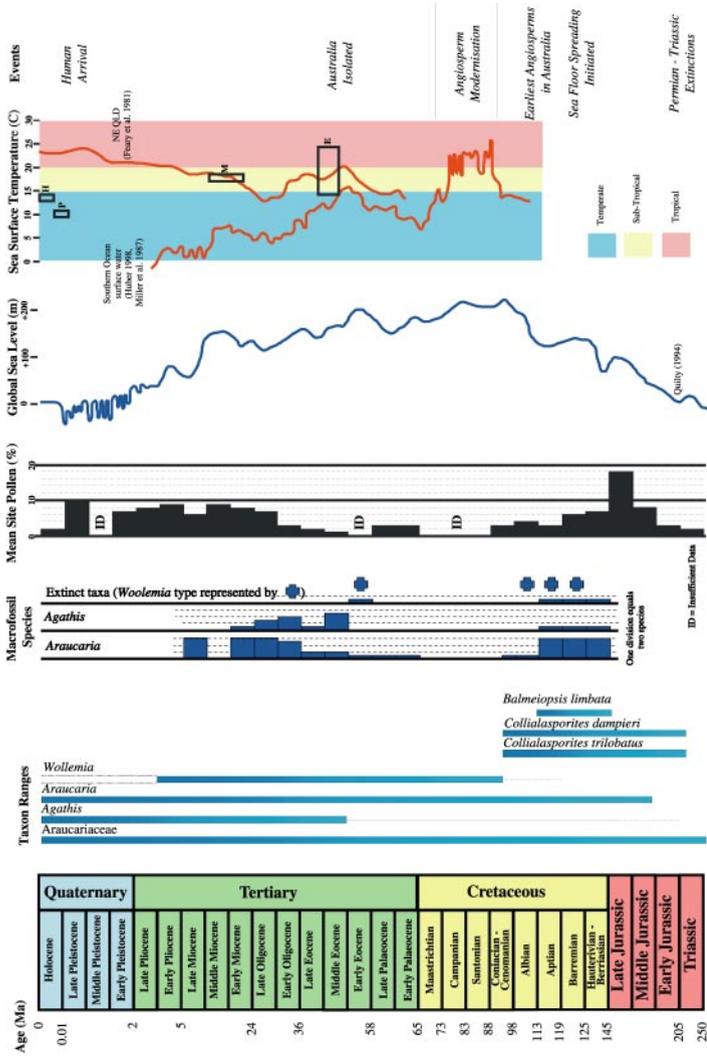


Figure 3 Australian records of Araucariaceae including taxon stratigraphic ranges, representation of predominantly southeastern Australian macrofossil species (data from Hill & Brodribb 1999) and average Araucariaceae percentage from pollen records shown on Figure 4, for individual geological periods, shown in relation to major environmental changes and events. Land temperature estimates from southeastern Australia: E – from leaf size index of Greenwood (1994), M – from overlapping bioclimatic ranges of pollen and macrofossil taxa from the brown coals of the Latrobe Valley (Kershaw 1997), P – from Last Glacial Maximum pollen data (Kershaw 1998), H – from bioclimatic profile of an early Holocene occurrence of the aquatic *Brasenia* (Lloyd & Kershaw 1997).

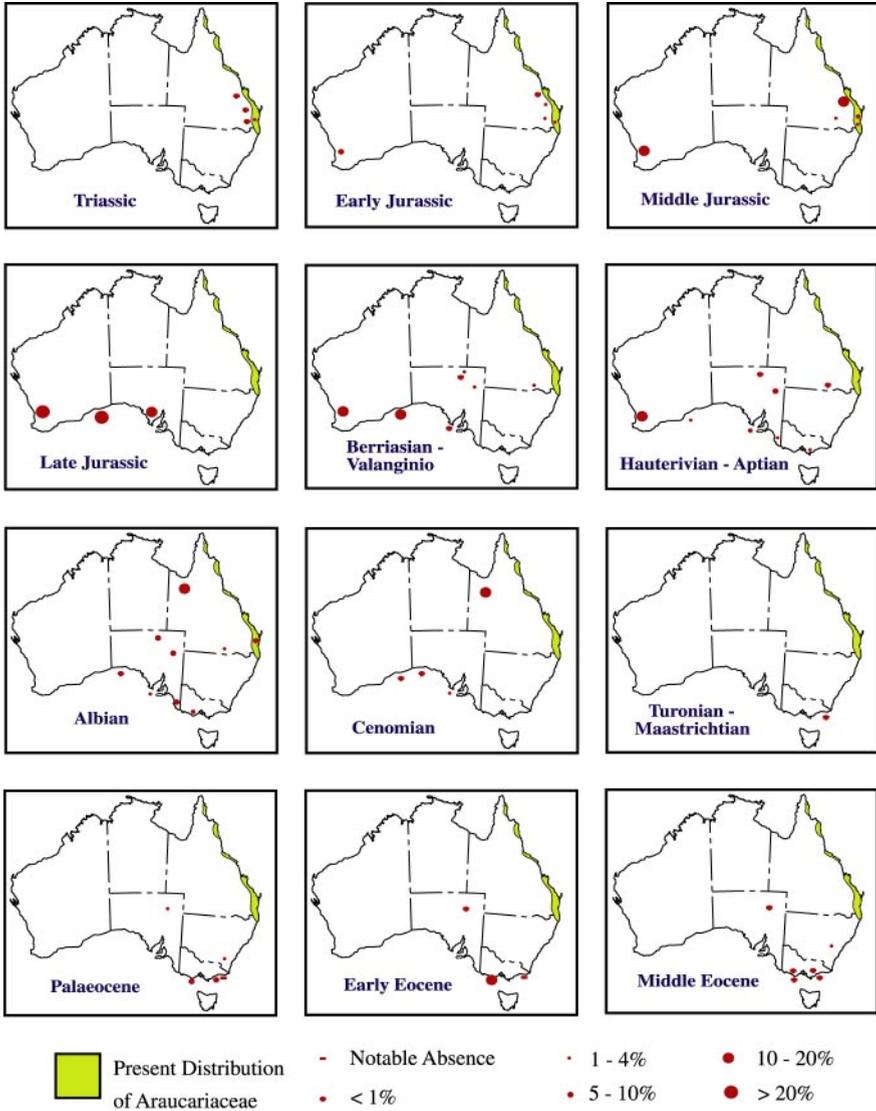


Figure 4 Average percentages of Araucariaceae pollen for geological time periods in Australian fossil sites; (*above*) Triassic - Middle Eocene; (*next page*) Late Eocene-Holocene (from a variety of sources).

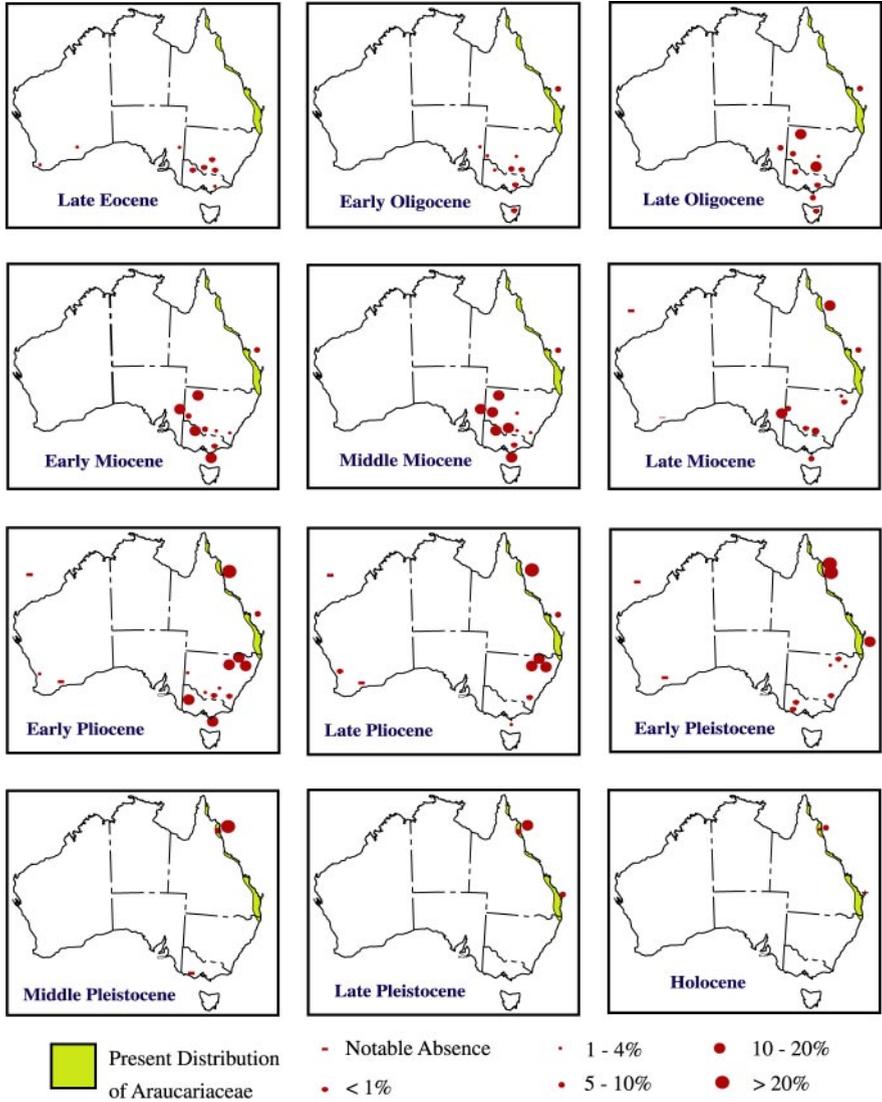


Figure 4 (Continued)

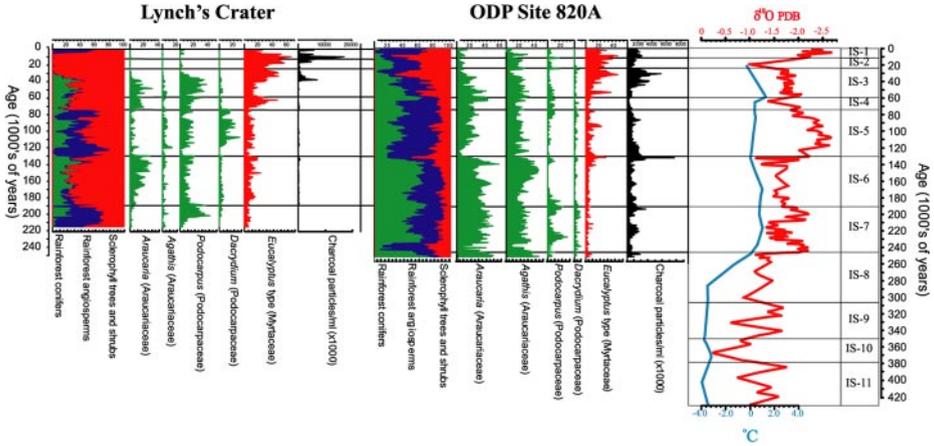


Figure 5 Selected attributes of the pollen records of Lynch's Crater (Kershaw 1986) and ODP 820 (Moss 1999) in relation to the oxygen isotope and inferred sea surface temperature change records from ODP 820 (Peerdeman et al. 1993). All pollen values are expressed as percentages of the sum of total dryland forest taxa for each sample.

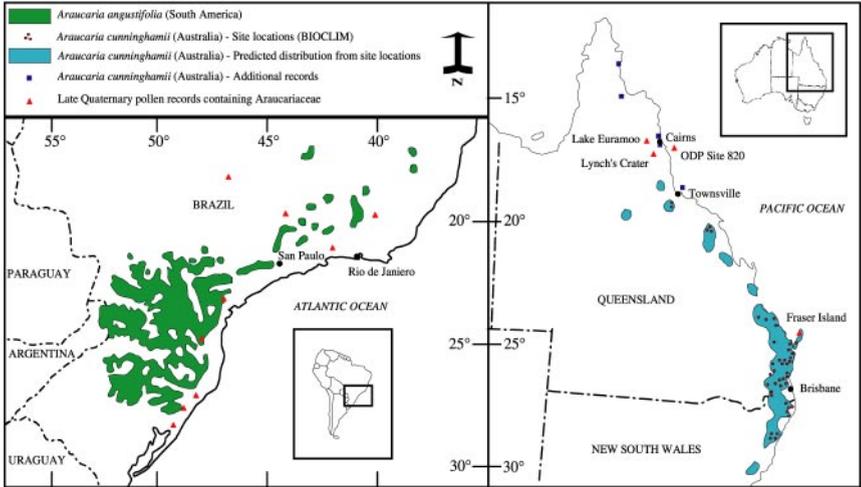


Figure 6 Distribution of *Araucaria angustifolia* in southeastern South America (from Veblin et al. 1995) and location of late Quaternary records containing *Araucaria* (from Berling 1998, Ledru et al. 1998), site records and predicted bioclimatic distribution of *Araucaria cunninghamii* in Australia (after Nix 1991), and location of major late Quaternary pollen records containing Araucariaceae.