New light on the origins of Australia's flora

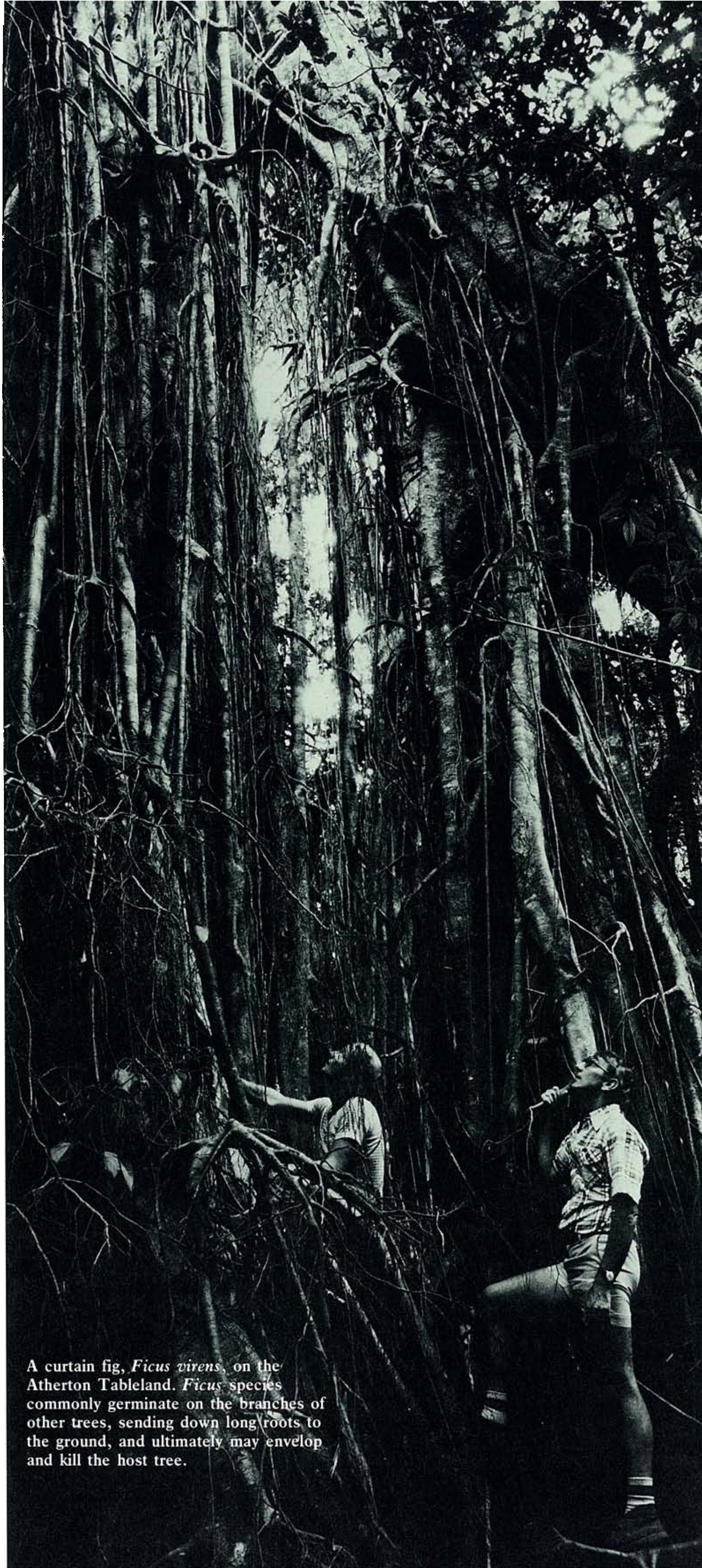
The Australian flora has fascinated science for two centuries. An estimated 80% of its species and more than 30% of its genera are found nowhere else in the world, easily the highest figures for any continent.

Only at family level does its common ancestry with the floras of other continents become clearly evident. Its distinctiveness testifies to a long history of isolation and independent evolution — and yet, paradoxically, two of the three primary elements in our flora have long been accepted as being of external origin.

The Australian sclerophyll element, typified by our eucalypt forests and woodlands, clearly evolved within Australia. It dominates our landscapes, halting at the margins of rainforests on the eastern coast and surrounding rainforest pockets in northern Australia.

The rainforests represent a fusion of the other two floral elements — the so-called Indo-Malesian element of tropical species that predominates in northern rainforest and the 'Antarctic element', represented by broad-leaved evergreen or deciduous rainforest beeches, sassafras, and conifers, that predominates in temperate rainforests.

More than a century ago the renowned English botanist Joseph Hooker first proposed that the Indo-Malesian rainforest type was merely an outlier of the great rainforests of south-eastern Asia, basing his view on the strong similarity



A curtain fig, *Ficus virens*, on the Atherton Tableland. *Ficus* species commonly germinate on the branches of other trees, sending down long roots to the ground, and ultimately may envelop and kill the host tree.

between the two. More recently, a convenient route for Hooker's invasion was provided with evidence that 10–14 million years ago a global lowering of sea levels produced an unbroken land bridge between Asia and Australia, and that a number of near-connections have occurred since then.

The Antarctic element has been regarded as an immigrant from the south, the legacy of an ancient connection between Australia and Antarctica, for which there is good fossil evidence. The Antarctic beeches, *Nothofagus* spp., and conifers such as *Araucaria* occur as fossils in Antarctica and as living plants in South America, suggesting that Antarctica was their centre of origin.

But today a new view of the origins of the Australian flora is emerging. The theory of plate tectonics or 'continental drift' has allowed a new interpretation to be made of the presence of the two supposedly alien elements in our rainforests, while studies of fossil pollen have provided a history of our vegetation stretching back more than 100 million years. Detailed studies in the rainforests themselves are also yielding new clues to their origins.

An Antarctic beech, *Nothofagus moorei*, in Lamington National Park, south-eastern Queensland. Antarctic beech pollen has been found in 80-million-year-old sediments in southern Australia.

Rainforest may be ancient

Dr Len Webb and Mr Geoff Tracey, of the Rainforest Ecology Section of the CSIRO Division of Plant Industry, have reached some conclusions that run counter to conventional theory. For example, they believe:

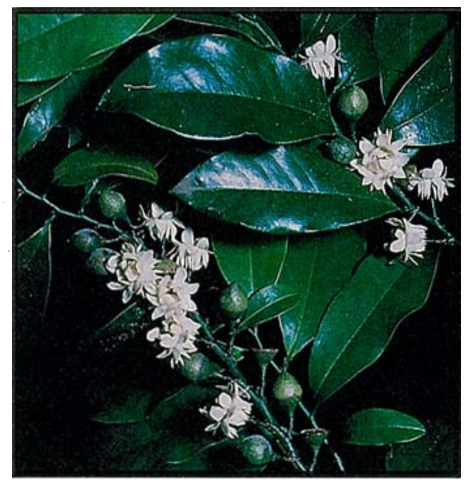
- ▶ The Indo-Malesian element in the flora represents the most ancient Australian flora.
- ▶ Far from being a receptacle for 'second-hand' immigrant floras of other continents, Australia was probably a centre, or part of a centre, for the evolution and radiation of primitive flowering plants.
- ▶ Australia's rainforests have spread in very recent times from nucleus 'refuge' areas where some of the world's most primitive flowering plants have survived the rigours of more than 100 million years of climatic change.
- ▶ While the clearing of land for agriculture has almost wiped out the large refuge areas of the coastal lowlands and tablelands, most of the smaller areas have escaped destruction because of their inaccessible locations and the robustness of their species.

Dr Webb believes the key premise in Hooker's theory of the origin of the Indo-Malesian plants is in fact its greatest weakness — the rainforests of Asia and Australia are too similar to have resulted from the random processes involved in long-distance dispersal or migration via land bridges.

Hooker's linking of Australian and Asian rainforests was intuitive. In modern times, ecologists have wrestled with the problem of measuring the similarities.

This is enormously difficult. The myriad plant species of the rainforests form complex communities that defy usual methods of classification. The dense packing of species, vertically as

Three of the world's most primitive flowering plants. The first two, *Idiospermum australiense* (left) and *Australobaileya scandens* (above), occur only in Australian rainforest and are the only representatives of their families. The third, *Eupomatia laurina* (below), is one of two species in a family limited to Australia and New Guinea.



Australia was probably a centre for the evolution and radiation of primitive flowering plants.

well as horizontally, makes 'head counting' very time consuming even in a small area, and there is no guarantee even then that the chosen area is representative of that particular tract of rainforest.

Dr Webb and Mr Tracey concluded that the only feasible first step was to classify rainforest by its structural type, not its component species. They devised a classification system (see *Ecos* No. 6) that describes rainforest according to its species complexity, general leaf size, presence of certain dominant plant types, and an evergreen or deciduous habit. The system offers, for the first time, an opportunity to compare structurally similar rainforests in different regions — even in different continents.

Dr Webb reasoned that structurally similar types of rainforest growing in similar environments would be most likely to share a common ancestry, which could be detected by the sharing of certain plant genera.

If Hooker was correct and rainforests have migrated large distances from a centre of origin in Asia, communities most remote from each other should show the fewest similarities. This is because of the lack of opportunity for genetic exchange between distant communities and the effect of other factors, such as species loss during migration and random genetic drift.

Sharing of genera

But when Dr Webb made an informal comparison of structurally similar rainforests in India's Western Ghats and Australia's Cooktown–Ingham region, he found they shared 47 genera — a remarkable figure considering the 8000 km between them. Even New Guinea, which would have been a staging point for Hooker's Indo-Malesian invaders, could only provide 41 matching genera, despite the fact that it has been connected to Australia in the recent past and still remains close enough for some genetic contact.

Dr Webb accepts that certain plants in our rainforests are genuine invaders — for example, some of those with wind-borne seeds, like orchids. But ecological studies into the way rainforests are organized, how their seeds are dispersed, and the quite narrow environmental requirements of their species offer further evidence that Australia's northern rainforests are not the result of invasion from south-eastern Asia.

Rainforests can only migrate as a community, for they are composed of many layers of vegetation that depend upon each other and upon the internal environment that the rainforest creates for itself. The likelihood of migratory birds or any other natural agent carrying a full spectrum of seeds from mature rainforest, not to mention the successional stages leading up to it, and depositing them at some environmentally favourable site hundreds or even thousands of kilometres away is extremely small.

If rainforests cannot migrate intact over long distances, how can the presence of similar plant communities in sites as widely separated as India and Australia be explained? Dr Webb believes there is now sufficient evidence to suggest they evolved as part of the flora of the ancient supercontinent of Gondwanaland, and were carried to their modern positions by Gondwanaland's break-up (see the box on page 9).

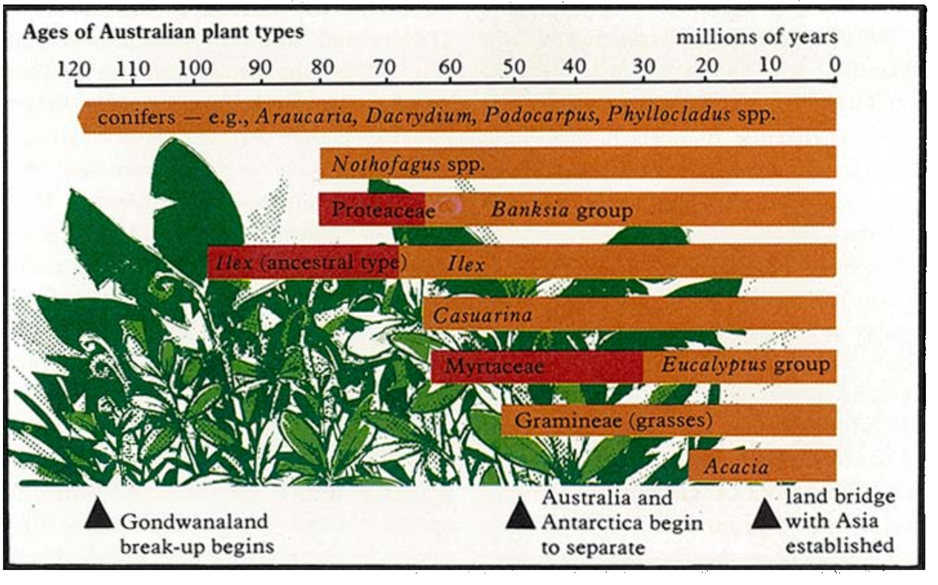
The climate in Gondwanaland between 200 and 60 million years ago would have favoured a warm temperate to a subtropical-type flora, and the Gondwanic rainforest could have been the progenitor of the modern rainforests of Australia, India, Africa, Madagascar, and South America. India and Australia were quite close together in the Gondwanic land mass until about 115 million years ago, and India's proximity to Madagascar (see the map) helps explain the close affinities between Indian and Madagascan rainforest.

One piece of evidence raises the possibility that the Gondwanic rainforest may have actually begun its spread from a region of which Australia was a part. Dr Webb points out that, despite their very small area, the rainforests of north-

Moisture-laden offshore winds provide a permanently wet environment for rainforest on the upper slopes and summit of Mount Bellenden Ker, Qld.

One type of refuge area where plant species can survive dry epochs is so-called gallery rainforest bordering permanent streams.

The chart shows the approximate times when some of the important members of the Australian flora appear in the fossil pollen record, including the rainforest indicator, *Ilex*. Rainforest was present long before Australia came into conjunction with south-eastern Asia.



Pollen from rainforest species can be found in 70-million-year-old sediments in southern Australia.

eastern Australia and nearby Pacific islands contain the greatest assemblage of primitive flowering-plant families in the world. Asian rainforests have a greater number of primitive genera and species, but he believes many of Australia's genera and species have been lost through climatic change and the leaching of nutrients from our ageing soils.

Single-species survivors

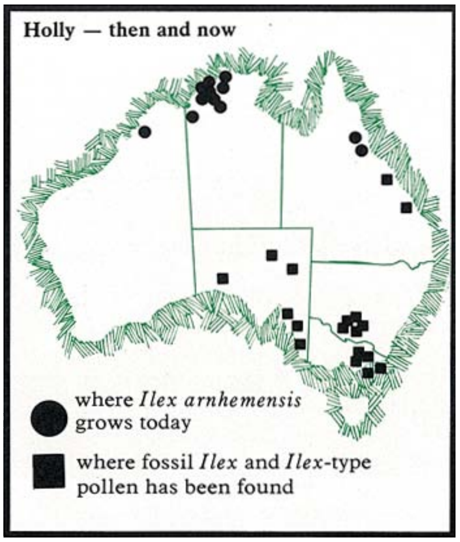
Some rainforest genera in Australia are represented by a single species. For example, north-eastern rainforests have a number of single-species genera in the Proteaceae family, presumably the last survivors of formerly diverse groups.

Australian rainforests have come through some severe times by comparison with those in the more stable climate of south-eastern Asia. The instability of the Australian climate, combined with the progressive decline in the richness of our soils in the absence of volcanic renewal, may have been responsible not only for the decline in diversity in our rainforests but also for the emergence of a new vegetation type.

Dr Webb and Mr Tracey note that two of the dominant families of today's Australian dry-leaved flora, the Myrtaceae and Proteaceae, have rainforest relatives that tend to favour lower-fertility soils. As the climate dried out, such plants may have evolved harder leaves and other drought-avoidance mechanisms and then diversified into the familiar sclerophyll vegetation of our landscapes today.

The resilience of certain rainforest plants in the face of dry conditions can be seen today in semi-arid areas. Genera such as *Cochlospermum*, *Flindersia*, and *Pittosporum* managed to adapt to drier conditions as the rainforests that once covered much of the continent retreated. Today these genera are split between diametrically opposite environments.

If rainforest was the progenitor of today's sclerophyll flora, the subtropical Gondwanic flora cannot take all the credit for its emergence. The southern Gondwanic flora, the so-called Antarctic



Australia's only holly species, *Ilex arnhemensis*, occurs today only in northern rainforest. However, fossil *Ilex* pollen is present in 15- to 70-million-year-old sediments from southern Australia, and *Ilex*-type pollen in even older sediments. This suggests that much of Australia has been covered by rainforest in the past.

element, almost certainly provided the Proteaceae family, which contains such genera as *Banksia*, *Grevillea*, and *Hakea*.

Two experts on this important family, Dr Lawrie Johnson and Dr Barbara Briggs, of the Sydney Herbarium, have modified their theories on its origin and spread in the light of evidence for a southern supercontinent. Where formerly they suggested it spread between the southern continents by a tropical route, they now conclude it was part of the warm, moist flora of southern Gondwanaland and was dispersed when that continent broke up. The Proteaceae occur in Africa, Madagascar, India, Australia, New Zealand, and South America, and as fossils in Antarctica.

Some of its most primitive species are found in the northern rainforests of Queensland, and only Australia has all five sub-families represented in its flora — facts that Dr Johnson and Dr Briggs cite as evidence that the family originated within the part of Gondwanaland that became the Australian land mass. They believe the same may apply to two other important Australian families that occur elsewhere — the sedge-like Restionaceae (Australia and Africa) and possibly also the Myrtaceae (all southern continents), which includes our own ubiquitous eucalypts.

The new picture of Australia as a primary centre for the evolution and spread of flowering plants is further supported by the fossil pollen record, which firmly contradicts the theories for an immigrant flora.

The pollen chronicle

Hooker's 'invasive' rainforest could not be older than about 12 million years, the time when Australia finally drifted to a connection with South-east Asia. Yet fossilized pollen from rainforest species can be found in 70-million-year-old sediments in southern Australia.

Dr Helene Martin of the University of New South Wales School of Botany has been studying fossil pollen recovered from deep bores in the Murray Basin area of southern New South Wales. More than 300 m beneath the roots of saltbush in the semi-arid zone south of Hay in the Riverina region, she found fossilized pollen from a species of holly.

Australia's only holly species, *Ilex arnhemensis*, occurs today in lowland rainforests in the far north. But the quantity of *Ilex* pollen in deep sediments in the Riverina indicates that it was an important member of the Australian flora for about 40 million years. With it occurs pollen of the 'Antarctic invader' *Nothofagus*, specifically *Nothofagus 'brassii* type', which is now extinct in Australia. Slightly younger sediments from the same area contain fossil pollen from other species found today only in rainforest. Pollen of the Antarctic beech *Nothofagus 'fusca* type' dates back about 65 million years.

Modern patterns of rainforest are no more than 12 000 years old.

Fan palms, *Liguala ramseyi*, dominate a tract of lowland tropical rainforest in northern Queensland.

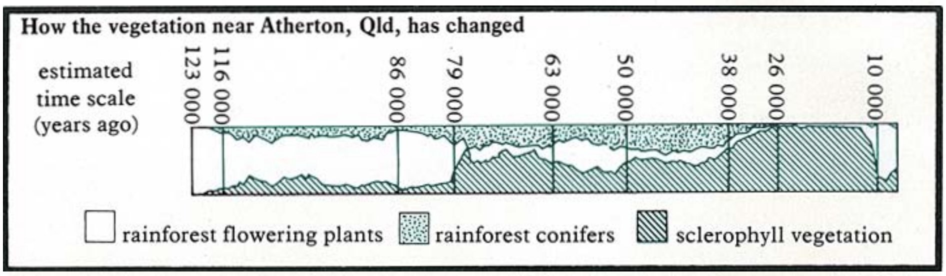
The fossil record reveals that not only were so-called Indo-Malesian species present in Australia 80 million years before it came into proximity with south-eastern Asia, but that the Antarctic species were also present 15 to 30 million years before Australia and Antarctica separated in the final event of Gondwanaland's break-up. Like Dr Webb and a growing number of Australian scientists, Dr Martin believes the customary division of the Australian flora into 'native Australian', Indo-Malesian, and Antarctic elements is no longer applicable.

For much of its history, as revealed by the fossil pollen record, large parts of Australia have had a quite stable moist climate favourable to rainforest. The climate apparently began to dry gradually about 40 million years ago, probably about the time that the Australian sclerophyll element began to develop. However, the emergence of this vegetation was slow, and may have resulted from the ageing and loss of nutrients of our soils rather than from climatic change.

Recent major changes

By comparison, the past 2 million years have been climatically unstable, with major changes taking place in the continent's vegetation in relatively brief time scales.

Dr Peter Kershaw, of the Geography Department at Monash University, has been studying fossil pollen from crater lakes on the Atherton Tableland of northern Queensland, and has compiled a record of the regional flora that indicates how the climate has fluctuated during the past 120 000 years. One of his



The chart shows the relative abundance of rainforest conifers, rainforest flowering plants, and sclerophyll vegetation in the fossil pollen record. During the last glacial period, which ended about 10 000 years ago, sclerophyll vegetation was dominant. Afterwards, rainforest flowering plants re-emerged. Present conditions are roughly comparable to those 86 000–79 000 years ago, and to those more than 116 000 years ago.

most surprising findings is that the modern patterns of rainforest are no more than 12 000 years old. Far from being in decline when Europeans arrived 200 years ago, they were in an expansion phase that began at the end of the last glacial period.

During that glacial period the climate was cooler and effectively drier than today, and the rainforests retreated into small areas where permanent moisture remained available and other environmental conditions remained favourable. Although the Atherton sediments represent only the regional flora, Dr Kershaw is confident they also reflect global climatic trends, as there is close agreement with records compiled from oxygen isotope ratios in marine sediments from the southern Indian Ocean and equatorial Pacific.

Two million years ago the flora of the Atherton region was not unlike that present in southern Australia about 40 million years earlier, according to the pollen record. But the last glacial period seems to have pushed some durable species past their limit, even after so many million years of survival.

Nothofagus 'brassii' (deciduous Antarctic beech), and the conifers *Phyllocladus* sp. (celery-top pine), a *Dacrydium* species (related to the huon pine), and *Dacrycarpus* all disappeared at Atherton. Presumably, they became extinct in the whole of mainland Australia not long afterwards.

If the Atherton record accurately reflects what was happening to the climate of Australia at large and the extinction processes in its vegetation, the last glacial period must have seen Australian rainforest shrink to one of the smallest areas in its long history. And yet it sur-

The rainforests of north-eastern Australia and nearby Pacific islands contain the world's greatest assemblage of primitive plant families.

Rainforest trees at risk

Many of the plants of our rainforests are at risk of extinction because of their limited distribution. A recent survey by Dr Webb, Mr Tracey, and other rainforest experts in the coastal arc from the Kimberleys in Western Australia, across the northern coast, and down the eastern coast into Tasmania points to the urgent need for conservation. They checked the distribution of 1316 rainforest tree species at 561 selected sites, ranging from small patches of rainforest to areas within larger tracts.

While the survey could not possibly cover all of Australia's rainforest, Dr Webb believes its results reliably indicate the rarity of many species. No species was found at more than 129 of the 561 sites; 30% occurred at no more than three sites, and 56% at no more than ten. Many species recorded as occurring at more than one site had only small populations at each, or a single major population and several small outlying occurrences remote from it.

Thus these species may be at greater risk than the figures for the number of sites where they were found indicate. The table shows the numbers of species found at 10 sites or fewer.

Species found at ten or fewer sites

Number of species and percentage of total	Number of sites where found
173 (13·1%)	1
131 (10·0%)	2
100 (7·6%)	3
64 (4·9%)	4
73 (5·5%)	5
56 (4·3%)	6
42 (3·2%)	7
36 (2·7%)	8
27 (2·0%)	9
35 (2·7%)	10

vived to begin spreading again at the end of the Ice Age.

Dr Kershaw's finding that its modern distribution dates back 12 000 years at most suggests rainforest has a very efficient means of 'sitting out' dry epochs that drastically reduce its range. The great antiquity of some of the plant species in our rainforests, particularly the very primitive flowering plants of north-eastern tropical rainforests, also points to such a mechanism.

Refuges for rainforest

In February last year, a rainforest conference in Venezuela heard evidence that even the great rainforests of the Amazon basin, Mexico, and Africa have in the recent past retreated to pockets representing only fractions of their maximum size.

Among the first plants to recolonize rainforest areas are stinging trees (*Dendropnides moroides*). At maturity this young plant will provide shade for species less tolerant of light.

Temperate rainforest in Alfred National Park, south-eastern Gippsland. This rainforest type is commonly found mingled with large eucalypts.

All the evidence suggests that, in dry periods, rainforest contracts to small areas where conditions remain favourable. Such areas vary in size from hundreds of square kilometres to perhaps only a few hectares.

Dr Webb and Mr Tracey have substantial evidence that the islands of rainforest now occurring right down the eastern coast are themselves the products of smaller islands that have expanded out of refuge areas to re-coalesce after the last glacial period. These nucleus areas are still identifiable, even though they form a continuum with the surrounding rainforest. The zones where their expanding margins have flowed into each other are also identifiable because the vegetation still has not settled into stable communities, and some of the species have still not colonized the new areas.

Dr Webb says any conservation program for what remains of our rainforests must concentrate on these nucleus areas, since they are living botanical museums, the very lifeblood of the rainforest. Most of them are probably intact. Their protected locations would tend to insulate them from the activities of Man, as well as from drought, fire, and invasion by the sclerophyll vegetation.

Dr Webb and Mr Tracey have identified a number of important refuge areas, but have concentrated on identifying the types of locations where they occur, as there are probably a great number of them. The chances are that no two will have the same assemblage of species because of the random effects of extinctions and genetic drift operating on them.

Dr Webb believes the areas of greatest botanical importance are those harbouring the most primitive flowering plants, and these are concentrated in northern Queensland. Of the 14 families of flowering plants recognized as truly primitive, eight occur there within a 6000-sq-km area. Two of these, the Austrobaileyaceae and Idiospermaceae, are represented nowhere else in the world, and a third, the Eupomatiaceae, is shared only with New Guinea.

Dr Webb describes the area as a botanical Noah's Ark — except that this Ark is laden with veritable dinosaurs.

Graeme O'Neill

The fossilized grain of holly pollen (*Ilex* sp.) from 40-million-year-old sediment in southern Australia, in the centre of the upper photo, bears a close resemblance to pollen of Australia's only modern holly species *I. arnhemensis* (lower), found only in permanently wet rainforest.

More about the topic

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Birth of the southern continents

Biological evidence for the existence of a southern supercontinent in prehistoric times has been known for at least a century. For example, the Antarctic beeches, *Nothofagus* spp., are found in Australia and South America, and occur as fossils in Antarctica.

The plant family Proteaceae occurs in all the southern continents, with fossils in Antarctica, and some genera — for example, *Orites*, *Lomatia*, and *Oreocallis* — are actually shared by Australia and South America. The world's largest birds, the flightless ratites, are also distributed among the southern continents — ostriches in Africa, emus in Australia, moas (now extinct) in New Zealand, and rheas in South America. These biological affinities between continents used to be attributed to the existence of ancient land bridges or to long-distance dispersal of species by sea.

The theory of continental drift was first proposed by a German scientist, Alfred Wegner. He suggested in 1912 that, long ago, all the world's continents had been part of a single land mass, which he named 'Pangaea'. Orthodox science rejected the idea for many years, as no mechanism was known that could shift massive continents around on the surface of the earth.

However, geological evidence for continental drift began to accumulate. The continents clearly fitted together well, and the matching of their outlines was even more dramatic when their submerged continental shelves were taken into account. Certain rock types 'dovetailed' between the continents, and matching plant and animal fossils pointed to a common ancestry.

Only in the past decade, however, has the missing mechanism for rifting and moving continents apart been found. The continents are believed to be carried on great crustal plates that, being lighter than the earth's molten core, float upon it and are moved by powerful convective currents in the magma. Wegner's Pangaea is now generally accepted, as is evidence that it broke into two supercontinents, Laurasia and Gondwanaland.

These two supercontinents also broke up. About 120 million years ago, Gondwanaland began fragmenting into the modern southern continents and India, with the final event, the separation of Antarctica and Australia, occurring around 50 million years ago. The sequence of the break-up deduced from geological studies fits well with that inferred from biological evidence.

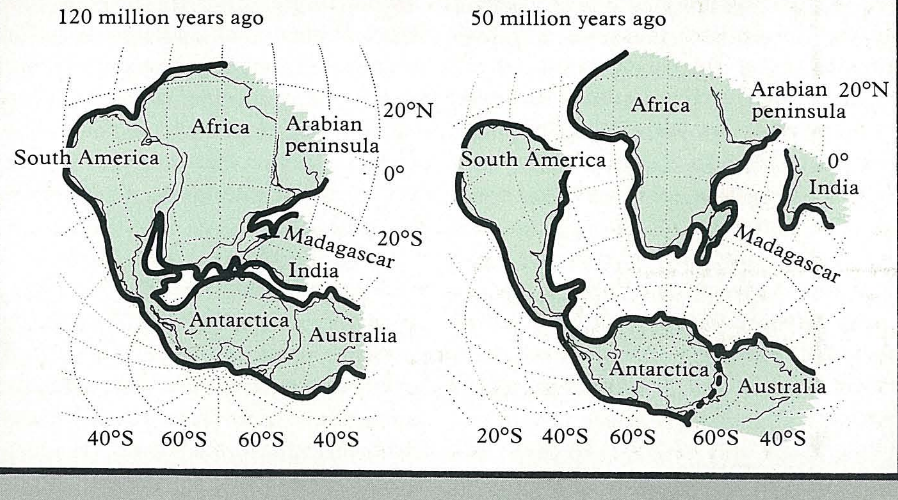
The absence of *Nothofagus* species from Africa, for example, points to Africa's early separation from the main Gondwanic mass. Supporting evidence comes from the Proteaceae — Africa shares no genera with Australia and South America. In the Jurassic period, about 200 million years ago, Gondwana straddled the globe between latitudes 70°S and 30°N (see the diagram).

Around 120 million years ago, Africa began to rift from South America, which remained connected to Antarctica and Australia. Rifting also initiated India's isolation from the other continents. By 80 million years ago large gaps had opened between South America and Africa, Africa and India, and India and Australia.

The elongated mass comprising what are now South America, Antarctica, and Australia still remained as a barrier to the establishment of a circumpolar oceanic current, and the southern continents enjoyed a quite stable climate ranging between moist temperate and tropical because of the 'homogenizing' effect of currents that mixed equatorial with polar water. Even though Antarctica was nearing its present position, it remained free of glaciation.

About 60 million years ago Africa and South America were widely separated

The break-up of Gondwanaland



The southern supercontinent began breaking up into the modern southern continents about 120 million years ago. By 50 million years ago, most of the continents were nearing their present positions, and Australia was starting to break free from Antarctica to begin its drift northwards. Jagged outlines indicate areas where Gondwanaland's boundaries have been obscured.

and only a narrow link remained between Antarctica and South America. Australia and Antarctica had begun to rift. By the ponderous standards of continental drift, India was speeding towards a violent collision with southern Asia, which would ultimately create the world's highest mountain range, the Himalayas.

By 40 million years ago the continents were approaching their modern positions. Australia was still moving northwards from a more southerly position than it occupies today, having broken free from Antarctica. During the next 15 million years the opening of gaps between South America and Antarctica, and later between Australia and Antarctica, cleared the way for a circumpolar current. Then, relatively undiluted by warmer waters, the polar seas began to cool and the glaciation of Antarctica began.

Hoop pine (*Araucaria cunninghamii*) survives in a protected gully, surrounded by sclerophyll vegetation.

As the climate began to cool, vegetation changes occurred in Australia with the disappearance of some of the more tropical plants from its southern areas. The sclerophyll element of the Australian flora began to expand about this time, although climate may have been less important than the ageing of our soils in its proliferation.

About 15 million years ago another climatic threshold was crossed when Australia's northerly movement brought it into conjunction with the Indonesian archipelago, blocking another route for the mixing of polar and equatorial waters. The Antarctic ice sheet began to form at this time, and its ebb and flow since then appears to have been an important factor in the relative instability of the climate of Australia over the past two million years, and in changing vegetation patterns.

Few scientists today question the theory of continental drift, in spite of its unacceptability only two decades ago. Now an equally revolutionary theory has been suggested by two scientists from CSIRO's Division of Mineral Physics.

Dr Brian Embleton and Dr Phillip Schmidt have analysed data from fossil magnetism studies in North America, Africa, and Australia and discovered that all three continents are in the same positions relative to each other and the earth's core as they were more than 2000 million years ago.

Their analysis is based on information that has been quoted many times in the scientific literature, so there is no reason to doubt its validity. But how can three continents that, according to continental drift theory, have been drifting around the surface of the globe, be in the same position they occupied eons ago?

Dr Embleton and Dr Schmidt have suggested two explanations, both of which require, in their own words, 'an open mind':

- In the distant past, the earth may only have been 60% of its present size, with all the continents forming a single, continuous mass on its surface except for some shallow seas. If so, their separation would have been the result of the earth expanding, not random drifting.

- Continental drift may be a cyclic phenomenon, with continents joining up, and then separating to return to 'remembered' ancient positions by some unknown mechanism. The stable positions of Africa, North America, and Australia today could indicate each has found its preferred location while other continents continue to drift at rates of several centimetres a year.

The 'global continent' theory suggested by Dr Embleton and Dr Schmidt is not new. In 1958 Dr S. W. Carey, Professor of Geology at the University of Tasmania, demonstrated that models of the continents could be fitted together on a globe, to form not merely a single continent, but one that virtually covered the whole globe. Dr Carey believes the globe is still expanding today.

Both Dr Embleton and Dr Schmidt know their findings are likely to be controversial, but say they are the only possibilities that fit the evidence. Dr Embleton points out that the odds against three continents occupying their ancient positions today purely by chance are astronomical.