Lucy Cranwell Lecture 1992
Australia's fossil floras and living Gondwanan forest remnants
420 million years of evolution of the Australian Flora

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It is a great honour to have been asked to deliver the Lucy Cranwell lecture for 1992. I did not know until I started to prepare this lecture how significant Lucy Cranwell's contribution had been to understanding the prehistoric world in which I have been mental-journeying lately. While she tramped the hills and mountains of New Zealand as a systematic botanist and then became a pioneer in palynology I was growing up in Southern Rhodesia, fascinated by plants, drifting continents and the wonders of nature. I did not know then that her work on Nothofagus would be part of the background to understanding Gondwana, the supercontinent in which I live mentally these days. I have escaped there, preferring the prehistoric world where all the problems have sorted themselves out during geological time and where all the once-endangered species are peacefully extinct. It is a more comfortable place than the modern world where one feels powerless to cure the problems caused by human over-population and its attendant ills. I think that had I been priviledged to meet Lucy Cranwell I might have felt that we were on the same wavelength.

Australia is an ancient landmass. Parts of Western Australia have rocks containing zircon crystals that were part of the early crust of the Earth when it cooled 4200 million years ago, and some of the oldest evidence of life found anywhere occurs in stromatolitic limestones in Western Australia -- dated at 3500 million years. It was early organisms with green photosynthetic pigment, the hallmark of plants, that produced oxygen as a by-product of their production of carbohydrates and steadily built up the oxygen in the atmosphere to a point at which higher plants and animals could function. We tend to forget the fundamental importance of plants as regulators of the atmosphere through time, including now, and the fact that 99.9% of food chains on Earth today are based on plants.

The 420 million years of plant life that I am going to describe tonight are a small slice of geological time. The sequence of fossil floras through time shows evolution of the biosphere and reminds us of the natural laws that govern the living planet. It was Charles Darwin who studied the simple ecosystems on the Galapagos Islands and recognised that **environmental change is the driving force of evolution, and natural selection the agent.** Small brown finches, adapted to the different conditions which applied in the islands, had become new species, distinct from those that had originally colonised them, in order to survive. What we need to remember is that while environmental change results in evolution, **too rapid environmental change causes extinction.** And rapid is measured in geological time, not man-time.

Co-evolution of Life and the environment has been the rule since the beginning of time. One cannot separate evolution of flora or fauna from evolution of the environment. James Lovelock has suggested that the Earth acts like an enormous living organism with all its systems, organic and inorganic, in balance -- **GAIA** the living planet. Before the arrival of the human species the biosphere was kept in dynamic balance -- each parcel of land or ecosystem having its carrying capacities or niches. Balance is a pre-requisite for the health and well-being of the planet -- a fact that we are beginning to realise at this late stage. Humans in their disproportionate numbers have upset the natural balances and operate outside the laws that had governed the biosphere up to the time of their arrival. They have been able to do this because they are the first species with technology.

The fossil record shows us the evolution of plants and animals through time. In addition, palaeogeographic reconstructions made by "reading" the rocks enable us to know how the arrangement of land and sea have changed. Australia was part of the supercontinent **Gondwana** for most of its history. South America, Antarctica, Africa, Arabia, Madagascar, India and Australia were the major components of Gondwana. About 175 million years ago an eastern province -- Pacifica -- of which New Zealand and New Caledonia are the only parts left above the sea, was added.

Early geographers had noticed that the continents, especially Africa and South America, fitted neatly against each other when the ocean between them was closed, and wondered whether perhaps lands might once have been joined. It was the work of the botanist Joseph Hooker 150 years ago which first lent some respectability to the theory that the configuration of land and sea had been different in the past. On voyages in the Southern Ocean in the 1840s with James Ross (after whom the Ross Ice-shelf is named) he saw the similarity of southern floras -- particularly the distribution of Antarctic Beech. The forests of Nothofagus in South America, islands of the Southern Ocean, Tasmania and New Zealand, and the disjunct distribution of members of many southern families in the now-separate southern lands suggested to him that there had been a previous connection between continents. He dicussed the idea with Charles Darwin and they agreed that such a previous connection, which included a vegetated Antarctica, was the only explanation for the facts.

As fossil floras were investigated, starting with a knowledge of those of the Gondwana Series in India, it became evident that the prehistoric floras of southern lands showed a previous connection with each other and also with India. The Glossopteris flora of the Permian, in particular, occurred in all the southern continents, as well as in India. Additional evidence from fossil faunas and the discovery of more and more disjunct distribution patterns in living plants and animals added weight to the argument. Dr Alex du Toit's geological evidence of the presence of the same strata on the opposing margins of continents now separated by oceans led to formulation of the theory of Continental Drift. General acceptance only came in the 1960s when technology had advanced to a stage where it could be proved that the crust of the Earth is divided into plates that move in relation to each other -- and the Science of Plate Tectonics has established the previous existence of supercontinents.

In the Late Silurian, about 420 million years ago, life started to invade the land. Up to that time life had been confined to the waters of the globe. Oxygen levels in the atmosphere had to reach a level where the ozone layer was sufficiently dense to cut out some solar radiation before the land could be colonised. All the phyla of invertebrates had evolved in the sea by this time, and fish -- the first vertebrates -- had evolved by 470 million years ago, 50 million years before life ventured onto the land. (Look well at little Arandaspis the earliest fish who swam in the Larapintine Sea that bisected a tropical Australia then -- she is our greatest-of-great grandmother, because from fish came amphibians and then reptiles and mammal-like reptiles, and finally mammals including us.) The plant kingdom up to the time of invasion of the land consisted of Algae only -- phytoplankton and seaweeds. With the move to the land development of vascular plants occurred and evolution of the divisions of the plant kingdom commenced.

If plants had not managed to colonise the land, life would have been confined to the water. When plants established a zone on water margins, animals could start their move into a land environment as well.

The Baragwanathia flora of Victoria is one of the oldest land floras. It contains the Lycophyte Baragwanathia (whose relatives are the tassel ferns that we know today little changed after 420 million years) and Psilophytes ancestral to ferns and horsetails, gymnosperms and angiosperms. (Psilotum today is close in structure and behaviour to these ancestral plants.) Australia lay in low latitudes, mainly in the northern hemisphere and much of what is now eastern Australia had yet to develop.

By Devonian times 380 million years ago life was well adapted to swamps, still tied to watery habitats. It was the evolution of seeds in plants (replacing the need for free water and two generations in reproduction by spores) and of eggs in vertebrates (developed by reptiles -- making them the first true land animals) that progressively severed the ties with water. Arborescent lycopods like Leptophloeum grew to considerable size. Amphibians were the dominant vertebrates on the land.

During the Carboniferous Australia moved from straddling the Equator towards the South Pole. Its flora of lycopods and horsetails, related to that which was responsible for coal formation in tropical Euramerica, became increasingly impoverished. The Carboniferous/Permian ice age was approaching and a low-growing tundra vegetation of rhacopterids with shrubby lycopods and horsetails and seed ferns grew as best it could under the harsh conditions. An ice age sheet covered half of Australia during the ice age, wiping out flora and fauna and setting the stage for a new burst of evolution when conditions improved in Early Permian.

The Glossopteris flora evolved as the ice retreated. Earliest Gangamopteris occurs at Bacchus Marsh in Victoria in glacial sediments. Australia's Permian coal deposits result from plant growth in cold-to-cool temperate bogs, more like those of Scotland today than the steamy swamp forests that had produced northern hemisphere coal in the Carboniferous. In the high latitude situation winters were dark and cold, if not freezing. The Glossopterids show many different reproductive structures and appear to have been a group that could have evolved in many different directions. Associated with them were early cycadophytes, ginkophytes, conifers, equisetaleans and ferns.

Towards the end of the Permian world climates warmed up, coal swamps and Glossopterids disappeared and the vegetation changed. The first podocarp and araucarian conifers and the first forked-frond seed ferns appeared. A marked extinction event with shallow marine invertebrates particularly affected occurred to separate the Permian and the Triassic, but the vegetation seems to have adapted and changed prior to and progressively through this time.

In the Triassic, which was warm worldwide with no polar ice, there was much aridity in middle latitudes. Australia had a more humid climate as the South Pole was at Bourke in western New South Wales. (Anyone who has travelled through the intensely arid outback and passed through Bourke will find the idea of a Pole there as slightly incongruous!) Vegetation had to contend with long months of darkness in winter. The Dicroidium flora developed in Gondwana, and presumably did not spread into the northern hemisphere because of the barriers created by subtropical and tropical deserts. This was the time of Pangaea, and the southern supercontinent was connected to the northern Laurasia.

A reconstruction of the Sydney Basin about 200 million years ago shows that it was a vast floodplain, rather like Bangladesh is today. Rivers flowed into it, mainly from Antarctica, carrying the hugh amounts of sand that have formed the massive Hawkesbury Sandstone which characterises the Sydney region today and forms the Blue Mountains. Lycopods that grew in the mangrove niche were like small palms with woody trunks and crowns of whorls of leaves. Conifers, cycadophytes and ginkgophytes lived in drier areas and Dicroidium and Lepidopteris probably formed heathlands. Some of the plants, like Xylopteris, show adaptation for drought resistance, which implies that even in these high latitudes there may have been seasonally dry periods. Giant Amphibians were still abundant and reptiles, including early crocodiles, were around.

The Jurassic Period was a time of global warmth and good rainfall and the ancient vegetation of conifers, cycads, ginkgophytes and ferns grew all over Pangaea. This was the time of Dinosaurs -- reptiles still ruled, and though small mammals were about by now they were an invisible part of the fauna. Birds had also evolved by Jurassic times (they and dinosaurs shared an ancestor and I once attended a symposium where a vertebrate palaeontologist asked whether dinosaurs should be classed as birds, or birds as dinosaurs!) Pterosuars were the main flying vertebrates.

By Middle Jurassic, about 175 million years ago, a new eastern province of Gondwana was added with the uprising of Pacifica along what is now Australia's eastern margin. Volcanic high ground developed on this land and rivers ran from it into eastern Australia. New Zealand and New Caledonia are the only parts of this landmass still above the sea. Pacifica received a quota of Jurassic plants. (The reconstructions showing this eastern Gondwanan province in four developmental stages were produced by Graeme Stevens of DSIR in Wellington.)

During Jurassic times rifting of supercontinents commenced. The times at which seafloor was produced separating the different continents varied. In Australia's case rifting between Antarctica and Australia and the formation of a wide rift valley started at 160 million years ago -- at first by continental extension (thinning of the Earth's crust). Final separation only occurred at 45 million years ago when the trailing edge (Tasmania and the South Tasman Rise) cleared Antarctica. India had moved away with opening of the Indian Ocean from 132 million years ago. It collided with Asia at about 50 million years, pushing up the Himalayas. Its plate and Austalia's then fused, so Australia's northward movement since it became an island continent has resulted in more interacton between India and Asia. Pacifica started rifting from the Eastern Australian margin about 80 million years ago and by 60 million years ago widening of the Tasman Sea had been completed and New Zealand and New Caledonia were in their present situations in relation to Australia.

Tasmania was in a hinge position between Antarctica and Australia when they were separating, and between Pacifica and Antarctia/Australia while the Tasman Sea was opening. As a result the Earth's crust in the Tasmania region was cracked and thinned. It has been estimated that 5000 cubic kilometres of molten magma were emplaced underneath Tasmania as a result. Today remnants of this volcanic rock are exposed as the dolerites of Cradle Mountain and other landscape features. Some of the melt came to the surface to crystallise as basalt. Cavaties in the basalt, formed when gases escaped, later were infilled by silica in the percolating groundwaters and agates and other semi-precious gemstones resulted.

The Lune River gemfield in S.E. Tasmania owes its origin to the basalts that covered the area in the Jurassic -- a consequence of Gondwana's rifting. My book, just released, **Time in Our Hands,** describes the gemfield, its stones, and in particular the petrified plant material that resulted from the eruption of basalt. A siltstone comprising volcanic ash, soil and plant material formed beneath the basalt. Today most of the basalt and siltstone have eroded away and the silicified gemstones and petrified plant remains are found in a gravel beneath the soil. My interest in the collections form the area started whem I found a perfectly petrified Bennettitalean cycadophyte polycarp in a private collection in Hobart. It had been there, a cut and polished lapidary specimen, among agates and onyx, unrecognised for 25 years. Fortunately the lapidary had cut a median longitudinal section to polish. Details of the seed/sterile scale layer are preserved. Seeds with two cotyledons and an extended micropyle are visible. The possible relationship of Gnetales like Ephedra and Gnetum is suggested. The polycarp has a piece of its stem attached and it has been possible to match small stems with the same internal anatomy.

Very large amounts of petrified wood -- up to 30% by weight of gravel samples -- are found at Lune River. Much of it appears to be conifer, some is enhanced as lapidary specimens by having suffered extensive or pocket rot prior to fossilisation. The petrified tree-fern stems that are much sought after by collectors (who have been stripping the gemfield for 30 years) are beautiful. Replacement of tissues with different coloured agate and opal enhances them and results in magnificent clarity of internal structure. Jim Frazier, who does the marvellous fossil photography for my books, has developed a new technique for illustrating anatomy. We do not have to cut thin sections for examination under a microscope. Using cut and polished lapidary specimens, special lighting techniques including fibreoptic sources and a macro lens he has made a real breakthrough in scientific illustration.

On the Australian mainland almost the whole of the eastern sector became an inward-draining region during the Jurassic. Sedimentary rocks laid down in it became the aquifers of the Great Artesiam Basin. The region is the Jurassic has been likened to the Amazon basin, but the high latitude situation and the absence of angiosperms imply that it must have been very different. Kauri Pine (Agathis), Araucarians and podocarps, and Pentoxylalean cycadophytes are abundant in the beautiful Palbragar Fish Bed flora.

During the Early Cretaceous global sealevel was high. Australia was a very flat land then as now and it was inundated. An island sea, entering the Great Artesian Basin from the Gulf of Carpentaria and flowing into all the major continental Basins, reduced the area of land to four island blocks. World climates were changing as lands started to move. Sealevels peaked between about 116 and 110 million years ago. An all-Australian dinosaur, the Muttaburrasaurus left his bones in the inland sea in Queensland. The vegetation of the times was largely of all the ancient plants, and the earliest angiosperms were appearing in the rift zone sediments between Australia and Antarctica and as rare members of the forest in the southern part of the continent.

The Late Cretaceous was a time of maximum global change. Continents were on the move, global climate was changing and there was much volcanism. Very deep weathering of rocks and formation of leached profiles characterise Australia at this time. It has been suggested that acid rain might have been a global phenomenon -- a product of volcanic activity.

Pollen records from the rift valley system between Australia and Antarctica and from what little evidence there is on the mainland tell us that tall open-forests of podocarps and araucarians had Proteaceae of many genera, Ilex, Winteraceae and other angiosperms. The rift seems to have acted as a cradle for evolution of Proteaceae and it is interesting to find that some of the genera like Adenanthos and Stirlingia are sclerophyll while others were tropical forest genera. Knightia which today is one of the remaining New Zealand genera originated in the rift. Nothofagus was present in small proportions.

At the end of the Cretaceous, 65 million years ago, the Terminal Cretaceous Event saw dinosaurs and ammonites and many other things become extinct. Whole books have been written speculating about this extinction -- and everything from a nuclear-winter type cataclysm due to asteroid impact to much less drastic scenarios has been suggested. A great number of species survived ... the plants in the southern hemisphere carry on through the interval, birds and most reptiles other than dinosaurs, pterosaurs and some sea monsters did not disappear. After the Late Cretaceous time of change modern-style flora dominated by angiosperms and a fauna dominated by mammals was established.

The Early Palaeocene cool temperate rainforest dominated by Huon Pine and other podocarps, with abundant araucarians including Agathis, was widespread. Myrtaceae was sometimes abundant. Late Palaeocene to Early Eocene forest was warm temperate with a suggested mean annual temperature of 20°C and about 1400 mm of rain. Some forests were dominated by Cunoniaceae, others by Myrtaceae. The Nothofagus component was small or absent.

In the Middle Eocene, 45 million years ago, Australia became an island continent and started drifting northwards. If you go to Central Australia today, as I have just done, and visit two localities close to Lake Eyre South you will be forcibly struck by the contrast between the gibber and saltbush desert of today and the forest of 45 million years ago. At Stuart Creek an amazing flora is preserved in Eyre Formation silcrete. Every boulder on the ridges and every bit of scree on the slopes is decorated with leaves. This was a land of meandering streams, of gallery forests, of marshlands and oxbow lakes. Now it is the sump of Australia -- many metres below sealevel, where a few desert Acacias and hardy grasses and desert herbs exist precariously, dormant between the unpredictable rains. At Nelly Creek mumified leaves are found in a carbonaceous mud beneath the salt-encrusted sand of the river. With cuticles perfectly preserved and some tissue between, they can be identified to living genera, and a spore and pollen assemblage in the mud is also diagnostic, confirming the age of this simple notophyll vine forest ... Brachychiton, Casuarina, Banksii, leaves of Myrtaceae and fruits of Eucalyptus, podocarps, araucarians, Cunoniaceae ... and many others. Other silcrete floras occur near Woomera further south in South Australia and a frond of a palm, Archontophoenix, is a spectacular specimen from there.

When Australia separated from Antarctica, and when the Drake Passage developed between South America and Antarctica a little later, a circum-polar current developed. As Antarctica became progressively more isolated it cooled and its ultimate refrigeration, which dates to about 35 million years ago for the first ice cap, set the world on train towards an ice age. Times of ice build up were arid times in Australia and times between were better watered and warmer. The general trend was to drier, more seasonal conditions. Rainforest started to contract into the more uniformly wet areas with better soils, sclerophyll was sorted out to expand in less favourable parts, and the overall trend was from forest to open woodland and later to grassland and chenopod shrubland.

20 million years ago the Centre near Lake Eyre was still well-watered and had gallery forests. Freshwater dolphins lived in the lakes. Flamingoes (which have been absent from Australia for the last 400,000 years) were abundant. A large number of different marsupials lived in the forest, including the first koalas, and there were big running birds

and crocodiles.

Sudden cooling and drying events punctuated the warm and wetter Miocene -- one at about 15 million and a marked one at 6 million -- the terminal Miocene event. A great expansion of polar ice then caused world-wide aridity. Sealevels fell, stranding the Mediterranean Sea which evaporated, to refill when sealevels rose again. A sharp contraction of forest and increase in grassland resulted in Australia.

In Africa the humanoid apes came down from the trees as their forest disappeared and started to walk upright on the savannah. In order to survive in an environment for which they had not been designed they adopted technology. Fire and the manufacture of stone artefacts enabled them to compete. It is suggested that it was the development of manual dexterity in the fashioning of weapons and tools that led to the development of a big brain. For an ape man to become a hu-man he first had to become a lapidary! and with the development of technology the troubles of the world were just beginning.

In the Pliocene in Australia a fauna of megabeasts evolved (but no ape-men). Giant wombats, Diprotodon, giant pythons, echidnas, and enormous short-faced kangaroos.

When the northern ice cap formed about 2.4 million years ago the world was right in an ice age. Fluctuations between glacial stages, when so much water was locked in ice that sealevels fell by up to 200 m and aridity was a feature of all climates, and interglacials when seas rose and it was wetter and warmer, became the pattern. While the northern hemisphere was greatly affected by ice, Australia suffered desiccation and was cooler and much windier during glacials. A mosaic of vegetation types contracted and expanded as climate fluctuated. The blown-sand deserts that characterise central Australia are a result of the increased windiness and aridity of glacial stages. The spinifex, mulga, mallee and dune/swale vegetation types of modern Australia evolved to suit the new environments created by the ice age. Australia became the driest vegetated continent, more than two-thirds under extremely arid regimes, more than half desert.

When the Aboriginals came to the continent at least 60,000 years ago, and we now think it may have been 140,000 years ago, they added a new dimension. They brought regular and devastating fire to a dry and fiery land and pollen records show that this completely changed the vegetation. Except for the small pockets of gondwanan forest on the eastern coast and in Tasmania, the selection of fire-tolerance became a feature of vegetation. Fire had probably been a significant determinant of components of vegetation from Late Miocene onwards, and Aboriginals merely accelerated the process. They hunted the megabeasts to extinction ... Like Man in all the other continents -- Quaternary extinctions were the result of their activity. (I do not have to convince you in New Zealand where the extinction of Moas within 500 years by Maoris is one of the best documented examples, and where much of the lowland forest was decimated by their fire.)

Today the remnants of Australia's gondwanan forest form a chain of refugia along the east coast. Their extent has been greatly decreased by logging. The wet tropical forests of Queensland are closest to the original mixed forest that was in Australia in the Eocene before separation from Antarctica. There has been a sifting of components to suit the conditions that now prevail. Nothofagus is confined to Tasmania and pockets in south-east Australia. The northernmost outpost occurs in the ranges near the Queensland/New South Wales border in the Lamington National Park.

Tall forests is the most critically endangered "species" worldwide. We need to fight to preserve every bit of the ancestral forest that remains. It is a resource beyond price, and Australia's forest remnants are indeed "dinosaur forests" as described by David Bellamy, each an entity that has evolved through 60 million years ... and surely deserving of total protection.

"Tribes' claims create poser" - *Pomaderris apetala* at Musick Point, Auckland

R.O. Gardner

The photograph on p. 29 of a comprehensively-illustrated history of the Howick and Pakuranga districts (La Roche 1991) caught my attention. Rangitoto is in the background, and in the foreground are some bushy plants, not immediately identifiable partly through there being no person or object to give a scale.
The caption states:

> Tainui (Pomaderris apertula [sic]). This shrub or small tree is found naturally only on Musick Point and from Kawhia Harbour to the Mokau River. It is said that stakes of Tainui were used as floor boards in the Tainui canoe when it came from Hawaiiki. While the canoe was at Musick Point some stakes took root and hence this isolated grove today. This is further scientific botanical evidence supporting the well-documneted oral traditional history of the Tainui canoe.

After examining the location map on p. 282 of the book I had thought that these plants might be growing on the cliff edge on the western side of the point, perhaps in native coastal vegetation. But the field-work proved arduous only in prospect; one drives almost to the end of the peninsula, passes across the enormous defensive ditch of the pa site to the former radio station building now owned by Telecom, and there on the last 50 metres or so of the headland, on the very irregularly hollowed and terraced ground, are numerous quite large trees of Pomaderris apetala.

These trees are those shown in the photograph and immediately one notices how this plant can form "groves" by sending up strong new trunks from fallen-down ones. Leaving aside the question of the ultimate ("Hawaiiki") origin of P. apetala (except to say that the Tainui is supposed to have visited the the Hauraki Gulf before going on to Mokau), it cannot be denied that this plant might very well have the ability to resurrect itself from canoe-flooring stakes, and an experiment along these lines would be very interesting. The plant is recorded in Flora N.Z. IV as having naturalized at various places around the country. Presumably this is by seeding, but its ability to clone may also have influenced "naturalized" status.

There are strong reasons to be disinclined to accept that P. apetala here is of ancient Maori origin. The first and to my mind insuperable objection is that neither Kirk nor Cheeseman knew of these plants. The second is that the plants are not found in the scrub of the coastal cliff and its edges, not even at the west end of the defensive ditch -- this damp-bottomed scrubby area, which has some manuka, Pseudopanax lessonii, Pittosporum crassifolium and old hawthorn, might be expected to harbour relictual vegetation. P. apetala occurs in half a dozen or so groves (i.e. pure stands), and the largest individuals are all about the same size, c. 8 m tall, 40 cm basal diameter. Seemingly, they are