Lucy Cranwell Lecture for 2008

THE ORIGIN OF NEW ZEALAND'S FLORA: HOW MUCH DO WE REALLY KNOW?

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Unravelling the history of terrestrial plant and animal life on our island archipelago is a challenging topic that poses more questions than it provides answers. Although I am sure that our explanations will remain that way for well into the foreseeable future, this is a good point in time to pause and contemplate what we know and were we should be going. We live in an age where DNA technology is entering daily life but more than that, it is also providing the raw data on which the history of life can be better understood. As we shall see, DNA is not only a substitute for the lack of fossil information – but a gateway to the future understanding of New Zealand biogeography.

The discipline I am talking about is known as 'historical biogeography', which, in its simplest form, is a branch of science that tries to explain what lives where and why. Today, this discipline comprises three widely separate lines of inquiry: from geology comes the knowledge of plate tectonics and the history of land masses in 'deep time' as well as the findings of palaeontology derived from studies of the fossil record; from biology comes the study of genealogical relationships i.e. biosystematics (taxonomy) and phylogenetic reconstructions (evolutionary trees); and from geography comes location data or distribution maps. In other words, historical biogeography investigates the evolution of organisms in space and time (Knapp 2005). By blending these three lines of evidence together, biogeographers can construct hypotheses to explain where our flora (or fauna) has come from, at what time in history it achieved its present distribution and, maybe, even how it might have got here. On an isolated, mobile and unstable landscape like New Zealand, clearly the timing of changes in climate, sea levels, and topography will all have a huge impact on the evolution of its terrestrial life. It is an exciting subject because it is for ever moving forward with new understanding; its hypotheses are continually subject to confirmation (or denial) whenever new data turns up and, ultimately, all aspects of the jigsaw must fit satisfactorily together to give a meaningful and believable picture of history.

Aucklander, Lucy Cranwell-Smith (1907-2000), as it turns out, was a significant pioneer in this field. She was mentored by none other than Leonard Cockayne in the 1920s and 1930s and employed at the Auckland War Memorial Museum 1929-1944. She enjoyed combining tramping with botanising, and teamed up with Lucy Moore for joint fieldwork in plant ecology. On an Easter trip in 1929, the 'two Lucies' climbed to Te Moehau bog, from where the samples they took sparked Lucy Cranwell's interest in the pollen deposits of peat bogs (RSNZ 2000). Lucy published papers on fossil pollens from New Zealand and Antarctica between 1939 and 1973, paving the way for later palynologists like R. A. Couper, M. McGlone and D. Mildenhall to describe the botanical composition of the flora of New Zealand throughout its history (e.g. Mildenhall 1980). This near-continuous, sequential, pollen record is invaluable for interpreting the history of plant life in New Zealand. It stands in stark contrast to the equivalent animal fossil record (terrestrial animals) which gives only two 'windows' on the past – one in the Miocene period (about 16-19 million years ago (MY)) and another very recently during the Holocene (1-10 thousand years ago) (Tennyson 2010).

Tonight, rather than reviewing the whole subject, I will discuss what I believe to be the main issues and especially the quality of the evidence that we use to draw our conclusions. Are we making good progress? Are we 'nearly there'?

My first approach is to consider the status of the fossil record in New Zealand arising from Lucy's research. Pollen grains are quite exceptional for the quality of the historical evidence they provide. They are found in many kinds of sediments, are essentially indestructible, and in the right places, will survive intact for immense periods of geological time. Their main disadvantage is that they can be windblown, often over great distances, and the deposits can sometimes be reworked by water erosion. The alternative to these microfossils is the discovery of macrofossils – fossils of the actual fragments of the plants themselves. Where they occur, these 'real' plant fossils (leaves, fruits, wood etc) are more informative, particularly in relation to the actual community they lived in, the appearance of the plants, any damage from herbivory or diseases. Unfortunately, plant macrofossils are rare in relation to the pollen deposits. Any fossil amounts to a 'real data point' for historical biogeographic interpretation, just like the 'real' data on distribution maps. Without fossils to pinpoint times and places of occurrence, the interpretation of genetic data for biogeography would be virtually impossible (e.g. Lee et al. 2007).

New Zealand is said to be one of the best places in the world to study historical biogeography. In fact, Dr Gareth Nelson, one of the founders of our modern approach to biogeographic analysis, said 'explain New Zealand and the rest of the world falls into place' (Nelson 1975). The unique endemic biota, its isolation in the SW Pacific Ocean, and the reasonably well known geological history, make it a fertile ground for 'beautiful theories' about the origins of plants and animals (Giribet & Boyer 2010). Yet the enormous time since New Zealand was part of another more ancient landmass (Gondwana) is so great (80 MY) that most of the evidence has been obliterated. Without fossils, as is the case with many plant groups and virtually all animals, we would remain in the dark when we came to unravel their historical story, but for the qualities of the magic DNA molecule. So the second part of my approach is to explain the information that can be gleaned from this molecule, which has a built-in memory of biological events in deep time. If only we could interpret these historical events without ambiguity, we would have our answer to the questions - where did it come from and when. In reality, however, there are limitations to what can be gained from DNA – firstly, it is only accessible from living species (apart from certain vertebrates that have left their ancient bones in caves, sand dunes or swamps); secondly, each gene gives a slightly different evolutionary story, and thirdly, there is the important question of calibration for a molecular clock which is one of the products of DNA analysis (Heads 2005).

Four major issues in New Zealand biogeography today are: 1) What, if any, of the living heritage from continental Gondwana remains with us today? 2) How severe was the impact of the 'Oligocene drowning', which occurred 23 million years ago? 3) What is the balance of *vicariant* (came with the original land) versus *dispersed* (blown/drifted across the ocean) lineages in the New Zealand biota? 4) And finally, can we establish a realistic age for the arrival of each lineage of plants or animals in New Zealand? (Gibbs 2006). One thing I have learnt from my biogeographical studies is that each lineage of organisms is likely to have a different history – one cannot generalise from specific cases, and one can never assume, for instance, that the story told by beech trees is going to be the same as that told by moas. It is here that the great advantage of the DNA molecule lies, because it tells us only about the history of the lineage that we have taken our samples from. Leaving issue 1) aside for the moment, how should we interpret the status of the 'drowning' hypothesis which occurred at the end of the Oligocene period? The basic question is - what is the quality of our evidence?

A geological interpretation which describes inundation by the sea at this time has been around since the 1870s but surfaced again in 2001 (Campbell 2001). The most obvious tangible evidence in favour of submergence comes from the presence of Oligocene limestones in patches all around New Zealand. These rocks were formed under the sea at that time. From a more theoretical angle, there are also 'buoyancy' arguments which relate to the thinness of the continental crustal block that split from Gondwana, implying that it was not thick enough to remain permanently above sea level and hence slowly sank during the 55+ MY after separation. From the point-of-view of terrestrial life, it is the extent of drowning that is all-important. If total drowning occurred, then life was extinguished altogether, in which case every organism here today, from a tuatara to a titoki tree, must have found its way across the sea to colonise New Zealand since the end of the Oligocene. Alternatively, if some forms of life persisted on islands that remained above sea-level during the inundation, then at least some of our pre-Oligocene heritage could still be alive today. If terrestrial life was able to persist through the 'drowning' then, of course, there is the possibility that descendents of Gondwanan survivors still remain. You would think the difference between these two scenarios (total drowning versus partial drowning) would be excruciatingly obvious, even 23 MY later. Yet, until the 'total drowning' hypothesis was resurrected in 2001, our researchers intent upon explaining the history of New Zealand's plant life had not been aware of any natural break in the continuous record of plants living in New Zealand (Mildenhall 1980). Life simply went on uninterrupted. New plant forms arrived and old ones went extinct, but the rates of change seemed no more remarkable during the Oligocene than at other times. Unfortunately the animal fossil record is too sparse to shed any light on this issue. At present, biologists are scrambling for evidence for and against the possibility of total drowning, but are unable to form a consensus. Essentially, this evidence is coming from DNA studies of both plant and animal groups.

In recent years there have been a spate of publications based on molecular studies of New Zealand lineages, many of which claim to shed light on the drowning issue. Their main argument is that if their study organism can be interpreted as having colonised New Zealand sometime after the 23 MY drowning date, then the case is in favour of drowning (Mc Glone 2005, Trewick et al. 2007), whereas if their interpretation finds colonisation is most likely to have occurred well before this, then only partial submergence is supported (Giribet & Boyer 2010). Needless to say, the fossil record is a significant component of these interpretations, since it is used to calibrate the estimates of deep time. Interestingly, to date the prevailing finding for our endemic plant groups has been overwhelmingly in favour of a total drowning scenario (Winkworth et al. 2005). In other words, these studies are confirming that the plant lineages in question did not colonise New Zealand until relatively recently and certainly much later than the 23 MY drowning event. It might have been hoped that the goal would be to examine a balanced sample of different lineages but, unfortunately, most of the studies seem to have focussed on the montane and alpine flora; a habitat that is only about 5-10 MY old and hence ripe for the establishment of new plant groups (e.g. *Veronica* (*Hebe*), *Abrotanella, Gnaphaliae, Myosotis, Ourisia, Ranunculus, Scleranthus*). *Dracophyllum* is an interesting case because the fossil pollen record indicates that it, or a near-relative, occurred in New Zealand in the Eocene period (40-50 MY) (Mildenhall. 1980), yet molecular analysis implies colonisation of the present stock from Australia during the Pliocene (7-8 MY) (Wagstaff pers. comm.).

The *Dracophyllum* case is not exceptional. Southern beech (*Nothofagus*) has always been regarded as an icon of Gondwana and the tectonic break-up of the southern continents. It has the fossil record to back it up. Fossil beech pollen is so abundant and widespread in the southern lands of Australia, New Zealand and South America that we can be confident, from the absence of pollen on the African continent that it never occurred there. This excellent pollen record also tells us that southern beech is well past its prime today, with many more extinct species than extant ones. This genus is known from New Zealand pollen and leaf fossils as far back as 65 MY. Yet a recent molecular study (Knapp et al 2005) has concluded that the present types of *Nothofagus* living in New Zealand have colonised from Australia at about the time of the 'drowning'. The same conclusion can be reached from conventional phylogenetic analyses based on structural plant attributes, without recourse to molecules. The point here is that this conclusion flies in the face of what had previously been conventional wisdom about *Nothofagus* ecology, namely that it was very slow to spread and an 'impossible' candidate for dispersal across an ocean (Swenson & Hill 2001) Which do you believe … the prejudice that leads to a vicariant explanation? Or the analysis that provides a dispersal explanation? Hence the title of this talk.

This is a good point to introduce some animal examples into the discussion. I will first mention a parallel case to *Nothofagus*, namely that of the gigantic ratite birds (or more strictly 'palaeognaths'), another group of classic Gondwanan significance. Conventional wisdom has always had it that these flightless birds must have walked to their present destinations on separate southern continents – ostriches to Africa, elephant bird to Madagascar, emu and cassowary to Australia, moa and kiwi to New Zealand and rhea to South America (Fleming 1979). There has been intense interest in resolving a satisfactory phylogeny. Until very recently, all efforts, based on both structural and molecular characters, to achieve this end had placed a group of small flying South American palaeognaths (tinamous) in the position of outgroup, with the large flightless birds considered as a monophyletic group – hence implying that flight had been lost once in a common ancestor and never regained. If this event occurred prior to the Gondwana break-up then, the argument goes, they must have walked. But now, with a very comprehensive genetic data base, recent analyses are indicating that perhaps tinamous are not a basal outgroup to the flightless ratites and that flight loss might have occurred a number of times in the history of these birds (Harshman et al. 2008, Phillips et al. 2010). These authors are suggesting that such an interpretation opens the way for a fresh approach to ratite evolution in which the birds could have flown to their present destinations across the ocean and then lost their wings. They also cite a famous phrase of Thomas Huxley: "*the great tragedy of science – the slaying of a beautiful theory by an ugly fact*" Again I must ask, how much do we really know?

As an invertebrate biologist, I am unable to proceed without giving the 'small creatures that rule the world' a chance to offer their evidence to this debate. I have combed the literature for examples of phylogenetic studies that treat certain New Zealand taxa, in the same way as the plant studies referred to above. When viewed collectively, the majority of these studies indicate that colonisation of New Zealand occurred very much earlier than the plant examples cited, i.e. well prior to the Oligocene 'drowning'. That is, our invertebrates seem to be generally older than our plants. Many are insects, including the large wetas (Pratt et al. 2008), jaw-moths, mayflies, kauri weevils, also peripatus (Allwood et al. 2009), koura (freshwater crayfish) (Crandall et al. 1999), centipedes and harvestmen (Giribet & Boyer 2010) as well as flax snails and paryphantid snails. Other examples, like the plant cases above, indicate much more recent arrival times as in cicadas (Arensburger et al. 2004), ghost moths (Brown et al. 1999), katipo spiders (Griffiths et al. 2005), wolf spiders (Vink & Paterson, 2003) and a freshwater shrimp (Page et al. 2005). My own research, which has taken me to all the southern continents, is targeted towards some tiny but highly significant little moths called jaw-moths (Micropterigidae). They are ideal candidates for biogeographic research because they represent the most archaic of all Lepidoptera (moths and butterflies) with beautiful fossils from Jurassic amber (140 MY) and they are distributed on all the world's continental land masses. As for most Lepidoptera, they are herbivores, but in this case rely on liverworts, ferns, and other pre-angiosperm plants for their food. From a world phylogeny, that is being compiled by my colleague David Lees, using molecular data, we can estimate that the deep basal splits of lineages within the family probably occurred during the existence of the Pangean and Gondwanan super-continental land masses (i.e. prior to 120 MY) and that so far as New Zealand's fauna is concerned, their lineages began well before the opening of the Tasman Sea. Thus, until this study is superseded by a more comprehensive ratite-type study, our data indicate moth lineages that are considerably older than the land they live on. They are most unlikely to have dispersed to New Zealand across the ocean after the 'drowning'. As an aside, it is interesting to note that the majority of New Caledonian moths in this family (and their biodiversity there is higher than anywhere in the world) are derived directly from New Zealand and in fact represent New Zealand forms that happen to survive on an island that was once part of the former continental Zealandia, prior to its 'drowning'.

My final case studies are freshwater invertebrates that are confined to cool freshwater streams and rivers. These small, ancient forms of insect and crustacean life show a remarkable affinity between Chile, New Zealand and eastern Australia. Although not many taxa have been thoroughly analysed at this time, collectively they represent a whole community that would have great difficulty dispersing across the ocean to reach their present destinations after the drowning of New Zealand. None are tolerant of marine conditions, most have short-lived, very weakly-flying adults. Their close relationships which exist only between these three southern continental areas can best be explained in terms of a common sharing of freshwater habitats when the now-separate continents were joined through Antarctica. The tectonic break-up of these isolated lands occurred between 80 MY (for New Zealand) and about 35 MY (for Australia and South America). Throughout these times, Antarctica linked the three lands and was clothed in cool temperate forests, dominated by *Nothofagus*. Ice began to accumulate over Antarctica about 14 MY ago.

To return to the four issues posed earlier, it should be evident that none have clear answers. In all cases, we can marshal the published evidence in defence of a variety of viewpoints, often diametrically opposed to one another. For the question of what, if anything, of the original Gondwanan flora and fauna remains here today, we can say that overall the answer is probably very few plants, but quite a lot of animals, including a number of small invertebrates, and especially those living in moist habitats or running fresh waters. A landmark study some years ago came to this same conclusion, based on a survey of all relevant southern hemisphere phylogenetic research at the time (Sanmartin & Ronquist 2004). Plants are biogeographically more mobile than animals, with their microscopic spores and seeds, and often requiring only a single individual for establishment, compared with the chance of getting multiple individuals of both sexes of adults to establish a new animal population. The theme of the Oligocene drowning arises in many publications, but they offer no unambiguous conclusions. The outcome depends largely upon which lineage is being researched. Likewise, the question of vicariance or dispersal can be extremely difficult to resolve. 'Total drowning' proponents must be prepared to falsify all examples of implied vicariance because dispersal is the default position and each well-substantiated example of vicariance can be regarded as a nail in the coffin of the total drowning hypothesis. Finally, examples which propose an age for individual lineages in this country are steadily increasing in number but how much credence can we place on such estimates at this stage?

What can be stated is that New Zealand is not an ark full of Gondwanan relics. Nor is it a subset of Australian life, which it might be if all our biota had established since a postulated drowning event. We desperately need more well-researched examples to fill the gaps in our understanding. We also need to reject stories that rely on 'absence of evidence' and, above all we must learn to carry our hypotheses lightly. Who knows which of the 'beautiful theories' we accept today will still be acceptable in 50 years time!

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Botanical excursion to Sydney, New South Wales, Australia

Mike Wilcox, Christine Major and Maureen Young

Summary

A group of 15 Auckland Botanical Society members spent nine days from 4-13 September 2009 exploring the plants of the Sydney region. It was spring, and flowering was abundant. The places visited were the Cronulla coast, Kamay Botany Bay National Park at Kurnell, Royal National Park from Bundeena and Waterfall, the Blue Mountains (Katoomba, Wentworth Falls, Blackheath, Mt Banks, Mt Wilson, Mt Tomah Botanic Gardens), Royal Sydney Botanic Gardens and NSW National Herbarium, and Berowra Valley Regional Park. The visit gave us a good appreciation and introduction to the Australian flora and the great importance there of the families Myrtaceae, Proteaceae, Fabaceae, Ericaceae, Rutaceae and Casuarinaceae – all well represented and ubiquitous on our field trips. Orchids and ferns were other groups to particularly grab our attention. Every place visited had some new plants for us to discover and enjoy. Vegetation types we studied were coastal dunes, cliffs and heaths; mangroves; dry sclerophyll forests; wet sclerophyll forests; cool-temperate rainforest; and various kinds of open heathlands and cliff communities, including hanging swamps. We were predominantly on the Triassic Narrabeen and Hawkesbury Sandstone formations. The weather was pleasantly fine and warm in Sydney (22-30°C) and cool and sometimes breezy in the Blue Mountains (3°C in the morning, 14-16 °C in the day).

Programme

As far as we know the Auckland Botanical Society has not previously had a group trip to Australia. We all found it a most rewarding experience, and saw a wonderful array of plants and spectacular scenery in one of Australia's best and most convenient places to study the native flora. Our group was *Jan Butcher*, *Colleen Crampton*, *Barrie McLeay*, *Gretta McLeay*, *Anne Fraser*, *Leslie Haines*, *Christine Major*, *Helen Preston Jones*, *Juliet Richmond*, *Doug Sheppherd*, *Alison Wesley*, *Diana Whimp*, *Mike Wilcox* (leader), *Nancy Wilcox*, *Maureen Young*. We stayed in youth hostels, and got around by bus, ferry, train or hired minibuses.

Thursday 3 September: Travel to Sydney.

Friday 4 September: On foot along the foreshore at Cronulla, looking at coastal cliff plants. By bus from Cronulla to Kurnell. Visited the Kamay Botany Bay National Park via Yena Track, Banks & Solander Track and Muru Track. Accommodation at Cronulla Beach Youth Hostel.

Saturday 5 September: By ferry from Cronulla to Bundeena, and then on foot to Jibbon Beach, Port Hacking Point, and a coastal walk in Royal National Park (Fig. 1), returning to Bundeena. Accommodation at Cronulla Beach Youth Hostel.