

# GEOLOGY AND GENES III



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**Geological Society of New Zealand  
Allan Wilson Centre for Molecular Ecology and Evolution**

## **Geology and genes III**

**Extended abstracts for papers presented at the  
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**Editors**

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Cover images, clockwise from top

Mt Ruapehu erupting in July 1996, from Ohakune.,

Bat tooth from the St Bathans Fauna (19-16Ma)

The 44's, part of the Chatham archipelago,

South Island alpine flower *Ourisia caespitose*,

Moraine divide between Von (left) and Oreti (right) Rivers, breached by a channel that allowed migration of galaxiids until 12000 years ago.

Male *Geodorcus sororum*, an island endemic from The Sisters, Chatham Islands.

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Organisers: Steve Trewick, Matt Phillips, Roger Cooper.

## INTRODUCTION

This volume contains the extended abstracts of papers presented at Geology and Genes III, a conference jointly sponsored by the Geological Society of New Zealand and the Allan Wilson Centre for Molecular Ecology and Evolution. This, the third in what we can now safely identify as a series of occasional meetings continues the theme of previous conferences in 1994 and 1998. The first had the more specific theme, Geological history, changing shorelines and the origin of the New Zealand biota and was held under the aegis of the Systematics Association of New Zealand (SYSTANZ) on November 25<sup>th</sup> 1994. The second, titled simply Geology and Genes was jointly sponsored by the Geological Society of New Zealand and SYSTANZ, and held on March 24<sup>th</sup> 1998.

The primary purpose of these meetings has been to bring together biologists and geologists so they can exchange knowledge and opinion in their respective areas of expertise in order that our mutual understanding of the origin and development of the New Zealand biota might be improved. In the first meeting a key question related to the extent and nature of past shorelines (especially those of Oligocene New Zealand), and how changes in the area and distribution of land might have influence biological evolution.

The second Geology and Genes meeting included papers that continued the debate about the age and origins of the New Zealand biota. It also provided a forum for a molecular, geological and biogeography papers relating to a broad range of taxa and a wide temporal scale. This trend towards diversification of topics continues in Geology and Genes III with papers appraising the history and current status of New Zealand biogeographic thought, the application of emerging theory and analytical techniques to ever larger data sets, and a wide array of geological processes and fossil discoveries. Perhaps most encouraging is the fact that the conference includes research from teams of geologists and biologists working together to examine biotic evolution in the New Zealand landscape. Several of these collaborations are the direct products of previous meetings in this series.



**New Zealand's extinct raptors: legendary and imaginary.**

Michael Bunce, *Ancient DNA Laboratory, School of Biological Sciences and Biotechnology, Murdoch University, Western Australia.*

In the 700 years since human occupation over a hundred of New Zealand's native bird species became extinct. Among these extinction events are three raptor species: *Harpagornis moorei* (the Haast's eagle), *Haliaeetus australis* (the Chatham Island eagle) and *Circus eylesi* (Eyles's harrier). Using ancient mitochondrial DNA extracted from fossil bones we have investigated the evolutionary history of these three species. The data shows that one species never existed and is a taxonomic "blunder", another has a predictable recent ancestor and the third has increased in size by 10-15 times in only a short evolutionary timeframe. This spectacular evolutionary change illustrates the potential speed of size alteration within lineages of vertebrates and represents yet another example of the remarkable evolutionary processes that occur within island ecosystems.



The Haast's eagle attacking a moa. With an estimated wingspan up to 3m and a mass of 10-14kg the Haast's eagle was the top predator in New Zealand's pre-human ecosystem. DNA extracted from the bones of this extinct eagle shows it was closely related to one of the worlds smallest eagles (Australia's "Little Eagle"). Artwork courtesy of John Megahan.

### Vicariance and molecular clocks: a test of inter-drainage fish transfer via river capture

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River capture is a geomorphological process through which stream sections are displaced from one catchment to another, and it may represent a dominant facilitator of inter-drainage transfer and cladogenesis in freshwater-limited taxa. However, few studies have been conducted in a manner to explicitly test the biological significance of river capture. Reconstruction of phylogenetic relationships can shed light on the history of both drainages and their associated freshwater biota. If river capture is responsible for the distribution of a freshwater-limited taxon, we expect to see genetic relationships reflective of historical rather than contemporary catchment boundaries. While several genetic studies have inferred a role of river capture in the distribution of freshwater-limited taxa, many were conducted without knowledge of river capture *a priori*, and hence had no expectation that the process might have been influential. Alternatively, if knowledge of river capture existed *a priori*, only a single taxon was surveyed. Consequently, the broader biogeographic significance of river capture is unknown. Multi-species phylogeographic studies are needed in regions where river capture is known to have occurred *a priori*, based on independent geological or biogeographic evidence.

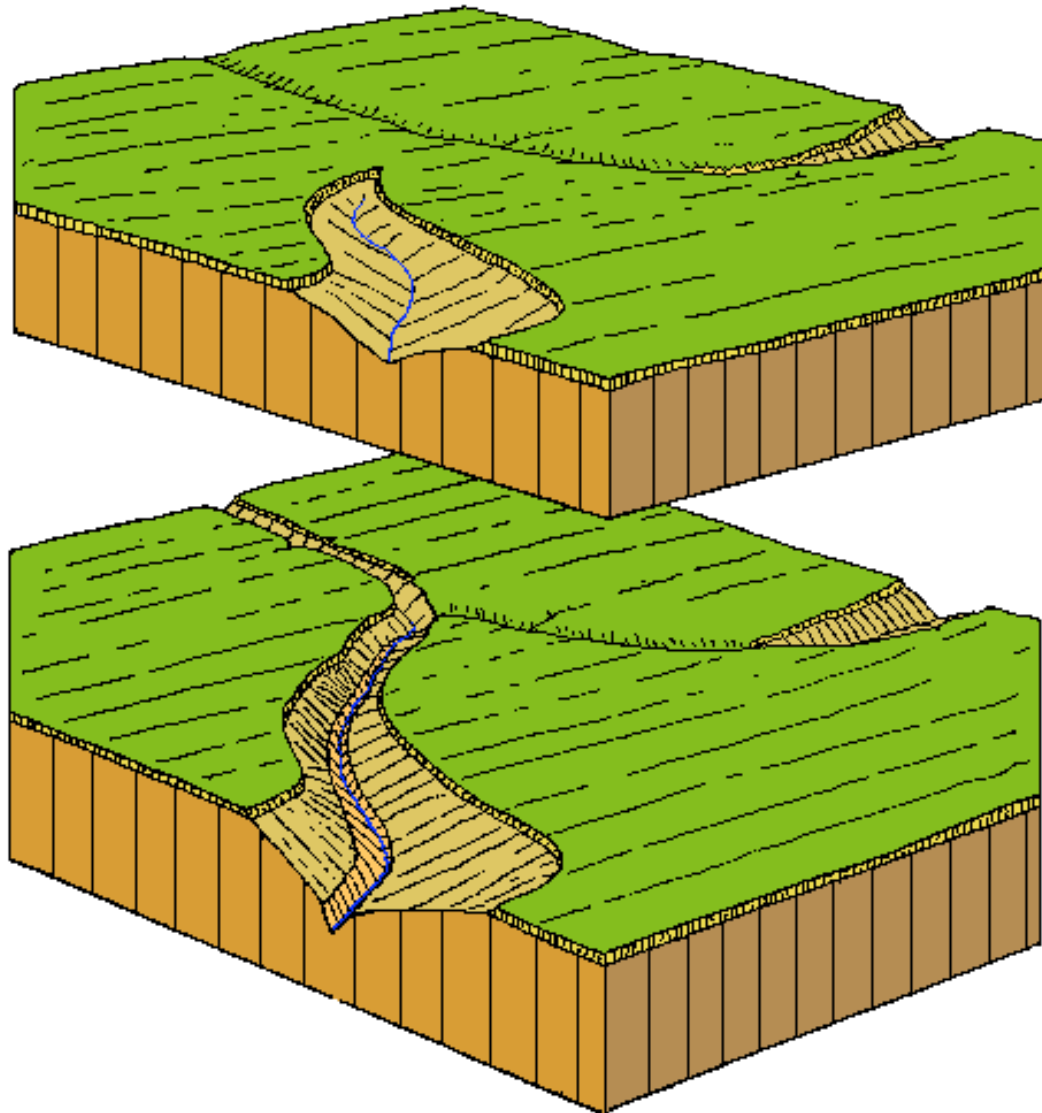
Here we present a multi-species phylogeographic analysis to test whether the non-migratory fish fauna of the Von River (South Island, New Zealand) is the product of a well-documented Late Quaternary river capture event, that isolated this river from the Oreti (Southland) and linked it to the Clutha. The divide between the Von and Oreti rivers has been low for all the Quaternary, and ice moved southwards into the Von valley during Quaternary glaciations of the Wakatipu basin. River terrace profiles and moraine erosion indicate that the Von River flowed south into the Oreti during the South Von (>130 ka BP) and White Burn (ca. 60–70 ka BP) glacial advances, but that northward drainage into the Clutha River system was restored subsequently in each case. Carbon dates obtained from terrace-embedded organic matter place the most recent restoration of northward drainage at 11–13 ka BP.

MtDNA phylogeography (control region and cytochrome *b* DNA sequence data) and analysis of nuclear orthologues of mtDNA sequences indicate that ‘flathead’ *Galaxias* of the Von River (n=31, three sites) have greatest genetic affinities with those of Southland (*G. ‘southern’*, n=142, 27 sites)—and the Oreti River in particular—rather than with those of the Clutha River (*G. sp. ‘D’*, n=73, 32 sites), into which the Von presently drains. Likewise, ‘roundhead’ *Galaxias* of the Von (n=52, four sites) have greatest genetic affinities with those of Southland drainages (*G. gollumoides*, n=223, 58 sites), rather than with those of the Clutha River (*G. pullus*, *G. anomalus*, *G. gollumoides* of the Nevis tributary; n=68, 32 sites). Consequently, river capture is responsible for the only non-migratory fish lineages presently known from the Von River.

Calibrations of a molecular clock against the age of this recent (11–13 ka BP) river capture event returns divergence rates of 8–27% sequence divergence per million years. These rates are faster than most estimates previously derived for fishes (0.5–1.7% Ma<sup>-1</sup>), but are consistent with the new ‘time dependency of molecular rates’ hypothesis. Under this hypothesis, faster rates of molecular evolution are observed for molecular clocks calibrated



against recent ( $<1$  Ma BP) rather than older events. Most fish clocks calibrated to date fall into the latter category, derived from events occurring over 3 Ma BP.



**River capture.**

### On the turn of a scallop

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The Chatham Islands represent the isolated eastern-most exposure of the New Zealand continent, Zealandia. They lie at the eastern end of the Chatham Rise, a relict edge of eastern-most Gondwanaland. The oldest rocks include basement Paleozoic-Mesozoic Chatham Schist and terrestrial Cretaceous sediments and volcanics. These are overlain by a well-developed marine sequence of latest Cretaceous to Paleogene age. The Neogene record is scant but is also marine. So, for much of Cenozoic time, the Chatham Islands area has been more or less submarine. But could it have been totally submarine? And if so, when exactly? Answers to these questions have fascinating biological implications.

On February 1 2004, we embarked on a three-year Marsden Fund project involving geologists and biologists at GNS, Massey University and Lincoln University, three private contractors, three research students, and several research associates. On the basis of compelling evidence, we started with the premise that the islands were completely submerged until about four million years. To our amazement and delight, we now have hard evidence for emergence less than one million years ago.

Early in 2005, we made a surprising discovery, thanks to Chatham Island farmer Robert Holmes: a new limestone formation near The Horns at the SW corner of Chatham Island. It is fossil-bearing with conspicuous *Pecten novaezelandiae*, the modern species of scallop, which has a known age range in the New Zealand region of about one million years. Early this year, 2006, we mapped the extent of the limestone over several kilometres. It is well above sea level with the highest record of fossils at 205 m.

To our astonishment, the limestone is in turn overlain by another previously unrecognised formation comprising about 100 metres of volcanic rocks: lava flows and palagonitic volcanic ash. This formation effectively forms the highest land surface on Chatham Island, and the highest point in the Chathams as a whole at just under 300 metres a.s.l. We have no doubt about the relationship of these remarkably young volcanic rocks to the underlying limestone formation, or the interpretation of their eruption submarine.

Our observations confirm regional uplift of the eastern end of the Chatham Rise within the last one million years. As yet we do not understand the underlying cause of uplift, but one or more of at least three crustal processes must be at work: volcanism, mantle plume inflation, tectonism. These are testable as they operate at different scales, but will involve geophysical analysis that is beyond the scope of our immediate project.

We are now able to calculate rates of uplift and have been able to establish that there is apparent differential uplift, with highest rates in southern Chatham, significantly lower rates in northern Chatham, and minimum rates in central Chatham. Accordingly, we can now offer a geological explanation for the shape of Chatham Island. By extrapolation of flat surfaces developed in the Pitt Island landscape, as well as the Mangeres, Southeast, the Forty Fours and the Sisters, we are confident that the entire Chatham Islands area has been affected. Variation in rates of uplift is secondary to a regional warping effect.

### **Investigating the potential of LENZ in evolutionary studies on the New Zealand alpine flora**

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In high-elevation areas of New Zealand, many genera have radiated to produce ecologically and morphologically distinct yet genetically similar species. Currently, the relative extent to which geological history, ecological factors, and genetic factors have each contributed to the patterns of diversification is largely unknown. The recent development of the Land Environment New Zealand (LENZ) system (Manaaki Whenua - Landcare Research) provides an exciting new tool for analyses of spatial and environmental data. The potential of this tool is that it provides an objective framework for developing hypotheses and understanding of plant distributions and habitats. When integrated with studies of DNA sequence variation, there is the promise of helping to achieve an unprecedented level of understanding of species radiation.

Predictive modelling of species distributions generally involves combining known localities from collection records with environmental data to produce an environmental envelope for a species, which is then used to extrapolate to other areas with similar environmental parameters. The resulting species distribution model may then be used and statistically compared to study factors potentially important in its distribution and evolutionary history. Predictive modelling has been greatly facilitated by Geographic Information Systems (GIS) techniques, which allow incorporation of spatial data with digitised maps of environmental variables that commonly structure a species macro-distribution. In New Zealand, the recently developed LENZ GIS system has been used to relate environmental variables to current and past distributions of New Zealand lowland flora. In LENZ, the landscape is divided into areas of similar environmental conditions based on a measure of environmental distance that is calculated from digitised maps of climatic and physical variables.

Here we report observations on the potential of LENZ for modelling the complex alpine environment. We use the models developed to address evolutionary questions concerning range expansion of alpine flora in the North and South Islands of New Zealand. The aims of our study have been to: 1) compare two GIS approaches (methods A and B) using LENZ to model NZ alpine plant distributions for accuracy (method A vs. method B; collections-based locality data vs. precise GPS locality data); and 2) use resulting environmental envelope data to address evolutionary questions in two case studies for which we have geographic and molecular data, *Ranunculus* (Ranunculaceae) and *Ourisia* (Plantaginaceae).

We developed two approaches to create predictive models for species distributions. Method A estimates a species environmental envelope based on LENZ environmental divisions, whereas method B (modified from Rutledge *et al.* 2004) extrapolates the environmental envelope from the underlying LENZ environmental data. We expected method B to predict a less accurate species distribution than method A, because with method A, only areas with an identical

classification to the known localities were included in the model, whereas in method B, areas with similar classification were also included. We also predicted that the models developed using precise GPS locality data would be more accurate than the models based on the less-precise collections-based data.

We implemented the above methods for species of *Ranunculus* (*R. insignis*, *R. nivicola* and *R. verticillatus*) and two species of *Ourisia* (*O. caespitosa* and *O. sessilifolia*). We found that, for alpine *Ranunculus* and *Ourisia*, the predicted model using method A closely matched the known distribution, and as expected method B showed greater range of habitats. Interestingly, there were no large differences in predictive models based on data of varying precision.

*Ranunculus*: Phylogenetic analyses of New Zealand alpine *Ranunculus* have suggested that this genus initially radiated into alpine habitats during the late Tertiary in the South Island of New Zealand (Lockhart *et al.* 2001; Carter *et al.* unpublished). Subsequently, two species from different breeding groups (*R. insignis* and *R. verticillatus*; Fisher 1965) expanded their ranges into the North Island of New Zealand, where a third (allopolyploid) species, *R. nivicola*, is also found. An explicit evolutionary model (McBreen and Lockhart 2006) built for New Zealand alpine *Ranunculus* contains a reticulation involving *R. nivicola* that indicates *R. nivicola* is a likely allopolyploid hybrid formed between *R. insignis*- and *R. verticillatus*-like ancestors. Using LENZ we have sought to address the question of whether *R. nivicola* extends the geographic range of alpine *Ranunculus* in the North Island into areas that would not be otherwise occupied by the putative parental species. Using data from methods A and B, we found that there are fine-scale ecological differences between these three species, however the environmental parameters studied here do not explain observed differences in distribution between *R. nivicola* and *R. insignis*.

*Ourisia*: Phylogenetic analyses of *Ourisia* have shown that the New Zealand species are a monophyletic group derived from a South American ancestor that subsequently radiated within New Zealand (Meudt & Simpson 2006; Meudt *et al.* unpublished). The twelve New Zealand species vary in geographic space (from sympatric to allopatric) and occur in a range of habitats and elevations (Meudt 2006). Using LENZ, we address the question of whether these environmental differences may have played a role in shaping species diversity within *Ourisia* by comparing species envelopes to one another, paying particular attention to sister pairs. For example, preliminary results from a pair of closely related species, *Ourisia caespitosa* and *O. sessilifolia*, which have largely sympatric ranges in the South and Stewart Islands and can occur in the same habitat, show that there is little difference in their potential distributions, but further statistical evaluation is necessary. We are currently expanding our study to include all species of New Zealand *Ourisia*.

In conclusion, we found that LENZ enabled us to devise an environmental envelope that was capable of distinguishing *R. verticillatus* from *R. insignis* and *R. nivicola*. Further exploration of the environmental data is necessary to determine whether we will be able to differentiate between habitats of *R. insignis* and *R. nivicola*, and between *O. caespitosa* and *O. sessilifolia*. The inclusion into the LENZ database of additional biotic and abiotic variables, as well as more data points from alpine areas, will be important in this endeavour.

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**The time dependency of evolutionary rates and issues with  
dating recent evolutionary events.**

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Recent work has indicated that molecular evolutionary rates appear to exhibit time dependency, in that rate estimates vary according to the time period across which they are measured. This is most noticeable in short-term measurements, such as the use of a molecular clock to estimate the timing of recent evolutionary events, and generally leads to a considerable over-estimate of divergence times. The estimated rates appear to follow a negative exponential curve, with the most rapid estimates resulting from short-term measurements within families, or populations and the slowest from fossil calibrations. The key issue appears to be the essential difference between rate estimates below the species level (which are primarily measuring polymorphism within populations) and the much slower rate recorded above the species level (generally calculated with a fossil date) which measure the mutation rate. The latter is the small proportion of polymorphisms that get actually fixed in a species lineage (by drift, or selective processes) over time.

When fossil-calibrated species rates are used to examine evolutionary events within the past 1-2 Ma, the result will generally be a considerable over-estimate of divergence times, while the opposite is likely to be true for coalescent calculations. We have determined a mathematical equation to explain this relationship using only simple parameters and standard population genetics theory for neutrally evolving sites. The theoretical data matches empirical studies surprisingly well, and indicates that it may be possible in many circumstances to estimate the contribution of polymorphism to genetic divergences, and therefore to obtain more accurate dating estimates. We apply this calculation to a number of key evolutionary events and observe major changes in date estimates. This process is likely to be important in New Zealand evolutionary studies given the major role of environmental changes during the Pleistocene.

**Equilibrium marine diversity dynamics in New Zealand  
Cenozoic shallow marine molluscs**

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In recent years several authors have questioned the reality of a widely accepted and apparently large increase in global marine biodiversity through the Cenozoic. This apparent increase has been variously explained by exponential, logistic and hyperbolic growth models. Here we use the rich and uniquely well documented shelfal marine mollusc fauna from New Zealand (NZ) to test this question at a regional scale. Because the NZ data were generated by a small number of workers and have been databased over many decades, we have been able to either avoid or quantify many of the biases inherent in analyses of past biodiversity. In particular, our major conclusions are robust to several potential collection, taphonomic and systematic biases and methodological uncertainties, namely non-uniform sampling through time, non-uniform loss of aragonitic faunas, biostratigraphic range errors, taxonomic errors, choice of time bins, choice of analytical protocols, and taxonomic rank of analysis.

The number of taxa sampled increases through the Cenozoic; this is the “raw” diversity pattern (Fig. 1). Once diversity estimates are standardized for sampling biases, however, we see no evidence for an increase in mollusc diversity in the NZ region through the mid- to late Cenozoic (Fig. 1). Instead, diversity has been approximately constant for much of the past 40 Myr and, at the species- and genus-levels, has declined over the past ~5 Myr. This suggests that total diversity on the isolated NZ continent was in dynamic equilibrium for much of the Cenozoic. Assuming that this result is representative of other taxonomic groups and other temperate faunal provinces, then it suggests that the postulated global increase in diversity is either:

1. an artefact of sampling bias or analytical methods;
2. resulted from increasing provinciality;
3. or was driven by very large increases in diversity in tropical regions.

Using existing data, it is not possible to say which of these possibilities is most likely to be correct. Recent global-level analyses are in conflict and support both explanations 1 and 3; in the latter case, there is some evidence for a dramatic increase in the latitudinal diversity gradient through time related to an increase in absolute and relative tropical diversity.

From the NZ data, we see no evidence for a species-area effect on diversity. Likewise, we are unable to demonstrate a relationship between marine temperature and diversity, although this question should be re-examined once refined shallow marine temperature estimates become available.



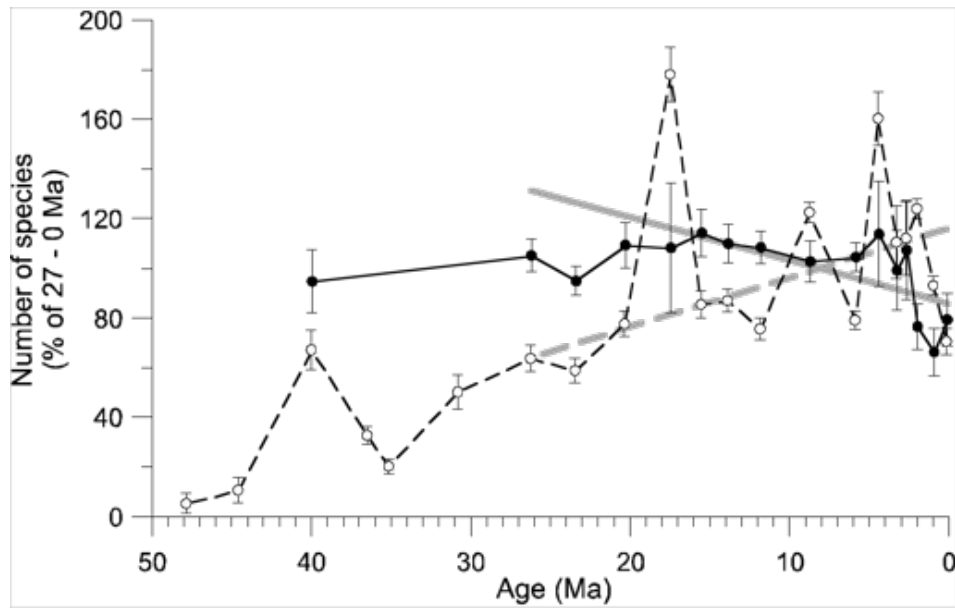


Figure 1) Raw (dashed black line) and sampling-standardized (solid black line) marine mollusc diversity curves for New Zealand for the past 50 million years. General trends in post-Early Oligocene data are shown by robust linear regressions (thick grey lines).

### Coevolution of landscape and galaxiid fish, Southland, New Zealand

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Southland is drained by four main rivers, Mataura, Oreti, Aparima and Waiau, with broad gravel valleys associated with each. The rivers discharge from high mountain hinterlands that were heavily glaciated during the Quaternary. The Mataura, Oreti and Aparima were interconnected at various times during the late Quaternary, and constitute a broad braid plain formed by coalescence of alluvial fans (Table 1). Further connections between these three rivers occurred at times of lowered sea level, when the rivers merged into an east-draining gravel plain that is now submerged beneath Foveaux Strait (Table 1). Native non-migratory galaxiid fish occur sporadically in the catchments of the coalesced Mataura, Oreti and Aparima plains. There has been widespread genetic homogenisation of these fish populations over the plains, with <0.9% mtDNA divergence. The various river interconnections that accompanied the evolution of the Southland plains both onshore and beyond the current shoreline (Table 1), has facilitated the genetic homogenisation through the Late Quaternary.

In contrast, the Waiau River follows a separate course farther west, and discharges towards the offshore Solander Trough to the west of Foveaux Strait. The Waiau River is separated from the Southland plains by mountains such as the Takitimu and Longwood Ranges that have been uplifted along the Moonlight Fault. galaxiid fish in the Waiau catchment are morphologically similar to those of the Southland plains, but are genetically distinct. There is a minimum mtDNA divergence of 2.4% between Waiau fish and the fish in the Mataura, Oreti, and Aparima Rivers.

*Table 1. Summary of river connections (shaded) between Oreti catchment and other Southland rivers, and age estimates of those connections based on terrace dating and correlations (partly after Turnbull 2000 and Turnbull & Allibone 2003). X = no connection; ? = unknown. \* = date from tephra (McIntosh et al. 1990).*

Oxygen Isotope Stage	Dated terrace	Connections for fish migration from Oreti River to:			
		Waiau R	Aparima R	Mataura R	Von R
Stage 1 (<12 ka)		X	via Foveaux plain (now submerged)		X
Stage 2 (12-24 ka)	11-13 ka	X			via Southland Plains (coalesced alluvial plains)
Stage 4 (59-71 ka)		X			
Stage 6 (128-186 ka)	145 ka	X			
Stage 6-8?		via gravel divide to Mararoa River	?		
Stage 8 (245-303 ka)	240 ka*		?		
Stage 10 (>340 ka)			?		

The lowest divide between the Waiau catchment and the Oreti catchment (the westernmost of the tributaries to the main Southland Plains) is a narrow bedrock ridge that links the mountain hinterland with the Takitimu Range. This bedrock ridge has been overtopped by glacial outwash at various times during the Quaternary, coinciding with major glacial advances, allowing wet connections between Mararoa River (Waiau catchment) and Oreti River (Table 1). The last time this low ridge was overtopped was about 145-240 ka, based on regional correlation of river terraces and a new OSL date (Table 1). The divide is formed in two places by gravel terraces of this age range. Since that last overtopping and formation of wet connections between the two catchments, the catchments have remained separated.

Populations of galaxiid fish that are genetically similar to those of the Southland Plains also occur in the Von River, a tributary of the Clutha catchment, to the north of the Oreti catchment. This is the only population of these fish in the Clutha catchment (apart from the Nevis valley; see below) that contains a wide variety of other genetically diverse galaxiids. The fish in the Von catchment have <0.1% mtDNA divergence from galaxiids in the nearby Oreti catchment, suggesting that separation of the galaxiid populations occurred relatively recently (possibly Holocene) compared to the Waiau separation.

The drainage divide between the Von and Oreti catchments was formed by a moraine ridge that was deposited 130-190 ka. At that time, the water flowed south from the Von (Clutha) catchment towards the Oreti catchment, although this drainage reversed when the ice retreated. A later glacial advance (60-70 ka) again caused water to flow from the Von to Oreti catchment, breaching the moraine divide. This breach persisted as a wet connection between the catchments until about 11 ka (based on new carbon dates; Table 1) when northward drainage resumed in the Von to the Clutha. The streams at the divide are now incised sufficiently that no wet connections can occur, even in times of flood. The timing of the severance of the wet connection between the Von and Oreti is consistent with that predicted by the genetic differences between the galaxiid populations.

Long-term wet connections may occur between catchments in Southland via swampy land on low divides between the above-described river systems. These swamps can drain in both directions, allowing fish to migrate through the swamp complex. This pathway is only relevant to fish that seek this type of habitat, such as *Galaxias gollumoides*. A *G. gollumoides* population in the Nevis valley (Clutha catchment) has also been separated from Southland (Mataura River) populations by tectonically-driven river capture (Waters et al. 2001). This process is slower than the climate-driven processes described above, and occurred between 300 and 500 ka.

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**Goodbye Gondwana, Hello Australis: a fresh look at the vicariance/dispersal debate**

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It has recently become fashionable to refute the ‘classic’ Gondwanan heritage hypothesis when considering the history of New Zealand’s modern fauna and flora. A spate of publications on molecular phylogenetic research has drawn attention to the dispersability of plants to the point where even the ‘impossibility’ of *Nothofagus* dispersal has been disputed. If nothing else, these studies show that we can easily be fooled into believing that we can predict the dispersability of organisms from their biological attributes. As we enter a new surge of interest in southern hemisphere molecular phylogenetic research, we need to take stock of the big picture. How good is the vicariance evidence? What was the role of the ‘Oligocene drowning? Is the *entire* New Zealand flora an example of trans-oceanic dispersal? What about the animal examples, and how about the silent majority, those ‘insignificant’ invertebrates that comprise 80% of our biodiversity? The argument for land-based inheritance of parts of our biota is not dead yet. Our present level of understanding will be reviewed and a case made for the launch of a new supercontinent, ‘Australis’ to explain New Zealand’s biological heritage.

**Neogene paleogeography of central North Island: evidence for a southward migrating  
and persistent Miocene-Pliocene seaway across the island  
until about 1-2 Ma**

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We are undertaking a programme of basin analysis across Wanganui, eastern Taranaki, King Country, and central Hawke's Bay regions, mainly to improve understanding of the depositional architecture and tectonic development of basins to assist efforts in petroleum exploration. These regions are dominated by extensive late Paleogene and Neogene marine sedimentary successions, which are exposed in the landscape and moderately accessible to field investigations. Our work has involved re-evaluation of stratigraphy, geological mapping at 1:50,000 scale, development of biostratigraphy and chronostratigraphy, and detailed facies analysis and sequence stratigraphy of units to get a better idea of the linked depositional systems through time and the overall pattern of basin infilling. As our resources allow, we have been linking the exposed stratigraphy to subcrop occurrences of related beds, mainly in Taranaki Basin, through the use of open-file exploration data acquired by the petroleum industry. In many respects our key information is summarized in paleogeographic maps, which are being iterated into improved approximations as we cover more ground and improved understanding of the basin histories emerges.

A major gap in information occurs across the Taupo Volcanic Zone and the Coromandel Volcanic Region. It is evident that significant thermally-driven domal uplift and associated erosion over the Taupo Volcanic Zone prior to the Pleistocene outbreak of volcanism has removed most, if not all, of the marine Neogene succession in this area, and this creates some uncertainty in interpretations of the Neogene paleogeography. In addition, we have a better understanding of western-central North Island geology than for central-eastern North Island, largely due to the more complex structure in the east coast region. A further complication in developing a Neogene paleogeography for eastern parts of North Island is its southward translation through time driven by coupling of the upper (Australia) plate with the subducting Pacific plate. We have used a modification of King (2000) as the basis for the relative positions of the eastern coastline in relation to the western coastline.

The Oligocene is usually regarded as the peak of inundation of the New Zealand landmass. In western North Island the Oligocene Te Kuiti Group accumulated in shelf environments, but there were prominent ridges that probably remained above sea level, although it is likely that the whole of northern and eastern North Island was below sea level. At the end of the Oligocene central-western North Island appears to have subsided rapidly to upper bathyal depths with accumulation of the Mahoenui Group. Bathyal mudstone and flysch deposits of this group are erosionally truncated immediately west of the Taupo Volcanic Zone, suggesting that deep water continued to the east. During the late-early Miocene (Altonian) changes in the location of active faults associated with far-field effects of the developing continental collision zone to the south, resulted in part of the Mahoenui depocentre being inverted and eroded, and the accumulation of Mokau Group coal measures. A deep water basin probably existed in the Waikato region (Waitemata Group), reflecting broad flexural downwarp of the crust (Australia plate) related to the emplacement beneath the region of the subducted slab of Australia plate (Kamp and Furlong 2006). The pattern we see through the rest of the Miocene is the southward migration of this seaway and related sedimentary basin. The land on the southern margin of this seaway undergoes marine onlap, reflecting flexural downwarping of

the crust driven by processes in the mantle. This land is the northern margin of the continent-continent collision zone associated with the Southern Alps, which itself migrated southward as the plate boundary zone evolved. Concomitantly a landmass in northern North Island and on the northern side of the seaway progressively expanded to the south uplifting marine sediments. During the Pliocene the Wanganui Basin, extending into Hawke's Bay, developed as the main part of the seaway across North Island. During the late Pliocene, coastal hills developed along coastal Hawke's Bay and Wairarapa reflecting emergence of the inboard part of the accretionary prism. The Ruahine and Tararua Ranges are Pleistocene basement-cored features resulting from crustal shortening and reverse faulting in response to coupling across the shallow part of the subduction thrust between the Australia and Pacific plates.

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[http://www.crownminerals.govt.nz/petroleum/conference/papers/Poster\\_papers\\_23.pdf](http://www.crownminerals.govt.nz/petroleum/conference/papers/Poster_papers_23.pdf)

### **The drowning of Zealandia: evidence and implications**

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The geology of New Zealand mainland, the Tasman Sea and the SW Pacific Ocean tells us that Zealandia broke away from Gondwanaland c. 85 Ma and then slowly sank 1,000 to 3,000 metres over a period of c. 60 million years. This process resulted from crustal stretching and thinning of continental crust, coupled with thermal cooling, with consequent loss of buoyancy and hence sinking of Zealandia. It may well have culminated in complete submergence c. 25 Ma.

This suggestion is a fascinating and interesting idea and is worthy of critical scientific consideration, and especially so because of the implications for our understanding of the origins and antiquity of the modern terrestrial New Zealand biota.

Furthermore, this idea has considerable merit because so much of Zealandia (90%) is submergent to this day. It is pertinent to ask: why is 10% of it above sea level? Why is Zealandia not all submerged? In terms of crustal dynamics, the answer is simple. About 25 Ma, plate boundary collision became vigorous resulting in tectonic emergence of New Zealand. This process is ongoing. In a sense, the New Zealand landmass is being held up against its will, and were the tectonism to diminish or cease, New Zealand would subside back to an ambient level commensurate with submerged Zealandia.

As a science community, we have assumed that there has always been land here in New Zealand, and this explains to a considerable degree, our understanding that our endemic biota is descended directly from Gondwanaland.

We challenge this interpretation and accordingly have examined the geological record that New Zealand has to offer in terms of a very different point of view: that Zealandia completely sank. Our studies have shown that the geological evidence for the existence of islands during latest Oligocene to earliest Miocene time is either non-existent or so wanting that we can confidently conclude that if any islands did exist they were small and short-lived.

It therefore follows that the modern terrestrial biota is not descended from archaic ancestors residing on proto-New Zealand (Zealandia) when it broke away from Gondwanaland. Rather, it has evolved from accidental arrivals since New Zealand became emergent. For all that, the modern biota is indeed derived from lands of Gondwanan heritage, simply because our nearest lands (Australia, New Caledonia, South America, Antarctica) support biotas that have indeed evolved largely from Gondwanan stock.

This research has grown from exploration of regional planar surfaces in the New Zealand landscape and particularly the Waipounamu Erosion Surface as expressed in Otago and the Chatham Islands, and is supported by the ChEARS Marsden Project.



**Fossil flowers, fruit, fungi, leaves, diatoms, sponges, fish and insects from a Central Otago lake deposit: a diverse 20 million year old forest-lake ecosystem**

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Studies of the flora and fauna preserved in an Early Miocene maar lake near Middelmarsh, Central Otago are providing an unrivalled opportunity to examine and reconstruct part of New Zealand's paleobiodiversity, in this case a 20-million year old forest-lake ecosystem. The plant material includes diatoms, algae, a wide variety of pollen and spores, a pollen-bearing flower, fruit, several types of fungi, bark, and huge numbers of complete and fragmentary leaves with preserved cuticle. The fauna collected to date includes freshwater sponge remains, numerous intact fish, insect feeding traces and the first record of *in situ* scale insects.

**Geological setting** The plant and animal fossils are preserved in a c. 75-100+ m thick, finely laminated diatomite deposit that accumulated for perhaps 100,000 years in a deep, 1.5 km diameter maar lake. Except for relict boulders of a thin Paleogene pebbly sandstone cover, and outcrops of c. 20 m.y. old fine-grained basalt around its margin, the lake deposit is surrounded by Otago schist.

Two depositional facies are recognized in 12 m of fresh (unoxidised) diatomite beds exposed in two mining pits. A thinly laminated diatomite facies comprising ~60 % of the succession consists of light and dark couplets of average thickness <0.5 mm (Fig. 1A). These laminae that we interpret as biogenic varves are composed mainly of diatoms; the dark laminae also contain abundant siliceous leiospheres and amorphous organic matter. By analogy with seasonal biological cycles of modern lakes, light-coloured laminae reflect enhanced diatom production when conditions (light, temperature, nutrients) were optimal during spring, while dark laminae accumulated during late summer- autumn. The second facies comprises 'speckled beds', black sapropelic diatomite beds up to 150 mm thick, also composed mainly of a single diatom taxon. Speckled beds incorporate pale diatomite flecks, fine woody plant matter and leaves, and invariably have a 1-5 mm thick capping layer of white diatomite. They were deposited at intervals of hundreds of years, from sediment gravity flows generated from the failure of plant matter-rich diatom ooze accumulating around the lake margins. Periodic variations in couplet thickness of 3~10 years compare with Late Quaternary records of ENSO (El-Niño Southern Oscillation) variability and indicate that the southern New Zealand climate was strongly seasonal and ocean-influenced during the Early Miocene.

**Lake biota** The lake was a closed system with virtually no abiogenic sediment. The layers are made up almost entirely of diatom frustules with some freshwater sponge spicules and tiny siliceous chrysophycean stomatocysts (algal resting spores). The diatom flora is overwhelmingly dominated by a single mucilaginous species, *Encyonema jordanii* (formerly *Cymbella*) that was attached to submerged aquatic plants such as *Myriophyllum* (water milfoil). We envisage that the entire lake surface was likely covered with floating plants, and that after the spring bloom, the diatoms dropped to the lake bed, while the decaying plants floated to the lake margins. Sponges may have encrusted plant material such as stems of water plants and dead leaves, or may have been anchored to soft sediment near the lake margins.

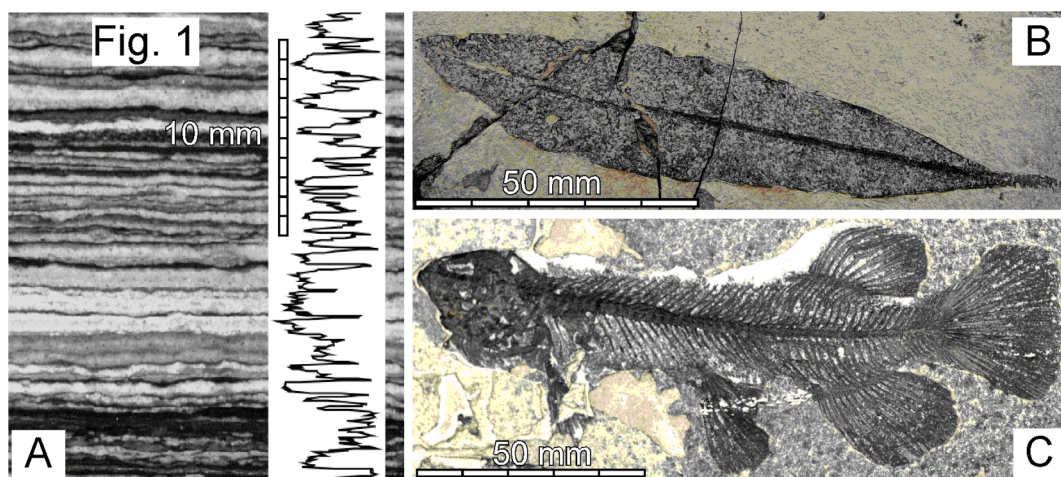
Limited excavations in the upper few metres of the deposit have yielded several entire fish skeletons up to 15 cm long that belong to a new species of galaxiid (Fig. 1C). These fish were probably lake-locked, lazy, skulking, wetland/lake margin predators, living on insects and possibly small crustaceans and gastropods. Their exquisite preservation confirms that the lake bottom waters were anoxic as there is no trace of predation, bioturbation or disturbance other than minor bacterial decay.

**Forest ecosystem** Surrounding the lake was an open evergreen forest: all the plant remains in the diatomite including small pieces of bark, rare flowers, stems, fruits, seeds and leaves must have either fallen in to the lake or been blown in from close by. One 20 mm diameter insect-pollinated flower was preserved complete with anthers and *in situ* pollen. Identification of pollen and spores from the matrix on the same bedding plane as the flower produced a list of more than 55 pollen types, including undescribed taxa (Bannister *et al.* 2005). Some of the numerous angiosperm leaves (Fig. 1B) have both upper and lower surface cuticles present and we now have cuticle preparations for some 280 individual leaves representing several families and genera. Most are dicots, but there are 5 different monocots, one conifer, and no ferns, although these are well-represented in the spore list. The leaves appear to be mainly from forest trees and lianes with moderately thick cuticles. About 40% of the leaves are Lauraceae, including several species each of *Beilschmeidia*, *Cryptocarpa*, and possibly *Endiandra*.

Three fungal associations are recognised to date: wood-rotting fungi on bark; saprophytic fungi as spores and perithecia within the cuticle envelope; and epiphyllous fungi (e.g. microthyriaceous cysts and subcuticular *Vizella*). Scale insects attached in life position to the upper surface of an angiosperm leaf are a recent discovery. Plant-insect relationships through time are of immense interest; other leaves show evidence of insect damage, and it is likely that more insects will be found at the site.

This low-elevation site is of major importance in any study of New Zealand's paleobiodiversity. Its age is well-constrained at c. 20 m.y., when global climate was much warmer than at present, though apparently seasonal as shown by the diatomite varves. Some of the biota has close living representatives in New Zealand, but many taxa no longer live locally. The Foulden Maar is the nearest Southern Hemisphere equivalent to the Eocene World Heritage Site at Messel in Germany.

Bannister, J.M., Lee, D.E., & Raine, J.I. 2005. Morphology and palaeoenvironmental context of *Fouldenia staminosa*, a fossil flower with associated pollen from the Early Miocene of Otago, New Zealand. *New Zealand Journal of Botany* 43: 515-525



**The Westland Forest Gap Revisited:  
Implications Based on Population Histories of Mycophagous Beetles**

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As demonstrated on both continents and islands, climatic and tectonic disturbances are responsible for the dispersal and separation of populations that may culminate in the formation of new species. On continental islands, such as New Zealand, it is expected that the pattern is similar, but the effects of local disturbance is not well known. The origin and maintenance of the *Nothofagus* beech forest gap in Westland, New Zealand, has challenged scientists seeking geological and biological explanations for the large number of species absent from the 150 km long area. The gap does not contain endemic plant species, but, interestingly, there are a few insects indicating that the Westland gap is an unusual area composed of many absentee species with remarkably few endemics.

While glacial disturbance is accepted as an important and perhaps the main cause of forest disjunctions in the South Island, the distribution of Pleistocene ice in the Southern Alps does not correspond exactly with past and present distributions of *Nothofagus* suggesting that other processes may be operating to maintain the Westland gap. Ecological (e.g., species competition), pedological (soil fertility and disturbance), and behavioural (slow re-colonization rates) factors have been proposed as factors that promote the lack of species, even though modelling of *Nothofagus* distributions show that the species may be perfectly capable of living in the Westland gap. We attempt to determine historical processes by examining the population structure of two species of fungus feeding beetles that are weedy, flight-capable, and widespread throughout New Zealand: *Brachynopus scutellaris* (Staphylinidae) inhabits rotten logs and is not present in the beech gap and *Hisparonia hystrix* (Nitidulidae) is contiguous through the gap and is found commonly on sooty mould growing on several tree and shrub species, but mainly beech and tea trees. The distributions of the two fungus feeding beetles will provide independent assessment of the beech gap and help to determine if the gap is correlated with patterns of haplotype diversity, and ultimately, ecological or historical causes.

Both species show north and south haplotype distributions while *Hisparonia hystrix* recolonised the gap as shown by definitive mixing with few central haplotypes. Based on coalescence dating methods, beetle lineages of *B. scutellaris* on either side of and within the beech gap indicate that the gap was formed at least 15,000 years ago and less than 209,000 years ago, and is therefore a long term phenomenon. Phylogenetic imprints from both species reveal similar patterns of population divergence corresponding to recent glacial cycles, favouring a glacial explanation for the origin of the beech gap.

Post-gap colonization by *H. hystrix* may have been facilitated by the spread of tea trees to the area, which may be better at dispersing than *B. scutellaris* which may be constrained by fungal host and/or microhabitat. The gap-excluded species *B. scutellaris* is found in both beech and podocarp-broadleaf forests flanking the Westland gap suggesting that there is a common effect on its distribution and that of *Nothofagus* and other species excluded from central Westland.

See figure on page 27.

### **How might volcanism influence evolution?**

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In addressing this question I have been asked to begin by providing an overview of the volcanic history of New Zealand. Indeed, volcanic activity has accompanied much of New Zealand's geological history, most commonly being associated with subduction at various times along the length of the country. However volcanism in post-Jurassic time is probably of most relevance to the history of our terrestrial flora and fauna, during New Zealand's separation from Gondwana and its isolated passage into the Southwest Pacific.

Beginning in the Cretaceous, subductive volcanism is recorded throughout the east coast North Island and north-east coast South Island. Elsewhere, small-scale intraplate and rifting basaltic volcanism is widespread.

Throughout the Tertiary in the South Island, widely scattered areas of intraplate volcanism are recorded. Best known are the large Miocene shield volcanoes of Banks Peninsula and the Dunedin volcano. On Chatham Island the Red Bluff Tuff is ubiquitous throughout the lower Tertiary. In upper Tertiary times the volcanic shields of the Auckland Islands and Campbell Island were emplaced, as volcanism continued in the Chatham Islands and around Timaru.

During mid-Tertiary and Quaternary time volcanicity in the North Island was predominantly related to convergence along the Pacific-Australian plate boundary. Subduction began in the Miocene of the Northland peninsula with a basalt-andesite-rhyolite association which became subsequently realigned in the Pliocene along the Coromandel Peninsula and Kaimai Ranges. In Quaternary time rotation of the northern East Coast "microplate" led to inception of the Taupo Volcanic Zone (Wallace et al. 2004). During this time intraplate volcanism in the Northland and Auckland regions was widespread.

There seem to be two major types of volcanic influence on organisms' habitat. First is a direct or "causal" influence where volcanic activity is directly responsible for an organism's survival or demise. Volcanic survival would include thermophilic organisms around deep sea hydrothermal vents (black smokers) or in geothermal hot water pools of the Central North Island. Volcanic demise would involve the extinction of an organism from volcanic processes such as overwhelming lava flows, lahars/jokulhlaups, pyroclastic flows, volcanic gases, tephra fall or volcanogenic tsunamis. But another way in which a causal influence might take place would be in a rare period of increased global volcanic activity or volcanic conflagration, where the global climate becomes so severely impacted an organism becomes extinct. The "ignimbrite flare-up" in Southwestern North America during Oligocene time has been referred to as the largest Phanerozoic episode of explosive volcanism on Earth (Cather et al. 2003). Such conditions may have also prevailed at the Permian-Triassic boundary. Implied in these episodes is a realisation that volcanic ash may contribute readily available iron to iron-limited ocean waters, stimulating phytoplankton growth and vastly increasing carbon production to influence global paleoclimate.

Second is an indirect or “opportunistic” influence where organisms take advantage of a specific volcanic habitat but it did not necessarily have to be volcanic. Examples would include:

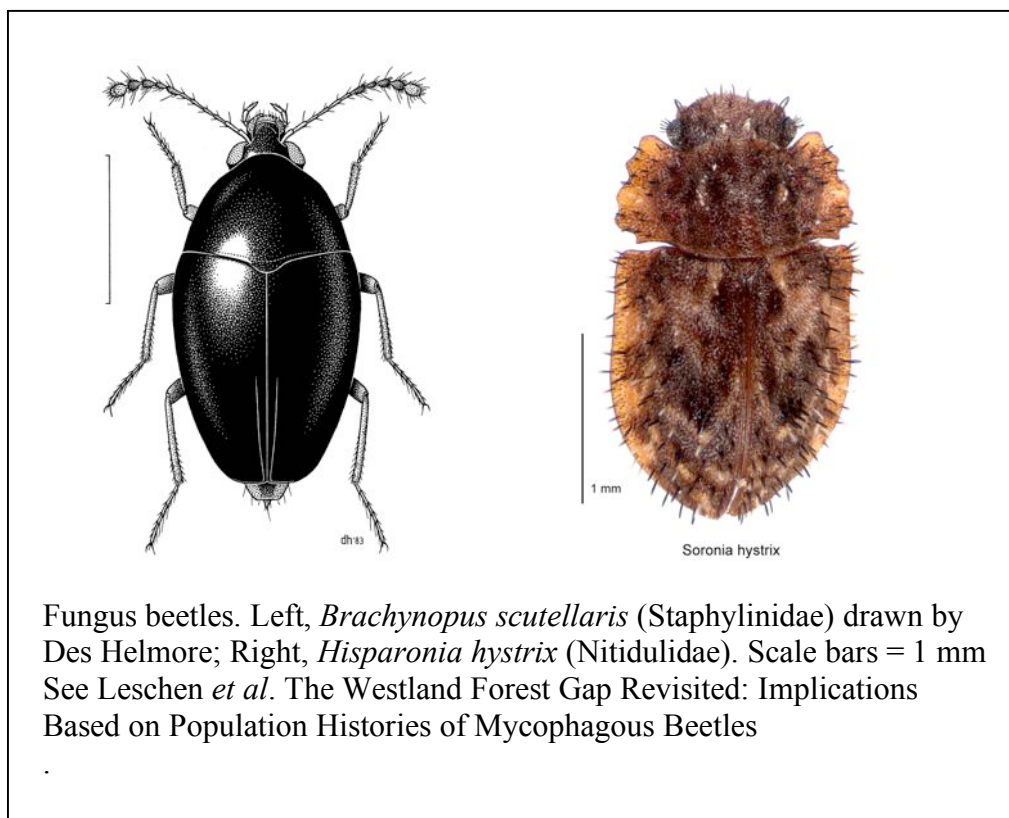
1. alpine and subalpine plants specific to volcanic mountains, such as Ruapehu and Taranaki/Egmont where the latitude is of greater significance to survival than the rock type
2. the specific environmental niches of the different latitudes and altitudes of the volcanic islands of the Pacific. DNA profiling is providing some exciting discoveries in understanding these influences.

Selected examples of these influences will be discussed in detail, followed by an anomaly.

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Wallace, L.M., Beavan, J., McCaffrey, R. & Darby, D. 2004. Subduction zone coupling and tectonic block rotations in the North Island, New Zealand. *Journal of Geophysical Research* 109, B12406. 21pp.



### Recent and emergent: Molecular analysis of the biota supports a young Chatham Islands

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The Chatham Islands, 800 km east of Christchurch, and their biota have long been thought to be of ancient origin with land being present since the Cretaceous. The islands are remnants of a large, extinct stratovolcano that erupted 80-70 million years ago (Ma) in the Late Cretaceous (Campbell et al., 1994). When the Tasman Sea started to open about 85 Ma, the New Zealand continental landmass, including the Chathams, rifted away from the eastern margin of Gondwanaland, carrying with it a full complement of plants and animals (Stilwell, 2006). The Chathams are thought to have been stable since then, with only minor sporadic volcanism. Their current subdued geomorphology is thought to be the product of long, slow erosion. The assumption has been that despite subsequent subsiding of the New Zealand continental landmass (including most of the Chatham Rise), there has always been land at the Chathams supporting an ancient biota. Biological hypotheses for the Chathams have generally been influenced by this geological scenario (e.g. Craw, 1988). New geological evidence (see Campbell et al this issue; and Campbell, 1998), however, suggests that the Chatham Islands may have emerged from the sea less than 3.8 million years ago.

Biologists have also questioned the older dates for the Chathams as there are some prominent absences and peculiarities in the modern Chatham Islands fauna and flora that suggest comparatively recent arrival with little evidence of an isolated heritage of great antiquity (Pole, 1994; Emberson, 1995). For example, only 2% of the Chatham Island beetle genera are endemic, much less than that of other island groups of similar size and 'apparent age'. By comparison, beetle genera endemism on the New Zealand mainland is 70% (Emberson, 1995). Furthermore, existing genetic evidence from insect genera reveals relatively minor Chatham-mainland divergences (Trewick, 2000).

We used a molecular approach to obtain evidence for the extent of divergence between taxa on the Chatham Islands and their closest relatives on mainland New Zealand. If the Chathams have emerged within the last 3.6 million years, then we would expect to see a relatively low level of genetic divergence (or variation) between Chatham endemics and close relatives in mainland New Zealand. Conversely, if the Chathams have had a long history as emergent land then at least some of the endemic taxa should have a relatively high level of genetic divergence with, perhaps, no close relatives on the mainland. We genetically surveyed species across a broad taxonomic and ecological range of the Chatham Island plants and animals. We sequenced gene regions that have been used extensively in population genetic and phylogenetic studies and evolve at rates suitable for our work and for which comparable data were available. For the animals we mainly used the mitochondrial gene regions COI and COII while for plants we used ITS. We obtained sequences for 16 plant and 9 animal genera from the Chatham Islands and several mainland close relatives for each of these taxa.

In all cases the genetic level of divergence between the Chatham and mainland species was relatively low (Table 1). Calibrating these levels of divergence to both known estimates of rate of change for a given gene region and to other dated speciation events, e.g. alpine species forming during mainland mountain uplift, allowed a reasonable estimate of timing for these events. Even allowing for considerable variation in molecular evolutionary rates, these data

support the hypothesis of a recent phylogenetic separation of Chatham and mainland taxa during the Pliocene (6-2 Ma). Divergence times are, therefore, at least an order of magnitude more recent than that suggested by vicariance hypotheses and supports the geological evidence of a recently emerged Chatham Islands.

Our findings have important implications for the Chatham Islands' biota. Foremost is that all of the species on the island have dispersed and colonised over a large water gap. We look forward to a new era of research on the Chathams where patterns and rates of speciation among different taxonomic groups will be examined along with the roles that niche spreading, multiple colonization and niche divergence and allopatric speciation and habitat switching play in divergence. Also, of interest is identifying characteristics that may have predisposed the current biota to dispersal and island establishment.

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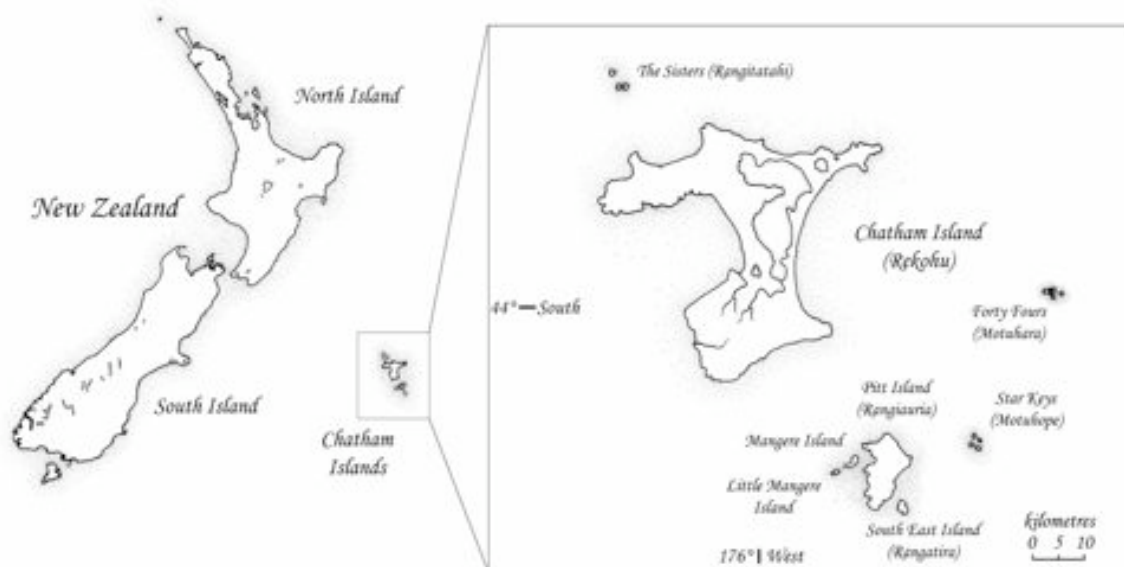
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Table 1. Examples of genetic divergence between Chatham Island and mainland species. Note that the closest relative may not have been identified and that these distance may therefore over-estimate the actual distance. However, if this is the case then the true levels of divergence will be even smaller than identified in the table.

Genus	Gene region	Distance	Genus	Gene region	Distance
Plants					
<i>Aciphylla</i>	ITS	0.024	<i>Hebe</i>	ITS	0.002
<i>Embergia</i>	ITS	0.050	<i>Leptinella</i>	ITS	0.047
<i>Gentiana</i>	ITS	0.006	<i>Olearia</i>	ITS	0.023
Invertebrates					
<i>Mecodema</i>	COI&II,16S	0.017	<i>Hadramphus</i>	COI	0.028
<i>Amychus</i>	COI	0.038	<i>Geodorcus</i>	COI	0.115
<i>Talitropsis</i>	COI	0.023	<i>Celatoblatta</i>	COI	0.044
<i>Anisolabis</i>	COI&II	0.004			

### New Zealand mainland and the Chatham Island archipelago



**“Nothing exists for one cause”; putting biology back into evolution**

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The opening phrase of the title is from Charles Darwin's notebooks (Schweber 1977). It is a double reminder, firstly that mainstream evolutionary theory is not just about describing nature but is particularly looking for mechanisms or 'causes', and secondly, that there will usually be several causes affecting any particular outcome. The second part of the title is our concern at the almost universal rejection of the idea that biological mechanisms are sufficient for macroevolutionary changes, thus rejecting a cornerstone of Darwinian evolutionary theory. Our primary aim here is to consider ways of making it easier to develop and to test hypotheses about evolution. Formalizing hypotheses can help generate tests.

In an absolute sense, some of the discussion by scientists about evolution is little better than the lack of reasoning used by those advocating intelligent design. Our discussion here is in a Popperian framework where science is defined by that area of study where it is possible, in principle, to find evidence against hypotheses – they are in principle falsifiable. However, with time, the boundaries of science keep expanding. In the past, some aspects of evolution were outside the current boundaries of falsifiable science, but increasingly new techniques and ideas are expanding the boundaries of science and it is appropriate to re-examine some topics.

It often appears that over the last few decades there has been an increasingly strong assumption to look first (and only) for a physical cause. This decision is virtually never formally discussed, just an assumption is made that some physical factor 'drives' evolution. It is necessary to examine our assumptions much more carefully. What is meant by physical factors 'driving' evolution, or what is an 'explosive radiation'. Our discussion focuses on two of the six mass extinctions, the fifth being events in the Late Cretaceous, and the sixth starting at least 50,000 years ago (and is ongoing).

*Cretaceous/Tertiary boundary; the rise of birds and mammals.*

We have had a long-term interest (Cooper and Penny 1997) in designing tests to help evaluate whether the processes of microevolution are sufficient to explain macroevolution. The real challenge is to formulate hypotheses in a testable way. For example the numbers of lineages of birds and mammals that survive from the Cretaceous to the present is one test. Our first estimate was 22 for birds, and current work is tending to increase this value. This still does not consider lineages that survived into the Tertiary, and then went extinct later.

Our initial suggestion was probably too narrow in that it lumped four models from Penny and Phillips (2004) into one model. This reduction is too simplistic in that we need to know about survival and ecological and morphological divergences during the Late Cretaceous, and whether Crown groups of avian or mammalian orders may have existed back into the Cretaceous. More recently (Penny and Phillips 2004) we have formalized hypotheses about dinosaurs and pterosaurs, with the prediction that interactions between mammals (and ground-feeding birds) and dinosaurs would be most likely to affect the smallest dinosaurs, and similarly interactions between birds and pterosaurs would particularly affect the smaller pterosaurs. There is now evidence for both classes of interactions, with the smallest dinosaurs and pterosaurs declining first, as predicted. Thus, testable models are now possible.

*Mass extinction number six: human impacts.*

On a broad scale, there is a good correlation between time of human arrival, and increased extinctions (Hurles et al. 2003; Martin 2005; Figure 1). However, it is necessary to distinguish different time scales (Penny 2005) and on a finer scale there are still large numbers of possibilities. In Hurles et al. (2003) we mentioned habitat modification (including the use of

fire), introduced plants and animals (including kiore) in addition to direct predation (the 'overkill' hypothesis). We need also to consider prey switching that occurs in early human societies, as evidenced by the results of Wragg (1995) on the middens of different ages on Henderson Island in the Pitcairn group. In addition, the presence of human-wary or human-adapted animals will affect the distribution in the subfossil record. A better understanding of human impacts world-wide, in conjunction with pre-scientific knowledge will make it easier to discuss the issues by removing 'blame'. While continued spontaneous generation was accepted universally, there was the expectation that animals continued to reappear.

New Zealand is one of the very best locations in the world to study many of these issues. Apart from the marine fossil record, some human-impact events are extremely recent and the remains less disrupted by time.

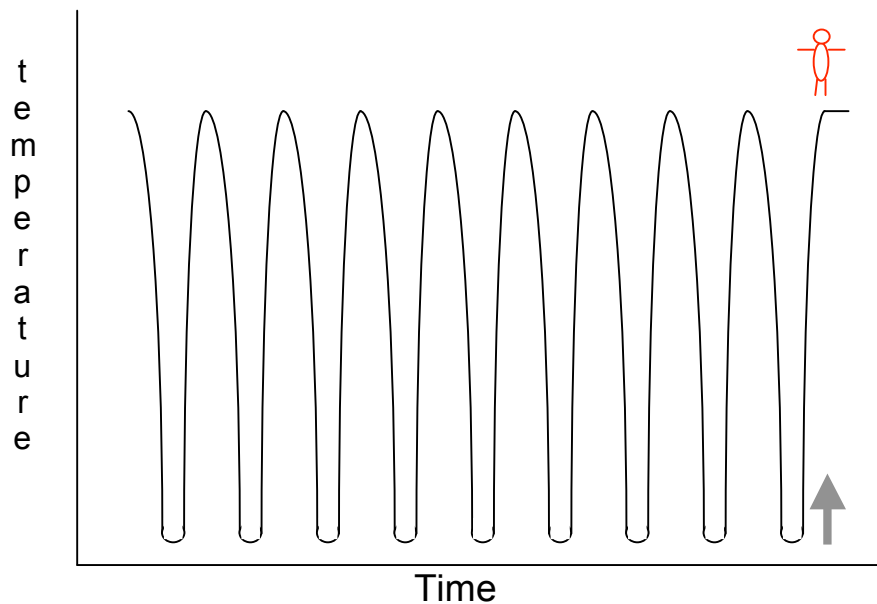


Figure 1. Cartoon of a succession of Ice Ages with extinctions of megafauna indicated by the arrow, more or less when humans first appeared. On a large-scale it is clear that human effects are a much better potential explanation than 'climate change', but fine-scale results are necessary to evaluate the effect of a range of direct and indirect factors.

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**Chloroplast phylogeography of the forest fern *Asplenium hookerianum*.**

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The study of spatial patterns of genetic variation, or phylogeography, in numerous European trees has indicated the presence of multiple refugia where forest remained *in situ* through the recent glacial period (Petit et al. 2003). Because each species can have an idiosyncratic pattern, investigating multiple species is desirable to develop an accurate picture of how communities were affected by climate change.

Few phylogeographic studies of plants have been carried out in New Zealand. However, New Zealand can be divided into regions with high (north of the North Island, north of the South Island, south of the South Island) and low (south of the North Island, and the middle of the South Island) numbers of endemic vascular plant species (McGlone et al. 2001). Forest refugia during the last glacial have been postulated in the endemic rich areas (Wardle 1963).

Gardner et al. (2004) have recently investigated chloroplast DNA sequence variation in the five endemic forest tree species of *Metrosideros* subgenus *Metrosideros* (including pohutukawa and rata). They recorded 12 haplotypes at the *trnL-trnF* locus amongst 200 samples. Although polymorphisms were shared across the species, the numbers of haplotypes were noticeably higher in Northland, Coromandel, and north-west Nelson; all areas of postulated forest refugia.

We have conducted a phylogeographic investigation of Hooker's spleenwort fern, *Asplenium hookerianum*, after earlier study revealed infraspecific variation at the *trnL-trnF* locus (Perrie & Brownsey 2005). *Asplenium hookerianum* is found throughout New Zealand, although it is generally more common in the east, reflecting a preference for drier habitats. Contemporary collections indicate that it is an obligate forest-dweller.

We obtained sequence data for c.10 individuals from each of twenty populations. 25 haplotypes were recorded, with most populations possessing multiple haplotypes. The geographic distribution of haplotypes in *Asplenium hookerianum* does not mirror that in *Metrosideros*. Haplotype numbers were not higher in areas of postulated forest refugia or in regions of high species endemism. The most haplotype-rich population was Banks Peninsula, with six haplotypes found in 10 individuals.

Even populations neighbouring glaciated areas contained multiple, and in some cases unique, haplotypes. The very rich haplotype diversity in *Asplenium hookerianum* is extremely unlikely to have all originated within the last c.14 000 years. Consequently, in order to accrue the observed present-day genetic diversity, either:

- (1) Populations, including those near glaciated areas, must have survived more or less *in situ* for a long period; i.e., beyond the last glacial period. Because *Asplenium hookerianum* is an obligate forest dweller, forest survival would also be implied.
- (2) If many populations only date from c.14 000 years ago, atypically high gene-flow must have occurred from unidentified refugial areas. The usual post-glacial colonisation pattern, with only a few haplotypes occupying the glaciated area because of successive founder events

and most diversity remaining in refugia, was not observed in *Asplenium hookerianum* (but is in *Metrosideros*).

In comparison, only one haplotype was found in populations around Lake Taupo, which assumedly post-date c.200 A.D. This suggests that, in this region at least, chloroplast gene flow has not been sufficiently high to introduce multiple haplotypes.

At a broader level, *Asplenium hookerianum* populations in the east and centre of the North Island were characterised by a different subset of haplotypes to populations in the South Island and north and south of the North Island. Statistical analysis (Templeton 1998) of this pattern rejected the null hypothesis of no significant association of genetic variation with geography. This implies that chloroplast gene flow is not sufficiently high to obliterate phylogeographic structure at this level. Whether the differentiation of the eastern and central North Island populations is an idiosyncrasy of *A. hookerianum*, or a reflection of some geological event remains to be seen. The discrepancy between *Metrosideros* and *A. hookerianum* nevertheless reinforces the desirability of phylogeographic study of additional New Zealand forest species.

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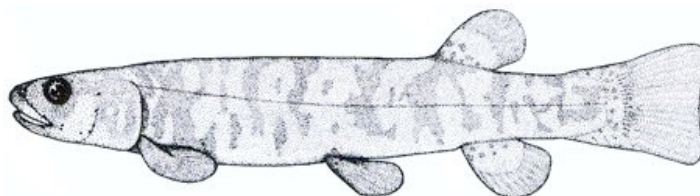
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**Geological dates and evolutionary rates: coevolution of rivers and their biotas**

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Geologically-derived calibrations of DNA sequence divergence provide a key method for testing evolutionary hypotheses and for understanding timeframes of biodiversification. To this end, many researchers have relied upon "accepted" rates of DNA evolution derived from early phylogenetic studies (calibrated using fossil data) (typically 1-2% mtDNA divergence per million years), under the assumption that these are applicable across timescales and across taxonomic boundaries. However, recent studies using Holocene calibration points have yielded substantially faster divergence rates for some taxa. To shed light on this apparent incongruence, it is essential to undertake calibrations across a wide range of geological ages.

We present a molecular clock calibration system based on geologically-dated river capture events. Changes in drainage geometry can effect vicariant isolation of freshwater taxa, and thus provide a predictive framework for associated phylogeographic studies. As a case in point, New Zealand's Pelorus and Kaituna rivers became geologically isolated from the larger Wairau River system approximately 130 ka. We conducted mtDNA phylogeographic analyses of two unrelated freshwater-limited fish taxa native to these river systems (*Gobiomorphus breviceps*: n = 63; *Galaxias brevipinnis*: n = 95). Consistent with predictions based on drainage history, phylogenetic analysis of combined control region and cytochrome *b* sequences yielded reciprocally monophyletic clades of Pelorus-Kaituna and Wairau haplotypes for each species. Molecular calibrations based on this river reversal event approximate to 10% mtDNA sequence divergence per million years, and are therefore substantially faster than traditionally accepted mtDNA divergence rates for fishes. A survey of freshwater phylogeographic literature reveals numerous examples in which the ages of recent evolutionary events may have been substantially overestimated through the use of "standard" calibrations. We recommend that - wherever possible - biologists should start to reassess the conclusions of such studies using more appropriate molecular calibrations derived from recent geological events.



**The St Bathans Fauna – first insight into Neogene Terrestrial  
vertebrate faunas in New Zealand.**

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The Early Miocene (16-19 million-year-old) sediments of the Bannockburn Formation, Manuherikia Group near St Bathans in Central Otago, South Island, have produced in excavations made since 2001, New Zealand's first comprehensive terrestrial vertebrate Neogene fauna. Shallow lacustrine sediments deposited in a large (c. 5,600 km<sup>2</sup>) palaeo-Lake Manuherikia are the source of this fauna. Taphonomic biases reflecting water transport and current sorting restrict the fossils to disarticulated relatively small bones, but it is still one of the richest Neogene deposits for bird bones in the world.

Fish remains numerically dominate with both bones and otoliths attesting to only 2 groups (galaxiids and gobies) being present in the fauna. A single vertebra is identified as a frog that is not a leiopelmatid. Many bones are referred to squamates (skinks and geckoes) and indicate a generic diversity greater than that in the Recent fauna. Sphenodontids are represented by 2 tooth-row fragments. A crocodilian is represented by several teeth, scutes and post cranial bones.

Bird bones are numerous with at least 25 species of birds represented by bones, and probable moa, Aves: Dinornithiformes, by eggshell. Anatids dominate the fauna with 6 species in 5 genera, making it the most diverse Neogene 'duck' fauna known worldwide. Most anatid fossils represent two species of dendrochenines, but a tadornine (shelduck) is common as well. A diving petrel (Pelecanoididae: *Pelecanoides*) is represented, extending the geological range of this genus worldwide from the Pliocene to the Middle Miocene, at least. Charadriiformes (gulls and waders) are represented by a large species of gull (Laridae), and at least two small waders the size of *Charadrius bicinctus* (banded dotterel) and *Calidris ruficollis* (red-necked stint). Phoenicopteriformes (flamingoes) are tentatively included in the fauna on the basis of a single worn fossil. Pelecaniformes (cormorants, pelicans and allies) are represented by a femur of a pelican. Gruiforms (rails and allies) are represented by one specimen similar to *Aptornis* and abundant rail (Rallidae) bones, including a common flightless species and a rarer slightly larger taxon, about the size of *Gallirallus philippensis*. Accipitrids are represented by 2 bones referable to an eagle slightly smaller than the wedge-tailed eagle. Pigeons are known by just a single ulna, but parrots (Psittacidae) are represented by several specimens from 3 species ranging in size from that of kea to parakeet, but are not referable to any Recent genus. An owl nightjar (Aegothelidae: *Aegotheles* sp.) is represented by a single tarsometatarsus clearly more similar to *A. novaezealandiae* than to any other species in the genus indicating a middle Miocene origin for this recent species. A single ulna is identified as a swiftlet (Apodidae: *Collocalia* sp.). Passerines are quite well represented with a minimum of 3 taxa, with the largest a member of the Cracticidae that today include magpies and currawongs. A majority of passerine bones appear to belong to a bellbird-sized honeyeater. The absence of some waterbirds, such as anserines (including swans), grebes (Podicipedidae) and shags (Phalacrocoracidae), among the abundant bones of other waterbirds, indicates their probable absence from New Zealand in the Early-Middle Miocene.



Mammals: At least 8 specimens are certainly identified as bats: two molars, the proximal ends of three radii, 2 distal humeri and a fifth metacarpal. At least four new bat species are represented by these fossils and include a mystacinid, a vespertilionoid (but not of the indigenous *Chalinolobus* lineage) and an archaic bat most closely resembling a group of cosmopolitan bats (archaeonycteridids) that died out elsewhere >45 Ma. While yet limited, this fauna has affinities with Palaeocene and Oligo-Miocene Australian faunas. Three specimens (2 mandible symphyses, femur) are referable to a stem therian mammal of a hitherto unknown lineage and indicate survival of a third Mesozoic vertebrate lineage in NZ long after rifting from Gondwana 82Ma.

Associated with these vertebrates are molluscs. Freshwater species (Hyridellids and Hydrobiids) are common but not uniformly present, and of considerable interest are specimens of terrestrial pulmonates of several species similar to Charopidae.

Taken together this assemblage attests to a more diverse terrestrial fauna than the Recent fauna indicating losses of several major groups (crocodilians and several bird families, some bats and an ordinal level taxon of mammals) since the Middle Miocene. Presence of the terrestrial mammal indicate survival of an hitherto unknown Gondwanan Mesozoic mammal lineage on NZ for a minimum of 60Ma, through the Oligocene marine transgression along with other relict taxa such as sphenodontids and leiopelmatids. The rich avian record will allow testing of hypotheses of dispersal events from Australia and so the origination of the recent fauna.



Fossils such as this bat tooth from the St Bathans Fauna (19-16Ma) are changing views on the evolution of the NZ fauna.

