GEOLOGY & GENES IV

This is the fourth of an irregular series of meetings bringing together geologists and biologists who share an interest in the history of life. This years meeting coincides, almost to the day, with the 200th year since the birth of Charles Darwin (12 February 1809). This is a salient reminder of the purpose of our meetings. Darwin and his contemporaries were naturalists who drew on all types of evidence. Observation and inference from the realms of earth and life science were both contributors in their learning. Indeed Darwin was in his early years rather more a geologist than a biologist and key influences in his thinking were Adam Sedgwick and Charles Lyell. Thus we come together in the expectation, or at least hope, that the expression, exchange and combination of our ideas, evidence and analysis might result in something nearing the significance of Darwin's achievements. At the very least we must emulate Darwin's contribution as a rational, freethinking humanitarian.

Organised by Steve Trewick (Massey University)
Norton Hillier (Canterbury Museum)
Roger Cooper (GNS Science).

Assisted by Joy Wood, Susan Adams and others (Allan Wilson Centre for Molecular Ecology and Evolution).

Cover Image: From Stagpoole V.M. (2002) The New Zealand Continent, 1:7 500 000.
Institute of Geological & Nuclear Sciences Ltd Geophysical map GPM15.
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I am quite charmed with Geology, but, like the wise animal between two bundles of hay, I do not know which to like the best; the old crystalline group of rocks, or the softer and fossiliferous beds. When puzzling about stratification, &c., I feel inclined to cry "a fig for your big oysters, and your bigger megatheriums." But then when digging out some fine bones, I wonder how any man can tire his arms with hammering granite.

(Charles Darwin. 1834. Letter to J.S.Henslow *in* Darwin, F. 1887. Life and Letters of Charles Darwin vol. I, p249. John Murray, London.)

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GEOLOGICAL CONSIDERATIONS RELATING TO THE CHATHAM ISLANDS, MAINLAND NEW ZEALAND AND THE HISTORY OF NEW ZEALAND TERRESTRIAL LIFE

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These people represent a large and diverse team of biological and geological researchers that has been individually and collectively investigating aspects of the submergence-emergence history of the New Zealand landmass during the past 100 million years of Cretaceous-Cenozoic time.

This team is a classic example of 'Geology and Genes' at work: a blending of biological and geological minds. For us, it all began in the Chatham Islands.

In this paper we shall confine ourselves to the geological precepts and considerations that have shaped and determined our interpretations. However, in so doing we shall draw on our experience working together as part of a three-year (2004-2007) Marsden Fund project exploring the antiquity of the Chatham Islands land surface.

Our objective is to provide some insight into the basis of our convictions and per force try to express the limits of our geological confidence. We hope that this may be of some value to biologists, especially those with little or no geological background.

Much of our thinking has been presented in recent scientific publications by Trewick et al. (2007), Landis et al. (2008), and in more popular literature such as Campbell & Hutching (2007) and Campbell (2008).

In crustal terms, New Zealand and New Caledonia are continental islands. They are the biggest remnants of a much larger tract of continental crust that is below sea level. Indeed, they may be regarded as the emergent parts of a largely submerged eighth continent, Zealandia. In terms of surface area, the 2,500 metre isobath is a proxy for defining the limits of Zealandia. On this basis, the continental crust of Zealandia is almost half the size of Australia, or about the size of India. What happened? The geological implication is that Zealandia was a continent that has subsequently sunk. Why did it sink and when? And why are New Zealand and New Caledonia emergent? Why are they too not submerged?

These questions were brought into sharp focus during our research in the Chatham Islands (176° W, 44° S) located c.850 kilometres due east of Christchurch on the Pacific Plate, well in-board of the active Australia-Pacific plate boundary that runs through mainland New Zealand.

Our research shows that the Chatham Islands became emergent less than 3 million years ago (Ma). The hard evidence for this is the recognition and mapping of a formation of submarine volcanic and associated sedimentary rocks in southwest Chatham Island that now form the highest topography in the Chathams. Age determination of these rocks is based on radiometric dates (Ar/Ar dating of hornblende crystals) and fossils (molluscs).

The mechanism for uplift is as yet uncertain but active mantle inflation of regional extent is suspected rather than a localised volcanic effect or far-field plate boundary tectonic collision effect. For all that, the Chatham Islands have been the locus of dominantly terrestrial intra-plate basaltic volcanism during Late Cretaceous time, and much smaller scale largely submarine intra-plate basaltic volcanism during Paleocene to Eocene and Miocene to Pleistocene time. More importantly, our investigations in the Chatham Islands have led to the realisation that they offer a unique subaerial glimpse of undeformed Zealandia. By contrast, New Zealand and New Caledonia are highly deformed.

Our subsequent research in mainland New Zealand has shown that the geological evidence for continual presence of land since Zealandia rifted away from Gondwanaland c.83 Ma is inconclusive. Furthermore, a reasonably compelling geological argument can be made for maximum submergence c.23 Ma and acknowledges the logical possibility of total submergence.

Though unproven one way or the other, we encourage the scientific community to explore this idea: that the New Zealand region of Zealandia may have been totally submerged c.23 Ma. Seminal to this idea is the recognition and significance of a regional marine-cut geomorphic feature within the New Zealand landscape, the Waipounamu Erosion Surface. This idea, the substantive drowning of Zealandia, has set a new paradigm for understanding the antiquity and origins of native biotas of New Zealand and New Caledonia. The potential implications are profound and the sinking of a continent over represents a geological phenomenon of global significance.

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THE PLIOCENE FOSSIL RECORD OF SOUTHERN OCEAN DIATOMS: RAPID EVOLUTIONARY TURNOVER AND NONLINEAR RESPONSES TO ENVIRONMENTAL CHANGE

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Southern Ocean phytoplankton are highly sensitive to climatic forcing (measurable response of productivity and ecology to surface warming incurred over last century) and may in turn modulate coupled carbon cycle-climate dynamics to some extent, via poorly understood biological feedbacks. In order to address how phytoplankton species migrate, evolve, and go extinct on longer timescales and greater climatic extremes (as predicted by the IPCC), we use high-resolution geologic records from the Pliocene (5.3-1.8Ma), the most recent time in Earth's history when atmospheric temperatures and $p\mathrm{CO}_2$ were higher than they are today.

Our new, robust reconstruction of the history of diatom origination and extinction in the Southern Ocean uses a regional database of microfossil records and paleomagnetic and radiometric age constraints from 25 Late Neogene drillcores (Cody et al. 2008), and constrained optimization models of quantitative biostratigraphic correlation and seriation (Sadler 2006). The approach constrains the most probable Plio-Pleistocene chronology of diatom species appearance and disappearance to within ±33kyrs, on average. Such high temporal resolution is virtually unprecedented in analytical paleobiology for any fossil clade, and reveals discrete episodes of major upheaval in the Pliocene that stand out in sharp contrast to the preceding 10 million years of uniformly slow turnover (Cody et al. submitted).The vast majority of turnover in Figure 1C represents autochthonous speciation and extinction of Antarctic endemics, rather than migration. Alternative model sequences verify that apparent pulses in turnover rate are *not* artifacts of stratigraphic incompleteness, reworking, sample size, or taxonomic bias (Cody et al. submitted).

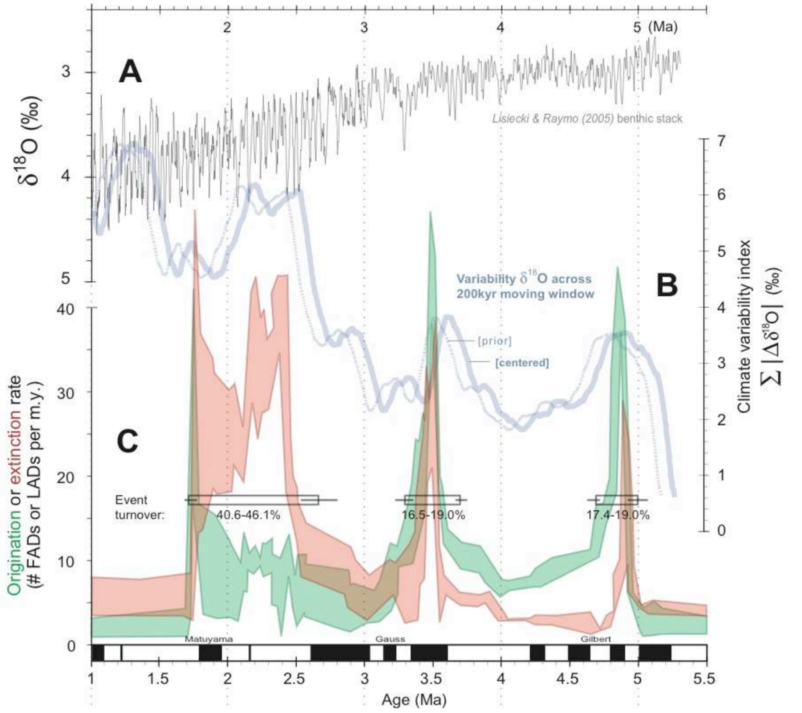

Figure 1. Plio-Pleistocene origination (green) and extinction (red) rates of Antarctic marine diatoms, after Cody et al. (submitted). Maxima and minima indicate the ±33kyr uncertainty in FAD and LAD event ages. Climate variability index (light blue line) represents the total variation in δ^{18}O values over a 200kyr moving window.

Of particular interest are two ~200kyr-long turnover pulses that occurred near 5.0Ma and 3.5Ma. Both events involved abrupt but short-lived rises in both origination and extinction rates to 5-10 times Miocene background levels, near-synchronous appearances of new forms in at least 8 separate genera (most notably *Thalassiosira* and *Fragilariopsis*), extinctions in at least 6 genera (counting less widely distributed/documented taxa), and net species turnover of ~18% (Cody et al. submitted). These significant episodes have not previously been documented in this or any other marine fossil group.

Diatom turnover pulses predate dramatic Pliocene stepwise changes in climate (Lisiecki & Raymo 2005; Naish et al. submitted), but dramatically coincide with peaks in climate variability (Figure 1B). Extreme climatic and oceanographic variability on different temporal and spatial scales may have provided new niche space in heterogeneous habitats and increased selection pressure through higher levels of disturbance.

A consistent 100kyr lag of peak fossil turnover behind peak climate variability suggests either that processes of climate-induced evolution and extinction in pelagic phytoplankton are extremely slow, or that variability acted more as a precondition than a trigger of rapid turnover in marine diatoms (Cody et al. submitted). Other possible triggers include extreme warmth, coupled with partial deglaciation of Antarctica (Harwood 1991). Considerable paleoecological evidence (Naish et al. submitted; Whitehood & Bohaty 2003; etc.) indicates warmer than present conditions in the Ross Sea and offshore Southern Ocean at ~4.9 and 3.5Ma, though geochemical paleothermometry is needed for confirmation. The deglaciation and transgressive flooding of continental margins would have provided ample incised, semi-isolated microenvironments and fjords conducive to vicariant speciation (Harwood 1991).

There is evidence of an approximately concurrent radiation among fossil Globorotalid foraminifera of the SW Pacific during a ~0.4myr interval near the base of the Pliocene (Hornibrook 1984), suggesting that in at least one case turnover may have propagated up Southern Ocean food chains. However, evidence of similar, synchronous events is conspicuously lacking from Pliocene fossil sequences around the world.

In contrast, a later episode of rapid extinction of Antarctic diatoms between ~2.6 and 1.7Ma (Figure 1C) has numerous analogs in the paleontological literature; similar late Pliocene extinctions are documented in marine and terrestrial organisms globally, especially warm-adapted groups. Approximately 70% of taxa present in the Early Pliocene regional assemblage went extinct between 2.5-1.7Ma; most of this biodiversity loss was never recovered. This high mortality is comparable to the most extreme Plio-Pleistocene "mass extinctions" in North Atlantic mollusks (Stanley & Campbell 1981), generally attributed to oceanic cooling with deterioration of global climate in the Late Pliocene.

Cooling is also implicated in Antarctic diatom decline: the onset of the extinction pulse (Figure 3) closely coincides with the abrupt decrease in Southern Ocean SST and perturbations in the carbon cycle at about 2.58Ma (Hodell & Ciesielski 1991). Further, Late Pliocene diatom extinction appears to be closely related to the reorganization of the global silica cycle, which involved the collapse of a coastal high-biosiliceous productivity belt ~2.5Ma from sea-ice expansion, and the establishment of a new hub of biosiliceous productivity and sedimentation to the north ~1.93Ma (Cortese et al. 2004).

It is unlikely that the pace of turnover in Pliocene diatoms was controlled by intrinsic factors arising from tight associations between species (i.e. coordinated stasis; Ivany 1996): fossil diatom species appear to respond individualistically to their environment. However, the punctuated nature of observed turnover suggests that the ecosystem's response to extrinsic forcing is nonlinear, determined in part by thresholds – either in the biological response to gradual environmental change, or in the environmental response to gradually changing boundary conditions, which the biota simply reflect (Cody et al. submitted).

The imprecise dating and controversial interpretation of available paleotemperature proxy records is such that no single paleoenvironmental explanation can be assumed or ruled out at this time. Antarctic phytoplankton evolution and extinction is likely driven by changes in ocean circulation (wind mixing, thermohaline, upwelling), water column stratification (temperature and salinity gradient, wind mixing, thermocline vs. photic zone depth, meltwater, precipitation), turbidity, or water chemistry (pH, salinity, nutrient levels) that are not captured by available paleoclimate proxy records. Although the nature and dynamics of Antarctic ice sheets and climate remain controversial (e.g. Kennett & Hodell 1993), it is clear that Early Pliocene environmental perturbations were sufficiently profound to bring about rapid evolution and extinction in planktic diatom assemblages as well as dramatic changes in biogeography and productivity of siliceous phytoplankton in general (Cody et al. submitted).

The remarkable stability of the assemblage since ~1.5 Ma, even in the face of increasing amplitude and changing periodicity of glacial-interglacial cycles (Lisiecki & Raymo 2005), suggests that modern species are adapted to high levels of disturbance, and that communities are able to migrate with the advance and retreat of sea-ice, ocean fronts, and surface water isotherms, with only a trickle of biodiversity loss (Cody et al. submitted). It is unclear whether Antarctic diatoms will be able to similarly accommodate future climate change (which will fundamentally alter the current disturbance regime and exceed the envelope of climatic variation to which these organisms are adapted, as per Toggweiler & Russell 2008) without major loss of diversity or evolutionary turnover. Further paleoecological study will assist in establishing the sensitivity and likely response of this important ecosystem.

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A NEW GEOLOGICAL MODEL OF CENOZOIC NEW ZEALAND SUGGESTS A COMPLEX PHYLOGEOGRAPHIC HISTORY FOR NEW ZEALAND TERRESTRIAL TAXA.

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The new model of North Island Cenozoic palaeogeography developed by Kamp *et al.* has a range of important implications for the evolution of New Zealand terrestrial taxa over the past 30 Ma. Key aspects include the prolonged isolation of the biota on the North Island landmass from the larger and more diverse greater South Island, and the founding of North Island taxa from the potentially unusual ecosystem of a small island around Northland.

The prolonged period of isolation is expected to have generated deep phylogenetic splits within taxa present on both islands, and an important current aim should be to identify such signals in surviving endemics to start building a picture of the historical phylogeography, and inferred ecology of both islands through the Cenozoic. Given the potential differences in founding terrestrial species and climatic conditions, it seems likely that the ecology may have been very diferent between the North and South Islands.

New genetic data from the 10 or so species of extinct moa suggest that the radiation of moa was much more recent than previously suggested, and reveals a complex pattern that is inferred to result from the interplay of the Cenozoic biogeography, marine barriers, and glacial cycles.

WHAT CONTROLS SPECIES LONGEVITY IN MARINE MOLLUSCS? - THE ROLE OF TRAIT INTERACTIONS

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What determines the duration of a species? The influence of the external environment has received considerable attention and extinction rates have been linked to climate change, bolide impact, competition, predation etc. Undoubtedly there is an element of chance also. But are there intrinsic properties of species that influence the likelihood of survival over geological time? Our study looks at survivorship probabilities of New Zealand Cenozoic mollusc species during times of background extinction. We analyze relationships among a range of ecological and biological traits - geographic range size, body size, life mode (whether infaunal or epifaunal), larval type (planktotrophic or nonplanktotrophic) and feeding type (bivalves: filter-feeder or other; gastropods: carnivore or other) - in order to identify those that are associated significantly with species duration. Of these, geographic range is a trait emergent only at the level of the species, whereas the other four traits are properties of the individuals that comprise the species.

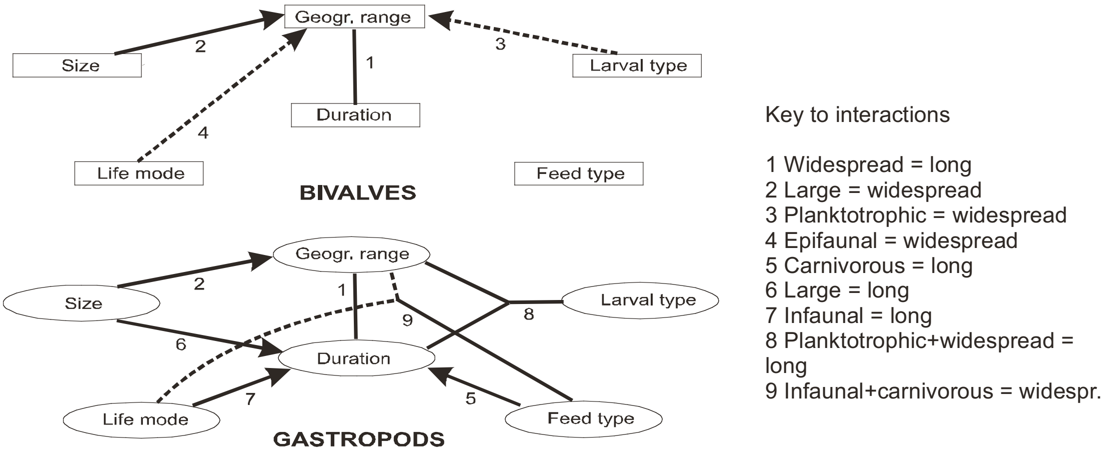
We also wish to separate, as far as possible, interactions between traits that can be attributed to a shared inheritance rather than to an ecological association. Thus, for example, two species with the same feeding type, say filtration, may share this feature because of common inheritance, rather than because it confers ecological-evolutionary advantage. Associations between traits that result apparently from shared inheritance are identified at the level of taxonomic families by stratified randomised resampling; in this way we separate putative, truly ecological associations from phylogenetic effects (Fig. 1).

Two-way and multi-way associations between traits have been analysed using log-linear modelling. This method makes no assumptions about predictor and response variables, treating all as response variables. This is important given that we are testing for poorly understood interactions between several variables, more than one of which may be dependent (notably, duration and geographic range – see Foote et al. 2008). Our main conclusions are as follows:

1. Increased geographic range is strongly associated with increased duration, a finding reflected in all tests. This confirms a pattern that is becoming firmly established in a wide range of organisms (Hansen 1978; Gaston, 2003; Jablonski 1987, 1996; Jablonski and Hunt 2006; Foote et al. 2007, 2008). Our randomised log odds ratio subsampling (Fig. 2A, B) suggests that in neither bivalves nor gastropods is this relationship a result of shared inheritance, which is not to say that geographic range itself is not a heritable trait at the species level (Jablonski 1987; Jablonski and Hunt 2006; see also Webb and Gaston 2003 for a contrary view). Geographic range is also strongly positively associated with body size, consistent with a trend found widely in the animal kingdom. This relationship appears to be a direct one in both bivalves and gastropods and not a result of indirect

mediation through one or more of the other traits studied. Again, in neither group is this relationship inferred to be a result of phylogenetic effects.

FIG. 1 Relationships between duration, geographic range, and other traits in bivalves and gastropods, based on two-way and multi-way (modeling) comparisons. Dashed lines indicate associations that are inferred to reflect shared inheritance. Arrowheads suggest the direction of the effect, on the assumption that an organismal trait can affect an emergent trait but not vice versa.



2. In bivalves, a planktotrophic larval type is associated directly with large range size; our data suggest that this association may result from shared inheritance. In gastropods, although planktotrophic larval type and large geographic range are not directly associated in a two-way interaction, they are associated through the three-way interaction term duration*geographic range*larval type. Larval type in gastropods might therefore influence range size by ‘hitch-hiking’ on the duration-larval type relationship; this association does not appear to be a phylogenetic effect. Our results for bivalves and gastropods are consistent with the commonly reported relationship between wide range size and planktotrophic larval type (Hansen 1978; Gaston 2003; Jablonski 1987; Jablonski and Hunt 2006), although in bivalves the association may be through shared inheritance

3. Large body size is associated with increased range size in both bivalves and gastropods, and with increased survivorship in gastropods only. These associations appear not to be the result of shared inheritance.

4. An infaunal life mode is associated with a decreased risk of extinction in gastropods, consistent with the view that predation plays a major role in extinction probability in the Cenozoic (Vermeij 1987). However, the association apparently is driven by shared inheritance rather than ecology (Fig. 2C, D) and may not be as strong as other interactions. In gastropods, infaunality is similarly associated with large range size through a three-way interaction involving carnivorous feed type. In bivalves, however, the relationship is reversed; infaunality is associated with reduced range size, an association also driven by common ancestry (Fig. 1).

5. In summary, for the traits examined here, bivalves have a relatively small number of simple two-way associations whereas gastropods have more complex interactions involving three-way associations among traits. This suggests a more complex ecology for gastropods and no doubt reflects their wider range of feeding types and life habits. Increased extinction probability in gastropods is linked with many other factors including

restricted geographic range, nonplanktotrophic larval type, noncarnivorous feeding type, small body size and epifaunal life mode. In bivalves, increased extinction probability is associated just with restricted geographic range.

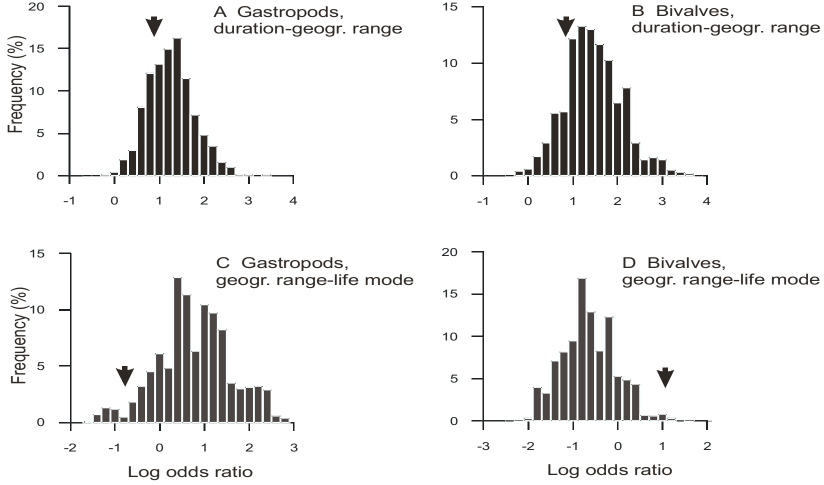


FIG. 2 Histograms of log odds ratios for two-way interactions between selected pairs of traits, calculated from 1000 randomised subsamples stratified on taxonomic families. The log odds ratio is a measure of the strength and direction of association between the traits of each pair; a log odds ratio of zero indicates no association. The arrow indicates the log odds ratio observed in the full data set. Where this arrow lies close to the mode in the randomised data (6A, B), strong phylogenetic effect is inferred to be negligible. Conversely, where the observed overall odds ratio is widely separated from the histogram mode (6C, D), the overall interaction is likely to be influenced by shared inheritance. See text for discussion.

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SPECIES IN THE FOSSIL RECORD: HOPELESS MONSTERS OR HOPEFUL MESSENGERS?

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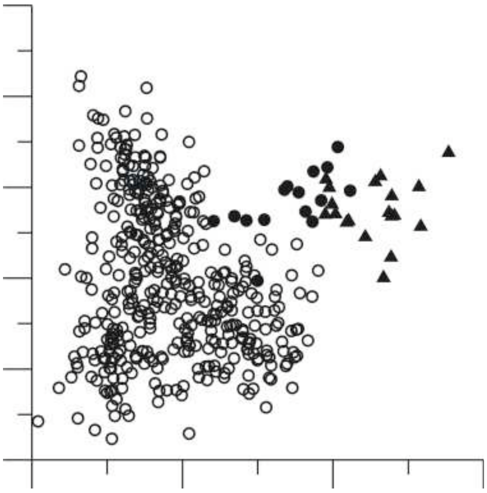
The definition of the species concept and the operational recognition of species are highly contentious problems; they are topics upon which "more paper has been consumed … than any other in evolutionary and systematic biology" (Wiley, 1978, Systematic Zoology, 27:17). These problems are acute when considering species in the fossil record, which may, or may not, be equivalent to species living today. The issue bears upon patterns of diversification, extinction and evolution as inferred from the fossil record: can these historical patterns be interpreted in terms of biological processes observed in living communities of plants and animals? Specifically, we wish to know: a) whether fossil morphospecies accurately reflect biological species identified using molecular approaches; and b) how well data from such morphospecies can reproduce molecular phylogenies? In studying morphospecies, is the paleontologist faced more often than not with hopeless monsters that confound interpretation, or hopeful messengers that convey meaningful information?

To explore the two questions posed above, we have obtained molecular phylogenetic and morphological data from two very different groups of living molluscs from New Zealand: marine volutid gastropods and freshwater unionid bivalves. Both groups lack abundant, discrete, hard-part morphological characters. The volute dataset is based on 11 nominal species living at subtidal to outer shelf depths. Approximately 7500 base pairs of mitochondrial DNA have been sequenced from these species and phylogenies were reconstructed using maximum likelihood and Bayesian methods. To study morphological variation within and between volute taxa, we used two approaches: geometric morphometric description of five landmarks and six semi-landmarks around the shell, and Fourier shape analysis of the aperture. The unionid dataset is based on three nominal species found in lakes and rivers throughout New Zealand. The molecular analysis is based on a 500 base pairs fragment of mitochondrial DNA with an independent test using nuclear DNA. Morphological variation within the unionids has been described using Fourier shape analysis of the shell outline.

Regarding the first of our questions, comparisons of molecular and morphometric data indicate that, in general, morphological data are able to discriminate molecular species with some success, even in morphologically "challenging" groups. This conclusion is not contingent on the *a-priori* identification of biological species. We illustrate this here with data from three closely related volutes that are readily separated in low-dimensional morphospaces based on landmarks and outlines (Fig. 1). Furthermore, the morphometric data apparently detect supra-specific separations (Fig. 2) – in this case, the separation of the volutid genera *Spinomelon* and *Alcithoe* (Fig. 2), which was poorly resolved previously. These encouraging results lend confidence to some taxic paleobiological analyses of diversity, extinction and evolution based on fossil morphospecies – at least for the case of molluscs.



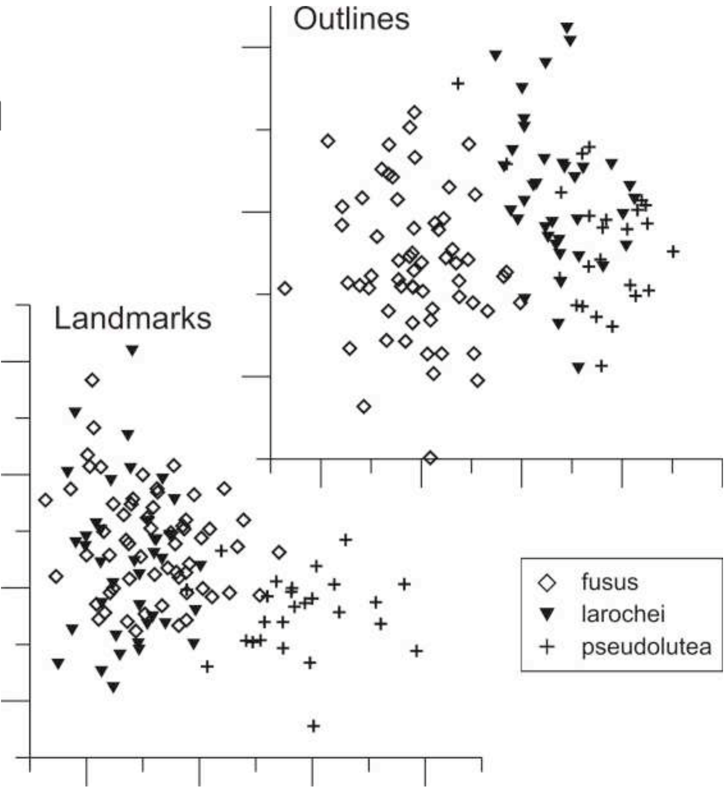


Figure 1) Canonical variate (CV) analyses based on landmark and outline morphometric data for three closely related species of volute, *Alcithoe fusus*, *A. larochei*, and *A. pseudolutea*. In both cases, the *x*-axis is the first CV, the *y*-axis is the second CV. The three species are clearly separated in the morphometric analyses, although in this example, the analyses must be interpreted in combination.

Figure 2) Canonical variate analysis based on landmark morphometric data for volutes in the genera *Alcithoe* (open symbols) and *Spinomelon* (closed symbols). Prior to molecular analysis, the assignment of species to these genera and, indeed, the validity of the genera, were uncertain. This figure shows that the genus *Spinomelon* occupies a discrete region of morphospace.

Regarding the second question posed above, our results suggest that reconstruction of phylogenies based solely on morphology is more challenging, especially in groups lacking abundant, discrete characters. Importantly, however, it seems that the incorporation of continuous, morphometric characters into morphological phylogenies can yield significant congruence with molecular phylogenies. New cladistic algorithms allow for the inclusion of continuous characters within analyses without the need for discretization. Further, these methods can use value ranges that might span, for example, the mean plus or minus one standard error. In the case of the New Zealand volutes, cladistic analyses based only on discrete characters fail to resolve any meaningful phylogeny. In contrast, incorporation of continuous morphometric characters yields a result that is much closer to the molecular phylogeny (Fig. 3).

Taken together, these results give us cause for optimism: at least in the groups studied and perhaps for many or most molluscs, we suggest that fossil morphospecies can accurately reflect biological species identified using molecular approaches and can be used to reproduce meaningful phylogenies. Our fossils are hopeful messengers!

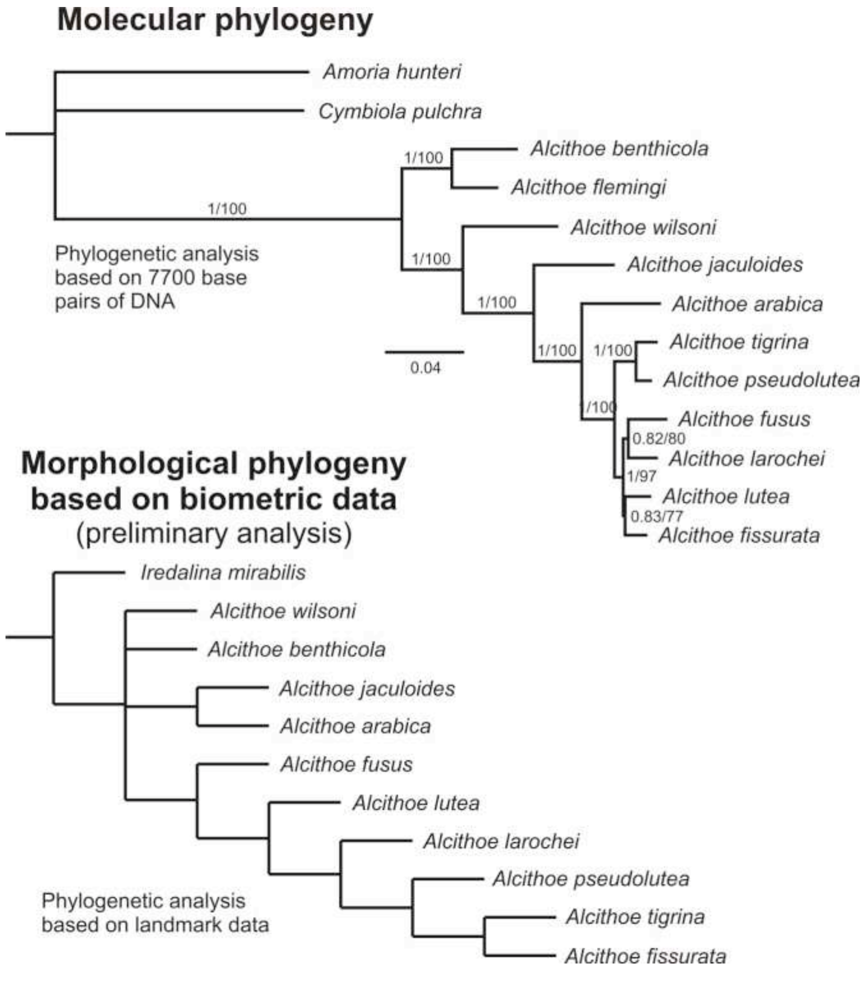


Figure 3) Phylogenies for New Zealand volutes based on molecular and morphometric data. The morphometric analysis utilised a small number of discrete characters and 8 continuous characters, these being median canonical variate (CV) scores for the first eight CV axes based on landmark analysis. Note that the morphological phylogeny is incomplete and preliminary, but shows very encouraging similarities to the molecular phylogeny.

THE ROLE OF NEW ZEALAND FOSSILS IN THE PHYLOGENY OF WHALES AND DOLPHINS (CETACEA)

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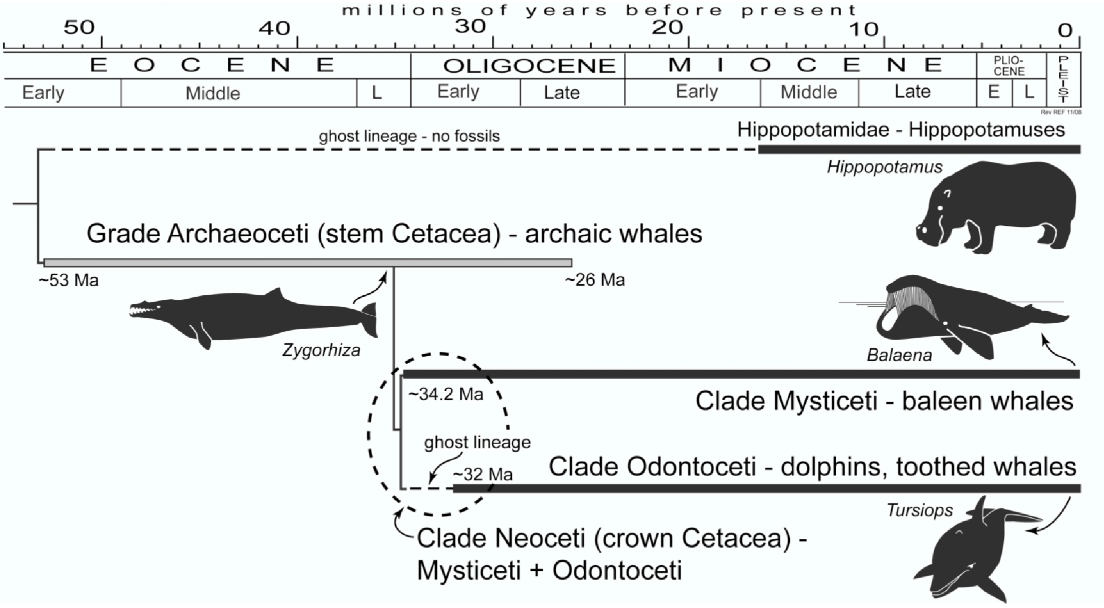
Whales and dolphins (Cetacea) provide a notable example of macroevolution linked to change from terrestrial to fully aquatic life. In contrast to the uncertain early history of most orders of mammals, cetacean origins can be tracked confidently to early Eocene (~53 Ma) beginnings (Gingerich 2005). The cetacean fossil record includes substantially complete and well-dated fossils that reveal the history of change in habitat, functional systems, and diversity. New Zealand fossils contribute both by elucidating the early fossil history of "modern" Cetacea (Fordyce 2009), and by calibrating molecular phylogenies (e.g. Nikaido et al. 2001, Sasaki et al. 2005). The weakness of fossils is their fragmentary nature and difficulty of interpretation; the great strength is that they provide the only direct, hard evidence of evolution, often representing extinct clades, morphologies, and lifestyles.

The 2 extant groups of Cetacea are sister taxa, traditionally suborders: Odontoceti, toothed whales and dolphins (echolocators), and Mysticeti, baleen whales (filter feeders). These 2 clades comprise crown-Cetacea, or Neoceti. The third suborder is the paraphyletic Archaeoceti (stem-Cetacea), an extinct and mainly Eocene cluster of archaic species currently in 5 families. Figure 1, below, shows a simple guide to relationships, with clade ranges plotted against time (slightly modified from Marino et al. 2007).



The earliest archaeocetes are known only from the Tethys and subequatorial north Atlantic. These animals mark the move from land to water (Gingerich 2005); they include 4-legged presumably amphibious species, some of which have the double-pulley astragalus in the ankle – indicating origin from amongst the Artiodactyla as suggested by W.H. Flower in the 1800s and recently corroborated by molecular signals.

By later Middle Eocene, 37-38 Ma, archaeocetes reached New Zealand waters, represented by 2 species of dolphin-sized Dorudontinae (Basilosauridae) and perhapsa larger zeuglodont (Basilosaurinae: Basilosauridae). Elsewhere, comparable archaeocetes of basilosaurid grade ranged beyond the Tethys into temperate regions, indicating that cetaceans had by now a fully pelagic lifestyle. Such habits are reflected in the recently proposed clade Pelagiceti: Basilosauridae + Neoceti.

New Zealand fossils add significantly to cetacean history during the latest Eocene and Oligocene. This time of significant change in ocean circulation and global climates coincided with the origins of many of the higher-level clades that have persisted to modern days. Most of the fossils are from the Waitaki region, South Island; most are housed in the Geology Museum, University of Otago.

New Zealand Oligocene mysticetes include early fossil members of modern clades. A fragmentary right whale (Balaenidae) indicates that the slow-swimming skim-feeding habits arose by ~28 Ma. *Mauicetus parki*, ~24 Ma, is a putative early rorqual (stem-Balaenopteridae) which presumably fed by lunge-gulp feeding; other *Mauicetus*-like fossils are older, from ~26 Ma. Thus, 2 key modern lineages, with divergent feeding habits, were established early in Late Oligocene times. As yet, New Zealand fossils give no clue about the origin of two other crown families, represented by the extant pygmy right whale (*Caperea*) and gray whale (*Eschrichtius*); judging from molecular and morphological phylogenies, both have long ghost lineages. One other baleen whale group is notable in New Zealand: the enigmatic dawn-mysticetes (Eomysticetidae) include 5+ species of narrow-jawed presumed gulp feeders with a ~4 M yr record, overlapping temporo-spatially with the stem right whale and stem rorquals.

The stratigraphic record for the 3 clades of toothless baleen whales indicates an Early Oligocene radiation not, however, represented by New Zealand fossils. Further, it is clear that early mysticetes had teeth (whether solely toothed, or with teeth and baleen is moot), but New Zealand lacks the diversity of Oligocene toothed mysticetes seen in the North Pacific. Our most significant toothed stem-Mysticeti is cf. *Llanocetus* which, at ~33-34 Ma, is close to the base of the clade – a little younger than the oldest species, *Llanocetus denticrenatus* (~34.2 Ma, Antarctica).

Whereas the record of Mysticeti reveals functional shifts in feeding mode (toothed, then baleen) within the clade, extant phylogenetic bracketing and functional reconstructions both suggest that the Odontoceti echolocated from the beginning. The oldest named odontocete, *Simocetus rayi* (Early Oligocene ~32 Ma, North Pacific) shows features consistent with echolocation. Globally, the early Oligocene record is sparse, but the diversity of Late Oligocene families indicates that, as with mysticetes, the Early Oligocene was a time of major radiation. Significantly, many of the Late Oligocene family-clades are extinct, and carry no signal through into molecular phylogenies.

Consider the Platanistoidea, today represented only by the endangered Ganges/Indus River dolphins: stem-platanistoids from New Zealand include several species in each of the extinct clades Squalodontidae, Squalodelphinidae, Waipatiidae, and enigmatic Dalpiazinidae. Such early diversity in a crown-clade is lost to molecular analysis. In contrast to the early diversity of platanistoids, there is only a sparse concurrent Oligocene global record of sperm whales (Physeteroidea), no firm reports of beaked whales (Ziphiidae), and minor reports of true dolphins (Delphinoidea). One New Zealand fossil delphinoid is noteworthy: cf *Kentriodon* sp. (Port Waikato), at ~23 Ma, implies a long ghost lineage for the Inioidea, which is the presumed sister clade to the Delphinoidea.

Inioids encompass 3 extant species of "river dolphins" (*Inia, Pontoporia, Lipotes*), and scattered fossils currently no older than 12-15 Ma. Today, in contrast to the Late Oligocene, platanistoids are nearly extinct, while delphinoids are highly diverse – with species of Delphinidae dominating the extant Cetacea (36-37 of 88 species). Whether the mirror-image pattern of diversity over time for platanistoids versus delphinoids reflects abiotic or biotic causes – for example, climate change versus competition – is moot.

The fossil record often turns up the unexpected. One real surprise of the last decade is the recognition in New Zealand of several species of "relict" Archaeoceti from Oligocene rocks around 26 Ma. The fossils are 6-8 M yr younger than the former "last" archaeocetes, and the earliest Neoceti, of the Late Eocene. Hitherto, it was assumed that archaeocetes went extinct through competitive displacement as the Mysticeti (filter-feeders) and Odontoceti (raptorial echolocators) radiated. However, the New Zealand "relict" Archaeoceti occur in the same strata as crown-Mysticeti and crown-Odontoceti: they clearly coexisted for some millions of years. Why are there no reports of such occurrences elsewhere in the world?

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NICHE STABILITY IN NZ BIRDS: INTEGRATING PHYLOGENY, MORPHOLOGY, LIFE HISTORY AND PALEONTOLOGY

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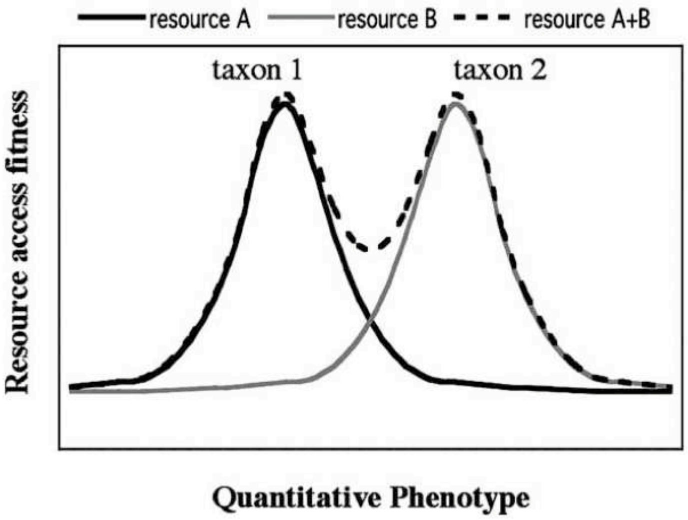
Sequence data is increasingly giving us a reproducible picture of the phylogeny of the major groups of living organisms – but what do we do with the phylogenies? Given our increased knowledge of phylogeny, it is a waste of good morphological data to attempt only to build phylogenies from that data. But if we have a phylogeny from molecular data then we can use other data, including morphological, life history, ecological and paleontological data to infer many of the important biological processes that occurred during history, including testing of basic theories about how fast major adaptive changes occur during evolution.

Some of the necessary theory as been developed (Figure 1, see Poole et al. 2003), and is based on the evolutionary-stable niche-discontinuity (ESND) model. This predicts that some lineages will keep evolving within a similar range of niches, but will not easily diverge into a different niche while that is still occupied by another relatively well adapted group. The basic reasoning is that in any population individuals have to compete both with their close relatives (for resource A), as well as with individuals in the other group (for resource B). This means that there are selective forces maintaining a lineage within its pre-existing life-history strategy, as well as other selective forces from competing with unrelated groups (B). The basic conclusion is that there will be some long-term (on a geological timescale) maintenance of lineages with in a particular life-history strategy.



Much less often, a more major shift will occur when a competing group is lost, or the ecological resources are partitioned in a different way.

Turning to NZ avian groups, we are finding that for ratites, the traditional model of ratite monophyly (apparently supported by morphology, nuclear and mitochondrial data) is not correct. Instead of the flighted tinamous being sister to all cursorial (unflighted) ratites, we have shown they are sister to moa, deep <u>inside</u> the ratite grouping (and this agrees with nuclear data). This implies multiple losses of flight among the ratite lineages. We propose that large size and cursoriality, and consequently loss of flight were selected for among Early Tertiary ancestors of modern ratites in filling parts of the eco-space vacated upon the K/T boundary extinction of mid-large sized terrestrial vertebrates, including dinosaurs.

Another interesting group are the Pelecaniformes. With the exception of ducks and geese, aquatic birds were inferred by Sibley & Ahlquist (1990) to form (more or less) a single evolutionary group. However within this group, traditional morphological characters do not necessarily group together, and may have arisen many times. For example flamingos group with grebes (who don't group with loons) rather than other long legged waders. The totipalmate feet of Pelecaniformes are also morphological convergence in part. Our results confirm pelicans group with the shoebill (near other wading birds) suggesting pelicans are 'aberrant long-legged waders' (Van Tuinen et al 2001). On the other hand, members of the core Pelecaniformes (gannets, darters and shags) do group together, and have been morphologically stable in their niches for a very long time.

Another long-lived group are pigeons, and these are an interesting group in that both
a) they seem to have occupied a similar niche for many tens of millions of years, and
b) there appears from a range of sequence data to be a genuine continuum from individual birds, to populations, sibling species, regional species complexes to higher order groups.
In this case there is no evidence for any discontinuity between micro- and macro-evolution, they are parts of a continuum.

It has been known since the work of Sibley & Ahlquist (1990) that many deep lineages of Passeriformes occur primarily in Australia; this appears to be a source of this most speciose of avian orders. However, recent work is providing evidence that passeriforms also have basal lineages in New Zealand as well – making Australasia the source of the avian lineages that then radiated out and took over the world. As the phylogeny of basal passerines is resolved, we will be able to date the origins of these lineages, and the ones that radiated out of Australasia. What non-passerine groups were present in Eurasia at the time passerines radiated out? Were they displaced and out-competed? These and many other questions follow on from a dated passerine phylogeny.

Given these four examples, it is appropriate time to integrate our knowledge from many areas of research, and we welcome all those who have information to contribute. It does appear that many taxonomic groups have long-term stability in their primary life history strategy.

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ASSISTED PASSAGE – EARLY MIOCENE TRANSPORT OF INSULAR TERRESTRIAL BIOTA TOWARDS NEW ZEALAND BY A MOVING TECTONIC PLATE

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Recent hypotheses (Landis et al. 2008) imply that post-rifting subsidence and Cenozoic differential uplift within Zealandia make it unlikely that the terrestrial biota of Gondwanan affinities on its two main emergent areas - New Caledonia and New Zealand - have simply been in place since the continent parted from Gondwanaland. Geological evidence suggests that the extent of differential submergence and uplift of respective landmasses and islands was such that repopulation must have been more likely than endemism. If this was the case, newly emerged or re-emerged areas would most likely require dispersal over water. It is therefore useful to investigate the regional geology and plate tectonics for likely migration corridors or conveyors that would have shortened or even bridged the gaps between land areas, the most obvious being between New Caledonia and New Zealand (Chaproniere 1980). In this paper, we present evidence that some volcanic and tectonic islands in the Norfolk Basin – Three Kings Ridge area actually moved southeastwards in the early Miocene, carrying their terrestrial ecosystems a little closer to New Zealand.

Tectonic reconstructions predict that before the Miocene the Three Kings Ridge, which is part of a Loyalty-Three Kings- Northland Plateau volcanic arc, lay alongside the Norfolk Ridge. Today, the Three Kings Ridge lies some 250 km southeast of the Norfolk Ridge, having been rifted off and moved there by backarc plate tectonics in the early half of the Miocene (Figure 1) (Mortimer et al. 2007). The plate carrying the Three Kings Ridge and Northland Plateau and a number of seamounts, slid along the Reinga Ridge–Northland continental margin of New Zealand, and in its wake, an extensional backarc basin – the Norfolk Basin – was opened. Within the Norfolk Basin and on the Northland Plateau, are small plateaux and ridges composed of faulted blocks and volcanic edifices. Some of these, along with some peaks of the Three Kings Ridge and some solitary seamounts on the plate, have flat tops and limestone caps signifying wave erosion. Meffre et al. (2006) proposed that a number of islands existed on the Three Kings and southern Loyalty ridges at times from the Late Eocene to Early Miocene, including a very large, tectonically up-thrust island in the Norfolk Basin itself between the earliest Oligocene (38 Ma) and earliest Miocene (23 Ma), which may have foundered before the Middle Miocene. Early Miocene, discontinuous, tectonic emergence of the Norfolk Ridge System, the strip of Mesozoic Zealandia that supports the land masses of New Caledonia and Northland, has also been proposed (Herzer and Mascle 1996; Herzer et al. 1997; Herzer 1998), which would have shortened the over-water distances for serendipitous migration of terrestrial biota. Indeed, on the southern Norfolk Ridge System, the sequence of Cenozoic subsidence and uplift suggests that the axis of emergence moved from northwest to southeast in the Early and Middle Miocene, in effect allowing terrestrial biota to ride a wave of uplift towards Northland.

Not all former islands have been discovered, and few have been sampled. We present a map (Figure 1) showing 17 features where shallow-water fauna have been collected and identified, or where wave-planed tops or flat limestone caps are known from seismic profiles. We infer that they were once islands or adjacent to land, and plot the possible trajectories, based on plate tectonics, of those which have moved.

Seafloor spreading is thought to have been active in the Norfolk-South Fiji backarc basins from Early Oligocene to Middle Miocene time. Based on Northland tectonic history and radiometric ages of seafloor basaltic crust, the most likely time that spreading would have affected the Norfolk Basin is between 23 and at least 19 Ma (Early Miocene), and possibly 15 Ma (Middle Miocene) (Mortimer et al. 2007); 23 – 15 Ma is the time-frame we have chosen for calculating approximate “back-of-an-envelope” island trajectories.

To show the amounts by which the islands on the moving plate may have brought terrestrial biota closer to New Zealand, the location and maximum and minimum ages of each shallow-water sample are projected onto a straight line drawn between the southeastern tip of mainland New Caledonia and Auckland (Figure 2), and the distances displayed from a simple calculation. The rocks are mainly clean bioclastic algal limestones and well sorted sandstones, and most of their ages fall within ca. 25-15 Ma (broadly the early half of the Miocene). In three instances fossil ages are supported by Ar-Ar radiometric ages of associated crystalline rocks. The period of likely exposure is taken as the period between the maximum and minimum fossil ages, which is probably young for some samples, as clean shallow-water limestones might only have formed after islands were eroded and submerged. Taking 15 Ma as the end of relative plate motion, and 36 km/My as the speed at which 290 km of basin opening took place over 8 My, the period of migration is calculated as the maximum age minus 15 Ma, and the length of the path in km as that number times 36. The resulting trajectories are shown on Figure 1. Although roughly derived, these trajectories illustrate that tectonic movement of this archipelago might have helped terrestrial biota to reach New Zealand from the New Caledonia region either by shortening the direct open-water distance or by moving into the path of favourable ocean currents.

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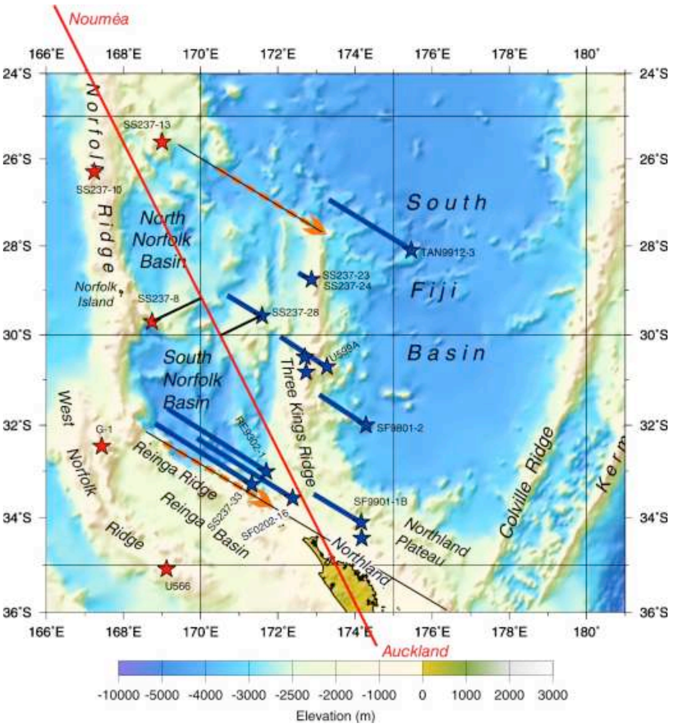

Fig. 1 Dredge stations (stars) with photic zone or very shallow-water rocks, and the trajectories of those features that have moved to their present location (blue). Blue star tracks show potential southeastward transport of biota on islands using an estimated Norfolk Basin opening rate of 36 mm/yr (290 km over the period 23-15 Ma). Red stars are on the Australian plate, which is fixed in this diagram. Thin black lines are faults along which the Three Kings ridge moved. Dashed orange arrows show the amount of displacement of the Three Kings Ridge. The stations are projected onto the red line in Figure 2.

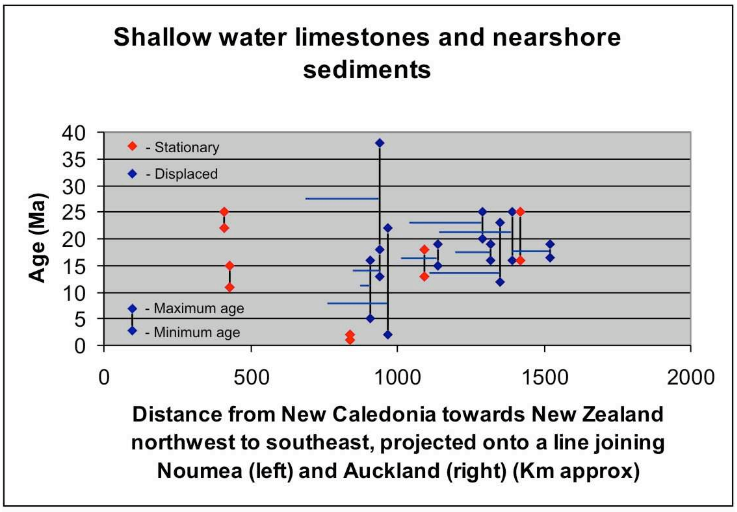

Fig. 2 Locations and ages of shallow-water rocks projected on a line between New Caledonia and New Zealand. Banners (horizontal lines) show distance of transport parallel with the line while shallow-water/terrestrial conditions may have prevailed. The vertical placement of the banners has no age significance.

ENHANCING MOLECULAR ANALYSIS WITH RIGOROUS PALEONTOLOGICAL SAMPLING PROBABILITIES

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When molecular and paleontological data are combined in a phylogenetic framework, fossil information is primarily used to calibrate divergence times in molecular clock analyses. Recent studies of the New Zealand Fossil Record File Electronic Database (FRED) (Crampton et al. 2003) have generated a wealth of statistical data (Cooper et al. 2006, Crampton et al. 2006a, Foote et al. 2007) that could be highly informative for molecular clock analysis. One particular element that seems promising for direct combination with molecular analysis is sampling probabilities for taxa in each stage of the New Zealand geological timescale (Crampton et al. 2006b).

Crampton et al. (2006b) present estimates for the per stage sampling probabilities for both species and genera. The probabilities the authors present are "the mean average probability that any taxon ranging though an entire given stage will have been sampled and recorded at least once from that stage". It is plausible to use these values as approximations for the probability that a taxon first sampled in a given stage originated in that stage (figure 1). In terms of the probability of origination, these values are likely to be over-estimates, as the sampling probabilities are for complete stages so taxa originating during a stage will only represent a portion of that probability. However, these sampling probabilities will serve to test the utility of this data in generating more accurate molecular clock inferences.

Initially, these data could serve to generate more informed calibration priors for Bayesian molecular clock analysis. Prior probability distributions can be generated to more closely match that of the fossil record sampling probability data. The caveat to detailed prior tuning is that, depending on the type of prior distribution used, the Bayesian sampling can stray from prescribed bounds. A novel approach is to use these sampling probabilities to inform the likelihood of a molecular analysis. Divergence times of a node with associated fossil data could be given a likelihood value based on the sampling probability data (see Figure 1). For a phylogeny of New Zealand marine molluscs, where there can be a large number of calibrated nodes, several of these values could be assigned to relevant nodes and summed across the tree. Different trees of the same taxa set could then be compared directly based on concordance to the fossil record with greater mathematical rigor than possible under previous approaches.

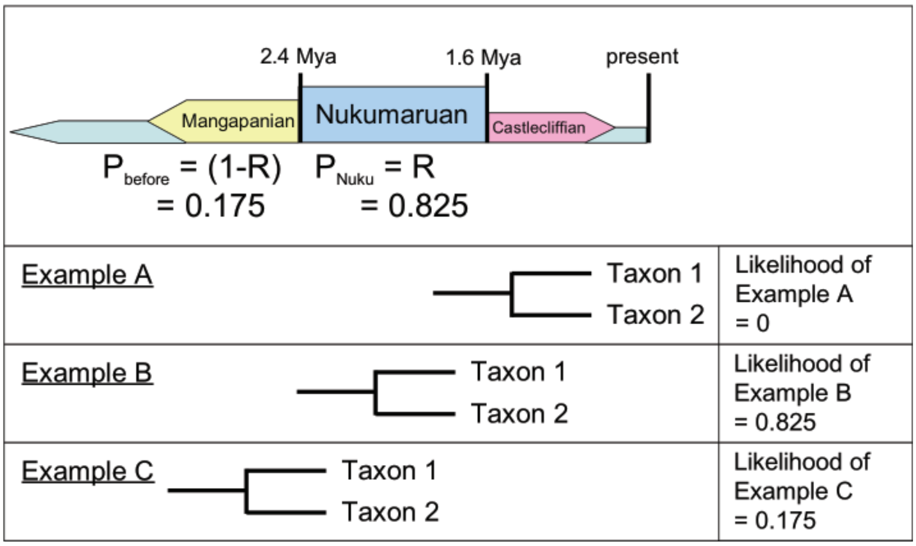

Figure 1: Using fossil sampling probabilities as likelihood values in molecular clock analysis.

Suppose that Taxon 1 and Taxon 2 are thought to have diverged from a common ancestor in the Nukumaruan stage, based on the presence of the first fossil of Taxon 1 in this stage. P_{Nuku} is the probability that Taxon 1 evolved in the Nukumaruan, and P_{before} is the probability that taxon 1 diverged before the Nukumaruan. P_{Nuku} is approximated by R, the sampling probability for species in the Nukumaruan from Crampton et al (2006b). P_{before} will therefore be equal to (1-R). These values can then be attached to a molecular analysis as depicted in examples A, B and C. If a molecular analysis returns a result indicating a divergence in the Castlecliffian this node will have a probability of 0, as fossil evidence shows that Taxon 1 existed in the Nukumaruan. The likelihood of a node such as example B, a divergence in the Nukumaruan, will be 0.82. In the case of example C where the inferred divergence occurred before the Nukumaruan the likelihood of that node would be 0.175. When there are several nodes with associated fossil data the values could be summed across the tree to get a probability of the tree based on the fossil record.

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NEW ZEALAND'S DIPLODACTYLINE GECKOS – A SPECIOSE ENDEMIC RADIATION WITH PROBABLE VICARIANT, GONDWANIC ORIGINS

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New sequence information from the nuclear Rag-1 and Phosducin and mitochondrial ND2 genes has been added to an existing 16S dataset (Hitchmough unpublished; Chambers et al. 2001; Pringle 1998; Chong 1999) to provide more confidence in reconstruction of deeper levels of the phylogeny of New Zealand geckos and their relatives. A more comprehensive coverage of outgroups within the Diplodactylinae (and Pygopodidae) and additional geographic coverage within some New Zealand species was also included.

Monophyly of the New Zealand radiation of at least 40 species is confirmed. Possible dates of initiation of radiation within New Zealand and of divergence from the closest outgroups will be discussed. It is possible that the depth of divergence is consistent with a vicariant Gondwanic origin 80 million years ago. However, the same pattern would be seen if there had been dispersal to New Zealand from Australia at any time between the separation of New Zealand from Gondwana and the first divergence within New Zealand, combined with extinction of all close sister groups.

Our data do not support a particularly close relationship between the New Zealand and New Caledonian radiations, unlike the smaller dataset of Chambers et al. (2001) which weakly supported such a relationship in a trichotomy with the northern Australian genus *Pseudothecadactylus*. These two east Tasman groups now appear to be derived independently from Australian ancestors, and *Pseudothecadactylus* is strongly supported as the sister group to the New Caledonian radiation. The Australian Diplodactylines are now recovered, though with poor support, as the sister group to the New Zealand radiation. Also in Australia, the Carphodactylidae and the legless, snake-like Pygopodidae are more distant outgroups.

Within New Zealand, the same major clades are recovered and the relationship among them is similar to what has been seen previously (allozyme results of Hitchmough 1997 and unpublished 16S and Cyt-B results). *Naultinus* (the diurnal green geckos) is nested well within *Hoplodactylus* (the nocturnal brown and grey geckos).

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LATE EOCENE PALMS, FERNS AND FUNGI, LATE OLIGOCENE PODOCARPS, PROTEACEANS AND EPACRIDS, EARLY MIOCENE ORCHIDS, FISH AND INSECTS: HOW EXCEPTIONAL FOSSIL DEPOSITS IN OTAGO AND SOUTHLAND ARE EXPANDING WHAT WE KNOW ABOUT THE HISTORY OF THE NEW ZEALAND TERRESTRIAL BIOTA

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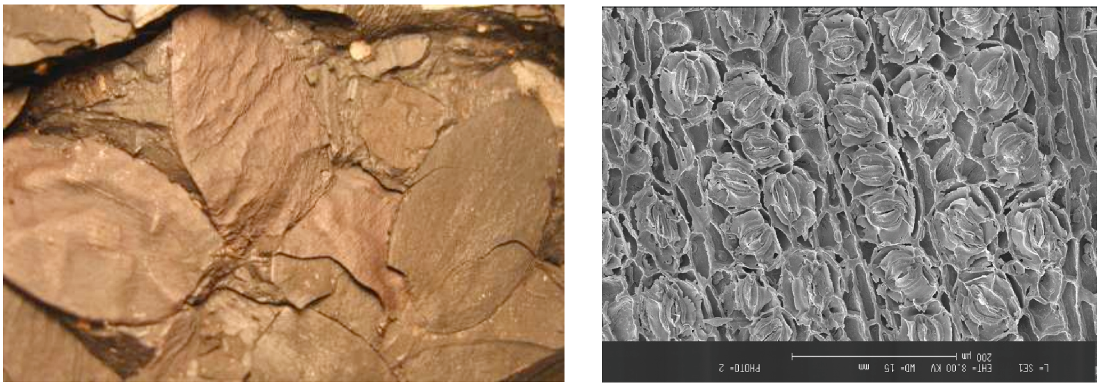
New fossil discoveries are providing new perspectives about the history of the New Zealand terrestrial biota since its break away from Gondwana some 80 million years ago. A major current topic of debate is the timing and extent of the Oligocene marine transgression, and its influence on the terrestrial biota. Was there major (or complete) loss of the fauna and flora in the Oligocene, and a total replacement in the Early Miocene? Such problems are best resolved by investigation of exceptional fossil deposits of Late Eocene, Oligocene, and Early Miocene age such as those recently discovered in Otago and Southland, and incorporation of the fossil evidence into molecular phylogenies.

At three sites, the Pikopiko Fossil Forest, the Newvale Mine leaf beds, and a diatomite deposit at Foulden Maar, organically preserved plant and animal macrofossils can be reliably identified, the deposits can be dated with precision, the paleoenvironment determined, and the flora and fauna can be placed in an ecological context. These deposits span the key time interval from Late Eocene to Early Miocene when the New Zealand land area was reduced to a minimum for the Cenozoic, perhaps to a series of islands occupying an area of 20,000 km^2 (about the size of New Caledonia).

In situ tree stumps of the Late Eocene Pikopiko Fossil Forest (left), and fern frond (right).

The *in situ* Pikopiko Fossil Forest, near Tuatapere in western Southland, was a lowland forest growing on fertile alluvial soils on a flood plain during the Late Eocene (c. 35 Ma) when New Zealand's climate was warm and humid. Forest litter preserved in mudstone of the Beaumont Formation contains numerous angiosperm leaves, fragmentary fern fronds, wood and araucarian bark. The leaves include dicots such as *Metrosideros* sp., Lauraceae, and monocots including a palm (*Calamus*) and leaves and stems of a liane (*Smilax* or *Ripogonum*). Pollen of *Casuarina*, several types of Proteaceae, and *Nothofagus* (*Fuscospora* and *Brassospora)* is present. Pikopiko Fossil Forest has 20 miospore types and six species of fern macrofossils, two of which are fertile (*Cyclosorus* and *Todea*).

Fern spores are common fossils in New Zealand, but their presence must be interpreted with caution as spores may be readily transported. In contrast, fern macrofossils indicate that the plants were growing near the fossil site, as fronds decompose *in situ*. The diversity and abundance of ferns at Pikipiko implies that ferns dominated the forest understorey as in modern New Zealand rainforests. A diverse range of epiphyllous fungi on the angiosperm leaves indicates a high rainfall, and leaves and fruit of the rattan palm, *Calamus*, as well as pollen of *Cupania* (Sapindaceae) and *Austrobuxus* (Euphorbiaceae) indicate a subtropical climate in southern New Zealand in the Late Eocene.



Agathis foliage (left), and leaf cuticle (right) from the Late Oligocene Newvale leaf bed.

At Newvale Mine, Waimumu, Southland, a diverse assemblage of fossil leaves with excellent cuticular preservation occurs in a leaf bed in the Late Oligocene (c. 25 Ma) Gore Lignite Measures. The leaf layers represent litter horizons laid down in pools on the surface of an ombrotrophic forest mire that formed on an extensive low-lying coastal plain. Highly acidic water ponded in depressions prevented microbial decay of the foliage which represents the swamp forest community growing within a few metres of the site. Taxa represented by both leaves and pollen include several conifers (*Phyllocladus*, *Dacrycarpus, Dacrydium* and *Podocarpus)*, a species of *Agathis*, and a variety of angiosperms including *Nothofagus (Brassospora*-type), *Gymnostoma*, epacrids, and several proteaceans as well as species of Cunoniaceae and Sapindaceae. The Newvale locality provides the first record of leaves belonging to an extinct species of *Phormium.* Numerous detached leaves of *Agathis* are present, and amber coloured resin found throughout the Gore Lignite Measures is likely to be derived from *Agathis*, which has a long history in the New Zealand region.

At the Early Miocene (c. 20 Ma) Foulden Maar site near Middlemarch, Otago, freshwater fish, sponges, pollen-bearing flowers and numerous leaves are preserved throughout a >100 m thick, finely laminated diatomite lake deposit. The most common fish is the oldest known fossil of the Southern Hemisphere genus, *Galaxias*. More than 55 pollen types are present. Cuticle preparations of more than 500 leaves indicate that most are from forest trees and lianes with moderately thick cuticles. Most leaves are of dicots, but there are several monocots, including orchids, and one conifer, a large-leaved extinct species of *Podocarpus*. About 40% of the leaves are from the family Lauraceae, including species of *Cryptocarpa* and *Litsea*. Wood-rotting fungi on bark, saprophytic fungi as spores and perithecia within cuticular envelopes, and epiphyllous fungi are present. A newly discovered fertile frond at Foulden is identified as a species in the family Davalliaceae, and provides a link between a well-preserved fern macrofossil and a spore type of previously uncertain affinity. The length and continuity of the record of fern fossils in New Zealand confirms that many families and genera have a long history in New Zealand, rather than being recent arrivals.

Many leaves carry insect feeding traces, and examples of *in situ* scale insects attached to angiosperm leaves, and hair-tuft mite domatia provide rarely preserved examples of plant-animal interactions. A dozen different types of insect fossils have now been collected from the diatomite, expanding the total number of (pre-Quaternary) Cenozoic insects known from New Zealand deposits from two to 14. These new insects include a winged ant (Hymenoptera), a termite (Isoptera), four different examples of Coleoptera, and a species of Hemiptera.

Insect fossil (left) and *Galaxias effusus* Lee, McDowall & Lindqvist (right) from the Foulden Maar.

In conclusion, lagerstätten deposits with exceptionally well-preserved fossils such as those at Pikopiko, Newvale and especially Foulden Maar provide crucial evidence for past climates, information on stratigraphic ranges of key plant and animal groups, and evidence for extinctions. They highlight the role that the New Zealand region has played in the development of global terrestrial paleobiodiversity. Perhaps most importantly, fossils from these deposits provide well-dated calibration points and support for molecular phylogenies.

For instance, the evolutionary history of monocot plants is the subject of intense international research. There is particular interest in family Orchidaceae, which, although representing the largest family of flowering plants with c. 25,000 species, has almost no fossil record. This apparent lack of fossils has reinforced the idea that they are likely to be one of the most recently evolved groups even though DNA studies suggest that they may instead be one of the oldest families of monocots. Our discovery in the Foulden Maar sediments of organically preserved leaf macrofossils representing two genera of epiphytic orchids provides the first evidence for timing of diversification of Epidendroideae, the largest subfamily of orchids, and supports an ancient (Late Cretaceous) origin for Orchidaceae.

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BEETLES UNRAVEL THE LAST GLACIAL MAXIMUM HISTORY OF SOUTH ISLAND FORESTS

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New Zealand's last glacial coldest period (LGCP), around 28,000-18,000 yrs ago[1], consisted of three major glacial advances, the first of which began with major cooling around 34,000 yrs ago[2]. Glaciation had a massive impact on the landscapes and ecosystems of the South Island, and the nature and severity of its ecological impact remain poorly understood. New Zealand lacked the great ice sheets of North America and Eurasia, but it also lacks the continental landmass across which temperate forest communities could retreat[3], so many species found on the South Island today must have survived the LGCP within part of their modern geographical range. Pollen records from this period indicate that most unglaciated parts of the South Island and lower North Island were covered in grasslands during the LGCP, with continuous forests limited to north of 36º S latitude[4]. However, temperature depression alone was not sufficient to explain such limited forest cover[5], and increased dryness, severe winds and incursions of freezing polar air masses have all been implicated in rendering the South Island inhospitable for forest species[6]. In spite of these conditions, pollen evidence does exist for forest survival in small, sheltered refugia, from which they expanded during glacial retreats[7]. In addition, high levels of species endemism and diversity in the flora of the Nelson region have been interpreted as indicative of a major survival centre during the LGCP[8].

A better impression of where and how many forest refugia survived is needed to accurately reconstruct LGCP conditions for New Zealand. We aim to identify the locations of putative South Island forest refugia using fossil remains of native forest beetle species, and comparative phylogeography and ecological niche modeling for five modern members of the beetle fauna. New Zealand has had a dynamic geological history, and the ability to investigate the past using multiple disciplines will greatly enhance our ability to interpret the impact of geological events on the modern flora and fauna.

Insect fossil deposits are invaluable records of ancient ecosystems because they provide a precise, dateable snapshot of a particular place in time. Detailed studies of New Zealand insect fossil assemblages[9,10] have indicated that Coleoptera communities during the LGCP were associated with similar ecosystem types as today, but in different locations, and demonstrate dispersal of communities across the landscape occurs in response to environmental change[11]. The presence of temperate forest species such as *Bembidion actuarium* Broun (Coleoptera: Carabidae) at South Island localities during the LGCP gives us an indication of what environmental conditions must have been at those sites to enable their survival.

Phylogeography is well-suited to identifying regions of long-term forest survival because even short-term absence from a location would erase the genetic evidence of refugia[12]. If forest species had primarily survived in and migrated from northern New Zealand, the long-established northern populations would host the greatest genetic diversity[3], including private haplotypes not present in more recently colonized areas[13]. Successful dispersers would have dominated the genome of leading-edge populations, resulting in southern regions with lower genetic diversity[3]. Alternatively, if New Zealand forest species were able to survive in several small South Island refugia, these areas could be identified as hotspots of genetic diversity scattered across the landscape, differentiated from each other and the larger northern refugia by the presence of unique genetic lineages[13].

Ecological niche modeling incorporates species' modern distribution information and GIS maps of environmental data to test the possible extent of historical and current ranges[14]. Where modern and paleoclimate conditions are known for a region, ecological niche models (ENMs) for a species can be developed and tested on a species' present distribution and then projected onto past climate data to identify regions of potentially suitable habitat.

Phylogenetic and niche model results for the first New Zealand beetle species, *Agyrtodes labralis* (Broun) (Coleoptera: Leiodidae), indicate survival in LGCP refugia largely concordant with those known from insect fossils. Private haplotypes are concentrated around Kaikoura, Marlborough, Nelson, and south along the west coast to Franz Josef Glacier. In particular, the northeastern populations (Kaikoura/Sounds) and north-central populations (Pelorus/Golden Bay) are each comprised of nearly all private haplotypes, and have been geographically isolated from the remaining clades predating the LGCP. ENMs project the most suitable habitat conditions for *A. labralis* in Abel Tasman and the Marlborough Sounds, with a small population centre in Kaikoura and diffuse populations along the west coast of the South Island and around Stewart Island where land has been submerged since the LGCP. LGCP forest insect fossil sites on the South Island include the Awatere Valley[15], Howard Valley in south Nelson[16], Lyndon Stream in northern Canterbury[9], and Westport[10]. Geology of fossil sites and ENMs suggest that water availability, rather than cool glacial temperatures, was a vital determining factor for forest presence/absence. At each location the local hydrology was disrupted by mass movement, tectonic activity or glacial outwash and aggradation, resulting in long-term water availability in otherwise dry ecosystems.

The combined picture from these three techniques is one of forest survival throughout the LGCP in long-term refugia in the northern South Island. Forests in the southern South Island would have existed either in a shifting mosaic of short-term refugia, survived in coastal areas no longer emergent, and/or expanded into the south from populations elsewhere. Phylogenetic and ENM evidence suggests that a combination of these three scenarios resulted in the distribution patterns we see today.

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WHEN DID NEW ZEALAND'S BIRDS EVOLVE?

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A wealth of new research has greatly increased our knowledge of the origins of New Zealand's unique avifauna. Fossil and molecular evidence indicate that the ancestors of some taxa evolved earlier than suspected, e.g. stitchbirds, while others evolved later than previously believed, e.g. Haast's eagle. Some taxa appear to have their origins in the Cretaceous, e.g. moa and New Zealand wrens, while others evolved only in the Pleistocene. The arrival of taxa in Zealandia is debated but most evidence suggests a long history for a few, with the majority arriving over-water since New Zealand's separation from Australis.

EVOLUTION IN NEW ZEALAND: GETTING IT IN PERSPECTIVE.

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Cowie & Holland (2006) argued for a renewed recognition of biotic dispersal as an important and sometimes the only means of origination of lineages in allopatry (geographically separate ranges). As evolutionists studying terrestrial snails on volcanic islands in the Pacific, Cowie & Holland (2006) were frustrated by the persistence of some biologists to relegate dispersal to a minor role, one that was apparently untestable and worse, one that obscured the "true" biogeographic patterns resulting from vicariance. The melding 1970-80's of cladistic and plate tectonic theory underpinned a programme that at best sought to understand the history of continents with reference to the distribution of organisms. However the attempts to explain biotic composition by vicariance biogeography alone yielded an absurd debate centred on the false dichotomy of dispersal versus vicariance; the confusion perhaps arising partly from poorly identified objectives.

Cowie & Holland (2006) noted that a focus on vicariance biogeography resulted in a focus of research on continents and continental islands, despite the clear evidence of dispersal as a major process on oceanic islands as identified by Charles Darwin (Trewick & Cowie 2008). Clearly there are a great many oceanic islands on earth, and even if their total area is small compared to the continents they represent a large number of colonisation events by a huge variety of plant and animal groups. In these terms alone it could be argued that dispersal is a major process underlying diversity on earth. However, it is also evident that on continents (or any landscape) allopatric speciation, through sundering of populations by various biotic and abiotic means (some of which can be defined as vicariance) is important in diversification. Dispersal and vicariance are mechanisms that can limit gene flow among populations and thus facilitate the independent evolution via genetic drift and/or natural selection of the populations. Other mechanisms with the potential to induce the same type of biological outcome (speciation) include mate recognition systems, host shifts and hybridisation (see recent review by Morgan-Richards et al. 2009).

In terms of biodiversity, dispersal and vicariance both influence the same core feature of biological systems- gene flow. Vicariance results in a reduction of gene flow between sundered populations. Dispersal is a property of organisms that maintains gene flow and habitat occupation[1]. The idea that dispersal could facilitate gene flow and contribute to biotic diversification seems paradoxical. We know that even in the face of (weak) selection, gene flow (dispersal) actually limits speciation [hence the conundrum of species range limits raised by Haldane (1954)]. However, the efficiency of dispersal varies in space and time so that the susceptibility of a population to isolation is in part dependent on characteristics of the organisms involved; phylogeographic studies since the 1980's have shown the extent to which gene flow within species is discontinuous even within land areas. Gene flow (dispersal) is influenced by extrinsic factors such as habitat

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[1] A distinction can and often is made between "normal" life-history dispersal and stochastic, passive, long-distance dispersal (LDD). In fact they are parts of the same continuum.

fragmentation (abrupt e.g. volcanic eruption or gradual e.g. climate change or, on a large scale, continental drift).

A child can see that dispersal is an important agent in biology. By coincidence, young Ted Trewick (aged 8) discovered an example just as this abstract was being written. The native diving beetle, *Rhantus* was in a wheelbarrow containing rainwater just two days old-15/1/09.

Cowie & Holland (2006) cautiously set aside New Zealand from their discussion, because it is a continental island. Trewick *et al.* (2007) argued that, the fact that NZ is formed from continental crust rather than oceanic crust should not be taken as proof positive that the biology of NZ and is fundamentally different from that of oceanic islands (see also Trewick & Morgan-Richards in press). The biology of NZ might be quite different from almost all other islands, but to plead a special case without evidence is simply poor science. Indeed, little if any comparison has been made of biology of different oceanic archipelagos let alone between these and continental islands[2]. In a "Darwin 200" themed edition of the *Philosophical Transactions of the Royal Society*, London- Evolution on Pacific Islands, Darwin's Legacy, Trewick & Cowie (2008) focused on molecular evidence on the development of terrestrial faunas of islands in the Pacific region. The volume consists of five biological reviews, and eight science papers on particular taxa. The edition also has a useful comparative review of the geology of Pacific islands, a summary of scale, timing and process (Neall & Trewick 2008).

With respect to the development of biotas in the Zealandia region in particular, a number of observations are made in two recent reviews (Goldberg *et al.* 2008, Grandcolas *et al.* 2008), and third on the Chatham Islands (Trewick *et al.* in prep.) and references there in.

- In some cases of undersampling (for any reason), species-level molecular phylogenies may not provide answers to questions of age and process in development of biotas. Singleton (relict) lineages are unlikely to yield any biogeographic information, while taxa with sparse lineages will be equivocal. Even apparently well-sampled taxa may, through recent extinction, yield misleading phylogenies; the more recent events are more likely to be reliably inferred. Taxa that are well represented in extant regional biotas and are ecologically (and phylogenetically) diverse have greatest potential for informing on biogeography and the processes that drive it (Pratt et al. 2008). NB. Sparse and poorly assigned fossil biotas can similarly result in misinterpretation.
- Integration of phylogenetic, fossil and ecological information is necessary for us to understand how assemblages evolve over time (see Gibb *et al.* this edition).
- Extent of endemism does not directly equate to length of biotic isolation. High species level endemicity is the expected outcome of even short-term isolation (breakdown of gene flow) through the agencies of genetic drift (e.g. closely related North Island giant weta- *Deinacrida fallai* vs *D. heteracantha*) or selection (e.g. Haast's eagle). Furthermore, distinctive forms and ecologies are common on islands and may not indicate ancient origin (e.g. Haast's eagle evolved in Pleistocene probably from a small Australian

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[2] Prior to the acceptance of continental drift, New Zealand's biota was viewed as an island biota.

eagle, and the kakapo presumably evolved flightlessness since extinction of mammals Miocene or later).

- Bearing in mind that there three times as much time passed between separation of Zealandia and maximum submersion in the Oligocene than between the maximum submersion and the present day, a focus on Gondwanan break-up is likely to be (and is) deceptive. In fact, on the basis of vicariance, we might expect greater parity between the biota of New Zealand and that of New Caledonia rather than with other parts of Gondwana, yet so far this does not appear to be the case. This provides another indication of the extent of extinction and replacement (via colonisation and/or speciation).
- Young species radiations are important in the New Zealand biota (Linder 2008). Their existence demonstrates the influence of changing landscape, climate and species interactions on assemblages. This does not preclude the possibility that some lineages may have persisted *in situ* since separation of Zealandia but it is a reminder that any (in time or space) is the product of evolution not stagnation.

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THE ORIGINS OF PLACENTAL MAMMALS: PROBLEMS INTEGRATING MOLECULAR DIVERGENCE TIME MODELS AND FOSSIL DATA.

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The relationships and origins of the placental mammals were a favorite problem of Darwin and Huxley, as they were considered a key part of understanding the history of life on earth. In contrast to some of their better-known achievements, they made relatively little progress on this problem. It is Gregory's (1910) work that is often looked at as the anchor point for these studies in the first half of the nineteenth century. At this time, he accurately identifies most of the 18 orders of placental mammals.

At the close of the twentieth century, there was a flurry of new activity on this problem, including the tree of Waddell, Okada and Hasegawa (1999). This tree was a quantitatively significant advance. For the first time it correctly identified all the main lineages and clades of placental mammals, and what are currently recognized as the 18 orders of placental mammals. It rebuilt the classification of placental mammals following phylogenetic principals and estimated the age of the clades. Many of these newly proposed superorders (e.g., Laurasiatheria, Supraprimates, Boreotheria, Atlantogenata) have now been "tested" with both sequences (e.g., Waddell, Kishino and Ota 2001, Waddell and Shelly 2003) and a variety of rare genomic events (e.g., Kreigs et al. 2006, Waddell et al. 2006). They remain unfalsified, while alternatives such as the morphologically originated hypothesis Epitheria, now seem rather unlikely (Waddell et al. 2006).

Here I examine how reliably the exact and relative ages of these groups are estimated. Estimation of these times increasingly uses models “of the rate of evolution of the rate of evolution” like those developed by Sanderson (1997), Thorne, Kishino and Painter (1998) and Kitazoe et al. (2007). Despite use of these methods, there remains a dichotomy in the estimated age of the first placental. For example, calibrating with fossils from within Laurasiatheria (e.g., the horse/rhino or whale/hippo split) suggests an old age for the root (100-130 mybp), while calibrating within Supraprimates (informally called Euarchontoglires, e.g. human/tarsier, rabbit/pika or basal rodent splits) suggests a much younger root (80-100 mybp, Waddell, Ota, Kishino 2001, Waddell 2007).

These estimates of the age of the root imply rather different biogeographic histories, occurring during quite different phases of the break up of the continents. There are both issues of the duration of the internodes and the exact age of clades. For example, the ancestral lineage of Atlantogenata appears to be of relatively short duration (almost certainly less than 5 million years, Waddell 2007). If this clade was caused by the opening of the South Atlantic ~95 million years ago (Waddell, Okada and Hasegawa 1999), then it is also possible that this vicariant event followed soon after a dispersal, perhaps from the north. Alternatively, if the root of placentals is less than 90 million years old, there is the probability of some quite dynamic dispersal involving early placental mammals.

In assessing the progress in estimating early placental divergence times, it is essential to take both an historical perspective, and to recognize current deficiencies in both the models and the data (not necessarily the familiar dichotomy of fossils versus molecules).

Major issues surrounding molecular divergence time estimation are discussed. These include estimation of edge lengths on substitution trees and testing models of the rate of evolution of the rate of evolution. It is of course essential to both understand and model the fossil data, which calibrates the molecular tree to real time. Significant problems with current methods of analysis are discussed and possible advances are described.

Acknowledgements

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ORIGIN, DIVERSIFICATION, AND CLASSIFICATION OF THE AUSTRALASIAN GENUS *DRACOPHYLLUM* (RICHEEAE, ERICACEAE)[1]

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The genus *Dracophyllum* (Ericaceae) has a fragmented distribution in Australasia, but reaches the greatest level of species richness and morphological diversity in New Zealand. We investigated evolutionary processes that contribute to this disparity in species richness by comparing DNA sequences from members of *Dracophyllum*, its close relatives *Richea* and *Sphenotoma* (together constituting Tribe Richeeae), along with more distant relatives in the Ericaceae. We created complementary data sets for the chloroplast-encoded genes *mat*K and *rbc*L. Both Bayesian and maximum likelihood analyses were conducted to assess the robustness of our phylogenetic inferences. The results were largely congruent and when analyzed in combination provided greater resolution. In our analyses, Tribe Richeeae formed a monophyletic group that diverged during the Eocene (at least 33.3 Ma) with a crown radiation during the early Miocene (at least 16.5 Ma) that resulted in two disjunct lineages. This date corresponds roughly to the onset of aridification in central Australia. The Western Australian genus *Sphenotoma* formed an isolated evolutionary lineage, while *Dracophyllum* and *Richea* together formed a second lineage restricted to Eastern Australia, Lord Howe Island, New Caledonia and New Zealand. The relationships of the Tasmanian endemic, *Dracophyllum milliganii*, remain an enigma. It was ambiguously placed in our analyses either emerging as sister to *Sphenotoma* or to the *Dracophyllum*/*Richea* clade. *Richea* was polyphyletic; we recovered two distinct lineages of *Richea*, traditionally recognized as *R.* sect. *Cystanthe* and *R.* sect. *Dracophylloides*; these were nested within *Dracophyllum*. Because *Richea* is polyphyletic, the status of this genus (and the respective infrageneric classifications of *Dracophyllum* and *Richea*) may be equivocal. The New Caledonian and New Zealand species of *Dracophyllum* dispersed from Australia; we document two independent episodes of long-distance dispersal in the late Miocene to early Pliocene. Low levels of sequence divergence suggest a rapid and recent species radiation in these two island archipelagos largely within the last 3--6 million years. This radiation accompanied Pliocene uplift of the New Zealand Southern Alps and episodes of glaciation during the Pleistocene.

NEW ZEALAND'S ST BATHANS FAUNA: AN UPDATE ON ITS COMPOSITION AND RELATIONSHIPS

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Discovery of an Early Miocene terrestrial fauna near St Bathans, Otago was made during stratigraphic mapping in the 1970s. Investigation of this site, the only insight into the terrestrial vertebrate faunas of New Zealand for the whole Tertiary, began anew in 2001 with the first fieldwork to recover fossils. Prior to our work, the fauna was known to include two presumed waterfowl species and a crocodilian. First to be published as a result of these renewed investigations, in 2006, was New Zealand's inaugural terrestrial mammal, a member of a possibly unknown basal group and dubbed the waddling mouse. The first holistic analysis of the fauna was published in 2007. In this, the fauna was named the St Bathans Fauna, and 23 taxa of birds were reported, with six species formally described, as well as the presence noted of sphenodontids, skinks, geckoes, bats, abundant fish and a crocodilian. The discovery of the 'waddling mouse' was the stimulus for establishment of a joint UNSW, University of Adelaide, Museum of New Zealand Te Papa Tongarewa and Canterbury Museum project to continue investigation of the fauna in the period 2007-2009. Here we summarize the fauna known to date.

Several thousand bones are now catalogued, most being waterfowl. A minimum of 30 bird taxa are now known (Table 1- page 43), with the waterfowl fauna extended to include six described anatids and two undescribed anserines. Descriptions are in press or submitted for the first flamingo-relative (a *Palaelodus* species), the first columbid, the first heron and the first passerine species from the Tertiary of New Zealand. The palaelodid augments the previously known Australasian fauna of two species from Oligo-Miocene sediments in Australia. The heron is the first Tertiary record for the family in Australasia. The pigeon is the sister taxon of *Hemiphaga* and suggests that the New Zealand Pigeon has a lineage extending from the Early Miocene in New Zealand. Because it is member of a fairly derived lineage among pigeons, this fossil species suggests a diverse fauna is yet to be discovered in Australia from where no Tertiary columbids are yet described. The smallest bird in the fauna, represented by four specimens, is clearly a member of the endemic Acanthisittidae, sister group to all other passerines in the world. Within this family, the fossil species appears to be sister to Rifleman and more derived than all other genera, indicating that the radiation of Recent acanthisittids in NZ, dates from no later than the Early Miocene.

Other vertebrates include amphibians, reptiles and mammals. Frog or anuran fossils are rare, but reveal a minimum of three taxa. One leiopelmatid frog (cf. *Leiopelma* n. sp. magn. *L. hamiltoni*) is represented by two vertebrae. A larger leiopelmatid is represented by a humerus. Significantly, a single procoelous vertebra represents probably a neobatrachian frog, a group unknown in the Recent New Zealand fauna but which includes four families of Australian and Melanesian frogs (Myobatrachidae, Hylidae, Microhylidae, Ranidae).

Reptile fossils are relatively common, with about 100 squamate bones now known and a similar number of crocodilian fossils. The squamates, with only skinks and geckoes present, do not differ from the living genera *Oligosoma* (skinks) or *Hoplodactylus* (geckoes). Sphenodontidae, of which the extant Tuatara (*Sphenodon*) is the only living representative, is represented by three fragmentary specimens that are not distinguishable from Recent *Sphenodon* jaws. The presence of endemic New Zealand type skinks and geckoes in the early Miocene doubles recent estimates of the age of this group based on molecular clock estimates.

The identity of St Bathans's terrestrial mammal remains elusive, but further remains have been found. A significant number of bat fossils now reveals a minimum of four taxa in at least three families. One of these is a member of the present endemic Mystacinidae, and another represents a new family related to South American noctilionoids. The latter is known by the only mammal teeth known from the fauna, upper and lower molars, as well as dentary fragments and postcranial bones.

Several of the avian taxa are still only known by one fossil e.g., *Palaelodus*, the columbid new genus, *Collocalia*, and *Aegotheles*, and several other taxa, notably the waddling mouse, by less than 5 specimens. These observations show that while the available sample is relatively large, it has not yet revealed the faunal diversity contained in these fossil deposits. Without doubt, continued investigations will reveal more taxa and allow the circumscription of those known rather imperfectly at present.

In addition to these vertebrates, a diverse range of invertebrates includes aquatic hyriid and sphaerid clams, hydrobiid gastropods (2 spp), several cf. charopid land snail taxa, and freshwater crayfish.

The St Bathans Fauna reveals that in the Early Miocene, 19-16 Ma, New Zealand had a vertebrate fauna that in many ways was similar to the present one. The major change since then has been the extinction of several major groups – a crocodilian, an anuran, one bat family and two bird families. Specifically, the endemic families New Zealand is renowned for, Leiopelmatidae, Sphenodontidae, Mystacinidae, and among birds Acanthisittidae and Dinornithiformes, were all members of this fauna. Moreover, in waterbirds, lizards and all other taxa in which taxonomic circumscription and or phylogenetic analyses or assessments have been possible, the fauna reveals endemism at the species and generic level. It is clear that had New Zealand been totally inundated during the Oligocene high stand in sea level then all New Zealand's special endemic taxa had to disperse to and colonise Zealandia during the first 3-4 million years of the Miocene, with no subsequent additional such taxa arriving. We interpret the St Bathans Fauna as one already reflecting a long in situ faunal evolution based on an initial vicariant component augmented by ongoing dispersal.

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Table 1. A summary of vertebrate taxa other than fish from the St Bathans Fauna. Data from Worthy *et al.* (2006, 2007, 2008, submitted a, b); Scofield *et al.* (submitted); Jones *et al.* (submitted) and unpublished data.

Higher taxon or Family	Genus	Species
Anura		
Leiopelmatidae	cf. *Leiopelma*	magn *L. hamiltoni*
	cf. *Leiopelma*	magn *L. markhami*
Family indet.	Genus indet.	sp. indet. 1
Reptilia		
Crocodilian, family indet.	Genus indet.	sp. indet. 1
Sphenodontidae	cf. *Sphenodon*	sp. indet.
Gekkonidae	cf. *Hoplodactylus*	sp. indet. 1&2
Scincidae	cf. *Oligosoma*	sp. indet. 1&2
Aves		
?Dinornithiformes	Genus indet.	sp. indet. 1
Pelecanoididae	*Pelecanoides*	*miokuaka*
Anatidae	*Manuherikia*	*lacustrina*
	Manuherikia	*minuta*
	Manuherikia	*douglasi*
	Miotadorna	*sanctibathansi*
	Dunstanetta	*johnstoneorum*
	Matanas	*enrighti*
	Anserine genus indet. A	sp. indet. 1
	Anserine genus indet. B	sp. indet. 2
Palaelodidae	*Palaelodus*	sp. nov.
Accipitridae	Genus indet. (eagle)	sp. indet. 1
	Genus indet.	sp. indet. 2
Ardeidae	Genus nov.	sp. nov.
Gruiformes, family indet.	Genus indet.	sp. indet. 1
Rallidae	Genus indet.	sp. indet. 1
	Genus indet.	sp. indet. 2
Laridae	Genus indet.	sp. indet. 1
cf. Charadriidae	Genus indet.	sp. indet. 1
	Genus indet.	sp. indet. 2
Columbidae	Genus nov.	sp. nov.
	Genus indet.	sp. indet. 1
Psittacidae	Genus indet.	sp. indet. 1
	Genus indet.	sp. indet. 2
	Genus indet.	sp. indet. 3
Aegothelidae	*Aegotheles*	sp. indet. 1
Apodidae	*Collocalia*	sp. indet. 1
Passeriformes		
Acanthisittidae	Genus nov.	sp. nov.
Cracticidae	Genus indet.	sp. indet. 1
Family indet.	Genus indet.	sp. indet. 2
	Genus indet.	sp. indet. 3
Mammalia		
Microchiroptera		
Mystacinidae	Genus indet.	sp. indet. 1
Vespertilionidae	Genus indet.	sp. indet. 1
	Genus indet.	sp. indet. 2
Family nov.	Genus nov.	sp. nov.
'Waddling mouse', fam. nov.	Genus indet.	sp. indet. 1