

# **'GeoGenes V'**

## **Geology and Genes V 2014**

*A meeting of mudstone and molecules*



## BIBLIOGRAPHIC REFERENCE

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## COVER IMAGES

**Top left:** Geologically modern beetle trapped in dried mud; the beetle carapace, associated pollen, trackway, rain-drop impressions, and mud cracks, if incorporated into the rock and fossil records, would all provide data about the life and times of that beetle. Photo: James Crampton.

**Top right:** Dinosaur hunting in Late Cretaceous sandstone, Mangahouanga Stream, Hawke's Bay. The enclosing vegetation probably resembles the forest that was grazed by the dinosaurs themselves. Photo: James Crampton.

**Centre:** Part of a paleogeographic map of central New Zealand for the Early Pleistocene, 2.4 million years ago. The outline of modern-day New Zealand shown in pale grey. Image: Kyle Bland, modified from Fig. 4C in Trewick and Bland, 2012. Fire and Slice: palaeogeography for biogeography at New Zealand's North Island/South Island juncture. *Journal of the Royal Society of New Zealand* 42: 153-183.

**Bottom left:** Blue duck, whio, *Hymenolaimus malacorhynchos* (family Anatidae), an endemic torrent duck that is one of a small number of species remaining of New Zealand's once very large 'duck' fauna. Waiau River, Hawke's Bay. Photo: James Crampton.

**Bottom right:** Mapping in the 'Ruataniwha Strait' (see central map) – ~2 million year old Pleistocene limestone overlying mudstone, Te Muna area, Wairarapa. The limestone contains a rich fauna of shallow-marine molluscs that occupied current-swept submarine highs within the Ruataniwha Strait. Photo: James Crampton.

***‘GEOGENES V’***  
***GEOLOGY AND GENES V 2014***

***A meeting of mudstone and molecules***

**2<sup>nd</sup>-3<sup>rd</sup> July, 2014**

**Museum of New Zealand Te Papa Tongarewa, Wellington**

Editors

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## Geology and Genes V

In 1962, the New Zealand biologist, paleontologist and geologist, Sir Charles Fleming, wrote:

“In our age of specialisation ‘the seamless coat of learning has been so rent and tattered’ that it is difficult to synthesise data even from the several branches of Natural History.”<sup>1</sup>

Some may argue that this situation has not changed or, perhaps, that it has worsened. In response, however, the occasional ‘*Geology and Genes*’, or ‘*GeoGenes*’, meetings<sup>2</sup> continue to bridge disciplinary silos, and to encourage thinking in the great traditions of Natural History using the tools of modern molecular biology, ecology, geology and paleobiology. Thus, molecular biologists probe the antiquity of clades, paleontologists squeeze the fossil record in order to resolve processes happening at ecological scales, and geologists map Zealandia’s ancient bays and mountains: at the interface of all these disciplines we are gaining new insight into New Zealand’s wonderful biological history.

<sup>1</sup> Fleming, C. A., 1962. New Zealand biogeography; a paleontologist’s approach. *Tuatara* 10 (2): 53-108.

<sup>2</sup> *GeoGenes* meetings were held previously in 1994, 1998, 2006 and 2009.

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# MAP



## City Attractions

1. Colonial Cottage Museum
2. National War Memorial & Carillon
3. Mount Victoria Lookout
4. Embassy Theatre
5. The Film Archive
6. Westpac St James Theatre
7. Downstage Theatre
8. Bats Theatre
9. Overseas Terminal
10. Museum of New Zealand Te Papa Tongarewa
11. Circa Theatre
12. The Opera House
13. Wellington Convention Centre/ Michael Fowler Centre/ Wellington Town Hall
14. Wellesley Boat
15. Civic Square/ City Gallery/ Capital E/ Wellington City Library/ Wellington i-SITE Visitor Centre
16. Adam Art Gallery
17. The Events Centre Wellington
18. Museum of Wellington City & Sea
19. New Zealand Academy of Fine Arts
20. Cable Car/ To Cable Car Museum/ To Carter Observatory
21. Botanic Garden
22. Government Buildings Historic Reserve/ DOC
23. Parliament Buildings/ Beehive
24. Archives New Zealand
25. Wellington Cathedral
26. National Library/ Alexander Turnbull Library
27. Old St Paul's
28. Katherine Mansfield Birthplace

## Accommodation Providers

29. Brentwood Hotel
30. Harbour City Motor Inn
31. Mercure Hotel Willis Street
32. Mercure Hotel Wellington
33. Comfort Hotel Wellington
34. Wildlife House Backpackers
35. base Backpackers
36. YHA Wellington
37. The Bay Plaza Hotel
38. Kingsgate Hotel Oriental Bay
39. Museum Hotel de Wheels
40. Duxton Hotel Wellington
41. West Plaza Hotel
42. Just Hotel
43. Copthorne Hotel Wellington Plimmer Towers
44. CityLife Wellington
45. James Cook Hotel Grand Chancellor
46. InterContinental Wellington
47. Hotel Ibis Wellington
48. Novotel Capital Wellington
49. Quest on Johnston
50. Quest Atrium
51. The Wellesley
52. Downtown Backpackers
53. Bolton Hotel
54. The Portland Hotel of Thorndon
55. Thorndon House B&B

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# CONFERENCE PROGRAMME

**Wednesday July 2<sup>nd</sup>**

The meeting will be held in the Icon Room Level 2, Te Papa

	Surname	First Name	Title
<b>09:00 – 09:10</b>	<b>REGISTRATION</b>		
<b>09:10 – 09:20</b>	<b>Greetings and Opening</b>		
<b>09:20 – 10:30</b>	<b>Session 1: Macroevolution</b>		
09:20	<b>Keynote 1</b>	Marshall Charles	Discovering the ecological and evolutionary rules of biodiversity change.
10:10		Crampton James	Fluctuating extinction selectivity in graptolites from very high resolution survivorship analysis.
<b>10:30 – 11:10</b>	<b>Morning break</b>		
<b>11:10 – 12:30</b>	<b>Session 2: Marine Molluscs</b>		
11:10		Hills Simon	The evolution of New Zealand <i>Alcithoe</i> , an integration of molecular and paleontological evidence.
11:30		Gemmell Michael	Interpreting <i>Buccinulum</i> taxonomy at the confluence of morphologic and molecular techniques.
11:50		Collins Katie	Anchors and snorkels: heterochrony, form and function in New Zealand crassatellid bivalves.
12:10		Vaux Felix	Integrated phylogenetics of a neogastropod genus.
<b>12:30-14:00</b>	<b>Lunch and posters</b>		
<b>14:00 – 15:30</b>	<b>Session 3: Paleogeographies</b>		
14:00	<b>Keynote 2</b>	Kamp Peter	Cenozoic paleogeography of New Zealand.
14:50		Bland Kyle	Geology for biology: Plio-Pleistocene paleogeography of New Zealand's North Island – South Island juncture.
15:10		Strogen Dominic	Paleogeography of the Taranaki Basin during the latest Eocene to Early Miocene and implications for the "total drowning" of Zealandia.
<b>15:30 – 16:00</b>	<b>Afternoon Break</b>		
<b>16:00 – 17:20</b>	<b>Session 4: Evolution and Paleoenvironment</b>		
16:00		Jordon Greg	Directional evolution of cell size – adaptation, genomes and ancestral state reconstruction.
16:20		Reichgelt Tammo	Temperature-driven foliar physiognomic divergence of the New Zealand flora since the Early Miocene.
16:40		Daly Elizabeth	Following fossils and living lineages. Investigating variation in shell shape and genetics of <i>Placostylus</i> through time.
17:00		Powell Nick	Are cryophily and nocturnality of New Zealand's iconic endemics legacies of Cretaceous polar cold and darkness?
<b>Posters</b>	Posters will be displayed for the duration of the Meeting	Wood Jamie	Extinct Holocene birds of the Chatham Islands: ancient dna provides new taxonomic and phylogenetic insights.
		Prebble Joe	Ranges of New Zealand pollen through the Cenozoic

## Thursday July 3<sup>rd</sup>

		Surname	First Name	Title
09:00 – 09:10	<b>House Keeping</b>			
09:10 – 10:20	<b>Session 5: NZ Miocene Biotas</b>			
	09:10	<b>Keynote 3</b>	Worthy Trevor	Updating the record from the Early Miocene St Bathans fauna, Central Otago and its significance for documenting the assembly of New Zealand's terrestrial biota.
	10:00		Conran John	Exceptional terrestrial biotas from Miocene New Zealand.
10:30 – 11:10	<b>Morning break</b>			
11:00 – 12:20	<b>Session 6: NZ Terrestrial Biotas</b>			
	11:00		Tennyson Alan	The evolution of <i>Nestor</i> parrots.
	11:20		Mitchell Kieran	Ancient dna reveals pre-Oligocene diversification in the acanthisittid wrens ( <i>Acanthisittidae</i> ).
	11:40		Hitchmough Rod	A robust phylogeny for New Zealand geckos and their immediate outgroups.
	12:00		Simon Chris	Phylogeography of six North Island, New Zealand cicadas and their relationship to multiple biogeographic boundaries suggests a re-evaluation of the Taupo line.
12:30-14:00	<b>Lunch and posters</b>			
14:00 – 15:30	<b>Session 7: NZ, Dynamic land and Fauna</b>			
	14:00	<b>Keynote 4</b>	Penny David	The importance of integrating geology and biology.
	14:50		Campbell Hamish	Zealandia: Latest geological perspectives.
	15:10		Scofield Paul	A remarkable mid-Pliocene Volant marine fossil bird assemblage alters our understanding of marine bird evolution in the Pliocene.
15:30 – 16:00	<b>Afternoon Break</b>			
16:00 – 16:45	<b>Session 8: Discussion session</b>			
	16:00		All participants	Setting a research agenda at the intersection of geology and biology in New Zealand.
	16:30	<b>Closing</b>		

## Friday July 4<sup>th</sup>

**Field trip** – details to be announced at meeting.

## ABSTRACTS



Juvenile specimen of Marlborough rock daisy, *Pachystegia insignis* (family Asteraceae), growing out of Eocene limestone, Mead Stream, Clarence valley, Marlborough. The genus *Pachystegia* contains, arguably, three species and is one component of New Zealand's large endemic flora. The Eocene limestone in Mead Stream contains abundant microfossil evidence of greenhouse climates and 'hyperthermal' climate events that occurred between about 56 and 35 million years ago. Photo: James Crampton.



## GEOLOGY FOR BIOLOGY: PLIO-PLEISTOCENE PALEOGEOGRAPHY OF NEW ZEALAND'S NORTH ISLAND–SOUTH ISLAND JUNCTURE

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Biogeography seeks to explain the distribution of biological diversity in space and time. Contrasting regional endemism and diversity highlight central New Zealand as an area of interest to biogeographers and evolutionists. This area, which extends from Taupo to northern South Island, is also of interest to geologists as it encompasses a zone of intense tectonic deformation related to subduction of the Pacific Plate and the transfer of relative plate motion from the subduction thrust to the Alpine Fault. Cook Strait, a marine breach across the trend of New Zealand's extensive axial ranges, is a geologically young feature, and the shape and position of what we now consider to be "North" and "South" islands has changed significantly during the past 4 million years. These changes have likely influenced the biogeography of the region.

A series of paleogeographic reconstructions, produced using updated geological mapping and other recently compiled data sources, depict the latest Neogene (c. 4 to 0 Ma) development of central New Zealand (Trewick & Bland 2012, Bland et al. 2013). The maps illustrate the general type of inferred terrestrial topography, in particular the distribution of mountains >1000 m. The maps show that much of southern North Island was submerged until c. 1.5 Ma. Until the relatively recent formation of Cook Strait during the past 0.5 million years, the Wellington area was geographically part of northern South Island. The Kaimanawa area was probably terrestrial from the latest Miocene, with mountainous topography developing during the early-Late Pliocene and Late Pliocene in the Kaimanawa and Kaweka ranges, respectively. By contrast, the Ruahine-Tararua ranges, which are the dominant topographic features in southern North Island today, are relatively young, having formed since c. 1 Ma.

The implications for the late Neogene biogeography of central New Zealand are considerable in terms of habitat availability for terrestrial species and opportunities for range shifting of both terrestrial and coastal organisms.

### References:

- Bland, K. J., A. J. W. Hendy, P. J. J. Kamp and C. S. Nelson. 2013. Macrofossil biofacies in the late Neogene of central Hawke's Bay : applications to palaeogeography. *New Zealand Journal of Geology and Geophysics* 56: 200–222.
- Trewick, S. A. and K. J. Bland. 2012. Fire and slice: palaeogeography for biogeography at New Zealand's North Island/South Island juncture. *Journal of the Royal Society of New Zealand* 42: 153–183.

## ZEALANDIA: LATEST GEOLOGICAL PERSPECTIVES

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Any understanding of the origins of the native terrestrial biota of New Zealand requires consideration of the geological history of New Zealand and its continental heritage as part of Zealandia and Gondwana.

This presentation offers some of the latest geological thinking and maps on this topic and is timely because the authors have just completed a popular book entitled: 'Zealandia: our continent revealed', which will be published in late August, 2014.

This is also an opportunity to take stock of the remaining geological uncertainties that pertain to 1) biological versus tectonic timing of separation/isolation of Zealandia from Gondwana in the Late Cretaceous interval 105-85 million years ago, and 2) interpretations of permanent land during Late Oligocene to Early Miocene time. These 'uncertainties' are largely about imprecise age control on rock formations (terrestrial versus marine), geological (sedimentary, volcanic and tectonic) events and rates of processes, and the nature of the fossil record.

### References:

Mortimer, N. and H. Campbell. 2014 (in press). *Zealandia: our continent revealed*. Penguin Books Ltd, Auckland. 272 pp.

# ANCHORS AND SNORKELS: HETEROCHRONY, FORM AND FUNCTION IN NEW ZEALAND CRASSATELLID BIVALVES

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We combine new growth-rate estimates for nine species from three genera of New Zealand Crassatellidae (Bivalvia: *Spissatella*, *Eucrassatella* and *Triplicitella*) with previously-published shape and size data and recent phylogenetic analysis, to identify heterochronic processes in their evolution.

$\delta^{18}\text{O}$  measurements identify annual high-low couplets in macroscopic shell banding, allowing estimation of total age-at-death for individual shells. From this, growth-rates and mean ages can be derived for each species for the first time. Shape and size data for adult, immature and juvenile size classes from Crampton & Maxwell (2000) are recalibrated with reference to these new ages, and the most recent phylogeny of the New Zealand Crassatellidae (Collins et al., accepted) provides the ancestor-descendant framework within which heterochronic processes are identified. Paedomorphosis and peramorphosis are both present within the clade, with an overall tendency towards size increase, and a general coupling of shape and size dissociated from lifespan.

Morphological variability and response to environmental pressure in this non-siphonate group is restricted by anatomical constraints. Two form-groups of associated suites of shell characters within the study taxa have been identified: heavy, armoured “anchors” and relatively highly-sculptured, elongate “snorkels”. Heterochrony produced the variation in developmental timing that led to the association of traits that characterise each form-group. Anchors and snorkels represent different ‘solutions’ to the problems of life as a non-siphonate, infaunal bivalve.

## References:

- Collins, K. S., J. S. Crampton and M. Hannah. Accepted. Stratocladistic analysis and taxonomic revision of the character-poor New Zealand crassatellid bivalves *Spissatella* and *Eucrassatella*. Journal of Molluscan Studies.
- Crampton, J. S. and P. A. Maxwell. 2000: Size: all it's shaped up to be? Evolution of shape through the lifespan of the Cenozoic bivalve *Spissatella* (Crassatellidae). Geological Society of London, Special Publications 177: 399–423.

## EXCEPTIONAL TERRESTRIAL BIOTAS FROM MIOCENE NEW ZEALAND

John G. Conran<sup>1,\*</sup>, Uwe Kaulfuss<sup>2</sup>, Daphne E. Lee<sup>2</sup>, Jennifer M. Bannister<sup>2</sup>,  
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<sup>3</sup> Georg August Universität, Courant Research Centre Geobiology, Göttingen, Germany.

Exceptional fossil sites are giving new insights into the floras and particularly the terrestrial invertebrate faunas of Oligocene to Miocene New Zealand. They include lacustrine diatomite deposits at Foulden and Hindon Maars and amber deposits at Roxburgh, Hyde and Cosy Dell.



At Foulden Maar, a diverse arthropod assemblage, including members of the Araneae, Plecoptera, Isoptera, Hemiptera, Coleoptera, Hymenoptera, Trichoptera, Odonata and Diptera, chiefly represents ground-dwelling taxa of forest floor and leaf litter habitats, mostly from subfamilies and genera still present in the modern fauna. A newly discovered biota from Hindon Maar includes beetles with rarely-preserved structural colour (Fig. A), several weevils (Fig. B), pollen-bearing flowers including Araliaceae (Fig. C), fish with skin and mouthparts preserved (Fig. D), and a fossil feather. A preliminary study of amber from three Cenozoic sites has revealed diverse mites, a variety of spiders and their web remains with prey, a pseudoscorpion and several Collembola. Inclusions of insects include Coleoptera, Hymenoptera, Heteroptera and Diptera, as well as Psocoptera and Lepidoptera. Other significant fossils in amber include nematodes and a variety of fungi, including sooty moulds. To date, we have collected ~260 terrestrial arthropods from all these sites, representing 33 families in 14 orders. Many of these new fossils represent groups with a poor fossil record for the entire Southern Hemisphere.

These *Lagerstätten* deposits, which preserve soft delicate tissues such as flowers, fish skin and mouthparts, insect wings, eyes and colour, and feathers, are of international significance. They provide fossil evidence for the antiquity of some of New Zealand's terrestrial plants and animals as well as potential time-calibration points for phylogenetic studies.

## FLUCTUATING EXTINCTION SELECTIVITY IN GRAPTOLITES FROM VERY HIGH RESOLUTION SURVIVORSHIP ANALYSIS

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<sup>3</sup> Department of Earth Sciences, University of California, Riverside, California 92521, USA.

Is extinction risk related to time since first appearance of a taxon (“taxon age”)? This question is of particular relevance today as extinction rate increases because of human activities, but also because it relates to controls of long-term biodiversity dynamics in general. Based on studies of the fossil record, extinction risk has been inferred generally to be either independent of taxon age (the “Law of Constant Extinction” as in Red Queen evolution) or to be inversely related to taxon age (at least, at the genus level or higher). The latter pattern is assumed to reflect the expectation of increased species richness and geographic range with increased taxon age, properties that are likely to promote extinction resistance. Here we exploit a very high-resolution database of Paleozoic zooplankton to examine extinction selectivity in relation to taxon age. Our data comprise continuous (unbinned) time series of origination and extinction for 1802 of the most common graptoloid species over virtually the entire history of the group (Ordovician-Silurian, 74 m.y.). The time series derive from quantitative biostratigraphic analysis of 518, globally distributed stratigraphic sections, have an average time resolution of 37 k.y., and span several major extinction events including the Late Ordovician Extinction Event.

We have examined age selectivity at the species level using logistic regression of cohort age *versus* proportion surviving for multiple cohort survivorship curves that intersect each of many time bins through the Ordovician and Silurian. We have analysed the data using imposed time bins varying from 0.25 m.y. to 1 m.y. in duration; our adopted results are robust to sensitivities related to time-binning protocols. Age-selectivity of extinction can be detected through about half of Ordovician and Silurian time, and occurs in short, sharp pulses separated by intervals during which no selectivity can be detected. During the Ordovician, with minor exceptions, extinction risk was inversely related to taxon age. In contrast, in the late Katian and Silurian, with an extinction rate significantly higher and more volatile than that of the Ordovician, age-selective extinction fluctuated between negative (favouring long-lived species) and positive (favouring short-lived species). The mechanism for this striking pattern is the subject of on-going investigation, but is likely to lie in global patterns of oceanic circulation, nutrient flux and temperature gradients, as inferred previously by us for species richness and extinction rate changes (Cooper et al. 2014).

### Reference:

Cooper, R. A., P. M. Sadler, A. Munnecke and J. S. Crampton. 2014. Graptoloid evolutionary rates track Ordovician-Silurian global climate change. *Geological Magazine* 151: 349-364.

# **FOLLOWING FOSSILS AND LIVING LINEAGES. INVESTIGATING VARIATION IN SHELL SHAPE AND GENETICS OF *PLACOSTYLUS* THROUGH TIME**

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Evolutionary and ecological processes are intrinsically linked. Evolution shapes the form and behaviour of organisms, whereas ecology generates selection and provides opportunities for adaptation. Here we examine evolutionary processes acting on ecological timescales. We use morphological, genetic and biogeographic information of extant and sub-fossil *Placostylus* landsnails to explore patterns of speciation, geneflow and hybridization among populations.

New Zealand is home to three endemic species of the SW Pacific landsnail genus *Placostylus* Beck, 1837. Sister groups are found in New Caledonia. New Zealand species are restricted to the Te Pahi district in northernmost mainland and some offshore islands. Sub-fossil remains have been recovered from 13 horizons spanning a short timeframe ~5000ybp with isolated fossils dating to ~40,000ybp. These sub-fossil deposits are found close to extant populations.

Shells of adult *Placostylus* are characterized by a thickened apertural lip, formed at sexual maturity, after which the growth in shell size stops (Penniket 1981). Original morphological descriptions (Powell 1979) were influenced by the size, position and number of tubercles around the aperture of the shell and other characteristics such as colour. Subsequent studies have used traditional shell measurement techniques to compare shell size and aperture between populations with limited success; however Penniket (1981) found a relationship between distance from the sea, type of forest cover and shell morphology. A recent geomorphometric analysis of New Caledonian *Placostylus* (Dowle 2014) was used to compare shell morphology to mtDNA and nuclear genetic data. Results showed that shell morphology was related to environment and concordant with genetic data, suggesting that environment is driving the formation of ecotypes in New Caledonian *Placostylus*.

Here we aim to study changes between and within populations through time to the present day, testing the mode of morphological evolution, and placing modern variation into the context of variation over thousands of generations.

## **References:**

- Dowle, E. J. 2014. Rates of molecular evolution and gene flow. Unpublished Ph.D. thesis, Massey University, New Zealand.
- Penniket, A. S. W. 1981. Population studies of land snails of the genus *Placostylus* in the North of New Zealand. Unpublished M.Sc. thesis, University of Auckland, New Zealand.
- Powell, A. W. B. 1979. New Zealand Mollusca. William Collins Publishers Ltd, Auckland.

## INTERPRETING *BUCCINULUM* TAXONOMY AT THE CONFLUENCE OF MORPHOLOGIC AND MOLECULAR TECHNIQUES

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Discrepancies between species delimitations inferred using different approaches are problematic for the reconstruction of accurate paleophylogeographic accounts of species evolution. As phylogenies are being reexamined with the use of increasingly powerful molecular tools, established taxonomies are being reconsidered. This is the case in a wide range of taxa. Recently Hills et al. (2012) have uncovered and resolved an example of this in *Alcithoe*, a marine mollusc genus found in NZ waters.

An initial investigation into the genus *Buccinulum* has uncovered inconsistencies between the current classifications and molecular phylogenies. *B. Colensoi*, *B. vittatum vittatum* and *B. vittatum littorinoides* make up a group of three lineages based on morphology and geography. These however are represented by only two lineages based on the mtDNA gene cytochrome oxidase 1: *B. vittatum vittatum* and a complex of *B. colensoi* and *B. vittatum littorinoides*. It has been shown that single gene trees are not always representative of true phylogenies, and phylogenies built on multiple loci are generally more robust (e.g., Spinks et al. 2014). Using next generation sequencing DD-rad Seq, we aim to confirm the molecular phylogeny for *Buccinulum* using multiple loci, both mitochondrial and nuclear. We then want to bring together morphometric and molecular methods. To do this the shells have been analysed using morphometric techniques to determine the amount of variation in the lineages and establish if any morphologic variation has relationship with the new phylogenies. If possible we hope to extract morphological characteristics which are taxonomically or phylogenetically informative.

Extending these methods into the fossil record is a broader goal of this project. New Zealand has one of the most complete marine fossil records for the last ~50 million years (Crampton et al. 2006). With a better understanding of the relationship between morphology and molecular phylogenies we plan to explore the evolutionary mode of species which have lineages extending from the fossil record into the living fauna.

### References:

- Crampton, J. S., M. Foote, A. G. Beu, R. A. Cooper, I. Matcham, C. M. Jones, P. A. Maxwell and B. A. Marshall. 2006. Second-order sequence stratigraphic controls on the quality of the fossil record at an active margin: New Zealand Eocene to Recent shelf molluscs. *Palaios* 21: 86–105.
- Hills, S. F. K., J. S. Crampton, S. A. Trewick and M. Morgan-Richards. 2012. DNA and morphology unite two species and 10 million year old fossils. *PLoS ONE* 7: e52083.
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## THE EVOLUTION OF NEW ZEALAND *ALCITHOE*, AN INTEGRATION OF MOLECULAR AND PALEONTOLOGICAL EVIDENCE

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Comprehensive integration of paleontological and molecular data remains a sought-after goal of evolutionary biology. The reciprocal illumination of these two fields is leading to a greater understanding of the evolutionary history of the New Zealand marine mollusc genus *Alcithoe* H. & A. Adams, 1853. Mitochondrial DNA sequence was used to infer a well-resolved phylogeny for *Alcithoe*. Molecular phylogenetics helped to clarify the taxonomy of the genus, which suffers from a paucity of discriminating morphological characters. Combined with morphometric analysis, these data demonstrate the synonymy of *A. knoxi* with *A. wilsoni*, enabling the confident application of ~10 million year old *A. knoxi* fossils in dated phylogenetic analysis. Our calibration regime utilised fossil occurrences of living species together with fossil sampling probabilities to generate prior distributions for Bayesian inference of divergence times in *Alcithoe*. This approach yielded a well-supported tree with divergence times that are consistent with the fossil record. The pattern of diversification implied by the molecular phylogeny indicates that most *Alcithoe* speciation has occurred relatively recently. However, this appears to be at odds with the fossil record, in which more taxonomic diversity is observed to have occurred in the past. Using our time-calibrated molecular phylogeny and diversification rates for New Zealand Mollusca calculated from paleontological data, we examine the diversification process in the *Alcithoe* lineage during the Cenozoic. Our results show that for *Alcithoe*, diversification of the living taxa is not representative of the complete evolutionary history of the lineage. Finally, as any explicit incorporation of fossil taxa into phylogenetic analysis will necessarily involve morphological characters, we examine the consistency of morphology and phylogeny in *Alcithoe*. In evaluating disagreement between molecular and morphological data in *Alcithoe* we found that an ecological variable, maximum habitat depth of species, is correlated with a significant conflicting signal in the morphological dataset.

## **A ROBUST PHYLOGENY FOR NEW ZEALAND GECKOS AND THEIR IMMEDIATE OUTGROUPS**

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The New Zealand gecko phylogeny published by Nielsen et al. (2011) contained some surprises. The New Zealand and New Caledonian Diplodactylinae gecko radiations are each monophyletic, but they are not sister groups as previously hypothesised. Each is independently derived, with different sister clades in Australia, where all the more distant immediate outgroups are also found. Divergence of the New Zealand radiation from its sister group pre-dates the Oligocene but does not appear to be old enough to indicate a vicariant, Gondwanic origin (40.2 mya; 95% highest posterior density estimate 28.9–53.5). The estimated date for the basal split within the radiation is 24.4 mya (range 15.5–33.8), but at least two different-sized gecko taxa are present in the 16–19 mya Saint Bathans fauna. The New Zealand radiation contains seven distinct clades that we have recognised as genera, and about 40 species. Most species have Pliocene divergence dates. Considerable species diversity and local phylogeographic structure indicates persistence *in situ* or only very local movement in much of the South Island during the Pleistocene. The high taxonomic and ecological diversity of the group is extremely unusual for a temperate landmass. Additional discoveries remain likely.

### **References:**

Nielsen S. V., A. M. Bauer, T. R. Jackman, R. A. Hitchmough and C. H. Daugherty. 2011. New Zealand geckos (Diplodactylidae): cryptic diversity in a post-Gondwanan lineage with trans-Tasman affinities. *Molecular Phylogenetics and Evolution* 59: 1–22.

# DIRECTIONAL EVOLUTION OF CELL SIZE - ADAPTATION, GENOMES AND ANCESTRAL STATE RECONSTRUCTION

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Recently we showed evolutionary associations among cell sizes in tissues in the diverse plant family Proteaceae (Brodribb et al. 2013). In some clades the cells of epidermis, mesophyll and xylem of leaves are all large, in others these cells are relatively small. Furthermore, these associations appear to be ancient, reaching in some cases deep into the Cretaceous.

Two mechanisms underlie these links: developmental links between structurally independent cells, mediated by genome size and possibly other genetic factors; and a link related to ecology - species from open environments tend to have larger cells than closed forest species. The links with environment is at least partly independent of genome size. Furthermore, there are potential links with atmospheric CO<sub>2</sub> concentration, especially with the guard cells of the stomata (the microscopic valves that regulate the evaporative loss of water while leaves absorb CO<sub>2</sub>).

We present phylogenetic and fossil evidence for the evolution of stomatal size in Proteaceae. Ancestral state analyses suggest that stomata in the Cretaceous and Paleogene were large (~45µm long) and increased in a few clades of open environments and decreased in other clades, especially those of rainforest. However, the fossil evidence shows stomata were small in the Cretaceous, became even smaller during the early Paleogene, and then increased substantially. These trends are apparent both overall and within clades. The trends in stomatal size broadly match global trends in both the incidence of vegetation type and atmospheric concentration in CO<sub>2</sub>. The fossils therefore show a pattern of directional evolution in response to environment. Furthermore, the older fossils have considerably smaller stomata than predicted by the ancestral state analyses, supporting the idea that ancestral state analyses based on parsimony or Brownian motion can be substantially affected by directional evolution. Impacts on other models of ancestral state reconstruction are as yet unknown.

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Brodribb, T. J., G. J. Jordan and R. J. Carpenter. 2013. Unified changes in cell size permit coordinated leaf evolution. *New Phytologist* 199: 559-570.

## **CENOZOIC PALEOGEOGRAPHY OF NEW ZEALAND**

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We have developed a set of paleoenvironment and paleogeography maps for New Zealand at 1 m.y. intervals through the Cenozoic. These maps are built upon base maps of the distribution of Paleozoic and Mesozoic basement terranes, changes in the distribution of which take account of the c. 800 km of right-lateral displacement through New Zealand during the past 27 m.y., for which a numerical model has been developed. This model is also used to relocate formations mapped in outcrop (QMap series) to the positions in a fixed-Australia frame-of-reference appropriate to the time they accumulated through sedimentary or volcanic processes. The paleoenvironment maps are supported by an extensive database that includes present location, stratigraphic age, lithofacies and environments of deposition for each Cenozoic formation, together with an extensive text file that details most of the information published about Cenozoic formations across New Zealand. The paleogeography maps are a derivative of the paleoenvironment maps and interpret the location of particular boundaries (e.g. coastline, shelf edge) and geomorphic features (e.g. mountains, rivers, submarine fans) through time.

# DISCOVERING THE ECOLOGICAL AND EVOLUTIONARY RULES OF BIODIVERSITY CHANGE

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There are two primary ways of assaying diversity change in deep time – the fossil record and molecular phylogenies. Molecular phylogenies can be developed for any living group, but have the severe limitation of (typically) excluding all extinct species. The fossil record does not have the same ascertainment bias, but for many groups it has the severe limitation of being taxonomically, morphologically, temporally, and geographically incomplete. Here, following Quental and Marshall (2013), I show how very rich fossil records can be identified and used to make sophisticated inferences about the ecological and evolutionary rules of biodiversity change. Specifically, I show how the richest fossil records of 19 monophyletic families of terrestrial mammal that are either extinct, or in diversity decline, can be use to establish that: 1) Their diversity change had a deterministic component, and was not just due to stochastic fluctuations; 2) Diversity change was diversity dependent (something that cannot be determined with molecular phylogenies); 3) The diversity trajectories were, on average, temporally symmetric (the rise and fall in diversity had approximately equal durations); 4) Increased extinction rate and decreased origination rate were equally important in driving diversity loss; 5) The final extinction rate approximately equalled the initial origination rate, and the final origination rate approximately equalled the initial extinction rate.

The diversity dependence evokes McArthur and Wilson's theory of island biogeography, and modelling the data within this framework, with the extension of having a time-varying carrying capacity, suggests that the diversity of each clade only transiently equaled the implied equilibrium diversity – the processes that drove diversity loss in these clades were non-equilibrial and overwhelmed diversity-dependent processes. This result offers resolution to a long-standing debate in paleobiology, suggesting that while diversity dependence exists, it only plays a secondary role in shaping long-term trends in diversification.

## **Reference:**

Quental, T. B and C. R. Marshall. 2013. How the Red Queen drives terrestrial mammals to extinction. *Science* 341:290-292.

## ANCIENT DNA REVEALS PRE-OLIGOCENE DIVERSIFICATION IN THE ACANTHISITTID WRENS (ACANTHISITTIDAE)

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It is well established that the Oligocene marine transgression drastically reduced the land area of New Zealand, with some suggestions of complete submergence. While geological evidence is largely equivocal on the extent of the inundation, biogeography remains a powerful tool for addressing this question. The most convincing biogeographic evidence against complete submergence would be the existence of multiple pre-Oligocene lineages in an endemic clade. However, very few native New Zealand taxa meet this criterion, as most appear to diversify well after the Oligocene, or are only represented by a single relict species. Still others are equivocal, having crown-age estimates with error margins extending either side of the putative submergence. The acanthisittid wrens, as one of the most diverse New Zealand bird families, offer a powerful test of this hypothesis that has not been fully explored. Molecular data were previously only available for three of the seven Recent species (five extinct, two extant): the rifleman (*Acanthisitta chloris*), rock wren (*Xenicus gilviventris*) and extinct bush wren (*Xenicus longipes*).

We sequenced mitochondrial genomes of three extinct species (stout-legged wren, *Pachyplichas yaldwyni*; Stephen's Island wren, *Traversia lyalli*; bush wren, *Xenicus longipes*) and the remaining extant species (rock wren, *Xenicus gilviventris*) using a combination of hybridisation enrichment and high throughput next-generation sequencing. Molecular dating demonstrates unequivocally that the lineage leading to the Stephen's Island wren diverged from the common ancestor of *Xenicus*, *Pachyplichas* and *Acanthisitta* prior to the Oligocene. As a result, two wren lineages survived through the Oligocene period, providing compelling evidence against complete submergence, as the acanthisittids are ill suited to long-range, overwater dispersal. This finding also provides clues about Oligocene paleoecology, and the ecological characteristics of taxa that were successful during this period. Phylogenetic analyses further suggest that the two *Xenicus* species (the extant rock wren and extinct bush wren) are not monophyletic, and instead the extinct stout-legged wren and rock wren are sister taxa, indicating a need for taxonomic reassessment of the group.

## THE IMPORTANCE OF INTEGRATING GEOLOGY AND BIOLOGY

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There is plenty of space for a positive interaction between paleontologists and molecular evolutionists and, combined, their data are particularly powerful. Biologists perhaps need to take more note of the fact that the young Charles Darwin was a geologist, and that he was soon convinced of the superiority of the geological approach of Charles Lyell for explaining events in the past by mechanisms that can be studied in the present (and Lyell included extraterrestrial impacts here). Biologists became more aware of Darwin's work after he started to apply the principles he had learned in geology, to biology (see Fig 1. of Penny 2011). This principle of uniting past events with current processes/mechanisms is very powerful (Penny 2009, 2010). So in order to get the maximum information from our data we need to integrate information from the past with mechanisms we can study in the present.

The specific case we examine here in more detail is the origin of the large group of oscine passerines. It is thought that this group originated in Australia and, although there are few early fossils, the earliest are found in Australia (though they are few in number, and there is a gap of several million years before later ones are found). However, combining that limited knowledge with evolutionary trees from sequence data shows, we think, that there is some good agreement? So we have studied the relationships of modern passerines, and the data appears to fit with the fossil evidence, including the later finds from Europe.

### References:

- Penny, D. 2009. Charles Darwin as a theoretical biologist in the mechanistic tradition. *Trends in Evolutionary Biology* 1: e1.
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- Penny, D. 2011. Darwin's theory of descent with modification versus the biblical Tree of Life. *PLoS Biology* 9: e1001096.

# ARE CRYOPHILY AND NOCTURNALITY OF NEW ZEALAND'S ICONIC ENDEMIC LEGACIES OF CRETACEOUS POLAR COLD AND DARKNESS?

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New Zealand's terrestrial fauna is widely regarded as unusual, and the iconic endemics including weta (Rhaphidophoridae, Henicidae), kiwi (*Apteryx*), *Xenicus* (a flightless rock-wren) and tuatara (*Sphenodon*) are considered bizarre by some authors. The nature and timing of the pressures that influenced their evolution have not, however, been specified.

Amongst other unusual attributes, most or all of the iconic endemics possess highly specialised physiological functions that facilitate low-temperature activity or survival. Whereas the cryophily of individual taxa has been recognised, it has not hitherto been realised that all the iconic endemics are cryophilic. Development of cryophily in several unrelated taxa cannot be readily ascribed to the availability of cold niches created by Neogene tectonism or Pleistocene climatic deterioration. Cryophily is more plausibly related to some harsh pre-Neogene climate endured by ancestral forms. Paradoxically, it probably reflects Cretaceous climatic conditions.

Although the Cretaceous is regarded as a period of global climatic warmth, Late Cretaceous New Zealand was probably cold because it lay at near-polar latitudes and vigorous tectonism induced high topographic elevations. Evidence for extensive Late Cretaceous glaciation comes from lithostratigraphic relations in southern New Zealand and offshore, where a heterolithic unconformity separates Cenomanian and older rocks from overlying Campanian and younger strata. This unconformity, the Waipounamu erosion surface (LeMasurier & Landis 1996) is currently regarded as a subaerially developed feature modified by marine processes. However, such an origin is difficult to reconcile with observed geological relations, and the surface, which formed in  $\sim 10^7$  years at high paleolatitudes during an episode of global cooling, can instead be interpreted as a Late Cretaceous subglacial floor.

Cryophily in the iconic endemics may in effect be a paleoclimatic signal reflecting the coldness of Cretaceous high latitudes. This view is supported by the fact that the ability of each iconic endemic form to tolerate cold is coupled with a fine degree of adaptation allowing activity in low-light conditions. I suggest that the ability to exploit dark habitats arose simultaneously with development of cryophily, and ultimately reflects the prolonged winter darkness of Late Cretaceous near-polar New Zealand.

These considerations support the view that New Zealand's iconic endemics are the evolutionary derivatives of a Cretaceous near-polar fauna.

## Reference:

LeMasurier, W.E. and C. A. Landis. 1996. Mantle-plume activity recorded by low-relief erosion surfaces in West Antarctica and New Zealand. Geological Society of America Bulletin 108: 1450-1466.

## **RANGES OF NEW ZEALAND POLLEN THROUGH THE CENOZOIC**

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The New Zealand Fossil Spores and Pollen Catalogue (<http://www.gns.cri.nz>) documents >830 species of fossil spores and pollen from the New Zealand (NZ) region that have been recorded in the scientific literature. It includes a detailed synonymy for each taxon, key illustrations, and in some cases suggested modern botanical affinities. In the catalogue, information on the biostratigraphic range of each taxon is restricted to the level of geological period, although more detailed range information is available for a small subset (~100) in the NZ Geological Timescale (Cooper 2004).

We have produced detailed range charts for the >330 Cenozoic taxa that appear in the Catalogue, using information from the New Zealand Fossil Record File (FRED). FRED (<http://www.fred.org.nz/>) is a database that records fossil localities in NZ and nearby regions, including SE Pacific Islands and the Ross Sea region of Antarctica. FRED contains about 98,000 locality records registered at regional recording centres since 1946, and > 5,000 records of Cenozoic pollen assemblages.

The range of each taxon has been extracted by counting the number of times each taxon has been recorded in FRED per New Zealand geological stage. Individual FRED entries have not been checked for accuracy, no consideration has been given to sampling biases, and therefore these data are not suitable for deriving absolute range information. Nevertheless, the relative frequency plots provide an indication of relative abundance through time, as well as showing where critical observations of earliest and latest occurrences may be sought.

### **Reference:**

Cooper, R.A. (ed.). 2004. The New Zealand Geological Timescale. Institute of Geological and Nuclear Sciences Monograph 22, Lower Hutt, 284pp.

# TEMPERATURE-DRIVEN FOLIAR PHYSIOGNOMIC DIVERGENCE OF THE NEW ZEALAND FLORA SINCE THE EARLY MIOCENE

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Leaf architecture is highly dependent on the environment in which a plant is growing. There are optimal growth forms for leaves in specific climatic types and therefore leaf assemblages from climatically similar areas can have the same morphological features, even though they may be taxonomically highly variable. The dataset of the Climate Leaf Analysis Multivariate Program (CLAMP) employs ~400 plots worldwide with more than 20+ species each, with standardized measurements for 31 physiognomic variables, including size, shape, margin morphology, base and apex shape, using Canonical Correspondence Analysis (Wolf 1993). This dataset is used to approximate climatic variables by cross-correlating standardized physiognomic characteristics of modern and fossil floras with measured or modelled climatic variables from the modern dataset (Spicer et al. 2009).

In southern New Zealand, nine fossil leaf floras were collected that range in age from the earliest Miocene (~23 Ma) to the Middle–Late Miocene boundary (~11 Ma). Applying CLAMP to these floras reveals distinct climatic differences between Miocene paleoenvironments and those of modern New Zealand (Reichgelt et al. 2013). These differences are predominantly reflected by temperature variation, whereas the precipitation regime appears to have changed little. From a climatological perspective, progressive northward migration of the Subantarctic Front since the early Miocene has caused New Zealand to go from a subtropical to a cold-temperate climate.

The difference between modern and Miocene New Zealand foliar characteristics represents directional selection and adaptation of the flora to the changing environmental circumstances. Miocene leaf physiognomy is closely comparable to modern day southern Queensland and Lord Howe and Norfolk Islands. Closer investigation of the specific morphological characteristics reveals that the most strongly selected traits were leaf size and base shape, whereas serrated margin frequency and apex shape were not subject to selection.

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# **A REMARKABLE MID-PLIOCENE VOLANT MARINE FOSSIL BIRD ASSEMBLAGE ALTERS OUR UNDERSTANDING OF MARINE BIRD EVOLUTION IN THE PLIOCENE**

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The mid-Pliocene (between 3.3 and 3.0 million years ago) is the most recent time in Earth's history when mean global sea temperatures were substantially warmer than today for a sustained period. As an oceanic landmass, the evolution of New Zealand fauna has been dependent on the sea. Whereas penguins are well known in the New Zealand Pliocene, the published record of volant birds is minimal, with only a couple of bony toothed bird (Pelagornithidae) fossils and a single shearwater (Procellariidae) crania described. Here we detail new records of bony-toothed birds (Pelagornithidae), albatross (Diomedidae) and petrels (Procellariidae) from the Tangahoe Formation (Waipian; mid-Pliocene) of New Zealand's North Island. These records alter our ideas about the evolution and biogeography of New Zealand's marine avifauna, and also give us new insights into the timing of evolution of waterbirds worldwide. Study of these fossils using CT scanning and modern medical imaging has enabled us to establish better than ever before the relationships of these fossils to modern taxa. We discuss the paleoenvironment of New Zealand during this biologically crucial epoch and discuss how radical changes in climate, currents and biogeography that occurred in the Pleistocene may have affected the evolution of seabirds worldwide.

## PHYLOGEOGRAPHY OF SIX NORTH ISLAND, NEW ZEALAND CICADAS AND THEIR RELATIONSHIP TO MULTIPLE BIOGEOGRAPHIC BOUNDARIES SUGGESTS A RE-EVALUATION OF THE TAUPO LINE

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Comparative biogeographers have long questioned the extent to which co-distributed species respond similarly to environmental change. The best evidence for such responses would be identical patterns of cladogenesis in multiple co-distributed taxa. Complete evolutionary independence – where each species responds differently to environmental stimuli – would be of no predictive value for unstudied species. Throughout the Pleistocene, NZ experienced repeated low temperatures, increased aridity, glaciers, and dramatic shifts in biota. At glacial maxima, many forest species are hypothesized to have existed only in small refugia, while during interglacials, populations are hypothesized to have expanded to meet populations from other refugia at contact zones. Here we examine present-day interglacial phylogeographic patterns for six North Island, New Zealand forest and shrub cicada taxa in the genus *Kikihia*, using mitochondrial DNA data. We compare our results to mitochondrial phylogeographic patterns in other invertebrate taxa in order to identify common boundaries and infer the geological events most likely to be important in geographic genetic differentiation. Species were identified by morphology and species-specific courtship songs and collected throughout the North Island of New Zealand. Mitochondrial DNA sequences (1,382 bp, 180 individuals) from seven co-distributed cicadas of the genus *Kikihia* were analyzed using phylogenetic (maximum likelihood, Bayesian) methods and Bayesian molecular dating techniques (BEAST). The results from these phylogeographic analyses and those of previously studied plant and animal species from the North Island of New Zealand were compared with respect to hypothesized biogeographic boundaries. Five species of *Kikihia* show various degrees of concordance with intraspecific mitochondrial clade biogeographic boundaries found in previously studied taxa. Four species (*K. ochrina*, *K. cutora*, *K. laneorum*, and *K. cauta*) show diversification older than the last glacial maximum (LGM, 20,000 y), whereas two species (*K. scutellaris* and *K. dugdalei*) show only post-LGM diversification. Despite species idiosyncrasies, we do see the imprint of historical biological events. Three previously described biogeographic boundaries, including the Kauri Line, Northland Line, and the NW-SE Line, are identified in North Island New Zealand *Kikihia* species. We also identify a new zone of interest in the East Cape region present in recently diverged taxa. Forest species are generally most closely associated with the Kauri Line and/or Northland Line or show only recent and insignificant genetic differentiation. Species that occupy shrub/hill habitats respond most strongly to the NW-SE line and East Cape boundary. We suggest that the importance of the Taupo line has been exaggerated and that the importance of the NW/SE mountain axis has been overlooked.

# PALEO GEOGRAPHY OF THE TARANAKI BASIN REGION DURING THE LATEST EOCENE TO EARLY MIOCENE AND IMPLICATIONS FOR THE “TOTAL DROWNING” OF ZEALANDIA

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Late Eocene–earliest Miocene (~40–21 Ma) strata in the Taranaki Basin provide important new regional paleogeographic and tectonic constraints not available from onshore outcrops. Six paleogeographic maps of the Taranaki Basin and surrounding areas (~142,000 km<sup>2</sup>), have been produced using extensive well, seismic reflection, and outcrop data. These data record three broad periods of sedimentation in the eastern and southern Taranaki Basin region characterised by: variable transgression and initial deformation (c. 40–30 Ma), maximum transgression with moderate deformation (c. 30–21 Ma) and regression with accelerated deformation (<21 Ma). Local sedimentation patterns were influenced by reverse faulting which produced depocentres and topographic highs, particularly adjacent to the Taranaki Fault System. Reverse faulting commenced as early as c. 40 Ma and may signify the onset of incipient subduction beneath the North Island. In common with other parts of New Zealand the Taranaki Basin region reached maximum marine inundation in the Waitakian (c. 23 Ma). However, the deposition of thick clastic sediments in eastern parts of Taranaki Basin, as well as in other regions of central Zealandia, such as the East Coast and Murchison basins, suggests the presence of a significant non-marine hinterland supplying sediment to the basin throughout the Oligocene and Early Miocene, and is *inconsistent* with total Oligocene drowning of Zealandia. These results are detailed in Stroger *et al.* (2014).

## References:

Stroger, D. P., K. J. Bland, A. Nicol and P. R. King. 2014. Paleogeography of the Taranaki Basin region during the latest Eocene–Early Miocene and implications for the “total drowning” of Zealandia. *New Zealand Journal of Geology and Geophysics* 57: 1–18.

## THE EVOLUTION OF *NESTOR* PARROTS

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The New Zealand *Nestor* parrots (kaka (*N. meridionalis*) and kea (*N. notabilis*)) are globally significant because, together with kakapo (*Strigops habroptilus*), they form a 40+ million year old (Ma) superfamily (Strigopoidea) that is sister taxa to all other parrots. Here, we review recent research that has provided exciting insights into the history of *Nestor* parrots. New molecular research indicates that the kakapo and *Nestor* lineages separated 23-29 Ma (Rheindt et al. 2014, Wood et al. in press). The earliest fossils of this group are three species related to *Nestor* from the 16-19 Ma deposits at St Bathans, Central Otago. New molecular research has dated the separation of the kaka and kea lineages to 2.3-4.4 Ma (Rheindt et al. 2014, Wood et al. in press), supporting Fleming's 'classic' theory of *Nestor* diversification, i.e., kea evolving under alpine/glacial conditions c.2.5 Ma and kaka evolving in low altitude/warmer forest habitat. We discuss how this alpine/lowland split fits with new Holocene fossils, which show that kea also lived in the North Island during the Holocene (Tennyson et al. in press); therefore apparently kea is not in fact an obligate 'alpine' species and the evolution of kaka and kea may be more complex than previously thought. Kaka evolved into four distinctive taxa within the New Zealand archipelago (Norfolk Island *N. productus*, Chatham Island *N. n.sp.*, North Island *N. m. septentrionalis* and South Island *N. m. meridionalis*). We present new data on size differences between the North and South Island taxa and describe the extinct *Nestor* parrot from the Chatham Islands. The Chatham species has a relatively large femur:humerus length ratio and broad pelvis compared to mainland kaka; it separated from the mainland form c.1.5 Ma.

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## INTEGRATED PHYLOGENETICS OF A NEOGASTROPOD GENUS

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Due to their frequent preservation in the fossil record, marine mollusc shells are used regularly to track long-term ('macro') evolutionary trends in morphology. Research that investigates the relationship between patterns of morphological change and estimations of genetic evolution is popular (Hunt 2013), but most studies are restricted to short geological timeframes, have inconsistent sampling, focus on broad taxonomic groups, or suffer from a low diversity of extant species. Importantly, studies that combine paleontological and molecular data often fail to directly address the assumptions of both datasets. In particular, investigations of punctuated evolutionary hypotheses frequently also become side-tracked by conflated arguments (Pennell *et al.* 2014), and produce overly complicated models.

We are conducting an integrated phylogenetic investigation of the Neogastropod genus *Penion* ('siphon whelks'). We will use the resulting phylogeny as a model to test the assumptions of stasis, geologically rapid change in morphology, and the association of morphological change with genetic divergence and speciation. *Penion* represents an ideal dataset for this investigation since there is a rich fossil record from New Zealand for the past 21 million years (extending to 66 Ma). Of equal importance, the genus also exhibits a significant diversity of extant endemic species, and there are suitable outgroup species within and beyond New Zealand. Crucially in order to study morphological change, both the extant organisms and fossil specimens exhibit high rates of morphological variation (purported to be intra- and interspecific).

The study is also of interest as very little is known about Neogastropod phylogenetics (Hayashi 2005). We are using mtDNA genomics, anonymous nDNA markers, and next-gen ddRAD sequencing to assess the genetic variation and relationships among groups. To assess morphology we will be applying geometric morphometrics and testing whether traditional morphologically-based species definitions in extant and fossil lineages are accurate.

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## EXTINCT HOLOCENE BIRDS OF THE CHATHAM ISLANDS: ANCIENT DNA PROVIDES NEW TAXONOMIC AND PHYLOGENETIC INSIGHTS

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Molecular analyses of Holocene bird bones from the Chatham Islands, 800km east of New Zealand, have begun to resolve the taxonomies of extinct avifauna from the islands and provide new insights into their evolutionary histories. Our poster summarises the main findings from these new studies. 1) The Chatham duck (*Pachyanas chathamica*) was actually nested in *Anas*, and was basal in the brown teal lineage, having diverged ca. 0.69 – 1.8 million years ago (Mitchell et al. 2014). 2) The Chatham Islands parrot (*Nestor* n. sp.) diverged from its sister taxon, the New Zealand kaka, ca. 0.53 – 3.29 Ma, and was distinguished by a longer beak, broader pelvis and larger femora (Wood et al. in press). 3) A small *Megadyptes* penguin occurred formerly on the Chatham Islands, and is nested within the hoiho (*Megadyptes antipodes*) mitochondrial DNA diversity, although it was ca. 40 % smaller than modern individuals of this species and ca. 20 % smaller than the extinct Waitaha penguin (*M. waitaha*). 4) Mitochondrial DNA analyses of the crested penguin bones from the Chatham Islands are ongoing. Initial results are inconclusive as to whether the bones represent a distinct species, as previously thought, but raise the possibility that some are from erect-crested penguins (*Eudyptes sclateri*), reflecting the natural northernmost limit of this species. 5) Mitochondrial DNA analyses show that the Chatham Island rails *Gallirallus dieffenbachii* (Dieffenbach's rail) and *Cabalus modestus* (Chatham Island rail), are both nested within the widespread genus *Gallirallus*, but represent two separate colonisation events of the Chatham Islands. 6) The Chatham Island merganser (*Mergus* n. sp.) represents a new species, distinct from the Auckland Island merganser (*Mergus australis*) (Williams et al. in review), and genetic work is currently in progress to elucidate the relationships of these taxa. Taken together, the results of all these studies (particularly the molecular dating of Chatham lineages and synonymisation of Chatham-endemic genera with widespread genera) provide further evidence for the relatively recent emergence of the Chatham Islands, and the rapid rates of morphological specialisation that can occur in island bird taxa.

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## UPDATING THE RECORD FROM THE EARLY MIOCENE ST BATHANS FAUNA, CENTRAL OTAGO AND ITS SIGNIFICANCE FOR DOCUMENTING THE ASSEMBLY OF NEW ZEALAND'S TERRESTRIAL BIOTA

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New Zealand has long been renowned for having a terrestrial vertebrate fauna dominated by birds. Furthermore, it is/was characterised by high endemism, especially at generic and specific levels. Whereas birds dominate the pre-human Holocene terrestrial fauna, in terms of both taxonomic diversity and habitat exploitation, until recently it was not known if this was a relatively recently acquired characteristic or one derived in geological antiquity. The Holocene fauna was diverse at higher taxon levels, but depauperate within families, with the largest radiations being the seven species of acanthisittid wrens and the nine moa in three families and six genera. Mammals appear to have been less diverse, with a complete absence of terrestrial mammals apart from bats. Their role was in part replaced by a suite of large browsing birds. Moreover, the modern herpetofauna lacked diversity at high taxonomic levels, with squamates restricted to just skinks and geckos, and a complete absence of turtles and crocodilians. However, such paucity is offset by the presence of the endemic leiopelmatid frogs and the tuatara, both globally significant relictual members of otherwise extinct higher clades. It is further offset by the only recently appreciated fact that the skinks and geckos exhibit the most diverse radiations within a vertebrate family in New Zealand, with some 54 *Oligosoma* skinks (39 described) and 42 diplodactylid geckos (seven genera, 20 described species) recently recognised.

The composition of the 'original' pre-human fauna is well known thanks to an outstanding Quaternary fossil record, so what has been lost following human impacts is documented perhaps better than for any other landmass. The *questions* that paleontological investigations can and are now addressing include: 'Has the New Zealand terrestrial vertebrate fauna always had these recent characteristics? How and when was this biota assembled?' This presentation will outline how the investigations of the Early Miocene St Bathans Fauna provide an unprecedented insight into such questions.

The St Bathans Fauna is diverse and minimally includes the following taxa. Molluscs: Freshwater taxa: Hyriidae (one sp.); Bulimidae (*Glyptophysa* sp.); Tataeidae (two-three spp. formerly Hydrobiidae); and Latiidae (*Latia manuherikia*). Land molluscs: Punctidae (one sp.), Charopidae (five spp.) and Rhytididae (one sp.). These are the oldest records for land molluscs from New Zealand, considerably predating the previous Late Pliocene limit. Crustacea: a freshwater crayfish *Paranephrops fordycei* and 'giant' ostracods *Mytilocypris* aff. *preanuncia*, from a group that live in temporary lacustrine environments, often with high salinity, across southern Australia. Vertebrates. Teleosts include a total of six families and 15 species, but Galaxiidae (six spp. *Galaxias*), Eleotridae (four spp. *Mataichthys*, gudgeons),

and Retropinnidae (two spp. *Prototroctes*, graylings) were the principle fish inhabitants of paleolake Manuherikia. Amphibia – Leiopelmatidae (two spp. *Leiopelma*). Reptilia included a crocodilian, a ?meiolaniid turtle, a sphenodontid, and minimally two skinks and two diplodactylid geckos. Aves now include about 40 species (Worthy et al. 2013a, b): Dinornithiformes (two spp.), Apterygidae (the kiwi *Proapteryx micromeros*), Pelecanoididae (the diving petrel *Pelacanoides miokuaka*), Anatidae (four spp. *Manuherikia*, *Miotadorna sanctibathansi*, *Dunstanetta johnstoneorum*, *Matanas enrighti*, *Cereopsis* sp., and one anserine indet.), Accipitridae (one eagle, one ?kite), Ardeidae (the herons *Matuku otagense*, *Pikaihao bartlei*), Aptornithidae (adzebill *Aptornis? proasciarostratus*), Rallidae (two<sup>+</sup> rails), Charadriiformes (one laromorph, two waders), Columbidae (*Rupephaps taketake*, one ?dove), Psittaciformes: Nestorinae (four parrots: three spp. *Nelepsittacus* plus one indet.), Aegothelidae (one owl-nightjar, *Aegotheles* sp.), Apodidae (one swiftlet, *Collocalia* sp.), Family indet (one sp.), Passeriformes: Acanthisittidae (*Kuiornis indicator*), and six<sup>+</sup> spp. fam. et. gen. undetermined). Mammalia: five bats (two<sup>+</sup> spp. Mystacinidae, one sp. Vespertilionidae, one sp. from a new family, one sp. et fam. indeterminate), and two terrestrial taxa (order & family indeterminate).

The St Bathans Fauna originates mainly from the basal 25 m of the Bannockburn Formation. To date its age is poorly constrained but is generally considered to be late Early Miocene (19-16 Ma). The underlying Dunstan Formation has floral similarities with that from the 23 Ma Foulden Maar and documents a transition from fluvial to swampland environments, which in turn grades into the lacustrine facies of the Bannockburn Formation without any apparent unconformity. These observations suggest that the lower Bannockburn Formation around St Bathans and its St Bathans Fauna is more likely to be early Altonian, closer to 19 Ma, than late Altonian. However, at levels >35 m above the base of the Bannockburn, limited faunal turnover is evident with the formerly dominant taxon *Manuherikia lacustrina* replaced by a new undescribed form. Analyses of other taxa (fish, rails) are not advanced enough to know whether there are other parallel turnovers. These changes may correlate with floral changes such as the transition from the Casuarinaceae to the Asteraceae-Chenopodiaceae zones documented by Pole and Douglas.

The faunal content of the St Bathans Fauna will be discussed with reference to selected recent molecular analyses. Notably, the fauna contains several taxa with divergence age estimates (in parentheses) from analyses of DNA that considerably predate the Oligocene marine highstand, indicating long histories for their lineages in Zealandia: *Latia manuherikia* (c.85 Ma) from South American sister taxon Chilinidae; sphenodontid reptiles and leiopelmatid frogs, sister groups of squamates and remaining frogs respectively; acanthisittid wrens (*Kuiornis indicator*), the sister group of remaining passerines; moa (58.1 Ma) though the crown group is c.7 Ma; kiwi (c.50 Ma) from elephant birds (Mitchell et al. 2014); *Mystacinids* (51-41 Ma); diplodactylid geckoes from Australian relatives (c.40 Ma); *Nestor* from the *Strigops* lineage c.28–29 Ma. Some taxa represent lineages that probably dispersed to Zealandia in the Early Miocene, after the Oligocene highstand, e.g. the fruit pigeon lineage (*Rupephaps*) and the skinks. Recent molecular analyses enable the predictions that among the bones of unstudied passerines, the oriole *Turnagra* lineage (c.20 Ma), the magpies and kin or cracticids (c.25 Ma), kokako and stitchbird (c.45 Ma), and yellowhead *Mohoua* lineage (32 Ma) should all be present. Conversely, the New Zealand honeyeaters are deeply embedded in Australian meliphagids and diverged c.12 Ma from them, so if honeyeaters are present in the St Bathans Fauna, they are unlikely to be related to tui or bellbird.

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