



Hello New Zealand

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ABSTRACT

Islands of the Pacific Ocean have long fascinated evolutionists. Oceanic islands, generally the products of volcanic activity, provide natural experiments as biological populations are well delimited and the age of islands can be determined using radiometric dating. ‘Continental islands’, including New Caledonia and New Zealand, provide equally valuable opportunities for evolutionary study. For students of New Zealand biogeography, the peculiar composition of the biota coupled with a limited interpretation of geology has resulted in the widespread acceptance that the flora and fauna is primarily ancient and of vicariant Gondwanan origin. There is increasing evidence from molecular data that much of this biodiversity is the product of evolution following relatively recent colonization. Such data have prompted biologists to consider geological information on New Zealand in more detail. At the heart of the issue is the question of whether modern New Zealand has a terrestrial link through time with the continent Zealandia that split from Gondwanaland some 80 Ma. Zealandia, which includes New Caledonia, Lord Howe Island and several of the subantarctic islands, is now largely submerged, and New Zealand’s present terrestrial existence is the product of tectonic activity initiated around 26 Ma. We argue that for the purposes of biogeographical interpretation, New Zealand can be treated as an oceanic island.

Keywords

Evolution on Pacific islands, Gondwana, island biogeography, moa’s ark, oceanic islands, Zealandia.

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Cowie & Holland (2006) give a timely reminder of the biological importance of islands. The crux of their paper is the significance of oceanic islands in the study of biological evolution. Island biodiversity is not just an outcome of the lottery of arrival and extinction (MacArthur & Wilson, 1967), but of adaptive speciation. However, in terms of evolution on Pacific islands, Cowie & Holland (2006) set New Zealand apart, as many have done before, as being continental – the implication being that the evolution of New Zealand biota is somehow subject to different processes from those of oceanic islands. Is this justified?

New Zealand has long been of interest to biogeographers and other biologists. Conservationists, phylogeneticists, ecologists, evolutionists and geneticists alike all draw attention to the distinctive nature of New Zealand plants and animals and it is widely held that this distinctiveness is the result of ancient isolation/origin. New Zealand’s position in the Southern

Hemisphere, its relatively large size compared to other islands of the Pacific and its distinctive assemblage of biota characterized by many taxonomic absences, the presence of apparently archaic lineages and aberrant species have all attracted attention. However, the accepted idea that New Zealand is an ancient continental landmass distinguishes it from oceanic island systems that are foci for evolutionary study, and in particular for the study of the role of dispersal (Cowie & Holland, 2006). The archipelagos of Hawaii and the Galapagos are of volcanic origin, and their terrestrial surfaces are the product of hot-spot volcanism. These islands are the tops of substantial volcanoes built upon oceanic crust. The age of these islands can be estimated accurately using radiometric methods (e.g. Fleischer *et al.*, 1998), and their biota can be definitively inferred as having originated via dispersal. The attraction oceanic island systems hold for evolutionists is that they represent natural experiments with definable histories and

population parameters in which to observe speciation (Emerson, 2002; Gillespie & Roderick, 2002).

New Zealand is the terrestrial part of Zealandia, a large submerged continental crustal fragment that rifted from Gondwanaland in Late Cretaceous time. The Gondwanan origin of Zealandia is undisputed. However, this geological heritage has been conflated with a Gondwanan origin of the flora and fauna: because the underlying substrate is Gondwanan in origin, then by implication the biota must also be as old (e.g. Stevens, 1980). This simple and attractive notion assumes a geological mechanism (plate tectonics) for permanent land and biological distribution. As a result, attention has focused on distribution patterns rather than exploration of alternative causal processes for the origin of New Zealand's native biota (McDowall, 2004). This approach reached its zenith with the panbiogeographical school that stressed the ancientness of New Zealand's biota (Craw, 1988; Craw *et al.*, 1999). Such a view has become intimately linked with a sense that New Zealand is something of a lost world, an ancient microcosm, a prehistoric 'moa's ark' (Bellamy *et al.*, 1990). This belief is deeply engrained in the psyche of biologists, and innumerable scientific papers, talks and books relating to the biology of New Zealand are prefaced with phrases like 'New Zealand has been isolated for 65 Myr' or 'the biota of New Zealand has lived in isolation for 80 Myr'. As early as 1883 Alfred Wallace stated 'we are justified in concluding that, during the whole Tertiary period at least, if not for much longer New Zealand has maintained its isolation'. Stevens *et al.* (1988) stated 'New Zealand, [was] isolated for at least the last 100 Myr'. Jared Diamond (1990), whose inferences continue to influence and reflect current opinion, echoed this view: 'Dry land has persisted in the New Zealand region for at least the last 100 Myr'. Belief in the ancient isolation of New Zealand and its biota remains central to the thinking of many biologists, and is widely used as the benchmark for estimating the age of radiations. For example, Baker *et al.* (2005) used a date of 82 Ma, without geological referencing, for the split between moa and other ratites.

A form of cosy 'reciprocal illumination' has resulted in biogeographical interpretations settling into a comfortable self-fulfilling prophecy – flimsy knowledge of geological history fits with assumptions about natural history (Waters & Craw, 2006). Fleming (1979) circumscribed this approach by constructing a hypothesis for the origins of the New Zealand biota and proposing biogeographical elements of various antiquity and affiliation. The evidence for this hypothesis was gleaned from assumed natural history and taxonomic similarity. Hence, tuatara and leiopelmatid frogs have no close extant relatives outside New Zealand. Weta and peripatus are considered to have low dispersal ability. Moa, chironomids and beech have a distribution fitting with the pattern of Gondwanan break-up. All of these are identified as archaic/palaeoaustrian elements. A modern dispersal element includes mostly birds that are nearly identical to their counterparts in Australia or elsewhere. Fleming's (1979) valuable synthesis of geological and biological information has been highly influ-

ential, due in part to the accessibility of the geological information in his book for biologists.

Daugherty *et al.* (1993) asked whether New Zealand is a small continent or a large island, and cited examples of the biota that are generally taken as indicators of both these conditions, but did not explore the geological evidence directly. The emergence of DNA sequence methods appeared to do little to alter the mix and match hypothesis of Fleming (1979). At that time most analyses of molecular data were still cladistic and interested in topology rather than timing of divergence. Patterns of divergence tended to mirror a Gondwanan break-up scenario with the nearest relatives of New Zealand biota present in Australia. Very few researchers noted that a dispersal scenario would also posit the up-wind and up-current Australia as the location of close relatives.

A landmark paper that had wide influence on biologists introduced evidence for a substantial Oligocene biodiversity 'bottleneck' within the New Zealand biota to explain younger patterns of diversification in moa, and by implication other biota (Cooper & Cooper, 1995). The significant reduction in land area during Oligocene time that was identified as the cause of this bottleneck has generally been represented as the result of erosion and marine transgression (advancement of the sea due to rise in sea level), and led to the conception of the Oligocene drowning hypothesis (Cooper & Cooper, 1995). Cooper & Cooper (1995) noted that the outline of New Zealand was very different in the Oligocene but, crucially, for biologists the questions have tended to be 'how much of New Zealand went under?' rather than 'how much of Zealandia went under?' New Zealand needs to be reconsidered as a separate entity to Zealandia. Only then can we pose the necessary question 'when did New Zealand emerge'?

The notion of the antiquity of the New Zealand biota is founded on the assumption that emergent land has continuously existed in the area since the break-up of Gondwanaland, but this relationship between tectonics and continental land is naively misconstrued. In geological terms, 'continental' means composed of continental rather than oceanic crust. This concept of two distinct crustal types has only become fully appreciated since the advent of plate tectonic theory in the late 1960s. We now know that for continental crust to be emergent as land it has to be thick enough to stand above sea level. The continental fragment that rifted away from Gondwanaland is referred to as Zealandia (Luyendyk, 1995; Mortimer, 2004). Other terms have been applied, such as 'greater New Zealand' (Stevens *et al.*, 1988), 'New Zealand Plateau' (NIWA) and Tasmantia (Storey, 1996; McLoughlin, 2001), but none of these terms have found as much favour as Zealandia. Zealandia is large, almost half the size of Australia, and includes New Zealand, the Campbell Plateau, Challenger Plateau, Lord Howe Rise, Norfolk Ridge, Chatham Rise and New Caledonia (Fig. 1). Zealandia moved north-eastwards with respect to eastern Gondwanaland, with the opening of the Tasman Sea. The oldest sea floor in the Tasman Sea is about 85 Myr and the youngest is about 65 Myr. As it rifted, Zealandia was stretched and thinned, effectively losing buoyancy, and sinking some

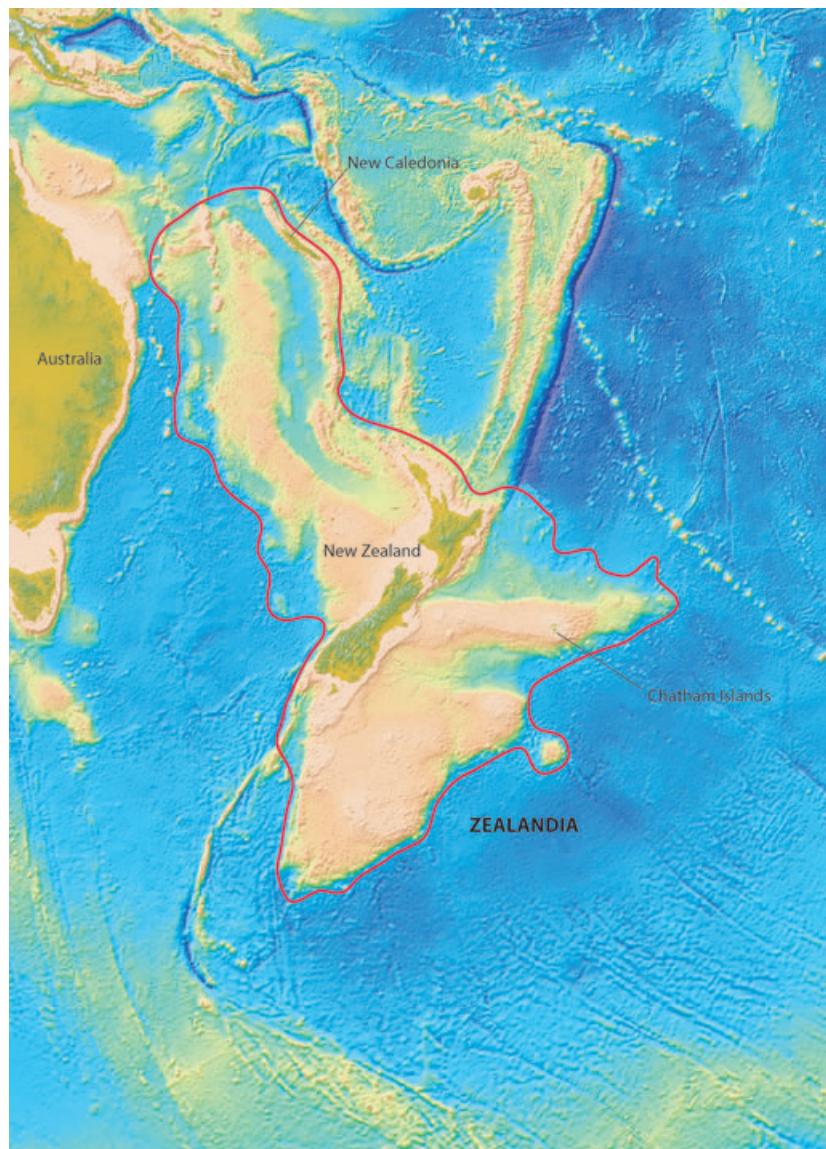


Figure 1 Zealandia. The approximate extent of the continental crust beneath New Zealand (red line, old Zealandia at time of Gondwana break-up). [From Stagpoole V.M. (2002) *The New Zealand Continent*, 1:7 500 000. Institute of Geological & Nuclear Sciences Ltd Geophysical map GPM15. Institute of Geological and Nuclear Sciences, Lower Hutt].

2000–3000 m. This is an inevitable consequence of reduction in thickness of continental crust. The Late Cretaceous and Palaeogene geology of New Zealand is testimony to this process: gradual inundation of the sea (transgression) culminating in latest Oligocene time about 25 Ma (Suggate *et al.*, 1978; C.A. Landis, H.J. Campbell, J.G. Begg, A.M. Paterson & S.A. Trewick, in prep.). Today, the continental crust of Zealandia, including New Zealand, is, in geological terms, thin (20–25 km). The continental crust beneath Australia is about 35 km thick and hence more buoyant.

Modern New Zealand owes its existence not to continental drift but to plate boundary collision. This has been vigorous and sustained since being initiated abruptly 26 Ma in latest Oligocene time (Sutherland, 1999; Cande & Stock, 2004). This activity is prominently expressed along the Alpine Fault, where tectonism has generated > 460 km of lateral motion and, since the Pliocene (5 Ma), 20 km of uplift resulting in the formation of the Southern Alps (Kamp *et al.*, 1989; Kamp, 1992;

Whitehouse & Pearce, 1992). If the tectonic forces at work were to diminish or cease, the crust beneath New Zealand would slowly drop back to the ambient repose of greater Zealandia, well below sea level. Similarly, New Caledonia is the product of plate boundary collision initiated 35 Ma in Late Eocene time (Paris, 1981).

The geological evidence for the survival of any ancient terrestrial parts of Zealandia at the end of Oligocene time (26 Ma) is very weak (Landis *et al.*, 2006), due in part to the destructive impact of later tectonics, although attempts to estimate Oligocene shorelines have been made (Fleming, 1962; Suggate *et al.*, 1978). If any of Zealandia remained emergent it was an exceedingly small part. Landis *et al.* (2006; in prep.) argue that any islands must have been ephemeral: small and short-lived. Furthermore, they argue that the geological evidence permits the idea of total drowning of Zealandia. At present, there is insufficient geological evidence to compellingly demonstrate permanent land or total immersion.

Therefore both perspectives must be considered as real possibilities. One problem is a lack of precision in determining the age of key fossil biotas, especially terrestrial fossils, and also a lack of taxonomic resolution of many fossils below family level.

Geologically, New Zealand has emerged from the sea since Early Miocene time (25 Ma to present). Therefore, although comprising continental crust, New Zealand is effectively an oceanic archipelago, albeit one of great age and of predominantly tectonic rather than volcanic origin. Can such a history accommodate the biology? Our work on the Chatham Islands may offer some insight. The Chatham Islands have long been assumed to be ancient land because this fitted with a preconception about the vicariant origin of biotas (Craw, 1988). It is now evident from geological (Campbell *et al.*, 1994, 2006; Campbell, 1998), taxonomic (Emberson, 1998) and molecular data (Trewick, 2000; Trewick *et al.*, 2005; Paterson *et al.*, 2006) that the extant Chathams emerged from the sea 1–3 Ma. This implies that the ancestors of all of the extensive Chatham's flora and fauna have arrived in a geologically short period across a significant water gap (> 800 km). This includes unlikely candidates such as freshwater fish, lizards and many flightless insects. Our findings imply that a newly emergent New Zealand would quickly gain high diversity levels. Molecular data record the arrival of colonizing taxa. The finding that modern *Nothofagus* beech must have arrived by dispersal (Knapp *et al.*, 2005) supports the proposition that the entire modern flora could be of dispersal origin (Pole, 1994, 2001; and see McGlone, 2005). Numerous studies have produced results that are compatible with the emergent New Zealand hypothesis but disquieting under the continental/vicariant hypothesis. For example, freshwater fish (Waters *et al.*, 2000) and plants (Hurr *et al.*, 1999; Meudt & Simpson, 2006) across the Southern Hemisphere, wolf spiders (Vink & Paterson, 2003) and ferns (Perrie *et al.*, 2003) across the Tasman Sea, *Metrosideros* across the Pacific (Wright *et al.*, 2001) have obvious recent dispersal histories.

Of course an emergent New Zealand archipelago does not preclude Zealandia having had a Gondwanan (vicariant) biota prior to submergence in the Oligocene, or the possibility that some lineages survived. What this hypothesis does say is that there was an abrupt discontinuity in species composition of New Zealand as a result of the submergence of Zealandia (Pole, 2001). A paradigm shift is needed to approach the biology of New Zealand from the perspective of a relatively young, dynamic evolutionary environment rather than the assumption of an archaic ark. However, the recent New Zealand Geology and Genes conference in July 2006 clearly demonstrated that consensus on the origin of the New Zealand biota is yet to be achieved.

Reconciling the origins of the land of New Zealand with the biology and taxonomic distinctiveness of the biota might result in a very different interpretation of the history and nature of the biodiversity. To this end molecular data will continue to provide invaluable and challenging insights. For example, the extinct New Zealand giant eagle (formerly

Harpogornis moorei), the largest known of its kind, was not an ancient endemic evolved during many millennia of isolation but was the product of impressive adaptive response during the Pleistocene following dispersal of a small ancestor (Bunce *et al.*, 2005). Whereas biologists have previously simply ignored the significance of absences from the biota, it is now easier to explain this condition for New Zealand. For example, the absence of terrestrial mammals and snakes from New Zealand becomes increasingly problematic as the timing of their radiation is pushed back deeper into the Cretaceous (Murphy *et al.*, 2001; Rich & Vickers-Rich, 2004; Apesteguia & Zaher, 2006). With a more recent emergence of New Zealand, the absence of mammals and snakes is easier to understand as they tend to be the last to colonize over significant water gaps. Therefore, explaining the extent of diversity (in some groups) becomes far more interesting as do the mechanisms of dispersal and colonization. One challenge rests with explaining why New Zealand has representatives of lineages, such as leiopelmatid frogs and tuatara, that have gone extinct elsewhere. An emergent New Zealand hypothesis would suggest that these lineages had colonized during the last 25 Myr and that their close relatives have gone extinct elsewhere, but perhaps these taxa are indeed the descendants of the lucky few survivors from Zealandia that persisted through a period of small, ephemeral islands.

If, as Diamond (1997) suggests, New Zealand is biologically the closest thing we can come to exploring another planet, then recognition of its emergent origin is profound indeed. Far from diminishing the biota, the 'alien' forms, ecology, behaviour and assemblage are revealed to be the products of a dynamic evolutionary environment, and not relics of a bygone age. New Zealand belongs as part of the story of island evolution in the Pacific and the evolutionary narrative played out there rivals that on tropical, volcanic island systems (Cowie & Holland, 2006).

REFERENCES

- Apesteguia, S. & Zaher, H. (2006) A Cretaceous terrestrial snake with robust hindlimbs and a sacrum. *Nature*, **440**, 1037–1040.
- Baker, A.J., Huynen, L.J., Haddrath, O., Millar, C.D. & Lambert D.M. (2005) Reconstructing the tempo and mode of evolution in an extinct clade of birds with ancient DNA: the giant moa of New Zealand. *Proceedings of the National Academy of Sciences USA*, **102**, 8257–8262.
- Bellamy, D., Springett, B. & Hayden P. (1990) *Moa's ark, The voyage of New Zealand*. Viking, New York.
- Bunce, M., Szulkin, M., Lerner, H.R.L., Barnes, I., Shapiro, B., Cooper, A. & Holdaway, R.N. (2005) Ancient DNA provides new insights into the evolutionary history of New Zealand's extinct giant eagle. *PLoS Biology*, **3**, 44–46.
- Campbell, H.J. (1998) Fauna and flora of the Chatham Islands: less than 4 m.y. old? 'Geology and genes'. *Geological Society of New Zealand Miscellaneous Publication*, **97** (ed. by R.A. Cooper and C. Jones), pp. 15–16.

- Campbell, H.J., Andrews, P.B., Beu, A.G., Maxwell, P.A., Edwards, A.R., Laird, M.G., Hornibrook, N. de B., Mil-denhall, D.C., Watters, W.A., Buckeridge, J.S., Lee, D.E., Strong, C.P., Wilson, G.J. & Hayward, B.W. (1994) Cretaceous-Cenozoic geology and biostratigraphy of the Chatham Islands, New Zealand. *Institute of Geological and Nuclear Sciences Monograph*, **2**, 1–269.
- Campbell, H.J., Begg, J.G., Beu, A.G., Carter, R.M., Davies, G., Holt, K., Landis, C. & Wallace, C. (2006) On the turn of a scallop. *Geological Society of New Zealand Miscellaneous Publication*, **121** (ed. by S.A. Trewick and M.J. Phillips), p. 9.
- Cande, S.C. & Stock, J.M. (2004) Pacific-Antarctic-Australia motion and the formation of the Macquarie Plate. *Geophysics Journal International*, **157**, 399–414.
- Cooper, A. & Cooper, R.A. (1995) The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **261**, 293–302.
- Cowie, R.H. & Holland B.S. (2006) Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *Journal of Biogeography*, **33**, 193–198.
- Craw, R.C. (1988) Continuing the synthesis between panbiogeography, phylogenetic systematics and geology as illustrated by empirical studies on the biogeography of New Zealand and the Chatham Islands. *Systematic Zoology*, **37**, 291–310.
- Craw, R.C., Grehan, J.R. & Heads, M. (1999) *Panbiogeography – tracking the history of life*, Oxford Biogeography Series 12. Oxford University Press, New York.
- Daugherty, C.H., Gibbs, G.W. & Hitchmough, R.A. (1993) Mega-island or micro-continent? New Zealand and its fauna. *Trends in Ecology & Evolution*, **8**, 437–442.
- Diamond, J.M. (1990) New Zealand as an island archipelago: an international perspective. *Ecological Restoration of New Zealand Islands. Conservation Sciences Publications No. 2* (ed. by D.R. Towns, C.H. Daugherty and I.A.E. Atkinson), pp. 3–8. Department of Conservation, Wellington.
- Diamond, J. (1997) *Guns, germs and steel: the fates of human societies*. Random House, London.
- Emberson, R.M. (1998) The beetle (Coleoptera) fauna of the Chatham Islands. *New Zealand Entomologist*, **21**, 25–64.
- Emerson, B.C. (2002) Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. *Molecular Ecology*, **11**, 951–966.
- Fleischer, R.C., McIntosh, C.E. & Tarr, C.L. (1998) Evolution on a volcanic conveyor belt: using phylogeographic reconstructions and K-Ar-based ages of the Hawaiian Islands to estimate molecular evolutionary rates. *Molecular Ecology*, **7**, 533–545.
- Fleming, C.A. (1962) New Zealand biogeography – a paleontologist's approach. *Tuatara*, **10**, 53–108.
- Fleming, C.A. (1979) *The geological history of New Zealand and its life*. Auckland University Press, Auckland.
- Gillespie, R.G. & Roderick, G.K. (2002) Arthropods on islands: colonization, speciation, and conservation. *Annual Review of Entomology*, **47**, 595–632.
- Hurr, K.A., Lockhart, P.J., Heenan, P.B. & Penny, D. (1999) Evidence for the recent dispersal of *Sophora* (Leguminosae) around the Southern Oceans: molecular data. *Journal of Biogeography*, **26**, 565–577.
- Kamp, P.J.J. (1992) Tectonic architecture of New Zealand. *Landforms of New Zealand*, 2nd edn (ed. by J.M. Soons and M.J. Selby), pp. 1–30. Longman Paul, Auckland.
- Kamp, P.J.J., Green, P.F. & White, S.H. (1989) Fission track analysis reveals character of collisional tectonics in New Zealand. *Tectonics*, **8**, 169–195.
- Knapp, M., Stockler, K., Havell, D., Delsuc, F., Sebastiani, F. & Lockhart, P.J. (2005) Relaxed molecular clock provides evidence for long-distance dispersal of *Nothofagus* (southern beech). *PLoS Biology*, **3**, 38–43.
- Landis, C.A., Campbell, H.J., Begg, J.G., Paterson, A.M. & Trewick, S.A. (2006) The drowning of Zealandia: evidence and implications. *Geological Society of New Zealand Miscellaneous Publication*, **121** (ed. by S.A. Trewick and M.J. Phillips), p. 21.
- Luyendyk, B.P. (1995) Hypothesis for Cretaceous rifting of East Gondwana caused by subducted slab capture. *Geology*, **23**, 373–376.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ, USA.
- McDowall, R.M. (2004) What biogeography is: a place for process. *Journal of Biogeography*, **31**, 345–351.
- McGlone, M.S. (2005) Goodbye Gondwana. *Journal of Biogeography*, **32**, 739–740.
- McLoughlin, S. (2001) The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Australian Journal of Botany*, **49**, 271–300.
- Meudt, H.M. & Simpson, B.B. (2006) The biogeography of the austral, subalpine genus *Ourisia* (Plantaginaceae) based on molecular phylogenetic evidence: South American origin and dispersal to New Zealand and Tasmania. *Biological Journal of the Linnean Society*, **87**, 479–513.
- Mortimer, N. (2004) New Zealand's geological foundations. *Gondwana Research*, **7**, 261–272.
- Murphy, W.J., Eizirik, E., O'Brien, S.J., Madsen, O., Scally, M., Douady, C.J., Teeling, E., Ryder, O.A., Stanhope, M.J., de Jong, W.W. & Springer, M.S. (2001) Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science*, **294**, 2348–2351.
- Paris, J.-P. (1981) Géologie de la Nouvelle-Calédonie. *BRGM Mémoire*, **113**, 1–278.
- Paterson, A.M., Trewick, S.A., Armstrong, K., Goldberg, J. & Mitchell, A. (2006) Recent and emergent: molecular analysis of the biota supports a young Chatham Islands. *Geological Society of New Zealand Miscellaneous Publication*, **121** (ed. by S.A. Trewick and M.J. Phillips), pp. 27–29.
- Perrie, L.R., Brownsey, P.J., Lockhart, P.J., Brown, E.A. & Large, M.F. (2003) Biogeography of temperate Australasian *Polystichum* ferns as inferred from chloroplast sequence and AFLP. *Journal of Biogeography*, **30**, 1729–1736.
- Pole, M.S. (1994) The New Zealand flora – entirely long-distance dispersal? *Journal of Biogeography*, **21**, 625–635.

- Pole, M.S. (2001) Can long-distance dispersal be inferred from the New Zealand pant fossil record? *Australian Journal of Botany*, **49**, 357–366.
- Rich, T.H. & Vickers-Rich, P. (2004) Diversity of early Cretaceous mammals from Victoria, Australia. *Bulletin of the American Museum of Natural History*, **285**, 36–53.
- Stevens, G.R. (1980) *New Zealand adrift*. Reed, Wellington.
- Stevens, G., McGlone, M. & McCulloch, B. (1988) *Prehistoric New Zealand*. Heinemann Reed, Auckland.
- Storey, B.C. (1996) Microplates and mantle plumes in Antarctica. *Terra Antarctica*, **3**, 91–102.
- Suggate, R.P., Stevens, G.R. & Te Punga, M.T. (1978) *The geology of New Zealand*. Department of Scientific and Industrial Research, Wellington.
- Sutherland, R. (1999) Basement geology and tectonic development of the greater New Zealand region: an interpretation from regional magnetic data. *Tectonophysics*, **308**, 341–362.
- Trewick, S.A. (2000) Molecular evidence for dispersal rather than vicariance as the origin of flightless insect species on the Chatham Islands, New Zealand. *Journal of Biogeography*, **27**, 1189–1200.
- Trewick, S.A., Goldberg, J. & Morgan-Richards, M. (2005) Fewer species of *Argosarchus* and *Clitarchus* stick insects (Phasmida, Phasmatinae): evidence from nuclear and mitochondrial DNA sequence data. *Zoologica Scripta*, **34**, 483–491.
- Vink, C.J. & Paterson, A.M. (2003) A combined molecular and morphological phylogenetic analysis of the New Zealand wolf spider genus *Anoteropsis* (Araneae: Lycosidae). *Molecular Phylogenetics and Evolution*, **28**, 533–544.
- Wallace, A.R. (1883) *Australasia: Stanford's compendium of geography and travel*. Edward Stanford, London.
- Waters, J.M. & Craw, D. (2006) Goodbye Gondwana? New Zealand biogeography, geology, and the problem of circularity. *Systematic Biology*, **55**, 351–356.
- Waters, J.M., Andres-Lopez, J. & Wallis, G.P. (2000) Molecular phylogenetics and biogeography of galaxiid fishes (Osteichthyes: Galaxiidae): dispersal, vicariance, and the position of *Lepidogalaxias salamandroides*. *Systematic Biology*, **49**, 777–795.
- Whitehouse, I.E. & Pearce, A.J. (1992) Shaping the mountains of New Zealand. *Landforms of New Zealand*, 2nd edn (ed. by J.M. Soons and M.J. Selby), pp. 144–160. Longman Paul, Auckland.
- Wright S.D., Yong, C.G., Keeling, D.J., Dawson, J.W. & Gardner R.C. (2001) Stepping stones to Hawaii: a trans-equatorial dispersal pathway for *Metrosideros* (Myrtaceae) inferred from nrDNA (ITS + ETS). *Journal of Biogeography* **28**, 769–774.

BIOSKETCHES

Steve Trewick, Adrian Paterson and Hamish Campbell

have collaborated on research relating to the age and formation of land surfaces of the Chatham Islands with a particular interest in the rates and modes with which the endemic biota has developed. Steve Trewick (Massey University) and Adrian Paterson (Lincoln University) share interests in speciation and evolution of a broad range of taxa with a particular focus on the biota of New Zealand. Hamish Campbell (GNS Science) is a geologist with particular interest in geochronology, geological mapping, stratigraphy and tectonics.

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