Goodbye Gondwana? New Zealand Biogeography, Geology, and the Problem of Circularity

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BIOGEOGRAPHY, MULTIDISCIPLINARY RESEARCH, AND CIRCULAR LOGIC

Vicariance is potentially a key biogeographic process (Rosen, 1978) that physically disrupts populations—typically through geological upheaval—and leads to genetic divergence and speciation (Avise, 2000). One of the most dramatic and best-known cases of vicariance is the perceived role of plate tectonics in mediating the widespread "Gondwanan" distribution of taxa currently limited to southern landmasses such as Africa, South America, Australia, New Zealand, and New Caledonia. Following the general acceptance of plate tectonic theory, vicariance biogeographers (e.g. Rosen, 1978; Nelson and Ladiges, 2001; Humphries, 2000; Ebach et al., 2003) have explained the wide southern distributions of ratite birds, freshwater fishes, and southern beeches, for example, as essentially passive phenomena shaped by geology.

Vicariant biogeographic inferences should ideally be based on a combination of biological and geological information. When such distinct fields of scientific research intersect, however, there is potential for associated "multidisciplinary" inferences to be clouded by circular reasoning. Bishop (1995) noted such a problem when considering geological versus biological evidence for river capture, a geomorphological process thought to effect vicariant isolation of freshwater-limited taxa (Mayden, 1988; Waters et al., 2001). To demonstrate a causal relationship between these geological and biological phenomena (e.g. cladogenesis of freshwater fish lineages mediated by vicariance), Bishop (1995) argued that geomorphological and organismal evidence should be assessed independently. If not, he explained, there is potential to invoke a geologically-mediated process which may not have occurred. Although a few studies of freshwater vicariance have indeed examined geological and biotic data independently (e.g. Mayden, 1988; Waters et al., 2001; Burridge et al., 2006), it is more common to merely invoke a geological explanation a posteriori on the basis of biological data (e.g. McDowall, 1990; Musyl and Keenan, 1992; Waters et al., 1994; Gollmann et al., 1997; Hurwood and Hughes, 1998; Engelbrecht et al., 2000; Kreiser et al., 2001). In many of the above cases that lack independent geological analysis, there are plausible biogeographic alternatives to drainage rearrangement, including migration across flooded divides, aridification, or lowland/marine dispersal (Bishop, 1995).

More broadly, a similar tendency towards circularity may apply to biogeographic inference at the intercontinental scale. The isolated landmass of New Zealand (NZ), 2000 km east of Australia, presents a fascinating system for biogeographers, as a variety of biological and geological processes could potentially explain the origin of its unique biota (e.g. Cooper and Millener, 1993; Pole, 1994). We suggest that NZ biogeography represents another case in which geological and biological explanations apparently lack independence. Specifically, we argue that the "Gondwanan" ancestry typically ascribed to components of NZ's biota (Cooper and Millener, 1993; Bellamy et al., 1990) lacks geological support. Instead, the geological "evidence" has largely been driven by the general assumption that NZ has a Gondwanan biota (Fleming, 1962, 1979), which results in circular logic. We therefore argue that the NZ-Gondwana story has achieved a level of prominence, driven by this circularity, where the whole is considerably greater than the sum of the parts.

GONDWANA RIFTING AND OLIGOCENE DROWNING

There is general geological agreement that NZ separated from Australia with the opening of the Tasman Sea about 80 million years ago (Molnar et al., 1975). This was the event that was reputedly responsible for NZ's Gondwana biota (Fleming, 1962, 1979). Survival of the terrestrial descendants of this Gondwana biota, however, requires that at least some of the NZ landmass remained above sea level since the rifting event. While there is certainly abundant evidence that NZ was emergent for most of that 80 Ma, Oligocene drowning of the landmass may also have occurred (Campbell and Landis, 2003).

The current state of geological knowledge regarding Oligocene geography and geology of NZ can be summarised in the following points:

1. The NZ continental block was stretched and thinned during the extensional breakup of Gondwana and rifting from Australia. Crustal thickness was typically 17–25 km (Adams, 1962): almost all of this thinned

crust became progressively submerged between Cretaceous and Oligocene. Most of the NZ continent is still submerged because of this thin crust.

2. The current emergent parts of the NZ continental crust block has been lifted above sea level by collisional tectonism and associated crustal thickening beginning in the late Oligocene or early Miocene (Cooper et al., 1987).

3. Evidence for widespread Cretaceous to Oligocene submergence of NZ is both direct (marine sediments) and indirect (wave-cut surface on basement; LaMasurier and Landis, 1996).

4. There is no direct evidence for continuously emergent land through the middle Tertiary (e.g., a continuous sequence of nonmarine sediments from Eocene to Miocene).

5. There is local evidence for land in the Oligocene (e.g., Turnbull et al., 1975; King et al., 1999), but this is almost invariably overlain or underlain by evidence of marine incursion. The Oligocene lasted more than 10 million years, and resolution of rock ages is too low to allow conclusive definition of times of complete submergence, or of persistence of an emergent archipelago.

6. There are many areas in the mountainous parts of NZ where all evidence of Tertiary history has been eroded. Hence it is not possible to discount either subsidence or emergence in the Oligocene in these areas.

Available geological data thus neither confirm nor reject Oligocene drowning of NZ. From a purely physical point of view, points 1, 3, and 4 strongly suggest that NZ was fully submerged in the Oligocene (e.g., Campbell and Landis, 2003). However, it is also possible to create maps of emergent Oligocene islands based on a lack of evidence to the contrary, associated with points 5 and 6, and the veracity of such maps is scientifically untestable at present. Fleming (1962, 1979) had no problem in mapping such islands because he was a biogeographer and believed that a "Gondwana" fauna and flora provided the extra evidence needed to discount complete Oligocene drowning. Similar biogeographical input has underpinned subsequent paleogeographic reconstructions of the Oligocene as well (e.g., King et al., 1999).

Genetic Evidence that NZ Biota Survived Oligocene Drowning?

The mere presence of taxa on rifted islands such as NZ provides little evidence to help discriminate between vicariant versus dispersalist biogeographic explanations. Oceanic dispersal of terrestrial species may appear implausible, but a number of such events have indeed been documented (see de Queiroz, 2005). Furthermore, features such as flightlessness may have evolved repeatedly in some groups (e.g. Emerson and Wallis, 1995; Trewick, 1997; Worthy and Holdaway, 2002), following island colonisation. Fossil records typically lack sufficient specimens and/or phylogenetic information to reliably infer species divergence dates (e.g. McDowall and

Pole, 1997). Hence, additional information is required before biological arguments for and against vicariant origins can be evaluated.

In recent times, biogeographers and systematists have begun to use molecular data to infer evolutionary relationships among groups of related taxa. Many such studies also assess biogeographic history using molecular calibrations that are themselves based on correlations between geological data points and genetic divergence (e.g. fossil record; isthmus formation; island formation; river capture). Molecular methods therefore present a means of discriminating between alternative biogeographic hypotheses (e.g. dispersal versus vicariance). It may sometimes be difficult, however, to discriminate between such hypotheses on the basis of genetic data alone.

First, many biogeographic and phylogenetic studies rely on molecular clocks developed for distantly related taxa. This could be problematic, as interspecific variation in rates of molecular evolution is thought to be substantial. For instance, Bermingham et al.'s (1997) analysis of mtDNA variation among 19 geminate pairs of marine fish taxa separated by the Panama Isthmus (approximately 3 Ma) yielded a wide range of transisthmian divergence values (5.0 ± 3.9%; range 0.2–12.4%). In the absence of a well-constrained molecular calibration, it might be might be difficult to discriminate between alternative biogeographic hypotheses (e.g. ancient vicariance versus ancient marine dispersal of cichlid fishes: see Farias et al., 1999; Briggs, 2003; Sparks and Smith, 2005). In the case of NZ taxa, reasonably accurate calibrations are required to discriminate between vicariant origins (Gondwana rifting 80 Ma) versus post-Oligocene colonization (e.g. dispersal 25 Ma). Second, a particular genetic divergence event (e.g. sphenodontians versus other reptiles), no matter how well dated, is not necessarily attributable to a specific geographic location.

We therefore suggest that researchers should begin to re-examine NZ biogeography to see if post-Oligocene colonisation can be rejected for any extant lineages. The following appraisal of some key NZ "Gondwanan" taxa suggests that support for vicariant origins is lacking in some cases and, at best, unconvincing in others.

Reptiles

Tuatara (*Sphenodon*) represents an ancient reptilian lineage now restricted to NZ. The genetic divergence of sphenodontians from other reptiles (Rest et al., 2003), however, predates the separation of NZ from Gondwana by over 100 Ma, and is therefore uninformative with regard to NZ's geological history. Fossil evidence only shows clearly that the ancestors of tuatara were widespread across the globe during the Triassic. All that can be concluded, therefore, is that sphenodontians have become extinct elsewhere in the world, while their continuing presence in NZ provides no information on the age or location of divergence between tuatara and these extinct lineages.

Oceanic dispersal may be an important biogeographic process for lizards. As a case in point, the

Mascarene Islands endemic skink *Leiolopisma telfarii* and related Mascarene taxa are nested phylogenetically within a clade of Australasian skinks (Carranza et al., 2001; Austin pers. comm.). It therefore appears that long-distance rafting from Australasia may best explain their colonization of the western Indian Ocean. In light of this finding, Trans-Tasman dispersal of skinks may also be biogeographically plausible. Indeed, given the evidence for oceanic dispersal in chameleons (Raxworthy et al., 2002), *Anolis* lizards (Calsbeek and Smith, 2003), geckos (Carranza et al., 2000; Austin et al., 2004; Vences et al., 2004; Carranza and Arnold, 2005), and skinks (Carranza et al., 2001), we see no reason why such explanations should be considered inapplicable for any component of NZ's reptile fauna (e.g. *Hoplodactylus*; *Naultinus*; *Oligosoma*).

Frogs

The NZ endemic genus *Leiopelma* represents a morphologically primitive and genetically divergent anuran lineage that, together with the North American *Ascaphus*, is sister to other extant frogs (Roelants and Bossuyt, 2005). The divergence between *Leiopelma* and *Ascaphus* is presented as relating to the rifting of Laurasia and Gondwana approximately 180 Mya. As is the case for tuatara (above), this divergence date easily precedes the separation of NZ from Gondwana, and is thus biogeographically uninformative for southern relationships. Roelant and Bossuyt's (2005) assumption that the divergence of *Leiopelma* necessarily correlates with "the loss of any terrestrial passage" to NZ 82 Mya may therefore be unwarranted. Indeed, elsewhere in the Southern Hemisphere, frogs have apparently dispersed across marine barriers "between Africa, Madagascar, Comoros and the Seychelles" (Vences et al., 2003). It might seem odd that only this *ancient* frog lineage successfully dispersed to NZ when many additional lineages that currently exist in the Australasian region apparently failed to do so; but we reiterate that the lack of extant relatives in nearby landmasses does not *prove* a NZ vicariant origin for *Leiopelma*.

Ratites

This group of large flightless birds appears to be a good candidate for vicariance, and is represented in NZ by both extinct (moa) and extant (kiwi) lineages. Cooper et al.'s (2001) ratite phylogeny based on 10.8 kb of mtDNA supported the monophyly of ratites relative to their flighted ancestors (tinamous; South America). The parsimonious assumption of a single loss of flight for Palaeognathes, however, is not a certainty: there are numerous avian lineages that have undergone repeated loss of flight, and this asymmetric evolutionary process is particularly common on predator-free islands such as NZ (Trewick, 1997; Worthy and Holdaway, 2002). It remains plausible, therefore, that ratites could have flown to NZ and subsequently evolved flightlessness. Cooper et al. (2001) "confirmed that the moa and kiwi are not monophyletic, and represent separate invasions of

New Zealand." Under a molecular clock calibrated on the *assumption* that moas are truly Gondwanan (82 Ma), genetic data suggest kiwi arrived in NZ by dispersal only 68 Ma. The mtDNA analysis of Haddrath and Baker (2001) similarly requires dispersal of kiwi to NZ. But this conclusion clearly begs the question: if dispersal was possible for the ancestors of kiwi, why not for moa? Moreover, the lack of geological calibration points for ratites (e.g. phylogenetically informative fossil data) limits the associated conclusions on the timing of dispersal: faster calibrations more typical of vertebrate mtDNA would give substantially younger dates for the "separate invasions" of NZ ratites.

Kauri

Stöckler et al. (2002) presented genetic data for *Agathis* representatives from Australia, New Caledonia and New Zealand, with nuclear *rbc*L sequences indicating substantial genetic divergence between NZ *A. australis* and other extant southern taxa. Although no molecular calibrations were attempted, these authors concluded that their data presented "the strongest evidence to date that New Zealand was not completely submerged during the Oligocene." As supporting evidence, Stöckler et al. (2002) cited palynological evidence "consistent with the existence of continuous forests" throughout NZ's Oligocene, and pointed to morphological similarity of 100 Mya fossil and extant NZ kauri. We argue that the suggested geological evidence is lacking. In addition, the fossil from northern South Island clearly predates NZ's separation from Gondwana, so it seems highly unlikely this ancient "*Agathis*" lineage was restricted to NZ at that time. Interestingly, there is a fossil record of *Agathis* in NZ and southern Australia to at least as young as Miocene (Pocknall, 1989; Hill and Brodribb, 1999). As with tuatara, therefore, the question remains: at what point did this ancient "*Agathis*" lineage become extinct in Australia and on other southern landmasses? Without such knowledge, it seems premature to reject post-Oligocene arrival of NZ *Agathis*.

Nothofagus

Southern beeches provide perhaps the best-known example of a "Gondwanan" distribution. Molecular analysis indicates that all NZ *Nothofagus*, however, are genetically similar to Australian taxa (Linder and Crisp, 1995; Knapp et al., 2005). Although some *Nothofagus* intercontinental relationships are consistent with vicariance, this trans-Tasman association "can only be explained by long-distance dispersal" approximately 30 Mya (Knapp et al., 2005). Molecular calibrations for these taxa are based on a rich and phylogenetically informative fossil pollen record, and enable the authors to reject strictly vicariant explanations.

Galaxiid Fishes

The freshwater family Galaxiidae comprises a mixture of diadromous (marine-tolerant) and freshwater-limited

fishes that exhibit a striking southern-temperate distribution (McDowall, 1990). There has been ongoing debate as to whether this wide southern range reflects vicariance (Rosen, 1978) or dispersal (McDowall, 1978). mtDNA analysis suggests that the six-month duration of the marine juvenile phase of diadromous galaxiids is sufficient to facilitate sporadic trans-Tasman dispersal (Waters et al., 2000a). Furthermore, all NZ species belong to clades that also include diadromous Australian relatives: (1) *Neochanna* (Waters et al., 2000b; Waters and McDowall, 2005); (2) *Galaxias maculatus* and landlocked derivatives (Waters et al., 2000a, 2001); (3) other *Galaxias* spp, including kokopu species, koaro, and landlocked derivatives (Waters et al., 2000b; Waters and Wallis, 2001; Waters and McDowall, 2005). Despite a NZ galaxiid fossil record dating back to the Miocene (McDowall and Pole, 1997), the phylogenetic affinities of extant NZ galaxiids are best explained by post-Oligocene dispersal from Australia to NZ.

LONG DISTANCE DISPERSAL

Sanmartin and Ronquist (2004) presented a comprehensive meta-analysis of austral biogeography, and concluded that "the dominant pattern in plants, (southern South America (Australia, NZ)), is better explained by dispersal, particularly the prevalence of trans-Tasman dispersal between New Zealand and Australia." Indeed, Tasmania and NZ, which have been isolated geologically for 82 Ma, share over 200 plant species (Jordan, 2001). Sanmartin and Ronquist (2004) concluded, by contrast, that southern animal patterns were more consistent with vicariance. It should be noted, however, that many of these southern Gondwanan pattern (SGP) taxa include no NZ representatives (e.g. marsupials; Mydidae; Megascelinae) and/or remain to be analysed genetically (e.g. Peripatopsidae; Trichoptera; Mycetophilidae).

Dispersal is increasingly recognised as a dominant biogeographic mechanism (McDowall, 1978; Diamond, 1987, 1988; Pole, 1994; Waters et al., 2000a; Wright et al., 2000; Price and Clague, 2002; De Queiroz, 2005). Although many biogeographers still interpret biotic distributions as passive phenomena shaped largely by geology (e.g. Croizat et al., 1974; Rosen, 1978; Craw et al., 1999), recent evidence shows that dispersal is common (e.g., Hurr et al., 1999; Trewick, 2000; Winkworth et al., 2002; De Queiroz, 2005). Long-distance rafting, for instance, is increasingly accepted as an important biogeographic process (Wheeler, 1916; Heatwole and Levins, 1972; Scheltema, 1995; Censky et al., 1998; Austin, 1999; Waters and Roy, 2004). Interestingly, the difficulty some researchers have accepting dispersal seems to be rooted more in philosophy than biological reality: they simply consider dispersal events to be unimportant, ad hoc, and untestable phenomena (Ball, 1975; Craw, 1979; Craw et al., 1999; Humphries, 2000). Some of these biogeographers appear to be interested in "area relationships" to the exclusion of underlying biogeographic processes and associated explanations involving specific taxa (see Ebach et al., 2003; McDowall, 2004). Nevertheless, to

ignore dispersal—an important ecological and biogeographic process—for these reasons is akin to throwing out the baby with the bathwater. Fortunately, molecular methods now provide a clear means of distinguishing between recent dispersal versus ancient vicariance (Trewick, 2000; Trewick and Wallis, 2001; Waters and Roy, 2004; De Queiroz, 2005), even under very rough molecular calibrations.

CONCLUSIONS

Gondwana has received strong support as an explanation for NZ's unique biota, and this notion of ancient origins is certainly appealing. While we are not specifically rejecting the possibility of a Gondwanan ancestry for some elements of NZ's flora and fauna, we caution researchers against a circular approach to this question. Analysis of geological evidence in isolation provides no evidence for continuous terrestrial landscapes during NZ's late Oligocene. Moreover, there is compelling evidence that much of NZ's supposedly Gondwanan biota arrived post-Oligocene, and that new species continue to arrive (Worthy and Holdaway, 2002). It should also be remembered that vicariance and dispersal are not mutually exclusive processes: in some cases recent trans-Tasman gene flow may have "overwritten" the genetic signatures of more ancient biogeographic events. Regardless, the onus is now on geologists, palaeontologists, and molecular phylogeneticists to provide convincing independent evidence for the continuous survival of NZ biota through the Oligocene and beyond. Otherwise, it might indeed be "goodbye Gondwana" (McGlone, 2005).

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