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## Society of Systematic Biologists

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Reviewed work(s):

Source: *Systematic Biology*, Vol. 50, No. 4 (Aug., 2001), pp. 602-609

Published by: [Oxford University Press](#) for the [Society of Systematic Biologists](#)

Stable URL: <http://www.jstor.org/stable/3070857>

Accessed: 18/12/2012 17:57

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# Points of View

Syst. Biol. 50(4):602–609, 2001

## Finding Fault with Vicariance: A Critique of Heads (1998)

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The renaissance of plate tectonics (Wegener, 1915), the growth of Hennigian systematics (Hennig, 1950), the development of molecular dating methods (Zuckerlandl and Pauling, 1962; Hillis et al., 1996) and the emergence of phylogeography (Avice et al., 1987) have placed biogeographic data at center stage of evolutionary debate (Avice, 2000). In cases where geological history is well-understood, biogeographic scenarios can be erected, based on molecular data (Thorpe et al., 1994; Lessios et al., 1999). In cases where alternative biogeographic hypotheses already exist, molecular data can be used to distinguish between them (Barendse, 1984; Bowen et al., 1989). On the other hand, molecular surveys have sometimes revealed unexpected patterns from which previously unknown histories and processes have been inferred (Avice, 1992; da Silva and Patton, 1998). New techniques enable geology and biology to develop more synergistically, whereby patterns revealed by one discipline can be used as an hypothesis for testing by the other.

The dynamic tectonic and volcanic history of New Zealand presents an array of possible questions relating to vicariance biogeography. Dominant among extant physical features is the 600-km-long Alpine Fault (Fig. 1), the continental boundary between Pacific and Australian plates, which has experienced as much as 20 km of uplift in the last ~5 million years (MY) (Batt et al., 2000; Chamberlain and Poage, 2000) and 480 km of lateral displacement in the last 25 MY (Kamp, 1992; Whitehouse and Pearce, 1992). The resulting Southern Alps facilitated extensive glacier formation during the Pleis-

tocene (Fig. 2), with some glaciers still reaching low altitudes in the current interglacial period. Many animal and plant species on South Island show disjunct distributions, typified by the "beech-gap" where southern beech (*Nothofagus*) and many other taxa are absent from the central narrow "waist" of South Island. These distributional gaps have generally been ascribed to glacial annihilation in the central region (Cockayne, 1926; Willett, 1950; Wardle, 1963; Burrows, 1965; Dumbleton, 1970), which is characterized by steep mountains (west) and recent alluvial gravel outwash (east; Fig. 2). Subsequent post-Pleistocene recolonization is hypothesized to have taken place from forested glacial refugia to the south and north (Forster, 1954; Holloway, 1954; Wardle, 1963). In contrast, McGlone (1985) considered the beech gap on the west coast to be the result of local conditions favoring podocarps, but evidence for this interpretation is lacking (Leathwick, 1998).

The role of Pleistocene glaciation in shaping current biotic distributions in New Zealand has been questioned by some zoologists (Craw, 1989) and botanists (Heads, 1989). These authors adopt a pan-biogeographic approach, the central philosophy of which is to focus on "the role of locality and place in the history of life" (Craw et al., 1999:4). Heads (1998) has recently published a series of 72 distribution maps for plant and animal taxa in South Island, New Zealand: algae, lichens, mosses, monocots, dicots, molluscs, annelids, and arthropods. These distributions typically comprise a cluster of points in the northwest (Nelson region; west of the Alpine Fault), and another

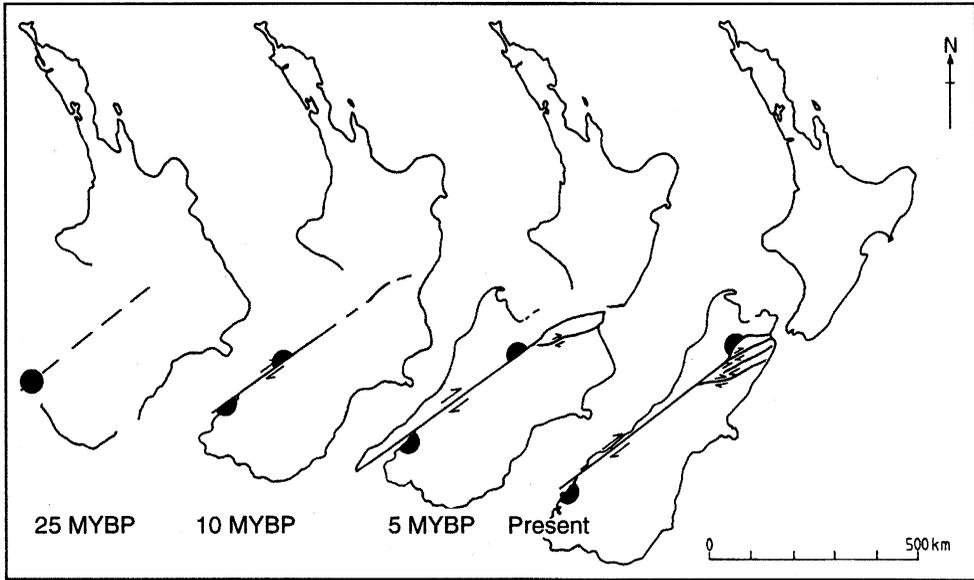


FIGURE 1. Map of New Zealand, showing displacement of South Island landmasses as a result of displacement along the Alpine Fault over a 25-MY period (after Kamp, 1992). The approximate position of the current coastline is shown on all maps. The black area represents the distribution of a hypothetical taxon fractured by this movement.

cluster in the south (Otago, Southland; east of the fault) (his Figs. 2–7). Heads argues that this biological disjunction along the Alpine Fault is a reflection of the ancient but ongoing vicariant process of lateral plate displacement, as opposed to the recent eradication of central populations by

glaciation: Previously continuous distributions have been torn apart by northeast versus southwest tectonic movement. The purpose of this paper is to examine Heads' contention critically and suggest some ways of resolving the debate.

NINE PROBLEMS WITH HEADS (1998)

1. *Disjunct Distributions Generate Rather than Distinguish Hypotheses*

The method of Heads (1998; henceforth Heads98) involves solely collation of distribution maps. However, disjunct distributions alone cannot be used to support alternative hypotheses. The two quite distinct processes of vicariance through lateral plate movement and eradication by glaciation are alternative explanations for the same pattern of disjunct distributions. Heads98 carries out no data analyses, nor makes any prediction that could distinguish the two processes. His approach is rhetorical rather than scientific.

2. *Disjunct Taxa Used as Examples Are Mainly Conspecifics*

Heads98 tells us that: "Disjunct taxa at different ranks from subspecies to family (Pleurophascaceae [monotypic moss family], Nothofagaceae [southern beech]) were

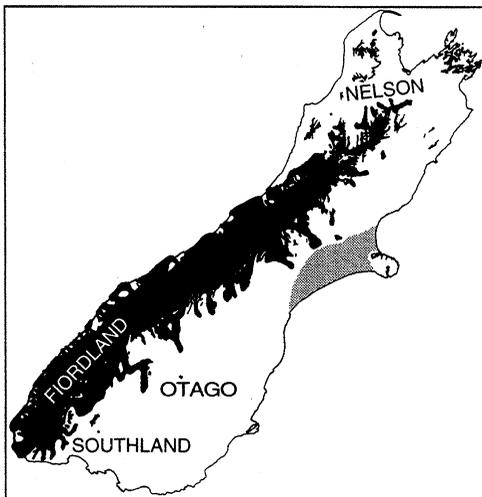


FIGURE 2. Map of South Island, New Zealand, showing maximal extent of Pleistocene glaciations (black) and river gravel aggradation (gray) (after Suggate et al., 1978).

observed" (p. 165; [our brackets]). The figure legends suggest, however, that the great majority of disjunct distributions involve conspecifics. Judging by the Linnaean nomenclature in the legends, 51 cases are within species, 4 are within species group or complex, 1 is within subgenus, and the remaining 16 are within genera. Indeed, we can see no mapped examples that involve disjunction higher than the species level. Of the 51 within-species disjunctions, 5 are within a form, variety, or subspecies.

It has long been recognized that one cannot equate taxonomic rank across different groups. For example, humans and chimps (originally placed in different families) are about as genetically distinct as sibling species of some groups such as *Drosophila* (King and Wilson, 1975). For mainly this reason, some authors have suggested rescaling Linnaean classification along molecular lines (Avice and Johns, 1999), whereas others go further and advocate abolishing taxonomic rank altogether (Mishler, 1999). Although morphological evolution can proceed at quite different rates across taxa (Simpson, 1944; Cherry et al., 1978; Larson, 1989), we think it highly unlikely that the majority (71%) of sister taxa in this study should remain conspecific (as implied by the absence of even subspecific notation) after an independent evolutionary history of 25 MY. For most groups, the average duration of an entire genus in the fossil record is far shorter (Stanley, 1979). Invoking gene flow across the gap to explain taxonomic cohesion is problematic (Ehrlich and Raven, 1969) and requires an explanation for the absence of intervening populations. We feel that the large majority of these examples are more likely to represent recently disrupted distributions (in some cases, maybe clines) rather than vicariant distributions dating from the early Miocene.

We are unclear what Heads98 means by his statement that family-level disjunctions were observed (Pleurophascaceae, Nothofagaceae). In the case of the Nothofagaceae, four species of one genus (*Nothofagus*) each have discontinuous distributions in South Island (McGlone, 1985); only one of these is mapped in Heads98 (his Fig. 3D). The Pleurophascaceae, as Heads98 notes, comprises just one species, also found in Tasmania. Although this species has a discontinuous distribution, that does not constitute evidence

of interfamilial disjunction. Possibly Heads meant that all South Island members of these two families show the disjunction.

### 3. Selective Sampling of Taxa

Most of the 72 maps depicted in Heads98 do indeed show strikingly disjunct distributions, and a repeated pattern requires explanation. Although 72 instances is an impressive sample size, one is left wondering how many other taxa do not conform to this pattern. Recent surveys and estimates of New Zealand species make reference to, for example, 178 species of earthworm, >1,000 terrestrial molluscs (Daugherty et al., 1993), >2,000 lepidopterans (Brian Patrick, pers. comm.), 5,026 dipterans, 6,740 beetles, 1,363 hemipterans, and 870 hymenopterans (Emberson, 1998). This faunal biodiversity is represented by about 20 cases in Heads98, representing about 0.1% of taxa. Some of these are not found on South Island, but the proportion is nonetheless small and, we suggest, nonrandom. Critically, taxa appear to have been chosen specifically because they show a disjunct distribution. Quoting from Heads98 (p. 165): "... only 'marker' distributions such as narrow endemics in Nelson and Fiordland will demonstrate fault displacement clearly." Although it is possible that the effect of an ancient vicariant process might be overlain (even obscured) by recent dispersal of different organisms, selection of taxa that "demonstrate fault displacement clearly" is circular reasoning. With an a priori bias in selection of taxa, it could be questioned whether Heads98 can even claim to have evidence of a consistent pattern, let alone process.

An examination of some of the source literature cited by Heads98 reveals many examples of taxa with distribution patterns inconsistent with the fault hypothesis (i.e., those that straddle the fault, some of which are widespread). Many of these taxa were not mentioned by Heads98, presumably because they do not show clear disjunction. Heads (1998:171) himself stated:

The hypothesis of biological displacement on the Alpine fault could be falsified biogeographically, by demonstrating a standard pattern of distribution which crosses the fault without apparent disruption.

For example, Heads98 cited examples of plecopterans that show disjunct

distributions (apterous species of *Vesicaperla*, *Halticoperla*, and *Notonemoura*) but ignored other genera of the same families that show quite different patterns of distribution (e. g., *Spaniocercoides* and *Zelandobius* [McLellan, 1991, 1993]). Additionally, we note that *N. latipennis* exists well to the east of the divide (43°5'S 171°35'W) near Arthur's Pass (McLellan, 1991), although Heads' Figure 6A does not show this point. For orthopterans, Heads98 includes *Alpinacris crassicauda/tumidicauda* (his Fig. 5J), which show a clear north–south and east–west disjunction, but omits *Papirides nitidus/dugdali*, which also show a north–south disjunction, but being *P. nitidus* found both east and west of the divide in the north (Bigelow, 1967). For the plant genus *Celmisia*, Heads includes three species, but not the alpine *C. traversii*, which is widespread on both sides of the fault in northern South Island, and widespread in western Southland (Given, 1984), a distribution more consistent with extirpation in the central region.

Moreover, in some cases Heads98 appears to have been selective within genera. For example, for *Vesicaperla*, he pooled the distributions of four species, but omitted *V. townsendi*, which is found in the central westcoast region (McLellan, 1993). The justification for this omission is apparently because it has vestigial wings rather than being apterous (his Fig. 5, p. 167). Heads98 listed two instances of disjunction in the lepidopteran genus *Stigmella*: one based on a single species (*S. progonopsis*) and a second on two species (*S. hamishella* and *S. aliena*). However, 24 other species with various other ranges in South Island, many of them local, have been recorded (Donner and Wilkinson, 1989), and it is not clear under which criteria Heads98 chose these particular species. More specifically, on what basis did he combine the distributions of *S. hamishella* and *S. aliena*, when any number of other *Stigmella* species permutations would have given quite different distribution patterns? Descriptions of these two species, and morphologically similar species, strongly suggests that they are not sister taxa. Similarly, the Anthicidae (coleopteran) genus *Paratrochus* includes some 35 species (McCull, 1982) but Heads98 picked just one, *P. hamatus*. Another coleopteran family comprises, in New Zealand, six genera and 25 species, presenting various patterns of in-

trageric distribution, but Heads98 selected just one species, *Trichananca [sic] fulgida*. *Trichananca* is represented by a single species in New Zealand but many species are known from Australia (Werner and Chandler, 1995). The source cited by Heads98 (Werner and Chandler, 1995:32) states: "The single species found in New Zealand appears to be an introduction from New South Wales..."; this condition ought to exclude it from any study of New Zealand vicariance biogeography.

#### 4. Ecological Constraint

Much of South Island's remaining forest is in Fiordland and Nelson. Reconstructions of prehuman forest cover show that most of South Island was covered in beech (montane) or podocarp (lowland) forest. In central and eastern regions, this habitat was broadly destroyed by fire soon after Maori settlement 1,000 years ago, and locally by European settlers over the last 150 years (Molloy et al., 1963). Pleistocene glacial periods may also have reduced the extent of forest cover. Some of central South Island is still dominated by glaciers that reach low altitudes because of steep terrain (3764 m to sea level in 36 km in the case of Mt. Cook) and high precipitation (as much as 12 m per year west of the divide; Griffiths and McSaveney, 1983). Elsewhere, to the east of the divide, little forest remains: The scenery is dominated by grazed and burnt highland tussock, highly modified arable lowlands, unstable braided rivers, and extensive hydro lakes. Thus there is simply much more ecological opportunity to observe sister taxa towards the geographical extremes of the island.

#### 5. Incomplete Sampling of Taxa

The disjunct northern and southern distributions in South Island may, to some extent, reflect sampling effort. Fiordland (Southland) and Nelson are widely recognized locations for endemism in the alpine zone (Heads, 1997). The central region has a well-recognized but smaller alpine biota but is dominated by higher mountains and agriculturally modified lowland/montane communities, which are of less attractive to biologists. Some of the gaps may not in fact be gaps, as indeed Heads recognized (1998:170).

### 6. *Dispersal Is Invoked Only When It Fits the Hypothesis*

Heads readily invokes range expansion to explain distributions that cross the fault (his Figs. 3–4), but ignores the longer-term implications of this process (1998:170). To keep pace with geological movement of 480 km over 25 MY requires only an average of 19 mm of organismal “dispersal” per year. This rate of spread should present little challenge to even a plant with no means of seed dispersal. Conversely, the major impacts of glaciation may have been felt until ~14,000 years ago (the end of the last glacial period), so any disjunction caused by local extinction might well persist to the present. Under the glacial extirpation model, one might expect closure of gaps at a rate proportional to the ability of the species to expand its range. Thus, where habitat allows, species with great dispersal potential might already have continuous distributions, whereas others may have expanded their range only minimally. This latter case has been made for *Nothofagus* (Leathwick, 1998) and as a more general prediction in the tropics (Endler, 1982).

### 7. *Current-Day Evidence Supports Glacial Extirpation*

Glaciers are typically several hundred meters deep, scouring and shearing away rock substrate under immense pressure. Few if any multicellular organisms can survive this treatment, so wholesale local extinction must happen as glaciers extend. Although New Zealand was not covered in a Pleistocene ice sheet to the same extent as northern Europe or North America, ice dominated the current alpine and subalpine regions of South Island (~30% of land area; Fig. 2). The evidence for recent coalescence in species that have recolonized glaciated regions in the northern hemisphere is abundant (Hewitt, 1999).

### 8. *The Alpine Fault Is Only Recently Alpine*

Many of the species included in Heads98 are restricted to the alpine zone. However, the alps have existed for  $\leq 5$  MY, emerging after ~300 km of lateral movement had already occurred. One would have to propose that ancestral lowland forms remained extant for most of that time before speciating into alpine forms independently at opposite

ends of South Island while, in most cases, retaining morphological similarity. This scenario stretches parallelism beyond belief.

### 9. *Land Surfaces Have Not Been in Continuous Existence*

Geological evidence indicates that during the Oligocene and early Miocene the (then) southern region was largely under sea, sea level at maximum reaching 24–23 MYA (LeMasurier and Landis, 1996). That was when the current Nelson and Southland regions were adjoining and starting to part. The current Nelson and Fiordland land masses may not have been fully emergent until the late Miocene, some 12 MYA. In the alpine region, some 16 km of the total 20 km of uplift (Kamp, 1992), and  $90 \pm 20$  km of plate convergence (Walcott, 1998) have been eroded by a combination of large landslips and very heavy precipitation (Griffiths and McSaveney, 1983), and much of the eroded material has been deposited in the lowlands through large braided river systems. Original land surfaces and rock types may be totally different from what was present 25 MYA.

## DISCUSSION

### *What We Are Not Saying*

We are not saying that biogeographers should ignore current distribution of taxa in their analyses. To the contrary, we applaud the plea by Heads and others to look carefully at distribution maps. We contend, however, that distributions alone are generally insufficient to answer many questions in biogeography (Waters and Wallis, 2000); rather, they are usually the stimulus to suggest hypotheses that can explain these distributions (Bowen et al., 1989). Current distributions are but a single dimension of biogeographic reconstruction and they are potentially affected by numerous extrinsic (geologic, catastrophic, climatic, biotic) and intrinsic (demographic, dispersal) factors, which change through time and comprise the complex history of a species (Schneider et al., 1998). To stop at distribution takes biogeography little beyond the original scope of Darwin and Wallace. If one is to use distributional data alone, specific predictions that differentiate hypotheses should be made at the outset (Endler, 1982; Mayr and O’Hara, 1986).

We are not suggesting that dispersalist (in this case, genetic cohesion/connectedness until the Pliocene or Pleistocene) explanations are preferable to vicariant ones in biogeography. Again, to the contrary, to assume Croizatian linkage of life and earth evolving together appears to us to be a preferable null hypothesis, but it is an hypothesis that (like all others) has to be falsifiable.

We are not suggesting that vicariance is not important in the evolution of any of these species. Some disjunct pairs may owe their cladogenesis to the ancient vicariant event, perhaps by virtue of very low dispersal ability (some plants), or to specific habitat requirements, perhaps driven by geology (e.g., Red Hills, West Otago, Fiordland; Red Hill, Richmond Ranges, Nelson), if these can persist despite erosion. We contend that these questions require an empirical rather than a rhetorical answer. Currently, the evidence is not available to distinguish recent (<1.8 MYA) from ancient (25 MYA) events. Molecular data offer an obvious solution, as has been suggested by other biogeographers (McGlone, 1985).

#### *Ancient Vicariance or Recent Glacial Extirpation?*

Although some predictions about current extents of distribution can be made, based on ecology and life-histories of some specific taxa, these will generally give only circumstantial evidence in favor of one hypothesis. Examples of these have been expressed elsewhere (McGlone, 1985) and we will not go into them here. We simply wish to make some predictions that are testable in the realm of molecular phylogenetics and evolution. A key premise of our predictions is that if disjunct distributions are explained by ancient vicariance, then dispersal along or across the fault must be virtually nonexistent over a long time frame. First, under the ancient vicariance hypothesis, sister taxa of Nelson forms west of the divide should reside in Otago-Southland east of the divide. Second, there should be sharp phylogeographic breaks across the Alpine Fault. Third, and perhaps most tellingly in this case, molecular divergence between northern and southern forms should reflect of 25 MYA as opposed to <1.8 MYA.

Other processes have also been invoked to explain the paucity of endemics or gaps

in the central region of South Island. A major Oligocene drowning event took place ~30 MYA, reducing New Zealand to series of low-lying islands (Cooper, 1989). There is some debate about the extent and timing of this drowning event, but it clearly falls in much the same time frame as the ancient vicariance hypothesis, so the two effects could be very difficult to distinguish. Additionally, McGlone (1985) has proposed a "tectonic hypothesis", which includes Miocene, Pliocene, and Pleistocene speciation resulting from a variety of processes (mainly mountain building and changes in sea level ranging from very recent (<0.5 MYA) to ancient (>20 MYA). This hypothesis is essentially a pluralist approach that deemphasizes the role of glaciation and allows a variety of drivers for New Zealand speciation, some of which would of course be hard to distinguish from the extreme position of Heads98. It is not our intention here to exhaustively list all possibilities, and indeed they may each hold in some circumstances. If pattern and depth are not consistent with ancient vicariance, then glacial extirpation is one main, but not sole, alternative. The time frame suggested by a molecular clock is likely to be crucial to a resolution. Current thought is that most of the movement (420 km) happened during the last 11 MY (Sutherland, 1994), which could ameliorate, though not invalidate, some of our criticisms.

#### *Directions for New Zealand Phylogeography*

Competing hypotheses such as these offer a framework for research programs that can improve our understanding of the history of the New Zealand flora and fauna. The wealth of information available in DNA sequence data and an ever-improving understanding of rates of molecular evolution and phylogeny construction can provide the data required to distinguish between sufficiently distinct and well-defined hypotheses. Initial work in this area points to Pliocene mountain building rather than early Miocene vicariance as an initiator of lineage divergence in widespread alpine species (Emerson and Wallis, 1995; Trewick et al., 2000; Buckley et al., 2001). Biogeography has grown in sophistication from an era of story-telling to one of more rigorous hypothesis-testing, although unanticipated patterns that require formulation of new hypotheses may

always appear. Robust answers to phylogeographic questions ultimately require a multispecies approach (Schneider et al., 1998), and endemic invertebrate groups offer several advantages: They are phylogenetically numerous and diverse, are often abundant as organisms, and have a wide range of vagilities and ecologies. Although initial phylogeographic studies tended to focus on vertebrates (Avise, 1998, 2000; Taberlet et al., 1998), the broader information content of invertebrate groups is now beginning to be tapped (Emerson and Wallis, 1995; Roderick and Gillespie, 1998; Gómez-Zurita et al., 2000; Juan et al., 2000; Trewick 2000; Trewick et al., 2000; Buckley et al., 2001). Finally, using the process of reciprocal illumination, biologists and geologists should work together to produce a more complete picture of the evolution of both the distinctive New Zealand biota and its dramatic landscapes.

#### ACKNOWLEDGMENTS

We particularly thank Bill Lee and Jon Waters for detailed comments on this paper. Mary Morgan-Richards, Chris Simon, and Steve Wagstaff also made useful suggestions. This research was supported by University of Otago Research Grant 99/753, the Hellaby Indigenous Grasslands Research Trust, and FoRST NZST Postdoctoral Fellowship UOO704 (SAT).

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Received 27 June 2000; accepted 28 August 2000  
Associate Editor: R. Olmstead