



# Biogeographic disjunction along the Alpine fault, New Zealand

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Eighty taxa (subspecies, species, species groups, genera and families) showing disjunction along the New Zealand Alpine fault (Australian/Pacific plate boundary) are documented and mapped. Four plant divisions, including 14 seed plant families, and four animal phyla, including 13 orders of insects, are represented. The disjunction has usually been explained by glaciers having wiped out central populations. However, the gap is often occupied by a related taxon and many alpine taxa are involved, and so extinction by glaciation seems unlikely as an explanation. It is proposed that the disjunction has been caused by the 480 km of lateral displacement on the fault.

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**ADDITIONAL KEY WORDS:**—biogeography – disjunction – seed plants – *Nothofagus* – insects – plate tectonics – transform fault.

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## INTRODUCTION

Since the time of Darwin biogeographic data have played a critical role in evolutionary studies. Modern explanations of biogeographic patterns often involve

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observations from geology, and by now there are many examples of 'reciprocal illumination' between geology and biology. The New Zealand Alpine fault is a major tectonic feature; it is a transform fault, or fault zone, located on the mutual boundary of the very large Australian and Pacific tectonic plates and has undergone 480 km of right-lateral displacement over the last 25 million years. It is suggested here that this movement on the fault has had the direct effect of pulling apart plant and animal populations, leading to the Fiordland-Otago/Nelson disjunction seen in many taxa with widely differing ecological requirements.

#### LITERATURE REVIEW: BIOLOGY

At the beginning of this century New Zealand geologists proposed that massive ice-sheets had totally overwhelmed the vegetation of the South Island in a former glacial epoch. Biologists such as Thomson (1909) replied that the floristic evidence was against this, as there was so much endemism in the South Island flora. Cockayne (1921) likewise argued for certain areas having preserved 'alpine' flora during glaciation. Nevertheless, Cockayne (1926) suggested that glaciation had indeed eliminated the 'southern beech' *Nothofagus* from the west coast for 100 miles south of the Taramakau River. This explanation of a major biological disjunction has dominated several decades of biogeographic, ecological and evolutionary research.

Willett (1950) extended Cockayne's ideas on 'glacial control' of *Nothofagus* and also discussed the land snail genus *Paryphanta*. He proposed elimination of taxa from heavily glaciated regions with survival in unglaciated refugia beyond a widespread periglacial zone, and subsequent reinvasion of previously glaciated areas. Willett discussed Powell's (1937) idea of geological control of speciation in land snails by Miocene seas, but did not accept it.

In a botanical study, Holloway (1954) pointed out that both Fiordland and western Nelson must have acted as refugia "little affected" by the last glaciation and that extensive forests would have survived there. Similarly Forster (1954), working on forest fauna, suggested that "Willett's assumptions of the effect of glaciation on the flora were too sweeping."

Wardle (1963) mapped disjunct areas of endemism in the northern and southern South Island and continued with the theme of glacial control. He suggested that the northern South Island (Nelson and Marlborough) was more diverse than the southern South Island (Southland and Otago), and that this was because it had been more important as a refugium/centre of survival. Wardle noted that in the waist of the South Island (Westland and Canterbury) there are fewer endemics even among alpine groups and it was proposed that the alpine flora has been negatively affected by glaciation. Wardle allowed a large degree of forest survival in SE Otago and elsewhere in the South Island.

Burrows (1965) did further mapping of disjunct areas of endemism in northern and southern South Island. Disjunctions between the two regions were again explained in terms of the glacial refugia hypothesis. Burrows proposed more refugia than Wardle, in southern Fiordland, Southland, Otago and Stewart Island, and argued that "plants survived the height of the last glaciation in many places". Indeed, "many species were favoured by the large number of open habitats."

Possible effects of Alpine fault movement on living communities in New Zealand were first proposed by Henderson (1985) in a thesis chapter entitled 'Cenozoic tectonics and biogeography'. Here Henderson discussed the biogeographic significance of Cretaceous terrane suturing and showed that many disjunctions between Nelson and Fiordland can be at least partly explained by displacement along the fault.

McGlone (1985) and Rogers (1989) have given a full discussion of the glacial control hypothesis and much evidence against it. The hypothesis cannot explain why so many disjunct taxa are plants of upland, even alpine habitats. McGlone showed that the hypothesis must be rejected as a general explanation for disjunction and endemism unless future work (1) demonstrates close correlations between plant distributions and ice-free refugia, (2) can substantiate range expansion of supposedly restricted taxa, or (3) shows that dispersal abilities of restricted plants are less than widely distributed relatives. McGlone also discussed possible indirect effects of tectonic uplift on plant populations.

Further, very significant evidence against the glacial theory is the fact that in very many cases the distribution gap in the middle of the South Island (central Westland and Canterbury) is not absolute, but is occupied by a closely related, usually congeneric, taxon. Craw (1989) has emphasized this important point in a discussion of the beetles *Lyperobius* and *Etheophanus* and the plants *Celmisia* and *Ourisia*. Westland is not simply a region of absence, but like Canterbury is also a centre of endemism.

In a previous paper (Heads, 1989) several examples of Alpine fault disjunction in plants and animals were documented and correlated with lateral displacement on the fault.

#### LITERATURE REVIEW: GEOLOGY

Wellman & Willett (1942) mapped the Alpine fault in its southern part, from Abut Head to Milford Sound, and noted the dextral offset of rivers. Wellman (reported in Benson, 1952) recognized "nearly 200 miles" of right-lateral offset on the Alpine fault. With its recognition in plate tectonics theory as a plate boundary, the Alpine fault was established as one of the earth's major structural features (Berryman *et al.*, 1992). Berryman *et al.* include the Wairau fault as part of the Alpine fault which gives a feature 650 km long running the length of the South Island. Rocks older than the fault, and the fossil populations in them, have been pulled apart by movement on the Alpine fault. For example, the ammonoid *Durvilleoceras* occurs only in Permian strata in Upukerora Valley, NW Southland and on d'Urville I. in the Marlborough Sounds (Pillai *et al.*, 1991).

Authors such as Smale (1991) envisage an inception of the fault in the latest Oligocene-early Miocene (25 Ma). At this time the plate boundary began to propagate through New Zealand and the fault represents the onland portion of a trench-trench transform (Browne, 1992; Kemp, Green & Tippett, 1992). Offset of south Westland moraines indicates an average fault displacement rate over the last 17 ka of 27 mm/yr (Sutherland & Norris, 1995).

In the central segment of the fault there has been ramping of continental Pacific crust over the continental Australia plate and the Southern Alps are the surface manifestation of uplift of the leading edge of the Pacific plate crust. Uplift was

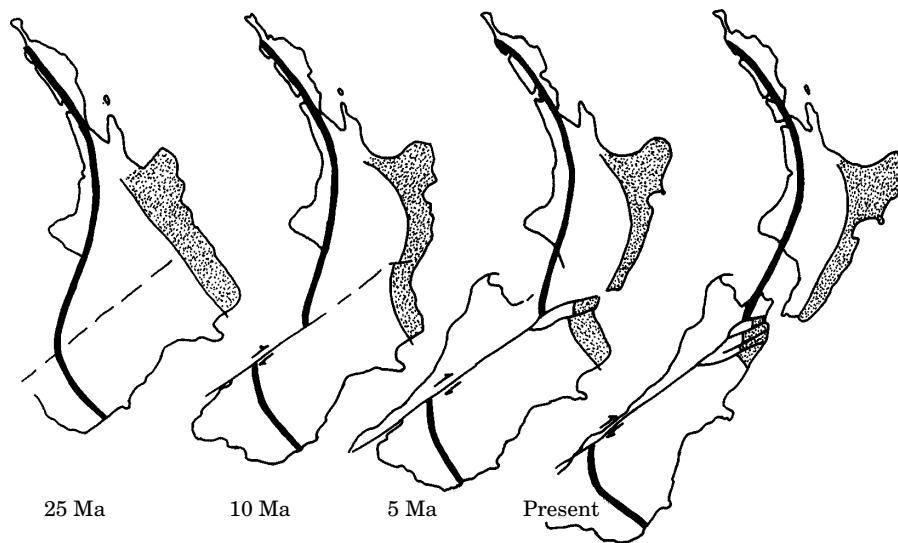


Figure 1. A model of the age and origin of recurved arcs in New Zealand in relation to movement on the Australian–Pacific plate boundary, including the Alpine fault sector. Dun Mountain terrane and associated magnetic anomaly as heavy black. Reconstruction at 25 Ma shows the future position of the Alpine fault as a broken line. Pahau subterrane (younger Torlesse) stippled (after Kamp, 1987).

initiated at 8 Ma (Tippett & Kamp, 1993). The northern portion of the transform consists of a series of fault splays (Fig. 1), the Marlborough fault system (Browne, 1992) or Marlborough Shear Zone (Jiu Shan Yang, 1991), connecting the northern end of the Alpine fault with the Hikurangi subduction zone, offshore along the eastern North Island. In the south, beyond Milford Sound the fault curves to SSW (Wellman, 1984).

The fault continues to be active. A large seismic event related to the last major movement on the central portion of the Alpine fault occurred in the middle 17th to early 18th century. Swamp or forest floor material in northern Fiordland has been inundated by up to 0.5 m of sand and gravel and large silver beech trees growing on the Alpine fault scarp have been topped at heights of 8–15 m above ground level by movement on the fault (Cooper & Norris, 1990). J. Wardle (1967) has also illustrated the dramatic effects of fault movement on New Zealand vegetation, and P. Wardle (1980) suggested that a major earthquake in 1730–40 led to the establishment of even-aged stands of *Metrosideros* and *Weinmannia* in Westland (cf. Stewart & Veblen, 1982).

The model of Alpine fault displacement illustrated here (Fig. 1) has the important feature that it accepts different degrees of displacement at different points on the fault. In particular, displacement is less in Marlborough and further north, where displacement is distributed across several faults and taken up in distributed shear. Thus displacement between, for example, Otago and Nelson is much greater (the full 480 km), than between southern Marlborough and Nelson/Wellington. North of Hokitika where the fault is joined by the Hope fault and others, slip on the Alpine fault drops off markedly. To-day the Hope fault carries most of the plate boundary deformation from the Alpine fault to the Hikurangi subduction zone offshore and the Wairau section is largely a relic feature (Berryman *et al.*, 1992).

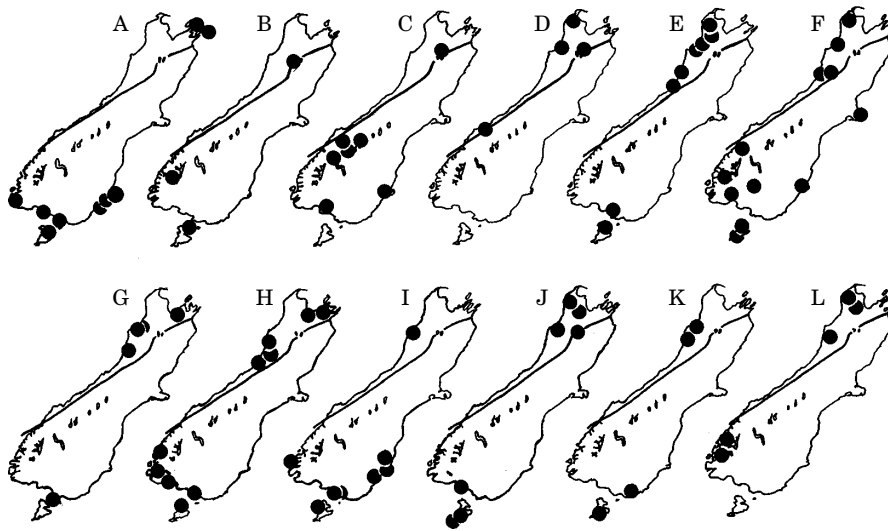


Figure 2. Red algae: A, *Apophlaea* (Moore, 1961; Batham, 1965; specimens in OTA). Lichens: B, *Anzia jamesii*, C, *Xanthoparmelia australasica* (Galloway, 1978, 1980). D, *Pseudocyphellaria hookeri*, E, *P. knightii*, F, *P. lividofusca*, G, *P. chloroleuca* (Galloway, 1988). Bryophytes: H, *Hypnodendron colensoi* (Touw, 1971). Monocotyledons: I, *Hierochloa fusca* (Zotov, 1973), J, *Astelia nivicola* var. *moricae*, K, *A. linearis* var. *linearis*, L, *A. subulata* (Moore, 1966).

#### METHODS

A survey was made of published distribution maps of New Zealand taxa for the presence of Alpine fault disjunction. Several examples are given below from sources where no map has been published, but no attempt has been made to retrieve all these from the literature.

#### RESULTS

Disjunct taxa at different ranks from subspecies to family (Pleurophascaceae, Nothofagaceae) were observed, as were disjunct sister group affinities. All distributions involving disjunctions between at least Taramakau River–Haast or an equivalent distance (240 km), and which are also disjunct on the eastern South Island (absent in the Canterbury region) are illustrated here (Figs 2–7). It is important to note that a taxon which was widespread before fault displacement will be equally widespread after movement, and only ‘marker’ distributions such as narrow endemics in Nelson and Fiordland will demonstrate fault displacement clearly (cf. the Dun Mountain ophiolite terrane, Fig. 1).

In many cases, such as Nelson–Stewart I. disjunction or Nelson–central/east Otago disjunction (Fig. 3A,B,J,L), movement on the fault only accounts for part of the disjunction and further research on the paleogeography of the region west of Stewart Island before Alpine fault movement is needed. In other cases (e.g. Figs 3E, F, 4C, H) disjunction is almost exactly equivalent to Alpine fault movement.

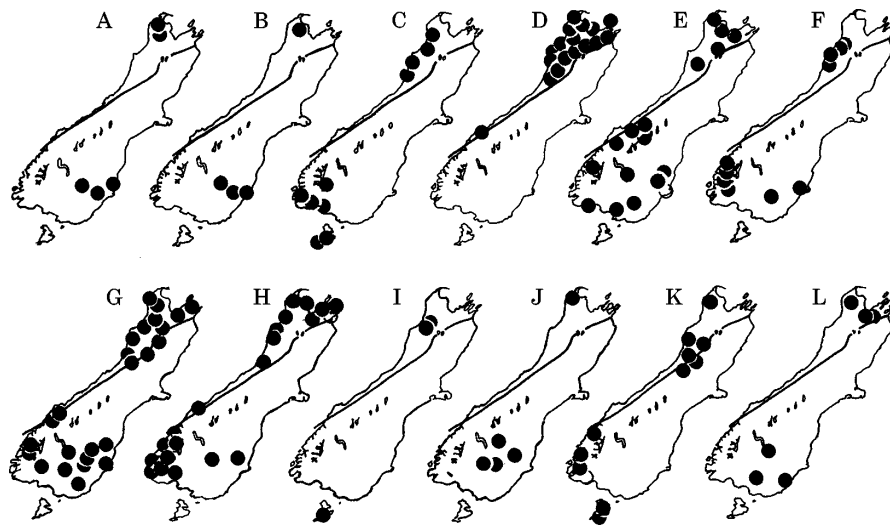


Figure 3. Monocotyledons (continued): A, *Simplicia* (Zotov, 1971), B, *Rytidosperma tenue* (Otago) and *R. pulchrum* (Nelson) (Connor and Edgar, 1979), C, *Elrharta* [*Petriella*] *thomsoni* (Burrows, 1965). Dicotyledons: D, *Nothofagus truncata* (Wardle, 1984), E, *Peraxilla colensoi* (Burrows, 1965; Barlow, 1966), F, *Dracophyllum politum* (Fiordland, Otago) and *D. densum* (Nelson) (Burrows, 1965), G, *Kellera laxa* (Heads, 1990), H, *Pimelea gnidia* (Heads, 1994b), I, *Aciphylla stannensis* (Stewart I.) and *A. trifoliolata* (Nelson) (Dawson, 1980), J, *Gingidia baxterae* (Dawson, 1967; Webb, 1977), K, *Mitrasacme novaezelandiae* (Burrows, 1965), L, *Myosotis tenericaulis*.

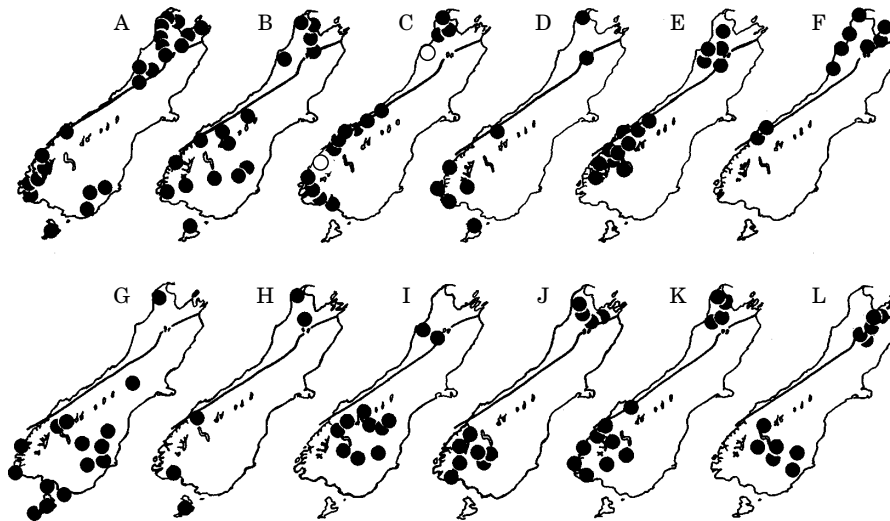


Figure 4. Dicotyledons (continued): A, *Coprosma* sp. aff. *parviflora* (Heads, 1989), B, *Leonohebe hectorii* and related species (Heads, 1994d), C, *Leonohebe mooreae*. Populations with adaxial stomata: open circles (Heads, 1992, 1994d), D, *Parahebe cataractae* group (Heads, 1994e), E, *Hebe cockayneana*, F, *Hebe gracillima* (Heads, 1993), G, *Euphrasia dyeri* (Heads, 1994c), H, *Ourisia modesta* (Heads, 1994a), I, *Ourisia glandulosa* (Heads, 1994a), J, *Senecio* [*Brachyglottis*] *revolutus* (Otago, Fiordland) and *S. adamsii* (Nelson) (Burrows, 1965), K, *Celmisia petriei* (Burrows, 1965), L, *C. prorepens* (Otago) and *C. sinclairii* (Nelson) (Petrie, 1895; Allan, 1961; specimens in OTA).

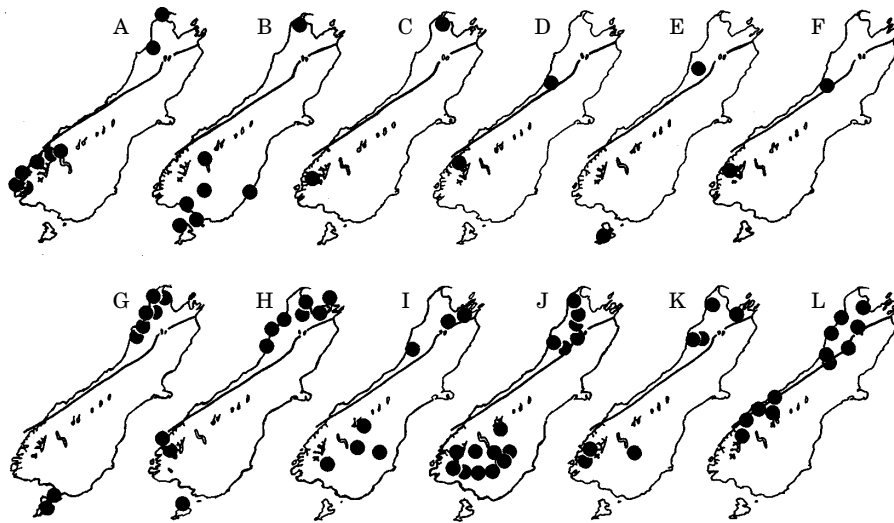


Figure 5. Mollusca: A, *Ptychodon blacki* (Climo, 1989), B, *Ptychodon* subgen. *Solemia* (Climo, 1978), C, *Zelandiscus* (Climo, 1989). Annelida: D, *Diporochaeta intermedia*, E, *Decachaetus*, F, *Deinodrillus benhami* (Lee, 1959). Arthropoda: Class Arachnida: G, *Karamea*, H, *Nuncia* (Forster, 1954). Class Insecta: Protura: I, *Tasmanentulus intermedius* (Tüxen, 1985), Orthoptera: J, *Alpinacris* (Bigelow, 1967) (in addition to the overall distribution of this endemic genus there is one possible record of the Nelson species in Fiordland), K, Plecoptera: apterous species of *Vesicaperla* (McLellan, 1993), L, *Halticoperla* (McLellan, 1991).

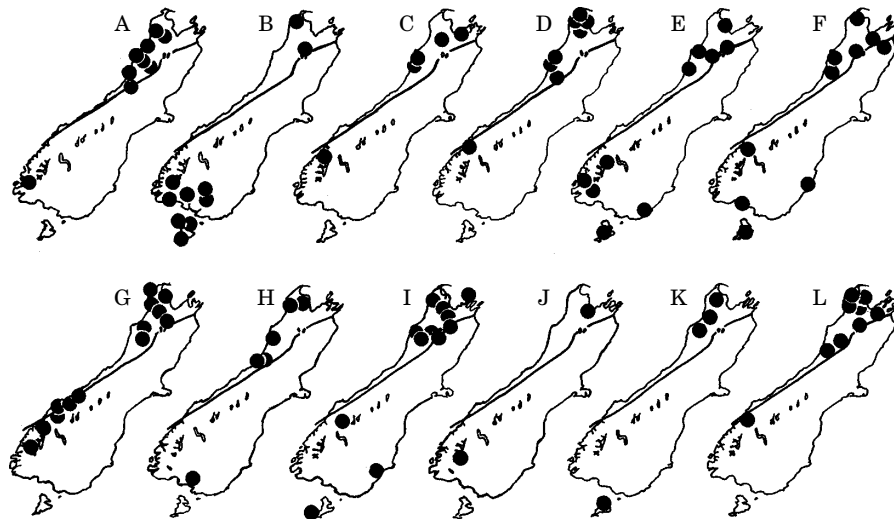


Figure 6. Class Insecta: Plecoptera (continued). A, *Notonemoura* (McLellan, 1991). Hemiptera: B, *Tripetochoris rudis* (Malipatil, 1977). Heteroptera: C, *Rhopalimorpha alpina* (Larivière, 1995). Homoptera: D, *Novothymbris* "zealandica group", E, *Novothymbris* "cithara group" (Knight, 1974), F, *Scaphetus brunneus* (Otago and Stewart I. specimens are slightly different from northern populations) (Knight, 1975). Coleoptera: G, *Paratrochus hamatus* (McCull, 1982), H, *Clambus saturnus saturnus*, I, *Sphaerotherax* (Endrödy-Younga, 1990), J, *Trichanancha fulgida* (Werner and Chandler, 1995). Trichoptera: K, *Rakiura vernale*, L, *Tarapsyche olis* (Ward, 1995).

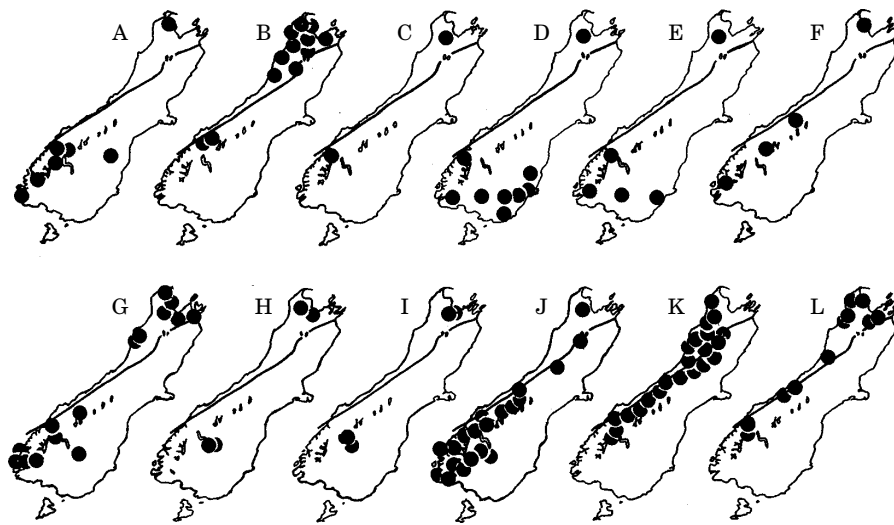


Figure 7. Class Insecta: Trichoptera (continued). A, *Hydrobiosis johnsi*, B, *Aoteapsyche philpotti* (Ward, 1995), C, Lepidoptera: *Stigmella hamishella* (Fiordland) and *S. aliena* (Nelson), D, *Stigmella progonopsis* (Donner & Wilkinson, 1989), E, *Harmologa pontifica* (B. Patrick, pers. comm. Feb. 1996). Diptera: F, *Dilophus alpinus* (Harrison, 1990), Hymenoptera: G, *Diphoropia sinuosa* brachypterous forms (Naumann, 1988), H, *Ophelosia stenopteryx*, I, *O. keatsi* (Berry, 1995). J, *Chionohebe ciliolata* (Dicotyledons) (Hheads, 1994d), K, *Celmisia armstrongii* (Dicotyledons) (Given, 1980), L, *Pycnocentria gunni* (Trichoptera) (Ward, 1995).

#### SYSTEMATIC OCCURRENCE OF TAXA DISJUNCT ALONG THE ALPINE FAULT

##### *Plants*

Marine taxa have not been examined in detail, but one example is given here from the red algae. The New Zealand endemic genus *Apophlaea* shows complete disjunction between northern and southern South I. (Fig. 2A). The systematic position of this 'enigmatic' genus is 'uncertain' (Hawkes, 1983), and it is presumably a phylogenetic relic of considerable age. Other unmapped red algae also show the disjunction. *Heterosiphonia tessellata* is at Three Kings Is., North I., Chatham Is., northern South I., and disjunct at Stewart I. *Polysiphonia rhododactyla* is recorded in the North I. (Bay of Plenty and Cook Strait) and the Marlborough Sounds, and is disjunct at Fiordland and Stewart I. (Adams, 1994).

Seven disjunct lichens and bryophytes are mapped (Fig. 2B–H). In addition, the lichen *Knightiella splachnirima* ranges in southern New Zealand (Dunedin, Awarua, Stewart I., Auckland Is.) and is disjunct in the north at Denniston Plateau (Galloway, 1985). The lichen *Pannaria crenulata* is disjunct between Stewart I./Fiordland and Greymouth (Galloway, Jones & Jørgensen, 1983). The moss family Pleurophascaceae has only one species, *Pleurophascum grandiglobum*, found in Tasmania and the South Island where it is disjunct in Fiordland (Percy Saddle) and in the north at Arthur's Pass, Paparoa Ra., Denniston Plateau and NW Nelson (Burgoo Stream) (Bartlett, 1985). (The whereabouts of a Westland locality, 'Okatira' (=Hokitika? Okarito?), referred to by Sainsbury [1955] has not been traced). Sainsbury writes that "the position of the family is not obvious". In his revision of *Sphagnum* in New Zealand,



Fife (1996) mapped *S. simplex* and *S. compactum* each disjunct between Nelson and Otago.

There are many examples of disjunction in the seed plants in addition to the classic case of *Nothofagus* and some are given in Figures 2–IL, 3, 4. In the Scrophulariaceae, Wardle (1993) has referred to a “whipcord hebe gap” coincident with the beech gap. *Leonohebe mooreae* shows the disjunction and anomalous populations of this taxon with adaxial stomata in Nelson (Denniston Plateau) and Fiordland (Caswell Sound) also show the disjunction very precisely (Fig. 4C). Although *Celmisia prorepens* and *C. sinclairii* (Fig. 4L) were placed in separate sections of the genus by Allan (1961) they show striking similarities (Mark & Adams, 1995) and Given (1969) has treated them in the same section of the genus.

Another cryptic case may occur in *Epilobium alsinoides*, an “enormously complex species” (Raven & Raven, 1976). Subsp. *alsinoides* ranges south from the North Island only to NW Nelson and the Alpine fault (at the Wairau V.). Nevertheless, “here and there in the South Island, especially in Otago”, are encountered plants “reminiscent” of subsp. *alsinoides*. They are placed in subsp. *atriplicifolium* by Raven and Raven, but have the pubescent capsules and rounded leaves that distinguish subsp. *alsinoides*.

A further unmapped example is *Gentiana saxosa*, recorded in the southern South I. (Dusky Sound, Bluff, Catlins) and Stewart I. and disjunct in north Westland (Hokitika) and Nelson (Charleston) (Cheeseman, 1925).

### Animals

Examples are mapped from the phyla Mollusca, Annelida and Arthropoda (Figs 5–7). In the insects there are examples from the orders Protura, Orthoptera, Plecoptera, Hemiptera, Heteroptera, Homoptera, Coleoptera, Trichoptera, Lepidoptera, Diptera and Hymenoptera.

Other unmapped examples include the earthworm genus *Eudinodriloides* of west Nelson, which has its closest affinities with certain ‘quasi-prostatic’ species of *Microscolex* found only on the New Zealand subantarctic islands (Lee, 1959).

In the insect order Psocoptera, the *Austropsocus insularis* group includes species from the New Zealand subantarctic islands, Stewart I. and Chatham I., and *A. salmoni*, in the south at Cascade Creek, Fiordland, and with disjunct records in the north: Lake Rotoiti, Lake Rotoroa and Karori Thornton, Wong & Smithers, 1977). In the cockroaches, order Blattodea, Johns (1966) recorded *Celatoblatta subcorticaria* in Nelson, Marlborough and north Canterbury, and disjunct in the wetter, cooler forests of Fiordland, coastal Southland and Stewart I.

Watt (1974) has mapped the beetle genus *Philpottia* from central Fiordland, Southland and Dunedin, and disjunct in the north from Arthur’s Pass to Nelson.

Collier (1993) has mapped South Island regions with high numbers of freshwater invertebrate species with restricted distribution in NW Nelson/N Westland and Fiordland, but numbers are low in central and south Westland. This phenomenon of biodiversity, although not a taxon as such, also conforms to Alpine fault displacement. Regional levels of biodiversity in New Zealand have been mapped for speciose plant and animal groups (Heads, 1997) and the following groups showed disjunct concentrations of biodiversity in Nelson and Otago: *Pseudocyphellaria* (lichens),

Scrophulariaceae (seed plants), Ambositrinae (Hymenoptera), Hepialidae (Lepidoptera), Notonemouridae (Plecoptera) and Antartoperlinae (Plecoptera).

In the Vertebrata there are two possible, clinal examples in the endemic New Zealand bird family Acanthisittidae. *Acanthisitta chloris*, the rifleman, has brighter yellow populations (subsp. *citrina*) in Fiordland and mountain districts of Otago and Nelson. Oliver (1974) recorded subsp. *citrina* from Chalky, Dusky, Doubtful and Caswell Sounds. 'Bourke Hut' (at Burke R.?), 'Makaroro' (=Makarora?), and, in the north, "mountains of Nelson". Falla, Sibson & Turbott (1979) write that "Further field work and taxonomic study are needed". In the same family, *Xenicus gilviventris* subsp. *rineyi* has been recorded from Fiordland. Similar birds occur in NW Nelson. The birds are a dark olive green, and there is wing flicking and bobbing behaviour and strong sexual dimorphism. In central South I. birds are brown, there is no wing flicking and less sexual dimorphism (Sue Heath, pers. comm. Feb. 1996; Heather & Robertson, 1996).

#### DISCUSSION

Possible objections to the correlation proposed here include the fact that small, obscure taxa are easily overlooked by collectors. The minute Hymenoptera (Moranilini) shown in Figure 7H–I may turn up in central South Island localities, although other species of Moranilini were found there. Data from very poorly collected groups were not included here, and of course are not usually mapped in the first place. Many of the taxa mapped here are fairly conspicuous and the overall pattern is seen in very many groups.

Poorly resolved taxonomy and misidentifications can also confuse biogeographic analysis. The approach taken here to counter this problem is to use large numbers of taxa in the analysis (cf. Banareescu 1990–95: 1426). In earlier work (Heads, 1990, 1992, 1993, 1994a,b,c,d,e) more detailed studies of individual taxa showing Alpine fault disjunction have been made. Further ecological-scale mapping would shed more light on the problem.

The question as to why individual taxa have not spread across the fault into neighbouring communities raises the general question as to why species do not expand into neighbouring communities, whether or not they are being pulled apart on a fault. Because of the disjunct distributions they exhibit, it seems likely that the taxa illustrated have not dispersed into surrounding communities. However, there is some evidence of relatively minor range expansion across the fault, e.g. at Arthur's Pass (Fig. 3G) and Jackson's Bay (Fig. 3H, 4F). There is also some evidence that populations may have been stretched out along the fault zone itself, giving narrow, almost linear distributions (Fig. 7J,K,L).

In the southern part of the South I. there is comparatively little land to the west of the fault. Taxa may be absent here because there is no suitable habitat. However, as indicated above, in very many cases the gap is filled by a closely related taxon with similar ecology. Considering the data presented in Figures 2–7, it is clear that the disjunction is shown in taxa with widely differing ecological requirements. This also leads to the conclusion that historical, rather than ecological, factors are of primary importance in producing the disjunction.

Long-distance dispersal from Nelson to Fiordland could be suggested as an

explanation for the disjunction, but would hardly explain such precise patterns as that of *Leonohebe mooreae* together with its disjunct 'adaxial stomata' populations at Caswell Sound and Denniston Plateau (Fig. 4K) and an endemic variety in Westland National Park (Heads, 1992). Long-distance dispersal does not explain the disjunction in groups such as terrestrial worms or molluscs, and Haase (1992) has argued against long-distance dispersal from northern refugia as an explanation for the disjunction in *Nothofagus*.

The Oligocene marine transgression in New Zealand is sometimes assumed to have devastated the terrestrial biota. This recalls the earlier debate between geologists who claimed that glaciers had totally devastated the vegetation, and biologists who disagreed. Lee & Lee (1994) and Cooper & Cooper (1995) have noted that there are major differences in estimates of the land area at the peak of the transgression, which vary from 20% to 50% of the present area.

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. An example would be a distribution in central Westland and Canterbury only, but no case of this is known. A check of the small-leaved shrubs mapped by Wilson (1991) revealed no examples. Patterns crossing the fault do occur at the northern end of the fault, but here geological displacement is minimum.

In this study the distribution of taxa beyond South and Stewart Islands was not noted. In many cases this will be of interest. For example, Endrödy-Younga (1995) recorded the Alpine fault disjunct *Sphaerothorax* (Fig. 6I) from Australia and southern South America, and concluded that it was a Gondwana relic. It is a common pattern for taxa disjunct on the fault to be present in southeast Australia (e.g. *Kelleria laxa*, Fig. 3G). In this way the disjunction on the fault is connected with the more well-known Gondwanic disjunctions.

#### CONCLUSIONS

Disjunction along the fault appears to be a widespread phenomenon seen in all major plant and animal groups and in taxa with widely differing ecology. There are examples of taxa from marine and terrestrial environments, from high and low altitude, from wet and dry habitat, and from forest, shrubland and grassland. The taxa involved also show a wide range of dispersal mechanisms.

In many distributions the southern end of the Paparoa Ra. separates northern from central Westland populations, with the northern form reappearing in south Westland. Before Fault movement, the picture would have been simpler, with the northern and southern populations then together in the north, and the central Westland populations in the south.

Disjunction on the fault also explains why many Fiordland/Nelson groups (e.g. Figs 2C, 3D,F,G,H) are absent on the west coast and also on Stewart Island. Before fault displacement these taxa would have had a simpler distribution, present in the north and absent in the south.

The disjunctions between Fiordland and Nelson, with their related taxa sandwiched in the middle in Westland, seem to indicate the presence of numerous, small, constantly moving refugia which have preserved regional biogeographic pattern,

rather than restriction of biota to a small number of large, distant refugia with subsequent reinvasion from there. There may well be range expansion of certain taxa across the fault, but this does not explain the disjunction in the first place. In a similar way, the classic Pleistocene *Pecten* sequence in Wanganui basin is much more complex in fine detail than earlier workers were aware of and its major features “appear to have been controlled by the ecology of the deposition site [cf. many refugia] rather than by wider-scale migrations caused by temperature changes” (Beu & Maxwell, 1990).

Distribution maps are available for comparatively few New Zealand taxa, but the superb *Fauna of New Zealand* series is providing a wealth of new information on biodiversity. A series of maps of the New Zealand flora would be extremely useful. A great deal of biogeographic information is published but not mapped, and so is relatively inaccessible. For example, in virtually all monographs on larger groups in New Zealand there are references to breaks in distribution and disjunctions which are compatible with Alpine fault movement.

The Alpine fault is such a major feature that movement along it must have had a significant effect on the living communities, even if the effect has not been as simple as that suggested here. Judging from their Gondwanic distributions many New Zealand groups, or at least their immediate ancestors, are old enough to have been exposed to fault movement ever since its inception. There are other large faults in New Zealand, some of which correlate with earlier positions of the plate boundary and possibly involve lateral displacement. In a similar way biogeographic disjunction along plate boundary faults has also been proposed in the Caribbean, where Pacific biotas have been carried eastward (Croizat, 1964; Durham, 1985), and may also occur in California and New Guinea/eastern Indonesia.

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