

Integrating earth and life sciences in New Zealand natural history: the parallel arcs model

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Abstract Attention is drawn to the parallel arc patterns permeating much of New Zealand biogeographic structure. The fracturing and creation of such parallel arcs by tectonic movement and erosion has brought about vast disjunctions in many plant and animal groups. The major arcs of distribution correlate with zones of tectonic activity such as plate and terrane margins, fracture zones, and belts of granitic intrusion. Other arcs may be the result of evolution along the Tertiary shores of inland bodies of water. The altitude of many communities in New Zealand also appears to conform to biogeographic and tectonic trends, with higher altitude communities having been derived by the uplift of mid-Tertiary lowland-coastal communities. Evolution is interpreted here as proceeding largely by phases of population reorganisation, for example in the formation of Cretaceous hybrid swarms, and "recrystallisation" in which ancient ranges are "frozen", even in weedy taxa. Such processes correlate spatially with zones of tectonic and physiographic disturbance.

Keywords evolution; biogeography, panbiogeography; geology; parallel arcs model; tectonics

INTRODUCTION TO NEW ZEALAND BIOGEOGRAPHY

In a global context the New Zealand flora and fauna can be broadly interpreted as an amalgam of affinities based in and around the Indian Ocean (Gondwanaland groups – Fig. 1a) and affinities of the Pacific Ocean (Fig. 1b). A third series of affinities ranging along the "Tethys" track: New Zealand – Melanesia – central Asia – Mediterranean is also important, and is illustrated in Fig. 19 where it comprises an extension of a circum-Pacific pattern.

With respect to differentiation within New Zealand, Colenso (1868) proposed one of the first biogeographic classifications. He suggested that the North Island could be divided into six regions, with the divisions between these corresponding to certain lines of latitude. Such areas are often taken to represent regions of animal and vegetable life reflecting, above all, climate. Of course, there is a broad lowering of temperature between, for example, Kaitiaki in the far north and Wellington in the south, as well as many biological differences. However, although "latitudinal" schemes as used by Colenso and others (e.g., Allan 1961) have historical importance, lines of latitude fail to account for a great number of distribution patterns.

Among such "anomalous" distributions in New Zealand are wide disjunctions—striking gaps in the range of a plant or animal often hundreds of kilometres across. The meaning of these gaps has remained controversial. Related anomalous patterns include distributions of biological groups which follow island arcs such as: Hen and Chickens – Poor Knights – Three Kings (Fig. 4a) but are absent on the mainland, which is geographically much closer to the individual islands involved than these are to each other. Many such anomalies in the distribution of groups in New Zealand have been documented and discussed in some detail (e.g., Croizat 1952–1968; Cranwell 1962; Craw 1983, 1985; Henderson 1985; Grehan 1987; Heads 1987), and this work has developed the idea that the distribution of living forms in the region follows a series of more or less parallel arcs. This

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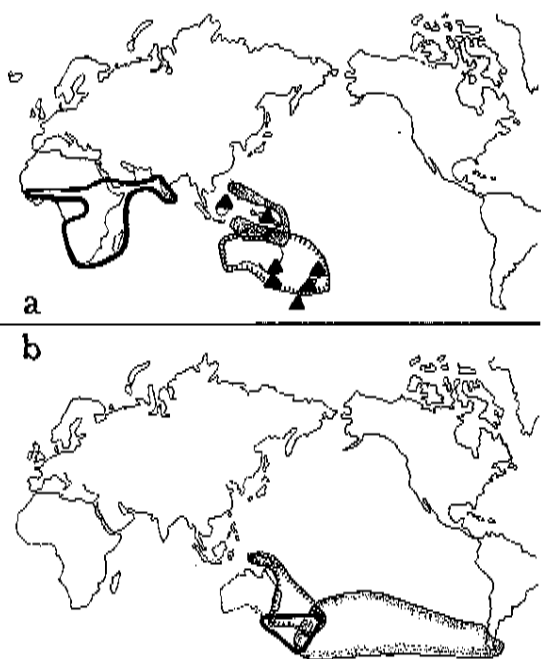


Fig. 1 a, An Indian Ocean affinity in Thymelaeaceae (Angiosperms). Thick line: *Gnidia* s.l.; stippled: *Thecanthes*; hatched line: *Pimelea*; triangles: *Kelleria* (Domke 1934). b, A Pacific Ocean affinity in Scrophulariaceae (Angiosperms). Thick line: *Leonohebe*; hatched line: *Parahebe*; stippled line: *Hebe* (Heads 1987).

idea originated with Croizat (1958) who mapped biological tracks as parallel arcs around New Zealand. It is of interest that these show a striking correlation with structural analyses presented by geologists in the following decades (Fig. 2), providing a good example of the predictive value of Croizat's work. Naturally, biologists in New Zealand to-day have access to much more biogeographic data for the region than did Croizat, and can extend his original analyses. Croizat (1952: 182) proposed that: "New Zealand stands as a land-bastion, surrounded by a half-crumbled insular arc, Norfolk Island–Kermadec Islands–Chatham Island–Bounty Island–Antipodes Island–Campbell and Auckland Islands–Macquarie Island. Whether this arc is actually single, or made out of lesser arcs and their branches (e.g., Lord Howe Island–Three Kings Islands–Chatham Island, matching the arc Norfolk Island–Kermadec Islands–Chatham Island etc., described above) we do not know. The fact seems to us clear, however, that dispersal speaks for New Zealand being the largest remnant of some land once massive in these quarters."

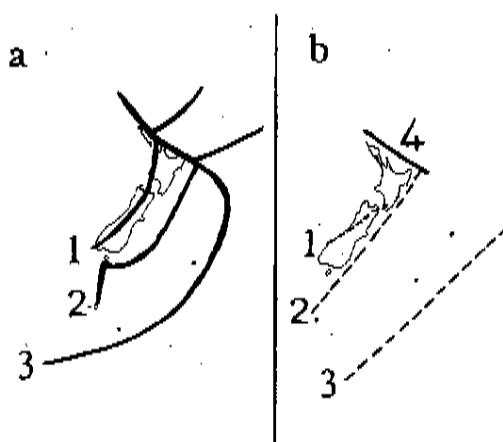


Fig. 2 Aspects of structure in and around New Zealand. a, Croizat's 1958 analysis (fig. 242, cf. his fig. 229A, 241 etc.). b, Features from Cullen's 1967 analysis. 1 = Alpine Fault, 2 = Waipounamu Fracture, 3 = Antipodes Fracture Zone, plus (4) = Vening Meinesz Fracture Zone (Kamp 1986).

Here it may be useful to provide a short explanation of two of Croizat's key terms and concepts: "dispersal" and "node". The idea, current in North American "vicariance biogeography" (Nelson & Platnick 1981), that Croizat somehow simply rejected dispersal is false. Croizat rejected certain authors' interpretations and conceptions of this process, not the process itself.

In modern biogeography, simple records of distribution are interpreted, or given a meaning, with respect to a fundamental process of change of position. Such a process has generally been labelled dispersal or migration—for example Clements & Shelford (1939) proposed a very broad concept of migration which would include "any and all changes of position". Croizat simply enlarged the concept even further. He argued that a workable concept of dispersal/migration must involve, in addition to simple change in position (Croizat's "translation in space"), a factor of form-making. This is because form-making by itself, for example the evolution of a character, may change the geographic position of that character, without any of the physical movement of individuals always assumed as fundamental by authors such as Clements & Shelford (1939) or Nelson & Platnick (1981) in their own concept of "dispersal"/"migration".

The meaning of organic dispersal—the synthetic process of spacing, timing, and form-making which gives rise to the distribution of plants and animals

and their characters over the face of the earth—is for Croizat the fundamental problem of biogeography (Croizat 1952-1968). Croizat's work is the most recent in-depth study of the broad phenomena of dispersal in plant and animal life.

Croizat described certain areas as biogeographic "nodes". Travelling into a node, one becomes aware that new plants and animals are present, and that others are now absent. The new forms may be restricted to the node or may be widespread in yet other regions. In general, a biological node (hinge, gate, articulation, beginning or end of a track, centre, etc.) can be characterised as a locality or region where plants and animals manifest:

- 1 presence, for example of endemic forms (found there and nowhere else),
- 2 absence, for example of groups found widely elsewhere,
- 3 phylogenetic and geographic relationships or affinities with several different areas at once,
- 4 boundary zones—where taxa begin (come into existence), and/or end (go dead), phylogenetically and geographically.

All four phenomena are typically present at nodes of major significance, and one or more are present at minor nodes. Fleming (1978) attributed all four characters to New Zealand, which thus constituted a node in his analysis. However, panbiogeographic work (as cited above) has shown that "New Zealand" is a composite structure—a whole galaxy of nodes—rather than a single node. Croizat's (1958, 1968) analysis of New Zealand is based on the concept of parallel arcs (Fig. 2) and cites boundaries such as Egmont - East Cape, and nodes such as Three Kings Islands, and Awarua (the latter included in this paper with the Foveaux Strait centre - Fig. 8). A series of nodes constitutes a track or biogeographic "arc" or "sector", and it should be noted that a track can be a track of absence—a zone of disjunction or gap—as well as a track of presence. Because a track may be one of absences, a track in general is neither simply a cladogram, nor simply a phenogram, nor simply a minimal spanning tree. This does not mean that a track can then mean anything to anyone, as areas of absence, for example in New Zealand, are clearly delimited and amenable to scientific investigation (see this paper and that by Craw in this issue).

Returning to New Zealand biogeography, it is clear that disjunctions and other "anomalies" have traditionally been explained very much case by case, with appeals made to: migration by "special means"

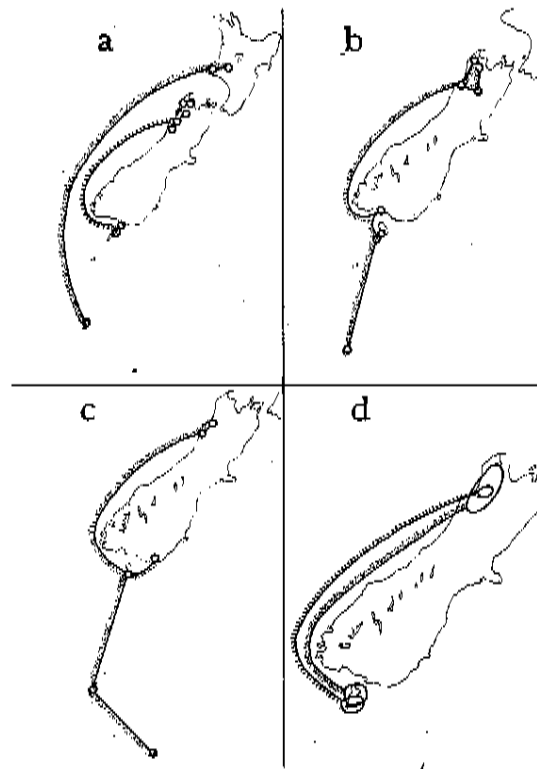


Fig. 3 a, Stippled line: *Perionyx* (Annelida: Oligochaeta). *P. egmonti* at Taranaki, *P. helophilus*, *P. perionychopsis* and *P. shoeanus* at Auckland Is (Lee 1959). Hatched line: *Karamea* (Opiliones). *K. lobata*, *K. tricerata*, and *K. tuthilli* at Grey River-Nelson, *K. trailli* at Bluff and northern Stewart I (Forster 1954). b, Stippled line: *Astelia linearis* var. *linearis* (Angiosperms: Liliaceae) (Moore 1966). c, Stippled line: *Astelia subulata* (Liliaceae) (Moore 1966, plus herbarium records). d, Stippled line: *Rakiura*, monotypic with *R. vernale* (Trichoptera: Helicopsychidae) (Cowley 1978; Henderson 1987). Hatched line: *Aciphylla stannensis* on Stewart I, and its closest relative *A. trifoliolata* of west Nelson (Angiosperms: Umbelliferae) (Dawson 1980).

of dispersal, mistakes of classification, human activity such as early Polynesian introductions, extinction of intermediate populations, poor collecting, or factors of past or present local ecology such as climate. However, such distribution patterns and, above all, their repetitive occurrences in many groups with different "means of dispersal" are often frankly admitted to constitute unexplained anomalies or curious puzzles.

Some standard disjunctions are illustrated below for the purpose of giving a brief summary of New

Zealand biogeography. The diagrams are intended to illustrate broad trends in dispersal, and not details of distribution, many of which could not be reproduced at the scales used. Further details are available in the references cited. My own bias is towards the seed-plants, and I am grateful to Drs Craw, Grehan, Henderson, and Climo for having shared information and ideas on dispersal in other groups, in particular insects and molluscs.

To begin with, there exists a series of related disjunctions in the southwest of the New Zealand region. Fig. 3 gives examples of oligochaete worms, insects and seed-plants ranging between Auckland – Campbell Is in the far south, north to the North Island (Taranaki). In these patterns all or large sectors of the South Island are not involved. Geologically and biologically, the northern part of Stewart Island could be taken to include points on the southern coast of the South Island such as Bluff (Fig. 1a). This "Foveaux Strait centre", whose biota often points to that of the Longwood Range to the west and/or the Catlins to the east, can also act in dispersal largely independent from Otago, Fiordland, and Canterbury, instead showing, as in Fig. 3, a strong affinity with the northwest South Island: Paparoa Range – northwest Nelson.

Moving to an apparently unrelated part of New Zealand, Fig. 4 shows various northeast arcs of dispersal in seed-plants, reptiles and barnacles. Biological form-making on these arcs was clearly recognised over a century ago. Hooker (1871) realised that: "It is a remarkable fact that many of the Barrier Island plants differ permanently, though slightly, and some strongly and specifically, from those of the adjacent mainland, indicative of a long geographical severance." In a discussion of endemism on Three Kings Islands Cranwell (1962) noted that Croizat (1958) stressed the importance of a "relict or 'horstian' component" in this sector of New Zealand biology. Croizat subsequently (1964) continued his analysis of the northeast New Zealand "horsts" in dispersal, citing ferns. Recently Watt (1982) accepted a Poor Knights – Three Kings connection in a study of invertebrate affinities. In summary, the islands of north Auckland (Three Kings, Poor Knights, Hen and Chickens, Mokohinau, Great and Little Barrier, etc.) often show striking endemism. Many groups manifest curious affinities among the islands but are absent from the mainland. In similar patterns, dispersal centred on the islands involves rare, isolated mainland populations, especially at or near North Cape, Whangarei Heads, and Cape Colville. Further inland, yet another series of tracks runs straight up

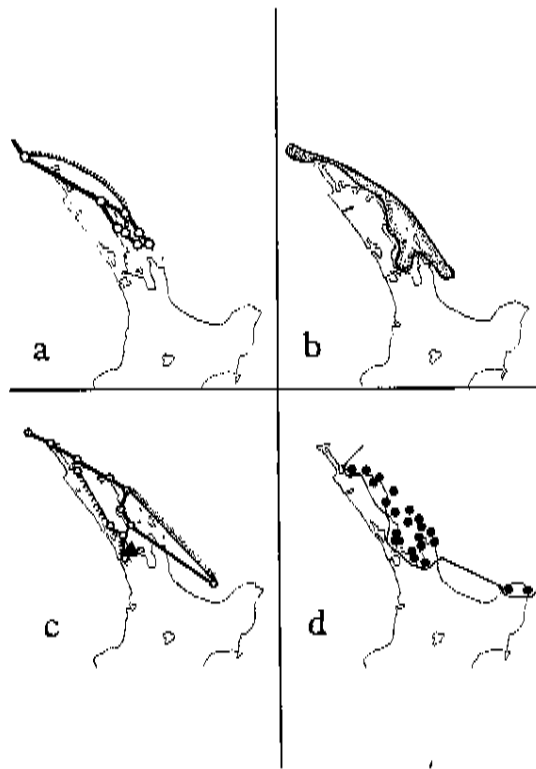


Fig. 4 a, Solid line: *Nestegis apetala* (Angiosperms: Oleaceae) also at Norfolk I (Eagle 1982). Hatched line, reading from north to south: Three Kings Is, Poor Knights Is, Hen and Chickens Is *Meryia* (Angiosperms: Araliaceae) in New Zealand; Three Kings, Poor Knights, and Hen and Chickens. *Cordyline kasper* (Angiosperms: Agavaceae): Three Kings and Poor Knights. *Alectryon grandis* (Angiosperms: Sapindaceae): Three Kings and Poor Knights (Cheeseman 1925; Beever 1984). b, *Leiopisma suteri* (Reptilia: Scincidae) (Towns 1974). c, Barnacles (Crustacea: Cirripedia). Stippled line: *Tetraclita aoranga*. Solid line: *Balanus tintinnabulum linzei*. Hatched line: *Balanus variegatus*. Triangle: *Balanus amphirite*. (Foster 1978). d, *Beilschmiedia tawaroa* (Angiosperms: Lauraceae) (Wright 1984).

the middle of north Auckland peninsula (north of Auckland isthmus, itself a complex biogeographic centre). This pattern of parallel or nested arcs, dividing up northern New Zealand between east and west (Fig. 4c, 5c) is clearly seen in many groups of marine, aquatic and terrestrial organisms. Further southeast many distributions show a notable disjunction between North Auckland – Coromandel Peninsula, and the East Cape region, with a conspicuous gap in the Bay of Plenty (Fig. 4d).

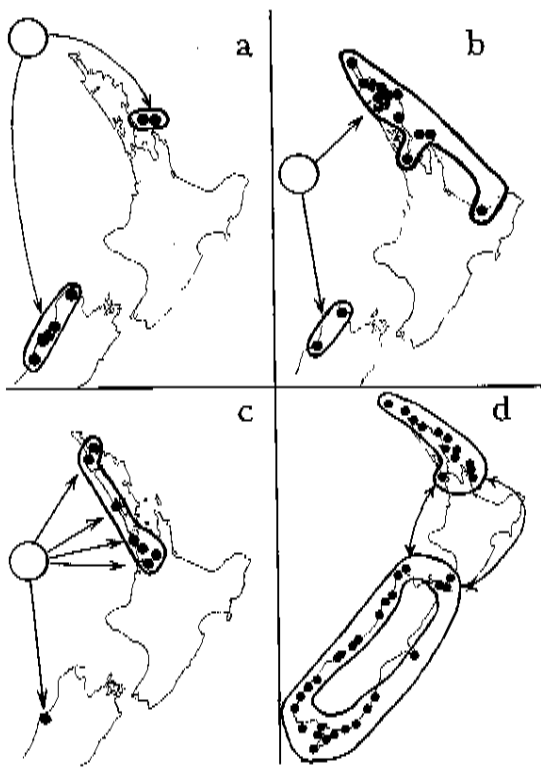


Fig. 5 Baseline, or centre of gravity, of dispersal, represented by circle. a, *Metrosideros parkinsoni* (Angiosperms: Myrtaceae) (Atkinson et al. 1962). b, *Sticherus flabellatus* (Pteridophyta: Gleicheniaceae) (Given 1982). c, *Utricularia protrusa* (Angiosperms: Lentibulariaceae) in New Zealand (Moar & Mason 1975). d, *Asplenium obtusatum* (Pteridophyta: Aspleniaceae). Northern massing: *A.o.* subsp. *northlandicum*, southern massing: *A.o.* subsp. *obtusatum* (Brownsey 1977).

Although the biogeographic affinities of the northern arcs often lie with Norfolk I, the Kermadecs, and Polynesia, they are also clearly connected with southern sectors of New Zealand (Fig. 5), in fact, often with the southwest arcs discussed above and illustrated in Fig. 3. Disjunction between northeast sectors and northwest South Island (Fig. 5) is generally seen in groups in which a main massing of forms occurs, as seems reasonable, to the northwest of New Zealand, in east Australia, Lord Howe I, Norfolk I, the island of New Guinea, and/or New Caledonia. Thus northern New Zealand may be "entered" by a double, split track, involving a forking or pincer-shaped structure, in much the same way as Fig. 3c illustrates tracks in the shape of "claspers"

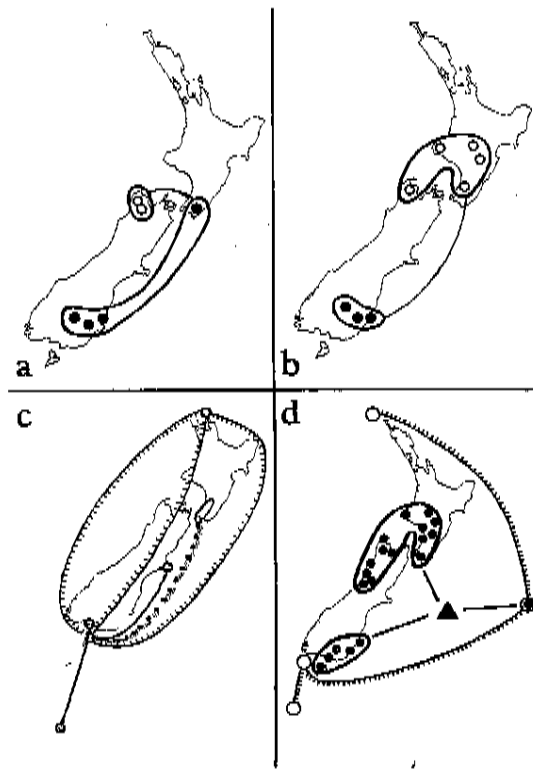


Fig. 6 a, *Simplicia* (Gramineae). Open circles: *S. buchananii*, dots: *S. laxa* (Zotov 1971). b, An affinity in *Rytidosperra* (Grasses). Dots: *R. tenue*, open circles: *R. pulchrum* (Connor and Edgar 1979). c, Solid line: the annelid worm *Plutellus*. Auckland Is: *P. aucklandicus*, Foveaux Strait: *P. stewartensis*, Banks Peninsula: *P. parvus*. (Lee 1959). Hatched lines: three possible tracks connecting breeding populations of the petrel *Pterodroma cooki*: Little and Great Barrier Is in the north, Codfish I (by Stewart I) in the south (Falla et al. 1979). Dotted stippled line: *Trillochorema* (Trichoptera) (Henderson 1985). d, Large, open circles connected by hatched line: breeding stations of the mollymawk *Diomedea bulleri*. Smaller dots connected by solid line: *Libertia pergrinans* (Angiosperms: Iridaceae) (Moore 1967), baseline of dispersal as triangle.

put on New Zealand from the southwest. Ties between the northeast arcs and the Cook Strait region are very common—in Fig. 5d, possible connections via the east as well as the west are shown.

To complete the circuit of New Zealand, Fig. 6 illustrates further nested arcs, this time lying to the east of New Zealand. Stewart I, Dunedin, Chatham Is, and Cook Strait appear as especially important nodes in such patterns, as are the other nodes already considered in the northeast, e.g., East Cape.

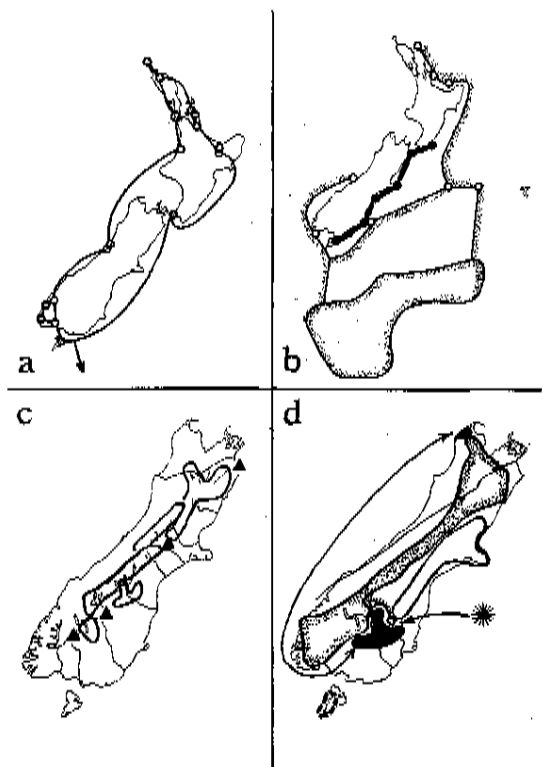


Fig. 7 a, *Pannaria crenulata* (Lichenes). All records mapped except Campbell I (Galloway et al. 1983). b, *Neophrynichthys* (Pisces) in New Zealand. Stippled: *N. angustus*. Solid line: *N. latus*. (*N. magnicirrus* endemic at Macquarie I) (Nelson 1977). c, Five related forms of *Aciphylla* (Angiosperms: Umbelliferae). Reading from south to north: *A. lecomtei*, *A. montana* var. *montana*, *A. montana* var. *gracilis*, *A. similis*, *A. monroi* (Dawson 1979). Nodes (triangles) at (south to north): Eyre Mts, upper Clutha, Torlesse Ra, Awatere River mouth. d, Related forms in *Gingidium* (Angiosperms: Umbelliferae). Stippled: *Gingidium decipiens*, black: *G. enysii* var. *baxterae* (populations connected by double-headed arrow), hatched line: *G. enysii* var. *spathulatum*, solid line: *G. enysii* var. *enysii* (Dawson 1967; Webb 1977). Northern Rock and Pillar Range indicated with asterisk and arrow.

In the light of the patterns already illustrated, distributions such as that of the lichen *Pannaria crenulata* (Fig. 7a) can be explained with reference to standard connections. Both western and eastern arcs are clearly involved, with the possibility of limited entry inland by nodes at Fiordland, Waikaremoana/Whakatane (northeastern North Island), and Kaitaia.

Nested arcs are equally obvious in marine and terrestrial taxa. For example, Fig. 7b shows two

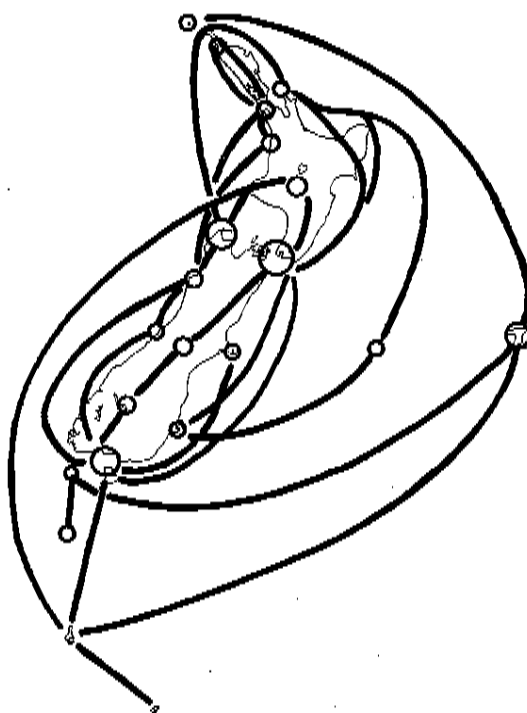


Fig. 8 A diagram obtained by juxtaposing several of the tracks and nodes shown in Fig. 1-5, and adding *Cotula potentillina* (Angiosperms: Compositae): Auckland Is-Chatham Is (Lloyd 1972).

related fishes with largely vicariant distributions, coming together at Dunedin.

To complete a brief review of New Zealand biogeographic patterns, inland New Zealand patterns are illustrated in Fig. 7c and d. Similar northeast striking patterns are repeated in many groups, with boundaries at all possible combinations of many inland nodes. Four main nodes—Eyre Mts, Dunstan Mts, Torlesse Ra, and Awatere River—are shown in Fig. 7c, d. The marked disjunction between Central Otago and northwest Nelson evident in *Gingidium* (Fig. 7d.) will be discussed below. *Gingidium* also shows especially clearly how a node at the northern Rock and Pillar Range may be involved with dispersal to the southwest (*G. enysii* var. *baxterae*), northwest (*G. enysii* var. *spathulatum*), and northeast (*G. enysii* var. *enysii*).

Fig. 8 has been compiled by putting together most of the tracks and nodes shown in Fig. 3-7 to integrate the patterns already considered. This serves

as an introduction to discussion of geological structures and events possibly relevant to the life of the region. Although Fig. 8 may indicate a very complex situation relative to the biogeography of the geologically stable continental shields (generally these are the geographical cores of the continents), the patterns illustrated can be compared with other geologically dynamic regions such as the Caribbean and Melanesia (Croizat 1958).

BIOGEOGRAPHY AND GEOLOGY OF NEW ZEALAND

The southwest Pacific is a major region of crust intermediate between continental and oceanic character (Aronson 1968). The New Zealand region itself shows a continental orogenic history. It is made up of huge thicknesses of material representing all the stratigraphic systems—Palaeozoic, Mesozoic, Tertiary, and Quaternary. Geosynclinal sedimentation and uplift, regional metamorphism, volcanism, and intrusion of plutonics have all taken place over wide areas of the New Zealand plateau, a structure which extends to Auckland, Campbell, and Chatham Is. Vast belts of folding are a characteristic feature, and the sedimentary beds commonly show very rapid lateral thinning. This indicates that the New Zealand region has suffered intense disturbance in its ecological and geological history; events or periods of upheaval are proposed here as phases of profound ecological and evolutionary reorganisation for ancestors of the extant flora and fauna. Thus, New Zealand has a key role to play in the development of modern theory. Indeed, Grindley (1974) has written: "successive orogenies have been superimposed through Phanerozoic time giving a complexity of structure that has made this [New Zealand] a testing ground for geologists and a graveyard for tectonic theories."

A very generalised view of the New Zealand plateau (Fig. 9) reveals New Zealand as a zone where at least three separate geological structures of more or less independent history and geographic affinities come together in a fractured, reverse S-shape structure. The New Zealand region straddles the present boundary between the Pacific and Australian plates (barbed line in Fig. 9). In modern geology three main kinds of plate margin have been proposed to account for global patterns: convergent margins, divergent margins, and transforms, with the latter linking convergent and/or divergent margins. To the north of New Zealand, the Pacific

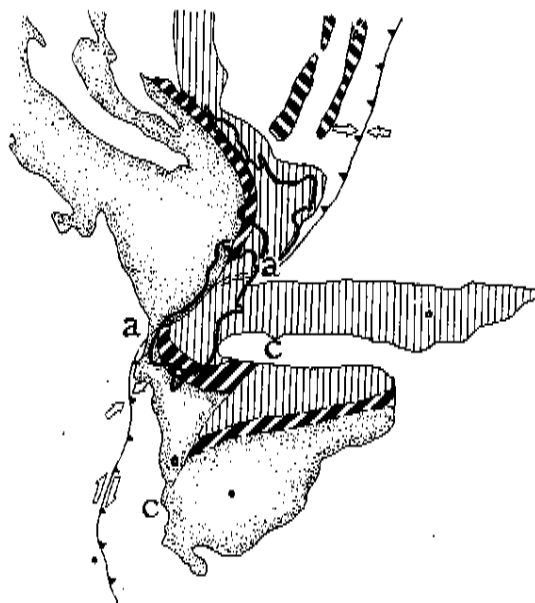


Fig. 9 A highly generalised view of geological terranes in the New Zealand region. Stippled: Tuhua terrane. Thick, oblique hatching: volcanic arc terranes (SW-NE hatching: Hokonui group of terranes, SE-NW hatching: Colville Ridge, Kermadec Is etc). Fine vertical hatching: Torlesse and Caples terranes. (After Howell et al. 1985). At a-a the Alpine Fault, at c-c the Campbell Fault.

plate to the east is proposed to be subducting beneath the Australian plate to the west. To the south, the Australian plate is being subducted beneath the Pacific plate. These two sectors of convergent margin, subduction zones dipping in opposite directions, are connected by a transform—the Alpine Fault.

At first sight Fig. 9 appears to bear little relationship with the nested arc phenomena of New Zealand biogeography. However, the fracturing of the geological arcs evident at the Alpine Fault (a-a in Fig. 9) and the Campbell Fault (c-c) is of great significance. The possible biological consequences of such major displacements include the formation of disjunction by the pulling-apart of populations. The faults here illustrated could not, on their own, explain all the biological disjunctions. However, with the development of the concept of the region as a complex of separate microplates, or terranes, the possibility of considerable movements between terranes emerges. Of course, a great deal of disjunction observed in terrestrial organisms may be explained with reference to past land, where now is

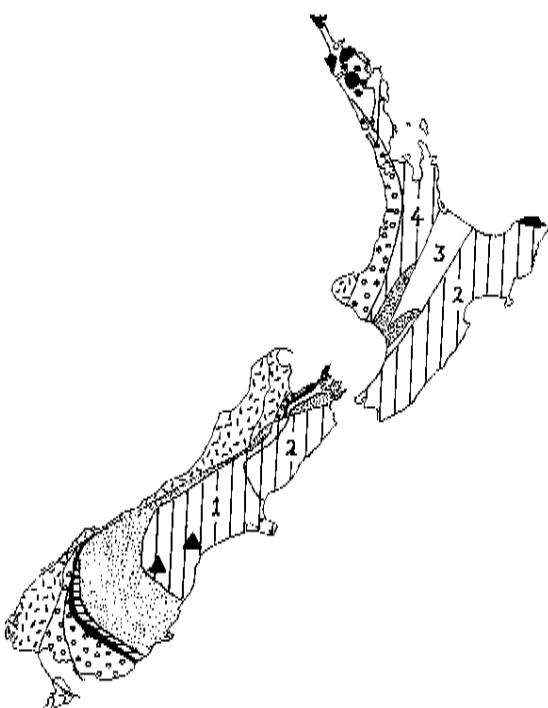


Fig. 10 Geological terranes of New Zealand (after Bishop et al. 1985; Spörli 1987 etc.). Scattered short lines: Western Province. Small circles: Brook Street and Murihiku terranes (the former to the west, the latter to the east). Heavy black in South Island: Dun Mountain-Maitai terrane. Horizontal hatching: Caples terrane. Stippled: Haast Schist. Vertical hatching: Torlesse terrane (1 = Older Torlesse, 2 = Younger Torlesse, 3 = Taupo Graben, 4 = Waipapa terrane, triangles = Akatarawa terrane to the southwest, Kakahu terrane to the northeast). North Island Tertiary terrane: solid black at North Cape, north Auckland, and East Cape mark the Whangakea, Tangihua, and Matakaoa Volcanics, respectively.

sea, having been lost by normal processes of sinking and erosion. Large sectors of land have been, and are being, lost this way all around New Zealand, and result in tracks disappearing out to sea, sometimes with fragments preserved on islands.

A more detailed picture of New Zealand basement terranes (Fig. 10) reveals greater complexity. Ten terranes have been proposed by Coombs (1985), and these are all "suspect", in that "they may once have occupied significantly different positions with respect to their neighbours than is now the case." Information supplied by Coombs enables a brief characterisation of the different terranes.

West of the Median Tectonic Line are the rocks of the "Western Province", representing a fragment of a Palaeozoic continental margin with possible pre-Cambrian basement. However, the nature of pre-Cambrian basement in New Zealand, if any, is still an open question (cf. Aronson 1968). In Western Province rocks, two separate terranes of Paleozoic sedimentary belts are recognised, and these were brought into contact in Palaeozoic (Devonian) time. Such early events cannot concern us here, but the record of subsequent granite emplacement in the Western Province through the Mesozoic, culminating in the Early Cretaceous, concerns an epoch of direct significance for modern biogeography. Correlation of belts of granite emplacement with tracks of plants and animals will be considered below.

In addition to the two Western Province terranes referred to above is the Western Fiordland Orthogneiss (maximum age of emplacement Early Cretaceous). This is a volcanic arc-related terrane that was involved in a Cretaceous collision event and was subsequently, but still in Cretaceous time, juxtaposed against rocks to the east.

The Median Tectonic Line (MTL) separates Western and Eastern Provinces. "Enigmatic" fault slivers, the largest of which is named as the Drumduan terrane, occur in the zone of the MTL, but are not shown on Fig. 10. They recall such "sliver" distributions along the MTL as that of the plant genus *Ili* (Fig. 24).

The "Hokonui Assemblage" includes the Brook Street, Murihiku, and Dun Mountain-Maitai terranes, accreted to the Western Province at some time/s in the Mesozoic, possibly in the Cretaceous.

The Brook Street terrane, including sediments of Permian to Cretaceous age, is described by Coombs as an "elongate sliver" of a volcanic arc complex which was once "substantially wider".

The Murihiku terrane is composed of a 15 km thickness of Triassic and Jurassic arc-derived sediments. According to Coombs it is "not demonstrably derived from Brook Street." There is some evidence for the presence of continental crust beneath the arc that did supply the detritus.

In the Dun Mountain-Maitai terrane the Permian Dun Mountain Ophiolite Belt, a "major tectonic and geophysical marker throughout New Zealand" (Spörli 1987), is overlain by the arc-derived sediments of the Upper Permian Maitai Group. (The two may be continuous with the Murihiku). Coombs cites evidence from the Maitai for a Cretaceous collision event which raised metamorphic conditions.

The Caples terrane, representing the margin of a volcanic arc, comprises metamorphosed Permian–Triassic sediments of low metamorphic grade, grading by increasing metamorphism into the Haast Schist. The provenance of the Caples sediments was volcanogenic but the ash beds so numerous in the (now) nearby Murihiku, are rare or absent, implying some relative displacement. Spörli (1987) regards the Waipapa terrane as the North Island equivalent of the Caples, but here (Fig. 10) the Waipapa is treated as part of the Torlesse.

Howell et al. (1985) place the Torlesse terrane in a group of terranes characterised as: "oceanic rocks mixed with continentally derived sediments (geosynclinal deposits)". The Older Torlesse (Rakaia) terrane largely comprises Permian–Triassic greywacke, probably derived from an active continental margin. These rocks grade southwestward by increasing metamorphism into the Haast Schist. The Haast Schist thus involves a "cryptic suture" of Caples and Torlesse terranes in which the metamorphic overprint has obliterated stratigraphic relations (Howell et al. 1985).

Within the Torlesse, the Kakahu terrane, by the Opihi River near Geraldine, comprises 15 km² of mélanged sediments and volcanics, including Carboniferous fossils. The Akatarawa terrane, northwest by Lake Avicmore on the Waitaki River (between Otematata and the Kirkliston Range) comprises 5 km² of sediments and volcanics. It includes Fusulinid foraminifera (Protozoa) of Tethyan affinities known elsewhere in New Zealand only at Whangaroa, north Auckland, in the Waipapa terrane. The Younger Torlesse (Pahau) terrane, apart from a younger age (late Jurassic–early Cretaceous), is very similar to the Older Torlesse (Rakaia) terrane. The boundary between the two is much less well-defined than the boundaries between the other terranes.

In the North Island, Tertiary terranes are of special biogeographic interest. The Whangakea, Tangihua, and Matakaoa Volcanics are related seamount bodies emplaced in the Tertiary along the line: North Cape–Kaitaia/Dargaville–East Cape (Brothers 1982), and on a similar sector the Northland and East Coast Allochthons have been related by Spörli & Ballance (1985).

In the following pages brief chronological and regional outlines of New Zealand geology compiled from standard geological texts are given, and juxtaposed with certain parallel phenomena in biology. Details of how such parallel structures in earth and life are related are not known. The aim of

this paper is to report some preliminary, broad geographical correlations. Also, no attempt is made here to provide lists of taxa involved in any one pattern, rather, examples are introduced simply to illustrate general kinds of patterns. The first case considered, that of the Alpine Fault Zone, is treated in a little more detail as an example of how a study could be developed, but even here, very many groups other than those illustrated show the same kind of pattern.

THE ALPINE FAULT ZONE: BIOLOGICAL DISJUNCTION ALONG A TRANSFORM

For much of its length the major structural boundary known as the Median Tectonic Line runs along a transform—the Alpine Fault Zone ("Alpine Fault"), which as we have already seen (Fig. 9, 10) is an important structure in its own right. The timing of, (a) the formation of the reverse S-bend (an "orocline") in New Zealand and, (b) the movement on the Alpine Fault have both been controversial ever since Wellman proposed 480 km of dextral displacement on the Alpine Fault in 1948. (Standing on either side of a fault, movement is "dextral" if the other side appears to have moved to the right, "sinistral" if to the left). Kamp's (1987) model (Fig. 11) of a pre-Tertiary bending to give the orocline structure, and an additional upper Tertiary bending with lateral displacement on the Alpine Fault seems to account for different sets of palaeomagnetic and geological data. A crucial feature of this model is that it accepts different amounts of displacement at different points on the fault (cf. Lillie 1980). In particular, the more brittle Western Province rocks have been cracked by the fault, whereas the softer schist and Torlesse were stretched out along the fault. Thus displacement between, for example, Otago and Nelson is much greater (the full 480 km), than between Marlborough and Nelson/Wellington. This model proposes no simple displacement on a single fracture in the North Island, but suggests instead that relative plate motion has been taken up by distributed clastic deformation. These ideas are of direct interest to biogeographic patterns.

There exists a series of biological distribution patterns involving disjunctions on the west coast of the South Island—a few examples are illustrated in Fig. 12–17. (These arcs are similar in general structure to those illustrated in Fig. 2–7 for other parts of New Zealand.) There are many more examples known, for example in molluscs, and it is proposed here that

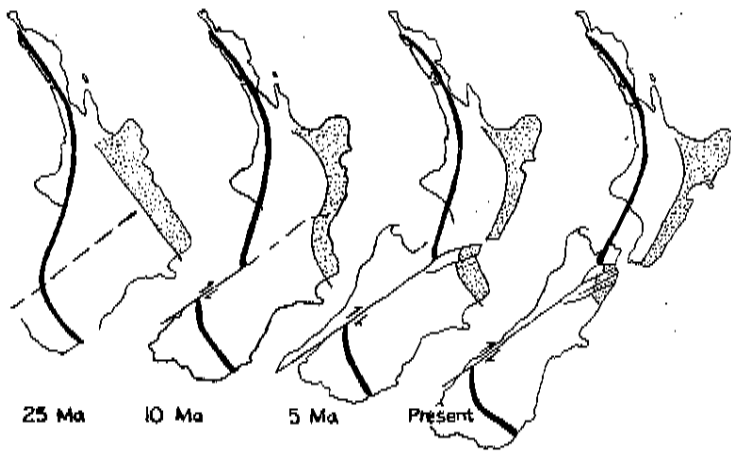


Fig. 11 A model of the age and origin of recurved arcs in New Zealand in relation to movement on the Australian-Pacific plate boundary, including the Alpine Fault sector. Dun Mountain terrane and associated magnetic anomaly as heavy black. Reconstruction at 20 million years before present shows the future position of the Alpine Fault as a broken line. Pahau subterrane (younger Torlesse) stippled. (After Kamp 1987).

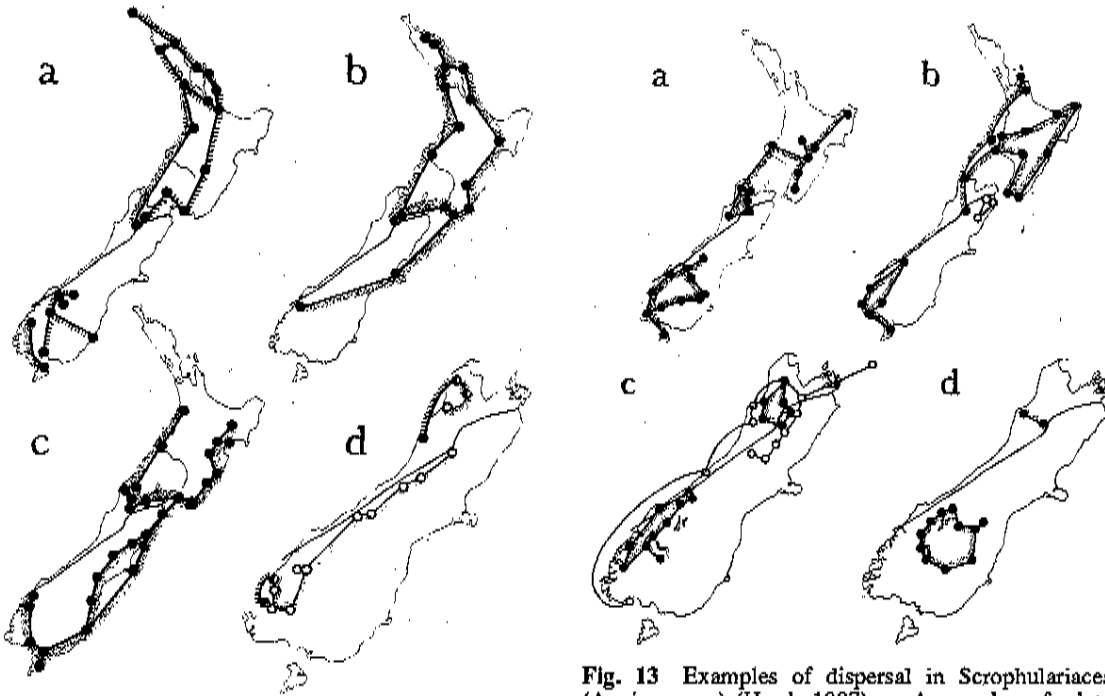


Fig. 13 Examples of dispersal in Scrophulariaceae (Angiosperms) (Heads 1987). a, A complex of related forms in *Leonohebe* (*L. laingii*, *hectorii*, *coarctata*, *subsiniis*, and *tetragona*). b, the *Parahebe catarractae* complex (currently treated as four subspecies). c, Dots connected by stippled line: *Hebe cockayneana*. Open circles connected by hatched line: *H. canterburiensis*. d, *Ourisia glandulosa*.

Fig. 12a, Stippled line: *Anzia* in New Zealand (*A. jamesii*) (Lichens) (Galloway 1978). Hatched line: *Xanthoparmelia australasica* (Galloway 1980). b, *Grammitis ciliata* (ferns) (Parris & Given 1976). c, *Asplenium lyallii* (ferns) (Brownsey 1977). d, Stippled line with open circles: *Astelia nivicola* var. *nivicola* (Angiosperms: Liliaceae). Hatched line with dots: *A. nivicola* var. *moriceae*. Half-filled circles: both forms present (Moore 1966).

such patterns were formed when whole communities were pulled apart by movement on the Alpine Fault. Naturally, if a group of plants or animals (or rocks) was widespread throughout New Zealand before the movement on the fault, it will be just as widespread after fault movement, and no disjunction will be apparent. If, on the other hand, before fault movement a group had a restricted range, for example, present only at Paparoas – northwest Nelson in the west, and Otago in the east, after movement on the fault a “disjunction” will be evident. The question as to why groups did not spread across the fault as movement took place along it, into neighbouring communities, raises the general question as to why many groups do not spread, whether or not they are being pulled apart on a fault.

Fig. 12 shows examples of lichens, ferns, and seed-plants exhibiting Otago/Fiordland – Nelson disjunctions which are easily explained as a direct result of pull-apart along the fault. Fig. 13 gives examples from four genera of a single family of flowering plants (Scrophulariaceae). Fig. 14 adds examples from *Celmisia* (Compositae) and *Coprosma* (Rubiaceae), and thus the general phenomenon is clearly manifest in the larger genera of New Zealand dicots. Turning to animals, Fig. 14c gives an interpretation of the dispersal of two oligochaete worms in terms of greater displacement to the south end of the fault, with less displacement to the north. Many other Alpine Fault disjunctions in the invertebrate fauna are also known (cf. Fig. 15). Vertebrates are comparatively undifferentiated in New Zealand, and to my knowledge there are no obvious signs of disjunction along the Alpine Fault. However, in birds, Oliver (1955) referred to the alpine rifleman (*Acanthisitta chloris citrina*: Acanthisittidae), as recorded from Fiordland and Nelson only.

If movement on the Alpine Fault disrupted terrestrial communities, adjacent marine communities may also be predicted to have suffered similar events. There is evidence for this being the case in, for example, brachiopods, molluscs, crustacea, and echinoderms (Fig. 16). Elsewhere (Heads 1983) I have discussed similar parallels between the dispersal of terrestrial and marine groups of the Pacific Plate.

The distribution outside New Zealand of taxa involved in Alpine Fault disjunction is of direct interest to distribution within New Zealand. One example only can be considered here. *Nothofagus*, the southern beeches, and their intercontinental distribution: Australasia – southern South America,

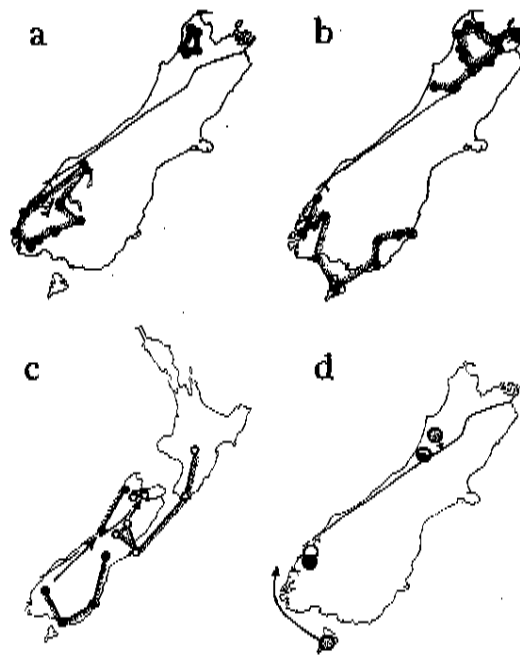


Fig. 14 a, *Celmisia petriei* (Angiosperms: Compositae) (Burrows 1965). b, *Coprosma* sp. aff. *parviflora* (Angiosperms: Rubiaceae) in South Island. (Herbarium records. Paparoas population: Mr A.P. Druce, pers. comm.). c, Stippled line: *Neochaeta* (*N. forsteri* and *N. salmoni*). Hatched line: *Plagiochaeta sylvestris* (Oligochaete worms) (Lee 1959). d, Oligochaete worms. Solid circles: *Deinodrillus benhami*. Open circle: *Diporocheata intermedia*. Half-filled circle: both species present. Stippled circles: *Decachaetus* in New Zealand: *D. minor* (Paparoas) and *D. violaceus* (Stewart I) (Lee 1959).

are well-known (Fig. 17). *Nothofagus* is related to: Balanopaceae of the southwest Pacific, the northern *Fagus* and *Betulaceae*, the trans-central Pacific *Castanopsis* and *Lithocarpus*, and the trans-tropical Pacific *Trigonobalanus*. Also related to these forms is Casuarinaceae of the Indian and western Pacific Oceans. Thus *Nothofagus* is the southern Pacific component of a vast aggregate of forms, the Fagales, whose members come to a very significant parting of the ways at the west-central Pacific (Croizat 1952, 1968).

Present main massings, whether of the families and subfamilies in the west Pacific, of *Nothofagus* in New Zealand (see below), or of absences in Africa and India, are reflections, above all, of prior massings and absences. In situ evolution of the main modern groups in the complex was probably more or less over by the early Tertiary. Subsequent range

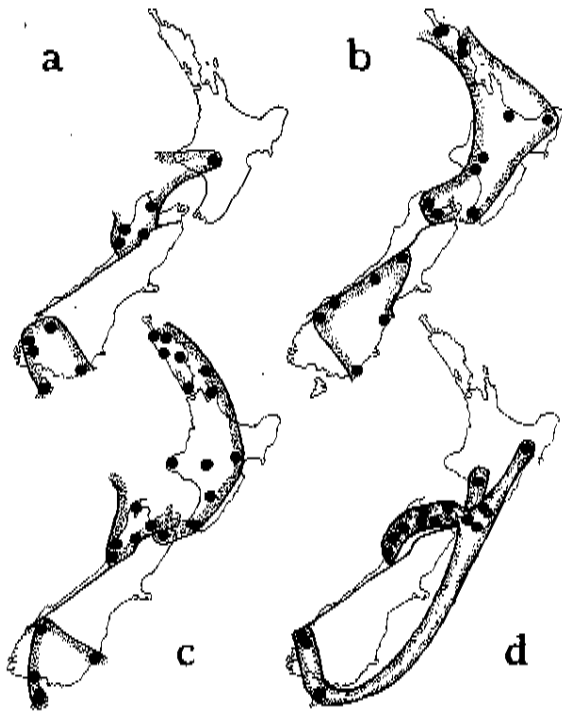


Fig. 15 a, *Novothybris* "cithara group" (Insecta: Homoptera). *N. cithara*, *N. notialis*, *N. peregrina*, and *N. vagans* (Knight 1974a). b, *Xestocephalus ovatus* (Homoptera) (Knight 1974b). c, *Scaphetus brunneus* (Homoptera) (Knight 1975). d, *Nuncia* subgen. *Nuncia* (*N. grandis*, *N. conjuncta*, *N. arcuata*) (Opiliones) (Forster 1954).

expansions and contractions have taken place through the Tertiary, but the major massings have remained where they evolved. This view is based on the assumption that outlying species and minor massings are much more likely to become extinct than major massings. In Fagaceae a great deal has been read into the fossil record. Ideas on phylogeny and dispersal have even been derived directly from the time of appearance of characters in the fossil record, but the available fossils actually give less information than living plants. For example, the living records of large genera such as *Lithocarpus* represent a vast amount of biogeographic, ecological, and morphological information. In another example, the fossil record suggests that most of the evolution within *Nothofagus* had taken place by the early Tertiary (Hill & Read 1989), but this was already clear from biogeographic and tectonic data.

Ecologically, Fagaceae have clear phylogenetic roots by the shore. Species of *Nothofagus*,

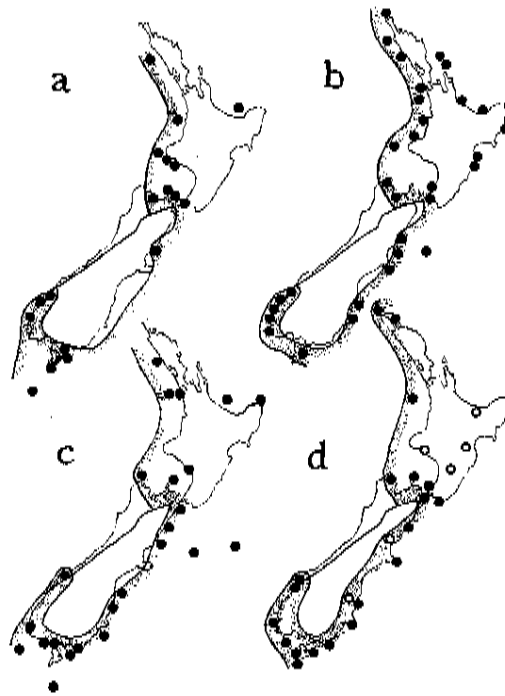


Fig. 16 a, *Evechinus chloroticus* (Echinoidea) (McKnight 1969). b, *Divaricella* (Mollusca: Bivalvia: Lucinidae) in New Zealand (*D. huttoniana*) (Luckens 1972). c, *Nectocarcinus* (Crustacea) in New Zealand (Main 1974). d, *Notosaria nigricans* (Brachiopoda). Closed circles: living populations, open records: fossil records (mid Miocene-Pleistocene) (Lee 1978).

Castanopsis, *Lithocarpus*, and *Quercus* are known down to sea-level. For example, *Castanopsis argentea* is found not far from the shore in West Java, and *Quercus subsericea* is found on rocky sea-shores in Malaya at 0–10 m altitude, facing the mangrove (Soepadmo 1972). Buttresses and stilt-roots are often present in several species of *Lithocarpus* and *Castanopsis*. In New Zealand, *Nothofagus* often grows by the sea-shore. From this base, *Nothofagus* ranges high into the mountains of New Guinea where it has been uplifted during orogeny. The idea that *Nothofagus* is simply limited to cool altitudes is incorrect. For example, in New Caledonia three species of *Nothofagus* grow in the tropical lowlands. Van Steenis (1971) notes that "it appears not well possible to correlate the altitudinal behaviour of *Nothofagus* in New Caledonia with environmental factors". Similarly, within the New Guinea region, *Nothofagus* is present on the biogeographically important d'Entrecasteaux

Archipelago at a distinctly lower altitude than on mainland New Guinea. In this instance latitudinal and longitudinal tracks interact with altitudinal trends, with the overall pattern largely mediated by tectonics. Ancestral "Fagaceae" undoubtedly utilised ancient sea-coasts and lake shores in the phase of modernisation during which *Nothofagus*, *Lithocarpus*, and the other genera came to maturity.

Since Baillon (1880) described the genus *Balanops* of Queensland, New Caledonia, Vanuatu and Fiji, it has been placed, usually in its own family if not its own order, with the Fagales. Like the other Fagales and allied plants in Hamamelidae (= Amentiferae), *Balanops* represents a pre-floral/proto-floral level in the evolution of fully normal (i.e., technically angiospermous) flowering plants from gymnospermous ancestors (Croizat 1961 cf. Mabberley 1978). Muller (reported in Soepadmo 1972) admitted that the pollen of *Nothofagus* is morphologically so isolated from that of the rest of Fagaceae, where it is usually placed, that if only pollen was known a palynologist would be at a loss to place it in any family. However, Baillon's original placement of *Balanops* finds support with Zavada & Dilcher (1986), who report that the pollens of *Nothofagus* and *Balanops* share interesting similarities. Whatever the final, formal taxonomic disposition of these two genera, the affinities discussed by Baillon, and Zavada & Dilcher are clearly of relevance, both phylogenetically and biogeographically, to the general problem of *Nothofagus* dispersal.

Broad patterns of morphological differentiation within a group, e.g., *Nothofagus* plus *Balanops*, are of equal, if not greater, biogeographic importance than exact distributional records, although the latter are necessary for detailed analysis. From the time of Mirbel through to the modern classifications the basic subdivision of *Nothofagus* has been made on the characters of leaf vernation, that is, how the leaves are folded in the bud. However, it was only recently that this character was examined in the New Zealand species (Philipson & Philipson 1979), with the result that modifications must be made to earlier classifications. The known distribution of the kinds of leaf vernation in *Nothofagus* is as follows (see Fig. 17a): leaves conduplicate in bud—New Guinea, New Caledonia; leaves plicate in bud—Tasmania, southern South America; leaves plane in bud—southeast Australia, New Zealand, southern South America; leaves revolute in bud—New Zealand.

The groups described by the vernation character thus show a clear degree of biogeographic as well as

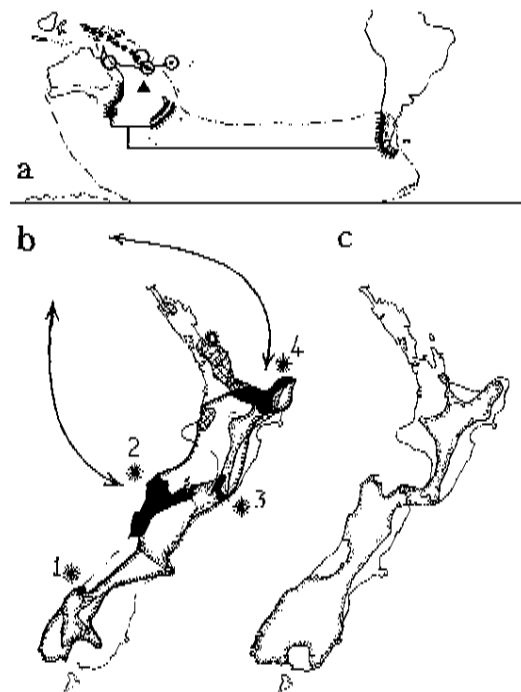


Fig. 17 a, *Nothofagus* groups: dotted line: populations with conduplicate vernation, hatched line: plane vernation, solid line: revolute vernation, stippled line: plicate vernation. Open circles: *Balanops* (*Balanopaceae*). Thin broken line: range of fossil pollen. (van Steenis & van Royen 1966; Philipson & Philipson 1979; Baines 1981). Triangle: the approximate location of a major biogeographic articulation in this affinity. b, Distribution of *Nothofagus* revolute-leaved group. Hatched line: *N. fusca*, stippled line: *N. solandri*, cross-hatching: *N. truncata*, solid black regions, with asterisks and numbered 1–4: all three species present. (Wardle 1984). c, The plane leaf-vernation group of *Nothofagus* in New Zealand: *N. menziesii*.

morphological individuality, and furnish convenient sections in *Nothofagus*. This view stands in some contrast with two recent treatments. That of Philipson & Philipson (1988) differs mainly in the ranking of the groups. Hill & Read (1989) make a gallant attempt to correlate extant pollen types with other characters, but the cuticle characters they favour are rather subtle, and they end up making the unlikely separations of *N. gunnii* from *N. pumilio*/*N. antarctica*, and *N. betuloides*/*N. nitida*/*N. dombeyi* from *N. menziesii*/*N. cunninghamii*/*N. moorei*. In any event, both of these revisions overlook an important aspect of shoot differentiation. Personal observations indicate the presence of brachyblasts

in various plicate-leaved species, with decussate phyllotaxis evident on these in *N. antarctica*. This recalls the seedling axis of certain *Nothofagus* (Philipson 1988), the brachyblasts of adult *Fagus*, and the whorled phyllotaxis of *Trigonobalanus* and *Balanops*. A monograph of *Nothofagus* is badly needed.

With respect to the vernation groups listed above, southeast Australia, New Zealand, and southern South America each manifest a similar degree of differentiation, with two groups each, and sharing a total of three groups, 75% of the total. The New Caledonian scores are similar, with one group of *Nothofagus* present plus the very different *Balanops*, possibly distinct to family level, with the total degree of differentiation at least balancing that manifest in the three southern groups. Related forms in Fagaceae occur in the forests of Australia and New Guinea. This gives a "centre of gravity" of massing in the overall affinity somewhere in the triangle: Queensland - Fiji - Lord Howe I. This node acts as a hinge or articulation pivotal to two pales of dispersal, one north and one south of the central Tasman Sea. Bearing in mind the possibility of such a central Tasman Sea node, the New Zealand distribution of the two groups present can now be examined.

The revolute-leaved group, known only from New Zealand, has three species, massing as shown in Fig. 17b. There are four regions (figured in black and numbered 1-4 in the figure), where all three species are present. Two of these zones of main massing (nos. 2 and 3) are connected by standard tracks involving the "Cook Strait centre" (Fig. 8). The very local centre by the lower Arawata River (no. 1), located virtually on the Alpine Fault and within view of the Dun Mountain Ophiolite Belt, is disconnected by at least 300 km along the Alpine Fault with the Nelson-Wellington main massing. The massing in Nelson remains north of the Wairau Fault, often regarded as an extension of the Alpine Fault. Thus the main massing in this revolute-leaved group ranges northwest of the Alpine Fault, apart from a minor outlier (Arawata River) disconnected along this same fault. A connection between northwest Nelson and the central Tasman Sea node would be normal. Finally, the Mamaku-East Cape-Waikaremoana zone of massing (no. 4) shows disconnections between Bay of Plenty and Nelson-Wellington. As illustrated above by *Utricularia* and *Metrosideros* (Fig. 5), there is a standard biogeographic connection between northwest Nelson and the northeast arcs, via the northwest of New

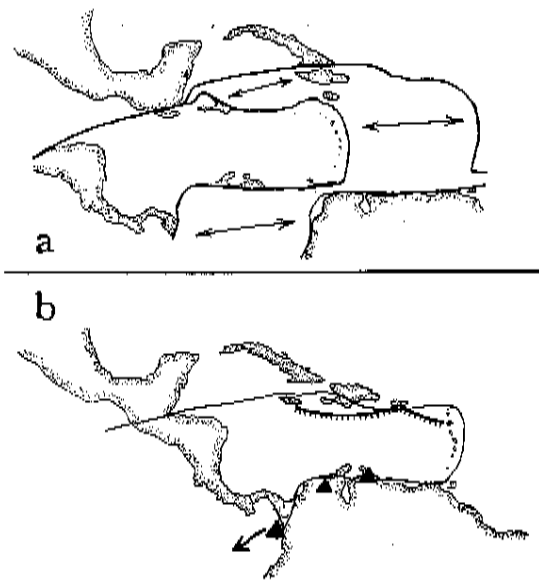


Fig. 18 Aspects of Caribbean geology and biogeography. a, reconstruction for late Eocene. Arrows mark sea-floor subducted since the Eocene (after Durham 1985). b, Present geography and structure. Hatched line: *Bazzania pycnophylla* (liverworts - Hepaticae) (Croizat 1964:126). Triangles: *Mellitella* (Echinoidea) (Durham 1985). The arrow indicates the remaining records of the genus—all are Pacific.

Zealand. In *Nothofagus*, disconnection could also be via the east of North Island (cf. *Asplenium* in Fig. 5d).

Finally in *Nothofagus*, the only New Zealand representative of the plane-leaved group (ranging: Australia-New Zealand-South America) is *N. menziesii* (Fig. 17c). It is present in all four areas of main massing in the revolute-leaved group, and is largely absent north of the Bay of Plenty massing. It is conspicuously present south of the Arawata massing, notably in the Dunedin-Catlins region, an area which is biogeographically related to the ranges of similar species (*N. nitida*, *N. dombeyi*) in southern South America.

The idea of biological disjunction along a transform being caused by lateral movement along the transform is not new. Croizat (1964) and Durham (1984) (see Fig. 18) invoked this same process to explain tracks around the Caribbean basin, showing patterns which reflect the deformation of the New Zealand region on the other side of the Pacific. 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 elaborates on the biogeographic significance of Cretaceous terrane suturing, and shows how many disjunctions between Nelson and Fiordland/Stewart I can be at least partly explained by displacement along the Alpine Fault. He also discusses other processes involved in disjunction such as the tectonic or erosional removal of terranes or sectors of terranes, and proposes the Alpine Fault Zone as a region of high tectonic activity correlated with the generation of high diversity in groups such as Trichoptera.

THE RANGITATA OROGENY AND SINCE

Three main episodes of plutonic and metamorphic activity have been recognised in New Zealand, dated at pre-Cambrian, mid-Palaeozoic, and late Palaeozoic–Mesozoic (Aronson 1968). The latter phase, related to the Rangitata Orogeny, will be considered here in more detail.

The Rangitata Orogeny (Lillie 1980), often considered to have culminated in the lowermost Cretaceous, is marked by, (a) the end of deposition in the New Zealand Geosyncline, (b) a metamorphic unconformity with Cretaceous and Tertiary rocks much less indurated than the older rocks, and (c), plutonism and metamorphism. The Rangitata Orogeny is sometimes extended to include the upper Tertiary Kaikoura Orogeny, and probably more or less all of the Mesozoic is involved, with a final uplift taking place in late Cretaceous. Spörli (1987) writes: "A major change in the tectonic regime took place in the Cretaceous. Over most of New Zealand, the Neocomian stratigraphic hiatus is marked by a profound unconformity." Subsequently, sediments were deposited in a tectonic setting of extension and rifting.

Much of this view of geological history is based on analyses involving data from palaeontology. In texts on the biogeography of fossil biotas it is often assumed that the distribution of fossil organisms must be analysed separately from that of living organisms. In Fig. 16d an attempt was made to indicate that the two can easily be integrated in analysis. On a larger scale, Fig. 19 illustrates major structural parallels between patterns of distribution in fossil and living groups. Two groups are illustrated. *Monotis* is a group of Mesozoic shellfish, *Coriaria* is a group of still-extant flowering plants. Both are present in many Pacific sectors, and connect via Tethys tracks (e.g., north India) with the

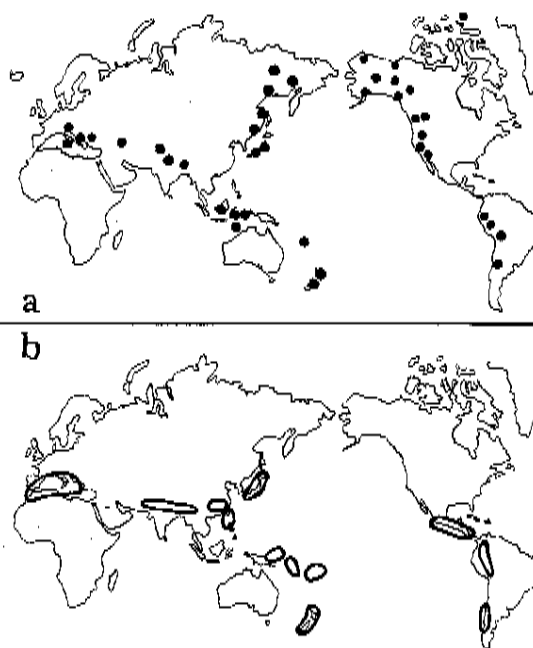


Fig. 19 a, *Monotis* (Mollusca: Bivalvia) faunas (Silberling 1985). b, *Coriaria*, comprising a monogeneric family of angiosperms. (Melville 1981).

Mediterranean. Both are notably absent in Australia, Africa south of the Atlas Mts, northern Asia-Europe, and the eastern Americas (see du Rietz 1940 and Croizat 1958 for examples of this pattern in living taxa). The process by which older life may "float" on younger stratigraphy is illustrated in Fig. 20.

Interaction between a "cold", austral biota and a "warm" Tethyan biota is a standard theme in the palaeontology and neontology of New Zealand. For example, Permian shallow water marine beds at Parapara, northwest Nelson, contain a "cold" fauna more similar to correlative faunas of Tasmania and New South Wales than to those of Southland, illustrating a trans-Tasman link also seen in many extant taxa. In contrast with such affinities westwards towards forms of the eastern Australian synclines, other New Zealand Mesozoic taxa show affinities with "warmer" Tethyan elements absent in east Australia, but known in Melanesia, Asia, Europe (cf. *Monotis* and *Coriaria* – Fig. 19, *Hebe* "ciliate disc group" – Fig. 28, *Carpodetus* (Angiosperms: Saxifragaceae): New Zealand and New Guinea). Many Triassic forms are confined to New Caledonia and New Zealand (the two comprising the "Maorian

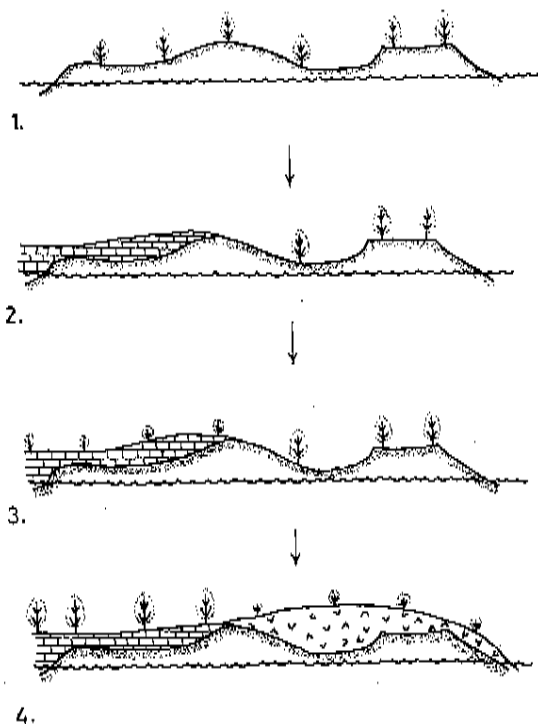


Fig. 20 A hypothetical example to illustrate the process of old life "floating" on young stratigraphy. 1, A Mesozoic peneplain with ancient biota, represented by trees. 2, Mid-Tertiary marine transgressions and subsequent uplift has left much of the substratum covered with thick limestones. These are soon colonised by seedlings, shown in 3. 4, Upper Tertiary volcanics have covered the rest of the basement, but are themselves now colonised by the limestone populations. The result is that the Mesozoic life-forms, simply through ordinary means of survival, "float" on the much younger Tertiary strata, remaining more or less in situ (cf. the small dimensions of many migrating basins ("geosynclinettes") in New Zealand's history). By similar means of survival (= "living on"), sundering or erosion of the Tertiary strata leading to the exhumation of the peneplain would result in the main massing of the biota being deposited back down onto the Mesozoic strata, as in, for example, communities living on now exposed schist and granite.

Province" of the palaeontologists) but affinities between these two areas are also clearly evident in the extant biota, for example, *Xeronema* (Angiosperms: Liliaceae) at Poor Knights, Hen and Chickens, and New Caledonia only (Moore & Edgar 1967). In the Permian, fossil assemblages in alternating beds show affinities with southeast Australia (a "cold" fauna) and Tethys (a "warm" fauna) (Lillie 1980). Both these affinities can also be detected in the Mesozoic, Tertiary, and extant biotas.

Tethys tracks running here more or less with the longitudes interact with circum-Antarctic tracks in southern New Zealand, and with a connection: Queensland/New South Wales border - Lord Howe I - Norfolk I - Kermadecs in northern New Zealand.

Following the initiation of rifting in the Cretaceous, during the Tertiary (especially in the Oligocene) shallow seas spread widely over several sectors of New Zealand, including some localities which are now topographically alpine. As Fleming (1979: 52) wrote: "Geologists are rather uncertain about the whereabouts of land at the height of the Landon [Oligocene] transgression", and this has led to differences in the reconstructions of geography, such as those presented by Fleming (1979: 46) and Kingma (1974: 152) based on geological data. Sequences of Landon beds are particularly well exposed in the Waitaki region, where all give evidence of very shallow-water, near-shore conditions of deposition. (The beds are remarkable for the very diverse faunas of penguins and other birds they contain.) In such shallow water environments coastlines are drastically affected by comparatively slight movements of the shelf as well as eustatic sea-level changes (dramatic lowering of sea-levels in Oligocene time is suggested by Keigwin & Keller 1984), and a complex, ever-changing system of inland shallow seas and islands is proposed. This would explain the survival of biogeographic centres correlated with events of the Rangitata Orogeny. The highest altitude Tertiary sediments in New Zealand are Oligocene beds which reach 1600m by Lake Wakatipu. Other similar outliers of Oligocene shallow-water coastal beds in what are now mountains give evidence of shallow embayments ancestral to the present alpine landscape, and such physiographic evolution correlates with the morphological, taxonomic, and biogeographic affinity between the alpine and coastal life of to-day. These Oligocene coastlines were themselves probably sites of continued biological form-making, as weedy taxa invaded and evolved on the land exposed by shifting and gradually shrinking inland seas. Form-making in such instances may have led to distribution in concentric rings, as seen in Central Otago (Fig. 23c) and also in southern Stewart I (Fig. 24d).

The Kaikoura Orogeny, clearly in evidence in the late Miocene, inherited its structural trends from the Rangitata Orogeny. Thus Lillie (1980) writes: "the opening up of the northeast fractures during the early Cretaceous produced a fabric which, intensified by subsequent shearing along that line, eventually became the trend for the major foldings that ensued

in Tertiary times". Northeast trending dispersal patterns have been illustrated above in Fig. 7c,d.

The major effects of upper Tertiary to Quaternary tectonics on the living communities included: first, rapid changes of altitude with the Kaikoura Orogeny; and second, great extinction in areas such as the lowlands of Nelson, Westland, Canterbury, Central Otago, and Southland which suffered repeated depositions of massive amounts of piedmont gravels. The North Island biota also suffered great extinction, with huge ignimbrite eruptions beginning in the lowermost Pliocene. Lillie (1980) sees these last as the result of the pulling apart of a gigantic sphenochasm (a triangular opening, with one side of a fold belt swinging away from parallel), "splitting a former domical mass of greywacke occupying the site of the central Volcanic region." (The South Island region too, of course, has also suffered splitting—by the Alpine and Campbell Faults, for example). Endemism in the central North Island, often restricted to very small sectors of the Ruahine and Kaimanawa Mts (a sliver of Haast Schist is exposed in the latter), represents a relic of the central North Island before it was split. In general, Lillie sees the Central Volcanic region as a rift zone comparable to those of East Africa and the Rhine, and in particular as the meeting point of two grabens, the Hauraki graben, and a northeast trending Taupo graben including White Island.

Developing McKay and Cotton's ideas on the faulted origin of New Zealand valleys and ranges, Lillie has stressed the importance in this region of "land forms dominated by tectonics", writing: "to my mind, all the present major land forms ["life-forms" could be added] of New Zealand are directly related to tectonics, so that very broadly all present great ranges are complex faulted anticlines and the big valleys are basically synclinal. Such major forms are essentially 'consequents' ". The faults along which the main alpine valleys were excavated in late Miocene time will in many instances date back to the later phase of the Rangitata Orogeny.

With local exceptions the whole New Zealand land area is currently rising at orogenic rates (0.2 – 10 mm per year, Grindley 1974), and at certain places on the Alpine Fault uplift rates of between 10 and 15 mm per year may be estimated (Lillie 1980). Such movements have marked ecological significance with respect to rapid changes in altitude of communities—these rates would give 100 m change in altitude in only 6700 – 10 000 years.

THE NEW ZEALAND PLATEAU, CONSIDERED AREA BY AREA

The Subantarctic

Katz (1982) has written: "Geologic and geophysical evidence suggests that a New Zealand – West Antarctica split ... cannot be explained by usual models of continental separation", and he suggests that this apparently unusual style of tectonic evolution may be caused by a relatively small area – which became the New Zealand microcontinent – having split off from a much larger and more stable continental mass "along a preexisting line of weakness which was the original junction between two different tectonic provinces." (Emphasis added). Katz accepts continental separation between New Zealand/Campbell Plateau and Marie Byrd Land at 81 Ma. Before this date the New Zealand/Campbell Plateau region was subjected to the Rangitata Orogeny, with folding and faulting, metamorphism, uplift, and erosion. Such activity on the "preexisting line of weakness" between the Campbell Plateau and Marie Byrd Land can also be implicated with the evolution of biological zones in the region, for example the major biological differentiation between Macquarie I/Antarctica and Auckland Is/Campbell I. The biota of the Macquarie I region shows clear connections with the New Zealand plateau as well as with circum-Antarctic tracks. The sector represented in today's geography by: Macquarie–Auckland–Campbell Is, also maintains a biota which points to its previous existence as an area of lands, which at some stage extended northwards to include Dunedin and the Chatham Is.

Davey & Christoffel (1978) consider the Campbell Magnetic Anomaly System, extending from east of Auckland Is to points 900 km eastwards between Antipodes and Bounty Is, to be a dextrally offset continuation of the Stokes Magnetic Anomaly (associated with the Dun Mountain and Ophiolite Belt). Thus, they proposed a transcurrent fault, aligned NE from Auckland Is named the "Campbell Fault" (Fig. 9). Discussing this fault, Barron & Harrison (1979) emphasise that: "The Alpine Fault is only one aspect of a complex boundary which resulted from the convergence of the Campbell Plateau with New Zealand." They consider that Cullen's Waipounamu Fracture (Fig. 2b), running parallel with the Campbell Fault, was the plate boundary at 60 Ma. Geological and palaeomagnetic data can here be synthesised with that from biogeography, where there is considerable information on relations among and within the

subantarctic islands. For example, the phylogenetically important *Leonohebe benthamii* links Auckland and Campbell Is; and nested tracks within the Auckland Is (Heads 1986) are possibly involved with the formation of the Auckland Islands Slope, where the Campbell Plateau drops off steeply into the Emerald Basin.

As an introduction to some further considerations in geology discussed below, Fig. 21–26 illustrate a biogeographic “transect” through the southern South Island from the Fiordland terranes in the west to the Torlesse in the northeast. Some major geological boundaries and tectonic zones which will be discussed below are illustrated in Fig. 21a, and these are drawn in as thin lines in Fig. 21–26.

It should be noted that through processes such as those outlined in Fig. 20 it is quite normal for young strata to maintain a life much older than the actual rocks, without there having been any substantial migration involved. Likewise, by processes of erosion, younger life may be “deposited” on older strata while remaining more or less in situ. Thus the correlation shown here between tectono-stratigraphic terrane boundaries and plant and animal distributions does not mean that these terranes were necessarily involved as “rafts”, merely that the evolution of the terrane boundaries has been connected with the evolution of plants and animals. Truncation or even virtual disappearance of terranes (considered below) means that the terranes of the past have also been involved.

Beginning with the geologist's Southwest Fiordland (Fig. 21a), this region is the locality of a number of interesting biological phenomena. For example, the daisy *Senecio bifistulosus*, with very distinctive dimorphic foliage, is known only from here (Fig. 21b). Here and elsewhere in Fiordland the subalpine shrubland is often composed largely of one of two species of *Leonohebe*, *L. mooreae* in the west and *L. odora* in the east (Fig. 21b). These two meet and replace each other at a line running in Fiordland largely along Central Fiordland, and extending eastwards in the south to the Longwood Range. Along this line runs a narrow zone where the two overlap.

Anisotome (Angiosperms: Umbelliferae) (Fig. 21c,d) shows the southwest to northeast sequence of parallel arcs particularly clearly. *A. lyallii* holds the outermost sectors and related forms occur in the islands to the south. *A. flexuosa* is wide in Otago and Southland, and in addition holds Central Fiordland and Stewart I, largely vicariant with *A. lyallii* in a pattern comparable in broad terms with that of

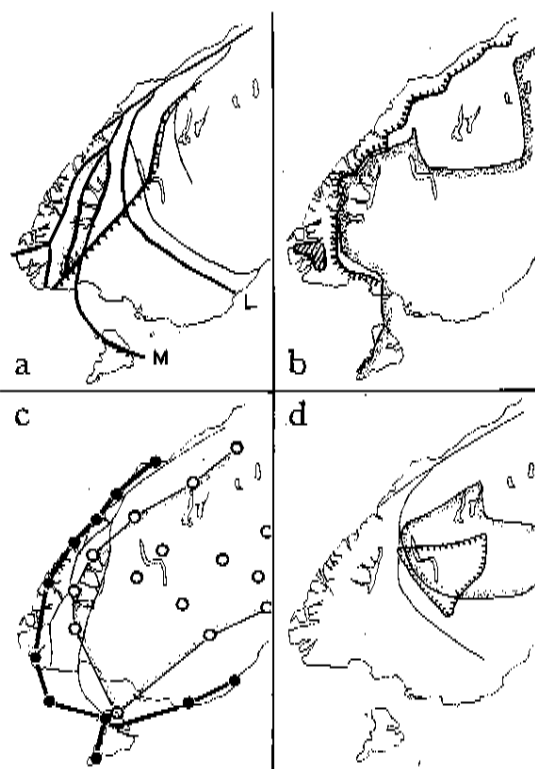


Fig. 21 a, Some geological boundaries and tectonic zones in southwest New Zealand. Fiordland stippled, divided into southwest, western, central, and eastern sectors. Fiordland is bound by the Alpine Fault to the north, the Moonlight Tectonic Zone (hatched), and the Median Tectonic Line (M). L indicates the boundary, marked in part by the Livingstone Fault, separating the Dun Mountain-Maitai terrane to the south, from the Caples terrane to the north and east. The fine line running north of this last line is the metamorphic boundary between the Caples and the Haast Schist. The forked line running with the Moonlight Tectonic Zone in the north is the Pounamu Ultramafic Belt. b, Hatched line: eastern limit of *Leonohebe mooreae*, stippled line: western limit of the closely related *L. odora* (Angiosperms: Scrophulariaceae) (Heads 1987). The mutual boundary lies largely along central Fiordland, with some overlap between the two species along this sector. Hatched region in southwest Fiordland: *Senecio bifistulosus* (Simpson 1974). c, Closed circles connected by thick line: *Anisotome lyallii*, open circles enclosed in stippled line: *A. flexuosa* (Angiosperms: Umbelliferae) (Dawson 1961). d, Stippled line: *Anisotome brevistylis*, hatched line: *A. caucicola* (Dawson 1961).

Leonohebe mooreae and *L. odora*. Further to the northeast, however, *Anisotome* displays rather different patterns, with *A. brevistylis* and *A. caucicola* (Fig. 21d) centred on the Caples terrane and Haast Schist, northeast of the Livingstone Fault.

It is not surprising that the diverse *Celmisia* (Angiosperms: Compositae) is also subject to the "decomposition" of Fiordland. *C. semicordata* is represented in Western Fiordland with the type subspecies, but eastwards is apparently absent in Central and Eastern Fiordland (Fig. 22a). This absence is probably related to the widespread presence in Fiordland of the related *C. coriacea*. South of Lake Manapouri, near the Median Tectonic Line the species reappears as subsp. *stricta*. This ranges northeast by the Moonlight Tectonic Zone to the Eyre Mts and the Caples - Schist boundary. Beyond this boundary lies the third and final subspecies, *aurigans*.

Ourisia (Angiosperms: Scrophulariaceae) (Fig. 22b) shows patterns similar to those of *Leonohebe*, *Anisotome*, and *Celmisia*, with, for example, *O. caespitosa* present in Eastern and Central Fiordland. The Moonlight Tectonic Zone and Caples-Schist boundary zone correlate with boundaries in this and related species. The very distinctive *Euphrasia integrifolia* is a nodal form phylogenetically, showing equally possible connections with a number of sections in this genus. It ranges (Fig. 22c) in southern parts of Central and Eastern Fiordland, and northeastwards, by the Moonlight Tectonic Zone, to the Livingstone Fault.

Hebe sect. *Subdistichae* (Angiosperms: Scrophulariaceae) in southern New Zealand (Fig. 22d) illustrates largely vicariant form-making among: Hump Ridge by the Median Tectonic Line in the south (*H. canterburiensis*), northern sectors of Central Fiordland (*H. cockayneana*) and the Garvie Mts (*H. dilatata* and *H. crawii*). *H. crawii* connects the Takitimu Mts, by the Moonlight Tectonic Zone, with the Haast Schist, across a broad sector of the "Hokonui Assemblage" of terranes avoided by *H. cockayneana*.

A more or less linear concentration of forms is evident along Central Fiordland in *Parahebe linifolia* and its allies (Angiosperms: Scrophulariaceae) (Fig. 23a) with notable absences in Western, Southwestern, and Eastern Fiordland, and the "Hokonui Assemblage". *P. linifolia* and *P. planopetiolata* are widespread only east of the Livingstone Fault. In a related genus, a similar pattern can be seen in *Ourisia confertifolia* and *O. spathulata* (Fig. 23b), with the connection between Fiordland and the Caples made near the Hollyford. A group of forms in *Leonohebe* sect. *Flagriformes* (Fig. 23c) illustrates the alternative southern connection across the "Hokonui Assemblage" along the line of the Moonlight Tectonic Zone, with *L. imbricata* at Eastern Fiordland

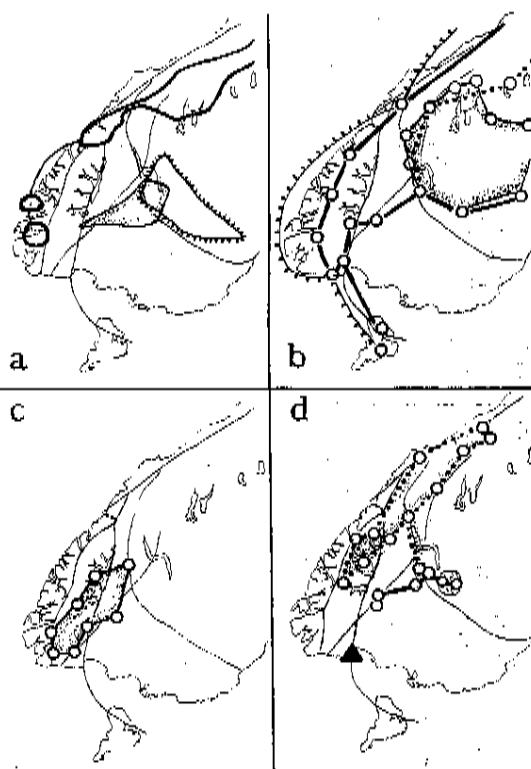


Fig. 22 a, *Celmisia semicordata* (Angiosperms: Compositae). Thick lines: subsp. *semicordata*, stippled line: subsp. *stricta*, hatched lines: subsp. *aurigans*. The related *C. coriacea* is widespread in Fiordland. (Given 1980). b, *Ourisia* (Angiosperms: Scrophulariaceae). Hatched line: *O. modesta*, thick line: *O. caespitosa* var. *caespitosa*, dotted line: western limit of *O. caespitosa* var. *gracilis*, stippled line: *O. glandulosa* (Heads 1987). c, Stippled line: *Euphrasia integrifolia* (Angiosperms: Scrophulariaceae)—phylogenetically a key form (Heads 1987). d, *Hebe* sect. *Subdistichae* in southwest New Zealand. (Angiosperms: Scrophulariaceae). Dotted stippled line: *H. cockayneana*, continuous line: *H. crawii* (total range), triangle: *H. canterburiensis*, stippled circle: *H. dilatata*.

(Mt Burns and Mt Cleughearn) and the Eyres. Once into the Caples and Haast Schist the group becomes much more diverse. Reading from outside to inside, *L. propinqua*, *L. poppelwellii*, and *L. subulata* form a concentric series of rings with localities such as Roxburgh at the centre. This sort of dispersal suggests form-making by the shores of progressively diminishing inland bodies of water, such as were present during the Tertiary, out of an ancestral complex of the Torlesse-Haast Schist-Caples terranes. Like these "whipcord" members of

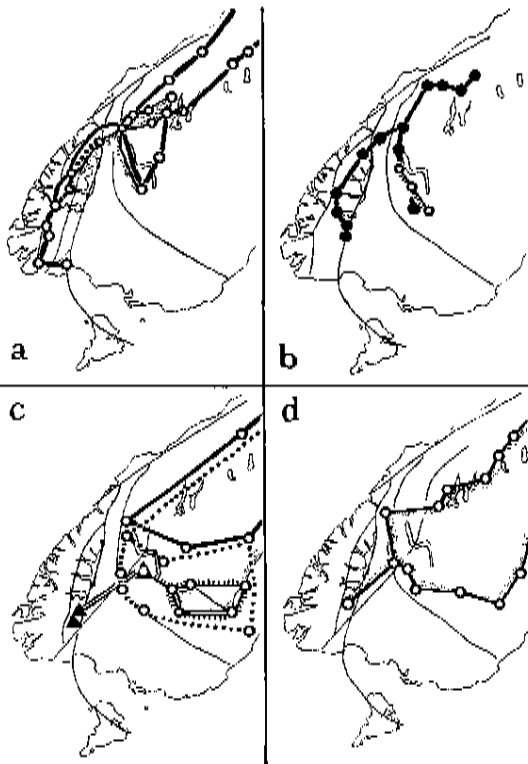


Fig. 23 Examples from Scrophulariaceae (Angiosperms) (Heads 1987). a, Continuous line: *Parahebe linifolia*, dotted line: *P. laxa*, stippled line: *P. planopetiolata*. b, Thick line: *Ourisia confertifolia*, hatched line: *O. spatulata*. c, thick line: *Leonohebe lycopodioides*, dotted line: *L. propinqua*, hatched line: *L. poppetwellii*, triangles and double line: *L. imbricata*, stippled line: *L. subulata*. d, *Hebe buchananii*.

Leonohebe (replaced in Fiordland by *L. hectorii* and *L. laingii*), *Hebe buchananii* (Fig. 23d) holds Fiordland only in the east, with records at Green Lake/Hunter Mts in the south and the Darrans to the north. Yet again, once beyond the Livingstone Fault dispersal is widespread.

Patterns of dispersal at the eastern margin of Fiordland, correlated spatially with the Median Tectonic Line, are illustrated in Fig. 24. Although the ferns *Hypolepis rufobarbata* and *H. millefolium* are widespread in Fiordland, in this region *H. ambigua* (Fig. 24a) ranges west only to the Median Tectonic Line. Also in ferns, *Asplenium obtusatum* and *A. lyallii* divide up Fiordland between themselves (Fig. 24b), with the former only at Western Fiordland, the latter generally east of the Median Tectonic Line. The interesting crucifer genus *Iti* is so far known

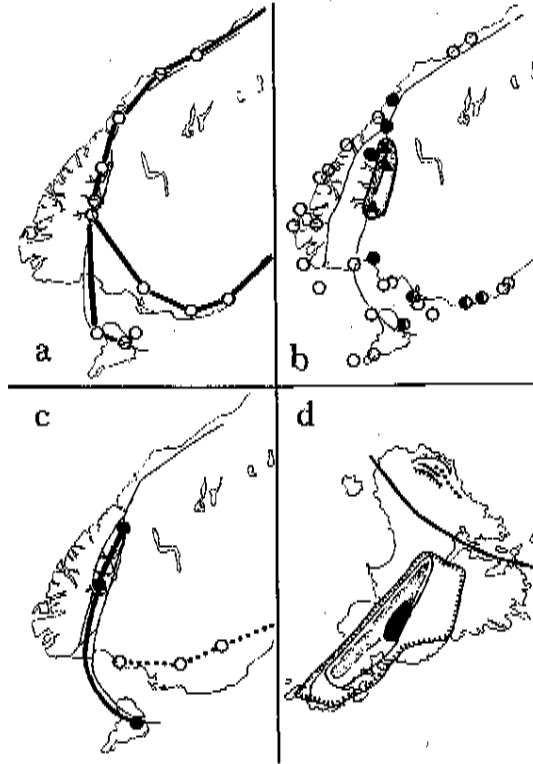


Fig. 24 a, *Hypolepis ambigua* (Pteridophyta: Dennstaedtiaceae) (Brownsey & Chinnock 1984). Two other species of *Hypolepis* are widespread in Fiordland. b, Open circles: *Asplenium obtusatum*, closed circles: *A. lyallii*, half-closed circles: both species. (Pteridophyta: Aspleniaceae) (Brownsey 1977). Triangles in stippled ellipse: total known range of *Iti* (Angiosperms: Cruciferae) (Garnock-Jones and Johnson 1987). c, *Nuncia* subgen. *Micronuncia* (Arthropoda: Opiliones) in southwest New Zealand. Thick line and closed circles: *N. roeweri seditiosa*, open circles with dotted line: *N. roeweri callida* (Forster 1954). d, Angiosperms in Stewart I north and south of the Median Tectonic Line. Northern Stewart Island: Stippled line: *Gentiana gibbsii* (Gentianaceae), dotted line: *Aciphylla traillii* (Umbelliferae), continuous line: *Celmisia* aff. *durietzii* (Compositae), hatched line: *Chionochloa* aff. *flavescens* (Gramineae). Southern Stewart Island: hatched line: *Chionochloa lanea*, continuous line: *Celmisia polyvena*, broken stippled line: *Aciphylla cartilaginea*, black: *Aciphylla stannensis* (Wilson 1987).

only from localities on or by the Median Tectonic Line (Fig. 24b).

Nuncia subgen. *Micronuncia*, a group of harvestmen, "comes apart" in southern New Zealand (Fig. 24c) with *N. roeweri callida* on or just west of the Median Tectonic Line, and *N. r. seditiosa* ranging east of the Line across Southland. In Stewart I,

parallel arcs of endemism in the north and concentric rings of endemism in the south, illustrated here in seed-plants (Fig. 24d), are both separated by the Median Tectonic Line.

East of the Median Tectonic Line there is a standard, northeast striking pattern of distribution involving southwest outliers (typically at the Takitimu Mts in Brook Street terrane) connecting via the Moonlight Tectonic Zone with the Caples terrane and Haast Schist. This pattern is illustrated in Fig. 25a–d for various seed-plants. The localised distribution of *Hebe biggarii* (Fig. 25a) serves to highlight the important sector (Eyre Mts, Garvie Mts, etc.) by the intersection of the Moonlight Tectonic Zone and the Livingstone Fault. The same sector is also held by *Celmisia spedenii* and *C. philocremna* (Fig. 26a), the latter a curious species combining characters of different sections. Also included in Fig. 26a is *C. inaccessa*, holding the quadrangle: Thompson Sound–Caswell Sound–Doon Saddle–Mt Luxmore. This is an important type of dispersal, and serves to illustrate a narrow zone of endemism straddling Western, Central, and Eastern Fiordland. The axis: Caswell Sound–Doon in particular is manifest in many groups, Caswell Sound, for example, being the only locality where *Leonohebe odora*, widespread in North, South, Stewart, and Auckland Is, reaches Western Fiordland (Fig. 21b).

Leonohebe sect. *Densifoliae* (*L. densifolia* and *L. uniflora*) meets sect. *Leonohebe* (*L. ciliolata*) in northwest Otago (Fig. 26b) somewhere by: Hector's Col–Mt Turner–Mt Alta, at the Moonlight Tectonic Zone and the Pounamu Ultramafic Belt (these two belts are not shown in the figure as they run so close to *L. uniflora*). *Leonohebe cheesemanii* and *Epilobium purpuratum* (Fig. 26c) also illustrate dispersal ranging from the northern Moonlight Tectonic Zone–Pounamu Ultramafic belt northeastwards into the Haast Schist and Torlesse terrane.

Finally in this brief transect from the Fiordland terranes to the Torlesse terrane, *Kelleria laxa* (Angiosperms: Thymelaeaceae) and *Ranunculus crithmifolius* (Angiosperms: Ranunculaceae) (Fig. 26d) range respectively north and south of the Waihemo Fault Zone, a contact between Haast Schist and sedimentaries of the Torlesse.

The geological basis of the zones outlined in Fig. 21a and discussed biogeographically above would appear to be of interest to the general problem of dispersal in New Zealand, and will be discussed here in a little more depth, in the same regional sequence.

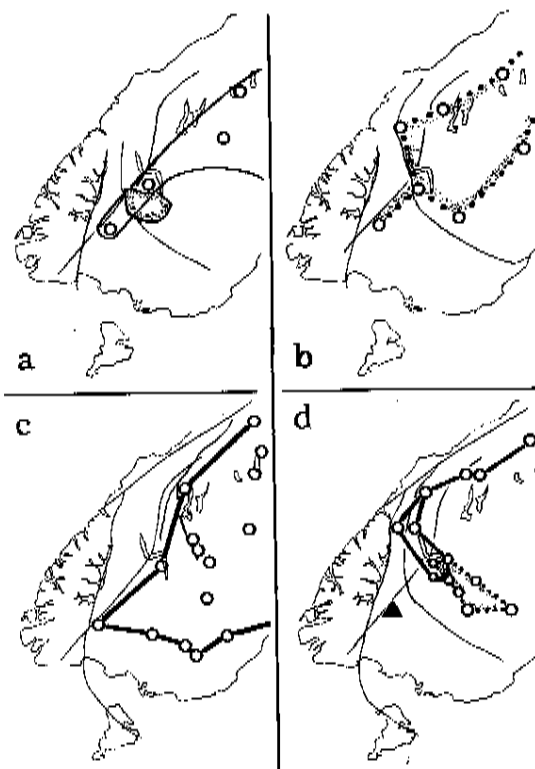


Fig. 25 a, Open circles in thick line: *Ranunculus haastii* (Angiosperms: Ranunculaceae) (Fisher 1965). Stippled line: *Hebe biggarii* (Angiosperms: Scrophulariaceae) (Heads 1987). b, *Parahebe decora* (Scrophulariaceae) (Heads 1987). c, *Epilobium pictum* (Angiosperms: Onagraceae) (Raven & Raven 1976). d, Three related species in or near *Parahebe*. Triangle: *Parahebe* sp. nov., thick line: *P. birleyi*, dotted stippled line: *P. trifida* (Heads 1987).

Fiordland

Suggate et al. (1978) describe the "Post tectonic intrusives" of Fiordland, dated mainly around the early Cretaceous. These include the Dea's Cove Granite (Secretary Island), the Murchison Granite (eastern Kepler and Murchison Mts north to the North Arm of Lake Te Anau), the Pomona Granite (Potteriti–Mt Tiitiroa–northern tip of Lake Te Anau, with a western outlier by the Doon River), and the Kakapo Granite (southwest Fiordland from Resolution Island to Lake Hakapoua, to be compared with the Rakeahua Granite of Stewart Island). Granite plutonism is generally associated with metamorphism in fold belts, and indicates a phase of profound geological, physiographic, and biological reorganisation. When finally exposed, granite in

Fiordland weathers easily to a sand providing ideal growth conditions for many plants.

Oliver & Coggon (1979) revised the highly complex geology and structure of Fiordland, which they divided into four major regions (Fig. 21a). Their "Southwestern Fiordland", including the Preservation Granite, ranges south of Dusky Sound to include Chalky and Preservation Inlets. "Western Fiordland" includes the Western Fiordland Orthogneiss and ranges west of the heads of Dusky, Doubtful, and Milford Sounds. "Central Fiordland", including its own granites and granodiorites, ranges east of this axis to: Lake Hauroko—middle arm of Lake Te Anau—head of Milford Sound, and "Eastern Fiordland", including the Pomona and Murchison Granites, ranges east from here to the eastern shores of Lakes Te Anau and Manapouri (and the Hollyford Fault System). These sectors correlate closely with some of the major biogeographic tracks of the area, as does the Resolution Fault Zone, just offshore between Breaksea Sound and its intersection with the Alpine Fault near Milford Sound.

Biogeographic tracks ranging between the vicinity of Lake Monowai (southern Fiordland) and the Eyre Mts (Caples terrane and Haast Schist) often either avoid the Takitimu Range (e.g., *Nothofagus fusca*, *Kelleria villosa*), or arc present only as a "sliver" in the extreme north of the range. Such tracks, as well as those illustrated above, correlate well with what Norris and colleagues (Norris et al. 1978; Norris & Carter 1982) have discussed as the Moonlight Tectonic Zone, a zone of tectonic instability which has traversed the area between Te Waewae Bay and the Shotover River (across five terranes) probably from pre-Tertiary time onwards (Turnbull 1980). The present surface expression of this zone is the Moonlight Fault System, as well as the biogeographic patterns illustrated by the examples in Fig. 22, 23c,d, and 25. The intersection of the Moonlight Tectonic Zone with northwest striking structure in the Eyre Mts is thus correlated with a major centre of intersecting tracks and endemism (Fig. 25a, 26a). D. Craw (1985) has traced the Moonlight Fault from the Shotover northwards, via the Wilkin forks, ultimately to the Burke River, some 250 km from Te Waewae Bay. Craw treats the fault as a major regional feature, associated with the fourth of five deformation phases recognised in the schist, and directly involved, for example, with the uplift of the Mt Aspiring region which reaches 2980 m. It is also implicated with the ecology and biogeography of plants in and around Mount Aspiring National Park, for example as a distributional

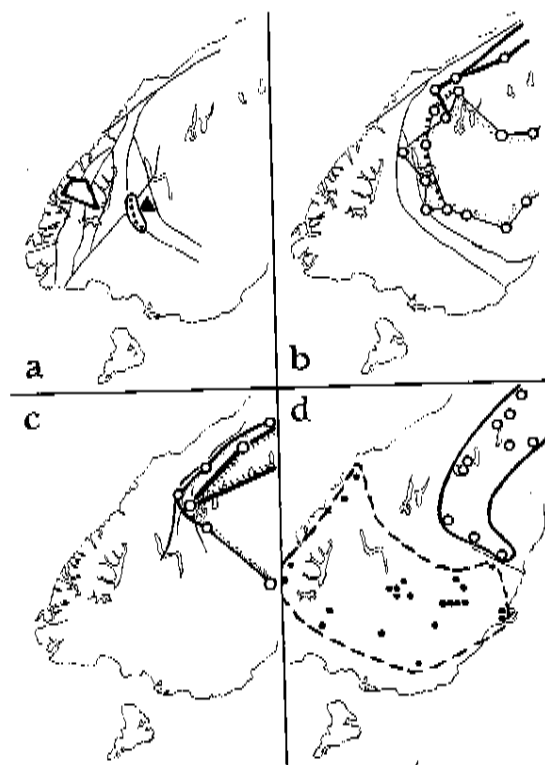


Fig. 26a, Stippled quadrangle: *Celmisia inaccessa* (Angiosperms: Compositae), dots enclosed in ellipse: *C. spedenii*, triangle: *C. philochemna* (Given 1971; Lee & Given 1984). b, Thick line: *Leonohebe ciliolata* (Scrophulariaceae), stippled line: *L. densifolia* (also in southeast Australia), hatched line: *L. uniflora*. (Heads 1987). c, Hatched line: *Leonohebe cheesemanii* (Heads 1987), stippled line: *Epilobium purpuratum* (Angiosperms: Onagraceae) (Raven & Raven 1976). d, Open circles enclosed in thick line: *Ranunculus crithmifolius* (Angiosperms: Ranunculaceae) (Fisher 1965). Dots in broken line: *Kelleria laxa* (Angiosperms: Thymelaeaceae) (Heads 1987). The fine line running between the two ranges represents the Waihero Fault Zone.

boundary between *Leonohebe* sects. *Densifoliae* and *Leonohebe* (Fig. 26b), as an eastern limit (e.g., *Hebe cockayneana*—Fig. 22d) and as a western limit (e.g., *Ourisia glandulosa*—Fig. 22b).

West Coast-Nelson

Many biologists now accept that aspects of east/west differentiation in the New Zealand biota are at least as important as the north/south, latitudinal patterns perceived by Colenso (1868). Like Croizat's track "1" in Fig. 2, the Median Tectonic Line separates the

New Zealand "mainland" into two provinces, east and west. North of Fiordland, the Western Province, dislocated by the Alpine Fault, is represented by Nelson, and the West Coast. Nodes of dispersal at the Paparoa Range (between the Taramakau River and Westport) have already been illustrated (Fig. 3a; 13a,c,d; 14b,d; 15a,c,d), and Jackson's Bay marks a second node in the region of major importance.

Offshore wells west of the Paparoa Range and Cape Egmont have encountered Western Province rocks which are usually inferred to extend out along the Lord Howe Rise (Cooper 1979). Precursors of extant central trans-Tasman links are represented by Lower Paleozoic affinities (for example in graptolites) between Fiordland/northwest Nelson and southeast Australia, and in the southeast Australia–Nelson affinities displayed in the Permian "cold" faunas mentioned above. Further north the probability of Mesozoic land west of Kawhia is indicated by the presence of huge granite boulders in the beds of Kawhia Syncline (Murihiku terrane).

In west Nelson the Karamca and Golden Bay terranes are intruded by belts of granite—Grindley (1974) characterised his "Rotoroa–Fiordland Zone" (forming about half of the Western Province) as a "zone of anatexis". The granite belts and bounding faults run roughly with the longitudes, in contrast with the NE trends of Tertiary folding. Most of the Paleozoic faults have had a complex history, having typically been rejuvenated in the Rangitata Orogeny (Cooper 1979). The north-south orientation of the granite batholiths is of general biogeographic interest, and the obvious comparison is with similarly oriented boundaries in Fiordland rocks and life. In west Nelson the Paparoa and Karamca batholiths are conspicuous, and in the east the Separation Point batholith runs Pikikiruna Range (Abel Tasman National Park)—Motueka River—Mt Murchison. Parts of the Paparoa batholith and the associated Berlins Porphyry (behind Westport) are dated (Suggate et al. 1978) as Jurassic–Cretaceous, and it is also proposed that a major part of the Separation Point batholith was also emplaced in the early Cretaceous. Several biogeographic regions in Nelson appear to trend likewise with the longitudes, and require analysis.

Following the compression and uplift of the Jurassic–Cretaceous phases of the Rangitata Orogeny, the development of extensional tectonics and a West Coast Rift System took place (Laird 1981). Laird illustrates the fault systems inferred to have been active during the late Cretaceous in the western portion of New Zealand (Fig. 27). The Cape Foulwind

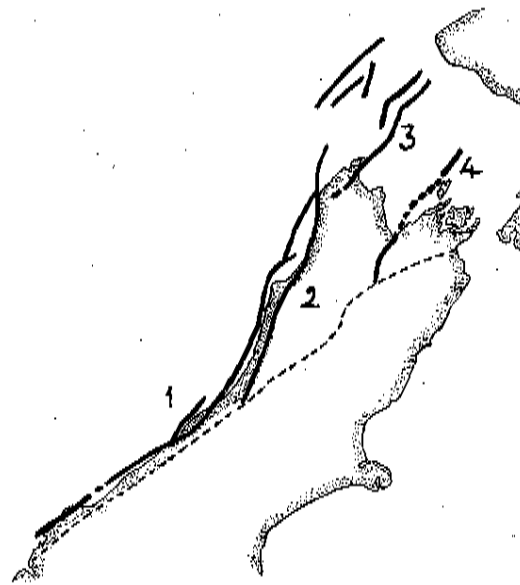


Fig. 27 Western New Zealand fault systems inferred to have been active during the late Cretaceous. Broken line: Alpine Fault. 1: Cape Farewell Fault Zone. 2: Paparoa Tectonic Zone. 3: Wakamarama Fault. 4: Waimea-Flaxmore Fault System. (After Laird 1980).

Fault Zone stretches north from Jackson Head and the Open Bay Islands out to sea, ranging a short way inland by Okarito/Abut Head (cf. for example *Hebe canterburiensis* at Omocroa, Fig. 11c; the white heron *Egretta alba* and royal spoonbill *Platalea regia* at Okarito, Falla et al. 1979; the Okarito kiwis, *Apteryx* aff. *australis*), and thence running out to sea parallel with the coastline to Cape Foulwind and Heaphy Bluff. Inland and parallel with this zone is the Paparoa Tectonic Zone, also of considerable biogeographic interest. It ranges NNE from the Alpine Fault near the Hokitika River, and by the Paparoa and Buller Geosynclines to near Westport, whence it follows the coast to Heaphy Bluff. The Wakamarama Fault extends NE from Cape Farewell and joins the Kiwi and Cape Egmont Fault Zones. Running parallel to and east of this line are the Waimea and Taranaki Faults, intersecting the coast near Patea (and the Patca-Tongaporutu Basement High) and between the two lines lies the Taranaki graben. The Kapuni oil wells are located on this graben; the Maui wells lie immediately west of the Cape Egmont Fault Zone (cf. differentiation in the *Parahebe catarractae* complex, Fig. 13b). Croizat (1958) proposed correlation between biogeographic

tracks and the localities of oil deposits. Katz (1968) reviewed the potential oil formations in New Zealand, which are all found on epicontinental, unstable shelf areas. The characteristic lithologic assemblage of possible source sequences is of the shale-sandstone-coal type, and "its environment is a transitional one of the near-shore marine and deltaic or estuarine-brackish to freshwater zone". Katz quotes Bitterli: "environmental conditions for the formation of bituminous sequences ... are often created at the turning points in the paleogeographic history", and notes that "it is not uncommon for argillaceous sediments lying just above major unconformities to be good source rocks. Rich growth of organic material often took place on land during several periods represented by such unconformities." It is the nature and ecology of this "rich growth" associated with turning points in geographic history which is of interest to both biogeographer and oil geologist.

On the eastern boundary of the Western Province, biogeographic tracks illustrating correlation with the Median Tectonic Line are illustrated in Fig. 24.

Murihiku

The Southland Syncline is generally believed to have been continuous with the Nelson and South Auckland (or Kawhia) Synclines. In the north Lillie (1980) writes that "the fossiliferous and very regularly folded Mesozoic beds are stopped abruptly by a transverse fault at Port Waikato, and no similar strata occur to the north until we disembark at New Caledonia", where terrigenous sequences "bear a remarkable similarity" (Spörl 1987) to the New Zealand Murihiku. These synclines together comprise a vast fold involving the shelf sediments of the Murihiku terrane. As in the Kawhia Syncline, coarse granitic detritus is common in various conglomerates of the Southland Syncline. Enormous thicknesses of volcanic material are now located along both its southwest flank (Bluff-Takitimus-Pyke: Brook Street terrane) and its northeastern flank (Balclutha-West Dome-Pyke: Maitai terrane), but these may not have always been so close to each other—the Brook Street terrane in particular may have had little to do with the others. To the north the Southland Syncline becomes narrowed and eventually largely faulted out, and is represented by the highly deformed Key Summit Syncline. The final record of sedimentation in the Southland Syncline is a sliver of Upper Jurassic shallow shelf—estuarine sediments in the Pyke Valley, and the syncline terminates generally with freshwater and terrestrial beds, as in the Kawhia Syncline.

Biogeographic ranges showing correlation with the Murihiku are given in Fig. 21d, 22, 23, 25, 26a, b.

Lillie (1980) writes that "From the data of Otago we can deduce clearly that the north-west trend of faults was well established in the very early Cretaceous immediately after or by the Rangitata Orogeny, but we also see that many faults with a north-east trend cut across the north-west trending folds and that these too were formed before the upper Cretaceous." The northeast trends are clear in the biogeography of very many groups (e.g., *Gingidium*, Fig. 7d; *Aciphylla*, Fig. 7c; *Kelleria villosa*, *K. multiflora*, *K. croizatii*, Heads 1987).

Caples terrane

This represents only a part of a once much larger arc terrane. Modern magmatic arcs are 2–400 km wide, and the Caples, Maitai, Murihiku, and Brook Street terranes have probably all been substantially narrowed subsequent to their formation. Landis & Blake (1987) consider that the different arcs which supplied the sediments of the Maitai and Caples have been removed by subduction, faulting, or erosion, and these vanished terranes may have also contributed plants and animals.

Haast Schist

The Haast Schist Group represents a regionally metamorphosed sector defined texturally (Bishop et al. 1976), and best exposed in Otago (over some 26 000 km²) where it lies between, and grades into, the Caples terrane to the southwest and the Torlesse terrane to the northeast. Other assemblages, such as that represented by the Aspiring terrane (Norris & Craw 1987) were probably also involved in the formation of the Haast Schist. The original sediments were deposited in Carboniferous to Jurassic time, with most of the metamorphism probably occurring from the early Mesozoic through to the Jurassic-Cretaceous. Bishop et al. (1976) conclude: "Lithostratigraphic units of both Torlesse and Caples rocks may be traced into the Haast Schist terrane from opposite directions. The Haast schists may thus represent the metamorphosed amalgamation of two distinct rock suites, derived from separate source areas." The formation of such metamorphosed suture zones could also have led to phenomena such as the formation, by the end of Cretaceous time, of hybrid swarms involving more or less modern forms in groups such as *Hebe* and *Coprosma*.

The boundary between the Caples and the Haast Schist, defined by the degree of metamorphism,

correlates with boundaries in many Otago plants and animals (Fig. 22a,d, 25b, 26a,b and also in the Blue Mts, Patrick et al. 1985). To the north, the boundary of the schist with the Torlesse is more complex, but the boundary by the Waihemo Fault Zone is especially well-marked biogeographically (Fig. 26d).

Structure within the schist zone is of greater complexity than in most New Zealand strata, indicating a particularly dynamic history of rocks and biota in the region. In comparison with some aspects of internal structure, metamorphic zones in the schist appear relatively simple. A biotite zone marks a central axis: Duncdin—Central Otago—northwest Otago, representing a southern sector of the Otago—Kaimanawa geanticline (Suggate et al. 1978). Cooper (1976), Cooper & Reay (1983), and Reay & Cooper (1984) have studied and mapped the Pounamu Ultramafic Belt (the source of nephrite boulders), which they recognise as “an important structural element” of the Haast Schist. It ranges: Mill Stream (Upper Maruia) to Waitaha, and thence “disappears into” the Alpine Fault, reappearing at Makawhio (= Jacobs) R—Haast R—Wilkin R. It branches in the vicinity of Mt Aspiring, with one line leading to Dead Horse Creek—Bushy Creek (near Moke Lake), the other to: Spring Burn (near Roaring Meg) — Clyde. Cooper & Reay write that “the PUB probably represents a slice of upper crust and mantle with its overlying pelagic and quartzo-feldspathic sedimentary cover tectonically emplaced during collision and accretion of the Torlesse—Haast Schist terrane with the western sediments of the Caples terrane... The collision event forming the accretionary prism of the present Torlesse terrane marks an early phase (probably late Triassic) of the Rangitata Orogeny in New Zealand.” Biogeographic tracks and boundaries recalling the Pounamu Ultramafic Belt are exemplified in Fig. 26b,c.

Torlesse terrane

The Torlesse terrane, composed of Carboniferous—Jurassic sediments, forms the lowland basement and most of the mountains from near the Waitaki River (north Otago) to north Auckland, and makes up about half the area of the main islands of New Zealand. The beds are highly fractured and folded. Describing the Torlesse, Bradshaw et al. (1981) emphasised that the presence of this “great volume of predominantly continent-derived quartzo-feldspathic material on the Pacific side of the convergent margin suite ... comprises the main geotectonic problem in New Zealand”, and Campbell (1974) has described the provenance of the Torlesse

as “one of the most perplexing problems in New Zealand geology.”

Discussing the Doubtless Bay—Kawau Island Waipapa Group of the Torlesse, Suggate et al. (1978) cite Bell & Clarke's (1909) conclusion that the source of the sediments lay to the northeast (the sediments coarsen in that direction). In the same year Speight (1909), proposing a “subtropical Pacific continent”, cited important early work in geology and biology by Suter, Forbes, Hutton, von Ihering, Hedley, Pilsbry, and Baur in support of a lost “Pacifica” continent, and affinities between Rapa and Chatham Is in, say, *Hebe* (total range of this genus given in Fig. 1b) could be added.

The idea of an eastern source for Torlesse and Cretaceous sediments was proposed by Kingma (1974), citing granite pebbles and boulders in Cretaceous beds of Hawkes Bay. Lillie (1972, 1980) observed that “granites appear in such distant parts of the New Zealand plateau as the Snarcs, Bounty Islands and Auckland Islands”. He also emphasised the abundance of granitic detritus in the Torlesse (from the boulder-beds of the North Island west coast and Great Barrier Island, down to the graywackes and argillites), and noted clast size increasing to the east. These suggested an eastern granitic and metamorphic foreland. Gage (1980: 99) discussed the possibility that a “vanished land mass [“an attractive speculation”] has been engulfed by the denser rocks of the sub-crustal mantle while the expanding Pacific Ocean floor has been overriding the eastern margin of our piece of the Australian—Asian continent”.

MacKinnon (1983) recently reviewed the Torlesse terrane—“part of the largely Mesozoic ... circum-Pacific graywacke suite that is commonly inferred to represent accreted subduction complexes”, and concluded that “compositional and textural immaturity of the sandstone and the enormous volume of the Torlesse signify a substantial mountainous source ... the source is interpreted to have been a major, active, volcano-plutonic arc”. Like Kingma, Bradshaw & Andrews (1973) proposed an eastern source for the Torlesse, with important palaeogeographic implications, and this has been supported by Retallack (1979) and Kamp (1980). Kamp argues that the sediments could have been derived from a very extensive eastern land-mass (“Pacifica”), which would account for the presence of similar quartzo-feldspathic sediments in California. Likewise, passing from the west of New Caledonia through the island to the east, Avias (1953, 1955) described (1) a former western landmass

"Tasmania", (2) a "geosynclinal intramelanesien" extending from New Zealand through New Caledonia to New Guinea, (3) a former eastern landmass, "Archcofijia", extending east to Marshall's Andesite Line.

The Torlesse has a comparative rarity of volcanic material such as is abundant in the Murihiku. Conversely, living forms such as the annelid worms *Titahia* and *Torlessia* (= *Terebellina*), described as "the most distinctive fossils of the Torlesse" by Fleming (1970), have never been found in the Murihiku, apart from one notable record (in Campbell 1974), of *Titahia* at Akatore in the far east of Otago (cf. patterns in the living flora of the east coast of Otago).

In the Permian, Fusulinid Foraminifera are known in the Torlesse of Whangaroa, north Auckland, and in the Akatarawa terrane of north Otago, but nowhere in the Murihiku. Such records suggest early, important biogeographic differentiation, whereas other groups show affinities between Torlesse and Murihiku. Lillie discusses the outcrop at Whangaroa with fossils "unlike any other in the [extensive] New Zealand Permian, and with distinct resemblances to the faunas of south-east Asia and of North America". Thus the Torlesse connects with northern Pacific sectors. Suggate et al. (1978) note that the absence from the Torlesse of the bivalves *Rhaetavicula*, *Otapiria*, and *Meleagrinnella*, widespread globally and in the Murihiku, is "puzzling". From the New Zealand Triassic-Jurassic, Campbell (1974) cites the brachiopods *Burmihynchia* (Burma, Yunnan, Japan, India, Africa, Europe) and *Halorella* (Indonesia-Europe, Oregon), known in New Zealand from the Torlesse only. Campbell discusses the disparity between the Torlesse and Murihiku faunas, with some "Tethyan" elements found only in the Torlesse. Living forms (*Hebe* "ciliate-disc group", Fig. 28; *Xeronema* as cited above) also show this Tethys-Torlesse pattern, and Croizat (1958, 1964) repeatedly emphasised the global importance of Tethys tracks (Fig. 28) in ancient and modern dispersal.

The Torlesse has been divided into a number of sub-terraces with different histories proposed for each. The development of such analyses will be of much interest to New Zealand biogeography which is, to a massive extent, the biogeography of the Torlesse. Two small terranes within the Torlesse, the Akatarawa terrane by Lake Aviemore, and the Kakahu terrane by Geraldine, stand out as distinct. Of the Akatarawa, Bishop et al. (1984) write: "The distinctive [Tethyan] fauna is completely unlike

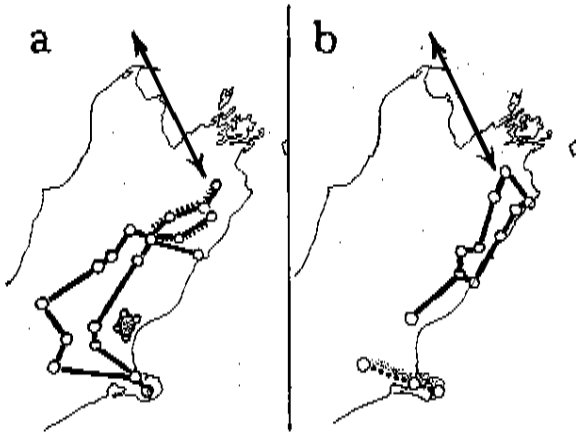


Fig. 28 The total New Zealand distribution of the "ciliate disc group" of *Parahebe* (currently placed in *Hebe*), arrows indicate the nearest affinity, in New Guinea. Thick line: *H. raoulii* var. *raoulii*, stippled quadrangle: *H. raoulii* var. *maccaskilli*, hatched line: *H. raoulii* var. *pentasepala*. b. Thick line: *H. hulkeana*, dotted stippled line: *H. lavaudiana* (Heads 1987).

other Permian faunas in South Island, and with the unique sandstone petrography indicate the Akatarawa terrane should be regarded as exotic." Of the Kakahu terrane, these authors write that: "Kakahu rocks have not been related convincingly to other Torlesse rocks, including the enclosing Permian strata. The Kakahu terrane, or at least the limestone-chert-volcanic portion is therefore regarded as a suspect terrane, with possible affinities with the Permian Akatarawa terrane." The sector marked by this "possible affinity" is of considerable biogeographic interest as it runs along part of the important track: Rock and Pillar-Torlesse Range which displays considerable endemism. (For examples see *Hebe* sect. *Glaucæ*, Heads 1987, and millipedes, Johns 1979). Likewise, in phytogeographic work Burrows (1968) has described the track: Hunters Hills-Four Peaks-Mt Peel-Mt Hutt-Torlesse-Puketeraki-Tekoa-Tinline (= Terako) - Seaward Kaikoura Range (Here the Kirkliston Range could possibly be included with the Hunter's Hills, and the Inland Kaikoura Range with the Seaward Kaikoura Range.)

Southeastern South Island

Eastern biogeographic arcs are illustrated above (Fig. 6), and bathymetric and paleomagnetic studies in the area southeast of the South Island have revealed structures striking northeast, parallel to much on-land faulting and cutting across basement terrane boundaries. Cullen (1967) proposed the name "Antipodes Scarp" for the sharply defined, more or

less linear eastern boundary of the Campbell Plateau, and wrote that "it is significant that northward extrapolation of this trend truncates the eastern extremity of the Chatham Rise." Cullen suggested "a primary tectonic origin" for the Antipodes Scarp, and if this is taken to include the eastern end of the Chatham Rise a structure with strike length in excess of 1600 km is indicated. Cullen viewed this as a "truly major tectonic feature" and named it the "Antipodes Fracture Zone" (see Fig. 2b), attributing its origin to late Mesozoic fracturing resulting from NE-SW crustal compression. Cullen's analysis also indicated that a structural zone, the Waipounamu Fracture, separates the Campbell Plateau and Chatham Rise from mainland New Zealand. Although the importance of these fracture zones has perhaps been overshadowed by the recognition of the Campbell Fault (Fig. 9), they remain of interest to biogeography, where Waipounamu dispersal is an important, if as yet unexplained, occurrence. Recently, Carter (1988) has described faults arranged en echelon off the southeast South Island, in what is proposed as the Waipounamu Fault System. Carter proposes two phases of movement: 1, extensional tectonics in the early-mid Cretaceous creating the Great South Basin off Catlins-Dunedin, and 2, mid-Cenozoic reactivation with gentle uplift, folding and faulting.

Just inland from the east Otago coast, the Cretaceous Henley Breccia is deposited on the east side of the northeast striking Titri Fault, which probably thus marked a fault-line scarp in Cretaceous time. Benson (1941) writes: "the present Taieri-Waihola-Tokomairiro depression, which is a faulted syncline resulting from post-Pliocene crust-movement, is parallel to and at most a few miles west of the Mid-Cretaceous fault-bounded depression. Once again the tectonic character of eastern Otago seems remarkably persistent." (cf. Mutch & Wilson 1952). The Titri Fault and related northeast striking structures can be contrasted with the northwest strike of the Waihemo or Shag River Fault Zone in north Otago (Fig. 26d), active in the Rangitata Orogeny, with later rejuvenated movement. *Kelleria dieffenbachii* (Thymelaeaceae) ranges widely between New Guinea and the Auckland Is, but grows at low altitude (60 m) only at Pukehiwitahi, near Shag Point (Heads 1987). Elsewhere, even at the subantarctic Auckland Is, the species ranges only above 450 m. This sort of "anomaly" occurs in many plants and animals at Shag Point, where a tussockland community typical of the low-alpine in other areas is found at sea-level. This is correlated with the

particular tectonic setting of the area: it is the point at which the Waihemo Fault Zone and the Kakanui/Horse Ranges intersect the coastline. In this zone, "The greatest fault movements took place during the middle Cretaceous, when the high rank schist on the west formed the upthrow side of what was then a normal fault system. After late Miocene time movement took place in the opposite direction, the eastern side being elevated by reverse faulting to form the Kakanui Range." (Mutch 1963). The same zone is also, not surprisingly, a northern and southern boundary of distribution (Fig. 26d), a possible centre of endemism (for example, the chiton *Notoplax facilis*), and a possible site of disjunction in orchids, with taxa known from only here and Banks Peninsula (Dr B. Molloy, DSIR Lincoln, pers. comm.).

Further north on the east coast, dispersal around Marlborough connects via the Cook Strait centre with Nelson, Wellington, the northeast arcs (*Asplenium* Fig. 5d), and directly out of New Zealand, for example to New Guinea (*Hebe* "ciliate disc group", Fig. 28).

Eastern and Northern North Island

Varietal differentiation within *Hebe parviflora* (Fig. 29) illustrates vicariant dispersal out of a baseline parallel to the Cretaceous-Tertiary Geosyncline, a double sided basin which ran along the east coast of the North Island (Lillie 1980).

Considering the northeastern North Island, it is appropriate to recall a warning given by Du Rietz (1940). He observed that Wegener's map of a "Pangaea", made up of Gondwanaland (South America, Africa, India, and Australasia) and Laurasia (North America, Europe, Asia) "suits the facts of transatlantic and Andean trans-tropical connection, but... seems impossible to reconcile with the facts of an old trans-Malaysian connection... Trans-tropical Pacific affinities also seem impossible to reconcile with Wegener's model, and are widespread (Croizat 1958; *Trigonobalanus*; the affinity between *Hebe rapensis* of Rapa I, and the Chatham Is forms of *Hebe*; *Fuchsia* (Angiosperms: Onagraceae): New Zealand-Tahiti-South and central America). Such affinities have led to ideas on ancient lands, floras, and faunas to the northeast of New Zealand which could have supplied the primaevial New Zealand/s with sediment and biota. Tropical Pacific dispersal generally involves New Zealand, if at all, by the northeast arcs described above.

Ballance et al. (1982) relate the geology of northern North Island to that of eastern North Island. They write: "northwestern North Island presently

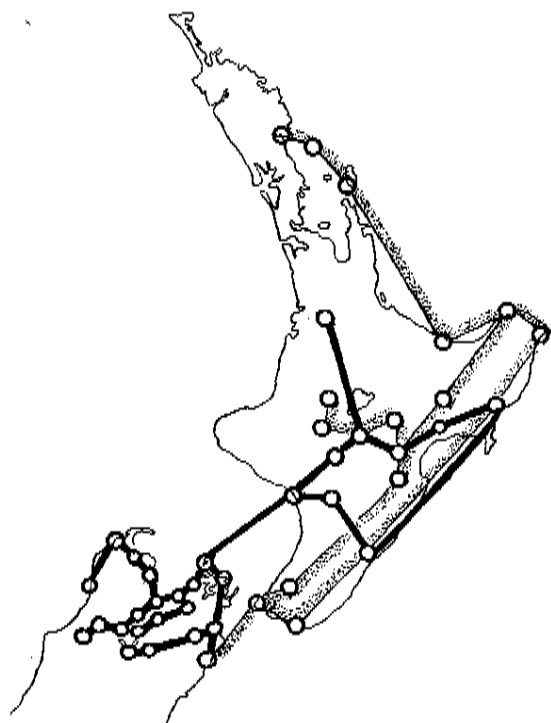


Fig. 29 Stippled line: *Hebe parviflora* var. *arborea*, thick line: *H. parviflora* var. *angustifolia* (Heads 1987).

contains arc volcanics of Miocene and Pliocene age, but has no recognisable accretionary prism. Eastern North Island is an accretionary prism of Miocene and Pliocene age, but lacks an adjacent arc of the same age; its adjacent arc, the Taupo Volcanic Zone is no more than 2 M.Y. old. Eastern and northwestern North Island are therefore thought to have been adjacent to each other during the Miocene and Pliocene, and as a consequence of that conclusion some system of late Pliocene and younger transcurrent displacement and rotation between eastern and western North Island is strongly indicated." Ballance et al. suggest that displacement took place along a postulated transform fault, a precursor of the present Vening Meinesz Fracture Zone. This latter zone (see Fig. 2b) is of great biogeographic interest, being oriented northwest-southeast off eastern North Auckland, and correlating with biological arcs to the northeast. The zone was illustrated and discussed by Croizat (1952, 1958), and was named and introduced to geologists by van der Linden (1967). This latter author recognised two distinct tectonic systems in the vicinity of New Zealand, and these had earlier been discussed as the "syntaxis" of Suess and the

"chiasma" of Fleming (1970). One system, striking NNE-SSW, is manifest in the Alpine and Campbell Faults. The second, including the Vening Meinesz Fracture Zone, is a NW-SE striking trend (cf. Lord Howe Rise - Campbell Plateau) extending northwest to Queensland and the Coral Sea, and southeast past the Chatham Islands to the Ellanin Fracture Zone System (Molnar et al. 1975; Weissel et al. 1977). Malahoff et al. (1982), studying magnetic anomalies, accept the Vening Meinesz Fracture Zone as "an active transform fault during the period of development of the Kupe Abyssal Plain between 35.5 and 25.5 m.y. separating the actively spreading basin from the North Island of New Zealand."

Summerhayes (1969) correlated the northwest strike and development of New Zealand features such as Lord Howe Rise-Campbell Plateau with the activity of (1) Van Bemmelen's Indian Ocean megaundation, and (2) Menard's Darwin Rise. The crest of the latter runs with the Cook and Line Islands, and the Rise showed a pronounced phase of development in the Cretaceous, sinking since that time (cf. Fleming 1970; King 1983: 134; Schlanger et al. 1981).

To the north of New Zealand Davey (1982) showed that the structurally complex South Fiji Basin is bounded by NNE trending features: Three Kings Rise on the west, and on the east the Lau Colville Ridge, and Kermadec Is-Tonga Is. The remaining four structural features in the area range generally NW-SE. Reading from north to south these are: South New Hebrides Trench-Hunter Fracture Zone, Julia Fracture Zone, Lindsay Fracture Zone, and, by the Northland Plateau, the Vening Meinesz Fracture Zone. This last, acting in its role as a transform, is implicated by Davey as fundamental in the development of South Fiji Basin-North Island. The line, or rather the set of arcs nested around it and "hitting" northeastern New Zealand, is of great palaeogeographic significance, indicating a particularly dynamic zone tectonically along which northeastern flora and fauna "invaded" New Zealand.

Thrasher (1986) has described basement structure in the region off Coromandel Peninsula as faulted into fault angle depressions and grabens, and a northwest striking trend is evident. Other geological structure running parallel with the Vening Meinesz Fracture Zone includes North Island plutonism, known (in exposed rocks) only at: North Cape (Cretaceous), Cape Karikari (Cretaceous), and northwest Coromandel (Miocene), a track which is closely allied to similar arcs in plant and animal records (Fig. 4).

Upper Cretaceous marine beds of the North Auckland peninsula, although very disturbed (emplaced above Oligocene and Miocene beds as the Onerahi Chaos) show "very striking resemblances" (Lillie 1980) to those of the Cook Strait—East Cape Cretaceous-Tertiary Geosyncline, recalling the many biogeographic connections between the "Cook Strait centre" and northeast Auckland. Southwest of East Cape the sediments have been judged autochthonous by some, but near the Cape itself Stevens & Speden (1979) write that structure is quite different: "the sequence is dominated by decollement slices emplaced in late Oligocene—Miocene time and largely allochthonous". The Matakaoa Volcanics (Fig. 10) formed by middle Cretaceous and lower Tertiary magmatic activity, accreted as a seamount terrane during the middle Tertiary (Gibson 1987). The Tangihua and Wangakea Volcanics are similar accreted ophiolitic sea-mount bodies in north Auckland (Brothers 1983). Likewise an affinity between Northland and East Coast Allochthons has been proposed by Spörl & Ballance (1985).

The East Cape region has a peculiar biogeographic significance, involving connections with northeast arcs, Cook Strait, and Chatham Is. As Kirk (1897) wrote: "the chief interest of the district arises from its exhibiting such a remarkable admixture of plants characteristic of the extreme north of the colony with others of a peculiarly southern type. Nowhere else do we find associated genera offering such a remarkable contrast when considered with regard to their geographical distributions as *Pisonia* and *Euphrasia*, *Sideroxylon* [*Planchonella*] and *Aciphylla*, *Persoonia* and *Gentiana*, *Vitex* and *Calceolaria* [*Jovellana*]; while the number of species which attain their northern or southern limits is perhaps larger than could be found in any other district of similar area in the North Island." This can be compared directly with the well-known combination of far-northern and far-southern components in the Chatham biota (cf. Fig. 8).

In conclusion, it appears that the problematic history of the Torlesse is intimately involved, in biogeography and presumably also in geology, with the connection: Vening Meinesz Fracture Zone—Chatham Rise—Campbell Plateau, in other words, with the series of biogeographic arcs to the east of New Zealand.

Geology and ecology in New Zealand

In proposing ideas on chronology in evolution, a traditional approach is to use fossil evidence. How-

ever, fossil evidence is virtually absent for many groups extant in New Zealand. What seems to be a viable alternative is to correlate biogeographic patterns with tectonics. This was the method which Croizat (1952–1968) developed and refined on a global scale, and the correlation of tectonic change with the development of biological communities, in particular with the altitude of the latter, had earlier been proposed by a series of New Zealand ecologists. Details in such accounts may be incorrect—what is emphasised here is the method of analysis and synthesis.

In an early example of this method, Kirk (1871) contributed biogeographic data to a geological debate. He wrote: "The frequent occurrence of several species of maritime plants in the Waikato District, far beyond the present range of tidal waters, appears to call for special remark from its important geological bearings. Dr. Hochstetter was, I believe, the first to advance the theory, 'that the whole Middle Waikato basin was but recently a shallow arm of the sea or a far extending estuary.' The accuracy of this opinion has however been impugned; it may therefore be advisable to recapitulate the maritime plants observed in and about the river and adjacent lakes and marshes." Kirk proceeds to list eight species (records from, for example, Crustacea could be added), and concludes: "It is readily admitted that littoral plants may occasionally be found in inland situations from accidental causes, but in the present case the number of species, and the wide area over which they collectively extend, afford forcible proof that the cause of their growth must be found in the district having been formerly a shallow estuary, probably connected with the Frith of the Thames."

Hutton's views on biogeography, for example that birds migrating between New Zealand and Melanesia follow old coast lines (Hutton 1872) match Kirk's, and both mark an early phase of integration in the earth and life sciences by two of New Zealand's most perceptive naturalists.

In his study on the plant geography of the Waimakariri, Cockayne (1900: 101) wrote: "Amongst the plants found [at the lower Waimakariri gorge] are a number which, so far as I know, rarely occur at any distance from the sea, and this seems to strongly favour Captain Hutton's theory, the crucial point of which is that the sea at one time came up to this spot. Of these plants *Linum monogynum*, *Parsonsia rosea*, *Chenopodium triandrum*, and *Angelica geniculata* may be especially cited."

Describing limestone cliffs and rocks bounding Te Whanga lagoon on Chatham I, Cockayne (1902)

wrote: "At one time the base of the cliffs was laved by the waters of the ocean, so that they are closely related to maritime cliffs. From such cliffs, as before described, they differ in their inland position, and consequent freedom from the influence of salt water, also in the very different nature of the rock. Many of their plant inhabitants are *doubtless part of the original flora ... taking the case of New Zealand it seems well-established that sea-coast plants can continue to occupy an inland ancient maritime station.* Mr. T. Kirk [1871] has called attention to such an instance, and I have also shown that *Angelica geniculata* occurs at the lower Waimakariri Gorge, on the upper Canterbury Plains, a station which Captain Hutton brings good evidence to show was formerly maritime." [Italics added].

In his account of the coastal vegetation of South Island, Cockayne (1907) devoted his Chapter 11 to the "occurrence of coastal plants inland", again citing Kirk (1871), as well as *Metrosideros excelsa* at Lakes Taupo and Rotoiti (by Rotorua), and other examples from South Island. He writes: "How far all the above cases denote a former shrinkage of the land and extension of the coast-line inland is not for a botanist to settle but certainly, so far as geological evidence goes at present, they are suggestive, to say the least." Cockayne also cites *Asplenium obtusatum* (for its Fiordland range see Fig. 24b) and *Senecio lautus* on limestone at Castle Hill and Weka Pass, concluding logically that: "If such a distribution is correlated with the marine origin of the rocks, then it is evident that species can exist under special conditions for enormous periods of time." (These ideas can be compared with the process outlined in Fig. 20). Cockayne's Chapter 10 is titled "mountain plants on the coast", and he cites *Claytonia australasica* and *Helichrysum selago* at Dunedin, *Cordyline indivisa* at Fiordland, and several species at Cook Strait. He also noted that "coastal scrubs ... are frequently closely related to subalpine scrub, both ecologically and floristically". Cockayne undoubtedly sensed the significance of such observations, writing that "the subject is of too much importance for a brief treatment", although in his later magnum opus (Cockayne 1928) published in Germany they are hardly mentioned.

Diels (1896) regarded the malvaceous plant *Plagianthus divaricatus* as a mangrove, and Mepham & Mepham (1985) treat it as a "potential mangrove"—an arborescent species growing in tidal zones. Beddie (1935) described a population from 600 ft altitude on an uplifted spur near Palliser Bay. Interpreting this, he writes: "One possible, and I

think probable, explanation of *Plagianthus divaricatus* occurring at this altitude is that when the river-bed was elevated to its present position a saltmarsh containing a patch of *P. divaricatus* was also raised to form a part of the spur ... Possibly *Hymenanthera crassifolia* shared in the upheaval ... Probably ... many former constituents of the saltmarsh found it impossible to accommodate themselves to life on the bare, steep spur ... [*P. divaricatus*] seems able to bear up with the altered conditions and to flower and fruit prolifically ... it is not a question of a few stray plants, but a quantity of them, and, personally, I cannot understand their getting established there except as members of an upraised salt-marsh." In the Wellington earthquake of 1855 (magnitude 8?) the Palliser Bay shoreline was raised at least 3 m (Lillie, 1980), and the possible ecological implications of such movements were clearly considered by Beddie.

Overseas, the direct effect of tectonic change on altitude and evolution of biological communities has been explored both by authors discussing spectacular cases (for example, inland mangroves on rapidly rising land) and also those writers such as Croizat who accept it as a normal and universal phenomenon. Tolmachev (1970) described the process of formation of highland floras, in which "the height rises with its vegetational cover, namely with its flora, which will ultimately become orophytic ... the adaptational amplitudes of the different species and their hereditary conservatism varies. Accordingly some species of the rising highland will remain without any apparent changes in their nature, whereas other species, adapting to their new conditions, will be transformed into new "daughter" species, and finally, other species, being unable to adapt to the changing conditions, will perish." Tolmachev emphasized the fundamental significance of the "Floral and vegetational character of a certain area on the earth's crust before its rise to the ultimate altitude. The importance of this moment is frequently not fully appreciated in investigations of the origin of orophytic floras, although their nature (especially that of the more recent formations) will largely depend on it." [Emphasis added].

Such tectonic intervention in the determination of community altitude may also explain the phenomenon of "Massenerhebung", in which the altitudinal vegetation belts are "telescoped" on lower mountains away from major axial ranges (e.g., in Morobe Province and the Bismarck Archipelago in Papua New Guinea, and Fiordland-Subantarctic Is in New Zealand). The major ranges, with their biota,

have been lifted higher. Naturally, biogeographic nodes (for example at Jackson Bay, Shag Point, The Nuggets, Cook Strait) play a fundamental role in determining where tracks intersect the coastline and other altitudinal zones.

Conclusions

With respect to the general processes involved in biological evolution, du Rietz (1940) has argued that: "It has grown into a habit amongst most biologists [Hooker and Darwin are cited] to assume that a taxonomic unit must have originated within a single region and from there spread over the distribution area it now occupies ... however ... it seems to be equally possible for a genus or any taxonomic unit to differentiate or 'crystallize' out of its more polymorphic ancestral syngameon simultaneously over a very large area ... it would then be unnecessary to assume any trans-tropical migrations for bipolar units later differentiated." (emphasis added). I have examined some implications of this idea above and elsewhere (Heads 1985). Evolution is here treated as occurring over broad fronts, both phylogenetically and spatially. Thus, the ancestral complexes which would eventually become recognisable as modern families of flowering plants, for example, are envisaged as already being somewhat diverse at the time of the change from gymnospermy to angiospermy, i.e., the closure of one or more of the gynoecial coats to form a style. This last is an example of a simple, widespread development manifest in the modernisation of most seed-plants at some stage in the Mesozoic. It is clear that we study characters or phenomena in general along a track, not just taxa, and "angiospermy" itself is thus interpreted as massively polyphyletic by origin, although monophyletic by tendency. This is confirmed by the complex, reticulate affinities of angiosperm families such as Thymelaeaceae and Flacourtiaceae. The main biogeographic massings of Palaeozoic-early Mesozoic ancestors are considered here to have provided the matrix from which the post-Mesozoic patterns developed.

In this paper, attention has been drawn to the parallel arc patterns permeating much of New Zealand biogeographic structure. The fracturing and creation of such parallel arcs by tectonic movement and erosion has brought about vast disjunctions in many plant and animal groups. Nested arc patterns of distribution in Indonesia-Papua New Guinea, the Caribbean, and New Zealand have been analysed at length by Croizat (1952-1968), who correlated

biogeographic patterns in these regions with tectonic history. In a contemporary development of Croizat's thought, Craw (1982) has examined Howell's (1980) model of New Zealand as the composite "mosaic" of exotic terranes accreted by subduction. It is suggested, with reason, that the suturing proposed by Howell would have had profound geological, geographical, and biological effects.

The major arcs of distribution in these regions of active margins correlate with zones of tectonic activity such as plate and terrane margins, fracture zones, and belts of granitic intrusion. Other arcs may be the result of evolution along the Tertiary shores of inland bodies of water.

The altitude of many communities in New Zealand also appears to conform to biogeographic and tectonic trends, with higher altitude communities having been derived by the uplift of mid-Tertiary lowland-coastal communities.

Evolution is interpreted here as proceeding largely by phases of population "re-melting", for example, in the formation of Cretaceous hybrid swarms of weeds, and "recrystallisation", by which standard ranges are "frozen", even in weedy taxa. Such processes correlate spatially with zones of tectonic and physiographic disturbance. In groups such as *Coprosma* and *Hebe* hybrid swarms which formed and were set in place in the Rangitata Orogeny have retained a very high potential to hybridise, which may be released, for example in cultivation. A major theme in New Zealand geology is the rejuvenation of tectonic features, and this gives rise to repeated phases of great disturbance along particular sectors. Communities of both wetlands and better drained areas have been present and affected by such change. New Zealand as a region of "disturbed wetlands" maintains the derivatives of ancient mangrove and swamp forest communities, including the lowland, montane, and alpine swamps and bogs of to-day. The wetlands have probably always been diverse phylogenetically—they would have been particularly extensive during the Oligocene—and have provided a source for the biota of modern forests and grasslands.

Although the relics of the Oligocene swamp forests and mangroves are of the greatest interest, in many groups the current New Zealand biota is generally depauperate. Dominant elements are those with a higher "coefficient of survival", and in many ways the biotas of what are now fully terrestrial localities resemble those of marine rock stacks. There are few mammals and more lizards, few vertebrates in general (exception: seabirds!) and

more invertebrates. The seed-plants are dominated by herbs and shrubs, often with weedy, pioneer ecology. The seed-plant flora is quite depauperate, in comparison with New Caledonia for example, and stands in contrast with the lichen flora, recently described as "one of the most interesting and best preserved in the world to-day" (Galloway 1985).

Modern developments in accreted terrane tectonics have led to the idea (Landis & Blake 1987) that terranes hundreds of kilometres wide may have disappeared from within the New Zealand region. These vanished terranes possessed rocks, plants, and animals, some of which would have been transferred to encroaching terranes (cf. the simple example given in Fig. 20) and would have eventually given rise to modern plants and animals.

If plant populations may be seen as sedimentary or metamorphic "strata", some are also very liable to be totally removed by biological "erosion", especially locally. The disappearance of *Leonohebe cupressoides* shrubland in the lakes region of Otago because of human activity is a dramatic example (Heads 1987). However, even after such "erosion" a tremendous amount of comparative biogeographic data remains, linking past and present. A great many elements of the current biota may be characterised as "weeds of tectonically active zones" which, despite this ecology, maintain precise patterns of endemism clearly articulated by standard nodes. Examples include cliff and scree plants in Scrophulariaceae, including fault-scarp colonisers such as *Hebe cockayneana* (Fig. 13c, 22d), the diverse swamp forests running along the Alpine Fault Zone, *Griselinia-Fuchsia* forests growing on steep fault-scarps around Dunedin, and the *Nothofagus* forests of Wellington, where Wardle (1967) has illustrated the dramatic effects on plant communities of even minor fault movement.

Ideas such as those outlined here can be applied even to such supposedly "advanced", recently-evolved groups as the tube-flowered plants. For example, if seed-plants ancestral to the extant Scrophulariaceae were subjected to a major "modernisation event" in the mid-Jurassic to mid-Cretaceous, with subsequent differentiation at specific and subspecific levels into the Tertiary, then the chronology proposed is easily congruent with that of Melville (1966) for *Hebe*, Hong (1984) for Veronicaceae, and Barker (1982) for *Euphrasia*. This is also consistent with, for example, affinities along the track: New Zealand-South America in *Hebe*, *Jovellana*, *Ourisia*, and *Euphrasia*. This would also explain why, for example, the extant biogeographic

patterns bear such little relationship with current physiography. With respect to the ecological history of these Scrophulariaceae, a Pacific ancestral complex is required, probably comprising woody plants of the shore and its hinterland, with habitat in well-drained sites such as coastal cliffs and rocks, as well as poorly drained areas such as coastal lagoons and swamps (cf. Retallack & Dilcher 1981). This range of ecology would characterise Mesozoic forms which at some stage were subjected to a phase of "modernisation", during which the major taxonomic and biogeographic massings currently observed were laid down. Subsequent tectonic events disrupted the earlier ecology and the Kaikoura Orogeny placed many low altitude populations at higher altitude. However, ancient water relations are quite possibly conserved in what are to-day alpine snow-banks and rock-fields.

Modernisation events in the history of earth and life may last some millions of years, for example the various phases of the Rangitata Orogeny may have lasted some 80 million years. During such phases the ancestral matrix of contemporary life and rocks is altered in a process of remelting and recrystallisation, in which rocks, landscapes, and biotas are metamorphosed as one.

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