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Biogeography and evolution in the Hebe complex (Scrophulariaceae): Leonohebe and Chionohebe

MICHAEL J. HEADS

RÉSUMÉ

HEADS, M. J. (1994). Biogéographie et évolution dans le complexe Hebe (Scrophulariaceae): Leonohebe et Chionohebe. *Candollea* 49: 81-119. En anglais, résumés français et anglais.

Les cinq espèces de *Chionohebe* et des 31 espèces de *Leonohebe* néo-zélandaises sont cartographiées. Leurs centres de distribution et les vicariances sont analysés. Les deux genres montrent leur plus grande différenciation dans les montagnes de l'Île du Sud, où se trouvent 33 des 36 espèces. Les centres d'endémisme et les barrières de répartition se rencontrent à Fiordland, Otago Centrale, Nelson, Marlborough et le long des Alpes du Sud. Le complexe *Hebe* a probablement subi une phase majeure de modernisation et de développement vicariant pendant le Mésozoïque, plutôt qu'une récente dispersion sur des longues distances à partir de l'hemisphère nord.

ABSTRACT

HEADS, M. J. (1994). Biogeography and evolution in the Hebe complex (Scrophulariaceae): Leonohebe and Chionohebe. *Candollea* 49: 81-119. In English, French and English abstracts.

Distributions of the five species of *Chionohebe* and the 31 species of *Leonohebe* are mapped and analysed with respect to patterns of geographic massing and vicariance. The two genera show their greatest differentiation in the mountains of South Island, New Zealand, with 33 out of 36 species present there. Centres of endemism and breaks in distribution occur in Fiordland, central Otago, Nelson, Marlborough and along the Southern Alps. It is concluded that the *Hebe* complex underwent a major phase of modernisation and vicariant form-making during the Mesozoic, rather than following recent long-distance dispersal from the northern hemisphere.

KEY-WORDS: Biogeography — Evolution — *Chionohebe* — *Leonohebe* — *SCROPHULARIACEAE* — New Zealand.

1. Biogeographic Affinities of the New Zealand Digitaleae

The tribe Digitaleae is one of the most diverse groups of flowering plants in New Zealand, where it is represented by a group of related genera referred to here for convenience as the *Hebe* complex (HEADS, 1992, 1993a,b).

As an introduction to the more detailed biogeography of the *Hebe* complex, some of its broader geographic affinities can be considered. HOOKER (1864) described *Veronica sensu lato* (including the *Hebe* complex) as "A very large European, Oriental and New Zealand genus, comparatively rare in other parts of the globe. In New Zealand it forms a more conspicuous feature of the vegetation than in any other country, both from the number, beauty and ubiquity of the species, from so many forming large bushes, and from the remarkable forms the genus presents. The species ... present numerous intermediate forms between many more distinct-looking ones [and] vary extremely in all their organs ..." Despite changing taxonomy, notably the elevation of several groups to

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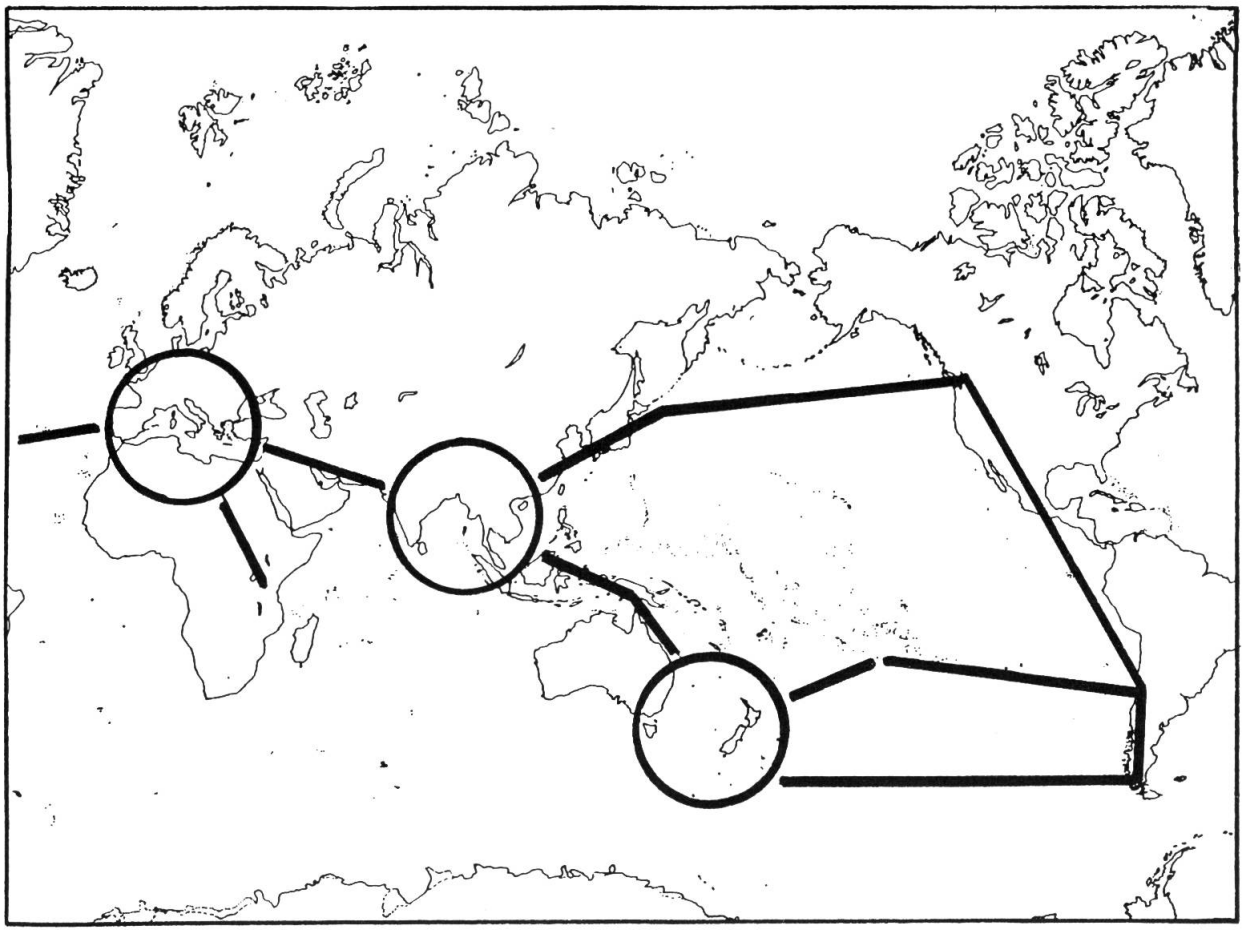

Fig. 1. — Some affinities of the New Zealand Scrophulariaceae, showing Hooker's three centres for *Veronica*, plus other tracks of this and allied genera.

generic rank, HOOKER's statement remains an accurate biogeographic summary — New Zealand is indeed a most "conspicuous" centre, both of species and "remarkable forms", in a biogeographic track: New Zealand — Orient — Europe (Fig. 1). This distribution pattern is standard for many organisms and has been related to biological evolution having taken place along the coasts of the Mesozoic Tethys Seas (CROIZAT, 1968a, b). Along this track HONG (1984) emphasized Australasia and South Asia as the two main centres of frequency and diversity for the tribe Veroniceae.

The *Hebe* complex includes the genera *Hebe*, *Chionohebe*, *Parahebe* and *Leonohebe*, and *Ourisia* is also related. All but the last were formerly placed in *Veronica*.

Veronica L. is currently recognised as a largely northern hemisphere genus, ranging with some 300 species in Australasia, Eurasia, Africa and North America. There are only about 15 species in Australasia and possibly none indigenous to New Zealand (but see KIRK, 1896; CHEESEMAN, 1925, and OLIVER, 1944). The main massing of *Veronica* is thus largely vicariant with the southern *Hebe* complex, and the two groups are clearly allied, for example, through members of *Parahebe*.

The genera of the *Hebe* complex range overall from an Antarctic Pacific baseline: Auckland Islands/Campbell Islands — Patagonia/Falkland Islands, north to southern Ecuador (*Ourisia* only), and through New Zealand, New Guinea, Tasmania and southeast Australia. *Hebe rapensis* is known only from Rapa Island, in the Tubuai (= Austral) Islands. (Fig. 2 shows the range of all the genera except *Ourisia*). *Detzneria* Schlechter ex Diels 1929, endemic to mountains of New Guinea (VAN ROYEN, 1983) is distinctive, but clearly allied with the *Hebe* complex (cf. HONG, 1984). This monotype is a shrub with large, dark blue or reddish-blue flowers reported as cleistogamic by SMITH (1982), and with a 5-merous calyx and corolla.

Ourisia is usually placed in Digitaleae, but may have no special affinity with the *Hebe* complex. Authors such as BENTHAM (1835) have placed *Ourisia* with *Sibthorpia*, a genus of Africa, the Mediterranean and Central and South America (CROIZAT, 1967: 125), and CROIZAT (1968a: 105) noted that the two genera "would vicariate [geographically] well enough". HEDBERG (1955) saw the closest ally of *Sibthorpia* in the monotypic *Ellisiophyllum* of India, Japan, Taiwan, Philippines and east New Guinea (AIRY SHAW, 1973). *Ellisiophyllum* in turn has at times been placed under *Ourisia* (noted by OHWI, 1965) and is treated as a genus of Tribe Veroniceae s.str. by authors such as TSOONG (1979). The species is currently generally treated as a family Ellisiophyllaceae Honda, showing affinities with Scrophulariaceae (BACKER, 1951), Hydrophyllaceae and *Littorella* (Plantaginaceae) (BAILLON, 1890). AIRY SHAW (1973) regards Ellisiophyllaceae as "intermediate between Scrophulariaceae, Hydrophyllaceae, Polemoniaceae and Primulaceae. YAMAZAKI (1957b) gives details of the very interesting embryology. Other affinities between Scrophulariaceae and Hydrophyllaceae undoubtedly exist. For example, on the other side of the Pacific *Ourisia californica* Bentham of California has been placed in *Hesperochiron* of Hydrophyllaceae (BENTHAM & HOOKER, 1876).

The broader affinities of the *Hebe* complex are unclear, but some interesting suggestions have been made. BENTHAM (1846) placed *Veronica* s.l. and *Ourisia* together with *Aragoa*, the latter comprising five species of conifer-like shrubs of the Colombian and Venezuelan Andes (PENNELL, 1937). BENTHAM (1846) and BENTHAM & HOOKER (1876) regarded *Aragoa* as closely and strongly related to *Veronica* sect. *Hebe*, and *Aragoa* was also aligned with *Hebe* s.l. by BAILLON (1888). This affinity requires investigation but the habit characters at least appear to show a trans-Pacific connection, a pattern already known within *Hebe* s.s., *Ourisia*, and other genera in the family. Like *Leonohebe*, *Aragoa* is phylogenetically rather marginal to the bulk of Scrophulariaceae. DON (1836) treated *Aragoa* as a monogeneric family placed, like *Ellisiophyllum*, between Scrophulariaceae and Polemoniaceae, while HONG (1984) treated *Aragoa* in a monogeneric tribe of Scrophulariaceae.

Further allies of the *Hebe* complex were given by BAILLON (1888), who proposed the following sequence in his Digitaleae: *Lafuentea* (2 species of Spain and Morocco), *Ourisia* (South Pacific), *Scoparia* (20 species of tropical America), *Capraria* (4 species of warm America and the West Indies), *Oftia* (2 species of South Africa, often treated in Myoporaceae), *Hemiphragma* (monospecific: western Himalayas — Assam), *Sibthorpia* (5 species of Africa, the Mediterranean, central and South America, map in CROIZAT, 1968b), *Veronica* s.l. (incl. *Hebe* etc.) and *Aragoa*.

WETTSTEIN (1891) placed *Ourisia* with *Lafuentea* (Spain and Morocco) and *Oreosolen* (3 species of Tibet/Himalayas). Also from Tethyan sectors are *Picrorhiza* Royle ex Bentham and *Neopicrorhiza* Hong, two monotypic genera of the western and eastern Himalayas respectively both treated in Veroniceae by HONG (1984).

YAMAZAKI (1957a) and HONG (1984) considered *Veronica* s.str. to be related to *Besseya* (7 species of North America, mainly in the Rocky Mts.) and *Synthyris* (9 species of the mountains of western North America). Clear connections in the far North Pacific are displayed by *Veronicastrum*, a relative of *Veronica* with one species in Afghanistan, China, Taiwan, northeast Asia and one in northeast North America (HONG, 1984; AIRY SHAW, 1973).

Put together, these affinities result in a complete Pacific circuit (Fig. 1), and a Tethys track: New Zealand — Mediterranean — Caribbean. The Pacific circuit is well-known in many plants, for example *Gaultheria* (Ericaceae). The sector: southwest Pacific — Chile — Colombia — western U.S.A., is discussed by CHIN *et al.* (1991) and shown to be a distribution pattern equally important for plants of land and sea. Tethys tracks have been described in many plant and animal groups by CROIZAT (1968a, b).

These biogeographic observations support HONG's (1984) conclusion that "the *Hebe* group must not be considered the derivative of *Veronica*, it has its own developmental history based on a different geographical, morphological and chromosomal background from that of *Veronica*." In fact many of the genera referred to above are geographic and phylogenetic vicariants of each other, and have probably differentiated from a common ancestor.

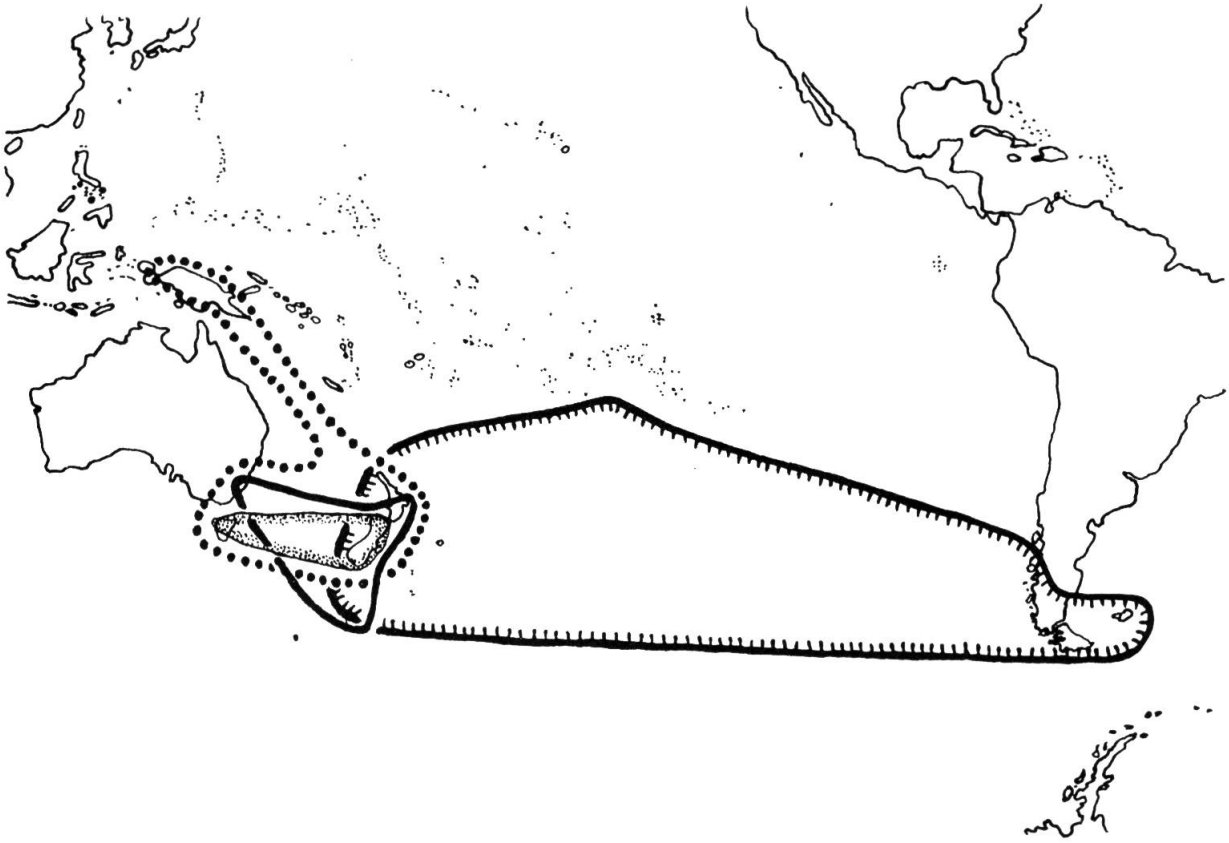

Fig. 2. — Hatched line: *Hebe*. Solid line: *Leonohebe*. Dotted line: *Parahebe*. Stippled line: *Chionohebe*.

2. Distribution of the Hebe complex in and around New Zealand

CHEESEMAN (1925) summed up what he called the "peculiar" distribution of the species of *Veronica* s.l. within New Zealand: "Twenty-one are confined to the North Island, and no less than 61 to the South Island, while only twelve species are found in both Islands. Five are endemic in the Chatham Islands, 2 in the Auckland and Campbell Islands, and 1 in the Kermadec Islands." South Island is thus a main centre in this pattern, and details for *Chionohebe* and *Leonohebe* are given below. The distribution patterns seen in the group are not really "peculiar" as CHEESEMAN suggested, but rather recur in many taxa, such as *Coprosma* (Rubiaceae) and *Nothofagus* (Fagaceae) (HEADS, 1989).

Chionohebe occupies a southern Tasman Sea range: Tasmania — South Is. *Leonohebe* encloses this, being present at Auckland Is. — Campbell Is. — Stewart Is. — South Is. — southern North Is. — southeast Australia, and notably absent along an arc: Chatham Is. — northern North Is. — Three Kings Is. (Fig. 2). In these two genera there is a concentration of forms at what are to-day inland (and often alpine) localities (Fig. 3). In contrast with *Leonohebe* and *Chionohebe*, the main massing of the comparatively homogeneous *Hebe* lies further east, the group ranging: Auckland Is. — Campbell Is. — Chatham Is. — New Zealand — Three Kings Is. — Kermadec Is. — Rapa Is. — southern South America/Falkland Is. *Parahebe* is recognised here from southeast Australia and Tasmania, but is most diverse in New Zealand and New Guinea, biogeographically intermediate between the western *Chionohebe* and *Leonohebe*, and the eastern *Hebe*. *Ourisia* is a classic Antarctic Pacific group, ranging in Australasia and southern South America. Thus the overall pattern in the *Hebe* complex (Fig. 2) is largely one of vicariance among the genera, the pattern resembling that found, for example, among the subgenera of *Astelia* (Liliaceae) (GOOD, 1974, Fig. 50). There

is some geographic overlap, largely restricted to within the New Zealand region, but within that region the genera have concentrations of diversity in very different regions, for example *Leonohebe* in the southwest (Fig. 3), *Hebe* in the north of South Is. (HEADS, 1993a).

3. Chronology of differentiation

According to one traditional view, groups such as the *Hebe* complex have been derived from the northern hemisphere in relatively recent times — Tertiary or even Quaternary — with even more recent spread eastwards from Australia to New Zealand (RAVEN, 1972; RAVEN & AXELROD, 1972; FLEMING, 1979). This interpretation continues to cause considerable debate (for example, the articles in MATTHEWS, 1989) and over the years has been questioned repeatedly. For example, BROWN (1935) recognised affinities between the Rapa Island endemic *Hebe rapensis* (Brown) Garnock-Jones, and Chatham Is. forms of *Hebe*. BROWN was also aware that "The distribution of sect. *Hebe* is remarkably like that of *Nothofagus*", and rather than invoking the usual "chance dispersal" concluded that: "*Hebe* is a primitive group with a history in Polynesia probably dating as far back as the Cretaceous". This chronology was supported by MELVILLE (1966), who observed that: "The separation of the New Zealand block from the Chilean fragments of South America was late enough ["end of the Cretaceous or Paleocene"] to account for the identity of the small number of *Hebe* species in the latter area with their New Zealand congeners." Ties between Australasia and South America are also shown by *Jovellana*, *Ourisia*, and *Euphrasia* as well as other Scrophulariaceae, and these are all accepted here as being derived from Mesozoic patterns. BARKER (1982) accepted similar chronology for distribution patterns in *Euphrasia*, and likewise HONG (1984) suggested that Veroniceae may have existed "before the break-up of communications between Australasia, Antarctica and South America". HONG, like BROWN (1935) also noted that "the present distribution of the *Hebe* complex is in detail comparable with *Nothofagus*," and this is certainly true. For example, within the New Zealand region similar pull-apart disjunctions occur in *Hebe*, *Leonohebe*, *Nothofagus* and *Coprosma* along a geological transform, the Alpine Fault Zone (HEADS, 1989). This indicates distribution patterns which predate massive upper Tertiary movement on the Fault Zone. Together with the New Zealand — South America patterns and Tasman Sea patterns, both correlating with patterns within New Zealand, this indicates a Mesozoic history of the group in the South Pacific.

4. Ecology

New Zealand members of Digitaleae are found from sea-level through to the upper limit of seed-plants in the Southern Alps. For example, *Hebe chathamica* grows on maritime cliffs where there is a maximum of spray (MOORE, 1961), while *Parahebe birleyi* and *Leonohebe haastii* occur at the highest altitudes attained by seed-plants in New Zealand: 2930 m, at Mt. Cook (MARK & ADAMS, 1973). In New Zealand *Veronica* s.l. CHEESEMAN (1925) referred to thirteen species never seen far from the sea, fourteen purely lowland species, and fifty nine purely montane or alpine species. Altitudinal range of taxa is interpreted here largely as a direct function of geological processes such as uplift, downwarping and erosion (HEADS, 1989). The distribution of *Hebe* and *Leonohebe* and the east-west vicariance between the genera, or their immediate ancestors, in the southwest Pacific (or their immediate ancestors) is Cretaceous or earlier in age (see last section) and the east-west vicariance within the New Zealand region is probably of similar age. The prior western biogeography of *Leonohebe* and *Chionohebe* meant that these genera were more caught up in the Kaikoura orogeny mountains than was *Hebe*, and their small "leaved" shrub habit, discussed in HEADS (1993b), accounts for their survival there. The morphogenetic history of *Leonohebe* and *Chionohebe* meant that they were pre-adapted to high stress environments in both drier and wetter mountains.

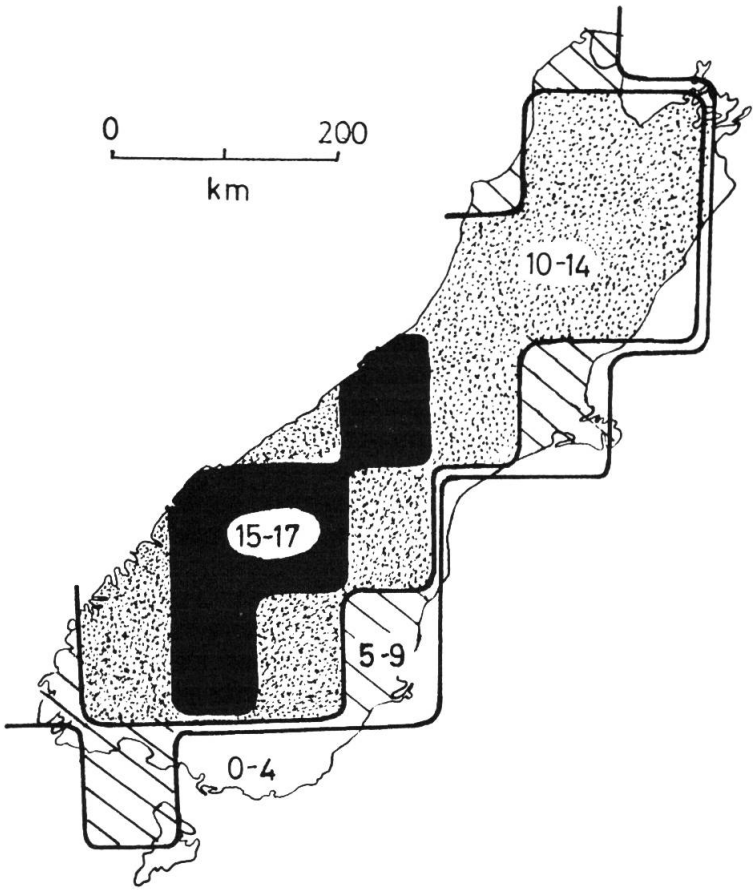

Fig. 3. — Map showing number of species of *Chionohebe* and *Leonohebe* in each degree square in South Is.

Throughout their altitudinal and geographic range most of the New Zealand Digitaleae grow in open sites. Comparatively few species are found in forest (*Hebe vernicosa*, *H. canterburiensis*, *H. corriganii*, *H. salicifolia*, *Leonohebe odora* (rarely), the *Parahebe catarractae* complex, *P. decora* and *Ourisia macrophylla*). Most of the species favour rocky sites and act as pioneer weeds on the bare rock outcrops of coastal and alpine cliffs, rocky gorges, road cuttings, and especially the vast areas of bare rock in the mountains (MOORE, 1975; pers. obs.). Some members of New Zealand Digitaleae are characteristic of peaty or swampy sites, both at low altitude (*Hebe salicifolia* var. *paludosa* by coastal swamps and lagoons, *H. gracillima*) and at high altitude (*Parahebe trifida*, *Chionohebe glabra*).

Leonohebe and *Hebe* dominate many of the shrublands of New Zealand, from the *Hebe elliptica* shrublands of southern coasts through to the subalpine "*Hebe* shrublands" of COCKAYNE (1958: 274). These shrublands are often ecotonal, occupying the forest-grassland margin, and some have a particularly diverse biota.

Although wild hybrids appear to be uncommon in the *Hebe* complex, many have appeared in gardens. Present patterns of differentiation in the group as a whole may well represent the vicariant derivatives of hybrid swarms formed and "frozen" in place during phases of evolution and hybridisation in the Mesozoic (HEADS, 1989; 1990b; 1993a, b). The ancestral potential to hybridise has been suppressed, but only superficially, and is released in cultivation. The weedy, pioneer ecology of these plants and their potential ability to hybridise occur, in an apparent paradox, with highly precise biogeographic patterns articulated by standard centres of endemism and disjunctions. These patterns are shared with other groups which have excellent means of dispersal, such as Compositae (HEADS, 1989). It appears that these patterns were established in their main outlines in ancestral

forms at the time of major tectonic disturbances in the Mesozoic. How such precise patterns are maintained for so long is not really understood. A field study of ecological relationships between biogeographic vicariants, even a distribution map of plants at a boundary, would be of great value.

5. Panbiogeographic treatment: concepts and terms

The species of *Chionohebe* and *Leonohebe* (Table 1) are mapped below and their distributions analysed below with respect to vicariance. Vicariance, or the structural relationship of replacement or representation of forms or taxa, may be by main massing, with some secondary overlap (e.g. *Leonohebe* and *Hebe*, Figs. 2 and 3), or it may be very precise (e.g. *Leonohebe* spp., Fig. 14). Vicariance takes place at or by nodes. These are points or regions where taxa or characters show geographic breaks in distribution, endemism, notable absence, and/or diverse, disjunct geographic affinities (HEADS, 1989; HENDERSON, 1991). Series of nodes are termed tracks. The nodes shown by *Leonohebe* and *Chionohebe* are nearly all in South Is., New Zealand, and these are mapped in Fig. 4. (In this preliminary analysis no attempt has been made to quantify the relative importance of the different nodes). Vicariance may be geographic, chronological, phylogenetic, ecological or any combination of these. The principle of vicariance means that a taxon, character, or any biological phenomenon, may be technically absent as such, but may be represented by a related group or phenomenon. Vicariant patterns are not due to invasion, or lack of it, by one of a series of taxa, but to *in situ* differentiation of descendants out of an ancestral complex which was always already widespread and differentiated.

In panbiogeographic analysis the distribution of a form, whether past or present, takes on a special significance. In discussion of terrestrial forms it may seem strange to refer, for example, to the triangle: Ben Lomond (Tasmania) — Fiordland (New Zealand) — Nelson (New Zealand), when virtually all of this region is currently sea. However, such a geographic taxon is a natural area, exemplified by the range of a taxon such as *Chionohebe ciliolata*. The main problem here is not one of ecology, for example whether a group is terrestrial or marine, but a general problem of how and why these three points relate in biogeography and tectonics, and, conversely, why the current "New Zealand" and "Australia" are of such little importance in this and other distribution patterns. Such patterns, whether "eroded" or "expanded", are usually relictual and related to Mesozoic tectonic disturbance initiating phases of biological modernisation.

The maps provided here show semi-generalised outlines only, except where there are very few records. In the latter case all localities are shown, connected by "tracks" which are not joined to enclose any area with further records. For ease of reference, collection localities are generally referred to mountain ranges, rather than to individual peaks. At a higher level of resolution different sectors of many of these ranges will prove to have different biotas, for example the northern and southern ends of the Dunstan Mts. (M. Heads and B. Patrick, field obs.).

Distribution records were obtained from my own field observations and collections, the collections at OTA, CHR and AK, data communicated personally by Dr. A. F. Mark, Dr. P. Johnson, Mr. A. P. Druce and Mr. B. Patrick, and a survey of the many published records.

Chionohebe Briggs & Ehrendorfer (1976: 1)

Distribution. — AUSTRALIA: Tasmania (one species shared with New Zealand). NEW ZEALAND: South Island (five species).

The massing of the genus is clearly in the southern sector of South Island, where one species is western, one is northeastern, and the three remaining species divide up central Otago about a point near Pisa Ra.

The species are characteristic of alpine, rocky areas such as fellfield, ridges and outcrops, and often contribute to areas of "cushion vegetation". One species, *C. glabra*, is restricted to more permanently wet sites.

1. *Chionohebe* 1. *C. ciliolata*, 2. *C. pulvinaris*, 3. *C. thomsonii*, 4. *C. glabra*,5. *C. myosotoides*.

2. *Leonohebe*

Sect. *Densifoliae*: 1. *L. densifolia*, 2. *L. uniflora*.

Sect. *Leonohebe*: 3. *L. ciliolata*, 4. *L. tetrasticha*, 5. *L. cheesemanii*, 6. *L. tumida*.

Sect. *Connatae*: 7. *L. epacridea*, 8. *L. haastii*, 9. *L. ramosissima*, 10. *L. petriei*.

Sect. *Apiti*: 11. *L. benthamii*

Sect. *Salicornioides*: 12. *L. annulata*, 13. *L. salicornioides*, 14. *L. armstrongii*, 15. *L. ochracea*

Sect. *Aromaticae*: 16. *L. cupressoides*

Sect. *Flagriformes*: 17. *L. laingii*, 18. *L. hectorii*, 19. *L. coarctata*, 20. *L. subsimilis*, 21. *L. tetragona*, 22. *L. imbricata*, 23. *L. propinqua*, 24. *L. poppelwellii*, 25. *L. subulata*, 26. *L. lycopodioides*.

Sect. *Buxifoliatae*: 27. *L. pauciflora*, 28. *L. odora*, 29. *L. anomala*, 30. *L. mooreae*, 31. *L. pauciramosa*, 32. *L. masoniae*.

Table 1. Synopsis of *Chionohebe* and *Leonohebe*.

1. Chionohebe ciliolata (Hook. f.) Briggs & Ehrendorfer (1976: 2). (Fig. 5).
Pygmea ciliolata Hook. f. (1864: 217).

Recorded from lands bordering the south Tasman Sea: Tasmania (Ben Lomond) — Fiordland — northwest Nelson. The Tasmania — Fiordland populations (comprising *C. ciliolata* var. *fiordensis* Ashwin) seem most closely related to each other. Two other geographic varieties in South Is., one central (var. *ciliolata*), and one northern (var. *pumila*) were described by ASHWIN (1961), but none of the three appear to be clear-cut. The species is replaced on and east of a line: Mt. Alta — Arthur's Pass — St. Arnaud Ra. by *C. pulvinaris* (the pattern in NW Nelson is complex). In the south the species is replaced on and east of a line: Garvie Mts. — Eyre Mts. — Humboldt Mts. — Matukituki V. (by Mt. Aspiring) — Wilkin V. by *C. thomsonii*, *C. glabra* and *C. myosotoides*.

Here, as in many other groups, the taxa relate western South Island more closely to southeastern Australia than to eastern South Island. The Cretaceous opening of the Tasman Sea has apparently disrupted a prior pattern, which must be Cretaceous or earlier in origin. The eastern boundary of the species in the south, and possibly the boundary with the next species are related geographically and possibly by origin to the Moonlight Tectonic Zone (HEADS, 1989).

2. Chionohebe pulvinaris (Hook. f.) Briggs & Ehrendorfer (1976: 2) (Fig. 5).
Pygmea pulvinaris Hook. f. (1864: 217).

This ranges from Mt. Alta — Arthur's Pass — St. Arnaud Ra., eastwards to Rock and Pillar Ra. — Mt. Torlesse — Tapuaenuku (Inland Kaikoura Ra.), being an eastern vicariant of *C. ciliolata* and a northern vicariant of the Otago species (*C. thomsonii, C. glabra* and *C. myosotoides* — Fig. 6). The notable gaps in range between *C. pulvinaris* populations at Rock and Pillar and at Mt. Alta, and between these populations and *C. ciliolata* at Eyre Mts./ Garvie Mts. are filled by the three following central Otago species.

3. Chionohebe thomsonii (Buchanan) Briggs & Ehrendorfer (1976: 2) (Fig. 6).
Pygmea thomsonii Buchanan (1882: 353).

Known from the arc: Umbrella Mts. — Eyre Mts. — Humboldt Mts. — Wilkin Valley — Ben Ohau Ra. — Benmore Ra. — Mt. Pisgah (Kakanui Ra.), and notably absent from: Pisa Ra. — Rock and Pillar Ra., where it is replaced by *C. myosotoides*.

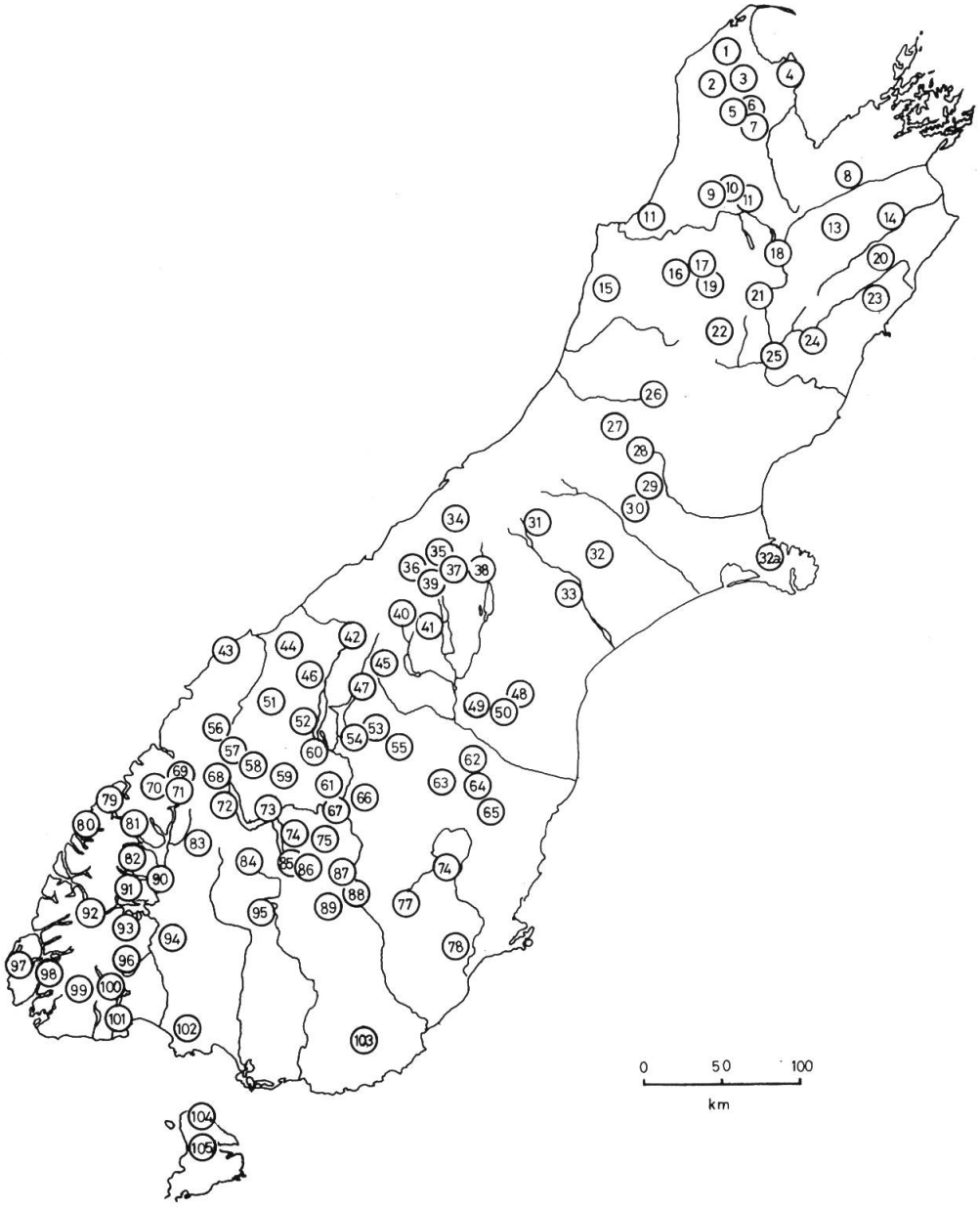

Fig. 4. — Locality map of the nodes in South Island displayed by *Chionohebe* and *Leonohebe*.
1, Wakamarama Ra.; **2,** Anatoki; **3,** Gouland Downs; **4,** Abel Tasman National Park; **5,** Mt. Peel; **6,** Cobb V.; **7,** Mt. Arthur; **8,** Richmond Ra.; **9,** Matiri Ra.; **10,** Mt. Owen; **11,** Denniston Plateau; **12,** Hope Ra.; **13,** Mt. Bounds; **14,** Altimarlock and Black Birch Ra.; **15,** Paparoa Ra.; **16,** Victoria Ra.; **17,** Mt. Mantell; **18,** St. Arnaud Ra.; **19,** Glenroy V.; **20,** Tapuaenuku (Inland Kaikoura Ra.); **21,** L. Tennyson; **22,** Lewis Pass; **23,** Seaward Kaikoura Ra.; **24,** Mt. Terako; **25,** Hanmer; **26,** Harper's Pass; **27,** Arthur's Pass; **28,** Cass; **29,** Torlesse Ra.; **30,** Big Ben Ra.; **31,** Arrowsmith Ra.; **32,** Mt. Somers; **33,** Mt. Peel; **34,** Waikukupa Ra.; **35,** Mt. Cook; **36,** Douglas Ra.; **37,** Liebig Ra.; **38,** Godley Valley; **39,** Sebastopol; **40,** Hopkins R.; **41,** Ben Ohau Ra.; **42,** Mt. Brewster; **43,** Cascade R.; **44,** Selbourne Ra.; **45,** Ahuriri R.; **46,** Wilkin V.; **47,** Mt. Arnould; **48,** Hunter's Hills; **49,** Benmore Ra.; **50,** Kirkliston Ra.; **51,** Mt. Aspiring; **52,** Mt. Alta; **53,** Lindis Pass; **54,** Mt. Grandview; **55,** St. Bathans Ra.; **56,** Olivine R.; **57,** Forbes Mts.; **58,** Richardson Mts.; **59,** Harris Mts.; **60,** Mt. Roy; **61,** Pisa Ra.; **62,** St. Mary's Ra.; **63,** Mt. Ida Ra.; **64,** Dansey Pass; **65,** Kakanui Mts.; **66,** Dunstan Mts.; **67,** Cromwell; **68,** Humboldt Mts.; **69,** Homer Saddle; **70,** MacKinnon Pass; **71,** Dore Pass; **72,** Greenstone V.; **73,** Queenstown; **74,** The Remarkables; **75,** Carrick Ra.; **76,** Rock and Pillar Ra.; **77,** Lammerlaw Ra.; **78,** Maungatua; **79,** George Sound; **80,** Caswell Sound; **81,** Lake Hankinson; **82,** Murchison Mts.; **83,** Livingstone Mts.; **84,** Eyre Mts.; **85,** Hector Mts.; **86,** Garvie Mts.; **87,** Old Man Ra.; **88,** Roxburgh; **89,** Umbrella Mts.; **90,** Lake Te Anau; **91,** Kepler Mts.; **92,** Wilmot Pass; **93,** Hunter Mts.; **94,** Takitimu Ra.; **95,** Mid Dome; **96,** Green Lake; **97,** Dusky Sound; **98,** Lake Mike; **99,** Cameron Mts.; **100,** Lake Hauroko; **101,** Hump Ridge; **102,** Longwood Ra.; **103,** Mt. Pye; **104,** Mt. Anglem; **105,** Mt. Rakeahua.

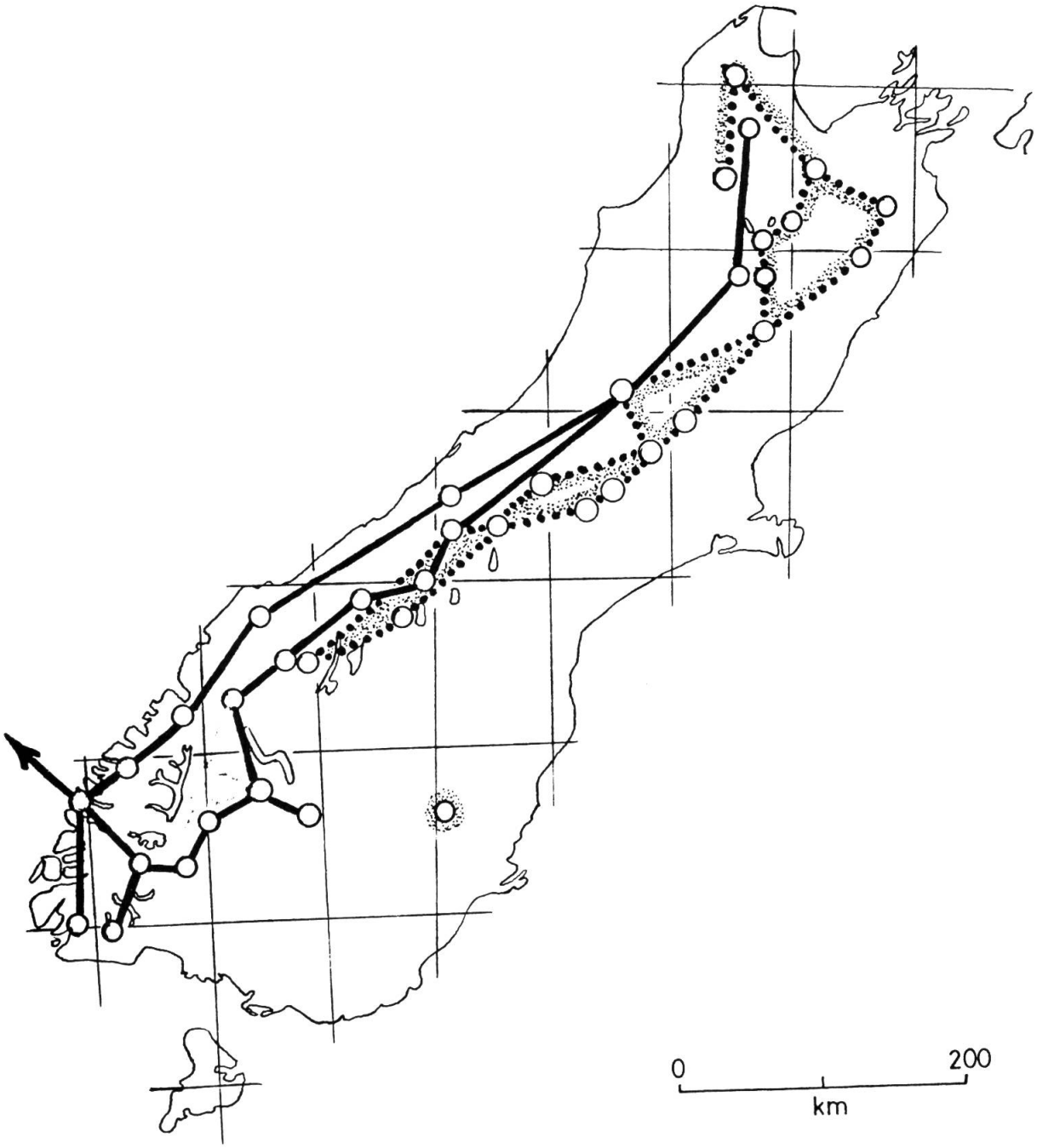

Fig. 5. — *Chionohebe ciliolata*: continuous line, plus Ben Lomond, Tasmania; *C. pulvinaris*: dotted stippled line.

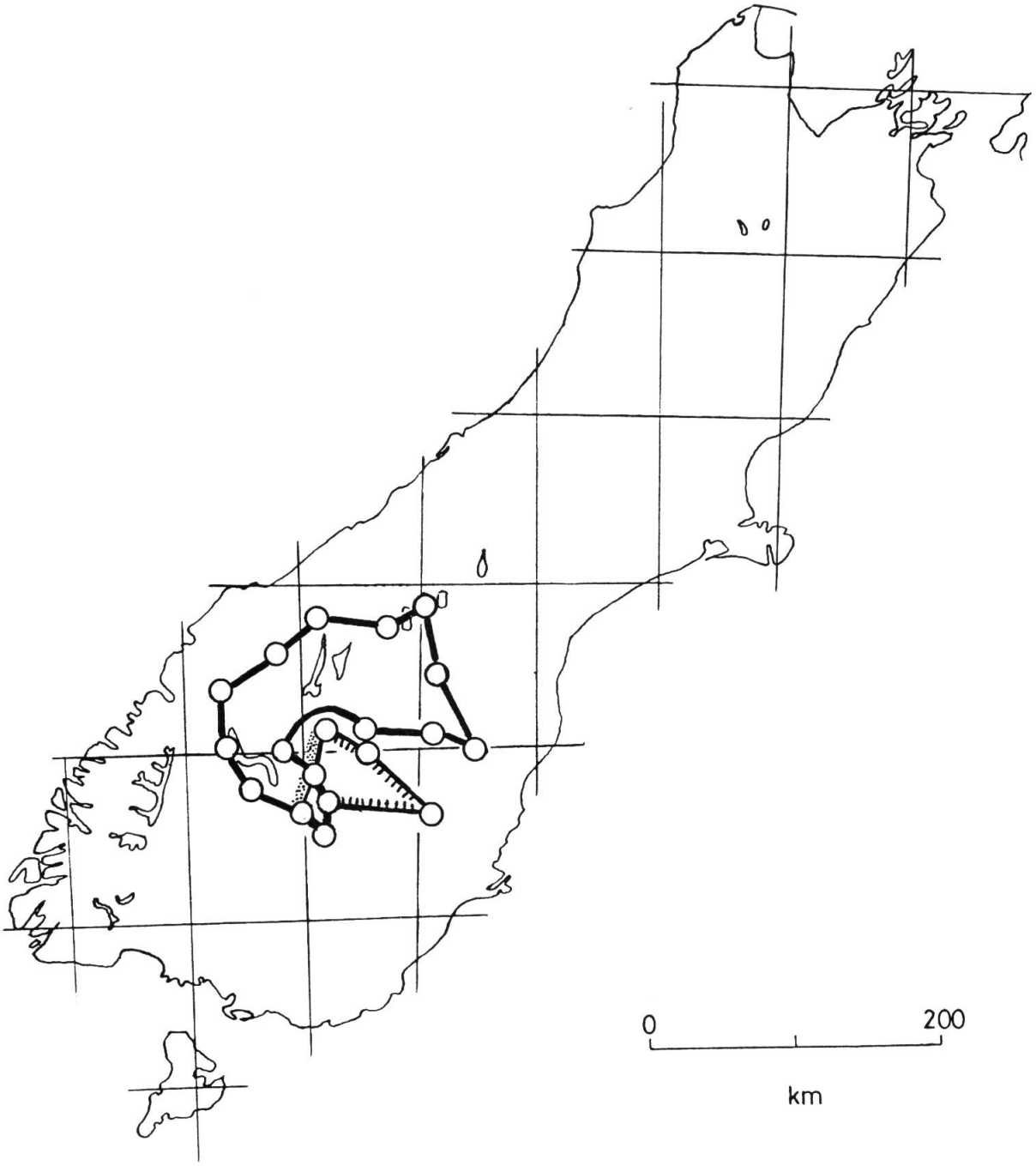

Fig. 6. — *Chionohebe thomsonii*: continuous line; *Chionohebe glabra*: stippled line; *C. myosotoides*: hatched line.

4. Chionohebe glabra (Cheesem.) Heads (1987: 4). (Fig. 6).
Veronica thomsonii var. *glabra* Cheeseman (1906: 540).

Known only from Garvie Mts. — Carrick Ra. — Pisa Ra., growing at 1500 — 1800 m in moist sites in snowbanks (cf. MARK & BLISS, 1970). The plants are very distinctive, both morphologically and ecologically. ASHWIN (*in litt.* 31.iii.1965, held at OTA) noted the affinities of these plants with *C. myosotoides*.

5. Chionohebe myosotoides (Ashwin) Briggs & Ehrendorfer (1976: 2). (Fig. 6).
Pygmea myosotoides Ashwin (1961: 975).

Recorded from: Pisa Ra. — Dunstan Ra. — Old Man Ra. — Rock and Pillar Ra. The species is accepted here for distinct populations with abaxial leaf pubescence as dense as or denser than adaxial pubescence. On both surfaces pubescence reaches only halfway down the leaf from the apex. Occasional plants with only sparse hairs indicate a close relationship with *C. glabra*.

The last three species illustrate a common pattern of central Otago endemism, being confined to the greater central Otago region: Umbrella Mts. — Eyre Mts. — Humboldt Mts. — Wilkin V. — Ben Ohau Ra. — Benmore Ra. — Mt Pisgah (Kakanui Ra.) — Rock and Pillar Ra. The three species divide the area up into three sectors, centred on Pisa Ra. by the town of Cromwell, with two forms highlighting the southeastern region: Pisa Ra. — Garvie Mts./Old Man Ra. — Rock and Pillar Ra. In accounting for this distribution, the history and influence of inland Tertiary seas should be considered as well as Mesozoic tectonics and palaeogeography.

Leonohebe Heads (1987: 4)

Distribution (Fig. 2). — AUSTRALIA: Mt. Kosciusko and Munyong Mts. (1 species, shared with South Island, New Zealand). NEW ZEALAND: Auckland Is. (2 species, 1 shared with Campbell Is.); Campbell Is. (1 species); Stewart Is. (3 species, all shared with South Is.); South Is. (c. 30 species), North Is. (3 species, 1 shared with South Is., north to Taranaki — Tongariro — Hikurangi).

Habitats range from marshes to cliffs, and from southern coasts to 2930 m altitude.

Accurate distribution maps of several *Leonohebe* and *Hebe* species in Canterbury were given by MACDONALD (1980, 1981, 1982).

Leonohebe sect. *Densifoliae* Heads (1987: 4)

Rock-dwelling plants found on ledges, in crevices, and in rockfields. AUSTRALIA: Mt. Kosciusko (SE New South Wales) and Munyong Mts. (Victoria). NEW ZEALAND: southern South Island.

Any collections of this section or sect. *Leonohebe* from between St. Bathan's Ra. and Hopkins Valley would be particularly interesting.

1. Leonohebe densifolia (F. Muell.) Heads (1987: 4) (Fig. 7).
Chionohebe densifolia (F. Muell.) Briggs & Ehrendorfer (1976: 2).
Pygmea tetragona (Hook. f.) Ashwin (1961: 874).
Veronica dasyphylla Kirk (1896: 519).

The New Zealand range of the species is a good example of central Otago distribution, being bounded by: Rock and Pillar Ra. — Lammerlaw Ra. — Mid Dome — Eyre Mts. — Humboldt Mts. — Wilkin V. — Kirkliston Ra. — Mt Pisgah (Kakanui Mts.). In the western part of its range the species occupies southeast Australia (Mt. Kosciusko and Munyong Mts.), thus almost duplicating the trans-Tasman track of *Chionohebe ciliolata* (South Is. — Tasmania). Such a track is

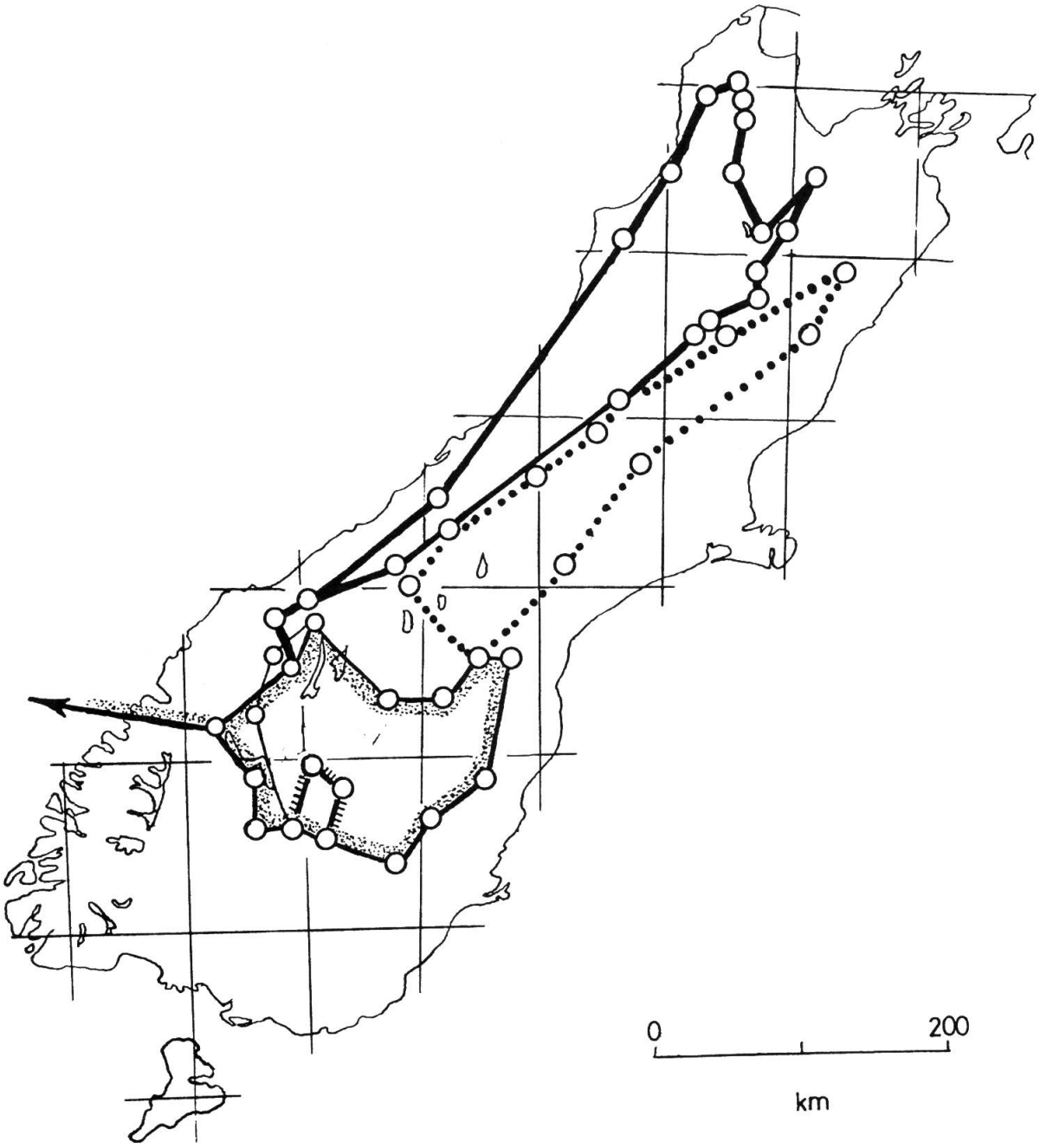

Fig. 7. — *Leonohebe densifolia*: stippled line, plus Mt. Kosciusko, glabrous calyx populations: hatched line; *L. uniflora*: fine line; *L. ciliolata*: thick continuous line; *L. tetrasticha*: dotted line.

unknown within species of *Parahebe* and *Hebe*, both more typical genera of Scrophulariaceae. Unlike *Chionohebe ciliolata*, *L. densifolia* and sect. *Densifoliae* are notably absent from Fiordland west of the Median Tectonic Line, and from Tasmania. To the south, a possible vicariant on the Takitimu Ra. is represented by an undescribed species close to *Parahebe trifida* (*Mark* 2.ii.1971, OTA, Excelsior Peak).

This range of *L. densifolia* is similar to that of the central Otago species of *Chionohebe* (above), for example Mt. Alta plays a similar role as node in the two groups.

Differentiation within *L. densifolia* requires study, as more than one entity is involved. *Veronica dasyphylla* var. *subacuta* Simpson & Thomson 1942 is recorded from Eyre Mts., Old Man Ra. and Rock and Pillar Ra., while *V. dasyphylla* var. *minor* Simpson & Thomson 1942 was described from Mt. St. Mary Ra. Trifid-leaved populations are known at two localities: upper Lauder Creek, northern Dunstan Mts. (*Mark* 10.ii.1985, OTA, all leaves trifid), and St. Bathans Ra. (*Mark* 25.ii.1964, OTA — calyx pubescence long and eglandular, leaves very long ciliate and occasionally trifid). *Baylis* (OTA) The Crater, Kakanui Mts., has pieces with small, rounded leaves bearing a rim of inward turned hairs apically and adaxially. All these forms have a pubescent, sometimes glandular-pubescent calyx.

Plants with the calyx broad and glabrous except for marginal hairs are known from southern localities: Old Man Ra., Carrick Ra., Garvie Mts. and Umbrella Mts. *Rance & Dickinson* 10.xi.1985 (OTA), Umbrella Mts., with a glabrous calyx, is notable through its bright blue corolla. Collections from Richardson Mts. (*Mark* 4.xii.1967, OTA) and Old Man Ra. (*Mark* 30.xii.1964, OTA) also have the surface of the calyx lobes glabrous, but are small-leaved cushion plants. The distribution of plants with glabrous calyces is mapped in Fig. 7.

2. Leonohebe uniflora (Kirk) Heads (1987: 5). (Fig. 7).
Pygmea armstrongii (Buchan.) Ashwin (1961: 875).

This poorly understood form is recorded only along the arc: Garvie Mts. — Hector's Col (by Mt. Aspiring) — Mt. Turner (Wilkin V.). It has the phyllotaxis and corolla shape of *L. densifolia*, and the species has been considered to be a simple hybrid between *L. densifolia* and one of the species of *Chionohebe*. However, as MARK & ADAMS (1973) and GIVEN (1981) point out, the range of *L. uniflora* extends further west than that of *L. densifolia*, notably at Hector's Col.

Leonohebe sect. *Leonohebe*

This section vicariates to the north of sect. *Densifoliae* in the same way that *Chionohebe pulvinaris* and *C. ciliolata* vicariate to the north of the central Otago *Chionohebe* species. Sections *Densifoliae* and *Leonohebe* are vegetatively similar but their flowers and fruits differ.

3. Leonohebe ciliolata (Hook. f.) Heads (1987: 5) (Fig. 7).
Hebe ciliolata Cockayne & Allan (1927: 39).

This vicariates to the west of *L. densifolia* and *L. tetrasticha*, and occurs on and west of a line: Mt. Alta/ Haast Ra. (north of Mt. Aspiring) — Mt. Cook — Arthur's Pass — Lake Tennyson — Richmond Ra. — Anatoki (NW Nelson).

4. Leonohebe tetrasticha (Hook. f.) Heads (1987: 5) (Fig. 7).
Hebe tetrasticha Cockayne & Allan (1927: 39).

This species vicariates to the east of *L. ciliolata*, ranging on and east of the line: Hopkins Valley — Mt. Cook — Arthur's Pass. WILSON (1976) reports a possible west-east cline between these two species in Mount Cook National Park. *L. tetrasticha* vicariates to the north of *L. densifolia*

at the Kirkliston Ra. Marlborough populations (Doubtful R., Mt. Terako, Mt. St. Bernard) treated as *tetrasticha* by Cheeseman, have been identified as *ciliolata* by Mr. A.P. Druce (pers. comm., 1987).

5. Leonohebe cheesemanii (Buchanan) Heads (1987: 5) (Fig. 8).
Hebe cheesemanii (Buchanan) Cockayne & Allan (1927: 39).

This species ranges west to: Mt. Alta — Mt. Dobson (Hopkins Valley) — Godley Valley — Cass — Lake Tennyson — Mt. Bounds, and east to: Kirkliston Ra./ Hunters Hills — Mt. Somers — Terako — Tapuaenuku (Inland Kaikoura Ra.)/Altimarlock. This last pair of stations forms an important eastern sector shared with *L. tumida* (below), (cf. *L. epacridea* and *L. ramosissima*). Like *L. tetrasticha*, *L. cheesemanii* is a northern vicariant of *L. densifolia* (vicariating at: Mt. Alta — Kirkliston Ra.), and vicariates to the east of *L. ciliolata*.

6. Leonohebe tumida (Kirk) Heads (1987: 6) (Fig. 8).
Hebe tumida (Kirk) Cockayne & Allan (1927: 39).

This distinctive species is perhaps near *L. tetrasticha*, as CHEESEMAN (1925) suggested. It shares the sector: Tapuaenuku — Altimarlock with *L. cheesemanii*, but is otherwise largely vicariant to the north of that species. It ranges west to Richmond Ra. (to Gordon's Knob) — St. Arnaud Ra.

Leonohebe sect. *Connatae* Heads (1987: 6)

This section is notably absent from the southeastern region of endemism in central Otago (Rock and Pillar Ra. etc., cf. *Chionohebe*), but is represented there by *Leonohebe* sects. *Flagriformes* and *Densifoliae*.

7. Leonohebe epacridea (Hook. f.) Heads (1987: 6). (Fig. 9).
Hebe epacridea (Hook. f.) Cockayne & Allan (1927: 42).

L. epacridea ranges on shingle slopes, in crevices and in fellfields, north from: Livingstone Mts. — Eyre Mts. — Garvie Mts. to Snowden Ra. (NW Nelson, between Anatoki and Cobb Valleys). It skirts central Otago by the arc: Garvie Mts. — The Remarkables — Richardson Mts. — Mt. Roy (by Lake Wanaka) — Lindis Pass — St. Bathans Ra. — Mt. Domett (Kakanui Mts.), but is notably absent from Pisa Ra. — Dunstan Mts. — Rock and Pillar Ra. Patterns of distribution showing presence on Kakanui Mts. but absence on nearby Rock and Pillar Ra. (or vice versa) are common, and can be correlated with activity on the Waihemo Fault Zone (HEADS, 1989). This species' nearest relative is undoubtedly *L. haastii*, and *L. epacridea* is largely vicariant to the east of that species, especially in Otago and south Canterbury.

8. Leonohebe haastii (Hook. f.) Heads (1987: 6).
Hebe haastii (Hook. f.) Cockayne & Allan (1927: 42).

Scree, fellfield, rock-clefts. Differs from the previous groups by its endemism in central Canterbury.

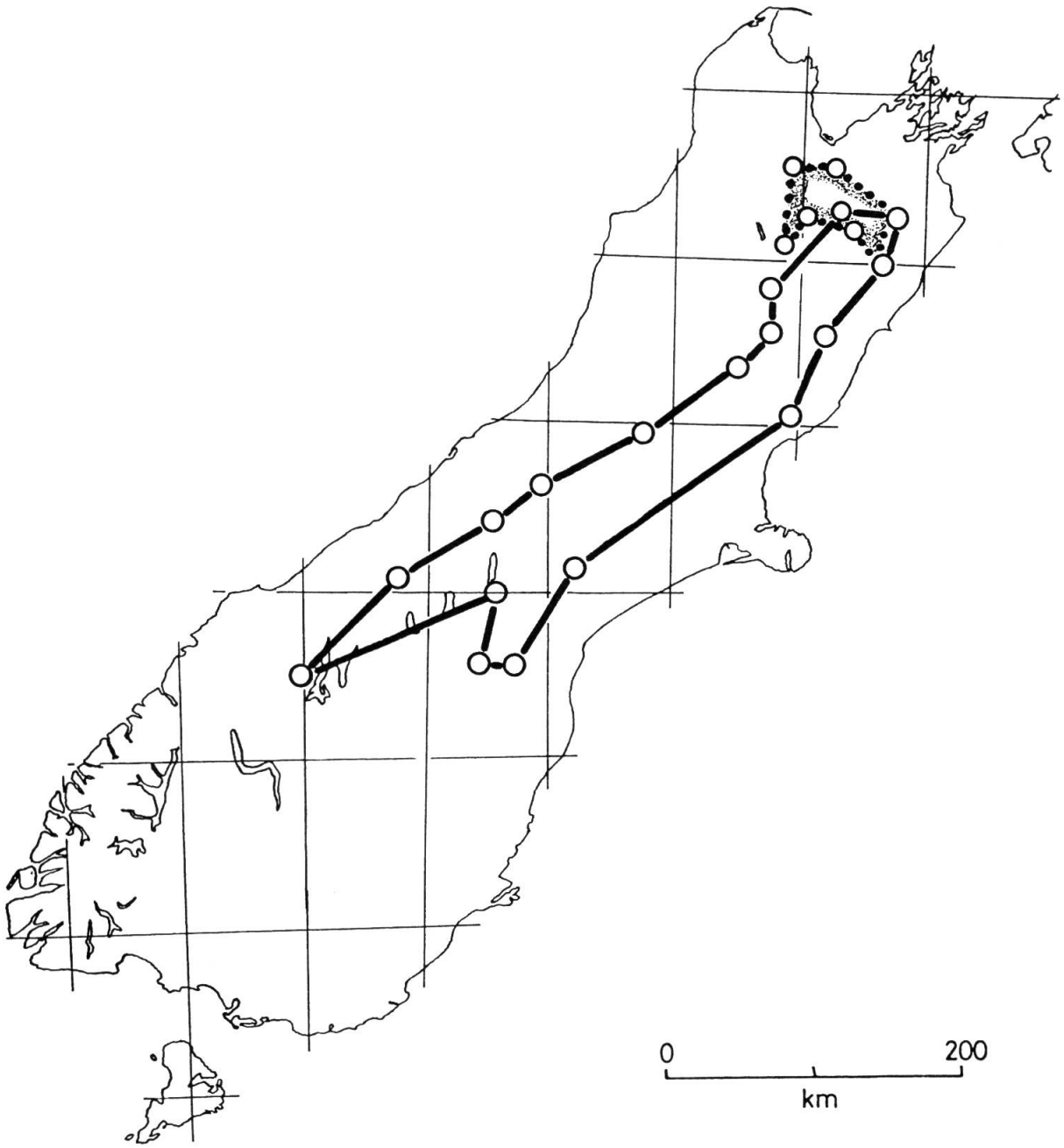

Fig. 8. — *Leonohebe cheesemanii*: continuous line; *L. tumida*: dotted stippled line.

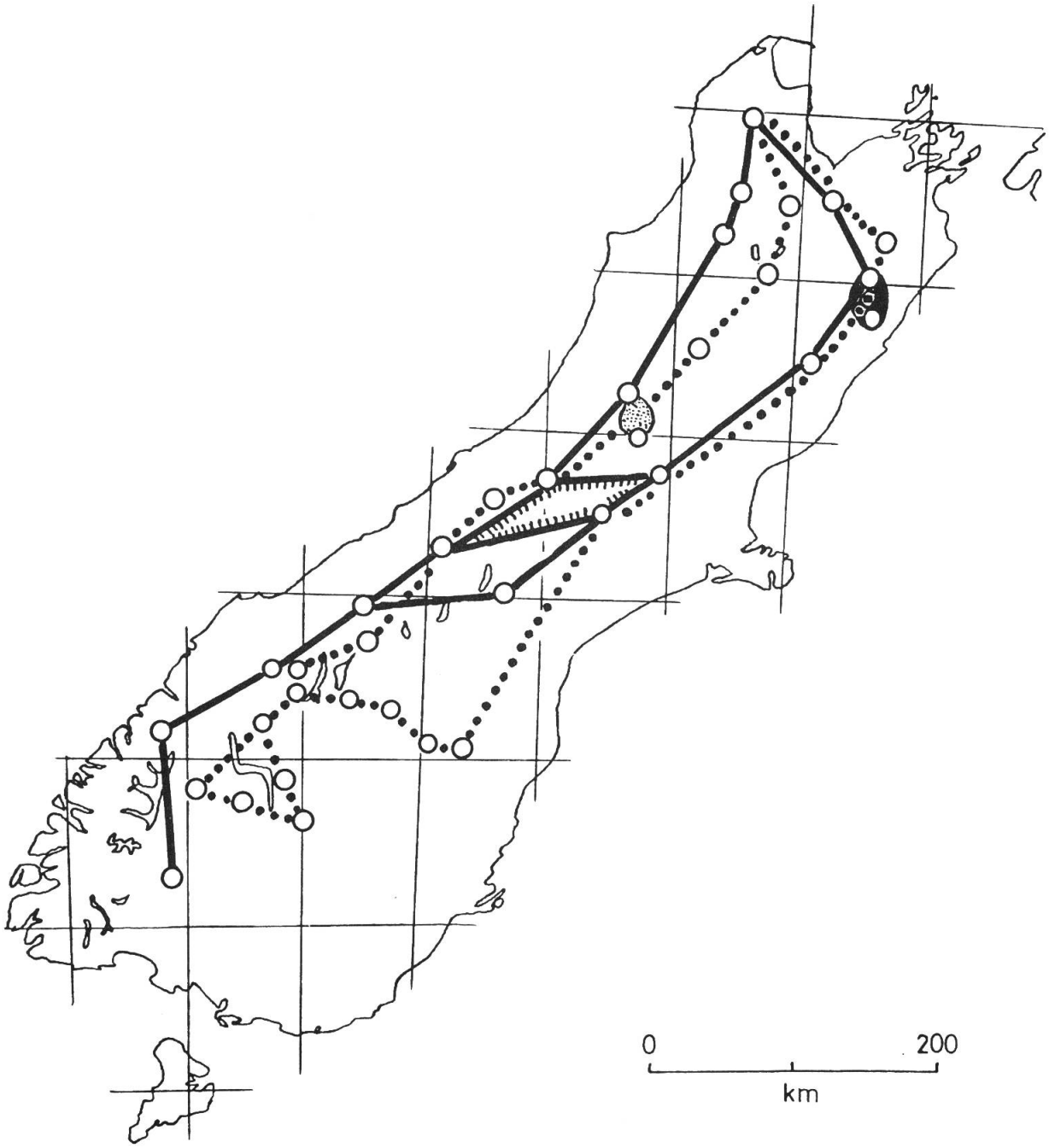

Fig. 9. — *Leonohebe haastii* var. *haastii*: hatched line; *L. haastii* var. *macrocalyx*: stippled; *L. haastii* var. *humilis*: continuous line; *L. epacridea*: dotted line; *L. ramosissima*: solid black.

8a. Leonohebe haastii var. **humilis** (Simpson) Heads (1987: 6) (Fig. 9).
Hebe haastii var. *humilis* (Simpson) Moore (1961: 940).

This is the widespread form of the species, ranging: Takitimu Ra. — MacKinnon Pass — Mt. French / Hector's Col (both by Mt. Aspiring), north to Cobb Valley (NW Nelson).

8b. Leonohebe haastii var. **haastii** (Fig. 9).
Hebe haastii (Hook. f.) Cockayne & Allan (1927: 42)

This ranges between Mt. Cook and Mt. Torlesse. In Mt. Cook National Park, WILSON (1976) records this variety only in the east, vicariating with var. *humilis*, known only in the west of the park. The biogeographic boundary thus runs to the east of the main geographic divide. The possible cline between *L. tetrasticha* and *L. ciliolata* (above) follows a similar track.

8c. Leonohebe haastii var. **macrocalyx** (Armstrong) Heads (1987: 6) (Fig. 9).
Hebe haastii var. *macrocalyx* (J. B. Armstr.) Cockayne & Allan (1927: 42).

Known only from the Arthur's Pass region (Waimakariri — Otira), an important northern boundary (e.g. Hectorellaceae) and southern boundary (e.g. *Traversia* — Compositae) in many groups.

9. Leonohebe ramosissima (Simpson & Thomson) Heads (1987: 7) (Fig. 9).
Hebe ramosissima Simpson & Thomson (1943: 29).

A distinctive local endemic of moist, rocky debris at high altitude on Manakau (Seaward Kaikoura Ra.) and Tapuaenuku. SIMPSON & THOMSON (1942) suggested that *L. ramosissima* and *L. petriei* are each other's closest relatives, with both being related more distantly to *L. epacridea* and *L. haastii*. The inflorescence of *L. petriei* is quite distinct from that of the other three species, but these three at least do seem related.

10. Leonohebe petriei (Buchanan) Heads (1987: 6) (Fig. 10).
Hebe petriei (Buchanan) Cockayne & Allan (1927: 42).

Moist sites in rocky debris, in crevices and on ledges. KIRK (1896) proposed this as "the most remarkable plant added to the Otago flora by the energetic Petrie". It is perhaps the most difficult species to place in the *Hebe* complex, and CHEESEMAN's classification is followed here for lack of any better alternative. The distribution of the species as a whole trends northeast between Mt. Burns (by Green Lake)/Takitimu Ra. and Mt. Repulse (northern Harris Mts., by Mt. Aspiring and Mt. Alta), thus following the Moonlight Tectonic Zone. It is not unusual for plants centred on this sector of the Median Tectonic Line to show unusual character combinations (e.g. the locally endemic *Iti* — Cruciferae, HEADS, 1989).

10a. Leonohebe petriei var. **petriei** (Fig. 10).

Takitimu Ra. — Livingstone Mts. — Lake Harris (Humboldt Mts.) east to Garvie Mts. — Pisa Ra. — Mt. Repulse (Harris Mts.).

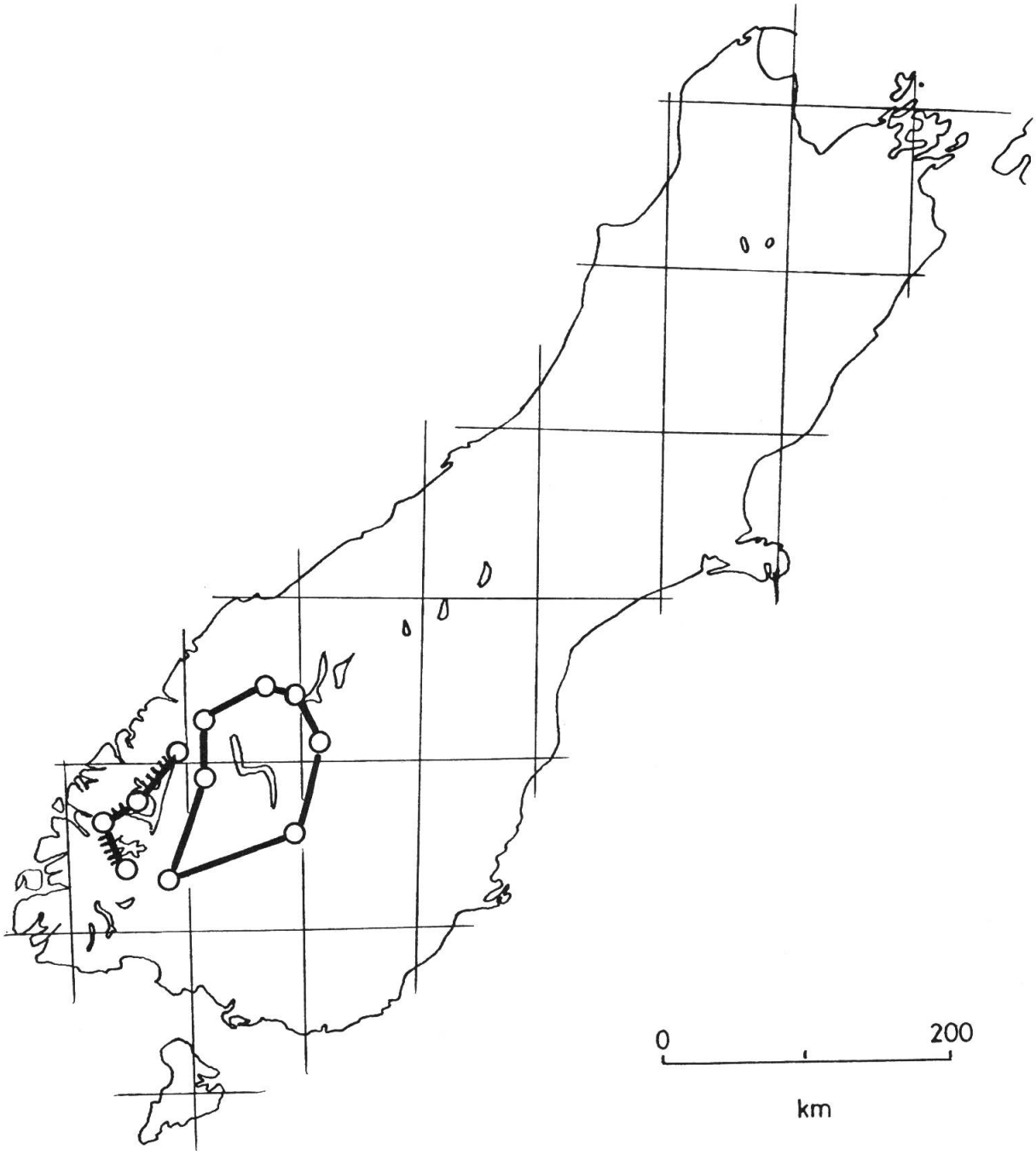

Fig. 10. — *Leonohebe petriei* var. *murrellii*: hatched line;
L. petriei var. *petriei*: continuous line.

10b. Leonohebe petriei var. **murrellii** (Simpson & Thomson) Heads (1987: 6) (Fig. 10).
Hebe petriei var. *murrellii* (Simpson & Thomson) Moore (1961: 938).

This ranges: Mt. Burns (by Green Lake) — Kepler Mts. — Murchison Mts. — Dore Pass, vicariating with the type variety at the Te Anau — Manapouri basin and the Median Tectonic Line.

Leonohebe sect. *Apiti* Heads (1987: 7)

The affinities of this curious monotype, *L. benthamii* from the New Zealand subantarctic islands, have long been debated. HOOKER (1844) gave a lengthy discussion with excellent illustrations. Later (1864) he referred to the species as "very distinct ... a most beautiful and remarkable plant ... quite unlike any New Zealand congener" and allied it with plants in *Hebe* group "Paniculatae" of MOORE (1961). CHEESEMAN (1925) followed Hooker closely in this (CHEESEMAN's "Subdivision B" of *Veronica* is identical with HOOKER's "Section 6"), but placed *L. benthamii* next to *V. macrantha* (and see CHEESEMAN, 1914). As suggested above, *Hebe* group "Paniculatae" and *Hebe macrantha* could both be allied in *Parahebe*. With respect to *L. benthamii*, MOORE (1961) took the novel step of placing the species with neither *V. macrantha* nor "Paniculatae", but instead with plants treated here as *Leonohebe* sect. *Connatae*. This affinity is supported by inflorescence symmetry and displays a track: Auckland Is. — Campbell Is. — Takitimu Mts. (*L. haastii*, *L. petriei*). This direct tie: Auckland Is./Campbell Is. — Fiordland avoids Stewart Is. — Solander Is. — southwest Fiordland, and would possibly fit into the series of parallel arcs of distribution described elsewhere (HEADS, 1989). A similar tie is shown between *L. benthamii* with *Hebe macrantha*, the affinity suggested by CHEESEMAN (1925). A tie with *Hebe* "Paniculatae", i.e. Auckland Is./Campbell Is. — Banks Peninsula, would be more unusual, but similar disjunctions along the east of South Is. occur in several plants and animals (HEADS, 1989).

In sum, this species was allied with *Parahebe* s.l. (incl. *Hebe macrantha* and *H.* group "Paniculatae") by HOOKER and CHEESEMAN, but is placed in *Leonohebe* by MOORE and myself, and in addition shares chromosome number and habit with a third genus, *Hebe*. It appears to be a particularly informative phylogenetic relict, recombining characters of the different genera.

11. Leonohebe benthamii (Hook. f.) Heads (1987: 7) (Fig. 11).
Hebe benthamii (Hook.f.) Cockayne & Allan (1927: 43).

The species is known from Auckland, Adams, and Disappointment Islands, all in the Auckland Islands group, and from Campbell Island. It thus ranges more widely in the subantarctic region than other Scrophulariaceae, such as those restricted to the northeast sector of the Auckland Islands. On the Auckland Islands JOHNSON & CAMPBELL (1975) record *L. benthamii* as "common from near sea-level to the hill-tops, particularly in tussock grassland, usually in wet sites."

Leonohebe sect. *Salicornioides* Heads (1987: 7)

The four known species form a series of more or less vicariant taxa ranging: Hump Ridge — Takitimu Mts. — Humboldt Mts. — Cobb V. — Tapuaenuku. The northeast "strike" of the tracks parallels that of much faulting in New Zealand. The group is notably absent from most of Fiordland and Otago.

12. Leonohebe annulata (Petrie) Heads (1987: 7) (Fig. 12).
Hebe annulata (Petrie) Cockayne & Allan (1927: 41).

Known only from rock faces at Takitimu Mts. and "Kurow Mts." (probably St. Mary's Ra.), on a trans-Otago track bound in the southwest by the Median Tectonic Line, and in the northeast by the schist/greywacke boundary. This comprises the southern vicariant of *L. salicornioides* and *L. armstrongii*.

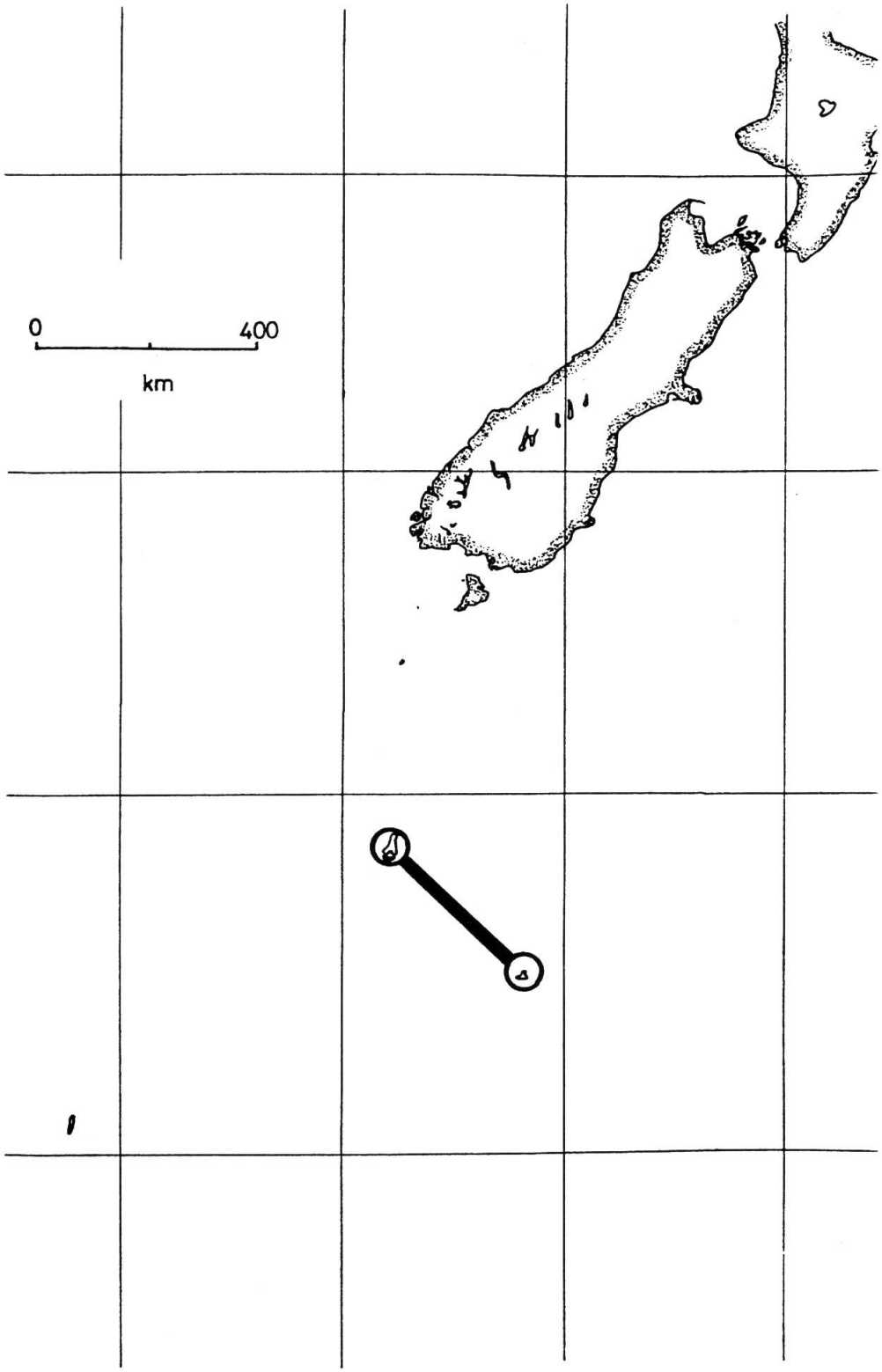

Fig. 11. — *Leonohebe benthamii*: Auckland and Campbell Islands.

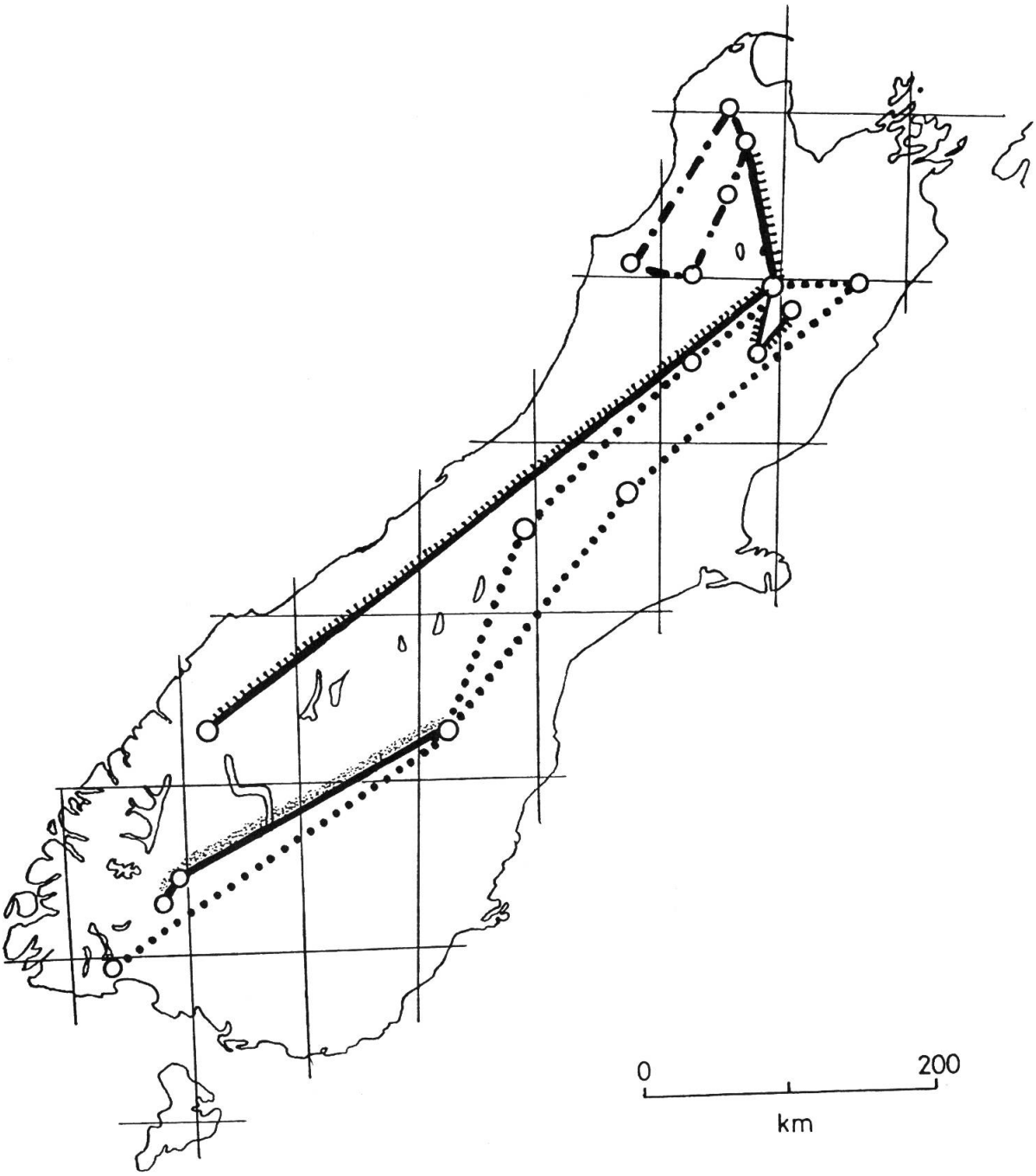

Fig. 12. — *Leonohebe annulata*: stippled line; *L. salicornioides*: hatched line; *L. armstrongii*: dotted line; *L. ochracea*: broken dotted line.

13. Leonohebe salicornioides (Hook. f.) Heads (1987: 7) (Fig. 12).
Hebe salicornioides (Hook. f.) Cockayne & Allan (1927: 40).

Usually in very wet ground, known from Humboldt Mts. and disjunct in the north at Hanmer — Lake Tennyson / Tarndale — Cobb Valley.

14. Leonohebe armstrongii (Armstrong) Heads (1987: 7) (Fig. 12).
Hebe armstrongii (J. B. Armstr.) Cockayne & Allan (1927: 40).

This is an eastern vicariant of the last species, and ranges from Mt. Kurow (= Mt. Kohurau, St. Mary's Ra.), north via Clyde Valley (by Arrowsmith Ra.) and Castle Hill — Amuri, to the line: Wairau Gorge (by L. Tennyson and St. Arnaud Ra.) — Tapuaenuku. A sterile specimen from "Hump Mts." (probably Hump Ridge on the south coast) (*Speden*, CHR) appears to be closer to *L. armstrongii* than to *L. annulata*.

15. Leonohebe ochracea (Ashwin) Heads (1987: 7) (Fig. 12).
Hebe ochracea Ashwin (1961: 936).

Paparoa Ra. (Buckland Peak etc.), east to: Mt. Mantell — Mt. Owen — Mt. Arthur — Mt. Peel. This comprises the west Nelson vicariant of the section and meets *L. salicornioides* at the Cobb Valley/Mt. Arthur centre. This node, like others, is an important mutual boundary, as well as being a centre of local endemism (e.g. *L. masoniae* var. *rotundata*).

Leonohebe sect. *Aromaticae* Heads (1987: 8)

The section caters for a single very distinctive species.

16. Leonohebe cupressoides (Hook. f.) Heads (1987: 8) (Fig. 13).
Hebe cupressoides (Hook. f.) Cockayne & Allan (1927: 42).

Usually on river-flats and terraces, from Lammerlaw Ra. — Garvie Mts. — "Te Anau" (CHEESEMAN, 1914) — The Remarkables/Queenstown — Mt. Grandview (by Lake Hawea) — Lindis Pass — upper Ahuriri V. — Arrowsmith Ra. — Harper's Pass, north to Lake Tennyson/upper Wairau V. on the west, and between Mt. Torlesse and Tapuaenuku on the east. The distribution pattern is suggestive of evolution along the coasts of inland seas which ranged from central Otago through to Marlborough in Tertiary times.

Agricultural practices have led to the demise of this plant in several parts of its range. Already in 1882 BUCHANAN observed that *Veronica* "has suffered much by the settlement of the Lake districts", where *V. cupressoides* was "once abundant".

Leonohebe sect. *Flagriformes* Heads (1987: 8)

Known from sectors of Stewart Is., South Is., and North Is., in shrubland and tussockland, expecially in wetter areas near streams and seepages.

Species 17 — 21 below (perhaps better treated as five or six subspecies of a single species) comprise a series of vicariant taxa ranging from: northern Stewart Is. — Lake Mike (SW Fiordland) in the south, north to: Rock and Pillar Ra. — Mt. Cook, and disjunct from there to: Paparoa Ra. — Hikurangi. The group's absence in eastern Marlborough (Tapuaenuku etc.) is conspicuous. It is replaced there by the closely allied *L. lycopodioides*. The group shows a notable disjunction along a geological transform, the Alpine Fault Zone, as do many other plant and animal taxa in the region (HEADS, 1989).

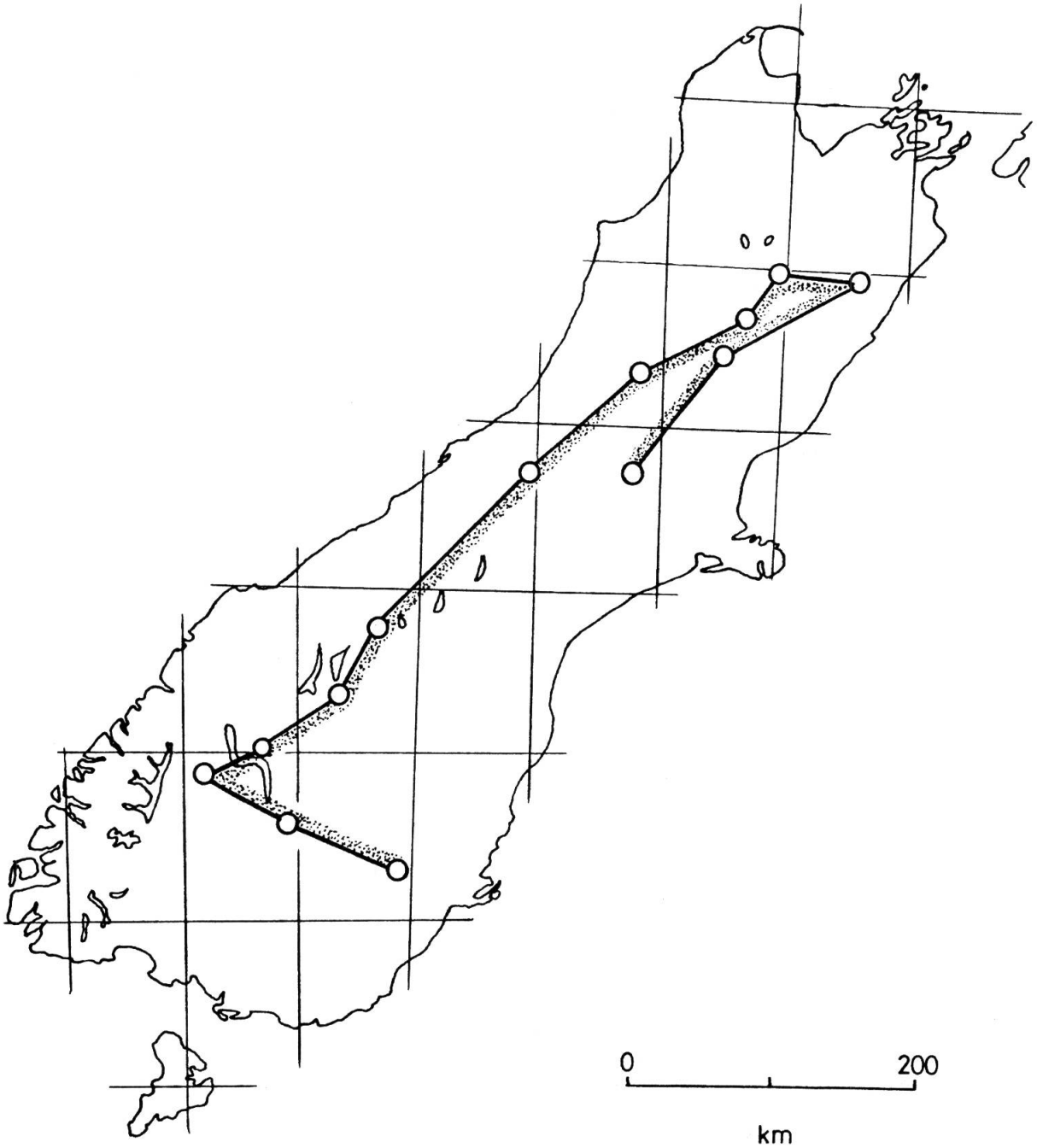

Fig. 13. — *Leonohebe cupressoides*: stippled line.

17. Leonohebe laingii (Cockayne) Heads (1987: 8) (Fig. 14).
Hebe laingii (Cockayne) Cockayne & Allan (1927: 40).

Damp grassy meadows along the arc: Mt. Anglem (Stewart Is.) — Lake Mike — Caswell Sound (western Fiordland), encircling the distribution of *L. hectorii* to the southwest.

18. Leonohebe hectorii (Hook. f.) Heads (1987: 8).
Hebe hectori (Hook. f.) Cockayne & Allan (1927: 40).

The distribution of this complex on a triangle: eastern Fiordland — Rock and Pillar Ra. — Mt. Cook, is closely comparable with that of taxa such as *Hebe buchananii*.

18a. Leonohebe hectorii var. **hectorii** (Fig. 14).

In contrast with *L. laingii*, this ranges along an eastern Fiordland arc: Lake Hauroko — Borland Saddle (southern Hunter Mts.) — Murchison Mts. — Humboldt Mts. — Big Bay — Mt. Brewster — Mt. Cook, and east to Takitimu Ra. — Mid Dome — Mt. Arnould. Many Fiordland specimens previously identified as *L. laingii* seem to be closer to *L. hectorii*. *Mark*, Feb. 1970 (OTA), from Stillwater Valley, Fiordland (between Doon V. and George and Caswell Sounds) is one of the most problematic specimens. It comes from a locality which, based on a study of other taxa (HEADS, 1989), lies near the boundary of two parallel arcs of distribution. The collection has foliage with reasonably conspicuous, yellow apical thickening abaxially (the reduced equivalent of the mucro), as in *L. hectorii*. The abaxial ridge is more developed than in other Fiordland *L. hectorii* and this points to *L. laingii*, but overall the specimen seems closer to *L. hectorii*.

18b. Leonohebe hectorii var. **demissa** (Simpson) Heads (1987: 8) (Fig. 14).
Hebe hectori var. *demissa* (Simpson) Ashwin (1961: 931).

Central Otago populations of *L. hectorii* from: Garvie Mts. — Old Man Ra. — Rock and Pillar Ra. — Mt. Pisgah (Kakanui Mts.), all show a distinct cusp at the leaf apex. These populations include the type of var. *demissa*, from Rock and Pillar Ra. Further west, plants from Forbes Mts. and Harris Mts. (Coronet Peak and Shotover Saddle) have a small cusp, while plants from the Livingstone Mts., Fiordland and Mt. Brewster have no cusp. Distribution of this cline: *L. laingii*, *L. hectorii* var. *hectorii*, *L. hectorii* var. *demissa* (with possible intermediates) thus follows a west-east sequence of nested arcs.

19. Leonohebe coarctata (Cheesem.) Heads (1987: 8) (Fig. 14).
Hebe coarctata (Cheesem.) Cockayne & Allan (1927: 40).

This is restricted to Nelson from a line: Mt. Stevenson (Paparoa Ra.) — Gouland Downs, east to: St. Arnaud Ra. — Moa Park (Abel Tasman National Park), sharing the western part of its range with *L. ochracea*, but showing significant eastern extensions to St. Arnaud Ra. — Moa Park.

20. Leonohebe subsimilis (Col.) Heads (1987: 9) (Fig. 14).
Hebe subsimilis (Col.) Ashwin (1961:929).

Both the type variety and *L. subsimilis* var. *astonii* (Petrie) Heads are recorded at: Pouakai (Taranaki) — Ruahine Ra. — Tararua Ra. They connect with *L. coarctata* by a track: Taranaki

Gouland Downs, and meet *L. tetragona* at the northwest Ruahine Ra. This last region is a node of pivotal importance in the dispersal of Scrophulariaceae such as *Ourisia* and *Euphrasia*, as well as *Leonohebe*.

21. Leonohebe tetragona (Hook.) Heads (1987: 9) (Fig. 14).
Hebe tetragona (Hook.) Cockayne & Allan (1927: 39).

This ranges from northwest Ruahine Ra., northwest to Kaimanawa Ra./Mt. Ruapehu, and northeast to Kaweka Ra. — Hikurangi, the northern limit of the section and the genus.

The following five species comprise another complex of closely related taxa ranging in central South Island between Mt. Burns (by Green Lake) in Fiordland and Richmond Ra. in Nelson. This group is largely vicariant to the east of the last group. All of its species are present in central Otago, but the group is absent from Stewart Is., and most of Fiordland and Nelson. The concentric ring pattern of endemism in central Otago again suggests evolution along the shore region of gradually shrinking Tertiary seas. Similar "bathring dispersal" can be seen in Australia, for example in *Eucalyptus* — Myrtaceae (HEADS, 1990b).

22. Leonohebe imbricata (Petrie) Heads (1987: 9) (Fig. 15).
Hebe imbricata (Petrie) Cockayne & Allan (1927: 42).

This is the southern member of the group, being found at: Mt. Cleughearn — Mt. Burns (both by Green Lake) — Eyre Mts., and vicariating at Eyre Mts. with *L. poppelwellii*. The connection SE Fiordland — Eyre Mts. is standard, being shared with taxa such as *Nothofagus fusca* — Fagaceae (HEADS, 1989).

23. Leonohebe propinqua (Cheesem.) Heads (1987: 9) (Fig. 15).
Hebe propinqua (Cheesem.) Cockayne & Allan (1927: 41).

Usually found on poorly drained areas in tussockland, north from an arc: Humboldt Mts. — Livingstone Mts. — Mid Dome — Maungatua to: The Remarkables — Mt. Ida. There is an early collection from "Rangitata River". The distribution of this species surrounds that of the next two, giving concentric rings of alpine endemism centred near Roxburgh. This high altitude endemism can be compared with low altitude endemism in the same region in, for example, *Hebe pimeleoides* var. *rupestris*. This SE central Otago node can be distinguished from the node at Pisa Ra. seen in *Chionohebe*. In the latter, high altitude endemism is complemented by low altitude endemism at Cromwell, for example in locally endemic Coleoptera (*Prodontria lewisi* — Scarabaeidae).

24. Leonohebe poppelwellii (Cockayne) Heads (1987: 9) (Fig. 15).
Hebe poppelwellii (Cockayne) Cockayne & Allan (1927: 41).

This is a classic southern central Otago endemic, with a range: Eyre Mts. — Garvie Mts. — Old Man Ra. — Rock and Pillar Ra. — Umbrella Ra. — Lammerlaw Ra. Four out of five of the species in this group meet at or along an axis: Eyre Mts. — Humboldt Mts.

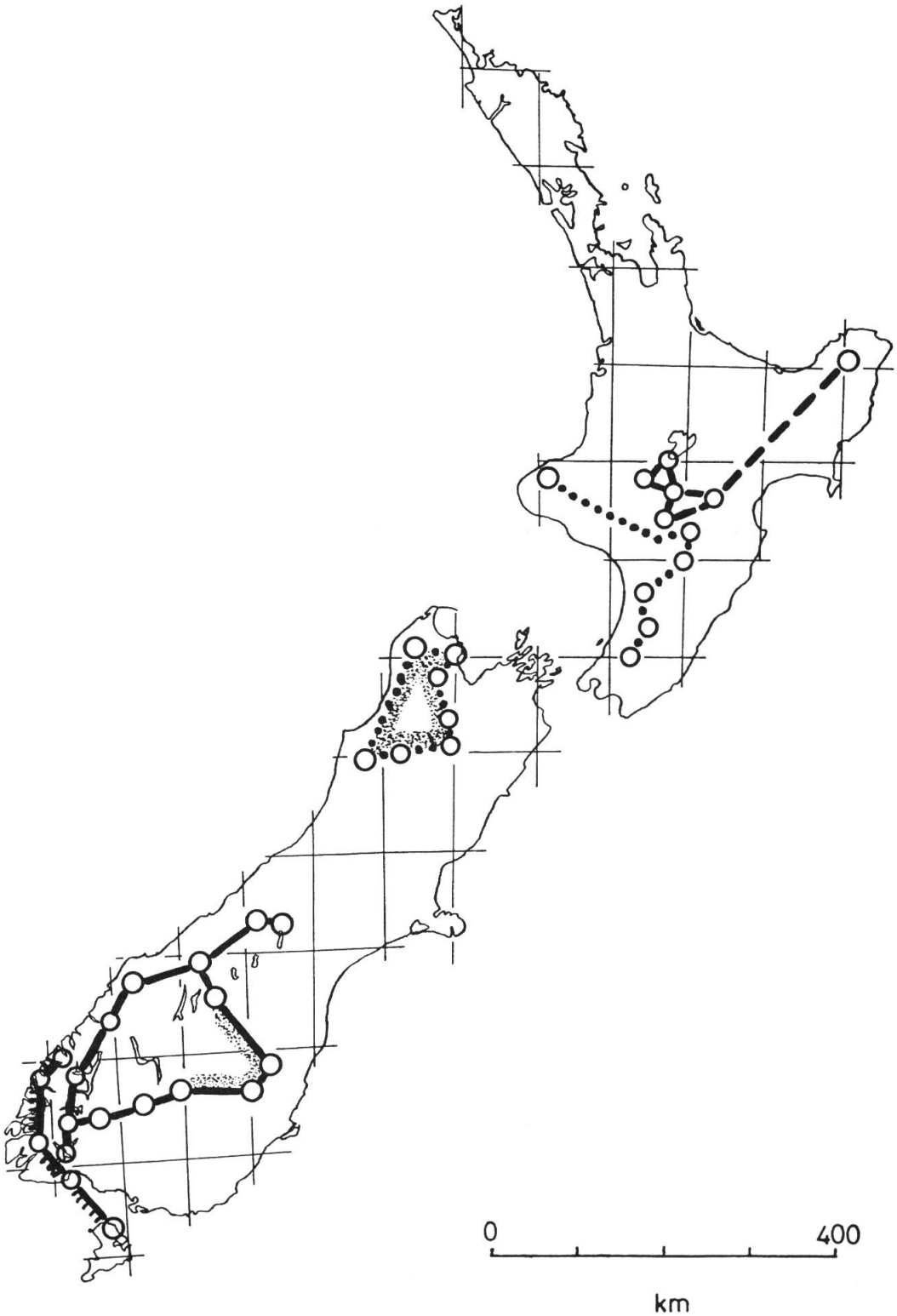

Fig. 14. — *Leonohebe laingii*: hatched line; *L. hectorii* var. *hectorii*: solid line; *L. hectorii* var. *demissa*: solid stippled line; *L. coarctata*: dotted stippled line; *L. subsimilis*: dotted line; *L. tetragona*: broken line.

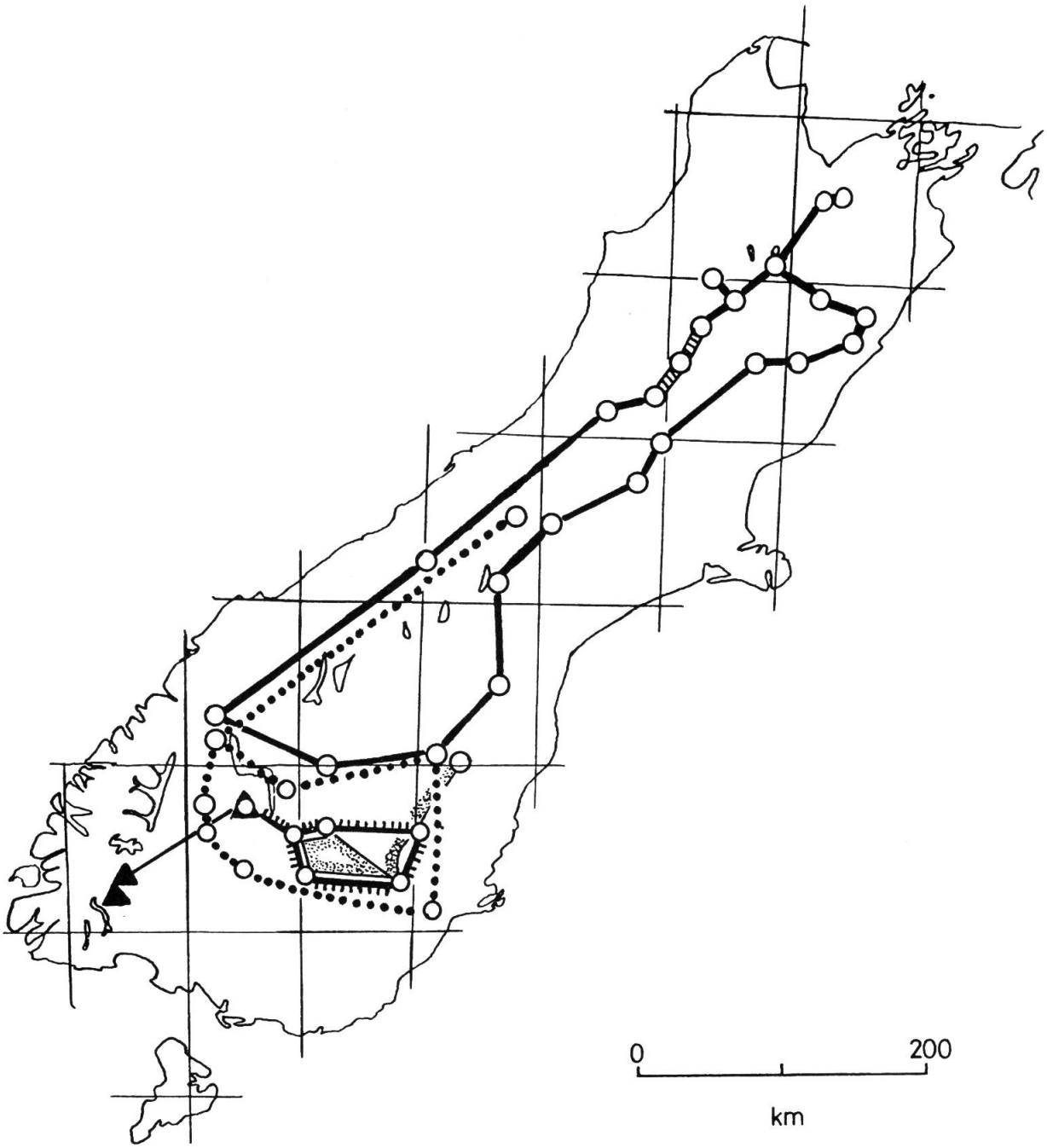

Fig. 15. — *L. imbricata*: triangles; *L. propinqua*: dotted line; *L. poppelwellii*: hatched line; *L. subulata*: stipple; *L. lycopodioides* var. *lycopodioides*: continuous line; *L. lycopodioides* var. *patula*: double hatched line.

25. Leonohebe subulata (Simpson) Heads (1987: 9) (Fig. 15).
Hebe subulata Simpson (1952: 427).

Garvie Mts. — Old Man Ra. — Umbrella Mts. — Lammerlaw Ra. — Dansey Pass (between Mt. Ida and Kakanui Ranges). Specimens from the latter locality (*Heads & Patrick*, Nov. 1986, OTA) are very similar to those from the Lammerlaw Ra. and other areas, having a leaf cusp but no ribs, and shoots c. 2 mm in diameter. Garvie Mts. plants are similar, but shoots are 3-5 mm diameter, with a very stout leaf cusp. Mt. Ida Ra. plants (*Heads, Keogh, Tangney & Patrick*, 12.i.1985, OTA, Fig. 2b) have leaves with the yellow, cartilaginous margin connecting with the similarly textured longitudinal "ribs", and are referred to *L. lycopodioides*. Thus there is apparent vicariance between the two species at: Mt. Ida/Dansey Pass. In its morphology *L. subulata* approaches *L. hectorii*, particularly var. *demissa*. However, this latter variety is basically eastern, where populations of *L. subulata* are quite distinctive. In central localities the convex leaf margin of *L. hectorii* generally contrasts with the concave margins of *L. subulata*, but the two are closely related.

26a. Leonohebe lycopodioides (Hook. f.) Heads (1987: 9) (Fig. 15).
Hebe lycopodioides (Hook. f.) Cockayne & Allan (1927: 40).

This has a western limit at: Greenstone R. (*Matthews*, AK) — Humboldt Mts. — Mt. Cook — Arthur's Pass — Glenroy Valley — Richmond Ra., and an eastern limit at: Mt. Ida — Hunter's Hills — Mt. Torlesse — Manakau (Seaward Kaikoura Ra.), reaching south to the southern Dunstan Mts. (*Rance* 27.iii.1986, OTA, Leaning Rock Ck.). This comprises the northeastern vicariant of the other forms in this complex, replacing the central Otago *L. poppelwellii* and *L. propinqua* to the north in the same way that *L.* sect. *Leonohebe* replaces sect. *Densifoliae*. *L. lycopodioides* continues through to Richmond Ra. — Seaward Kaikoura Ra., but is notably absent from west Nelson. The species shares leaf ribbing with *L. poppelwellii* which has leaves shorter and more obtuse, has the leaf cusp of *L. subulata*, and is also close to *L. imbricata*.

26b. Leonohebe lycopodioides var. **patula** (Simpson & Thomson) Heads (1987: 9) (Fig. 15).
Hebe lycopodioides var. *patula* Simpson & Thomson (1943: 164).

This holds the central sector: Harper's Pass (by Arthur's Pass — cf. *Hebe venustula*, *H. canterburiensis*, etc.) — Lewis Pass. ASHWIN (1961) noted affinities with *L. poppelwellii*, and wrote that the variety "might better be placed there". This affinity would follow a disjunction along similar lines to that of *Ourisia glandulosa* (HEADS, 1989).

Leonohebe sect. *Buxifoliatae* Heads (1987: 10)

Members of this section are important ecologically and dominate large areas of shrubland. The group, revised in HEADS (1992), is also phylogenetically important as certain species combine the bud structure of *Hebe* with the inflorescence of *Leonohebe*. Biogeographically the group is distinct through its presence at eastern localities.

27. Leonohebe pauciflora (Simpson & Thomson) Heads (1987: 10) (Fig. 16).
Hebe pauciflora Simpson & Thomson (1943: 166).

From Caswell Sound — Dusky Sound in the west, this distinctive species ranges southeast to South Caroline Burn (Lake Hauroko) — Wilmot Pass — Upper Iris Burn (Kepler Mts.) — Murchison Mts. The sector: Caswell Sound — Murchison Mts., here a northern boundary, is a southern boundary in *Parahebe planopetiolata* (at Doon Valley) and a centre of local endemism in, for example, *Celmisia* (Compositae) (HEADS, 1989). General vicariance is evident between *L. pauciflora*

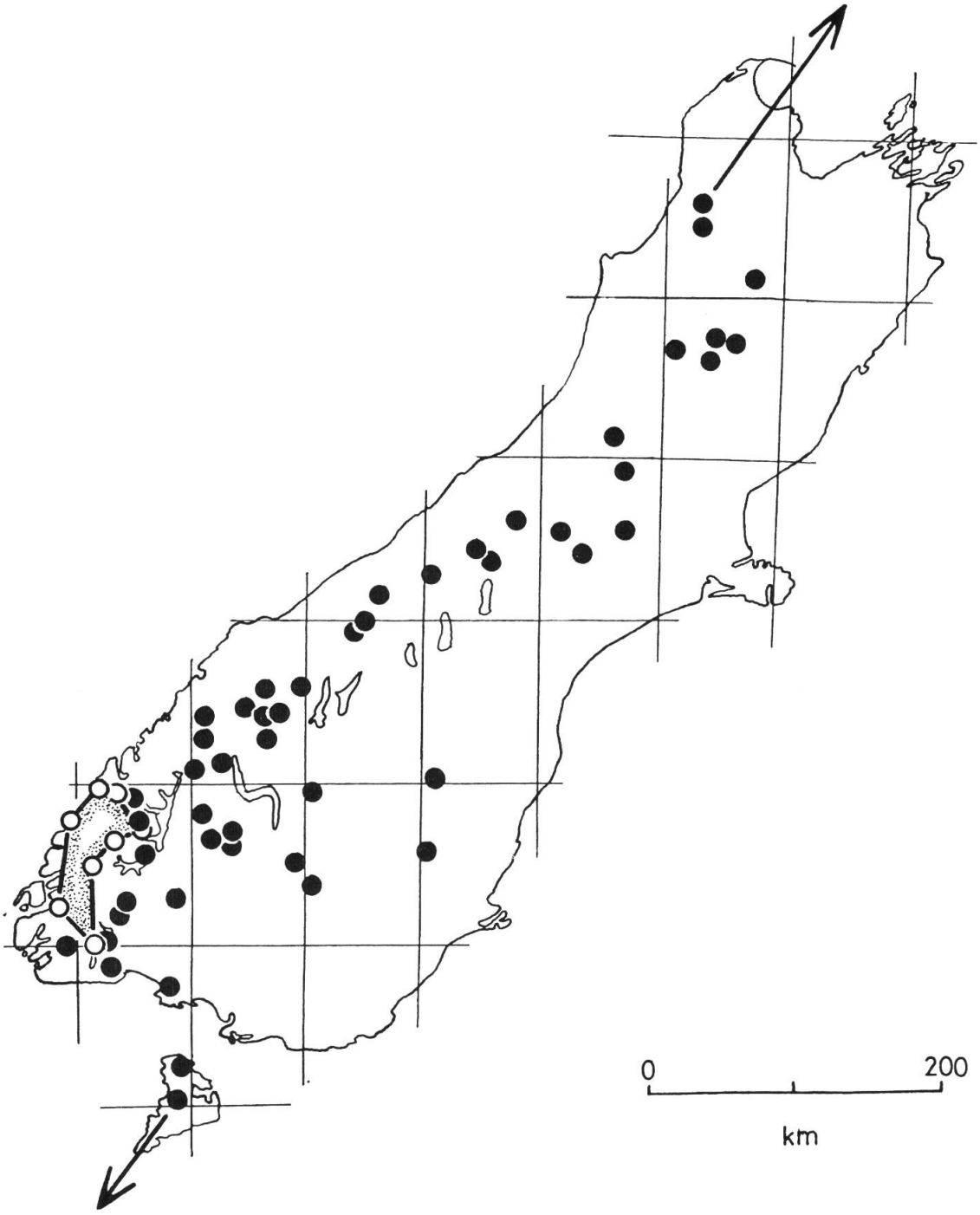

Fig. 16. — *L. pauciflora*: stippled line; *L. pauciramosa* var. *pauciramosa*: circles (also at NE Auckland Is. and Mt. Taranaki).

and *L. pauciramosa*, with the ranges of the two species overlapping only at South Caroline Burn (Lake Hauroko) and Murchison Mts. *L. pauciramosa* is present in southwest Fiordland (Lake Monk, in the Cameron Mts.) where *L. pauciflora* appears to be absent.

28. Leonohebe odora (Hook. f.) Heads (1987: 10) (Figs. 17, 18).
Hebe odora (Hook. f.) Cockayne (1929: 472).

This is the most wide-ranging species of the genus and abounds in many shrublands. The only Auckland Islands specimens I have seen are from northeast Auckland Island, in agreement with JOHNSON & CAMPBELL's (1975) note: "occasional in forest and scrub at low altitudes but not collected from Adam's Island". Likewise *Hebe salicifolia* in the Auckland Islands is recorded only from the northeast. In contrast, groups such as *Kelleria* (Thymelaeaceae), with Indian Ocean rather than Tasman-Pacific affinities, are recorded in the Auckland Is. only at Adam's Island (HEADS, 1990a). *L. odora* is widespread in Stewart and nearby Big South Cape Is., and from here ranges west to the Longwood Ra. and to the north-striking boundary: NW Kaherekouau Mts. (north of L. Hauroko) — Caswell Sound. North of Caswell Sound it ranges west to: Homer Saddle — O'Leary Pass (between the Dart and Olivine valleys). From here it is disjunct to Worryline Stream (Ben Ohau Ra.) — Lily Stream, Liebig Ra. (thus not entering Mount Cook National Park) — Arthur's Pass — Paparoa Ra. — Gouland Downs. It is found northwards in North Island to the line: Taranaki — Tongariro — Hikurangi, proposed by CROIZAT (1968b) as an important boundary. This is also the northern limit of the genus. *L. odora* ranges east to: Mt. Pye (Catlins) — Dunedin — Mt. Herbert (Banks Peninsula) — Jack's Pass — Mt. St. Bernard (Inland Kaikoura Ra.) — Altimarlock (Black Birch Ra.) — Ruahine Ra. — Hikurangi. This is the only species in the genus present in the far east of South Is., notably at Catlins, Dunedin and Banks Peninsula, although it is absent from Chatham Islands. A possible segregate, *Veronica anomala*, is apparently restricted to eastern localities in South Is. An interesting gap in the records is apparent between O'Leary Pass (north of Forbes Mts.)/Dunstan Mts. in Otago and Worryline Stream (Liebig Ra.)/Mt. Peel in Canterbury (Fig. 18). This large disjunction apears to be real, but the status of this generally conspicuous shrub in areas such as Mount Aspiring National Park remains to be worked out.

29. Leonohebe mooreae Heads (1987: 10) var. **mooreae** (Fig. 19).

This ranges from the far west of Fiordland east to: Longwood Ra. — Hump Ridge — South Caroline Burn — Percy Saddle (between Hunter Mts. and Wilmot Pass). Along this arc it meets *L. odora* at its western limit. North of here it ranges to central Fiordland — Homer Saddle — Upper Olivine River — Drake and Selbourne Ranges. Up to this point there is general vicariance with *L. odora* to the east (overlap at Caswell Sound) but north of here a gap (filled by *L. pauciramosa*) opens up between the two species. There appear to be no collections of either *L. odora* or *L. mooreae* from a region: Wilkin Valley — Mount Cook National Park. From the mouth of the Cascade River, *L. mooreae* ranges northwards along Westland to the Douglas Ra. From here the species is disjunct to the line: Denniston Plateau — Gouland Downs — Mt. Stevens (Wakamarama Ra.), west to Lake Sylvester (by Cobb V.), and with a possible record (sterile specimens) from Richmond Ra. Plants with adaxial stomata are known only from Caswell Sound and Denniston Plateau, which recalls the only localities where *L. odora* reaches the west coast: Caswell Sound, Paparoa Ra., and northwest Nelson (Fig. 21).

29b. Leonohebe mooreae var. **telmata** Heads (1987: 10) (Fig. 19).

Known only from Westland National Park at Douglas Range, head of Waikukupa R., and Mt. Fox. This variety extends the range of the species slightly north of the Westland limit of the type variety, but it basically straddles this northern limit at the point of disjunction.

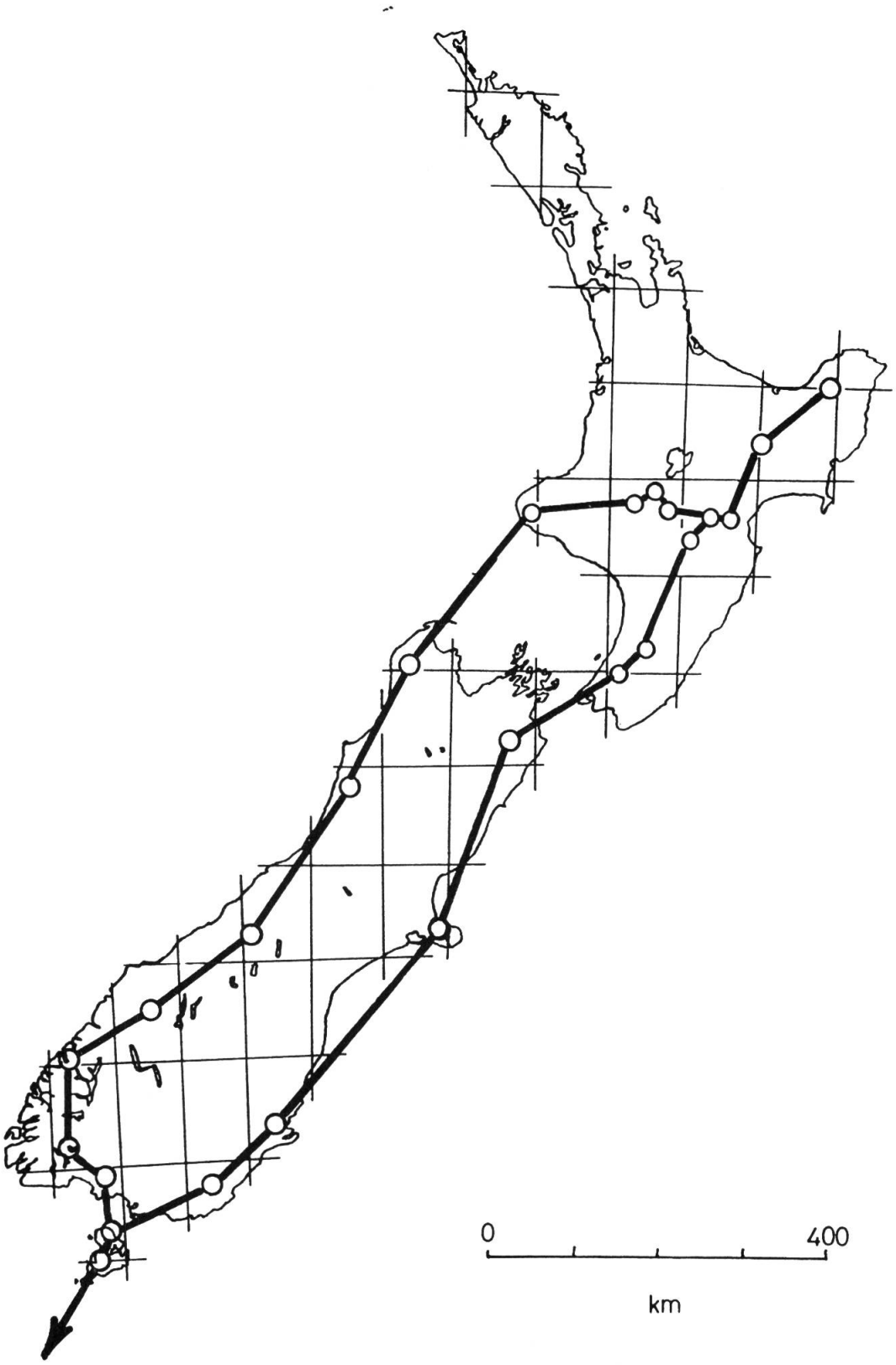

Fig. 17. — *Leonohebe odora*: continuous line (plus NE Auckland Islands).

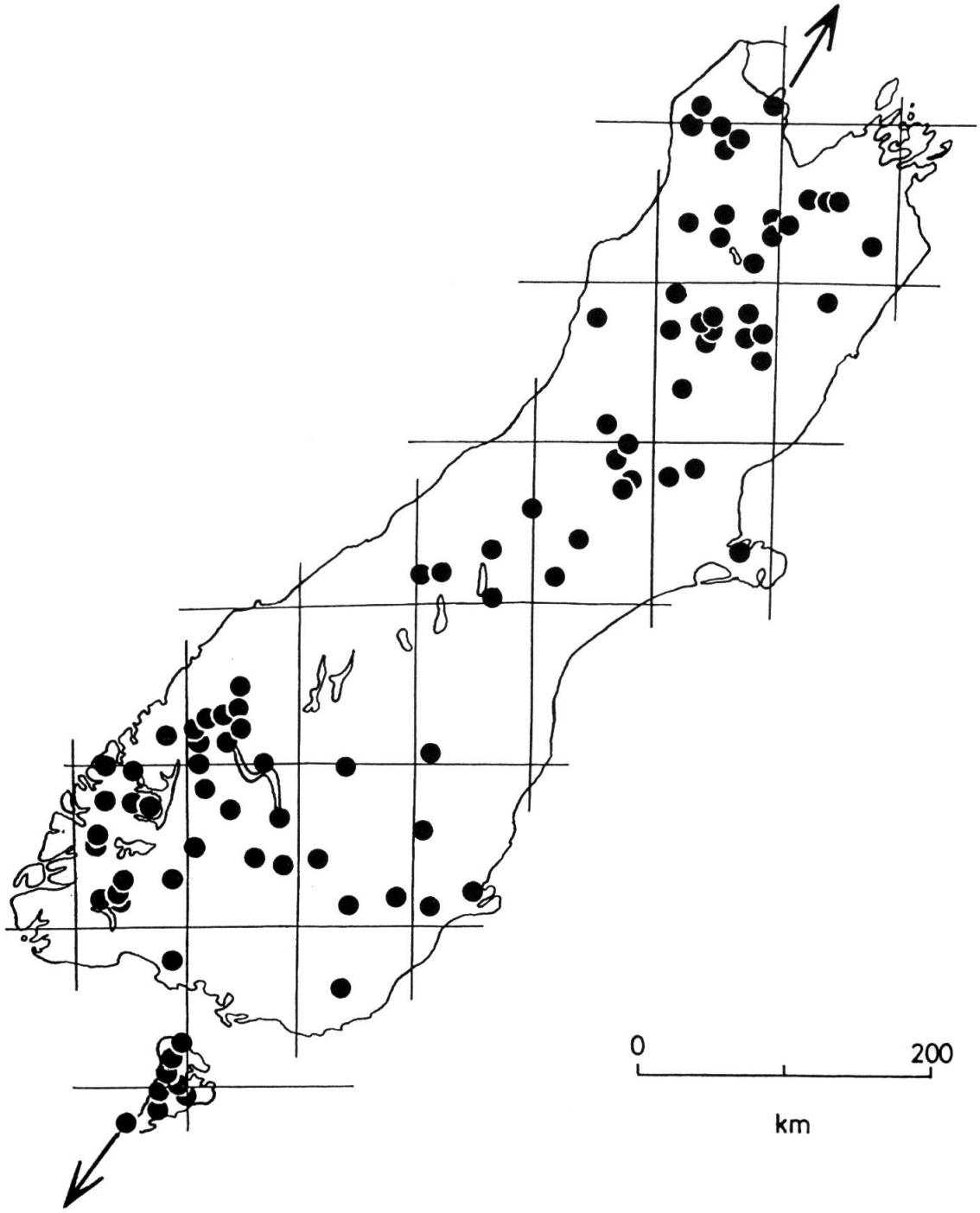

Fig. 18. — *Leonohebe odora* South Island distribution.

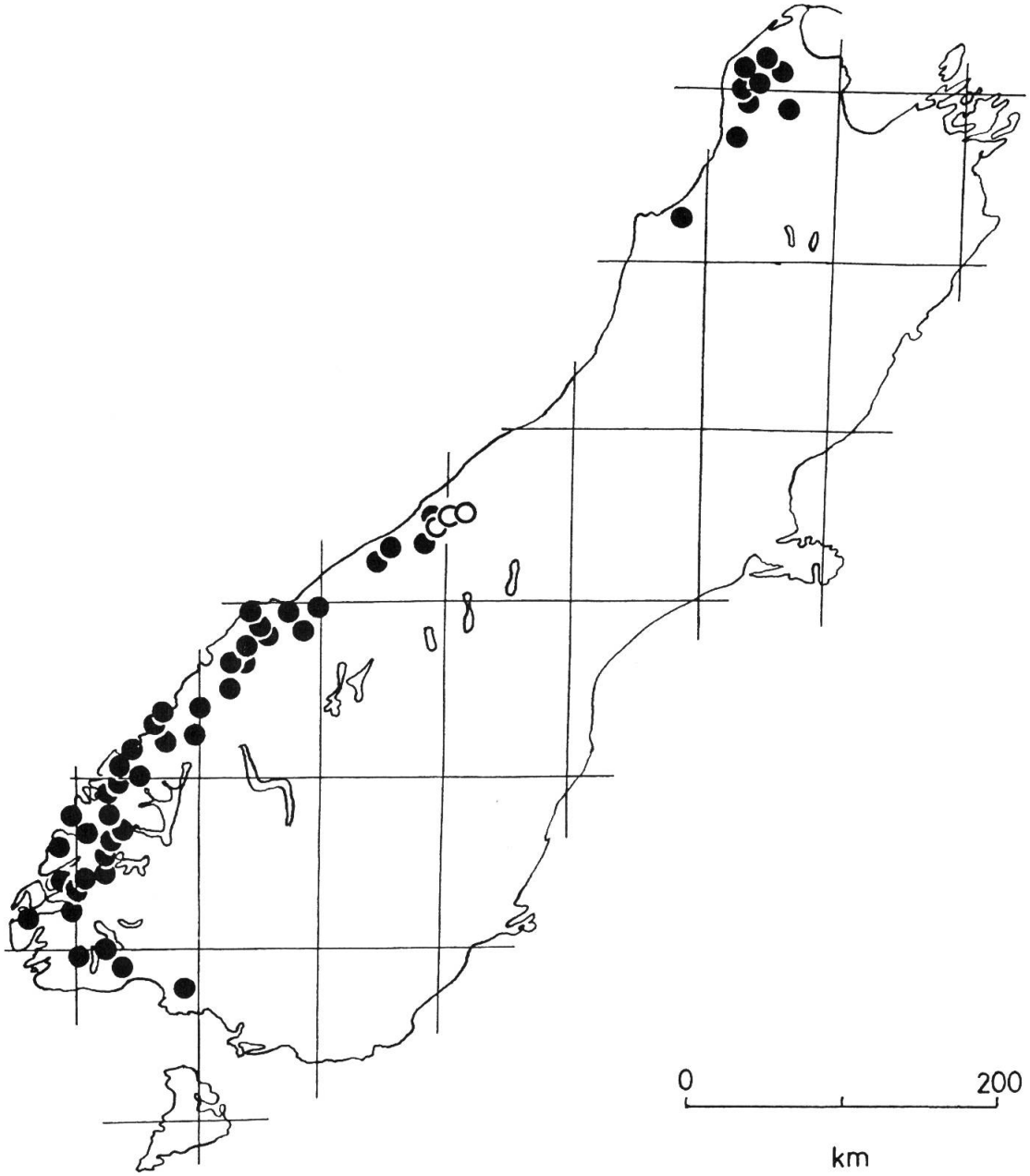

Fig. 19. — *Leonohebe mooreae* var. *mooreae*: closed circles; *L. mooreae* var. *telmata*: open circles.

30. Leonohebe pauciramosa (Cockayne & Allan) Heads 1987: 10) (Fig. 16).
Hebe pauciramosa (Cockayne & Allan) Moore (1961: 925).

Auckland Is., in the NE only (Port Ross); Stewart Is., north of the Rakeahua R. only (Mts. Rakeahua and Anglem). In South Is., west to: Longwood Ra. — Hump Ridge — Lake Monk/Cameron Mts. — Green Lake — Mt. Luxmore (Kepler Mts.) — Lake Hankinson (species in *eastern* Fiordland only), and further north to Lake Harris (Humboldt Mts.) — Bryneira Ra. (by Olivine R.) — Mt. Aspiring — Mt. Brewster — Godley Valley (apparently absent from large sectors of Mount Cook National Park) — Arthur's Pass — Rahu River (by Victoria Ra.) — Matiri Ra./Pike Peak (Allen Ra., NW Nelson) — Taranaki. There is very precise vicariance between *L. pauciramosa* and *L. mooreae* in Fiordland, Westland and Nelson, but the two are geographically sympatric in the region: Lake Monk — Hump Ridge — Longwood Ra. The generally central distribution of *L. pauciramosa* extends east to: Umbrella Mts. — Rock and Pillar Ra. — Mt. Ida in Otago, and Mt. Somers — Thirteen Mile Bush (by Big Ben Ra.) in Canterbury.

31. Leonohebe masoniae Heads (1987: 10) (Fig. 20).

This species is largely restricted to west Nelson where it vicariates to the north of *L. pauciramosa*.

31a. Leonohebe masoniae var. **masoniae**

The variety holds an eastern line: Cobb Ridge — Lookout Ra. — Hope Ra., and ranges west from here to Burgoo Stream, Slate Ra. (Gouland Downs), Garibaldi Ridge, Little Wanganui Saddle, Matiri Ra. and Denniston Plateau. There is also a disjunct population at Worryline Stream, Ben Ohau Ra., and this apparent disjunction can be compared with other western disjunctions in *L. mooreae*, *Hebe gracillima* and other groups (HEADS, 1989). This variety is generally vicariant to the west and south of the following variety.

31b. Leonohebe masoniae var. **rotundata** Heads (1987: 10) (Fig. 20).

This is restricted to Mt. Arthur, Mt. Peel, Lake Sylvester and near Cobb Dam, giving a distribution with a radius of some 8 kilometers.

Conclusions

The main aim of this project was to provide a preliminary analysis of the phylogeny and distribution of a large group of plants in New Zealand. Unfortunately, other studies with similar aims either fail to deal with even putatively monophyletic groups (e.g. studies on New Zealand members of a group only), or simply map species in alphabetical order. Previous studies have also lacked detailed areographic analysis. The clearest finding of this study is that taxa show a very high degree of vicariance at all ranks, often displayed in strikingly precise patterns. The explanation for this is more controversial.

Biogeographic patterns within New Zealand such as those outlined here are usually explained in terms of taxa reinvading areas in relatively recent times, with a relatively small number of relics being acknowledged. For example, FLEMING (1979:91) accepted and mapped hypothetical migrations of *Hebe cheesemanii* and *H. decumbens* into previously "severely glaciated" regions in the central South Island (itself a centre of endemism) from "refugia" in the north. The particularly high number of nodes — sometimes interpreted by other authors as "refugia" — seems to contradict

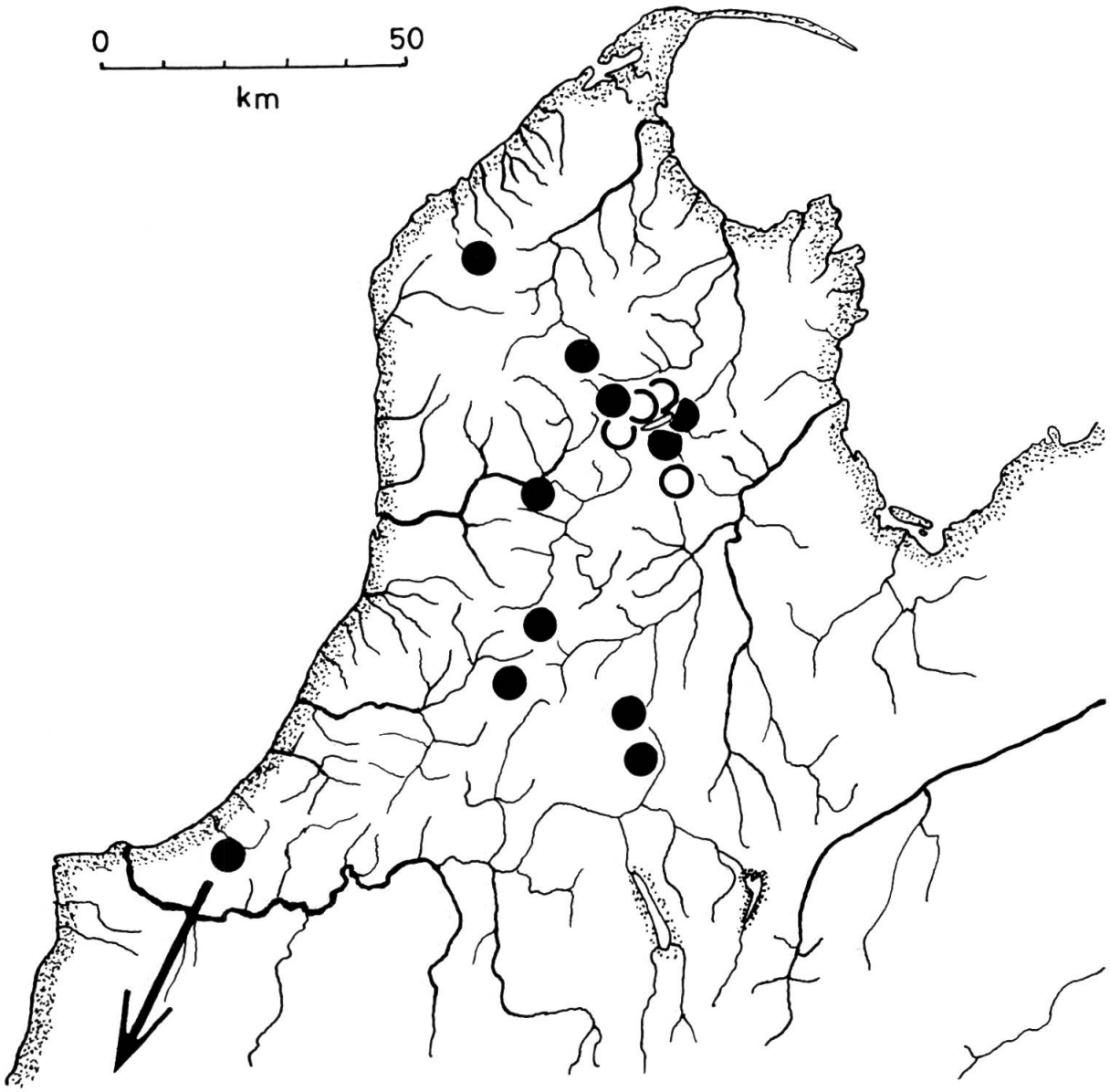

Fig. 20. — *Leonohebe masoniae* var. *masoniae*: closed circles; *L. masoniae* var. *rotundata*: open circles.

the general premise of "refugium theory", that there were relatively few refugia, and that there were large areas with no refugia. In the groups studied here it would seem rather that different elements were always already present on "ecological islands" of many different kinds, such as nunataks and rocky knolls in forest. The nodes described here (Fig. 4), while too numerous to be "refugia" in the usual sense, are still fewer than might be expected if dispersal was random, and many nodes feature in several taxa. Most of these nodes are important also for other groups of plants and animals and their history has been explained elsewhere (HEADS, 1989) in terms of Mesozoic and Tertiary geology. The refugium theory as developed for South America was criticised extensively by CROIZAT (1975), and more recently GENTRY (1989) has noted that the idea was accepted "almost instantaneously", and "often quite uncritically".

Biogeographic patterns within the broader southwest Pacific region are also controversial. For example, authors such as RAVEN (1972) have discussed the general problem of plant groups which show considerable diversity and endemism in the New Zealand region, but are absent in Australia, or display little diversity there (e.g. the *Hebe* complex, *Coprosma* — Rubiaceae, *Epilobium* — Onagraceae, *Celmisia* — Compositae, *Myosotis* — Boraginaceae, *Aciphylla* — Umbelliferae, *Poa* — Gramineae, and *Carex* — Cyperaceae). Similar chromosome numbers, interfertility and apparent hybridism among the species of these genera caused RAVEN to think that the "species explosions" or "adaptive radiations" seen in New Zealand in these genera have been recent and rapid. RAVEN (cf. FLEMING, 1979) even suggested that the open habitats occupied by these genera (e.g. alpine grasslands, coastal moors) developed for the first time in New Zealand in the Pleistocene — New Zealand having been previously "almost entirely forested". Raven and other authors interpret the New Zealand groups in question, as well as many others, as having been derived from Australia, and ultimately, the northern hemisphere (RAVEN & AXELROD, 1972). The traditional biogeographic interpretation supported by RAVEN and FLEMING invokes northern hemisphere ancestors, followed by long distance dispersal, and Pliocene-Pleistocene radiations, whereas the model favored in the present paper implies southern hemisphere ancestry, no long distance dispersal, much vicariance, and Mesozoic radiations. The following points seem to favor the model used here rather than that of RAVEN et al.:

1. Different external biogeographic affinities of New Zealand taxa (e.g. *Leonohebe* with Australia, *Hebe* with Pacific islands and South America) dated as Mesozoic by correlation with tectonics, show different patterns within New Zealand (*Leonohebe* in the west, *Hebe* in the east) which can also be correlated with Mesozoic tectonics (HEADS, 1989).

2. Open habitats are always already present, even in such tall forests as those of central Africa. Open areas must always have existed in and around New Zealand forests, and this accounts for pockets of distinct, often locally endemic, open habitat taxa in and around present forests.

3. Current hybridism in the New Zealand flora now appears to be much rarer than has often been supposed. Earlier authors seem to have been misled by comparatively cryptic differentiation among the many species of small-leaved shrubs in *Hebe*, *Leonohebe*, *Coprosma* and *Olearia*. The different taxa accepted in this paper have distinct character combinations throughout their respective ranges which are bounded by features of tectonic significance. The differences among the species are admittedly sometimes very slight and species are sometimes interfertile. However, this indicates neither recent, rapid, nor continuing evolution in these genera. In fact, this information indicates nothing about the geological era in which the differentiation, rapid or otherwise, took place. Similar patterns of vicariance between taxa of different ranks, as shown above (e.g. Figs. 5-8), imply that degree of differentiation is *not* proportional to the time since vicariant formmaking. It also implies a general phase of modernisation, during which some taxa at a node differentiated to the level of genus, some to subgenus or species, and some only to the level of "cryptic" species, subspecies, "cytotype", etc.

   It is suggested here that dating can be done more effectively by correlating biogeography with tectonics. For example, South America — New Zealand affinities can be assumed to date to Mesozoic times, especially if endemism is involved.

4. There are many groups which are highly diverse in Australia, but absent or with little diversity in New Zealand (e.g. *Eucalyptus*, Leguminosae, Proteaceae). These groups may be represented in New Zealand and the Pacific by vicariants, (e.g. *Metrosideros* for *Eucalyptus*). The absence of the Australian groups east of the Tasman Sea, like the presence there of *Hebe*, etc., may be due simply to phylogenetic causes, with the ancestral populations of one region evolving into one taxon, and those of another region into a vicariant taxon, rather than to any invasion by long distance dispersal.

ACKNOWLEDGEMENTS

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REFERENCES

AIRY SHAW, H. K.(1973) *'J. C. Willis' Dictionary of the Flowering Plants and Ferns'.* 8th Ed. (Cambridge University Press: London).

ASHWIN, M. (1961). Euphrasia, Hebe (whipcord species), Parahebe, and Pygmea. *Flora of New Zealand* vol. 1. (ed. by H. H. Allan). Government Printer, Wellington.

BACKER, C. A. (1951). Hydrophyllaceae. *Flora Males.* I, 4: 207-209.

BAILLON, H. (1888). *The Natural History of Plants.* Vol. 8. Transl. M. Hartog. Reeve, London.

BAILLON, H. (1890). Sur l'Ellisiophyllum. *Bull. Mens. Soc. Linn. Paris* No. 103 (Janvier 1890): 817.

BARKER, W. (1982). Taxonomic studies in Euphrasia L. (Scrophulariaceae). A revised infrageneric classification, and a revision of the genus in Australia. *J. Adelaide Bot. Gard.* 5: 1-304.

BENTHAM, G. (1835). Caractères des tribus et des genres de la famille des Scrophularinées. *Ann. Sci. Nat. Bot.* (ser. 2) 4: 177-188.

BENTHAM, G. (1846). Scrophulariaceae. *Prodromus Systematis Naturalis Regni Vegetabilis* (ed. by A. de Candolle) 10: 320-586; 589-598. Masson, Paris.

BENTHAM, G. & J. HOOKER (1876). Scrophularineae. *Genera Plantarum* 2: 913-980. Lovell Reeve, London.

BRIGGS, B. G. & F. EHRENDORFER (1976). Chionohebe, a new name for Pygmea Hook. f. (Scrophulariaceae). *Contrib. Herb. Aust.* 25: 1-4.

BROWN, F. B. H. (1935). Scrophulariaceae. Flora of Southeastern Polynesia. Vol. III. Dicots. *Bernice P. Bishop Mus. Bull.* Vol. 130.

BUCHANAN, J. (1882). On the alpine flora of New Zealand. *Trans. Zealand Inst.* 14: 342-356.

CHEESEMAN, T. F. (1906). *Manual of the New Zealand Flora.* Government Printer, Wellington.

CHEESEMAN, T. F. (1914). *Illustrations of the New Zealand flora.* Government Printer, Wellington.

CHEESEMAN, T. F. (1925). *Manual of the New Zealand Flora.* 2nd Ed. Government Printer, Wellington.

CHIN, N., M. BROWN & M. HEADS (1991) The biogeography of Macrocystis (Lessoniaceae). *Hydrobiologia* 215: 1-11.

COCKAYNE, L. (1929). New combinations in the genus Hebe. *Trans. New Zealand Inst.* 60: 465-467.

COCKAYNE, L. (1958). *The Vegetation of New Zealand.* 3rd (reprint) Edition. Engelmann/Cramer, London.

COCKAYNE, L. & H. H. ALLAN (1927). The present taxonomic status of the New Zealand species of Hebe. *Trans. New Zealand Inst.* 57: 11-47.

CROIZAT, L. (1967). An introduction to the subgeneric classification of Euphorbia. II. *Webbia* 22: 83-202.

CROIZAT, L. (1968a) Introduction raisonnée à la biogéographie de l'Afrique. *Mem. Soc. Broteriana* 20: 1-451.

CROIZAT, L. (1968b) The biogeography of the tropical lands and islands east of Suez — Madagascar. *Atti Ist. Bot. Univ. Crittogam. Pavia.* ser. 6, 4: 1-400.

CROIZAT, L. (1975). Biogeografia analitica y sintetica ("Panbiogeografia") de las Americas. *Bol. Acad. Cienc. Fis., Mat. Nat.* Caracas. 35 (103-106). 890 pp.

DON, D. (1836). Sur les caractères de certains groupes de la classe des Personées. *Ann. Sci. Nat. Bot.* 5 73-82.

FLEMING, C. A. (1972). *The Geological History of New Zealand and its Life.* Oxford University Press, Auckland.

GENTRY, A. H. (1989). Speciation in tropical forests. *In*: L. B. HOLM-NIELSEN, I. C. NIELSEN & H. BALSLEV (Eds.), *Tropical Forests: Botanical Dynamics, Speciation, and Diversity*, pp. 113-134. Academic Press, London.

GIVEN, D. (1981). *Rare and Endangered Plants of New Zealand.* Reed, Wellington.

GOOD, R. (1974). *Geography of Flowering Plants.* 4th Ed. (New York: Wiley).

HEADS, M. J. (1987). New names in New Zealand Scrophulariaceae. *Otago Bot. Soc. Newslett.* 5: 4-11.

HEADS, M. J. (1989). Integrating earth and life sciences in New Zealand natural history: The parallel arcs model. *New Zealand J. Zool.* 16: 549-585.

HEADS, M. J. (1990a). A revision of the genera Kelleria and Drapetes. *Austral. Syst. Bot.* 3: 595-652.

HEADS, M. J. (1990b). Mesozoic tectonics and the deconstruction of biogeography: a new model of Australasian biology. *J. Biogeogr.* 17: 223-225.

HEADS, M. J. (1992). Taxonomic notes on the Hebe complex (Scrophulariaceae) in New Zealand. *Candollea* 47: 583-95.

HEADS, M. J. (1993a). Biogeography and biodiversity in Hebe, a South Pacific genus of Scrophulariaceae. *Candollea* 48: 19-60.

HEADS, M.J. (1993b). Morphology, architecture and taxonomy in the Hebe complex (Scrophulariaceae). *Adansonia*. In press.

HEDBERG, O. (1955). A taxonomic revision of the genus Sibthorpia L. *Bot. Not.* 108: 161-191.

HENDERSON, I. (1991). Biogeography without area? *Austral. Syst. Bot.* 4: 59-71.

HONG DE-YUAN (1984). Taxonomy and evolution of the Veroniceae (Scrophulariaceae) with special reference to palynology. *Opera Bot.* 75: 1-60.

HOOKER, J. D. (1844). *Flora Antarctica*. Reeve, London.

HOOKER, J. D. (1864). *Handbook of the New Zealand Flora*. Reeve, London.

JOHNSON, P. & D. CAMPBELL (1975). Vascular plants of the Auckland Islands. *New Zealand J. Bot.* 13: 665-720.

KIRK, T. (1896). Notes on certain veronicas and descriptions of new species. *Trans. New Zealand Inst.* 28: 515-531.

MACDONALD, A. D. (1980). Distribution maps of Hebe in Canterbury as an extension of the Canterbury checklist. *J. Canterbury Bot. Soc.* 14: 40-45.

MACDONALD, A. D. (1981). Distribution maps of Hebe in Canterbury. *J. Canterbury Bot. Soc.* 15: 32-35.

MACDONALD, A. D. (1982). Distribution maps of Hebe in Canterbury. *J. Canterbury Bot. Soc.* 16: 73-76.

MARK, A. F. & N. ADAMS (1973). *New Zealand Alpine Plants*. Reed, Wellington.

MATTHEWS, C. (1989) (Ed.). Panbiogeography special issue. *New Zealand J. Zool.* 16(4).

MELVILLE, R. (1966). Continental drift, Mesozoic continents and the migrations of the angiosperms. *Nature* 211: 116-119.

MOORE, L. B. (1961). Hebe (except whipcord species) and Ourisia. *Flora of New Zealand*. Vol. 1. (ed. by H. H. Allan). Government Printer, Wellington.

MOORE, L. B. (1975). Hebe. *New Zealand Nat. Heritage* 6: 2133-2138.

OHWI, J. (1965). *Flora of Japan* (English transl.). Smithsonian Institution, Washington.

OLIVER, W. R. B. (1944). The Veronica-like species of New Zealand. *Rec. Dominion Mus.* 1: 228-231.

PENNELL, F. W. (1937). Taxonomy and distribution of Aragoa and its bearing on the geological history of the northern Andes. *Proc. Acad. Nat. Sci. Philadelphia* 89: 425-432.

RAVEN, P. H. (1972). Evolution and endemism in the New Zealand species of Epilobium. *Taxonomy, Phytogeography and Evolution*, (ed. by D. H. Valentine). Academic Press, London.

RAVEN, P. H. & D. I. AXELROD (1972). Plate tectonics and Australasia palaeobiology. *Science* 176: 1379-1386.

SIMPSON, G. (1952). Notes on some New Zealand plants and descriptions of new species. (No. 5). *Trans. Roy. Soc. New Zealand* 79: 419-435.

SIMPSON, G. & J. S. THOMSON (1943). Notes on some New Zealand plants and descriptions of new species. *Trans. Roy. Soc. New Zealand* 73: 155-171.

SMITH, J. M. B. (1982). The alpine flora. *In:* VAN ROYEN, P. (Ed.), *The Alpine Flora of New Guinea* 1: 51-61. Cramer, Vaduz.

TSOONG, P. C. (1979). Clavis generum. (1). *Fl. Reip. Pop. Sin.* 67(2): 4.

VAN ROYEN, P. (1983). *The Alpine Flora of New Guinea.* Vol. 4. Cramer, Vaduz.

WETTSTEIN, R. VON (1891). Scrophulariaceae. *In:* ENGLER, A. (Ed.), *Nat. Pflanzenfam.* Teil 4, Abt. 3b: 39-107.

WILSON, H. (1976). *Vegetation of Mount Cook National Park, New Zealand*. Department of Lands and Survey, Wellington.

YAMAZAKI, T. (1957a). Taxonomical and phylogenetic studies of Scrophulariaceae — Veroniceae with special reference to Veronica and Veronicastrum in Eastern Asia. *Journ. Fac. Sci., Univ. Tokyo.* Sect. 3, 7: 91-125.

YAMAZAKI, T. (1957b). Seed formation of Ellisiophyllum pinnatum var. reptans. *Bot. Mag. Tokyo* 70: 162-168.

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