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Autor:	Heads, Michael
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Biogeography and biodiversity in *Hebe*, a South Pacific genus of Scrophulariaceae

MICHAEL HEADS

ABSTRACT

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

This paper includes distribution maps of the 67 species of *Hebe* s.str., arranged according to their presumed affinities. Notes on critical localities and patterns of vicariance are given. A pronounced massing of species occurs in Nelson/north Marlborough provinces. Many of the distributions within New Zealand can be correlated with Mesozoic tectonics, as can the New Zealand — Rapa Is. — southern South America disjunction within sect. *Hebe*.

RÉSUMÉ

HEADS, M. (1993). Biogéographie et biodiversité chez *Hebe*, genre de Scrophulariacées du Pacifique Sud. *Candollea* 48: 19-60. En anglais, résumés anglais et français.

Cet article comprend des cartes de répartition des 67 espèces d'*Hebe* s.str. arrangées selon leur rapports putatifs. Des notes sur les localités critiques et les exemples de vicariance sont données. Une concentration marquée des espèces se situe dans les provinces de Nelson et du Marlborough septentrional. Beaucoup des distributions en Nouvelle-Zélande peuvent être mises en corrélation avec des tectoniques Mésozoïques tout comme la disjunction: Nouvelle-Zélande — Ile Rapa — Patagonie dans la sect. *Hebe*.

KEY-WORDS: Biogeography — Biodiversity — *Hebe* — SCROPHULARIACEAE — South Pacific — New Zealand.

1. Introduction

Hebe is a genus of shrubs and small trees widespread in the South Pacific (Fig. 1). Two of the three sections and most of the species are confined to New Zealand (HEADS, 1987, 1992, 1993a, b). Many of the species are reasonably well understood and well represented in herbarium collections. The aim of this paper is to provide an overview of the biogeography of the genus rather than a full revision of the species. Data were collected from study of the material in New Zealand herbaria, from critical appraisal of published records and from personal field observations.

2. Biodiversity

Even in the narrow sense used here *Hebe*, with 66 species in New Zealand, is probably still the most diverse plant genus in that country. Next in size ALLAN (1961) lists 58 species for *Celmisia* (Compositae) and 50 for *Epilobium* (Onagraceae). Assessing biodiversity in this way, simply by

counting numbers of species, can be criticised, as in many cases it will be misleading (VANE-WRIGHT & al. 1991; FAITH, 1992). For example, in southern Africa the single species of *Welwitschia* probably represents greater biodiversity than does a species of *Combretum* or *Ficus*. FAITH (1992) suggested that "features" of organisms, rather than taxa such as species could be used in studies of biodiversity. It is true that "features", or characters, are the raw data of taxonomy and biodiversity, and emphasizing these is a sound approach in biology. For example, Linnaeus insisted that students learn more than one classification of a group, and thus emphasized the recombination of characters rather than any rigid hierarchy. Nevertheless the practical problems of dealing directly with such large amounts of raw data would be daunting in preliminary studies of biodiversity which presumably should deal with groups that are as large as possible. In cases such as *Hebe* it is clear that any taxonomy is useful, above all, as a summary or at least a sample of a vast amount of variation in populations where characters recombine in a kaleidoscopic way. The taxonomy used here is only one possible arrangement, but general conclusions, such as Nelson/northern Marlborough being a centre of diversity, would also be shown in many alternative classifications. The general principle that taxa and taxonomies can be used in comparative biogeographic analysis if the samples used are large enough (CROIZAT, 1964) seems valid.

Species and subspecies density of *Hebe* in New Zealand is shown in Fig. 2. Even when using species density as a convenient approximation of biodiversity, many errors are involved as well as the phylogenetic problem mentioned already. The understanding of the main evolutionary trends in the group is nowhere clear enough to allow the production of a credible dichotomous cladogram, and different species are broadly or narrowly defined (see below). Nevertheless the classification used here is more or less workable as a summary of the variation and the large numbers of species involved here give a good sample. The massing in Nelson comprises a species density fully three times that found through much of New Zealand. The pattern of massing is relatively simple, centred on Nelson/northern Marlborough, and tailing off first through South Is., and then through the rest of New Zealand. The Nelson/northern Marlborough massing of *Hebe* lies to the northeast of those of *Leonohebe* and *Chionohebe*, reflecting a fundamental vicariance, but is located on the same two degree squares (41-42°S, 172-174°E) as the main massing of *Pimelea* (Thymelaeaceae) species in New Zealand (Heads, in prep.)

3. Biogeographic nodes

In the case of *Hebe*, massing of species coincides geographically with what has been referred to as a major biogeographic node at Nelson (HEADS 1989, Figs. 12-17; HENDERSON, 1991). Biogeographic nodes can be characterised as centres of biological presence (endemism) and absence, as margins of distribution, and as points of disjunction. In addition, nodes can be the sites of anomalies in altitudinal range, e.g. the usually montane *Kelleria dieffenbachii* occurring near sea-level only at Shag Point, New Zealand (HEADS, 1990). Nodes also feature as centres of biodiversity, as in *Hebe* at Nelson, and as centres of "bizarre" and "grotesque" forms, e.g. Madagascar or Australia, the vegetation of the latter having been described as "Flora at the masked ball" (Correa da Serra, quoted in ARBER, 1970). Possibly the most bizarre *Hebe*, *H. townsonii*, has stiff, lanceolate leaves with marginal domatia, and is also found in Nelson. This massive diversity in Nelson/northern Marlborough has considerable implications for conservation. The scenery in the region is not as spectacular as that in the higher Southern Alps further south and is consequently less well-known internationally and generally more developed, with fewer and smaller national parks.

Determining the age of the Nelson massing is a key problem in understanding its history and significance. The group of genera in the "Hebe complex" is certainly pre-Cretaceous: New Zealand — Australia connections occur in *Leonohebe* and *Chionohebe*, New Zealand — New Guinea connections occur in *Parahebe*, and New Zealand — Rapa Is. — southern South America ties are found in *Hebe*. The Nelson massing — as a massing — and its geographic location are probably Mesozoic, although particular species may have changed since then. There has been major tectonic activity

in Nelson, including upper Mesozoic granite emplacement, and a general correlation between geology and biogeography in the region was suggested by HEADS (1989). Recently HAY (1992) has also accepted species stasis over 100 m.y. for certain Araceae.

Nelson as a node may show connections with S.E. Australia directly (*Oreopanax*—*Poranthera*—Euphorbiaceae), or with the northeast New Zealand "horsts" (HEADS, 1989). In *Hebe*, despite a Nelson main massing, there is no New Zealand — Australia connection. The trans-Tasman ties in *Leonohebe* and *Chionohebe* range between SE Australia and southern South Island.

Rapa Island (Austral Is.) features prominently in the distribution of *Hebe* with an endemic species there related to the Chatham Is. species. This affinity is an extension of the common "outer arc" endemism in the New Zealand region involving the Subantarctic Is., Chatham Is., Three Kings Is. etc., and related to evolution along the Vening Meinesz Fracture Zone (HEADS, 1989). The New Zealand — Rapa Is. tie is found widely throughout plant life. Another particularly interesting example is the dicot shrub genus *Corokia*, restricted to New Zealand, Rapa Is., Lord Howe Is. and a very small area in eastern Australia (near the MacPherson/Macleay Overlap) (EYDE, 1966). The Rapa Is. *Corokia*, endemic there, was treated by BROWN (1928) as a new genus linking eastern Asian and eastern North American species of *Cornus*. This is a very interesting role for the central South Pacific to play, especially as *Corokia* itself has such interesting relationships. It has been placed in Rhamnaceae, Cornaceae, and in Saxifragaceae Escallonioideae with *Argophyllum* (Australia and New Caledonia). Eyde reports that "*Corokia* has generalised pollen and wood characters in common with a number of families". Rarely, two adjacent corolla lobes are united for most of their length. *Argophyllum* and *Corokia* share an unusual hair type with Loranthaceae and the related Proteaceae, with Compositae and Asclepiadaceae in the Tubiflorae, and with Pittosporaceae, the latter more closely related to *Corokia*. Even within Scrophulariaceae the massive blue and red-flowered members of *Hebe* sect. *Occlusae* begin to have the appearance of *Corokia*, as the flower of these *Hebe* species is hardly zygomorphic and the posterior corolla lobe is only slightly deflexed. The affinities of *Corokia*, although clear enough in general, are very wide. In this the genus resembles other linking forms of the south Pacific region such as *Alseuosmia*, *Corynocarpus*, *Griselinia* and *Donatia*. It is very difficult to see these forms as anything but relicts from an early phase of angiospermy, when many connecting forms still existed and family limits were not as clear cut as they are to-day. Likewise, it is difficult to see the distribution of these families in the south Pacific as due to migration by chance long distance dispersal, following the primary differentiation of angiosperm families elsewhere. The South Pacific is interpreted here as a primary centre of differentiation in its own right which has led to the existence there of relic plants with relic distributions.

The New Zealand — Patagonia disjunctions in *Hebe salicifolia* and *H. elliptica* have often been explained as the result of long distance dispersal, largely because there is no apparent difference between the New Zealand and the South American populations. However, in related plants trans-Tasman ties occur in *Leonohebe* and *Chionohebe* (same species), *Ourisia* (related species) and *Parahebe* (very different species), and New Zealand — New Guinea connections are seen in *Parahebe*. These connections are usually accepted as indicating Mesozoic age (HEADS, 1989). In addition, the New Zealand — South America connection of *Hebe* spp. is also seen in other Scrophulariaceae (*Ourisia*, *Euphrasia*, *Jovellana*). These facts suggest that the disjunction in *Hebe* is a normal component of the standard New Zealand — Patagonia track seen in many organisms and attributed to Mesozoic evolution and the subsequent break-up of Gondwanaland. In *Hebe* the species involved have shown a notable lack of differentiation over tens of millions of years (cf. HAY, 1992; CROIZAT, 1964).

4. Species concepts

Hebe is a mix of broad and polymorphic species such as *H. pinguifolia*, other species which are smaller, well-defined local vicariants, and intermediates between these two. Probably many plant species in New Zealand could be better treated as subspecies, with broad species concepts like those of ornithology. However, before this lumping can be done biogeographic studies are

desirable — the information available for birds is unusually good. Also, the new subspecies must not be subsequently ignored simply because they are treated below the rank of species, which is perhaps not as "special" as it is often assumed to be. Ornithologists argue with reason that the unit of conservation of birds should be the subspecies. So possibly in the future many New Zealand species will be seen as vicariant subspecies. Nevertheless, in the present state of botanical knowledge, to maintain consistency throughout Scrophulariaceae and related groups most taxonomic units in *Hebe* are best described as species.

5. Hybridism

Hybridism has, no doubt, played an important part in the evolution of the New Zealand flora, but the products now seem largely "fixed". A tendency in botany to identify the inevitable residue of difficult specimens as "hybrids" has sometimes developed as a substitute for undertaking time-consuming taxonomic enquiry, and this is especially obvious in the large genera *Hebe* and *Coprosma*. Taxonomic publications on these groups have virtually ceased to appear despite the fact that many new, distinctive taxa await description. Workers have probably been put off by the idea that hybridism is rampant and so diversity must be hopelessly complex. Likewise the nearly total absence of distribution studies (maps, analyses, etc.) of these groups may be attributed to the dominant concept of long-distance, chance dispersal.

6. *Hebe* as an example of "adaptive radiation"

Three main trends or clines are evident in the ecology of *Hebe*. Species are found:

1. From open types of landscape (most species) to closed, more or less shaded forest.
2. In a sequence of habitats with different water-relations: wetlands — streamsides — dry banks — rocks (limestone, greywacke, schist, volcanics).
3. In an altitudinal range from the littoral (both sea-cliffs and coastal lagoons) to the high alpine zone.

Combinations of positions on these three axes give a wide range of species ecologies.

The diverse ecology of a group like this is usually interpreted as the result of an "adaptive radiation" within the group, the group supposedly having developed by radiating out from a single species ancestor. This concept of a uniform ancestor (or "stem species") has been criticised elsewhere (HEADS, 1985). In *Hebe* the evidence suggests (HEADS, 1992, 1993a, b) that the differentiation in trends 1. and 2. above may have already been present in an ancestral complex which only later became modernised as *Hebe* and related genera. This differentiation perhaps even goes back to a gymnospermous ancestor, and it is interesting that the vegetative architecture of *Hebe townsonii* is similar to that of some African Podocarpaceae. Ancestral water relations (swamp forms, rock forms) are conserved in descendant taxa, even after these have been left stranded inland.

With respect to altitude (trend 3), the ancestral Mesozoic complex which gave rise to *Hebe* etc. probably comprised forms of the coasts and lowlands, like the ancestors of many angiosperms. Due to their prior distribution, some groups (e.g. *H.* sect. *Glaucae*) were subsequently stranded inland following Tertiary and Quaternary uplift and receding of inland seas, and have even survived uplift to alpine heights. So in terms of altitude the pattern of ecological differentiation is not the result of one species of proto-*Hebe* invading newly risen mountains and then differentiating. The altitude of populations is interpreted here as a more or less direct outcome of the geological processes of uplift and erosion changing the altitude of the land and the plant communities already there. In seeing alpine plants as those that survived uplift, very little importance is attributed to "adaptation". Rather "adaptive structure", such as small, coriaceous leaves, is seen as pre-adaptation already present in the ancestors and not primarily adaptive in the currently alpine plants. Data on altitude are not included here and warrant a separate study.

Hebe and other angiosperm taxa can be construed as groups which show correlated tendencies, e.g. in flower and fruit morphology, but which are massively polyphyletic in terms of their origin from a diverse ancestor. The vast amount of “parallelism” (and “incongruence”) evident in angiosperm characters is neither an accident, nor the result of selection pressure or “adaptive radiation”, but is simply inherited by different groups from an *already diverse* ancestor.

In conclusion, evolution in *Hebe* did not take place as an “adaptive radiation” from a “stem species”, but rather as a modernisation of an already diverse group, widespread in the South Pacific. This modernisation event was not recent — the Quaternary Ice Ages had little effect on the main aspects of distribution (HEADS, 1993b) — but Jurassic/Cretaceous, that is, at the same time as the last modernisation event for life in general. It is not surprising that the group, and groups with similar distributions, are structurally intermediate between tribes and families, and also show standard intercontinental disjunctions.

Hebe Commerson ex A. L. de Jussieu (1789)

Distribution: Patagonia and Falkland Is. (2-3 spp.), Rapa Is. (Austral Is.) (1 sp.), New Zealand (throughout — ca. 66 spp.). In New Zealand the genus ranges from northern and southern coasts to the high alpine zone (2100 m: *H. buchananii*). The overall geographic range of *Hebe* is shown in Fig. 1 which depicts sect. *Hebe*. The two remaining sections are confined to North and South Is. of New Zealand.

Cutting across the classification used here is the “parallel” or “incongruent” occurrence of leaf pubescence in different groups in the same geographic region. In sect. *Subdistichae* and sect. *Hebe* (and also *Leonohebe* sect. *Apiti*) leaf pubescence is concentrated on outer arcs of the New Zealand region (“horstian” dispersal — HEADS, 1989), in particular along the northeast sector: Three Kings Is. — northeast Auckland — Chatham Is. Within the context of sect. *Glaucae*, itself a group of inland South Is., the two pubescent forms (*H. gibbsii* and *H. allanii*) are also located on an outer eastern arc. The peculiar ciliolate corolla lobes of *H. speciosa* are also found in a species restricted to what is virtually an insular arc (Fig. 13), this time in the west.

Hebe sect. *Subdistichae* Heads (1987)

Species 1-5 form a loose series of forms (*H. vernicosa* is placed on Fig. 4 for the sake of clarity). The group (Fig. 3) is concentrated in S.W. South Is. (Hump Ridge — Wilmot Pass — Eyre Mts. — Garvie Mts.) and N.W. South Is. (west Nelson). As well as these disjunct massings there are disjunct species (*H. cockayneana*, *H. canterburiensis*) in these same areas. This pattern has been interpreted (HEADS, 1989) as the result of pulling apart of populations on the Alpine Fault. In Nelson the distribution of *H. cockayneana* is enclosed in that of *H. canterburiensis*, a distinctive concentric pattern repeated in the next map, Fig. 4.

1. Hebe cockayneana (Cheeseman, 1906) Cockayne & Allan (1926). Fig. 3.

Shrubland and tussock grassland. The southern massing ranges from Wilmot Pass/Mt. George and Eyre Mts./Humboldt Mts. north to Cascade Valley — Lake Sweeney (just to the east of the Alpine Fault)/Mark’s Flat. Further north, disjunct populations occur at Ada Pass (by Lewis Pass)/Travers Ra. (on the Alpine Fault), north to Mt. Peel. The boundaries by the Fault and the extent of lateral displacement involved strongly suggest that the disjunction in this species is a result of movement on the Alpine Fault. The species shows some affinity with *Leonohebe odora* in leaf texture and colour, and CHEESEMAN notes (1925): “The blackish colour of the leaves when dried [cf. several members of *Leonohebe*] is very peculiar.”

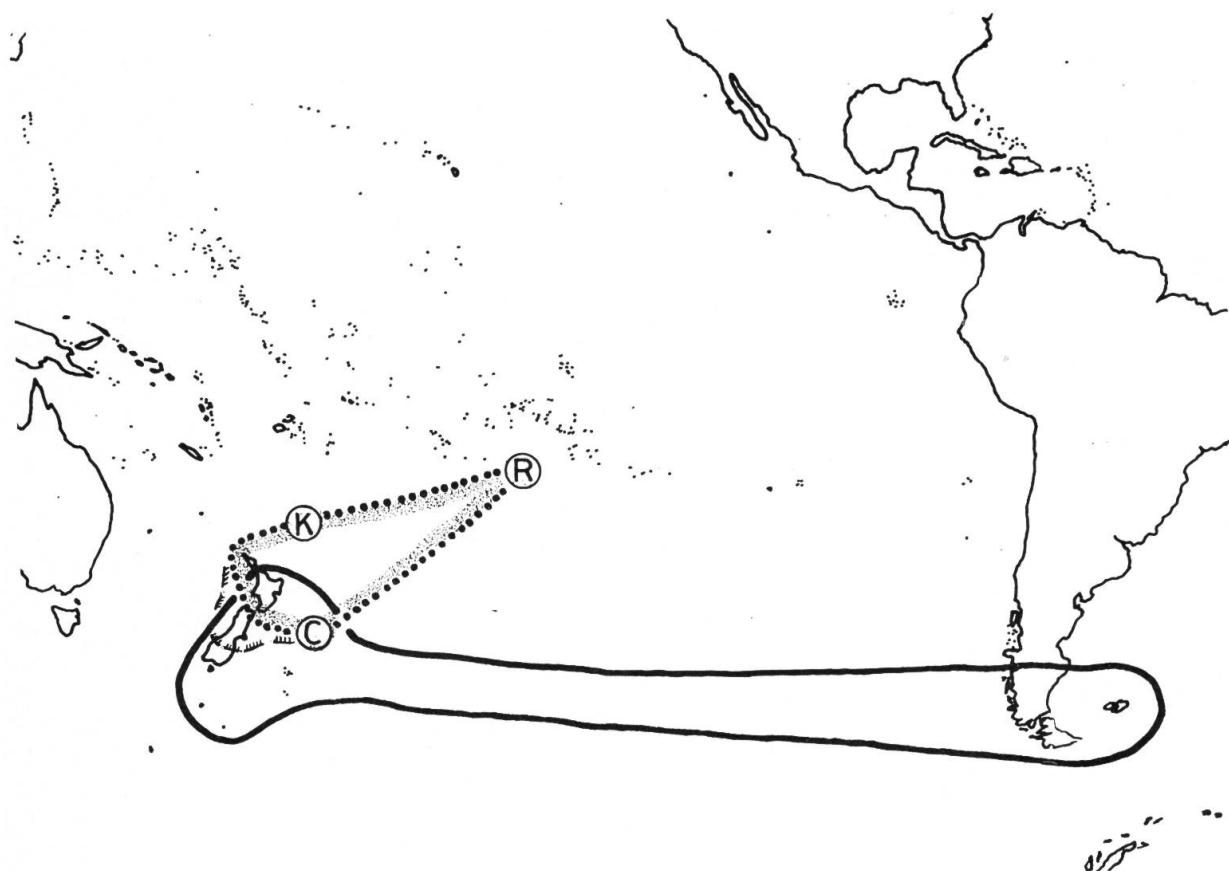


Fig. 1. — Distribution of *Hebe* beyond New Zealand.
Hebe sect. *Hebe* ser. *Hebe*: solid line.

Hebe sect. *Hebe* ser. *Occlusae* without the *traversii* complex: dotted stippled line, with the *traversii* complex: broken hatched line.
 R = Rapa Is.; K = Kermadec Is.; C = Chatham Is.

2. *Hebe dilatata* Simpson & Thomson (1943); Heads (1992). Fig. 3.

Debris slopes, Garvie Mts.

3. *Hebe crawii* Heads (1987). Fig. 3.

Talus slopes, boulderfield, fellfield, shrubland. Takitimu Mts., Eyre Mts., Garvie Mts., Umbrella Ra. (see also HEADS, 1992).

4. *Hebe canterburiensis* (J. B. Armstrong, 1879) Moore (1961). Fig. 3.

Known in the west only from Hump Ridge (Southland), Omoeroa (*Wardle*, CHR) and Waimangaroa. MOORE (1961) refers to these populations as possibly comprising a distinct variety. The track connecting these localities skirts *H. cockayneana* and *H. crawii* to the west, with all three species occurring close to each other only at a triangle: Hump Ridge — Takitimu Mts. — Wilmot Pass. The main part of the distribution of *H. canterburiensis* ranges from: Arthur's Pass — Paparoa Ra. — Lake Sylvester, east to Esk V. (mid-Waimakariri) — upper Wairau — Red Hill. This distribution encloses that of *H. cockayneana*, with the boundaries meeting only near Mt. Peel.

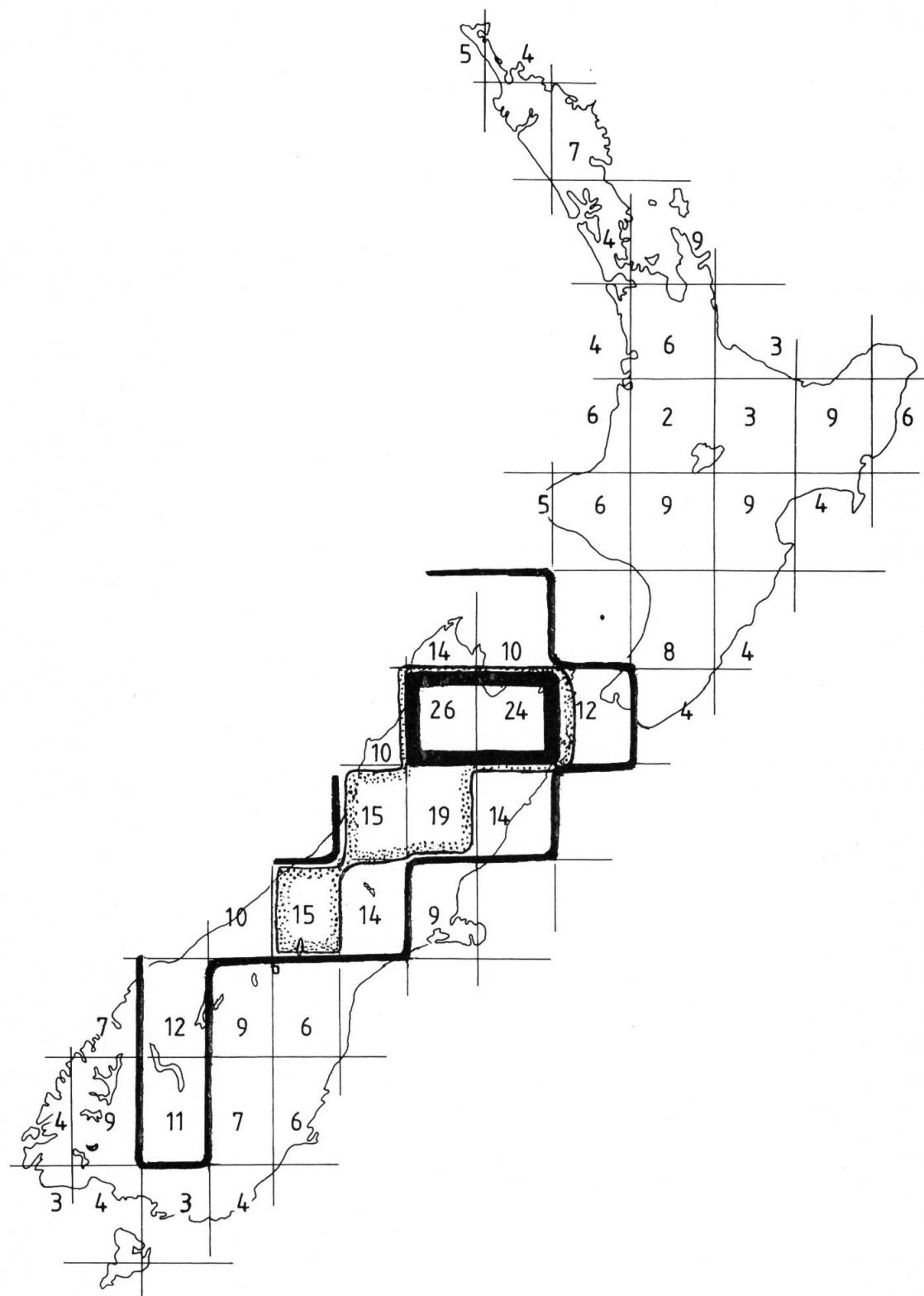


Fig. 2. — Numbers of species, subspecies and varieties of *Hebe* in each degree square of New Zealand.

5. *Hebe vernicosa* (Hook. f., 1864) Ckne. & Allan (1926). Fig. 4.

In *Nothofagus* forest and tussock-shrubland from: Paparoa Ra. — Burgoo Stream (N.W. Nelson) east to: Amuri Pass — upper Wairau — Bounds Ra. — Mt. Piripiri (by Picton).

6. *Hebe venustula* (Colenso, 1895) Ckne. (1929) (retransferred by Moore, 1961), incl. *H. brachysiphon* Summerhayes (1927). Fig. 4.

This shrubland plant shares the western base-line: Paparoa Ra. — northwest Nelson (Gouland Downs) with *H. vernicosa*, but extends south to Arthur's Pass — Mt. Oxford (mid-Waimakariri), and north to Mt. Taranaki (= Mt. Egmont). The boundary: mid-Waimakariri — Terako — Kekerengu — Cape Palliser — Pahaoa Gorge connects at Cape Palliser with the boundary: Gouland Downs — D'Urville Is. — Palliser. A second track holds the centre of North Is.: Mt. Taranaki — Waimarino — Ruahine Ra. — Kaweka Ra. — Mt. Hikurangi. The Tararua Ra. is thus skirted by the two tracks in a peculiar "pincer" arrangement. This absence from the Tararua Ra. complements the role of the range as a centre of endemism in, e.g., *H. evenosa* (Fig. 18). Just like *H. canterburiensis*, the distribution of this species encloses the northern South Is. populations of *H. cockayneana*, with the boundaries meeting only at Mt. Peel. *H. venustula* also encloses the distribution of the previous species and this pattern is basically a repeat of that shown by *H. cockayneana* and *H. canterburiensis*.

7. *Hebe rigidula* (Cheeseman, 1906) Ckne. & Allan (1926). Fig. 5.

Rocky places, sometimes by the side of streams, along the more or less linear track: Lewis Pass — Wairau Gorge — Richmond Ra. — D'Urville Is. — Kawhia. This central track contrasts with the South Is. — North Is. connections of *H. venustula*. In the context of other related species (Fig. 6) it acts as a central vicariant of parallel tracks in the west (*H. divaricata* — *H. diosmifolia*) and in the east (*H. rupicola* — *H. colensoi*). In the South Is. its distribution conforms to the mutual boundary of *H. divaricata* and *H. rupicola* with striking precision.

8. *Hebe divaricata* (Cheeseman, 1906) Ckne. & Allan (1926). Fig. 6.

In forest and shrubland on rocks and by streamsides at: Aorere Valley (NW Nelson) — Red Hill — Pelorus Sound. CHEESEMAN (1925) regarded this as "very close indeed to *H. diosmifolia*", and the corymbose inflorescence of these two species and *H. insularis* is distinctive in the tribe, although inflorescences of several other members of this section may show some primary branching. The far west connection between the two species: Aorere — Waipoua is a notable disjunction.

9. *Hebe diosmifolia* (A. Cunn., 1836) Ckne. & Allan (1926). Fig. 6.

Banks of rivers and creeks, waterfalls, shrubland and cliffs on the west of North Auckland at: Waipoua — Ahipara, through to the eastern line: Whangarei — Bay of Islands — Karikari Peninsula — North Cape. MURRAY & al. (1989) studied the various forms of *H. diosmifolia* and discovered the existence of two chromosome races, one diploid and one tetraploid. These authors state that the races "do not show a very clear pattern of geographic separation", but their records of tetraploids at Rarawa, Karikari Peninsula and Te Paki, with diploids to the west, indicate a pattern of vicariant parallel arcs which is standard in this region (HEADS, 1989).



Fig. 3. — *Hebe cockayneana*: dotted stippled line. *H. crawii*: hatched line. *H. dilatata*: stippled circles. *H. canterburiensis*: solid line.

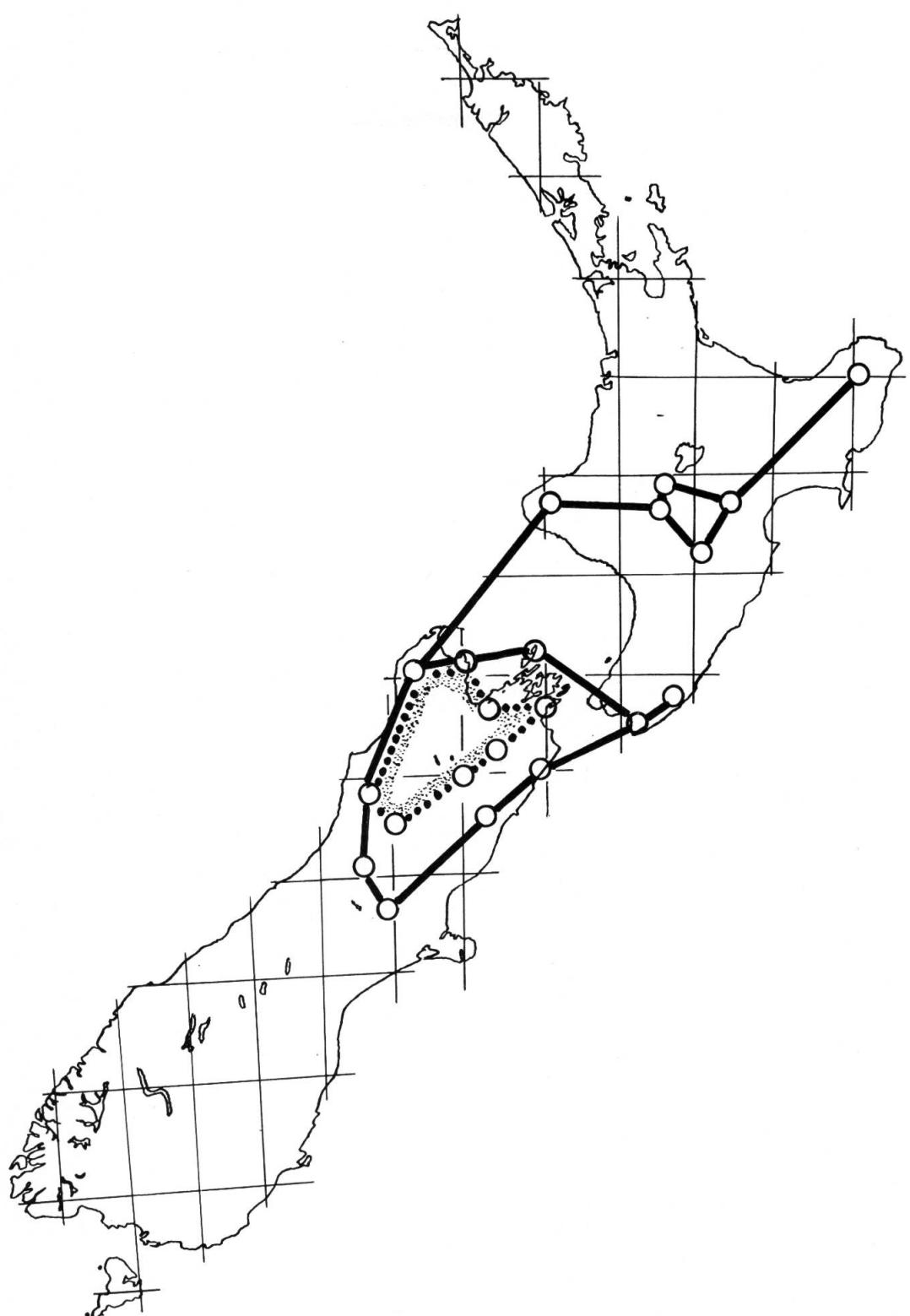


Fig. 4. — *Hebe vernicosa*: dotted stippled line. *H. venustula*: continuous line.

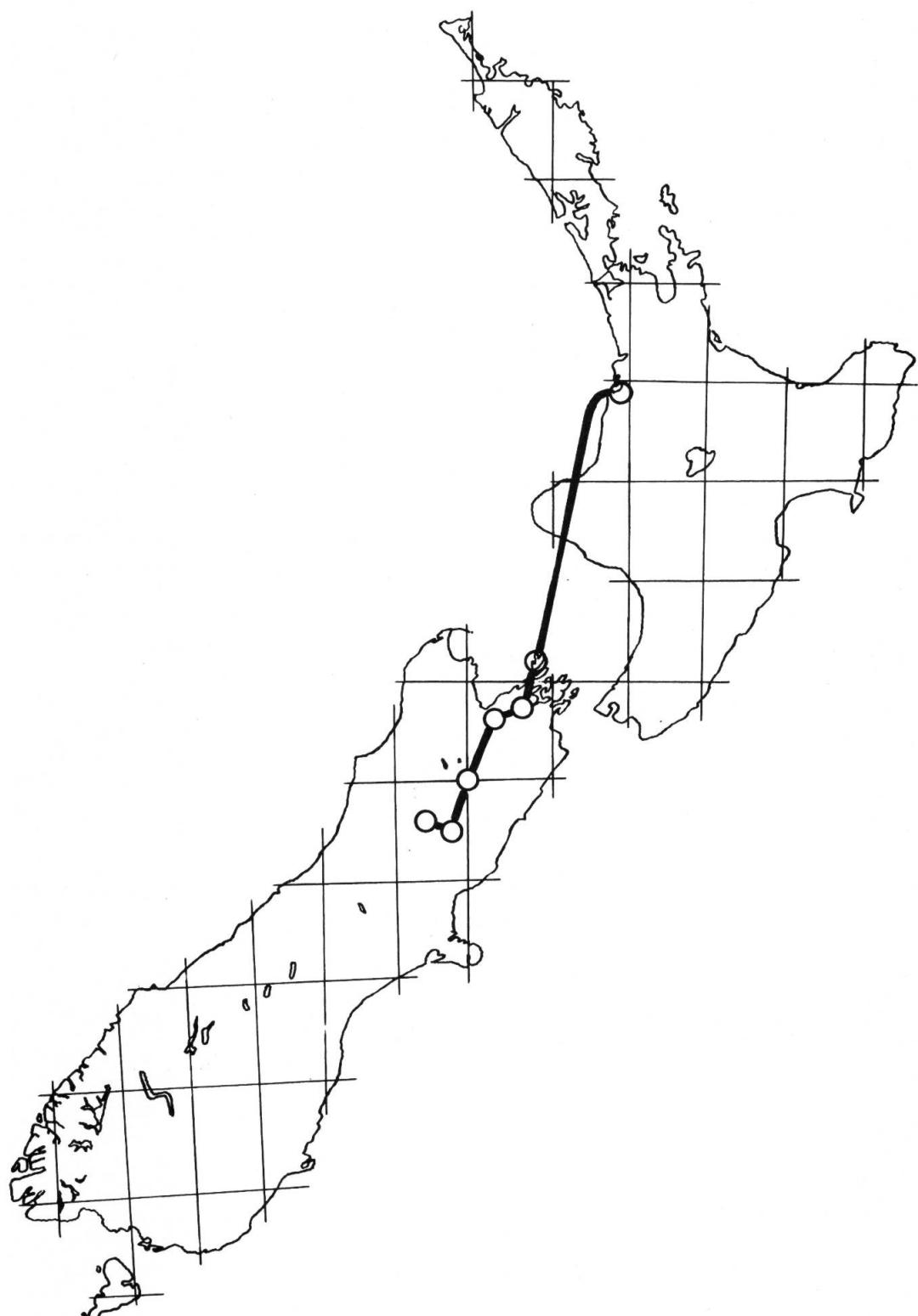


Fig. 5. — *Hebe rigidula*: continuous line.

10. *Hebe rupicola* (Cheeseman, 1906) Ckne. & Allan (1926). Fig. 6.

Rocky places on and east of a line: Red Hill — Wairau Gorge — Tekoa, to the axis: Terako — Kekerengu, thus vicariating (at Red Hill) with *H. divaricata*. The boundary between the two species is itself tracked closely by *H. rigidula*, and thus a “centre” or “track” of endemism acts at the same time as a boundary or limit of distribution/dispersal. This phenomenon can also be seen in the South Is. at, for example, the Eyre Mts. — Garvie Mts., at the Takitimu Mts., and at Caswell Sound — Doon V. — Murchison Mts. (*Leonohebe pauciflora*, *Parahebe planopetiolata*). The distribution of *H. rupicola* is directly comparable with that of *Parahebe catarractae* subsp. *martinii*. Its nearest ally is probably *H. colensoi* (CHEESEMAN, 1925). This affinity (indicated on Fig. 6) shows an eastern connection between North and South Islands (Kekerengu — Moawhango), complementing the western connection in *H. divaricata*/*H. diosmifolia*, and the central connection in *H. rigidula*.

11a. *Hebe colensoi* (Hook. f., 1864) Ckne. (1929) var. *colensoi*

11b. *H. colensoi* var. *hillii* (Colenso, 1896) Moore (1961). Fig. 6.

This dimorphic species is known from cliffs and stony ridges in the triangle: northwest Ruahine Ra. (Moawhango) — Kaimanawa Ra. — Kaweka Ra.

12. *Hebe insularis* (Cheeseman, 1897) Ckne. & Allan (1926). Fig. 6.

Rocky places, fissures and ledges on sea-cliffs of Three Kings Is. Plants of *H. insularis* are variable, being glaucous or not, decumbent (rare in this section) or erect shrubs, and MOORE (1961) reports that some leaf buds lack the sinus. Moore also observed that the indumentum when best developed resembles that of some Chatham Is. species (ser. *Occlusae*). The species is clearly highly polymorphic, showing complex affinities with sects. *Hebe* and *Glaucae* as well as with *Subdistichae*. In *Leonohebe* an equivalent node would be Auckland — Campbell Is., where *L. benthamii* shows affinities with several different groups.

For *H. insularis* HAIR (1967) records and illustrates a chromosome number of $n = 20 +$ fragment. The “extra fragment” chromosome, also known as an “accessory” or “supernumerary” chromosome, is usually called a “B chromosome”. It is unknown elsewhere in New Zealand Scrophulariaceae, where chromosome numbers have proved useful in taxonomic studies (HEADS, 1992, 1993a). The B chromosome system, although widespread in gymnosperms, angiosperms, platyhelminths, molluscs, arthropods and vertebrates (JONES & REES, 1982), is highly “anomalous” in its distribution, as it may be present within a species in only some organs of some individuals of some populations. It is also anomalous in its behaviour at meiosis and non-Mendelian patterns of inheritance. In many organisms the B system is deleterious, and it is often regarded as “parasitic” (JONES & MATTHEWS, 1983; THOMSON, 1984). JONES & REES (1982) write: “while B chromosomes are not essential for normal growth and development, their effects upon the phenotype are manifold, often pronounced, and sometimes startling.” Although Jones & Rees assume that B chromosomes are derived from the normal A chromosome complement, they note that “there is no example to date which records in detail the origin and evolution of a particular B chromosome.” STEBBINS’ (1971) conclusion seems reasonable: “the evolutionary origin of accessory chromosomes is still largely a matter of hypothesis and conjecture. The fact that, with few exceptions, they show no signs of homology with chromosomes of the basic set, and are completely different in size and morphology, suggests that in most species which have them they are not recently derived from the basic chromosomes.”

This view is compatible with the pivotal biogeographic and phylogenetic position held by *H. insularis*.

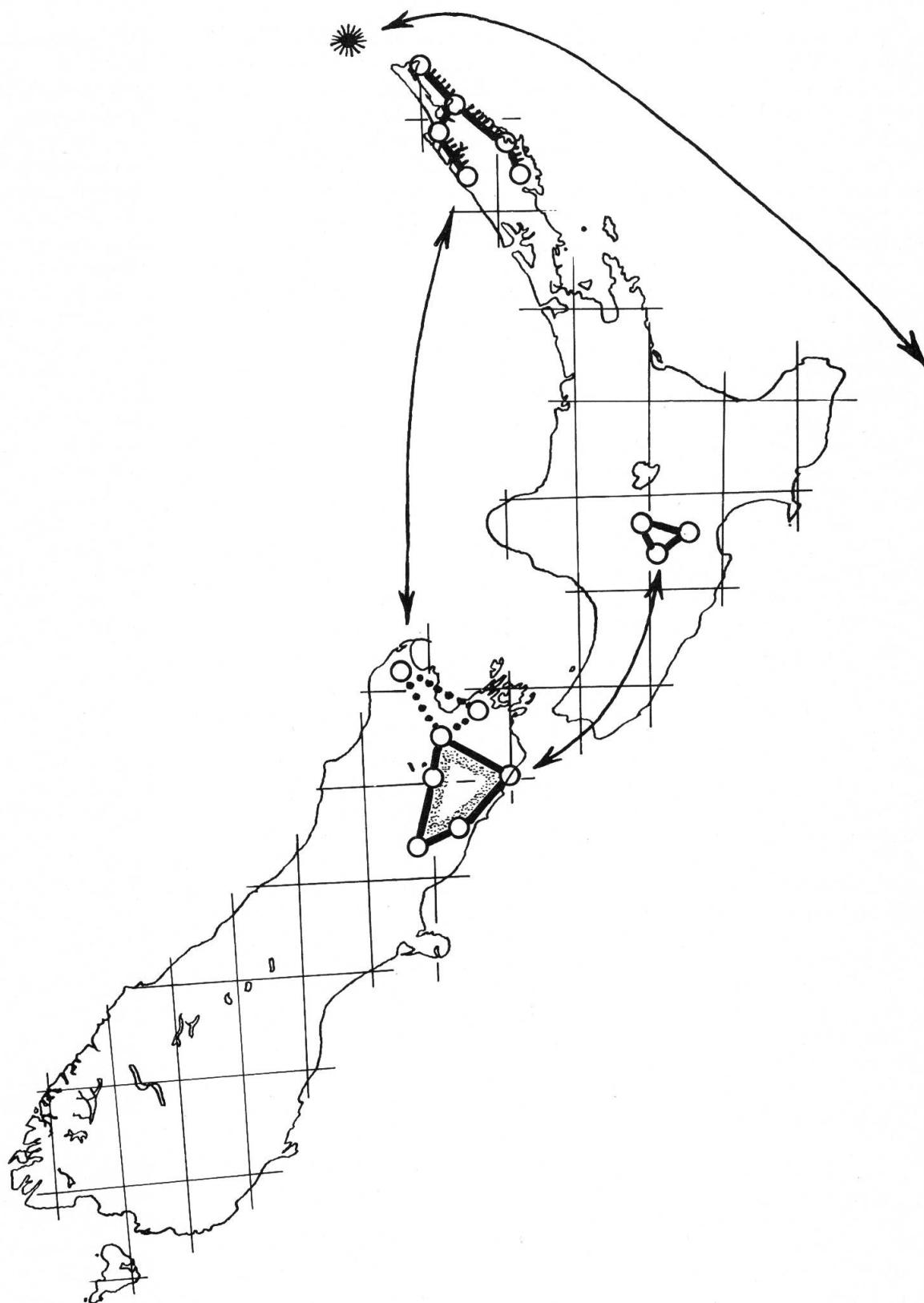


Fig. 6. — *Hebe divaricata*: dotted line. *H. diosmifolia*: hatched line. *H. rupicola*: stippled line. *H. colensoi*: continuous line. *H. insularis*: asterisk (affinities with Chatham Is. species indicated by arrow).

In a synthesis of the largest and smallest scales in biology, CROIZAT (1984) interpreted evolutionary development as a function of (a.) molecular biology and (b.) biogeography, and some recent work utilises this approach. For example, KIMURA (1983) mapped the geographic distribution of alleles (at the alcohol dehydrogenase and esterase-1 loci) in Japanese fishes. The biogeographic basis of the patterns is obvious from the maps provided by Kimura, and is used by him to argue for "neutral", i.e. non-adaptive, vicariant evolution. Similarly, BERMINGHAM & AVISE (1986) analysed molecular zoogeography of American fishes with reference to restriction fragment length polymorphisms in mitochondrial DNA. They introduce their paper with a summary of Croizat's views on vicariance of widespread ancestral biotas along standard tracks. Among their results, a major east-west break in *Lepomis punctatus* is found to be "remarkably concordant in geographic placement" with a main break in *Amia calva*, and this intraspecific pattern is itself "remarkably ... highly concordant" with patterns of other fish species, thus giving similar biogeography at different taxonomic levels. As these authors argue, "it seems likely that similar historical factors might account for both phenomena", and they provide a discussion of historical geology. They conclude that: "any interpretations of population genetic structure that fail to consider the possible influence of history in shaping that structure, may be seriously inadequate." In another molecular study of relevance to general evolution and biogeography, BEVERLEY & WILSON (1985), on the basis of estimated amino acid sequence divergence, have argued that Drosophilinae have been evolving at the location of the Hawaiian Archipelago for at least 40 m.y., i.e. older than the present terrestrial rock strata.

The history of the enigmatic B chromosomes would thus seem amenable to biogeographic analysis. For example, WESTERMAN (1975) studied B chromosomes in the New Zealand grasshopper *Phaulicridium marginale* at 9 North Is. and 3 South Is. sites. By far the highest frequency of B chromosomes was recorded at Black Jack, NE Coromandel Peninsula, which shows many biogeographic connections with the Three Kings Is. (via the "northeast horsts" — HEADS, 1989), the site of the B chromosomes in New Zealand Scrophulariaceae.

Hebe sect. *Glaucae* Heads (1987)

These plants are characteristically found on rocky platforms and outcrops and in shingle, generally favouring better drained sites. The group is found in inland South Is. (lowland to alpine) and nearer the coast in the northeast of the island. This contrasts with groups such as *Leonohebe* (HEADS, 1993b) and *Kelleria* (Thymelaeaceae, HEADS, 1990) which occur at the coast in the south of South Is. Close affinities exist with the fleshy-leaved members of sect. *Hebe* (*H. elliptica*, *H. obtusata* etc.) which are found along present coastlines, and these vicariate with the inland sect. *Glaucae*, members of which appear to be stranded along old coastlines. Sect. *Glaucae* is also linked, via *H. crawii* and *H. insularis*, with sect. *Subdistichae*.

In species 13-19 the flowers are sessile, and the lowermost bracts opposite (MOORE, 1961). The group is confined to a strip ca. 60 km wide running down the centre of the island between Manapouri and Nelson.

13. *Hebe buchananii* (Hook. f., 1864) Ckne. & Allan (1926). Fig. 7.

Rock outcrops, fellfield and cushion vegetation. From Green Lake/Hunter Mts. the species ranges north to Eyre Mts./Livingstone Mts. — Humboldt Mts./Darran Mts. — Mt. Alta — Mt. Cook/Liebig Ra. (cf. *Leonohebe mooreae*, *Ourisia remotifolia*). It extends eastwards to Mid Dome — Umbrella Mts. — Lammermoor Ra. (Patrick, OTA) — Rock and Pillar (where Moore records the "most divergent form") — Dansey Pass — Kirkliston Ra. — Mt. Peel — Two Thumb Ra. (cf. *Leonohebe hectorii*). Chromosome number is generally $n = 40$. HAIR (1967) identifies specimens from Canyon Ck. (Ahuriri), Mt. Maud (Central Otago) and Rock and Pillar ($n = 20!$) as "*Hebe* aff. *buchananii*". In addition, larger forms approach *H. pinguifolia*. Leaves are reflexed in MARK & WELLS, 1965, Old Man Ra., OTA, giving the appearance of *Leonohebe epacridea*. This specimen has ovaries with long, straight, erect pubescence, unlike that of more typical *H. buchananii* from

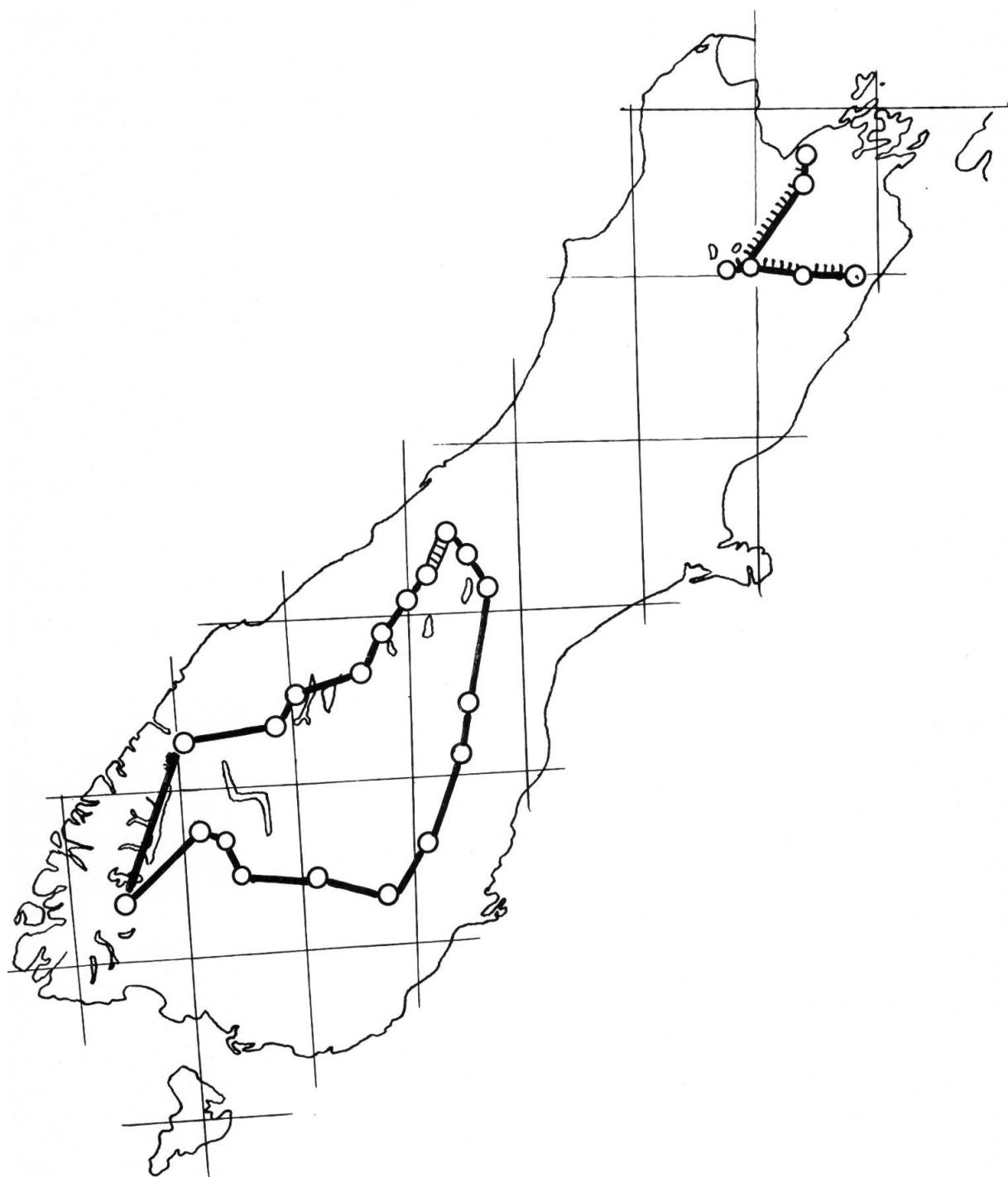


Fig. 7. — *Hebe buchananii*: continuous line. Large-leaved populations of *H. buchananii*: double hatched line. *H. carnosula*: hatched line.

the same range (e.g. Wells, 1966, OTA). Rock and Pillar specimens have medium length, shaggy ovary pubescence, and disc to fully 1/2 the length of the ovary. Three OTA collections from Hooker Valley and Malte Brun identified, understandably enough, as *Leonohebe pauciramosa*, have no sinus and are here treated as a large-leaved form of the *H. buchananii* complex (Fig. 7). (In the *H. buchananii* var. *major* folder at AK are very interesting Mt. Cook specimens. Matthews, Mt. Kyeburn, also filed here, is possibly *H. biggari*). Typical *H. buchananii* is recorded from Mt. Cook National Park by WILSON (1976) who suggests that the large-leaved form is the result of hybridism between *H. buchananii* and *H. subalpina*. The quite restricted geographic distribution of the form would seem to argue against this.

14. *Hebe carnosula* (Hook. f., 1864) Ckne. (1929). Fig. 7.

From Travers Ra./St. Arnaud Ra. east to Tapuaenuku, and northeast to Mt. Richmond and Dun Mt. (Bryant Ra.). CHEESEMAN (1925) regarded this as: "very closely allied to *V. pinguifolia*", and it also appears to be a northern vicariant of *H. pimeleoides*.

15. *Hebe pimeleoides* (Hook. f., 1864) Ckne. & Allan (1926).

15a. *Hebe pimeleoides* var. *pimeleoides*. Fig. 8.

From a western margin: Queenstown — Shotover V. — Hopkins V. — Godley V. — Arthur's Pass — Fowler's Pass (by Lake Tennyson) — Rainbow R. (upper Wairau), this ranges east to: Mt. Ida — Lake Heron — Port Cooper (Banks Peninsula) — Mt. Symons (by Tapuaenuku).

15b. *Hebe pimeleoides* var. *rupestris* Ckne. & Allan (1926). Fig. 8.

Recorded only from: Queenstown — Kawarau Gorge — Dunstan Mts. — Chatto Ck. — west above Lake Roxburgh, and so restricted to sectors of the Kawarau — Clutha — Manuherikia system of lowlands (Central Otago). This lowland distribution complements alpine endemism in the same geographic region at Pisa Ra., Old Man Ra. etc. HAIR (1967) records *H. pimeleoides* var. *rupestris* from Alexandra with $n = 20$, but records a *Hebe* aff. *pimeleoides* var. *rupestris* (from near Roxburgh) with $n = 40$ (as in *H. buchananii*).

15c. *Hebe pimeleoides* var. *minor* (Hook. f., 1867) Ckne. & Allan (1926). Fig. 8.

Lake Heron and central Rangitata. On *Holloway*, Queenstown (CHR), Moore has written "plant (b) at top right very closely matches the type of *V. pimeleoides* var. *minor* at Kew which appears to be only small because of hard growing conditions." However, a Canterbury plant growing at Botany Division (D.S.I.R) Lincoln, identified by Dr. Garnock-Jones (pers. comm., 1987) with *H. pimeleoides* var. *minor*, is strikingly distinct and similar plants have been collected by Mr. Enright from Mt. Ida (cf. *H. pinguifolia*, *H. pareora* and *H. amplexicaulis*).

15d. *Hebe pimeleoides* var. *glaucocaerulea* (J. B. Armstrong, 1879) Ckne. & Allan (1926). Fig. 8.

Lake Tekapo — Mt. Arrowsmith.

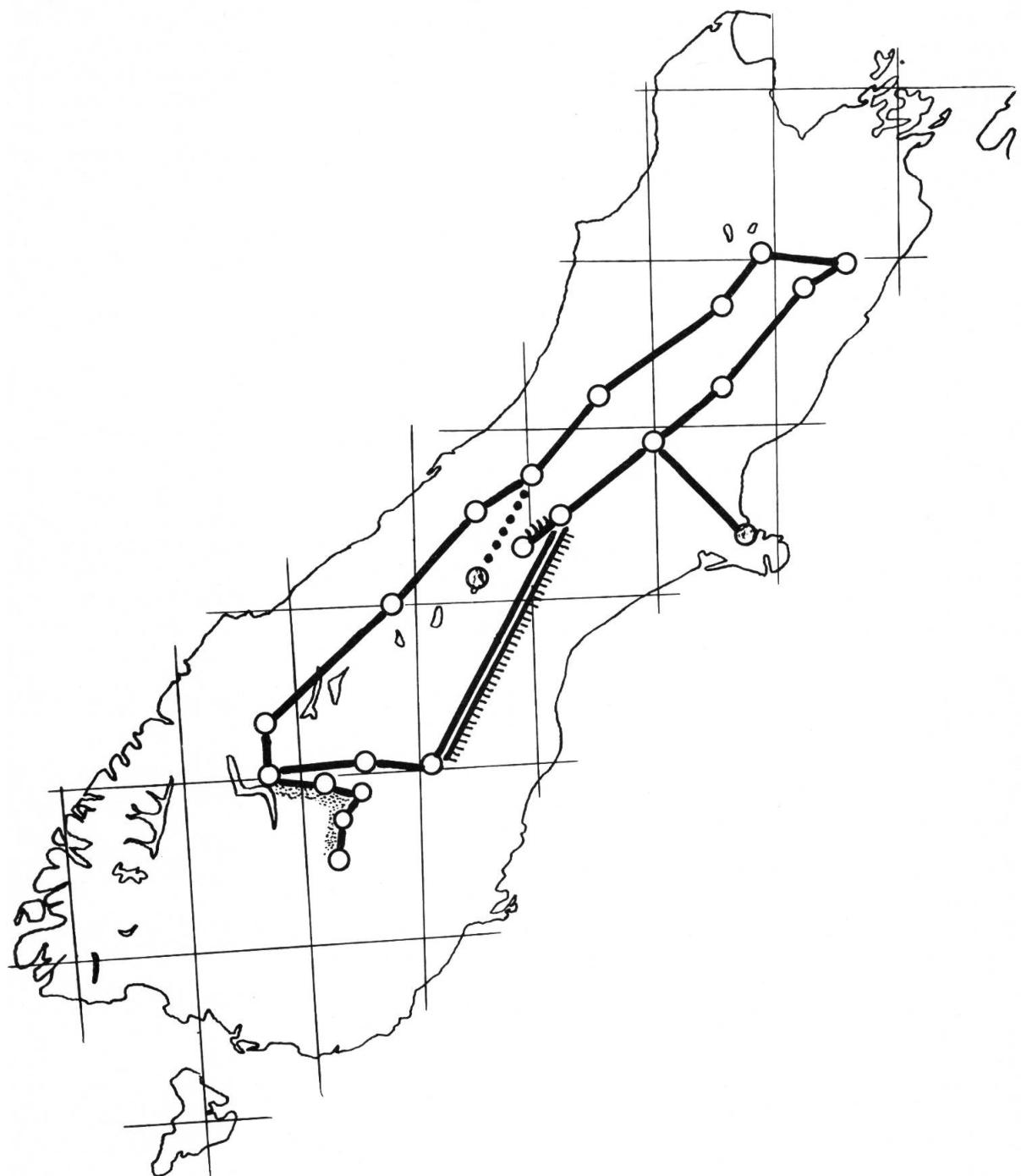


Fig. 8. — *Hebe pimeleoides* var. *rupestris*: stippled line. *H. pimeleoides* var. *pimeleoides*: continuous line. *H. pimeleoides* var. *glaucocaerulea*: dotted line. *H. pimeleoides* var. *minor*: hatched line.

16. *Hebe pinguifolia* (Hook. f., 1864) Ckne. & Allan (1926). Fig. 9.

Rock outcrops and debris, open tussock grassland and herbfield. From a southern limit: Mt. Arnould — St. Bathans Ra. — Hawkdun Ra. — Mt. Pisgah (Kakanui Mts.), this complex of populations extends north on the west along a track: Mt. Arnould — Mt. Cook — Arthur's Pass — Amuri — Lake Tennyson — Richmond Ra. Records on the east are known along the arc: Mt. Pisgah — Four Peaks — Mt. Somers — Mt. Hutt — Torlesse Ra. — Puketeraki. In Mt. Cook National Park, WILSON (1976) records the species in the east only (Godley V.) (cf. *Leonohebe haastii*, *L. tetrasticha* and *L. odora*/*L. mooreae*). The varied forms currently included under this species require further study. A plant in this general affinity and probably of wild origin cultivated at Otago University Botany Department has inflorescences regularly terminal, and another plant in Dunedin Botanical Gardens had a branch with leaves in whorls of three.

17. *Hebe pareora* Garnock-Jones & Molloy (1983). Fig. 9.

Rock outcrops. Hunters Hills — Opihi Gorge.

18. *Hebe amplexicaulis* (J. B. Armstrong, 1879) Ckne. & Allan (1926), incl. *H. allanii* Ckne. (1926). Fig. 9.

Rocks in tussock grassland between Mt. Peel Ra. (Canterbury) and Mt. Somers. SPEIGHT & al. (1911) record the species from Mt. Arrowsmith, as well as *H. pinguifolia* and *H. pimeleoides*, but not *H. buchananii*, but I have not seen specimens and the locality is not included on the map. The lamina of *H. allanii* (Mt. Peel — Four Peaks), is covered on both sides with dense pubescence. GARNOCK-JONES & MOLLOY (1983) treat this as intraspecific variation within *H. amplexicaulis*. Together with *H. pareora*, this demonstrates polymorphism on southeast Canterbury sectors. A plant cultivated at Dunedin Botanic Gardens had a branch with leaves in whorls of three, as noted for *H. pinguifolia* above. I have not noticed this character elsewhere in the genus, or indeed the tribe, although the floral bracts are whorled in some *Ourisia* species.

19. *Hebe gibbsii* (Kirk, 1896) Ckne. & Allan (1926). Fig. 9.

Richmond Ra. — Bryant Ra. CHEESEMAN (1925) regarded *H. carnosula* as its nearest ally, but it is possibly closer to *H. amplexicaulis* (and *H. allanii*).

The flowers in species 20-24 are shortly pedicellate, and the lowermost bracts not opposite. The five species form a series of vicariants ranging between Central Otago and NW Nelson.

20. *Hebe biggarii* (Ckne., 1916) Ckne. (1929). Fig. 10.

Thomson Mts. — Northern Eyre Mts. (Mt. Dick) — southern Eyre Mts. (upper Windley Stream) — Mt. Cameron (Garvie Mts.) — Mid Dome — East Dome (southern Garvie Mts.). The species is located on the intersection of the Moonlight and Tapanui Tectonic Zones, a notable centre of endemism (HEADS, 1989).

21. *Hebe decumbens* (J. B. Armstrong, 1879) Ckne. & Allan (1926). Fig. 10.

Rocky sites in grassland from Arthur's Pass National Park — Spenser Mts. — upper Wairau, east to: Terako — Ben More Ra. (by Waima) — Altimarlock (by Awatere).

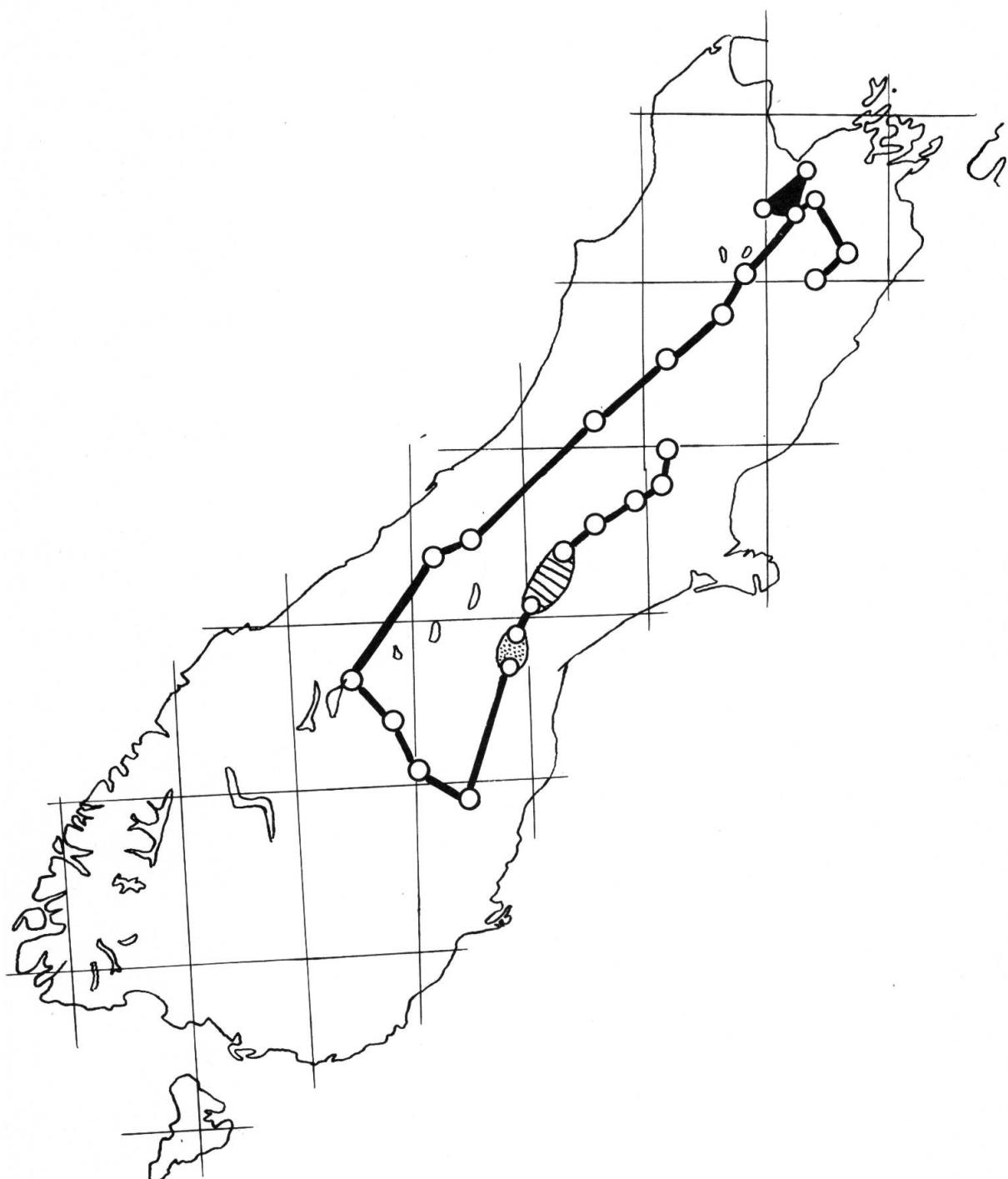


Fig. 9. — *Hebe pinguifolia*: continuous line. *H. pareora*: stipple. *H. amplexicaulis*: hatched. *H. gibbsii*: black triangle.

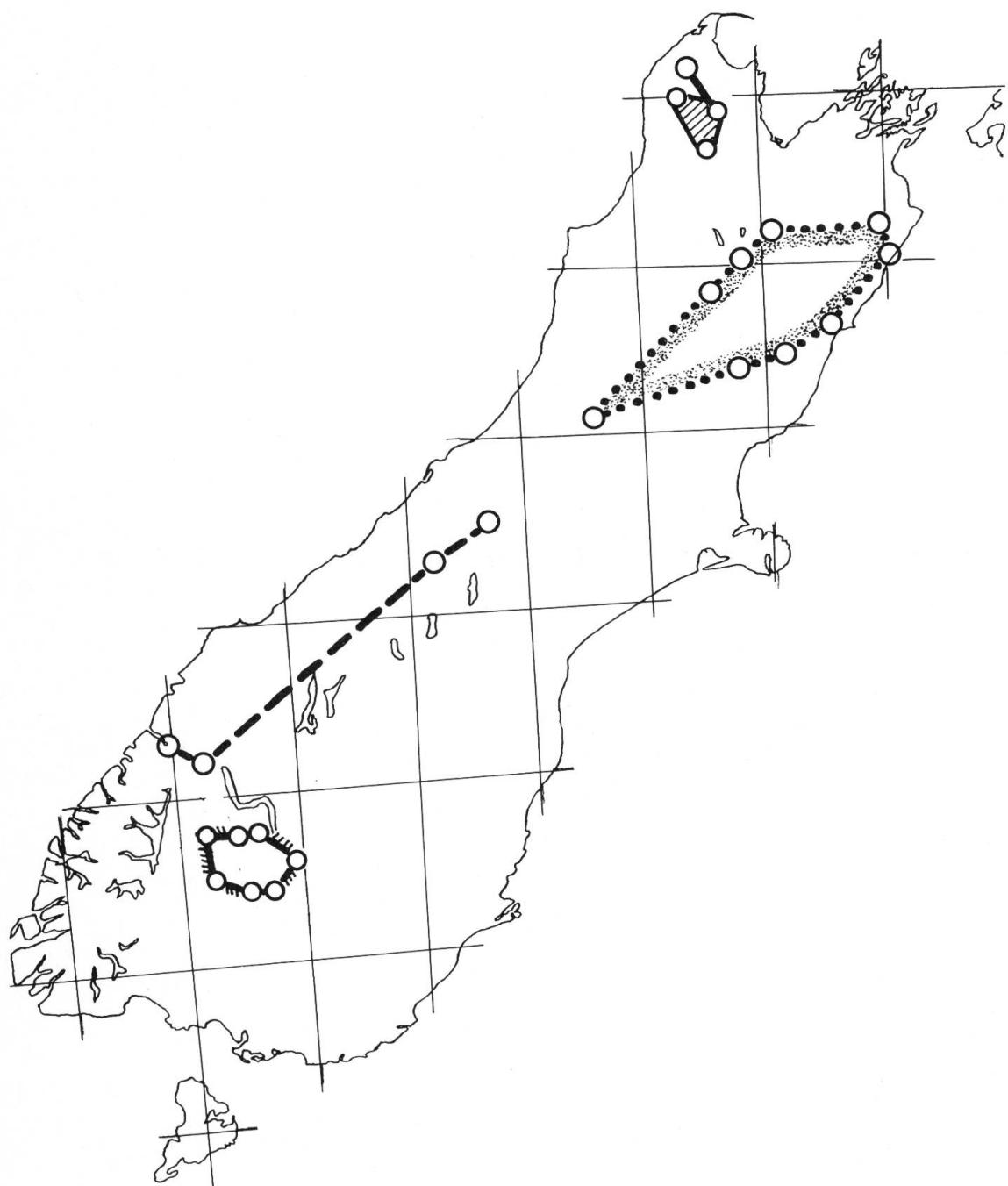


Fig. 10. — *H. biggarii*: hatched line. *H. matthewsii*: broken line. *H. albicans*: hatched. *H. recurva*: continuous line. *H. decumbens*: dotted stippled line.

22. *Hebe matthewsii* (Cheeseman, 1906) Ckne. (1929). Fig. 10.

Humboldt Mts., Milford Sound, "Canterbury Alps" (*Haast, Armstrong*).

23. *Hebe albicans* (Petrie, 1917) Ckne. (1929). Fig. 10.

Mt. Arthur — Cobb Valley — Mt. Lockett — Gouland Downs. Collections from Takaka Hill (e.g. *Druce*, CHR) mark a population linking *H. albicans* and *H. recurva*.

24. *Hebe recurva* Simpson & Thomson (1940). Fig. 10.

Rock platforms on river banks. Aorere R. (N.W. Nelson — near Bainham) — (?) Takaka, thus acting as the northwest Nelson vicariant of the group.

Hebe sect. Hebe ser. Hebe**25. *Hebe elliptica* (Forst. f., 1786) Pennell (1921). Fig. 11.**

A very distinct species of coastal rocks and cliffs in Patagonia and Falkland Is., and also found on the outer New Zealand arc: Auckland Is. — Campbell Is. — Chatham Is. (This is the only member of Tribe *Digitaleae* at the Chathams other than the endemic Chathams group of *Hebe* ser. *Occlusae*). From this outer arc it reaches north centrally in New Zealand to the inner islands: Snares — Big South Cape Is. — Stewart Is. — Solander Is. — South Is. — Open Bay Is. (Jackson Bay) — North Is. The species ranges north on the east at: Cape Wanbrow (Oamaru) — Rangitata (*Kirk*, OTA) — Lyttelton (Banks Peninsula) — Clarence R. between Dillon and Acheron R. (*Kirk*, CHR), and at many localities along the west coast.

There is considerable geographic differentiation within the species. The distinctive leaf margin pubescence is least developed in Subantarctic Is. specimens (MOORE, 1961). COCKAYNE (1905) described the Open Bay Is. population as "a distinct variety" with "remarkably large leaves". Blue flowers can be seen on plants from Jackson Bay, and are also conspicuous at Bobby's Head north of Dunedin.

The pubescence and more or less crenulate margin of *H. elliptica* are very reminiscent of *L. benthamii*. Also of interest are the unusual "mucronate" pinching on the leaf of *H. elliptica*, and the sometimes subsucculent texture of the leaves. Moore notes specimens from a Punta Arenas garden with most twigs terminating in flowers (cf. the plants of *H. pinguifolia* noted above), showing affinity away from the usual *Hebe* arrangement and towards that of *Leonohebe*. The large flower and fruit of *H. elliptica* recall "*Hebe*" *macrantha*, probably best regarded as a *Parahebe*.

25a. *Hebe elliptica* var. *crassifolia* Ckne. & Allan (1926) Fig. 11.

Known from: below Mt. Taranaki — Kapiti — Titahi Bay, vicariating with the type variety at Cook Strait, and between northwest Nelson and Mt. Taranaki.

26. *Hebe salicifolia* (Forst. f., 1786) Pennell (1921). Figs. 12, 16.

Forest and shrubland of southern New Zealand and the coast of Chile at about the same latitude (MOORE, 1961). In New Zealand the species ranges at: Auckland Is. (known only from a bay south of Lindley Point (northeast Auckland Is.) — Stewart Is. — South Is., where it is

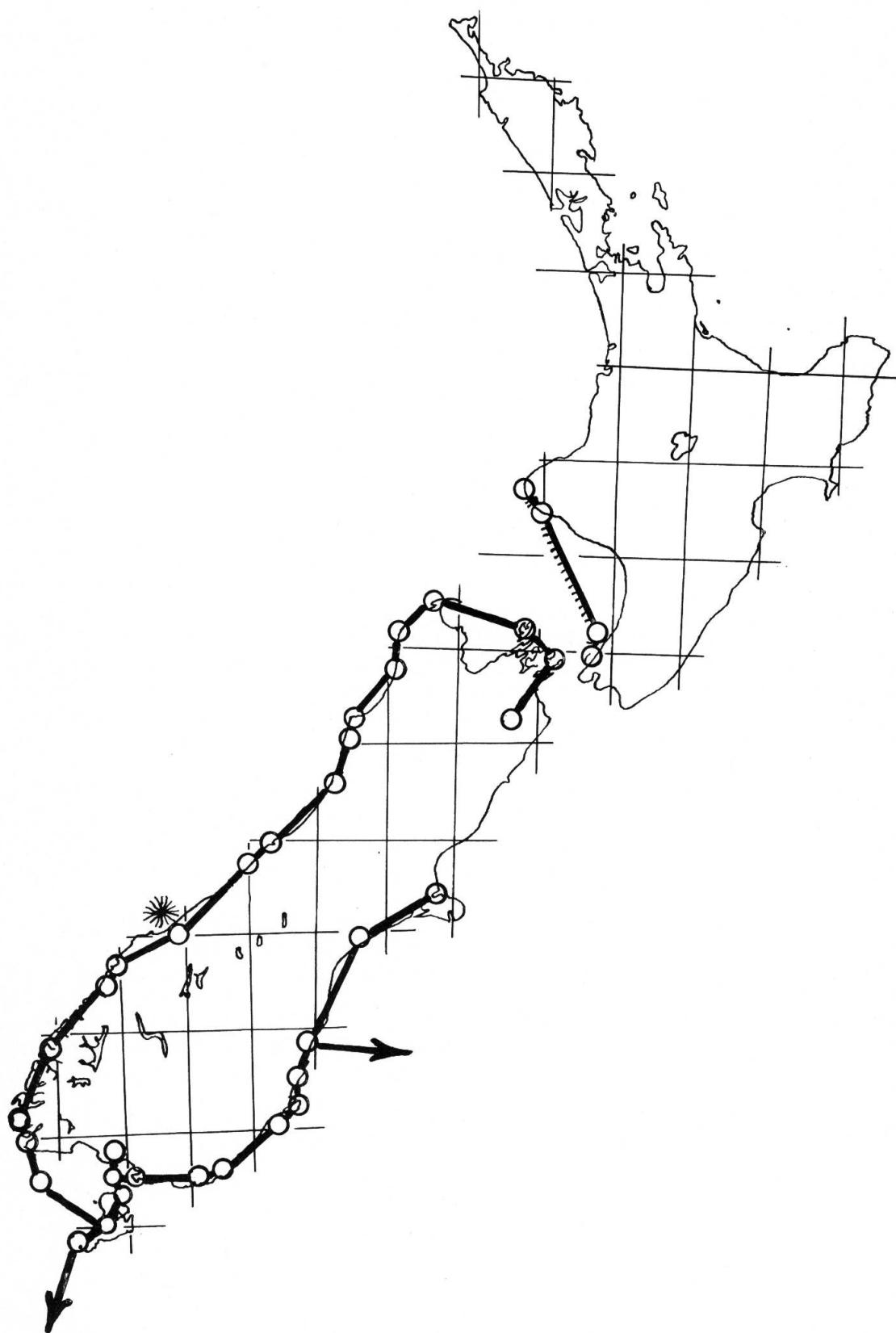


Fig. 11. — *Hebe elliptica* var. *elliptica*: continuous line (plus Auckland, Campbell, Chathams, Snares Is., and southern South America), Open Bay Is. population: asterisk. *H. elliptica* var. *crassifolia*: hatched line.

widespread throughout from near the coast to the interior, except northeast of a line: Takaka — Richmond Ra. — Chalk Ra. (Kekerengu) where it is absent. Here it is replaced by *H. stricta* of ser. *Occlusae* (Fig. 16).

27. *Hebe amabilis* (Cheeseman, 1906) Ckne. & Allan (1926), incl. *H. blanda* (Cheeseman, 1906) Pennell (1921). Fig. 12.

Southern South America and New Zealand: Stewart Is./Bluff, north on the east coast to Green Is. — Port Chalmers (both by Dunedin) and north on the west to Anita Bay, near Milford Sound. Johnson 1979, CHR, from Puysegur Point is annotated by Dr. P. Garnock-Jones as “*salicifolia* × *elliptica* or backcross ... however the specimen is by no means intermediate.” Similarly, distinctive plants not intermediate between these two species, as well as the two species themselves, may be seen in southeast Otago (*Heads*, OTA). These are tentatively referred to *H. amabilis*.

28. *Hebe corriganii* Carse (1930). Fig. 12.

This very close relative of *H. salicifolia* favours lowland situations quite close to running water on small streamside flats in rocky gorges (CARSE, 1930). (This ecology may approach that of the more or less “rheophytic” *Parahebe catarractae*). The species is also found in the montane forests of Taranaki — Kaimanawa Ra. — Raukumara Ra. where it is the only *Hebe*. The species ranges: Westport — Mt. Taranaki — northwest Ruahine Ra. — Hikurangi, and in addition holds the northwest extensions: Kuratau (between south Hauhangaroa Ra. and Taupo) — Pureora — Pirongia (cf. Kawhia as a northern limit in, for example, *H. rigidula*), and: Maungapohatu (north of Waikaremoana) — McLaren’s Falls (Tauranga) — Karangahake Gorge/Ohinemuri R. (near Waihi/Paeroa).

29. *Hebe pubescens* (Bentham, 1846) Ckne. & Allan (1926). Fig. 12.

Open forest from Thames through Coromandel Peninsula to Great and Little Barrier Is. The population on these two islands is regarded by EAGLE (1982) as a distinct form and MOORE (1961) notes that plants from Coromandel Peninsula may vary considerably in their pubescence. CHEESEMAN (1925) regarded *H. pubescens* as “very near *H. stricta*”, and in addition it is a northern vicariant of *H. corriganii*.

30. *Hebe* sp. “v” of Eagle (1982). Fig. 12.

Known only from the Mokohinau Is. Eagle cites ESLER (1978), who writes that the population: “does not fit comfortably into the description of any species. The plants are much less hairy than typical *H. pubescens*.” Here the form is treated as a northern vicariant of *H. corriganii* and *H. pubescens*.

31. *Hebe gracillima* (Kirk, 1896) Ckne. & Allan (1926). Fig. 13.

Damp or swampy places, at Big Bay (Waiuna Lagoon) and Cascade R. mouth, and from there with disjunct populations at Mt. Davy (Greymouth) — Westport (“especially abundant in swamps between Fairdown and Waimangaroa” — MOORE, 1961) and north to Gouland Downs — Abel Tasman National Park. The species ranges east to: Motupiko — Whangamoa. In contrast with taxa such as *H. cockayneana*, the west coast disjunction cannot be explained by simple displacement on the Alpine Fault. EAGLE (1982) notes that the sinus is “very small, sometimes obscure” and CHEESEMAN (1925) compared the species with *H. acutiflora* (and *H. parviflora*) both of Ser. *Occlusae*.

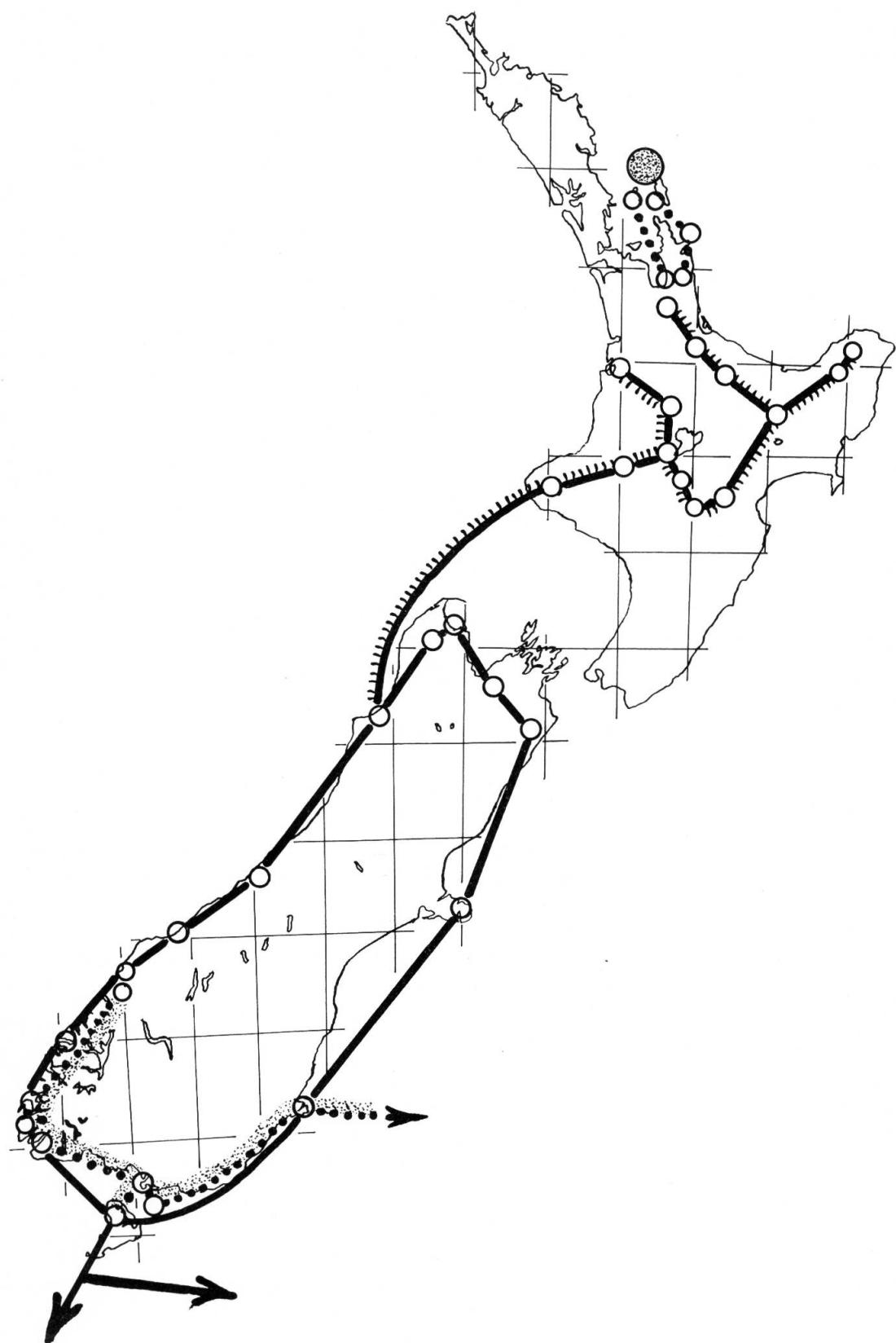


Fig. 12. — *Hebe salicifolia* var. *salicifolia*: continuous lines, plus northeast Auckland Is. *H. amabilis*: dotted stippled line, plus southern South America. *H. corriganii*: hatched line. *H. pubescens*: dotted line. *H. sp. "v"*: stippled circle.

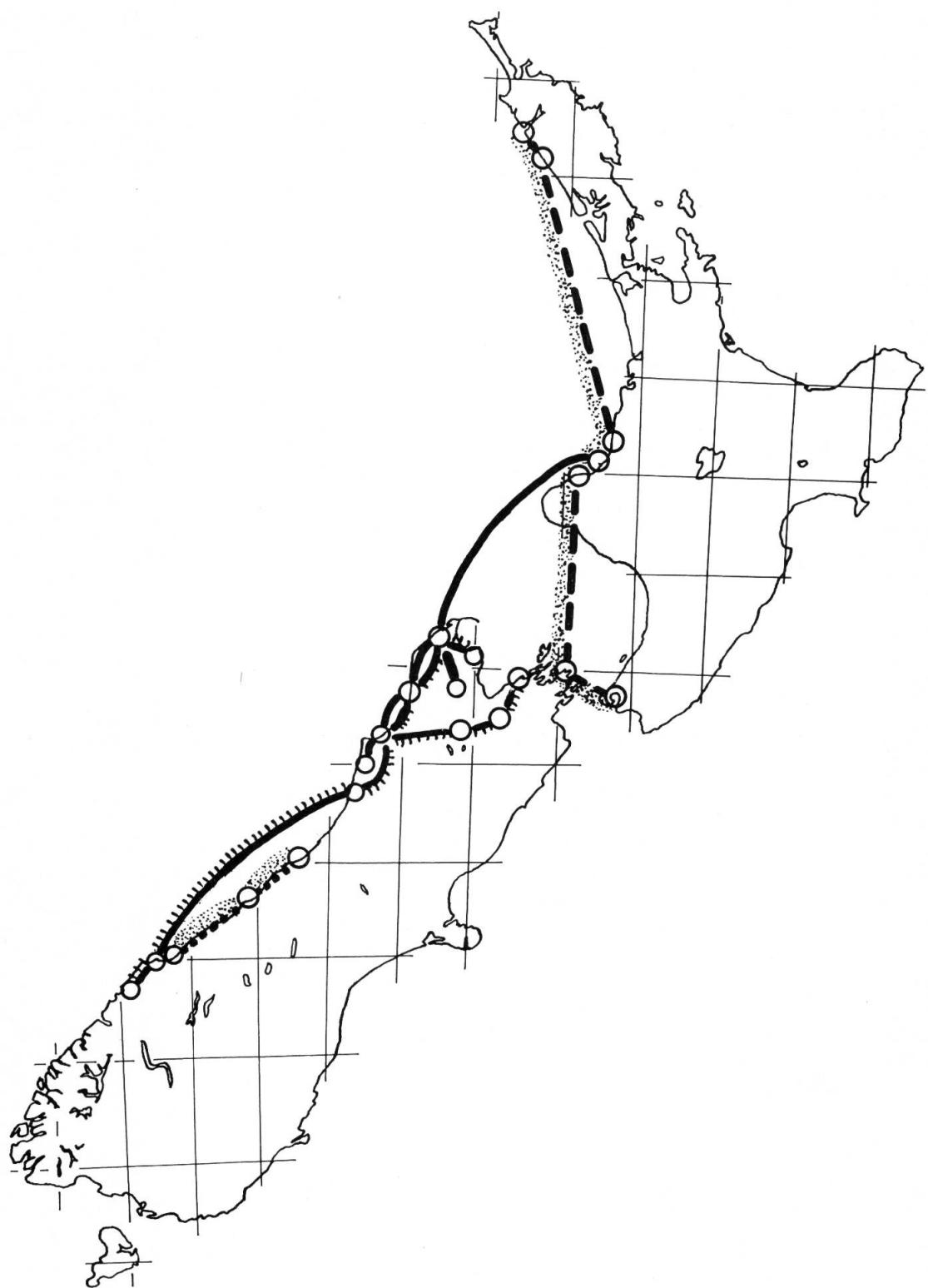


Fig. 13. — *Hebe gracillima*: hatched line. *H. salicifolia* var. *paludosa*: dotted stippled line. *H. townsonii*: continuous line. *H. speciosa*: broken stippled line.

32. *Hebe salicifolia* var. *paludosa* (Ckne. 1916) Ckne. & Allan (1926). Fig. 13.

Swamp margins and coastal lagoons between Arawata River and Jackson Bay, and in Westland National Park north of Cook R. but abundant only from Waitangiroto R. (by Okarito) northwards (WARDLE, 1975). Wardle also notes that in north Westland the variety appears to grade into *H. gracillima*, and MOORE (1961) suggested that *H. salicifolia* var. *paludosa* is a hybrid between *H. salicifolia* and *H. gracillima*. In Fig. 13 it is mapped north to Lake Ianthe (the type locality).

33. *Hebe townsonii* (Cheeseman, 1913) Ckne. & Allan (1926). Fig. 13.

Riverbanks, cliffs and limestone outcrops from Fox River (west of Paparoa Ra.) north to Mt. Burnett (N.W. Nelson) (this sector shared with *H. gracillima*), from there southeast to Mt. Arthur, and northeast to Mt. Messenger. On the under-surface of the leaves, just within the margin, there is a row of small pits, or "domatia", similar to those seen on leaves of *Coprosma* (Rubiaceae). These glands appear to be the last trace of the epiphyllous inflorescences of the early angiosperms, left over after the hemming-in of growth responsible for the modern angiosperm leaf took place (HEADS, 1984). The character, apparently unique in tribe Digitaleae, suggests that the species is relictual and the disjunct, far western localities may reflect the former existence of lands to the west (HEADS, 1989).

34. *Hebe speciosa* (A. Cunn., 1836) Ckne. & Allan (1926). Fig. 13.

A remarkably rare and local species confined to cliffs near the sea, and often drenched with sea-spray. Localities are: 1. Cook Strait: Port Nicholson (Wellington) — Titirangi Bay (outer Pelorus Sound), 2. the short sector: Urenui — Tongaporutu — Mokau (near Awakino), and 3. Maunganui Bluff — Hokanga Heads — Cape Reinga. Tongaporutu is very near Mt. Messenger, the locality also featured in disjunction by *H. townsonii*. The tie: D'Urville Is. — Kawhia is also seen in *H. rigidula* (Fig. 5). CHEESEMAN (1925) gave *H. speciosa* first position in his treatment of *Veronica*. In contrast, MOORE (1967) noted the ease with which many different forms could be derived from a "protohebe" similar to *Leonohebe odora*. (This is more easily understood than the fact that her 1961 treatment of *Hebe* sens. lat. begins with *H. diosmifolia*). Following *H. speciosa* in Cheeseman's treatment are Chatham Is. species of ser. *Occlusae*, and then *adamsii*, *bollonsii*, *obtusata* and *macroura*, all forms of ser. *Occlusae* found on modern coasts. This treatment warrants further consideration, as the division of sect. *Hebe* into ser. *Occlusae* and *Hebe* may not be the best possible (HEADS, 1993a). An alternative division might involve series based on *H. salicifolia*, *H. stricta* etc.; *H. elliptica*, *H. speciosa*, *H. macroura*, etc., *H. traversii* etc.

Hebe sect. Hebe ser. Occlusae Heads (1987)

All species in this large series have leaves (except midrib and margins) glabrous, except: *H. ligustrifolia* (NE Auckland — North Cape) — "minute pubescence at extreme base"; *H. breviracemosa* (Kermadec Is.) — "fine pubescence on both surfaces near base"; *H. barkeri* (Chatham Is.): "peculiar indumentum which gives a velvety texture to the leaves" (MOORE, 1961); *H. chathamica* (Chatham Is.) "leaves sometimes hairy on both surfaces"; *H. traversii* (northern South Is.) "minute pubescence on upper surface near base and on upper margin". It seems significant that four out of five of these occur along "horstian" tracks (HEADS, 1989) of N.E. North Is., and that the pubescent member of sect. *Subdistichae*, *H. insularis*, is found at Three Kings Is.

35. *Hebe rapensis* (F. Brown, 1935) Garnock-Jones (1976).

Known only from Rapa Is. (Fig. 1). It resembles Chatham Is. species closely, and shows less affinity with species of the main islands of New Zealand (MOORE, 1967; GARNOCK-JONES, 1976). Its closest affinities lie with *H. barkeri* and *H. dieffenbachii*. The subauriculate leaf base and pubescent corolla tube of these species clearly indicate a direct tie: Chatham Is. — Rapa Is.

The following three species are endemic to the Chatham Is. Their leaves are often more or less amplexicaul and the plants are often low growing and more or less prostrate. The three species show an ecological trend from maritime sites through to tableland forest.

36. *Hebe dieffenbachii* (Bentham, 1846) Ckne. & Allan (1926).

Chatham Is. (Fig. 1). Coastal or rocky places, limestone cliffs, lagoon rocks, also peaty lake margins. Plants cultivated at Canterbury University show massive branches which are more or less horizontal and prostrate and are produced at an angle approximating 90°, as in the well-known "divaricate" habit of many New Zealand shrubs. The vegetative buds are massive and square, and can be compared with those of *H. chathamica*, which appears to be a less woody version of *H. dieffenbachii*. At about 1 cm diameter the branches of *H. dieffenbachii* produce prolific adventitious roots.

37. *Hebe chathamica* (Buchan., 1875) Ckne. & Allan (1926).

Chatham Is. (Fig. 1). "Maritime cliffs where there is maximum of spray ... not uncommon on rocks near the sea" (MOORE, 1961). Recorded by CHEESEMAN (1925) as a "prostrate or trailing shrub".

38. *Hebe barkeri* (Ckne., 1899) Ckne. (1929).

Chatham Is. (Fig. 1). This is taken here to include *H. gigantea* (Ckne.) Ckne. & Allan which "occasionally reaches a height of 40 feet, with a stout and evident trunk" (CHEESEMAN, 1925). The species is an important constituent of lowland and tableland forest and appears to be an inland vicariant of the last two species.

39. *Hebe macroura* (Bentham, 1846) Ckne. & Allan (1926), *H. stricta* var. *macroura* (Bentham) Moore (1961). Fig. 14.

This ranges at a Cook Strait triangle: Maud Is. — Palliser Bay — Rimutaka Ra. road summit. This last locality is the only inland record of this species — elsewhere it is a purely littoral plant of sea-cliffs. From the Cook Strait region it ranges north on the east to Opotiki — Motiti Is., and north on the west to Raglan Harbour. MOORE (1961) reports that: "On very exposed coasts plants may be almost prostrate with much similarity to *H. obtusata* and some of these remain decumbent in cultivation."

40. *Hebe obtusata* (Cheeseman, 1916) Ckne. & Allan (1926). Fig. 14.

On sea-cliffs along the west Auckland sector: Manukau Heads — Muriwai. In CHR is a folder of Wellington specimens (*Wall*, Island Bay; *Mason*, Titahi Bay; *Zotov*, Ohau Bay; *Rawson*, Pukerua

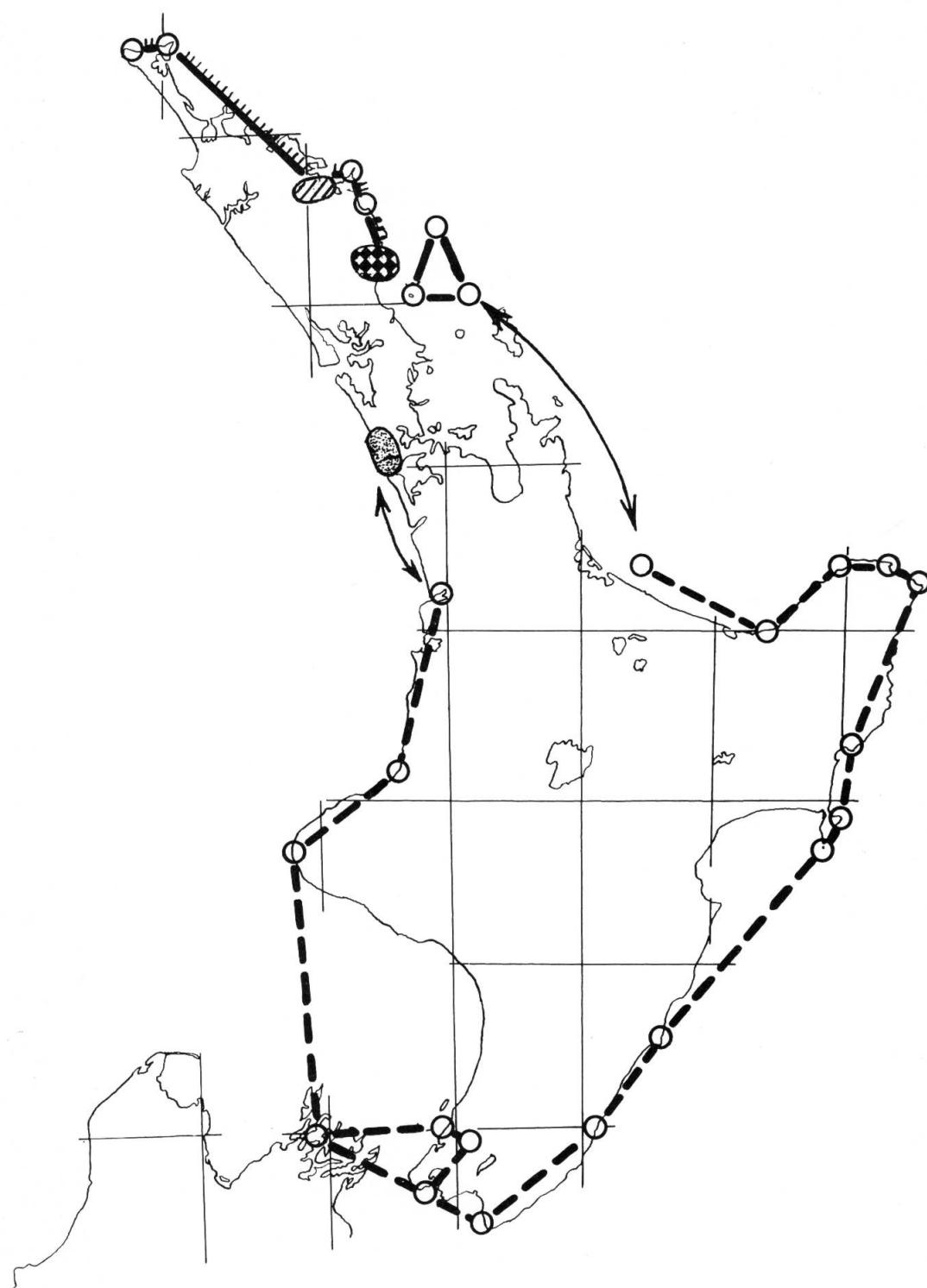


Fig. 14. — *Hebe macroura*: broken line. *H. obtusata*: stippled. *H. bollonsii*: triangle. *H. sp. "m"*: circle with squares. *H. ligustrifolia*: hatched line. *H. acutiflora*: hatched circle.

Bay) identified by Cheeseman and others (but not Moore) with *H. obtusata*, which again shows the close affinities between *H. macroura* and this species.

41. *Hebe bollonsii* (Ckne., 1912) Ckne. & Allan (1926). Fig. 14.

Coastal shrubland on Poor Knights Is., Hen and Chickens Is. and Mokohinau Is. CHEESEMAN (1925) regarded this as "probably nearest to *V. macroura*", implying a horstian connection: Mokohinau Is. — Motiti Is. (Fig. 14).

42. *Hebe* sp. "m" of Eagle (1982). Fig. 14.

Steep rocky slopes at Whangarei and Bream Heads. Eagle's illustration indicates that the affinities of this form may lie with *H. bollonsii*, and this would give a standard biogeographic connections (HEADS, 1989). The two can be regarded here as western and eastern vicariants of each other.

43. *Hebe ligustrifolia* (A. Cunn., 1836) Ckne. & Allan (1926). Fig. 14.

Open shrubland and forest margins along the arc: Whangarei Heads — Bay of Islands — North Cape.

44. *Hebe acutiflora* (Bentham, 1846) Ckne. (1929). Fig. 14.

Bay of Islands: "under the falls of Kerikeri", and in nearby Puketi State Forest. Placed by MOORE (1961) and earlier writers with *H. ligustrifolia*.

45. *Hebe breviracemosa* (W. R. B. Oliver, 1910) Ckne. & Allan (1926).

Coastal and inland cliffs of Raoul Is. (Kermadec Is. — Fig. 1). Previously known populations in other habitats have been eaten out by goats. Mr. W. R. Sykes (pers. comm. 1986) compares this species with *H. macrocarpa* (recorded at, for example, North Cape and Great Barrier Is.), rather than with *H. bollonsii*.

46a. *Hebe macrocarpa* var. *macrocarpa* (Vahl, 1794) Ckne. & Allan (1926). Fig. 15.

The type variety is found to the west of the other two varieties, and has flowers coloured white or a pale mauve soon fading to white. It ranges from North Cape, south on the west to Kaitaia — Mt. Karioi, and on the east to Mangonui — Coromandel Peninsula — Kaimai Ra. — Tolaga Bay/Poverty Bay. MOORE (1961) records the species south on the west to Taranaki, and notes that Collingwood and Karamea specimens "might belong here", but I have not seen specimens, and EAGLE (1982) records it south only to Coromandel Ra. and Waikato. A specimen from Kennedy Bay (N.E. Coromandel Pen.) (Carse, CHR) has dichotomising inflorescences. Also in this vicinity Moore notes that an "especially distinct" form is found on the Coromandel Ra. from Te Moehau to Castle Rock (cf. endemism N.E. of North Is. in *H. bollonsii* etc.).

46b. *Hebe macrocarpa* var. *latisepala* (Kirk, 1896) Ckne. & Allan (1926). Fig. 15.

Great and Little Barrier Is. Flowers bluish-purple.

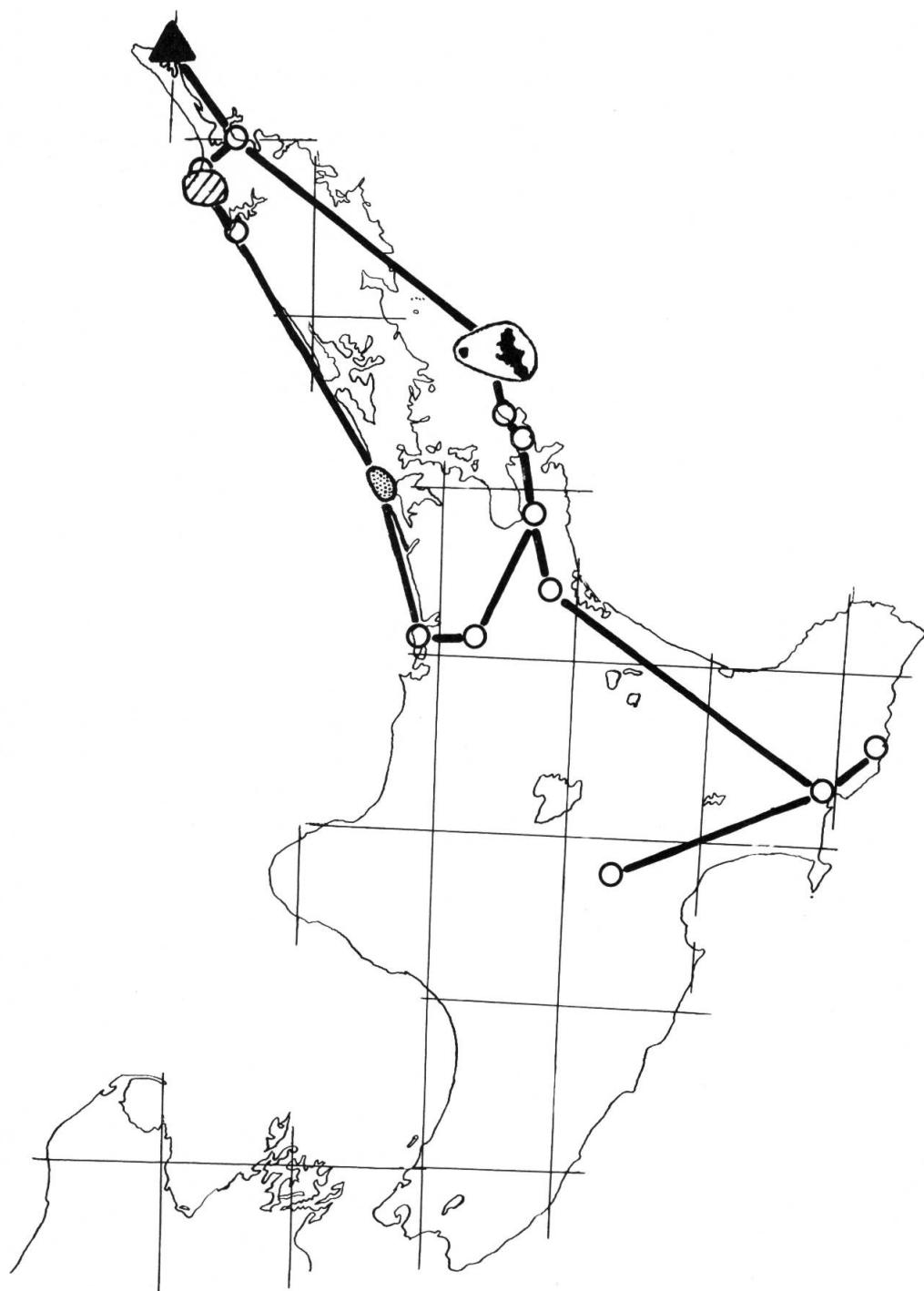


Fig. 15. — *Hebe macrocarpa* var. *macrocarpa*: continuous line. *H. macrocarpa* var. *brevifolia*: solid triangle. *H. macrocarpa* var. *latisepala*: Great and Little Barrier Is. (in black). *H. sp. "x"*: hatched ellipse. *Veronica × bishopiana*: stippled ellipse.

46c. *Hebe macrocarpa* var. *brevifolia* (Cheeseman, 1906) Moore (1961). Fig. 15.

North Cape only. Flowers reddish-purple. This was placed under *H. speciosa* (ser. *Hebe*) by CHEESEMAN (1925), and is regarded as a distinct species by EAGLE (1982). The chromosome number is an aneuploid variant: $n = 59$. However, MOORE (1962) cites a specimen from Whangarei Heads which "could be as well placed here as in var. *latisepala*" and CHEESEMAN (1925) and KIRK (1896) recorded var. *latisepala* from Whangarei Heads as well as the Barrier Is. It seems to be a question of a complex ranging along the usual "horstian" track: North Cape — Whangarei Heads (cf. *H. ligustrifolia*) — Great and Little Barrier Is. The differentiation of purple corollas evident here along this track connects with red-blue coloured flowers on the southern arc: Chatham Is. — Subantarctic Is. (e.g. Compositae, Umbelliferae, *Leonohebe benthamii*). Purple flowers are also known centrally (e.g. *H. pimeleoides*), but apparently in fewer groups than along the outer arcs.

47. *Hebe* sp. "x" of Eagle (1982). Fig. 15.

West of Herekino, near Kaitaia. The affinities of this may be closer with the forms shown on Fig. 14 (*H. obtusata*, *H. macroura*, etc.). In any case, it seems quite distinct and highlights the node at Kaitaia which operates as both a southern and northern boundary in many groups, for example within the genus *Dracophyllum* (Epacridaceae).

48. *Veronica* × *bishopiana* Petrie (1926). Fig. 15.

"Rocky knobs between Huia Hill and Little Huia, near Manakau North Heads, Waitakere Ra." (MOORE, 1961). EAGLE (1982), citing MEAD (1972), notes that this form is regarded by local botanists as a distinct species of *Hebe*. The same west Auckland node shown in *H. obtusata* is also seen here.

49a. *Hebe stricta* var. *stricta* (Bentham, 1846) Moore (1961). Fig. 16.

Like *H. salicifolia* in South Is., the type variety of *H. stricta* is widespread through North Is., mostly on banks, ranging between North Cape and Manawatu Gorge. It is also present on Hen and Chickens Is., Great and Little Barrier Is. and Mayor Is. (Bay of Plenty), with specimens from the last showing abnormal inflorescences (cf. *H. macrocarpa* at N.E. Coromandel Peninsula).

49b. *Hebe stricta* var. *lata* Moore (1961). Fig. 16.

On rocks in tall tussock grassland above treeline: Kaimanawa — Kaweka — Maungaharuru Ranges. At the latter locality it meets the following variety, and from there both follow the linear track: Maungaharuru — Waikaremoana — Arowhana — Hikurangi/Honokawa.

49c. *Hebe stricta* var. *egmontiana* Moore (1961). Fig. 16.

Shrubland above treeline along the arc: Mt. Taranaki — Ruapehu — Ruahine — Hikurangi. The central North Is. boundaries of *H. stricta* would possibly have been interpreted by earlier biogeographers as the result of waves of migration. But the boundaries coincide with tracks of endemism (HEADS, 1989), and there is no reason to see them as anything but the normal result of form-making along the standard axis: Taranaki — Waimarino — Hikurangi.

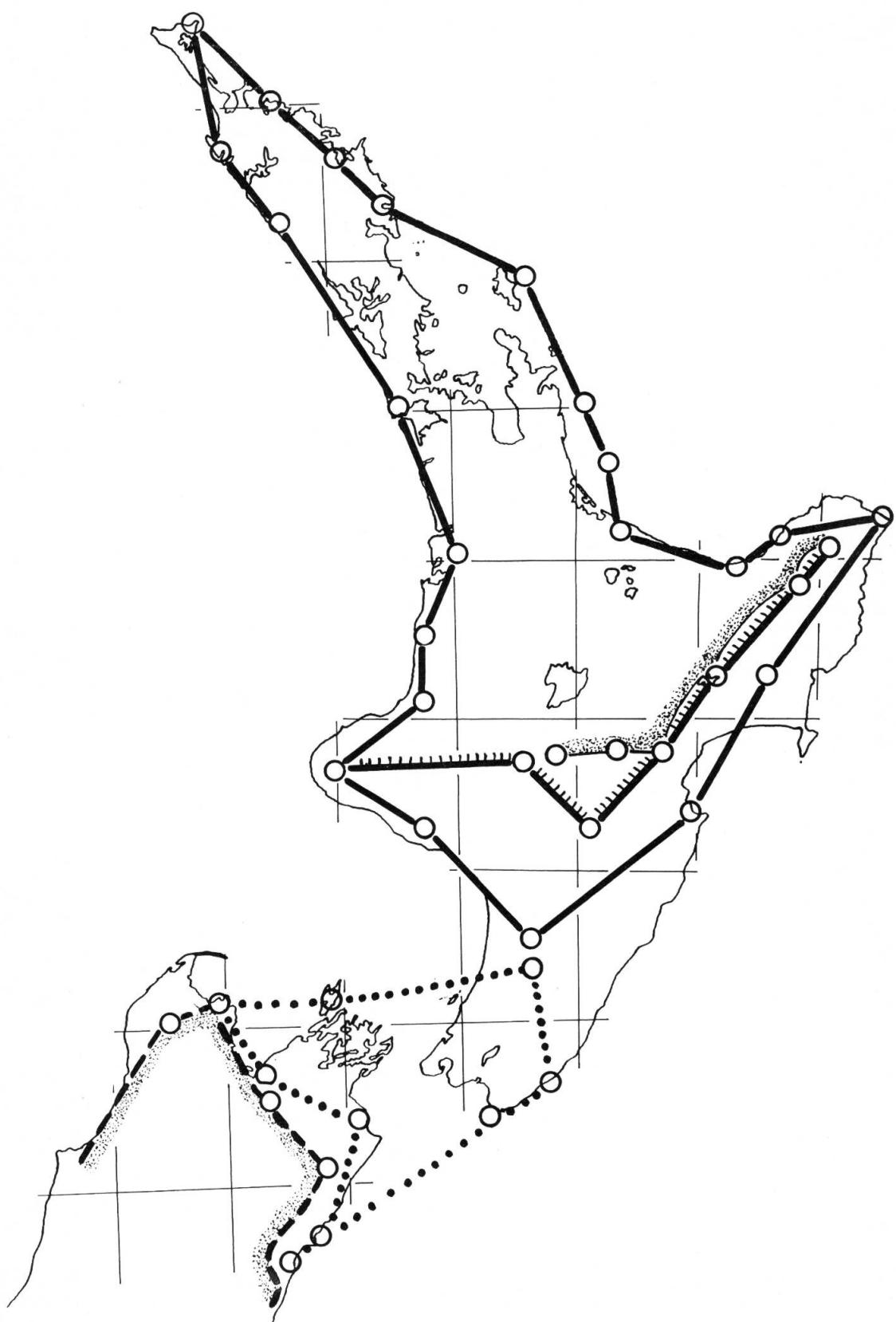


Fig. 16. — *Hebe stricta* var. *stricta*: continuous line; *H. stricta* var. *lata*: stippled line. *H. stricta* var. *egmontiana*: hatched line. *H. atkinsonii*: dotted line. *H. salicifolia* (northern limit only): broken stippled line.

49d. *Hebe stricta* var. *atkinsonii* (Ckne., 1916) Moore (1961). Fig. 16.

Tall shrubland, especially on banks. The variety has a northern limit: Ligar Bay — D'Urville Is. — north Tararua Ra. (Moore has it north to "40°" but I have not seen specimens), and a southeastern boundary: Conway R. near Hundalee — Kaikoura — Pahaoa. By the western boundary (Ligar Bay — Maitai Valley — Awatere mouth — Kaikoura — Conway R.) it vicariates neatly with *H. salicifolia* (where Cheeseman placed all of *H. stricta* as a variety). As MOORE (1975) noted: "Cook Strait is not an effective barrier in this instance". In fact for these and many other plants and animals the Cook Strait region is an important centre in its own right (HEADS, 1989). The distinction between ser. *Hebe* and ser. *Occlusae* is the presence or absence of a bud sinus, but a collection of *H. stricta* from Kahutara R., Waiau — Kaikoura Road (Druce, CHR) includes plants with a small sinus, as well as plants without a sinus. In a population 1 mile north of the Conway R. on the Hundalee Hills all plants observed were without sinuses. At Okarahia Stream, plants have some buds with small sinuses, and some without sinuses (Heads, OTA). These populations and locations are of special phylogenetic and biogeographic interest as they threaten the major division of sect. *Hebe* into ser. *Hebe* and ser. *Occlusae*. Nevertheless, in nearly all populations of nearly all species of sect. *Hebe* the sinus character is constant, and so remains of special biogeographic interest and taxonomic value. After all, any one taxonomic system can only summarise character distribution which may, as in sect. *Hebe*, involve much complex recombination.

50. *Hebe carsei* (Petrie, 1924) Ckne. (1929).

"Margins of forest and woods, Waimarino Plain" (south west of Lake Taupo — not mapped) (type). MOORE (1961) gives further records from Tongariro National Park. COCKAYNE & ALLAN (1926) regarded this as a hybrid of present-day species (*H. venustula* and *H. stricta*), but Moore indicates that the combination of characters displayed by *H. carsei* is not simply that of these species. This seems quite likely, as Waimarino is an important subcentre of the Waimarino — Taupo — N.W. Ruahine centre of endemism (HEADS, 1989).

Species 51-67 comprise "Group b" of MOORE's (1961) synopsis of ser. *Occlusae*. This group includes the "*traversii* complex" which has long been a difficult group for students (ALLAN, 1940). MOORE (1975) describes the group as comprising "about a dozen species ... grouped on the basis of small leaves and well-defined shortish compact spikes of white flowers. They are mostly rounded shrubs of hill country or subalpine scrub."

51. *Hebe* sp. "n" of Eagle (1982). Fig. 17.

Mainly near the coast, in shrubland on mudstone slopes, also inland on river banks, from Wairoa to north of Gisborne and Motu R. headwaters. Judging from Eagle's illustration the affinities of this species are probably with *H. parviflora*, and it shares a sector of the eastern baseline held by the other forms of this species.

52. *Hebe parviflora* (Vahl, 1794) Ckne. & Allan (1926). Fig. 17.

The type specimen of the type variety if not known, and all information available for the species is presented here under two additional varieties. MOORE (1961) writes that "*H. parviflora* sens. lat. includes not just two clear-cut taxa as Cheeseman implied but possibly four or five more or less distinct entities."



Fig. 17. — *Hebe parviflora* var. *arborea*: stippled line. *H. parviflora* var. *angustifolia*: continuous line. *H. sp. "n"*: solid black.

52a. *Hebe parviflora* var. *arborea* (Buchan., 1874) Moore (1961). Fig. 17.

These narrow-leaved trees grow up to 8.5 m tall with a trunk “nearly 2 feet in diameter at the base” (KIRK, 1896). From the east coast the range extends on forest edges and river flats at the southern sectors: Wellington — Woodside Gorge (Waima — by Kekerengu), centrally to Kaimanawa — Waimarino — Hauhangaroa, and on the northern sector: “Bay of Plenty” — Great Barrier — Hen and Chickens — Whangarei Heads.

52b. *Hebe parviflora* var. *angustifolia* (A. Rich., 1832) Moore (1961). Fig. 17.

Rocky and well-drained places on the coast and in river valleys, especially cliffs, up to the montane zone. This shares the east coast baseline with *H. parviflora* var. *arborea*, at least on the sector: Owahanga (between Castlepoint and Cape Turnagain) — Gisborne. In addition, a population at Kaimanawa Mts. connects with one at Rukuhia (Waikato) in the northwest, and Wanganui — D’Urville Is./Trio Is./Chetwode Is. in the southwest. Further tracks extend in South Is. to Waima R. (ties are here also possible with Owahanga etc.), Rotoiti, Owen R., and Collingwood — Karamea. With respect to the manner in which the tracks emerge out of the east coast “baseline” (HEADS, 1989), *H. parviflora* var. *angustifolia* exhibits a large measure of vicariance with *H. parviflora* var. *arborea*.

53. *Hebe traversii* (Hook. f., 1864) Ckne. & Allan (1926). Fig. 18.

Cliffs, banks, streamsides and shrubland east to a line: Four Peaks/Mt. Peel — Mt. Terako — Waima R., and west to a line: Liebig Ra. (for other boundaries near here see *Leonohebe*) — Arthur’s Pass National Park — Gouland Downs (N.W. Nelson).

54. *Hebe strictissima* (Kirk, 1896) Moore (1961). Fig. 18.

Forest margins or occasionally within forest on Banks Peninsula, east of a line: Lyttelton — Port Hills — “between Birdling’s Flat and Little River”. This is a very closely related vicariant of *H. traversii*.

55. *Hebe treadwellii* Ckne. & Allan (1926). Fig. 19.

Stony ground from Drake Ra. (Waiatoto)/ south branch Wilkin R., north to Mt. Cook, with a northern record at Victoria Ra.

56. *Hebe leiophylla* (Cheeseman, 1906) Ckn. & Allan (1926), *Veronica parviflora* var. *phyllireaefolia* Hook. f. (1854).

Type from “Nelson” (not mapped). This is a poorly understood form, compared by Cheeseman with *H. strictissima*, but in need of revision.

57. *Hebe brockiei* Simpson & Thomson (1942). Fig. 19.

Recorded from between Amuri Pass and the nearby Lake Mann and also from Fog Peak, Torges Ra. MOORE (1961) noted that through characters of leaf, inflorescence and flower “this closely approaches *H. subalpina*”, while habit and leaf shape “resemble rather *H. pinguifolia*”. This



Fig. 18. — *Hebe traversii*: continuous line. *H. strictissima*: triangle on Banks Peninsula. *H. truncatula*: crossed circles. *H. evanosa*: stippled.

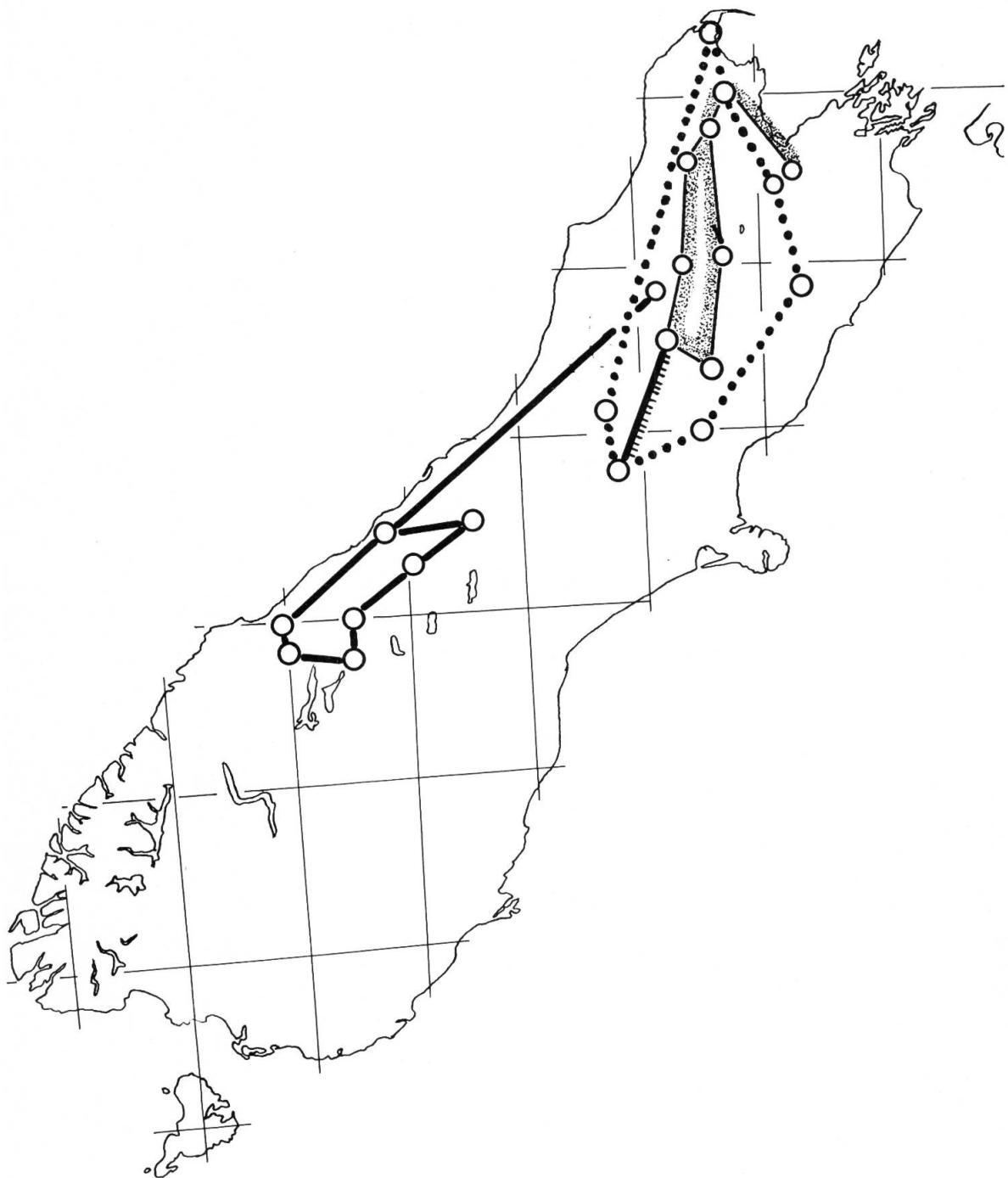


Fig. 19. — *Hebe treadwellii*: continuous line. *H. brockiei*: hatched line. *H. glaucophylla*: dotted line. *H. topiaria*: stippled line.

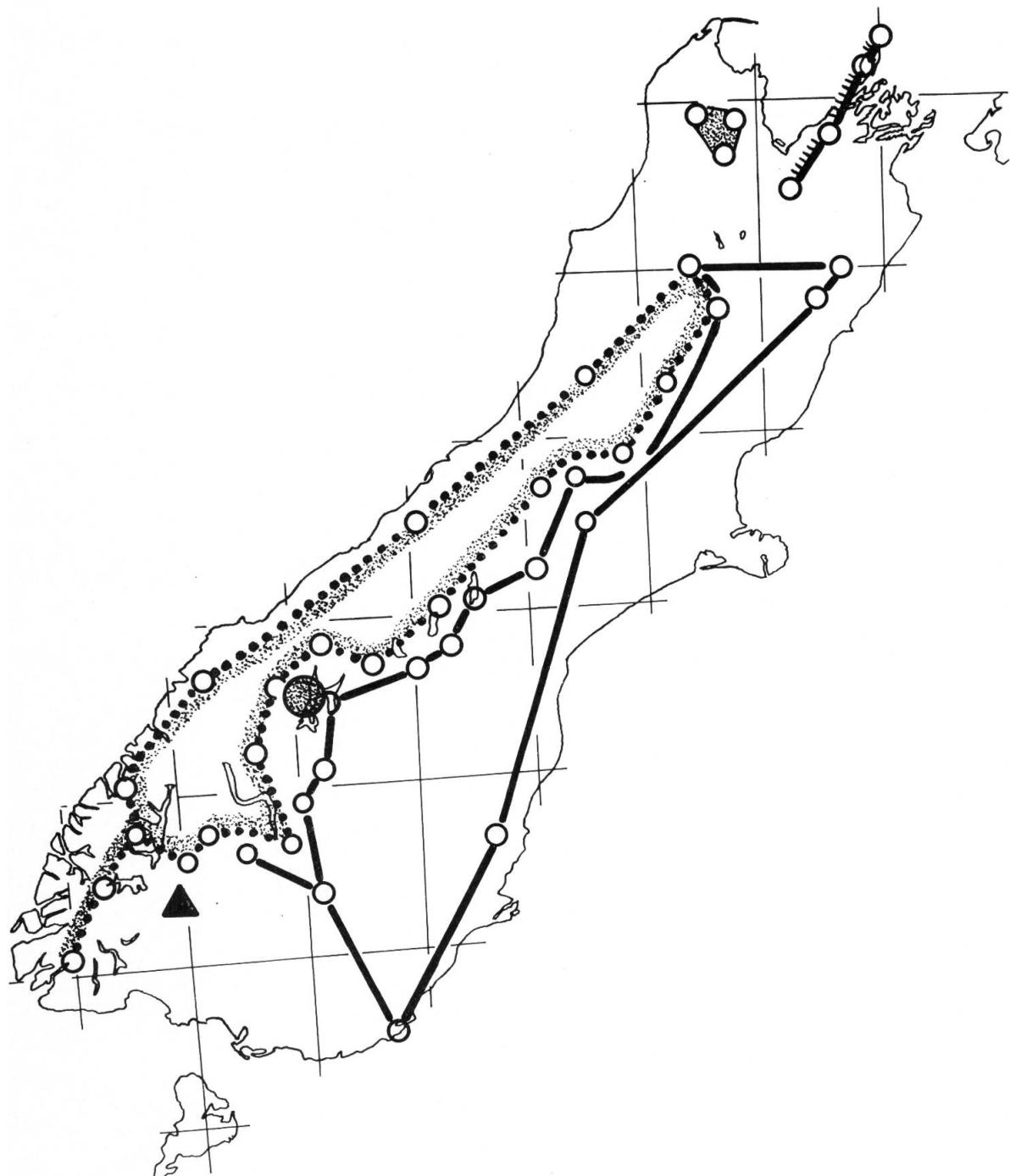


Fig. 20. — *Hebe urvilleana*: hatched line. *H. fruticeti*: stippled circle. *H. subalpina*: dotted stippled line. *H. rakaiensis*: continuous line. *H. aff. rakaiensis*: black triangle. *H. sp. "o"* stippled triangle.

is not the only time putative members of South Is. Ser. *Occlusae* approach Sect. *Glaucae*. Here the species is interpreted as an eastern vicariant of *H. treadwellii*, with which it seems to be allied (cf. also *H. obovata* (Kirk) Ckne.), as well as vicariating, at Amuri Pass, with *H. topiaria*. Differences between this species and *treadwellii* and *obovata* need to be clarified.

58. *Hebe glaucophylla* (Ckne., 1899) Ckne. (1929). Fig. 19.

Shrubby banks and gullies in tussock grassland within the circuit: Arthur's Pass National Park — Mt. Burnett (N.W. Nelson) — Red Hill — Molesworth — Broken River. HAIR (1967) notes that the Red Hill population "regularly has a very small sinus", and so threatens the current classification of ser. *Occlusae* — ser. *Hebe* in the same region as do *H. stricta*/*H. salicifolia* populations.

59. *Hebe topiaria* Moore (1961). Fig. 19.

Amuri Pass and Tekoa north (via Faerie Queen and Glenroy R.) to Wangapeka/Mt. Arthur — Takaka Hill. With the exception of one additional record: Mt. Starveall (Richmond Ra.), the range of the species is surrounded by that of *H. glaucophylla* (cf. sect. *Subdistichae* in Nelson — Fig. 3).

60. *Hebe truncatula* (Col., 1899) Moore (1961). Fig. 18.

At or just within forest margins on the Ruahine Ra. This is placed by MOORE (1961) with *H. evenosa*. Both species have the glabrous style and ovary of *H. urvilleana*, *H. fruticeti* and *H. subalpina*.

61. *Hebe evenosa* (Petrie, 1916) Ckne. & Allan (1926). Fig. 18.

Upper edge of forest in the Tararua Ra.

62. *Hebe urvilleana* Oliver (1944). Fig. 20.

In *Leptospermum* (Myrtaceae) shrubland on ultramafic rocks, along the linear track: Mt. Starveall (Richmond Ra.) — Red Hill — Whangamoa — D'Urville Is. — Stephen's Is. This linear dispersal can be compared with that of *H. rigidula* and folding in the Nelson — Kawhia syncline (HEADS, 1989). OLIVER (1944) writes that the species: "comes close to *H. fruticeti*", and MOORE (1961) places the two together.

63. *Hebe fruticeti* Simpson & Thomson (1940). Fig. 20.

Shrubland in the Estuary Burn catchment below Mt. Alta. This form, *H. urvilleana*, and a distinct population of the Takitimu Mts. all lie along the mutual boundary of *H. rakaiensis* and *H. subalpina*.

64. *Hebe subalpina* (Ckne., 1899) Ckne. & Allan (1926). Fig. 20.

Shrublands, especially on banks by streams, from Long Sound (near Lake Mike) north to Glenroy Valley/Lake Tennyson. The most prominent eastern population is that of the Garvie Mts. The apparently restricted distribution in Fiordland south of Murchison Mts. complements an apparent absence from Paparoa Ra.

65. *Hebe rakaiensis* (J. B. Armstrong, 1881) Ckne. (1929). Fig. 20.

Steamsides and rocky outcrops, on the east at False Islet (Catlins coast) — Kakanui Mts. — Rakaia — Hodder R. (by Tapuaenuku), west to: Eyre Mts. — Umbrella Mts. — Hawea etc., generally vicariant with *H. subalpina*, with some geographic overlap at Glenroy Valley — Lake Tennyson. The small-leaved *Occlusae* population of the Takitimu Mts. (Fig. 20) has been identified with both *H. subalpina* and *H. rakaiensis*, but seems to be distinct from both. This needs study, as does the observation that Umbrella Mts. has, in addition to typical *H. rakaiensis*, an entity of distinct appearance (*Dickinson*, OTA) in this general affinity.

66. *Hebe* sp. "o" Eagle (1982). Fig. 20.

N.W. Nelson: Peel Ra. — Arthur Ra. — Lockett Ra. These populations appear to be close to *H. subalpina* but have the ciliate leaf margins and pubescent capsules of *H. rakaiensis*.

67. *Hebe* sp. aff. *?subalpina*

Plants collected by Dr. P. Johnson from limestone cliffs in the Murchison Mts., Fiordland, and cultivated at the Department of Scientific and Industrial Research, Dunedin, belong to an unnamed species possibly related to *H. subalpina*. Neither flowers nor fruit are known.

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