Zeitschrift: Candollea : journal international de botanique systématique = international journal of systematic botany

Herausgeber: Conservatoire et Jardin botaniques de la Ville de Genève

Band: 49 (1994)

Heft: 1

Artikel: Biodiversity and biogeography in New Zealand Ourisia (Scrophulariaceae)

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DOI: https://doi.org/10.5169/seals-879526

Biodiversity and biogeography in New Zealand Ourisia (Scrophulariaceae)

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RÉSUMÉ

HEADS, M. J. (1994). Biodiversité et biogéographie chez Ourisia (Scrophulariaceae) en Nouvelle-Zélande. *Candollea* 49: 23-36. En anglais, résumés français et anglais.

Cet article réunit des remarques et des cartes de répartition pour les 17 espèces d'*Ourisia* de Nouvelle-Zélande, arrangées selon leur rapports putatifs. Des notes sur les localités critiques et les exemples de vicariance sont donnés. Une concentration marquée des espèces de la Nouvelle-Zélande se situe dans la région des montagnes Humboldt. Les disjonctions le long de la faille alpine (l'exemple "beech gap") sont évidentes pour plusieures espèces d'*Ourisia*, ces disjonctions s'expliquant par les mouvements latéraux, au tertiaire, le long de la faille ayant divisé les populations. De la même façon, les disjonctions trans-Pacifiques et trans-Tasmaniennes dans le genre s'expliquent par la séparation de l'Australie, de la Nouvelle-Zélande et de l'Amérique du Sud.

ABSTRACT

HEADS, M. J. (1994). Biodiversity and biogeography in New Zealand Ourisia (Scrophulariaceae). *Candollea* 49: 23-36. In English, French and English abstracts.

This article includes distribution maps and notes for the 17 New Zealand species of *Ourisia*, arranged according to their presumed affinities. Notes on critical localities and patterns of vicariance are given. A pronounced massing of the New Zealand species occurs in the Humboldt Mts. region. Disjunctions along the Alpine Fault (the "beech gap" pattern) are evident in several *Ourisia* species and can be explained by Tertiary lateral movement on the Fault pulling apart populations. Similarly, the trans-Pacific and trans-Tasman disjunctions in the genus can be explained by the rifting apart of Australia, New Zealand and South America.

KEY-WORDS: Seed-plants — Distribution — South Pacific — Vicariance — Plate tectonics.

Introduction

Ourisia Commerson ex de Jussieu 1789, a genus of herbs with most species in New Zealand and SW South America (Fig. 1), is a classic example of trans-Pacific disjunction. DONAT (1935) mapped the genus and compared the range with that of several other groups. His map of *Caltha* L. sect. *Psychrophila* DC. (Ranunculaceae), for example, shows a range almost identical to that of *Ourisia*. This disjunct pattern is now generally accepted as representing break-up of a Gondwanaland group. In *Ourisia* it occurs in a family usually regarded as being among the most recently derived of all plants. Within New Zealand, *O. lactea, O. glandulosa, O. modesta,* and the affinity *O. goulandiana — O. macrocarpa* subsp. *macrocarpa* all show disjunction along the Alpine Fault. This pattern is locally referred to as the "beech gap" since *Nothofagus* (Fagaceae) is strangely absent there. The Alpine Fault represents a plate boundary (a transform), and lateral movement on the Fault during the Tertiary is proposed to have separated the regions of maximum diversity in New

CODEN: CNDLAR
ISSN: 0373-2967
49(1) 23 (1994)

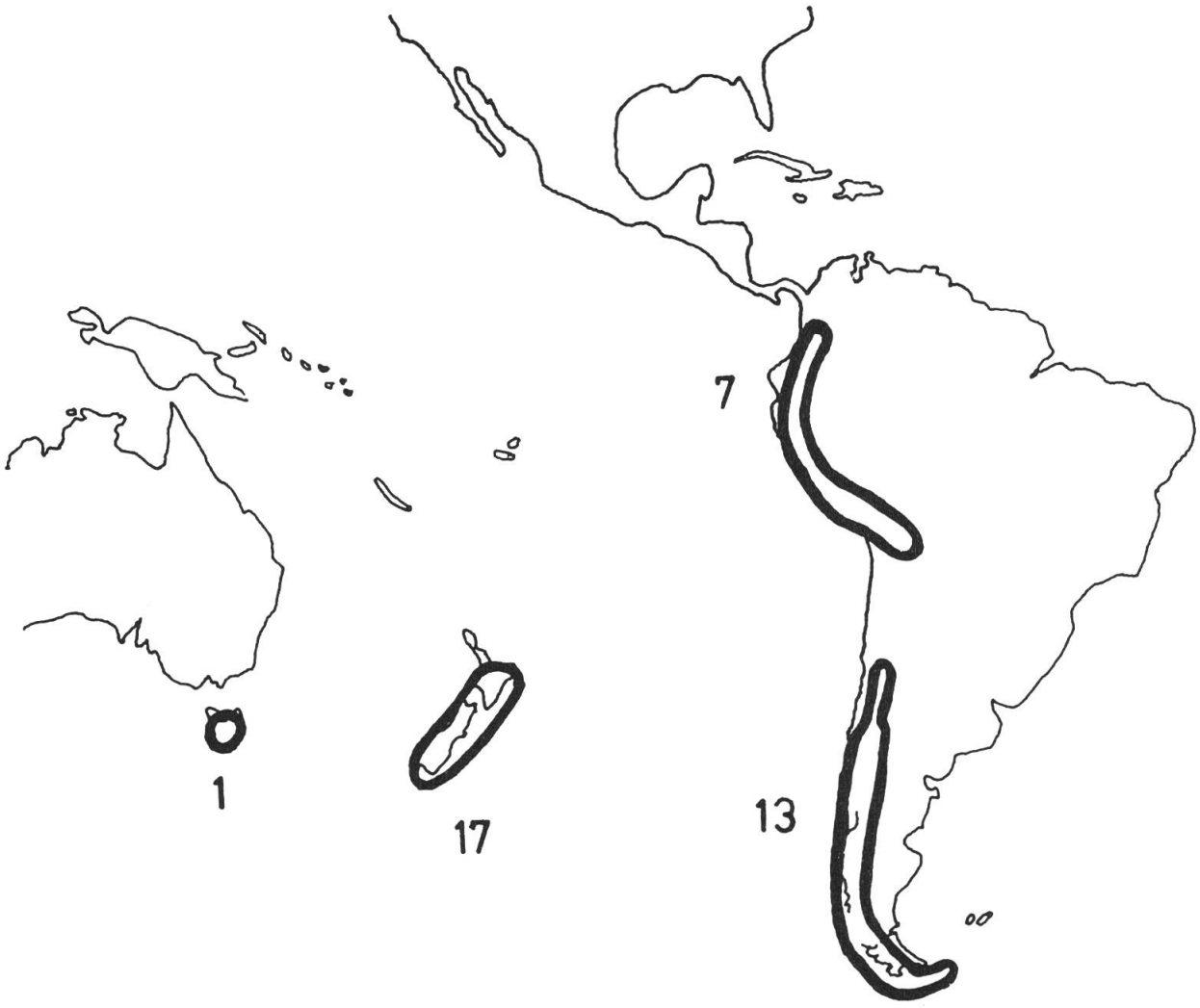

Fig. 1. — Distribution of *Ourisia*, with numbers of species (modified after DONAT, 1935).

Zealand *Nothofagus* by 180 km (HEADS, 1989), and led to striking absences and disjunctions in forest taxa (e.g. *Nothofagus*), alpine taxa (e.g. *Ourisia*) and in marine organisms (HEADS, 1989). The question as to why groups did not spread across the fault into neighbouring communities as movement on the fault took place raises the general question as to why many groups do not spread, whether or not they are being pulled apart on a fault. The "beech gap" is usually explained as a result of Pleistocene glaciation wiping out West Coast populations. This seems unlikely for at least two reasons. As indicated, the phenomenon is widespread throughout terrestrial and marine organisms with totally different ecologies. For example, *Ourisia* is largely alpine in New Zealand and is abundant around glaciers. A second objection to the usual theory is that the "gap" is often "filled" with a related taxon. For example, the gap in *O. lactea* subsp. *lactea* is filled by *O. crosbyi* (Fig. 4), the gap in *O. glandulosa* and *O. modesta* is filled by *O. caespitosa* (Fig. 7).

The affinities of *Ourisia* appear to be diffuse and complex, with some forms even resembling Gesneriaceae (HEADS, 1993a). At least some species have the wrong corolla aestivation for the subfamily Rhinanthoideae where the genus is usually placed. This is also true for some members of the *Hebe* complex (HEADS, 1993a), and these southern groups threaten to destabilise the basic divisions of the family. *Ourisia* also displays a disconcerting recombination of characters at the tribal level, having the united stigmas of the Veroniceae emend. Thieret but the divaricate anther cells of Digitaleae emend. Thieret (THIERET, 1967).

Ourisia comprises a single species of Tasmania, about 17 New Zealand species (some revised by ARROYO, 1984), and ca. 12 species of western South America. In South America DONAT (1935) mapped the genus north to northern Colombia, while ARROYO (1984) listed it north to southern Ecuador, but according to Dr N. H. Holmgren (*in litt.* 30.11.1992) the northernmost species are *O. chamaedrifolia* Benth. (Bolivia, Peru, Ecuador, southern Colombia) and *O. muscosa* Benth. (Pichincha Province, Ecuador).

Ourisia in New Zealand

The maps in this article have been prepared from a study of herbarium material, critical evaluation of published and unpublished records and personal field observations.

Members of the genus in New Zealand favour moist, open places such as upland streamsides, damp banks, forest margins, open boggy ground, subalpine shrubland, alpine grassland, herbfield, snowbanks and fellfield. The genus ranges from sea-level up to 2100 m (7000') (MARK & ADAMS, 1973).

Numbers of species and subspecific taxa per degree square are shown in Figure 2. There is a clear main massing in the region of the Humboldt Mts., already recognised as "an unusually rich locality for alpine plants" by CHEESEMAN (1914) and now constituting part of Mt Aspiring National Park. Secondary levels of massing are evident in Stewart I. and western South I.

In New Zealand plants floral bracts are either whorled or paired. Members of Group 1 below (*O. macrocarpa, O. macrophylla, O. goulandiana, O. lactea, O. colensoi, O. crosbyi* — Figs. 3, 4) have bracts whorled. This is equivalent to the first group of four species in MOORE's (1961) key, although in her synopsis *O. macrocarpa* is excluded on the basis of calyx division. The species is regarded here as a phylogenetic linking form. Members of Group 2 (Figs. 5-7) have paired bracts.

Group 1

1a. Ourisia macrocarpa Hook. f., Fl. N. Z. 1: 198. 1854 subsp. **macrocarpa** (Fig. 3).

From Lake Monk, north via both western (Secretary I.) and eastern (Hunter Mts.) Fiordland, to Humboldt Mts. and Simonin Pass by Red Mountain.

1b. Ourisia macrocarpa subsp. **calycina** (Colenso, Trans. N. Z. Inst. 21: 97. 1889) Arroyo, New Zealand J. Bot. 22: 460. 1984 (Fig. 3).

From Skippers Ra. (between Lakes McKerrow and Alabaster) and Cascade Saddle north, on and west of a line: Mt. Cook — Arthur's Pass — Glenroy Valley — Mt. Starveall (Richmond Ra.) — Mt. Goul (NW Nelson). The apparently interdigitating boundary with subsp. *macrocarpa* at: Skippers Ra. — Red Mt. — Cascade Saddle lies in a seldom explored area, and requires further study.

2. Ourisia goulandiana Arroyo, New Zealand J. Bot. 22: 451. 1984 (Fig. 3).

Known only at Gouland Downs. ARROYO writes: "*O. goulandiana* has close affinities with both *O. macrophylla* Hook. f. and *O. macrocarpa* Hook. f. (with which it is sympatric) ... its essentially glabrous, subcordate dark green leaves in particular recall *O. macrocarpa* var. *macrocarpa* from Fiordland." This is a Fiordland — Nelson disjunction of the type discussed by HEADS (1989) and attributed to pull-apart of populations on a geological transform, the Alpine Fault. ARROYO continues: "the completely divided calyx lobes [of *O. goulandiana*] are extremely similar to those found in *O. macrophylla* [incl. *O. lactea*], which interestingly is not represented on the Gouland

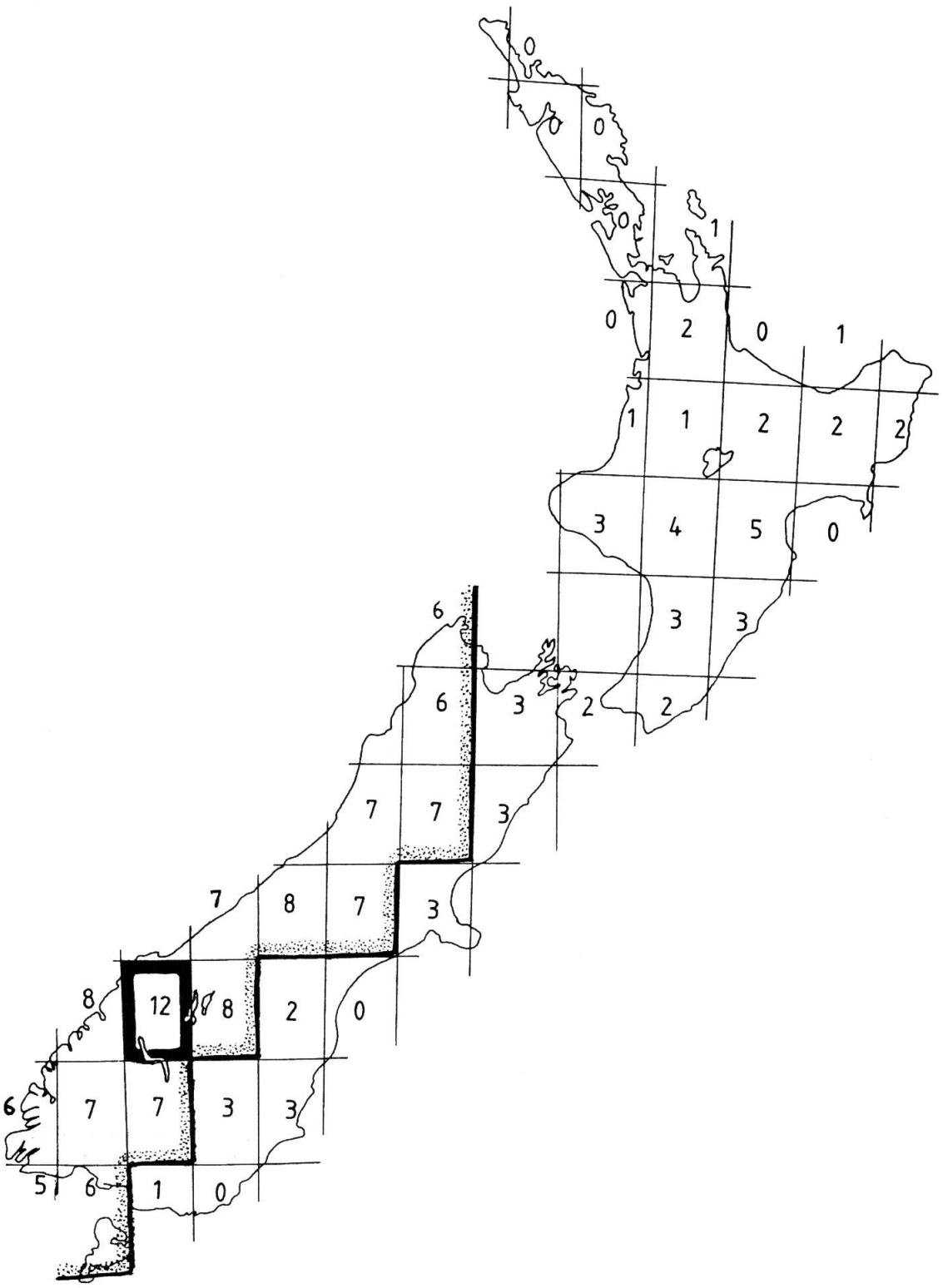

Fig. 2. — Numbers of species and subspecies of *Ourisia* per degree square in New Zealand. Regions including 0-5, 6-10, and 10- species/square are demarcated.

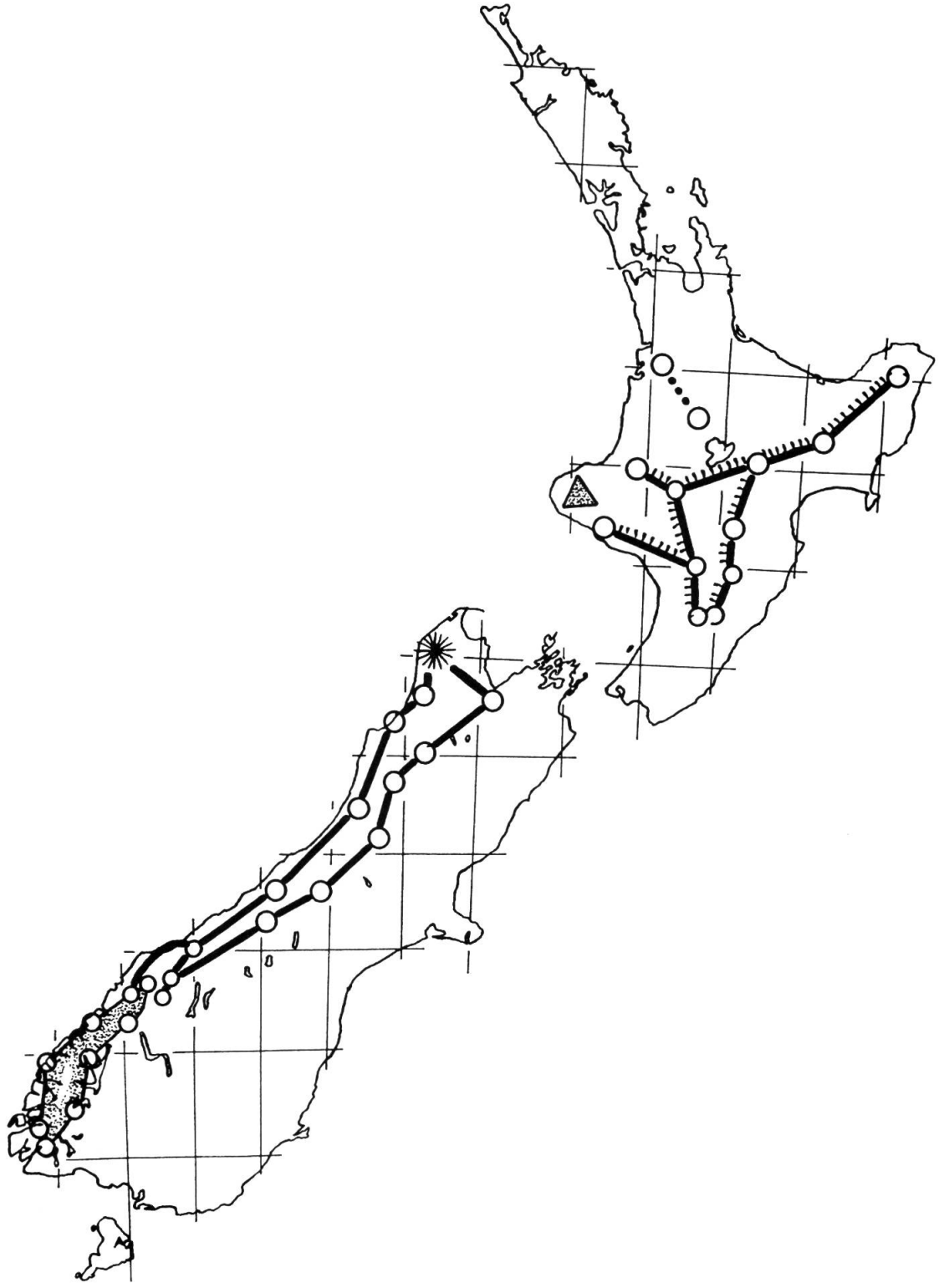

Fig. 3. — *Ourisia macrocarpa* subsp. *macrocarpa*: stippled line; *O. macrocarpa* subsp. *calycina*: continuous line; *O. goulandiana*: asterisks; *O. macrophylla* var. *macrophylla*: triangles; *O. macrophylla* var. *robusta*: hatched line; *O. macrophylla* var. *meadii*: dotted line.

Downs in spite of its wide distribution in the North and South Islands" While it may be true that *O. macrophylla* is not present *as such* at Gouland Downs, the precise location of this absence seems to indicate that its absence there is not absolute, and *O. macrophylla* is probably "represented" at Gouland Downs — by the populations referred by Arroyo to *O. goulandiana*. This is a good example of a centre of endemism also acting a a centre of absence (HEADS, 1989).

3a. Ourisia macrophylla Hook., Ic. Pl. tt. 545, 546. 1843 subsp. **macrophylla** (Fig. 3).

Locally endemic at Mt. Taranaki (= Mt Egmont) and nearby Pouakai Ra.

3b. Ourisia macrophylla subsp. **robusta** (Colenso, T. N. Z. I. 17: 246. 1886) Arroyo, New Zealand J. Bot. 22: 461. 1984 (Fig. 3).

Bounded by Patea — Manawatu in the south, this ranges north to: Tangarakau Gorge (20 km SE of Mt. Messenger) — Waimarino — Panekiri (Lake Waikaremoana) — Hikurangi.

3c. Ourisia macrophylla var. **meadii** Moore, Fl. N. Z. 1: 974. 1961 (Fig. 3).

This variety, characterised by petiolar hairs and leaf shape, is not accepted by ARROYO (1984) who regards it as clinal with *O. macrophylla* subsp. *robusta*. Whether clinal or not, the distribution of the form, at Mangakino Gorge — Pirongia, is of equal interest as this dispersal relates to a node at Kawhia seen also in, e.g., *Hebe rigidula* and *H. macrocarpa* (HEADS, 1993b).

4a. Ourisia lactea (Moore, Fl. N. Z. 1: 974. 1961) Arroyo, New Zealand J. Bot. 22: 459. 1984 subsp. **lactea** (Fig. 4).

Two tracks in southern South I.: Stewart I. — Doubtful Sound, and Flagstaff (Dunedin) — Garvie Mts. — Upper Routeburn Valley (Humboldt Mts.) connect at McKinnon Pass. Distribution is disjunct from there to: Punakaiki (by Paparoa Mts.) — Peel Ra. (NW Nelson), east via Arthur's Pass and Red Hill to Te Ao Whekere (Seaward Kaikoura Ra.) — Banks Peninsula. The overall disjunct pattern is very similar to that of, e.g., *Kelleria laxa* (Thymelaeaceae) (HEADS, 1990), with the gap filled by *O. crosbyi* (below).

4b. Ourisia lactea subsp. **drucei** (Moore Fl. N. Z. 1: 973. 1961) Arroyo, New Zealand J. Bot. 22: 459. 1984 (Fig. 4).

This holds two tracks: Mt. Taranaki — Ruapehu — Panekiri — Hikurangi, and: Tararua Ra. — Ruahine Ra. — Kaimanawa Mts. — Ruapehu.

The tracks of the two subspecies of *lactea* connect at: Peel Ra. (NW Nelson) — Mt. Taranaki, and Seaward Kaikoura Ra. — Tararua Ra.

5. Ourisia crosbyi Cockayne, Trans. N. Z. Inst. 47: 113. 1915 (Fig. 4).

Throughout Fiordland (on and west of a line: Hauroko — Murchison Mts. — McKinnon Pass). Also with the usual additional records at Stewart I. — Longwood Ra., and north of Fiordland along a line: Skippers Ra. — Mueller R. — Alex Knob — Arthur's Pass, neatly "filling in" the disjunction of *O. lactea*.

Fig. 4. — *Ourisia lactea* subsp. *lactea*: continuous line; *O. lactea* subsp. *drucei*: stippled line; *O. crosbyi*: dotted line; *O. colensoi*: hatched line.

6. Ourisia colensoi Hook. f., Handb. N. Z. Fl. 218. 1864 (Fig. 4).

This has a curious linear distribution, ranging south — north across North I.: Rimutaka Ra. — Tararua Ra. — Ruahine Ra. — Kaimanawa Ra. — Kaweka Ra. — Te Aroha — Te Moehau. The last locality is the northern limit in New Zealand of many taxa (e.g. *Kelleria* — Thymelaeaceae, HEADS, 1990) and is virtually the same northern limit as that of *Parahebe catarractae* at Cape Colville (ASHWIN, 1961). The tracks of *O. colensoi* together with those of *O. lactea* and *O. colensoi* form a "X" with the intersection near the Kaimanawa Mts., which is a standard pattern in North Island biogeography (HEADS, 1989). This zone of intersection is also a notable centre of endemism, e.g. *O. vulcanica* (Fig. 7), *Parahebe spathulata* (ASHWIN, 1961).

Group 2

This group (Figs. 5, 6) comprises ARROYO's (1984) "*sessilifolia* complex".

7a. Ourisia sessilifolia (Hook. f., Handb. N. Z. Fl. 218. 1864) subsp. **sessilifolia** (Fig. 5).

Stewart I. — South Caroline Burn (Lake Hauroko) northwards, on and west of a line: Mt. Burns — Takitimu Mts. — Eyre Mts. — Humboldt Mts. — McKerrow Ra. — Ohau Ski Basin — Mt. Fox (NW of Mt. Cook). The subspecies has a second disjunct massing in northern South Island, with a focus near Lake Tennyson. The localities are: Nelson Tops (near Lake Sumner) — Amuri Pass — Spenser Mts.; "Kaikouras"; Mole Tops (Nelson Lakes National Park) — Mt. Kendall (Karamea) — Cobb V. — Mt. Domett (Peel Ra.).

7b. Ourisia sessilifolia subsp. **splendida** (Moore, Fl. N. Z. 1: 974. 1961) Arroyo, New Zealand J. Bot. 22: 461. 1984 (Fig. 5).

Sealy Ra. (by Mt. Cook) — Arthur's Pass — Mt. Trovatore (by Lewis Pass). This subspecies thus fills the gap: Mt. Cook — Lewis Pass seen in the range of subsp. *sessilifolia*, and resembles *O. crosbyi* filling the gap in the range of *O. lactea*. CRAW (1989) has discussed these and other taxa which "close" the mid-South I. gap, and which appear to indicate Canterbury/Westland centres of form-making active before the rise of the Southern Alps.

8. Ourisia remotifolia Arroyo, New Zealand J. Bot. 22: 449. 1984 (Fig. 5).

From SW Fiordland: Lake Mike — Lake Monk (a common boundary — cf. *Euphrasia integrifolia* Petrie, pers. obs.), this follows a largely linear track extending north to: Mt. Burns — Irene Saddle — Homer Saddle — Fohn Saddle — Copland Ra./Mt. Sefton (by Mt. Cook). Its distribution is thus completely enclosed by that of the related *O. sessilifolia*.

9. Ourisia confertifolia Arroyo, New Zealand J. Bot. 22: 447. 1984 (Fig. 6).

This distribution comprises three sectors, which come together at the Humboldt Mts.: 1. Mt. Cuthbert (by Lake Monowai) — Percy Saddle (west of Lake Manapouri) — Mt. Soaker (Kepler Mts.) — Nitz Creek (Franklin Mts.) — Homer Saddle — Fiery Col (northern Humboldt Mts.); 2. Mid Dome — southern and northern Humboldt Mts. 3. Humboldt Mts./Mt. Earnslaw — Waiatoto Valley — McKerrow Ra. — Mt. Brewster (cf. *Parahebe catarractae* breaking off its range here at the lower Young V.).

Fig. 5. — *Ourisia sessilifolia* subsp. *sessilifolia:* continuous line; *O. sessilifolia* subsp. *splendida:* dotted line; *O. remotifolia:* stippled line.

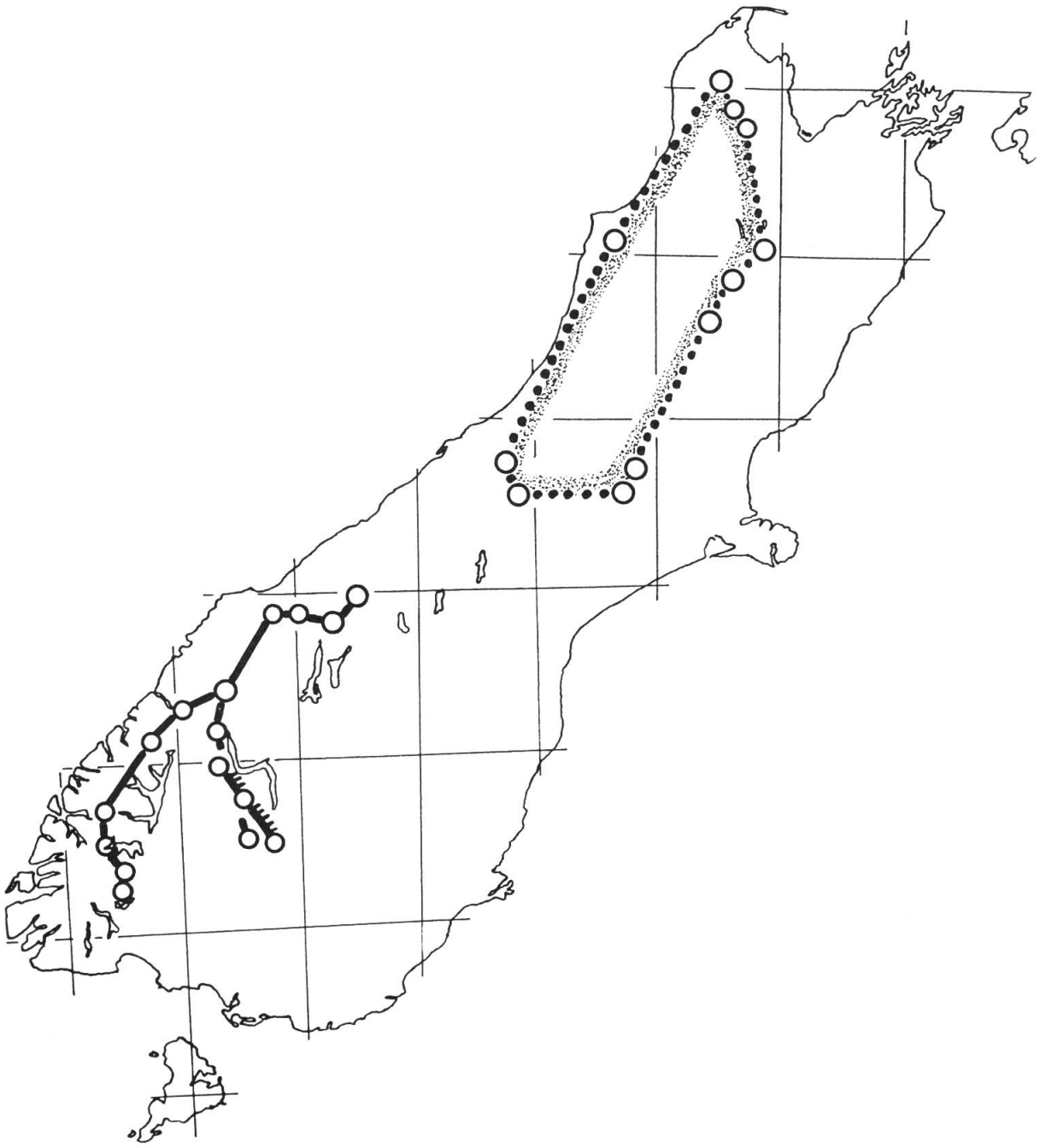

Fig. 6. — *Ourisia confertifolia:* continuous line; *O. spathulata:* hatched line; *O. simpsonii:* dotted stippled line.

10. Ourisia spathulata Arroyo, New Zealand J. Bot. 22: 451. 1984 (Fig. 6).

This ranges: East Dome (southern Garvie Mts.) — Eyre Mts. — Thomson Mts. and appears to "fill in" the range of *O. confertifolia* between Mid Dome and southern Humboldt Mts. The sector of endemism (cf. *Hebe biggarii, H. dilatata* — HEADS, 1992, 1993b) also acts as a limit or boundary of distribution in, e.g., *Leonohebe subulata, L. densifolia* and *L. haastii* (HEADS, 1993b).

11. Ourisia simpsonii (Moore, Fl. N. Z. 1:974. 1961) Arroyo, New Zealand J. Bot. 22: 462. 1984 (Fig. 6).

This ranges from a western limit: Lord River (upper Wanganui R.) — Mt. Misery (by Mt. Potts) — Paparoa Ra. — Mt. Goul, east to Torlesse Ra. — Wairau Gorge — Mt. Arthur. The southern limit by the upper Rangitata is the same as that of, e.g., *Parahebe linifolia* (ASHWIN, 1961).

Group 3

This group is based on *O. caespitosa* and *O. glandulosa*, markedly anisophyllous species with two rows of small leaves and two of large.

12. Ourisia caespitosa Hook. f., Fl. N. Z. 1: 198. 1853 (Fig. 7).

Northern Stewart I. (Mt. Anglem) — Lake Monk — Peel Ra. (NW Nelson), east to: Hump Ridge — Mt. Cuthbert — Takitimu Mts. — Eyre Mts. — Umbrella Mts. — Rock and Pillar Ra. — Kirkliston Ra. — Mt. Peel — Puketeraki — Te Ao Whekere. This last node connects with eastern North Island records: Tararua Ra. — Ruahine Ra. — Ruapehu/Tongariro — Hikurangi. The southern South I. distributions of this and related species have been correlated with terrane boundaries and tectonic zones (HEADS, 1989).

On the basis of bract shape and number of flowers per inflorescence the extensive collections in OTA are easily sorted into the two entities which follow, despite ARROYO's (1984) view that variation is clinal.

12a. Ourisia caespitosa var. **caespitosa** (Fig. 7).

This has bracts lobed, calyx lobes broad to apex, and two flowers in each bract pair. Generally there are two pairs per inflorescence, sometimes there are three pairs. There is never just a single flower. Leaves are larger and more lobed than in the following variety. This is widespread from Stewart I. to northern South I. and eastern North I., but in southern South I. ranges east only to: upper Beans Burn (Humboldt Mts.) — Mt. Aspinall — McKerrow Ra. — *Upper* Godley Valley (*Scott*, 5000', OTA).

12b. Ourisia caespitosa var. **gracilis** Hook. f., Handb. N. Z. Fl. 738. 1867 (Fig. 7).

This has leaves smaller and less lobed than the preceding variety, with entire bracts and calyx lobes narrowed apically. Generally the inflorescence comprises a single flower in a pair of bracts. At most there are two flowers, placed one above the other. This form is found mainly in central Otago, west to: upper Eyre Creek — Thomson Mts. — O'Leary Pass (Humboldt Mts.) — Mt. Roy — lower Young Valley — *Lower* Godley Valley (*Scott*, 5000', OTA) — Ohau Ra. This more or less meets the eastern limit of var. *caespitosa*. MARK & ADAMS (1973) state that var. *gracilis* "accompanies var. *caespitosa* in Canterbury and Western Otago".

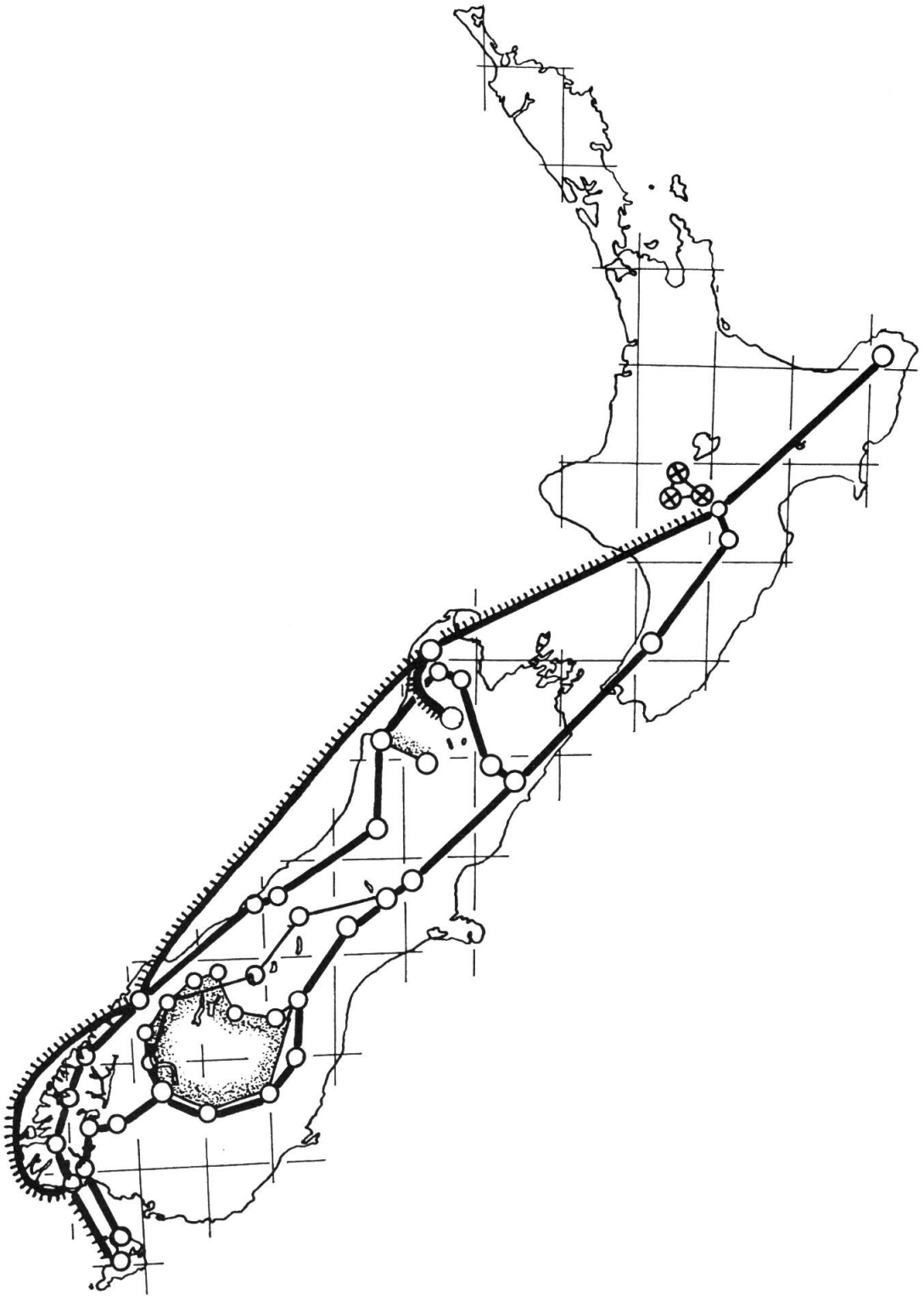

Fig. 7. — *Ourisia caespitosa* var. *caespitosa:* continuous line; western limit of *O. caespitosa* var. *gracilis:* fine line; *O. vulcanica:* crossed circles; *O. glandulosa:* stippled line; *O. modesta:* hatched line.

13. Ourisia cockayneana Petrie, T. N. Z. I. 29: 426. 1897 (not mapped).

Mt. Burns — Eyre Mts. — Cleddau V. — Humboldt Mts. — Mt. Earnslaw, disjunct to Hokitika R. — Arthur's Pass. ARROYO (1984) regards this as a hybrid of *O. macrocarpa* and *O. caespitosa*. However, no consistent difference is obvious between plants from near Arthur's Pass, where *O. macrocarpa* is represented by subsp. *calycina*, and those from further south where only subsp. *macrocarpa* is known (MOORE, 1961). Probably more than simple current hybridism is involved, and the apparent disjunction along the Alpine Fault is a standard pattern (HEADS, 1989).

14. Ourisia vulcanica Moore, Fl. N. Z. 1: 974. 1961 (Fig. 7).

Kaimanawa Mts. — Ruapehu/Tongariro. This includes plants formerly placed in *O. colensoi*, but MOORE (1961) notes that the affinities are rather with *O. caespitosa*.

15. Ourisia glandulosa Hook. f., Handb. N. Z. Fl. 219. 1864 (Fig. 7).

The southern, main massing of this species is a good example of the broader kind of central Otago endemism. A virtually identical pattern is seen in *Leonohebe densifolia*, disjunct to Kosciusko (HEADS, 1993a). Records are known on and within the line: Mt. Jumbo (Wilkin V.)/Mt.Alta — Humboldt Mts. — Eyre Mts. — Umbrella Mts. — Rock and Pillar Ra. — Mt. Pisgah — Hunters Hills — Kirkliston Mts. TOWNSON (1907) records the species at the Paparoa Ra., and the specimen '*Burke* 1985, Glenroy Valley' (CHR) probably also belongs here. This is a further example of disjunction along the Alpine Fault.

16. Ourisia prorepens Petrie, T. N. Z. I. 25: 272. 1893.

Type from Humboldt Mts. Status unclear. MOORE (1961) suggested that it may be a hybrid involving *O. caespitosa*, *O. glandulosa* and possibly other species.

Group 4

17. Ourisia modesta Diels, Fedde Repert. 7: 114. 1909 (Fig. 7).

This species differs altogether in size of flower and general appearance from all the other New Zealand species, and Diels (quoted in COCKAYNE, 1909) regarded it as closest to *O. breviflora* Benth. of Fuegia and *O. integrifolia* R. Br. of Tasmania. Localities are: Rakeahua Valley (Stewart I.) — Waitutu — Lake Alabaster — Tophouse (north of Lake Rotoiti) — Gouland Downs — north-west Ruahine Ra. (cf. *Euphrasia disperma*).

The far western arc of disjunct localities displayed by this species is correlated with an affinity (*O. integrifolia*) across the South Tasman Sea. This resembles *Kelleria laxa* — Thymelaeaceae (HEADS, 1990), which has a similar "beech gap" disjunction in South I., as well as a trans-Tasman disjunction. These two disjunctions can be explained by (a) the opening of the Tasman Sea and (b) lateral displacement on the Alpine Fault.

ACKNOWLEDGEMENTS

This work was supported by a Fellowship from the Miss E.L. Hellaby Indigenous Grasslands Research Trust and carried out in the Department of Botany, University of Otago. I thank the Directors of CHR, AK and WELT for permission to work through their collections of Scrophulariaceae, and Drs. P. J. Garnock-Jones, P. Weston, J. B. Wilson and the late Dr. L. B. Moore for reading versions of this article and making helpful suggestions.

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