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Biogeographic studies in New Zealand Scrophulariaceae: tribes Rhinanthaeae, Calceolarieae and Gratioleae

MICHAEL J. HEADS

RÉSUMÉ

HEADS, M. J. (1994). Étude biogéographique des Scrophulariaceae: Les tribus Rhinanthaeae, Calceolarieae et Gratioleae. *Candollea* 49: 55-80. En anglais, résumés français et anglais.

Les espèces Neo-Zélandaises de Scrophulariaceae des tribus Rhinanthaeae, Calceolarieae et Gratioleae sont cartographiées et commentées. Une importante concentration des espèces se situe au West Nelson au même endroit qui a le plus grand nombre d'espèces de *Hebe* (Scrophulariaceae, Digitaleae). Les quatre sections d'*Euphrasia* néo-zélandais montrent des centres de distribution vicariants en Nouvelle-Zélande avec des répartitions vicariantes ou affinités en dehors de la Nouvelle-Zélande en Australie, Nouvelle-Guinée, Juan Fernandez et en Amérique du Sud. Des fleurs péloriques ont été trouvées pour la première fois dans la flore de la Nouvelle-Zélande en *Mazus* dans la localité de Cannibal Bay en sud-est d'Otago, là, où le *Hebe rakaiensis* atteint sa limite australe. L'importance biogéographique de ce centre est en relation avec le synclinal de Southland.

ABSTRACT

HEADS, M. J. (1994). Biogeographic studies in New Zealand Scrophulariaceae: tribes Rhinanthaeae, Calceolarieae and Gratioleae. *Candollea* 49: 55-80. In English, French and English abstracts.

This article gives distribution maps and notes for the New Zealand members of Scrophulariaceae tribes Rhinanthaeae, Calceolarieae and Gratioleae. A main massing of species occurs in west Nelson, in the same degree square that has the highest number of *Hebe* species (Scrophulariaceae tribe Digitaleae). The four sections of New Zealand *Euphrasia* show vicariant massings within New Zealand together with vicariant ranges or affinities outside New Zealand in Australia, New Guinea, Juan Fernandez and South America. Peloric flowers are recorded for the first time in the New Zealand flora in *Mazus* at a locality (Cannibal Bay, SE Otago) where *Hebe rakaiensis* reaches its southern limit. The biogeographic importance of this centre is attributed to its association with the Southland Syncline.

KEY-WORDS: Biogeography — RHINANTHAEAE — CALCEOLARIEAE — GRATIOLEAE — SCROPHULARIACEAE — New Zealand

Introduction

Distribution maps and notes are given below for the New Zealand members of Scrophulariaceae in tribes Rhinanthaeae (one genus), Calceolarieae (one genus) and Gratioleae (five genera). New Zealand members of Rhinanthaeae (*Euphrasia*) were revised by ASHWIN (1961), the other groups were treated by ALLAN (1961). The remaining New Zealand Scrophulariaceae are all members of the *Hebe* complex (tribe Digitaleae) (HEADS, 1992, 1993a, b).

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. Species and subspecies

density of the group treated below is shown in Fig. 1. A main massing is evident in west Nelson, in the same degree square that has the highest number of *Hebe* species (HEADS, 1993a, b).

Mr. A. P. Druce (pers. comm. 1989) has indicated the existence of several undescribed species of *Euphrasia* in Nelson, which would accentuate this pattern of massing.

Tribe Rhinanthae

Euphrasia L. 1753

A recent infrageneric classification of *Euphrasia* (BARKER, 1982) recognises 14 sections.

Four sections are recorded in New Zealand (see below). Five sections are restricted to Australia. Four of these (*Phragmostomeae*, *Striatae*, *Australes*, *Scabrae*) are present in Tasmania, and the fifth (*Lasianthera*) is restricted to the mountains of SE mainland Australia.

Sect. *Paradoxae* comprises a single species, *E. formosissima*, with a distinct habit and known only from Juan Fernandez Is. BARKER (1982) notes the "generally agreed remote relationship of the species to the neighbouring South American species [sect. *Trifidae*] and emphasizes instead an affinity with sect. *Novaezeelandiae* of New Zealand (Fig. 2). This link is also known in other plants. For example, *Coprosma* (Rubiaceae) ranges between Australasia and Juan Fernandez but is absent from mainland South America, while Juan Fernandez species of *Ranunculus* and *Haloragis* are closer to New Zealand species than to South American ones (DU RIETZ, 1931).

Euphrasia sect. *Trifidae* caters for the South American species, which range from Falkland Is./Tierra del Fuego north to NW Argentina (or possibly Peru — see BARKER, 1982). The section is closely related to *E. disperma* (sect. *Anagosperrae*) of New Zealand.

Sect. *Atlanticae* caters for two species of the Azores. These show a syndrome of characters (regarded by BARKER, 1982, as primitive) found elsewhere only in Taiwan, Malesia, Australasia and Juan Fernandez. This affinity thus shows connections around the Atlantic, Indian and Pacific Oceans, but is notably absent from the continents of Africa, Asia and America.

Sect. *Malesiana* includes thirteen species of Ceram, Borneo (Kinabalu), Philippines (Luzon) and Taiwan. This section is geographically vicariant to the north of sect. *Pauciflorae* known from New Zealand, New Guinea and Sulawesi (Fig. 3).

Finally, sect. *Euphrasia* includes 90 species found north of a line: Japan — Himalayas — Morocco.

The overall pattern in the genus is dominated by 9 of the 14 sections occurring at a South Tasman Sea centre: Tasmania/SE Australia/New Zealand. Globally, *Euphrasia* has many southern sections but only one north of a line: Japan — Himalayas — Morocco (i.e. a Tethys boundary). This pattern, with high levels of diversity in the southern hemisphere and relatively homogeneous groups in the north resembles that of many groups, such as the *Hebe* complex of genera.

Although *Euphrasia* is very widespread, its origins by vicariance with other genera seem likely. BARKER (1982) cites Wettstein's suggestion of a common origin of *Euphrasia* with genera such as *Bartsia*. This latter genus shows what Barker describes as a "somewhat complementary" (i.e. vicariant) range to that of *Euphrasia*: mountains of tropical Africa, northern and central Andes. Also vicariating to the north of *Euphrasia* is *Lamourouxia*, with 30 species of Mexico and tropical South America (AIRY SHAW, 1973) and placed next to *Euphrasia* by BAILLON (1888).

Many of the distributions seen in *Euphrasia* are particularly clear examples of standard biogeographic patterns. For example, CROIZAT (1952: 19-23) homologised the South Pacific "baseline" of distribution in *Euphrasia* with that of *Nothofagus*, Monimiaceae and *Carex*. Globally he compared the distribution of *Euphrasia* with that of *Libocedrus* s.l. (living and fossil records) and proposed ecological and geographic vicariance between *Euphrasia* and Bignoniaceae. Within New Zealand, CROIZAT (1968) drew attention to the southern massing of *Euphrasia* (in South Island rather than North Island) (cf. *Hebe*, HEADS, 1993a) and to the importance of a North Island boundary: Cape Egmont — East Cape.

BARKER (1982) has also described homologous distributions in *Euphrasia*, *Nothofagus/Fagus*, and Scrophulariaceae tribe Veroniceae, and adds that Australian Mimulineae (*Elacholoma*, *Peplidium*, *Microcarpaea*, *Glossostigma*) "have disjunct trans-Pacific connections which may be as ancient". Elsewhere in the family *Jovellana* (see below) also has trans-southern Pacific links. Barker's conclusion, that *Euphrasia* had evolved in the Cretaceous before the breakup of Gondwanaland, seems unavoidable.

The New Zealand sections of *Euphrasia* show more or less distinct centres of massing within the region, correlating with distinct ranges and affinities outside New Zealand. Sect. *Anagospermae* masses in SW South I., and is closely related to sect. *Trifidae* of South America (Figs. 2, 5). Sect. *Novaezeelandiae* masses in Fiordland and Nelson, and is closely related to sect. *Paradoxae* of Juan Fernandez Is. (Figs. 2, 6). Sect. *Pauciflorae* masses in NW Nelson and is also in New Guinea and Sulawesi (Fig. 3, 7, 8). Sect. *Cuneatae* is in the western North I. and also in NE New South Wales (Fig. 4, 9). In this way the four sections show clear vicariance both within and beyond New Zealand, resembling the situation seen in the genera in the *Hebe* complex (HEADS, 1993a, b).

The global distribution patterns of the sections of New Zealand *Euphrasia* (New Zealand — Juan Fernandez, New Zealand — South America, New Zealand — New Guinea/Sulawesi, New Zealand — Australia) are accepted by Croizat, Barker and others as resulting from Mesozoic evolution followed by disruption. These patterns correlate with more or less vicariant main massings in New Zealand in, respectively, SW South I., Fiordland/Nelson, Nelson, and North I. This vicariance within New Zealand can also be interpreted as Mesozoic in age (HEADS, 1989). There is no reason to assume that this differentiation is any younger than the formation of the other sections of the genus with their own geographical centres of massing.

A biogeographic cline in plant architecture in *Euphrasia* appears to follow a northward sequence of the New Zealand biogeographic centres. The southern *Anagospermae* have a very fluid, plagiotropic morphology compared with the northern, orthotropic shrub *E. cuneata*. This cline in architecture resembles that of *Kelleria* (Thymelaeaceae, HEADS, 1990). In this genus the southern South I. plants form prostrate cushions and mats with adventitious roots, but further north in New Guinea there are only orthodox ericoid shrubs.

ASHWIN (1961) noted that in all New Zealand species of *Euphrasia* there are "patches of minute brown glands between the veins on the undersurface [of the leaves]." BARKER (1982) added that "the sessile glands occur on the lower surface in dense patches always in rows parallel to and just inside the margins." These glands recall the "domatia" of forms such as *Hebe townsonii*. These and similar structures may represent relic traces of earlier phases in the evolution of the leaf (HEADS, 1984).

Euphrasia sect. *Anagospermae* (Hook. f. 1879) Barker 1982 (Fig. 5)

This comprises four southern New Zealand species and includes the only forms of the genus at Stewart I. It also includes *E. disperma* (= *Siphonidium* Armstr.), a bizarre species with a filiform corolla tube up to 7 cm long and 1 mm wide. One-seeded fruits are very rare or unknown in Scrophulariaceae but the common form of *E. disperma* has one-seeded, asymmetric fruits (ASHWIN, 1961: 842; Fig. 33). SIMPSON (1977) described germination in this species, and illustrated the distinctive root "collet". Through *E. disperma* sect. *Anagospermae* is closely related to sect. *Trifidae* (South America) and more remotely to sects. *Novaezeelandiae* (New Zealand), and *Paradoxae* (Juan Fernandez).

1. *Euphrasia repens* Hook. f. 1854. (Fig. 5).

Sandy, shingly and boggy places on coasts. Cockayne (quoted in ASHWIN, 1961) describes the distribution on a Foveaux Strait centre (HEADS, 1989): "common on Dog, Centre and Ruapuke Islands [small islets in the strait] but rare on Stewart Id." The species is known on Stewart I. at Table Hill, and on South I. at Lake George and Riverton beach (both by the Longwood Ra.),

marshes near Oreti R. mouth (the type locality of *E. umbellata* Petrie), and east to Fortrose (near Awarua) and Fraser's Beach. *Baylis*, Secretary I., 800' (OTA) has been identified with this species.

2. *Euphrasia dyeri* Wettst. 1896. (Fig. 5).

Boggy places on mountains. SW Stewart I. (Big South Cape I., Port Pegasus, Mason Bay), west to West Cape — Humboldt Mts. — Richardson Mts., disjunct from there to Mt. Goulard (NW Nelson) (*Mair* 1962, CHR). The species ranges east to: Longwood Ra. — Blue Mts. — Maungatua — Rock and Pillar Ra. — Mt. Kyeburn (by Mt. Ida) — Mt. Somers.

This is morphologically very similar to the last, but the two are geographically distinct. ASHWIN (1961) writes that they occupy "quite different habitats", but the only clear difference in habitat seems to be altitude, and populations from intermediate altitudes (e.g. that of Secretary I.) may be difficult to place.

3. *Euphrasia integrifolia* Petrie 1915. (Fig. 5).

From SW. Fiordland (Lake Mike — Lake Monk, a standard boundary, cf. *Ourisia*, pers. obs.), NE through Fiordland (South Caroline Burn, Lake Hauroko — Mt. Cleughearn — Mt. Burns — Wilmot Pass/Percy Saddle — Murchison Mts.) to the Livingstone Mts. and Takitimu Mts. The general SW-NE alignment along the Moonlight Tectonic Zone (HEADS, 1989) suggests that the species may yet be found in, for example, the Eyre Mts.

4. *Euphrasia disperma* Hook. f. 1879. (Fig. 5).

Siphonidium longiflorum J. B. Amstr. 1881. *E. wettsteiniana* Du Rietz 1931.

Sea-level to 1000 m, usually in boggy or muddy places, in stunted vegetation on gley podzols and in bogs bordering coastal lagoons (WARDLE, 1975). Jackson Bay (Cascade R. and Dismal Swamp) — Okarito and nearby Five Mile Creek — Bald Hill Grey R. — Paparoa Ra. — Denniston Plateau/Mt. Rochfort -Karamea, and finally disjunct to Reporoa Bog in NW. Ruahine Ra. (see Fig. 6 for the last locality).

E. wettsteiniana Du Rietz 1931 was proposed to cater for material from Paparoa Ra./Denniston Plateau/Mt. Rochfort (near Westport), which is a standard biogeographic centre (HEADS, 1989).

Euphrasia sect. *Novaezeelandiae* (Du Rietz 1948) Barker 1982. (Fig. 6)

This comprises four New Zealand species only and is related to sects. *Paradoxae*, *Anagosperrae* and *Trifidae*. It is found to the north of the Stewart I./Foveaux Strait euphrasias, and has centres of massing in Fiordland — Otago, and Arthur's Pass — Karamea.

5. *Euphrasia australis* Petrie 1911. (Fig. 6).

From SW. South I. (Hump Ridge — Lake Monk — Resolution I. — Secretary I. — Clinton Saddle — Olivine Ra.) this ranges east to a line: Lake Hauroko — Takitimu Mts. — Umbrella Mts. — Humboldt Mts. — Wills R.

6. *Euphrasia zelandica* Wettst. 1896. (Fig. 6).

From the western localities: Lake Monk — Cascade R. — Arthur's Pass — Victoria Ra. — Peel Ra. — Mt. Ruapehu, this ranges east to: Umbrella Mts. — Maungatua — Hunters Hills — Banks Peninsula — Altamarlock — Tararua Ra. — Ruahine Ra. — Kaimanawa Mts. — Mt. Hikurangi.

The range of this widespread species is truncated in the western South I. Apparent absences occur at Resolution I. and Hump Ridge, where the species is replaced by *E. australis*, at Paparoa Ra. — Karamea, where it is replaced by *E. cockayneana*, and finally at Mt. Lyell — Goulund Downs, where it is replaced by *E. cheesemanii*. The relationship between the wide, eastern *E. zelandica* and the three species found on and west of its western boundary resembles the pattern seen in *Leonohebe odora*/*L. mooreae* (HEADS, 1992).

7. *Euphrasia cockayneana* Petrie 1894. (Fig. 6).

Paparoa Ra. (Sewell Peak etc.) — Karamea, inland to mid-Waimakariri — Arthur's Pass — west Matakītaki Valley.

8. *Euphrasia cheesemanii* Wettst. 1900. (Fig. 6).

Mt. Lyell (by Denniston) — Goulund Downs, inland to Mt. Arthur — Bull Creek (northern Spenser Mts.). There is general vicariance with *E. cockayneana*, and also vicariance at Goulund Downs with all other members of sect. *Novaezeelandiae*.

Euphrasia sect. *Pauciflorae* Barker 1982. (Figs. 7, 8)

Known from New Zealand (6 spp., massing at Goulund Downs — Mt. Peel), central New Guinea (9 spp.) and Sulawesi (1 sp. on Mt. Loemuet). This arc can be compared with affinities in *Parahebe*, *Libocedrus* (Cupressaceae) and *Carpodetus* (Saxifragaceae) which range: New Zealand — New Guinea, skirting Australia to the northeast. The New Zealand subsection of sect. *Pauciflorae* is keyed out by BARKER (1982) next to sect. *Striatae*, known from Tasmania and the eastern highlands of Victoria (Baw Baw Plateau, Fig. 3).

9. *Euphrasia townsonii* Petrie 1912. (Fig. 7).

Paparoa Ra. (Mt. Stevenson, Buckland Peaks) — Mt. Rochfort (near Westport) — Goulund Downs, east to: St. Arnaud Ra. — Mt. Arthur.

10. *Euphrasia monroi* Hook. f. 1864. (Fig. 7).

Goulund Downs — Mt. Mantell (between Maruia and Matakītaki Rivers) — Trovatore (by Lewis Pass), east to: Raglan Ra. — Mt. Richmond — Dun Mt./Mt. Tinline (Bryant Ra.).

11. *Euphrasia laingii* Petrie 1912. (Fig. 7).

Goulund Downs — Amuri Pass, south to Arthur's Pass — Hopkins R. (Lake Ohau) — Mt. Peel — Craigieburn, east to Chalk Ra./Ben More (south by the Waima (= Ure) R.). The population at Mt. Stokes (Marlborough Sounds) was previously usually referred to *E. monroi*, but CHR specimens have been determined as *E. laingii* by Dr. W. Barker. ASHWIN (1961) treated the plants as

E. monroi, but noted that they are "not quite typical". This recalls the "difficult" *Kelleria* population at this locality (HEADS, 1990), endemism there in *Celmisia macmahonii* (Compositae, ALLAN, 1961), and other patterns such as those of *Hebe stricta* var. *atkinsonii* and *H. macroura* which involve boundaries at a "Cook Strait centre" (HEADS, 1989, 1993).

12. *Euphrasia drucei* Ashwin 1961. (Fig. 8).

Tararua Ra. — Ruahine Ra. This connects with populations of the related *E. laingii* at Ben More — Mt. Stokes.

13. *Euphrasia petriei* Ashwin 1961. (Fig. 8).

From Fiordland (Mt. Burns — Secretary I. — Tutoko Saddle), east to Livingstone Mts. — Eyre Mts. — Humboldt Mts. — Olivine Ra., and in central Otago, on and within the circuit: Hector Mts. — Pisa Ra. — Dunstan Mts. — Garvie Mts. — Rock and Pillar Ra. Specimens from these localities can be distinguished from larger-flowered plants from: Mark's Ra. — Franz Josef Glacier — Mt. Peel (NW Nelson), east to: Mt. Brewster — Mt. Cook — Arthur's Pass — Faerie Queen. ASHWIN (1961) notes that the two forms are "more or less geographically separated". She also noted that on Hector and Pisa Ranges "dwarf densely tufted forms appear very distinct ... could receive varietal recognition." However, the classification of the populations of *E. petriei* appears to be less straightforward than the recognition of, for example, *Ourisia caespitosa* var. *gracilis* in a similar region (pers. obs.), and they are not figured on the map (Fig. 8).

14. *Euphrasia revoluta* Hook. f. 1854. (Fig. 8).

Ocean Peak (Humboldt Mts.) — Remarkables, north on the west to Mt. Brewster — upper Callery V. — Mt. Peel (NW Nelson), and east to: Mt. Torlesse — Lake Tennyson — Tararua Ra. — Ruahine Ra. Here a baseline: Peel Ra. — Franz Josef — Humboldt Mts. is shared with *E. petriei*, but otherwise there is general vicariance between the two species.

Euphrasia sect. *Cuneatae* Barker 1982 (Figs. 4, 9)

This comprises two species only: *E. cuneata* of central New Zealand, and *E. ramulosa* of montane to subalpine NE New South Wales. The section as a whole is related to the monotypic sect. *Phragmostomae*, with *E. phragmostoma* of coastal cliffs and heaths of Tasman Peninsula, SE Tasmania. Similar disjunct affinities between Tasmania and NE New South Wales (the "MacPherson-Macleay Overlap") have been discussed by CROIZAT (1964: 157).

15. *Euphrasia cuneata* Forst. f. 1786. (Fig. 9).

In the west this holds the series: Green Hill Stream (NW Nelson coast near Cape Farewell) — Mt. Taranaki — Ngawhakatara (= The Lady, near Kawhia) — Wahine Rock, Kaimai Ra. In the south it ranges east to: L. Ellesmere (by Banks Peninsula) — Awatere V. — Aorangi Ra. — Mahia — East Cape. The disjunct record at L. Ellesmere is notable, and recalls endemism at Banks Peninsula (e.g. *Hebe strictissima*, HEADS, 1993a).

Tribe Calceolarieae

Jovellana Ruiz & Pav. 1798

Within tribe Calceolarieae KRÄNZLIN (1907) recognised three genera: *Calceolaria* with 200 species ranging north from Falkland Is./Tierra del Fuego along the Andes to Mexico, *Perodittia* monotypic in Peru, and *Jovellana* with two species of Chile (between Concepción and Islos de Chonos) and four species (only two currently recognised) of New Zealand. The tribe and *Jovellana* thus span the South Pacific. HUTCHINSON (1973) mapped the genus and wrote: "The range of *Jovellana* ... points to the probability of a former land connexion between these now widely separated regions." CHEESEMAN (1925) regarded *Jovellana* as "hardly separable from *Calceolaria* ... from which it differs in the two lips of the corolla being nearly alike in size, whereas in *Calceolaria* the lower lip is very much larger than the upper." However, this morphological distinction has a standard, disjunct biogeography, and CHEESEMAN (1914) regarded *Jovellana*/*Calceolaria* as "striking proof of a special relationship between the flora of South America and New Zealand." The genus and tribe are notably absent from large sectors of northern and southern New Zealand. In Patagonia *Jovellana* is absent from the far south (Falkland Is. etc.) where other taxa, such as *Drapetes* (Thymelaeaceae, HEADS, 1990), are endemic.

1. *Jovellana sinclairii* (Hook. f. 1843) Kränzl. 1907. (Fig. 10).

This was regarded by HOOKER (1853) as "very nearly allied to *Calceolaria punctata* of south Chili". Distribution follows an arc in NE North I.: Haparapara R. (eastern Bay of Plenty) — Hick's Bay — East Cape — Tolaga Bay — Wairoa — Maungaharuru Ra. — Kaweka Ra. — Ikawetea R. (NW Ruahine Ra.) — Rangitikei R. east of Taihape. The last locality may be a lowland section of the important biogeographic centre at NW Ruahine Ra. (cf. *Euphrasia disperma*, Fig. 5).

2. *Jovellana repens* (Hook. f. 1854) Kränzl. 1907. (Fig. 10).

From a baseline: East Cape — Poverty Bay shared with *J. sinclairii*, this ranges west to Waioeka Gorge (near Opotiki) — Ngatukituki (over the Kaimai Ra. from Tē Aroha) — Wairata, and southwest to: Waikareiti/Panekiri (both by L. Waikaremoana), and the central triangle: Kaweka Ra. — Ohakune — Ruahine Ra. From here the species ranges south to Tararua Ra. — Rimutaka Ra., and southwest to: Herangi Ra. (by Awakino R.) — Mt. Taranaki — Anatoki (NW Nelson) — Karamea — Lake Brunner — Arthur's Pass — upper Karangarua R.

Tribe Gratiroleae

THIERET (1967) described this as "a large assemblage of obviously related genera ... characterised by a uniformity of seed type that is found in no other tribe of the Scrophulariaceae." The tribe is unknown in western Fiordland, and has only very restricted distribution in Stewart I. and Auckland Is. In these sectors it is largely replaced by members of the tribes Digitalae and Rhinanthae.

1. *Glossostigma* Wight & Arn. 1836. (Fig. 11).

This comprises some five species of New Zealand, Tasmania, Australia and India (ALLAN, 1961; VAN BALGOOY, 1971). Early records from Africa (Cape of Good Hope) are now usually

discounted (e.g. AIRY SHAW, 1973). Allan records the New Zealand species "from coastal to lowland ... in shallow waters, often entirely submerged", or "below hightide level submerged for a good many hours daily". CHEESEMAN (1877) observed that tensions set up in the style are released on light contact by a rapid movement of the style through at least 180°, with consequences for pollination. This recalls the tensions set up in the "traumatichorous" corollas of Indonesian *Stemodia* (Scrophulariaceae — Gratioleae) and *Stachytarpheta* (Verbenaceae) which are pushed out upon irritation (BACKER & BAKHUIZEN VAN DEN BRINK, 1965).

Pending investigations by Dr. W. Barker, the separate ranges of the New Zealand forms of *Glossostigma* (two species ?) have not been distinguished. The genus ranges east to North Cape — Tutira (Hawkes Bay) — Wickliffe Bay Otago Peninsula) / Waiholā (Dunedin) — Stewart I., and *G. elatinoides* Benth. 1854 is recorded from Chatham Is. The genus is apparently absent in Fiordland west of a line: Te Anau — Poteriteri, and is possibly also absent in southern Stewart I.

2. *Limosella* L. 1753.

A genus of some 15 species of New Zealand, south and east Australia, Eurasia, Kerguelen, Africa, North and South America.

1a. *Limosella lineata* Glück 1934 var. *lineata*

GLÜCK (1934) records this from Africa (South Africa, Madagascar, Fernando Po, Ethiopia), Kerguelen and Possession Is., SW and SE Australia, Tasmania, New Zealand and South America (north to Peru). This is a standard austral or Gondwanic range. ALLAN (1961) notes that similar forms of the variety are found in New Zealand, Tasmania and Australia.

In New Zealand (Fig. 12) the variety ranges as follows: Enderby I. (NE Auckland Is., cf. *Hebe salicifolia*, HEADS, 1993a, b) — Chatham Is. — Stewart I. (Mason Bay only), South and North Is. On the main islands it ranges west to: Lake Hakapoua (by Lake Monk) — Lake Katherine (George Sound), and from Fortrose (near Awarua) north to East Cape — North Cape.

1b. *Limosella lineata* var. *spathulata* Glück 1934.

GLÜCK (1934) records this from South Africa, Namibia and New Zealand (North Auckland, *Carse*) only. This range, like that of the last variety, is a classic Gondwanic distribution, but this taxon is centred clearly on the Indian Ocean. This complements the Pacific Ocean tracks seen in *Euphrasia*, *Jovellana*, the *Hebe* complex, etc.

2. *Limosella curdieana* F. Muell. 1875. (Fig. 12).

Recorded from SE Australia (Victoria, New South Wales) and New Zealand. In GLÜCK's (1934) treatment it forms a group with *L. capensis* of South Africa and *L. grandiflora* of South Africa and Namibia. The affinity, like *L. lineata* var. *spathulata* above, is centred on the Indian Ocean.

In New Zealand the species is known only from "near Black Horse Hotel" (Manuherikia Valley, PETRIE, 1896) and Catlins R., Owaka (near Cannibal Bay, SE Otago).

3. *Limosella* sp.

Mr. A. P. Druce has informed me (pers. comm. 1989) that there is a third New Zealand species of *Limosella* on the Taranaki coast (Opunake).

3. *Gratiola* L. 1753. (Fig. 13).

Some 20 species of New Zealand, Tasmania, south and east Australia, east Asia and Eurasia (VAN BALGOOY, 1971). The genus is recorded in New Zealand from coastal to lowland bogs and swamp margins on and within the circuit: North Cape/Spirits Bay — Kaitaia — Manakau — Taranaki — Cape Farewell — Westport — Notown (near Blackball) — Okarito — Big Bay — Te Anau/ Manapouri/Hauroko — Awarua — Chatham Is. — East Cape — Whangarei — North Cape. The genus is apparently absent in: west and central Fiordland — Stewart I. — Auckland Is. — Catlins.

Here the separate distributions of the two species accepted by ALLAN (1961) for New Zealand, *G. nana* Benth. 1846 and *G. sexdentata* A. Cunn. 1838, are not distinguished. Both of these also occur in Australia and Tasmania.

4. *Mimulus* L. 1753.

This comprises ca. 120 species of western North and South America (where species are most numerous), Juan Fernandez, New Zealand, Tasmania, Australia, west Malesia, southeast Asia, east Asia, Eurasia, Africa (AIRY SHAW, 1973; VAN BALGOOY, 1971). The single New Zealand species is also in Australia.

1. *Mimulus repens* R. Br. 1810. (Fig. 14).

In saltmarshes, coastal damp sands, marshy ground and meadows, from North Cape south to Cape Egmont — Otaki — Porirua — Wairau R. mouth — Blind R. (by Cape Campbell), and from there south on the west coast to Okarito, and on the east to Kaituna (by Lake Ellesmere and Birdling's Flat) — Otago Peninsula — Waituna Lagoon. Also in Australia (Tasmania, Victoria, South Australia).

5. *Mazus* Lour. 1790.

This comprises ca. 20 species of East Asia (the centre of diversity of the genus), SE Asia, Malesia, Philippines, New Guinea, east Australia, Tasmania and New Zealand (AIRY SHAW, 1973; VAN BALGOOY, 1971). Recorded in New Zealand from lowland to lower montane swamp margins, boggy ground, forest edges and damp grassland.

1. *Mazus radicans* (Hook. f. 1854) Cheesem. 1906. (Fig. 15).

From Lake Manapouri — Martyr R. (Jackson Bay) — Mt. Taranaki/Pouakai Ra. this ranges east to: Waituna Lagoon — Blueskin Bay (by Dunedin) — Naseby — Hanmer — Tararua Ra. — Maungaharuru Ra. — Kaweka Ra. — Atiamuri and nearby Lake Rotorua.

2. *Mazus pumilio* R. Br. 1810. (Fig. 15).

This species, closely allied to the Indian *M. rugosus* by CHEESEMAN (1925), is found in Australia, Tasmania and New Zealand. In New Zealand it ranges from: Cape Maria van Diemen (west of North Cape) — Ahipara — "lower Waikato", east to: Thames — East Cape — Wanganui — Pencarrow (by Port Nicholson, Wellington) — Banks Peninsula — Alexandra — Lowburn (by Pisa Ra.). Vicariance in the north and east with *M. radicans*, and the inland records from central Otago are noteworthy.

3. *Mazus* sp. (Fig. 15).

At False Islet (Cannibal Bay, SE Otago) a population of an unnamed *Mazus* species occurs in damp dune hollows by the sea with *Leptocarpus* — Restionaceae (Heads Dec. 1986, OTA). Flowering shoots terminate in either one flower, or a pair of flowers back to back, or a pair fused as a peloric structure (Fig. 16), with the calyces and corollas fused, 8 stamens, and two ovaries closely appressed but not fused. All three forms are common. This seems to be the first record of peloria in New Zealand plants. Peloria in Scrophulariaceae are discussed by SUTTON (1987). The general significance of pelorisation as the process by which an ancestral strobile could be condensed to form a modern flower is discussed by HEADS (1984). Stewart I. plants illustrated and described by WILSON (1982) as *Mazus radicans* probably belong to the same species. Wilson records these plants on the west coast of Stewart I. from east Ruggedy (north of Mason Bay) to Mason Bay. This *Mazus* species is thus vicariant to the south of the other species and ranges north to a biogeographic centre by False Islet, also known as the southern boundary of *Hebe rakaiensis* (HEADS, 1993a) and as one of only two New Zealand localities of *Limosella curdieana* (at nearby Owaka, and also in Central Otago. Tectonically and ecologically the False Islet region also has particular significance as the point at which the axis of the Southland Syncline, the major tectonic structure of the region, intersects the coastline. The geology and biogeography of the region is discussed further by HEADS (1989).

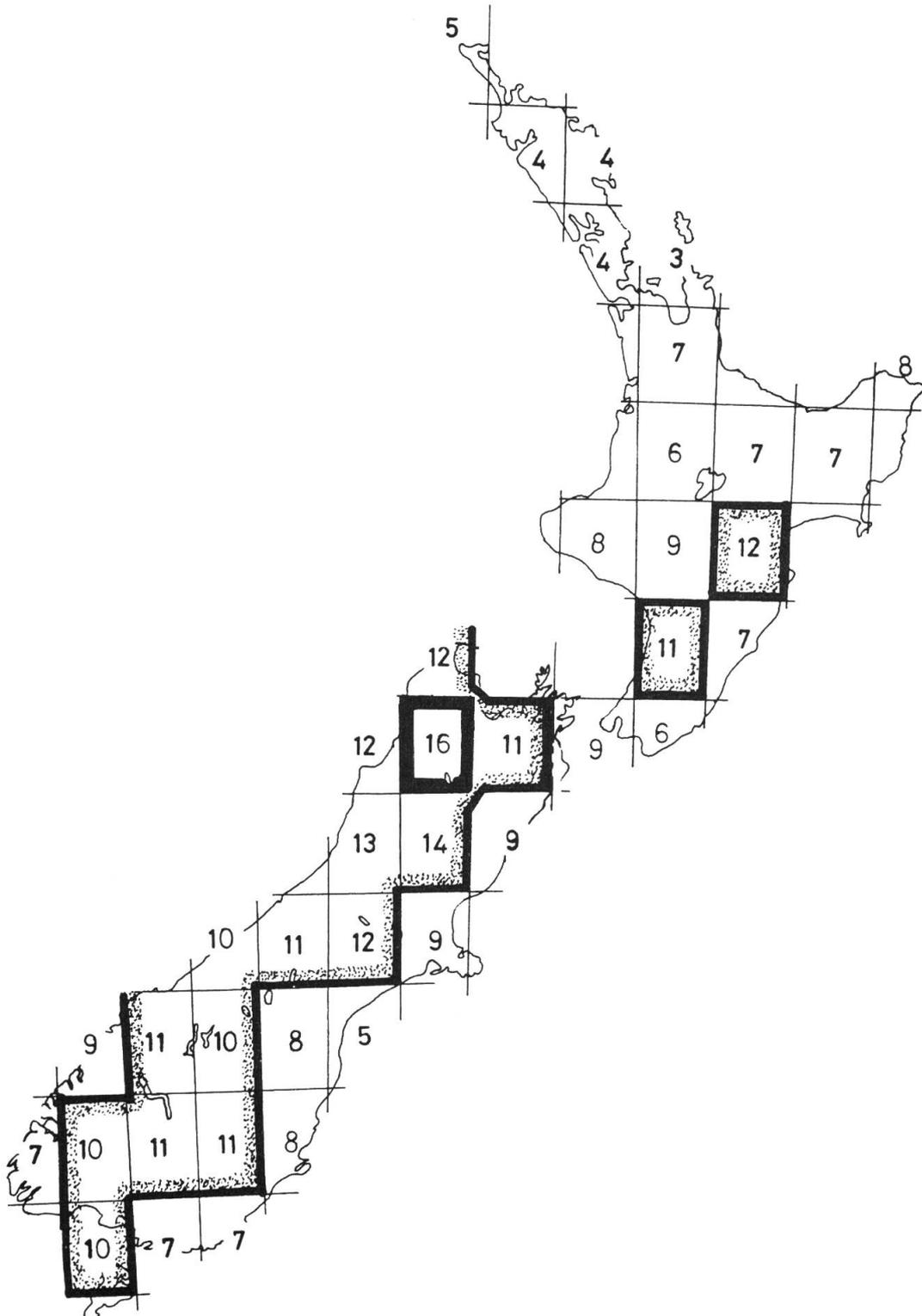


Fig. 1. — Numbers of species and subspecies of Rhinanteae, Calceolarieae and Gratioleae in each degree square of New Zealand. Regions with 0-9, 10-14 and 15-16 taxa/square are demarcated.

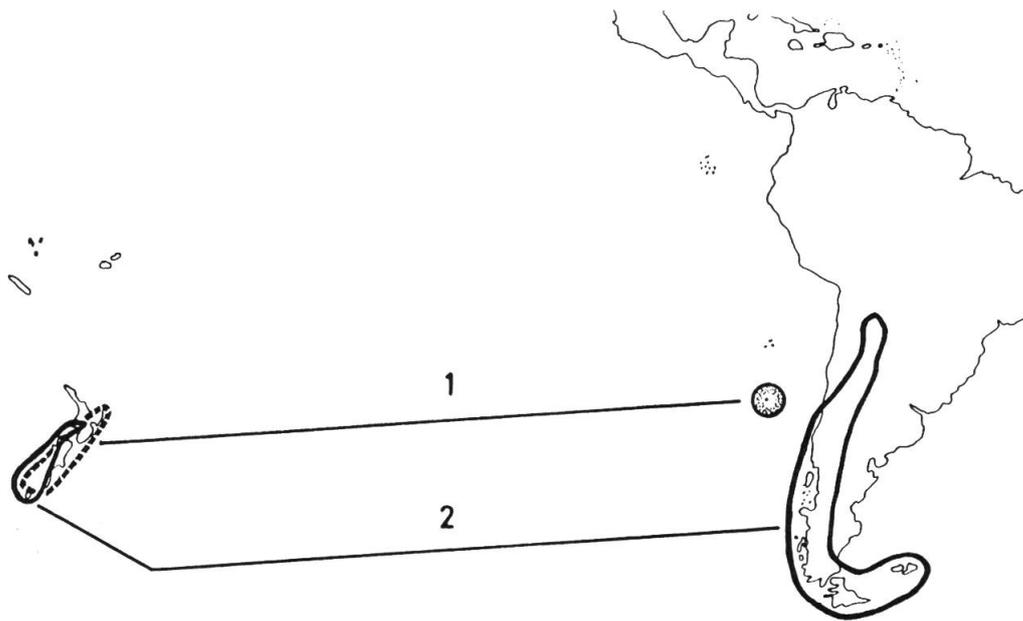


Fig. 2. — Track 1 indicates affinity between *Euphrasia* sect. *Novaezeelandiae* (broken line, New Zealand) and *E.* sect. *Paradoxae* (stippled circle, Juan Fernandez Is.). Track 2 indicates affinity between *E.* sect. *Anagosperrae* (especially *E. disperma*) and *E.* sect. *Trifidae* (South America).



Fig. 3. — *Euphrasia* sect. *Pauciflorae* (stippled, New Zealand, New Guinea, Sulawesi), and its closest relative, *E.* sect. *Striatae*, (solid black, Australia).

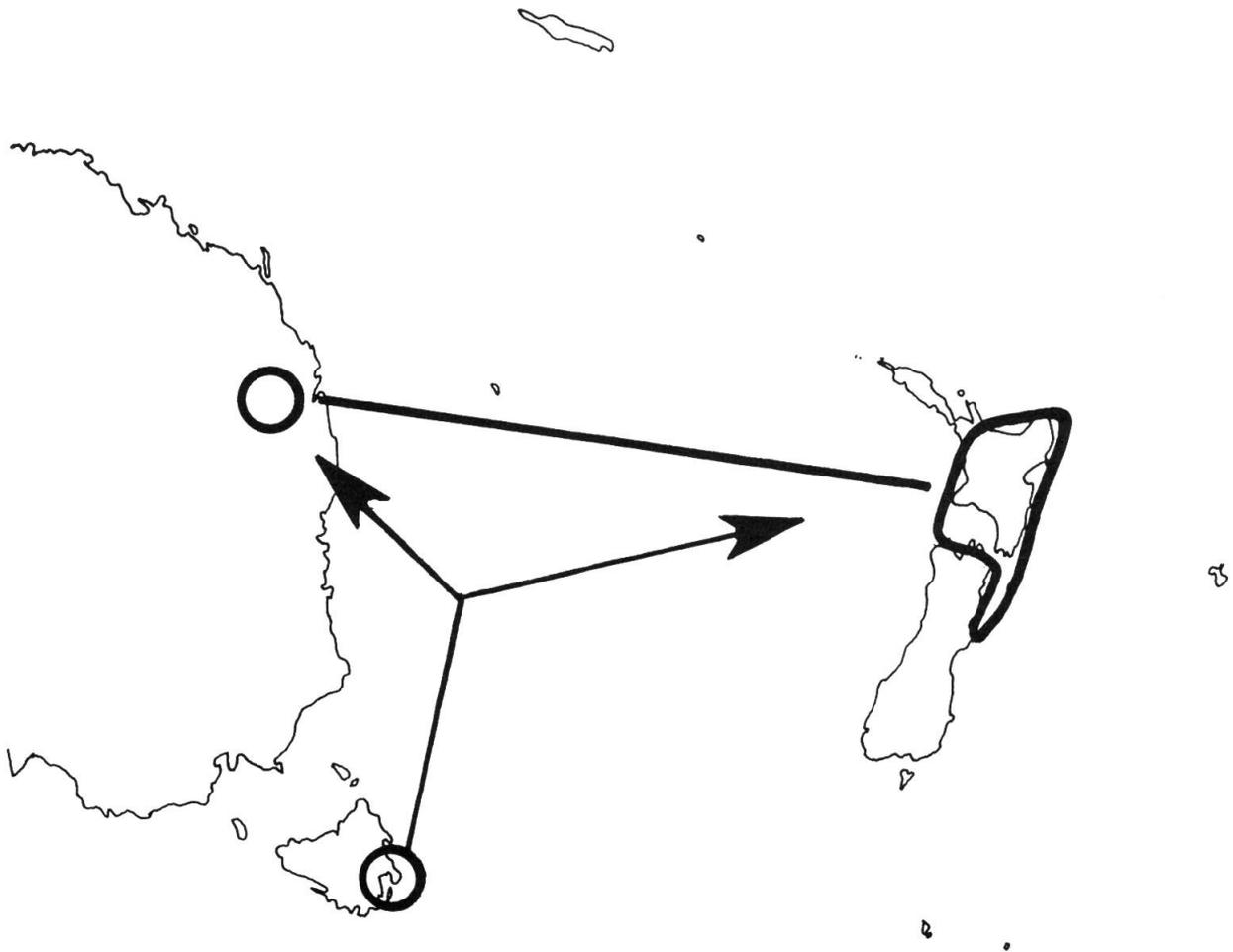


Fig. 4. — *Euphrasia* sect. *Cuneatae* (New Zealand, NE New South Wales) and its closest relative, *E.* sect. *Phragmostomeae* (Tasmania).

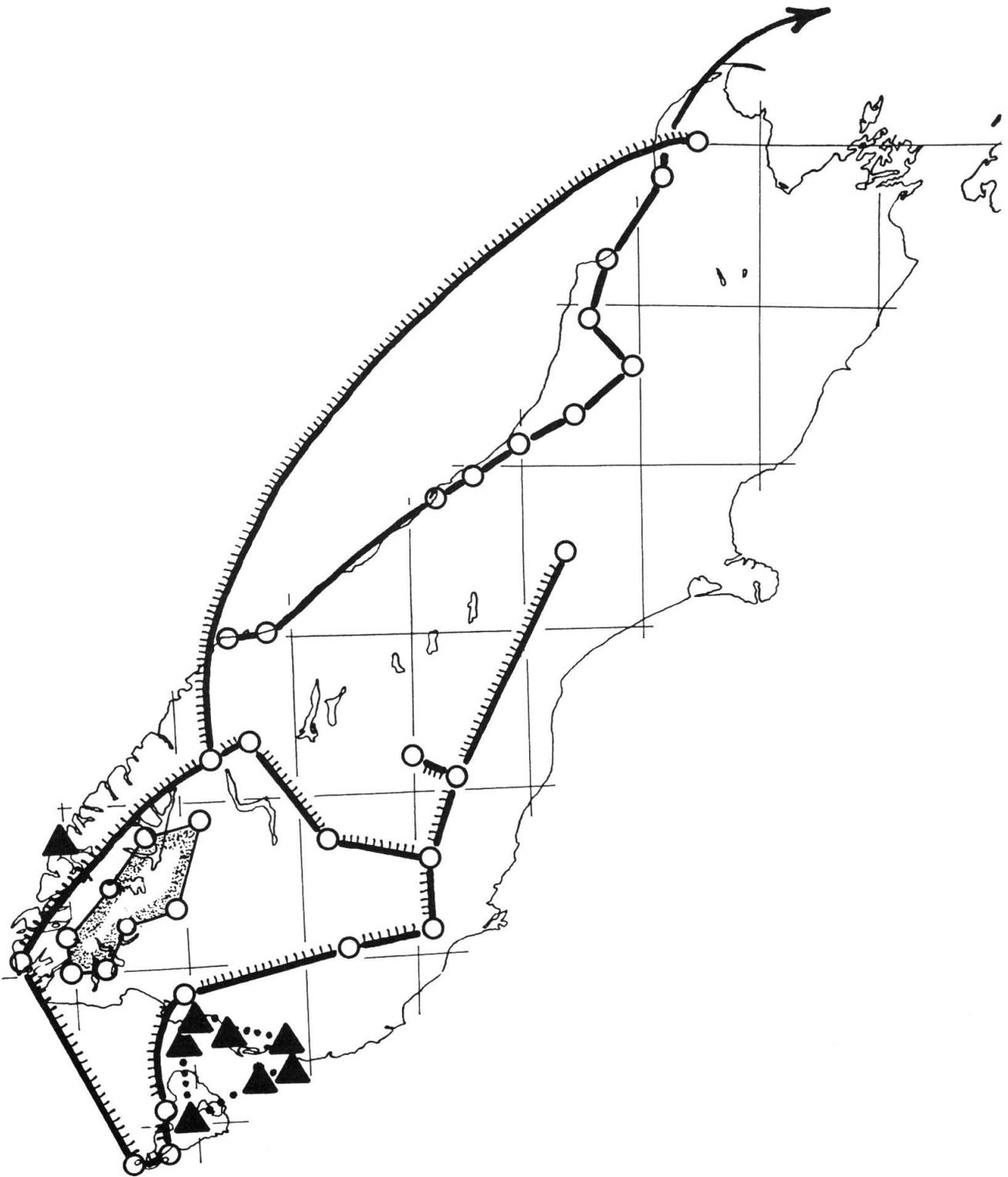


Fig. 5. — *Euphrasia* sect. *Anagosperrae*. *E. repens*: triangles; *E. dyeri*: hatched line; *E. integrifolia*: stippled line; *E. disperma*: continuous line (plus Reporoa, NW Ruahine Ra. — for this locality see Fig. 6).



Fig. 6. — *Euphrasia* sect. *Novae-zelandiae*. *E. australis*: hatched line; *E. zelandica*: continuous line; *E. cockayneana*: stippled line; *E. cheesemani*: dotted line. NW Ruahine Ra. indicated by arrow.

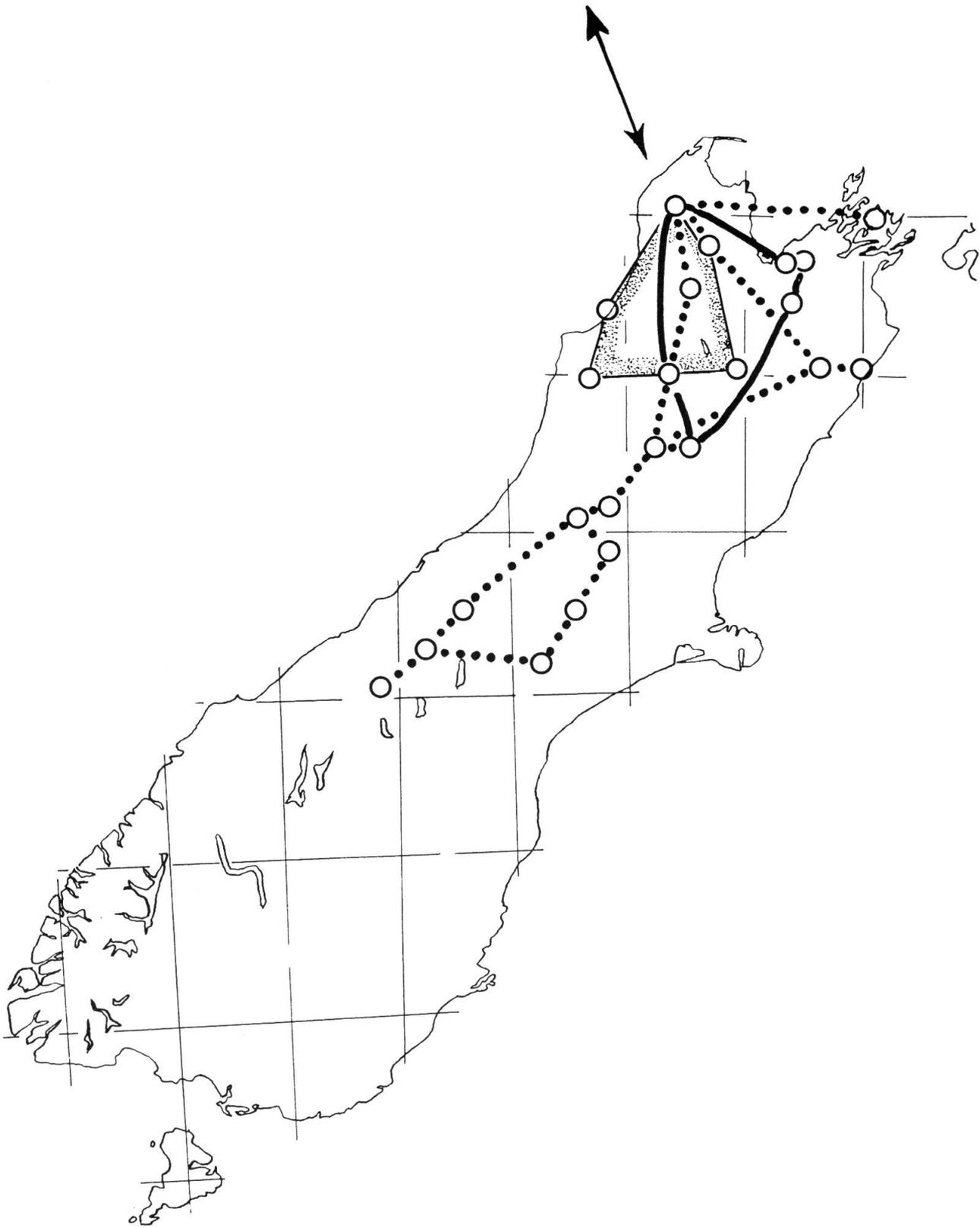


Fig. 7. — *Euphrasia* sect. *Pauciflorae* (in part). *E. townsonii*: stippled line; *E. monroi*: continuous line; *E. laingii*: dotted line.

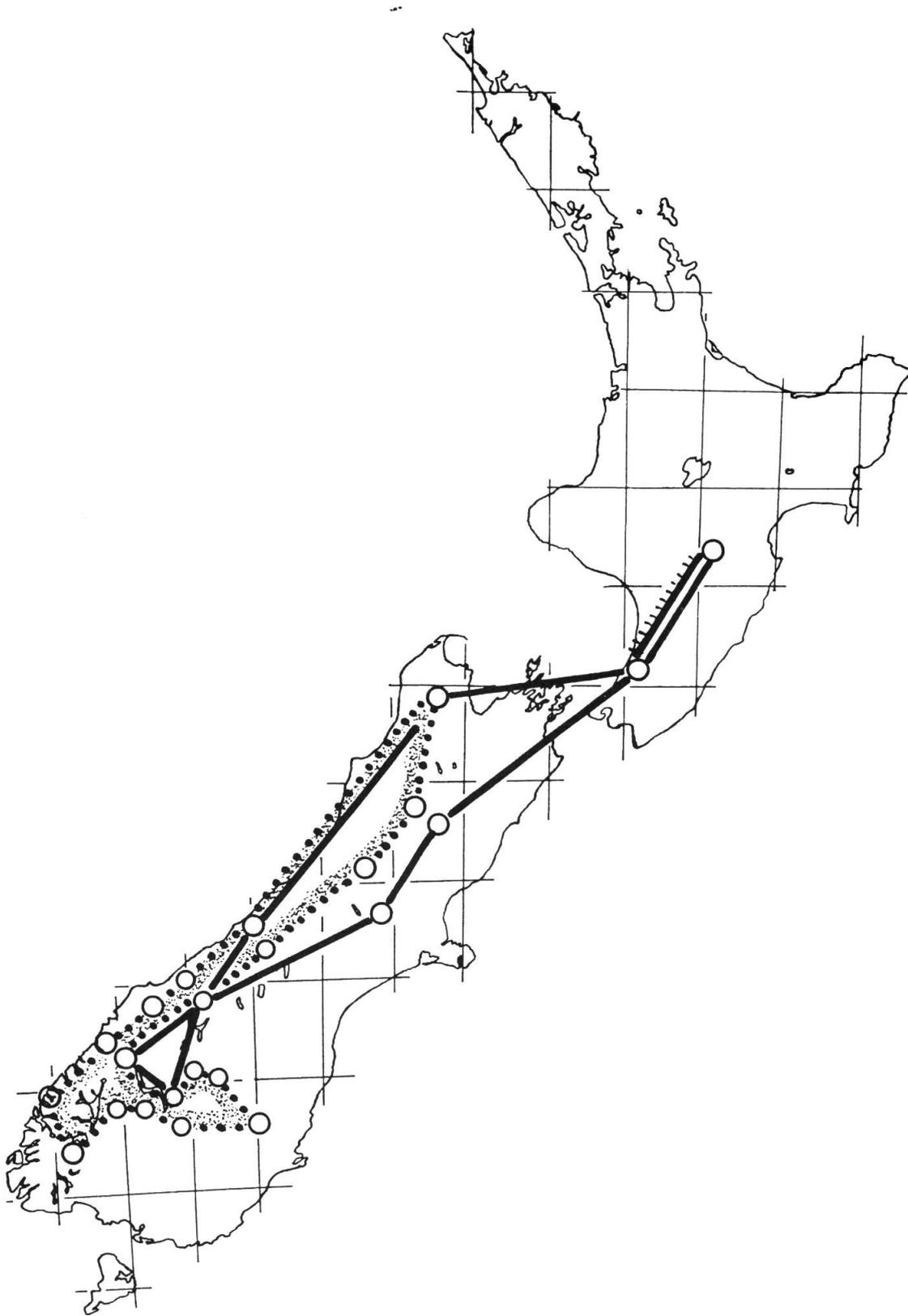


Fig. 8. — *Euphrasia* sect. *Pauciflorae* (in part). *E. drucei*: hatched line; *E. petriei*: dotted stippled line; *E. revoluta*: continuous line.

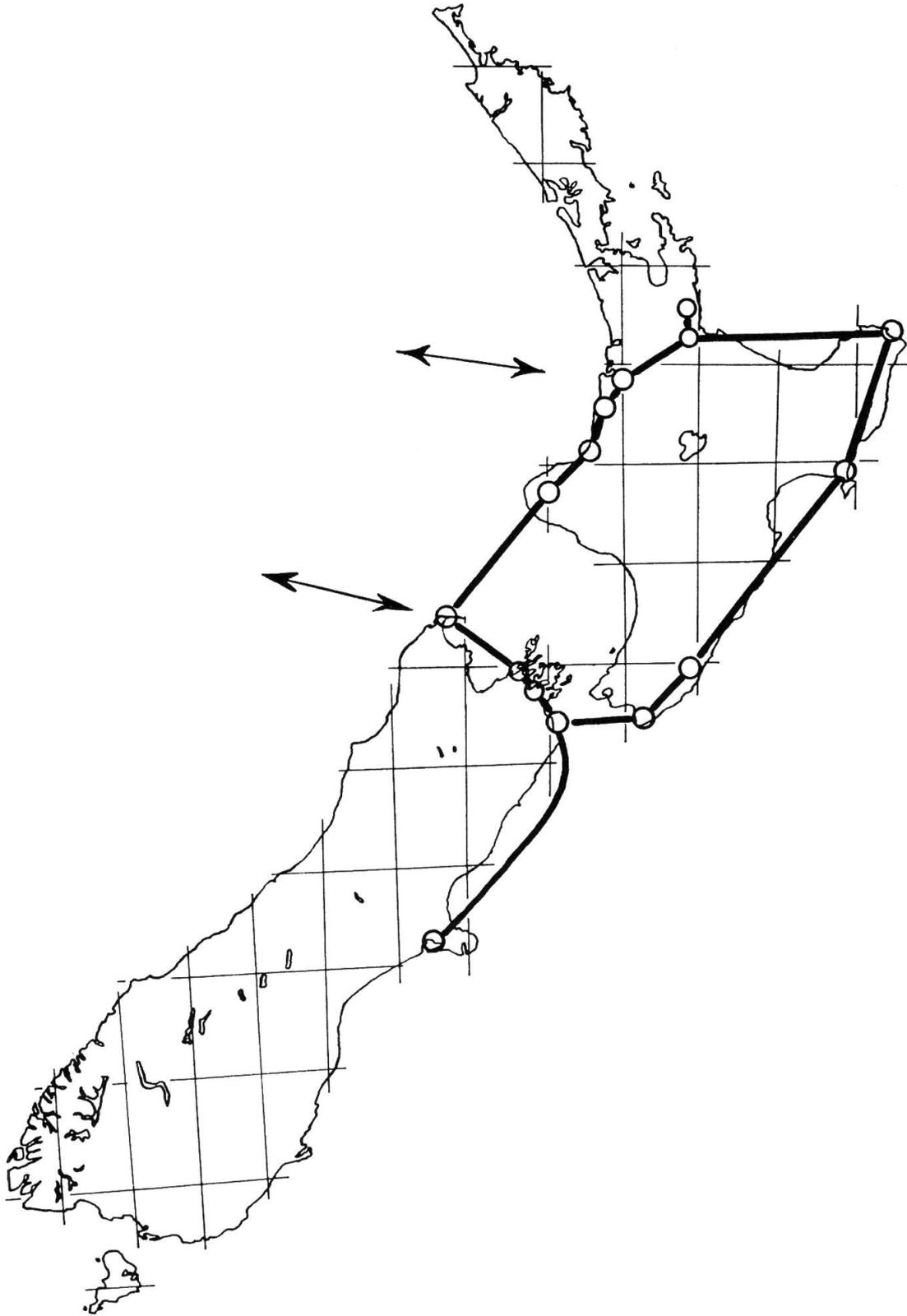


Fig. 9. — *Euphrasia cuneata*: continuous line.

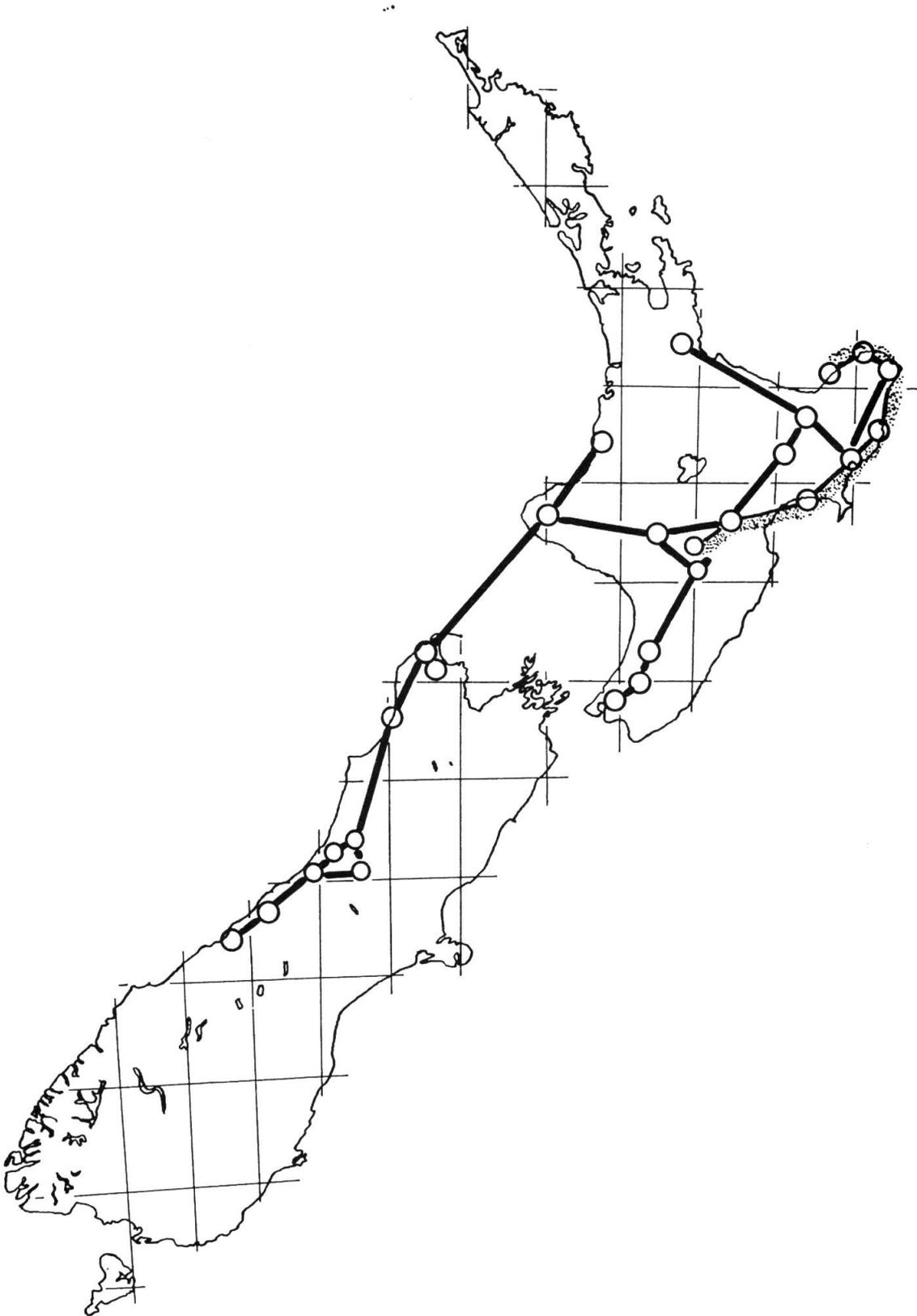


Fig. 10. — *Jovellana sinclairii*: stippled line; *J. repens*: continuous line.

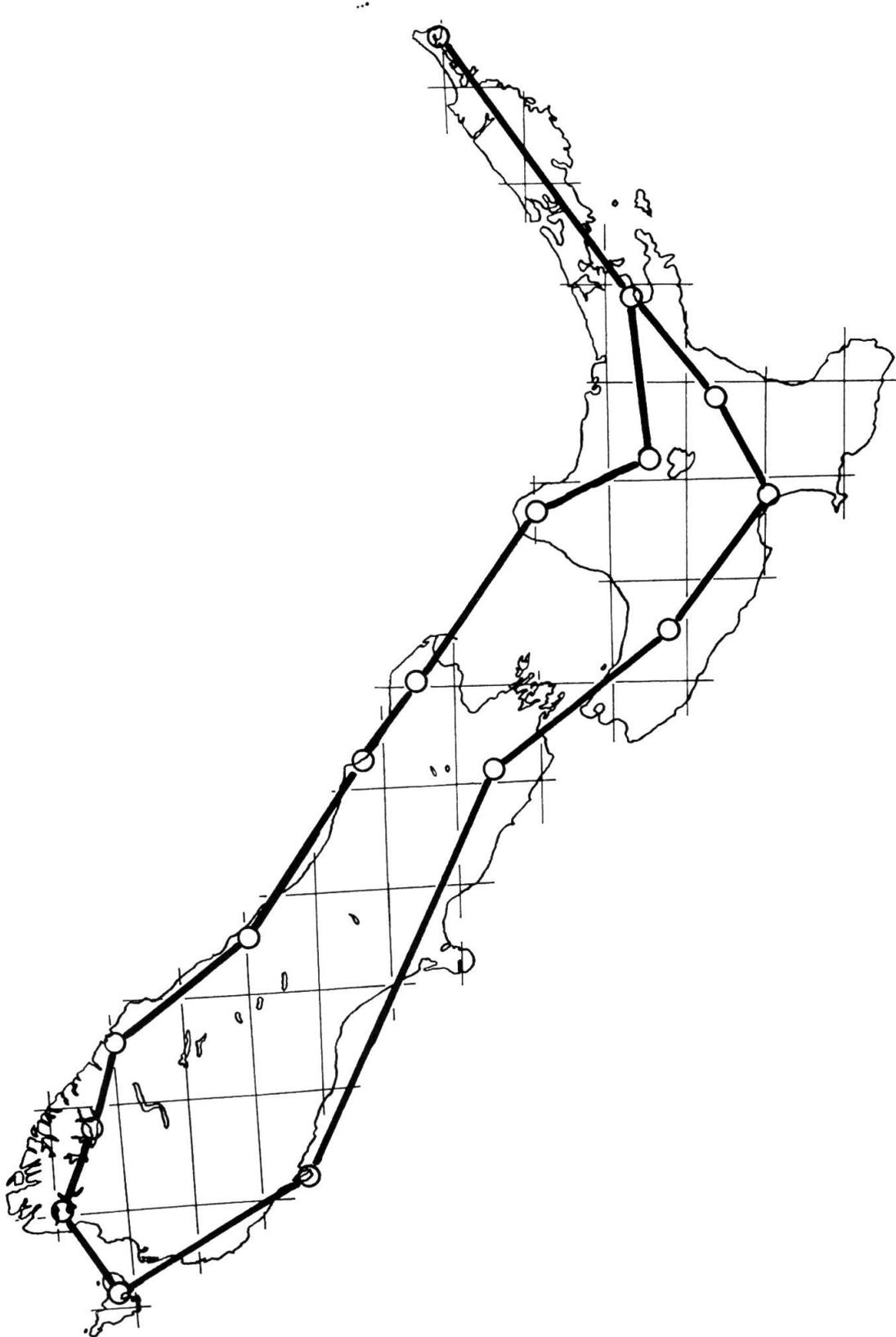


Fig. 11. — *Glossostigma* in New Zealand.

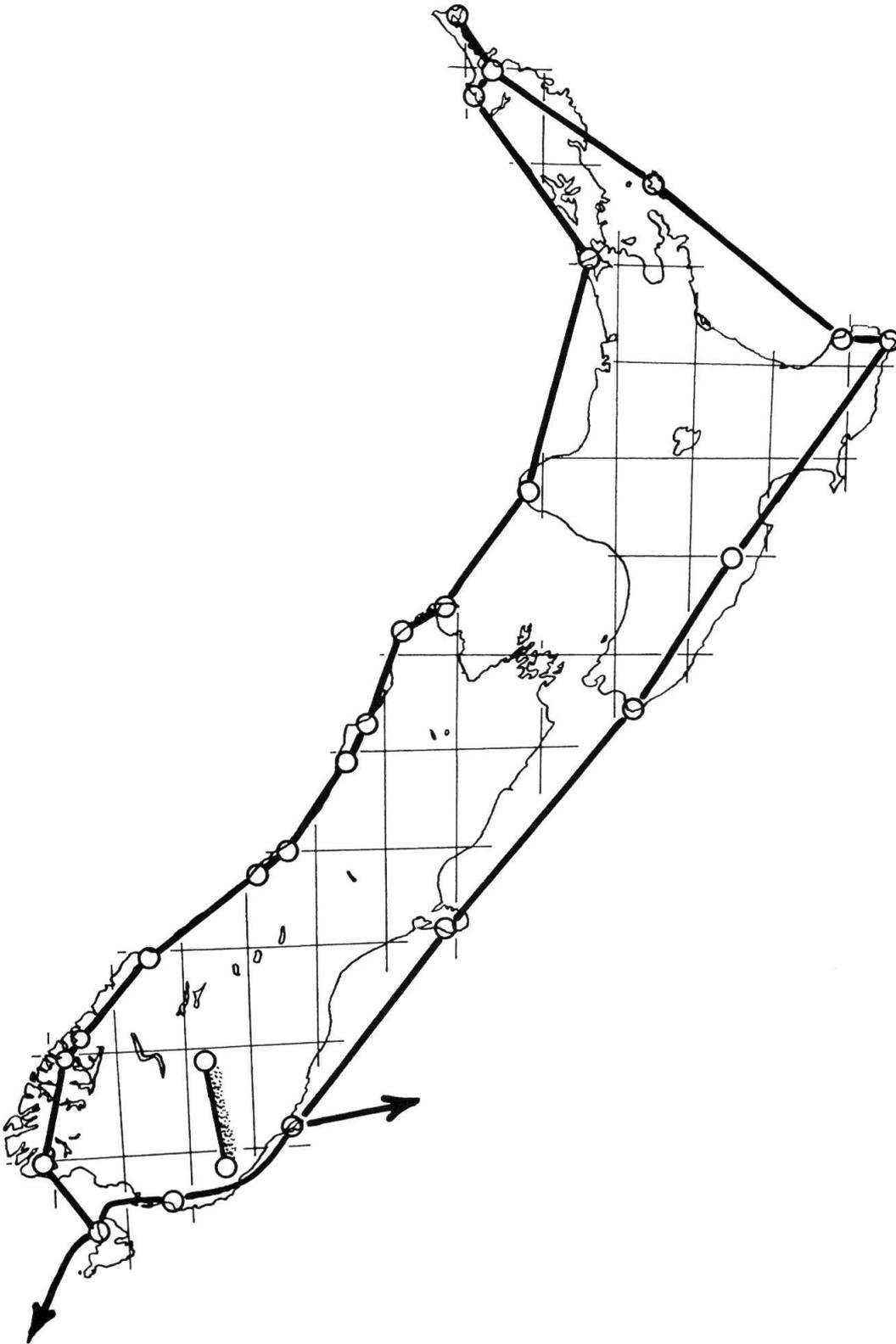


Fig. 12. — *Limosella lineata*: continuous line (plus Chatham Is.); *L. curdieana*: stippled line.

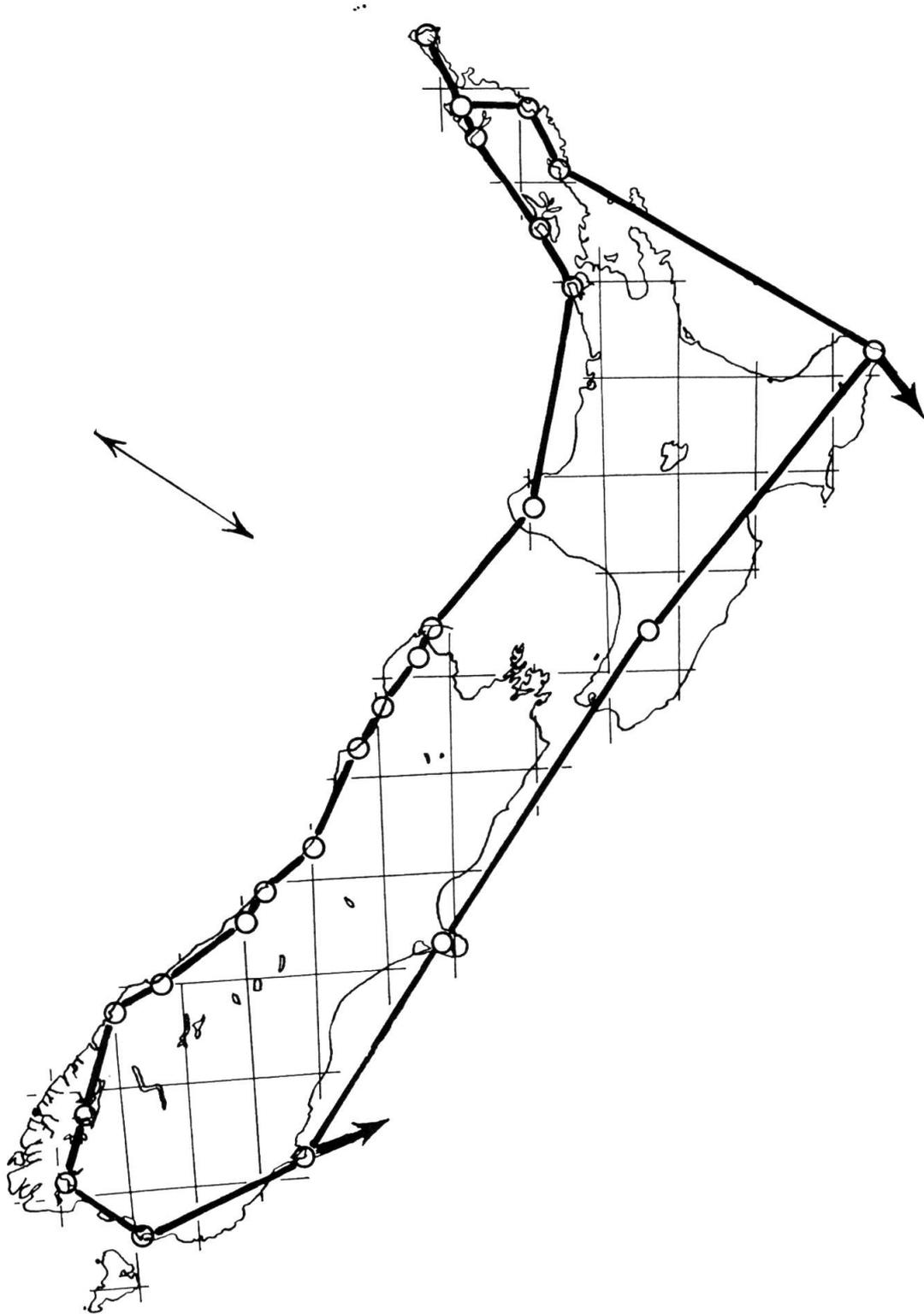


Fig. 13. — *Gratiola* in New Zealand (plus Chatham Is.).

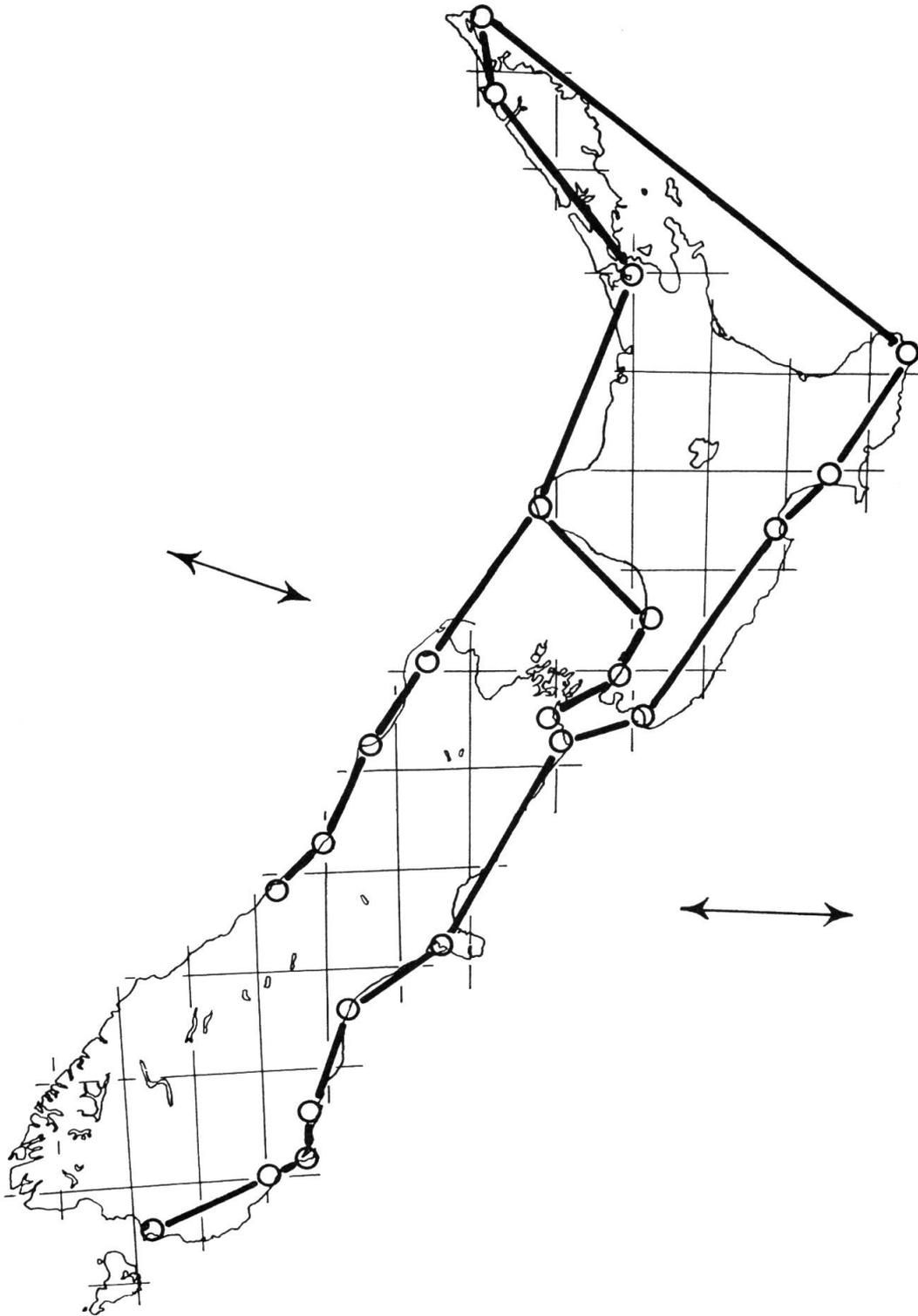


Fig. 14. — *Mimulus repens*: continuous line.

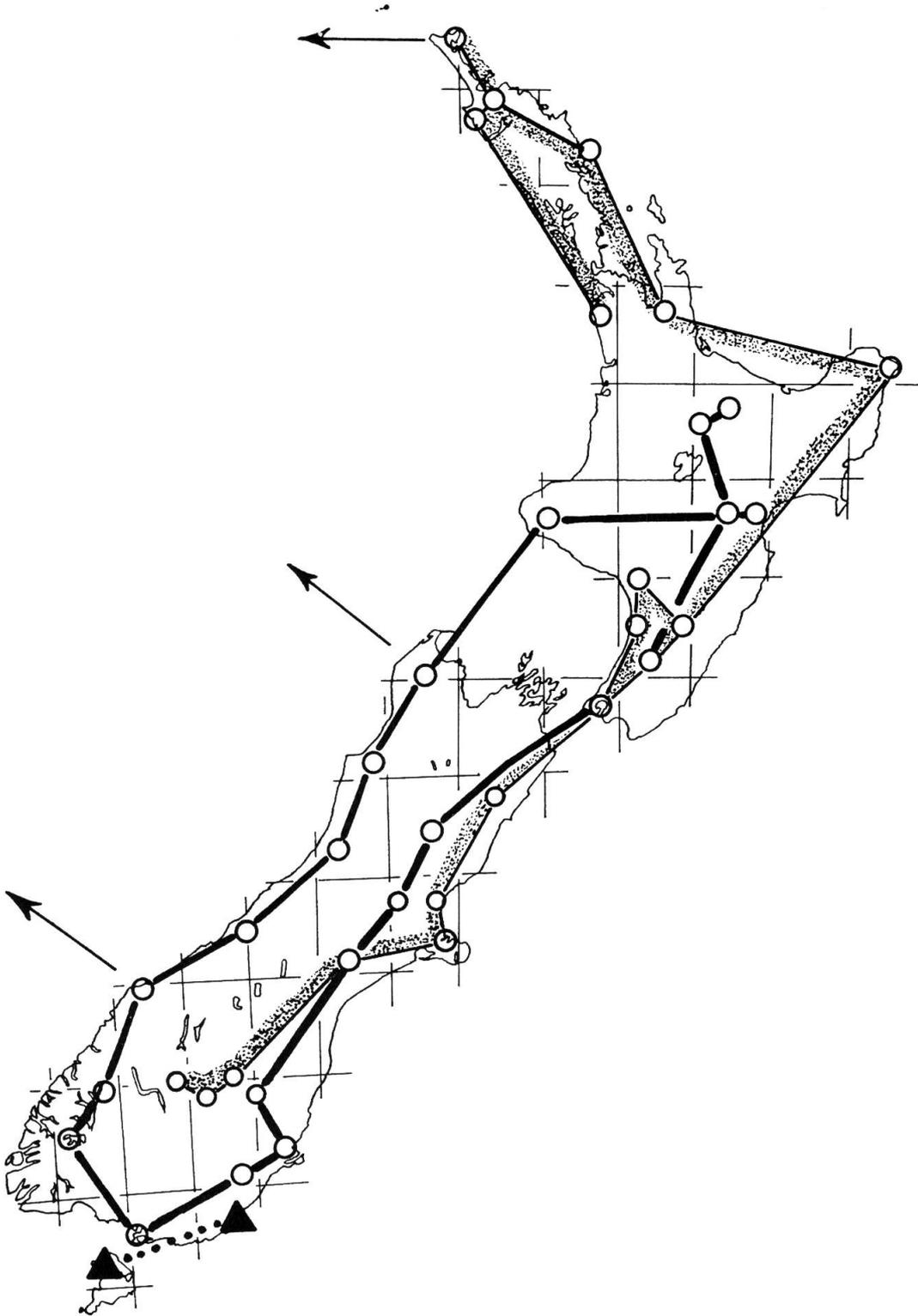


Fig. 15. — *Mazus radicans*: continuous line; *M. pumilio*: stippled line; *Mazus* sp.: triangles and dotted line.

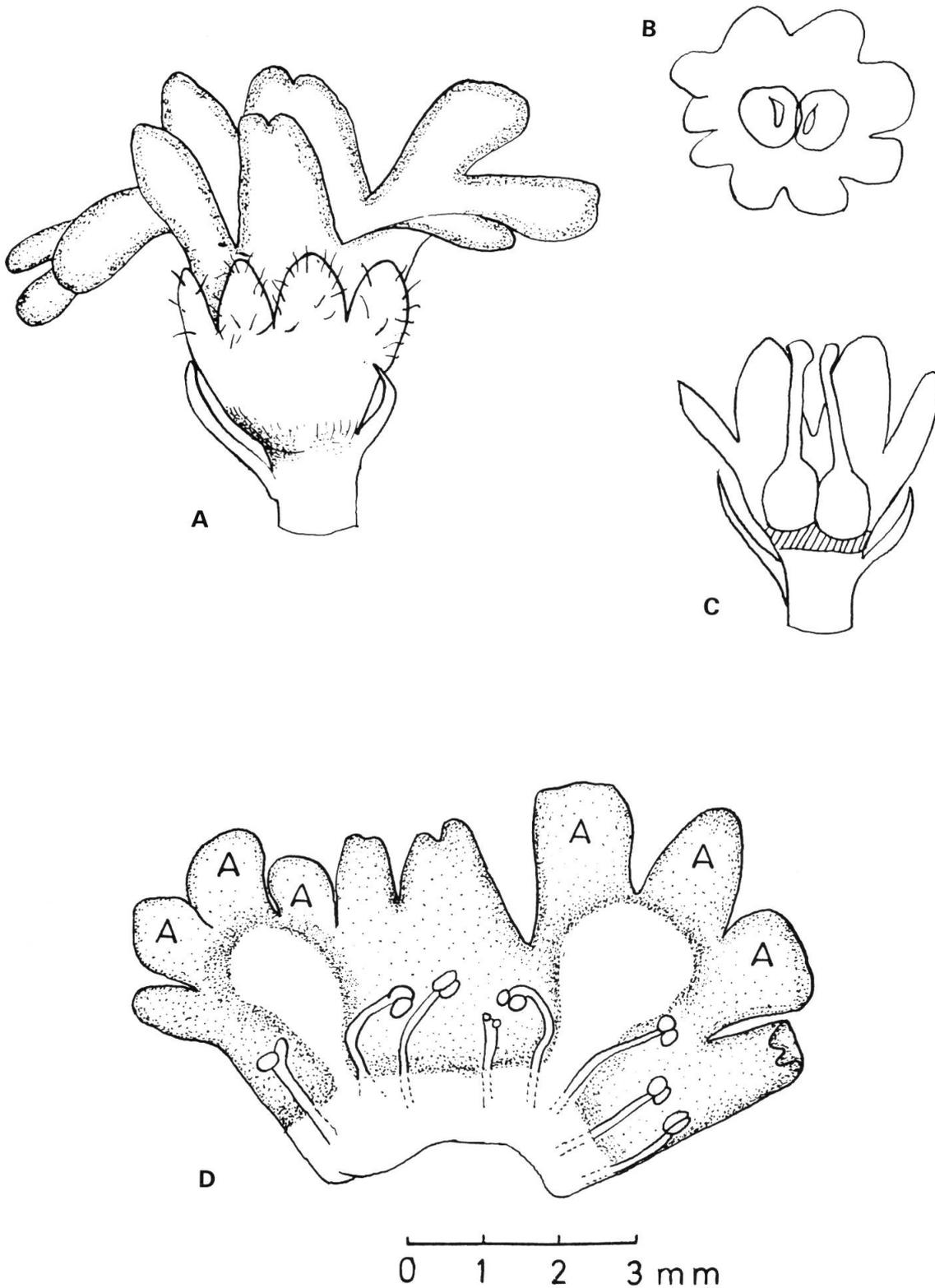


Fig. 16. — The peloric flower/inflorescence of *Mazus* sp. (Heds, November 1986 False Islet, SE Otago, OTA). **A.** Lateral view of the peloria with 2 bracts, 9 calyx lobes and 10 corolla lobes. **B.** View of the 9 calyx lobes and 2 ovaries (corolla removed). **C.** Lateral view. **D.** Corolla with adnate stamens/staminodes. Anterior corolla lobes labelled "A". Blank areas are yellow in nature, and stippled areas are purple.

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REFERENCES

- AIRY SHAW, H. K. (1973). *J. C. Willis' Dictionary of the Flowering Plants and Ferns*. 8th ed. Cambridge University Press, Cambridge.
- ALLAN, H. H. (1961). *Flora of New Zealand*. Vol. 1. Government Printer, Wellington.
- ASHWIN, M. (1961). *Euphrasia*. In: ALLAN, H. H. (Ed.), *Flora of New Zealand*. Vol. 1, pp. 849-60. Government Printer, Wellington.
- BAILLON, H. (1888). *The Natural History of Plants*. Vol. 8. Transl. M. Hartog. L. Reeve, London.
- BACKER, C. A. & R. C. BAKHUIZEN VAN DEN BRINK Jr. (1965). *Flora of Java*. Vol. 2. Noordhoff, Groningen.
- BALGOOY, M. M. J. VAN (1971). *Plant Geography of the Pacific*. Rijksherbarium, Leiden.
- BARKER, W. R. (1982). Taxonomic studies in *Euphrasia* L. (Scrophulariaceae). A revised infrageneric classification, and a revision of the genus in Australia. *J. Adelaide Bot. Gard.* 5: 1-304.
- CHEESEMAN, T. F. (1877). Notes on the fertilisation of *Glossostigma*. *Trans. New Zealand Inst.* 10: 353-356.
- CHEESEMAN, T. F. (1914). *Illustrations of the New Zealand Flora*. Government Printer, Wellington.
- CHEESEMAN, T. F. (1925). *Manual of the New Zealand Flora*. 2nd ed. Government Printer, Wellington.
- CROIZAT, L. (1952). *Manual of Phytogeography*. Junk, The Hague.
- CROIZAT, L. (1964). *Space, Time, Form: The Biological Synthesis*. Publ. by the author, Caracas.
- CROIZAT, L. (1968). The biogeography of the lands and islands east of Suez/Madagascar. *Atti Ist. Bot. Univ. Lab. Crittogam. Pavia ser. 6, 4*: 1-400.
- DU RIETZ, G. E. (1931). Two new species of *Euphrasia* from the Philippines and their phytogeographic significance. *Svensk. Bot. Tidskr.* 25: 500-542.
- GLÜCK, H. (1934). *Limosella-Studien*. *Bot. Jahrb.* 66: 488-566.
- HEADS, M. J. (1984). Principia Botanica: Croizat's contribution to botany. *Tuatara* 27: 26-48.
- HEADS, M. J. (1989). Integrating earth and life sciences in New Zealand natural history: the parallel arcs model. *New Zealand J. Zool.* 16: 549-586.
- HEADS, M. J. (1990). A revision of *Kelleria* and *Drapetes* (Thymelaeaceae). *Australian Syst. Bot.* 3: 595-652.
- HEADS, M. J. (1992). Taxonomic notes on the *Hebe* complex (Scrophulariaceae) in the New Zealand mountains. *Candollea* 47: 583-595.
- HEADS, M. J. (1993a). Biogeography and biodiversity in *Hebe*, a South Pacific genus of Scrophulariaceae. *Candollea* 48: 19-60.
- HEADS, M. J. (1993b). Morphology, architecture and taxonomy in the *Hebe* complex (Scrophulariaceae). *Adansonia*. In press.
- HOOKE, J. D. (1853). *Flora Novae-Zelandiae*. Reeve, London.
- HUTCHINSON, J. (1973). *The Families of Flowering Plants*. Clarendon Press, Oxford.
- KRÄNZLIN, F. (1907). Scrophulariaceae — Antirrhinoideae — Calceolarieae. In: ENGLER, A., *Das Pflanzenreich*, Fam. IV, 257c, Heft 28.
- PETRIE, D. (1896). List of the flowering plants indigenous to Otago. *Trans. New Zealand Inst.* 28: 540-591.
- SIMPSON, M. J. A. (1977). Fruit characters and seed germination of *Euphrasia disperma* Hook. f. *New Zealand J. Bot.* 15: 181-183.
- SUTTON, D. A. (1987). Peloric flowers in the tribe Antirrhineae (Scrophulariaceae). *Watsonia* 27: 337-338.
- WARDLE, P. (1975). Vascular plants of Westland National Park (New Zealand) and neighbouring lowland and coastal areas. *New Zealand J. Bot.* 13: 497-545.
- WILSON, H. (1982). *Stewart Island Plants*. Field Guide Publ., Christchurch.