Experimental Taxonomic Studies on Species of *Cardamine* Linn. in New Zealand

By G. G. PRITCHARD

Department of Botany, Victoria University College*

[*Received by the Editor, November 15, 1956.*]

Abstract

THE variation pattern in New Zealand species of *Cardamine* (*C. heterophylla, C. bilobata* and *C. corymbosa*), together with two introduced species (*C. hirsuta* and *C. flexuosa*) is outlined. Descriptions of plants cultivated in a uniform environment and the results of cytological, genetical and field studies are given and the bearing of this work on taxonomic problems presented by the New Zealand species is discussed. It is concluded that the New Zealand species, *C. heterophylla,* is distinct from the species *C. hirsuta* (in which it was formerly placed) and that a coastal variety, usually placed under *C. heterophylla,* belongs to the species *C. corymbosa.* Three forest races are recognised within *C. heterophylla.* A brief discussion of the alpine complex is given, but no taxonomic conclusions on this group are drawn.

INTRODUCTION

IT is not intended in the present paper to propose a taxonomic revision of the New Zealand species of *Cardamine* but rather to draw attention to a type of taxonomic problem commonly encountered in the New Zealand flora and to the importance of experimental methods in approaching such a problem.

The treatment of *Cardamine* in Cheeseman's "Manual of the New Zealand Flora" (1925) does not suggest that any great taxonomic difficulties are involved. Five species are recognised, of which only one, *C. heterophylla,* is at all widespread. The other four are restricted to the Subantarctic Islands or to isolated localities in the South Island mountains. However, if an attempt is made to fit the specimens of *Cardamine* in any of the large herbaria to this treatment, the difficulties will soon be apparent. A large array of forms will be found differing from each other in numerous vegetative and reproductive features. Only some of these can be placed in one or other of Cheeseman's species. Apart from this variability within the indigenous species, earlier treatments of the genus have included the New Zealand species, *C. heterophylla* (or *C. debilis*), in the widespread northern hemisphere species, *C. hirsuta,* and even Cheeseman in 1925 was hesitant to separate the two.

A monograph of the genus *Cardamine* by O. E. Schulz appeared in 1903. Schulz revived Forster's name *heterophylla* for the New Zealand plants placed by Hooker in the northern *C. hirsuta.* He also recognised several sub-units within *C. heterophylla* but no complete descriptions of these were given.

The present study includes forms from three of the New Zealand species, *C. heterophylla, C. corymbosa* and *C. bilobata,* and also the two introduced species, *C. hirsuta* and *C. flexuosa.*

EXPERIMENTAL METHODS

Collections were cultivated in an unheated glasshouse. Seed lost its viability very rapidly after a few weeks without the cause being discovered and therefore had to be sown immediately after collection. Chromosome counts are based on meiotic figures in pollen mother cells. Whole inflorescences were sectioned and

---

[*] This paper represents the results of a study submitted as a thesis for an M.Sc. degree.

Transactions of the Royal Society of New Zealand
Vol. 85, Part 1, pp. 75–89, 5 Text-figs., Nov., 1957

stained in Heidenhain's iron haematoxylin. Pollen fertility was determined by the method of Owczarzak (1952).

Many interracial and intraracial crosses were attempted. The New Zealand species and races are naturally self-pollinated. Emasculation of the flowers was carried out at the latest possible stage before anthesis (the anthers dehisce usually an hour or two before the opening of the flower). The female parent was isolated from the other plants and from air draughts but bagging was not attempted owing to the risk of damaging the small flowers. The stigma is receptive very shortly after

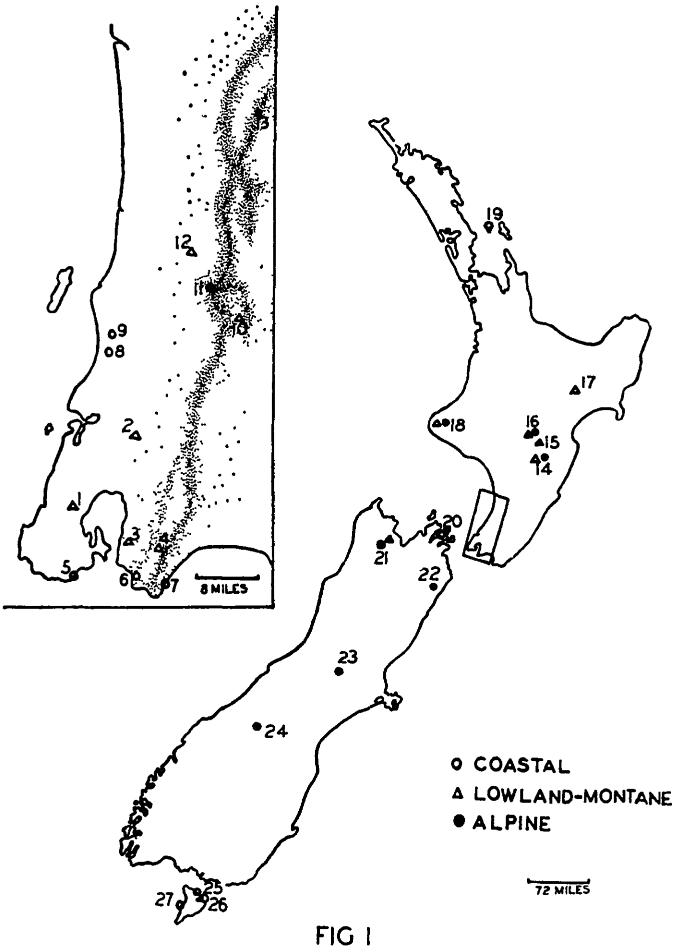


FIG I

Text-fig 1.—Localities from which plants have been obtained and grown under uniform conditions. 1, Khandallah Reserve, Wellington 2, Hutt Valley, Wellington 3, Butterfly Creek, Wellington. 4, Orongorongo Valley. 5, Cape Sinclair. 6, Mouth of the Wainui-o-mata River 7, West side of Palliser Bay. 8, Foot of Mt. Wainui, Paekakariki. 9, Steep cliff face near coast, Paekakariki. 10, Tauwharenikau Valley, South Tararua Mountains. 11, Mt Hector-Mt. Dennan, South Tararua Mountains. 12, Otaki Forks, South Tararua Mountains. 13, Mt Ruapi, North Tararua Mountains. 14, Rangiwahia Hut, Ruahine Mountains. 15, Reporoa Bog, North Ruahine Mountains. 16, Napier-Taihape road, Rangitikei Valley. 17, Near Lake Waikare-iti, Urewera Mountains 18, Dawson Falls, Mt Egmont. 19, Little Barrier Island 20, Marlborough Sounds. 21, Mt. Arthur Tableland. 22, Chalk Range, Inland Kaikoura Mountains. 23, Lake Lyndon. 24, Huxley River. 25, North-east coast, Stewart Island. 26, Near Oban, Stewart Island 27, Mason's Bay, Stewart Island Not shown on map: Enderby Island, Auckland Island group anthesis. After pollination the plants were kept in isolation for 48 hours, by which time, if the cross were successful, the fruit had started to develop.

Although seed was collected from the majority of these crosses, very little germinated. The seed was stored for 2–3 months and largely lost its viability in that time.

DESCRIPTIONS OF THE SPECIES AND RACES

The habitats sampled have been grouped into the following categories:—

(1) Open coast. Shingle beaches and rocky coastlines.
(2) Forest. Coastal, lowland- montane and sub-alpine forests of all types.
(3) Alpine. Alpine and sub-alpine habitats above the timberline—i.e., scrub, tussock, scree, etc.

Corresponding to these three habitat groupings, a fairly natural distinction between the races can be made

FOREST AREAS. Studies in the Wellington area established a provisional grouping into three native races which have been termed, "Glossy Leaf", "Narrow Petal" and "Long Style". Also present in certain areas are the two introduced species, *C. hirsuta* and *C. flexuosa.*

OPEN COASTAL AREAS. A single race has been found in open coastal areas. It is usually included in Hooker's variety *uniflora* of *C. heterophylla.* Also included under this heading is *C. corymbosa* from coastal regions in the Subantarctic Islands.

ALPINE AREAS. *North Island.* The Tararua and Ruahine Mountains have a relatively simple pattern. Two distinct races exist, one found on screes and open rocky areas (termed, for convenience, "Scree Race") and the other amongst tussock and scrub-tussock, ("Tussock Race"). Quite different types have been found in two isolated localities, Mount Egmont and limestone areas in the north-west Ruahine Mountains.

South Island. Such a complex array of forms exists in the South Island mountains that no full descriptions of them will be given in the present paper.

THE FOREST RACES AND THE INTRODUCED SPECIES

This group comprises the two introduced species, *C. hirsuta* and *C. flexuosa,* and the three native races, "Glossy Leaf", "Long Style" and "Narrow Petal". All five types have a basic morphological pattern in common.

In the vegetative state they consist of a compact rosette of leaves borne on a short stem with no elongation of internodes. The leaves are pinnate, with a terminal round or reniform leaflet which is usually larger than the lateral leaflets. The number of leaflets and shape of the terminal leaflet varies during development of the individual plant as well as between races, so that care must be taken to compare leaves from comparable positions on the plant. Following the development of the floral primordia, the stem elongates considerably. This elongated stem frequently bears leaves which subtend axillary inflorescences. These will be termed "cauline" leaves as distinct from "rosette" or "basal" leaves. In some species and races these two types of leaves have differently shaped pinnae. The inflorescence itself, in the forest races and introduced species, is a simple raceme with the flowers borne on short pedicels arranged in an open spiral on a long peduncle. The flowers are of the typical cruciferous pattern and seldom exceed 6 mm in diameter. The fruit is a siliqua with a uniseriate row of seeds.

Introduced Species

Cardamine hirsuta Linn. (Fig. 2)

Annual. Basal leaves in a compact rosette, pinnate, with 0–5 (usually 2–3) pairs of lateral pinnae and a terminal leaflet. Terminal leaflet always larger than the lateral leaflets, fairly broad and with definite auricles. Hydathodes at vein endings not conspicuous Upper surface of leaflets covered with scattered, fairly long hairs. Lateral pinnae rounded, decreasing in size toward the base of the leaf; petiole glabrous. Cauline leaves distinct from radical leaves; pinnae narrowed especially in the higher cauline leaves. Leaflets with a single palisade layer and 2-4 spongy mesophyll layers.

Flowering stems long (10–15 cm), straight and slender, glabrous and not pigmented; branched in the axils of cauline leaves. Flowers 15–20 on the main axis closely packed in the young stage, usually 2–3 open at a time. Flowers small (2–3 mm diam.); sepals green, with 2-3 hairs on the dorsal surface; petals small (2 mm x 1 mm), poorly differentiatd into stalk and limb; one or more petals often imperfectly developed. Stamens usually reduced to 4 (2 short laterals absent or occasionally one or both present). Ovary hairy or glabrous. Ripe siliqua yellowish, 1.5–2.5 cm long; style on mature fruit less than 1 mm. Seeds small, 1 mm diam., closely packed, 17–20 per siliqua.

Chromosome number: n = 8 (three metaphase II counts, also Manton (1932).

Flowering time: July-October.

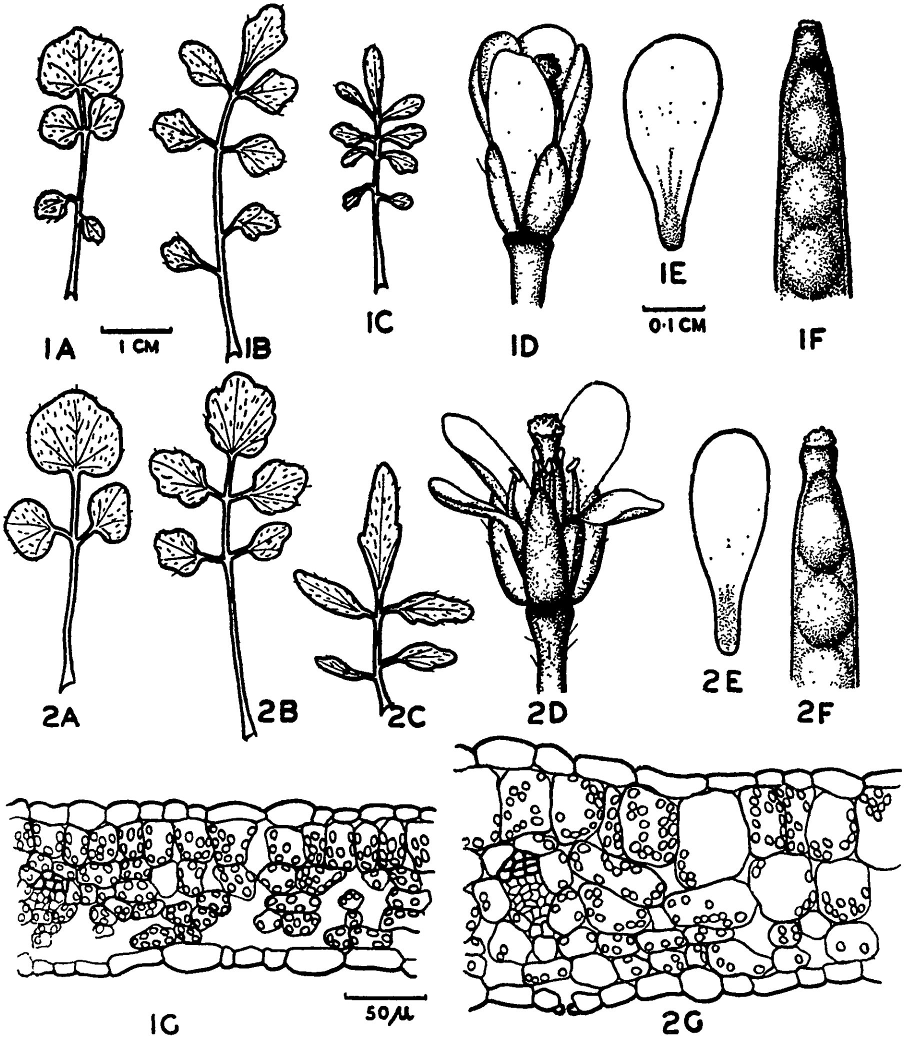


FIG. 2

Text-fig. 2.—The introduced Species—*C. hirsuta* (1) and *C. flexuosa* (2). A, Typical rosette leaf. B, Typical cauline leaf. C, Uppermost cauline leaf. D, Flower. E, Petal. F, Upper part of fruit showing style. G, T.S Leaf.

Cardamine flexuosa With. (Fig. 2).

Annual Basal leaves forming a compact rosette; pinnate with 0–5 (usually 2–3) pinna-pairs. Terminal leaflet the largest, similar in shape to that of *C. hirsuta.* Upper surface of the leaflets hairy. Hydathodes inconspicuous. Lateral pinnae rounded, decreasing in size toward the base of the leaf. Cauline leaves distinct from the rosette leaves, attenuation of the pinnae not as marked as in *C. hirsuta.* Leaves thicker than in *C. hirsuta* mainly due to increased cell size rather than to increased number of mesophyll layers.

Flowering stem stouter than in *C. hirsuta,* showing pronounced ribbing, quite hairy and often pigmented near the base. Strongly flexuose. 15–20 flowers on the main axis closely crowded in the early stages. Flowers a little larger than in *C. hirsuta,* petals seldom imperfectly developed. Stamens always 6. Siliqua as in *C. hirsuta* with a slightly longer style.

Chromosome number: n = 16 (based on a single metaphase 1 count, also Manton (1932).

Flowering time: August-October; seedlings may flower again in January or February.

Distinguished from *C. hirsuta* by the flexuose inflorescence stalk and by the fact that the pedicels stand out from the peduncle at a wide angle (best seen in the fruiting stage), whereas in *C hirsuta* they are nearer the vertical.

The Native Forest Races

Perennial. Basal leaves forming a looser rosette than in the introduced species; pinnate with 0–4 lateral pinna-pairs. Terminal leaflet usually the largest (not always in "Long Style") and with marked lobing. Hairiness of the lamina varying according to the race. Cauline leaves distinct from the rosette leaves in some races though never to the same extent as in the introduced species.

Flowering stem 10–18 cm long, glabrous, sometimes pigmented. Fewer flowers on the main axis than in *C. hirsuta.* Flowers varying in size according to the race, 3–4 mm or 5–6 mm diameter; usually perfectly developed, very rarely apetalous. Stamens always 6. Siliqua 1.5–2.5 cm long; style length varying according to the race. Seeds 1.5 mm diam —i.e., somewhat larger than in *C hirsuta* and *C flexuosa.*

(a) "**Glossy Leaf**" (Fig. 3).

Perennial, dying down to an underground rhizome after fruiting. Basal leaves forming a loose rosette; pinnate with 0–3 (usually 1–2) lateral pinna-pairs. Terminal leaflet larger than the lateral leaflets, conspicuously lobed, (cf. *C hirsuta*). Hydathodes inconspicuous. Upper surface of leaflets dark glossy green, glabrous except for a few marginal hairs. Lateral pinnae lobed, decreasing in size toward the base of the leaf. Petiole usually hairy near the base. Cauline leaves distinct from basal leaves, though not to the same extent as in *C. hirsuta;* pinnae sharply lobed. Leaflets with a single palisade layer and 3–4 layers of isodiametric cells.

Flowering stem long (10–15 cm), straight and slender, glabrous, sometimes developing a brownish pigment. 12–15 flowers on the main axis. Flowers larger than in *C. hirsuta* (5–6 mm diam.), all parts usually perfectly developed; sepals green or with a brown tint, glabrous; petals broad and well differentiated into stalk and limb. Stamens 6. Siliqua green or with brown or purple pigment; 1.5–2.5 cm long, style on mature fruit less than 1 mm. Seeds green when ripe, 1.5 mm diam.

Chromosome number: n = 24 (from several clear metaphase 1 counts in one population)

Flowering time: August to early December.

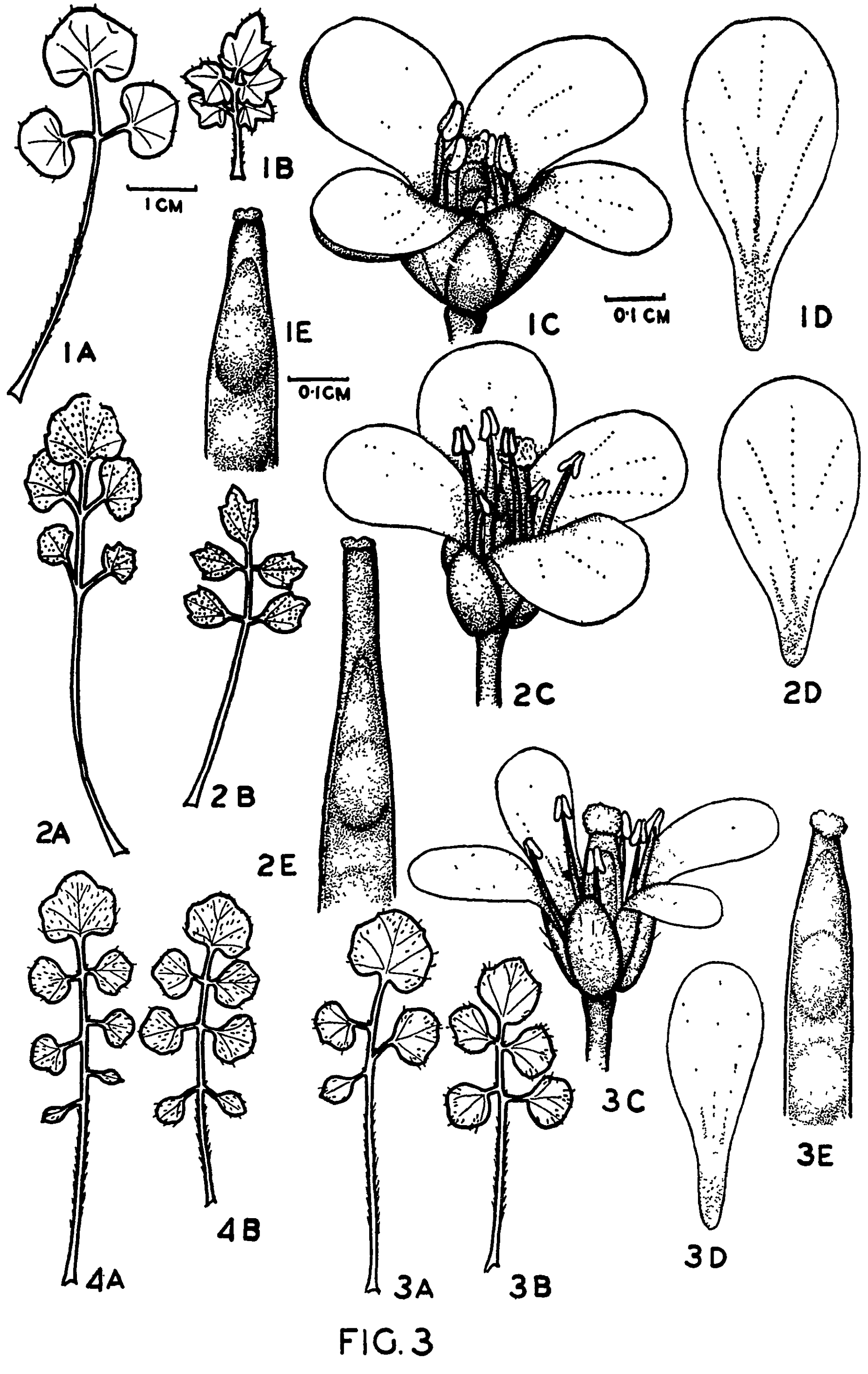
Areas from which plants have been collected and grown: Wellington—*Khandallah; Keith George Park, Hutt Valley; Tauwharenikau Valley, South Tararuas.* The plants from these three localities are almost identical. Since the plants of this race die back to an underground rhizome after fruiting—i e., during late summer and early autumn, they have no doubt been overlooked in many areas

(b) "**Long Style**" (Fig. 3).

Perennial, the leaves persisting after fruiting. Basal leaves forming a loose rosette; pinnate with 0–4 (usually 2–3) lateral pinna-pairs. Terminal leaflet often equal in size to the lateral leaflets or only slightly larger, smaller than in "Glossy Leaf", auricles often lacking. Hydathodes prominent at vein endings, 3–5 per leaflet. Anthocyanin pigmentation variable, usually present in the petiole and hydathodes. Upper surface of the lamina covered closely with fine short hairs (much shorter than in *C hirsuta*). Cauline leaves distinctive and narrow, sharply lobed. Pinnae of thicker texture than in "Glossy Leaf"; 5–6 layers of isodiametric cells; no marked palisade

Flowering stem 12–15 cm long, glabrous, usually pigmented. Flowers 12–15 on the main axis, same size as in "Glossy Leaf"; sepals glabrous, usually with a pink or brown pigment; petals broad, differentiated into stalk and limb. Stamens 6, anthers occasionally with a purple or pink pigment. Siliqua usually pigmented, 2–2.5 cm long; style comparatively long (4 mm, sometimes shorter - 2 mm). Seeds large, 1.5 mm, and relatively well spaced.

Chromosome number: n = 24 (6 diakinesis figures from 2 different populations).



TEXT-FIG. 3.—The Forest Races of *C. heterophylla*—"Glossy Leaf" (1), "Long Style" (2) and "Narrow Petal" (3, Tauwharenikau Valley and 4, Paekakariki). A, Typical rosette leaf. B, Typical cauline leaf. C, Flower. D, Petal. E, Upper part of fruit showing style.

Flowering time: late October-end of December (cf. " Glossy Leaf ").

Areas from which plants have been collected and grown: Wellington—*Khandallah: Hutt Valley; Paekakariki; Akatarawa; Orongorongo Valley; Tauwharenikau Valley; Otaki.* Ruahine Mountains: *Rangiwahia.* Urewera Mountains: *Lake Waikare-iti.* Mount Egmont: *Dawson's Falls.*

Local variation is shown in degree of pigmentation of the leaf, petiole and fruit; anther pigmentation, shape of the terminal leaflet and length of the style. In spite of this variation, the populations undoubtedly constitute a natural race.

(c) " Narrow Petal " (Fig. 3).

Perennial, leaves usually persisting after fruiting. Basal leaves forming a fairly compact rosette; petioles sometimes reflexed near the base resulting in a flattened rosette. Basal leaves pinnate with 0–4 (usually 2–3) lateral pinna-pairs. Terminal leaflets always larger than the lateral leaflets, shape variable, auricles usually present. Hydathodes at vein endings not as prominent as in " Long Style ". Hairiness variable, occasionally glabrous, usually scattered long hairs on the upper surface of the lamina, also on the petiole. Anthocyanin pigmentation varying from a very weak pink to a deep brownish-purple. Short colourless outgrowths (less than 1 mm) or small leaflets often present in the pinna axils Cauline leaves not usually distinctive but may be so in some forms (see Fig. 3). Anatomy: 4–6 layers of mesophyll sometimes with a one- or two-layered palisade.

Flowering stem 12–18 cm long, glabrous, usually slightly pigmented. Flowers 3–10 on the main axis, smaller than in " Long Style " and " Glossy Leaf " (3–4 mm diam.); sepals usually with a pink pigment and hairy; petals narrow and poorly differentiated into stalk and limb. Stamens 6. Siliqua yellow when ripe, 1.5-2.5 cm long. Style 1.5–2.5 mm long. Seeds pale yellow when ripe, usually well spaced in the siliqua.

Chromosome number: $n = 24$ (numerous metaphase 1 and 2 and diakinensis counts from 5 different populations).

Flowering time: late August-early December.

Areas from which plants have been collected and grown: Wellington—*Khandallah; Hutt Valley; South Coast (Palliser Bay and Wainui-o-mata River mouth); Paekakariki; Orongorongo Valley; Tauwharenikau Valley.* Rangitikei Valley: *Napier-Taihape Road.* N W. Ruahine Mountains: *near Reporoa under limestone outcrops.* Little Barrier Island. Marlborough Sounds: *Crail Bay* Stewart Island: *Vicinity of Oban.*

Local variation is shown in numerous features; shape of the terminal leaflet, hairiness, pigmentation of the leaves and stem, size of the flower and length of the fruit and style. Always characterised by narrower petals than in the other two forest races. Further study might show it to be a group of races, but no satisfactory division can be made at present.

DETAILED STUDIES

Ecological and genetical relationships between races in the field were studied at Khandallah reserve, Wellington, where the three native races and also *C. hirsuta* occur together. The selected area consisted of a strip of forest dominated by *Fuchsia excorticata, Melicytus ramiflorus* and *Hedycarya arborea* on the floor of a valley. On either side of a central streamlet, the canopy decreased in height, the forest ultimately giving place to exotic induced grassland covering the upper flanks and crests of the ridges (see Fig. 5a). Across this valley, a transect, 70 metres x 1 5 metres, was marked out and the position of every *Cardamine* plant present in the transect was plotted. The distribution of the races along this transect is shown in the form of a histogram in Fig. 5b. A definite distribution pattern is apparent. *C. hirsuta* and " Narrow Petal " are concentrated near the margins of the forest strip and fall off sharply towards the centre of the valley. " Glossy Leaf " shows a maximum a few yards inside the margin of the forest and then drops off more gradually toward the centre. " Long Style," on the other hand, reaches a maximum in the centre of the valley and decreases in density toward either flank.

Gradients in light intensity, soil moisture and possibly other factors exist along this transect, but little experimental evidence is available on the relative importance of these factors in governing the ecological distribution of the races.

A detailed examination of several other areas—Keith George Park, Hutt Valley; Orongorongo Valley; Tauwharenikàu Valley—has revealed the same pattern. *C. hirsuta* and " Narrow Petal " occupy the drier, well-lit parts of an area while " Long Style " favours the damper areas. " Glossy Leaf " is more tolerant of reduced light intensity and isolated individuals can be found well inside the forest margin.

A sample of 80 plants was taken along one edge of the transect and examined carefully with respect to all characters differentiating the races. No intermediates were found nor has any natural hybridism been detected in any of the areas.

The Race from Open Coastal Areas and C. corymbosa.

The race found on stony beaches and in sandy patches amongst rocks differs considerably from all of the forest races. The leaves are smaller than in the forest types and are more densely compacted into a rosette. Often they are simple with a single terminal reniform leaflet. If pinnate, the number of lateral pinna-pairs rarely exceeds two. The terminal leaflet does not show the lobing characteristic of most of the forest types. A more pronounced difference is in the development of the inflorescence. Whereas, in the forest races, flowering is preceded by stem elongation, this does not always occur in the coastal race. Usually, in the terminal inflorescence, the first few flowers appear to arise directly from the centre of the rosette on long pedicels. This is interpreted as a condensed form of the normal raceme—i.e., there is no elongation of the internodes between the uppermost leaf nodes and the flowering nodes. After two or three flowers have been produced in this way, the next internode may elongate up to 2–3 cm and bear three or four flowers in an apparent whorl at the top. The inflorescence may not elongate further or, alternatively, a second internode may elongate and bear another "whorl" of flowers. Occasionally, axillary inflorescences—i.e., those arising in the axils of the higher rosette leaves, may have an internode elongating below the last leaf so that a "cauline" leaf appears. Thus the inflorescence, though fundamentally of the

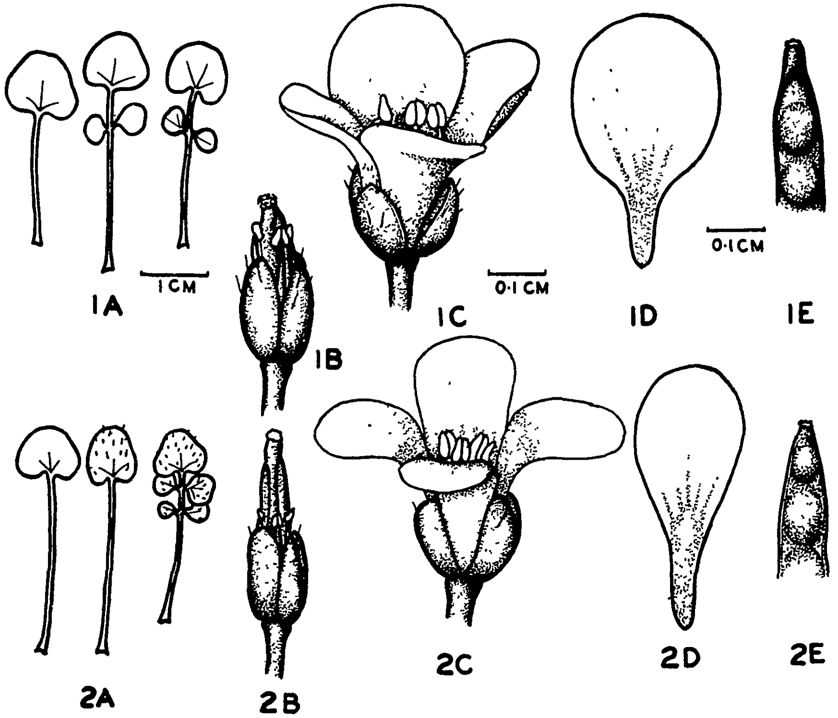


FIG 4

TEXT-FIG. 4.—The Mainland Coastal Race (1) and *C. corymbosa* (2). A. Rosette leaves. B. Apetalous and C, Petaliferous flower. D, Petal. E, Upper part of fruit showing style.

same pattern as in the forest races, does not have the regular elongation of internodes associated with the development of flowers.

Flowers borne in spring and early summer are similar to those of the forest races, but in late summer and autumn, apetalous flowers with only four stamens are produced. These apetalous flowers are presumably the same as the cleistogamous flowers described by Schulz in *C. corymbosa.* The ripe fruit is shorter than in the forest races (seldom exceeds 2 cm) and the seeds smaller (less than 1 mm diam.).

This coastal race has not yet been described in any taxonomic work, but is generally placed in the variety *uniflora* of *C. heterophylla.* However, there is a close resemblance between this coastal race and *C. corymbosa* (restricted by Cheeseman to the Subantarctic Islands). This resemblance has been borne out by cultivation of the two types under the same conditions. The name *uniflora* appears to be based on a misinterpretation of the inflorescence, the long pedicels arising from the centre of the rosette having been regarded as axillary peduncles with a solitary terminal flower.

A single description will suffice for both the coastal race and *C. corymbosa.*

Perennial, the leaves persisting after flowering and fruiting. Leaves smaller than in the forest races, arranged in a compact rosette; simple or pinnate, seldom more than two lateral pinna-pairs. Terminal leaflet cordate, lateral leaflets, when present, smaller than the terminal leaflet, more or less rounded. Hydathodes inconspicuous. Purple pigment occasionally present in the petiole base. Glabrous or with scattered long hairs on the upper surface of the lamina. Cauline leaves occasionally present, similar to the radical leaves, usually simple. Anatomy: 1–2 palisade layers and 3–5 layers of isodiametric cells.

Inflorescence a raceme with irregular development of internodes (see above). Flowers of two kinds: petaliferous flowers borne in the spring and apetalous autumn flowers; sepals green or purplish, usually with 2–3 hairs on the dorsal surface. Petals, when present, broad, well differentiated into stalk and limb in the mainland forms, poorly so in Subantarctic plants Stamens 6 in petaliferous flowers, reduced to 4 in apetalous flowers (2 short laterals missing). Siliqua rarely exceeding 2 cm, usually 1.5 cm, very slender. Style less than 1 mm. Seeds less than 1 mm and yellow when ripe.

Chromosome number: n = 24 (several metaphase counts from three different populations including Enderby Island).

Flowering time: September to April. (Flowers after December apetalous.)

Areas from which plants have been collected and grown: Wellington—*Cape Sinclair; Lake Wairarapa.* Stewart Island: *North-east coast; Mason's Bay.* Auckland Island.

Local variation is shown in hairiness and texture of the leaves; shape of the petals and length of the style on the fruit. The only characteristic distinguishing all the mainland forms from the Subantarctic Island form is the narrow petals of the latter.

The Alpine Races

These races will not be discussed in detail for two reasons. First, the sampling of the New Zealand alpine regions is very incomplete (see Fig. 1) and second, very little detailed field or experimental work has been done on those types that have been collected. With the exception of the two races found throughout the Tararua and Ruahine Mountains, no simple distribution pattern is apparent.

I. North Island Mountains

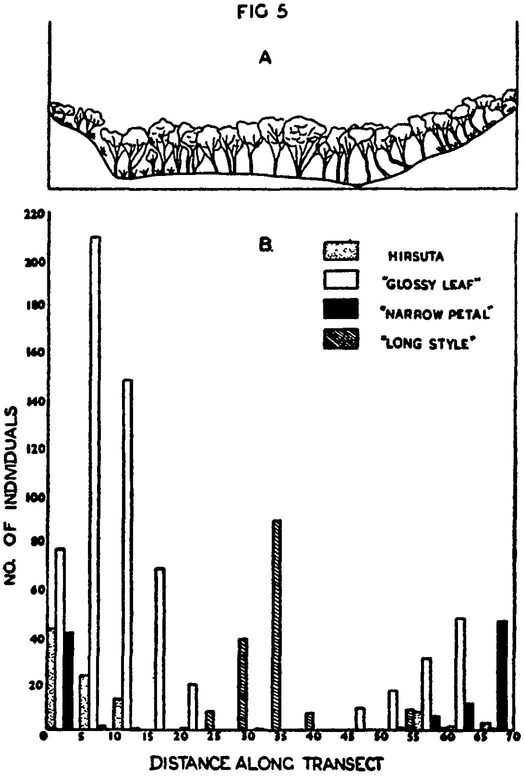
Two races are present throughout the subalpine tussock grasslands of the Tararua and Ruahine Mountains. One of these is found amongst the snowgrass tussock (*Danthonia sp.*) and occasionally in the scrub belt, the other on screes and in rock crevices. These will be termed the " Tussock Race " and the " Scree Race ".

(a) *The " Tussock Race "*

Perennial, leaves persisting after fruiting. Leaves arranged in a more or less compact rosette; simple or pinnate (rarely more than one pair of lateral pinnae). Terminal leaflet large, reniform, with up to 9 hydathode points. Lateral leaflets, when present, smaller and rounded. Hydathodes fairly conspicuous. Hairiness of lamina variable, glabrous or with numerous long hairs on the upper surface. Petiole glabrous. Pigmentation usually absent. Cauline leaves, when present, with elongated pinnae.

Flowering stem long (15–20 cm), glabrous and non-pigmented Flowers 8–12 on the main axis, similar in size to those of " Glossy Leaf " and " Long Style "; sepals green and

FIG 5



Text-fig. 5.—Ecological studies in the Khandallah Reserve, Wellington. A, Profile of forest along transect. B, Histogram showing frequency of the races along the transect.

glabrous; petals broad, well differentiated into stalk and limb. Stamens 6. Siliqua very large and broad, often 4 cm or more long and 2 mm broad; yellow when ripe. Style length variable, 2–4 mm. Seeds 2 mm in diameter, larger than in the forest races.

Chromosome number: n = 24. (two metaphase counts from one population).

Flowering time: early November to early January.

Areas from which plants have been collected and grown: South Tararua Mountains: Mt. *Dennan* (*4,010ft*). North Tararua Mountains: *Mt. Ruapai* (*4,150ft*). Ruahine Mountains: *near Rangiwahia Hut* (*4,000ft*).

Local variation is shown in hairiness and style length, otherwise the race is a very uniform one.

(b) *The "Scree Race"*

Perennial, leaves persisting after fruiting. Leaves forming a very compact rosette; pinnate with 0–3 lateral pinna-pairs Terminal leaflet the largest, reniform, seldom exceeding 1 cm in diameter; lateral leaflets decreasing in size toward the base of the leaf. Leaflets fleshy, dark glossy green, completely glabrous. Hydathodes inconspicuous. No traces of anthocyanin pigmentation.

Inflorescence type similar to that of *C. corymbosa* and the coastal race. Flowering stem short, seldom exceeding the leaves. Flowers 6–8 per peduncle, borne amongst the leaves, large, sepals green and glabrous; petals broad, well differentiated into stalk and limb. Stamens 6. (Apetalous autumn flowers have been seen in this race but not by the writer.) Siliqua 2–2.5 cm long, 1.5–2 mm broad. Valves with a brownish pigment. Stigma almost sessile. Seeds 1.5 mm diam. and greenish-brown when ripe.

Chromosome number: not determined.

Flowering time: December to January.

Areas from which plants have been collected and grown—South Tararua Mountains: Mt. *Hector* (*5,000ft*). North Tararua Mountains: *Mt. Ruapai* (*4,150ft*).

Another three races besides these two have been collected from isolated localities. One of these, found growing on the bases of *Carex secta* tussocks in the north-west Ruahine Mountains, bears a resemblance to the coastal race in rosette form, inflorescence development and apetalous flowers, but differs from it in certain details of the leaflet shape, hairiness and fruit characters. Another type of plant, also growing on the *Carex secta* tussocks a few miles from the first locality, has more in common with the forest races. In its natural habitat, a large sphagnum bog, it had a straggly, fragile stem intertwining with the tussocks but when cultivated, a definite rosette of leaves was formed. Finally on the tussock and boggy areas of Mt. Egmont, a third type, having some resemblance to *C. corymbosa,* was found. Whether these three forms have a wider distribution outside these localities is not known.

II. South Island Mountains

From the four widely separated areas from which collections have been studied under cultivation at least 13 different races apart from *C. bilobata* have been obtained. These are distributed as follows: Mount Arthur Tableland (north-west Nelson), 6; Chalk Range, Inland Kaikoura Mountains, 1; Lake Lyndon, 2; Huxley River, 4. No two of these localities have any race in common. These races show an almost complete range of morphological pattern from the small compact rosette and condensed inflorescence of *C. corymbosa* to the more open habit and elongated flowering stem of the forest races together with plants not referable to either of these patterns. A few unique morphological features are worthy of note.

Certain races possess a siliqua whose whole surface (though more particularly the valves) is covered with a dense tomentum of short and curved hairs. This siliqua type has been found on three dissimilar races.

(a) From the Lake Lyndon area. Herbarium records show that this race is fairly common in the Waimakariri headwater regions.

(b) From the Chalk Range, Marlborough. Plants otherwise identical but with a glabrous siliqua occur intermixed with plants having a tomentose siliqua.

(c) From rocky beaches on the north end of Kapiti Island (not an alpine locality).

It is possible that this results from a mutation which has arisen independently in the several areas, though no experimental evidence bearing on this is available. (Forster's type of *C. heterophylla* is described as having a densely pilose siliqua, Schulz (1903).)

Two plants collected from the Huxley River area were vegetatively identical but produced different types of flower. One plant had very small flowers (about the size of those of *C. hirsuta*) which were completely self-fertile. The other had flowers with large petals borne on very long pedicels. This plant set no seed by self-pollination and was apparently, therefore, self-incompatible. Even when crossed with the small-flowered plant no seed was set. As only one plant of this type was collected it may prove to be an abnormality.

Almost every race collected had its own peculiar leaflet shape. Many of these approached the cordate type of *C. corymbosa* leaflets. Apart from leaflet shape, many of the alpine races have other features in common with *C. corymbosa*—a condensed inflorescence, long pedicels, apetalous autumn flowers and small yellow seeds.

The species, *C. bilobata* Kirk, is distinguishable from all other forms by leaf shape. The leaves are simple, not pinnate. The earlier leaves are entire, usually spathulate with a broad petiole, the later leaves pinnatifid with one or sometimes two pairs of lobes beneath the terminal obovate portion. In its floral and fruit characters, this species closely resembles other alpine types. Cheeseman draws attention to the large flowers and long slender style on the fruit. In all specimens in the writer's collections, the flowers are not particularly larger than in other alpine types, and the style on the fruit is quite short. Specimens of this species have been obtained from the Lake Lyndon area, the Huxley River area, and from Roy's Peak, Wanaka.

These studies illustrate the complexity of the pattern in the South Island mountains and the difficulty of attempting to devise any systematic treatment until a much wider representation of races has been obtained. Chromosome counts from three of the races and also from *C. bilobata* all yielded the same number—n = 24. It appears that this complex state of differentiation must have been achieved in part, at least, on the homoploid level.

GENETICAL STUDIES

As mentioned earlier, comparatively little genetical evidence has been obtained in the present study, due largely to difficulties encountered in seed germination. From a large number of crosses carried out, only 10 different F 1 generation progenies have been obtained. Of the negative results, only three or four are sufficiently confirmed to regard the types involved as incompatible.

A. CROSSES WITHIN THE FOREST GROUP OF RACES

(1) Intraracial Crosses (i.e., between local variants).

"**Long Style**" variants:

Two different crosses within this race yielded F1 progenies.

(a) Khandallah Reserve, Wellington. ♀	×	Rangiwahia track, west Ruahine Mountains. ♂
Anther pigment lacking.		Purple anther pigment.

F1 plants vigorous. Anthers with weak pink pigment (weaker than in Ruahine plants).

Seed set: approximately 100 per cent. Pollen fertility: 90–95 per cent.

(b) Khandallah Reserve. ♀	×	Paekakariki. ♂
Anthocyanin pigmentation of leaves and peduncle weak.		Intense anthocyanin pigmentation.

F1 plants vigorous. Pigmentation intermediate.

Seed set: approximately 100 per cent. Pollen fertility: 90–95 per cent.

"**Narrow Petal**" variants.

Two different crosses within this race yielded F1 progenies.

(a) North-west Ruahine Mountains. ♀	×	Tauwharenikau Valley ♂
(b) South Wellington coast ♀	×	Paekakariki coast ♂

Parental differences mainly in leaflet shape and hairiness of the lamina.

F1 plants vigorous; intermediate in most characters. Fertility data have only been obtained in the second cross.

Seed set: 75 per cent. Pollen fertility: 70 per cent. (parents: 95–100 per cent.).

(2) Interracial Crosses.

"**Narrow Petal**" (Palliser Bay, Wellington) × "**Glossy Leaf**" (Hutt Valley, Wellington). F1 plants vigorous; leaflets glossy green with a few laminal hairs. Flowers even smaller than in "**Narrow Petal**". The plants were attacked by fungus before the fruit matured, so no data on seed set were obtained.

Pollen fertility: 15 per cent. (parents 95–100 per cent.).

"**Long Style**" (Tauwharenikau Valley) × "**Narrow Petal**" (North-west Ruahine Mountains).

F1 plants vigorous; petioles and hydathodes pigmented as in "**Long Style**". Terminal leaflet sharply lobed but with marked auricles.

Seed set: 13 per cent. Pollen fertility: 32 per cent.

"**Glossy Leaf**" (Hutt Valley, Wellington) × "**Long Style**" (Khandallah, Wellington).

Two crosses of this type were carried out. In both cases the siliqua developed; in one, a single seed was set, in the other, four seeds. All five seeds had abnormally distended testas. They were sown but did not germinate. Further crosses, however, are needed to establish the incompatibility of the parents.

B. CROSSES BETWEEN THE FOREST RACES AND *C. hirsuta*

Several crosses between the forest races and *C. hirsuta* were attempted, none of which yielded normal seed.

In one group of crosses (between "Narrow Petal" and *C. hirsuta*), a study of the comparative rates of pollen tube growth in the styles of self- and cross-pollinated plants was made. Several flowers of "Narrow Petal" were emasculated, and one set was self-pollinated while the other set was simultaneously cross-pollinated with pollen from *C. hirsuta.* After periods of (a) 1¼ hours and (b) 1¾ hours the ovary was removed from certain of the flowers of each set, fixed in acetic-alcohol and stained in acid fuchsin. By squashing out the style under a coverslip and examining with a microscope, the extent of growth of the pollen tubes (stained deep red) could be determined. After 1¼ hours in the self-pollinated plants the pollen tubes had traversed the tissues of the stigma and had reached the central strand of the style tissue. After 1¾ hours they had grown some distance down the central strand. In the plants pollinated with *hirsuta* pollen, the tubes had only slightly penetrated the stigma tissue after 1¼ hours and still had not reached the central strand of the style after 1¾ hours. Thus even if some cross-pollination occurred in nature, pollen tube competition would prevent fertilisation by foreign gametes. This experimental approach has not yet been applied to crosses within the forest races.

C. CROSSES BETWEEN *C. corymbosa* AND THE MAINLAND COASTAL RACE

C. corymbosa (Auckland Island) ×	Coastal Race (Cape Sinclair, Wellington)
Thin hairy leaves	Thick glabrous leaves
Nearly glabrous sepals	Hairy sepals
Narrow petals	Broad petals
Unpigmented siliqua, 1 cm long	Purple siliqua, 1·5 cm long

(These two races represent the extremes of the range of variation in this group. Plants from Stewart Island differ from *C. corymbosa* only in the shape of the petals.) F1 vigorous; anatomy of leaves and hairiness of the leaves and sepals and pigmentation of the fruit intermediate. Fruit even longer than in the Wellington plants—about 1·7 cm.

The F1 progeny flowered in January, so only apetalous flowers were produced. Seed set: almost 100 per cent. Pollen fertility: 85 per cent. (parents: 95–100 per cent.).

F2; vigorous plants showing segregation in leaf texture and hairiness. The two plants must thus have been sufficiently close genetically that no physiological unbalance was produced by recombination within the parental genotypes. This contrasts with the next cross to be described.

D. CROSSES BETWEEN *C. corymbosa* AND THE FOREST RACES

Only one cross of this kind has yielded F1 progeny.

C. corymbosa (Auckland Island) × "Narrow Petal" (Palliser Bay, Wellington).

F1 vigorous. Intermediate in leaf characters. The internode below the first flower elongated, but only about 1 cm. Most but not all of the internodes between the flowers elongated. The hybrids flowered in January when *C. corymbosa* is normally producing apetalous flowers. On any F1 plant could be found flowers ranging from the apetalous condition to the fully petaliferous state of "Narrow Petal". Staminal number also showed considerable variation on a single plant, including such intermediate states as five free stamens or four free stamens and two with fused filaments. Fruit varying in development from an unelongated state to normal development. Seed set: 6 per cent. Pollen fertility: 4 per cent.

F2. 14 plants of the F2 generation were obtained. A wide range of types from abnormalally developed sterile plants to fairly vigorous, highly fertile plants was obtained. Segregation was shown in leaflet shape and hairiness, inflorescence pattern, pedicel length, flower size and shape of the petals, hairiness of the sepals and length of the fruit. None of the F2 plants equalled the parental types in vigour—i.e., though the two parents can exchange genes to a limited extent, genetic recombination results in a certain degree of unbalance.

Although very little genetical work was carried out on the alpine types, one cross between the forest race " Long Style " and *C. bilobata* is of interest. An F1 generation of normal vigour was obtained, with pinnate hairy leaves lacking the characteristic sharply lobed leaflets and the strong anthocyanin pigmentation of " Long Style ". The flowers had large broad petals and glabrous sepals as in both parents. The style was 1–2 mm long (intermediate between the parents). Seed set was surprisingly high, most fruits having a full complement of seeds.

It is apparent that the variants within the races are highly interfertile, while an incomplete barrier to gene exchange exists in the F1 of interracial crosses. The introduced *C. hirsuta* does not appear to be able to cross with the native forest races. Genetical evidence confirms the close relationship between the subantarctic *C. corymbosa* and the mainland coastal race. Furthermore, a limited amount of gene exchange between the forest races and *C. corymbosa* can be achieved experimentally.

DISCUSSION

Emphasis has already been placed on the incompleteness of the experimental evidence and the need for a wider coverage of New Zealand before any final analysis of the problem can be made. However, a few conclusions stand out already.

Hooker, in 1853, had stated, " In Flora Antarctica, I left it doubtful whether the New Zealand plant (*C. debilis* = *C. heterophylla*) was the same as the *C. hirsuta* of Europe. I am now sure that it is so, being unable to trace any distinction, however slight, between the New Zealand and Scottish forms." This view was accepted by Kirk (1899) and by Cheeseman (1906), though the latter returned in 1925, not without hesitation, to Schulz's treatment (1903) in separating *C. heterophylla* from *C. hirsuta*. The validity of this separation has been confirmed in the present work where *C. hirsuta* was shown to differ morphologically, cytologically and genetically from the forest races of the New Zealand complex. The reservation must be made that other forms more closely related to *C. hirsuta* may exist in parts of the country unsampled in the present study, but this seems unlikely.

Secondly, it has been shown that the race from open coastal areas, formerly included in *C. heterophylla* var. *uniflora* is really only a minor variant of *C. corymbosa* which thus has a distribution from the Subantarctic Islands to at least as far north as Wellington. With regard to Hooker's var. *uniflora*, a taxonomic difficulty still exists. The type specimens of var. *uniflora* at Kew were collected by Colenso but no date or locality is given. The only indication given of their origin is a comment by Cheeseman (1925) that the variety was originally discovered by Mr Colenso in an alpine locality. Until a more detailed survey of the alpine localities has been carried out, the variety *uniflora* will have to be retained.

The third problem is that of the status of the forest races. They do not appear to intercross when occurring together in nature in spite of ecological overlap and an incomplete genetic barrier. It may be that a pollen competition mechanism similar to that demonstrated between *C. hirsuta* and " Narrow Petal " exists. Furthermore, the natural breeding habit—i.e., self-pollination, must be kept in mind when interpreting the genetic evidence. Since the infrequency of cross-pollination is in itself acting as a reproductive barrier, genetical isolation machanisms would not have the strong selective value that they would have in an outbreeding species. A similar situation is seen in the cereal grasses—wheat and oats—where the species are readily interfertile experimentally yet do not intercross when occurring together in nature.

In the author's opinion the name *heterophylla* should be restricted to the forest races (perhaps including certain South Island alpine races) and that the races, " Glossy Leaf ", " Long Style " and " Narrow Petal " should be ranked as varieties. At the present time no formal description is possible owing to the difficulty in relating these to the varieties of Schulz (1903). Furthermore, it is probable that several more varieties exist within *C. heterophylla* All forest specimens so far found in the North Island, the Marlborough Sounds and Stewart Island can be referred to one or other of the three races. Field studies in the montane beech forests of the Mount Arthur Tableland, however, show that a different pattern exists there, and herbarium specimens from the West Coast of the South Island show more in common with the Mount Arthur races than with the three races described in the present study.

A strong, though not absolute barrier exists between at least one of the forest races (" Narrow Petal ") and *C. corymbosa*. Furthermore, the ecological separation of these two groups is such that little cross-pollination would take place.

A taxonomic treatment of the alpine races must await more detailed collecting and experimental work. The two North Island races, the " Tussock Race " and the " Scree Race ", seem from morphological, ecological and geographical evidence to be quite distinct species. Of the South Island races, many clearly have affinities with *C. corymbosa* in such features as leaf form, condensed inflorescence, apetalous autumn flowers and fruit characters. Others appear to be more closely related to the forest races and yet others have features in common with both groups. Interspecific hybridisation may have contributed to this complex, but any such suggestions can only be highly speculative at this stage.

ACKNOWLEDGMENTS

I would like to thank members of the Botany Division, D.S.I.R. and of the Botany Department, Victoria University College, for help in collecting material; Professor H. D. Gordon and Miss L. B. Moore for help and criticism, and Mr. A. P. Druce for many collections from alpine areas and much useful information on the North Island alpine races.

LITERATURE CITED

CHEESEMAN, T. F., 1906. Manual of the New Zealand Flora. 1st. Ed. Government Printer, Wellington, N.Z. 1199 pp.

——— 1925 Manual of the New Zealand Flora. 2nd Ed. Government Printer, Wellington, N Z. 1162 pp.

HOOKER, J. D., 1853. Botany of the Antarctic Voyage of H.M.S. " Erebus " and " Terror " in the years 1839–1843. II. London.

KIRK, T., 1899. The Students' Flora of New Zealand and the Outlying Islands. Government Printer, Wellington, N.Z. 408 pp.

MANTON, I., 1932. Introduction to the general cytology of the Cruciferae *Ann. Bot.*, 42: 509–556.

OWCZARZAK, A., 1952. A rapid method for mounting pollen grains. *Stain Tech.*, 27: 249–251.

SCHULZ, O. E., 1903. Monographie der Gattung *Cardamine*. *Engler. Bot. Jahrb.*, 32: 280–623.

G G. PRITCHARD,
Department of Botany,
Victoria University College.