

A revision of the New Zealand, Subantarctic, and South American species of *Cotula*, Section *Leptinella*

David G. Lloyd

To cite this article: David G. Lloyd (1972) A revision of the New Zealand, Subantarctic, and South American species of *Cotula*, Section *Leptinella*, *New Zealand Journal of Botany*, 10:2, 277-372, DOI: [10.1080/0028825X.1972.10429156](https://doi.org/10.1080/0028825X.1972.10429156)

To link to this article: <http://dx.doi.org/10.1080/0028825X.1972.10429156>



Published online: 30 Mar 2012.



Submit your article to this journal [↗](#)



Article views: 231



View related articles [↗](#)



Citing articles: 31 View citing articles [↗](#)

A Revision of the New Zealand, Subantarctic, and South American Species of *Cotula*, Section *Leptinella*

DAVID G. LLOYD

Botany Department, University of Canterbury, Christchurch

(Received 21 December 1971)

SUMMARY

The taxonomic position, status, and characters of *Cotula*, and its subdivision into three sections are briefly described. Section *Leptinella* is considered a well-defined taxon and its characters and relationships are discussed. Twenty-five species from New Zealand, the Subantarctic islands, and South America are described and classified into two series, *Elongata* and *Radiata*. The following new taxa and names are described: series *Oligoleima* (from Australia and New Guinea), *Elongata* and *Radiata*; five new species, *C. dispersa*, *C. serrulata*, *C. calcarea*, *C. intermedia*, and *C. nana*; two new names, *C. albida* and *C. membranacea*; five new combinations, *C. rotundata*, *C. traillii* subsp. *pulchella*, *C. pectinata* subsp. *villosa*, *C. pectinata* subsp. *willcoxii*, and *C. pyrethrifolia* var. *linearifolia*; four new subspecies, *C. dispersa* subsp. *rupestris*, *C. dioica* subsp. *monoica*, *C. squalida* subsp. *mediana*, and *C. atrata* subsp. *luteola*.

INTRODUCTION

The genus *Cotula* L. contains approximately 80 species and is the largest of a number of genera in the tribe Anthemideae (Compositae) which are confined to or centred in the Southern Hemisphere. In the classification of *Cotula*, introduced by Bentham (1867) and followed below, there are three sections. Section *Cotula* includes the cosmopolitan species *C. coronopifolia* L. and occurs principally in South Africa. The second section, *Strongylosperma* (Less.) Benth., includes the widespread weed *C. australis* (Less.) Hook.f. and occurs mainly in the warmer parts of Australia, America, Asia, and Africa. The third section, *Leptinella* (Cass.) Hook.f., contains the remaining species of New Zealand, the Subantarctic islands, and South America, which are described below, as well as five Australian and New Guinea species which will be described elsewhere.

The New Zealand species are often regarded as being difficult to

distinguish and the species boundaries are poorly known (Hooker, 1864; Allan, 1961). Apart from the limited revisions made in the various Floras of New Zealand in the interval between Hooker's and Allan's publications, and the occasional publication of new species, the only paper on the morphology or taxonomy of New Zealand species is that by Edgar (1958). She described the nature of the florets and divided the New Zealand species into two natural groups on the basis of their stem anatomy.

The present author became interested in the New Zealand species of *Cotula* when he discovered that they possess a greater diversity of declinous breeding systems than was previously thought. As the evolution of the breeding systems could not be traced until the relationships of the species were known, investigations were extended to a taxonomic study of the species. After extensive field work, almost 500 accessions have been grown and compared at Christchurch under relatively uniform conditions. Numerous aspects of biology have been studied, including breeding systems, pollen stainability, chromosome numbers, crossing relationships, the performance of artificial hybrids, natural hybridisation, and the evolution of the habit and other characters. The present paper is the first in a series describing this work and is limited to the taxonomy of the New Zealand, Subantarctic, and South American species of section *Leptinella*.

THE GENUS *Cotula* L.

The genus *Cotula* L. officially dates from 1753, when Linnaeus described four species in the first edition of "Species Plantarum". During the next century the number of species increased slowly, mostly by addition of South African species, and the limits of the genus were changeable. The content of the genus has been more stable since Bentham's revisions in "Flora Australiensis" (1867) and "Genera Plantarum" (1873b). Since then, the only critical treatment of the genus on a world-wide scale is that of Hoffmann (1890-94), who included in *Cotula* the nine species of the South African genus, *Cenia* Juss. The one other major change in the content of *Cotula*, since Bentham's work, is the more recent inclusion of the two South African species formerly in *Otochlamys* DC., by Levyns (1941) and Phillips (1950).

The relatives of *Cotula* are not well known. Bentham (1873a), in "Notes on Compositae", informally grouped *Cotula*, with ten other smaller genera, into the "Cotuleae", an assemblage based in part on earlier classifications of the Anthemideae by Lessing (1832), Cassini (1834), and de Candolle (1838). Since Bentham's account, a number of changes in the limits of several genera have been made, but the group as a whole has not been discussed at all. At least two genera should be removed from the Cotuleae as recognised by Bentham—*Polygyne* Phil. (to *Eclipta* L., Cabrera, 1954) and *Ceratogyne* Turcz. (Turner, 1970). The remaining Cotuleae are largely grouped together

within the Anthemideae by the mutual possession of characters representing the loss or reduction in the habit and various parts— involucre, paleae, ray florets, pappus, number of corolla teeth and stamens (to four), and seed-sterility of disk florets. The decreases in the size and number of any of these parts could well have occurred independently in a number of different phyletic lines. Each genus of the Cotuleae, apart from *Cotula*, is a small, geographically limited, and morphologically well defined taxon, easily separated from *Cotula* by a number of positive attributes rarely shared by more than one genus.

The Cotuleae may not, therefore, be a natural group. But it is still likely that the closest relatives of *Cotula* are among the Southern Hemisphere genera of the Cotuleae, especially *Centipeda* Lour., and also *Sphaeromorphaea* DC., *Soliva* R. et P., *Plagiocheilus* Arn., and *Abrotanella* Cass. All these genera, at least, will have to be considered in the future in a critical review of the relationships of *Cotula*.

Although the content of *Cotula* has recently been rather stable, the genus is not well defined morphologically. There is extensive variety among *Cotula* species in the habit, leaf division, involucre, receptacle, and achenes which prevents these structures contributing much to the definition of the genus. *Cotula* can be defined only by a combination of two characters—tubular, reduced (or absent) corollas of the pistillate florets, and solitary, pedunculate heads. Even then, the latter character is marred by the very short peduncles of two New Zealand species, *C. maniototo* Petrie and *C. goyenii* Petrie. But the conclusion of Bentham (1873b) still seems valid, viz “The genus (*Cotula*) is natural enough, although scarcely distinct from the following of the tribe (*Centipeda*, *Plagiocheilus*, *Soliva*, etc.) and divided by various authors in diverse ways into genera or sections; it seems to us that it should be kept intact” (author’s translation).

SECTIONS OF COTULA

Within *Cotula* there are five groups of species, each of which has at some time been considered a separate genus, viz *Cotula sensu strictissimo* (section *Cotula* of Bentham, 1867), *Cenia* Juss., *Otochlamys* DC., *Strongylosperma* Less., and *Leptinella* Cass. These are arranged differently in the two formal classifications of *Cotula* by Bentham (1867) and Hoffmann (1890-94). Bentham excluded *Cenia* and *Otochlamys* from *Cotula* and regarded the other three groups as sections of *Cotula*. Hoffmann included *Cenia* in *Cotula* as a separate section and joined *Strongylosperma* and *Leptinella* as section *Pleiogyne* (Koch) Harvey.

Hoffmann’s classification of *Cotula* is unsatisfactory, since his sections *Cotula* and *Cenia* are closely similar and difficult to separate, whereas *Strongylosperma* and *Leptinella*, which he united, are quite distinct. Bentham’s classification is superior, but must be amended to take into account the more recent inclusion of *Cenia* and *Otochlamys*

in *Cotula*. Levyns (1941) has pointed out that the diagnostic characters of *Cenia* and *Otochlamys* are approached by certain species of section *Cotula sensu* Bentham. All three groups occur entirely or predominantly in South Africa, and in several respects they are more similar to each other than to either *Leptinella* or *Strongylosperma*. As a provisional solution, Bentham's classification is modified here by the inclusion of *Cenia* and *Otochlamys* in section *Cotula*.

The three sections have the following characters:

1. Section **Cotula**. Pistillate florets fewer than disk florets, usually in one (occasionally incomplete) row, occasionally absent or in more than one row. Corolla of pistillate florets absent or minute and fused with the ovary, narrower than the ovary and not inflated. Basic chromosome numbers, $x=8$ (Turner, 1970) and $x=10$ (Malik, 1960; Hair, 1962).

There are probably approximately 40 species, mostly in South Africa. A few species occur in North Africa and Australia and both the type species *C. coronopifolia* L. and *C. turbinata* L. are now widespread.

2. Section **Strongylosperma** (Less.) Benth. Pistillate florets more numerous than disk florets, in several rows. Corolla of pistillate florets absent or small and usually fused with the ovary, narrower than the ovary and not inflated. Basic chromosome number, $x=18$ (Diers, 1961; Hair, 1962; Mehra *et al.*, 1965*).

There are approximately eight species; three in Australia, of which the type species *C. australis* (Less.) Hook.f. is a widespread weed, an ill-defined number in Africa and Asia (often lumped under *C. anthemoides* L.), and one, *C. mexicana* (DC.) Cabr., in Central and South America.

3. Section **Leptinella** (Cass.) Hook.f. Pistillate and staminate florets in all proportions, heads sometimes unisexual; in bisexual heads, the pistillate florets are usually in more than one row. Corolla of pistillate florets present and evident, jointed to the ovary, tubular but sometimes compressed, as wide as the ovary at anthesis and inflated. Basic chromosome number, $x=13$ (Hair, 1962).

There are 30 species; 24 in New Zealand and the Subantarctic islands, 5 in Australia and New Guinea, and the type species *C. scariosa* (Cass.) Franch. in South America and the Falkland Islands.

The previous authors who have contributed to the diagnoses of the three sections, Hooker (1864), Bentham (1867), and Edgar (1958), all used somewhat different combinations of characters to distinguish the sections. Only the above characters appear to me to be sufficiently

*Mehra *et al.* give $n=18$ for *C. anthemoides* L. and $n=10$, $2n=20$ for *C. hemisphaerica* Wall. The identity of the latter plant is questionable, since *C. hemisphaerica* is one of the "species" included in *C. anthemoides sensu lato*.

constant to warrant inclusion in the diagnoses. The other characters used by earlier authors will be discussed below as far as they affect the differences between *Leptinella* and the other sections.

Each of the three sections possesses a different basic chromosome number or numbers. Hair (1962) and Turner (1970) have suggested three ways by which one basic chromosome number could be derived from the other two. But there is no evidence that any one of the sections has a combination of morphological characters of the other two and might have arisen by allopolyploidy. Speculation on the origin of the basic chromosome numbers in *Cotula* seems premature until the systematics of the genus and its relatives are better known.

Section *Leptinella* is the most distinct of the three *Cotula* sections. All species share two characters not found in sections *Cotula* and *Strongylosperma*, or in any other members of the Anthemideae—inflated pistillate corollas and a basic chromosome number of $x=13$. In addition, there are a number of other characters described below, particularly those associated with the prostrate habit, which are characteristic of *Leptinella*, but which are absent in some species or occur in a few species of sections *Cotula* and *Strongylosperma* as well. Altogether, the gap between *Leptinella* and the other sections indicates that *Leptinella* is a natural, monophyletic group with well-demarcated limits.

The characters distinguishing sections *Cotula* and *Strongylosperma* are less impressive. The South African species of section *Cotula* have one row or less of pistillate florets and many more disk florets. All species of section *Strongylosperma* have several rows of pistillate florets, which outnumber the disk florets. But there are three *Cotula* species* from outside South Africa which have pistillate florets in several rows, although they are still outnumbered by the disk florets. These species are tentatively assigned to section *Cotula*, but the boundary between sections *Cotula* and *Strongylosperma* needs clarification by the use of additional characters and further chromosome counts.

HISTORY OF SECTION LEPTINELLA

When Cassini (1822) described the first two species of section *Leptinella* as *Leptinella scariosa* Cass. and *L. pinnata* Cass., both from unknown localities, he considered that they were distinct from previously described Compositae. He mentioned several characters of section *Leptinella* which are rare or absent in related Compositae, including the distinctive pistillate corollas, the seed-sterility of the disk florets, the bracts on the peduncle, and the dilated upper part of the corolla of disk florets.

**C. cryptocephala* Sch. Bip. from Ethiopia and apparently undescribed *Cotula* species from the Malagasy Republic (Imerina, J. M. Hildebrandt, July 1880, cord) and Western Australia (Northam, collector unknown, 1 Sept. 1962, PERTH).

During the next twenty years, no further species were described in *Leptinella*, except that *L. scariosa* was redescribed as *L. acaenoides* Hook. et Arn.—see the description of *C. scariosa* (Cass.) Franchet. Two species of section *Leptinella* were described as *Strongylosperma reptans* Benth. from Australia and *Soliva tenella* Cunn. from New Zealand. Nevertheless the genus *Leptinella* was retained during this period in classifications of the Compositae by Lessing (1832), Cassini (1834), and de Candolle (1838).

In 1843, Koch combined several species of *Leptinella* and *Strongylosperma* and one species of section *Cotula* into a new genus, *Pleiogyne* Koch. In the next 20 years J. D. Hooker (1844, 1847, 1852, and 1864) described 15 species from Australia and New Zealand now included in section *Leptinella*. Hooker consistently ignored the genus *Pleiogyne* and affirmed the relationship of the Australasian species to *L. scariosa*. The first 11 species were described as *Leptinella* species (Hooker 1844, 1847, and 1852), except that one Australian species *C. filicula* (Hook.f.) Hook.f. ex Benth. was briefly put into another genus *Symphymera* Hook.f., which he suppressed in 1856. The last four species described by Hooker (1864) were named as *Cotula* species, when he reduced *Leptinella* to a section of *Cotula*. In the same year, Mueller described the last two species named as *Leptinella* species, from the Chatham Islands.

Since Hooker's publications, the number of described species has doubled and all have been named as *Cotula* species and assigned to section *Leptinella*. The classification of *Leptinella* as a group, however, has not been so consistent. In 1864, Hooker placed *Leptinella* as one of three sections of *Cotula*, together with section *Cotula* (including *Strongylosperma*) and section *Myriogyne* (Less.) Hook.f. (now the genus *Centipeda* Lour.). Bentham (1867 and 1873b) excluded *Myriogyne* from *Cotula* and raised *Strongylosperma* as a separate section, recognising for the first time the three sections accepted above. Bentham's concept of the genus and his subdivision into three sections have been followed since without significant change by Australasian authors. The only other change in the status of *Leptinella* was made by Harvey (1865) and copied by Hoffmann (1890-94), who resurrected *Pleiogyne* as a section of *Cotula* to include *Leptinella* and *Strongylosperma*. As discussed above, this was probably a retrogressive step as well as now being nomenclaturally invalid, since *Strongylosperma* was described before *Pleiogyne*.

CHARACTERS OF SECTION LEPTINELLA

The following account of the general morphology of section *Leptinella* applies to all *Leptinella* species, including those in Australia and New Guinea, unless otherwise stated. The order of treatment of the characters corresponds with that in the species descriptions.

HABIT AND BRANCHING PATTERN

One of the most obvious features of *Leptinella* is the prostrate perennial habit, with roots at most nodes and usually long internodes. The long slender stems presumably prompted Cassini (1822) to bestow the name *Leptinella* (Latin for *little thread*) on the group. The other sections of *Cotula* consist predominantly of decumbent annuals, but the habit does not completely distinguish section *Leptinella*. A perennial prostrate habit has evolved independently in a few species in both sections *Cotula* and *Strongylosperma*. Moreover one species of *Leptinella*, *C. featherstonii* (F. V. Muell.) Hook.f. is suberect, although probably derived from a prostrate ancestor (see under that species), and another species, *C. maniototo* Petrie, occasionally behaves as an annual.

The prostrate perennial habit probably depends on the lack of a severely unfavourable season for growth and maintenance, due to either cold or dry conditions. Species of section *Leptinella*, except *C. atrata* Hook.f. and *C. dendyi* Ckn. on mobile subalpine shingle slides, retain some leaves throughout the winter. There are no special protective mechanisms for winter conditions, although the number of leaves is usually reduced and growth is curtailed to various degrees in different species.

A considerable number of ancillary morphological features of section *Leptinella* are associated with the prostrate habit. One of these is the restriction of the growth of most axillary shoots, which either do not develop at all or have imbricate leaves on determinate shoots, described here as short shoots to distinguish them from the indeterminate rhizomes. The development of short shoots varies immensely between species. In some species they do not develop at all; in other species they form only a few reduced leaves and are scarcely emergent from the subtending leaf base; in many species they carry all or most leaves crowded on stems usually less than 2 cm long but able to grow out into indeterminate rhizomes under favourable conditions.

The only axillary buds which normally develop into rhizomes in section *Leptinella* are those at the flowering nodes, and if the rhizome internodes are short, those at several nodes immediately behind the flowering one. In the erect or decumbent species of the other *Cotula* sections and related genera, most axillary buds grow at approximately the same rate as the parent branch until the growth of the whole plant slows down, usually when flowering occurs.

Prostrate stems on the soil surface occupy an asymmetrical interface between the ground and the air. As a consequence, in many *Leptinella* species the rhizomes, leaves, and subsequently the short shoots arising from their axils are initiated and maintained in two rows, alternating on either side of the rhizome. However, spiral phyllotaxis is retained throughout the year in several species, usually those with underground rhizomes, and in the autumn and winter in a number of species

of series *Radiata* Lloyd. Short shoots, which tend to grow more vertically than the rhizomes, also have a spiral phyllotaxis, except in *C. maniototo*, where leaves are distichous on both the rhizomes and short shoots.

The position and growth of the peduncle in section *Leptinella* is also associated with the prostrate habit. In the decumbent species of the other sections of *Cotula*, the peduncles are terminal on leafy branches which decrease in thickness towards the head and elongate gradually from the bud to fruiting stages of head development. In section *Leptinella*, the axil of a flowering node contains a vegetative bud as well as the inflorescence bud. The latter develops a single head on a peduncle which is sometimes nude, but often has one or more small bracts along its length. The peduncle is of constant thickness and, except in *C. goyenii* Petrie, fully elongated at anthesis.

The habit of section *Leptinella* species is uniform in its general features but very diverse in detail. The prevailing form has evergreen rhizomes with distant nodes on the soil surface, and grows as part of a sward or develops into patches on bare ground. Several more specialised habits have evolved, including tufts from underground rhizomes in drier habitats, compact subalpine mats, summergreen clumps in mobile shingle slides, and subwoody erect branches.

LEAVES

No leaf characters completely separate any of the three sections of *Cotula* from the other two. Within each section, leaf division, shape, texture, and hairiness vary considerably, causing extensive overlap between sections. But *Leptinella* species may be distinguished from many species of the other sections by the possession of a distinct petiole (except in *C. goyenii*) and a leaf base which is closely wrapped around the enclosed stem and lacks pinnae.

The leaves of species of section *Leptinella* vary from simple and entire to 2-3 pinnatifid. In the species descriptions two terms are used to describe leaf divisions. A leaf division which is cut to the axis bearing it (i.e. the sinuses between the divisions reach to the axis) and is therefore of similar width to that axis, is known as a pinna (primary and less often secondary or tertiary). A leaf division which is not cut as far as the axis bearing it and is much narrower than the division on which it is borne is described as a tooth. Most simple leaves and pinnae of 1-pinnatifid leaves have teeth on their margins. Teeth are really only reduced pinnae; sometimes one sees transitions between teeth and pinnae, but the two are usually quite distinct.

EPIDERMAL HAIRS

The blunt, columnar, uniseriate hairs that occur on the achenes of many species of sections *Cotula* and *Strongylosperma* are absent in *Leptinella*. The two types of trichomes present in *Leptinella* also occur

in the other sections. Their distribution and abundance vary greatly between species of section *Leptinella* and they often provide useful characters to separate similar species.

Uniseriate hairs are composed of several short basal cells in a row, surmounted by one or more longer cells, of which the terminal cell has a pointed apex. They are invariably present on the leaves, rhizomes, peduncles, and phyllaries, but not the achenes, except in series *Oligoleima* (Hook.f.) Lloyd. The visible hairiness which the uniseriate hairs cause is extremely variable from species to species and depends on environmental conditions. Sometimes the hairs are very sparse and have short terminal cells with a wide lumen and narrow walls. Such surfaces appear glabrous until examined under the microscope. At other times the hairs are very dense and have long terminal cells with a narrow lumen and thick walls. The hairs then form an obvious dense cover.

Biseriate hairs are composed of two rows of several short basal cells and a pair of taller and broader, thin-walled (glandular?) cells at the apex. They are present on the leaves, florets, and achenes in considerable density in all species and on other surfaces at a lower density. They are colourless when fresh and are rarely visible with the unaided eye, but pits containing them are visible on thicker "glabrous" leaves, such as those of *C. pyrethrifolia* Hook.f. and *C. dioica* Hook.f. The biseriate hairs are more or less deciduous and not often useful as taxonomic characters, although those on the achenes especially have been used in many previous descriptions.

HEADS

Head size and shape vary greatly between species, providing useful taxonomic characters within section *Leptinella*, but they do not separate *Leptinella* from the other sections. The surface of the head made by the tips of the florets at anthesis is usually rather shallowly convex, but varies from almost flat to hemispherical or steeply convex (taller than wide). The phyllaries of section *Leptinella* tend to be more herbaceous than those of the other sections and are still fresh and green when the seeds mature. In monoecious species the phyllaries are usually in approximately two subequal rows and form a flat to campanulate involucre which does not retain the mature seeds. In the dioecious species of series *Elongata* Lloyd, the involucre of male heads is similar to that of monoecious species, but with fewer broader phyllaries. The involucre of pistillate heads, however, consists of several unequal rows of phyllaries. The inner phyllaries are longer and arch over the ovaries and corollas of the outer florets at anthesis, so the involucre may be described as urceolate. After anthesis, the inner rows of phyllaries continue to grow and enclose the head, so the mature seeds are trapped until the head withers and falls.

RECEPTACLE

Bentham (1867) and later authors used the shape of the receptacle as one of the characters defining the sections of *Cotula*. According to them, the receptacles of section *Leptinella* are conical, whereas those of the other sections are flat or convex. This is approximately correct, but there is too much variation in both sections *Leptinella* and *Strongylosperma* for receptacle shape to reliably separate the sections. In most species of section *Leptinella*, the receptacle is a low mound that would be better termed convex than conical. In other species it is truly conical or steeply convex or hemispherical or, varying in the other direction, almost flat in the pistillate heads of *C. dendyi*.

Another character used by Bentham (1867), and copied repeatedly in diagnoses of the *Cotula* sections, is the length of the floret pedicels. These peg-like protuberances covering the receptacle are readily seen after the fruits are shed. Bentham described the achenes of the pistillate florets as being borne on long stalks in section *Cotula*, sessile in *Leptinella*, and in either condition in *Strongylosperma*. These differences, which are associated with the breeding systems, are not as clear-cut as Bentham indicated. In all three sections, both pistillate and disk florets are borne on protruding pedicels.

In section *Leptinella*, the pedicels are very short, roughly one-tenth the length of mature achenes. The pedicels of the pistillate florets are slightly longer than those of the staminate florets, and since the pistillate florets are themselves slightly shorter than staminate florets, all florets reach the same level at the head surface. The situation is similar in the monoecious species of section *Strongylosperma*. In the gynomonocious species of sections *Strongylosperma* and *Cotula*, the pistillate florets lack a corolla and are much shorter than the disk florets, which have both a corolla and a full-sized ovary. In these species the pistillate florets have much longer pedicels, approximately equal in length to the ovaries, so again all florets reach the same level.

DISTRIBUTION AND SEX OF FLORET TYPES

Bentham (1867) described section *Cotula* as having a single row of pistillate florets, whereas *Leptinella* and *Strongylosperma* have several rows. Almost a century later, Edgar (1958) added that in section *Cotula* the disk florets are very numerous, while in *Strongylosperma* they are comparatively few. The two sets of observations, when combined, provide one of the few characters which reliably separate the sections. Section *Cotula* is distinguished by the pistillate florets being less numerous than the disk florets. Although there is usually only one row of pistillate florets, occasionally there is more than one row and a few species lack pistillate florets altogether. Section *Strongylosperma* differs in having pistillate florets which are more numerous than the disk florets and always in several rows. Species of section *Leptinella* generally resemble *Strongylosperma*, but the diversity of breeding systems causes both the number of rows and the proportions of the two floret types to vary over the range shown in the other sections.

The floret proportions are closely associated with the seed fertility or sterility of the disk florets. In section *Cotula*, as in most Anthemideae, most (or occasionally all) seed is produced by the more numerous disk florets, which are fertile and probably often self-pollinated. In section *Strongylosperma*, the more numerous pistillate florets produce most seed. This trend is continued further in the three species of *Strongylosperma* in which the disk florets are seed-sterile and functionally staminate. The disk florets are uniformly outbreeding further by subdioecious or dioecious conditions. In both *Leptinella* and *Strongylosperma*, the loss of seed production has been accompanied by morphological changes in the staminate florets, which have reduced ovaries and circular, undivided, non-receptive style apices which serve only to present the pollen for pollination. In section *Leptinella*, the ovary although reduced is still evident and clearly demarcated from the corolla. Edgar (1958) has described the abortion of the ovule in staminate florets.

PISTILLATE FLORETS

The pistillate florets of sections *Cotula* and *Strongylosperma* either entirely lack a corolla or have a small compressed corolla which is not obvious macroscopically and appears continuous with the broader, winged ovary. In contrast, the corolla of the pistillate florets of section *Leptinella* species is more conspicuous, round or compressed, jointed with the ovary, and "inflated" due to the presence of an air space between outer and inner layers. The distinctive pistillate corolla of *Leptinella* was immediately recognised by Cassini (1822) and Hooker (1844, p. 28). Hooker remarked that the continuity of the inner and outer layers at both the base and summit of the corolla and the distribution of the veins and "glands" (biserial hairs) indicate that the two layers represent the two surfaces of a hollow erect corolla and not two complete layers of a reflexed corolla. The function of the inflated corolla appears to be to cause nectar, which wells up in the narrow space between the inner layer and the style, to be exposed at the top of the corolla, an unusual feature in the Compositae. At the apex of the corolla are four small teeth, which are usually apparent but in some species are obscure or obsolete. The exact shape of the corolla varies greatly between species and is a useful taxonomic character (Fig. 1).

DISK FLORETS

The corolla of the disk florets of section *Leptinella* has only four corolla teeth and there are only four stamens, as in the other sections and related genera of the Cotuleae. (*C. mexicana* (DC.) Cabr. of section *Strongylosperma* has only three corolla teeth and stamens; see Caro, 1961.)

In all three sections of *Cotula*, the corollas of disk florets are narrower below and broader in the upper portion containing the anthers. In sections *Cotula* and *Strongylosperma*, the corolla is tubular (sometimes winged or, in the species formerly in *Otochlamys*, with a sheathing base extending over the ovary) and the upper expansion is relatively slight. The corolla teeth are small and more or less erect (but in the species formerly in *Cenia* the anterior lobe of the outermost disk florets is expanded into a pseudo-ray). There is only a narrow space between the anthers and the corolla, and the relatively narrow florets are tightly packed together. In section *Leptinella*, the lower part of the corolla of staminate florets is tubular and in some species inflated slightly, but much less so than the corollas of marginal florets. The broad portion of the corolla is usually about twice as wide as the lower part and cup-shaped. The florets are packed much more loosely than in the other sections. At anthesis, the relatively large and deeply cut teeth are horizontal or reflexed. Nectar wells up the narrow portion of the corolla into the base of the broad cup surrounding the anthers and is readily accessible to the small insects, usually Diptera, which visit the heads.

The size, shape, and colour of the corolla of staminate florets vary greatly among *Leptinella* species (Fig. 1). Otherwise the staminate florets provide almost no taxonomic characters to separate the species from each other or from those of the other two sections.

ACHENES

Hooker (1864) described the achenes of the pistillate florets of section *Cotula* (which corresponds to sections *Cotula* and *Strongylosperma* in the present classification) as having flat winged achenes, while section *Leptinella* was said to have non-winged achenes. This distinction almost separates all species of *Leptinella* from all species of sections *Cotula* and *Strongylosperma*. In the latter sections, the ovaries and later the achenes are strongly compressed, relatively thin, and almost flat. On either side of the fruit there is a conspicuous margin, which is usually thinner than the central portion covering the seed and of a different colour and texture. The joint width of the margins equals or exceeds that of the seeds, so the achenes are justifiably described as winged. The seeds of section *Leptinella* are usually bulkier than those of the other

FIG. 1.—Pistillate (right) and staminate (left) florets of five species of section *Leptinella*.

Series *Elongata* top row, left, *C. squalida* subsp. *mediana*; right, *C. potentillina*. Series *Radiata*, middle and bottom rows; left, *C. atrata* subsp. *atrata*; middle right, *C. minor*; bottom right, *C. pectinata* subsp. *villosa* (pollen emerging).



squalida



potentillina



atrata



minor



0 1mm



pectinata



sections and occupy most of the achene. The achenes are thick and vary in cross-section from almost round or tetragonal to clearly compressed, but still convex on the dorsal side at least. The margins, if evident at all, are usually narrower than those in the other sections and not different in colour or texture from the achene surface above the seed. There are considerable differences between the series of section *Leptinella* in achene shape, and these are described below.

CHROMOSOME NUMBER

The basic chromosome number in section *Leptinella*, $x=13$ (Hair, 1962), differs from that in the other sections, as described previously. The lowest number yet obtained is $n=26$. In both series *Elongata* and *Radiata* there is a complex series of polyploids, culminating in $n=ca. 156$ in series *Elongata* and $n=78$ in series *Radiata*. The chromosome counts mentioned in the species descriptions will be presented in a later paper.

SUBDIVISION OF SECTION LEPTINELLA

AUSTRALIAN AND NEW GUINEA SPECIES

The five species of section *Leptinella* from Australia and New Guinea are a natural group which share several features not seen in any New Zealand, Subantarctic, or South American species. The achenes of Australian species are distinctly compressed and have margins that jointly equal the seed in width. In this respect they are similar to the achenes of species of sections *Cotula* and *Strongylosperma*, particularly *C. alpina*. In contrast, the achenes of the remaining species of section *Leptinella* are compressed only slightly or not at all and have inconspicuous or obsolete margins. Another feature of the Australian species is that the corolla of the pistillate florets is persistent, whereas in the other species it is shed when the achene is released from the head or shortly afterwards.

The Tasmanian species of section *Leptinella* were put by Hooker (1847) into a separate subgenus of *Leptinella*, named *Oligoleima* Hook.f. because of the low number of involucre bracts. This feature does not entirely separate the Australian species from those in New Zealand, which have a wide range of phyllary numbers. Nevertheless, the five Australian and New Guinea species are sufficiently distinct to warrant taxonomic separation from the other species of *Leptinella*. A new series is proposed here to contain them: Series *Oligoleima* (Hook.f.) stat. nov., based on a subgenus of *Leptinella*, subgenus *Oligoleima* Hook.f., Lond. Jour. Bot. 6: 117, 1847. The type species is *C. longipes* (Hook.f.) Curtis.

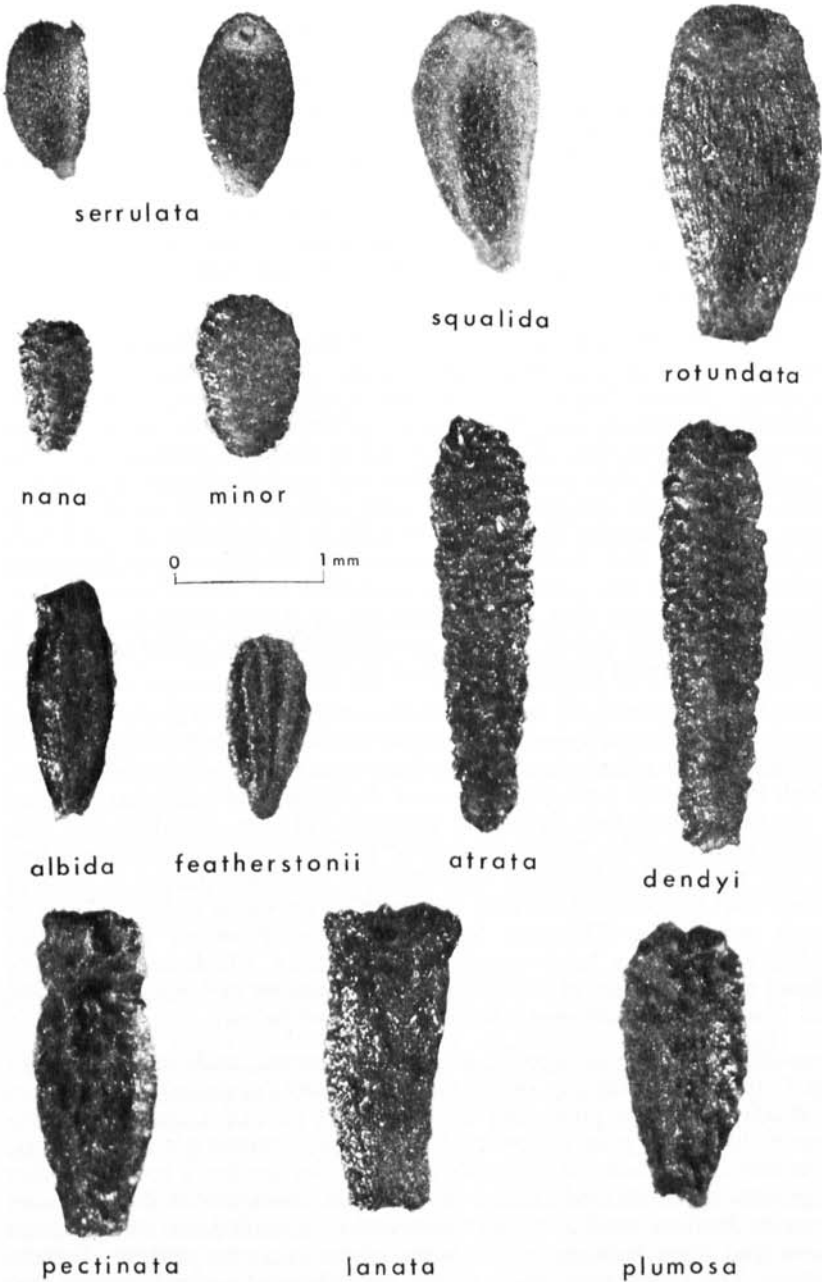


FIG 2.—Achenes of 12 species of section *Leptinella*. Series *Elongata*; top row from left, *C. serrulata* side view, *C. serrulata* ventral view, *C. squalida*, *C. rotundata*. Series *Radiata*; second row, *C. nana*, *C. minor*; third row, *C. albida*, *C. featherstonii*, *C. atrata* subsp. *atrata*, *C. dendyi*; bottom row, *C. pectinata*, *C. lanata*, *C. plumosa*.

NEW ZEALAND, SUBANTARCTIC, AND S. AMERICAN SPECIES

The first subdivision of New Zealand species was made by Hooker (1864), who informally split the 10 New Zealand species he recognised into two subgroups, with unisexual and bisexual heads respectively. His groups were continued in all subsequent New Zealand manuals and more species were added until Allan (1961) named them sections *Unisexuales* and *Bisexuales*. Allan's names are invalid, however, since no type species were designated. The *Unisexuales* should also have taken the name of the subgenus, *Leptinella* (also not validly published, as described below).

In an independent classification, Cockayne (1927) pointed out that the Canterbury species were divided into "patch-forming" and "turf-forming" species. Edgar (1958) then divided all New Zealand and Subantarctic species into two groups, primarily on the basis of stem anatomy. Cross-sections of the internodes of the stems (rhizomes) of the first group show eight vascular bundles and a narrow band of pericycle fibres between the bundles. In internode sections of the second group, there are four vascular bundles surrounded by a complete ring of fibres. Edgar observed that the first group contained Cockayne's patch-forming species, whereas the second group contained his turf-forming species. Moreover she noted that the two anatomical groups tended to differ in habitat and flower colour and corresponded to some extent to the unisexual and bisexual groups recognised by Hooker.

After examining all species for the characters previously used and numerous additional ones, the present author concludes that Edgar's classification is clearly superior to that based on the sex distribution, which is somewhat artificial because of the complex evolutionary history of the breeding systems in section *Leptinella* (Lloyd, unpublished). The groups recognised by Edgar are named in the taxonomic account below as two new series, *Elongata* and *Radiata*, with no change in content except that the South American species, *C. scariosa*, is added to her first group, now series *Elongata*. Species of series *Elongata* and *Radiata* typically differ in a large number of characters, which are apparently related to the habitats of the series. The differences in vegetative growth, floral morphology, and seed release are outlined below.

Vegetative Characters: Species of series *Elongata*, such as *C. squalida* and *C. perpusilla*, usually occur at low altitudes, in closed communities in which the plants grow into each other as part of a continuous permanent turf. The plants grow rapidly and have numerous short shoots. In winter they retain long internodes and suffer neither a total cessation of growth nor a marked change in internode arrangement. Most species of series *Radiata*, such as *C. pectinata* and *C. pyrethrifolia*, occupy more severe and open habitats in which the plants occur as shifting, discrete patches. The plants grow more slowly than those of series *Elongata* and have only a few small short shoots or none at all. When growth is checked at the end of the season the internodes become very closely clustered, in contrast with the long internodes produced earlier.

The branches of series *Elongata* are usually single (Fig. 9), since only the axillary bud at the flowering node is induced to grow rapidly into a rhizome when flowering occurs. In series *Radiata*, several axillary buds at and immediately behind the flowering node are usually induced to grow when flowering occurs, so several branches radiate in all directions from the clustered nodes (Fig. 23).

The leaves of most species of series *Elongata* are soft, with broad pinnae bearing many small teeth. The leaves of series *Radiata* are usually more coriaceous, with narrow pinnae usually lacking teeth, but they are sometimes toothed or more deeply cut into secondary or even tertiary pinnae.

Floral Characters: Some species of series *Elongata* are monoecious, but more of them are strictly dioecious, with clearly distinct male and female heads. The florets of series *Elongata* are an inconspicuous yellow-green and have relatively short corollas. Most species of series *Radiata* are monoecious, although three are subdioecious or contain subdioecious populations. In general, the heads of series *Radiata* are showier and contain more numerous and brightly coloured florets with longer, more slender corollas.

Fruit Characters: The achenes of series *Elongata* are bulky (Fig. 2) and mature slowly over 2 to 3 months. As they grow they crowd each other and become curved outwards and irregularly angled in cross-section. In the dioecious species, the inner phyllaries of pistillate heads elongate during achene development and usually enclose the florets completely until the head falls. In the monoecious species, the achenes fall from the head individually when mature.

The achenes of series *Radiata* are more slender (Fig. 2) and mature quickly, in 2 to 6 weeks in different species. The seeds remain uncrowded and straight. The phyllaries do not grow after anthesis and the mature seeds are readily released from the head.

Relationships of Species: Series *Elongata* is a rather homogeneous group. Most species are very similar and difficult to distinguish. Many hybrid combinations are known and several of these are widespread and common. The subgroups recognised in the summary below are not very distinct. *C. intermedia* is closer than the other species of series *Elongata* to series *Radiata* and is apparently an allopolyploid whose ancestors were members of the two series.

The species of series *Radiata* are much more heterogeneous and usually quite distinct from their closest relatives. There are several well-marked subgroups within series *Radiata*, viz *maniototo*; *nana*, *filiformis*, and *minor*; *dendyi* and *atrata*; *goyenii*, *albida*, *pectinata*, and *pyrethri-folia*; *lanata* and *plumosa*; *featherstonii*. Hybrids occur in relatively few combinations and only *C. dendyi* × *atrata* and *C. albida* × *pectinata* are at all common.

TAXONOMIC CONCEPTS

The difficulties experienced with the demarcation and identification of New Zealand *Cotula* species in the past have arisen from several sources. Many of the species are very similar and there is a paucity of constant qualitative features which can be used as reliable diagnostic characters. In the most difficult species groups, there are virtually no reproductive characters distinguishing the species. The vegetative characters are also confusing because of the extreme environmentally induced plasticity often shown. The species which are most widespread and most often encountered are also geographically variable. The variation patterns in *C. dioica* and *C. pectinata*, especially, are complex and clinal. In addition, several pairs of species, that are already difficult to separate, hybridise extensively.

In several species, such variation easily exceeds the morphological gap between the species and its nearest relatives. In such cases the differences between species may vary from area to area. It is not surprising, in view of these difficulties, that a number of species have not been recognised and that the characters, limits, and geographic distributions of other species have been uncertain.

Allan (1961) recognised 22 species in section *Leptinella* in New Zealand and the Subantarctic islands. Only eight of Allan's species are unchanged in name and basic content in the taxonomic treatment below, and three of these have had major amendments to their geographic distribution. Five species were recognised by Allan but have not been upheld below. On the other hand, seven species, including five new species, are recognised here but not by Allan. The net gain at the species level, apart from *C. scariosa* which Allan did not consider, is two species. Below the species level, six species are newly divided into subspecies and in one species, *C. pyrethrifolia* Hook.f., a marked local variant previously known as a separate species (*C. linearifolia* Cheesem.) has been reduced to a variety. All previously named varieties, apart from those now recognised as species or subspecies, have been dropped.

It seems advisable to outline the taxonomic concepts involved in the changes in classification of section *Leptinella*. A combined biological plus morphological species concept has been used. Groups of populations which are reproductively isolated from other such groups have been given the status of taxonomic species if they are also morphologically distinguishable. This means in effect that all biological species have been formally recognised as species except the cytological races in *C. squalida* and *C. pectinata*, which are distinguishable only by ploidy level.

The application of this species concept has resulted in the division of several species recognised by Allan (1961), which are actually pairs or trios of biological species coexisting in a more or less extensive region of overlap without losing their identity. Thus *C. atrata* Hook.f. and *C.*

dendyi Ckn. have been re-separated, in agreement with Cockayne (1915); *C. serrulata* Lloyd has been removed from *C. perpusilla* and the three species formerly identified as *C. minor* Hook.f. have been raised to specific level as *C. nana* Lloyd, *C. dispersa* Lloyd, and *C. membranacea* Lloyd. (The name *C. minor* is assigned to the species previously known as *C. haastii* Kirk).

The variety category has been used in the past in *Cotula*, as in other genera, to cover a wide range of diverse, usually undefined biological situations, including various patterns of geographic variation. In this paper a variety is accepted in only one species, to denote an obvious but local facies of a species. Although the variety recognised, *C. pyrethriifolia* var. *linearifolia* (Cheesem.) Lloyd, is instantly recognisable by one character, it is subordinate to the more significant but less obvious and unnamed major phyletic division of the species.

Many New Zealand *Cotula* species show considerable geographic variation which is maintained under glasshouse conditions. The subspecies category has been employed for major phenetic segments which are distinguishable from the remainder of a species and have their own distinct geographical area. The geographic variation patterns fall into two classes, species with more or less continuous distributions and those with clearly disjunct distributions.

In the widespread species occupying large areas continuously without a major geographic barrier, there is often complex geographic variation in which several characters vary simultaneously in discordant clinal patterns. Where the segments of such patterns merge into each other, they have not received any taxonomic recognition, even although the extremes are sometimes strikingly different, as in *C. dioica* Hook.f. subsp. *dioica*. For this reason *C. angustata* Simp. and the varieties of *C. dioica* have been dropped. Subspecies are, however, recognised in one continuously distributed species, *C. pectinata*, in which three formerly allopatric phenons have expanded their ranges and now meet along two narrow zones of contact.

The most difficult taxonomic decisions have been the choice of taxonomic level for morphologically distinguishable, geographically isolated entities. There is no natural test of the degree of reproductive isolation between such allopatric phenons, so a loose yardstick, the minimum difference between sympatric species, has been used to determine their status. If the allopatric phenons are more dissimilar than the most similar pairs of sympatric species (excluding cytological races), they have been designated separate species. Thus the two pairs of closely related species, *C. squalida* and *C. scariosa*, and *C. minor* and *C. filiformis*, have been upheld, and *C. rotundata* and *C. calcarea* are separated from *C. dioica* and *C. perpusilla* respectively.

Differences between allopatric phenons which are consistent but less than those between sympatric species have been given subspecific recog-

dition in five species. In borderline cases, where the differences between the allopatric phena were not clearly fewer or greater than those between the closest sympatric species, the least possible change in formal status has been made. In particular, the Southland plants customarily included in *C. traillii* with plants from Stewart Island have been retained in *C. traillii* as a subspecies, rather than shifted to *C. squalida* or to a new species.

When allopatric phena lack universally present diagnostic features, so that adequate specimens cannot always be identified as belonging to one or the other phenon, they have been denied any formal taxonomic status. Hence *C. pyrethriifolia* var. *robusta* Simp. and *C. renwickii* have been dropped as separate taxa.

THE DESCRIPTIONS

The descriptions and measurements are based on plants collected in nature. The terms used for leaf shapes are those adopted by the Systematics Association Committee for Descriptive Biological Terminology (Taxon 11: 145-56 and Chart 1, 1962). In species with toothed pinnae, the segments of the pinnae margins are referred to as the proximal (nearest the petiole), outer (farthest from the rhachis), and distal (farthest from the petiole) margins. Floret lengths were measured from the base of the ovary to the tip of the outstretched corolla lobes. The gametic chromosome numbers (n) are those of the author: Dr J. B. Hair supplied the somatic numbers quoted ($2n$).

The representative specimens quoted are not comprehensive, but have been selected from a number of herbaria to encompass the geographical area and morphological range of a taxon. The herbaria names are abbreviated as in the Index Herbariorum Part I (Regnum Vegetabile 31, 1964). The full distribution of all species is shown in the distribution maps, where a single locality is indicated by one symbol, regardless of the number of collections made there, and separate localities are indicated only if they are more than 5 km apart. Interspecific hybrids are not included in the lists of representative specimens or maps, except for *C. squalida* \times *C. dioica* hybrids, which merge into *C. dioica* and are included with it.

SUMMARY OF SECTION LEPTINELLA

Series OLIGOLEIMA. Habit various; seeds compressed, with broad margins. 5 Australian or New Guinea species.

Series ELONGATA. Rhizome internodes long, branches single; seeds not compressed, without broad margins.

- A. Rhizomes at soil surface; pinnae glabrous, teeth entirely around pinnae margins.
2. *potentillina*. Chatham and Auckland Is., n=26, monoecious.
 3. *membranacea*. North and northern South Is., n=26, monoecious.
- B. Rhizomes at soil surface; pinnae not densely hairy, teeth uncommon on proximal margins.
1. *scariosa*. South America, n not known, dioecious.
 4. *dispersa*. Campbell Is., local throughout N.Z., n=26, monoecious or dioecious.
 5. *rotundata*. North Auckland, n=ca. 156, monoecious.
 6. *dioica*. Stewart, North and South Is., n=ca. 130, monoecious or dioecious.
 7. *traillii*. Stewart Is. and Southland, n=ca. 156, dioecious.
 8. *squalida*. North, South, and Stewart Is., n=ca. 78, 104, and 130, dioecious.
- C. Rhizomes underground; pinnae often densely hairy, teeth uncommon on proximal margins.
9. *perpusilla*. Southern North and eastern South Is., n=52, dioecious.
 10. *serrulata*. Eastern South Is., n=26, dioecious.
 11. *calcareo*. N.W. Nelson, n=52, dioecious.
- D. Rhizomes underground; pinnae not densely hairy, teeth few.
12. *intermedia*. South Canterbury, n=ca. 78, monoecious.

Series **RADIATA**. Rhizome internodes often short, branches us. clustered; seeds not or slightly compressed, without broad margins.

- A. Lowland-montane; prostrate; leaves linear or with minute pinnae.
13. *maniototo*. Southern North and southern South Is., n=26, monoecious.
- B. Lowland-montane; prostrate; leaves 1-pinnatifid, sts toothed.
14. *nana*. Southern North and northern South Is., n=26, monoecious.
 15. *filiformis*. Marlborough and N. Canterbury, n=26, monoecious.
 16. *minor*. Banks Peninsula, n=26, monoecious.
- C. Montane-subalpine; rhizomes buried; leaves 2-3 pinnatifid.
17. *dendyi*. Marlborough and Canterbury, n not known, sub-dioecious.
 18. *atrata*. Marlborough to N. Otago, n=26, monoecious.

- D. Montane-subalpine; prostrate; leaves 1-pinnatifid or palmatifid.
19. *goyenii*. Otago, $n=26^*$, subdioecious.
 20. *albida*. Otago, $n=26$, monoecious.
 21. *pectinata*. South Is., $n=26, 52$, monoecious.
 22. *pyrethrifolia*. Wellington and northern South Is., $n=ca. 78$, monoecious or subdioecious.
- E. Coastal-lowland; prostrate; leaves 2-3 pinnatifid or 1-pinnatifid and toothed.
23. *lanata*. Auckland and Campbell Is., $n=26^*$, monoecious.
 24. *plumosa*. Subantarctic Is., $n=26^*$, monoecious.
- F. Coastal; suberect; leaves simple.
25. *featherstonii*. Chatham Is., n not known, monoecious.

TAXONOMY

SECTION **LEPTINELLA** (Cass.) Hook.f., Handbook N.Z. Flora: 140, 1864.

Leptinella Cassini, Bull. Sci. Soc. Phil. Paris, Series 3, v.9: 127, 1882 (as genus).

Perennial or rarely facultatively annual, prostrate or rarely suberect. Peduncle axillary, nude or with 1-several reduced bracts. Heads either bisexual with any proportion of pistillate and staminate florets or unisexual or both. Corolla of pistillate florets present, evident, tubular, conical to cylindric, sts compressed, persistent or deciduous, *ca.* as wide as ovary at anthesis, jointed with ovary, inflated with a hollow space between the outer surface and an inner layer closely surrounding the style. Disk florets seed-sterile, functionally staminate; ovary reduced but evident and demarcated from corolla; style apex an undivided, circular, slightly concave disc. Achene thick, not flat, convex on the dorsal surface at least, not winged but with an obvious or obscure margin, lacking blunt columnar uniseriate hairs on the dorsal and ventral surfaces, rarely with tapering uniseriate hairs on the margins. Chromosome number, $x=13$ ($n=26, 52$ and *ca.* 78, 104, 130 and 156).

TYPE SPECIES: *Cotula scariosa* (Cass.) Franchet.

Allan's (1961) description of subgenus *Leptinella* was not validly published, since there was no reference to an earlier description of *Leptinella*.

*Chromosomes counted only as the somatic number. The equivalent gametic number is given here for easy comparison—see species descriptions.

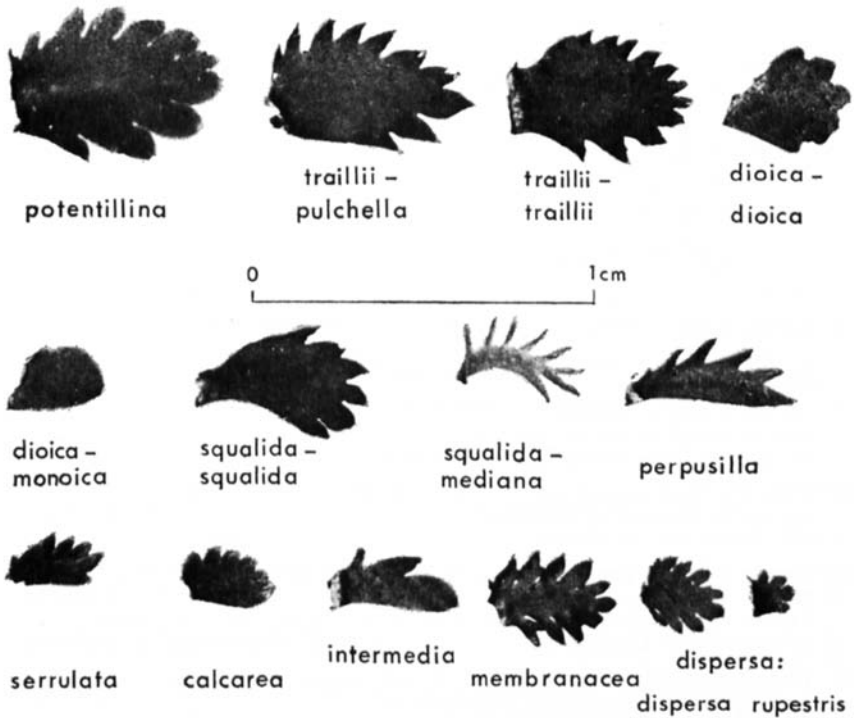


FIG. 3—Single pinnae from glasshouse-grown plants of taxa in series *Elongata*; Top row, from left, *C. potentillina*, *C. traillii* subsp. *pulchella*, *C. traillii* subsp. *traillii*, *C. dioica* subsp. *dioica*; middle row, *C. dioica* subsp. *monoica*, *C. squalida* subsp. *squalida*, *C. squalida* subsp. *mediana*, *C. perpusilla*; bottom row, *C. serrulata*, *C. calcarea*, *C. intermedia*, *C. membranacea*, *C. dispersa* subsp. *dispersa*, and *C. dispersa* subsp. *rupestris*.

KEY TO THE SPECIES

- 1. Leaves pinnately divided more than half way to the rhachis 2
 Leaves simple (any lobes cut less than half way to rhachis) or palmately divided 23
- 2. Leaves 1-pinnatifid (pinnae may have much narrower teeth) 3
 Leaves 2-3 pinnatifid (secondary and tertiary divisions hardly narrower than primary pinnae) 21
- 3. Pinnae small, ca. 1 mm long, linear 13. *C. maniototo*
 Pinnae larger, of lanceolate to orbicular order 4
- 4. Branches single. Rhizome leaves distant, even at apex. Short shoots obvious, with crowded leaves. Seeds plump 5
 Branches us. radiating from a cluster. Rhizome leaves several at apex, often remain crowded. Short shoots absent or reduced. Seeds slender 15

5. Rhizomes well buried, pale and wiry, with 0 or few leaves. Short shoots grow up from rhizome. Leaves us. hairy 6
 Rhizomes at or near soil surface, green to brown, bearing leaves. Short shoots grow out on both sides of rhizome. Leaves us. \pm glabrous 9
6. Leaves us. densely hairy. Pinnae close-set or overlapping, with many close, \pm oblong teeth 7
 Leaves glabrous to obviously hairy. Pinnae separated, with 0-many, more distant, triangular teeth 8
7. Leaves subfleshy, stiff, without brown pigment 11. *C. calcarea*
 Leaves not fleshy or stiff, us. with diffuse brown pigment on mature leaves 10. *C. serrulata*
8. Leaves almost glabrous to obviously hairy, membranous. Dioecious 9. *C. perpusilla*
 Leaves glabrous, \pm coriaceous. Monoecious 12. *C. intermedia*
9. Leaves \pm fleshy, glabrous, us. without brown pigment 10
 Leaves membranous or coriaceous (rarely fleshy on coastal cliffs), us. sparsely hairy and with brown pigment 12
10. Only proximal pinnae cut to rhachis, distal pinnae cut less far (cut almost to rhachis in Southland) 6. *C. dioica*
 All pinnae cut to rhachis 11
11. Leaves 2-12 cm long. Pinnae 6-15 pairs, with obvious teeth. Monoecious 2. *C. potentillina*
 Leaves us. less than 2 cm long. Pinnae 3-5 pairs, with 0 or inconspicuous teeth. Dioecious 4. *C. dispersa* (subsp. *rupestris*)
12. Plant small; rhizomes, peduncles slender. Leaves us. less than 2 cm long. Heads 1-3 mm diam., often bisexual 13
 Plant, rhizomes, peduncles stouter. Leaves us. more than 2 cm long. Heads 3-10 mm diam., unisexual 14
13. Pinnae broad to suborbicular. Teeth coarse, extended around margin on larger pinnae. Florets equal or exceed phyllaries 3. *C. membranacea*
 Pinnae us. narrower. Teeth smaller, predominantly on distal margin. Phyllaries exceed outer florets 4. *C. dispersa*
14. Leaves \pm coriaceous. Pinna teeth cut less than halfway across pinna, white-pointed. Coastal 7. *C. traillii*
 Leaves membranous. Pinna teeth cut *ca.* halfway across pinna, not white-pointed. Varied grasslands 8. *C. squalida**
15. Leaf bases, phyllaries and florets without dark veins. Reduced short shoots present at some nodes. Below 600 m alt. 16
 Leaf bases, phyllaries and often florets with 1-several dark veins. Short shoots absent. Us. above 1,000 m alt. 19
16. Rhizome with sparse short hairs. Pinnae not overlapping 17
 Rhizome covered with tangled woolly hairs. Pinnae overlapping 23. *C. lanata*
17. Plant minute. Rhizomes slender, up to 0.5 mm diam. Heads yellow-green, up to 2 mm diam. Leaves thin 14. *C. nana*
 Plant larger in all parts. Heads white. Leaves \pm thick 18

*The South American species, *C. scariosa*, would also key out here and is distinguished by the outer tooth on each pinna (i.e. that farthest from the rhachis) being larger than the others; in *C. squalida* all teeth are approximately equal in size.

18. Plant robust. Rhizomes up to 2 mm diam. Leaves 1-5 cm long. Teeth common, most on proximal pinnae. Heads 4-6 mm diam. 16. *C. minor*
 Plant smaller in all parts, rhizomes less than 1 mm diam. Leaves 0.5-2.0 cm long. Teeth rare. Heads 2-3 mm diam. 15. *C. filiformis*
19. Leaves thick, glabrous. Peduncles us. with several scattered bracts. Heads up to 1.8 cm diam., white, bisexual and/or unisexual 22. *C. pyrethrifolia*
 Leaves thinner, glabrous to densely hairy. Peduncles with 0 or 1 bract. Heads up to 1.0 cm diam., white or yellow-red, bisexual 20
20. Plant forming tight silver mats, covered with tangled hairs obscuring internodes and pinnae 20. *C. albida*
 Plant forming loose grey-green mats or patches, glabrous to densely hairy; some internodes and pinnae visible 21. *C. pectinata*
21. Rhizomes on ground surface. Leaves membranous, light green 24. *C. plumosa*
 Rhizomes buried under loose rocks. Leaves coriaceous, grey-green or purplish 22
22. Heads varying from all male to all female florets. Phyllaries exceed outer florets 17. *C. dendyi*
 All heads with many male and female florets. Phyllaries exceeded by outer florets 18. *C. atrata*
23. Leaves palmately divided 19. *C. goyenii*
 Leaves simple 24
24. Leaves linear 25
 Leaves of lanceolate to orbicular order 26
25. Leaves coriaceous. Heads 5-15 mm diam., on long peduncles 22. *C. pyrethrifolia* (var. *linearifolia*)
 Leaves membranous. Heads 2-3 mm diam., sessile 13. *C. maniototo*
26. Stems suberect. Teeth at leaf apex only 25. *C. featherstonii*
 Stems prostrate. Teeth not confined to apex of leaves 27
27. Leaves orbicular, sparsely hairy 5. *C. rotundata*
 Leaves narrower, glabrous 6. *C. dioica*

SERIES *ELONGATA* ser. nov.

Rhizomatis folia ad apicem singula; internoda consequenter maturans. Rami singuli. Achaenia curvata, non manifeste compressa, longitudine duplicatum latitudinem non aequantia.

Rhizome leaves single at apex, all distant; each internode elongates quickly behind the apex before the next appears. Branches single at flowering nodes. Short shoots develop at most nodes, carry all or most fully-developed leaves, with internodes which emerge from the sheath of the subtending rhizome leaf. Corolla of pistillate florets deciduous when fruit shed. Achenes curved, not markedly compressed, us. irregularly angled in cross-section from mutual pressure, length less than twice width, with inconspicuous margins.

TYPE SPECIES: *Cotula scariosa* (Cass.) Franchet.

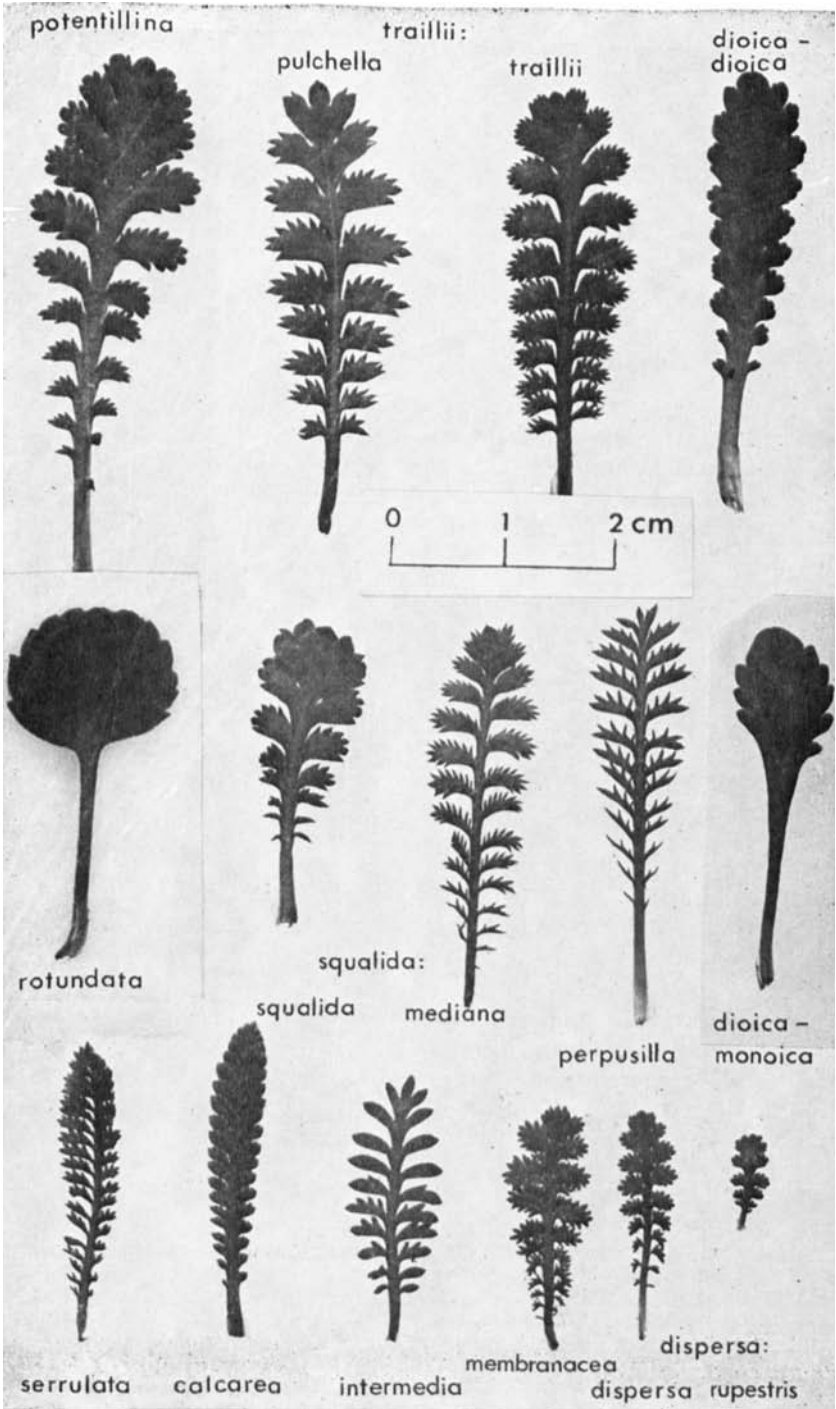
1. *Cotula scariosa* (Cass.) Franchet, Miss. Scientif. Cap.

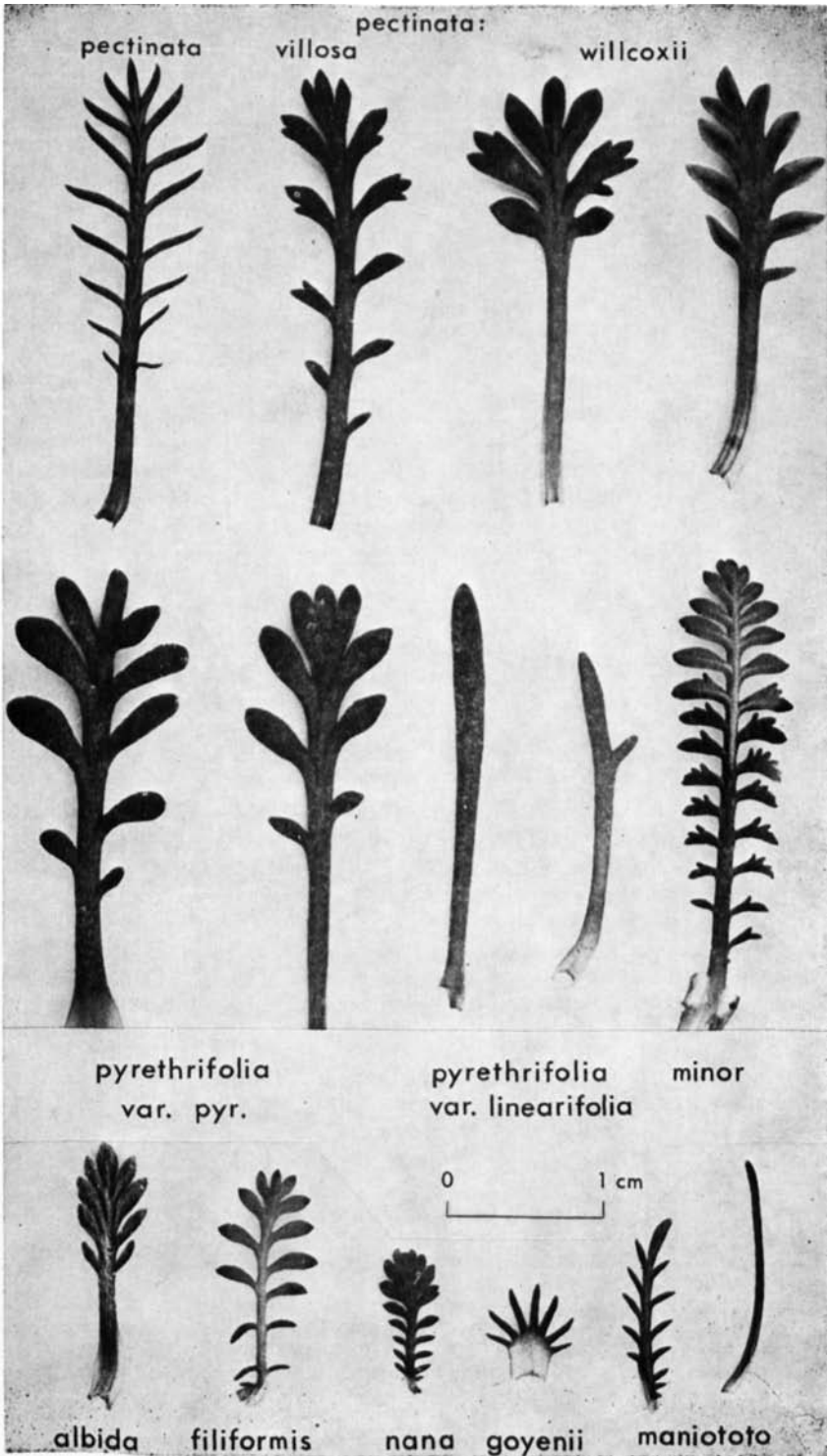
Horn 5: 344, 1889.

Leptinella scariosa Cassini, Bull. Sci. Soc. Phil. Paris 1822: 127.*Leptinella acaenoides* W. J. Hook. et Arn., W. J. Hook. Jour. Bot. 3: 325,1841. *Cotula acaenoides* (Hook. et Arn.) Alboff, Anal. Mus. La Plata Sec. Bot. 1: ix, 1902.*Cotula hombroni* Franchet, Miss. Scientif. Cap. Horn 5: 345, 1889.

A creeping perennial herb. Rhizomes at or near soil surface, green or dark, flexible and pilose when young, becoming pale, wiry and glabrous if buried, rather thick, 1.0–1.5 mm diam.; branches usually single at flowering nodes; leaves in two rows, single at apex, 0.5–2.0 cm apart. Short shoots alternate on both sides of rhizome, with 2–4 clustered or closely spaced leaves, sometimes converted into rhizomes with distant leaves. Roots rather thick and long, up to 1.0 mm diam. Leaves 1-pinnatifid, 1–5 × 0.3–1.0 cm; blade 0.5–3.0 cm long, elliptic to obovate, coriaceous, green, without brown pigment, sparsely pilose; midrib not raised on ventral surface; pinnae 6–12 pairs, equally spaced, distant or overlapping, cut to rhachis, elliptic; teeth on most or all pinnae, up to 10 per pinna, mostly on distal margin, cut *ca.* $\frac{1}{4}$ across pinna, even-sized except that outermost one is larger, triangular, obtuse, and apiculate. Peduncles borne on rhizomes or short shoots, us. longer than leaves, 1–6 cm, nude or with 1 simple bract, sparsely hairy. Dioecious. Pistillate heads 3–6 mm diam., up to 10 mm in fruit, surface convex; involucre urceolate; phyllaries 20–40 in 3 or more unequal rows, broadly elliptic, green, sparsely hairy with a broad red-brown scarious margin; inner phyllaries grow on to enclose subglobose fruiting head; florets 20 or more, *ca.* 1.75 mm long, curved, yellow-green, corolla slightly longer than wide, with unequal teeth. Staminate heads 4–8 mm diam.; involucre campanulate; phyllaries 5–10 in 1–2 subequal rows, not growing after anthesis; florets slightly more numerous. Achenes up to 1.6 × 0.9 mm, not or slightly compressed, almost round or irregularly angled from mutual pressure, with a pale unwrinkled papery surface turning brown and smooth. Flowers in spring and summer. Chromosome number not known. Fig. 13.

FIG. 4—Leaves from glasshouse-grown plants of New Zealand and Subantarctic taxa in series *Elongata*; Top row, from left, *C. potentillina*, *C. traillii* subsp. *pulchella*, *C. traillii* subsp. *traillii*, *C. dioica* subsp. *dioica*; middle row, *C. rotundata*, *C. squalida* subsp. *squalida*, *C. squalida* subsp. *mediana*, *C. perpusilla*, *C. dioica* subsp. *monoica*; bottom row, *C. serrulata*, *C. calcarea*, *C. intermedia*, *C. membranacea*, *C. dispersa* subsp. *dispersa*, *C. dispersa* subsp. *rupestris*.





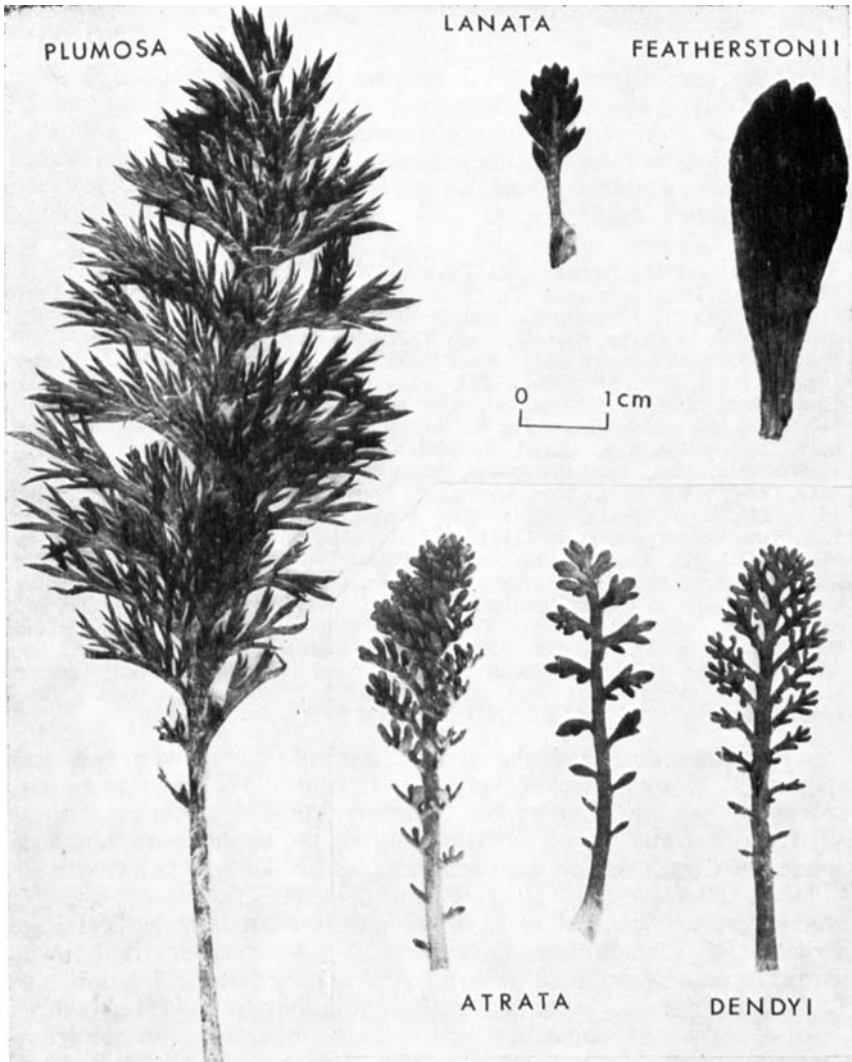


FIG. 6—Leaves of five species of series *Radiata*; top row, from left, *C. plumosa*, *C. lanata*, *C. featherstonii*; bottom row, *C. atrata* subsp. *atrata*, *C. atrata* subsp. *luteola*, *C. dendyi*.

FIG. 5—(left) Leaves from glasshouse-grown plants of taxa in series *Radiata*; Top row, from left, *C. pectinata* subsp. *pectinata*, *C. pectinata* subsp. *villosa*, *C. pectinata* subsp. *willcoxii* (two leaves); middle row, *C. pyrethrifolia* var. *pyrethrifolia* (two leaves), *C. pyrethrifolia* var. *linearifolia* (two leaves), *C. minor*; bottom row, *C. albida*, *C. filiformis*, *C. nana*, *C. goyenii*, *C. maniototo* (two leaves).

TYPE: See discussion below.

DISTRIBUTION: Chile; from the province of Valdivia to Cape Horn, common in diverse sites; stream and lake margins, swampy ground, clearings in *Nothofagus* forest, roadside, moist soil, and sea beaches are all mentioned on specimen labels. Argentina; Tierra del Fuego, Staten Island, Falkland Islands (and Nahuel Huapi National Park, Rio Negro; Cabrera, 1939). Fig. 7.

REPRESENTATIVE SPECIMENS: CHILE: VALDIVIA: S. José de la Mariquina, E. Wedermann 1172, F. Corral, H. Gunckel 3501, MO. Cordillera Pelada, Cerro Mirador, Ricardi, Marticorena and Matthei 1182, CONC. ORSONO: Summit Cordillera de la Carpa, Chilcon, Lago Todos los Santos, A. Pfister, CONC 10414. Ralum, A. Pfister, CONC 6014. Road from motel, Ensenada to Cochamo and Laguna Patos, J. L. Morrison 17574, MO. Puerto Montt, H. Koeppen 32, CONC. Huautrunes, Maullin, H. Gunckel, CONC 4035. CHILOE: Chepu, E. J. Godley 317, CHR. PIRUQUINA, Tramahué, C. Junge, MO 1022255. Cordillera San Pedro, E. J. Godley 496, CHR. CUCAO, E. Wedermann 293, F. Isla Talcán, C. Marticorena 1635, CONC. Islas Guaytecas, Melinka, M. Ricardi and C. Marticorena 4082, CONC. AYSÉN: C. Tres Montes, C. Darwin 483, K. Puyuhuapi, H. Behn, CONC 21252. MAGALLANES: Rio Bueno, A. Donat 355, NY. Ultima Esperanza, O. Magens, CONC 11511. Last Hope Inlet, Pen. Antonio Varas, Ynes Mexia 8005, NY. Estancia Rio de Los Palos, Isla Riesco, A. Pfister and M. Ricardi, CONC 11877. Punta Arenas, P. Dusén, MO 1617563. Straits of Magellan, Capt. Collinson, K. Caleta Josefina, Tierra del Fuego, Ricardi and Matthei 145, CONC. Puerto Williams, Navarino Island, E. J. Godley 1107, CHR. Hermite Island, Cape Horn, J. D. Hooker 55, K. Cape Horn, S.L., ex Dr. Beck, K. ARGENTINA: Tierra del Fuego: 80 km. inland from Rio Granda, Estancia la Esperanza, Ynes Mexia 7917, NY. Ushuaia, R. N. Luti 1652, CORD. (Staten Island), Dr Eights, K. FALKLAND IS.: West Falklands, E.V. 5, K.

When he described the genus *Leptinella* Cass. with two new species, *L. scariosa* and *L. pinnata*, Cassini (1822) had seen only specimens given to him by M. Godefroy from an unknown locality. W. J. Hooker and Arnott (1841) described the single South American species of *Cotula* section *Leptinella* as *L. acaenoides* Hook. et Arn. In "Flora Antarctica", J. D. Hooker (1844:28) "assumed" that *L. acaenoides* was identical to *L. scariosa*, and most later authors have accepted this identification. Cabrera (1939), however, reverted to the name *C. acaenoides* (Hook. et Arn.) Alb., stating that the description of *L. scariosa* "does not agree on the whole with the species in the southern parts of Argentina and Chile" (author's translation). The second of Cassini's species, *L. pinnata*, has never been equated with any later-described species.

Godefroy's specimens cannot now be traced at the Muséum National d'Histoire Naturelle, Paris (Professor J.-F. Leroy, pers. comm.) or at the Herbarium du Conservatoire, Geneva (Dr Claude Weber, pers. comm.). It is therefore necessary to attempt to identify Cassini's species from his descriptions. Despite Cabrera's statement quoted above, numerous characters in the description of *L. scariosa*, including prostrate stems, tufted short shoots, a single bract on the peduncle, pistillate heads, and female florets with an articulated inflated corolla, admirably describe the eight dioecious or partly dioecious species of *Cotula* series *Elongata*

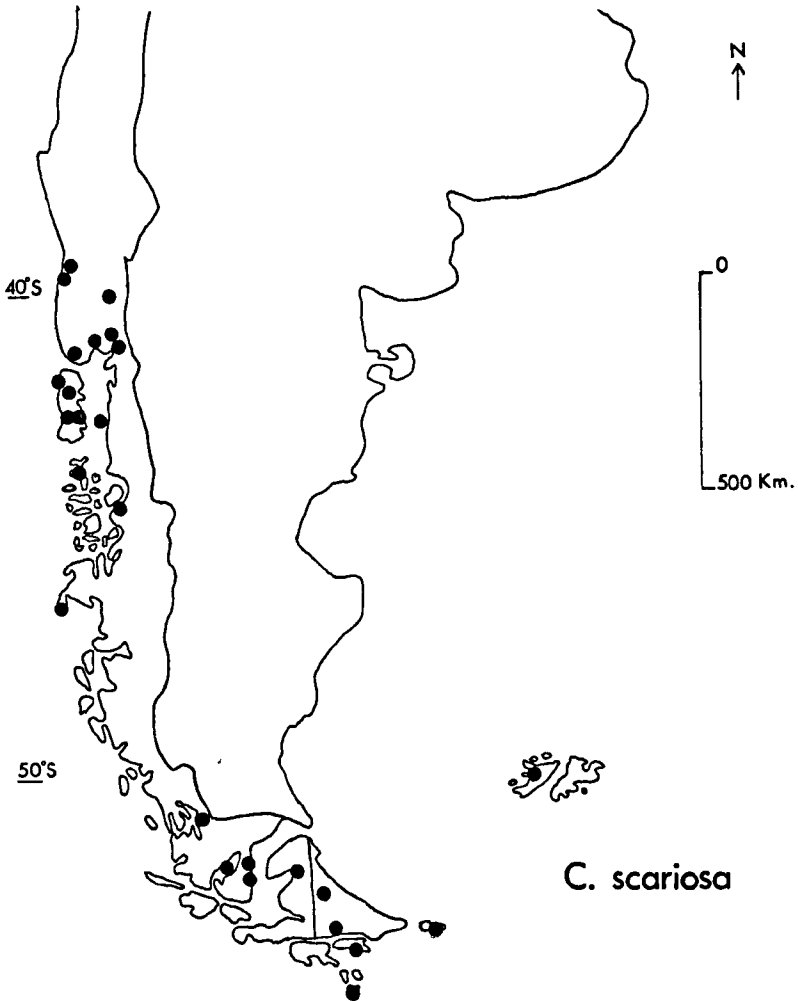


FIG. 7.—Distribution of *C. scariosa*. In this and subsequent maps, a collection is marked on the map only if it is from a point at least 5 km from all previous spots of the same taxon on the map.

and exclude all other possibilities. It is not possible to identify the species; on the grounds of their abundance over large areas in coastal and lowland sites, either the South American species or *C. squalida* would seem most likely. The identity of *L. pinnata* is less certain; if it is a *Cotula*, it is most likely to be one of the Australian species of section *Leptinella*.

The identity of *L. scariosa*, the type species of section *Leptinella*, cannot yet be finally settled. Godefroy's specimens could be re-

discovered in the future so it does not seem advisable to specify neotype material at this time. I have retained the name *C. scariosa* for the South American species, in accordance with most previous authors. This provisional solution causes the least nomenclatural disturbance at the moment. If the original specimens are located, this decision may be verified, or two species names may have to be changed.

Despite the considerable latitudinal distribution in South America (39°S to 55°S), *C. scariosa* appears, from herbarium specimens, to show no geographic variation throughout its range. The species most similar to *C. scariosa* is undoubtedly *C. squalida*; indeed it is difficult to find consistent differences between the two species. To separate them, one must resort to small and unusual details such as tooth distribution and shape. The leaves of *C. scariosa* are more coriaceous and have broader, less deeply cut teeth. In *C. scariosa*, the pinna tooth farthest from the rhachis is usually larger than the other teeth, whereas in *C. squalida* all teeth are similar in size. The specific differences are slight, but they are of a similar order to the differences between several other pairs of species in section *Leptinella*. *C. scariosa* is not closely related to the Australian species *C. reptans* Benth., as has been often stated, or to *C. mexicana* (DC.) Cabr. (section *Strongylosperma*), the only other native American species of *Cotula*.

C. scariosa is the only South American species of section *Leptinella*, which is otherwise confined to the Australian, New Zealand, and Subantarctic regions. The preponderance of species outside America, the geographic uniformity of *C. scariosa*, and the similarity between *C. squalida* and *C. scariosa* suggest that the ancestor of *C. scariosa* arrived from New Zealand by long-distance dispersal relatively recently. The wide Subantarctic distribution of *Leptinella* (Hooker 1852) is probably a secondary phenomenon of little phytogeographic significance.

2. *Cotula potentillina* (F. v. Muell.) Druce, Rep. Bot. Exch. Club Brit. Isles for 1916: 617, 1917.

Leptinella potentillina F. v. Muell., Veg. Chatham Is.: 28, plate 6, 1864.
Cotula muelleri Kirk, Stud. Fl. N.Z.: 324, 1899.

A diffusely creeping perennial herb. Rhizomes on soil surface, rather thick, pale, sparsely pilose; branches usually single at flowering nodes; leaves in two rows, single at apex, 0.5–4.0 cm apart. Short shoots alternate on both sides of the rhizome, with clustered leaves, sts converted into rhizomes with distant leaves. Roots slender and weak, up to 0.5 mm diam. Leaves 1-pinnatifid, 2–12 × 0.4–2.5 cm; blade 1–8 cm, obovate, subfleshy, yellow-green, without brown pigment, glabrous or almost so, midrib slightly raised on proximal part of ventral surface: pinnae 6–15 pairs, not overlapping, cut to rhachis or distalmost sinuses not quite reaching rhachis in larger leaves, elliptic; teeth on most pinnae, up to 12 per pinna, almost equally on distal and proximal

margins, cut *ca.* $\frac{1}{2}$ across pinna, triangular, obtuse or acute, occ. themselves with 1–2 teeth. Peduncles us. borne on rhizomes, us. longer than leaves, 2–7 cm, nude or with 1 simple bract, sparsely pilose. Monoecious. Heads 5–8 mm diam., surface hemispherical to steeply convex; involucre flat or spreading; phyllaries 15–30 in 2 or more subequal rows, elliptic to oblong, green, almost glabrous, with a narrow transparent scarious margin, not growing after anthesis; pistillate florets 60–200 in 4–6 rows, *ca.* 2.0 mm long, slightly curved, yellow-green; corolla slightly longer than wide, with unequal teeth; staminate florets more numerous. Achenes up to 1.5 × 0.8 mm, slightly compressed, almost round or irregularly angled, with a pale unwrinkled papery surface turning brown and smooth. Flowers in spring and summer. Chromosome number, $n=26$, $2n=52$. Figs. 1, 3, 4, 10.

LECTOTYPE: Chatham Islands, H. H. Travers, MEL 42211! Isotype at WELT (Herb. Petrie ex Herb. Mueller)!

DISTRIBUTION: Auckland and Chatham Islands, in wet, often saline conditions near the sea. Fig. 8.

REPRESENTATIVE SPECIMENS: CHATHAM ISLANDS: Awatotara Gorge mouth, collector unnamed, CHR 176558. Kaiara, J. F. Findlay, CHR 97215. Southeast Island, Brian Bell, CHR 159009. Near Lake Huro, B.G. Hamlin 657, 29 Jan. 1957, WELT. Near racecourse, L. Cockayne, Jan. 1901, WELT. AUCKLAND ISLANDS: Col. Bolton, 1850, K. Adams Island, I. G. Tennant, Nov. 1907, AK 10369. Ranui Cove, Ross Harbour, E. J. Godley, Jan. 1963, CHR 134220. Ranui Cove, B. A. Fineran, 1966, CANU 17066.

Cotula potentillina is a distinct species reaching a larger size than any other species in series *Elongata*. It is probably most closely related to *C. membranacea*. The two species share monoecy, outspread phyllaries, relatively large teeth extending entirely around the margin of pinnae, and a distribution not centred in the South Island.

The presence of *C. potentillina* in the Auckland Islands was not clearly recognised until Godley (1969) included it in a list of additions to the Auckland Islands flora. Godley suggested that it may have been accidentally introduced by a party of Chatham Island Maoris in the summer of 1842–43. J. D. Hooker, however, in 1840 collected a hybrid of *C. potentillina* × *C. plumosa* which is now in the Kew herbarium. The occurrence of *C. potentillina* on the Auckland Islands therefore predates the arrival of the Maoris and the species is presumably indigenous. Pure *C. potentillina* has been collected on the Auckland Islands on at least four subsequent occasions from 1850 to 1966 (see cited specimens). All collections have been from Ross Harbour (Godley, 1970, for information on Bolton's visit). The confusion arose from Hooker's description of the hybrid as *C. propinqua* Hook.f. in 1844 and his subsequent reduction of *C. propinqua* to a synonym of *C. lanata* (Hooker 1864: 142, erroneously citing Campbell Island as the locality).

The Chatham Islands plants are identical to those from the Auckland Islands in all respects.

3. *Cotula membranacea* nom. nov.

Soliva tenella Cunningham, *Annals Nat. Hist.* 2: 128, 1839, non *Cotula tenella* Meyer ex DC., *Prodr.* 6: 80, 1838.

A soft creeping perennial herb forming loose patches or part of a turf. Rhizomes at or near soil surface, green or dark, flexible, sparsely villous; branches usually single at flowering nodes; leaves in two rows, single at the apex, 0.5–2.0 cm apart. Short shoots alternate on both sides of the rhizome, with up to 6 clustered leaves, occ. converted into rhizomes with distant leaves. Roots numerous, slender, up to 0.4 mm diam. Leaves 1-pinnatifid, 1–4 × 0.4–1.5 cm; blade up to 3.5 cm long, obovate, membranous, bright green, often with the proximal pinnae especially covered with brown pigment, glabrous; midrib not raised on ventral surface; pinnae 6–10 pairs, not or scarcely overlapping, cut to rachis, broadly elliptic to suborbicular; teeth numerous, us. on all pinnae, up to 12 per pinna, extending completely around the margin or lacking on the proximal side, cut ca. $\frac{1}{3}$ across pinna, narrowly triangular to oblong, acute or mucronate, larger ones sts themselves with 1 or 2 teeth. Peduncles us. borne on rhizomes, ca. equal to leaves, 0.5–1.5 cm, nude or with 1 simple bract, sparsely pilose. Monoecious. Heads 2–6 mm diam.; surface convex; involucre upcurved to flat; phyllaries 8–12 in 2 subequal rows, broadly elliptic, green, glabrous, with broad red-brown scarious margins, not growing after anthesis; pistillate florets 20–45 in 2 or more rows, ca. 1.5 mm long, exceeding phyllaries, slightly curved, yellow-green; corolla slightly longer than wide, with almost equal teeth; staminate florets fewer, 10–15. Achenes up to 1.3 × 0.6 mm, slightly compressed, in section almost round or irregularly angled, with a pale unwrinkled papery surface turning brown and smooth. Flowers in spring. Chromosome number, $n=26$. Figs. 3, 4, 9.

LECTOTYPE: On the sides of fresh water streams generally in New Zealand, R. Cunningham 1834, $\kappa!$

DISTRIBUTION: North Island: North and South Auckland, and the west coast of Wellington. South Island: N.W. Nelson. A disjunct species, growing along the coast or inland at low altitudes, in wet low-lying conditions. Fig. 8.

REPRESENTATIVE SPECIMENS: AUCKLAND: Oruru Bay, Whatawhiwi Peninsula, H. Powell, CHR 78625. Mair Park, Whangarei, F. Duguid, CANU 16454. Near Port Fitzroy, Great Barrier Island, H. Carse and H. B. Matthews, Jan. 1919, CANTY (Carse Herb 1598/3). Awaroa Point, Little Barrier Island, L. B. Moore, CHR 59538. Kaihu, Northern Wairoa (River, Kaipara Harbour), T. F. Cheeseman, AK 10378. Waiau Creek, Manakau Harbour, H. Carse, WELTU 5142. Near mouth of Waikato River, H. Carse, AK 32051. Matata, Bay of Plenty, D. Petrie, March 1896, WELT. WELLINGTON: Near Hokio, W. of Levin, A. P. Druce, CHR 180510. Otaki Gorge Road, near Pukeatua Stream, F. Duguid, CANU 17226. Gollan's Valley, P. Stewart, CANU 17861. MARLBOROUGH: Keneperu, J. H. McMahon, April 1929, CANTY (Carse Herb. 1598/7). NELSON: Farewell Spit, M. J. A. Simpson, CHR 167551. Wharariki Beach, near Cape Farewell, M. J. A. Simpson, CHR 167670.

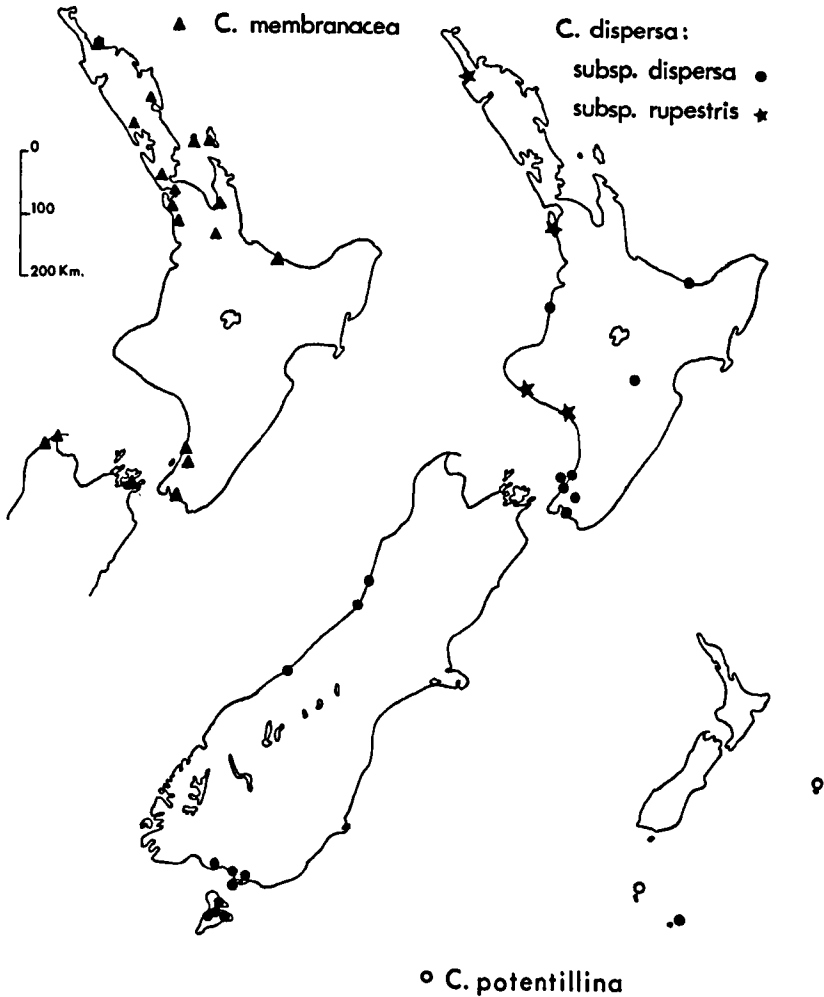


FIG. 8—Distribution of *C. potentillina*, *C. dispersa* and *C. membranacea*.

Soon after Cunningham described *Soliva tenella*, the basionym of *C. membranacea*, J. D. Hooker considered it a synonym of *C. dioica* (Hooker, 1852) and then of both *C. australis* and *C. dioica* (Hooker, 1864). Kirk (1899) considered *S. tenella* to be synonym of *C. minor* Hook.f. Since then *C. membranacea* has been one of the three species usually identified as *C. minor*. In this paper, the name *C. minor* is given to a fourth species. The epithet *tenella* has already been used in *Cotula*, so it is necessary to find a new name, *C. membranacea*, for Cunningham's species.

Cotula membranacea may be most closely related to the larger species *C. potentillina* (see under that species), but it is most difficult

to separate from *C. dispersa*. The most reliable diagnostic features of *C. membranacea* are the many obvious teeth running all around the margin of larger pinnae and the numerous female florets which are not obscured by the short phyllaries. In the Auckland area, *C. membranacea* is very distinct from *C. dispersa* subsp. *rupestris* in habitat and morphology and no hybrids are known. Farther south, there is a large gap in the distribution of *C. membranacea*. In Wellington *C. membranacea* is difficult to separate from *C. dispersa* subsp. *dispersa*, which is usually monoecious in that area; hybridisation may occur between the two species, which grow together in Gollan's Valley, at least.

4. *Cotula dispersa* sp. nov.

Planta parva vel nana. Folia 0.3–5.0 cm × 1–8 mm, membranacea vel carnosae; dentes plerumque limitati ad distales et exteriores margines pinnarum, triangulares. Monoica vel dioica. Capitula 1–3 mm diam., feminea capitula 4 mm ubi fructificantia. Flosculi 10–40.

A small or minute creeping perennial herb forming loose patches or part of a turf. Rhizomes at or near soil surface, slender, green or dark, flexible, sparsely villous; branches usually single at flowering nodes; leaves in two rows, single at the apex, 0.5–2.0 cm apart. Short shoots alternate on both sides of the rhizome, with up to 4 clustered leaves, occ. converted into rhizomes with distant leaves. Roots slender and weak, up to 0.3 mm. Leaves 1-pinnatifid, extremely variable in size and texture, 0.3–5.0 × 0.1–0.8 cm; blade 0.2–4.0 cm long, obovate, membranous (fleshy in some coastal situations), bright green, sts with brown pigment on proximal pinnae, ± glabrous, midrib not raised on ventral surface; pinnae 3–15 pairs, distant or distal ones slightly overlapping, cut to rhachis, elliptic or broadly so; teeth absent or 1–2 on larger pinnae or up to 10 on all pinnae, on distal and outer margins, sts extending partly onto proximal margin, small, cut ca. $\frac{1}{3}$ across pinna, triangular, acute to acuminate (obtuse and mucronate if fleshy). Peduncles us. borne on rhizomes, short but equal to leaves, 0.2–3.0 cm, nude, pilose. Dioecious or monoecious. Heads very small, 1–3 mm diam. (pistillate heads 4 mm in fruit); surface convex. Pistillate heads with urceolate involucre; phyllaries 8–22 in 2 or more unequal rows, broadly elliptic, green, almost glabrous, with a broad us. brown-tipped scarious margin; inner phyllaries grow on to enclose the subglobose fruiting head; florets 10–30, ca. 1.5 mm long, not exceeding phyllaries, curved, yellow-green, corolla slightly longer than wide, with unequal teeth. Staminate heads with hemispherical involucre; phyllaries 5–8 in 1–2 subequal rows, not growing after anthesis; florets slightly more numerous. Bisexual heads intermediate, with widely varying percentages of staminate and pistillate florets. Achenes up to 1.3–1.6 × 0.6–0.8 mm, slightly compressed, in section almost round or irregularly angled, with a pale unwrinkled papery surface turning brown and smooth. Flowers in spring. Chromosome number, $n=26$, $2n=52$. Figs. 3, 4, 9.

TYPE: Hollow in sand dunes, mouth of Mikonui River, Westland, 27 Jan. 1966, D. G. Lloyd 66074, CANU 17228.

DISTRIBUTION: North Island: throughout, but local; South Island: Westland, and the S. coast of Southland, locally abundant; Stewart Island: common; Campbell Island, known from one small area only. On estuaries and coastal cliffs, occ. inland on lake or river margins. Fig. 8.

KEY TO THE SUBSPECIES

Leaves up to 5 cm long, not fleshy. Pinnae 4–10 pairs, with obvious, narrow, acute teeth.4a. subsp. *dispersa*

Leaves up to 1.5 cm long, fleshy. Pinnae 3–5 pairs, with inconspicuous, broad, obtuse teeth4b. subsp. *rupestris*

4a. *Cotula dispersa* subsp. *dispersa*.

Leaves up to 3(–5) cm long, not fleshy; pinnae 4–10 pairs; teeth obvious, up to 10 per pinna, narrowly triangular or oblong, acute or acuminate. Peduncles 0.5–3.0 cm long. Monoecious or dioecious. Heads small, 2–3 mm diam. Chromosome number, $n=26$, $2n=52$. Figs. 3, 4, 9.

DISTRIBUTION: Gisborne to Southland, Stewart Island and Campbell Island. Local except in coastal Southland and Stewart Island. Usually coastal, in estuaries, wet depressions and cliffs, less often inland on river and lake margins.

REPRESENTATIVE SPECIMENS: GISBORNE: Morices Bay, 12 miles east of Opotiki, N. Potts, CHR 167336. HAWKE'S BAY: Taruarau River, Napier-Tāihape Road, D. G. Lloyd 67530, CANU. TARANAKI: 1½ miles south of Mohakitino River, Mokau, D. G. Lloyd 66366, CANU. WELLINGTON: South of Waikawa R. mouth, R. Mason, CHR 90885. Kapiti Island, N. end, A. P. Druce, CHR 6237. Western shore L. Wairarapa, D. G. Lloyd 67404, CANU. Gollan's Valley, P. Stewart, CANU 17857. WESTLAND: Taramakau R. mouth, D. G. Lloyd 65499, CANU. Ship's Creek, N. of Haast, D. G. Lloyd 67484, CANU. SOUTHLAND: Bluff Hill, G. Simpson, CHR 95252. STEWART ISLAND: Freshwater Inlet, G. Kelly, CANU 15558. CAMPBELL ISLAND: Above western cliffs, St. Col. Ridge, 300 feet, C. D. Meurk, CANU 13451.

4b. *Cotula dispersa* subsp. *rupestris* subsp. nov.

Folia usque ad 1 cm longa, carnosae. Pinnarum 3–5 paria. Dentes usque ad 5 per pinnam, inconspicui, ad apicem rotundati. Capitula perparva, 1–2 mm diam.

Leaves up to 1.5 cm long, fleshy; pinnae 3–5 pairs; teeth inconspicuous, up to 5 per pinna, broadly triangular, obtuse. Peduncles 0.2–0.5 cm long. Dioecious. Heads minute, 1–2 mm diam. Chromosome number not known. Figs. 3, 4, 9.

TYPE: Wet calcareous sandstone coastal cliffs, Castlecliff, Wanganui, A. Esler, April 1969, CANU 15541!

DISTRIBUTION: North Island; West Coast, N. Auckland to Wanganui, locally abundant beside streams, springs, and seepages on coastal cliffs.

REPRESENTATIVE SPECIMENS: NORTH AUCKLAND: Waihi, 20 miles north of Ahipara, T. F. Cheeseman, AK 10377. Kariotahi Gap, west of Waiuku, P. Hynes, CANU 15543. TARANAKI: Sea cliffs, Hawera, W. R. B. Oliver, WELT.

Although it is one of the three species previously confused under *C. minor* Hook.f., *C. dispersa* is not closely related to *C. minor* in the sense used herein. *C. dispersa* is a widespread but local species with extreme geographic variation. Most populations resemble a small version of *C. squalida*, probably its closest relative, but certain Wellington populations approach *C. membranacea* (see under that species). Most of the geographic variation is of a continuous nature, but plants on coastal cliffs from several North Island stations differ consistently in their small stature and fleshy leaves and are distinguished here as subsp. *rupestris*.

Sex expression is geographically variable. Subspecies *rupestris* and populations of subsp. *dispersa* from the Auckland Islands to South Westland and at Lake Wairarapa are dioecious. Westland and most North Island populations of subsp. *dispersa* are monoecious with varying proportions of male and female florets.

Occasional hybrids between *C. dioica* and *C. dispersa* subsp. *dispersa* have been observed. On the Wellington Coast some plants may be of hybrid origin between *C. membranacea* and *C. dispersa*. A number of *C. plumosa* × *C. dispersa* hybrids were collected by C. Meurk on Campbell Island. These are of special interest as one of the few known natural hybrids between species of series *Elongata* and series *Radiata*.

5. *Cotula rotundata* (Cheesem.) comb. nov.

Cotula dioica var. *rotundata* Cheeseman, Man. N.Z. Fl.: 359, 1906.

A creeping perennial herb forming a loose turf. Rhizomes on soil surface, rather slender, green or dark, flexible, sparsely villous; branches uncommon, usually single at flowering nodes; leaves in two rows, single at the apex, 1–3 cm apart. Short shoots alternate on both sides of the rhizome, with us. only 3 or 4 leaves but often converted into rhizomes with distant leaves. Roots slender and weak, up to 0.6 mm diam. Leaves simple, 1–5 × 0.5–1.5 cm; blade 0.5–1.5 cm long, suborbicular, membranous, yellow-green, without brown pigment, sparsely but evenly covered with long hairs, with a cuneate base and rounded apex, veins not evident on ventral surface, crenate; teeth 9–15 per pinna, around the distal $\frac{1}{2}$ – $\frac{2}{3}$ of blade, shallow, broadly triangular,

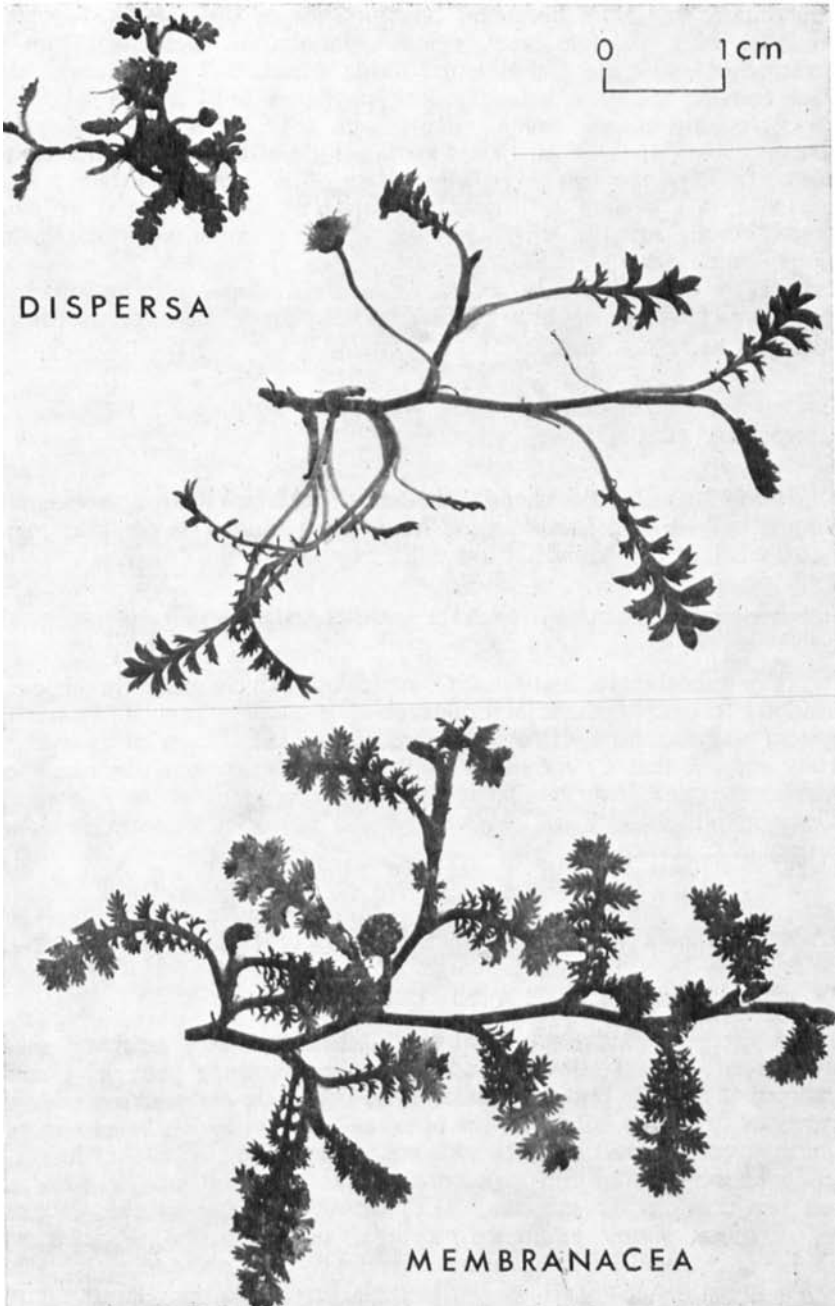


FIG. 9.—Plants of *C. dispersa* and *C. membranacea*. Top left, *C. dispersa* subsp. *rupestris*; middle, *C. dispersa* subsp. *dispersa* (from Stewart Island); bottom, *C. membranacea*.

mucronate. Peduncles borne on rhizomes, longer than leaves, 2–6 cm, nude or with 1 simple bract, villous. Monoecious, each plant with a mixture of staminate and bisexual heads. Heads 5–7 mm diam.; surface convex; involucre hemispherical; phyllaries 6–12 in 1–2 subequal rows, broadly elliptic, green, villous, with a broad, sts brown-tipped, scarious margin; inner phyllaries grow a little after anthesis to incompletely enclose the head; pistillate florets often 0, us. less than 5 but up to 12, in 1 incomplete row, ca. 2.0 mm long, slightly curved, yellow-green; corolla equal in length and width, with unequal teeth; staminate florets much more numerous, 40–90. Achenes up to 1.9×1.1 mm, not or slightly compressed, in section \pm round, with a pale unwrinkled papery surface turning brown and smooth. Flowers in summer. Chromosome number, $n = ca. 156$. Figs. 2, 4, 10.

LECTOTYPE (Allan, 1961): Cliffs, Waitakere West, Dec. 1880, T. F. Cheeseman, AK 10445!

DISTRIBUTION: North Island: the west coast of North Auckland, known only in two localities. At Maunganui Bluff it is confined to a narrow belt at the summit of low cliffs. Fig. 11.

REPRESENTATIVE SPECIMEN: NORTH AUCKLAND: Maunganui Bluff, J. Knight, AK 40179.

The suborbicular leaves of *C. rotundata*, which make the species instantly recognisable, the high chromosome number, peculiar breeding system and northern distribution are all unusual in series *Elongata*. They suggest that *C. rotundata* is a relic of an ancient phyletic line which separated long ago from the other species of series *Elongata*. There is no justification for the previous status of the species as a variety of *C. dioica*.

6. *Cotula dioica* (Hook.f.) Hook. f., Handb. N.Z. Fl.: 143, 1864.

Leptinella dioica Hook.f., Fl. N.Z. 1: 129, 1852.

A creeping, fleshy perennial herb. Rhizomes at or near soil surface, green or dark, flexible and \pm pilose, becoming pale, wiry and glabrous if buried; branches uncommon, us. single at flowering nodes; leaves in two rows, single at the apex, 0.3–3.0 cm apart. Short shoots alternate on both sides of the rhizome, with up to 5 clustered leaves, rarely converted into rhizomes with distant leaves. Roots us. slender and weak, up to 0.8 mm diam. Leaves very variable in size, shape, and divisions, simple to incised-pinnatifid, occ. pinnatifid, $0.7\text{--}12.0 \times 0.3\text{--}1.5$ cm; blade 0.5–7.0 cm, narrowly to broadly obovate or elliptic, fleshy, green, or glaucous, us. without dark pigment, \pm glabrous but dotted with sunken glandular hairs, midrib not raised on vertical surface, lobes (pinnae or teeth) 4–12 pairs, distant or the distal ones

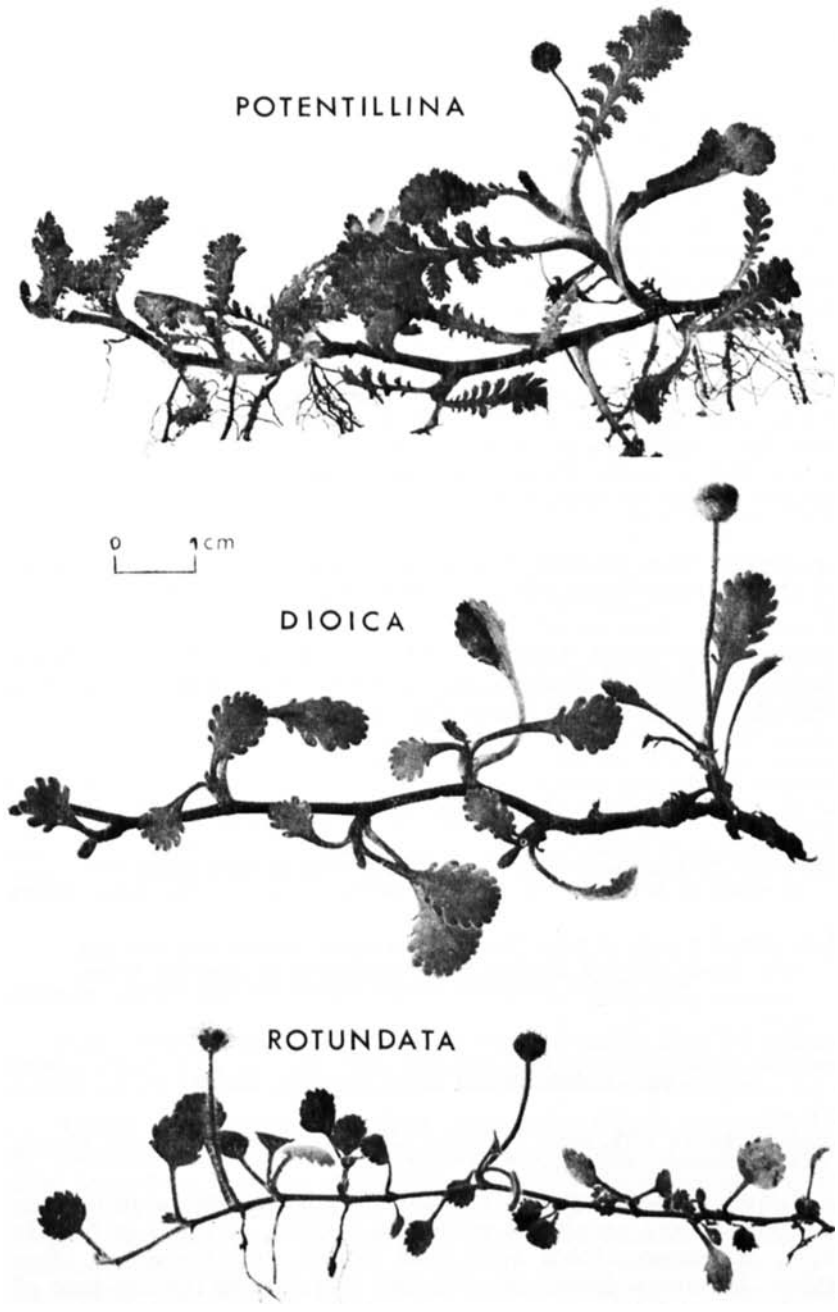


FIG. 10—Plants of *C. potentillina*, *C. dioica* subsp. *dioica* and *C. rotundata*.

overlapping, oblong to orbicular; proximal lobes cut to rhachis, sinuses of distal lobes usually not reaching rhachis, sts cut only 1/5 to rhachis at widest part of the leaf; teeth often absent but up to 6 per lobe, on the distal and outer margins, small, triangular, obtuse or rounded, apiculate. Peduncles us. borne on rhizomes, *ca.* equal to leaves, 1–6 cm, nude or with 1 simple bract, sparsely villous. Us. dioecious, occ. monoecious. Pistillate heads 2–7 mm diam., up to 10 mm in fruit; surface convex; involucre urceolate; phyllaries 10–30 in 3 or more unequal rows, broadly elliptic, green, glabrous, with a wide, often brown-tipped, scarious margin; inner phyllaries grow after anthesis to enclose subglobose fruiting head; florets 10–80, *ca.* 2–5 mm long, curved, yellow-green; corolla slightly longer than wide, with unequal teeth. Staminate heads 3–8 mm diam.; involucre hemispherical; phyllaries 5–10 in 1–2 subequal rows, not growing after anthesis; florets slightly more numerous. Bisexual heads predominantly staminate. Achenes up to 1.9 × 1.0 mm, slightly compressed, almost round or irregularly angled, with a pale unwrinkled papery surface turning brown and smooth. Flowers in spring and summer. Chromosome number, $n=ca.$ 130. Figs. 3, 4, 10.

LECTOTYPE: New Zealand, Colenso (no locality or date on specimen) K!, cited as Cape Turnagain by Hooker, 1852: 129.

DISTRIBUTION: North Island: from S. Auckland south, local. South Island: all districts, common on coast, less often inland from Marlborough to Otago. Stewart Island. Fig. 11.

KEY TO THE SUBSPECIES

Blade with 4–15 pairs of lobes. Lateral lobes often toothed, larger than or equal to terminal lobe. Heads unisexual 6a. subsp. *dioica*

Blade with 0–5 pairs of lobes. Lateral lobes entire, smaller than terminal lobe. Heads with 0–5 pistillate florets outside 10–30 staminate florets 6b. subsp. *monoica*

6a. *Cotula dioica* Hook.f. subsp. *dioica*

Cotula obscura Kirk, Stud. Fl. N.Z.: 327, 1899. *Cotula dioica* var. *obscura* (Kirk) Cheesem., Manual. N.Z. Fl.: 359, 1906.

Leaves incised-pinnatifid (pinnatifid from Dunedin south), often ± glaucous, very variable in shape and division, narrowly to broadly elliptic or obovate; lobes 4–12 pairs, oblong to suborbicular, often toothed; lowermost sinuses on each side extending to rhachis; base of most proximal lobes ± truncate; terminal lobe not distinctly wider (between sinuses) than lateral lobes. Dioecious, heads on one plant

either staminate or pistillate only; inner phyllaries of pistillate heads elongating after anthesis, enclosing fruit. Pollen grains with even spines and walls. Chromosome number, $n=ca. 130$. Figs. 3, 4, 10.

DISTRIBUTION: North Island: west coast of S. Auckland, Coromandel Peninsula, Wellington; not collected but perhaps present locally in intervening areas. South Island: estuaries throughout and inland in Marlborough, Canterbury, and the Otago Peninsula up to 1000 m, in boggy places. The northern populations are widely scattered, small, and largely confined to *Leptocarpus* marshes; the Wellington and especially the South Island coastal populations are abundant in a wide variety of estuarine habitats.

REPRESENTATIVE SPECIMENS: South AUCKLAND: Between Manukau and Waikato Heads, H. Carse, AK 10438, Thames Gold Field, T. Kirk 397, WELT. Raglan Harbour, Waitatuna R. mouth, D. G. Lloyd 7008, CANU. South end of Aotea Harbour, P. Hynes, AK 94171. WELLINGTON: East Wairarapa, Opouawe R. mouth, A. P. Druce, CHR 179461. MARLBOROUGH: Lagoon to north of Wairau R. mouth, R. Mason, CHR 88734. Raglan Range, opposite Red Hill, D. G. Lloyd 66105, CANU. Ure River, B. C. Aston, CHR 4070. Yeo Creek, Clarence Valley, H. A. Allan, CHR 95205. NELSON: Croiselles Harbour, Marlborough Sounds, D. G. Lloyd 67396, CANU. Rabbit Island, H. Talbot, CHR 127183. Ruataniwha Inlet, Golden Bay, D. G. Lloyd 67712, CANU. Wharariki, south of Farewell Spit, J. A. Petterson, CHR 77877. Karamea, G. Simpson, CHR 42175. Cape Foulwind, H. H. Allan, CHR 180151. WESTLAND: Taramakau R. mouth, D. G. Lloyd 66317, CANU. Commissioners' Bluff, between L. Windermere and Okarito, P. Wardle and I. R. Fryer, CHR 185707. Ships Creek, N. of Haast, D. G. Lloyd 67486, CANU. CANTERBURY: Boyle River, Lewis Pass, G. Simpson, CHR 95171. Waipara R., base of cliffs, W. R. B. Oliver, 21 Nov. 1909, WELT. Porter's Pass, H. H. Allan, CHR 42170. Akaroa, T. Kirk 397, CANTY. South east of Hinds R., R. Mason, CHR 169035. OTAGO: Duntroon, Waitaki R., G. Simpson, CHR 95204. Moeraki Point, G. I. Collett, CHR 168590. Lawyer's Head, west of Dunedin, G. Simpson, CHR 95174. Catlins R. estuary, D. G. Lloyd 66130, CANU. SOUTHLAND: Woodend, T. Kirk, AK 10433. Te Wae Wae Bay, D. G. Lloyd 66138, CANU. Dog Island, Foveaux Strait, G. I. Collett, CHR 148519. STEWART ISLAND: Mill Creek estuary, near Oban, D. G. Lloyd 6734, CANU.

6b. *Cotula dioica* subsp. *monoica* subsp. nov.

Folia interdum integra sed plerumque incisa-pinnatifida cum 1-5 triangularibus, integris lobis utrimque; loba terminalis lobis lateralibus maior. Monoica; capitula cum 0-5 femineis flosculis 10-30 masculos flosculos cingentibus.

Leaves yellow-green, rhomboid, obovate or elliptic, sts entire but us. incised-pinnatifid with 1-5 triangular entire lobes or teeth on each side; lowermost sinus on each side not usually extending to rhachis; base of blade cuneate; terminal lobe distinctly wider than lateral lobes. Monoecious; heads on each plant a mixture of staminate heads and bisexual heads with us. 1 or 2 but sts up to 5 pistillate florets in 1 incomplete row surrounding 10-30 staminate florets. Pollen grains functional but with walls irregular in thickness and spines lacking or underdeveloped. Chromosome number not known. Figs. 3, 4.

TYPE: Estuary, mouth of Makara River, Wellington, 30 July 1966, D. G. Lloyd 66240, CANU 17223.

DISTRIBUTION: North Island: the west coast of Wellington, in estuaries.

REPRESENTATIVE SPECIMENS: WELLINGTON: Hokio Beach, Levin, F. Duguid, CANU 15781. Waikanae estuary A. P. Druce, CHR 179550. *C. dioica* subsp. *dioica* × *C. dioica* subsp. *monoica*: S.E. side of Paremata Harbour, D. G. Lloyd 68063, CANU.

The closest relative of *C. dioica* is *C. squalida*. The differences between the two species vary throughout New Zealand. In the South Island, the fleshy incised-pinnatifid leaves of *C. dioica* are readily distinguished from those of *C. squalida* subsp. *mediana*, which are never fleshy and in which the sinuses between all pinnae are incised equally to the midrib. In the North Island, however, the distal sinuses of leaves of *C. squalida* subsp. *squalida* are not incised as far as the proximal sinuses and the leaves are sometimes fleshy, just as in *C. dioica*. There the best distinguishing features between the species are:

1. The relative distance between pinnae. In *C. squalida* subsp. *squalida* this is greater in the middle of the leaf than above and below. In *C. dioica*, the distance between pinnae is constant along the length of the leaf or increases slightly towards the base.
2. The basal sinuses of the leaves. In *C. squalida* subsp. *squalida* the basal sinuses reach to the midrib. In the North Island populations of *C. dioica*, none of the sinuses reach quite to the midrib.

It is thus possible to discriminate between pure plants of the two species throughout the country. Unfortunately hybrid plants are common from Kawhia to Canterbury and Westland, as either heterogeneous hybrid swarms or more uniform stabilised hybrid segregates. Back-crossing seems to be more frequent to *C. dioica* than to *C. squalida*. The limits of *C. squalida* are usually clear, but *C. dioica* often merges into the hybrids. Consequently the list and map (Fig. 11) of *C. dioica* specimens do not attempt to separate "pure" *C. dioica* plants and localities from those of hybrids with *C. squalida*. Occasionally hybrids are also found between *C. dioica* and *C. dispersa*, *C. perpusilla* or *C. calcarea*.

Another source of difficulty is provided by geographic variation, which is more obvious and complex in *C. dioica* than in any other species. In an attempt to describe the diversity, especially of leaf form, Allan (1961) recognised four varieties described by earlier authors. Two of these, *C. dioica* var. *pulchella* (Kirk) Cheesem. and *C. dioica* var. *rotundata* Cheesem. do not belong to *C. dioica* (see *C. traillii* and *C. rotundata* respectively). The other two varieties, *C. dioica* var. *obscura* (Kirk) Cheesem. and *C. dioica* var. *crenatifolia* Kirk, are arbitrary segments of a complex clinal variation pattern.

- *C. rotundata*
- *C. dioica* subsp. *dioica*
- ▲ *C. dioica* subsp. *monoica*
- ★ subsp. *monoica* × subsp. *dioica*

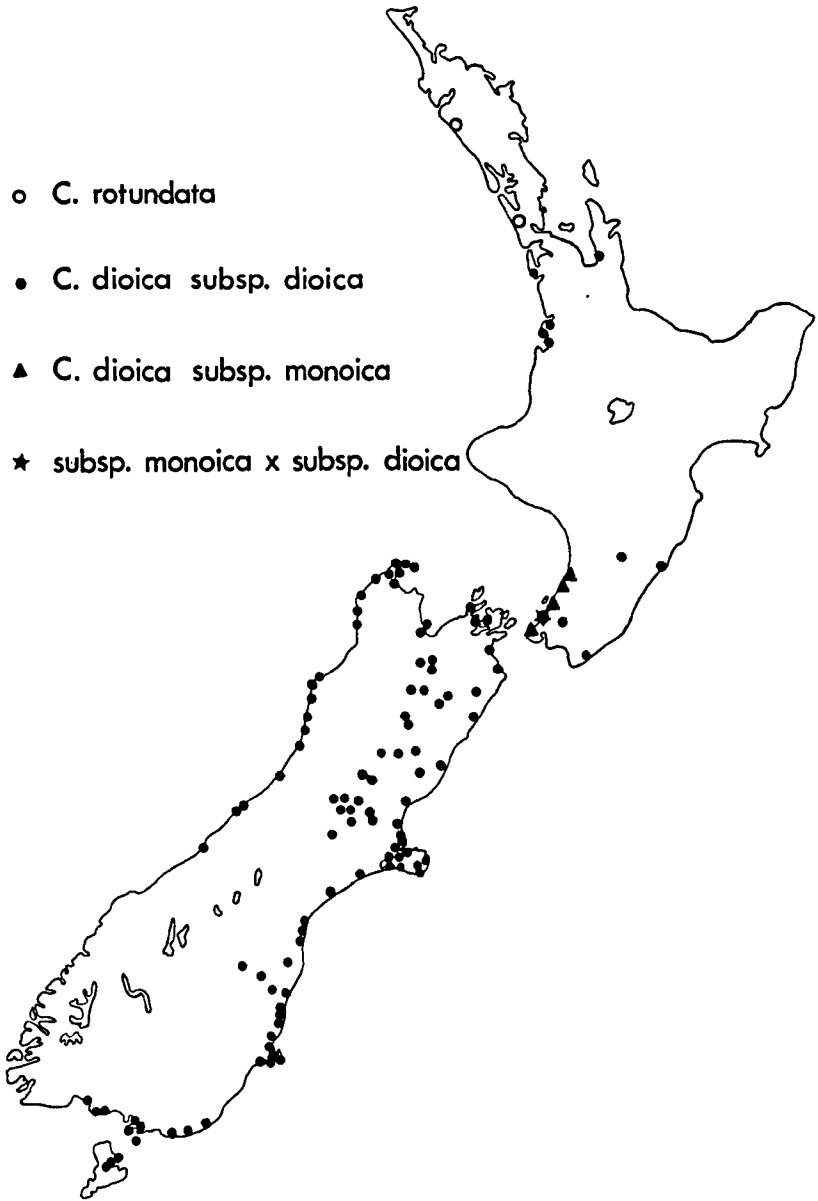


FIG. 11—Distribution of *C. rotundata* and *C. dioica* (including *C. dioica* × *C. squalida* hybrids).

Although the extremes of this continuous variation are spectacularly different, especially in leaf size and shape, they are linked by a series of intermediate populations. Hence they do not merit formal taxonomic status and will be described elsewhere.

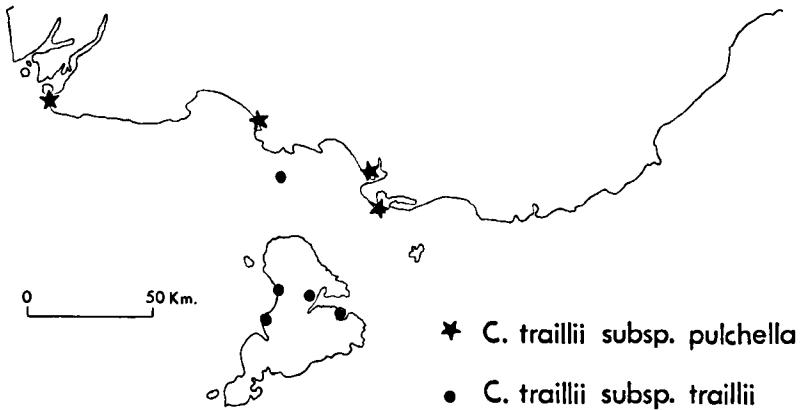
Most of the populations on the west coast of Wellington share several leaf and reproductive characters which set them apart from the diversity of forms elsewhere in New Zealand. They are separated above as subspecies *monoica*. Plants from the Paremata Harbour appear to be hybrids between the two subspecies.

Cotula dioica is widely used, usually under the name *C. pulchella*, in "weed" bowling greens, especially in the South Island. Plants have been introduced onto greens on a number of occasions since 1913 from natural populations, usually from Otago and Southland estuaries but occasionally from elsewhere (Miller and Martin, 1953). Now, after much transfer of plants between greens and intercrossing of the various populations, the cultivated material is very heterogeneous.

The epithet *dioica* was first used in *Cotula* in Banks and Solander's unpublished manuscript to describe a specimen from near Opuragi, Coromandel Peninsula. The description and accompanying plate match a specimen, AK 128751, of *C. squalida* subsp. *squalida* collected by Banks at Opuragi. When Hooker published the name *Leptinella dioica*, he quoted Banks and Solander's name, but not Banks' specimen. Consequently, the epithet *dioica* applies to the species customarily known as *C. dioica* and not to Banks and Solander's plant, now in *C. squalida*.

7. *Cotula traillii* Kirk, Stud. Fl. N.Z.: 324, 1899.

A creeping perennial herb forming a loosely matted turf. Rhizomes at or near soil surface, green or dark, flexible, villous; branches uncommon, us. single at flowering nodes; leaves in two rows, single at apex, 0.5–2.0 cm apart. Short shoots alternate on both sides of rhizome, with up to 6 clustered leaves, rarely converted into rhizomes with distant leaves. Roots slender and weak, up to 0.6 mm diam. Leaves 1-pinnatifid, 1–5 × 0.4–1.0 cm; blade 1–4 cm, obovate, ± coriaceous, dark green usually with brown pigment over proximal or all pinnae, sparsely villous; midrib slightly raised on proximal part of ventral surface; pinnae 4–10 pairs, equidistant, not overlapping, cut to rhachis, oblong to orbicular; teeth few or up to 10 per pinna, confined to outer margin or extending around distal margin as well, cut $\frac{1}{4}$ – $\frac{1}{2}$ across pinna, triangular, acuminate with a sharp pale sts deciduous point ± obscured by a tuft of parallel hairs. Peduncles us. borne on rhizomes, *ca.* equal to leaves, 1–4 cm, nude or with one simple bract, pilose. Dioecious. Pistillate heads 3–5 mm diam., up to 10 mm in fruit; surface convex; involucre urceolate; phyllaries 15–20 in *ca.* 3 unequal rows, broadly elliptic, green, without evident veins, ± villous, with a

FIG. 12—Distribution of *C. traillii*.

broad transparent brown-tipped scarious margin; inner phyllaries grow after anthesis to enclose the subglobose fruiting head; florets 20–70, *ca.* 2–5 mm long, curved, yellow-green; corolla slightly longer than wide, with unequal teeth. Staminate heads 4–6 mm diam., involucre hemispherical; phyllaries 5–10 in 1–2 subequal rows, not growing after anthesis; florets slightly more numerous. Achenes up to 1.9×1.0 mm, slightly compressed, in cross-section almost round or irregularly angled, with a pale unwrinkled papery surface turning brown and smooth. Flowers predominantly in spring. Chromosome number $n = ca.$ 156. Figs. 3, 4, 13.

LECTOTYPE (Allan, 1961): Stewart Island, T. Kirk (no date), WELT (Herb. Petrie)!

DISTRIBUTION: South Island, south coast; Stewart Island, coastal rocks. Fig. 12.

KEY TO THE SUBSPECIES

Leaves coriaceous, thick; teeth, small, closely-spaced ... 7a. subsp. *traillii*

Leaves less coriaceous, thin; teeth, coarser, more distant ... 7b. subsp. *pulchella*

7a. *Cotula traillii* Kirk subsp. *traillii*.

Leaves coriaceous, thick, dotted with glands, dark green, with brown pigment on all or only proximal pinnae; pinnae broadly obovate to suborbicular, width almost or *ca.* equal to length, with up to 12 small, closely-spaced, narrowly triangular teeth on distal and outer margins. Chromosome number, $n = ca.$ 156. Figs. 3, 4.

DISTRIBUTION: Stewart Island and adjacent islets.

REPRESENTATIVE SPECIMENS: STEWART ISLAND: The Neck, G. Simpson, CHR 95167. Freshwater River, G. Simpson, CHR 95178. Mason Head, M. Noonan, CANU 17060. Kilbride, M. Noonan, CANU 17062. CENTRE ISLAND: G. Collett, CHR 148709.

7b. *Cotula traillii* subsp. *pulchella* (Kirk) comb. nov.

Cotula pulchella Kirk, Student's Flora N.Z.: 328, 1899, pro parte. *Cotula dioica* var. *pulchella* (Kirk) Cheeseman, Man. N.Z. Flora: 359, 1906, pro parte.

Leaves less coriaceous, thinner and not us. dotted with glands, lighter green, with brown pigment only on proximal pinnae; pinnae oblong to broadly ovate, width less than length, with up to 4 (rarely to 10) more distant broadly triangular teeth confined to the outer margin or occ. extending onto distal margin. Chromosome number not known. Figs. 3, 4, 13.

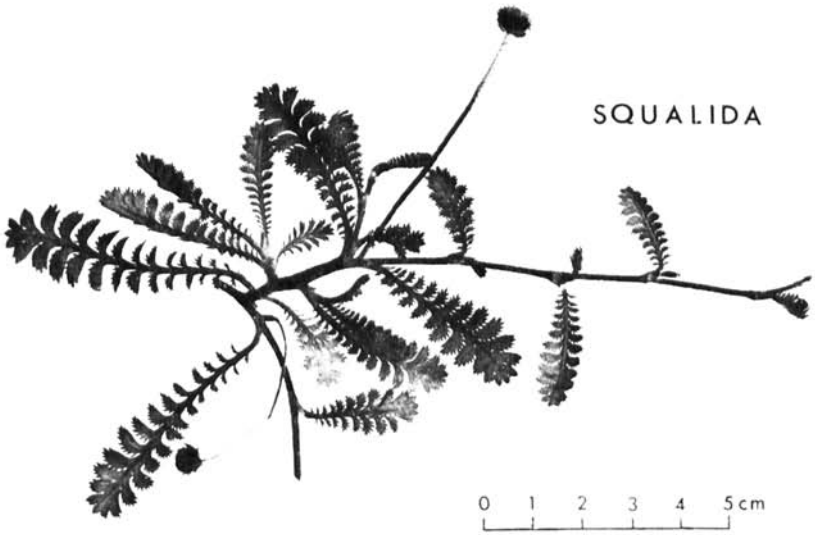
LECTOTYPE: Near Pilot Station, New River Head, Southland, T. Kirk, 12 Feb. 1890, WELT!

DISTRIBUTION: South Island: the south coast of Southland.

REPRESENTATIVE SPECIMENS: SOUTHLAND: Bluff Hill, Invercargill, L. M. Cranwell, CHR 27515. Stirling Point, Bluff, D. G. Lloyd 66133, CANU. Monkey Island Beach, Te Wae Wae Bay, D. G. Lloyd 66139, CANU. Puysegur Point, G. Collett, CHR 148050.

The dark, coriaceous but villous leaves and the many-toothed suborbicular pinnae of Stewart Island plants (subsp. *traillii*) enable them to be readily distinguished from Southland plants and all other species. Southland plants are intermediate between *C. traillii* subsp. *traillii* and *C. squalida* subsp. *mediana* and could be put in either species almost equally well on their morphology. They have been retained in their previous position in *C. traillii* and named as subspecies *pulchella* because they resemble subsp. *traillii* in their coastal habitat and occurrence within the area of *C. squalida*. Apparently both subspecies of *C. traillii* are reproductively isolated from *C. squalida*.

In Kirk's description of *C. pulchella* four different localities are cited. Specimens collected from these localities prior to 1899 and identified by Kirk as *C. pulchella* are now in several herbaria, particularly those of the Auckland and Dominion Museums. They represent three elements: *C. traillii* (from Southland only), *C. dispersa* subsp. *dispersa*, and *C. dioica* × *C. squalida*. Most of the collections are of Southland plants here included in *C. traillii* and the description fits these better than the other two elements. So the epithet *pulchella* is restricted here to Southland plants of *C. traillii* in the new combination *C. traillii* subsp. *pulchella*.



SQUALIDA



TRILLII



SCARIOSA

FIG. 13—Plants of *C. squalida* subsp. *mediana*, *C. trillii* subsp. *pulchella* and *C. scariosa*.

8. *Cotula squalida* (Hook.f.) Hook.f., Handb. N.Z. Fl.; 143, 1864.

Leptinella squalida Hook.f. Fl. N.Z. 1: 129, 1852.

A creeping, rapid-growing perennial herb, us. intermingled with other species in a turf, sts in patches colonising sand. Rhizomes at or near soil surface, green or dark, flexible, pilose, becoming pale, wiry and glabrous if buried; branches us. single at flowering nodes; leaves in two rows, single at the apex, 0.5–3.0 cm apart. Short shoots alternate on both sides of the rhizome, with 3–8 clustered leaves, under favourable conditions converted into rhizomes with distant leaves. Roots slender and weak, up to 0.8 mm diam. Leaves 1-pinnatifid, 0.5–10.0 × 0.3–2.0 cm; blade; 0.4–6.0 cm, elliptic or obovate, membranous (fleshy on coastal cliffs), bright green and often with brown pigment especially on proximal pinnae, us. sparsely pilose but glabrous to moderately pilose, midrib raised along most of ventral surface; pinnae 6–20 pairs, oblong to elliptic, often falcate, either all equidistant, not overlapping and cut to rhachis or (in subsp. *squalida*) distal pinnae closer and overlapping and not quite cut to rhachis; teeth us. present on larger pinnae at least, up to 10 per pinna, on distal margins, cut $\frac{1}{3}$ – $\frac{2}{3}$ across pinna, oblong, acute or acuminate. Peduncles us. borne on rhizomes, longer than leaves, 1–6 cm, nude or with 1 simple bract, sparsely pilose. Dioecious. Pistillate heads 3–5 mm, ca. 10 mm in fruit; surface convex; involucre urceolate; phyllaries 15–40 in 3 or more subequal rows, broadly elliptic, green, ± villous, with a broad brown-tipped scarios margin; inner phyllaries grow after anthesis to enclose subglobose fruiting head; florets 15–70, ca. 2.25 mm long, curved, yellow-green; corolla slightly longer than wide, with unequal teeth. Staminate heads 4–7 mm diam.; involucre hemispherical; phyllaries 5–10 in 1–2 rows, not growing after anthesis; florets slightly more numerous. Achenes up to 1.9 × 0.9 mm, slightly compressed, in section almost round or irregularly angled, with a pale unwrinkled papery surface turning brown and smooth. Flowers in spring and summer. Chromosome numbers, $n=ca.$ 78, 104 and 130, $2n=156$. Figs. 1, 2, 3, 4, 13.

LECTOTYPE: (Hawke's Bay), New Zealand, W. Colenso 4250, κ!

DISTRIBUTION: North and South Islands, Stewart Island, Chatham Island, common in wet places. Fig. 14.

KEY TO THE SUBSPECIES

Distal pinnae not cut entirely to rhachis, closer together and at a narrower angle to the rhachis than middle pinnae ... 8a. subsp. *squalida*

All pinnae cut to rhachis, equidistant and at a wide angle to the rhachis ... 8b. subsp. *mediana*

8a. *Cotula squalida* Hook.f. subsp. *squalida*.

Leaves membranous or fleshy; larger pinnae suborbicular to obovate, often *ca.* equal in length and width; distal pinnae not cut to rhachis, closer together and at a narrower angle to the rhachis than the middle pinnae and often overlapping; middle and proximal pinnae cut to rhachis, distant. Chromosome number, $n=130$. Figs. 3, 4.

DISTRIBUTION: North Island: south from Great Barrier Island and near Auckland, on coastal cliffs and inland on stony river-beds and montane grasslands, sea level to 1500 m, scattered but locally common; Chatham Islands: collected only once (recently), but indigenous as it differs from all North and South Island collections.

REPRESENTATIVE SPECIMENS: NORTH AUCKLAND: Tryphena Bay, Great Barrier Island, T. Kirk, 11 Dec. 1867, WELT. Nihotupu, Ball, Jan. 1886, AKU. Kennedy Bay, Coromandel, H. B. Matthews, AK 3206Z. Between Waikato and Manukau Heads, H. Carse, CANTY (Carse Herb. 1608/4). SOUTH AUCKLAND: Raglan township, D. Petrie, 1902, WELT. TARANAKI: 3 miles S. of Mokau, D. G. Lloyd 66365, CANU. Otakeho, South Taranaki, W. D. Burke, WELTU 8288. Mt Egmont, D. Petrie, CHR 68203. GISBORNE: Omaio, East of Opotiki, H. H. Allan, CHR 42172. Bank of Tapuaeroa R., East Cape, B. Sneddon, WELT 5159. Hangaroa R., A. P. Druce, CANU 15703. HAWKE'S BAY: Moeangiangi R., W. Colenso 4304, K. WELLINGTON: Rangitikei R., Kaimanawa Flats, A. P. Druce CHR 116325. Mangahua Stream, Tongariro National Park, I. A. E. Atkinson, CHR 151130. Waiohine-iti R., Tararua Mts, V. D. Zotov, CHR 4367. Owhiro Bay, South coast, D. G. Lloyd 67805, CANU. CHATHAM ISLANDS: North coast, Chatham Island, G. Kelly, CANU 15704.

8b. *Cotula squalida* subsp. *mediana* subsp. nov.

Pinnae oblongae vel ellipticae, quasi aequidistantes per laminam, sinus omnes ad rhachim incisi.

Leaves membranous; pinnae oblong or elliptic, length greater than width, all equidistant along the blade, at a wide angle to the blade and cut to the rhachis. Chromosome numbers, $n=ca.$ 78, 104, and 130, $2n=156$. Figs. 1, 2, 3, 4, 13.

TYPE: Riverbed, Waitaha River, Westland, 27 Jan. 1966, D. G. Lloyd 66078, CANU 17222.

DISTRIBUTION: South Island: from N.W. Nelson and inland Marlborough to Fiordland, sea level to 2000 m; Stewart Island. West of the main divide, it is ubiquitous in low tussock grasslands, on river-beds, and above tree line. East of the main divide it is moderately common

in wetter places, especially at higher altitudes north of Christchurch; farther south, it becomes progressively restricted to more western stations.

REPRESENTATIVE SPECIMENS: NELSON: Takaka-Totaranui track, M. T. Kalin, CANU. Dun Mt, G. O. K. Sainsbury, CANTY (Carse Herb. 1608/2). Hope Saddle J. Williman CANU 15632. Brunner Range, W. Townson, AK 10425. MARLBOROUGH: Raglan Ra., opposite Red Hill, D. G. Lloyd 66106, CANU. Mt Tapuaenuku, G. Simpson, CHR 68445. WESTLAND: Taramakau R. mouth, D. G. Lloyd 66319, CANU. Franz Joseph Glacier, H. H. Allan, CHR 3968, Haast R., Mt Aspiring N. P., A. F. Mark, OTA 21650. CANTERBURY: Upper Hurunui R., A. Wall, Oct. 1917, CANTY. Near Christchurch, R. M. Laing, CANU 4646. OTAGO: Upper Lake Hawea, D. Petrie, CHR 68204. Harris saddle (Routeburn-Hollyford Pass), M. Noonan, CANU 15689. Supper Cove, Dusky Sound, M. J. A. Simpson CHR 122130. STEWART ISLAND: Mt Anglem, A. F. Mark, OTA 7925.

Cotula squalida is easily the most common species in New Zealand, especially in the South Island. Morphologically it occupies a central position in series *Elongata*. Six other species, each more restricted in habitat and/or distribution, are more similar to *C. squalida* than to each other. They may be distinguished from *C. squalida* in the following ways:

1. *C. scariosa*: leaves more coriaceous, with more regular, less deeply incised teeth on the pinnae. The tooth farthest from the rhachis is usually larger than the others: in *C. squalida* all teeth are roughly equal in size.
2. *C. traillii*: leaves more coriaceous, with less deeply incised, hair-pointed teeth.
3. *C. perpusilla*: rhizomes underground, with more or less vertical short shoots, leaves smaller and hairier.
4. *C. dispersa*: smaller in all parts; sometimes monoecious.
5. *C. rotundata*: leaves simple and suborbicular; monoecious.
6. *C. dioica*: fleshy, incised-pinnatifid leaves, usually lacking brown pigment; sometimes monoecious.

All these species, except *C. rotundata*, can be confused with *C. squalida*. Two of them, *C. perpusilla* and *C. dioica*, hybridise extensively with *C. squalida* in some localities to form hybrid swarms as well as more uniform hybrid segregates, but in other localities each coexists with *C. squalida* with little or no hybridisation.

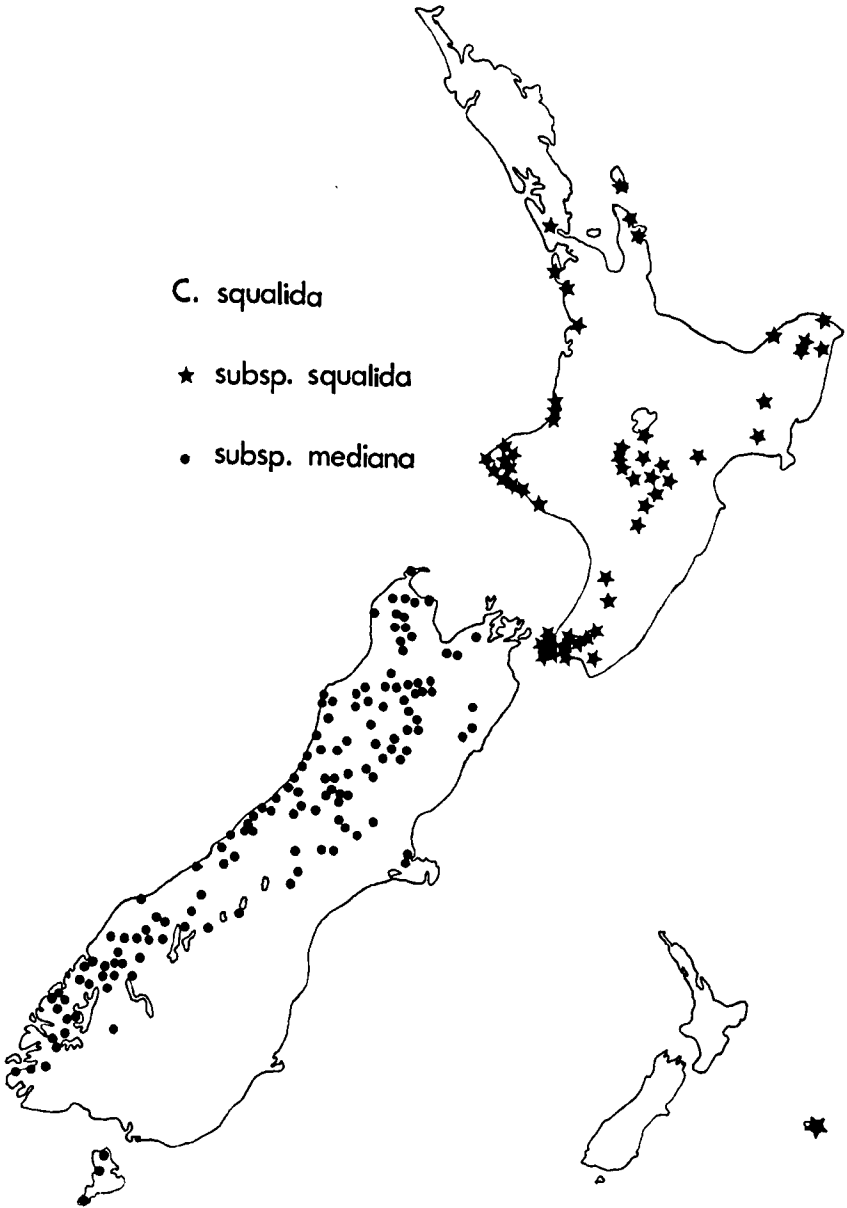


FIG. 14—Distribution of *C. squalida*.

In both the North and South Islands, *C. squalida* shows considerable geographic variation of a generally continuous nature. Despite this, populations from the two islands are separated by small but consistent differences in leaf shape and have been put into different subspecies. South and Stewart Island populations have pinnae which are all uniform in their distribution along the leaf, in the degree of incision, and the angle the lower margin makes with the rachis. In the leaves of North Island plants, the 1-3 terminal pinnae form a more or less distinct 'head'; this is apparent because the sinuses separating the terminal pinnae are less deeply incised, the lower margins of the terminal pinnae are at a narrower angle to the rachis, and the middle pinnae are more widely separated than those above and below. The differentiation of the terminal pinnae is barely apparent in some populations from the Volcanic Plateau, in which the reduced hairier leaves converge remarkably on *C. perpusilla*. Plants of the only Chatham Islands collection show the pinna differentiation weakly and so have been included with North Island plants in subsp. *squalida*.

9. *Cotula perpusilla* Hook.f. Handb. N.Z. Fl.: 143, 1864.

Leptinella pusilla Hook.f., N.Z. 1: 129, 1852; non *Cotula pusilla* Thunberg Prodr. Pl. Cap.: 162, 1800.

Cotula angustata Simpson, Trans. Roy. Soc. N.Z. 79: 435, 1952.

A small perennial herb with tufts of leaves in grassland turfs. Rhizomes us. well-buried, pale, wiry and glabrous; branches uncommon, us. single at flowering nodes; leaves spirally arranged reduced scales lacking blade and petiole, 0.5-2.0 cm apart. Short shoots growing upwards from the rhizome, with 4-8 tufted leaves at the apex. Roots slender and weak, up to 0.5 mm diam. Leaves 1-pinnatifid, 1-6 × 0.3-1.0 cm; blade 0.5-3.0 cm long, lanceolate to obovate, submembranous, light green but often proximal or all pinnae covered with brown pigment, us. moderately villous but glabrous to densely villous, midrib raised along most of ventral surface; pinnae 8-15 pairs, distant to overlapping, cut to rachis, oblong or obovate; teeth absent or up to 8 per pinna, on distal margins, not obscured by hairs, cut $\frac{1}{4}$ - $\frac{1}{2}$ across pinna, narrowly triangular, acute to acuminate, sts with a terminal tuft of hairs. Peduncles ca. equal to leaves, 1-3 cm, nude or occ. with 1 simple bract, villous. Dioecious. Pistillate heads 2-4 mm, up to 8 mm in fruit; surface convex; involucre urceolate; phyllaries 15-30 in 3 or more unequal rows, broadly elliptic, green, ± villous, with a broad often brown-tipped scarious margin; inner phyllaries grow after anthesis to enclose the subglobose fruiting head; florets 25-80, ca. 2.0 mm long, curved, yellow-green; corolla slightly longer than wide, with unequal teeth. Staminate heads 3-5 mm diam.; involucre hemispherical, phyllaries 5-10 in 1-2 subequal rows, not growing after anthesis; florets slightly more numerous. Achenes up to 1.6 × 1.0 mm,

slightly compressed in section, almost round or irregularly angled, with a pale unwrinkled papery surface turning brown and smooth. Flowers in spring. Chromosome number, $n=ca. 52$, $2n=104$. Figs. 3, 4, 16.

HOLOTYPE: (Turakirae, Wellington), Colenso 1942, $\kappa!$

DISTRIBUTION: North Island: near Dannevirke (19th century) and on the S. Wellington coast. South Island: from Richmond Range, Marlborough to Foveaux Strait, east of the main divide, common in short-tussock grasslands from sea level to 1500 m. Fig. 15.

REPRESENTATIVE SPECIMENS: WELLINGTON: Dannevirke, W. Colenso, AK 10407. Ngawhi Point, near Cape Palliser, G. Kelly CANU 17039. NELSON: Mt Robert, Nelson Lakes National Park, D. G. Lloyd 66380, CANU. MARLBOROUGH: Dashwood Pass, near Blenheim, D. G. Lloyd 67393, CANU. Molesworth, H. H. Allan, CHR 68456. Oaro, M. Noonan, CANU 15970. CANTERBURY: Lake Sumner, N. T. Moar, CHR 97582. Ellesmere Spit, I. Robbins, CANU 17019. Acheron R., near start of diversion race to L. Coleridge, E. Edgar, CHR 149570. Cameron R., D. G. Lloyd 66224, CANU. Lake Pukaki, G. Simpson, CHR 75702 (lectotype of *C. angustata* Simpson). Near Waimate, D. G. Lloyd 67360, CANU. OTAGO: Ahuriri saddle, M. T. Kalin, CANU 15986. Lake Wanaka, G. Simpson, CHR 201386. Rock and Pillar Ra., J. M. Ward, CANU 17025. Hills behind L. Waihola, G. Simpson, CHR 95247. SOUTHLAND: Wye Creek, L. Wakatipu, D. G. Lloyd 67216, CANU. L. Manapouri, mouth of Spey R., M. J. A. Simpson, CHR 111848. Otaitai Bush, Riverton, A. J. Healy, CHR 368453.

Three species with hairy leaves and underground rhizomes have previously been confused under the name *C. perpusilla*. The widespread *C. perpusilla sensu stricto* can be distinguished from the allopatric *C. calcarea* of northwest Nelson by the stiff fleshy leaves of the latter. *C. serrulata* is sympatric with *C. perpusilla* over much of the eastern South Island, but the hairier, more close-set pinnae and close oblong teeth of *C. serrulata* enable it to be distinguished on close examination. The North Island populations of *C. perpusilla* are morphologically intermediate between South Island populations and *C. serrulata*. The South and North Island populations of *C. perpusilla* share the same chromosome number, $n=52$, while *C. serrulata* has 26 pairs of chromosomes.

The separation of *C. squalida* and *C. perpusilla* is the most common and probably the most difficult task in the discrimination of New Zealand *Cotula* species. A paucity of universally applicable differential characters, extreme plasticity, geographic variation, and hybridisation all contribute to occasionally obscure the usual differences between the two species. *C. squalida* is more widespread, since *C. perpusilla* is absent from most of the North Island and west of the main divide in the South Island. Both species are common between Marlborough and South Canterbury, with *C. squalida* usually being more common in western areas and *C. perpusilla* predominating in eastern areas. *C. perpusilla* usually occurs in drier grasslands and extensively mixed populations are not common. The usual forms of the

two species are quite distinct, *C. perpusilla* being smaller with underground leafless rhizomes and hairier leaves. But both species occupy a wide range of habitats and approach each other in appearance as their habitats converge. Hybridisation between the species seems to be of limited occurrence in most areas, but especially in the Mackenzie Country hybrid segregates appear to occupy considerable areas. The total variation in both species from these several sources is such that it is not always possible to make a confident identification, particularly of dead material.

Simpson's species, *C. angustata*, is only one segment of a multi-dimensional continuous variation pattern within *C. perpusilla* and has accordingly been reduced to synonymy with *C. perpusilla*.

Allan (1961) designated a specimen from the Tarndale Plains, collected by Travers, as the lectotype of *C. perpusilla*. The choice was unnecessary and erroneous, as Colenso's specimen from Turakirae is the only specimen cited in the description of the basionym, *Leptinella pusilla* Hook.f., and must be the holotype.

10. *Cotula serrulata* sp. nov.

Rhizomata subterranea, pallida, rigidula. Folia imbricata, viva ad apices caulium determinantum, flexibilia, viridia vel glauca, folia matura plerumque rubiginoso pigmento ubique suffusa; pinnae \pm imbricatae; dentes usque ad 6 oblongi, obtusi, conferti, plerumque pilis obscurati. Dioica.

A small perennial herb with tufts of leaves in grassland turfs. Rhizomes us. well-buried, pale, wiry, and glabrous; branches uncommon, us. single at flowering nodes; leaves spirally-arranged, reduced scales lacking a blade and petiole, 0.5–1.5 cm apart. Short shoots, growing upwards from the rhizome, with 3–6 tufted leaves at the apex. Roots slender and weak, up to 0.4 mm diam. Leaves 1-pinnatifid, 0.7–2.0 \times 0.2–0.6 cm; blade 0.6–2.0 cm, elliptic or obovate, submembranous, green, or glaucous, older leaves often diffusely covered with brown pigment, moderately to densely silver-hairy, midrib raised along most of vertical surface but sts obscured by hairs; pinnae 8–20 pairs, close-set and us. overlapping, cut to rhachis, broadly obovate; teeth on all or most pinnae, up to 6 per pinna, on distal margins, cut ca. $\frac{1}{2}$ across pinna, close-set, oblong, obtuse, sts obscured by hairs. Peduncles us. borne on short shoots, ca. equal to leaves, 1–3 cm, nude or with 1 simple bract, villous. Dioecious. Pistillate heads 2–4 mm, up to 8 mm in fruit; surface convex; involucre urceolate; phyllaries 20–40 in 3 or more unequal rows, broadly elliptic, green, villous, with wide often brown-tipped scarious margin; inner phyllaries grow after anthesis to enclose subglobose fruiting head; florets 30–95, ca. 2.0 mm long, curved, yellow-green, corolla slightly longer than wide, with unequal teeth. Staminate heads 3–5 mm diam.; involucre hemispherical; phyllaries 8–15 in 1–2 subequal rows, not growing after anthesis; florets slightly

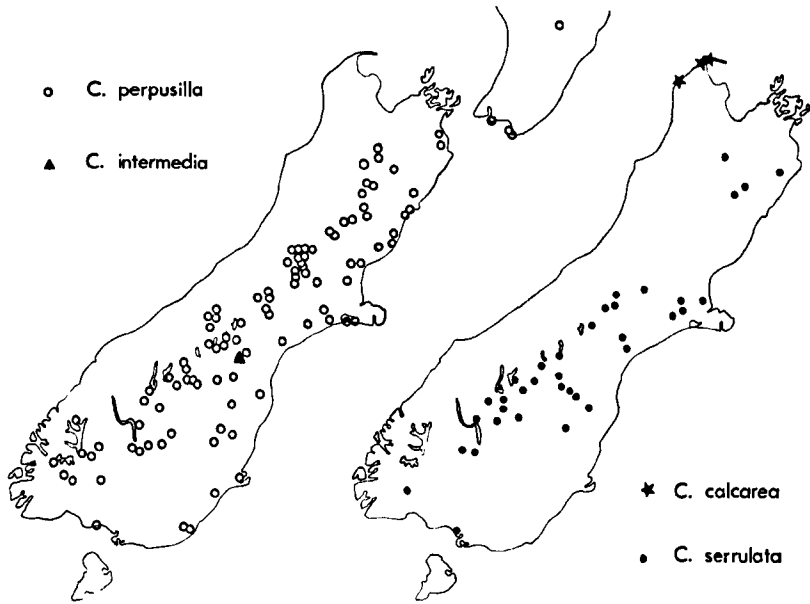


FIG. 15—Distribution of *C. perpusilla*, *C. serrulata*, *C. calcarea* and *C. intermedia*.

more numerous. Achenes up to 1.4×0.8 mm, slightly compressed, in section almost round, with a pale unwrinkled papery surface turning brown and smooth. Flowers in spring. Chromosome number, $n=26$, $2n=52$. Figs. 2, 3, 4, 16.

TYPE: Grassland above lake, south end of Lake Pukaki, Canterbury, 4 Feb. 1967, D. G. Lloyd 67296, CANU 17224.

DISTRIBUTION: South Island: from the Wairau R., Marlborough to Foveaux Strait (but not yet known between the Awatere R. and Christchurch), east of the main divide, sea level to 1500 m, in tussock grasslands of drier areas. North of the Rangitata R. it is not common and is largely restricted to flat river beds and terraces; in the Mackenzie Country and Central Otago it is much more abundant and varied in habitat. Fig. 15.

REPRESENTATIVE SPECIMENS: MARLBOROUGH: Chalk Ra., R. Mason and D. R. McQueen, CHR 84726. Wairau R. bed, opposite Red Hills, D. G. Lloyd 66103, CANU. Home ridge, Molesworth, H. H. Allan, CHR 95127. CANTERBURY: Shipley's Farm, Harewood, Christchurch, B. P. J. Molloy, CANU 17052. Rakaia R., 5 miles below confluence with Wilberforce R., D. G. Lloyd 66275-6,

CANU. Mesopotamia Stream, Rangitata R., M. Barker, CANU 12969. Between Winchester and Rangitata, S. Canterbury, A. J. Healy, CHR 45958. Waitaki Valley, J. M. Ward, CANU 17051. OTAGO: Kain's property, Hawea Flat, I. A. McNeur, CHR 79621. Dunstan Mts, H. H. Allan, CHR 68451. Kokonga (S. of Kyeburn), A. Wall, Jan. 1920, CANTY. SOUTHLAND: 3 miles south of Kingston, D. G. Lloyd 67215, CANU. Lake Monowai, G. Simpson, CHR 95211. Oreti Beach, R. Mason and N. J. Moar, CHR 75887.

There is no previous mention in the literature of the distinction between *C. serrulata* and *C. perpusilla*, although they are sympatric over a wide area. The geographical variability and environmentally induced plasticity of both species tend to obscure specific differences. They often grow intermingled in the same turf, although I have seen putative hybrid plants in only one locality, south of Kingston. No other hybrids involving *C. serrulata* are known.

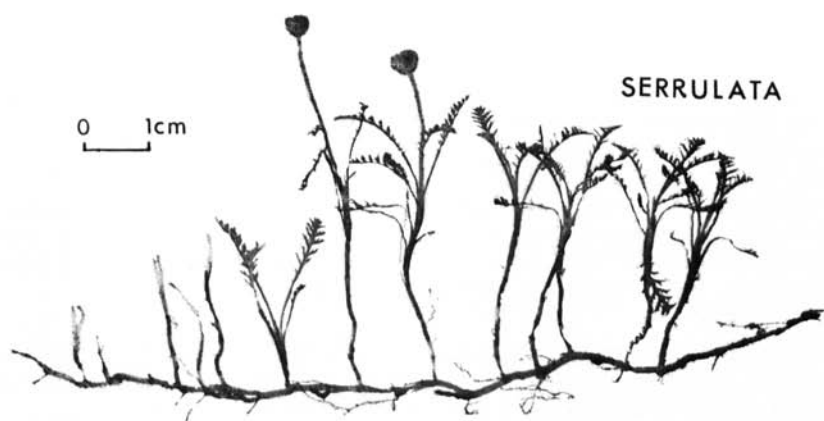
The populations in the Waitaki Valley, Mackenzie Country and Central Otago differ from others in that the leaves are blue-green rather than green in ground colour and have more silver hairs and less brown pigment. *C. serrulata* has not yet been collected between Christchurch and Central Marlborough and may be absent in this area.

11. *Cotula calcarea* sp. nov.

Rhizomata subterranea, pallida, rigidula. Folia imbricata, viva ad apices caulium determinantum, rigida, subcarnosa, chortica pilis partim obscurata; pinnae imbricatae; dentes usque ad 6 oblongi ad triangulares, obtusi. Dioica.

A perennial herb with tufted leaves in loose open mats. Rhizomes us. well buried, pale, wiry, and glabrous; branches uncommon, us. single at flowering nodes; leaves spirally arranged reduced scales lacking a blade and petiole, 0.5–2.0 cm apart. Short shoots growing upwards from the rhizome, with 3–8 tufted leaves at the apex. Roots slender and weak, up to 0.5 mm diam. Leaves 1-pinnatifid, 1–4 × 0.3–0.6 cm; blade 1–4 cm, oblong to elliptic, thick, subfleshy, and stiff, yellow-green, sts with brown pigment on proximal lobes, with a moderate to dense cover of long woolly hairs, midrib prominently raised along the ventral surface; pinnae 12–20 pairs, close-set and us. overlapping, cut to rhachis, broadly elliptic; teeth on most pinnae, up to 6 per pinna, on distal margins, cut ca. $\frac{1}{3}$ across pinna, close-set, narrowly triangular, obtuse. Peduncle us. borne on short shoots, ca. equal to leaves, 1–4 cm, nude or with 1 simple bract, villous. Dioecious. Pistillate heads 3–5 mm diam., up to 10 mm in fruit; surface convex; involucre urceolate; phyllaries 20–40 in 3 or more unequal rows, broadly elliptic, green, \pm villous, with a wide brown-tipped scarious margin; inner phyllaries grow after anthesis to enclose developing fruit; at maturity phyllaries bend

FIG. 16—Plants of *C. serrulata*, *C. perpusilla*, *C. calcarea* and *C. intermedia*.



SERRULATA



PERPUSILLA



CALCAREA



INTERMEDIA

outwards to partly expose fruit; florets 25–120, *ca.* 2.0 mm long, curved, yellow-green; corolla slightly longer than wide, with unequal teeth. Staminate heads 4–6 mm diam.; involucre hemispherical; phyllaries 8–15 in 1–2 subequal rows, not growing after anthesis; florets slightly more numerous. Achenes up to 1.6 × 0.8 mm, slightly compressed, in section almost round or irregularly angled, with a pale unwrinkled papery surface turning brown and smooth. Probably flowers in spring. Chromosome number, $n=52$. Figs. 3, 4, 16.

TYPE: Sand dunes and exposed conglomerate rock slopes, Wharariki Beach, N. of Westhaven Inlet, Nelson, 10 Dec. 1967, D. G. Lloyd 67736, CANU 17227; isotypes at AK, CHR, K, and WELT.

DISTRIBUTION: South Island: N.W. Nelson, on coastal limestone cliffs and adjacent sand dunes. Fig. 15.

REPRESENTATIVE SPECIMENS: Half-mile west of Cape Farewell, A. P. Druce, CHR 180853. Nguroa Beach, N. of Westhaven Inlet, D. R. Given, CANU 17040. Kaihoka, Westhaven Inlet, D. R. Given, CANU 17045. Kahurangi Point, N.W. Nelson, G. I. Collett, CHR 177766.

The relatively few previous collections of *C. calcarea* have usually been identified as the more widespread *C. perpusilla*. The species are closely similar and share the same chromosome number. In evolutionary terms, *C. calcarea* was probably derived from *C. perpusilla* as a coastal limestone ecotype. It is now separated from *C. perpusilla* by a considerable geographical barrier. Morphologically, *C. calcarea* is as distant from *C. perpusilla* as are *C. serrulata* and *C. squalida*, and so it has been given specific status.

Plants from Nguroa Beach, Kaihoka and Wharariki Beach were grown at Christchurch. The three populations are slightly different from each other, though they span a length of coastline only about 13 km long. At Wharariki Beach, *C. calcarea* and *C. dioica* are extensively intermingled, but only one hybrid plant was found.

12. *Cotula intermedia* sp. nov.

Rhizomata leviter defossa. Folia coriacea, ± glabra; pinnae non imbricatae; dentes pauci, triangulares, obtusi, plerumque in distalibus marginibus pinnarum. Monoica.

A small creeping perennial herb with tufts of leaves in turf. Rhizomes shallowly buried, initially dark, flexible, and sparsely pilose, becoming pale stiff and glabrous; branches uncommon, us. single at flowering nodes; leaves spirally arranged, 1–2 at the apex, 0.5–1.0 cm apart. Short shoots grow ± upwards from the rhizome, with up to 5 tufted leaves at the apex. Roots slender and weak, up to 0.6 mm

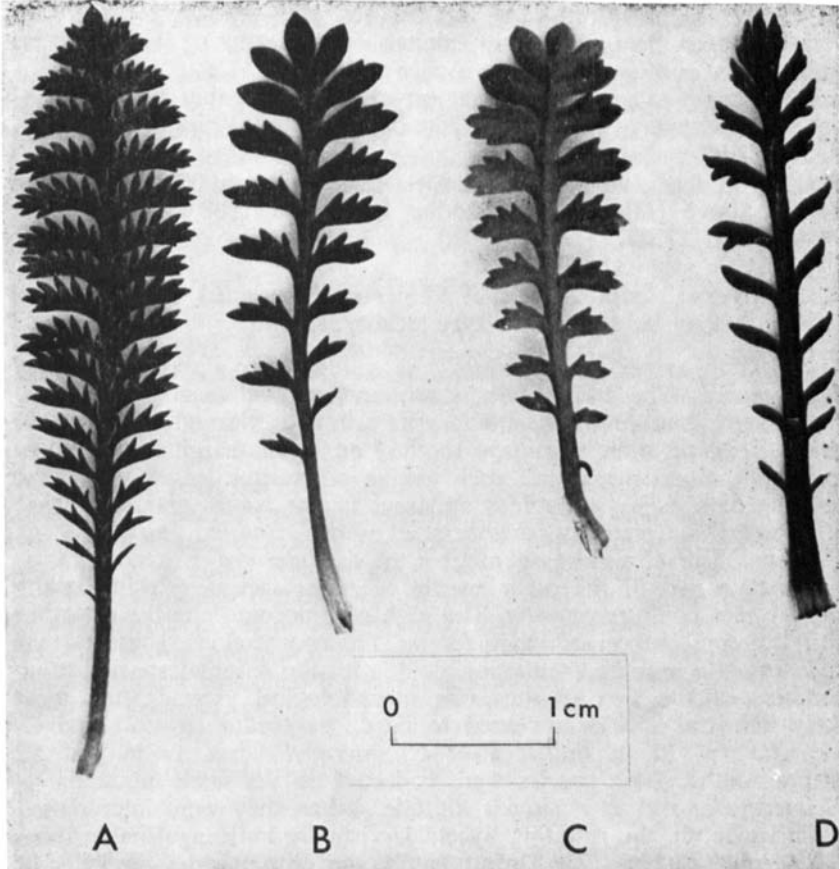


FIG. 17—Leaves of: A, *C. perpusilla* from the Hakataramea saddle; B, *C. intermedia* from above the Hakataramea saddle; C, an F_1 hybrid between A and D; D, *C. pectinata* from above the Hakataramea saddle.

diam. Leaves 1-pinnatifid, $0.8-4.0 \times 0.2-1.2$ cm; blade $0.4-3.0$ cm long, elliptic, coriaceous, light green, sts with brown pigment especially on proximal pinnae, glabrous; midrib sts slightly raised on ventral surface; pinna 4-10 pairs, not overlapping, cut to rhachis, elliptic; teeth us. few per pinna, up to 5 on distal margin and 3 on proximal margin, cut up to $\frac{1}{2}$ across pinna, triangular, obtuse. Peduncles us. borne on rhizomes, ca. equal to leaves, ca. 3 cm, \pm villous, nude or with 1 simple bract. Monoecious. Heads 4-5 mm diam.; surface convex; involucre hemispherical, phyllaries ca. 12 in 1-2 subequal rows, broadly elliptic, dark green, \pm villous, with wide brown scarious margin, not growing after anthesis; pistillate florets few, up to 10 in 1 incom-

plete row, ca. 2.0 mm long, almost straight, yellow-green; corolla slightly longer than wide, with almost equal teeth; staminate florets much more numerous, ca. 40. Achenes up to 1.3×0.9 mm, compressed, biconvex, golden brown, unwrinkled. Probably flowers principally in summer. Chromosome number, $n=ca. 78$. Figs. 3, 4, 16, 17.

TYPE: Wet flush, with *Caltha novae-zelandiae*, ca. 5,000 ft, Grampian Range, above Hakataramea Saddle, 17 March 1968, D. G. Lloyd 68044, CANU 17225.

DISTRIBUTION: South Island: S. Canterbury; collected only once and may not extend far beyond the type locality. Fig. 15.

In many respects *C. intermedia* resembles more glabrous plants of *C. perpusilla*. The two species share underground rhizomes, vertical short shoots and several characters in common with other species of series *Elongata*, such as pinnae toothed on distal margins and yellow florets. In other characters, such as the coriaceous leaves, monoecy, and the dark veins sometimes apparent in the leaves and phyllaries, *C. intermedia* resembles members of series *Radiata*, especially *C. pectinata*. The chromosome number of *C. intermedia*, $n=ca. 78$, is higher than that of the other species of either section growing in the general area of *C. intermedia*. The high chromosome number, together with the combination of characters of the two sections, suggests that *C. intermedia* may be an allopolyploid, with the parental species being members of the two sections. On morphological grounds, the most likely ancestral species appeared to be *C. perpusilla* ($n=52$) and *C. pectinata* ($n=52$ in the area of *C. intermedia* but $n=26$ and 52 further south). Both species were collected on the same mountain as *C. intermedia* and at a similar altitude. When they were intercrossed at Christchurch, the resulting hybrid is virtually indistinguishable from *C. intermedia* (Fig. 17). Unfortunately the chromosome numbers of these parents do not add up to that of *C. intermedia*. A doubling of the chromosome number in a *C. perpusilla* \times *pectinata* F_1 hybrid produced in the area cannot, therefore, produce a plant with the chromosome number of *C. intermedia*. So the origin of *C. intermedia* is at present uncertain, although there are two main possibilities:

1. *C. serrulata* ($n=26$) and not *C. perpusilla* ($n=52$) was the parent from series *Elongata*. *C. serrulata* occurs on the same mountain as *C. intermedia*, at a lower altitude. The cross *C. serrulata* \times *C. pectinata*, between plants from other localities, has been made but not grown. It is likely that such a hybrid would be extremely similar to *C. intermedia*, as other interseries hybrids which have been grown, such as *C. squalida* \times *C. pectinata*, are all remarkably alike.
2. *C. perpusilla* and an $n=26$ race of *C. pectinata* were the parents. This would require a previously larger range of either the lower ploidy level of *C. pectinata* or *C. intermedia*.

Although the characters and name of *C. intermedia* indicate a roughly equal similarity to species of the two series, *C. intermedia* is placed within series *Leptinella* as a matter of convenience. The habit and leaf shape of *C. intermedia*, which must provide the usual basis for identification, are more similar to other species of series *Leptinella* than to series *Radiata*. The extremely local distribution of *C. intermedia* argues against creating another series just for it.

SERIES *RADIATA* ser. nov.

Rhizomatis folia compluria ad apicem aggregata; folia matura aut omnia imbricata manent aut aliqua distantia fiunt. Rami plerumque aggregati. Achaenia non manifeste curvata aut compressa, biconvexa vel obscure tetragona, longitudine duplicatam latitudinem aequantia vel superantia, cum marginibus inconspicuis.

Rhizome leaves several clustered at the apex, either all remaining imbricate or some becoming distant as several internodes elongate gradually and simultaneously. Branches us. clustered, several radiating from flowering nodes and the nodes immediately behind. Short shoots absent or with few reduced leaves, with internodes within the sheath of the subtending leaf or us. converted into rhizomes if emerging from sheath. Achenes not markedly curved or compressed, length equal to or greater than twice width, with inconspicuous margins, biconvex or obscurely 4-angled.

TYPE SPECIES: *Cotula pectinata* Hook.f.

13. *Cotula maniototo* Petrie, Trans. N.Z. Inst. 14: 362, 1882.

A very small perennial (occ. annual) herb forming loose patches or an inconspicuous low matted turf. Rhizomes at or near soil surface, slender, less than 1 mm diam., often hidden within leaves, \pm villous, becoming wiry and glabrous when older; branches often difficult to discern, poorly differentiated from short shoots; leaves crowded in two rows, \pm horizontal, up to 10 clustered at the apex, imbricate or older ones gradually becoming up to 4 mm apart; short shoots at most nodes, initially with a few reduced leaves in the axils of rhizome leaves, often converted into rhizomes with distant leaves. Roots abundant, slender, up to 0.5 mm diam., white. Leaves variable, 0.2–2.5 cm long; blade up to 2.0 cm long, either 1-pinnatifid, lanceolate or oblong and up to 2 mm wide or (especially in winter) simple, linear and ca. 0.5 mm wide, thin, grass-green and glabrous to silky white and densely villous; midrib not raised on ventral surface; pinnae 0 or 1–2 minute lobes or up to 6 pairs, distant, subequal, shorter than the terminal lobe, linear, narrower than the rhachis, without teeth. Peduncles very short, less

than 1 mm long, nude. Monoecious. Heads almost sessile, small, 2–3 mm diam.; surface convex; involucre campanulate; phyllaries *ca.* 10 in 1–2 subequal rows, oblong, rather thin, green villous, with wide brown or reddish scarious margin, not growing after anthesis; pistillate florets 15–20 in 1–2 rows, *ca.* 2.0 mm long, straight, pale yellow and red-tipped; corolla four times as long as wide, with equal teeth; staminate florets *ca.* equal in number. Achenes up to 1.0 × 0.3 mm, slightly compressed, biconvex, green turning chocolate brown, unwrinkled and soft. Flowers in summer. Chromosome number, $n=26$, $2n=52$. Figs. 2, 5, 18.

LECTOTYPE (Allan, 1961): In moist hollows, covered by water in wet seasons, Maniototo Plains, Otago, D. Petrie (no date), WELT (Petrie Herb.)!

DISTRIBUTION: North Island: L. Wairarapa. South Island: south from L. Lyndon, Canterbury, east of the main divide, sea level to 700 m, locally common in its specialised habitat—soils with fluctuating water tables subject to periodic flooding and drying, especially lake margins and winter pools in moraines and river terraces. Fig. 19.

REPRESENTATIVE SPECIMENS: WELLINGTON: Western Lake Reserve, L. Wairarapa, R. Mason, CHR 65660. CANTERBURY: Lake Lyndon, T. Kirk, CHR 68170. Near Lake Coleridge, Rakaia R., D. G. Lloyd, 65549, CANU. Lake Camp, U. Ashburton Valley, R. Mason, CHR 145655. Near Mary Burn, Tekapo-Pukaki Road, D. G. Lloyd 66328, CANU. OTAGO: 4 miles south of Luggate, D. G. Lloyd 66183, CANU. Waipiata, Maniototo Plains, A. Wall, Jan. 1920, CANTY. SOUTHLAND: 3 miles south of Kingston, D. G. Lloyd 67214, CANU. Lake Te Anau, D. G. Lloyd 6745, CANU. Dam at Lake Monowai, G. Simpson, CHR 201391. Hokonui Hills, near Gore, D. Petrie, CANU 4647.

Cotula maniototo is easily distinguished from all other species of section *Leptinella* by the small narrow leaves. It is so distinctive in vegetative characters that it is not easily recognised as a *Cotula* when it is not in flower. In addition to the usual variation in compactness and hairiness, many populations have a unique seasonal heterophylly, producing simple linear leaves in the winter and pinnatifid leaves in the summer. This heterophylly and the ability of some, at least, of the populations to reproduce vegetatively by bulbils will be considered elsewhere.

14. *Cotula nana* sp. nov.

Perpusilla, diffuse repens. Rhizomata tenuia, minus quam 0.5 mm diam. Folia 0.4–2.0 cm × 2–4 mm; pinnarum 5–10 paria, distales pinnae confertae vel imbricatae et versus rhachim non plus quam circa 2/3 incisae, proximales distantiores et ad rhachim incisae. Capitula perparva, viridia.

A very small, frequently branching, creeping perennial herb forming small diffuse patches. Rhizomes on the soil surface, very slender,

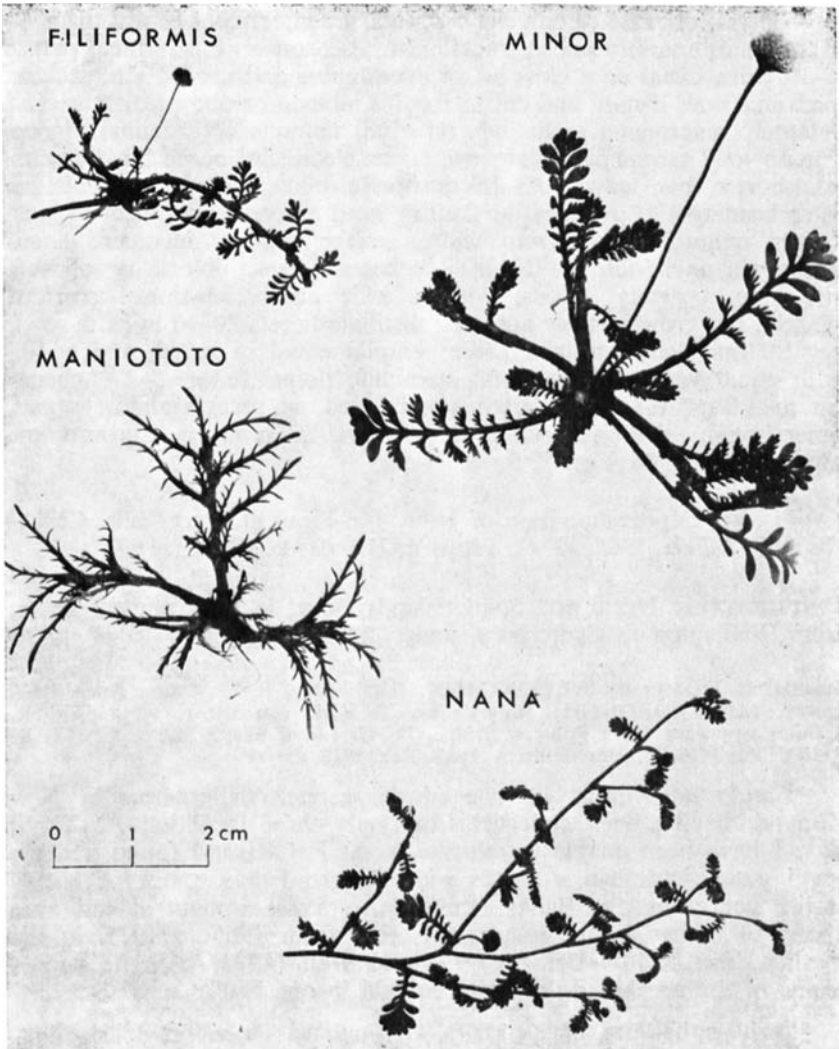


FIG. 18—Plants of *C. maniototo*, *C. nana*, *C. filiformis* and *C. minor*. All are glasshouse-grown plants and are laxer than is usual in nature.

less than 0.5 mm diam., green, soft, sparsely pilose; branches common, at the frequent flowering nodes and sts also at 1–3 nodes immediately behind; leaves 1–several at the apex but mostly distant, 0.5–1.0 cm apart. Short shoots variable, occ. few but us. at most rhizome nodes, often converted into rhizomes. Roots very slender and weak, up to 0.3 mm diam. Leaves 1–pinnatifid, 0.4–2.0 × 0.2–0.4 cm; blade

0.3–1.5 cm, obovate or narrowly so, thin, green, without brown pigment, glabrous or sparsely pilose, midrib not raised on ventral surface; pinnae 6–10 pairs, distal ones close-set or overlapping and cut *ca.* $\frac{3}{4}$ to rhachis, proximal ones distant and cut to rhachis, oblong or obovate, obtuse and minutely mucronate; teeth 0–3, on distal margins of proximal pinnae, cut up to $\frac{1}{2}$ across pinna, narrow, acute. Peduncles borne on rhizomes, us. shorter than leaves, 0.3–1.0 cm, nude, pilose, erect at anthesis, sts later bending 180° to bury the fruiting head among leaves. Monoecious. Heads minute, 1.5–2.0 mm wide; surface convex; involucre hemispherical; phyllaries *ca.* 20 in 2 subequal rows, oblong or obovate red-green, sparsely villous, with a wide sts brown-tipped scarious margin, not growing after anthesis; pistillate florets 20–40 in *ca.* 2 rows, *ca.* 1.0 mm long, straight, green; corolla equal in length and width, with equal very shallow teeth; staminate florets fewer, 5–7. Achenes up to 1.0 × 0.5 mm, slightly compressed, in section almost round, green-brown, shallowly wrinkled. Flowers in summer. Chromosome number, $n=ca.$ 26. Figs. 2, 5, 18.

TYPE: Wet depression, base of cliffs, Mt Pleasant, Port Hills, Christchurch, 13 Feb. 1965, D. G. Lloyd 65216, CANU 17221.

DISTRIBUTION: North and South Islands: local in bare, muddy places, from Wellington to Canterbury, under 400 m. Fig. 19.

SPECIMENS EXAMINED: WELLINGTON: Titahi Bay, B. C. Aston, April 1907, CANTY. MARLBOROUGH: Rai Valley, T. Kirk (no date), WELT. Rai R. 3 miles upstream from Pelorus Bridge, D. G. Lloyd 67395. CANU. CANTERBURY: Mt Pleasant, Port Hills, A. Wall, Feb. 1918, CANTY.

Cotula nana must be one of the rarest Angiosperms in New Zealand, having been collected from only three localities. At Titahi Bay, I have been unable to relocate it. At Rai River I found a single small patch less than a metre wide, before I was aware of Kirk's earlier collection. On Banks Peninsula, a small amount spread over about 10 m has been present each year from 1965 to 1971, in the locality described by Laing (1919) and Wall (1922). All the known plants of the species could easily be held in one hand.

Perhaps because of its rarity, *C. nana* has been previously considered conspecific with both *C. dispersa* and *C. membranacea* (under the name *C. minor*), but it is similar to the other two species only superficially, in its small size. In all critical characters it belongs to series *Radiata*, nearest to *C. filiformis*.

15. *Cotula filiformis* Hook.f., Handb. N.Z. Fl.: 142, 1864.

A creeping perennial herb forming open patches. Rhizomes on the soil surface, slender, less than 1 mm diam., brown, sparsely pilose; branches us. single at flowering nodes but sts 2–3 clustered; leaves

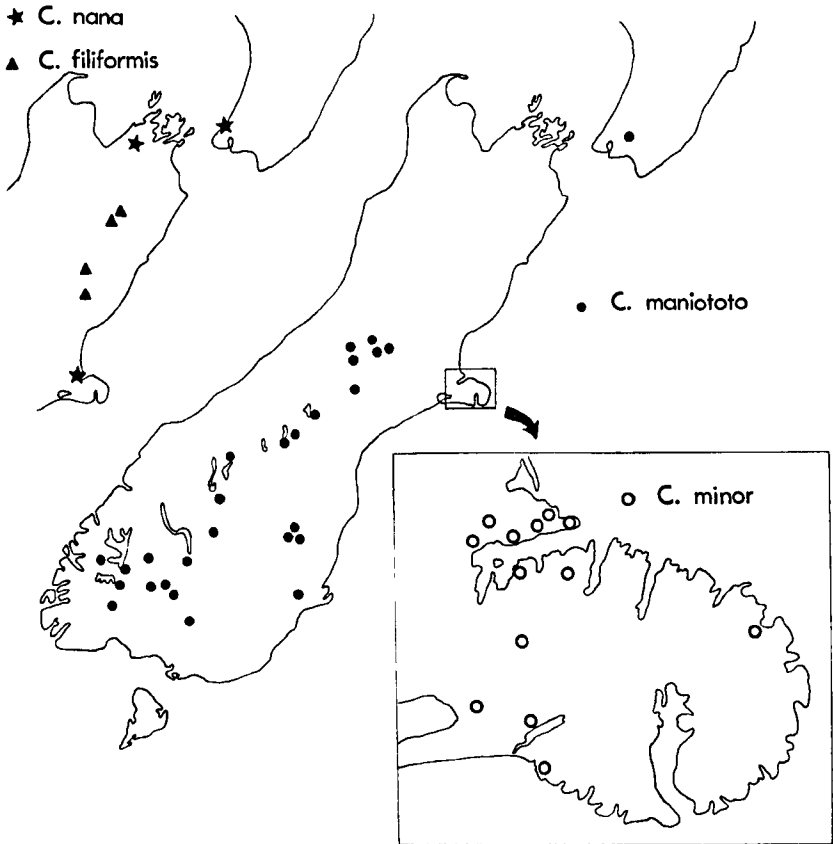


FIG. 19—Distribution of *C. maniototo*, *C. nana*, *C. filiformis* and *C. minor*.

3—many clustered at the apex, older leaves up to 1.5 cm apart. Short shoots absent or with 1—few small leaves. Roots slender, less than 0.5 mm diam. Leaves 1—pinnatifid, $0.3\text{--}2.0 \times 0.2\text{--}0.4$ cm; blade 0.2—1.5 cm, oblong to obovate, coriaceous, dull green, sts with brown pigment, \pm glabrous; pinnae 4—10 pairs, not overlapping, cut to rachis, obovate; teeth us. absent, occ. 1—3, on distal margins of proximal pinnae, cut $\frac{1}{2}\text{--}\frac{3}{4}$ across pinna, triangular, obtuse and minutely mucronate. Peduncles borne on rhizomes, longer than leaves, slender, 1—3 cm, nude or with 1 simple bract, pilose. Monoecious. Heads 2—3 mm diam.; surface convex; involucre outspread; phyllaries 8—14 in 2 equal rows, suborbicular, pilose, with a wide brown scarious margin, not growing after anthesis; pistillate florets 15—50 in 2 or more rows, ca. 1.0 mm long, straight, white; corolla twice as long as wide, with equal teeth; staminate florets ca. equal in number. Achenes 0.85×0.5 mm.

slightly compressed but almost round in section, pale brown, transversely wrinkled. Chromosome number, $n=26$, $2n=52$. Flowers in summer. Figs. 5, 18.

LECTOTYPE (Allan, 1961): Canterbury, 1862, J. von Haast 594, K!

DISTRIBUTION: Eastern South Island: Awatere R. valley, Hamner Plains and Balmoral, in dry grasslands at 300–600 m. Fig. 19.

REPRESENTATIVE SPECIMENS: MARLBOROUGH: Langridge Station, Upper Awatere R., L. B. Moore, CHR 87211. CANTERBURY: Hamner Plains, C. Christensen, Feb. 1914, CANU 4672. Balmoral, A. Wall, Nov. 1917, CANTY.

The closest relative of *C. filiformis* is the allopatric species *C. minor*, which is very similar but larger in all parts. The two taxa barely deserve separate specific status, but are retained here as species to avoid a dubious change and because the size differences give them very distinct appearances.

16. *Cotula minor* (Hook.f.) Hook.f. Handb. N.Z. Fl.: 142, 1864, pro parte.

Leptinella minor Hook f. Fl. N.Z. 1: 129, 1852 pro parte, non *Cotula minor* Caruel ex Boiss., Flora Orientalis 3: 358, 1875.
Cotula haastii Kirk, Stud. Fl. N.Z.: 325, 1899.

A creeping perennial herb forming open patches. Rhizomes on the soil surface, slender to stout, 0.5–2.0 mm diam.; branches produced earlier in season clustered, up to *ca.* 5 radiating from around a flowering node; branches produced later in season us. single at flowering nodes. Leaves 3—many clustered at the apex, under better conditions older leaves up to 2 cm apart. Short shoots absent or with 1—few small leaves. Roots \pm thick, 0.5–1.0 mm diam. Leaves 1—pinnatifid, 1–5 \times 0.3–1.0 cm; blade 0.3–4.0 cm, obovate, coriaceous, dull green, usually with brown pigment on proximal pinnae, \pm glabrous; pinnae 5–12 pairs, not overlapping, cut to rhachis, obovate, teeth 0 or up to 7 per pinna, us. restricted to proximal pinnae, on distal margins, cut $\frac{1}{3}$ – $\frac{2}{3}$ across pinna, oblong, obtuse and minutely mucronate. Peduncles borne on rhizomes, equal to or longer than leaves, slender, 2–5 cm, nude or with 1 simple bract, pilose. Monoecious. Heads 4–6 mm diam.; surface convex; involucre outspread; phyllaries 15–20 in 2 equal rows, suborbicular, pilose, with a wide brown scarious margin, not growing after anthesis; pistillate florets 70–130 in 2 or more rows, *ca.* 1.75 mm long, straight, white; corolla twice as long as wide, with equal teeth; staminate florets *ca.* equal in number. Achenes *ca.* 1.0 \times 0.5 mm, slightly compressed but almost round in section, pale brown, transversely wrinkled. Chromosome number, $n=26$. Flowers through the spring and summer and at a reduced rate in autumn and occ. winter. Figs. 1, 5, 18.

LECTOTYPE (Allan, 1961): Canterbury, Dr Lyall (no date or number), K!

DISTRIBUTION: Canterbury: Banks Peninsula, from sea level to 600 m, in dry exposed grassland and around the base of rocks. Fig. 19.

REPRESENTATIVE SPECIMENS: Canterbury Plains, near Christchurch, D. Petrie, WELT. Canterbury Plains, near Kowhai Corner, J. von Haast 393, Nov. 1864, CANTY. Godley Head, T. W. Rawson, CHR 82749. Victoria Park, Christchurch, D. G. Lloyd 66269, CANU. Diamond Harbour, J. M. Ward, CANU 17093. Mt Herbert, D. Petrie (no date), CANTY (Carse Herb. 1600/2). Base of hills above west end of Ellesmere Spit, D. G. Lloyd 65313, CANU. Okains Bay, D. G. Lloyd 67664, CANU.

When he described *Leptinella minor*, J. D. Hooker cited three collections, which belong to three species—*C. squalida* and *C. dispersa* as well as *C. minor* as defined here. Most of the characters in the description suit any of the three species equally well. Only one character, "occasional unisexual heads" describes *C. squalida* alone, and only the description of the plants as small suits *C. dispersa* best. On the other hand, several of the characters are more appropriate to the narrower concept of *C. minor* adopted here. Allan in 1961 designated Dr Lyall's specimen as the lectotype. His choice agrees with the element that best fits Hooker's description and must be followed. Unfortunately Kirk (1899) published another name, *C. haastii*, which has since been used generally for *C. minor*. Kirk ascribed the name *C. minor* to three other species which have not been previously distinguished from each other. These latter are described above as the new species, *C. dispersa*, *C. membranacea*, and *C. nana*.

In the vegetative state, *C. minor* has often been identified as the more common species *C. squalida*, because of the numerous teeth on the pinnae of larger leaves. But *C. minor* is easily distinguished by the restriction of teeth to the lower pinnae, which is unique in section *Leptinella*.

17. *Cotula dendyi* Cockayne, Trans. N.Z. Inst. 47: 118, 1915.

Cotula atrata var. *dendyi* (Cockn.) Cheesem. Man. N.Z. Flora: 993, 1925.

A somewhat fleshy perennial herb of 1 or more summergreen tufts of much-divided leaves among loose rocks. Rhizomes ascending, at rock surface when young, becoming deeply buried, up to ca. 1 cm long, thick, \pm fleshy, pale or reddish, with a few short deciduous hairs when young; branches often initially in clusters of up to 4 diverging from a flowering node and the nodes immediately behind, but few survive the first season; leaves usually remain crowded behind the apex, but sts eventually separate up to 2.5 cm apart. Roots numerous, very long and extensively branching, thick, up to 1.5 mm diam., fleshy. Leaves 2-pinnatifid, 2-5 \times 0.3-0.8 cm; blade 1-3 cm

long, narrowly obovate, coriaceous and subfleshy, grey-green, tinted with red pigment especially on primary and secondary axes, \pm pilose, midrib not raised on vertical surface; pinnae 8–12 pairs, cut to rhachis, distal ones overlapping, broadly elliptic and divided, reducing to distant oblong simple proximal pinnae; secondary pinnae up to 9 per pinna, equally on proximal and distal sides, cut to midrib of pinna, with rounded apices, turned up at an angle to blade, occ. with a linear lobe on one or both sides. Peduncles easily exceeding leaves, 3–8 cm, stout, pilose, with 6–15 evenly spaced bracts; lowermost bracts scarcely smaller than leaves, reducing evenly to simple and oblong or 1-pinnatifid uppermost bracts. Subdioecious; pistillate, staminate and bisexual heads all common. Pistillate heads large, up to 2 cm diam., surface almost flat; involucre spreading and upturned at the margin; phyllaries numerous, in 2–several unequal rows, grey-green with a reddish tinge, \pm pilose, not growing after anthesis; outer phyllaries exceeding florets, thick, simple and oblong or with 1–8 oblong lobes on both sides, without a scarious margin, gradually changing to thinner, simple, obovate inner phyllaries with a narrow scarious margin; florets 200–900 in numerous rows, 3.25–4.25 mm long, straight, pale yellow with brown corolla teeth, the whole floret rapidly turning brown after anthesis. corolla ca. 4 times as long as wide, with equal, obvious, diverging teeth. Staminate heads much smaller, less than 1 cm diam.: surface convex; involucre hemispherical; florets fewer, 120–450. Achenes up to 2.9×0.7 mm, slightly compressed, in section almost round, golden-brown, deeply wrinkled. Flowers in summer. Chromosome number not known. Figs. 2, 6, 21.

LECTOTYPE: Shingly Peak, Awatere (Valley), L. Cockayne, WELT! Cockayne visited the Shingly Range only once, on 14 Dec. 1911 (Hamlin, 1967), a few years before *C. dendyi* was described.

DISTRIBUTION: South Island: E. Nelson, Marlborough and Canterbury, on and east of the main divide, on mobile subalpine scree and adjacent bare ridges and summits, 1,000–2,000 m, common but in small populations with scattered plants. Fig. 20.

REPRESENTATIVE SPECIMENS: NELSON: Gordon's Knob, D. Petrie Jan. 1910, WELT. Camel, Travers Valley, A. P. Druce, CHR 82237. MARLBOROUGH: Team Saddle, Saxton River, M. T. Kalin and J. M. Ward 66354, CANU. U. Awatere Valley, A. F. Mark, OTA 27295. Mt Tapuaenuku, B. C. Aston, Dec. 1915, WELT. Mt Te Ao Whekere, Seaward Kaikoura Ra., D. G. Lloyd 67382, CANU. Mt Half Moon, Dillon River, A. Wall, Dec. 1926, CANTY. CANTERBURY: Wairau Gorge, Travers, K. Glacier Gully, Spencer Mts, T. Kirk, WELT. Mt St. Patrick, Clarence R., D. G. Lloyd 70030, CANU. Mt Miro Miro, Amuri Co., D. Petrie, CHR 23928. Evangeline Creek, L. Sumner, C. Ecroyd, CANU 17117. Between Ranger and Fenwick Streams, Poulter Ra., M. Heine, CANU 17115. Mt Pember, Puketeraki Ra., L. Moore and J. Clarke, CHR 174048. Fog Peak, Torlesse Ra., D. G. Lloyd 66040, CANU. Mt Bailey, Cragieburn Ra., A. Wall, Feb. 1923, CANTY. Mt Hutt, E. Atkinson, 1 Jan. 1931, WELT.

Among the bipinnatifid scree *Cotulas*, three distinct series of

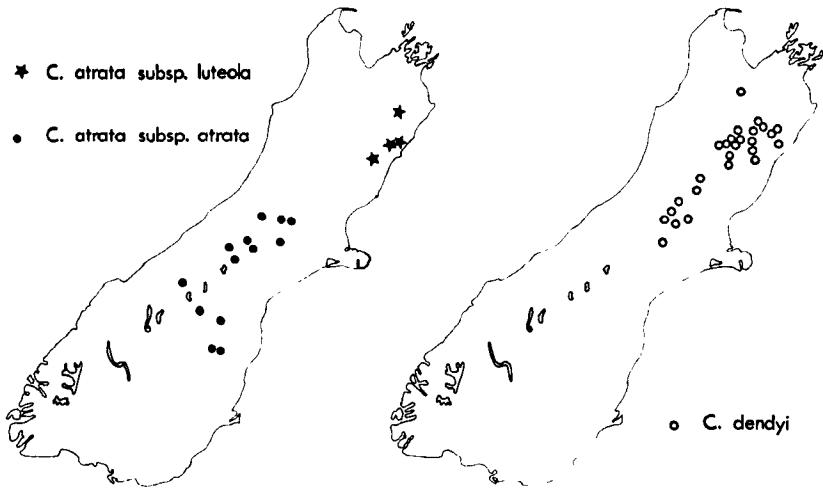


FIG. 20—Distribution of *C. atrata* and *C. dendyi*.

populations can be recognised on morphological features. They are described here as *C. dendyi* and *C. atrata* subspecies *atrata* and *luteola*. All three are similarly specialised in their vegetative characters and together they form one of the small groups of plants adapted to the mobile shingle slides of the eastern South Island mountains. They are all closely related and difficult to distinguish, especially in the vegetative state. Of the three taxa, *C. dendyi* is the most distinctive. It occurs sympatrically with both of the others, and so is reinstated as a separate species. The other two taxa are more similar to each other, and since they are geographically widely separated, they are described here as subspecies of *C. atrata*.

In the region of overlap of *C. dendyi* and *C. atrata* subsp. *atrata*, between the Torlesse and Hutt Ranges, hybridisation is quite extensive and a range of intermediate plants occurs. Further north, *C. dendyi* and *C. atrata* subsp. *luteola* have both been collected on several ranges, but never together as part of the same collection. No hybrids have yet been collected, but their common range is poorly explored.

Each of the three taxa has one or more features, unique and derived in the section, by which it can be recognised. Table 1, compares the three taxa for the more obvious differential characters.

Apart from the subspecific differences, there is little geographic variation in *C. atrata*. All populations of subsp. *atrata* appear to be indistinguishable. In subsp. *luteola*, the only difference noted between plants grown at Christchurch from the Black Birch Range and Mt

TABLE 1—A comparison of the characters of *C. atrata* subsp. *atrata*, *C. atrata* subsp. *luteola* and *C. dendyi*.

| CHARACTER | <i>C. atrata</i> subsp. <i>atrata</i> | <i>C. atrata</i> subsp. <i>luteola</i> | <i>C. dendyi</i> |
|--------------------|---------------------------------------|--|-----------------------------------|
| 1. Leaves | much divided, pinnules upturned | less divided, pinnules \pm flat | much divided, pinnules upturned |
| 2. Head diameter* | to 1.3 cm | to 1.2 cm | to 2.0 cm |
| 3. Head surface* | convex | paraboloid (steeply convex) | almost flat |
| 4. Phyllaries* | exceeded by outer florets, upturned | exceeded by outer florets, \pm flat | exceeding outer florets, upturned |
| 5. Receptacle | convex | conical | almost flat |
| 6. Floret colour | very dark red | yellow, with red tips | yellow, with red-brown tips |
| 7. Sex of heads | bisexual | bisexual | all female to all male |
| 8. Stigma exertion | temporary, short | permanent, far | temporary, short |

*Florets may be squashed out of the head during drying of herbarium specimens, obscuring head size and shape.

Terako was that in the former the red-tipped portion of the florets is more extensive, so that the unopened florets of the heads appear darker than in the Mt Terako plant. *Cotula dendyi*, however, shows considerable geographic variation, particularly in the division of the peduncle bracts and outer phyllaries, in head size, and in the frequency of bisexual heads. The variation is continuous and there are no clearly distinct segments of the species worthy of formal taxonomic recognition.

18. *Cotula atrata* Hook.f., Handb. N.Z. Fl.: 142, 1864, pro parte.

Habit, rhizomes and roots as in *C. dendyi*. Leaves 2-pinnatifid, 2-8 \times 0.5-1.3 cm; blade 1.5-6.0 cm long, obovate, coriaceous and subfleshy, grey-green tinted with red pigment especially on the primary and secondary axes, sparsely pilose, midrib not raised on ventral surface; pinnae 5-15 pairs, cut to rachis, distal ones close-set or overlapping, broadly elliptic and divided, reducing to distant oblong simple proximal pinnae; secondary pinnae 0-9 per pinna, equally on distal and proximal sides, cut to midrib of pinna, oblong or obovate, with rounded apices, flat or upturned, occ. with 1 or 2 small lobes on

either side. Peduncles scarcely longer than leaves, 3–12 cm, stout, pilose, with 4–10 evenly-spaced bracts; lowermost bracts scarcely smaller than leaves, reducing evenly to simple and oblong or little divided uppermost bracts. Monoecious. Heads 0.5–1.3 cm diam.; surface convex to paraboloid; involucre hemispherical or flat; phyllaries in 2–3 subequal rows, overtopped by mature florets, otherwise as in *C. dendyi*; pistillate florets 100–240 in several rows, 3.25–3.75 mm long, straight, pale yellow or very dark red and almost black; corolla ca. 5 times as long as wide, with equal, obvious and diverging teeth; staminate florets ca. equal in number. Achenes up to 1.8–2.8 × 0.8–1.0 mm, slightly compressed, in section almost round, pale brown or dark brown, deeply wrinkled. Flowers in summer. Chromosome number, $n=26$. Figs. 1, 2, 6.

LECTOTYPE: Province Canterbury, Sinclair and Haast 1860-61 (number and exact locality uncertain), $\kappa!$ (see below).

DISTRIBUTION: South Island: Eastern Marlborough, Canterbury and N. Otago, in the same habitat as *C. dendyi*. Fig. 20.

KEY TO THE SUBSPECIES

Corolla almost black; distal pinnae overlapping; secondary pinnae upturned 18a. subsp. *atrata*

Corolla yellow but dark-tipped; pinnae not overlapping; secondary pinnae \pm flat 18b. subsp. *luteola*

18a. *Cotula atrata* Hook.f., subsp. *atrata*.

Pinnae 8–15 pairs; proximal ones distant, distal ones us. overlapping; secondary pinnae up to 9 per pinna, oblong or obovate, upturned. Lower bracts on peduncle almost as divided as leaves, upper bracts simple or with few divisions. Involucre hemispherical; outer phyllaries us. pinnatifid, with up to 6 pairs of oblong lobes. Receptacle convex. Florets dark red; upper part of corolla almost black, lower part and ovary wine red; stigmas of pistillate and staminate florets not exerted far beyond the corolla, retracted into the corolla tube after anthesis (and during drying of specimens). Chromosome number, $n=26$. Figs. 1, 2, 6.

DISTRIBUTION: South Island: Canterbury and N. Otago.

REPRESENTATIVE SPECIMENS: Fog Peak, Torlesse Ra., D. G. Lloyd 66040-15, CANU 17109. Mt Enys, Cragieburn Ra., V. D. Zotov, CHR 21117. Mt Hutt, Canterbury, D. G. Lloyd 65244, CANU. U. Cameron R., Canterbury, D. G. Lloyd 66222, CANU. Mt Peel, R. S. Russel, OTA 2501. Mt Richmond, Two

Thumb Ra., A. F. Mark and N. M. Adams, OTA 25849. Above L. Ohau. W. Larson, OTA 6370. Ben More, W. R. B. Oliver, WELTU 5108. Mt Kyeburn, Otago, D. Petrie, WELT. Dansey's Pass, Kakanui Ra., J. E. Holloway, CHR 29509.

18b. *Cotula atrata* subsp. *luteola* subsp. nov.

Folia minus dissecta quam subsp. *atratae*; ultimae divisiones triangulares ad oblongas, planae vel leviter sursum inclinatae. Monoica. Involucrum planum; involucri squamae simplices, oblongae. Flosculi luteoli; corollae dentes cum exteriore apice lateritio.

Leaves less divided; pinnae 5–10 pairs, not overlapping; secondary pinnae up to 5 per pinna, triangular to oblong, flat or scarcely upturned. Bracts on peduncle simple or with 1–3 lobes on either side. Involucre flat; phyllaries all simple, oblong. Receptacle conical. Florets yellow, with the corolla teeth reddish brown; stigmas far exerted and not retracted after anthesis (or on dried specimens). Chromosome number, $n=26$. Fig. 6.

TYPE: Mt Terako, North Canterbury, L. B. Moore, CHR 97080!

DISTRIBUTION: Eastern Marlborough and North Canterbury, known only from four localities.

REPRESENTATIVE SPECIMENS: MARLBOROUGH: Black Birch Range, L. B. Moore, CHR 176951. Ridge to Mt Manakau, Seaward Kaikoura Ra., I. M. Ritchie, CHR 176066. Kahutara Saddle, W. Martin, Jan. 1932, WELT.

TYPIIFICATION OF *C. atrata*: The original description of *C. atrata* by J. D. Hooker in 1864 cited 5 localities. The specimens referred to are now on 2 sheets in the Kew herbarium. Specimens from 2 localities "Tarn-dale, Sinclair" and "Wairau Gorge, Travers" belong to *C. dendyi*. The other 3 localities are in Canterbury and are represented by 12 pieces on one sheet. There is no way of determining now which of the 3 cited localities each piece came from. The specimens are an equal mixture of 6 *C. atrata* subsp. *atrata* and 6 *C. dendyi* pieces. Both *C. dendyi* and *C. atrata* occur on Mt Torlesse, but the other 2 localities are well outside the known range of *C. dendyi*. So 2 of the 5 cited localities represent *C. dendyi*, 2 represent *C. atrata* subsp. *atrata* and 1 either *C. dendyi* or *C. dendyi* and *C. atrata*.

Most of the characters used in Hooker's description do not differentiate between the 2 species. Only the phrase "florets . . . black when dry" refers to 1 species, *C. atrata*. The epithet *atrata* alludes to the black florets of *C. atrata* subsp. *atrata*. In 1915 Cockayne described *C. dendyi* as a separate species. Then Cheeseman (1925) reduced *C. dendyi* to a variety of *C. atrata*. Allan (1961) followed Cheeseman, but he designated Travers' specimen from the Wairau Gorge as the lectotype of *C. atrata*. This choice is not acceptable, since the speci-

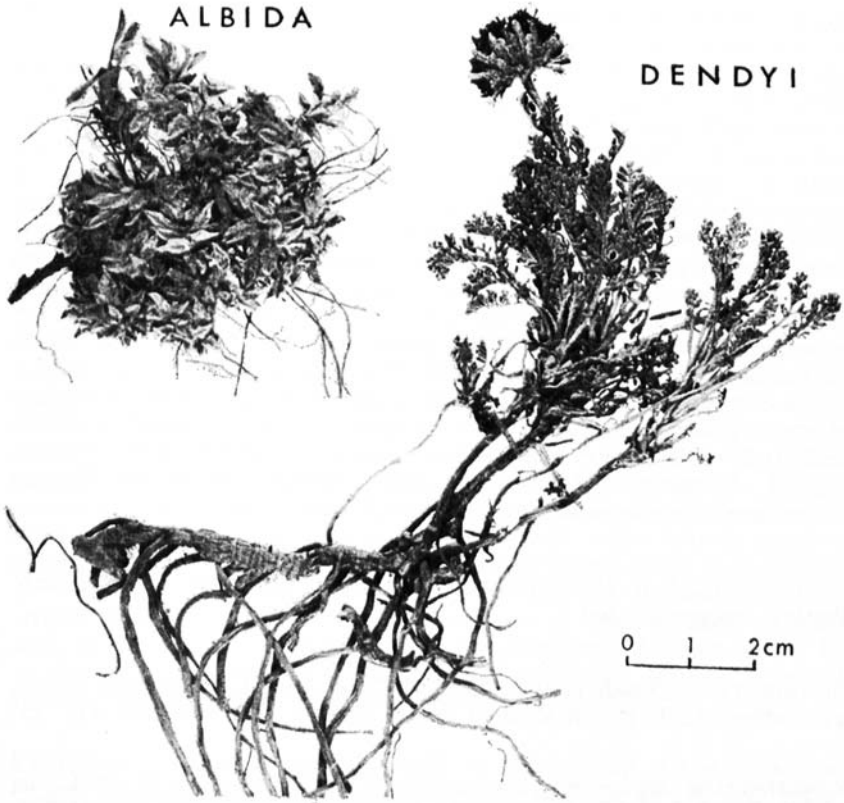


FIG. 21—Herbarium specimens of *C. albida* and *C. dندی*.

men does not belong to the typical variety recognised by Allan and does not match the description as well as other specimens cited by Hooker. The specimen chosen above as the lectotype is the left-hand specimen in the third row from the top of the sheet, and as far as can be judged is one of two pieces which belong to the label "Canterbury 1862, J. Haast, 642".

19. *Cotula goyenii* Petrie, Trans. N.Z. Inst. 18: 295, 1886.

A woody perennial herb forming tight mats 1–3 cm thick, in patches up to *ca.* 1 m wide. Rhizomes packed together, \pm horizontal and ascending at tips, obscured by crowded leaves; branches single or 2–3 clustered and diverging, at intervals of 0.5–3.0 cm; living leaves closely imbricate on apical *ca.* 0.5 cm of each stem; lower parts of

stems covered with persistent dead leaves. No short shoots. Roots issuing from lower parts of stems, slender but becoming subwoody, up to 0.5 mm diam. Leaves sessile, palmately divided, curved around stem, $4-6 \times 4-5$ mm; blade *ca.* 3 mm long, crescent shaped, coriaceous, dark green, with scattered short hairs; lobes us. 7, linear, subterete, in a half-circle with central lobes above shorter lateral lobes, acute to acuminate, cut to top of broad leaf base. Peduncles less or greater than leaves, up to 0.7 cm long, nude or with 1 small bract, pilose. Subdioecious? Heads not or scarcely emergent from mat surface, small, 2-4 mm diam.; surface convex; involucre hemispherical; phyllaries in 2 subequal rows, elliptic or oblong, thin, dark-green with wide, pale \pm keeled midrib, glabrous, with wide brown scarious margin, not growing after anthesis. Pistillate plants (?) with heads with 10-15 phyllaries and 20-45 pistillate florets; florets *ca.* 2.25 mm long, straight, yellow-red, corolla twice as long as wide, with equal teeth. Staminate plants (?) with heads with 8-12 phyllaries, 0 or 1-8 pistillate florets and 10-35 staminate florets. Achenes up to 1.3×0.65 mm, \pm compressed, biconvex, golden-brown shiny, scarcely wrinkled. Flowers in summer. Chromosome number, $2n=52$. Figs. 5, 23.

LECTOTYPE (Allan, 1961): Mount Pisa, 1885, D. Petrie, WELT! (Herb. Petrie); isotype at CHR!

DISTRIBUTION: South Island: Central Otago and E. Fiordland mountains above 1,300 m, on level or gently sloping ridge summits. Fig. 23.

REPRESENTATIVE SPECIMENS: Dunstan Mts, Central Otago, A. F. Mark, CHR 167259. Rough Peaks, L. Wakatipu, G. Simpson, CHR 95163. The Remarkables, above L. Alta, P. Wardle, CHR 179148. Hector Mts, A. F. Mark, OTA 23131. Mt Tennyson, Garvie Mts, D. G. Lloyd 66142, CANU. Carrick Ra., A. F. Mark, OTA 9054. Old Man Ra., B. Molloy and H. E. Connor, CHR 193071. Rock and Pillar Ra., E. Edgar, CHR 201994. Mt Burns, (Hunter Mts), D. R. Given, CHR 175017.

The compact woody branches and imbricate palmatifid leaves are unique in the genus and make *C. goyenii* difficult to assign to the correct genus, or even family, in the absence of reproductive structures. It grows intermingled with *C. pectinata* and *C. albida*, and occasional hybrids between *C. goyenii* and *C. pectinata* are found. (*C. goyenii* \times *albida*, if it occurs, is probably indistinguishable as herbarium specimens from *C. goyenii* \times *pectinata*). Such hybrids, with silky, pinnatisect leaves were named *C. goyenii* var. *pinnatisecta* by Kirk (1899, p. 326).

The breeding system of natural populations is not yet known in detail. Pistillate, staminate, and bisexual heads apparently occur in different proportions on various mountains, but larger samples must be analysed before it is certain whether all populations have two "sexes" of plants.

20. *Cotula albida* nom. nov.

Cotula pectinata var. *sericea* Kirk, Stud. Fl. N.Z.: 325, 1899, *Cotula sericea* (Kirk) Cockayne et Allan, Trans. N.Z. Inst. 57: 52, 1927, non *Cotula sericea* Linn. f. Suppl. 377, 1781, nec *Cotula sericea* Thunberg, Prodr. Pl. Cap. 1800.

A creeping perennial herb forming tight mats up to ca. 1 m wide, densely covered all over with long silky silver hairs. Rhizomes interwoven, \pm horizontal on soil surface or ascending and tightly packed, densely hairy; branches us. in clusters, up to 4 radiating from around a flowering node; leaves clustered near apex, remaining crowded or occ. older ones becoming up to 0.8 cm apart. No short shoots. Roots moderately stout for the size of the shoots, up to 0.5 mm diam. Leaves 1-pinnatifid, 4–10 \times 2–3 mm; blade coriaceous, dark green but hidden under a dense layer of woolly hairs; pinnae 4–8 pairs, very close-set and not easily discerned under the hairs, cut to rhachis, obovate, obtuse, without teeth. Peduncles longer than leaves, 1–2 cm, nude, densely woolly. Monoecious. Heads 3–10 mm diam.; surface convex; involucre subcampanulate; phyllaries ca. 20 in 2 subequal rows, oblong, grey-green but densely villous, with wide brown scarious margin, not growing after anthesis; pistillate florets 20–50 in 1–2 rows, 2.75 mm long, straight, pale yellow or yellow-red, sts with 1–2 dark stripes along corolla and ovary; corolla ca. 3 times as long as wide, with equal teeth; staminate florets more numerous. Achenes up to 1.6 \times 0.6 mm, \pm compressed, biconvex, golden-brown, scarcely wrinkled. Flowers in summer. Chromosome number, $n=26$. Figs. 2, 5, 21.

LECTOTYPE: Mount Cardrona, north of Arrowtown, Lake Wakatipu, Otago, D. Petrie (no date), CHR 68186!; ? isotypes at AK! and WELT!

DISTRIBUTION: Central Otago mountains, above 1,600 m. in herb fields. Fig. 22.

REPRESENTATIVE SPECIMENS: OTAGO: Old Man Range, D. Petrie, CHR 68186. Mount Pisa, D. G. Lloyd 66181, CANU.

It has been difficult to decide on the taxonomic status of *C. albida* and the boundary between *C. albida* and *C. pectinata*, because of the close similarity between the species and conflicts between species criteria. On the summits of Mts Cardrona and Pisa and The Old Man Range, but nowhere else as far as is known, there are silvery-white mat plants which are even more reduced, compact, and hairy than the extreme *C. pectinata* plants which can be found near or among them. The differences are confounded by the plasticity shown in *C. pectinata* and by considerable hybridisation between the two species. But chromosome counts indicate different levels of ploidy and the two phenotypes coexist despite the hybridisation between them. The present author feels these two entities deserve separation at specific level, in agreement with Cockayne and Allan, who separated Kirk's *C. pectinata* var.

sericea as *C. sericea*. The name *C. sericea*, however has been used previously (twice) for other species of *Cotula*, so the new name, *C. albida*, is presented here.

The situation is further confused by the occurrence of compact, densely hairy but greyish plants on the Wether and Hawkdun Ranges (cited under *C. pectinata* subsp. *villosa*). These latter plants are not definitely distinguishable from the extreme of the range of *C. pectinata* subsp. *villosa* on most mountains. The plants from the Wether Range, at least, have $n=26$, identical to *C. albida*, but differing from the $n=52$ found elsewhere in *C. pectinata*. If these plants are put into *C. albida* with the silver-hairy plants with the same chromosome number, and separated from *C. pectinata*, the resultant species could not always be morphologically distinguished. On the other hand, if all plants under consideration are put into *C. pectinata*, the older name, one would have on certain mountains two distinguishable biological species within a single taxonomic species. A compromise solution is adopted here, in which the distinct silvery, $n=26$ plants are retained as a species, *C. albida*, which is recognisable and is also reproductively isolated by ploidy level from the bulk of *C. pectinata*. The greyish $n=26$ plants from the Wether and Hawkdun Ranges are put into *C. pectinata*, which then possesses two ploidy levels which cannot be reliably distinguished by any morphological characters.

21. *Cotula pectinata* Hook.f., Handb. N.Z. Fl.: 142, 1864.

A highly variable creeping perennial herb forming loose patches on open ground or dense mats in closed herbfields. Rhizomes at or near soil surface, rather stout, up to 2 mm diam., dark, densely villous at least when young; branches in clusters of up to 4 radiating from around a flowering node or solitary at flowering nodes if internodes are long; leaves initially clustered at apex, sts remaining crowded, us. older ones becoming up to 2.0 cm apart. No short shoots. Roots often extensive and much-branched, stout, up to 1 mm diam. Leaves 1-pinnatifid, occ. simple, $0.7-4.0 \times 0.2-1.0$ cm; blade 0.5-3.0 cm, elliptic or obovate, coriaceous, silky green and densely villous to dark green and glabrous, midrib not raised on ventral surface; pinnae 1-10 pairs, occ. absent, close-set in exposed habitats but us. distant, cut to rhachis, oblong, obovate or linear, obtuse, teeth often 0 sts 1-3 pinna, mostly on proximal margin, cut ca. $\frac{1}{2}$ across pinna, triangular, obtuse. Peduncles longer than leaves, 1-10 cm, nude or with 1 simple bract, sparsely to densely villous. Monoecious. Heads 4-8 mm diam.; involucre subcampanulate; phyllaries 12-24 in 2 or more subequal rows, oblong, dark green or grey-green, with 1-3 dark veins sts obscured by sparse to dense hairs, with wide brown scarious margin, not growing after anthesis; pistillate florets 12-200 in 1-several rows, 2.25-2.75 mm long, straight, white or pale yellow-red, often with 1-2 dark stripes along corolla and ovary; corolla $1\frac{1}{2}$ -3 times as long as wide, with equal

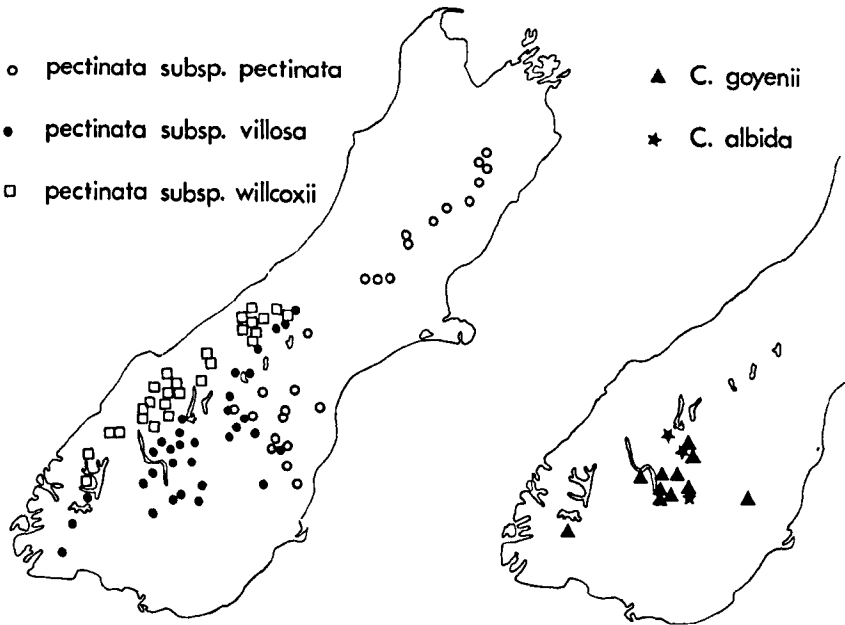


FIG. 22—Distribution of *C. goyenii*, *C. albida* and *C. pectinata*.

teeth; staminate florets more numerous. Achenes up to 2.1×0.7 mm, \pm compressed, biconvex, golden-brown, scarcely or deeply wrinkled. Flowers in summer. Chromosome numbers, $n=26, 52, 2n=52, 104$. Figs. 1, 5, 23.

LECTOTYPE (Allan, 1961): Canterbury Plains, 1862, J. von Haast, κ !

DISTRIBUTION: South Island: Marlborough to Southland, more often east of the main divide, 500–2,400 m, in a wide range of open grassland and herbfield habitats. Fig. 22.

KEY TO THE SUBSPECIES

- 1. Pinnae linear to narrowly obovate, usually more than 5 pairs, often hairy 2
- Pinnae broader, oblong to obovate, 5 or fewer pairs, glabrous 21c. subsp. willcoxii
- 2. Florets white 21a. subsp. pectinata
- Florets yellow to yellow-red 21b. subsp. villosa

21a. *Cotula pectinata* Hook.f. subsp. *pectinata*.

Plant forming loose patches or tight mats. Branches occ. solitary, usually in clusters of up to 4. Leaves clustered at the apex or older ones scattered along the rhizome; blade up to 3.0 cm long, elliptic or obovate, occ. broadly so; pinnae 1–10 pairs, occ. absent, linear and \pm cylindrical to flat and narrowly obovate. Leaves, peduncles and phyllaries almost glabrous to moderately villous. Florets white, 2.25–2.75 mm long. Achenes up to 2.1×0.7 mm. Chromosome number, $n=52$, $2n=104$. Fig. 5.

DISTRIBUTION: Marlborough to N. Otago, east of the main divide, in bare ground, especially on inactive scree and stony herbfields, usually not abundant.

REPRESENTATIVE SPECIMENS: MARLBOROUGH: Mt Murphy, Awatere R., J. M. Ward and M. T. Kalin 66359, CANU. CANTERBURY: (Mt) Terako, G. Simpson, CHR 95219. Shale Peak, Waiiau R., C. J. Burrows, CANU 6639. Puketeraki Ra., D. G. Lloyd 67701, CANU. Mt Enys, Cragieburn Ra., V. D. Zotov, CHR 21127. Fox Peak, W. Birchie, CHR 95221. Longslip Creek, Lindis Pass, 1700 ft A. F. Mark and J. Wells, OTA 15066. Mt Baldy, above Omarama Saddle, Wether Range, D. G. Lloyd 67506, CANU. Dansey's Pass, D. G. Lloyd 6701, CANU. Mt Kyeburn, B. C. Aston, Dec. 1898, CANTY (Carse Herb. 1601/1).

21b. *Cotula pectinata* subsp. *villosa* (Simp.) comb. nov.

Cotula villosa Simpson, Trans. Roy. Soc. N.Z. 79: 434, 1952, non *Cotula villosa* DC., Prodrromus 6: 79, 1838.

Leaves, peduncles and phyllaries occ. glabrous, us. moderately to densely villous. Florets yellow to yellow-red. Chromosome numbers, $n=26$, 52. Otherwise as in subsp. *pectinata*. Fig. 5.

LECTOTYPE (Allan, 1961): Mount Roy, Lake Wanaka, G. Simpson, 23 Dec. 1950, CHR 76029!

DISTRIBUTION: S.W. Canterbury, Otago and Southland, east of the main divide, common in grasslands and herbfields.

REPRESENTATIVE SPECIMENS: CANTERBURY: Macaulay R., C. J. Burrows, CANU 4639. Whale Stream, Ben Ohau Ra., M. T. Kalin 67629, CANU. Maitland Ra., L. Ohau, J. Mitchell, Massey Univ. Herb. (no date or no.). Above Lindis Pass, 4500 ft D. G. Lloyd 65516, CANU. Dansey's Pass, D. G. Lloyd 6702, CANU. Rock and Pillar Ra., E. Edgar, CHR 201997. Mt Baldy, above Omarama saddle, Wether Range, D. G. Lloyd 67509, CANU. Hawkdun Range, A. F. Mark and J. Wells, OTA 17807. SOUTHLAND: Upper Eyre Creek, Eyre Mts, A. F. Mark, OTA 26666. Mid-dome, R. Melville, CHR 140021. Green Lake, S.E. Fiordland, J. M. Ward 67093, CANU. Princess Range, J. Speden, 26 Jan. 1924, WELT.

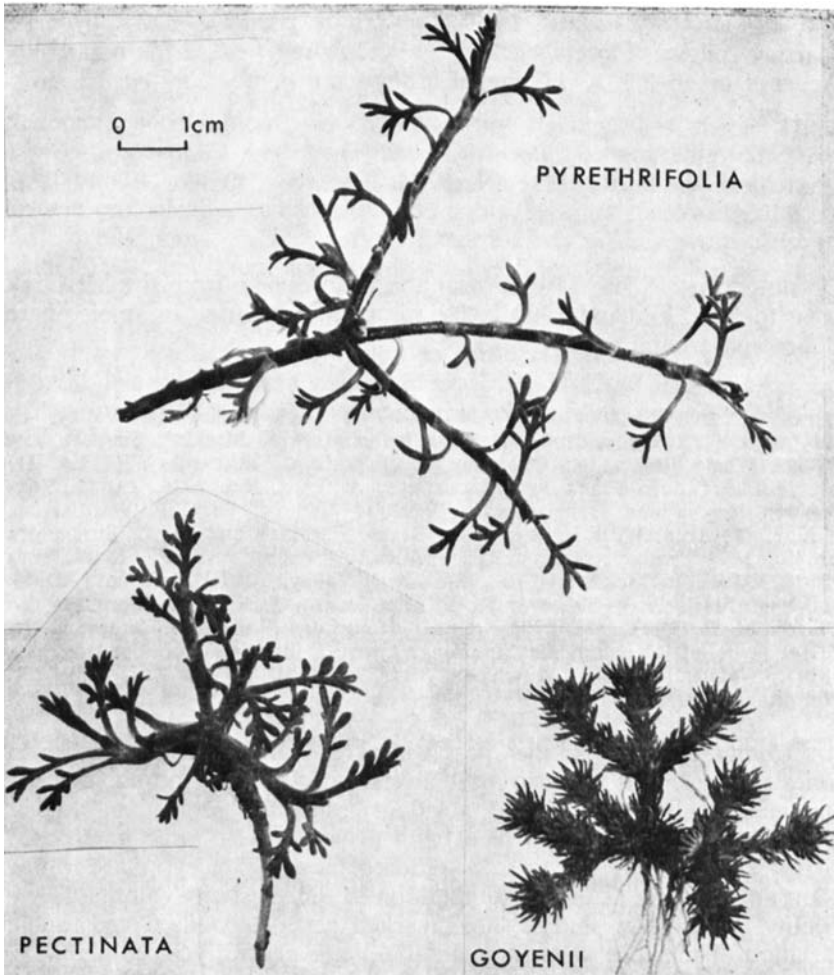


FIG. 23—Plants of *C. pyrethrifolia*, *C. pectinata* and *C. goyenii*. All are glass-house-grown plants and are laxer than is usual in nature.

21c. *Cotula pectinata* subsp. *wilcoxii* (Cheesem.) comb. nov.

Cotula wilcoxii Cheeseman, Trans. N.Z. Inst. 48: 212, 1916.

Cotula monticola Simpson, Trans. Roy. Soc. N.Z. 79: 434, 1952.

Plant usually laxer than other subsp., in diffuse irregular patches. Branches us. solitary at flowering nodes. Leaves us. scattered along rhizome; blade up to 1.0 cm long, broadly elliptic; pinnae 1-5 pairs,

flat, oblong to obovate. Leaves glabrous, peduncle and phyllaries sparsely pilose. Florets yellow to yellow-red, *ca.* 2.75 mm long. Achenes up to 2.3×1.0 mm. Chromosome number, $n=ca.$ 52, $2n=104$. Fig. 5.

LECTOTYPE (Allan, 1961): Near Mt Earnslaw, Otago, W. Willcox. AK 24966!

DISTRIBUTION: South Island: near the main divide, from the Mt Cook area to N. Fiordland, 900–2,400 m, beside streams, on moist bare slopes and around rocks.

REPRESENTATIVE SPECIMENS: CANTERBURY: Mid-Godley R. Valley, D. Scott, OTA 4478. Malte Brun, Mt Cook National Park, M. J. A. Simpson, CHR 204899. Whale Stream, Ben Ohau Ra., M. T. Kalin 67628, CANU. WESTLAND: Mt Moltke (above Franz Joseph Glacier), A. Wall, Jan. 1924, CANTY. Tops between Regina and Douglas Ras., Westland National Park, P. Wardle, CHR 179257. Mt Tole, Wills Valley, Haast R., A. F. Mark and M. L. Burke, OTA 23838. Mt Tyndar, Drake Ra., Waiatoto Valley, A. F. Mark, OTA 25704. OTAGO: McKerrow Ra., Makarora Valley, A. F. Mark, OTA 23343. South of Black Peak, Shotover R., P. Wardle, OTA 3329. Richardson Mts, W. Otago, A. F. Mark, OTA 27933. Upper Routeburn Valley, G. Simpson, CHR 75701 (type of *C. monticola* Simpson). Grave-Talbot Pass, G. Simpson, CHR 68447. Waterfall Creek (Murchison Mts, S. Fiord, L. Te Anau), W. R. Philipson, CANU 388.

Cotula pectinata is the most widespread and common species in series *Radiata*. It is also the most diverse species, both morphologically and ecologically. In sheltered positions, especially at lower altitudes, it is a lax almost glabrous plant with distant leaves, while in exposed higher situations it becomes a reduced, densely hairy, mat-forming plant approaching *C. albida*. In addition to this plasticity within a single locality, greenhouse studies show marked genetically-based geographic variation. The more western populations are generally more glabrous, with wider pinnae, and southern populations tend to be hairier in all parts. Variation patterns in these and other characters are complex, but three major groups of populations can be distinguished. Each occupies a considerable area largely separate from the other two, but there are peripheral contacts along two of the borders. Each of the population series is itself complex, but is distinguishable as a group by one or more morphological features and has a distinct ecology. The three population series are distinguished as subspecies.

Of the three subspecies, *villosa* is geographically and morphologically the central one. The other two subspecies are more closely related to *villosa* than to each other. Moreover, subsp. *villosa* comes into geographical contact with both subsp. *pectinata* and subsp. *willcoxii*, while the latter two are allopatric. The critical evidence for

the taxonomic status of all three involves the distinctions between subsp. *villosa* and each of the other two subspecies.

With regard to subsp. *pectinata* and *villosa*, there is only one character, floret colour, which invariably distinguishes them. Their general appearance and occurrence, however, is markedly different, since populations of subsp. *villosa* are much more abundant, more diverse ecologically, and hairier. The two subspecies meet along a long but narrow front, which curves from Dansey's Pass westwards to Lindis Pass and then northwards to the Two Thumb Range. Both subspecies have been found together on three mountains, and they probably meet elsewhere along the front. There appears to be considerable hybridisation where the two subspecies occur together, but at at least two of the observed localities, subsp. *villosa* has a generally higher distribution on the mountain, limiting their contact. Neither subspecies penetrates far into the range of the other. The situation closely resembles the zones of secondary hybridisation between parapatric taxa observed in animals (Mayr, 1963).

Subspecies *willcoxii* and *villosa* can usually be distinguished by the occurrence in *willcoxii* of a laxer habitat, fewer, broader, less hairy pinnae and larger heads. Subspecies *willcoxii* occurs near the main divide, while subsp. *pectinata* is usually found on drier mountains to the east. The few collections from the zone of intermediate climate between the two areas provide contradictory results.

In Otago and Southland, the westernmost populations of subsp. *villosa* resemble subsp. *willcoxii* so closely that herbarium specimens cannot be reliably identified as one or other subspecies. Under glass-house conditions, plants from the Eyre Mts and southern Fiordland are closer morphologically to subsp. *villosa* than to subsp. *willcoxii* and so are placed with the former. But a single live plant from Lake Ohau and herbarium specimens from the Shotover River are so nearly intermediate that they could equally well be placed in either subspecies. There may be a cline linking the subspecies in the middle part of their range.

In Canterbury, the characteristic form of subsp. *villosa*, with narrow somewhat hairy pinnae, extends farther west and overlaps slightly with subsp. *willcoxii* in distribution. On the Ben Ohau Range, the two subspecies occur together without apparent hybridisation (M. T. Kalin-Arroyo, pers. comm.). In this part of their range, subsp. *villosa* and *willcoxii* are distinct, in contrast to the continuum between them farther south.

The variability of *C. pectinata* plants is further confounded in some areas by polyploidy and hybridisation with *C. albida* (extensive) and *C. goyenii* (rare), as discussed under those species. The complex variation in *C. pectinata* will be considered in detail elsewhere.

22. *Cotula pyrethrifolia* Hook.f., Handb. N.Z. Fl.: 143, 1864.

A creeping perennial herb forming \pm discrete patches us. less than 1 m wide. Rhizomes on the soil surface or intertwined and lying on old decaying rhizomes, stout, 1–3 mm diam., dark and sparsely pilose, becoming woody and glabrous; branches us. clustered, up to 6 radiating from around a flowering node; leaves clustered at apex, but under better conditions older leaves up to 3 cm apart. No short shoots. Roots \pm extensive and stout, up to 20 cm long and 1 mm diam. Leaves 1-pinnatifid, occ. simple, 0.5–4.0 \times 0.3–1.0 cm (only *ca.* 1 mm wide if simple); blade 0.4–1.5 cm long, elliptic to obovate or broadly so, coriaceous, thick, dark green, glabrous, midrib not raised on ventral surface; pinnae 1–5 pairs, distant, cut to midrib, obovate, obtuse; teeth us. 0, occ. 1 on either side of larger pinnae, cut $\frac{1}{3}$ – $\frac{1}{2}$ across pinna, triangular. Peduncles longer than leaves, 2–12 cm, us. with 1–8 evenly spaced small linear bracts, occ. nude, sparsely pilose. Occ. monoecious, us. subdioecious with pistillate, staminate and bisexual heads common. Pistillate heads 0.5–1.5 cm diam.; surface flat or slightly convex; involucre hemispherical; phyllaries 20–110 in 2 or more subequal rows, oblong, dark green, with a single dark vein \pm evident, glabrous, with wide brown scarious margin, not growing after anthesis; florets 50–300 in numerous rows, 2.75–4.0 mm long, straight, white; corolla 2–4 times as long as wide, with equal teeth. Staminate heads larger, 0.5–1.8 cm diam.; surface convex; involucre spreading or flat; phyllaries 10–60; florets us. fewer, 40–300, occ. with a dark stripe down the broader part of the corolla. Bisexual heads intermediate; in subdioecious populations with all possible percentages of pistillate and staminate florets; in monoecious populations with 15–60 pistillate florets surrounding 50–90 staminate florets. Achenes up to 2.3 \times 1.0 mm, \pm compressed, biconvex, golden-brown or dark brown, scarcely wrinkled. Flowers in summer. Chromosome number, $n = ca.$ 78. Figs. 5, 23.

LECTOTYPE (Allan, 1961): Tarndale Plains, 4,000 ft, New Zealand Travers 35, κ !

DISTRIBUTION: North Island: Tararua Range. South Island: from Nelson and Marlborough south to the Two Thumb Ra, Canterbury; 600–2,000 m, along river margins and on rocky slopes and ridges. Fig. 24.

KEY TO THE VARIETIES

- Leaves 1-pinnatifid, with 1–4 pairs pinnae **22a. var. *pyrethrifolia***
 Leaves simple, linear, occ. with a single small lobe near the apex
 **22b. var. *linearifolia***

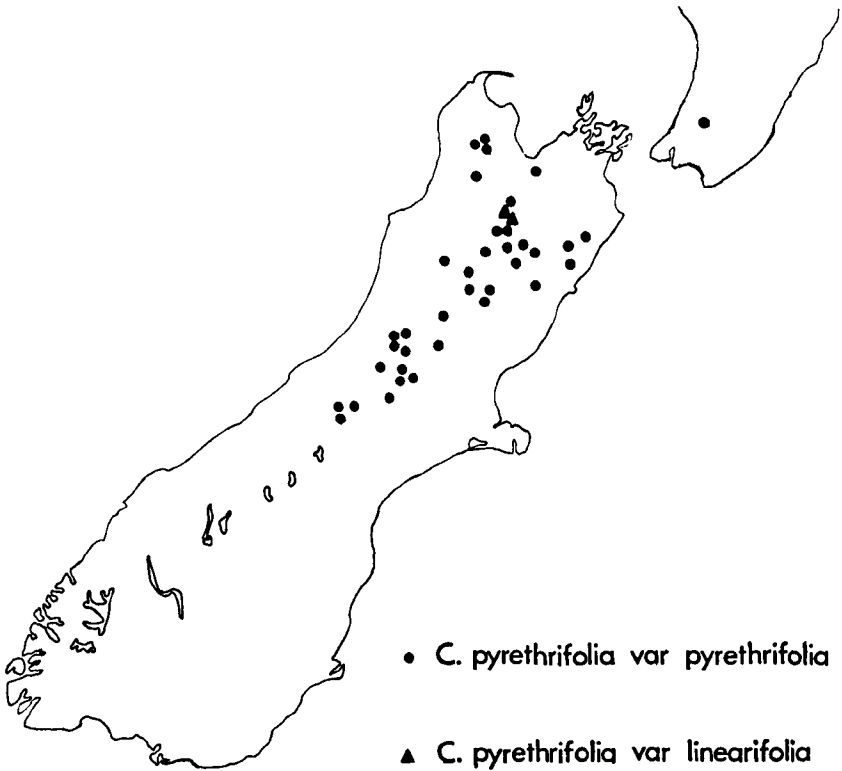


FIG. 24.—Distribution of *C. pyrethrifolia*.

22a. *Cotula pyrethrifolia* Hook.f. var. *pyrethrifolia*.

Cotula pyrethrifolia var. *robusta* Simpson, Trans. Roy. Soc. N.Z. 79: 433, 1952.

Leaves 1-pinnatifid, 0.5–4.0 × 0.3–1.0 cm, elliptic to obovate or broadly so; pinnæ 1–4 pairs, up to 5 mm long, distant, obovate. Achenes golden-brown. Chromosome number, $n=ca. 78$. Figs. 5, 23.

DISTRIBUTION: as for species.

REPRESENTATIVE SPECIMENS: WELLINGTON: Mt Hector, Tararua Ra., A. P. Druce, CHR 159845. Tararua Mts, N. Potts, CHR 75700 (type of *C. pyrethrifolia* var. *robusta* Simpson), CHR. MARLBOROUGH: Ben More, Ure River, A. Wall, CHR 68177. Team saddle (Saxton R.), J. M. Ward and M. T. Kalin, CANU 17189. NELSON: Cobb Valley, Mt Cobb, D. R. Given, CHR 190255. Mt Owen, D. G. Lloyd 65451, CANU. Ben Nevis, Richmond Range, D. H. Leigh, CHR 153836. Robert Range, Nelson Lakes National Park, A. P. Druce, CHR 159895. Victoria Range, D. G. Lloyd 65453, CANU. WESTLAND: Rangi Taipo, Jacksons, D. Petrie, Jan. 1893, WELT. Arthur's Pass, D. M. Calder,

CANU 7417. CANTERBURY: Mt St Patrick, Clarence R., D. G. Lloyd, 70053, CANU. Above Macmillan Stream, U. Hurunui R., D. G. Lloyd 67603, CANU. Mt Hamilton, Cragieburn Ra., R. Melville, CHR 68180. Upper Cameron River, D. G. Lloyd 66221, CANU. Cloudy Peak Ra., Rangitata R., B. Manson, CANU 17186. Trojan Valley, Two Thumbs Range, C. J. Burrows, CANU 17182.

22b. *Cotula pyrethrifolia* var. *linearifolia* (Cheesem.) comb. nov.

Cotula linearifolia Cheeseman, Trans. N.Z. Inst. 15: 299, 1883.

Leaves us. simple, entire, linear, 0.5–2.5 cm × 1 mm, occ. with a single oblong lobe up to 2 mm long near apex on one or both sides. Achenes dark brown. Chromosome number, $n=ca.$ 78. Fig. 5.

LECTOTYPE (Allan, 1961): Red Hills, Wairau Valley, alt. 4,500 ft, Jan. 1882, T. F. Cheeseman, AK 128753!

DISTRIBUTION: Red Hills and Raglan Range, border of Nelson and Marlborough, on serpentine soils.

REPRESENTATIVE SPECIMENS: Raglan Ra., Wairau Valley, T. F. Cheeseman, CANTY. Head of Motueka R., Red Hills, W. Martin, CHR 68176. Chrome Stream, Red Hills, D. G. Lloyd 66107, CANU.

In most areas, *Cotula pyrethrifolia* is readily distinguished from its closest relative, *C. pectinata*, by the thicker leaves and larger heads with white florets which vary from all male to all female in a head, even on the same plant. But the southernmost populations from the Two Thumbs to the Arrowsmith Ranges are more similar to *C. pectinata*, especially subspecies *willcoxii*, in having smaller leaves, shorter peduncles and smaller, invariably bisexual heads. They are still distinguished from *C. pectinata* subsp. *willcoxii*, however, by a chromosome number of $n=78$ and white florets. The differences between the southern populations and the bulk of *C. pyrethrifolia* probably represent the major phyletic division of the species, but they are difficult to observe. The recognition of the two groups as subspecies seems unwarranted in the absence of readily usable diagnostic characters.

The linear leaves of the plants described here as *C. pyrethrifolia* var. *linearifolia* enable this narrowly distributed edaphic ecotype to be readily distinguished. But in other respects, var. *linearifolia* plants closely resemble the pinnatifid populations surrounding them on all sides. The possession of one distinguishing morphological character, even a striking one, in a local race does not merit subspecific status. On the other hand, the recognition of a separate variety will ensure that the variation is not lost sight of.

North Island plants described by Simpson (1952) as var. *robusta* are supposedly "everywhere stouter". But populations from the South Island are plastic as well as geographically variable in size.

Populations from the two islands do not differ consistently in any character, so var. *robusta* cannot be maintained.

The only other striking geographical variation which persists under uniform cultivation involves Marlborough populations. The plants are generally smaller than those from elsewhere, with relatively broader pinnae. The extreme form, however, grades into the general populations, preventing the recognition of discrete taxa.

C. pyrethrifolia is not known to hybridise naturally with any other species.

23. *Cotula lanata* (Hook.f.) Hook.f., Handb. N.Z. Fl.: 141, 1864.

Leptinella lanata Hook.f., Fl. Antarct. 1: 25, tab. 19, 1844.

A robust but small-leaved, diffusely creeping perennial herb. Rhizomes on soil or rock surface, stout, 1–4 mm diam., covered with a thick mat of tangled woolly hairs but eventually becoming \pm glabrous, brown and slightly woody; branches us. clustered, up to 4 radiating from around a flowering node, often repeated every few nodes several times per season; leaves 2–4 clustered at the apex, most 2–5 cm distant. Short shoots us. absent, occ. present as a few reduced leaves. Roots largely confined to older stems, us. slender, up to 1 mm diam. Leaves 1-pinnatifid, 1.0–2.5 \times 0.4–1.0 cm; blade 0.5–2.0 cm long, broadly elliptic, thick, subfleshy, light green, with a few woolly hairs when young, especially on rhachis, later glabrous; midrib not raised on ventral surface; pinnae 3–5 pairs, distal ones overlapping, cut to rhachis, broadly elliptic or oblong if undivided; teeth up to 4 per pinna, on larger pinnae, mostly on distal margin, cut ca. $\frac{1}{2}$ across pinna, triangular, obtuse. Peduncles borne on rhizomes, longer than leaves, 1–3 cm, nude, slender but with a thick mat of woolly hairs. Monoecious. Heads 0.6–1.0 cm diam., surface hemispherical; involucre hemispherical; phyllaries ca. 30 in 2–3 subequal rows, broadly elliptic, thick and subfleshy, green with deciduous woolly hairs and a narrow us. transparent scarious margin, not growing after anthesis; pistillate florets 50–100 in 2 or more rows, ca. 3.0 mm long, almost straight, yellow-green, corolla twice as long as wide, with equal teeth, staminate florets fewer, 70–90. Achenes up to 2.3 \times 0.8 mm, not compressed, obscurely 4-angled, golden-brown, shiny, unwrinkled. Probably flowers from spring to autumn. Chromosome number, $2n=52$. Figs. 2, 6, 25.

LECTOTYPE (Allan, 1961): Auckland Is., J. D. Hooker 1447, κ !

DISTRIBUTION: Auckland and Campbell Islands, usually exposed coastal rocks and cliff tops, on peat or in rock crevices. Fig. 26.

REPRESENTATIVE SPECIMENS: AUCKLAND ISLANDS: Ewing Island, F. J. Fisher, CHR 134032b. Enderby Island, B. C. Aston, WELTU 5137. Cliffs close to sea, Carnley Harbour, L. Cockayne 2306, 23 Nov. 1907, WELT. CAMPBELL



FIG. 25—Plants of *C. plumosa* and *C. lanata*.

ISLAND: Cliff face, Courrejolles Peninsula, E. J. Godley, CHR 117997. South coast, R. L. O. (Oliver), 10 Dec. 1944, WELT. North of Penguin Bay, C. Meurk, CANU 15257.

The epithet *lanata* is appropriate, as the woolly rhizomes contrasting with the almost glabrous leaves give the species a distinct

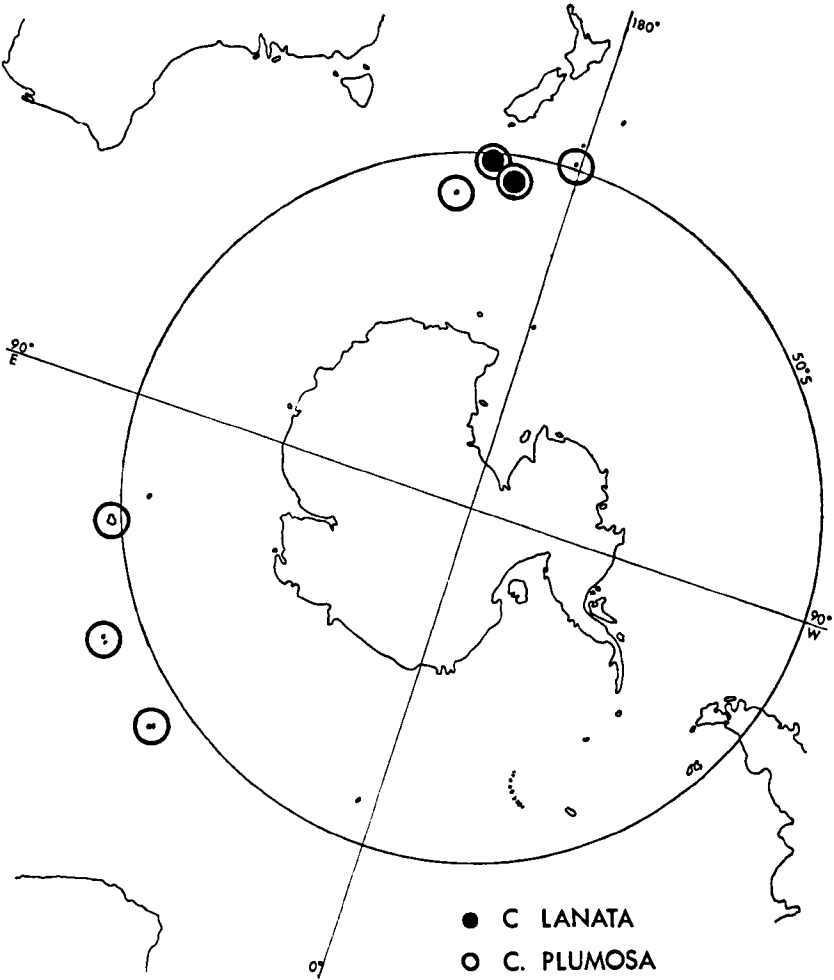


FIG. 26—Distribution of *C. plumosa* and *C. lanata*.

appearance. *Cotula lanata* hybridises occasionally with its closest relative, *C. plumosa*, where they occur together on Campbell and Auckland Islands, but such hybrids are not sufficiently abundant to create common problems of identification or to appreciably influence variation in either species.

24. *Cotula plumosa* (Hook.f.) Hook.f., Handb. N.Z. Fl.: 141, 1864.

Leptinella plumosa Hook.f., Fl. Antarct. 1: 26, tab. 20, 1844.

A highly plastic, shortly creeping perennial herb. Rhizomes on soil surface, us. very thick, up to 1 cm diam., green, hard, glabrous

to thinly but uniformly covered with tangled woolly hairs; branches single or clustered around flowering nodes, sts repeated several nodes later; leaves 4–8 tufted at the apex, older ones scattered up to 4 cm apart. Short shoots us. absent. Roots largely confined to older stems, up to 1 mm diam. Leaves very variable in size and divisions, 1–2 pinnatifid, 5–20 × 1–6 cm; blade 4–12 cm long, elliptic or broadly so, soft, light green, glabrous to moderately villous especially along rhachis, midrib not raised on ventral surface; pinnae 5–20 pairs, slightly overlapping, cut to rhachis, elliptic; secondary pinnae up to 13 per pinna, most on distal margin, cut to rhachis, simple and narrowly triangular or divided and elliptic; tertiary pinnae 0–6, mostly on outer margin of secondary pinnae, oblong or narrowly triangular; final divisions acute. Peduncles shorter than leaves, 6–12 cm, nude or with one simple or scarcely divided bract, with dense deciduous woolly hairs. Monoecious. Heads *ca.* 1 cm diam.; surface hemispherical; involucre hemispherical; phyllaries *ca.* 20 in 2 subequal rows, oblong or elliptic, thick, green, ± hairy when young, with a wide brown scarious margin (or tip only), not growing after anthesis; pistillate florets 90–260 in 3–6 rows, *ca.* 2.75 mm long, almost straight, yellow-green; corolla twice as long as wide, with equal teeth; staminate florets fewer or equal. Achenes up to 1.9 × 0.8 mm, not compressed, obscurely 4-angled, golden-brown, with a few shallow wrinkles. Probably flowers from spring to autumn. Chromosome number, $2n=52$. Figs. 2, 6, 25.

LECTOTYPE (Allan, 1961): Auckland Is., J. D. Hooker 1448, κ!

DISTRIBUTION: Antipodes, Campbell, Auckland, Macquarie, Kerguelen, Crozet, and Marion Islands, usually around harbours and bays in salt marshes and wet depressions, less often on bare ground inland and exposed ridges. Fig. 26.

REPRESENTATIVE SPECIMENS: AUCKLAND ISLANDS: Ewing Island, F. J. Fisher, CHR 134033. Adams Island, B. C. Aston, Nov. 1907, WELT (Herb. Petrie). CAMPBELL ISLAND: Camp Cove, Perseverance Harbour, W. B. Brockie 13 Dec. 1946, WELT. Tucker Cove, W. B. Brockie 19 Dec. 1946, WELT. Monument Harbour, J. H. Sorensen, 18 March 1947, WELT. Windlass Bay, R. L. Oliver, 5 Nov. 1944, WELT. Lyall Ridge, R. L. Oliver, 26 Nov. 1944, WELT. ANTIPODES ISLAND: E. G. Turbott, AK 26549. MACQUARIE ISLAND: H. Hamilton, AK 10363. KERGUELEN ISLAND: J. M. Coulter, F 994721.

Plants collected from different islands do not differ consistently in any character. As it occurs in a wide variety of habitats, *Cotula plumosa* is a highly plastic species; variation on Kerguelen Is. is described and figured in Chastain (1958). C. Meurk (pers. comm.) observed on Campbell Is. that "it attains its greatest luxuriance in salt marshes, sea elephant wallows and along sheltered water courses near the sea; while on exposed ridges, on peat or mineral soil, and on rocks it becomes dwarfed to superficially resemble *C. lanata*". Hybrids are occasionally found between *C. plumosa* and either *C. lanata*, *C. potentillina*, or *C. dispersa* (see under those species).



FIG. 27—Shoot of *C. featherstonii*. One of the radiating branches has been removed for clarity before the photograph was taken. The scale is in millimetres.

25. *Cotula featherstonii* (F. v. Muell.) Hook.f., Handb. N.Z. Fl.: 733, 1867.

Leptinella featherstonii F. v. Muell., Veg. Chatham Is.: 27, tab. 5, 1864.
Cotula renwickii Cockayne, Trans. N.Z. Inst. 47: 119, 1915.

A robust, luxuriant suberect perennial herb. Stems erect or later becoming decumbent, 0.2–1.2 m tall, thick, up to 6 mm diam., green, hard, subwoody at base, incompletely ringed at intervals with old leaf-scars and sparsely covered with short deciduous hairs; branches clustered, us. 3–4 diverging from a flowering node and the nodes immediately behind, often repeated at later nodes several times per season; leaves several clustered at the apex, older ones scattered 0.2–3.0 cm apart. Roots not seen. Leaves simple, almost sessile, 1.5–4.0 × 0.7–1.7 cm; blade obovate, narrowing into ill-defined petiole and leafbase, tender, grass-green, glabrous to thickly and evenly covered with soft, suberect, ± deciduous hairs, midrib and principal veins evident on both surfaces, with 0–3 shallow triangular obtuse teeth on either side just below the apex. Peduncles shorter than leaves, 1–2 cm, with 0 or a few small bracts, villous. Monoecious. Heads ca. 1 cm diam.; surface hemispherical; involucre hemispherical; phyllaries 10–15 in 1–2 subequal rows, broadly elliptic, rather thick, green with 1–3 brown veins evident, sparsely pilose, with a narrow transparent scarious margin around the apex only, not growing after anthesis; pistillate florets ca. 200 in 6 or more rows, ca. 2.0 mm long, almost straight, yellow-green; corolla ca. 3 times as long as wide, blunt, with equal teeth; staminate florets fewer, ca. 130. Achenes up to 1.5 × 0.7 mm, slightly compressed, chocolate-brown, striated with 2 lateral, 2–4 anterior and 2–4 posterior pale ribs, unwrinkled. Probably flowers from spring to autumn. Chromosome number not known. Figs. 2, 6, 27.

LECTOTYPE: Chatham Islands, damp rocks near the sea, S.E. side, H. H. Travers No. 27, MEL 42209! Isotype at WELT (Herb. Petrie ex Herb. Mueller)!

DISTRIBUTION: Chatham Islands (in the vicinity of mutton-bird nests, on peaty ground, Cockayne, 1901), near the coast of the main island and offshore islets. Fig. 28.

REPRESENTATIVE SPECIMENS: CHATHAM ISLANDS: Kaingaroa, W. Martin, CHR 68174. The Sisters Islands, L. C. Bell, CHR 83371. South East Island, G. Kelly, CANU 15608. Sea coast, Matarakau, N. Chatham Island, L. Cockayne, 4 Feb. 1901, WELT. Forty Fours Islets, Maori fishermen per F. A. D. Cox, WELT (Cockayne Herb, holotype of *C. renwickii* Ckn.)

Possessing a suberect habit, almost sessile leaves, and ribbed achenes, *C. featherstonii* is anomalous in section *Leptinella*. The leaves and achenes resemble those of *Centipeda* rather than other *Cotula* species, as Mueller (1864) observed in the original description

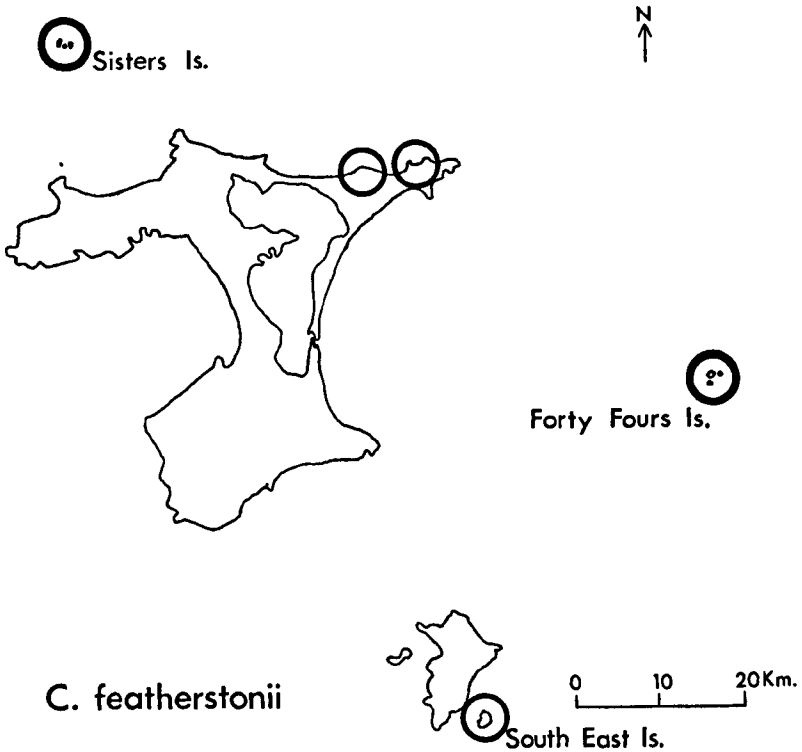


FIG. 28—Distribution of *C. featherstonii* in the Chatham Islands. The type locality, from the southeast side of Chatham Island, has not been indicated, as its exact position is not known.

of the species. But this resemblance is probably the result of secondary convergence, rather than an indication of close relationship between *Centipeda* and *C. featherstonii*. The female florets of *C. featherstonii* are characteristic of *Leptinella* and the size, texture, and teeth of the leaves differ from those of *Centipeda*. The clustered branches, monoecy, stem anatomy, and the shape of the involucre and florets in *C. featherstonii* clearly indicate affinities with other species of section *Leptinella*, series *Radiata*. Despite the peculiarities of *C. featherstonii*, its taxonomic position is evident.

The suberect habit with hard subwoody stems differs from all other species of *Cotula*, but is apparently derived from the prostrate condition found in other section *Leptinella* species. This is suggested by the position of the peduncles and the form of branching. In *C. featherstonii*, as in other *Leptinella* species, a head is borne on an axillary shoot which is additional to the vegetative axillary bud at the same node. Furthermore, the only axillary buds which develop into

vegetative shoots are those associated with the flowering nodes. This pattern of growth in *Cotula* is otherwise confined to prostrate species.

Cotula renwickii was described by Cockayne as a distinct species "evidently closely related to *C. featherstonii*, but easily recognised by its greater stature, its stem ringed with old leaf-scars, its thin glabrous leaves . . . , its shorter peduncles and much larger flower heads". Of these characters, *C. featherstonii* does in fact possess the leaf scars (Fig. 27). Moreover, the size of the plants, peduncles, and heads in the only two available sheets of *C. renwickii* appears to be within the wide range present in the more numerous collections of *C. featherstonii*. The remaining characters, the thickness and hairiness of the leaves, vary much in *C. featherstonii*: the leaves are initially hairy, but the hairs are sometimes lost very quickly. As Cockayne observed, the leaves are thinner and more glabrous in the sheets of *C. renwickii* from the Forty Fours Islets than is usual in *C. featherstonii*. But the differences are small and could easily be induced by conditions on the Forty Fours Islets. Since the differences between *C. featherstonii* and *C. renwickii* are so slight and perhaps not even genetically based, *C. renwickii* has been reduced to a synonym of *C. featherstonii*.

The habit of plants of *C. featherstonii* on The Sisters and Forty Four Islets is evident in photographs of the nest sites of albatrosses and mollymawks in figs. 10-13 in Knox (1957).

ACKNOWLEDGMENTS

I am grateful to the many collectors who have provided live and dried material, including Dr C. J. Burrows, Mr A. P. Druce, Mrs F. Duguid, Mrs P. Hynes, Dr M. T. Kalin-Arroyo, Mr G. C. Kelly, Mr C. Meurk, Dr B. P. J. Molloy, Dr M. Noonan, Miss J. M. Ward, Mr R. Wilson. The curators of the following herbaria allowed me to examine material: Auckland University; Auckland Institute and Museum; Massey University; Dominion Museum; Victoria University; Forest and Range Experiment Station, Rangiora; Canterbury Museum; Lincoln College Field Club; Botany Division, DSIR, Lincoln; University of Otago; Kew Herbarium; Chicago Natural History Museum; Michigan State University; Missouri Botanic Garden; New York Botanic Garden; National University of Cordoba; University of Concepción; National Herbarium of Victoria; Western Australian Herbarium; Bolus Herbarium, Cape Town; Central National Herbarium, India. I also wish to thank Mr R. Wilson for growing plants and Mr F. E. McGregor for assisting with the photographs. Dr J. B. Hair kindly supplied unpublished chromosome counts. Professor D. A. Kidd prepared the Latin diagnoses. Dr J. A. Caro provided information on the South American literature. Part of the work was done while the author held a Miss E. L. Hellaby Indigenous Grasslands Research Fellowship. A field trip to Fiordland was sponsored by the Royal Society of New Zealand.

REFERENCES

- ALLAN, H. H., 1961: "Flora of New Zealand", Vol. 1. Government Printer, Wellington.
- BENTHAM, G., 1867: "Flora Australiensis", Vol. 3. Reeve, London.

- 1873a: Notes on the classification, history and geographical distribution of Compositae. *Journal of Linnaean Society, Botany* 13: 335-577.
- 1873b: Compositae. In G. Bentham and J. D. Hooker "Genera Plantarum", Vol. 1. Reeve, London.
- CABRERA, A. L., 1939: Las Compuestas del Parque Nacional del Nahuel Huapi. *Revista del Museo de La Plata (N.S.)* 2, Sección botánica: 227-396.
- 1954: "Polygyne" y "Lefrovia". Universidad Nacional de Eva Peron, Notas del Museo 17 (Botanica No. 35): 167-71.
- CANDOLLE, A. P. 45, 1838: "Prodromus Systematis Naturalis", Vol. 6. Truethel and Würtz, Paris.
- CARO, J. A., 1961: Las especies de *Cotula* (Compositae) del Centro de la Republica Argentina. *Kurtziana* 1: 289-98.
- CASSINI, H., 1822: Proposition d'un nouveau genre de plantes (*Leptinella*). *Bulletin de la Société Philomathique de Paris, Series* 3, 9: 127-9.
- 1834: "Opusculs Phytologiques", Vol. 3. Levrault, Paris.
- CHASTAIN, A., 1958: La flore et la vegetation des Iles de Kerguelen. *Mémoires du Muséum nationale d'histoire naturelle, N.S. Ser. B (Botanique)* 11: 1-136.
- CHEESEMAN, T. F., 1925: "Manual of the New Zealand Flora", 2nd. ed. Government Printer, Wellington.
- COCKAYNE, L., 1901: A short account of the plant-covering of Chatham Island. *Transactions of New Zealand Institute* 34: 243-325.
- 1915: Some new species of New Zealand flowering plants. *Transactions of New Zealand Institute* 47: 111-8.
- 1927: Ecological Botany of the Canterbury Plains. In R. Speight *et al.* "Natural History of Canterbury". Simpson and Williams, Christchurch.
- DIERS, L., 1961: Der Anteil an Polyploiden in den Vegetationsgürteln der West Korbillere Perus. *Zeitschrift für Botanik* 49: 29-488.
- EDGAR, E., 1958: Studies in New Zealand *Cotulas*. *Transactions of the Royal Society of New Zealand* 85: 357-77.
- GODLEY, E. J., 1969: Additions and corrections to the flora of the Auckland and Campbell Islands. *New Zealand Journal of Botany* 7: 336-48.
- 1970: Botany of the Southern Zone. Exploration, 1847-1891. *Tuatara* 18: 49-93.
- HAIR, J. B., 1962: Basic chromosome numbers in *Cotula*. *Chromosome Information Service* 3: 41-2.
- HAMLIN, B. G., 1967: Itinerary of Leonard Cockayne's botanical expeditions. *Records of the Dominion Museum, Wellington* 5: 265-76.
- HARVEY, W. J., 1865: Compositae. In W. J. Harvey and O. T. Sonder (Editors) "Flora Capensis," Vol. 3. Reeve, London.
- HOFFMANN, O., 1890-94: Compositae. In A. Engler and K. Prantl (Editors) "Die Natürlichen Pflanzenfamilien". Vol. 4 (5): 87-391 Engelmann, Leipzig.

- HOOKER, J. D. 1844: "Flora Antarctica", Vol. 1: 25-9. Reeve, London.
- 1847: Flora Tasmaniae Spicilegium. *London Journal of Botany* 6: 106-25.
- 1852: "Flora Novae-Zelandiae", Vol. 1: 127-30. Reeve, London.
- 1856: "Flora Tasmaniae", Vol. 1: 191-4. Reeve, London.
- 1864: "Handbook of the New Zealand Flora". Reeve, London.
- HOOKER, W. J. and ARNOTT, G. A. W., 1841: Contributions towards a flora of South America and the Islands of the Pacific. *London Journal of Botany* 3: 310.
- KIRK, T., 1899: "The Student's Flora of New Zealand". Government Printer, Wellington.
- KNOX, G. A., 1957: General account of the Chatham Islands 1954 Expedition. *New Zealand Department of Scientific and Industrial Research, Bulletin* 122: 1-37.
- KOCH, C., 1843: Einiges über *Cotula*, *Strongylosperma* und *Cenia* Less. u De C. *Botanische Zeitung* 1: 37-42.
- LAING, R. M., 1919: The vegetation of Banks Peninsula, with a list of species (flowering-plants and ferns). *Transactions of New Zealand Institute* 51: 355-408.
- LESSING, C. F., 1832: "Synopsis Generum Compositarum". Duncker and Humbolt, Berlin.
- LEVYNS, M. R., 1941: Notes on *Cotula* and the description of a new species. *Journal of South African Botany*, July 1941: 131-4.
- MALIK, C. P., 1960: Chromosome number of some Dicotyledons. *Science and Culture* 25: 437.
- MAYR, E., 1963: "Animal Species and Evolution". Belknap Press, Cambridge.
- MEHRA, P. N., GILL, B. S., MEHTA, J. K. and SIDHU, S. S., 1965: Cytological investigations on the Indian Compositae. I. North Indian taxa. *Caryologia* 18: 35-68.
- MILLER, A. and MARTIN, W., 1953: History and composition of the Dunedin bowling greens. *Report of the Proceedings of the Conference of Bowling Greenkeepers and Green Superintendents, Dunedin, 20-22 May, 1953.*
- MUELLER, F. VON, 1864: "The Vegetation of the Chatham Islands". Government Printer, Melbourne.
- PHILLIPS, E. P., 1950: Descriptions and changes of name. *Journal of South African Botany* 16: 21.
- SIMPSON, G., 1952: Notes on some New Zealand plants and descriptions of new species (No. 5). *Transactions of the Royal Society of New Zealand* 79: 419-35.
- TURNER, B. L., 1970: Chromosome numbers in the Compositae. XII Australian species. *American Journal of Botany* 57: 382-9.
- WALL, A., 1922: "The Botany of Christchurch". A. H. and A. W. Reed, Wellington.