

The results of morphological studies are the main basis for the taxonomic treatment herein, but much useful comparative data have come from field studies, garden cultures, distribution patterns, artificial hybridisations, and chromosome counts. The term *species* when used here refers to a population system which is internally homogeneous with respect to most of the properties of its members and is separated from other related groups by discontinuities in morphology. These discontinuities have been shown to be the result of some genetic, geographical, and/or ecological barriers to any large-scale gene exchange. The term *subspecies* refers to two or more regional facies of a species which possess relatively minor distinguishing features; the term *variety* is not used. The foregoing statements refer to the taxonomic structure, which has seemed to be the most practical and useful method of handling the rather complex pattern of variation exhibited by this group of *Senecio* species.

Since the four species discussed in this paper have, at one time or another, been considered synonymous, the term "species complex" is used in this historical sense and does not connote the meaning of a group of closely related species. The treatment of this group of species was evolved as a result of the analysis and integration of a number of lines of evidence. It was necessary to examine all the available herbarium material of members of the complex and of related species, to collect living material, to observe populations in the field, to review pertinent literature, and to conduct breeding experiments and cytological investigations. Using these methods, it has been possible to construct a reasonably workable taxonomic framework into which the majority of the specimens of the complex fit and which seems to reflect natural relationships more adequately than have the previous taxonomic treatments of the group.

ACKNOWLEDGMENTS

It is a pleasure to take this opportunity to thank Professor H. D. Gordon and the faculties of the Botany and Zoology Departments at Victoria University of Wellington for their hospitality during my stay in New Zealand. Special thanks are due the late H. H. Allan, G. T. S. Baylis, T. Carrick Chambers, John W. Dawson, A. P. Druce, N. L. Elder, C. Leo Hitchcock, M. D. King, George Mason, Lucy B. Moore, Mrs. P. R. Woodhouse, Sheila Natusch, Graham Pritchard, Graeme Ramsay, Ross G. Robbins, G. M. Schulze, Margaret Simpson and Colwyn Trevarthen, who have contributed in various ways to the completion of this work. I would also like to thank the staffs of the herbaria for extending the use of their facilities and making loans during the course of the project. I am deeply indebted to A. R. Kruckeberg, of the University of Washington, for his valuable advice on many of the problems which arose from time to time. Finally, I gratefully acknowledge the generous financial support of the United States Educational Foundation in New Zealand.

KEY TO THE TAXA OF THE *Senecio lautus* COMPLEX

The roman numerals preceding the names of the taxa in the key refer to the sequence of the discussions of the taxa in the systematic section.

- (1) Plants annual or short-lived perennials, mainly coastal; leaves usually pinnatifid (2).
- (1) Plants perennial, usually not coastal, but if so (on the eastern coast of the South Island) then the leaves usually merely serrate, or if pinnatifid then the heads borne in corymbs (5).
- (2) Leaves membranous, 5-18 cm long, pinnatifid with broad lobes and broadly winged petioles; herbage arachnid-tomentose when young; Chatham Islands.

III. *Senecio radiolatus*

- (2) Leaves usually somewhat fleshy and otherwise not as above (3).
 (3) Heads large, the disk 1.5–2 cm in diameter; leaves to 10 cm long, pinnatifid; habitat the nesting grounds of sea-birds on offshore islands.

II. *Senecio sterquilinus*

- (3) Heads smaller, the disk well under 1.3 cm in diameter; leaves merely serrate, but if deeply pinnatifid then under 6.5 cm long and habitat not as above (4).
 (4) Plants fleshy and very succulent, low, sparingly branched; the leaves entire or pinnatifid with broad lobes, the leaf margins revolute; internodes shortened and the leaves subopposite or whorled at least below; ray florets recurved, the ligules under 4 mm long.

Ib. *Senecio lautus* ssp. *carosulus*

- (4) Plants fleshy, but not succulent; low or erect much-branched plants, the leaves usually pinnatifid at least above, the leaf margins not revolute; ray florets with ligules usually over 4 mm long and not revolute.

Ia. *Senecio lautus* ssp. *lautus*

- (5) Ligules absent; plants of scree of the North and South Island mountains.

IVd. *Senecio glaucophyllus* ssp. *discoideus*

- (5) Ligules present; plants of more stable ground (6).
 (6) Stems erect, branched from the base but usually simple above; leaves pinnatifid; heads usually borne in corymbs.

IVc. *Senecio glaucophyllus* ssp. *raoulii*

- (6) Stems erect or decumbent, but leaves not deeply pinnatifid (7)
 (7) Stems erect, branched at the base but usually quite simple above; leaves serrate; heads borne in corymbs; plants of higher altitudes in the northern South Island.

IVa. *Senecio glaucophyllus* ssp. *glaucophyllus*

- (7) Stems erect or decumbent, simple or more often freely branched above; leaves serrate or incised; heads borne loosely; plants of coastal areas in the eastern South Island.

IVb. *Senecio glaucophyllus* ssp. *basinudus*

HERBARIUM STUDIES

The following herbaria were visited or furnished loans of material of the species in the *Senecio lautus* complex; abbreviations which are used in the text and specimen citations are those suggested by Lanjouw and Stafleu (1956). The abbreviation marked with an asterisk is not listed by them and is original. Since many New Zealand collectors do not use collection numbers, the citations of representative herbarium specimens which follow the discussion of each taxon are transcriptions from the labels on the specimens. If duplicates are present in other herbaria these transcriptions should facilitate their identification. Specimens cited in the text are not listed again in the sections listing representative specimens.

Auckland Institute and Museum, Auckland (AK).

Bernice Bishop Museum, Honolulu (BISH).

Botany Division, DSIR, Christchurch (CHR).

Canterbury Museum, Christchurch (CANTY).

Royal Botanic Gardens, Kew (K).

British Museum, Natural History (BM).

National Herbarium of Victoria, South Yarra (MEL).

Museum of Natural History, Paris (P).

Otago University, Dunedin (OTU).*
Dominion Museum, Wellington (WELT).

SYSTEMATIC TREATMENT

Ia. *Senecio lautus* Solander ex Willd. Sp. Pl. 3: 1804. (ssp. *lautus*).

S. lautus Sol. Prim. Fl. N.Z., unpublished MS., after 1771.

S. lautus Forst. Fl. Ins. Austral. Prodr. 1786. nomen nudum.

? *S. angustifolius* Forst. (non L.) Fl. Ins. Austral. Prodr. 1786. nomen nudum.

S. neglectus A. Rich. Essai Fl. Nouv.-Zel. 258. 1832.

S. australis var. *β unidentatus* DC. Prodr. 6: 374. 1837. (Cited for N.Z. and Tasmania) pro parte.

S. lautus var. *α lautus* Hook. f. Fl. Nov.-Zel. 2 (1): 145. 1853. pro parte.

S. lautus var. *a* Cheesem. Man. N.Z. Fl. 373. 1906 (including *carnosulus*).

A variable, much branched glabrous to villous annual or short-lived perennial herb; the prostrate to ascending branches 15–35 cm long, leafy throughout, the stems often purplish-pigmented; lower leaves lance-ovate in outline, entire to sparingly toothed, petiolate, often withering early; middle cauline leaves 3–6.5 cm long, lance-ovate to oblong in outline, deeply once-pinnatifid, the principal lateral lobes remote, narrowly oblanceolate or linear, these lobes frequently entire or sparingly toothed, the lamina in the sinuses between the lobes usually entire; terminal lobe usually larger than the lateral lobes; upper leaves reduced, sessile, with a lacerate or nearly entire auriculate clasping base; heads cylindrical, borne loosely at the ends of branches throughout the plant; involucre 4.5–5.5 (7) mm high, the bracts numbering 11–13, villous at the often black tips; disk 5–10 mm in diameter; the ligules about 13, yellow, narrowly elliptic-oblong (3.5) 5–7 (9) mm long, rarely shortened and barely exceeding the involucre, 1.3–2 (2.7) mm wide; cypselas 2.5–3 mm long, grooved, strigose overall or merely in the grooves; *n* = 20. Fig. 2.

Senecio lautus has had an exceedingly confused nomenclatural history. This confusion stems from several sources, including application of the name to many Australian taxa, application of the name to other New Zealand species, and bibliographic and historical errors. The synonymy is difficult to work out since many of the early collectors were not careful in their notations on specimens. Original material of all the names listed in the synonymy has been seen with the exception of the De Candolle specimen.

The type specimen of the species is No. 15757 in Willdenow's herbarium preserved at Berlin-Dahlem; isotypes are at Kew and the British Museum (Natural History). In his cursory description of the species Willdenow (1804) cited only the Forsters' specimens and indicated the range of the species as simply New Zealand. Photographs of the Willdenow types of both *Senecio lautus* and *S. australis* were furnished through the kindness of Dr. G. M. Schulze of Berlin-Dahlem. The photograph of the fragment of *Senecio australis* leads to the conclusion that this name should probably not be considered synonymous with *S. lautus* since there is little resemblance between the two specimens. Schulze wrote that these specimens had been given Willdenow by Sprengel; according to Merrill (1954) Sprengel's specimens were originally from the Forster collections. Thus the lineage would appear to be quite clear. However, in 1826 Sprengel listed *Senecio lautus* and followed his short descriptive paragraph with the obscure statement "Falsum habet Willd.". Since this remark applies to the holotype it could have considerable importance were its significance known. At the present time an acceptance of the Forster specimen as valid would seem to be the wisest course to follow. Duplicates of this collection are at Kew and the British Museum (Natural History) and closely resemble the Willdenow specimen.

The type locality is unknown, but the ships carrying J. and G. Forster anchored at Dusky Bay for some weeks and in Queen Charlotte Sound on three occasions. Since the type collection was made just as the plants were coming into flower, it is likely that the collection was made by the Forsters on their second (November) visit to the Sound.

The typical subspecies of *Senecio lautus* occurs on cliffs, rocks, or sand dunes of the coastal areas of the North Island and probably in similar habitats along the northern and eastern portions of the South Island coast. It has also been collected from the Chatham Islands. Plants may occur as scattered individuals or in colonies of several dozen individuals. In flower September to June.

The precise limits of the distribution of *Senecio lautus* ssp. *lautus* are difficult to determine. In addition to the areas mentioned above, it has been reported from Stewart Island and vicinity by Cockayne (1909) and Poppelwell (1912; 1916; 1918). Since there are no specimens in New Zealand herbaria confirming these observations it is not known whether these reports refer to *Senecio lautus* or to one of the subspecies of *S. glaucophyllus* formerly considered as *S. lautus*. The species has not been reported or collected on the subantarctic islands (Hamilton, 1895; Chilton, 1909; Oliver and Sorensen, 1951). It has not been recorded from Lord Howe Island (Oliver, 1917) and the one Mueller specimen so labeled in the British Museum (Natural History) is an erectitoid *Senecio*. Laing (1915) reported that he "got a form of this (*Senecio lautus*) on the beach near the Cascades" on Norfolk Island. His specimen has not been seen, but another collection from this island (seen at the National Herbarium of New South Wales, Sydney) appeared to be closer to the Australian taxa formerly included in *Senecio lautus*. Cheeseman (1888) was doubtful about the specimens he saw on Macauley Island in the Kermadecs, noting that "only a few specimens (were) seen, and these so young that the identity is doubtful". Oliver (1909) reported the species from French Rock in this island group, but his specimen (WELT) is so badly damaged by insects that it cannot be identified with certainty.

Senecio lautus ssp. *lautus* is exceedingly variable throughout its range. This variability is due to the presence of a large number of biotypes within the populations as well as to the phenotypic plasticity of the various biotypes. Plants grown in the greenhouses at Wellington and Seattle showed both intrapopulation and interpopulation variation with respect to ligule length, head size, amount of pubescence, branching habit, stem pigmentation, and pattern of leaf dissection. Generally, the populations of this subspecies are more homogeneous in the northern portion of the North Island than they are in the southern half, particularly along the coast of Wellington province. In addition, the northern plants (and those from Nelson province) have a finer texture, smaller leaves, and smaller heads than the Wellington plants.

REPRESENTATIVE HERBARIUM SPECIMENS. North Island: North East Island, Three Kings, J. F. Buddle, 31/12/54 (AK 24111); Awanui Heads, North Auckland, H. B. Matthews, 1934 (AK 35383); Bream Trail, North Auckland, Hutson 26/11/48 (CHR 82601); Rangitoto Island (CHR 8222); Gannet Rock, Hauraki Gulf, B. E. G. Molesworth, 10/11/47 (AK 35379); Whale Bay, Raglan, P. Hynes 21/10/51 (AK 28049); New Harbour, Napier, W. R. B. Oliver, 27 Oct. 32 (WELT); East Cape, New Zealand, Dr. Sinclair (K); Tolaga Bay, Banks and Solander (BM); Base of Mt. Egmont, Dieffenbach (K); Mt. Egmont, manuka scrub, H. H. Allan 2/9/27 (CHR 10305); Rapanui, Wanganui, 7/3/1937 (CHR 18276); Lepperton, Taranaki (CHR 475); Terawhiti, Dec. '06 (WELT); Kapiti, manuka scrub, H. H. Allan, 2/9/27 (CHR 10304); near Paekakariki, V. D. Zotov, 21/11/44 (CHR 85773); Day's Bay, H. H. Allan (CHR 85770); Muritai, Wellington, L. B. Moore, 7/12/49 (CHR 67643). South Island: Naomi Island, Kenepuru Sound (CHR 83767); Paponga, Farewell Spit, J. A. Petterson, 13/11/54 (CHR 77891); Akaroa, T. Kirk, 10/1/76 (CANTY). Chatham Islands: Chatham Islands, W. Travers (WELT, MEL); Te Whanga Lagoon, Chatham Island, J. F. Findlay, Jan., 1955 (CHR 87403).

Ib. *Senecio lautus* ssp. *carnosulus* (T. Kirk) Ornduff hoc loc.

S. lautus var. *carnosulus* T. Kirk Students' Fl. N.Z. 341. 1899.

S. lautus var. *a* Cheesem. Man. N.Z. Fl. 373. 1906 (with ssp. *lautus*).

A stout-stemmed, fleshy, succulent annual or biennial herb; leaves thick, entire, or with a few broad, entire, lateral lobes, the leaf margins revolute; internodes shortened so that the lower leaves appear subopposite or whorled; heads obconic or cylindrical; the ligules 8–15, 3–4 mm long, recurved, often widely and irregularly spaced; cypselas frequently sericeous; $n = 20$. Fig. 8a, 8b.

There are no herbarium specimens extant labelled by Kirk as *Senecio lautus* var. *carnosulus* so far as can be determined. The neotype selected is a greenhouse grown plant from fruits collected by G. T. S. Baylis at sea level, Black Head, Dunedin, on January 1, 1956. His commentary on the wild plants was that they were "compact much-branched forms growing in rather argillaceous soil along the cliff base". The neotype has been sent to the herbarium of the Botany Division, D.S.I.R.

This subspecies is known definitely from only two South Island localities which are at the southern edge of the range of *Senecio lautus* ssp. *lautus*. These localities are: Punakaiki Beach and the environs of Dunedin. However, it would be expected to occur more or less sporadically throughout the range of ssp. *lautus*, particularly in regions with saline soils or in areas exposed to strong oceanic winds. In flower October to January.

This maritime ecotype is similar in its morphological characteristics to the coastal ecotypes of *Achillea borealis* noted by Clausen, Keck and Hiesey (1948). The taxonomic recognition of *Senecio lautus* ssp. *carnosulus* is complicated by the fact that some segments of genetically "good" ssp. *lautus* when growing under maritime conditions will produce ecads which are similar in their form to ssp. *carnosulus*. When these forms are brought into the greenhouse or are grown as progeny from collected fruits, the plants which develop are indistinguishable from the inland ecotypes of *Senecio lautus* which occur in the same region. On the basis of studies made to date there is no sure method of distinguishing true ssp. *carnosulus* from the "mimic" plants of ssp. *lautus*. However, the fact that this confusion can exist is not a sufficient reason for denying taxonomic recognition of ssp. *carnosulus*. It is probable that ssp. *carnosulus* is actually more common than herbarium collections indicate, since its compact and succulent nature make it a rather unattractive plant to collect and dry.

At least one collection (Seatoun, Wellington) showed characteristics intermediate between the two subspecies when grown in the greenhouse at Victoria University.

REPRESENTATIVE HERBARIUM SPECIMENS. South Island: Punakaiki, between Westport and Greymouth, 15/1/27, W. Mackay (CHR 60309); Punakaiki Beach, early Jan., 1953, I. W. Davey (CHR 81981); Foot of Black Head, Oct. 21, 1925, Marie C. Neal 332 (BISH); Dunedin, Lawyer's Head, Oct. 21, 1925, Marie Neal (BISH).

II. *Senecio sterquilinus* Ornduff nom. nov., hoc loc.

Senecio lautus var. γ *macrocephalus* Hook. f. Fl. Nov.-Zel. 1853.

A coarse, fleshy, thickly pubescent short-lived perennial herb; similar to *Senecio lautus* in aspect, but the central stem stout, erect, up to 90 cm tall; often a few secondary branches from near the base, but these branches less well developed; leafy throughout, the middle cauline leaves thick, to 10 cm long, with revolute margins, pinnatifid, with up to 10 lateral lobes, these often oblique to the midrib; upper leaves reduced, sessile, with an auriculate clasping base; heads large, the involucre 8 mm high, the bracts numbering 15 (21); disk 1.5–2 cm in diameter; ray florets (15) 21, yellow; ligules narrowly elliptic-oblong, 7 mm long and 3 mm wide; cypselas 3 mm long, strigose, becoming gelatinous when wet; $n = 20$. Fig. 3.

The only specimens in Hooker's possession marked *Senecio lautus* var. γ *macrocephalus* are three fragments at Kew collected by Colenso under his number 268 (Sheet 5/H1232/55). A search of the Hooker-Colenso correspondence by the Kew staff members revealed the following comments by Colenso regarding this collection:

"? *Senecio*, from an Islet in the Harbour, with a very large globular receptacle and involucre", dated 1846. According to N. L. Elder, Colenso was then living at the Waitangi Mission station in Hawke's Bay; this suggests that the islet is one of those in the inner harbour at Napier. Specimen No. 4 on the Kew sheet mentioned is here selected as the lectotype for this species. The specific epithet "*macrocephalus*" cannot be used since it has already been given at least twice to other *Senecio* species.

This species is known only from the sea-bird nesting grounds on Brothers Islands and the type locality. The only collections since that of Colenso were made on the main Brothers by an unidentified collector (WELT), by William Dawbin (WELT), and by me. However, Dawson (1954), noted that on Stephens Island "bird burrows are common between the tussocks, and large plants of *Senecio lautus* are numerous and widespread". Furthermore, Dawbin (1955 in litt.) reported that on Trio Island "there was a form resembling that at the Brothers at least in general appearance, large size, and thickness of leaves". In light of these remarks, it is probable that *Senecio sterquilinus* does occur on islands in Cook Strait other than the Brothers group. Collections from these islands would be highly desirable.

Through the courtesy of the Marine Department, Wellington, it was possible for me to visit the Brothers Islands in October, 1954, in order to observe this species in the field. The main island constitutes only a few acres in area, rises sharply from the sea, and is densely populated by burrowing petrels. The accumulation of faeces from these birds has resulted in an odorous, friable soil which is presumably very high in levels of phosphate and nitrate.

Senecio sterquilinus was abundant around the bird burrows and formed dense stands on the more sheltered portions of the island. In exposed spots dwarfed plants were seen, but even these plants retained the distinctive features of this species. This guano endemism is reminiscent of that in *Senecio antipodus* T. Kirk reported by Cockayne (1904).

It would be reasonable to assume that the coarseness and large size of *Senecio sterquilinus* are the results of the high soil fertility of its habitat. However, greenhouse grown progenies from the Brothers retained most of the features of their wild progenitors. These plants, grown in ordinary greenhouse soil, grew to the same average height of their parents and had their same large heads and number of floral parts.

REPRESENTATIVE HERBARIUM SPECIMENS. Brothers Island, Dawbin (CHR 71821a, b); Brothers Island, Cook Strait (WELT).

III. *Senecio radiolatus* F. Muell. Veg. Chatham Is. 25, Pl. IV. 1864.

Included in *S. lautus* by Hooker, Handb. N.Z. Fl., 724. 1864.

S. lautus var. *radiolatus* J. Buch. Trans. and Proc. N.Z. Inst. 7: 333. 1875. As to name but not as to material cited.

S. lautus var. *radiolatus* T. Kirk Students' Fl. N.Z. 1899.

A simple or strongly branched short-lived perennial herb with fibrous roots; stem stout, (13) 20-45 (90) cm tall, usually erect, grooved, leafy throughout, and often purplish in the lower portion; lowest leaves with a long, narrowly winged petiole, often withering early; middle cauline leaves broadly ovate in outline, 2.5-12 cm wide, 5-18 cm long, abruptly narrowed below the middle to a broadly winged, entire to toothed petiole; distal portion of the blade of the middle cauline leaves pinnately parted to nearly flabellate, the divisions again lobed, and these lobes acutely toothed, midrib prominent; upper leaves sessile, auriculate-clasping, somewhat reduced, the proximal portion pinnately parted or merely lobed, the ultimate teeth mucronate or acute; herbage arachnid-tomentose when young, becoming subglabrate with age; inflorescence terminal on the branches, corymbose-paniculate, the numerous heads cylindrical-urceolate when fresh, pressing to campanulate; involucre 6-9 mm high, the bracts linear, usually 14 or 21; disk 5-10 mm in diameter; ray florets numbering 10-14, often irregularly and widely spaced, the yellow, oblong or linear ligules 3-6 mm long, 1-1.5 mm wide; disk florets yellow; pappus white, copious, equalling or exceeding the corolla; cypselas 2.5-4 mm long, strigose overall or merely in the grooves; n = 40. Fig. 1.

The holotype of *Senecio radiolatus* is Travers No. 5, "Chatham Island, November. On sandy places at sea beach above level of the sea." It is in the National Herbarium of Victoria, South Yarra.

This species is endemic to the Chatham Islands, where it is apparently limited to sandy sea beaches, flat rocks, or rocky crevices near the sea (*vide* Cockayne, 1902; 1921). In flower November to February.

Senecio radiolatus has been collected only a few times; the early collections, including the type, consist of the upper portions of flowering plants. Various authors have considered *S. radiolatus* synonymous with or a variety of *S. lautus*. In his description of the species, Mueller (1864) allied it to *Senecio latifolius* (*S. solanderi* Allan) and *S. banksii*, or even the European *S. vulgaris* "should it prove annual".

Examination of living plants in the greenhouse and of available herbarium specimens suggests that the relationship of *Senecio radiolatus* to any of the above species is remote. It is here proposed that its closest alliance is with *Senecio antipodius* T. Kirk, an endemic of the heavily bird-manured soils of Antipodes Island. These two species are similar in many respects: they are both much-branched herbs with large leaves, the distal portions of which are expanded and pinnatifid, the petioles of which are broadly winged; they both have a conspicuous cobwebby tomentum and prominently veined leaves; and they are both endemics of islands a considerable distance from the main islands of New Zealand.

The few collections of *Senecio radiolatus* in herbaria show that it is morphologically a rather uniform species.

REPRESENTATIVE HERBARIUM SPECIMENS. Chatham Islands, Cox (WELT); N. coast of Chatham Is., L. Cockayne, Feb., 1901 (WELT, CANTY); Chatham Island, Travers 79 (MEL); Chatham Island, J. F. Findlay, January, 1955 (CHR 87402).

IV. *Senecio glaucophyllus* Cheesem.

This species is comprised of at least four geographical races which are recognised as subspecies. Most of the members of this species are easily fitted into their respective taxonomic niches, but there is a great amount of variation within the subspecies. In Marlborough plants with an admixture of characteristics used to distinguish three of the subspecies occur. Individuals from some localities are not readily assignable to any of the subspecies and will have to be identified arbitrarily. Moreover, on the seaward side of the range of *Senecio glaucophyllus* ssp. *discoideus* intermediates between this subspecies and presumably ssp. *basinudus* or ssp. *raoulii* are found. These plants have ligulate outer florets and occupy stable ground.

Severe disturbances of the natural vegetation of New Zealand have occurred since European settlement, particularly in the South Island. Fire, rabbit infestations, over-grazing, and the introduction of foreign plants and animals have resulted in profound changes in the biotic balance. Many plant species have nearly been eliminated; some plant associations have been destroyed and new ones formed. It is quite possible, therefore, that the high degree of variation within and between the South Island populations of *Senecio glaucophyllus* is the result of the breakdown of ecological barriers formerly separating the distinct regional populations of the species and/or the opening up of large unforested tracts for rapid colonisation by the plants.

IVa. *Senecio glaucophyllus* Cheesem. Trans. and Proc. N.Z. Inst. 23: 536. 1896. (ssp. *glaucophyllus*)

S. lautus var. *montanus* Cheesem. Man. N.Z. Fl. 1906. pro parte.

An erect, perennial herb, branched from the base but sparingly so above, the stems 15–60 cm tall, the aerial portions of the plant dying back in the winter and the next season's growth arising from basally clustered shoots; herbage glabrous and often somewhat glaucous; lower leaves 2 or more cm long, oblanceolate to obovate, obtuse or acute, sinuate-dentate to serrate,



FIG. 1—*Senecio radiolatus* (Chatham Island, CHR 82025). FIG. 2—*S. lautus* ssp. *lautus* (Makara Beach, Wellington). FIG. 3—*S. sterquilinus* (Brothers Island, Cook Strait). FIG. 4—*S. glaucophyllus* ssp. *raoulii* (Moemoe, Ruahines).



Fig. 5—*S. glaucophyllus* ssp. *glaucophyllus* (immature topotype, Mt. Arthur). Fig. 6—*S. glaucophyllus* ssp. *basinudus* (holotype, near Lake Ellesmere). Fig. 7—*S. glaucophyllus* ssp. *discoideus* (Blue Cliffs Station, near St. Andrews). Scale marked in dm. Photographs by the Still Photo Unit, University of Washington.



FIG. 8.—*Senecio latus* ssp. *carnosulus*. A—Punakaiki Beach, CHR 81981. B—Lectotype, Black Head, Dunedin. Scale marked in dm. Photographs by the Still Photo Unit, University of Washington.



tapering to a short petiole; middle cauline leaves similar in outline to the lower, up to 9 cm long, narrowing to a broad petiole or a clasping base; upper leaves often somewhat reduced and narrower, the uppermost clasping by an entire or lacerate auriculate base; heads campanulate, borne in a terminal corymb; disk 5–8 mm in diameter; heads radiate, the yellow ligules numbering 13–15, ovate or oblong, 2–6 mm long, 2–2.5 mm wide; involucre bracts linear, about 5 mm long; cypselas about 3 mm long, scabrid in the grooves. Fig. 5.

Specimen A on sheet 10601 (AK) collected by Cheeseman on Mt. Arthur, Nelson, at an altitude of 4,000 feet, January, 1886, is here selected as the lectotype for *Senecio glaucophyllus*.

The nomenclatorially typical subspecies of *Senecio glaucophyllus* occurs in the crevices of limestone rocks at altitudes of 2,000–4,000 feet in the Tasman mountains, the eastern section of the Lyell range, and possibly the Richmond range. Flowers December and January.

REPRESENTATIVE HERBARIUM SPECIMENS. South Island: Goulard Downs, January, 1927, A. Wall (CANTY); Gordon's Mountain, Nelson, alt. 3,000ft, January, 1882, TFC (AK 10590); Mt. Arthur, Nelson, 4,000ft, W. Townson (AK 10589); Mt. Arthur, Nelson, F. G. Gibbs (AK 10595); Mt. Arthur, J. Adams (AK 15762); Mt. Arthur, 3,800ft, January, 1933, Alfred Meebold, 17594 (BISH); Mt. Pat., Herb. F. G. Gibbs (CHR 582).

IVb. *Senecio glaucophyllus* ssp. *basinudus* Ornduff ssp. nov., hoc loc., a ssp. *glaucophyllo* differt absente caulium brevium ad basum per hiemem; caulis ramosus supra.

Similar to ssp. *glaucophyllus* in many respects; erect or prostrate herb, usually rather freely branched above, the aerial portions of the plant not dying back to the ground in the winter and hence the basally clustered shoots absent; heads borne rather loosely, not in terminal corymbs; measurements of the capitula as in ssp. *glaucophyllus* but the ligules of the ray florets from nearly absent to 3.5 mm long; $n = 50$. Fig. 6.

The type collection of this subspecies consists of plants collected by J. W. Dawson in July, 1954, on a road-cut of the Christchurch-Akaroa road at a point just north-east of the tip of Lake Ellesmere. The holotype has been deposited in the herbarium of the Botany Division, D.S.I.R.

This subspecies is found on dunes and cliffs along the coast from Lyttelton Hills southward to at least Dunedin; also collected at Cape Campbell. In flower October to March.

Most of the herbarium material of *Senecio glaucophyllus* ssp. *glaucophyllus* has been collected at Mt. Arthur and is morphologically rather uniform. On the other hand, the few collections of ssp. *basinudus* show that it is a variable entity in the field.

These two subspecies of *Senecio glaucophyllus* are superficially similar, but there is a good basis for recognizing them both: ssp. *glaucophyllus* occupies a montane habitat, ssp. *basinudus* is littoral; the former is erect and branched only from the base, the latter is erect or decumbent and freely branched above; the former bears its heads in a loose corymb, the latter in a loose panicle; the former dies to the ground during the winter and renews its growth the next season from basally clustered shoots, while the latter does not do this. These differences remain constant when plants are grown in the greenhouse and are considered of sufficient magnitude to justify the recognition of two subspecific taxa.

REPRESENTATIVE HERBARIUM SPECIMENS. South Island: Cape Campbell, L. B. Moore (CHR 85767); Port Hills, Christchurch, H. H. Allan, 19/12/40 (CHR 83768); Lyttelton Hills, H. H. Allan, 23/10/47 (CHR 83769); Oamaru, sea coast cliffs, H. H. Allan, Jan. 1929 (CHR 969); head of Dunedin Harbour, foot of

hill, in sand, Marie C. Neal 333, Jan. 2, 1926 (BISH); Allans Beach, Dunedin, G. T. S. Baylis, 2/1/1956 (OTU 003593); Catlin's River, Clutha Co., D. Petrie, March, 1891 (WELT).

IVc. *Senecio glaucophyllus* ssp. *raoulii* (Hook. f.) Ornduff comb. nov., hoc loc.

Senecio lautus var. β *Raouli* Hook. f. Fl. Nov.-Zel. 1853. pro parte.

Senecio lautus var. *montanus* Cheesem. Man. N.Z. Fl. 1906. pro parte.

A perennial herb (19) 25-40 (60) cm tall, branched from the base but usually simple above, the aerial portions of the plant dying back in winter and the next season's growth arising from basally clustered shoots; herbage glabrous or very sparsely pubescent when young, especially in the leaf axils; stems erect, often purplish below, leafy throughout, the leaves ascending and gradually reduced upwards; lower leaves 2-5.5 (8) cm long, often purplish beneath, the oblanceolate shallowly toothed blades narrowing to a long petiole; middle cauline leaves somewhat ascending, lanceolate-elliptic in outline, deeply pinnatifid, the lobes usually serrulate and somewhat remote, the blade of the sinuses between the lobes usually serrate; these leaves lacerate-clasping at the base; upper leaves much reduced and bract-like below the inflorescence; heads small, numerous, usually borne in a rather dense corymbiform panicle; involucre about 5 mm high, the linear bracts numbering about 13; ray florets yellow, the ligules broadly elliptic, 2-4 (5.5) mm long, 1.5-2 (2.5) mm wide; cypselas 2.8-3 mm long, pubescent in the grooves; n = 50. Fig. 4.

Specimen No. 4 on Kew sheet 3-H1232/55 (Colenso No. 85) is here selected as the lectotype for this subspecies. The Hooker-Colenso correspondence at Kew revealed that this collection was made "near the summit of barren and lofty hills. These hills were composed chiefly of pumice and ashes." The collection was made on January 5, 1842, while Colenso was on a journey between Waikare and Ruatuhuna. Hooker labelled several of his specimens as "var. β *Raouli*" and all of them correspond to the present concept of ssp. *raoulii*. This specimen was collected at Akaroa by Raoul and is an erectitoid *Senecio*. With this exception, all of Hooker's specimens were supplied by Colenso and appear to be North Island collections.

This subspecies occurs on rocky cliffs, amongst the tussock, or "as a single plant in most of the main river valleys" (N. L. Elder in litt.) at an altitude of 1,500-4,800 feet in the mountains just east of Lake Taupo, in the Kaimanawas, Ruahines, Huiaurus, and probably other ranges of the North Island volcanic plateau. In the South Island it has been collected in Marlborough and extreme northern Canterbury, and presumably occupies similar habitats there, except that it apparently descends to lower altitudes than in the North Island. In flower November to May.

This subspecies appears to be relatively uniform in the North Island, but as mentioned earlier, it appears to merge with other subspecies on the periphery of its South Island range. The South Island collections are characterised by a lesser amount of leaf serration and by the more remote nature of the leaf lobes than the North Island plants, but these differences are not considered to be of taxonomic significance.

REPRESENTATIVE HERBARIUM SPECIMENS. North Island: N.W. Ruahines, Mangaohane Station, Jan. 1946, A. P. Druce (CHR); Moawhango R., 12/3/53, Druce and Hamlin (CHR 79505); East of Taupo, ca. 2,000ft, K. W. Allison, 18/11/34 (CHR 17696); Mt. Tauhara, Taupo, alt. 3,000ft, TFC, Jan., 1889 (AK 10593); on scrub burn, Waiouru, 1931-32, T. E. Attwood (AK 35235); Ruahine Range, early Jan., 1914, B. C. Aston (WELT, 1910); Lake Taupo, Nov., 1897, D. Petrie (WELT, CANTY); Waiouru Plain, 3,350ft, Jan., 1911 (WELT); Kaimanawas, 12/14 (WELT). South Island: Ure Gorge, shaded limestone cliffs, Geo. Simpson (CHR 18939); Ward Pass, Archeron River side, H. H. Allan, 2/4/1945 (CHR 51285); Molesworth Hill, H. H. Allan, 30/3/1945 (CHR 51274); Mt. Highfield block, Waiau, L. B. Moore, 5/5/48 (CHR 62619); Waipara, river bed near township, H. H. Allan, 28/1/41 (CHR 85772); Boundary Creek,

limestone rocks, H. H. Allan, 5/1/29 (CHR 10187); Puki Puki R., Kaikoura Mts., Dec., '29, A. Wall (CANTY); Hammer, open places, 3,000ft, H. H. Travers, March, 1909 (P).

IVd. *Senecio glaucophyllus* ssp. *discoideus* (Cheesem.) Ornduff comb. nov., hoc loc.

Included in *S. lautus* var. *a lautus* by Hook. f. Fl. Nov.-Zel. 1853.

S. lautus var. *discoideus* Cheesem. Man. N.Z. Fl., 1906.

Low perennial herb, the stems arising from what appears to be a rootstock but is the main stem of the previous years covered by unstable scree; stems 9–15 (25) cm tall, erect or more often lax, simple, or branched from the base; herbage glabrous or seldom sparsely pubescent when young; stem leafy throughout, the leaves gradually reduced upward and often purplish pigmented on the lower surface; lower leaves 2–6 cm long, oblanceolate-ovate in outline, petiolate, shallowly toothed or pinnatifid; middle cauline leaves oblong-elliptic in outline, serrate to deeply pinnatifid, often with a clasping base; heads discoid, solitary or few, the disk 6–9 mm in diameter; involucre (4) 5–6 mm high, the bracts numbering about 13 (21); florets and pappus at length longer than the involucre; ligules of the outer pistillate florets absent; cypselas about 3 mm long, sparingly pubescent in the grooves; $n = 50$. Fig. 7.

Specimen B on sheet 10596 (AK) is here selected as the lectotype for this subspecies. It was collected by Cheeseman in January, 1880, on Mount Torlesse, Canterbury Alps, at an altitude of 3,500 feet. Cheeseman described *Senecio lautus* var. *discoideus* to include the large-headed, discoid, low plants from the South Island mountains which he felt were within the species. While he rarely based his descriptions on single specimens, the only material of this taxon in his herbarium which had been collected before 1906 are sheets 10596 and 10597 (AK). Since both collections are morphologically quite similar, a specimen in the earlier collection has been chosen as the lectotype.

This subspecies grows on unstable debris slopes of the mountain ranges east of the Southern Alps in Canterbury and Otago and has also been collected in the Kaikouras. A sole collection has been made in the Ruahines in the North Island. In flower December to January (one collection dated April).

This subspecies appears to be an ecotype adapted to unstable scree, a habitat in which many interesting plant species are found in New Zealand. The deep soil of the scree is stable, but there is much surface movement. According to Fisher (1952) ssp. *discoideus* avoids damage from the moving stones by bending before the rubble and later sending new shoots back to the surface.

One characteristic of this subspecies which has no obvious adaptive value is the absence of the ligule in the outer pistillate florets of the head. Haskell (1953) discusses the case of radiate and discoid forms in *Senecio vulgaris* L. and presumes the discoid form to have a greater reproductive capacity than the radiate form, although this idea is not supported satisfactorily. De Vries (1910) reported the discoid form of *S. jacobaea* L. on the dunes of North Holland and the radiate form of the species from the dunes of South Holland, but he offered no opinion as to the basis for this geographical separation.

The lack of ligules in *Senecio glaucophyllus* ssp. *discoideus* may not be an adaptive trait in itself, but perhaps may be one of the effects of a pleiotropic gene or a gene linked with one associated with other characteristics of the subspecies which adapt and limit it to the scree. Random fixation is not acceptable as an explanation for the presence of this character in the population, since presumably compatible populations of other radiate subspecies of *S. glaucophyllus* are known to occur on stable ground adjacent to populations of ssp. *discoideus*, yet the two forms retain their integrity. Just what the adaptive significance of this character is, if any, will have to remain problematical for the present.

REPRESENTATIVE HERBARIUM SPECIMENS. North Island: Ruahines, Te Atua Mahuru, ca. 4,800ft, N. L. Elder, Jan., '46 (CHR 63036). South Island: Big Hill, Molesworth, on scree fan, M. Simpson, 29/1/56 (CHR 90786); Yeo River, debris slope, 1/4/1945, H. H. Allan (CHR 51301); Kyeburn Crossing, Nov., 1892,

D. Petrie (WELT); Shingle slip, limestone hill between Broken and Porter rivers, Leonard Cockayne, Dec. 29, 1890 (WELT); Limestone rocks, Trellissick basin, 2,800ft, T. Kirk (WELT, 1908); Mts. behind Castle Hill, Canterbury, TFC, Jan., 1883 (AK 10597); Mt. Torlesse, open places, 2,500ft, 4/09 H. H. Travers (P); Mt. Hay, Two Thumb Range, Barker 352 (CHR 20454); S. Pisa Range, Jan., 1923, A. Wall (CANTY); Mt. Arnould, ca. 2,800ft, D. Petrie (WELT, 1908); Dunstan, approx. 3,500ft, I. A. McNeur 25/12/1949 (CHR 68905); Eweburn Valley, ca. 2,000ft, 10/1/11, D. Petrie (WELT).

BREEDING SYSTEM

An understanding of the breeding system of an organism may aid in interpreting the variation pattern in a taxon and may give some clues as to the limits and evolutionary potentialities of the group. For most of the flowering season the majority of the taxa of *Senecio* discussed in this paper are outbreeding. Flowering plants are visited on warm days by hover-flies (Syrphidae) and to a lesser extent by honey bees and bumblebees. The large number of hybrid seedlings on the benches under the plants in the greenhouse lends some support to the idea that most taxa are outbreeding, and further suggests that the pollinators of *Senecio* do not respect the boundaries of taxonomy or of ploidy in their activities.

Despite this primarily outbreeding nature, all the taxa are self-compatible. It appears that *Senecio glaucophyllus* ssp. *discoideus* and *S. lautus* ssp. *carnosulus* normally set a high percentage of selfed fruits. Furthermore, the sequence of events in the maturation of florets of all species is such that self-pollination will eventually occur if no pollinator makes a visit. This suggests that in poor weather, when pollinators are not active, self-fertilisation may be frequent. This combination of outbreeding and inbreeding is undoubtedly chiefly responsible for the mosaic of variation characteristic of most of the taxa of the *Senecio lautus* complex.

Apomixis has not been demonstrated in any of the species; emasculated heads of caged plants set no fruit.

CHROMOSOME NUMBERS

Although other numbers forming an aneuploid series have been reported, most of the *Senecio* species which have been investigated by various workers have diploid chromosome numbers in multiples of 10, ranging from 20 to 180 (Darlington and Wylie, 1956). The four species investigated in this paper are polyploids at various levels. For *Senecio lautus*, $n = 20$; *S. sterquilinus*, $n = 20$; *S. radiolatus*, $n = 40$; and for *S. glaucophyllus*, $n = 50$. Chromosome numbers were determined from squash preparations of microsporocytes stained with aceto-carmin. Meiosis was regular in all species. Buds were preserved in a fixative consisting of 3 parts 95% ethyl alcohol and 1 part glacial acetic acid.

Following is a list of plants which were used for the chromosome counts, the localities from which they were taken, and their collectors:

Senecio lautus ssp. *lautus*, $n = 20$: Motuhoropapa Island, Hauraki Gulf, Geo. W. Mason; Bream Head Peak, Whangarei Head, Geo. W. Mason; Little Barrier Island, Graeme Ramsay; Cape Turnagain, N. L. Elder; Paekakariki hill summit, R. Ornduff; Mana Island, R. Ornduff; Red Rocks Stream, near Wellington, R. Ornduff; Makara Beach, R. Ornduff; Pencarrow Head, near Wellington, R. Ornduff; Rimutaka summit, R. Ornduff; Mable Island, near Picton, R. Ornduff.

Senecio lautus ssp. *carnosulus*, $n = 20$: Punakaiki Beach, I. W. Davey; Black Head, Dunedin, G. T. S. Baylis.

Senecio sterquilinus, $n = 20$: Brothers Island, Cook Strait, R. Ornduff.

Senecio radiolatus, $n = 40$: Chatham Island, E. A. Madden.

Senecio glaucophyllus ssp. *glaucophyllus*, no count.

Senecio glaucophyllus ssp. *basinudus*, n = 50: near Lake Ellesmere, J. W. Dawson; Allans Beach, Dunedin, G. T. S. Baylis.

Senecio glaucophyllus ssp. *raoulii*, n = 50: Moemoe, northwest Ruahines, R. Ornduff *et al.*; Pohatuhaha, N. L. Elder; Ngaurooruru, N. L. Elder; Titiokura, N. L. Elder.

Senecio glaucophyllus ssp. *discoideus*, n = 50: Blue Cliffs Station, near St. Andrews, Mrs. P. R. Woodhouse.

ARTIFICIAL HYBRIDISATIONS

Crosses were made in all possible combinations of the four species discussed in this paper, and among all the infraspecific taxa. No living plants of *Senecio antipodus* were available. Since three of the species represent different levels of polyploidy, it would be expected that hybrids between them would be highly sterile as was the case. These interploid hybrids formed no viable pollen at all. However, hybrids between *Senecio lautus* and *S. sterquilinus*, both of which have the same chromosome number, were as fertile as their parents.

The hybrids obtained from the intraspecific crosses were of special interest because they indicated that despite the high degree of variation within the species, nearly all the infraspecific categories are highly interfertile. In a few instances, there is a reduction of fertility in the second generation. Fertility of the hybrids was determined by scoring stained and non-stained pollen grains mounted in cotton blue-lactophenol.

Since the four species are highly self-compatible, particular care had to be taken to prevent self-pollination during the course of the hybridisations. The heads of the seed parents were emasculated by removing the upper portions of the heads with a razor blade, thus removing the anthers but not the stigmas. The heads were then bagged until the stigmas were receptive, and then the pollinations were made. If the pollination was successful, the stigmas withered within a few hours and the cross was considered effected. The species of the *Senecio lautus* complex are freely crossable under greenhouse conditions, although such free crossability is not a universal feature of the genus.

The results of these breeding experiments show that individuals of three of the four species investigated here are intersterile. In addition to this effective isolating mechanism, *S. glaucophyllus* and *S. radiolatus* are completely allopatric, one being mainland and the other an insular endemic. *Senecio lautus* is spatially isolated from *S. glaucophyllus* over most of its range, although it occurs within the range of *S. glaucophyllus* ssp. *basinudus* in parts of the South Island coast. *Senecio lautus* and *S. radiolatus* are both found on the Chatham Islands. *Senecio sterquilinus* is presumably spatially isolated from all the other members of the complex and is endemic to a unique edaphic situation. Its close relationship to *S. lautus* is unmistakable on grounds of morphology and high hybrid fertility, and if the two were to occur together in nature a certain amount of hybridisation would be expected.

Senecio sterquilinus is treated as a distinct species because of the relatively large number of characters by which it differs from *S. lautus*. While hybridisation between these two species, if it does occur, could have a profound effect on their future evolution it would not necessarily affect their present taxonomic status.

The infraspecific taxa which are recognised within two of the species are generally compatible with one another. Consequently, the factors which serve to keep the subspecies of a species distinct over most of their range must be their different ecological requirements combined with spatial isolation. Intermediate forms do

occur, especially in *S. glaucophyllus*, but since genetic segregation does not occur when these intermediates are grown in cultivation it appears that these intermediates are stabilised biotypes.

The relationship of *Senecio lautus* to *S. glaucophyllus* is inferred from the morphological similarity of some of the subspecies of these species. One cannot assume a very close genetic relationship, however, because of the different chromosome numbers of the two species. It is possible that *S. glaucophyllus* originated long ago as an amphiploid hybrid between a *lautus*-like ancestor and a form similar to some of the 30-chromosome-pair species now in the New Zealand flora (latter chromosome numbers supplied by J. B. Hair in litt.).

Senecio radiolatus and *S. antipodus* appear to be more closely related to each other than to any other species. Kirk (1899) compared the latter species with the Fuegian *S. candidans*, but the resemblance is slight indeed.

THE RELATIONSHIP OF THE NEW ZEALAND *Senecio lautus* COMPLEX TO AUSTRALIAN TAXA

Many authorities have used the name *Senecio lautus* to apply to a remarkable diversity of Australian forms. All of the herbarium specimens of "*Senecio lautus*" and its allies in the National Herbarium of New South Wales, Sydney; the National Herbarium of Victoria, South Yarra; the State Herbarium at Perth; Kew; and the British Museum, Natural History, were examined. In addition, the few Australian specimens in American herbaria were examined.

Nine seed collections of "*Senecio lautus*" from New South Wales, Victoria, Tasmania, and Western Australia, representing extremes of morphology and habitat, were sown in the greenhouses at the University of Washington in Seattle. All of the plants which developed were found to have haploid chromosome numbers of 20. These plants were utilised in reciprocal crossing experiments with *Senecio lautus* ssp. *lautus* and *S. sterquilinus*. The range in fertility in the hybrids was between 10% and 70%, with the average about 50%. In addition to this partial sterility barrier there is a definite morphological discontinuity between the array of Australian forms and the relatively more homogeneous New Zealand forms.

It is concluded, therefore, that the interests of taxonomy would be best served by the exclusion of the Australian forms from the limits of *Senecio lautus*. The Tasman Sea provides an effective barrier to gene exchange between populations in the two countries and provides a convenient taxonomic boundary as well. To include any of the Australian forms in *S. lautus* would be unwise, since the transition from somewhat similar Australian forms to quite different races in Australia is gradual and would result in considerable taxonomic confusion. Consequently, *Senecio lautus*, already *sensu latissimo*, is considered a New Zealand endemic.

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