VEGETABLE SHEEP: A CHEMOSYSTEMATIC STUDY OF THE CASSINIINAE.

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VEGETABLE SHEEP: A CHEMOSYSTEMATIC STUDY OF THE CASSINIINAE

It is well known that there are few places in the Asteraceae where generic limits are more difficult to apply in practice than in the tribe Gnaphalieae subtribe Cassiniinae. This is the subtribe of the paper daisies, the Edelweiss, the cudweeds. These species are characterised by discoid floral heads with papery involucral bracts. This thesis presents the results of an investigation of the flavonoid chemistry of the major species present in Australasia from which an attempt to infer taxonomic relationships among the species based on the combination of chemical, morphological and ecological characters is made.

The exudate and vacuolar flavonoid profiles of six genera Cassinia R. Br., Ozothamnus R. Br., Raoulia Hook. f and Haeckeria F. Muell., Leucogenes R. Br. and Lawrencella Anderberg were established. The exudate chemistry consists of chalcones, dihydrochalcones and flavanones, several of which lack B-ring oxygenation, and quercetin 3-O- and 7-O-methyl ethers. Vacuolar flavonoids include galangin, eriodictyol-7-O-methyl ether, and a series of kaempferol and quercetin glycosides. Several combinations of these compounds occur in the taxa studied.

Species in this study form a number of relationships that show a strong correlation to geography, altitude and ecological conditions. The production of exudate flavonoids show a direct correlation to the amount of UV-B radiation. These relationships mimic the classical taxonomy proposed by Allan in 1961 for the New Zealand species and by Burbidge in 1958 for the Australian species. Differences in distribution of flavonoids are taken as evidence for recognition that the relationships between the genera are as complex as classical taxononomic studies suggest.

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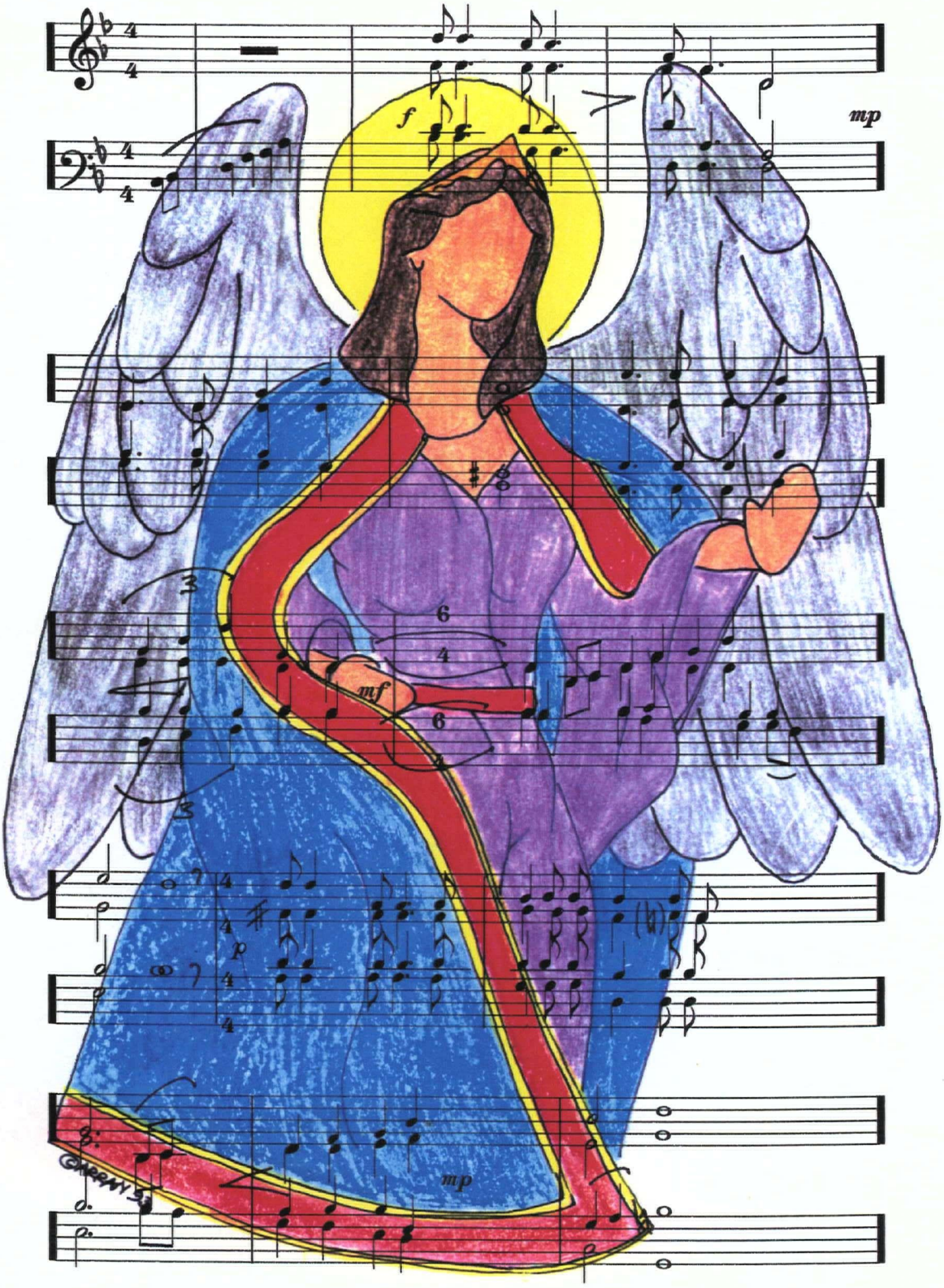
And lastly to Lesley (a real angel) and Neil, you taught me the life in music and the music of life.

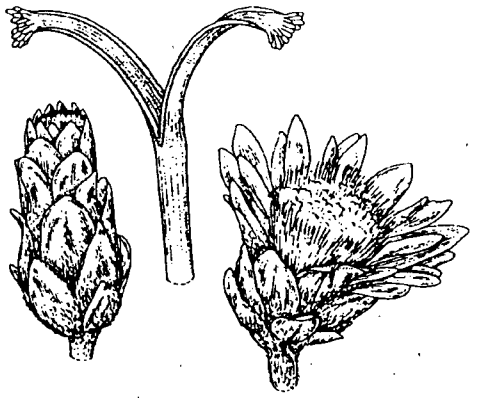


This thesis is dedicated to the memory of Neil Sutherland.
He showed me the music of life and the life in music.
Thank you for your gift.

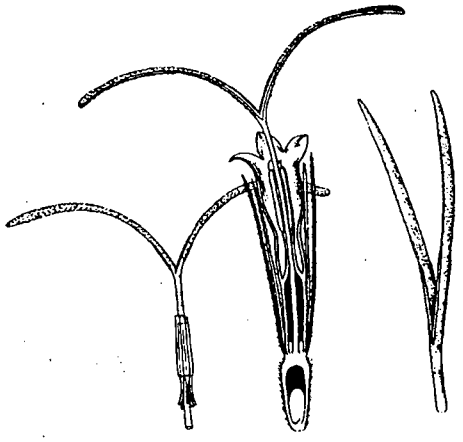
Introduction

In terms of species numbers the Asteraceae (Compositae) is the largest family of plants. According to Bremer (1994) this family comprises 1535 genera and over 23,000 species, arranged in 3 subfamilies and 17 tribes. Of these 17 tribes it is particularly difficult to define the generic limits in the tribe Gnaphalieae (Jeffrey, 1969). The Gnaphalieae sensu Anderberg consists of five subtribes (Gnaphaliinae, Cassininae, Loricariinae, Relhaniinae and Angianthinae), 167 genera and more than 2000 species making it one of the largest tribes in the family. The tribe has a worldwide distribution and is well represented in Australia, New Zealand and southern Africa. Most species are cosmopolitan and weedy colonizers of disturbed habitats, e.g., Gnaphalium uliginosum L. Some are commonly used in dried flower arrangements including the everlasting daisies(e.g., Helichrysum bracteatum Vent) the Edelweiss (Leontipodium R. Br. ex Cass.) , the cudweeds (Gnaphalium L..) and the pussytoes (Antennaria Gaert.).

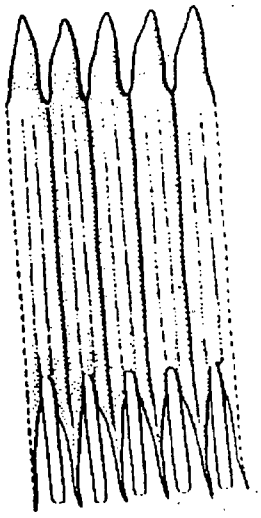
Bentham (1873b) defined the Gnaphaliinae by the presence of caudiculate or sometimes sagittate anthers with styles of the Vernonia Schreber, Senecio L. or Inula L. type (Fig 1). This is accompanied by the predominance of heterogamic yellow flowers with setose or plumose pappus elements. Four subtribes were characterized by filiform female florets (Tarchonanthinae, Filaginae, Plucheinae and the Gnaphalinae), four with ligulate female florets (Athrixinae, Inulinae, Buphthalminae and the Relhaninae) and one with homogamous flowers (Angianthinae). The taxonomic description of the Gnaphaliinae by Bentham (1873b) served as the basis for the classification systems of Hoffmann (1890) and Merxmüller et al. (1977). The revision of the Bentham system by Merxmüller et al. (1977), defined three subtribes (Inulinae, Athrixiinae and Gnaphalinae) within the Inuleae, based on palynological, cytological, anatomical and chemical data. Each subtribe included several sections. The Gnaphaliinae sensu Merxmüller et al. (1977) contains 200 genera and 2100 species with two major centres of geographic distribution, South Africa and Australia along with relatively poor representation in Eurasia, the Mediterranean and Indo-Malay regions where distribution of all the members of the Inuleae is limited.



Style branches of Gnaphalium (Inula type)



Style branches of Vernonia



Sagitate anthers

Figure 1. Style and anther types found in the Gnaphalieae. (after Zomlefler 1994)

Palynological investigations (Leins 1971 a, b, 1973, Besold 1970), showed the pollen of the Inuleae to be uniform throughout the 800 species investigated. In sharp contrast to this, the stylar morphology varied immensely among subtribes. The only common character in the Inuleae is that two marginal stigmatic rows exist. The Inuleae and Plucheeinae sensu Merxmüller et al. (1977) have the stigmatic rows fused to the tip of the stylar arms. In the other subtribes proposed by Merxmüller et al. (1977) the stigmatic ridges are separated by sterile hairs.

Reports of chromosome numbers in the Inuleae are confounded by the existence of apomictic series. For example in certain species of Antennaria Gaertner, Bayer (1988) linked apomixis to the formation of several polyploid agamic complexes each composed of several microspecies. More than 350 names have been proposed for the North American species of Antennaria. Bayer (1988) recognized eight diploid species present in North America, each with a related polyploid series. Chromosome counts in the Inuleae are often obscured by polyploidy. Contributions to the chromosome atlas of New Zealand highlight problems in the New Zealand Gnaphalieae. Dawson et al. (1993) concluded that many of the more easily recognized species of the genus Raoulia R. Br. are formed from several polyploid entities. The chromosome numbers in Raoulia, for example range from $2n = 2x_2 = 28$ to $2n = 8x_2 = 112$.

Bremer (1987) and Anderberg (1989) argued that the Inuleae sensu Merxmüller et al. (1977) is paraphyletic and that anomalous genera show a closer relationship with the Gnaphaliinae than with the Inuleae sensu lato. Anderberg (1991) rearranged the classification to reflect the view that the Gnaphaliinae and the Athrixiinae of Merxmüller et al. (1977) were each monophyletic. He defined a new tribe, the Gnaphalieae, with five subtribes. Many of the genera placed in this tribe were difficult to delimit and therefore were placed in one of the two larger genera, Helichrysum Miller or Gnaphalium L. Traditionally (Bentham 1873b) the number and distribution of female florets in the capitulum have played an important role in the taxonomic treatment of the Gnaphalieae.

Three recent attempts have been made to reconstruct the phylogeny of the Australasian Cassiniinae. The first (Anderberg, 1991,1994) (Fig 2.), was part of the circumscription of the

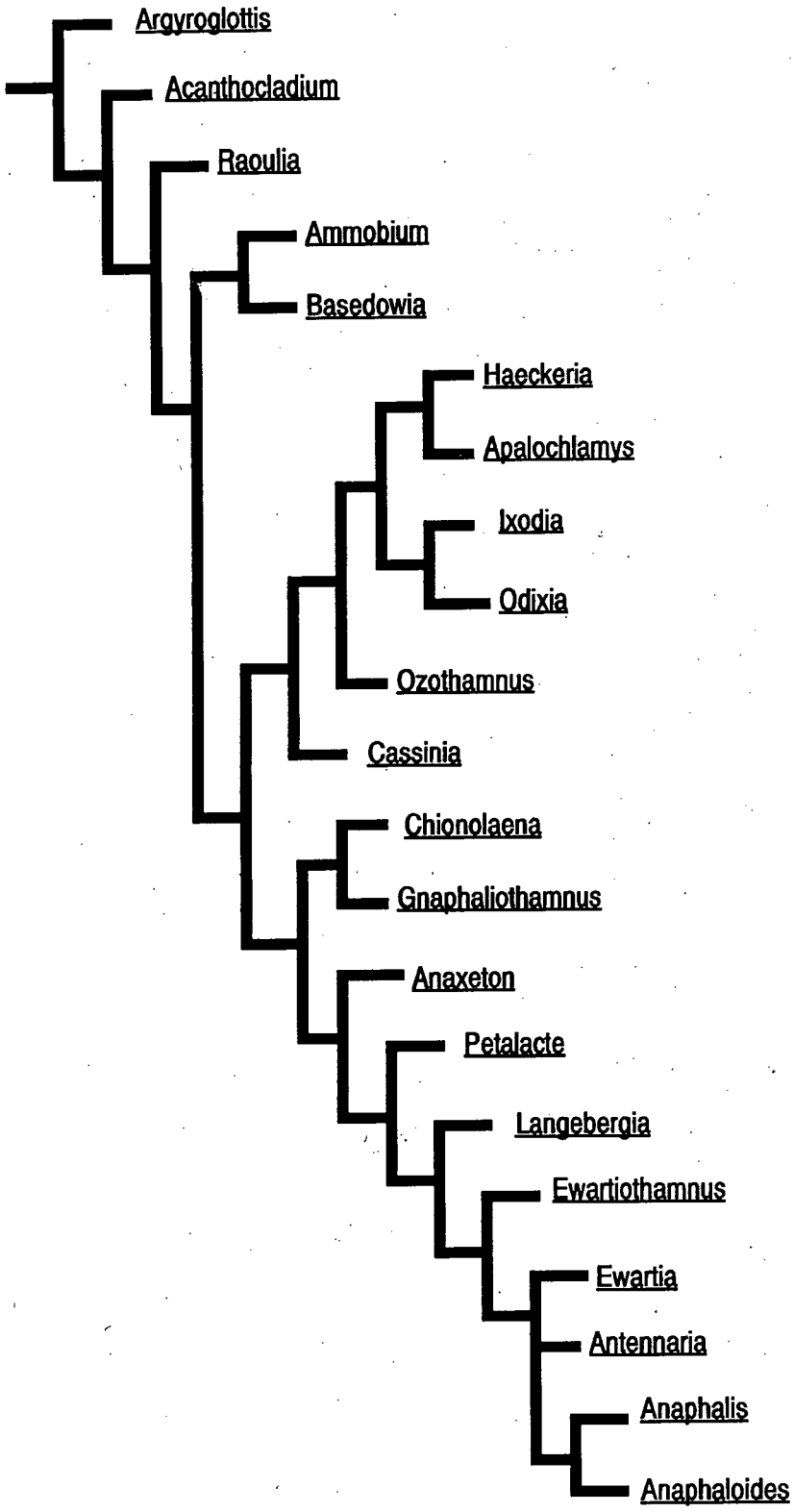


Figure 2. The strict consensus tree of the Cassiniinae sensu Anderberg.

Gnaphalieae as a new tribe within the Asteraceae. Anderberg (1991) described the tribe as having a basal grouping of unresolved genera that could not be placed in any of the subtribes and showed similarities to many genera assigned to other tribes.

The Gnaphalieae was divided into five subtribes, Angianthinae, Cassiniinae, Gnaphaliinae, Loricariinae and Relhaniinae,. Noting that the species of Cassinia R. Br. have many characters in common with the genus Ozothamnus R. Br., Anderberg (1991) created the subtribe Cassiniinae to include Cassinia, Ozothamnus and several smaller genera. The Cassiniinae is represented throughout Australia, New Zealand and New Caledonia by several genera. Cassinia is composed of 20 species occurring in Australia and New Zealand. Allan (1961) accepted five species and several regional varieties for Cassinia in New Zealand (C. amoena Cheesem., C. fulvida Hook. f., C. leptophylla (Forst. f.) R. Br., C. retorta A. Cunn. & DC., C. vauvilliersii (Homb. & Jacq.) Hook. f.). Cassinia leptophylla displays considerable local morphological differentiation but Webb (1988) reported that no set of characters can delimit more than one species. Characters used previously, e.g., size, shape, colour and number of receptacle scales, often vary continuously and independently among populations. Webb (1988) accepted one species of Cassinia endemic to New Zealand and attributed colour variation within the genus sensu Allan to an altitudinally controlled condition. The altitudinal colour variation is not as prominent in Australian Cassinia species as it is in the New Zealand species.

Many of the fifty-three species of Ozothamnus in Australia, New Zealand and New Caledonia, bear a striking resemblance to species of Cassinia. The genus was included as a section of Helichrysum by Bentham in the Flora Australiensis (1867). Burbidge (1958) elevated the section Ozothamnus to subgeneric status with two sections, Ozothamnus and Hebelaena. Anderberg (1991) elevated subgenus Ozothamnus sensu Burbidge to generic status moving all species in both sections to the resurrected genus. The taxonomic description of Ozothamnus by Burbidge (1958) highlighted ecological tolerances of the Australian species. These ecological tolerances point to a close relationship between Ozothamnus and the Australian Cassinia species. New Zealand Cassinia species are colonizers of open ground while the Australian species,

like the Australian species of Ozothamnus, are plants of damp forests. Anderberg (1991) found that Helichrysum was paraphyletic, and based on this discovery, proposed several smaller allied genera.

Cladistic analysis of a new monotypic genus Cremothamnus Puttock led Puttock (1994) to question Anderberg's (1991, 1994) analyses. The new genus could be placed tentatively either in the Lawrencella Lindl. group of the Angianthinae or within the Cassininae group allied with Ozothamnus R. Br. Analysis of the cladograms produced by Anderberg with the addition of this new genus, indicated that the subtribes were polyphyletic.

The initial analysis of Anderberg produced a phylogenetic arrangement for the 167 genera in the Gnaphalieae (Anderberg 1989). Seventy two of these genera were scored for the data matrix. Using Hennig86 version 1.5 parsimony program, five analyses were performed, one at the tribal level and four at the subtribal level resulting in 120 minimal length trees. The most important assumption of Anderberg's analysis was that the clades discovered were monophyletic after each taxon was added. Therefore the taxa shared synapomorphies with the clade to which they were added.

Puttock (1994) reanalyzed the data matrix used by Anderberg. The monophyly of the Cassiniinae was tested using four outgroup taxa: Gnaphalium, a representative of the sister clade to the Cassiniinae; Ixiolaena Benth.; Philyrophyllum O. Hoffm. and Lawrencella which had been used in Anderberg's analysis. The analysis produced 24 equally parsimonious trees of 140 steps, ten steps shorter than the published phylogeny for the subtribe Cassininae sensu Anderberg. The 90% consensus tree generated by Puttock (Fig 3.) showed that a number of polytomies, seven to be exact, existed, i.e., a number of taxa seemed to be so closely related to each other that relationships could not be resolved. Gnaphalium, the type genus for Anderberg's subtribe Gnaphaliinae, clusters with Anaphalis DC. and Anaphaloides (Benth.) Kirp. if Ixiolaena and Philyrophyllum were used as the out group taxa. None of the cladograms produced by Puttock (1994) were the monophyletic trees reported by Anderberg (1991, 1994). Puttock expanded the analysis to include all members of the tribe sensu Anderberg. The subtribes Loricariinae and the

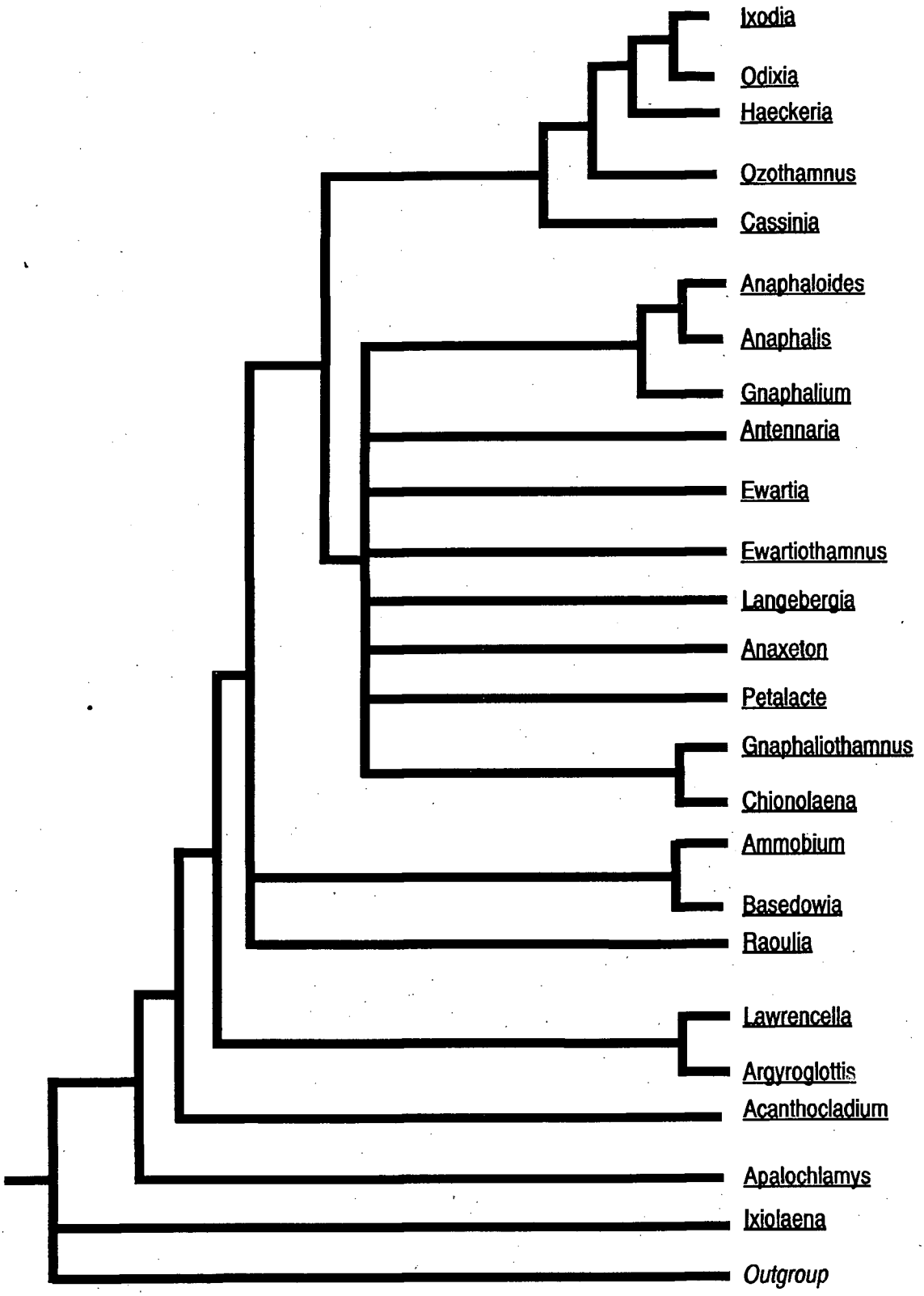


Figure 3. The strict consensus tree of the Cassiniinae sensu Puttock (1994)

Relhaniinae remained unaltered by the new analysis. Puttock's analysis differed from the cladograms published by Anderberg (1991). Five main clades were resolved, the Lucilia Cass. group (originally a group of species that Anderberg placed in the subtribe Gnaphaliinae) and the subtribes Loricariinae, Relhaniinae, Angianthiinae and the Gnaphaliinae. The major divergence from the cladograms published by Anderberg was that the Cassiniinae was submerged into the Gnaphaliinae. The Gnaphaliinae sensu Puttock contained the majority of Anderberg's Cassiniinae and Gnaphaliinae but excluded the Lucilia group, Apalochlamys Cass., Raoulia R. Br. and Argyroglottis Turcz. These differences reflect the redistribution of the Cassiniinae within the Gnaphaliinae. The position of the Australian genus Acanthocladium F. Muell. as the sister taxon to the Gnaphaliinae remains unchanged.

The proposed position of Cassinia R. Br. is relevant to the present study. Both Anderberg and Puttock placed Cassinia basal to the clade containing Ozothamnus R. Br., Haeckeria F. Muell., Ixodia R. Br. and Odixia Orchard. In Anderberg's scheme, Haeckaria and Apaloclamys comprised a sister clade to Ixodia and Oxidia. The submergence of the Cassiniinae into the Gnaphaliinae reflected the classical taxonomy (Bentham 1873a; Burbidge 1958) of the Cassiniinae with respect to Cassinia, Ozothamnus, Raoulia and Haeckaria. These taxa have at one time been placed in Helichrysum or Gnaphalium.

The phylogenies published by Anderberg (1991, 1994) and by Puttock (1994) concerned generic, not species, relationships. Breitwieser and Ward (1993) Investigated species relationships between forty-five species from ten genera. This study reported fifty-six "flavonoid" spots in a chromatographic study of the Australasian Gnaphalieae but no chemical structures were determined. Forty-five species, from 10 genera, were scored for flavonoid, leaf and floral characters. These characters were combined and used to construct a phylogenetic tree (Fig 4.). In Breitwieser's phylogeny the whipcord species of Ozothamnus formed a natural group. Ozothamnus dimorphus and O. depressus clustered to form a sister clade to O. coralloides and O. intermedium. This clade included O. parvifolius (Yeo) Anderberg. Ozothamnus parvifolius is known from several small populations in northwest Nelson, New Zealand. Breitwieser placed the

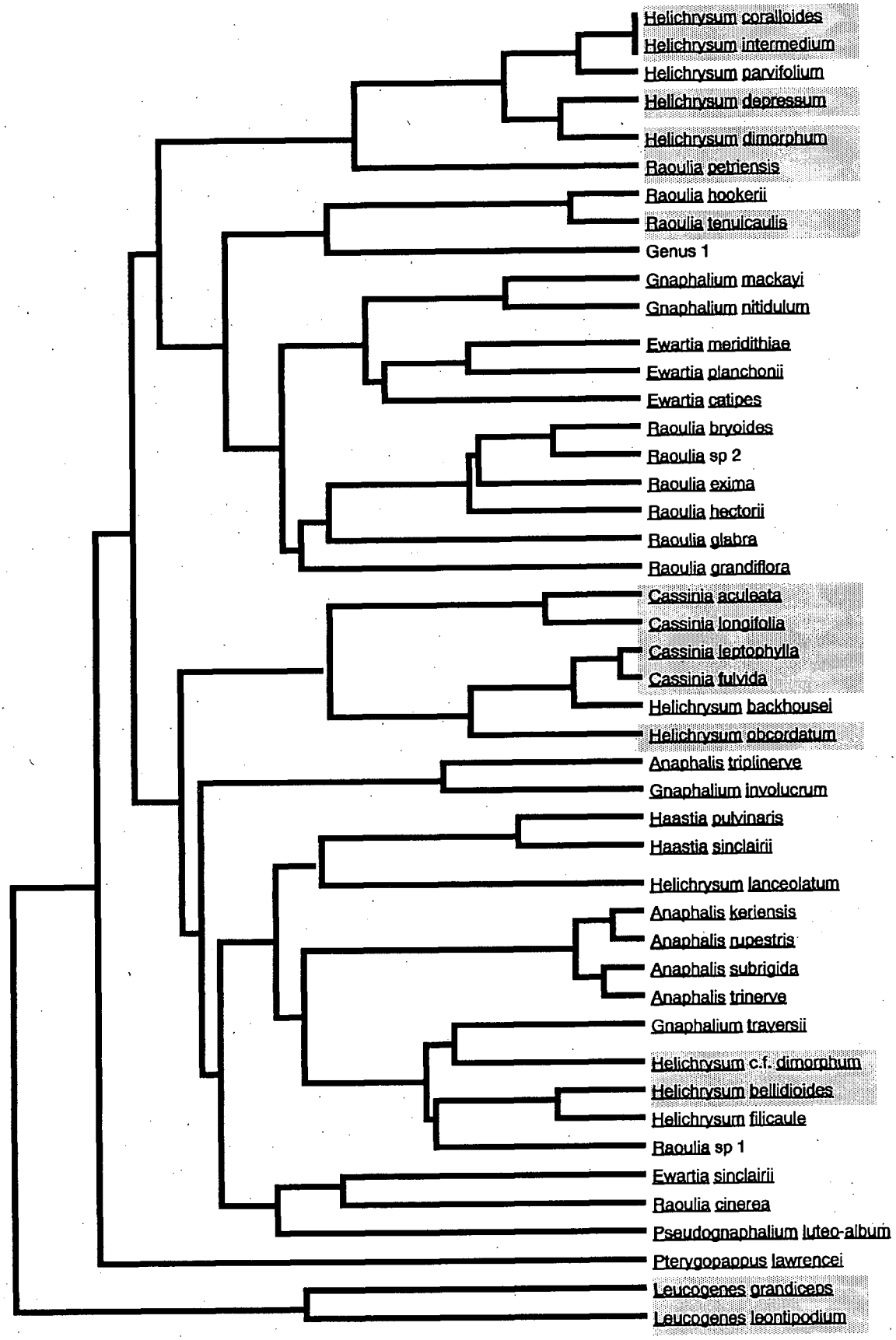


Figure 4. Species relationships within the Australasian Gnaphaliae sensu Breitwieser and Ward (1993)

= Taxa present in this study

whipcord* species of Raoulia, R. petriensis, as a sister taxon to the whipcord species of Ozothamnus. This phylogeny grouped the Australian and New Zealand Cassinia species. Breitwieser placed Cassinia in the same clade as the Australian alpine species of Ozothamnus, O. obcordatum, and with O. backhousei Hook. f. Ozothamnus backhousei is found in the tablelands of northwest Tasmania and has similar ecological requirements to some New Zealand Cassinia species. These tablelands are subjected to high winds and low winter temperatures (Curtis 1963). Of all the Australian species of Ozothamnus, O. backhousei is thought to be the closest relative of the New Zealand Cassinia species (Breitwieser pers. comm). According to Breitwieser and Ward (1993), Cassinia is related to the Haastia pulvinaris Hook. f., giant vegetable sheep, and Haastia sinclairii Hook. f. and the cudweeds sensu Drury (1972). Breitwieser and Ward (1993) proposed that Raoulia subgenus Raoulia sensu Allan and the alpine species of Ewartia Beauverd are closely related to the whipcord Ozothamnus species. Breitwieser and Ward (1993) investigated the herbaceous members of the Gnaphalieae from New Zealand. The Cassinia species and the Whipcord Ozothamnus species are the only woody representatives in the phylogeny sensu Breitwieser and Ward (1993).

The recent work by Anderberg (1991, 1994), Breitwieser and Ward (1993) and Webb (1988) has challenged the long standing beliefs concerning the relationships within this group of taxa. Additional data might help to resolve some of these issues. The combination of flavonoid data with ecological and morphological data, as attempted by Breitwieser and Ward (1993), may be more valuable if the structure of the compounds were known. With a knowledge of flavonoid biosynthesis and ecological conditions a better understanding of the relationships within the Australasian Cassiniinae may be achieved. Flavonoids are the most widely used secondary metabolites in plant taxonomy because of their structural diversity, stability and widespread occurrence within the plant kingdom. The variation in flavonoid structure arises from a number of sources including the oxygenation pattern of the basic skeleton. This skeleton can be substituted

* The term whipcord refers to the habit displayed by several families (Epacridaceae (Dracophyllum), Scrophulariaceae (Hebe) and the Rosaceae (Acaena), in alpine areas of New Zealand. From a distance the leaf and branch structure resembles braided rope or leather.

with various moieties such as glycosidic, methoxyl, prenyl, and sulfate groups. The number and position of these substitutions are important characters that determine flavonoid classes. The nature of the C-ring also contributes to the variation in structure. In addition it is absent in chalcones and dihydrochalcones and in aurones it consists of only five carbons instead of six as in other flavonoid classes

The stability of flavonoids and their ease of identification are the main advantages to their use in taxonomic studies. Commonly they can be extracted from either fresh or dried plant material, including herbarium specimens. Niklas and Gianassi (Gianassi and Niklas 1977, Niklas and Gianassi 1977a, b, 1978) demonstrated that flavonoids may be recovered from angiosperm fossils provided the plants have been fossilized under certain conditions. Whenever possible studies should use the same tissues, and compare plants of similar ages. Growth and developmental factors, as well as ecological conditions, may influence the accumulation of particular flavonoid types or classes (Menadue and Crowden 1983, Reid and Bohm 1994). The relative position of flavonoids in a two dimensional chromatogram is a useful taxonomic tool but determination of structures is prudent because our knowledge of flavonoid biosynthesis then makes it possible to assess degrees of similarity among flavonoid profiles.

There have been a number of chemical studies of flavonoids from the Inuleae sensu lato. Flavonoid composition has been reported for some 40 genera, approximately one sixth of the 250 or so genera considered by Merxmüller et al. (1977) to constitute the tribe. However, chemical composition of only eight genera and 21 species of Australasian members of the Inuleae, Plucheeae and Gnaphalieae sensu Anderberg have been reported. The summary of the flavonoid compounds reported from all genera that have Australasian members provided in this thesis are limited because while a large number of flavonoids have been reported in most cases no attempts were made to link the flavonoid occurrence with the systematic position of the taxa from which the compounds were isolated. The problem is whether the absence of a given compound in a report is real or simply whether it reflects a lack of detection.

Flavonoids have been used successfully to interpret evolutionary relationships in many groups of angiosperms (e.g. Fuchsia L., Averett et al. 1986, Crowden et al. 1977; Sophora L. Sykes and Godley 1968, Markham and Godley 1972; Podocarpaceae Berry et al. 1985, Markham and Whitehouse 1984, Markham, Webby and Vilain 1984). These interpretations often have been presented in a narrative fashion without specific indications of the kinds of relationships expressed. Also chemical data alone cannot easily provide an absolute timescale as to the divergence of taxa.

The aim of the research in thesis was to provide data for use in the classification and evolutionary analysis of relationships within the Australasian Gnaphalieae by carrying out a chemosystematic study of the flavonoids of members of this subtribe. The flavonoid data are combined with ecological, geographical and morphological data, to help address some of the biosystematic relationships. Thirty-eight species, representing six genera, were scored for flavonoid, leaf, floral, ecological and geological characters. These character scores were combined and used to construct a phylogenetic tree. Interpretation of the data requires an understanding of the ecological and geographical conditions in which the taxa in question exist which in turn requires a review of the biogeographical history of Australasia.

The nomenclature used in this thesis is based on published names. One has to be aware that some species have been misplaced. For convenience and expediency I begin with taxa in the taxonomic scheme sensu Anderberg (1991). The names for the New Zealand species of Cassinia, Leucogenes and Raoulia are those published in The Flora of New Zealand Volume 1 (Allan 1961). The names for species of Ozothamnus present in New Zealand and Australia follow those published by Anderberg (1991).

Table 1 Species included in this thesis.

Genus	Geographical Location	Species
Cassinia R. Br.	Australia	C. aculeata R. Br.
		C. arcuata R. Br.
		C. denticulata R. Br.
		C. laevis R. Br.
		C. longifolia R. Br.
		C. quinquefaria R. Br.
		C. rugata N. G. Walsh
		C. subtropica F. Muell.
		C. theodorii F. Muell.
		C. trinerve N. A. Wakefield
		C. uncata A. Cunn. ex DC.
	New Zealand	C. amoena Cheesem.
		C. fulvida var. fulvida (Hook. f.) Allan
		C. fulvida var. montana (Hook. f.) Allan
		C. leptophylla (Forst. f.) R. Br.
		C. vauvilliersii (Homb. & Jacq.) Hook. f.
Haeckeria F. Muell.	Australia	H. ozothamnoides (F. Muell.) P. S. Short
Lawrencella	New Zealand	L. bellidioides (Forst. f.) Anderberg
Leucogenes Beauverd	New Zealand (North Is.)	L. leontipodium (Hook. f.) Beauverd
	New Zealand (South Is.)	L. grandiceps (Hook. f.) Beauverd

Table 1 Species included in this thesis.

Genus	Geographical Location	Species
Ozothamnus R. Br	Australia	O. cordatus (DC.) Anderberg
		O. argophyllus (A. Cunn. ex Bentham) Anderberg
		O. dendroideus (Wakef.) Anderberg
		O. diosmifolius (Vent.) DC.
		O. hookerii Sond.
		O. obcordatus (F. Muell) DC.
		O. rosmarinifolius (Labil.) DC.
		O. stirlingii (F. Muell.) Anderberg
		O. coralloides Hook. f.
		O. depressus Hook. f.
		O. dimorphus (Ckn.) Anderberg
		O. intermedium (Simpson) Anderberg
		O. selago Hook. f.
Raoulia Hook f.	New Zealand	R. australis Hook. f.,
	Subgenus Raoulia	R. glabra Hook. f.
		R. hookeri var. albo-sericea (Col.) Allan
		R. hookeri var. apice-nigra (Kirk) Allan
		R. hookeri var. hookerii Allan
		R. monroi Hook. f.
		R. subsericea Hook. f.
		R. tenuicaulis Hook. f.
	Subgenus Mistura	R. petriensis Kirk

* O. argophyllus = O. ferruginea DC.

The Biogeography of the Southern End of the World: The New Zealand and Australian Botanical Regions.

The lands of the south temperate biogeoclimatic zone,Southern South America including Tierra del Fuego, southern Australia with Tasmania and New Zealand, have much in common geographically, geologically, biologically and climatically. No other substantial land areas share all their characteristics and although the southern tip of Africa extends into this zone it shows warm temperate affinities. The distribution of plants in the southern region of the world has interested biogeographers since the time of J. D. Hooker who published the Flora Antarctica (Hooker 1844) in which he emphasized the relationships between Tasmania, New Zealand and South America.

The New Zealand Botanical Region.

The geologic, climatic and biotic histories of New Zealand are known in greater detail than those of any other south temperate land. Its geographical and biological isolation over a long period of time created a unique and diverse flora in an environment that has sustained ancient forests, alpine wonders and plant species long since vanished from the rest of the world. Eighty-four percent of all flowering plants found in the New Zealand Botanical Region are endemic. New Zealand shares almost 80% of its vascular plant genera with Australia. (Cockayne 1917)

Of the world's larger islands, the two islands of New Zealand are the most remote from any continent. At its closest point New Zealand is 1900 km (1200 miles) from the nearest continental influence. In contrast, Japan and the United Kingdom are as close to their continental influence as New Zealand's North and South Islands are to each other. Other large island archipelagos, such as Indonesia and the Caribbean Islands, are a close-set series of islands linking two major continental areas. New Zealand is not so.

The New Zealand Botanical Region, stretching from the Kermadec Islands (30^{o}00'S, 178^{o}30'W) to Macquarie Island (54^{o}S,159^{o}E), stretches through approximately 25^{o} of latitude. It contains 40 endemic genera and one endemic family, the Dactylanthaceae (Allan 1961, Webb 1988).

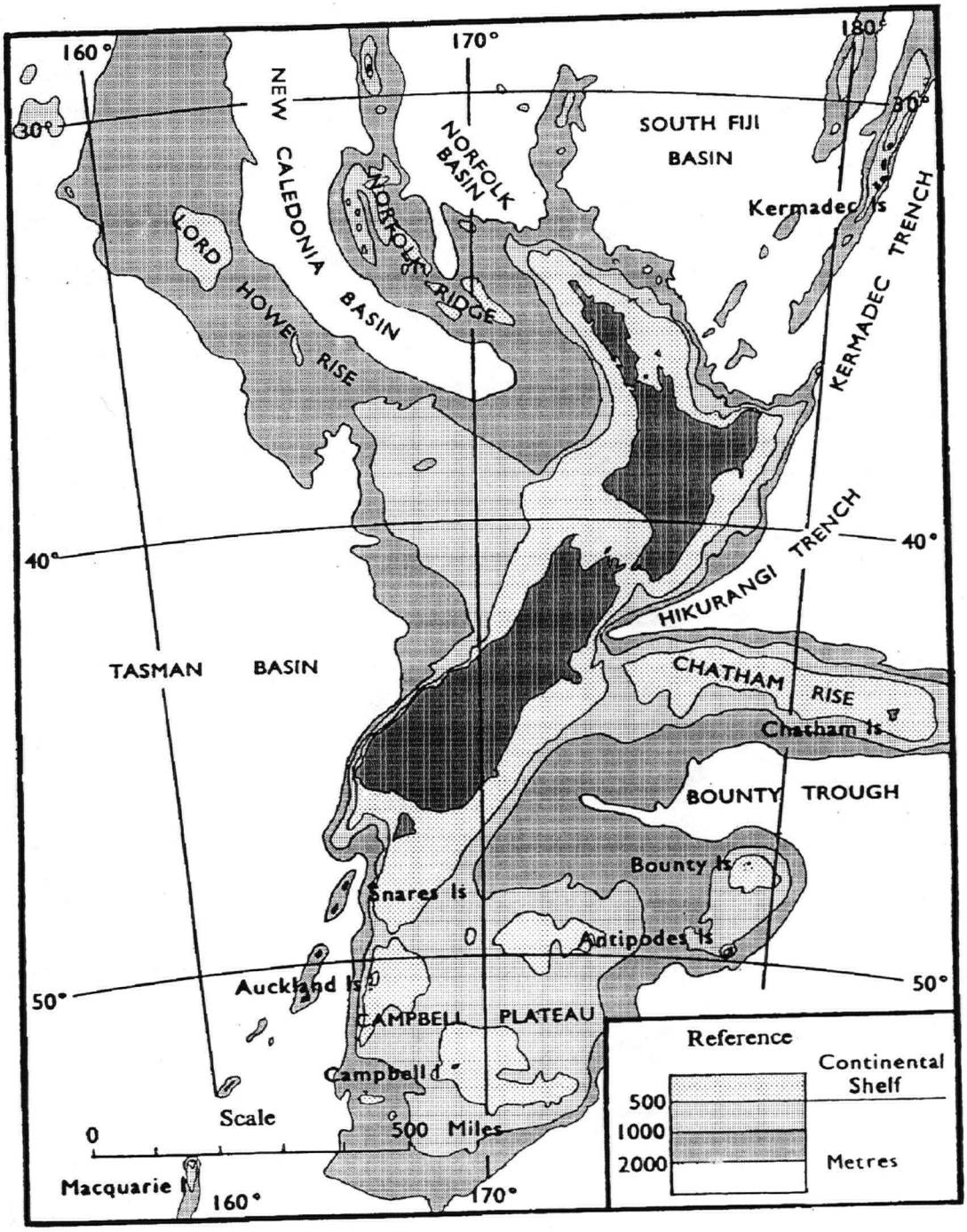


Figure 5. The New Zealand Geological and Botanical Region

The Kermadec Islands flora consists of 120 species, 15 of which are endemics (Oliver 1953, Sykes 1969, 1977), while that of Macquarie Island, which lies just outside the sub Antarctic convergence, is not particularly diverse containing 45 phanerograms, of which two are endemic, an unnamed orchid and Azorella maquariensis, an endemic carrot. The Chatham Islands (44°00'S,176°30'W), 820 km east of Christchurch, marks the eastern border of the region and supports 40 endemic species (Allan 1961). Stewart Island, (46°30'S, 168°00'W), known to the Maori as Rakioura, lies about 50 km off the south coast of the South Island of New Zealand and was isolated from the South Island as a result of seismic activity. Despite its proximity to a major landmass, the flora of Stewart Island has twelve endemic species (Allan 1961; Wilson 1987).

Two types of flora exist in New Zealand, one a predominantly lowland-montane forest and the other predominantly an alpine non-forest. (Fig 6). Cockayne (1917) defined botanical regions for New Zealand based upon agricultural, ecological, geographical and other biological factors and recognized a discontinuity of the flora through the centre of the North Island. Cook and Foveaux Straits were recognized as a barrier to the north-south dispersal of the flora through New Zealand. The Southern Alps, which form the backbone of the South Island, provided an east-west barrier. The most startling discovery made by Cockayne was that the Southern Beech or Nothofagus forests of the South Island were not continuous but are split by "the Westland Beech Gap". The Westland Beech Gap extends from Hokitika in the North, to Arthur's Pass in the South. A conifer-broadleaf forest replaces the Nothofagus forest in this region. In contrast, the Alpine flora is extremely fragmented in the North Island and is restricted to the central volcanic region around Mt. Ruapehu and Mt. Ngauruhoe. Continual volcanic eruptions in this area retard the recolonization of the area by forest-forming species. Extensive alpine vegetation exists in the South Island mountains at high altitudes. During glacial times alpine vegetation covered all but the coastal areas and warm valleys of New Zealand's South Island.

Wardle (1963) redefined the regions proposed by Cockayne based on the number of endemic species occurring in each. The number of endemics found between 38°S and 40°S and between 42° and 45°S is significantly lower than in the rest of New Zealand.

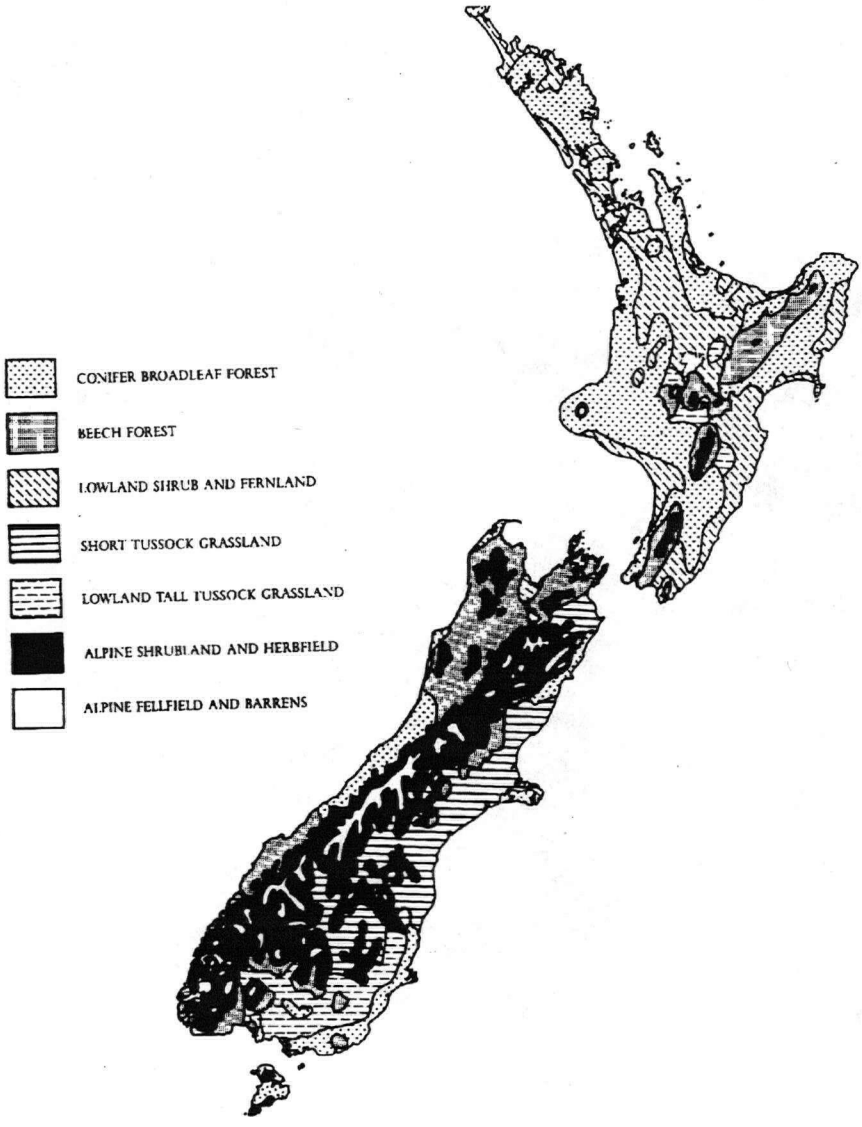


Figure 6. Vegetation Map of New Zealand (Dawson 1988)

Cockayne (1928) had already recognized that these latitudes corresponded to biological and ecological limits for many species in New Zealand. Northern North Island endemics are predominantly woody in nature. The Three Kings Islands, north of Auckland city, have 13 endemic species; 6 are trees, 4 are shrubs and 1 is a climber while the Auckland Islands, far to the south of the South Island, have 28 endemics, of which only 3 are shrubs. The 39th parallel is the limit for those species with tropical affinities such as Kauri (Agathis australis Salisb.) and Taraire (Beilschmiedia taraire (A. Cunn.) Benth. &. Hook. f.). The 45th parallel is the northern limit for those species with Sub-Antarctic or southern affinities. Wardle concluded that the nature of the endemics in an area was the best character to be used in the interpretation of floristic relationships.

The Australian Botanical Region

The Australian Botanical Region (Fig 7.), stretching from the Christmas Islands (10°35'S, 105°30'W) to the southern tip of Tasmania (43°S,149°E), covers approximately 30° of latitude. According to Burbidge (1963) the region contains 173 dicotyledon and 49 monocotyledon families comprising 1600 genera and 13,000 species. The world's largest families, the Orchidaceae, the Asteraceae, the Fabaceae and the Poaceae, are well represented but are exceeded in number by members of the Myrtaceae. There are 12 endemic families (Beadle 1981) and 540 endemic genera distributed within 92 families. Burbidge (1963) and Beadle (1981) both list these and show that by far the largest number of endemic species and genera are members of the Asteraceae. The habitats include rain forests (87 genera), soils of low fertility (195 genera), semiarid and arid zones (107 genera), and the cold alpine zone of Tasmania and the Kosciusko ranges of N.S.W. (19 genera).

Australia has a much drier climate than New Zealand resulting in the formation of different vegetation types (Beadle 1981), some of which are common to both countries. For example the cool moist Southern Beech (Nothofagus spp) forest extends through the eastern fringe of Australia and is common in Tasmania, the open alpine areas of northeastern Victoria and the South Island of

New Zealand. Before the arrival of humans this vegetation type occupied approximately 1% of the Australian continent.

Moist closed forests exist in scattered patches along Australia's eastern coast line, the northwestern parts of Western Australia and in the Northern Territory. These forests are classified into three types: tropical, subtropical and warm temperate. Tropical forests which are dominant in Queensland, northwestern parts of Western Australia and the Northern Territory, are commonly referred to as mesophyll forests. The subtropical forests are distributed in central Queensland and central New South Wales. Referred to as a notophyll forest (Dawson 1988), this is a mixed forest with tropical and temperate affinities. The warm temperate forests, extending through New South Wales and eastern Victoria, is a microphyll forest dominated by temperate genera. These forests share a number of genera with New Zealand: Elaeocarpus L., Beilschmedia Nees, Dysoxylum Blume, Syzygium Gaertner and the vines Freycinettia Gaudich., Ripogonum Forster & Forster f. and Parsonsia R. Br. In most cases of shared genera there are more Australian than New Zealand species. Woody vines and vascular epiphytes are conspicuous in the northernmost Australian forests but are less common in the latitudes shared with New Zealand's North Island. In Queensland, members of the Moraceae and the Araucariaceae are dominant emergent trees. This points to an increased tropical influence in these northern forests.

The moist Nothofagus forests extend through the coastal areas of southern Victoria and are the dominant vegetation type in Tasmania. As in New Zealand, the Australian Nothofagus forests have relatively few species in the understorey and few or no vascular epiphytes or lianas. Several other similarities with New Zealand exist. Members of the Cunnoniaceae, Weinmannia racemosa L. f. (Kamahi) in New Zealand and Ceratopetalum apetalum D. Donn. in Tasmania are the dominant species found associated with Nothofagus forests. The conifers Dacrydium Sol. ex Forst. f. and Phyllocladus L. C. Rich. & A. Rich. and the tree ferns Dicksonia L'Herr. spp. and Cyathea Smith spp., are common in gulleys and canopy gaps. Ecological species pairs exist with New Zealand in this forest type. Nothofagus cunninghamii (Hook. f.) Oersted, the Australian

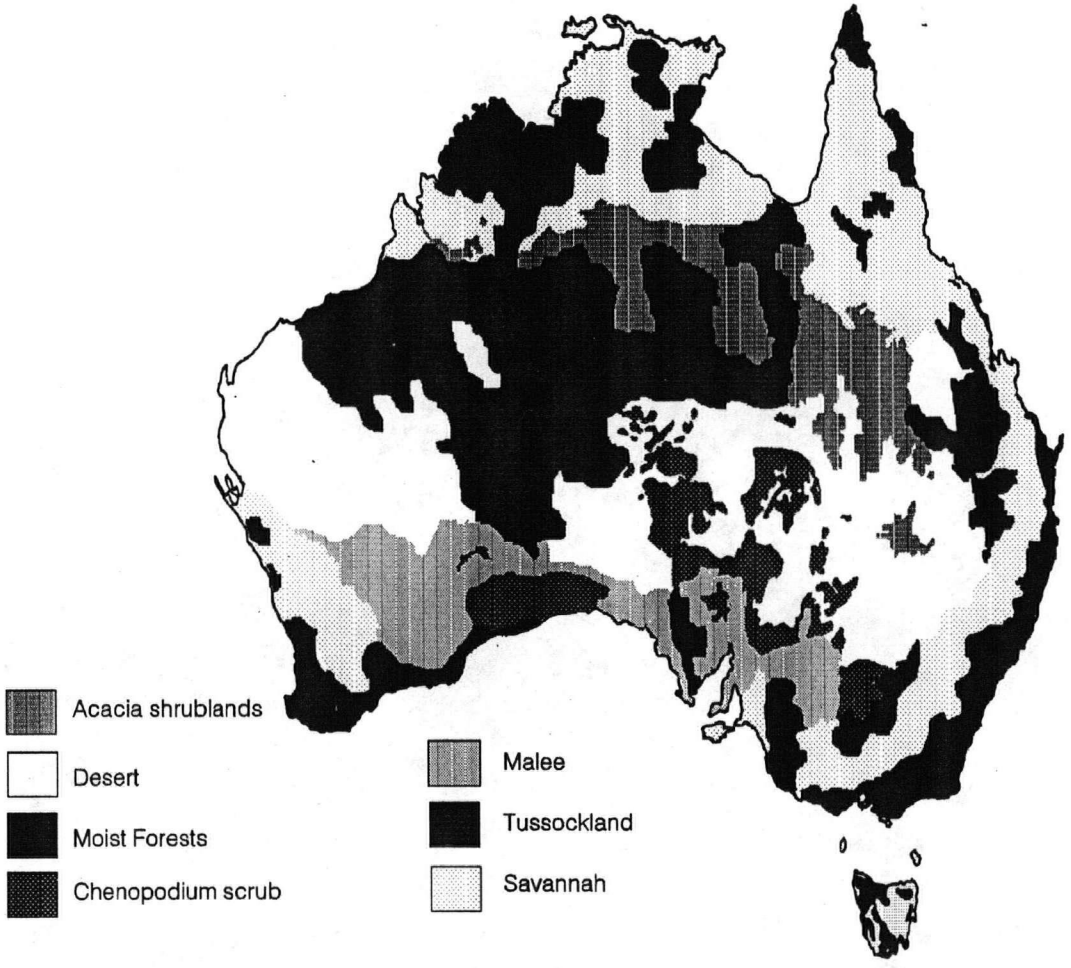


Figure 7. Vegetation Map of Australia (Adapted from Beadle 1981).

species and N. menzesii (Hook. f.) Oersted, the New Zealand species, are the dominant montane species.

Intermingled throughout the range of the Nothofagus forests in Australia are the open eucalypt forests. Trees in the eucalypt forest grow sufficiently apart that the crown does not form a continuous canopy. As a consequence, the ground is not heavily shaded. The wet sclerophyll forest is restricted to maritime southeast Australia and Tasmania and on the southwestern tip of Western Australia. Where the soils are locally fertile, tree ferns dominate the understorey but this forest is an indicator of generally poor soil conditions. Under infertile conditions the understorey is dominated by heath-like shrubs belonging to the Myrtaceae, Proteaceae or Casuarinaceae. In areas of extreme infertility and water stress, this forest is stunted and resembles a tall shrubland. This forest may also include species of Acacia Miller and is known in Australia by two names, Malee and Mulga.

Australia has generally low relief. It is only in the southeast and in Tasmania that mountains rise above treeline. Mt. Kosciuscko (36°15' 36"S, 148°12'E) is the highest point at 2194m. The mountains are formed from raised plateaus with fringing scarps. Glaciation was more severe in Tasmania than mainland Australia resulting in a larger number of mountainous sites. On mainland Australia, the subalpine zone, immediately below tree line (at approximately 1000m above sea level), is dominated by species of Eucalyptus known as 'snow gums.' In Tasmania the snow gums are replaced by the cold tolerant Nothofagus gunnii (Hook. f.) Oersted. More commonly, the valley floors are dominated by Danthonia DC grassland similar to the Chionocloa Zotov grass/tussocklands of New Zealand's Mackenzie basin. Above treeline, on well-drained fertile soil, the herbfield is dominated by Celmisia Cass., Euphrasia L. and Craspedia Forst. f. These species form an integral part of the New Zealand alpine vegetation. On the poorly drained sites, bogs dominated by peat mosses and sedges are common. Tasmanian sites are dominated by subantarctic genera similar to the Southern Alps in New Zealand.

Geology

The New Zealand Geological Region (Fig. 5) extends from New Caledonia eastwards to the Chatham Plateau and south to the Campbell Plateau (Fleming 1975). This "landmass" began to separate from the Australo-Antarctic margins of Gondwana approximately 82 million years ago (Stevens, 1980) causing a rift system that formed what is now the Tasman Sea. This sea impeded the dispersal of plant and animal species from the remnants of the super continent. Some elements of the biota did manage to bridge the proto-oceanic gap but essentially New Zealand was a floating raft with an isolated terrestrial biota.

The plant and animal groups adrift on this island raft were members of what are thought to be the most primitive of all and included the terrestrial gastropods typified by the giant carnivorous land snails Paryphanta, the ratite birds Dinornis and Apteryx and some of the more primitive members of the plant kingdom. Among the plants were representatives of the Winteraceae, the Araucariaceae and the Fagaceae (Nothofagus spp, the Southern Beeches). The Tasman Sea ceased spreading 60 million years ago by which time New Zealand and Australia were separated by the present distance (1700 km from North Cape to New Caledonia and 1900 km from Westland to Tasmania.) With the Norfolk and Lord Howe Rises devoid of volcanic hotspots, New Zealand has been disjunct from Australia for 80 million years. There was considerable exchange of species between New Caledonia and New Zealand. The Kermadec Islands, and their associated ridges, were island chains along which plants island hopped in northerly and southerly directions. The long isolation of the New Zealand archipelago has led to a high degree of endemism in both the flora and the marine fauna. The opening of the southern ocean between Australia and Antarctica and the opening of Drake's passage (between Tierra del Fuego and Graham's Land) caused the establishment of circumpolar sea currents, which combined with the winds of the "Roaring Forties" and "Furious Fifties" aided in west-east dispersal of both plant and animal species. Many of these genera no doubt arrived as a result of these winds. However action of these winds cannot explain the presence of forests that have a strong gondwanan element.

During the Cretaceous (65-140 million Y. B. P.) New Zealand was composed of an amalgam of low relief land blocks formed along the edge of Gondwana (Fig. 8). Australia at this time was connected to South America and Southern Africa, forming Gondwanaland. This supercontinent lay further south than Australia's present day position. At this time the Kermadec Islands were situated within the Antarctic circle and the South Pole was situated in the middle of the Campbell Plateau. The influence of the climate on the flora was most noticeable in New Zealand and Southern Australia. South temperate forests, consisting of podocarps, beeches, tree ferns and bryophytes covered the land. As the climate warmed in the interglacial periods of the Paleocene and the Eocene, the subtropical climate accompanied by higher rainfall and erosion, produced a highly dissected landscape dominated by Nothofagus species of the N. brassii pollen group (Cranwell 1939, Van Steenis 1971), Casuarina and mangroves. Mangroves and coconuts grew at 45^{o} S latitude, a latitude that today would not support that type of flora. The abundance of Nothofagus species in the forest reflects the cycles of subtropical warmth and glacial cold. The N. brassii pollen group reflects the tropical interglacial while the N. fusca and N. menzesii pollen groups indicate cooler glacial periods (Poole 1986). The geological instability of the boundary between the Pacific Plate and the Australian Plate increased significantly during the Oligocene. This activity led to an increase in the lateral shearing that ultimately distorted the shape of New Zealand into its present conformation. The instability continued throughout the Pliocene and Pleistocene. The cooling of the climate during this mountain-building period removed the tropical and subtropical elements from the vegetation of New Zealand. Among the notable reductions was the Nothofagus brassii group, a group that was prominent in New Zealand during the Cenozoic, but is now restricted to New Caledonia and New Guinea. (Dawson 1988) The ice age coincided with a period of intense tectonic activity. The rapid growth of the Southern Alps and other mountain ranges has been the major influence on the present day disjunctions in plant distributions (McGlone 1985).

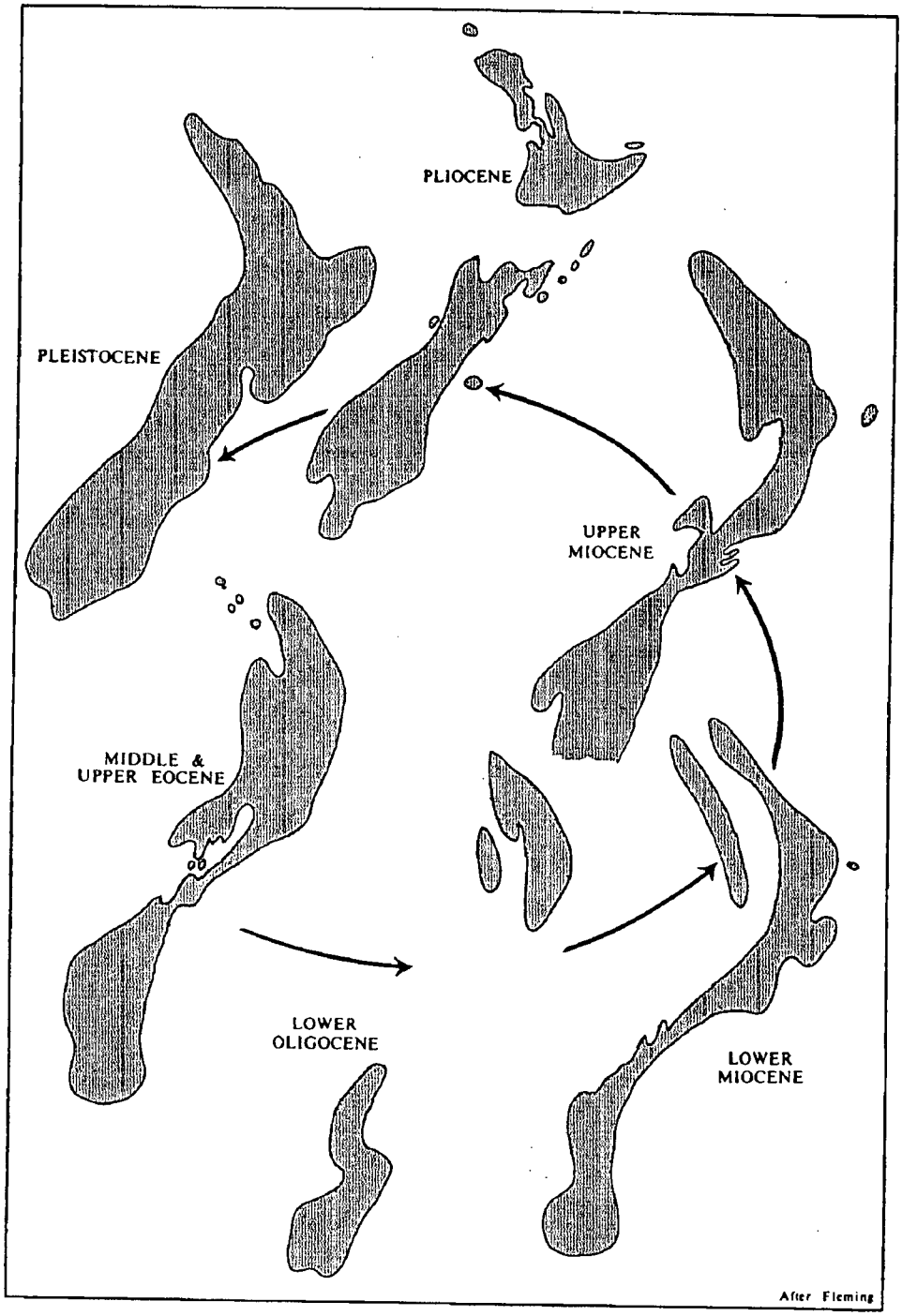


Figure 8. Coastlines of New Zealand (after Fleming 1975).

Meanwhile during the Eocene (Fig 9. 53 million Y. B. P.) Australia was locked together with Antarctica, South America, India and Africa as a single landmass (Gondwana) positioned at 30°S. As would be expected, many ancient groups of plants (including the cycads, tree ferns and the Southern Hemisphere gymnosperms) are distributed across the continents of the Southern Hemisphere that formerly comprised Gondwana (Page and Clifford 1981). During the Paleocene (53-65 million Y. B. P.) tectonic movements began to form a rift valley system that would eventually separate Australia from Antarctica. At this time Southern Australia was centered at 65°S and surrounded by a subtropical influence (Flemming 1975). There is little fossil evidence from this time in Australia. Most floral reconstruction's have been through palynological studies. The subtropical climate is confirmed by pollen analysis. Pollen profiles indicate widespread forests dominated by Podocarpus, Araucaria, the Myrtaceae and the Proteaceae. Forests of Nothofagus were rare and the tropical forests extended into areas of central Australia that are now dominated by scrublands. The final separation of Australia and Antarctica began during the Eocene (Fig 9. 53 million Y. B. P.) At first the warm moist climatic conditions persisted, but as the Eocene progressed the cooling of the seas surrounding Australia led to increased abundance of temperate Nothofagus forests. The climatic cooling trend continued through the Oligocene causing the formation of icecaps in Antarctica. This resulted in a general drying of the Australian landscape. which continued throughout the Oligocene and into the Miocene. During the latter part of the Miocene the climate reverted to a moist warm climate similar to the conditions found during the Eocene. Palynology suggests than an extensive forest of Nothofagus, Lauraceae and Myrtaceae dominated Australia. During this time Australia was situated between the latitudes it presently occupies and the Antarctic icesheets had reached their present extent. This indicates a progression toward a drier cooler climate. The glacial and interglacial oscillations led to the widespread disappearance of the tropical forest in all but the northern most parts of Queensland (Beadle 1981).

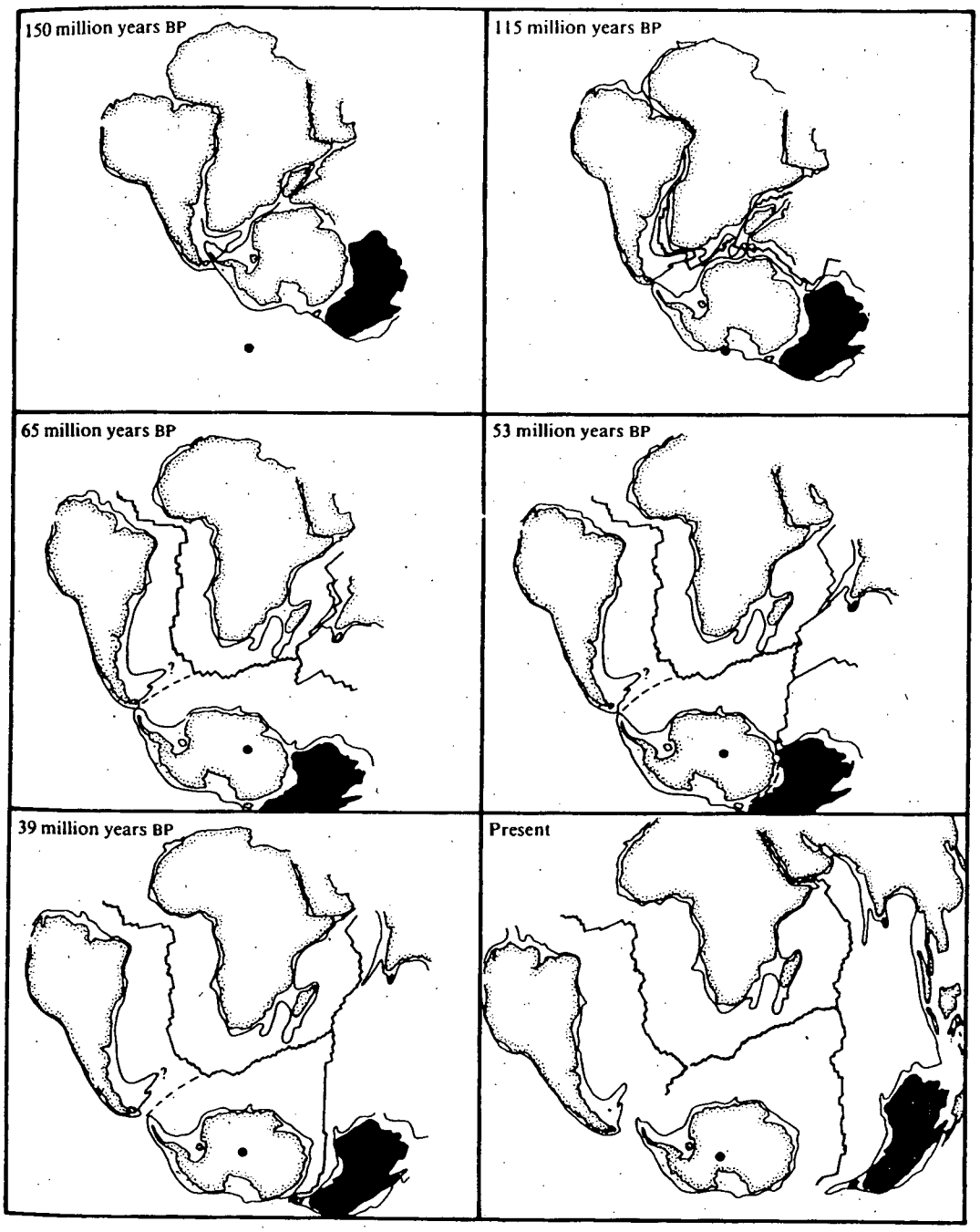


Figure 9. Geological Movements of the Australian Continent.

The disappearance of the rain forests left an arid, leached soil profile in which only the most tolerant plants (mostly Eucalyptus L' Herr. and Casuarina L.) could survive.

In contrast to the geological movements of Australia, New Zealand, sitting astride the boundary of the Pacific and Australian plates, moved as two independent pieces. Geological evidence (Stevens 1980) suggests that the southern part of the South Island was in a more northerly position than the central volcanic region is today. The constantly changing sea level accompanied by frequent volcanic and tectonic activity gave New Zealand a variety of shapes and sizes (Fig. 8.). This continual disruption of the land forced many species of southern affinities, such as Nothofagus and the southern gymnosperms in New Zealand, into refugia. The geological stability of the Pliocene and Pleistocene allowed colonization of suitable habitats by these refugial populations

Cockayne (1928) suggested that a few of the ancestors of the present alpine flora also survived in these refugia probably on rocky bluffs or outcrops during the warmer times. With the onset of glaciation these plants colonized the new cold sites. Cockayne's theory is apparently bolstered by the presence of some of the present day rocky shore genera, such as Aciphylla squarrosa J. R. et G. Forst. (Apiaceae) in the Cook Strait area, Celmisia lindsayi Hook. f. (Asteraceae) in Akaroa and Anisotome lyallii Hook. f. (Apiaceae) in south west Otago. This is very similar to the "nunatak hypothesis" of Fernald (1924). McGlone (1985) proposed that in New Zealand the rocky coasts, exposed outcrops and the high mountain tops acted as the refugia. There is a problem, however, with this theory. The alpine flora of New Zealand is dominated by herbaceous species while the fossil record indicates that there was a predominance of woody species. The theory can be modified by suggesting that soon after the herbaceous plants became common, long distance dispersal brought in the plants from the Northern Hemisphere. This does not mean that the lowland relatives of alpine plants are primitive. More likely, the alpine vegetation extended to the coastlines in the glacial eras. With each warmer interglacial the forest type vegetation would have been able to recolonize the lowland areas except for rocky, exposed sites. Wardle (1963) suggested that in the warmer pre-glacial times New Zealand would have extended

past the Campbell Plateau (Tasmantis) and would have been able to support a cool temperate forest flora. This, in turn, could have been a genetic bank for the engendering of mountain species. This hypothesis was based on genera and species shared between the mainland mountains and the Sub-Antarctic islands. The species endemic to the Sub-Antarctic islands could not migrate back to the mainland mountains before the more opportunistic colonizers arrived from the North.

Wardle (1968) later proposed that a small element of alpine flora may have been in New Zealand during the warmer times. This is partly documented by the fossil record. He lists 29 flowering plant species from 15 genera that are confined to cool, wet, infertile soils, which may have reached New Zealand by long distance dispersal. Of these, Nothofagus is a forest dominant, Stilbocarpa (Araliaceae) is a dominant herb in the southern islands and the rest are low growing mat forming plants that do reach alpine levels. It was suggested by Wardle (1968) that the alpine conifers Podocarpus nivalis Hook. (Snow Totara), Lepidothamnus laxifolius Hook. f. (Pigmy pine) and Phyllocladus asplenifolius var. alpinus (D. Donn) Parl. (Mountain Toatoa) may have survived to the present from the Tertiary. Hair et al (1967) showed that the shrubby forms, e.g., the alpine conifers, are cytologically more primitive than their forest relatives and so it is unlikely that the alpine conifers are derived from the forest relatives.

It has also been suggested that the alpine flora of New Zealand, Tasmania and the Andes has been derived from the now extinct mountain flora of Antarctica (Fleming 1962). This would imply, for the New Zealand flora, migration by way of the Sub-Antarctic Islands. Considering the poor dispersal properties of many New Zealand alpine species it is unlikely that this migration occurred.

Description of the subtribe Cassiniinae.

The Cassiniinae are shrubs or perennial herbs that may be dioecious (e.g., Antennaria Bayer 1988) or monoecious. The leaves are often clothed in glandular tomentum which may be reduced to minute glandular dots. The capitula may be disciform or discoid with several rows of brown or transparent papery involucral bracts. The bracts range in colour from white and yellow to red. The receptacle is either paleate or epaleate. The outer florets are filiform and female and usually are less frequent than the central perfect disc florets. The style in both floret types is truncated with apical hairs. The pappus is held in a single row and constructed from barbed capillary hairs. The subtribe is distributed world-wide but is concentrated most richly in the southern hemisphere especially in New Zealand, Australia and South Africa. The subtribe consists of 22 genera and approximately 300 species

Two generic groups were recognized by Anderberg (1991); the Cassinia group (to which the species in this study belong) and the Anaphalis group. The Cassinia group consists of two main genera, Ozothamnus and Cassinia, with four smaller allied genera, Ixodia, Oxidia, Haeckaria and Apalochlamys. The smaller genera are distinguished from the larger two by the lack of receptacular paleae.

Description of the species involved in this study

Cassinia R. Br.

Species of Cassinia are shrubs up to 5m in height with tomentose, linear to spathulate, sessile, alternate leaves. The glandular tomentum ranges in colour from fulvous to white. The homogamous capitulum is discoid and held in flat topped, terminal corymbs or panicles. The few disc florets present are hermaphroditic, while the tubular outer florets are predominantly female. The imbricate phyllaries range in colour from white through pink to brown. The receptacle is paleate and the paleae are white tipped. The outer florets are yellow if present. The achene is sometimes covered with glandular hairs. The 20 species are distributed in New Zealand and Australia. Cassinia is absent from the Northern Territory.

New Zealand Cassinia species.

Allan (1961) accepted 5 species and several regional varieties for New Zealand Cassinia (Fig. 9.). These species and varieties can be classified based on leaf exudate that ranges in colour from yellow to gray green.

The Yellow Exudate Species

Cassinia amoena Cheesem.

The smallest of the New Zealand Cassinia species, C. amoena, is a slender, much branched shrub, less than 1m in height. When mature the leaves are glabrous above and with a dense white woolly tomentum below. The disc florets are scaleless but surrounded by white tipped phyllaries. Cassinia amoena is known from only the type location, the serpentine outcrops of Kerr Point and North Cape. This is the rarest of the New Zealand species but is in cultivation at several botanical gardens including Otari Native Botanical Garden in Wellington. The flowering period is between November and January. This species has the most restricted altitudinal distribution, occurring only on the coastal cliffs at North Cape which are less than 100m above sea level.

Cassinia fulvida Hook. f. (syn: Cassinia leptophylla var. gamma Hook. f.)

The Golden Tauhinu, or Cottonwood, is a slender, much branched shrub, that reaches 2m in height. The sticky branches are clothed in a dense fulvous or yellow, woolly tomentum that extends to the underside of the mature leaves. Two varieties are recognized. Cassinia fulvida var. fulvida Allan is common from 40°S to Stewart Island in scrub from sea level to 1200m. Flowering period is between March and November. Cassinia fulvida var. montana Ckn. is a more compact shrub that has larger more obovate leaves than C. fulvida var. fulvida. The capitulum is commonly red caused by the numerous pubescent phyllaries. Cassinia fulvida var. montana is common in scrub from 500m to 1500m and is distributed from 42°S to 52 °S.

Cassinia vauvilliersii (Homb. & Jacq.) Hook. f. (syn: Ozothamnus vauvilliersii Homb. & Jacq. ex Decne.; Olearia xanthophylla Col.)

The Mountain Tauhinu is the largest of the New Zealand Cassinia species reaching over 3m in height. It is distinguished easily from the other species by the thick spreading and twisted branches. The whole plant is covered in a dense fulvous tomentum. Flowers are produced from September to December and range in colour from off-white through pink to red. The Mountain Tauhinu is found throughout New Zealand from 37°S to the Auckland Islands and is most common on soils of volcanic origin. A number of regional varieties from different soil parent materials have been described. Cassinia vauvilliersii var. serpentina Ckn. et Allan has been described from the serpentine outcrops of Dun Mountain in northwest Nelson and differs from typical specimens of C. vauvilliersii in habit and branching pattern. The tomentum in C. vauvilliersii var. serpentina is reported to be cottony in texture and brown in colour (Cockayne and Allan 1926). C. vauvilliersii var. pallida Allan, C. vauvilliersii var. albida Kirk and C. vauvilliersii var. canescens Allan are varieties of local distribution. These three varieties have been described from the valleys and plains of the Clarence, Awatere and Wairau Rivers in northeast Marlborough. The tomentum in C. vauvilliersii var. albida and C. vauvilliersii var. canescens is reported to be cottony in texture and white in colour (Cockayne and Allan 1926). In C. vauvilliersii var. pallida the tomentum is green. Webb (1988) attributes these varieties as unstable mutant forms of C. leptophylla

The gray-green exudate species

Cassinia leptophylla (Forst. f.) R. Br. (syn: Calea leptophylla Forst. f.)

The slender or fragrant Tauhinu is a spreading shrub, up to 3m tall, covered in a grey tomentum. The tomentum covers all parts of the plants including the capitula. The flowers are

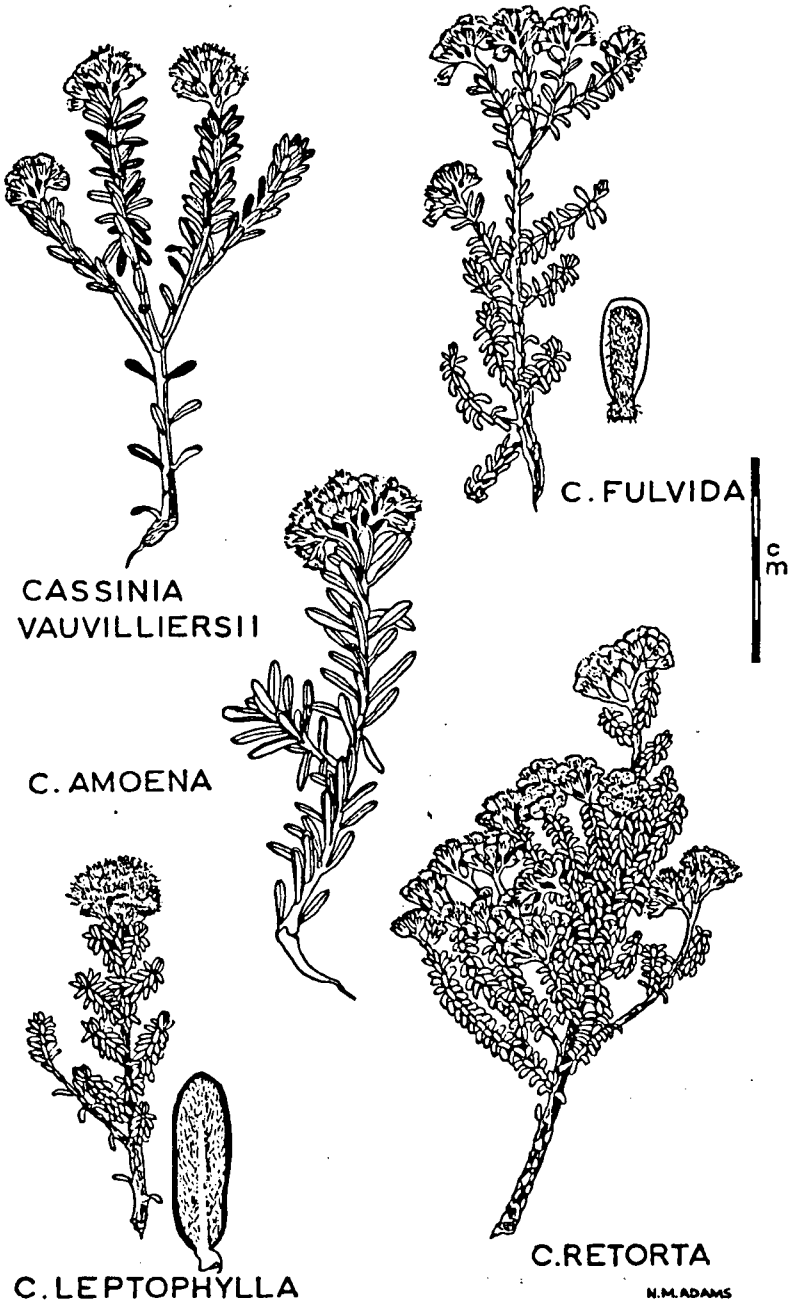


Figure 10. New Zealand Cassinia species (Poole & Adams 1963)

produced between November and January with a second flush in March and April. The flowers appear to range in colour from cream to pink caused by the phyllaries that surround the receptacle. This species is a common pioneer in all habitats and soil types. This species has the widest altitudinal and geographical distribution of Cassinia in New Zealand. It is found throughout the New Zealand botanical region from the Kermadec islands to the Auckland Islands and from sea level to 1500m. Cassinia leptophylla displays considerable local differentiation. Characters used previously, e.g., size, shape, colour and number of receptacle scales, may vary continuously within and among populations and they tend to vary independently of each other. Many plants are not referable to any previously described taxa. Webb (1988), while accepting only one endemic New Zealand species, described the forms of C. leptophylla as having a dense white tomentum on the young stems and on the lower surface of the leaves. This tomentum is often overlain with yellow glands. The concentration of these glands determines the colour and stickiness of the leaves and stems. All degrees of density of glands are found in alpine and subalpine plants. Plants with narrow leaves and a yellow tomentum are often referred to as C. fulvida. In the South Island and the lower North Island plants from higher elevations generally have much thicker branchlets, larger leaves and a deeper yellow tomentum than plants from lower elevations. Upland plants are referred to as C. vauvilliersii while lowland plants are referred to as C. leptophylla. Clearly, Webb attributes colour variation within the genus sensu Allan as an altitudinally controlled condition.

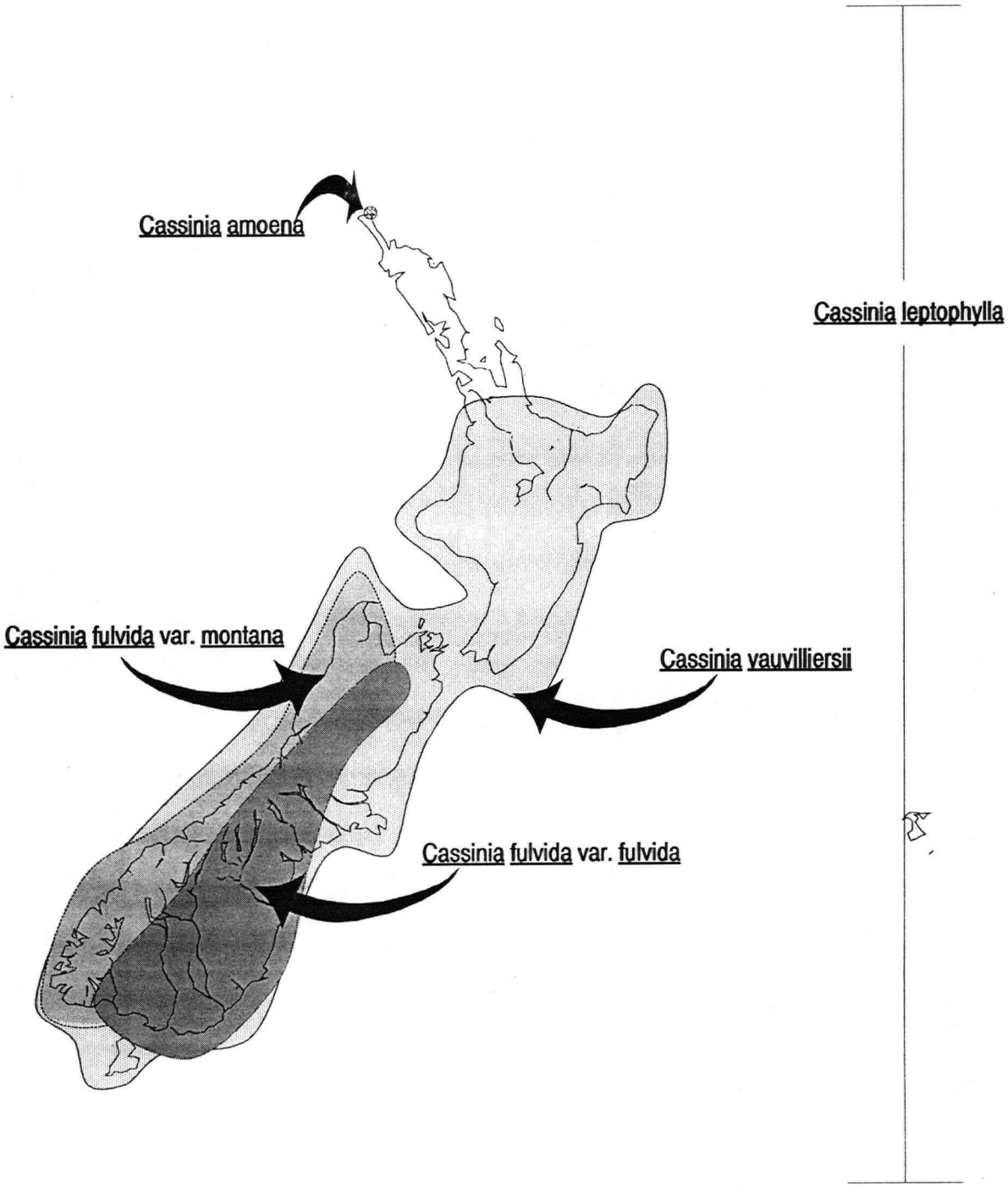


Figure 11. Distribution of Cassinia species in New Zealand

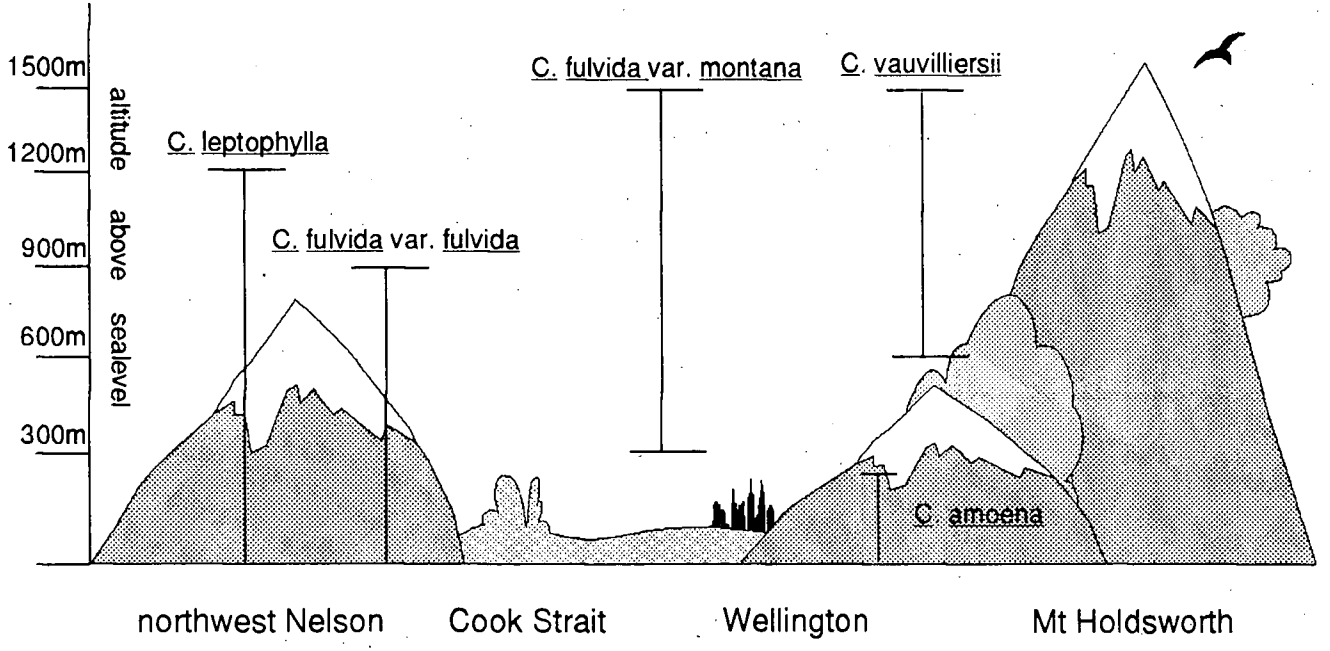


Figure12. Altitudinal distribution of New Zealand Cassinia species across 41°S latitude

Australian species of Cassinia

Anderberg (1991) noted that the species of Cassinia have many characters that are common to the genus Ozothamnus. Cassinia is defined by paleate receptacles that, in Anderberg's opinion, is a synapomorphy of the genus when compared with Ozothamnus and Haeckaria. The Australian species of Cassinia resemble species of Ozothamnus rather than New Zealand species of Cassinia. The leaf shape is linear lanceolate rather than spathulate and the leaves are not glandular. Ecological tolerances also seem to point to a closer relationship with Ozothamnus. New Zealand Cassinia tends to be an open ground colonizer while the Australian species such as Ozothamnus are damp forest plants.

Cassinia aculeata R. Br. (syn: Cassinia aculeata A. Cunn. ex DC.; Calea aculeata Labill. Cassinia affinis R. Br.; Cassinia adunca F. Muell.)

Dolly Bush is a small tree that reaches 3m in height. All parts of the plant are densely pubescent. The terminal capitula are white but can range in colour through pink to brown. Distributed in New South Wales, Victoria, Tasmania and South Australia, some specimens have been described as C. uncata var. uncata and as C. uncata var. affinis. All characters traditionally used in describing this species are highly variable and reflects the wide ecological tolerances of this species. Cassinia aculeata has the same habitat preferences as the New Zealand Tauhinu C. leptophylla

Cassinia arcuata R. Br. (syn: Cassinia paniculata Behr and Muell.)

This erect shrub grows up to 2m in height and has the widest geographical distribution of all Australian species. Cassinia arcuata is known as Chinese Scrub and occurs in Victoria, South Australia, New South Wales and in coastal areas of southern Western Australia. The white tomentum is restricted to the undersides of branches and leaves. Unlike the New Zealand species the flowers appear white or cream coloured based on the number of smooth bracts surrounding the receptacle.

Both C. aculeata and C. arcuata are common along forest margins and flower between February and March.

Cassinia denticulata R. Br.

This small tree is restricted in distribution to the river valleys of central New South Wales. It can be distinguished from other Australian species by the rusty tomentum that covers the underside of the leaves. The margins of the coriaceous leaves are minutely toothed. The character that distinguishes this species from other Australian species is the obovate leaves. Almost all other species have linear leaves.

Cassinia laevis R. Br. (syn: Cassinia laevis Endl. ex DC.)

Cassinia laevis is a slender shrub whose branches and undersides of the leaves are covered in a white tomentum. This species is distributed in southeast Queensland, the central plateaus of New South Wales and extends into South Australia. Common in forest margins C. laevis is usually found in association with Eucalyptus species.

Cassinia longifolia R. Br.

Often mistaken for C. laevis this slender shrub is covered with a rough white tomentum that is lost from the leaves at maturity. The flowers are larger than those of C. laevis and are mostly yellow in colour. This is the common floral colour of most Australian Cassinia species. Unlike the other species the bracts are opaque and so do not alter the colour of the flowers. Cassinia longifolia is distributed in New South Wales and southwest Victoria.

Cassinia quinquefaria R. Br. (syn: Cassinia quinquefaria Sond.; C. hygrophila A. Cunn; Achromolaena viscosa Cass.)

Common from the New England coast to the central Blue Mountains of New South Wales C. quinquefaria is a large glabrous shrub with straw coloured flowers.

Cassinia rugata N. G. Walsh

A tall shrub (fig 14) up to 3m in height, C. rugata is known from four populations restricted to southeastern Victoria. It was noted that this species showed affinity with Cassinia uncata (Walsh 1990). According to notes accompanying herbarium specimens deposited in MEL (J.H. Willis and A. C. Beauglehole MEL 504682; A. C. Beauglehole MEL 1560578, MEL 527146; A. C. Beauglehole and C. & D. Woolcock MEL 527127; H.I. Aston MEL 1560583; Walsh and A. C. Beauglehole MEL 1560555) this species is an intergeneric hybrid between Ozothamnus rosmarinifolius (Labill.) Anderberg and Cassinia aculeata (Labill.) R.Br. Walsh (1990) suggests there is more affinity with Cassinia uncata.

Cassinia subtropica F. Muell.

Cassinia subtropica, the most pubescent shrub of all Australian species, is covered in a fulvous tomentum. The red or brown flowers are produced close to the end of December and hence the local name is Christmas Bush. This species is restricted to the New South Wales coast and adjacent Queensland.

Cassinia theodori F. Muell.

Named by Ferdinand von Mueller for a colleague, this erect shrub has the tomentum restricted to the underside of the leaves. This species is restricted to New South Wales. Bentham and Von Mueller (1867) noted that the single floret in the capitulum was unusual for any Helichrysum species . This floret is surrounded by numerous chaffy bracts. They also noted that this species showed affinity with Cassinia arcuata.

Cassinia trinerve N. A. Wakefield

Upon first examination this species bears a resemblance to C. longifolia and C. laevis. However, this slender shrub is distinguished by the pair of marginal secondary veins. The leaf margins are recurved but do not obscure the marginal veins. This species is a common understorey shrub in New South Wales and southwestern Victoria.

Cassinia uncata A. Cunn. ex DC.

A shrub less than 1m tall, C. uncata occurs at the highest altitude of any Australian Cassinia species. Although rare in the Australian Capital Territory, C. uncata is common in the area to the south of Canberra, on the slopes of Mt Kosciusko and at higher altitudes in the Victorian Alps.

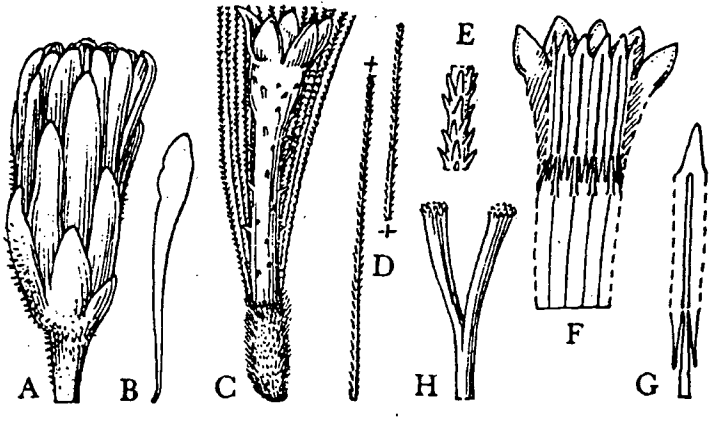


Figure 13. Cassinia vauvilliersii. A, capitulum x 6; B, receptacular scale x 6; C, floret x 12; D, E, pappus bristles x 100; F, corolla opened to show stamens x 12 G, anther x 24; H, style arms x 24. (Jeffrey 1969)

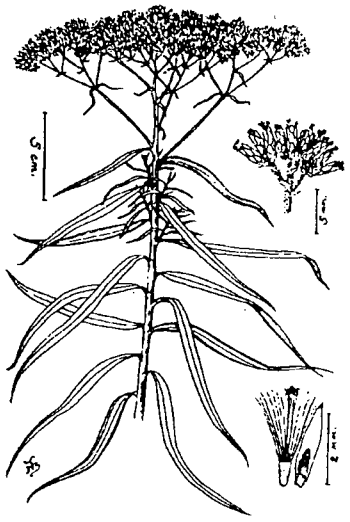


Figure 14. Cassinia longifolia (Jessop 1981)

Figure 15. Cassinia denticulata (Jessop 1981)

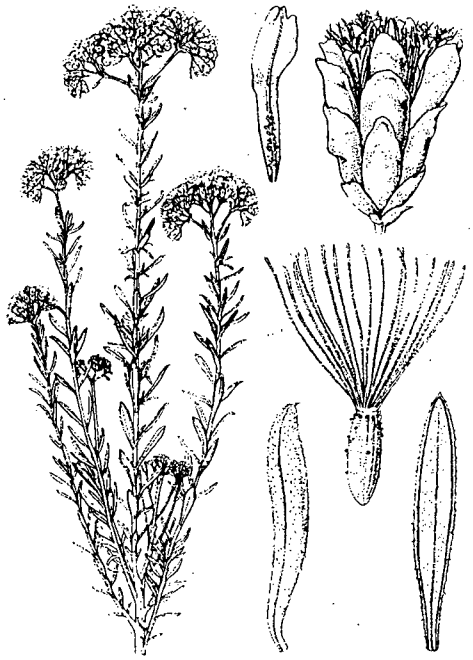


Figure 16. Cassinia rugata (Walsh 1990)

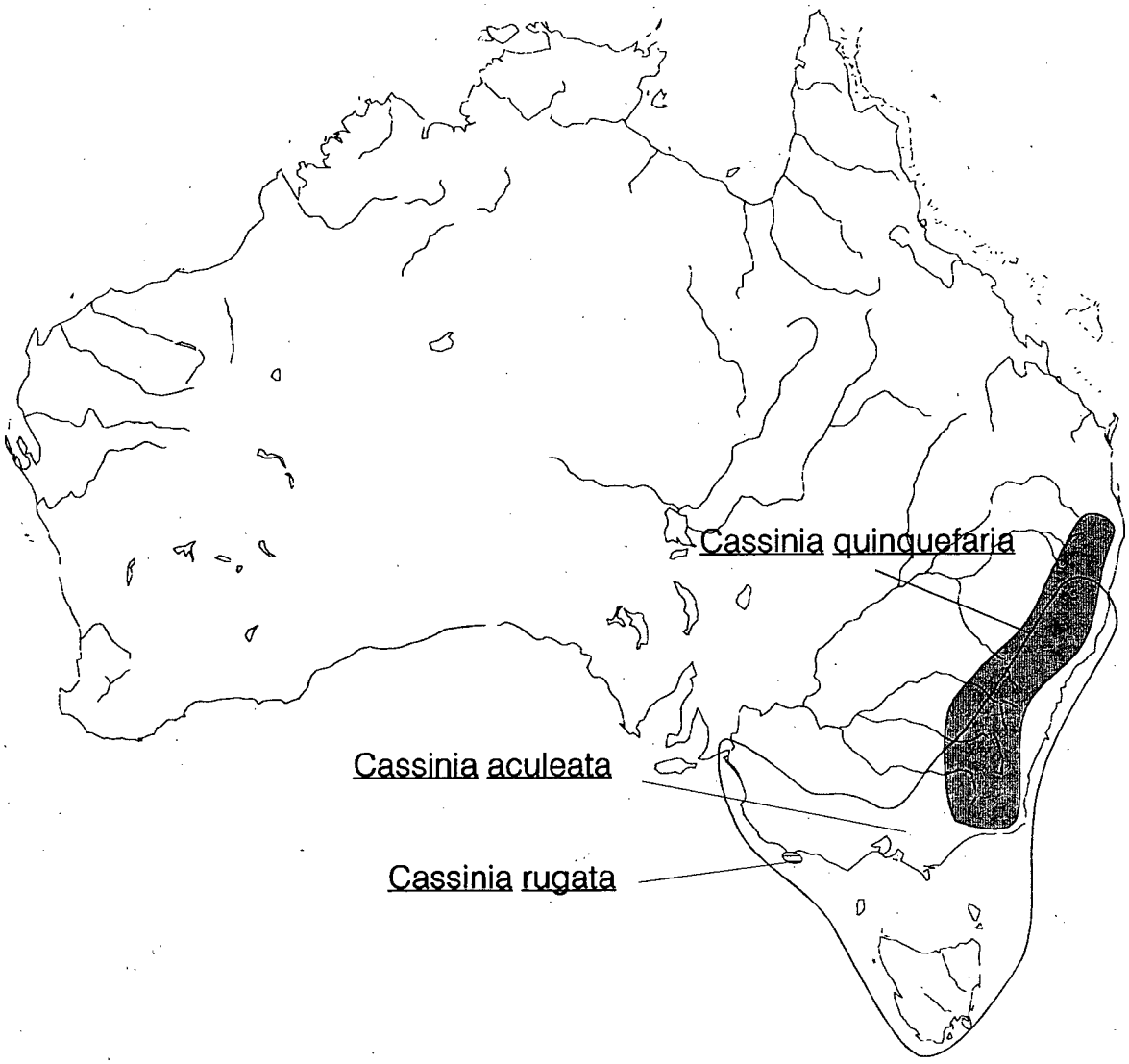


Figure 17. Distribution of Australian Cassinia species Cassinia trinerve and Cassinia longifolia are sympatric with Cassinia aculeata.

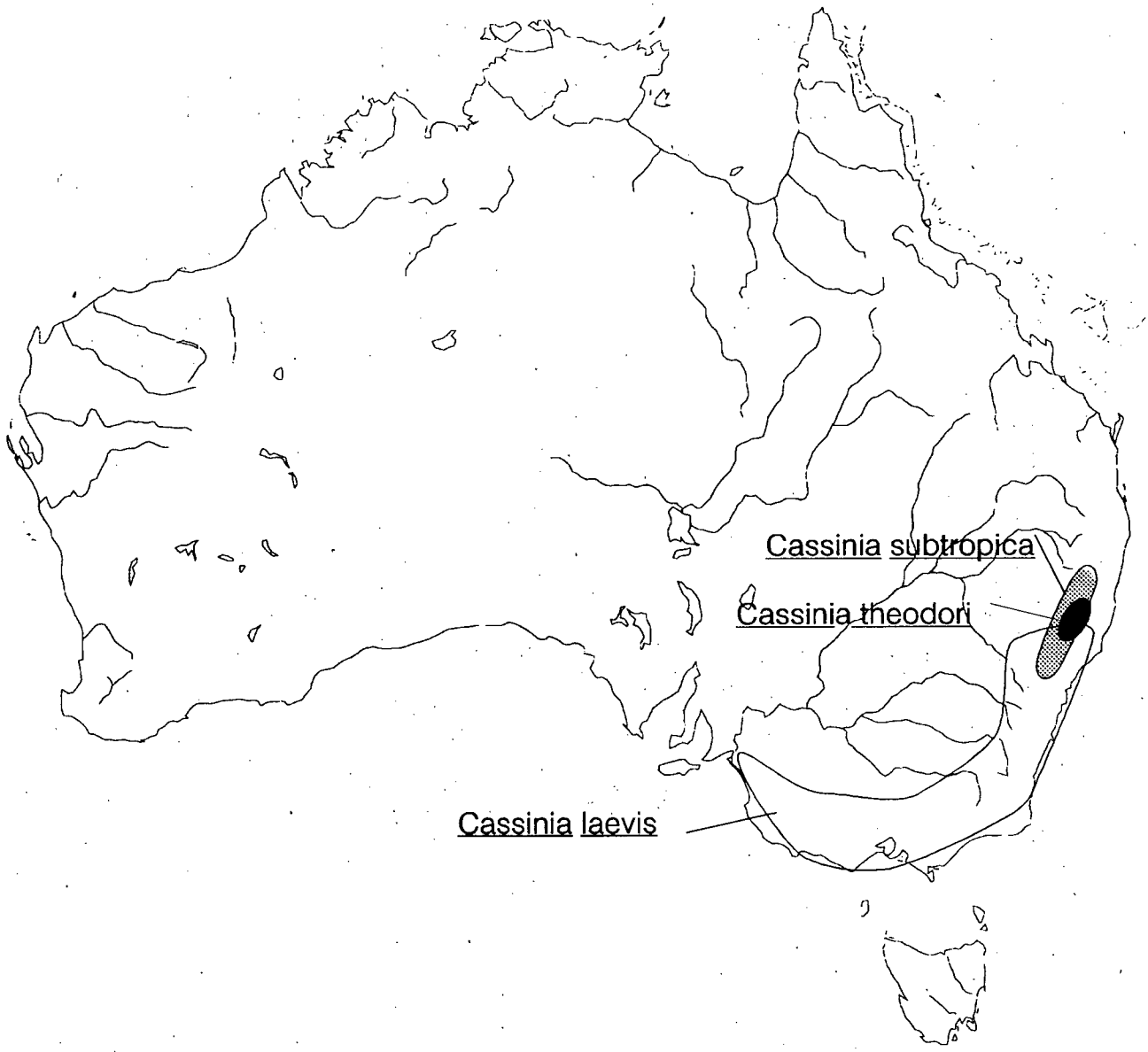


Figure 17 (contd.) Distribution of Australian Cassinia species

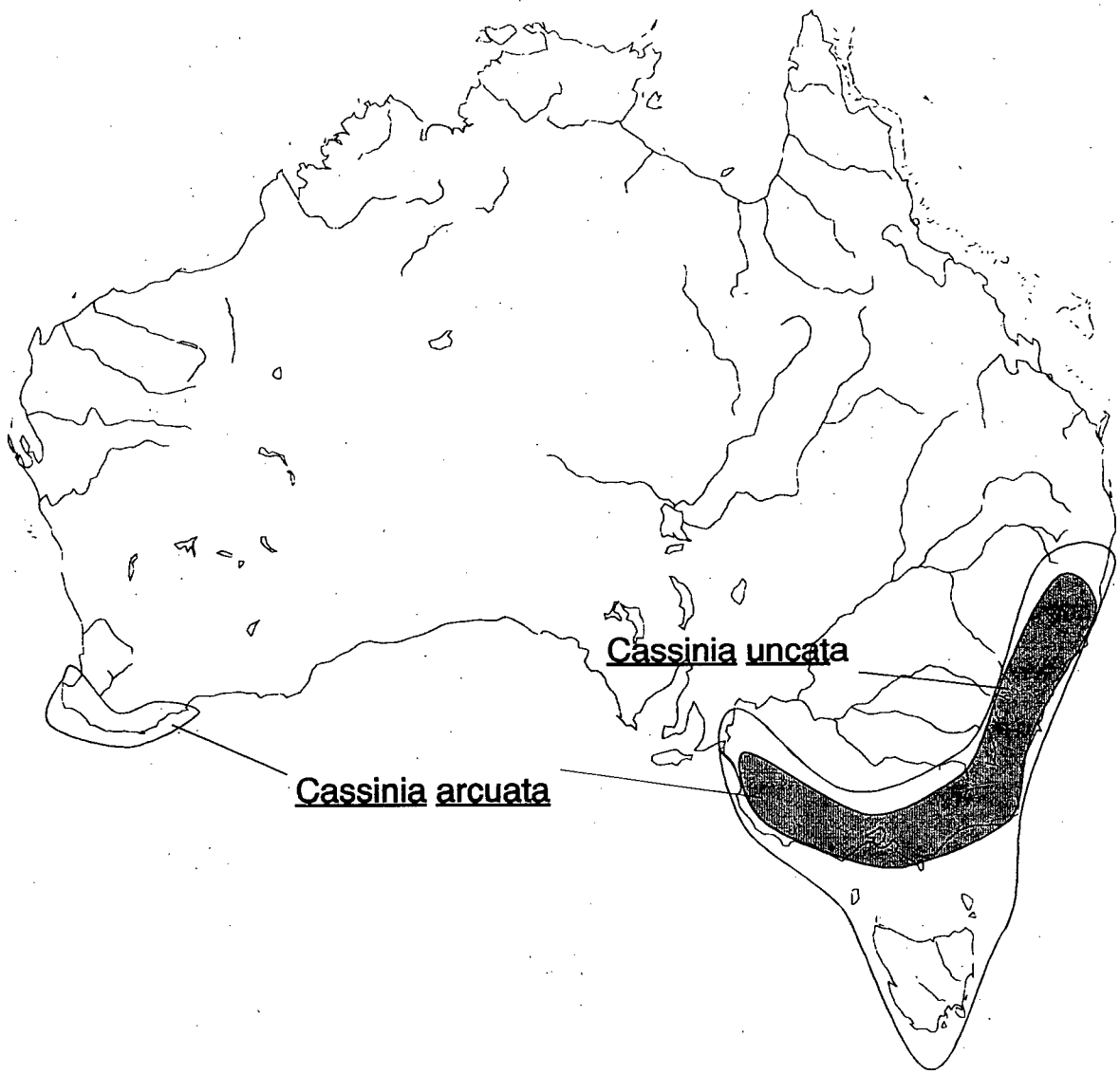


Figure 17 (contd.) Distribution of Australian Cassinia species

Ozothamnus R. Br. (Helichrysum Mill. section Ozothamnus Burbidge)

The genus Ozothamnus R. Br was included in Helichrysum as a section by Bentham in the Flora Australiensis (1867). Hooker (1853) and Rodway (1903) retained Robert Brown's genus. Burbidge (1958) elevated the section Ozothamnus to subgeneric status that included two sections Ozothamnus and Hebelaena. Anderberg (1991) elevated the subgenus Ozothamnus to generic status moved both sections into the newly resurrected genus. Fifty species are distributed throughout New Zealand and Australia. Anderberg (1991) did not recognize the sections of subgenus Ozothamnus sensu Burbidge but did note that Ozothamnus was paraphyletic. Some species of Ozothamnus bear a striking resemblance to the Australian species of Cassinia.

New Zealand Species of Ozothamnus

The New Zealand species of Ozothamnus were not included, by Burbidge (1958), in the revision of Helichrysum subgenus Ozothamnus. These plants differ dramatically from the species found in Australia. The major morphological difference between the Australian and New Zealand species is that the New Zealand representatives are low growing prostrate shrubs. These shrubs exhibit a "whipcord" habit, i.e., from a distance the leaf and branch structure resembles braided rope or leather. This habit is common also in the genus Hebe Comm. ex Juss. The New Zealand species are distributed in open montane habitats. The capitulum of the Australian representatives is bisexual while the New Zealand species produce capitula that are predominantly male.

Ozothamnus selago Hook. f. (syn Helichrysum selago (Hook. f.) Benth. & Hook. f.)

This is a small much branched whipcord shrub that reaches 20-50cm in height. The thick, crowded branches are covered in awl shaped, coriaceous leaves. The minute leaves are leathery on the free part and keeled on the back ending in a bony white tip giving the appearance of knobs rather than leaves. Ozothamnus selago is found throughout the southern uplands of the South Island. There are a number of allied species. Ozothamnus coralloides Hook. f., is endemic to the Kaikoura Mountains and O. selago var. intermedium (Simpson) Anderberg is endemic to the

Torless and Craigieburn Ranges and to montane habitats west of Lake Wakatipu. Druce (1987) recognized 5 types of O. selago var. intermedium.

Ozothamnus selago var. intermedium (Simpson) Anderberg (syn Helichrysum intermedium Simpson; Helichrysum selago var. intermedium (Simpson) Allan)

This small much branched whipcord shrub resembles O. selago. It may reach 20 cm in height. This species differs from O. selago in that there is a more pronounced keel to the scale-like leaves. In this species the florets are produced in equal numbers of male and female. Ozothamnus selago var. intermedium is restricted to montane habitats west of Lake Wakatipu.

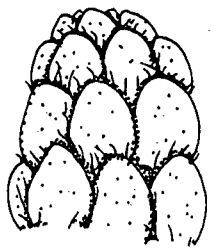
Ozothamnus coralloides Hook. f. (syn: Helichrysum coralloides (Hook. f.) Benth.)

This species is similar to O. selago except that it exhibits a more depressed habit. O. coralloides is common in montane and alpine habitats from 42°S to 43°S east of the main divide

Ozothamnus dimorphus (Ckn.) Anderberg (syn: Helichrysum dimorphum Ckn.)

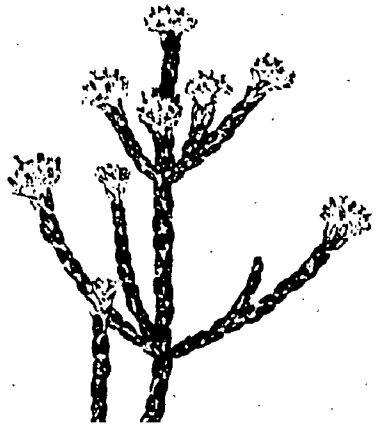
This is the only liana in the tribe Gnaphalieae. Slender flexible branches hold two leaf types. Juvenile and shade leaves are up to 5 mm long and are covered with a white woolly tomentum below. Adult leaves are similar to those of O. selago. A gradation of leaves exists between adult form and juvenile forms. Capitula are terminal with several ranks of phyllaries that cover a cylindrical involucre. The florets are perfect in O. dimorphus. The four known populations of this species are restricted to one area near the junction of the Poulter and Waimakariri rivers and Puffer Creek.

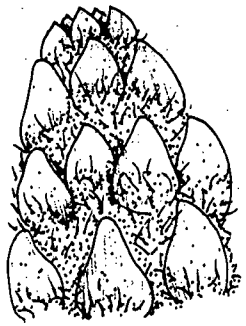
Habit O. coralloides



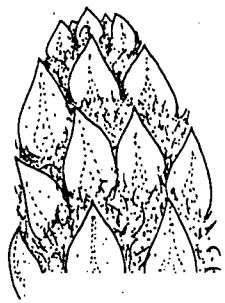
O. coralloides

Habit O. intermedium and O. selago





O. intermedium



O. selago

Figure 18. Leaf detail of the whipcord Ozothamnus species.

Ozothamnus depressus Hook. f. (syn: Helichrysum depressum (Hook. f.) Benth.)

Ozothamnus depressus is usually a depressed shrub that is less than 1m tall. The leaves resemble the adult form of O. dimorphus. The barbellate pappus is formed from hairs of uneven length. All other species of Ozothamnus in New Zealand have barbellate pappus hairs of even length. The minute grey leaves overlap each other and give the plant a withered appearance. Ozothamnus depressus is common on river beds in the South Island between 300 and 1200m and flowers between November and January

Australian species of Ozothamnus

In 1958 Burbidge re-examined Helichrysum section Ozothamnus. Raising Ozothamnus to the subgeneric level, Burbidge recognized two sections, section Ozothamnus and section Hebelaena. In contrast to the New Zealand members of Helichrysum subgenus Ozothamnus section Ozothamnus the Australian members were described as woody shrubs commonly with short internodes and small leaves. The capitula aggregate into dense corymbs held either terminally or at the end of short lateral branches. The flat receptacle is covered in deciduous tomentose phyllaries that enclose hermaphroditic florets. Section Hebelaena differs from section Ozothamnus in that the members are herbaceous perennials with weakly ascendant woody branches. In section Ozothamnus the capitula are loosely held in a panicle. Each capitulum is enclosed in persistent phyllaries. The type species for both sections is Ozothamnus rosmarinifolius.

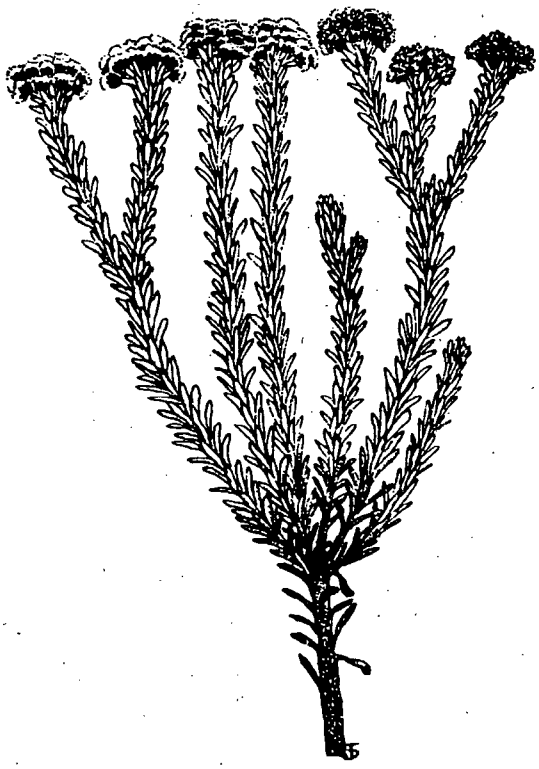


Figure 19. Ozothamnus depressus
(Curtis 1963)

Figure 20. Ozothamnus diosmifolius
(Curtis 1963)

Ozothamnus dendroideus (Wakef.) Anderberg (syn Helichrysum dendroideum Wakefield; H. ferrugineum sensu Bentham; H. ferrugineum (Labill.)Less. ex Steud.; Eupatorium ferrugineum Labill.; Chrysocoma ferruginea Spreng.; Ozothamnus ferrugineus DC.; Petalolepis ferrugineus Cass.)

Traditionally small leafed specimens of H. ferrugineum are referred to as Ozothamnus dendroideus. This small tree reaches up to 5m tall. The tomentum common in most members of the Cassininae is present on young branches but is lost at maturity. Ozothamnus dendroideus is common in mesic forests from New South Wales to Victoria. Wakefield (1951) claimed that this species is also found in South Africa. Burbidge (1958) transferred the South African species to a variety of Helichrysum sutherlandii.

Ozothamnus obcordatus (F. Muell) DC.

Ozothamnus obcordatus is the most easily recognized Australian species as the leaf shape is obcordate. All other Australian species have linear or lanceolate leaves. This species is a shrub 1.5 m tall covered with a rufus tomentum. Two subspecies were described by Short (1990) O. obcordatus ssp. obcordatus P. Short is common in the central mountains of Tasmania and along the coasts of Victoria and southeast New South Wales. Ozothamnus obcordatus (F. Muell.) DC ssp. major P. Short is found in alpine conditions around Mt Kosciusko.

Ozothamnus obcordatus (F. Muell) DC ssp. major P. Short
(syn H. obcordatum (F. Muell.) DC.; Cassinia obovata DC.) has larger leaves than ssp. obcordatus, up to 20 mm long. The tomentum is grey in this subspecies and is less prominent than that of ssp. obcordatus. Ozothamnus obcordatus ssp. major is alpine in distribution

Ozothamnus rosmarinifolius (Labil.) DC. (syn: H. rosmarinifolius (Labill.) Steud. ex Bentham; Eupatorium rosmarinifolium Labill.; Petalolepis rosmarinifolium Cass.; Chrysocoma rosmarinifolia Spreng.; Ozothamnus rosmarinifolius DC.)

This shrub reaches up to 2.5m tall and loses its tomentum upon maturity. The reddish outer floral bracts are slightly wrinkled in contrast to most other species in which they are smooth. Inner floral bracts are white giving the flowers a pink hue. Ozothamnus rosmarinifolius is distributed widely in Tasmania, Victoria and southeastern New South Wales and is found most commonly in association with mesic eucalypt forests.

Ozothamnus stirlingii (F. Muell.) Anderberg (syn; H. stirlingii F. Muell.)

All parts of this small tree are covered with a yellow exudate that rivals the exudate of Cassinia vauvilliersii in stickiness. The lanceolate leaves are up to 8 cm long and resemble C. trinerve possessing two marginal veins. The flowers appear pink due to the reddish outer phyllaries and inner phyllaries that are conspicuously white. The range of this species extends from southeast Victoria to southwest Queensland. It is a common pioneer species in open or disturbed habitats.

Ozothamnus diosmifolius (Vent.) DC. (syn H. diosmifolium (Vent.) Sweet; Ozothamnus diosmaefolius DC.; Gnaphalium diosmaefolium Vent.)

This small tree, up to 3m tall, is easily distinguished by the capitulum that is clad in white concave involucral bracts. These phyllaries are clawed at the tip and are not deciduous, as in the other Australian Ozothamnus species, when the achenes are formed. The species extends from the western slopes of the coastal mountain ranges of New South Wales into southeastern Queensland

Ozothamnus argophyllus (A. Cunn. ex Bentham) Anderberg (syn: Cassinia argophylla A. Cunn. ex Bentham; Helichrysum argophyllum (A. Cunn. ex Bentham) Wakefield; H. ferrugineus DC.; H. ferrugineus (Labill.) Sweet; H. ferrugineum var. gravesii (Rodway) Willis)

This species, along with O. dendroideus, was thought to form a complex that was treated by Bentham and Von Mueller (1867) in the Flora Australiaensis as Helichrysum ferrugineum. Burbidge (1958) treated the taxa of Bentham and Von Mueller as separate species noting that they formed a very closely related series and could be treated as subspecies. This species is found from the southern New South Wales coast to eastern Victoria and Tasmania.

Ozothamnus hookeri Sond. (syn: Helichrysum hookerii (Sond.) Druce; H. baccaroides F. Muell. ex Bentham; Baccharis lepidophyllum DC.; H. lepidophyllum Tovey & Morris; Ozothamnus lepidophyllus Hook.f.)

As in almost all other Australian Ozothamnus species this shrub is glabrous at maturity. This species is the only truly alpine Ozothamnus in Australia, confined to high alpine conditions in the Australian Alps and high elevations of Tasmania.

Ozothamnus cordatus (DC.) Anderberg (syn: Helichrysum cordatum DC.)

Burbidge placed this species in Helichrysum subgenus Ozothamnus section Hebelaena. Ozothamnus cordatus is a weakly woody perennial with spreading or weakly ascending tomentose branches. Leaves, as the name informs, are cordate and are covered with a white tomentum on the underside. The outer florets are almost exclusively male while the central florets are hermaphroditic. This species is endemic to the southwest coast of Western Australia.

Haeckeria F. Muell.

The taxonomic position of these shrubs has been the subject of great debate. Bentham and Von Mueller placed these species in Humea Sm. This genus is reported to be synonymous with Calomeria Vent. Mabberly (1991) recorded 14 African species for Calomeria while Anderberg (1994) states Calomeria is monotypic. Von Mueller recognized that the four species of Haeckeria endemic to Australia.

Haeckeria ozothamnoides (F. Muell.) P. S. Short (syn: Humea ozothamnoides F. Muell; Calomeria ozothamnoides Vent.)

Haeckeria ozothamnoides is an erect shrub that reaches 3m tall and produces a characteristically strong odour. This species differs from other Haeckeria species in that it is pubescent. Haeckeria ozothamnoides is distributed throughout Victoria.

Helichrysum bellidioides (Hook. f.) Willd.

One of the most easily recognised members of the paper daisies found in New Zealand is Helichrysum bellidioides (Hook. f) Willd. Anderberg (1991) elevated Helichrysum section Lawrencella to generic status. Lawrencella Lindl. was placed as the basal taxon of subtribe Angianthiinae. Lawrencella bellidioides (Forst. f.) Anderberg (syn Xeranthemum bellidioides Forst. f.; Gnaphalium bellidioides Hook. f.; Helichrysum bellidioides (Hook. f.) Willd.) is common throughout the New Zealand botanical region and extends its distribution from the main islands of New Zealand to Campbell, Auckland and the Antipodes Islands. Lawrencella bellidioides was classified by Bentham (1873) in Helichrysum section Xerochlaena.

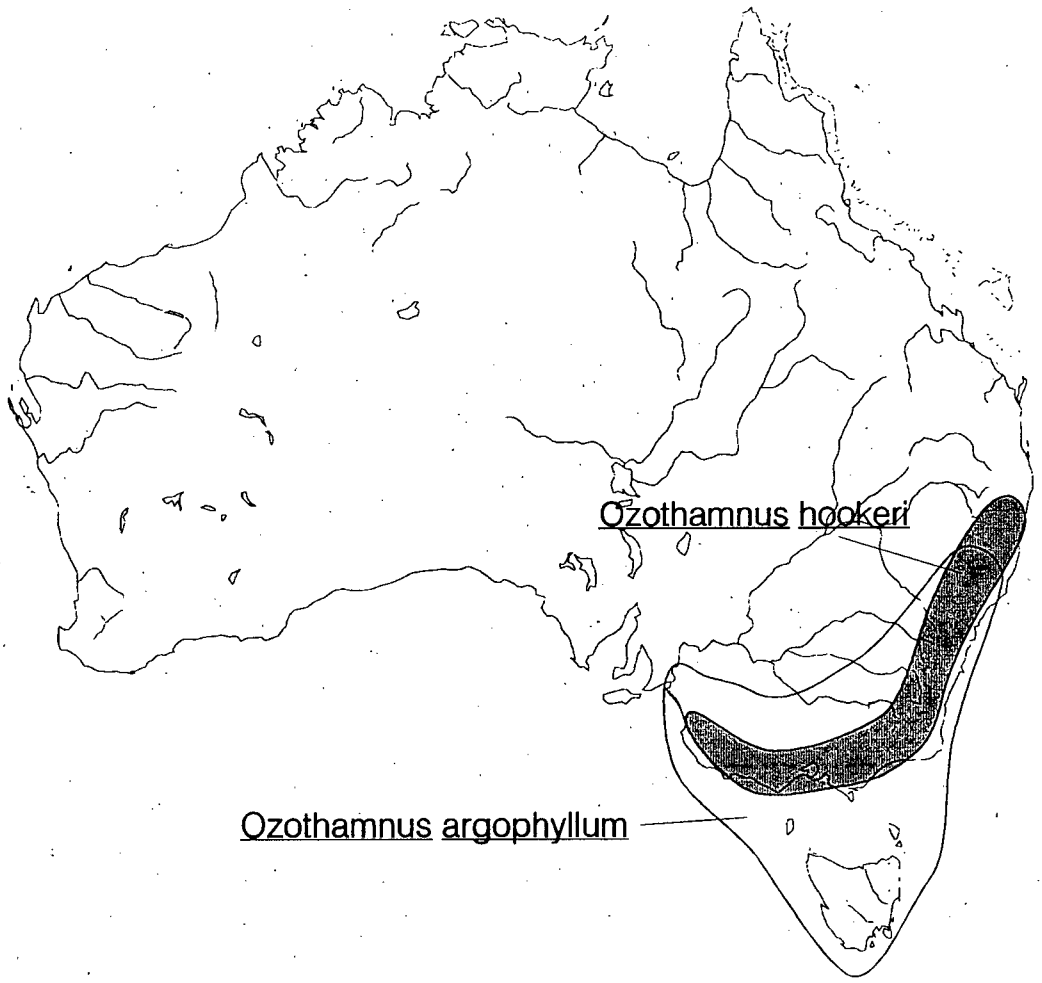


Figure 21. (contd.) Distribution of Australian Ozothamnus species

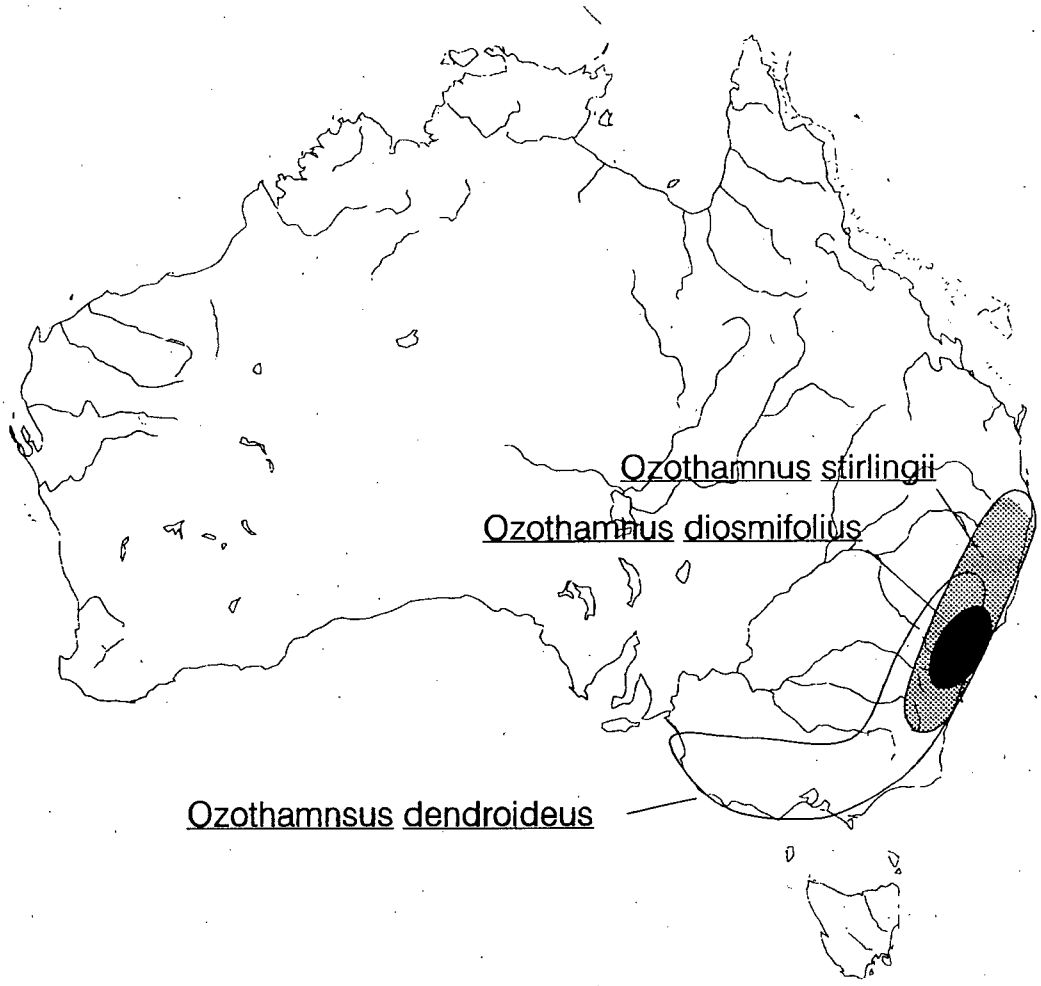


Figure 21. (contd.) Distribution of Australian Ozothamnus species.

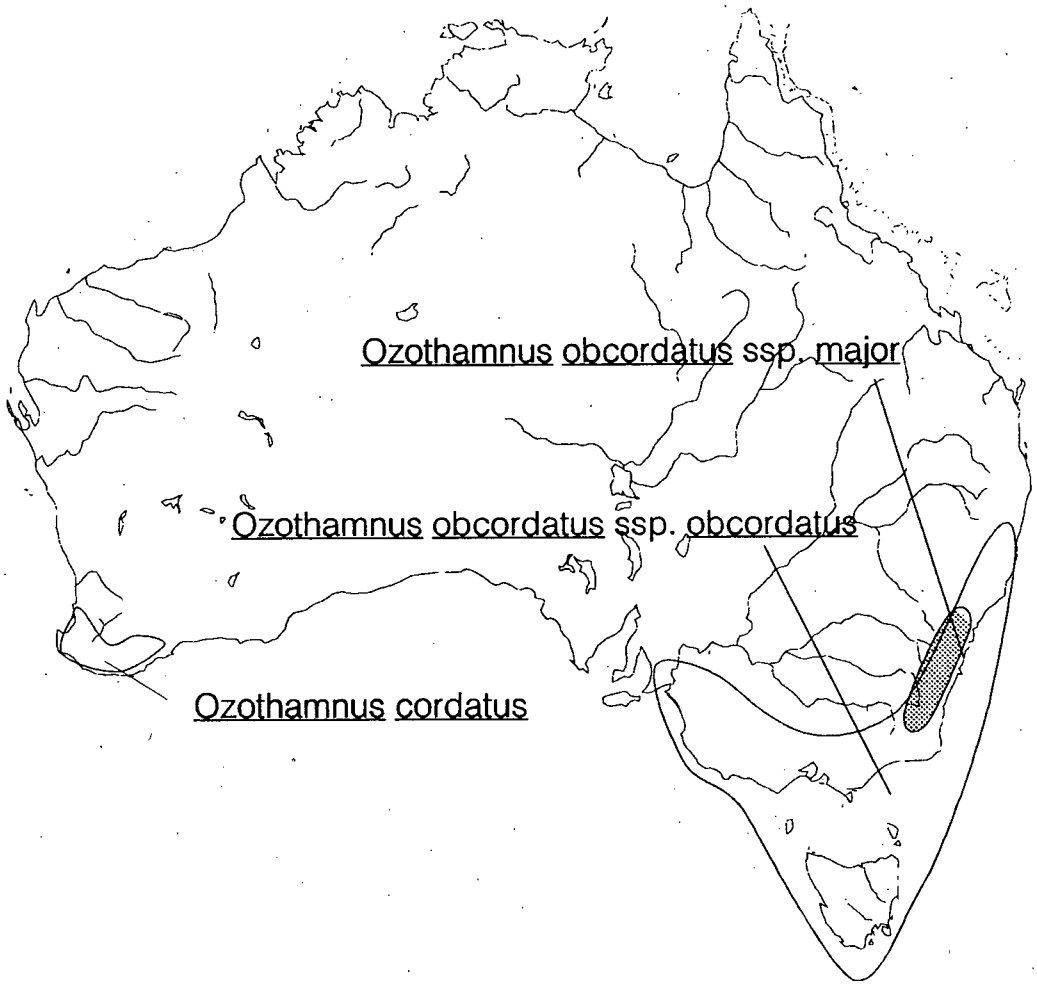


Figure 21. Distribution of Australian Ozothamnus species.

Raoulia

Raoulia Hook. f. is a genus comprising 20 species endemic to New Zealand. The plants are common in montane and subalpine shrublands throughout New Zealand (Allan, 1961). They are characterized by a low, creeping, mat or cushion-forming habit from which the common name, vegetable sheep, derives. The cushion habit is formed by stems and branches that are closely packed together and may be up to several metres long and 2 metres high. The branches and leaves are densely tomentose with the leaves pressed together and concealed by hairs. The overlapping leaves surround many axillary flower heads. Raoulia cushions are all morphologically similar Above, the stems branch repeatedly and toward their tips are covered with small woolly leaves packed exceedingly close together, and finally stems and branches are pressed into a hard rounded mass. Within the plant tuft peat, composed of rotting leaves and branches, holds water like a sponge and the final branches send roots into it. The woody main root serves chiefly as an anchor (Cheeseman 1925). The achenes are covered in a soft white down. Raoulia can be found from sea level to 3000m and flowers in December and January. As a result of intensive numerical analysis, Ward (1982) produced a key to the species of Raoulia.

Seven species (nine taxa) were studied for flavonoids: R. australis Hook. f., R. glabra Hook. f., R. subsericea Hook. f., R. hookeri Allan, var. hookeri, R. hookeri var. albo-sericea (Col.) Allan, R. hookeri var. apice-nigra (Kirk) Allan, R. monroi Hook. f., R. tenuicaulis Hook. f. and R. petriensis Kirk. Raoulia petriensis belongs to subgenus Mistura; the others to subgenus Raoulia.

The taxonomic history of Raoulia has not been a quiet one. The genus was described by Hooker (1853) but it was evident from a reexamination of the plants (Hooker 1864) that Raoulia was a taxon based more upon habit than upon good taxonomic characters that distinguish it from Gnaphalium sect. Helichrysum. Bentham (1873a) and Kirk (1899) retained Raoulia but with two sections, Leptopappus (subgenus Raoulia) and Imbricata (subgenus Psychrophyton). Kirk (1899) suggested that members of section Leptopappus could be accommodated by Gnaphalium and members of Imbricata by Helichrysum. Beauverd (1912) retained Raoulia with subgenus Raoulia

encompassing lowland/montane species and subgenus Psychrophyton encompassing montane/alpine species. This division was based on characters of the pappus and the number of flowers. This taxonomic division was substantiated by Solbrig (1960) in an investigation of the leaf venation of Raoulia. Subgenus Raoulia is composed of compact semicreeping plants with lanceolate appressed leaves. These leaves are characterized by three veins forming the vascular supply to the foliage leaf. The higher order venation is reticulate in pattern. Beauverd (1912) divided subgenus Psychophyton into three sections. The first, section Uninerve, is composed of species with one vascular trace entering the foliage leaf. The second, section Truncatae, is composed of those species with a truncated leaf apex and the third section Trinerves comprises those species with three vascular traces entering the foliage leaf. This set the scene for Allan's treatment in which 20 species, split within three subgenera and six sections, are recognized. Anderberg (1991) returned subgenus Psychrophyton to generic level. Ward (1993 a, b) suggested that the varieties of R. hookeri be elevated to specific status and that infrageneric taxa be dropped, but no formal treatment has been published. This degree of taxonomic indecision reflects the large amount of morphological variation within the genus. It is easier to recognize Raoulia as a genus than it is to determine the exact species. Anderberg (1991) believes Raoulia to be the ancestral or basal taxon to the two groups within the Gnaphaliieae subtribe Cassiniinae.

The New Zealand Edelweiss (Leucogenes Beauverd)

The New Zealand Edelweiss (Leucogenes Beauverd), which consists of two alpine species, is thought to have its nearest relative within the genus Leontopodium (Pers.) R. Br., the Northern Hemisphere or true Edelweiss (Anderberg 1991, 1994). Anderberg (1991, 1994) placed the New Zealand Edelweiss in Gnaphalieae subtribe Gnaphalinae as a basal taxon and a sister group to the Northern Hemisphere Edelweiss, Leontopodium and to Galeomma Rauschert, the African Edelweiss. The two South African species of Galeomma are prostrate herbs that bear a striking resemblance to Leucogenes but differ in pappus morphology.

Two species are assigned to Leucogenes, L. leontopodium (Hook. f.) Beauverd, the North Island Edelweiss and L. grandiceps (Hook. f.) Beauverd, the South Island Edelweiss. The North Island species differs from that found in the South Island in the size and shape of the leaves and the way they are held within the rosettes. The leaves are crowded to the ends of the rosettes in the North Island species and are loosely spaced in the South Island species. The major floral character that allows us to differentiate the species is the nature of the phyllaries. In L. leontopodium they are described as being tomentose and up to 5 mm in length, while in L. grandiceps they are up to 1 cm long and glabrous.

Leucogenes is known to hybridize with species of Raoulia R. Br. section Psychophyton in places where they are sympatric. Both species of New Zealand Edelweiss are alpine and occur above 1600m. Leucogenes leontopodium has a disjunct distribution within New Zealand. It is well known from the type locations in the Tararua ranges and Mount Hikurangi in the Coromandel. The North Island Edelweiss is common on other North Island Mountains including the central volcanoes. Leucogenes grandiceps, on the other hand, is restricted to the Southern Alps of New Zealand's South Island especially in the Torless and Craigieburn Ranges but its geographical range extends to Stewart Island.

As with so many other New Zealand representatives of the Gnaphalieae Leucogenes has had a confusing taxonomic history. Originally described by J. D. Hooker in the 1853 Flora of New Zealand, Leucogenes was included in Helichrysum (H. leontopodium Hook. f. and H. grandiceps Hook. f) but was unfortunately also described as a species of Gnaphalium (G. colensoi Hook. f.). These names were also used by Hooker (1864) in the handbook of the New Zealand flora. Thomas Kirk (1899) followed the scheme of Hooker in the Students Flora of New Zealand by placing both species in Helichrysum. It was not until reevaluation of several genera by Beauverd in 1912 that these species were placed in a genus separate from Gnaphalium or Helichrysum. The two species of Leucogenes are placed within the subtribe Gnaphaliinae sensu Anderberg, where they form a basal pair of taxa to the subtribe. Molloy (1995) described two new species of Leucogenes. Both are perennial evergreen, alpine subshrubs that form a polyploid series with

their nearest relative, L. leontopodium. Leucogenes neglecta Molloy is the tetraploid Marlborough Edelweiss and is restricted to the mountains between the Wairau and Awatere Rivers. Leucogenes tarahaoa Molloy is the octaploid Canterbury Edelweiss and is restricted in distribution to Mt Peel and Middle Mt Peel in Canterbury.

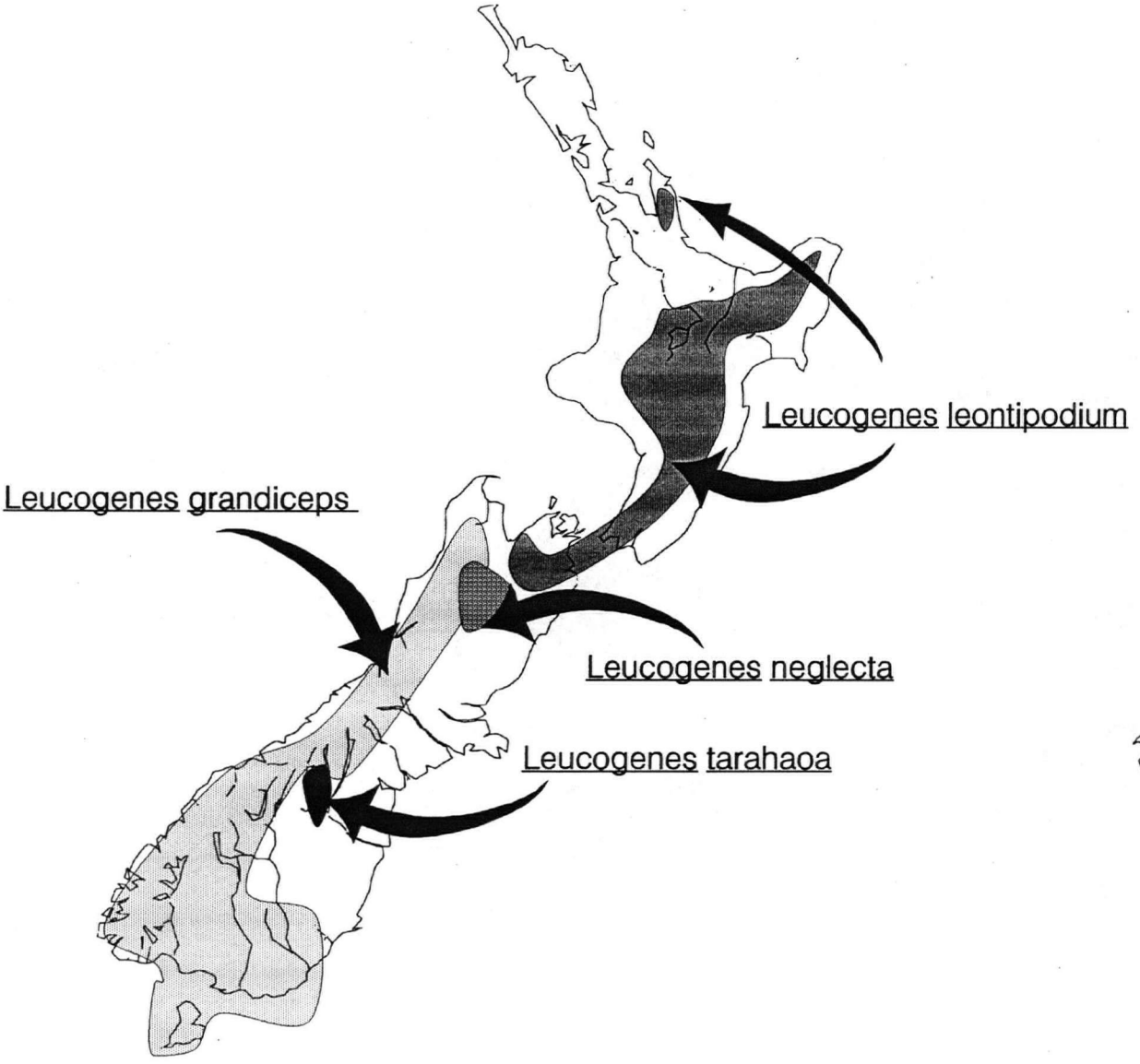


Figure 22. Distribution of the New Zealand Edelweiss

Previous flavonoid studies of the Inuleae, Plucheeae and Gnaphalieae

Information on the flavonoid composition of the Inuleae sensu lato has been reported for some members of 40 genera, approximately one sixth of the 250 or so genera recognised by Merxmüller et al (1977). By far the largest amount of this work has been concentrated on three genera: Inula L., Gnaphalium L. and Helichrysum Mill. Cladistic analyses of Inuleae s. l. (Bremer 1987, 1994; Anderberg 1989, 1991, 1994) suggested that the group was paraphyletic and led to the recognition of three tribes, Inuleae, Plucheeae and Gnaphalieae, which consist of 38, 28 and 180 genera, respectively. Reports of the chemical composition of the Australasian members of the three tribes are limited to only 8 genera and 21 species. In order to discuss possible relationships, a summary of the flavonoid compounds reported from genera that have Australasian members is presented here. It must be noted that although a large number of flavonoids have been reported the survey cannot be relied upon as being complete. In most cases no attempt was made to link the occurrence of compounds isolated with the systematic position of the taxa the compounds were isolated from. The problem, then is whether an absence of a given compound reflects a true absence or is due to the fact that the compound was simply not detected.

Some generalizations concerning the occurrence of flavonoids in these three tribes can be made. Isoflavones and compounds with 2',4',5'-trioxygenated B-rings are absent from all three tribes. Anthochlors (chalcones and aurones) and dihydrochalcones are abundant in the Gnaphalieae as are B-ring deoxyflavonoids (e.g., galangin, 3,5,7 trihydroxyflavone). Acylation of flavonoid classes has been reported for the Gnaphalieae. Jakupovic et al (1989) isolated acylated flavanones from Ozothamnus stirlingii (F. Muell.) Anderberg. Dihydroflavonols and 6-oxygenation occur more abundantly in genera of the Plucheeae and in Inuleae sensu strictu than in the Gnaphalieae. Hydroxylation of both the 6 and 8 positions is more common in the Gnaphalieae than in the other two tribes.

Inuleae s. s. is unique in lacking flavonoids with 8-oxygenation. Members of the Inuleae do produce 6,8 dihydroxyflavonoids and therefore have the capacity to oxygenate the 8 position. Members of the Inuleae also lack C-glycosylflavones. The Plucheeae exhibit no compounds unique to the tribe but shows quantitative differences with regard to the frequency of occurrence of the flavonoid classes. A further qualitative difference lies in the predominance of flavonols over flavones in members of the Plucheeae as compared to the other two tribes. Flavonols appear to be the most prevalent flavonoid reported in each tribe. The presence of sulfated flavonoids in the Inuleae s. s. and the Plucheeae distinguishes them from the Gnaphalieae. O-Methylated flavonoids occur widely in the three tribes. Differences in the levels of methylation exists in the three tribes, however, some members of Inuleae produce hexa-O-methyl flavonoids while the highest level of O-methylation is five in the other two tribes .

INULEAE CASSINI.

There are reports of flavonoid chemistry from two Australasian representatives of the Inuleae sensu Anderberg (1989, 1991, 1994), Blumea DC. and Dittrichia W. Greuer. The latter is an introduced weed in Australia. Blumea consists of about 100 species of shrubs or herbs, distributed through Africa, Asia and Australia. Flavonoids have been reported for four species. Anderberg (1994) suggests that many of these species could be placed within the Plucheeae. The earliest report was by Bose et al. (1968) who isolated 5-hydroxy-3,6,7,3',4'-pentamethoxyflavone (artemetin) from B. eriantha DC. Artemetin and 5,3',4'-trihydroxy-3,6,7-trimethoxyflavone (chrysosplenol-D) were also reported from B. lacera DC. (Rao et al. 1977) and two taxifolin methyl ethers, (2R,3R)-dihydroquercetin-4'-methyl and 7,4'-dimethyl ethers, were isolated from B. balsamifera DC. (Ruangrungsi et al. 1981). Kulkarni and coworkers (1987) reported 6-hydroxy-3,5,7,4'-tetramethoxyflavone and three flavonols with 2',5'-B-ring substitution from B. malcomii Hook. f. A reinterpretation of the spectral data led Markham (1989) to reassign structures to the trio of compounds. The revised structures are methyl ethers of quercetagetin (3,5,6,7,3',4' hexahydroxy flavone), quercetagetin 3,6,7-trimethyl ether, quercetagetin 3,6,7,3'-tetramethyl and

quercetagetin 3,6,7,3',4'-pentamethyl ether. A recent paper by Barua and Sharma (1992) described an unusual flavonoid methylation pattern. 3,5,2'-Trihydroxy-7,5'-dimethoxyflavanone was isolated from B. balsamifera (L.) DC. Two species of the genus Dittrichia are known to be naturalized in the Sydney area and in the Blue Mountains of New South Wales. Dittrichia viscosa (L.) Greuer yielded quercetin-7-methyl ether (rhamnetin) (Simöes & Nacimento 1990), quercetin-3,3'-dimethylether and (2R,3R)-dihydrokaempferol-7-methyl ether (Chiappini et al. 1982).

GNAPHALIIEAE Anderberg

Actinobole Fenzl ex Endl. is common in coastal Victoria, New South Wales, Northern Territory and South Australia. Three species are native to Australia. Jakupovic and coworkers (1988) reported 5,4'-dihydroxy-7-methoxyflavanone (sakuranetin) from A. uliginosum (A. Gray) H. Eichler.

Bellida Ewart is a monotypic Australian genus. Bellida graminea Ewart was shown to have luteolin and quercetin (Jakupovic et al. 1989).

Several of the 20 or so species that comprise the genus Cassinia have been examined for flavonoids. Cassinia arcuata R. Br. was shown to have 3,5,7-trihydroxyflavanone (pinocembrin) and it's 3-O-acetate (Zdero et al., 1991). Wollenweber (personal communication;) reported 5,7-dihydroxyflavanone (pinobanksin), pinocembrin, pinocembrin 3-O-acetate, 3,5,7-trihydroxyflavone (galangin), 3,5,6,7-tetrahydroxyflavone and 3,5,7-trihydroxy-6-methoxyflavone from C. quinquefaria R. Br. 3,5-Dihydroxy-6,7,4'-trimethoxyflavone (mikanin) has been reported from C. longifolia R. Br. (Zdero et al., 1987), C. aculeata (Labill.) R. Br. (Zdero et al., 1990) and C. laevis R. Br. (Jakupovic et al., 1988). Cassinia uncata Cunn. ex DC. afforded 5,7-dihydroxy-6,4'-dimethoxyflavone (pectolinaringenin) while quercetin was reported from C. subtropica F. Muell. (Jakupovic et al., 1988). Kaempferol 3-O-glucoside and 3-O-rhamnoside were also reported from the C. laevis (Jakupovic et al., 1988). A recent numerical phenetic analysis of leaf anatomy and flavonoids of New Zealand Inuleae (Breitwieser and Ward, 1993) included four species of Cassinia

(C. aculeata, C. fulvida, C. leptophylla and C. longifolia), but, unfortunately, offered only paper chromatographic fingerprints of the taxa studied.

Gnaphalium L, which encompasses the common cudweeds, is a large world-wide genus that consists of some 150 species. Flavonoid information has been recordedfrom fifteen of these. Flavonoid diversity is high in the genus with reports of chalcones, flavones and flavonols. B-Ring substitutions range from three to none and A-ring extra substitution at C-6 and C-8 and, in some cases, both. 2',4',4-Trihydroxy-6'-methoxychalcone 4'-O-glucoside has been identified from G. affine D. Don (Aritomi & Kawasaki 1974; Itakura et al. 1975) and from G. multiceps Wall by Maruyama et al. (1974) and by Ahluwalia and Rani (1976) who also synthesized the compound. Apigenin, luteolin and quercetin, either as aglycones or glycosides, in various combinations, have been reported from G. affine (Aritomi et al. 1964; Aritomi and Kawasaki 1974; Itakura et al. 1975), G. luteo-album (Pseudognaphalium luteo-album (L.) Hilliard & Burtt) (Meriçli 1980), G. pellitum H. B. & K. (Pseudognaphalium pellitum (HBK) Anderberg) (Torrenegra et al. 1978), G. rufescens H. B. & K.(Torrenegra et al. 1987) and in G. sylvaticum L. (Konopleva et al. 1978). Konopleva and coworkers (1978) also reported 5,7,4'-trihydroxy-3',5'-dimethoxyflavone (tricin) from G. sylvaticum, which appears to be the only B-ring trisubstituted flavonoid so far obtained from a member of the genus. Other simple O-methylated flavonoids have been reported, luteolin 7-methyl ether from G. rufescens (Torrenegra et al. 1987) and quercetin 7-methyl ether from G. pellitum (Torrenegra et al. 1978). Extra A-ring substitution is seen in 6-methoxyapigenin (hispidulin) in G. antenarioides DC. (Torrenegra et al. 1987) and 5,7,4'-trihydroxy-6,3'-dimethoxyflavone (jaceosidin) in G. luteo-album (Meriçli 1980). Several 6-hydroxy and 6-methoxy compounds have been reported from G. uliginosum L. by Konopleva et al. (1979 a, b): 6-hydroxyapigenin (scutellarein), 6-hydroxyluteolin, 6-methoxyluteolin (eupafolin, nepetin) and jaceosidin.

Table 2. B-ring Deoxyflavonoids of Gnaphalium species.

	Compound [a]												
Species	57/3	5/78	57/38	578/3	5/378	35/78	58/67	357/68	57/368	35/678	58/367	5/3678	5678/3
G. elegans [1]									+		+		+
G. gaudichaudianum [2]							+						
G. lanuginosum [1]			+										
G. luteo-album [3]			+					+					
G. obtusifolium [4]					+	+		+					
G. pellitum [5]		+											
G. robustum [6]	+		+	+	+					+			
G. undulatum [7]												+	
G. wrightii [7]		+											

a) Hydroxyl/methoxyl positions; 1) Torrenaga et. al. 1979, 1980; 2) Guerreiro et. al. 1982,; 3) Meriçli 1980; 4) Hänsel & Ohlendorf 1969; 5)Escarria et. al. 1977; 6) Urzua & Cuada 1989, 1990; 7) Bohlman and Ziesche 1980

The most unusual aspect of the flavonoid profile of Gnaphalium is the abundance of both flavones and flavonols that lack B-ring substitution, a character that distinguishes this tribe from the Inuleae s. s. and the Plucheeae. The simplest pattern reported was 5,7-dihydroxy-3-methoxyflavone (galangin 3-methyl ether) isolated from G. robustum (Pseudognaphalium robustum (Phil.) Anderberg) (Urzua & Cuadra 1989); the most highly substituted compound, 5-hydroxy-3,6,7,8-tetramethoxyflavone was identified from G. undulatum (Bohlmann & Ziesche 1980). 5,7,8-Trihydroxy-3-methoxyflavone occurs in G. robustum (Pseudognaphalium undulatum (L.) Hilliard & Burtt) (Urzua and Cuadra 1990)

Until the cladistic analysis of Anderberg (1991, 1994) Helichrysum Mill., with some 500 species, wasconsidered to be the largest genus in the Inuleae. Species of Helichrysum sensu Anderberg are Eurasian and African in distribution while the Australian and New Zealand representatives are now classified in 6 smaller genera. For clarity in this summary all species names are left as Helichrysum with the new generic and specific epithets of the Australasian members in brackets. The Australasian species are now treated as members of the genus Ozothamnus R. Br. Capitulae of some species, especially H. bracteatum Andr. (Bracteantha bracteata (Vent.) Anderberg & Haegi), 'straw flower', are dried and used as decorations. Flavonoid information is available for 54 species. A wide variety of flavonoid compounds, aurones, chalcones, dihydrochalcones, flavanones, dihydroflavonols, flavones, flavonols and anthocyanins, have been reported in various combinations. The existence of numerous compounds lacking B-ring substitution should be noted; such compounds have been reported from 38 species and involve all structural types except aurones and anthocyanins.

Another unusual B-ring substitution pattern was the report of 'bracteatin', and its glucoside 'bractein', from H. bracteatum (Bracteantha bracteata) by Hänsel et al. (1962) identified as two highly hydroxylated aurones. The structure of bracteatin was established as 4,6,3',4',5'-trihydroxyaurone, that of bractein as the 4-O-glucoside (Hänsel et al. 1962, 1963; Hänsel & Langhammer 1963). The chalcone with the corresponding substitution pattern, 2',4',6',3,4,5-trihydroxychalcone 2'-O-glucoside, and 4,6,3',4'-tetrahydroxyaurone (aurusidin) also occur in

Table 3. Unsubtituted, methylated and glycosylated chalcones in Helichrysum species.

	Chalcone [a]											
Species	2'4'6'/-	2'4'6'4/-	2'4'6'34/-	2'4'6'345/-	2'4'/6'	2'6'/4	2'4'4/6'	2'6'4/4'	2'/6'4'	2'4/6/4'glu	4'6'/4/2glu	6'/2'3'4'
H. achryoclinoides [1]								+				
H. acuminatum [2]	+											
H. affine [3]							+				+	
H. aphelexioides [1]					+							
H. arenarium [4,5]		+									+	
H. bracteatum [6,7,8,9]		+	+	+							+	
H. bractiferum [1]					+							
H. cooperi [10]							+			+		
H. cymosum ssp. calvum [11]						+						
H. graveolens [12]		+									+	
H. heterolasium [13]							+					
H. odoratissumum [14]							+					
H. oreophyllum [15]	+					+			+			
H. palasii [16]		+									+	
H. sutherlandii [17]												+
H. teniculum [11]						+						
H. triplinerve [1]					+			+				

1) Randriaminahy et al. 1992; 2) Bohlmann & Abraham 1979; 3) Aritomi & Kawasaki 1974; 4) Vrkoc et al. 1959; 5) Hänsel et al. 1960; 6) Kaufmann & El Baya 1969; 7) Rimpler et al. 1963; 8) Rimpler & Hänsel 1965; 9) Krishnamoorthy & Seshadri 1966; 10) Wright 1976; 11) Bohlmann et al. 1979a; 12) Çubukçu & Damatyan 1980, 1986; 13) Bohlmann & Abraham 1979a; 14) Van Puyvelde et al. 1989; 15) Jakupovic et al. 1986; 16) Çubukçu & Bingol 1984; 17) Bohlmann et al. 1978 a) Glc = glucose; Hydroxyl/methoxyl/other substiution

this plant (Rimpler et al. 1963; Rimpler and Hänsel, 1965; Kaufmann and El Baya 1969). Nair and coworkers (1989) reported both bractein and 4,6,3',4'-tetrahydroxyaurone 4-O-glucoside (cernuoside) from H. buddleioides DC. ex Wright.

Chalcones and their derivatives are prominent in the genus (table 2., 3., 4.). They vary in structural complexity from 2',4',6'-trihydroxychalcone, and its methyl ethers, through derivatives of 2',4',6',4-tetrahydroxychalcone to a series of O- and C-prenylated compounds some of which have undergone cyclization with neighboring hydroxyls to form dimethyl chromane/chromene derivatives.

Dihydrochalcones in the genus are not as widely distributed as are the chalcones. The simplest member of this group is 2',4',6'-trihydroxydihydrochalcone which was obtained from H. tenuifolium Killick (Bohlmann & Abraham 1979). Other B-ring deoxydihydrochalcones from Helichrysum are 2',6'-dihydroxy-3',4'-methylenedioxydihydrochalcone from H. sutherlandii Harv. and H. mundtii Harv. (Bohlmann et al. 1978). Helichrysum argyrolepis MacOwan (Bohlmann et al. 1984), H. forskahlii (Gmel.) Hilliard and Burtt) (Jakupovic et al. 1990), H. cymosum (L.) D. Don ssp. calvum Hilliard) and H. tenuiculum DC. (Bohlmann et al. 1979) accumulate A-ring modified dihydrochalcones. Helichrysum splendidum (Thunb.) Less. accumulates 2',4',6',4-tetrihydroxydihydrochalcone (Bohlmann & Suwita 1979) while H. monticola Hilliard afforded two isomers of 2',3',4',6',4-pentahydroxy-5'-C-geranyldihydrochalcone.

The simplest flavanone, which occurs in several species, is 5,7-dihydroxyflavanone (pinocembrin). Its 5-methyl ether is known from H. herbaceum (Andr.) Sweet (Bohlmann et al. 1979). Several 8-substituted pinocembrin derivatives were described from H. cymosum (L.) D. Don: 8-C-prenylpinocembrin, 8-hydroxy pinocembrin 7-methyl ether, 8-methoxy pinocembrin and 8-methoxy pinocembrin 7-prenyl ether (Jakupovic et al. 1989). Higher levels of prenylation, involving both O- and C-substitution, are seen in a series of pinocembrin derivatives isolated from H. rugulosum Less. (Bohlmann & Misra 1984). 8-C-Geranylpinocembrin, along with 8-C-prenyl and 8-C-derived prenyl pinocembrin have been identified from H. hypocephalum (Bohlmann & Abraham 1979d). 5,7-Dihydroxy-8-C-prenylflavanone was also described from

Table 4. C-prenyl and Cyclised c-prenyl chalcones in Helichrysum species.

Species	C-prenyl chalcones [a] 2'4'/6'/3'	2'4'6'/-/3'	2'6'/4'/3'	2'6'/4'/3'	Cyclised c-prenyl chalcones [a] 2'4'/-/3-	2'4'/-/5	2'6'/4'/3'	4'/2'/5
H. achryoclinoides [1]	+							
H. aphelexioides [1]	+					+		+
H. argyrolepis [2]	+							
H. athrixifolium [3]		+						
H. cymosum [4]			+				+	
H. krausii [7]					+			
H. retrorsum [8]		+						
H. rugulosum [8]		+						
H. teniculum [4]				+				

Table 5. O-prenylated and substituted chalcones in Helichrysum species

Species	chalcones [a] -/2'6'/3'4'mdo	2'4/6'/3'4'mdo	2'/6'/4'-o-pr	2'6'/-/4'-o-pr	2'6'4/-/4' -o-pr
H. aphelexioides [1]			+		+
H. athrixifolium [3]			+		+
H. forskahlii [5]			+	+	
H. glomeratum [6]		+			
H. retrorsum [8]				+	
H. rugulosum [8]			+	+	
H. sutherlandii [9]	+				

1) Randriaminahy et. al. 1992; 2) Bohlmann et. al. 1984; 3) Bohlmann & Ates Gören 1338; 4) Bohlmann et. al. 1979
5) Jakupovic et. al. 1990; 6) Bohlmann & Suwita 1979; 7) Jakupovic et. al. 1989; 8) Bohlmann & Misra 1984; 9) Bohlmann et. al. 1978
a) Hydroxyl positions/Methoxyl positions/Other substituents; Pr = prenyl; MDO = methylenedioxy

Table 6. Methylated, glycosylated and unsubstituted flavanones in Helichrysum species.

	flavanones [a]												
Species	57/-	7/5	5/7	57/8	58/7	574'/-	74'/-/5glu	74'/-/5diglu	574'/6	573'4'/-	573'4'/6	574'/3'	573'4'/8
H. acutatum [1]	+												
H. aphelexioides [2]	+												
H. apiculatum [þ3]						+							
H. arenarium [4,5,6,7,8,9,10]						+	+	+					
H. aurantiacum [11]						+							
H. bracteatum [21]										+			
H. bractiferum [2]			+										
H. calliconum [12]	+												
H. cymosum [16]	+			+	+								
H. graveolens [11,13]						+							
H. herbaceum [14]		+											
H. italicum [15]	+												
H. oreophyllum [17]	+												
H. palassii [18]						+							
H. plicatum [11]						+							
H. plinthocalyx [11]						+							
H. polyphyllum [9,11]						+	+						
H. rubicundum [11]						+							
H. stirlingii [19]	+												
H. tenuifolium [12]	+												
H. viscosum [§20]						+			+		+	+	+
H. zeyheri [17]	+												

1) Bohlmann & Abraham 1979a; 2) Randriaminahy et al. 1992; 3) Zdero et al. 1992 4) Vrkoc et al. 1975; 5) Jerzmanowska & Grzybowska1958; 6) Hänsel & Heise 1959; 7) Borkowski & Pasich 1961; 8) Prokopenko et al. 1972; 9) Zapesochnaya et al. 1972 10) Vrkoc et al. 1959; 11) Ovdienko et al. 1977; 12) Bohlmann & Abraham 1979b 13) Çubukçu & Damatyan 1980, 1986; 14) Bohlmann et al. 1979; 15) Freitag 1977; 16) Jakupovic et al. 1989; 17) Jakupovic et al. 1986; 18) Çubukçu & Bingol 1984; 19) Jakupovic et al. 1987; 20) Wollenweber et al. 1993; 21) Rimpler et al. 1963 þ) Reported as Chrysocephalum ambiguum (Turez.) Anderb. §) Reported as Bracteantha viscosa (DC.)A. Anderb. a) hydroxyl / methoxyl / other

Table 7. Substituted flavanones from Helichrysum species.

O-Prenyl flavanones [a]

Species	-/5/7 O-pr	5/-/7 O-pr	5/8/7-o-pr	54'/-/7 opr
H. athrixifolium [2]		+		+
H. cymosum [3]			+	
H. forskahlii [5]		+		
H. hirtum [1]		+		
H. retrorsum [1]				+
H. rugulosum [4]	+	+		

C prenyl flavanones [a]

Species	5/-/7O 8C	57/-/6	57/-/8	574'/-/8
H. athrixifolium [2]				+
H. cymosum [3]			+	
H. hypocephalum [6]		+	+	
H. retrorsum [1]				
H. rugulosum [4]	+	+		
H. thapsus [8]		+		

Other subtituted flavanones [a]

5/-/7-o-ner	57/-/8 O-ger	57/-/68 diC pr
	+	
+		
		+

1) Randriaminahy et al. 1992; 2) Bohlmann & Ates Gören 1988; 3) Jakupovic et al. 1989; 4) Bohlmann & Misra 1984; 5) Jakupovic et al. 1990; 6)Bohlmann & Abraham 1979a; 7)Bohlmann & Zdero 1983 a) Hydroxyl positions / Methoxyl positions / Other substituents; ner = neryl; ger= geranyl

H. hypocephalum Hilliard. Naringenin has been found in several species along with the 5-O-glucoside and the 4'-O-glucoside. 8-C-Prenylnaringenin and naringenin 7-prenyl ether were identified as components of H. athrixiifolium O. Hoffm. where they were accompanied by several prenylated chalcones (Bohlmann and Ates-Gören 1984). Eriodictyol and it's 3'-methylether (homoeriodictyol) were reported as components of H. viscosum Sieber ex DC. var. bracteatum F. Muell. (Bracteantha viscosa (Sieber ex DC.) Anderberg & Haegi) (Geissman et al. 1967). Eriodictyol was also reported from H. bracteatum (Bracteantha bracteata) along with 5,7,3',4',5'-pentahydroxyflavanone (Rimpler et al. 1963). Forkmann (1983) also observed this pentahydroxyflavanone from H. bracteatum. It is prudent to remind the reader that the presence of a given flavanone may merely reflect the natural occurrence of the corresponding chalcone a portion of which has undergone conversion to the cyclic form as a result of isolation procedures. Details of the occurrence of flavanones in the genus are given in Table 5 and 6.

Dihydroflavonols (3-hydroxyflavanones) have been reported from only a few Helichrysum species. 3,5,7-Trihydroxyflavanone (pinobanksin) has been obtained from H. tenuifolium (Bohlmann & Abraham 1979a), H. lepidissimum S. Moore (Jakupovic et al. 1989), H. platyterum DC. (Jakupovic et al. 1986) and from H. stirlingii F. Muell., where it occurs with its 3-acetate (Jakupovic et al. 1987). Two 3,5,7-trihydroxy-6-C-prenylflavanones differing in the stereochemistry at C-3, and (2R,2S)-3,5,7-trihydroxy-6-C-geranylflavanone have been identified as components of H. thapsus O. Hoffm. (Bohlmann & Zdero 1983).

B-Ring deoxyflavones and flavonols (Table 5) are also very common in Helichrysum. These range from the simplest, 5,7-dihydroxyflavone (chrysin), which occurs in H. tenuifolium (Bohlmann & Abraham 1979a), through an array of O-methylated compounds, to 3,5,6,7,8-pentamethoxyflavone from H. nitens Oliver & Hiern (Tomas-Barberan et al. 1988). The most frequently encountered compound, present in eight species, is 3,5-dihydroxy-6,7,8-trimethoxyflavone.

Table 8. B-ring deoxyflavones and flavonols from Helichrysum species

Species	Flavonoid [a] -/3567	-/35678	-/357	-/5/78-MDO	-/567	-/5678	-/57	-/578	35/67	35/678	35/78	357/-	357/68
H. arenarium [1]										+		+	
H. armenium [2,3]													
H. bracteiferum [4]												+	+
H. cephaloideum [5]													
H. chrysargyrum [6]													
H. decumbens [7]									+	+			
H. graveolens [3,8,9]										+			
H. herbaceum [6]						+	+						
H. heterolasium [10]													
H. italicum [11, 12]											+		
H. krausii [13]										+			
H. mimetes [5]													
H. mundii [14]				+			+	+					
H. nitens [15]	+	+	+		+	+	+						
H. noeanum [3]										+			
H. odoratissimum [16]										+			
H. orientale [17]										+			
H. pagophilum [18]										+			
H. pallasii [3,19]										+			
H. picardii [20, 21]													
H. platypterum [5]													
H. sanguineum [3, 22]													+
H. schimperi [23]					+								
H. tenuifolium [10]												+	

1) Vrkoc et. al. 1975; 2) Hänsel et. al. 1967, 1981; 3) Çubukçu 1982; 4) Randriaminahy et. al. 1992; 5) Jakupovic et. al. 1986; 6) Bohlman et al 1979; 7)Tomas-Lorente et. al. 1989; 8)Hänsel & Çubukçu 1972; 9) Çubukçu & Damatyan 1980, 1986; 10) Bohlmann & Abraham 1979a,b; 11) Opitz et. al. 1971; 12) Hänsel et. al. 1980; 13)Candy et. al. 1975; 14) Bohlmann et. al. 1978, 1980; 15) Tomas-Barberan et. al. 1988; 16) Van Puyvelde et. al. 1989; 17) Çubukçu 1976; 18) Bohlmann et. al. 1980; 19) Çubukçu & Bingöl 1984; 20) De La Puerte et. al. 1990; 21) Tomas-Lorente et. al. 1991; 22) Meriçli et. al. 1984; 23) Jakupovic et. al. 1990

Table 8. (contd.) B-ring deoxyflavones and flavonols from Helichrysum species

Species	Flavonoid a													
	5/367	5/3678	5/67	5/678	5/7	5/78	56/37	57/-	57/3	57/36	57/368	57/38	58/67	8/567
H. arenarium [1]														
H. armenium [2,3]									+					
H. bracteiferum [4]										+	+	+		
H. cephaloideum [5]	+													
H. chrysargyrum [6]							+							
H. decumbens [7]											+			
H. graveolens [3,8,9]									+					
H. herbaceum [6]													+	+
H. heterolasium [10]										+				
H. italicum [11, 12]										+				
H. krausii [13]														
H. mimetes [5]													+	
H. mundii [14]														
H. nitens [15]			+	+										
H. noeanum [3]														
H. odoratissimum [16]														
H. orientale [17]														
H. pagophilum [18]														
H. pallasii [3,19]														
H. picardii [20, 21]								+			+			
H. platypterum [5]								+						
H. sanguineum [3, 22]														
H. schimperi [23]	+		+	+	+	+								
H. tenuifolium [10]							+	+						

a) Hydroxyl positions/Methoxyl positions/Other substituents; Pr = prenyl; MDO = methylenedioxy

Extra A-ring oxygenation and/or O-methylation of otherwise unsubstituted flavonoids are uncommon in members of this genus. Quercetin 3-methyl ether has been identified in H. kraussii Sch Bip. (Candy et al. 1975) and H. odoratissimum Sweet (Van Puyvelde et al. 1989). The only quercetagetin derivatives recorded are the 7-O-diglucoside from H. stoechas DC. (Pinkas et al. 1973) and the 3,6,7,3',4'-pentamethyl ether (artemetin) from H. chionosphaerum DC. (Bohlmann et al. 1980-869). Helichrysum viscosum var. bracteatum (Bracteantha viscosum) accumulates 5,4'-dihydroxy-6,7-dimethoxyflavone and 5,7,4'-trihydroxy-6,3'-dimethoxyflavone (Geissman et al. 1967). Two 8-oxygenated compounds have been described: 7-hydroxy-5,6,8,4'-tetramethoxyflavone from H. herbaceum Sweet (Bohlmann et al. 1979) and 5,3',4'-trihydroxy-3,7,8-trimethoxyflavone (gossypetin 3,7,8-trimethyl ether) from H. splendidum (Bohlmann & Suwita 1979).

Species of Helichrysum also have the capacity to produce some apigenin, luteolin, kaempferol and quercetin derivatives. Flavones occur as 7- or 4'-O-glucosides, flavonols as 3- or 7-O-glycosides. Flavonol 3-O-(p-coumaroylglucosides) have been reported from H. kraussii and H. orientale Gaert. A quercetin 7-O-triglycoside, which yielded arabinose, galactose and xylose, was encountered in H. stoechas. Rimpler et al (1963) identified an 8-C-glucosylluteolin from H. bracteatum (Bracteantha bracteata) which is the only report of C-glycoflavonoid in the genus.

Cyanidin, as a glycoside, was reported by Rimpler et al. (1963) from H. bracteatum (Bracteantha viscosa). Pelargonidin and peonidin glucosides were reported from H. sanguineum Kostel by Meriçli et al. (1984).

South African members of Helipterum DC. are now classified as Syncarpha DC. and form the type species of the Syncarpha group of Gnaphalinae sensu Anderberg. The Australian species are now classified as Rhodanthe Lindl. and form the basal taxon in the Angianthinae (Anderberg 1994) Helipterum is a large genus, with about 60 species, distributed in South Africa and Australia. Zdero and coworkers (1989) reported 6-methoxyapigenin (hispidulin) from H. propinquum Fitzg. and H. corymbiflorum Schlecht., 6- methoxyluteolin (eupafolin) from the latter

and luteolin and chrysoeriol from H. tenellum A. Gray.

Leontopodium R. Br., which includes the true Edelweiss, is a genus of 30-40 species distributed in the mountains of Europe, central and eastern Asia and Japan. This genus is included in the survey as it is thought to be the genus most closely related to the New Zealand Edelweiss from which there are no published flavonoid data. Only two species appear to have been analyzed for flavonoids. Leontopodium alpinum Cass., the true Edelweiss, was shown to accumulate luteolin 7-O-glucoside and 4'-O-glucoside (Tira et al. 1970). Dashbalyn and Glyzin (1978) found apigenin and luteolin 7-O-glucosides in L. ochroleucum Beauverd.

Myriocephalus Benth. is an Australian genus with ten species. Jakupovic and coworkers (1991) isolated 5-hydroxy-3,7,4'-trimethoxyflavone from M. guerinae F. Muell. the only species studied for its flavonoid composition.

Merxmüller et al. (1977) considered the 10 species of Pseudognaphalium O.M. Hilliard & B. L. Burtt to be best accommodated in Gnaphalium while Anderberg (1991) recognized 80 species in Pseudognaphalium. The one species studied, P. luteo-album (L.) O.M. Hilliard & B.L.Burtt, has been referred to as Gnaphalium luteo-album and is the one cosmopolitan member of the genus found in New Zealand and Australia. Saleh et al.(1988), in a study of Gnaphaliinae of Egypt, included P. luteo-album from which they identified apigenin and luteolin 7-O-glucosides, kaempferol and quercetin 3-O- and 7-O-mono-glycosides and the two highly substituted compounds 5,4'-dihydroxy-3,6,7,8-tetramethoxyflavone and 5,4'-dihydroxy-3,6,7,8,3'-pentamethoxyflavone.

PLUCHEEAE Anderberg

Epaltes Cass., consisting of 15 species, is distributed in warmer parts of both hemispheres. The native Australian species is common in the wetter coastal habitats of the

continent. The sole source of flavonoid data appears to be the work of Nair et al. (1982) who found apigenin and luteolin 7-O-glucosides in E. pygmaea.DC.

Pluchea Cass is a genus of about 40 species that occur in warmer parts of both hemispheres and is the type genus for the Plucheeae sensu Anderberg. Flavonoid data for five or six of these show a diverse array of compound types. Polar flavonoids obtained from P. dioscorides DC. (Ahmed et al. 1987) were identified as kaempferol and quercetin 3-O-glycosides, isorhamnetin 3-sulfate, kaempferol, quercetin and isorhamnetin-3,7-disulfates and an apigenin 6,8-di-C-glucoside. 5,7,3'-Trihydroxy-4'-methoxyflavanone (hesperetin) 7-O-rutinoside and dihydroquercetin (taxifolin) 3-O-arabinoside were identified in soils associated with P. lanceolata Oliver & Heirn and discussed by the authors (Inderjit & Dakshini 1991) as possible germination and growth inhibitors. All other flavonoids from species of Pluchea are methylated compounds many of which also exhibit substitution at C-6. Quercetin-3,3'-dimethyl ether was isolated from Pluchea sericea Coville (Romo de Vivar et al. 1982), 5,7,4'-trihydroxy-3,6-dimethoxyflavone from P. chinogoya DC. (Chiang & Silva 1978), and a series of methyl ethers of kaempferol, 6-hydroxykaempferol, quercetin and quercetagetin from P. odorata Cass (Arriaga-Giner et al. 1983; Wollenweber et al. 1985). The only 8-substituted flavonol so far encountered in the genus is 5,7,3',4'-tetrahydroxy-3,6,8-trimethoxyflavone which Martino and coworkers (1976) obtained from P. sagittalis (Lam.) Cabrera.

Pterocaulon (Labill.) A.L. Cabrera & A.M. Ragonese, a genus of 25-30 species, enjoys a wide distribution, being known from tropical America, Madagascar and Mauritius, tropical Asia and Australia. Only two species have been investigated for flavonoids; Bohlmann et al. (1981) identified the 7-prenyl ethers of dihydrokaempferol (aromadendrin) and dihydroquercetin (taxifolin) from P. virgatum Less. Pterocaulon virgatum also yielded quercetin 3-O-glycosides, isorhamnetin and quercetin-7,3'-dimethyl ether (rhamnazin) (Debenedetti et al. 1983). The second species studied, P. purpurescens Malme, afforded quercetin, isorhamnetin and quercetagetin 3-methyl, 3,7-dimethyl, 3,3'-dimethyl and 3,7,4'-trimethyl ethers (Debenedetti et al. 1987).

Sphaeranthus consists of 40 species that range from tropical Africa through southern Asia to Australia. Anderberg (1991, 1994) considers this genus to be a heterogeneous assemblage that forms a species complex. Zdero et al. (1991) obtained isorhamnetin, quercetin-3,3'-dimethyl and 3,3',4'-trimethyl ethers from S. confertifolius Robyns. Jakupovic and coworkers (1990) reported "chrysosplenol" from S. bullatus Mattf. and S. suaveolens DC.

Materials and Methods

With some modifications the phytochemical methods used in this study follow those of Wilkins and Bohm (1976).

Isolation and Identification of Flavonoids

The exudate flavonoids were removed from the leaves by two brief rinses with dichloromethane (CH_2Cl_2). Analytical thin layer chromatography (TLC) was carried out with polyamide DC 6.6 0.25mm plates using ethyl formate:cyclohexane:formic acid:butyl acetate (50:25:2:23) as the solvent. Evaporation of the solvent provided an oily residue which was resolved using column chromatography on Polyclar AT. Columns were developed with CH_2Cl_2 - methanol mixtures with increasing concentration of methanol. Individual compounds were purified using TLC.

For the isolation of vacuolar flavonoids the dried, CH_2Cl_2-washed leaf samples were extracted repeatedly with 80% aq methanol at room temperature. The combined extracts of each sample were then treated as described by Wilkins and Bohm (1976). Each sample was subjected to 2D TLC on Polyamide DC 6.6 plates using water:n-butanol:acetone:dioxane (70:15:10:5) for the first development and 1,2-dichloroethane:methanol:butanone:water (55:20:22:3) for the second. After air drying the plates were sprayed with 0.1% diphenylboric acid ethanolamine complex (Naturstoffreagent A) in 1:1 methanol-water and allowed to stand for one hour for colour development. The plates were then examined under U.V. light (366nm) and scored for flavonoids. Where no discernible inter- and intra- populational differences were visible the extracts were combined to afford a greater working volume. Vacuolar flavonoids were isolated using column chromatography on Sephadex LH20 and purified using TLC according to Gornall and Bohm (1980). Structures were established using standard UV (Mabry et al., 1970) and MS methods (Markham, 1982). Purified glycosidic compounds were subjected to total and partial acid hydrolysis using trifluoroacetic Acid (TFA) and analyzed using methods described by Ceska and Stiles (1984) and Kartnig and Wegschaider (1971). Ultraviolet spectra were recorded in absolute

methanol. Their structures were established using standard UV (Mabry et al., 1970) and MS methods (Markham, 1982). All compounds identified are well known in the literature. Observed spectral data (appendix !!!) agreed completely with published information and chromatographic behaviour matched standard compounds.

Plant Material

Full details of collection location and associated ecological, altitudinal, edaphic and physical characteristics of populations are given in appendix 1. Plant samples were collected from sites listed below. The collections listed are those of A. R. Reid. Ranges of numbers indicate individuals from populations. MEL signifies the acquisition number of the specimen assigned by the National Herbarium of Victoria Melbourne Australia. Voucher specimens are deposited in MEL, WELTU, CANTU and UBC.

New Zealand

Cassinia amoena, Otari CAM, NZ 703; North Cape, NZ 1406; Cassinia fulvida var. fulvida, Porter's Pass NZ 702, NZ 770 - 774; Foggy Peak NZ 781 - NZ 786; Cave Stream NZ 775 - NZ 779; Mt Ffyfe NZ 791 - NZ 799, NZ 1400 - 1405; c. f. Cassinia fulvida var. fulvida Hurunui NZ 787 - NZ 790; Cassinia fulvida var. montana, Dry Stream NZ 1401 - NZ 1410; Cass River NZ 1411 - NZ 1418; Arthur's Pass NZ 701; Mt St. Bathans CFMMB 1 - 5; Old Man Range NZ 1450 - 1453; Cassinia leptophylla, Akatarawa NZ 714, NZ 717 - NZ 720, NZ 722, NZ 723; Makara Hill NZ 724, NZ 725; Karori NZ 709; Makara Beach NZ 710; Owhiro Bay NZ 706, NZ 707, Shannon NZ 1413 - NZ 1415; Wanganui River Road NZ 1417 - NZ 1420; Featherston NZ 1421 - NZ 1425; Pahiatua NZ 1426 - NZ 1430; Pencarrow NZ 1443 - 1444; Wainuiomata NZ 1445; Lake Ferry NZ 1446; Picton NZ 1459; Otari CLEP, NZ 708; c. f. Cassinia leptophylla, Awatere NZ 1455 - 1458, NZ 1454; Cassinia vauvilliersii, Mt. Holdsworth NZ 705, NZ 1426 - NZ 1430; Mangatoetoeiti NZ 735 - NZ 739; Te Piripiri Stream NZ 742 - NZ 746; Tukino Road NZ 748 - NZ 752; Rangipo NZ 753 - NZ 760; Waihohonu NZ 761 - 765; Tawhai Track NZ 1431; Whakapapanui NZ 1432 - 1435;

Pukeonake NZ 1436 - 1438; Pokaka NZ 1439 - 1442; Lawrencella bellidioides, Mt. Holdsworth NZ HB 1 - 5; Whakapapanui NZ HB 6 - 8; Pukeonake NZ HB 9 - 12; Pokaka NZ HB 13 - 16 Cave Stream NZ 913a - 920a; Dry Stream NZ 900 - 901; NZ 912 - 920; Leucogenes grandiceps, Mt St. Bathans NZ 619 - 624 Old Man Range NZ 613 - 618: Leucogenes leontipodium, Mt. Holdsworth NZ LL 1 - 6; Ozothamnus depressum, Cave Stream NZ 901a - 905a; Dry Stream NZ 902 - 904,921 - 927 Cass River NZ 936 - 939; Ozothamnus intermedium, Cave Stream NZ 905a - 912a; Dry Stream NZ 905 - 911; Cass River NZ 943 - 948; Ozothamnus selago, Cave Stream NZ 921a - 925a; Dry Stream NZ 928 - 935; Cass River NZ 940 - 942; Raoulia australis, Karori NZ 812 - 815; Makara Beach NZ 822, NZ 823; Featherston NZ 829 - 832; Pahiatua NZ 829 - 832; Mt. Holdsworth NZ 839 - 842 Rangipo NZ 856 - 859; Whakapapanui NZ 877 - 880; Pukeonake NZ 887, NZ 889; Pokaka NZ 1600 Pencarrow NZ 1607; Wainuiomata NZ 1611; Lake Ferry NZ 1613; Porter's Pass NZ 1614 - 1616; Foggy Peak NZ 1621; Cave Stream NZ 1626; Dry Stream NZ 1628 - 1630; Hurunui NZ 1634; Mt Ffyfe NZ 1636; Mt St. Bathans NZ 1638; Awatere NZ 1640 - 1643; Raoulia glabra, Porter's Pass NZ 613; Cave Stream ***** Dry Stream ***** Cass River *** ; Old Man Range NZ 546 - 550; Raoulia hookeri var. albo sericea, Wanganui River Road NZ 824 - 826; Mangatoetoeiti NZ 833 - 836; Te Piripiri Stream NZ 846 - 849; Tukino Road NZ 852 Rangipo NZ 860 - 864; Waihohonu NZ 865 - 870; Tawhai Track NZ 871; Whakapapanui NZ 872, NZ 873, NZ 874 - 876; Pukeonake NZ 884, NZ 885; Pokaka NZ 890 - 895 NZ 1601, NZ 1602; Old Man Range **** ;Otari NZ 1640: Raoulia hookerii var. apice-nigra, Mt Ffyfe NZ 1637, NZ 1638; Awatere NZ 1639; Raoulia hookeri var. hookeri, Makara Hill NZ 800 - 811; Karori NZ 818; Makara Beach NZ 816, NZ 817; Pencarrow NZ 1604 - 1606; Wainuiomata NZ 1608 - 1610; Lake Ferry NZ 1612; Foggy Peak NZ 1617, 1619, 1620; Arthur's Pass NZ 1632 - 1633;

Raoulia petriensis, Mt St. Bathans NZ 600 - NZ 605; Old Man Range NZ 606 - 612; Raoulia subsericea Foggy Peak NZ 1622; Cave Stream NZ 1627; Dry Stream NZ 1631; Arthur's Pass NZ 1635;

Raoulia tenuicaulis Mangatoetoeiti NZ 837, NZ 838; Te Piripiri Stream NZ 843 - 845; Tukino Road NZ 850, 851, 853 - 855; Whakapapanui NZ 881 - 883; Pukeonake NZ 888; Pokaka NZ 896 - 899; Porter's Pass NZ 1618; Foggy Peak NZ 1623 - 1625;

AUSTRALIA

Cassinia aculeata, Grants Picnic Ground NGW 3424, NGW 3426; Maroota Mt Franklin RR 2386, LGA 4121; Barwon River AR 3445 - 3447; Bungonia Heights SJ 6144; Wee Jaspers NGW 3316; Geelong AR 3440; Cassinia arcuata, Rushworth Road NGW 3421, NGW 3422; Grants Picnic ground, AR 3437 - 3440; Maroota AR 3441 - 3444; Mt Franklin LGA 4124; Cassinia laevis, Darling Downs PGW 1262; Cassinia longifolia, Geelong AR 3444; Rushworth Road NGW 3423; Grants Picnic Ground AR 3431 - 3434; Barwon River AR 3449; Cassinia quinquefaria, Wee Jaspers NGW 3358; Cassinia rugata, Portland NGW 3428 NGW 3429 NGW 2074 NGW 2075 NGW 2076; C. subtropica, Paluma MEL 2019336; Mt. Barney MEL 713584; Moreton MEL 1582763; Cawley Lookout MEL 1598778; Cassinia trinerve Grants Picnic Ground NGW 3425; Geelong AR 3441 - 3443: Barwon River AR 3450 - 3452; Cassinia uncata, Rushworth Road NGW 3420; Grants Picnic Ground AR 3427 - 3430;

Maroota AR 3435 - 3436; Mt Franklin LGA 4123; Wee Jaspers NGW 3359; Barwon River AR 3448; Haeckeria ozothamnoides Wee Jaspers NGW 3320; Pine Mt. MEL92300; Bowenya MEL680822; Killawarra MEL604651; MEL226952 Ozothamnus cordatum, Augusta RJC 8212, RJC 8213, RJC 8214; Ozothamnus dendroideum, Portland JJE 2095; Ozothamnus diosmifolius Portland BR 2385; Maroota NGW 4127; Mt Franklin LGA 4126 Wee Jaspers NGW 3319; Mt Gambier AR 3323; Ozothamnus ferruginea Rushworth Road NGW 3430; Grants Picnic Ground AR 2096, AR 2097; Maroota AR 2100 - 2103; Wee Jaspers NGW 3317; Mt Gambier AR 3321;: Nethercote Falls MEL675841; Dover Island MEL235449; Mt Wellington: MEL626535; Clarke's Island MEL529099; McLean's Bay MEL 529101; Ozothamnus hookerii Portland JJE 2093; Mt Gambier NGW 3324. Ozothamnus obcordatum Rushworth Road NGW 3426; Warrumbungle MEL1598551 MEL646158; Mt Lindsay MEL2014651; Egan Peaks: MEL673724;

Haycock Hill MEL671568; Ozothamnus rosmarinifolius JJE 2094; Maroota AR 3323; Mt Gambier AR 3322; Grants Picnic Ground AR 2098 - 2104; Mt Franklin LGA 4125; Wee Jaspers NGW 3318; Rolleys Flat MEL1559634; White Rocks River: MEL689342; Trial Harbour MEL235450; Arthur River MEL1617273; Corrina Road: MEL1606621 Ozothamnus stirlingii Mt Franklin LGA 4122; Hybrid C. uncata x O. obcordatum Rushworth Road NGW 3427

ANALYSIS PROCEDURES FOR THE GENERATION OF PHYLOGENETIC TREES

A data matrix was established using flavonoid structural features and the OTU's under study. The matrix was analyzed using PAUP (Swofford et. al. 1987) and the characters contributing to the make up of the cladogram were traced using MacClade version 3 (Maddison and Maddison 1992).

With any approach in determining relationships of phylogeny, certain cautions must be kept in mind. One major problem concerns qualitative verses quantitative variation in compounds. Documentation of the absence of a compound is essentially impossible, because with more plant material and more sensitive methods the component might be detected (Crawford 1978). A second problem involves proper comparison of compounds from the same organ of the plant. As has been stressed by many workers sometimes very different compounds are found in different organs.

The biosynthesis of flavonoid compounds and the genetic bases of different structures must be considered carefully. No discussion of flavonoid biosynthesis per se will be presented here as a number of reviewers cover this topic (Wong 1976; Grisebach 1979 Hahlbrock & Grisebach 1979 Manitto 1981 Stafford 1991 Vickery and Vickery 1981). The point that must be made is that although flavonoid biosynthesis has been studied in very few species of flowering plants, the basic steps to the various classes of flavonoids appear to be similar if not identical. Thus when flavonols, for example, occur in two separate species they most likely represent the product of the same biosynthetic pathway. Questions arise, however, with regard to the later steps in flavonoid biosynthesis such as hydroxylation, methylation and glycosylation. That is, it may be that these "window dressings" in the production of flavonoids normally sequestered by plants occur via

different mechanisms or are under different genetic control in different species of plants (Hahlbrock et. al. 1970; Wong 1976; Crawford and Levy 1978; Harrison & Strickland 1978; Tubak et. al. 1978 Forkman 1980) there is too little comparative data to assess with certainty the actual magnitude of these potential problems in phylogenetic studies. It must be pointed out, however, that these difficulties are no greater with flavonoids than with other characters more commonly used by (e.g. morphological characters). These difficulties may even be less problematic in flavonoid analysis because the basic biosynthetic steps from one class of compound to another, or from one structure to another, are better understood than the ontogeny of morphological features (Stuessy and Crawford 1983). This allows the formation of hypotheses of directionality of chemical character states based on inferences of biosynthetic (and presumably genetic) homology. These inferences are undoubtedly stronger when dealing with phylogenetic studies at the generic or specific level rather than the familial or ordinal level (Crawford 1978). The evolutionary directionality of flavonoids as determined for one group of plants may not be the same for all groups of plants. Certain broad-scale trends that seem to hold for a large group such as the Angiosperms (Crawford 1978; Gornall & Bohm 1978; Harborne 1977; Gornall et. al. 1979) may not apply to restricted taxa.

The homologies of the flavonoid character states must be evaluated before evolutionary comparisons can be made. The occurrence of the same structure between a pair of taxa is assumed to represent an evolutionary homology unless they have arisen via different biosynthetic pathways or they have the same biosynthesis, but in one case it is the original compound and in the other case it is a derived compound. Gornall and Bohm (1978) outlined perspectives on primitive, derived and highly derived compounds. Stuessy and Crawford (1983) feel that the problems in evolutionary homology are minor problems at the lower taxonomic levels as opposed to the higher taxonomic levels. The absence of a compound cannot safely be known to be homologous, because, as indicated before, their absence could have different biosynthetic bases.

To generate the data matrix certain assumptions must be made. We must assume that hydroxylation of flavonoids occur at the flavanone/chalcone stage of the biosynthetic pathway to form the basic classes. It is assumed that the enzymatic steps that produce the modifications of

the flavonoid skeleton are site specific not skeleton specific. For example a 7-O-glycosyltransferase will attach a sugar molecule at the 7 position regardless of the oxygenation pattern. With this in mind each taxon was coded for the flavonoid present based upon the position of substitution. Upon examination of the data matrix it was found that certain positional modifications existed in all taxa examined. These characters were the common flavonol B-ring oxygenation patterns that correspond to kaempferol and quercetin. In addition to the data obtained from the flavonoid analysis, morphological and ecological characters were scored for each taxon. All characters are unweighted and are assumed to be independent of each other. The data matrix was processed in PAUP using the heuristic search algorithm:- simple step, terminal branch length swapping. The search found 57 equally parsimonious trees of 229 steps each. The strict consensus tree of these 57 equally parsimonious trees was then transferred to M^{ac}Clade in order to trace the characters that changed on each branch. The computer program was asked to seek and disregard the invariant characters. That is all the characters not contributing to the variation were eliminated. All characters remained unweighted. For clarity the consensus tree is divided into three figures. Figure*** shows the combination of ecological and geographical characters that separate the species. Figure *** shows the total character changes for the New Zealand species and figure *** shows the total character changes for the Australian species.

CHARACTER STATES FOR THE ANALYSIS OF THE GNAPHALIEAE IN THIS STUDY

Chemical characters

1) 3574' tetra hydroxy flavone 0= absent 1= present

2) 6 hydroxy 0= absent 1= present

3) 5' hydroxy 0= absent 1= present

4) 3' hydroxy 0= absent 1= present

5) B-ring de-oxygenated 0= no 1= yes

6) glucose at the 3 position 0= absent 1= present

7) rhamnose at the 3 position 0= absent 1= present

8) glucose at the 7 position 0= absent 1= present

9) rhamno glucoside at the 3 position 0= absent 1= present

10) diglucoside at the 3 position 0= absent 1= present

11) Methoxy at the 3 position 0= absent 1= present

12) Methoxy at the 6 position 0= absent 1= present

13) Methoxy at the 7 position 0= absent 1= present

14) Methoxy at the 3' position 0= absent 1= present

15) 574'trihydoxyflavone 0= absent 1= present

16) 573'4'tetrahydroxyflavone 0= absent 1= present

17) 574' trihydroxyflavanone 0= absent 1= present

18) B-ring deoxyflavanone 0= absent 1= present

19) 3' hydroxyflavanone 0= absent 1= present

20) 7 methoxyflavanone 0= absent 1= present

21) 2'4'6'4 tetrahydroxychalcone 0= absent 1= present

22) B-ring deoxychalcone 0= absent 1= present

23) hydroxyl at 3' position of a chalcone 0= absent 1= present

24) 6 position deoxygenated on a chalcone 0= absent 1= present

25) methoxyl at the 4' position of a chalcone 0= absent 1= present

26) 3574' dihydroflavonol 0= absent 1= present

27) acetate at the 3 position of a dihydroflavonol 0= absent 1= present

28) dihydrochalcone 0= absent 1= present

ECOLOGICAL AND MORPHOLOGICAL CHARACTERS

29) soil type 0= alluvial coastal soil; 1 = loess deposits on soil parent materials derived from sedimentary sources; 2 = igneous derived soil; 3= serpentine derived soils; 4 = present on all soil types no preferences shown.

30) Island 0 = throughout New Zealand; 1= New Zealand North Island only; 2= New Zealand South Island only; 3 = Not New Zealand Australia including Tasmania.

31) Altitude ranges 0= coastal 0- 300m; 2 = lowland 300- 1000m; 3 = montane to alpine 1100-2000m; 4= plants present at all altitudes.

32) phyllary colour 0 = white; 1 = straw-yellow; 2 = yellow to pink; 3 = distinctly brown-red

33) bracts ranked 0 = bracts in a single series; 1 = double series; 2 = triple series; 3 = 4 ranked series; 4 = 5 ranked series; 5 = more than 5 ranks present.

34) bract apex 0= truncated or obtuse; 1 = rounded; 2 = acute

35) inner bracts hairy 0 = no; 1 = yes

36) inner bracts wrinkled 0 = no; 1 = yes

37) Tomentum 0 = none; 1 = white; 2 = yellow; 3 = orange.

38) Leaf size 0 = less than 1.5 cm x 0.5 cm; 1= greater than 1.5 cm x 0.5 cm

39) Leaf shape 0 = obovate 1= spathulate; 2 = ovate; 3 = linear; 4 = lanceolate; 5 = obcordate; 6 = scale like;

40) lamina margins revolute 0 = yes; 1= no

41) Habit 0 = tree; 1= shrub; 2 = herb

42) 0 = upright; 1 = prostrate

43) internodes 0 = distinct; 1 = short; 2 = not evident

44) Mature leaves 0 = alternate; 1 = spiral; 2 = distichous

ECOLOGICAL AND MORPHOLOGICAL CHARACTERS (cont.)

45) Head 0 = solitary; 1= panicle with curved receptacle; 2 = panicle with distinctly conical receptacle; 3 = corymb with flat receptacle;

46) Tomentum position 0 = absent; 1 = abaxial (below only); 2 = on both adaxial and abaxial sides.

47) Pappus shape 0= bristle; 1 = flattened; 2 = feather/barbellate; 3 = papilose; 4 = absent

48) Pappus shaft 0 = not present; 1 = present

49) Base distinct 0 = no; 1 = yes

50) Leaf angle 0 = $<45^{o}$; 1= $45\text{-}90^{o}$; 2 => 90^{o}

51) Receptacle terminal 0= no; 1 = yes

Raoulia as an out group.

In the analysis of the data matrix Raoulia subgenus Raoulia sensu Allan was used as the out group. Anderberg's (1991, 1994) analysis showed that the 11 species of Raoulia subgenus Raoulia sensu Allan formed a monophyletic group if R. chiliastra Mattf. (from Papua New Guinea) and Raoulia subgenus Mistura sensu Allan (R. petriensis) were included. Anderberg split Raoulia subgenus Psychrophyton from Raoulia sensu Allan, placing these true "Vegetable sheep" species into the genus Psychrophyton Beauverd. Raoulia subgenus Raoulia sensu Allan forms the basal taxon to the Gnaphaliinae in the phylogenetic trees of Anderberg 1991. This view echoed the taxonomic systems published by Ward (1982) and Allan (1961) both of whom suggested that these species formed a natural group. It is often easier to recognise Raoulia as a genus than it is to determine the exact species. Samples of Raoulia used in this study represented Raoulia subgenus Raoulia sensu Allan and Raoulia subgenus Mistura sensu Allan. The samples showed a uniform flavonoid profile (Reid & Bohm 1995) regardless of geographical, altitudinal or edaphic differences. All taxa present exhibited the same habit, that of a prostrate mat plant. In all cases the capitulum was terminal and enclosed in double-ranked white-tipped phyllaries. The tomentum was present abaxially.

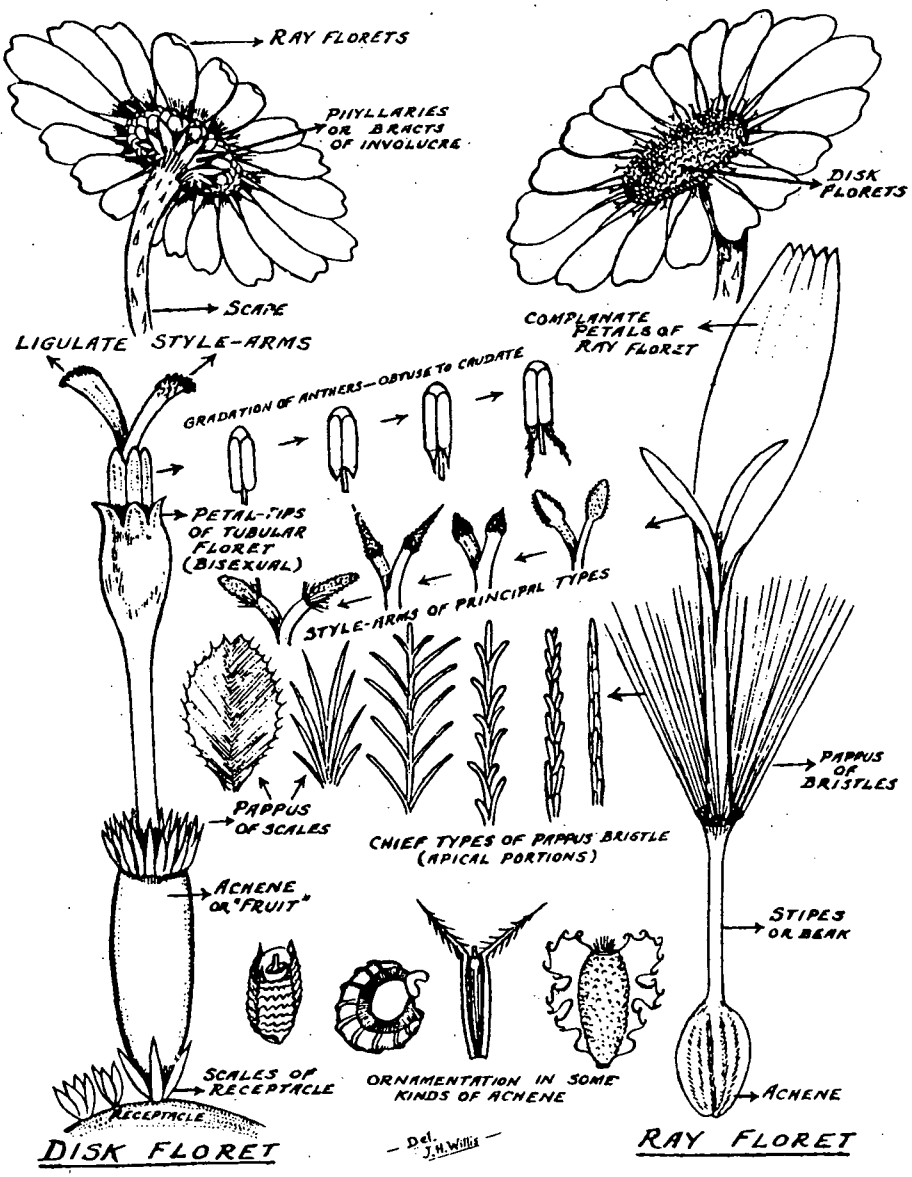


Figure 23. Floral Morphology of the Compositae
(Willis 1959)

Table 9 Data matrix of flavonoid, morphological and ecological characters used for cladistic analysis

	Characters																					
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Raoulia (out group)	1	1	1	1	0	1	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0
C. aculeata	1	0	1	1	0	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	0
C. arcuata	1	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1	1	0	1	0	0
C. amoena	1	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1	1	0	1	1	1
C. denticulata	1	0	1	1	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0
C. fulvida	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	1	1	1
C. montana	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1
C. laevis	1	1	0	1	0	1	1	0	1	0	1	1	1	1	0	0	0	0	0	0	1	0
C. leptophylla	1	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	1	1	1	0	0	0
C. longifolia	1	0	0	1	0	1	0	0	1	0	1	1	1	1	0	0	0	0	0	0	1	0
C. quinquefaria	1	1	0	1	1	0	0	0	1	1	1	1	0	0	0	0	1	1	1	1	1	0
C. rugata	1	0	0	1	0	1	0	0	1	0	1	0	1	0	1	1	1	1	1	0	1	0
C. subtropica	1	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
C. theodorii	1	0	0	1	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0
C. trinerve	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
C. uncata	1	0	0	1	0	0	0	0	1	0	1	1	0	1	1	1	1	1	0	1	1	0
C. vauvilliersii T	1	0	0	1	0	1	0	1	1	1	0	0	1	0	0	0	1	1	1	1	1	1
C. vauvilliersii H	1	0	0	1	0	1	0	0	1	1	1	0	1	0	0	0	1	1	1	1	1	1
O. coralloides	1	0	0	1	0	1	1	0	1	0	1	0	0	0	0	0	1	1	1	1	0	0
O. cordatum	1	0	0	1	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0
O. dendroideus	1	0	0	1	0	1	0	0	1	1	1	0	0	0	1	1	1	1	0	0	0	0
O. depressum	1	0	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0
O. dimorphum	1	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
O. diosmifolius	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
O. ferruginea	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0
O. hookeri	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	1	0	0
O. intermedium	1	0	0	1	0	1	1	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0
O. obcordatum	1	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
O. rosmarinifolius	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
O. selago	1	0	0	1	0	1	1	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0
O. stirlingii	1	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1	1	1	1	1	0
H. ozothamnoides	1	0	0	1	0	0	0	0	1	0	1	0	0	1	1	1	1	1	0	1	1	0

Table 9 Data matrix of flavonoid, morphological and ecological characters used for cladistic analysis

	Characters																
Taxon	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Raoulia (out group)	0	0	0	0	0	1	4	0	4	0	1	0	0	0	1	1	0
C. aculeata	0	0	0	0	0	0	0	3	1	2	2	0	1	0	0	2	3
C. arcuata	0	0	0	0	1	0	1	3	0	2	1	2	0	0	0	2	3
C. amoena	0	0	1	0	0	0	3	1	0	0	4	0	1	1	1	1	3
C. denticulata	0	0	0	0	0	0	0	3	0	1	2	0	0	0	2	2	1
C. fulvida	0	0	1	0	0	0	1	2	1	1	3	0	1	0	3	1	2
C. montana	0	0	1	0	0	0	1	2	2	1	3	0	1	0	3	1	2
C. laevis	0	0	1	1	0	0	0	3	0	0	2	2	0	1	2	2	3
C. leptophylla	0	0	0	1	0	0	0	0	0	0	2	2	0	1	2	2	3
C. longifolia	0	0	0	0	0	0	0	3	1	0	0	2	1	0	1	2	4
C. quinquefaria	0	0	0	0	1	0	1	3	0	0	5	2	1	1	3	2	3
C. rugata	0	0	0	0	0	0	0	3	0	0	5	0	0	1	1	2	3
C. subtropica	0	0	0	0	0	1	1	3	1	3	2	0	0	1	2	2	3
C. theodorii	0	0	1	0	0	1	0	3	0	1	2	2	0	0	2	2	4
C. trinerve	0	0	0	0	0	0	0	3	1	0	0	2	1	0	1	2	4
C. uncata	0	0	0	0	0	0	1	3	1	0	2	0	0	0	0	2	3
C. vauvilliersii T	0	1	1	1	0	0	2	1	3	1	3	0	1	0	2	1	1
C. vauvilliersii H	1	1	1	1	0	0	1	1	3	1	3	0	1	0	2	1	1
O. coralloides	0	0	0	0	0	0	1	2	3	1	4	0	1	0	0	1	6
O. cordatum	0	0	0	0	0	0	0	3	0	0	2	2	1	0	1	2	5
O. dendroideus	0	0	0	0	0	0	1	3	1	0	2	0	0	0	0	2	3
O. depressum	0	0	0	0	0	0	1	2	2	0	3	2	1	0	0	1	6
O. dimorphum	0	0	0	0	0	0	1	2	2	0	3	0	1	0	0	1	6
O. diosmifolius	0	0	0	0	0	0	1	3	1	0	2	0	0	0	0	2	3
O. ferruginea	0	0	0	0	0	0	1	3	1	0	2	1	1	0	0	2	4
O. hookeri	0	0	0	0	0	0	1	3	2	1	3	1	0	0	1	1	3
O. intermedium	0	0	0	0	0	0	1	2	3	1	4	0	1	0	0	1	6
O. obcordatum	0	0	0	0	0	0	0	3	0	0	2	0	0	0	0	2	5
O. rosmarinifolius	0	0	0	0	0	0	0	3	0	2	0	0	0	1	0	2	3
O. selago	0	0	0	0	0	0	1	2	3	1	4	0	1	0	0	1	6
O. stirlingii	0	0	0	0	0	0	1	3	1	0	?	?	?	0	?	2	4
H. ozothamnoides	0	0	0	0	0	0	1	3	1	1	0	0	0	0	2	2	3

Table 9 Data matrix of flavonoid, morphological and ecological characters used for cladistic analysis

Taxon	Characters											
	40	41	42	43	44	45	46	47	48	49	50	51
Raoulia (out group)	0	2	1	2	1	0	1	3	1	1	2	1
C. aculeata	0	0	0	0	0	3	1	1	1	1	1	0
C. arcuata	0	0	0	0	0	1	1	1	0	0	1	0
C. amoena	0	1	0	0	0	1	1	1	1	1	1	0
C. denticulata	0	0	0	0	0	1	1	1	0	0	1	0
C. fulvida	0	1	0	0	0	1	1	1	1	1	1	0
C. montana	0	1	0	0	0	1	1	1	1	1	1	0
C. laevis	0	0	0	0	0	1	1	0	0	0	1	0
C. leptophylla	0	0	0	0	0	1	1	1	1	1	1	0
C. longifolia	0	0	0	0	0	1	1	0	0	0	1	0
C. quinquefaria	0	0	0	0	0	2	1	1	0	0	1	0
C. rugata	0	0	0	0	0	3	1	0	1	1	1	0
C. subtropica	0	1	0	0	0	0	1	1	0	0	1	1
C. theodorii	0	0	0	0	0	1	1	1	0	0	1	0
C. trinerve	1	0	0	0	0	1	1	1	1	0	1	0
C. uncata	1	0	0	0	0	1	2	1	1	0	1	0
C. vauvilliersii T	0	1	0	0	0	1	1	1	1	1	1	0
C. vauvilliersii H	0	1	0	0	0	1	1	1	1	1	1	0
O. coralloides	1	1	0	2	1	0	1	3	0	0	0	1
O. cordatum	1	2	0	0	0	2	2	3	0	0	1	0
O. dendroideus	0	0	0	0	0	3	2	3	1	1	1	0
O. depressum	1	1	1	1	0	0	2	1	0	0	0	0
O. dimorphum	0	1	0	1	1	0	2	1	0	0	0	1
O. diosmifolius	0	0	0	0	0	3	1	3	0	0	1	0
O. ferruginea	0	0	0	0	0	1	1	1	1	1	1	0
O. hookeri	1	1	0	0	0	0	0	1	1	1	0	0
O. intermedium	1	1	0	2	1	0	1	3	0	0	0	1
O. obcordatum	1	1	1	0	1	3	2	3	0	0	1	0
O. rosmarinifolius	1	0	0	0	0	3	1	1	1	1	1	0
O. selago	1	1	0	2	1	0	1	3	0	0	0	1
O. stirlingii	1	0	0	0	0	1	?	?	?	?	1	0
H. ozothamnoides	1	0	0	0	0	1	2	4	0	0	1	0

Table 10. Flavonoids from Cassinia, Ozothamnus, Haeckeria, Lawrencella, Leucogenes and Raoulia.

	C. aculeata	C. amoena	C. arcuata	C. denticulata	C. fulvida var. fulvida	C. fulvida var. montana
galangin	-	-	-	-	-	-
kaempferol	+	+	+	+	+	+
quercetin	+	+	+	+	+	+
kaempferol 3 O-rhamnoside	-	-	-	-	-	-
kaempferol 3 O-glucoside	+	+	-	+	+	+
kaempferol 7 O-glucoside	-	-	-	-	-	-
kaempferol 3 O-rutinoside	+	+	+	+	+	-
quercetin 3 O-glucoside	+	+	+	+	+	+
quercetin 3 O-rutinoside	+	+	+	+	+	+
quercetin3 O-diglucoside	-	-	-	-	-	-
quercetagetin 3 O-glucoside	-	-	-	-	-	-
isorhamnetin 3 O-glucoside	+	-	-	-	-	-
myricetin3 O-glucoside	+	-	-	+	-	-
apigenin	+	-	-	+	-	-
luteolin	+	-	-	+	-	-
eriodictyol	+	-	-	-	-	-
eriodictyol 7 O-methyl ether	+	-	-	-	-	+
5,7 dihydroxyflavanone	+	-	+	-	-	-
5 hydroxy 7 methoxyflavanone (pinostrobin)	+	+	+	-	+	+
pinobanksin	+	-	+	-	-	-
2'4'6'4 tetrahydroxychalcone	+	-	-	-	-	-
2'6'4 trihydroxy 4' methoxychalcone	+	-	-	-	-	-
2' hydroxy 4' methoxychalcone	-	-	-	-	-	-
2'4'6' trihydroxychalcone	-	-	-	-	-	+
2'6' dihydroxy 4' methoxychalcone	-	+	-	-	+	+
2'4'34 tetrahydroxychalcone	-	-	-	-	-	-
2'6' dihydroxy 4' methoxy dihydrochalcone	-	+	-	-	+	+
kaempferol 3 O-methyl ether	+	-	-	-	-	-
quercetin 3 O-methyl ether	+	+	+	+	-	-
quercetin 7 O-methyl ether	-	-	-	-	-	-
quercetin 6 O-methyl ether	+	-	-	-	-	-

* = Lawrencella belidioides
° = Leucogenes

Table 10. Flavonoids from Cassinia, Ozothamnus, Haeckeria, Lawrencella, Leucogenes and Raoulia.

	C. laevis	C. leptophylla	C. longifolia	C. quinquifaria	C. rugata	C. subtropica	C. trinerve	C. theodorii
galangin	-	+	-	-	-	-	-	-
kaempferol	+	+	+	+	+	+	+	+
quercetin	+	+	+	+	+	+	+	+
kaempferol 3 O-rhamnoside	-	+	-	-	-	-	-	-
kaempferol 3 O-glucoside	+	+	-	-	+	+	+	+
kaempferol 7 O-glucoside	-	-	-	-	-	-	-	-
kaempferol 3 O-rutinoside	+	+	-	+	-	-	-	-
quercetin 3 O-glucoside	+	+	+	-	+	+	+	+
quercetin 3 O-rutinoside	+	+	+	+	+	+	+	+
quercetin3 O-diglucoside	-	+	-	+	-	-	-	-
quercetagetin 3 O-glucoside	+	-	-	+	-	-	-	-
isorhamnetin 3 O-glucoside	+	-	+	-	-	-	-	-
myricetin3 O-glucoside	-	-	-	-	-	-	-	-
apigenin	-	-	-	-	+	-	-	+
luteolin	-	-	-	-	+	-	-	+
eriodictyol	-	-	-	+	-	-	-	-
eriodictyol 7 O-methyl ether	-	-	-	+	-	-	-	-
5,7 dihydroxyflavanone	-	+	-	+	-	-	-	-
5 hydroxy 7 methoxyflavanone (pinostrobi	-	-	-	-	+	-	-	-
pinobanksin	+	-	+	+	+	-	-	+
2'4'6'4 tetrahydroxychalcone	+	-	-	-	-	-	+	-
2'6'4 trihydroxy 4' methoxychalcone	+	-	+	+	-	-	-	+
2' hydroxy 4' methoxychalcone	-	-	-	-	-	-	-	-
2'4'6' trihydroxychalcone	-	-	-	-	-	-	-	-
2'6' dihydroxy 4' methoxychalcone	-	-	-	-	-	-	-	-
2'4'34 tetrahydroxychalcone	-	-	-	-	-	-	-	-
2'6' dihydroxy 4' methoxy dihydrochalcone	-	-	-	-	-	-	-	-
kaempferol 3 O-methyl ether	-	-	+	+	-	+	-	-
quercetin 3 O-methyl ether	+	-	+	+	+	+	-	+
quercetin 7 O-methyl ether	-	-	-	-	-	-	-	-
quercetin 6 O-methyl ether	+	-	+	+	-	-	-	-

* = Lawrencella belidioides
° = Leucogenes

Table 10. Flavonoids from Cassinia, Ozothamnus, Haeckeria, Lawrencella, Leucogenes and Raoulia.

	C. uncata	C. vauvilliersii (H)	C. vauvilliersii (T)	Awatere	Hurunui	L. bellidioides*	O. coralloides
galangin	-	-	-	-	-	-	-
kaempferol	+	+	+	+	+	+	+
quercetin	+	+	+	+	+	+	+
kaempferol 3 O-rhamnoside	-	-	-	-	-	-	+
kaempferol 3 O-glucoside	-	+	+	-	-	+	-
kaempferol 7 O-glucoside	-	+	-	-	-	-	+
kaempferol 3 O-rutinoside	+	+	+	-	-	+	+
quercetin 3 O-glucoside	-	+	+	+	+	+	+
quercetin 3 O-rutinoside	+	+	+	-	-	+	+
quercetin3 O-diglucoside	-	+	+	-	-	+	-
quercetagetin 3 O-glucoside	-	-	-	+	+	-	-
isorhamnetin 3 O-glucoside	+	-	-	-	-	-	-
myricetin3 O-glucoside	-	-	-	-	-	+	-
apigenin	-	-	-	-	-	-	-
luteolin	+	-	-	-	-	-	-
eriodictyol	-	+	-	-	+	-	+
eriodictyol 7 O-methyl ether	-	-	+	-	-	-	-
5,7 dihydroxyflavanone	-	+	+	+	+	-	+
5 hydroxy 7 methoxyflavanone (pinostro	+	-	-	-	+	-	-
pinobanksin	-	-	-	-	-	-	-
2'4'6'4 tetrahydroxychalcone	+	-	-	+	+	-	-
2'6'4 trihydroxy 4' methoxychalcone	-	-	-	-	-	-	-
2' hydroxy 4' methoxychalcone	-	+	+	-	-	-	-
2'4'6' trihydroxychalcone	-	-	+	-	-	-	-
2'6' dihydroxy 4' methoxychalcone	-	-	+	-	-	-	-
2'4'34 tetrahydroxychalcone	-	+	-	+	+	-	-
2'6' dihydroxy 4' methoxy dihydrochalcon	-	-	-	-	-	-	-
kaempferol 3 O-methyl ether	-	-	-	-	-	+	-
quercetin 3 O-methyl ether	+	+	-	-	+	+	+
quercetin 7 O-methyl ether	-	+	+	-	+	-	-
quercetin 6 O-methyl ether	+	-	-	-	-	-	-

* = Lawrencella belidioides
° = Leucogenes

Table 10. Flavonoids from Cassinia, Ozothamnus, Haeckeria, Lawrencella, Leucogenes and Raoulia.

	O. cordatum	O. dendroideum	O. depressum	O. dimorphum	O. diosmifolius	O. ferruginea	O. hookeri
galangin	-	-	-	-	-	-	-
kaempferol	+	+	+	+	+	+	+
quercetin	+	+	+	+	+	+	+
kaempferol 3 O-rhamnoside	-	-	-	-	-	-	-
kaempferol 3 O-glucoside	+	+	-	+	+	-	-
kaempferol 7 O-glucoside	-	-	-	-	-	-	-
kaempferol 3 O-rutinoside	-	+	+	+	-	-	-
quercetin 3 O-glucoside	-	+	+	+	-	-	-
quercetin 3 O-rutinoside	-	+	+	-	-	-	+
quercetin3 O-diglucoside	-	+	+	-	-	-	-
quercetagetin 3 O-glucoside	-	-	-	-	-	-	-
isorhamnetin 3 O-glucoside	-	-	-	-	-	-	-
myricetin3 O-glucoside	-	-	-	-	-	-	-
apigenin	+	+	+	-	-	-	-
luteolin	-	+	-	-	-	-	-
eriodictyol	-	-	-	-	-	-	-
eriodictyol 7 O-methyl ether	-	-	-	+	-	-	+
5,7 dihydroxyflavanone	-	+	-	-	-	+	+
5 hydroxy 7 methoxyflavanone (pinost	-	-	-	-	-	-	-
pinobanksin	-	+	-	-	-	+	-
2'4'6'4 tetrahydroxychalcone	-	-	-	-	-	-	-
2'6'4 trihydroxy 4' methoxychalcone	-	-	-	-	-	-	-
2' hydroxy 4' methoxychalcone	-	-	-	-	-	-	-
2'4'6' trihydroxychalcone	-	-	-	-	-	-	-
2'6' dihydroxy 4' methoxychalcone	-	-	-	-	-	-	-
2'4'34 tetrahydroxychalcone	-	-	-	-	-	-	-
2'6' dihydroxy 4' methoxy dihydrochal	-	-	-	-	-	-	-
kaempferol 3 O-methyl ether	-	+	-	-	+	+	-
quercetin 3 O-methyl ether	+	+	-	-	+	+	-
quercetin 7 O-methyl ether	-	-	-	-	-	-	-
quercetin 6 O-methyl ether	-	-	-	-	-	-	-

* = Lawrencella belidioides
° = Leucogenes

Table 10. Flavonoids from Cassinia, Ozothamnus, Haeckeria, Lawrencella, Leucogenes and Raoulia.

	O. intermedium	O. obcordatum	O. rosmarinifolius	O. selago	O. stirlingii	Haeckaria ozothamnoides
galangin	-	-	-	-	-	-
kaempferol	+	+	+	+	+	+
quercetin	+	+	+	+	+	+
kaempferol 3 O-rhamnoside	-	-	-	-	-	-
kaempferol 3 O-glucoside	-	-	-	+	+	+
kaempferol 7 O-glucoside	-	-	-	-	-	-
kaempferol 3 O-rutinoside	-	-	-	-	-	+
quercetin 3 O-glucoside	+	+	+	+	+	+
quercetin 3 O-rutinoside	-	+	+	-	+	+
quercetin3 O-diglucoside	+	-	-	+	-	-
quercetagetin 3 O-glucoside	-	-	-	-	-	-
isorhamnetin 3 O-glucoside	-	-	-	-	-	+
myricetin3 O-glucoside	-	-	+	-	-	-
apigenin	-	+	-	+	-	+
luteolin	-	-	-	+	-	+
eriodictyol	-	-	-	-	-	-
eriodictyol 7 O-methyl ether	-	-	-	-	+	-
5,7 dihydroxyflavanone	-	-	-	+	+	-
5 hydroxy 7 methoxyflavanone (pinostr	-	-	-	-	-	+
pinobanksin	-	-	-	-	+	+
2'4'6'4 tetrahydroxychalcone	-	-	-	-	+	+
2'6'4 trihydroxy 4' methoxychalcone	-	-	-	-	-	-
2' hydroxy 4' methoxychalcone	-	-	-	-	-	-
2'4'6' trihydroxychalcone	-	-	-	-	-	-
2'6' dihydroxy 4' methoxychalcone	-	-	-	-	-	-
2'4'34 tetrahydroxychalcone	-	-	-	-	-	-
2'6' dihydroxy 4' methoxy dihydrochalco	-	-	-	-	-	-
kaempferol 3 O-methyl ether	+	-	-	-	+	-
quercetin 3 O-methyl ether	+	-	+	-	-	+
quercetin 7 O-methyl ether	-	-	-	-	-	-
quercetin 6 O-methyl ether	-	-	-	-	-	-

* = Lawrencella belidioides
° = Leucogenes

Table 10. Flavonoids from Cassinia, Ozothamnus, Haeckeria, Lawrencella, Leucogenes and Raoulia.

	Hybrid C. uncata x O. obcordata	L. leontipodium°	L. grandiceps°	Raoulia
galangin	-	+	-	-
kaempferol	+	+	+	+
quercetin	+	+	+	+
kaempferol 3 O-rhamnoside	-	+	-	-
kaempferol 3 O-glucoside	-	+	+	+
kaempferol 7 O-glucoside	-	+	+	-
kaempferol 3 O-rutinoside	+	-	-	+
quercetin 3 O-glucoside	+	+	+	+
quercetin 3 O-rutinoside	+	-	+	-
quercetin3 O-diglucoside	-	+	+	-
quercetagetin 3 O-glucoside	-	-	-	-
isorhamnetin 3 O-glucoside	-	-	-	-
myricetin3 O-glucoside	-	+	-	+
apigenin	+	+	+	-
luteolin	+	+	-	+
eriodictyol	-	-	-	-
eriodictyol 7 O-methyl ether	-	-	-	-
5,7 dihydroxyflavanone	-	-	-	-
5 hydroxy 7 methoxyflavanone (pinostrobin	+	-	-	-
pinobanksin	-	-	-	-
2'4'6'4 tetrahydroxychalcone	+	-	-	-
2'6'4 trihydroxy 4' methoxychalcone	-	-	-	-
2' hydroxy 4' methoxychalcone	-	-	-	-
2'4'6' trihydroxychalcone	-	-	-	-
2'6' dihydroxy 4' methoxychalcone	-	-	-	-
2'4'34 tetrahydroxychalcone	-	-	-	-
2'6' dihydroxy 4' methoxy dihydrochalcone	-	-	-	-
kaempferol 3 O-methyl ether	-	+	-	-
quercetin 3 O-methyl ether	+	+	-	-
quercetin 7 O-methyl ether	-	+	-	-
quercetin 6 O-methyl ether	-	-	-	-

* = Lawrencella belidioides
° = Leucogenes

DISCUSSION OF RESULTS: CHEMICAL, MORPHOLOGICAL, ECOLOGICAL AND GEOGRAPHICAL CHARACTERS FORMING THE CLADOGRAM

The clustering of the taxa in the cladogram is strongly influenced by ecology and geography (Fig. 24). With the exception of Ozothamnus hookeri, the taxa are grouped into those of Australian and those of New Zealand distribution. This geographical character, although included in the data matrix, was not used for the analysis and production of the parsimonious trees. Ozothamnus hookeri clusters with the "whipcord" species of Ozothamnus found in New Zealand. This species is one of the few Australian species of Ozothamnus that reaches alpine elevations. Ozothamnus obcordatum, O. cordatum and O. hookeri are found at higher elevations in the Blue Mountains of New South Wales, the Victorian Alps and the uplands of northwestern Tasmania. Ozothamnus hookeri has the smallest leaves of all Ozothamnus species found in Australia. The common leaf shapes in Australian Ozothamnus are linear or lanceolate. Ozothamnus hookeri, O. obcordatum and O. cordatum possess obcordate or spathulate leaves that are appressed to the main branch. The whipcord Ozothamnus clade forms a sister group to the New Zealand species of Cassinia. The geographical and ecological characteristics common to these two groups are 1) these taxa grow on soils that are formed from soil parent materials of Oligocene or Miocene age. 2) All species in this clade show a strong preference for open habitats but may also occur at forest margins.

The second clade(fig 26) contains Haeckeria and the Australian species of Cassinia and Ozothamnus. Australia's size, lack of high mountain ranges and generallly low relief direct the major rainfall patterns to the coast. This restricts suitable habitats for many plants to coastal regions no further than 200 km inland. Haeckeria and the Australian species of Cassinia and Ozothamnus occur within this coastal zone.

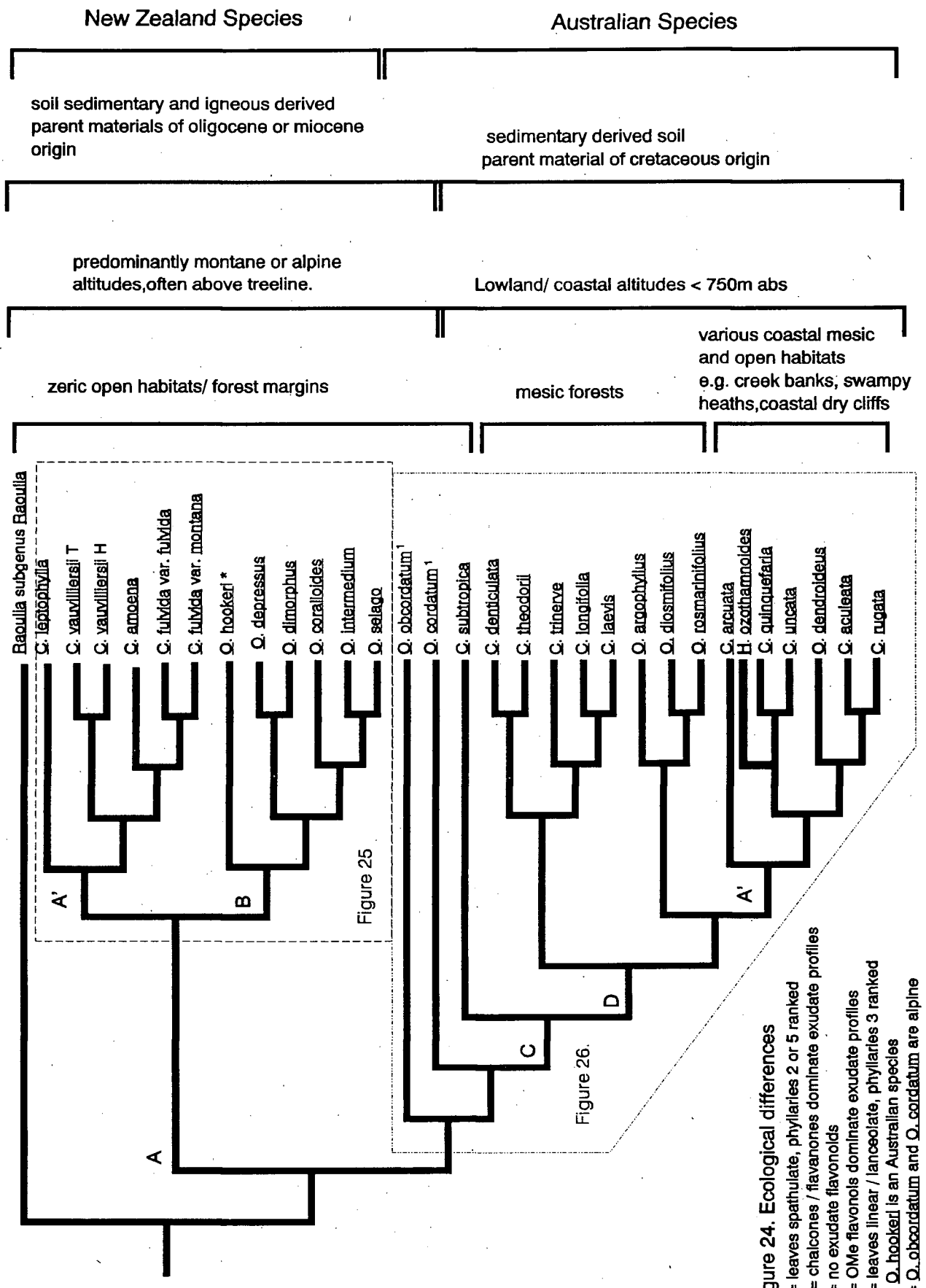


Figure 24. Ecological differences
A = leaves spathulate, phyllaries 2 or 5 ranked
A' = chalcones / flavanones dominate exudate profiles
B = no exudate flavonoids
C = OMe flavonols dominate exudate profiles
D = leaves linear / lanceolate, phyllaries 3 ranked
* = O. hookeri is an Australian species
1 = O. obcordatum and O. cordatum are alpine

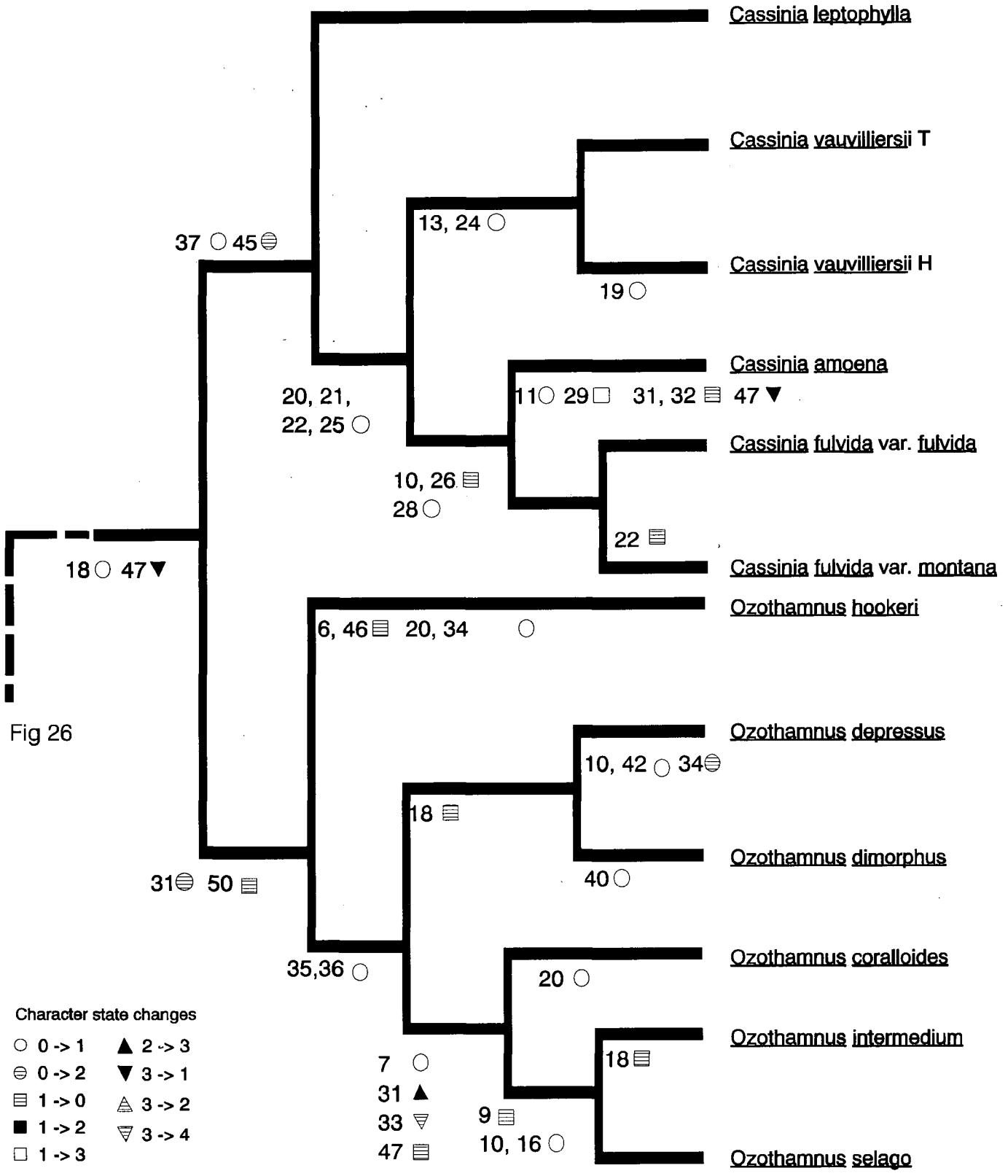


Fig 26

Figure 25. Strict consensus cladogram of the New Zealand species.

Fig 25

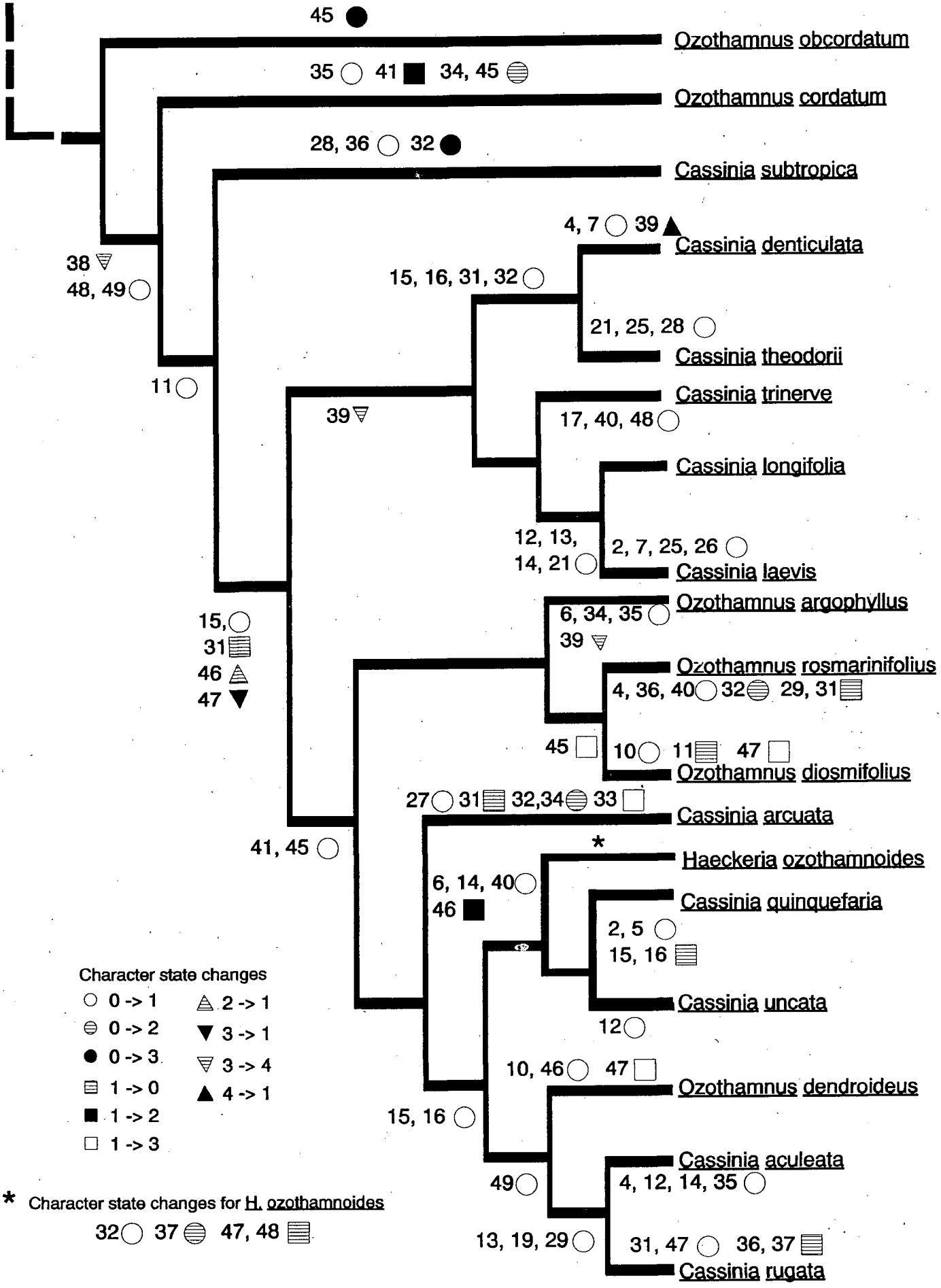


Figure 26. Strict consensus cladogram of the Australian Species.

Two major clades appear in the Australian taxa. The first contains those taxa that are common in mesic forest habitats (C. denticulata, C. theodorii, C. trinerve, C. longifolia and C. laevis). The second is further subdivided into one that contains O. argophyllus, O. diosmifolius and O. rosmarinifolius which are common understorey shrubs in mesic eucalypt forests of Victoria, southern New South Wales and Tasmania. The second subdivision contains taxa that occupy a variety of coastal habitats; C. arcuata, Haeckeria ozothamnoides, C. uncata, O. dendroideus, C. aculeata and C. rugata. These habitats range from coastal cliffs and plateaus in the case of C. arcuata to wet open river banks in the case of C. rugata. The presence of chalcones and flavanones in the exudate profile of members of this clade distinguishes the group from the other Australian clade.

Notes accompanying herbarium specimens deposited in the National Herbarium of Victoria (J. H. Willis and A. C. Beauglehole MEL 504682; A. C. Beauglehole MEL 1560578, MEL 527146; A. C. Beauglehole and C. & D. Woolcock MEL 527127; H. I. Aston MEL 1560583; Walsh and A. C. Beauglehole MEL 1560555) suggest that this species is an intergeneric hybrid between Ozothamnus rosmarinifolius (Labill.) Anderberg and Cassinia aculeata (Labill.) R.Br. Cassinia rugata differs from the proposed parents in a number of characters (Table 11). It does not represent an intermediate stage between either parent. Walsh (1990), while compiling a register of the rare and threatened plants of Victoria, investigated the taxonomic status of this species. Cassinia rugata is distributed in the upper catchments of the Fitzroy and Surrey Rivers, 25 km from Portland, southwest Victoria (Walsh 1990). Walsh described the new species as being closely related to Cassinia uncata Cunn. ex DC., a polymorphic species with several varieties. (Cooke 1986). Cassinia uncata differs from C. rugata in a number of characters (Table 11). Cassinia uncata and C. aculeata are not sympatric with C. rugata. The nearest known population of either proposed parent occurs in the Barwon River catchment, over 100 km to the east. Along with the geographical and morphological differences there are habitat differences. Cassinia rugata occurs in seasonally wet heathlands. These treeless sites are dominated by Allocasuarina paludosa (L.) L. Johnson, Baumea Gaudich. spp., and Juncus L. spp. Cassinia uncata, on the other hand, is

dominant in open dry malee scrublands common in the table lands of Victoria and southwest New South Wales. Cassinia aculeata has a similar habitat requirement to C. uncata inhabiting forest margins especially the transitional areas between forest and Malee scrub. Ozothamnus rosmarinifolius forms associations with mesic eucalypt forests in Tasmania, Victoria and southeastern New South Wales.

Comparison between the flavonoid and morphological characters of Cassinia and Ozothamnus as a whole, shows an affinity between Cassinia rugata and Cassinia aculeata, one of the parents proposed by J. H. Willis and A. C. Beauglehole (MEL 504682). It does not show a direct link to Cassinia uncata which is a part of a sister clade linked to C. aculeata and C. rugata (Fig. 26). The vacuolar flavonoid profile of Cassinia rugata consists of kaempferol, quercetin and their 3-O glucosides, quercetin 7-O methylether (rhamnetin), rutin and the common flavones apigenin and luteolin. Cassinia aculeata possesses a similar pattern of flavonoids, in addition to the flavonoids found in C. rugata, it accumulates kaempferol 3-O rutinoside, eriodictyol 7-O methyl ether and pinocembrin. Cassinia uncata does not accumulate eriodictyol 7-O methyl ether or pinocembrin nor does it contain apigenin, the 3-O glucosides of kaempferol, quercetin and quercetin 7-O methylether (rhamnetin). Ozothamnus rosmarinifolius has the simplest vacuolar flavonoid profile of the proposed parents. This profile consists of kaempferol and quercetin aglycones, the 3-O glucoside and the 3-O rhamno-glucoside of quercetin. The distinctive part of the profile of O. rosmarinifolius is the occurrence of quercetagetin 3-O glucoside. This flavonol also found in C. aculeata.

The exudate profiles of these species vary widely. The simplest pattern belongs to O. rosmarinifolius and includes one flavonol quercetin 3-O methyl ether. Cassinia rugata and C. uncata have relatively simple exudate flavonoid profiles, when compared to the other species forming this group, consisiting of quercetin 3-O methyl ether, pinocembrin 7-O methyl ether. C. rugata adds pinocembrin to this profile. The most complex exudate flavonoid profile of the proposed parents belongs to C. uncata. To the common set of exudate flavonoids C. uncata adds

2',4',6',4 tetrahydroxychalcone (chalconaringenin) and its 4-O methyl ether, pinocembrin and the 3-O methyl ethers of kaempferol and quercetin.

There are a number of morphological and ecological characters that separate C. rugata from C. uncata, the closest relative according to Walsh (1990). Cassinia rugata and C. aculeata both occur on wet coastal soils that are not subject to long periods of desiccation. C. uncata is common in areas that are much drier than C. rugata or C. aculeata on soil that is described as a subset of coastal Yellow Brown Earths (Stevens 1980), a classification that describes soils of sedimentary origin. The major difference between these habitats is the amount of rainfall each experiences. Floral and leaf tomentum characters separate C. rugata and C. uncata. Cassinia rugata bears capitula terminally in a corymb. Five ranks of wrinkled phyllaries envelop each capitulum. Cassinia uncata has a capitulum with smooth, double ranked phyllaries. In both these species the tomentum is cottony and bristly and occurrs on both the leaves and stems. Tomentum location differs. In C. uncata it covers the entire leaf and encloses the revolute margins whereas in C. rugata it is on the under surface of the leaf.

Ozothamnus dendroideus, C. rugata and C. aculeata are placed in the same clade. This is a result of the high degree of similarity between the vacuolar and exudate flavonoid profiles. The exudate profile of Ozothamnus dendroideus contains pinocembrin and the 3 -O methyl ethers of kaempferol and quercetin. The vacuolar profile consists of kaempferol and quercetin 3 -O glucosides, kaempferol 3-O rhamno-glucoside the common flavones apigenin and luteolin. This profile is very similar to that of C. aculeata. Ozothamnus dendroideus accumulates quercetin 3-O diglucoside in its vacuolar profile. This, accompanied by the lack of a tomentum and the barbellate pappus, are the major characteristics that separate O. dendroideus from C. aculeata and C. rugata. According to Curtis (1963) this species of Ozothamnus is common throughout Australia and occupies a similar ecological habitat to both C. aculeata and C. rugata. Ozothamnus dendroideus is found along forest margins and along creek and river banks. This habitat seems to combine the features of the two habitats occupied by the Cassinia species.

Three species, C. uncata, C. quinquefaria and Haeckeria ozothamnoides, form a sister clade to the C. rugata group. Chemically these species lack the flavones apigenin and luteolin which are common to the C. rugata sister clade. Cassinia uncata and C. quinquefaria possess dihydroflavonol and flavanone 3 acetates (Jakupovic et al. 1989). The flavonoid acetates are a part of the flavonoid profile of Ozothamnus stirlingii (Jakupovic et al 1989). Cassinia uncata, C. quinquefaria and Haeckeria ozothamnoides possess three acutely tipped ranked phyllaries which are yellow or pink in Cassinia arcuata and C. quinquefaria and brown in Haeckeria. The capitula are held in terminal panicles. Cassinia arcuata has linear leaves less than 3 cm long with obtuse or recurved tips and revolute margins. Cassinia quinquefaria, on the other hand has leaves greater than 4 cm long. Cassinia arcuata is a basal taxon to the clade containing C. uncata and its related species and the clade containing C. rugata and C. aculeata.

Ozothamnus rosmarinifolius is a common understorey shrub in the mesic eucalypt forests of Victoria (Curtis 1963). A number of morphological and chemical characters separate it from the complex containing C. rugata. Ozothamnus rosmarinifolius is a much branched shrub that holds the inflorescence in a terminal corymb. Each capitulum bears an individual floret on a flattened receptacle. This character is common in O. diosmifolius and O. argophyllus, two species that form a clade with O. rosmarinifolius. Also common to this group is a flattening of the pappus tip. Plants of this group possess a cottony, rather than bristly, tomentum which covers the organ in question with a fine mat of simple hairs that resemble fine cotton wool. A bristly tomentum is a covering of loosely matted, much branched hairs. The inflorescence of the C. rugata group is an axillary panicle. The common flavones, apigenin and luteolin, are absent from the O. rosmarinifolius clade.

The second major clade formed by the analysis includes five Australian species of Cassinia, C. denticulata, C. theodorii, C. trinerve, C. longifolia and C. laevis. Cassinia denticulata and C. theodorii are common in the tropical eucalypt forests of Queensland and northeastern New South Wales which occur between 300 and 1000m above sea level on the foothills of the Great Dividing Range. The remaining species are coastal in distribution. This geographical difference is accompanied by a difference in phyllary colouration. In C. denticulata and C. theodorii the

phyllaries lack the white tips that are common in almost all other Australian Cassinia species. Chemical characters also play a major role in the separation of these species from other Cassinia species. C. denticulata and C. theodorii both contain flavones, apigenin and luteolin but these are absent from the other three species in this clade. Cassinia denticulata and Cassinia theodorii can be resolved by flavonoid characters. Cassinia denticulata produces flavonol 3-O rhamnosides, flavonols that are absent from the vacuolar profile of C. theodorii. The exudate flavonoid profile of C. theodorii consists of chalcones and flavanones. The absence of the chalcones is the major character that separates the two species. Tthe two species have different habitat preferences although both species occupy the same geographical and altitudinal distribution. C. denticulata is most commonly a deep forest dweller while C. theodorii shows a preference for forest margins and open spaces. The three more southerly distributed Cassinia species, C. trinerve, C. longifolia and C. laevis are seperated from C. denticulata and C. theodorei on the basis of leaf shape. The former group have lanceolate leaves while the latter group has ovate-linear leaves. In the field it is often difficult to distinguish C. longifolia and C. laevis. Cassinia laevis is a slender shrub with a white tomentum that covers the branches and the underside of the leaves. Cassinia longifolia is also a slender shrub with linear or lanceolate leaves covered in a rough white tomentum. The characters most commonly used to distinguish the two species are the number of phyllary ranks and the shape of the phyllary tip (Curtis 1963). In C. longifolia the inflorescence is a dense panicle. Pure white obtusely tipped phyllaries surround each capitulum. In C. laevis the double ranked, acutely tipped phyllaries are opaque. The chemical profile of C. laevis includes 2',4,4' trihydroxychalcone, its 4' methyl ether, quercetagetin (3,5,6,7,3',4' hexahydroxy flavone) and flavonol 3 -O rhamnosides. The third member of this clade C. trinerve is easily distinguished from the previous pair by the lateral veins that run along the margin of the leaves and by the possession of a distinct shaft that bears the feathered pappus. The pappus of C. laevis and C. longifolia does not possess this shaft. Chemically C. trinerve lacks patuletin (3,5,7,3',4' pentahydroxy 6 methoxy flavone), quercetin 7-O methylether (rhamnetin), isorhamnetin and the common chalcone, chalconaringenin

(2',4',6',4-tetrahydroxychalcone). Cassinia trinerve accumulates luteolin. Both apigenin and luteolin are absent from C. laevis and C. longifolia.

The flavonoids of Ozothamnus stirlingii

Ozothamnus stirlingii is a common pioneer species in open or disturbed habitats. This species is common throughout southeastern Victoria and its range extends through New South Wales to southwest Queensland. All parts of this small tree are covered with a yellow exudate that rivals the exudate of C. vauvilliersii in stickiness. The yellow exudate is composed of pinocembrin and pinocembrin 7 methyl ether, 2',4',6',4 tetrahydroxychalcone, pinobanksin (3,5,7 trihydroxydihydroflavonol) and kaempferol 3-O methyl ether. A similar array of compounds is found in C. vauvilliersii and Haeckeria ozothamnoides. In contrast to the exudate profile, the vacuolar flavonoid profile is simple, consisting of the 3-O glucosides of kaempferol and quercetin and the 3-O rutinoside of quercetin (rutin). The occurrence of eriodictyol 7-O methyl ether is of interest as it is a part of in the vacuolar flavonoid profiles of a number of species, including C. quinquefaria, C. vauvilliersii from Tongariro National Park, C. aculeata and C. fulvida var. montana. This flavonoid is present in only one species of Ozothamnus, O. hookeri. Morphologically this species resembles C. trinerve, possessing lanceolate leaves up to 8 cm long. Each leaf has two marginal veins. The capitula appear pink from the reddish outer phyllaries and white inner phyllaries. Ecologically O. stirlingii is found in highly disturbed sites that resemble the habitats occupied by C. fulvida var. montana or C. leptophylla. Samples of O. stirlingii collected at the beginning of their flowering period (March) from the Brundabella Range in the southern part of the Australian Capital Territory (ACT) showed a considerable degree of morphological variation. The capitulum had not fully developed, therefore pappus characters could not be determined with any certainty. Phyllary morphology varied within each fully developed capitulum. In some species these phyllaries are wrinkled. Within the fully developed capitulum of these samples, phyllaries were both wrinkled and smooth. In some species there is a covering of fine hair on each phyllary. In some cases both glabrous and hairy phyllaries were present in the same capitulum. There was

no discernable pattern to the distribution of these phyllary conditions. The number of phyllary ranks varied from 2 to 5. Tomentum position also varied within this sample set. Some plants were completely covered with a soft white down. In other plants the tomentum was restricted to the underside of the leaves. Depending on the age of the branch, both conditions could be observed. With these characters coded as uncertain or missing (symbolized by ? in the data matrix) the phylogenetic tree produced scatters taxa, thought of as closely related, throughout the phylogenetic tree. Chemically the exudate profile points to a relationship with C. quinquefaria, C. aculeata or Haeckeria ozothamnoides. Morphological characters show a correlation with C. trinerve while ecological preferences, including altitude range and soil preferences, show a stronger correlation with C. fulvida var. montana or C. vauvilliersii from Tongariro National Park. Therefore O. stirlingii was excluded from the final analysis. Ozothamnus stirlingii is of unknown affinity, thus it cannot be placed with any certainty in any of the clades produced.

Relationships within the New Zealand Cassinia species.

Webb (1988) could not recognize more than one species of Cassinia, C. leptophylla, in the New Zealand flora. This species is treated as highly variable and forms an altitudinal complex. Webb (1988) described the forms of C. leptophylla as having a dense white tomentum on the young stems and on the lower surface of the leaves. Yellow glands cover the tomentum. The concentration of these glands determines the colour and stickiness of the leaves and stems. Subalpine and alpine forms show a wide variety of gland density. Clearly Webb considered colour variation within the genus sensu Allan as an altitudinally controlled condition. If this is so then plants transplanted from their altitudinal range to other altitudinal conditions should therefore, over time, change tomentum colour to the colour prevalent at the new altitude.

Several specimens representing the morphological variation of C. leptophylla sensu Webb are present in botanical gardens in New Zealand including Otari Native Plant Museum, in Wellington, the Christchurch Botanical Gardens (both of which are at sea level) and at Arthur's Pass National Park. A special soil mix is used to mimic the natural conditions of Cassinia amoena.

The Christchurch Botanical Gardens and Otari Native Plant Museum collections contain specimens of the genus sensu Allan, Cassinia fulvida var. fulvida and Cassinia leptophylla from low altitude, and Cassinia fulvida var. montana and Cassinia vauvilliersii from high altitude. The common garden site at Arthur's Pass National Park Headquarters contains plants transplanted laterally rather than an altitudinally. In all cases there has been no change in the tomentum colour. The altitudinal colouration must therefore must be genetically fixed rather than due to ecological conditions alone.

Samples of the New Zealand species of Cassinia collected from throughout their natural range (appendix 1) showed few differences between populations and individuals within populations. There were, however, geographical differences that corresponded to the genus sensu Allan (1961). The most complex exudate flavonoid profile observed was seen in C. vauvilliersii, five compounds in plants from Tongariro, six from Mt Holdsworth. Pigment differences between plants from these two sites are as great as differences between other pairs of taxa. Profiles of vacuolar flavonoids of plants from the different sites were also different, but the differences were less striking. It is interesting to note that the plants from the two sites grow on different substrata. Plants from Tongariro National Park were growing on weathered igneous substratum while those from Mt. Holdsworth grow on sedimentary-derived soil. The suggestion that these flavonoid profiles might be fixed in each of these areas gets support from the observation that a specimen of C. vauvilliersii (NZ 708) obtained from the Otari Native Botanical Garden gave exudate and vacuolar flavonoid profiles identical to those seen in plants collected from the native habitats. A sample of C. leptophylla (NZ 704) from the Otari Native Botanical Garden also exhibited flavonoid profiles identical to field collected plants.

Morphological and ecological characters separate C. amoena from the other fulvous species. The combination of characters suggests that C. amoena is a sister taxon of Cassinia fulvida var. fulvida and Cassinia fulvida var. montana. Cassinia amoena has longer leaves that the other species of Cassinia in New Zealand which resemble the leaf shape of Cassinia leptophylla. A soft grey tomentum that often possesses a slight yellow tinge covers the leaves of C. amoena.

The yellow tinge to the tomentum is a factor of the size of the leaves and of the density of the hairs producing this tomentum.

The differences in the exudate flavonoid chemistry have the greatest influence upon the cladogram produced (Fig. 24). Flavonol 3 -O diglucosides and flavonol 7 methyl ethers are the only vacuolar flavonoid compounds that influence the cladogram. The presence of the flavonol 7 methyl ethers is not surprising as the flavanone 7 methyl ethers and the corresponding 4' methoxychalcone are present. This groups the fulvous (yellow) species together and excludes Cassinia leptophylla. One flavonoid compound, pinocembrin, is present in the exudate profile of Cassinia leptophylla. The absence of quercetin 3-O diglucosides, dihydrokaempferol and 2',4',6',4 tetrahydroxy dihydrochalcone separates the South Island species C. fulvida var. fulvida and C. fulvida var. montana from C. vauvilliersii. Cassinia vauvilliersii occurs on two different substrata. The flavanone eriodictyol, present in the sample from sedimentary derived substrata, separates the Tongariro samples from the Mt Holdsworth sample.

The main chemical character separating C. amoena from the varieties of C. fulvida is the presence of quercetin 3-O methyl ether in the exudate profile of C. amoena. There are pronounced differences in phyllary morphology and colouration among the three taxa. The phyllaries are white in C. amoena and opaque yellow in C. fulvida and varieties. A flattening of the pappus is characteristic of C. amoena, while the pappus in the varieties of C. fulvida comprises a ring of short papillae. All three species occupy different altitudinal ranges (fig 12). Cassinia fulvida var. fulvida is common on the Canterbury Plains from 100m to 900m. Cassinia fulvida var. montana is common in upland and alpine conditions. Cassinia amoena is confined to the coastal serpentine cliffs of Kerr Point which are no more than 300m above sea level. Serpentine outcrops occur in several parts of New Zealand: in North West Nelson, in the Clarence and Awatere River valleys of Marlborough and on the Old Man Range. Several varieties of Cassinia vauvilliersii are described from these regions including varieties with white or grey tomentum and larger leaves than the typical specimens of Cassinia vauvilliersii. Samples of Cassinia "species" from two of these areas were collected. The first samples (NZ 787- NZ 790) were collected from the mouth of

the Hurunui River in eastern Marlborough. Plants of this population resemble C. leptophylla. A grey tomentum that has a slight yellow tinge is characteristic of plants in this population. The large spathulate leaves up to 1 cm in length. The midrib of the leaves is very prominent. The vacuolar flavonoid profile is simple consisting of the 3 -O glucosides of quercetin isorhamnetin and quercetagetin. The exudate flavonoid profile consists of pinocembrin, 2',4',3,4 tetrahydroxychalcone and 2',4',6',4 tetrahydroxychalcone. The first two are common to the profile of C. vauvilliersii from Mt. Holdsworth. The second sample population (NZ 1455-1458) was collected from the Awatere River valley between the Seaward and Inland Kaikoura Mountain Ranges. Plants of this population resemble C. fulvida var. fulvida. A greenish yellow tomentum is common on plants of this area. The large spathulate leaves may be up to 1 cm in length and achenes that are pubescent. These characters are found in populations of C. fulvida var. fulvida and C. vauvilliersii. The vacuolar profile is simple consisting of the 3-O glucosides of quercetin isorhamnetin and quercetagetin and eriodictyol. The finding of eriodictyol is interesting because the only other New Zealand species that accumulates this flavanone is C. vauvilliersii from Mt Holdsworth. The exudate profile of the Awatere sample shows a correlation with the Mt Holdsworth sample. It contains kaempferol and quercetin 3-O methyl ethers, pinocembrin and pinocembrin 7 methyl ether, 2',4',3,4 tetrahydroxychalcone and 2',4',6',4 tetrahydroxychalcone. The Awatere sample differs from the Mt. Holdsworth sample by the presence of pinocembrin 7 methyl ether.

The chemical data take on additional significance in view of their apparent genetic stability as shown by limited common garden study. The samples from Hurunui and Awatere represent subsets of the profiles of C. vauvilliersii from Mt Holdsworth. The flavonoid information points to the recognition of the two varieties; C. vauvilliersii var. albida Kirk (the Hurunui sample) and C. vauvilliersii var. pallida Allan (the Awatere sample).

Relationships within the New Zealand Ozothamnus species.

There is greater similarity between the Australian species of Cassinia and Ozothamnus than between the New Zealand and Australian species of Ozothamnus. The New Zealand species of Ozothamnus form a sister clade to the New Zealand Cassinia by a combination of morphological and chemical characters. This clade approximates the classification according to Allan (1961) and Druce (1987). Ozothamnus coralloides, O. intermedium and O. selago cluster together and form a sister clade to O. depressus and O. dimorphus. The major morphological characters that separate the Cassinia species from the Ozothamnus species are leaf angle and leaf shape. Leaves of the New Zealand Ozothamnus species are scale-like and appressed to the stem, giving the impression of plaited leather thongs. Plants exhibiting this habit are referred to as "whipcord", a habit common to many alpine taxa in New Zealand including Hebe (Scrophulariaceae), Coprosma (Rubiaceae) and Dracophyllum Labill. (Epacridaceae). Druce (1987) considers the whipcord habit a response to altitudinal conditions (Druce 1987). Included in this clade is one of the few small leaved alpine Australian species of Ozothamnus, O. hookeri. This species differs from the New Zealand species morphologically in that O. hookeri lacks a tomentum and also lacks the wrinkled, hairy and obtusely tipped phyllaries that are characteristic of the New Zealand species of Ozothamnus. Chemically Ozothamnus hookeri differs from the New Zealand species it clusters with by the absence of glycosylated flavonols and the presence of flavanones methylated at the 7 position.

Ozothamnus dimorphus and O. depressus upon first observation strongly resemble each other and are recognised by their straggling habit. Ozothamnus dimorphus is the only vine in the New Zealand Asteraceae and undergoes a distinct juvenile phase which may occur on any part of the plant. Suppression of this juvenile phase obscures the differences between O. dimorphus and O. depressus. Both taxa, present in the same region of central Canterbury, are covered with a grayish woolly tomentum that gives the plant the appearance of being desiccated. Morphologically O. dimorphus is distinguished from O. depressus by the shape of the leaf margins which are are

revolute in O. depressus and plane in O. dimorphus. Furthermore the phyllaries of O. depressus possess distinctly acute bracts which are clawed at their tip. Ozothamnus depressus, on the other hand, has flattened obtuse bracts that are never clawed. The major chemical factor that enables us to distinguish the pair is the accumulation of quercetin 3-O diglucoside by O. depressus, a feature lacking in O. dimorphus. Morphological and chemical characters separate O. depressus and O. dimorphus from the other New Zealand Ozothamnus species. The major chemical characters that separate the O. dimorphus clade from the O. selago clade are the loss of B-ring deoxy flavanones and flavonol 3-O rhamnosides. Ecologically the members of the two clades occur at different altitudes. Ozothamnus selago and its allied taxa are are common in the alpine fellfields on the major South Island mountain systems such as the Southern Alps and the Kaikoura range. Ozothamnus dimorphus and O. depressus are found at the lower limits of the alpine fell field but are much more common on the braided river beds of the Torless Range. These areas are approximately 700-1000m above sea level.

Ozothamnus coralloides and O. intermedium have been considered to be regional varieties of O. selago (Allan 1961). Druce (1987) elevated these varieties to species level noting that with O. selago the three species formed a natural grouping. Druce based his separation of the species on leaf and floral morphology. The cladogram (Fig. 24) shows a strong correlation to the classification system proposed by Druce (1987). The presence of pinocembrin separates O. selago from O. coralloides. This flavanone contributes to the overall grey waxy sheen to the leaves of Ozothamnus selago. Druce noted that plants referred to as Ozothamnus selago var. intermedium had more of a sheen to the leaves than does O. selago. Three chemical characters separate O. coralloides from O. intermedium. Characteristically O. selago and O. intermedium possess the flavone apigenin in their vacuolar profiles along with large quantities of quercetin 3-O diglucosides. Surprisingly the rutinosides of kaempferol and quercetin are absent from these two species. Quercetin 3-O rutinoside and the kaempferol equivalent are major components of the vacuolar flavonoid profiles of the other New Zealand Ozothamnus species.

The major chemical characters that separate species of Ozothamnus from the New Zealand Cassinia are the absence of chalcones and flavanones from the exudate flavonoid profile species. There are more morphological characters separating the two clades. The New Zealand Ozothamnus species has leaves that are appressed to the stem. In New Zealand species of Cassinia the capitulum is held in a panicle while the whipcord Ozothamnus species are characterized by a solitary inflorescence. The tomentum of the New Zealand Cassinia is more prominent than in New Zealand species of Ozothamnus where the tomentum is more apparent on the stems rather than on the leaves. Phyllary morphology may also be used to distinguish the two clades. In the New Zealand Ozothamnus clade phyllaries are white tipped and held in four ranks, while the New Zealand Cassinia possess phyllaries that are three, four or five ranked depending on the species. These phyllaries are usually straw-yellow but may be red tipped giving the overall appearance of pink flowers.

The New Zealand species, including O. hookeri, (Fig. 24) are separated from the Australian species of Cassinia and Ozothamnus by two major characters. The first is the presence of pinocembrin (5,7-dihydroxyflavanone), a flavanone common to all members of the New Zealand clade (Fig. 25) except Ozothamnus dimorphus and O. depressus. The second is the pappus shape. Common to all species in the New Zealand this clade is a flattening of the pappus. In the New Zealand clade the pappus forms a flattened ring that encircles the apex of the achene. In Australian species there is a wide range of pappus shapes, ranging from barbellate to feathered and in some cases the pappus is absent.

THE FLAVONOIDS OF RAOULIA SPECIES

Breitwieser and Ward (1993) reported seventeen "flavonoid" spots in their chromatographic study of the genus but no structures were determined. A dichloromethane leaf-wash of seven taxa collected from this study failed to reveal any non-polar phenolic compounds. The vacuolar components of seven species (nine taxa) were identified as kaempferol, quercetin, isorhamnetin and myricetin 3-O glucosides, kaempferol and quercetin 3-O rutinosides and the

flavone luteolin. No interspecific variation was detected, and in all cases where several specimens of a taxon were available identical flavonoid profiles were observed.

The degree of indecision in the taxonomic history of Raoulia reflects the large amount of morphological variation within the genus and is evident if we examine the three subgenera that presently constitute the genus. Subgenus Raoulia sensu Allan is characterized by a low growing mat habit composed of loosely intertwining branches. Subtle differences in phyllary and leaf morphology distinguish the species of these two subgenera. Subgenus Mistura is monotypic, represented by Raoulia petriensis. Ward (1982, 1993a) regarded Raoulia petriensis as an intermediary species between the "non-sheep" species of subgenus Raoulia and the "sheep" species of subgenus Psychrophyton. Ward (1982) recognizes three groups within Raoulia. The first group is similar to the subgenus Raoulia sensu Allan and includes prostrate mat forming plants that often root at the nodes. The leaves are small, entire and imbricate. In this subgenus the capitulum is solitary, terminal and sessile. The second group contains Raoulia petriensis and several "non-sheep" species that belong to subgenus Psychrophyton. The third group is similar to subgenus Psychrophyton sensu Allan. These are the pulvinate species, the true vegetable sheep, which form taprooted cushions. The present study showed that the flavonoid profile of members of two subgenera (three sections) is invariable, which suggests an underlying relationship within the genus. Furthermore, the pigment profile appears to be insensitive to the nature of the substratum upon which the plants grow. This edaphic insensitivity lies in contrast to the difference in flavonoid profiles seen in Cassinia vauvilliersii collected from two different soil types (Reid and Bohm, 1994). Raoulia contains flavones in common with members of Cassinia and Ozothamnus (Reid and Bohm, 1995.). This points to a possible relationship between these genera.

FLAVONOIDS OF HAECKERIA F. MUELL

There are four species of Haeckaria F. Muell. all of which are restricted to Australia. These species share the same ecological features as species of Ozothamnus and Cassinia. One species of Haeckeria, H. ozothamnoides was investigated for its flavonoid components. This

shrub is known as China Scrub or Dolly Bush, names that are also applied to Cassinia uncata. Haeckeria species are typically small, much branched shrubs with sessile tomentose leaves with revolute margins. The small discoid capitulum forms a terminal, flat topped corymb. Each floret is yellow and enclosed by brown involucral bracts.

The exudate flavonoid component consists of pinocembrin (5,7 dihydroxyflavanone) and its 7 methyl ether (pinostrobin) accompanied by naringenin (5,7,4' trihydroxyflavanone), 2',4',6',4-tetrahydroxychalcone and the 3-O methyl ethers of quercetin and kaempferol. The vacuolar profile contains the 3-O glucosides and 3-O rutinosides of kaempferol and quercetin accompanied by the flavones apigenin and luteolin.

Upon analysis of the data matrix we find that Haeckeria ozothamnoides clusters with C. uncata and C. quinquefaria (Fig. 24). The major chemical difference separating the three species is the formation of 6-O methoxy flavonols by C. uncata. Phyllary colour in Haeckeria is predominantly brown and may be yellow tipped while the phyllaries in C. uncata and C. quinquefaria are often white tipped. This clade shares a number of distinctive characters. Haeckeria ozothamnoides, C. uncata and C. quinquefaria produce isorhamnetin 3-O glucoside. The bristly or cottony tomentum, present on both the adaxial and abaxial sides of the leaves, is yellow due to the high concentration of 2',4',6',4-tetrahydroxy chalcone on the plant. All three species have leaves with revolute margins.

THE FLAVONOIDS OF THE NEW ZEALAND EDELWEISS

The New Zealand Edelweiss consists of two alpine species belonging to the genus Leucogenes (Hook. f.) Beauverd. Leucogenes grandiceps (Hook. f.) Beauverd occurs on the South Island and L. leontipodium (Hook. f.) Beauverd is the North Island Edelweiss. Anderberg (1991, 1994) placed the New Zealand Edelweiss in Gnaphalieae subtribe Gnaphalinae as a basal taxon and sister group to the Northern Hemisphere 'true' Edelweiss Leontipodium R. Br. ex Cass. Included in this assemblage is the South African Galeomma (two species) which includes prostrate

herbs that bear a striking resemblance to Leucogenes, but differs in pappus morphology. Both species of New Zealand Edelweiss are alpine and found above 1600m.

Flavonoid profiles did not vary among collections for each species but the two species differed significantly. Kaempferol 3-O rhamnoside, 3-O glucoside, 7-O glucoside, quercetin 3-O glucoside, and 3-O diglucoside constituted the more polar fraction of L. leontipodium. Leucogenes grandiceps showed a similar array of glycosides except that it lacked kaempferol 3-O rhamnoside but did have quercetin 3-O rutinoside. Trace quantities of quercetagetin 3-O glucoside were seen in L. leontipodium. The aglycone fraction of L. leontipodium consisted of apigenin, luteolin, kaempferol, quercetin, galangin (3,5,7-trihydroxyflavone), kaempferol and quercetin 3-methyl ethers, and quercetin 7-methyl ether. The aglycone fraction of L. grandiceps was much simpler, consisting only of apigenin, kaempferol, and quercetin. Leucogenes does not appear to be the subject of any detailed flavonoid analysis. Breitwieser and Ward (1993) included both species in their survey but no structures were determined. The flavonoids of 'true' Edelweiss have been reported, Tira et al. (1970) identified luteolin 7-O and 4'-O glucosides from Leontipodium alpinum Cass. while Dashbalyn and Glyzin (1978) reported apigenin and luteolin 7 -O glucosides from L. ochroleucum Cass. Leucogenes and Leontipodium are easily distinguished on the basis of their flavonoid profiles.

However, a more interesting observation may involve the differences between the two New Zealand species. Leucogenes leontipodium, the North Island species, occurs in tussock grasslands, whereas on the South Island, L. grandiceps occurs scattered in an open landscape termed fell field (Dawson 1988; Wardle 1991) which presents a harsher environment characterized by lower average temperatures, frequent frost, violent winds, and more intense sunlight. Wollenweber (1985) has suggested that production of lipophilic flavonoids may be of adaptive significance for plants in arid or semiarid habitats. Production of lipophilic flavonoids by L. grandiceps, thus, may represent a mechanism selected to counter effects of higher incident radiation and, possibly, desiccating conditions, experienced by plants in these habitats. However

several species of New Zealand native plants have a high degree of reflectance, indicating that other adaptations may play a role in the reduction of UV-B absorption (Robberecht et al. 1980).

Similarities with other Phylogenetic treatments.

There have been three recent attempts to reconstruct the phylogeny of the Australasian Gnaphalieae. The first (Fig 2.) was a part of the circumscription of the Gnaphalieae as a new tribe within the Asteraceae (Anderberg 1991, 1994). In that treatment, the majority of Australasian genera belonging to the Gnaphalieae sensu Anderberg, were placed within the subtribes Cassiniinae and Angianthinae. Puttock (1994) reanalyzed Anderberg's data matrix and suggested that these two subtribes were better placed within the subtribe Gnaphaliinae as they represent taxa with characters that were common in the larger subtribe. In this analysis (Fig 3.) the arrangement of the genera within the phylogenetic tree was not changed. Puttock (1994) suggested that the separation of the Cassiniinae and Angianthinae was artificial.

The phylogenies published by Anderberg and by Puttock concern generic not species relationships. The only attempt to resolve species relationships was the phylogeny published by Breitwieser and Ward (1993). This study reported fifty-six "flavonoid" spots for forty-five species representing ten genera of the Australasian Gnaphalieae. No structures were determined by these workers. The species were scored for flavonoid, leaf and floral characters and were used to construct a phylogenetic tree (Fig 4.).

Breitwieser's phylogeny clusters the whipcord species of Ozothamnus together in the same clade. Ozothamnus dimorphus and O. depressus cluster together to form a sister clade to O. coralloides and O. intermedium (Ozothamnus selago was unavailable for Breitwieser's study). As a sister taxon to the clade containing O. intermedium and O. coralloides Breitwieser places the "Whipcord" species of Raoulia, R. petriensis. Breitwieser's phylogeny also clusters the Australian and New Zealand Cassinia species together. Cassinia aculeata and C. longifolia, the two Australian representatives of Cassinia used by Breitwieser, cluster together and form a sister clade to the New Zealand species of Cassinia, Cassinia leptophylla and C. fulvida. Breitwieser places

the Cassinia species in the same clade as the Australian alpine species of Ozothamnus, O. obcordatum and with O. backhousei Hook. f. Ozothamnus backhousei is found in the table lands of northwest Tasmania and has similar ecological requirements as many of the New Zealand Cassinia species. These table lands are subjected to high winds and low winter temperatures accompanied by rain and frosts (Curtis 1963). It is thought that this species most resembles the New Zealand Cassinia species (Breitwieser pers. comm)

The clade containing the Cassinia species is related to a much larger group that contains the giant vegetable sheep Haastia pulvinaris Hook. f. and Haastia sinclairii Hook. f. and the cudweeds sensu Drury (1972). This clade does not include the "whipcord" Ozothamnus species. Breitwieser proposes that the whipcord Ozothamnus species are closely related to species of Raoulia subgenus Raoulia sensu Allan and the alpine species of Ewartia Beauverd and Gnaphalium. The two species of Leucogenes are more related to each other than to any other species.

The phylogeny proposed by the present study (Fig. 24) approximates the classical taxonomy of the New Zealand species of Cassinia and Ozothamnus proposed by Allan (1961). This phylogeny places the New Zealand members of Cassinia into a group consisting of the yellow exudate species C. amoena, C. fulvida and C. vauvilliersii which has the grey green exudate species, C. leptophylla, as the sister taxon. The New Zealand Cassinia group forms a sister clade to one formed by the whipcord Ozothamnus species. Here the true whipcords, O. selago, O. intermedium and O. coralloides form a sister clade to O. depressus and O. dimorphus. This group is also present in the phylogeny of Breitwiesser and Ward (1993) and approximates the relationships recognised by Druce (1987). The findings of Breitwieser and Ward (1993) differ somewhat from the phylogeny proposed by the present study. Breitwieser and Ward propose that the New Zealand Ozothamnus and New Zealand Cassinia species are not closely related to the other members of the two genera. This difference may be due to the fact that Breitwieser and Ward (1993) investigated the herbaceous members of the Gnaphalieae present in New Zealand and investigated relatively few woody representatives. The Cassinia species and the whipcord

Ozothamnus species are the only woody representatives in the phylogeny sensu Breitwieser and Ward (1993). All the other representatives investigated by Breitwiesser and Ward (1993) are herbaceous or non shrub mat forming plants.

The phylogeny proposed by Breitwiesser and Ward (1993) also clusters the Australian representatives of Cassinia with the New Zealand members. My proposed phylogeny shows that there is a greater similarity between the Australian members of Ozothamnus and Cassinia than between Australian and New Zealand taxa. The Australian forest dwelling members of Ozothamnus and Cassinia form a related complex. These species share ecological, morphological and chemical characters that make them distinct from their New Zealand counter parts. This difference in phylogenies, i.e., the fact that this study clusters the Australian members of Ozothamnus and Cassinia together and Breitwieser does not, is due to the sampling of the species used for the respective analyses. The present study concentrates on woody forest representatives of Australian taxa and the related New Zealand ones while Breitwieser concentrates on sub alpine or alpine representatives.

Table 11. Comparison of Cassinia rugata with closely related species

Species	Leaf shape texture	Stem Vestiture	Involucral Bracts	Receptacular Bracts	Achene	Habitat
O. rosmarinifolius	linear, herbaceous apex strait	cottony	unranked, tips spreading ± wrinkled	absent	glabrous pappus bristles flattened at tip	swampy heaths
C. aculeata	linear, herbaceous apex strait	bristly	unranked, erect smooth	present	glabrous, pappus bristles not flattened at tips	various not swampy heaths
C. uncata	linear, firm, apex recurved	cottony & bristly	ranked	present	glabrous, pappus bristles not flattened at tips	dry coastal
C. rugata	oblong to narrow apex recurved	cottony & bristly	+ ranked spreading wrinkled	present	glabrous, pappus bristles not flattened at tips	swampy heaths

Ultra violet light and flavonoids.

Analysis of the data matrix (table 10) revealed a number of relationships between the flavonoid patterns and ecological tolerances (Fig 24). The first is most pronounced in samples of the New Zealand species of Cassinia. There was little difference between populations and individuals within populations. There were, however, geographical differences that corresponded to the genus sensu Allan (1961). The most complex exudate flavonoid profile observed was seen in C. vauvilliersii, five compounds in plants from Tongariro, six from Mt Holdsworth. Pigment differences between plants from these two sites are as great as differences between other pairs of taxa. Profiles of vacuolar flavonoids of plants from the different sites were also different, but the differences were less striking. It is interesting to note that the plants from the two sites grow on different substrata. Plants from Tongariro National Park were growing on weathered igneous substratum while those from Mt. Holdsworth were on sedimentary-derived soil. The suggestion that these flavonoid profiles might be fixed in each of these areas gains support from the observation that a specimen of C. vauvilliersii (NZ. 708) obtained from the Otari Native Botanical Garden gave exudate and vacuolar flavonoid profiles identical to those seen in plants collected from the native habitats. A sample of C. leptophylla (NZ 704) from the Otari Native Botanical Garden also exhibited flavonoid profiles identical to field collected plants.

Substratum influences on the flavonoid profile are less pronounced between Australian species of Cassinia and Ozothamnus. This may reflect in part the age of the Australian continent and the distribution of the species. Most Australian species of Cassinia and Ozothamnus are restricted to specific ecological conditions in coastal areas (Fig 17, Fig 21). Cassinia aculeata has the widest ecological tolerances of all Cassinia or Ozothamnus species in Australia. The flavonoid profiles did not vary among collections for this species, regardless of the soil conditions.

Substratum differences are also seen in the New Zealand Edelweiss. The two species, L. leontipodium and L. grandiceps, differ in the size and shape of the leaves and the way these leaves are held within the rosettes. The two species also grow on soils derived from different soil parent materials. Leucogenes leontipodium, disjunct within New Zealand, is most commonly found

on igneous derived soils This species is well known from the type locations in the Tararua ranges and Mount Hikurangi in the Coromandel and is common on other North Island Mountains, including the central volcanoes. All of these areas have a long history of volcanic activity. Leucogenes grandiceps, on the other hand, is restricted to the Southern Alps of New Zealand's South Island and is common in the Torless and Craigieburn Ranges. These areas are sedimentary in origin and resulted from seismic events during the Rangitata Orogeny (the tectonic events that formed the present day Southern Alps) (Walcott 1979). The flavonoid profiles were invariable among collections for each species. The interesting observation involves the differences between the flavonoid profiles of the two New Zealand species. Leucogenes leontipodium, the North Island species, occurs in tussock grasslands, whereas on the South Island, L. grandiceps occurs scattered in an open landscape termed fell field (Dawson 1988; Wardle 1991) which presents a harsher environment characterized by lower average temperatures, frequent frost, violent winds, and more intense sunlight. The size and shape of the tussocks provide a microclimate in which several alpine species survive the harsh conditions (Cockayne 1967). Wollenweber (1985) has suggested that production of lipophilic flavonoids may be of adaptive significance for plants in arid or semiarid habitats. Production of lipophilic flavonoids by L. grandiceps, thus, may represent a mechanism selected to counter effects of higher incident radiation and, possibly, desiccating conditions, experienced by plants in these habitats.

It is not known whether the existence of different flavonoid profiles in plants growing on different soils reflects a cause and effect relationship. The phenomenon is not unique to Cassinia. Menadue and Crowden (1983) described different flavonoid profiles in species of Richea R. Br. (Epacridaceae) growing in Tasmania. Aurones were detected in populations growing in soils derived from igneous or sedimentary rocks but were not seen in plants from metamorphic rock-derived soils. Horovitz (1976) described two examples from the Ranunculaceae. In the case of Pulsatilla alpina Miller, differences between subspecies were observed. Subspecies alpina is a widespread calcicole with purple and white perianth, while ssp. apiifolia is a localized calcifuge with yellow flowers. In the case of Anemone coronaria L. three different combinations of flower colours

were seen depending on soil type. Monomorphic scarlet colonies were observed on all soil types, but polymorphic populations, consisting of purple or violet flowered plants with some pink, white and scarlet individuals, occurred on unleached, mineral-rich terra rosea overlying dolomite, or on cool, heavy alluvial soils. A third group, consisting mainly of white or pale pink flowered plants with some scarlet individuals, was restricted to leached terra rosea or basaltic soils. A similar set of chemical differences was found in Thymus pulegioides (Martionfi et al. 1994). These substratum differences are not restricted to flavonoid composition. Differences in alkaloid composition were reported from Geijera balansae Lindl. growing on difference substrata in New Caledonia (Ahond et al. 1979; Skaltsounis 1985).

The second correlation found in the analysis of the data matrix(table 10) is between habitat, UV-B radiation and the production of exudate flavonoids. Plants have evolved many "strategies" for defense against environmental pressures. These pressures may be: attack by pathogens or herbivores or competition from other plants for nutrients and space. Some defenses are physical, for example thorns or spines, others may be chemical in nature. Phenolic compounds, alkaloids (Levin 1971, 1976) and other secondary plant products have been implicated in plant defense e.g., cyanogenic glycosides (Ganders 1990), glucosinolates (Louda and Rodman 1983), cuticular waxes (Espelie and Hermann 1988), polyacetylenes (Marchant and Towers 1987) and terpenoid derivatives (Lincoln and Langenhein 1979). Carlquist (1970) described the flora of the Hawaiian Islands as being "exceptionally poor in poisonous plants". This view was based on descriptions of the poisonous plants of Hawaii by Arnold (1968). Arnold pointed out that most of the poisonous species in Hawaii are not native to Hawaii. Carlquist's conclusion implies that a plant has to be toxic to be effective in fending off attackers. It also implies that the major role of these compounds is to act as a feeding deterrent. The majority of island species continue to accumulate a wide array of secondary metabolites. These include metabolites that are quite toxic, e.g., tutin in Coriaria L. (Tutu), the glucose nitropropyl esters in Corynocarpus laevigatus J. R. et G. Forst. (Karaka) and alkaloids in Solanum laciniatum Ait. (Poroporo).

Until the introduction of a wide range of non native animals, by humans, New Zealand was devoid of terrestrial mammals. Due to the isolation of the archipelago, and the paucity of mammals, many birds have assumed roles that would have been occupied by mammals. Therefore it is possible that some of these secondary metabolites perform several functions, only one of which involves action as a feeding deterrent. Certain flavonoids, for example, can serve as UV shields, others can function in the attraction of pollination vectors (Harborne 1988), some play a role in controlling pollen tube germination and growth, while others act as messengers between roots and nodulating bacteria (Maxwell et al. 1989). If flavonoids are no longer required for their deterrent properties, because former herbivores are no longer a threat, the capacity to make the compounds may still be maintained because of their other properties. If evolution, without former predators or pathogens, involves loss of deterrent chemicals then we would expect to see a reduction in the frequency of occurrence of these compounds.

Plants are thought to employ a variety of mechanisms to protect themselves from ultra violet B (UV-B; 280- 320 nm) radiation. These protective mechanisms include leaf thickness, UV-B absorptive pigments and UV-B reflective properties. Light absorbing flavonoids have been implicated in protecting plants from the damaging effect of UV-B radiation. (Li et al. 1993). This hypothesis seems plausible as the UV-B absorbing flavonoids accumulate in leaf epidermal cells where they may protect the inner cell layers from UV-B radiation (Caldwell et al. 1983, Beggs et al. 1986). Flavonoid biosynthesis has been shown to be influenced by UV light (Stafford 1991)

A steep increase in solar UV-B radiation from the high to low latitudes results from the natural latitudinal gradient of decreasing ozone thickness and the shorter solar path lengths towards the equator (Caldwell et al. 1980). Even in temperate regions, the moderate levels of ambient UV-B reduce seedling growth of some crop plants (Becwar et al. 1982, Tevini et al. 1989, 1991). At lower latitudes, terrestrial vegetation is thought to be more resistant to UV-B radiation (Caldwell et al. 1982; Barnes et al. 1987). High UV-B flux may have an appreciable influence on plants in tropical ecosystems. If current levels of UV-B affect terrestrial plants, even small reductions in stratospheric ozone may be of concern. A marginal decrease in ozone levels will

result in a greater incidence of UV-B radiation in tropical areas than in temperate regions (Caldwell 1991; Madronich 1993). Between 1979 and 1992 a marked reduction in ozone levels within 15^{o} of the equator, over the southern ice caps of Antarctica and over New Zealand has been detected by the Total Ozone Mapping Spectrometer (TOMS) (Madronich and de Gruijl 1993). Based mostly on work with temperate-latitude agricultural plants, effects of UV-B radiation include growth reductions (Teramura 1983), damage to photo system II (PSII) reaction centres (Bornman 1989) and augmentation of UV-B absorbing epidermal flavonoids (Caldwell et al. 1983; Flint et al. 1985). Flint et al. 1985 showed that the concentration of phenolic compounds increased 5-15 % when plants were exposed to UV-B radiation. It was found that, as the dose of UV-B radiation increased the production of flavonoids increased significantly. This increase was found in barley (Hordeum vulgare L.), radish (Raphanus sativa L.) and soya bean (Glycine max L.) seedlings by Teramura and Caldwell (1983). This confirmed the work of Wellman (1974) who studied the regulation of flavonoid and phytochrome biosynthesis under various UV light conditions. Using cell cultures of parsley (Petroselinum hortense Hoffm.) Wellman showed that as the daily level of UV light increased the production of flavonoid compounds increased. The increase in secondary phenolic compounds, due to UV-B radiation, has been reported from a number of agricultural crops. Ambler et al. (1975) and Bennett (1981) showed that with increased UV radiation cotton (Gossypium herbaceum L.) petioles showed a marked increase in production of anthocyanins. These anthocyanins were distributed in both leaf epidermal cells and petiole cells of seedlings. Bennett (1981) concluded that these anthocyanins and other flavonoids provided ideal UV-B protection as they were transparent to visible light thus letting the visible wavelength through the epidermis to be used in photosynthesis, while the major flavonoid classes have UV absorption peaks within the range of UV-B radiation (200-320 nm).

There is tremendous natural variation in the daily effective UV-B radiation reaching the Earth's surface. This variation reflects not only latitudinal effects but is also a factor of elevation. UV-B irradiance increases as much as 43% from sea level to 3043m in Hawaii (Caldwell et al. 1980). Ziska et al. (1992) explored the altitudinal effect of UV-B irradience on plants grown from

seed collected from populations along an altitudinal gradient in Haleakela Crater National Park. Comparisons were made between the highest elevation and lowest elevation populations of Plantago lanceolata L., Oenothera stricta Ledeb. ex Link, Tetramolopium rockii Sherff., T. humile (Gray) Hbd., Hypochoeris radicata L. and Chamaesyce celastroides Boiss. Grown at a common altitude and under various degrees of UV-B irradiation measurements of chlorophyll levels, total biomass and growth characters and the UV-B protecting compounds were made. When grown in a UV-B environment, levels of UV-B absorbing compounds increased in low elevation samples of Plantago lanceolata and Chamaesyce celastroides. In contrast, increases in UV-B irradience did not result in increased production of UV-B absorbing compounds in plants from higher elevations. With the exception of Hypochoeris, the level of UV-B absorbing compounds produced in high elevations were comparable to those of low elevation populations.

There is a marked altitudinal difference in the distribution of the Australasian Gnaphalieae. In New Zealand the Gnaphalieae may be found above treeline in subalpine and alpine conditions (e.g., C. vauvilliersii, O. selago and Leucogenes leontipodium) and also on exposed areas such as cliff tops and beach fronts (e.g., Cassinia amoena and Gnaphalium traversii Hook. f.). The only Australian species of interest in the present context that regularly reaches alpine conditions is O. obcordatus. Differences also occur in habitat preferences. Australian members of the Gnaphalieae are commonly forest understorey or forest margin plants. They do colonize open spaces but these spaces are usually adjacent to forests or are in partial shade. There are also populational differences. In New Zealand members of Cassinia and Ozothamnus are found individually, that is, within a given geographical area, there are numerous isolated plants. In contrast to this the Australian species may form a continuous secondary understorey. These differences seem to be reflected in the exudate flavonoid profiles of the species. New Zealand species of Cassinia produce the richest exudate profile of all species in this study. The profile is heavily laden with chalcones, flavanones and methylated flavonols. These compounds are found in some Australian species but not in the same quantities as the New Zealand Cassinia species. This appears to be related directly to the habitats of these species. The alpine habitat of the New

Zealand species, combined with populations being discontinuous, allows a greater amount of light (of all wavelengths) to effect the plant. Caldwell et al. (1980) and Ziska et al. (1992) showed that UV radiation increases with altitude. The exudate flavonoids could therefore act as a UV filter. The transmission of UV light, especially UV-B, is reduced by the presence of these exudate flavonoids. Chalcones, flavanones and methylated flavonols absorb UV light between 250 and 350 nm and therefore screen out the characteristic UV-B wavelengths of 280- 320 nm. In Australia the forest canopy, in Nothofagus forests where it is closed, and in Eucalyptus forests where it may be either open or closed, provides an effective light filter. Therefore the production of exudate flavonoids is less important. The majority of species studied have simple exudate profiles consisting of one or two methylated compounds. The production of exudate flavonoids by Australian species is most pronounced in those species that are more commonly found at the forest margin or in rocky exposed areas. The richest exudate profile was seen in Ozothamnus stirlingii and Haeckeria ozothamnoides, both of these are common pioneer species in open or disturbed habitats. All parts of these small trees are covered with a yellow exudate that rivals the exudate of C. vauvilliersii in stickiness. Ecologically O. stirlingii is found in highly disturbed sites that resemble the habitats occupied by C. fulvida var. montana or C. leptophylla, while Haeckeria ozothamnoides prefers sites that have intermediate disturbance. These sites are characterized by a low scrub cover. In both habitats the amount of UV-B radiation is higher than that experienced by forest understorey plants.

However, it was noted by Robberecht et al. (1980) that a high degree of reflectance occurs in several species of native plants high on Haleakela, notably Geranium tridens Hbd. and Argyroxiphium sandwichense DC., indicating other adaptations may play a role in the reduction of UV-B radiation absorption. This reflectance was also noted in several species of New Zealand native plants (Druce 1987; Robberecht et al. 1980). A plant can modify the absorbance of harmful quantities of UV and near infrared light by changing either the reflectance or the transmission of the leaves through structural modifications: by the production in the cuticle or epidermis of pigments (e.g., anthocyanins) that absorb specific wavelengths of light and screen them out before

they reach the mesophyll; or by changing the orientation of the leaves reducing the amount of radiation incident upon the leaves. Excess heat energy resulting from the absorption of near infrared radiation can be dissipated by increased convectional heat loss through production of small leaves or by evaporative cooling (increased transpiration rates). Large quantities of leaf exudates are produced by representatives of a broad spectrum of plant groups (e.g., palms, pines, grasses, peas and eucalypts) and is especially prevalent among succulent plants from several families (e.g., Aizoaceae, Asteraceae, Cactaceae, Crassulaceae.) Structurally, the exudates consist of rod and platelike particles of long chain hydrocarbons especially alkanes, alcohols and wax esters deposited in varying proportions on the cuticle surface (Martin and Juniper 1970). Several investigators (Billings and Morris 1951, Ehleringer et al. 1976, Gates et al. 1965, Pearman 1966, Sinclair and Thomas 1970, Thomas and Barber 1974) have examined leaf spectral properties in the visible and near-infrared and have discussed their ecological significance.

Mulroy (1979) investigated the effect of these deposits in Dudleya brittonii Rose. In this investigation, glaucous leaves reflected more light than non-glaucous leaves. The exudate was removed from the leaves. The spectrum of these treated leaves showed an exact match to the reflective spectrum of non-glaucus leaves. Mulroy concluded that the exudate is responsible for the difference between the two leaf types. This reflective difference accompanied a transmittance difference. The thicker glaucous leaves showed negligible transmittance. It is tempting to speculate that the sole adaptive significance of these exudates lies in their spectral properties. This is however unwarranted. The deposition of leaf exudates occur in a wide variety of plants growing in a wide variety of habitats. Besides the distinctive spectral properties these deposits has several other properties. Thomas and Barber (1974a, b) have shown that water repellence of the wax confers frost tolerance to subalpine E. urnigera F. Muell. It has also been speculated that this water repellence also reduces chances of infection by fungal pathogens (Davies 1961 Heather 1967a 1967b).

Exudates of non-flavonoid nature are present in many of the alpine members of the Gnaphalieae present in New Zealand. The most prominent of these are Ozothamnus selago and

O. coralloides. If the leaves of these species are rubbed, a waxy coating can be removed revealing the dark green scale leaves. Analysis of these exudates revealed pinocembrin as the only flavonoid component. A number of blue and non-fluorescent compounds were observed in the exudate flavonoid chromatograms but none of these componds were characterised. This pattern was also observed in the chromatograms of C. leptophylla and L. leontipodium. Ozothamnus depressus and O. dimorphus appear, at first glance, to be similar to O. selago. Upon further investigation, it was shown that these two species obtain their grey appearance by the possession of a dense off white tomentum, rather than the formation of an exudate. No waxy exudate was extracted from the leaves of O. depressus and O. dimorphus.

Therefore it can be surmised that the production of a large quantity of exudate flavonoids is an adaptation to the high levels of UV-B radiation present in open alpine habitats. Flavonoids such as chalcones, flavanones and methylated flavonols are well suited to this role as they are transparent and absorb UV radiation between 220 and 350nm (UV-B wavelengths = 280- 320nm) thus allowing the passage of useful wavelengths of light while blocking the deliterious UV wavelengths.

Ultra violet light and Morphology

If exudate flavanoids are a survival mechanism produced in response to increased UV-B radiation in alpine or open habitats, why are there a number of subalpine and alpine members of the Gnaphalieae in New Zealand that do not produce or have reduced numbers of exudate flavonoids? The members of the Australasian Gnaphalieae that do not produce exudate flavonoids are species of Raoulia subgenus Raoulia, Cassinia and Ozothamnus from Australia, the whipcord species of Ozothamnus in New Zealand, Lawrencella bellidioides and Leucogenes grandiceps. Several ways exist for meeting the problem of harmful quantities of UV and near-infrared light. The production of flavonoids may be one mechanism. Another possible adaptation includes changing either the reflectance or the transmission of the leaves through structural modifications. The chemical modifications (as documented above) include the production of pigments (e.g., anthocyanins) that absorb specific wavelengths of light and screen them out before they reach the mesophyll. There are also a number of morphological modifications that also retard the passage of specific wavelengths of light. Changing the orientation of the leaves reduces the amount of radiation incident upon the leaves. Excess heat energy arising from the absorption of near-infrared radiation can be dissipated through the increased convectional heat loss that comes with having small leaves or by evaporative cooling (Mulroy 1979).

There is a tendency among higher plants for leaf pubescence to increase along an environmental gradient of decreasing precipitation. Hauri (1916) and Metcalfe and Chalk (1983) amde observations from which they inferred that pubescence is an adaptive feature of plants occupying arid habitats. Pubescence can potentially reduce the heat load of leaves by increasing the reflectance from the leaf surface which, in turn, reduces the amount of radiation absorbed. Leaf pubescence also can provide a stable air chamber or microclimate in which temperatures and evapotation rates are lowered. Ehleringer, Björkman and Mooney (1976) showed that the presence of leaf pubescence in Encelia farinosa A. Gray, a desert species of the Compositae, reduced the absorbance of photosynthetically active radiation (400-700nm) by 56% compared to a closely related non pubescent species, E. californica A. Gray. There is an ecological correlation to

this observation. Encelia farinosa, a common plant in the dry desert areas of southwestern United States in which pubescence increases through its growing season therefore modifying the energy balance in the leaf as UV radiation increases during this period.

The extreme habitats of some New Zealand Gnaphalieae and their peculiar growth forms had, by the turn of the century, inspired botanists to undertake studies to try to correlate anatomical features with the habitats of the plants. Lazeniewski (1896) described the leaf anatomy of Haastia pulvinaris O. microphyllus and O. selago and noted a correlation between morphology and xeric habitats. The xerophytic characters of the leaves are obvious in the New Zealand alpine members of the Gnaphaliaeae Raoulia, Leucogenes, Ozothamnus and Lawrencella this is achieved by a number of morphological adaptations. All species of Raoulia have small leaves and where a number of habitats are occupied by the same species the smallest leaf size is found in the most xerophytic conditions. These small leaves assume a vertical position relative to the ground surface and are closely appressed to the branchlets. These branchlets are compacted together to form the characteristic cushion form of Raoulia subgenus Psychrophyton. In many alpine species of both hemispheres these branchlets and small leaves are covered in dense tomentum. This covering of hair is not restricted to members of the Asteraceae, being found in alpine members of the Rosaceae (Acaena L.), Epacridaceae (Dracophyllum Labill.) and Caryophyllaceae (Scleranthus biflorus (J. R. & G. Forst.) Hook. f.).

In Raoulia the surface of the leaves is covered by a thick cap of trichomes which are long uniseriate multicellular hairs of a type commonly occurring in the Asteraceae (Metcalfe and Chalk 1983). The type of trichome is the same in all species but there are differences in the general appearance and distribution of hairs on the leaf surface (Fig 27). In both subgenera of Raoulia the growing tip is surrounded by a dense mat of fine hairs. The genus can be divided into two groups: species with leaves covered by a thick layer of tightly interwoven trichomes forming a felt like cap (Raoulia subgenus Raoulia sensu Allan) and those that have leaves with a cover of more or less straight and somewhat stiff hairs that usually point towards the tip of the leaves (Raoulia subgenus Psychrophyton sensu Allan). Finally R. subulata has glabrous leaves, whereas R. glabra has only

a few widely spaced hairs on the leaf surfaces. Species of Raoulia subgenus Raoulia sensu Allan usually have the entire leaf surface covered with a thick cap of interwoven hairs which may be as thick or thicker than the leaf tissue proper. On the other hand, species with stiff hairs (Raoulia subgenus Psychrophyton sensu Allan) have them concentrated towards the apical end and usually more dense on the adaxial surface of this region. These differences can be correlated with the pattern of apical growth. In Raoulia subgenus Raoulia sensu Allan the stems are more elongate and leaves more reflexed. On the other hand Raoulia subgenus Psychrophyton sensu Allan are true cushion plants. Their cauline leaves are numerous, imbricate and closely appressed; as a consequence only the upper third of the leaf is exposed. This condition is also seen in the New Zealand representatives of Ozothamnus. . These low growing prostrate shrubs exhibit a "whipcord" habit. The thick, crowded branches are covered in awl shaped, coriaceous leaves. The minute leaves are leathery on the free part and keeled on the back ending in a bony white tip giving the appearance of knobs rather than leaves. In one species, Ozothamnus selago var. intermedium, there is a more pronounced keel to the scale-like leaves. In Ozothamnus depressus the minute grey leaves overlap each other and give the plant a withered appearance. Leucogenes leontipodium , the North Island Edelweiss, occurs in tussock grasslands, whereas on the South Island, L. grandiceps occurs scattered in an open landscape termed fellfield (Dawson 1988; Wardle 1991) which presents a harsher environment, than that experienced by L. leontipodium, characterized by lower average temperatures, frequent frost, violent winds, and more intense sunlight. In all of these genera only the upper third of the leaf is exposed to the environment. A dense covering of trichomes would therefore create a microclimate to reduce water loss through transpiration and also reduce the effect of UV radiation on the photosyntheic tissues. According to Pyykkö (1966) this covering of trichomes is a response to solar radiation and is accompanied by a compact mesophyll. This compacted mesophyll is not present in the New Zealand members of the Gnaphalieae. Breitwieser (1990) examined leaf anatomical characters and found that the mesophyll in Raoulia species was not organised in any special way although in some species there were additional rows of palisade mesophyll. The mesophyll of Leucogenes was

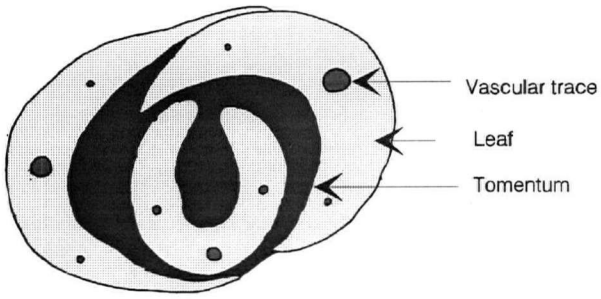
indistinguishable from parenchymatous tissues. Breitwieser concluded that the dense tomentum covering in members of the New Zealand Gnaphalieae negated any ecological advantage a compacted mesophyll might confer. This was also noted by Fowraker (1917) and by Hauri (1916) who also noted that the xeric conditions of high alpine areas produce additional morphological adaptations in response to light levels. These include schlerenchyma caps in Raoulia subgenus Psychrophyton and the water storage cells of Raoulia subgenus Raoulia.

The cushion form of Raoulia is apparently well fitted to the environment. Within this cushion a large amount of decaying leaves become enbedded, forming a peat. This phenomenon is not restricted to the Asteraceae being found in a number of families including the Epacridaceae, Rosaceae and Caryophyllaceae (Fowraker 1917). The peat like material, combined with the compactness of the cushion form a medium which has considerable water absorbing and holding capacity i.e., the body of the cushion acts as a sponge reservoir. The potential of such a mass of absorbent material renders the plant more or less independent of external nurtient and water sources. The large cushions of R. haastii are moist inside even when the shingle on which it grows is practically devoid of water for a considerable distance below the surface. The branches of this plant give off adventitious roots into the filling material and it is equivalent to a plant growing on humus. One feature of the leaves of all Raoulia species is their central mass of aqueous tissues. These water storage tissues are composed of large polygonal cells with few intracellular spaces (Fig 28). During heavy rainfall water is restored in this central tissue then released to photosynthetic tissues during times of drought. The most striking feature in the stem anatomy of Raoulia is the well developed endodermis. This structure has been associated with climatic and edaphic conditions commonly endured by steppe plants (Esau 1953; Haberlandt 1914). It is however more common to find a thickened endodermis in roots than in stems as an adaptation to the fluctuation water supply. In Raoulia the endodermis is thickened along the lateral walls forming a barrier similar to the casparian strip of angiosperm roots.

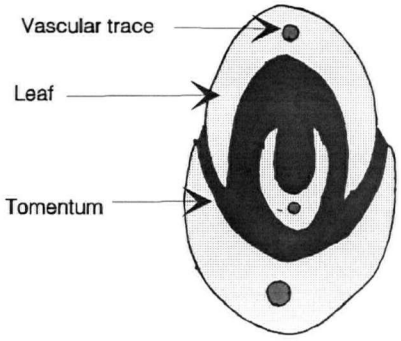
As pointed out by Metcalfe and Chalk (1983) it is unusual to find one species that possesses all known xeromorphic characters. The New Zealand representatives of the

Gnaphalieae are no exception. Their cuticle is between 5-10μ thick but the anticipated sunken stomata are positioned at the epidermal surface.

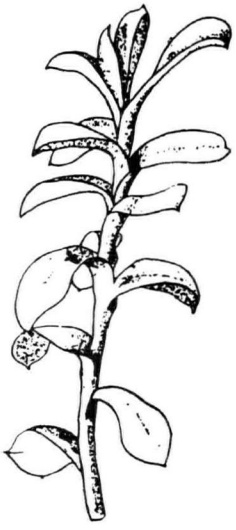
These anatomical adaptations are absent from the Australian representatives of Cassinia and Ozothamnus. The one species of Ozothamnus, O. obcordatum, that does reach alpine sites in Australia does not seem to possess any of the specialised xerophytic features prevalent in the New Zealand representatives. This reflects the distribution and habitat preferences of the Australian species. Australian members of the Gnaphalieae are commonly forest understorey or forest margin plants. In New Zealand, members of the Gnaphalieae are found as isolated individuals whereas, the Australian species may form a continuous secondary understorey. The lack of specialized xerophytic adaptations suggests a more favourable environment.



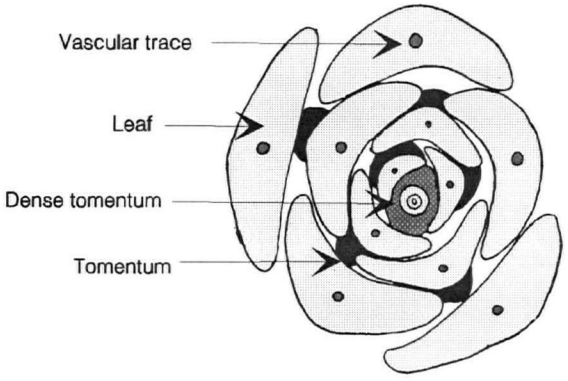
Raoulia australis



Raoulia monroi



Habit (R. glabra)



Raoulia glabra

Figure 27. Tomentum position in mat forming species of Raoulia.

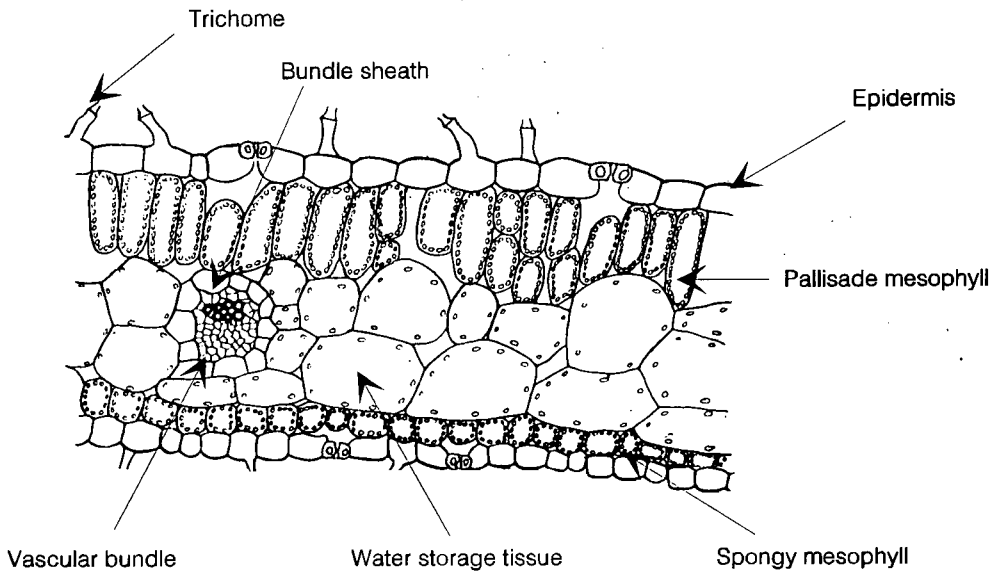


Figure 28. Transverse section of R. glabra leaf lamina.

Summary and conclusions.

Species in this study present a number of relationships that show a strong correlation to geography, altitude and ecological conditions. The production of exudate flavonoids show a direct correlation to the amount of UV-B radiation. These relationships correlate with the classical taxonomy proposed by Allan (1961) for the New Zealand species and by Burbidge (1958) for the Australian species.

Analysis of the combined flavonoid, ecological and morphological data, allows the formation of a cladogram that resembles the classical taxonomy sensu Allan (1961). The New Zealand Cassinia species appear to be a natural grouping formed from more than one species. This assemblage can be split into two groups, the species with yellow exudates and the species with green exudates. The first group consists of C. amoena, C. fulvida var. fulvida, C. fulvida var. montana and C. vauvilliersii. Memembers of this group is commonly found in alpine or exposed conditions. Varieties of Cassinia vauvilliersii described from the South Island include those with a white or grey tomentum and larger leaves than the typical specimens of Cassinia vauvilliersii. Samples of Cassinia "species" from two of these areas were collected. Plants (NZ 787- NZ 790) collected from the mouth of the Hurunui River in eastern Marlborough resemble C. leptophylla possessing a grey tomentum with a slight yellow tinge covering the large spathulate leaves. Plants (NZ 1455-1458) collected from the Awatere River Valley between the Seaward and Inland Kaikoura Mountain Ranges resemble C. fulvida var. fulvida and possess characters that are found in populations of C. fulvida var. fulvida and C. vauvilliersii. The exudate profiles in both samples show a correlation with C. vauvilliersii from Mt Holdsworth and each appear to contain subsets of that flavonoid profile. The flavonoid information supports the recognition of the two varieties; C. vauvilliersii var. albida Kirk for the Hurunui sample and C. vauvilliersii var. pallida Allan for the Awatere sample. The chemical data acquire additional weight in view of their apparent genetic stability as shown by limited common garden study.

The second group consists of one species, C. leptophylla. This common colonizer of open and disturbed habitats is the sister taxon to the yellow exudate species. These relationships follow

the classical taxonomy sensu Allan. Allan (1961) grouped the yellow exudate species together noting that there were several regional varieties. Webb on the other hand combined the New Zealand species into one. Cassinia leptophylla displays considerable local morphological differentiation but Webb (1988) reported that no set of characters could delimit more than one species. Characters used previously, e.g., size, shape, colour and number of receptacle scales, often vary continuously among populations and vary independently of each other. Webb (1988) attributed colour variation within the genus sensu Allan to an altitudinally controlled condition. Several transplant experiments have been attempted, in all cases exudate colouration does not change with altitude or geography. Individuals from sedimentary substrata showed a different exudate pattern to those of igneous substrata. A better understanding of the relationship between substratum composition and flavonoid profile could be achieved by the examination of samples of C. leptophylla from other serpentine areas of New Zealand.

This pattern of substratum differentiation was seen also in the two species of Leucogenes studied. The North Island species occurs on substrata of igneous origin while the South Island species occurs on sedimentary-derived soils. This is accompanied by habitat differences. Leucogenes leontipodium, the North Island species, occurs in tussock grasslands, whereas on the South Island L. grandiceps occurs scattered in an open landscape. Wollenweber (1985) has suggested that production of lipophilic flavonoids may be of adaptive significance for plants in arid or semiarid habitats. Production of lipophilic flavonoids by L. grandiceps, represent a mechanism selected to counter effects of higher incident radiation and, possibly, desiccating conditions, experienced by plants in these habitats.

In contrast to the pronounced differences in the flavonoids of New Zealand Cassinia the flavonoid profiles of Raoulia subgenus Raoulia were constant regardless of which taxon was investigated, the substratum origin or the geographical or altitudinal range of the taxon.

The whipcord New Zealand Ozothamnus species form a natural group that is related to O. hookeri, the Australian alpine species. This matches the taxonomy of Breitwieser and Ward (1993). Druce (1987) thought these species constituted a hybrid swarm formed from ecologically

restricted species. These species can be distinguished by the vacuolar flavonoid profiles. The New Zealand Ozothamnus species are alpine in distribution and share habitat preferences with O. hookeri and O. obcordatus. This may point to the way these species evolved.

The Australian Ozothamnus and Cassinia species show a number of similarities. Analysis of the data matrix clusters the forest species of Cassinia together. This group clusters with species of Ozothamnus that are found in various habitats. As the habitat becomes more open the amount of exudate flavonoids produced increases. The species that produce the greatest array of exudate flavonoids are the species in seasonally open habitats or those found on the forest margin. Orchard (1981), Walsh (1990) and Curtis (1963) all noted that the Australian species of Cassinia bore a stronger resemblance to Australian Ozothamnus species than to the New Zealand Cassinia species. Puttock (1994) and Orchard (1981) suggest that Cassinia is better accommodated in Ozothamnus than as an independent genus in its own right.

Cassinia rugata was thought to be an intergeneric hybrid between Ozothamnus rosmarinifolius and Cassinia aculeata. Cassinia rugata differs from the proposed parents in a number of characters (Table 11). It does not represent an intermediate stage between either parent. The proposed parents are not sympatric with C. rugata. Instead C. rugata is related to C. aculeata, a species that occupies similar habitats to C. rugata. Cassinia rugata is restricted to the Portland area of southwestern Victoria and is known from four populations and probably represents a relict population of a species that once had a wider distribution.

The cladogram (Fig 22) shows a correlation between the production of exudate flavonoids and UV-B radiation. There is a marked altitudinal difference in the distribution of the Australasian Gnaphalieae. In New Zealand the Gnaphalieae may be found above treeline in subalpine and alpine conditions (e.g., C. vauvilliersii, O. selago and L. leontipodium) and on exposed areas such as cliff tops and beach fronts (e.g., Cassinia amoena and Gnaphalium traversii Hook. f.). The only Australian species that regularly reaches alpine conditions is O. obcordatus. Differences also occur in habitat preferences. Australian members of the Gnaphalieae are commonly forest understorey or forest margin plants. They do colonize open spaces but these spaces are usually

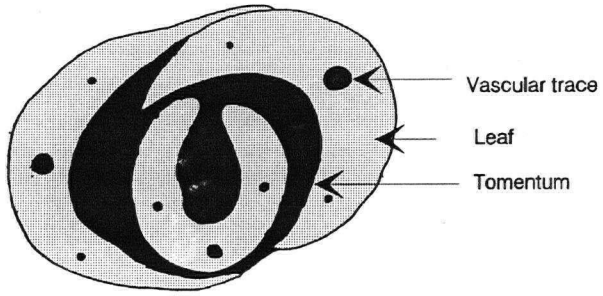
near forests or are in partial shade. The exudate profile of New Zealand Cassinia is heavily laden with chalcones, flavanones and methylated flavonols. These compounds are found in some Australian species but not in the same quantities as the New Zealand Cassinia species. This is related directly to the habitats of these species. The alpine habitat of the New Zealand species, combined with populations being discontinuous, allows a greater amount of light in all wavelengths to effect the plant. The production of exudate flavonoids therefore acts as a UV filter.

It was noted by Robberecht et. al. (1980) that a high degree of reflectance occurs in several species plants at high altitude, indicating other adaptations may play a role in the reduction of UV-B radiation absorption. This reflectance was also noted in several species of New Zealand native plants (Druce 1987). A plant can modify the absorption of harmful quantities of UV and near-infrared light by changing either the reflectance or the transmission of the leaves through structural modifications: by the production of citical or epidermalpigments (e.g., anthocyanins) that absorb specific wavelengths of light and screen them out before they reach the mesophyll; or by changing the orientation of the leaves, reducing the amount of radiation incident upon the leaves. Excess heat energy resulting in the absorption of near-infrared radiation can be dissipated by increased convectional heat loss by producing small leaves or by evaporative cooling (increased transpiration rates).

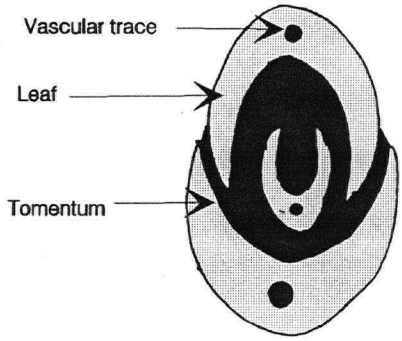
There are a number of subalpine and alpine members of the Gnaphalieae in New Zealand that do not produce or have reduced numbers of exudate flavonoids. The members of the Australasian Gnaphalieae that do not produce exudate flavonoids are species of Raoulia subgenus Raoulia, Cassinia and Ozothamnus from Australia, the whipcord species of Ozothamnus in New Zealand, Lawrencella bellidioides and Leucogenes grandiceps. A plant can lessen the levels of UV and near-infrared light acting on the leaves through chemical or structural modifications. There are also a number of morphological modifications that also retard the passage of specific wavelengths of light. Changing the orientation of the leaves reduces the amount of radiation incident upon the leaves. Excess heat energy resulting in the absorption of near-infrared radiation can be dissipated by increased convectional heat loss by producing small

leaves or by evaporative cooling (Mulroy 1979). Pubescence can potentially reduce the heat load of leaves by increasing the reflectance from the leaf surface. Leaf pubescence also can provide a stable air chamber or microclimate in which temperatures and evaporation rates are lowered. It is unusual to find one species that possesses all the xeromorphic characters possible (Metcalfe and Chalk 1983). For example a dense covering of hair correlated normally with raised rather than sunken stomata and with a thin cuticle rather than a thick cuticle. Leaf pubescence is not restricted to members of the Asteraceae, being found also in alpine members of the Rosaceae, Epacridaceae and Caryophyllaceae. In all of these genera only the upper third of the leaf is exposed to the environment. A covering of trichomes is a response to solar radiation and is accompanied by a compact mesophyll. It was also noted that the xeric conditions of high alpine areas produce additional morphological adaptations in response to light levels. These include schlerenchyma caps in Raoulia subgenus Psychrophyton and the water storage cells of Raoulia subgenus Raoulia (Fowraker 1917).

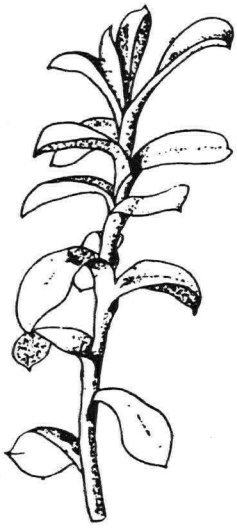
These anatomical adaptations are absent from the Australian representatives of Cassinia and Ozothamnus. The one species of Ozothamnus that does reach alpine conditions in Australia, O. obcordatum, does not seem to possess any of the specialized xerophytic features found in the New Zealand representatives. This reflects the distribution and habitat preferences of the Australian species. Australian members of the Gnaphalieae are commonly forest understorey or forest margin plants. In New Zealand representatives of the Gnaphalieae are found as isolated individuals. In contrast to this the Australian species may form a continuous secondary understorey. The lack of specialized xerophytic adaptations points to more favourable environment.



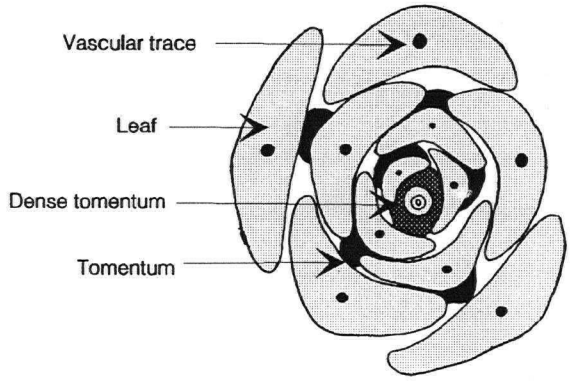
Raoulia australis



Raoulia monroi



Habit (R. glabra)



Raoulia glabra

Figure 27. Tomentum position in mat forming species of Raoulia.

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Appendix 1: Collection sites

NEW ZEALAND

Plant samples were collected from sites listed below. Where map references given they are based either upon the New Zealand Series 262 Topographical Maps (scale 1:250 000) or Series 273 map of Tongariro National Park (T19 Scale 1:80 000). Collection numbers are given after each species in parenthesis. MEL refers to aquisition numbers for the National Herbarium of Victoria South Yarra Victoria Australia

North Island

NCP NORTH CAPE
Location: Surville cliffs in Scenic reserve
Topography: Sea cliff and ridge
Substrate: Ultramafic alluvial derived soils.
Associated Vegetation: Pisonia toru, Euphrasia pseudocuneata, Leptospermum scoparium, Dracophyllum spp
Altitude: 100m ABS
Map Reference: 514:756 NZMS 262/1
Slope: 0-20^{o}
Species collected: Cassinia amoena (CAM, NZ703)

AKA AKATARAWA
Location: Akatarawa Hill Road opposite Burnard Gardens 3.7km from State Highway 1.
Topography: River terrace with thin stony soils.
Substrate: Loess.
Associated Vegetation: Senecio lagopus, introduced grasses, Beilschmedia tawa
Altitude: 200m ABS West facing
Map Reference: 687:028 NZMS 262/8
Slope: 5^{o}
Species collected: Cassinia leptophylla (NZ714, NZ717-NZ720, NZ722, NZ723)
* The description of this site is a for a number of populations. All populations are within 15 mins walking distance from the Map Reference

MAK MAKARA HILL
Location: On Makara Hill Road in reverting pasture 7 km from Karori Township, 2.6km from Makara township
Topography: Ridge top
Substrate: Loess thin stony soils on Yellow Brown Earths.
Associated Vegetation: introduced grasses, Ulex europeus
Altitude: 400m ABS
Map Reference: 651:991 NZMS 262/8
Slope: 10-25^{o}
Species collected: Cassinia leptophylla, (NZ724, NZ725) Raoulia hookeri var. hookeri (NZ 800-811)

KAR KARORI
Location: On Old Karori Hill Road in fallow pasture 3.7km from Karori Township,
Topography: Ridge top
Substrate: Loess thin stony soils on Yellow Brown Earths.
Associated Vegetation: introduced grasses, Ulex europeus
Altitude: 400m ABS
Map Reference: 655:990 NZMS 262/8
Slope: 10-25^{o}
Species collected: Cassinia leptophylla (NZ 709) , Raoulia hookeri var. hookeri (NZ 818), Raoulia australis (NZ 812-815)

MAB MAKARA BEACH
Location: Sea front cliffs at Makara 15km from Wellington GPO
Topography: Eroding cliff.
Substrate: Loess on Yellow Brown Earths
Associated Vegetation: Chionochloa, introduced grasses, Hebe, Dracophyllum
Altitude: 20m ABS North facing
Map Reference: 651:991 NZMS 262/8
Slope: 60^{o}
Species collected: Cassinia leptophylla (NZ 710), Raoulia hookeri var. hookeri (NZ 816, NZ 817), Raoulia australis (NZ 822, NZ 823)

OWH OWHIRO BAY
Location: Sea front cliffs at south of Wellington harbour
Topography: Eroding cliff.
Substrate: Loess on Yellow Brown Earths
Associated Vegetation: Chionochloa, introduced grasses, Hebe, Dracophyllum
Altitude: 20m ABS North facing
Map Reference: 658:984 NZMS 262/8
Slope: 60^{o}
Species collected: Cassinia leptophylla (NZ706, NZ707), Raoulia hookeri var. hookeri

SHA SHANNON
Location: On Old Karori Hill Road in fallow pasture 3.7km from Karori Township,
Topography: Alluvial flood plain of the Manawatu River
Substrate: Loess thin stony soils on Yellow Brown Earths.
Associated Vegetation: introduced grasses, Ulex europeus
Altitude: 200m ABS
Map Reference:
Slope: <10^{o}
Species collected: Cassinia leptophylla (NZ1413-NZ1415)

WAN WANGANUI RIVER ROAD
Location: State highway 7a 12km from Wanganui @ Ranana,
Topography: River Valley
Substrate: Loess thin stony soils on Yellow Brown Earths.
Associated Vegetation: introduced grasses, Ulex europeus , Beilschmedia tawa
Altitude: 400m ABS
Map Reference:
Slope: 25^{o}
Species collected: Cassinia leptophylla (NZ1417-NZ1420), Raoulia hookeri var. albo sericea (NZ 824-826)

FEA FEATHERSTON
Location: On Rimutaka Hill Road in fallow pasture 1.3km East of Featherston Township,
Topography: River Valley
Substrate: Loess thin stony soils on Yellow Brown Earths.
Associated Vegetation: introduced grasses, Ulex europeus , Beilschmedia tawa
Altitude: 400m ABS
Map Reference: 704:008 NZMS 262/8
Slope: 25^{o}
Species collected: Cassinia leptophylla (NZ1421-NZ1425), Raoulia australis (NZ 829-832)

PAH PAHIATUA,
Location: At gates of Pahiatua Golf club
Topography: River Valley
Substrate: Loess thin stony soils on Yellow Brown Earths.
Associated Vegetation: introduced grasses, Ulex europeus , Beilschmedia tawa
Altitude: 400m ABS
Map Reference: 750:079 NZMS 262/8
Slope: 25^{o}
Species collected: Cassinia leptophylla (NZ1426-NZ1430) Raoulia australis (NZ829-832)

HOL MT HOLDSWORTH
Location: Tararua Mountains near Holdsworth hut
Topography: mountain ridge above treeline
Substrate: Loess on Yellow Brown Earths, greywacke base
Associated Vegetation: Chionochloa rubra, Nothofagus solandrii (krumholtz), Hebe spp, Dracophyllum spp, Aciphylla spp, Pseudopanax simplex var. sinclairii
Altitude: 1450m ABS
Map Reference: 714:036 NZMS 262/8
Slope: 30^{o}
Species collected: Cassinia vauvilliersii (NZ 705, NZ1426-NZ1430), Raoulia australis, (NZ 839-842) Helichrysum bellidioides, Leucogenes leontipodium

TOE MANGATOETOEITI
Location: Tongariro National Park. Desert Rd side at sign post 690/9.60 ERP.
Topography: Volcanic Plateau 100m on army side of road
Substrate: Volcanic derived soils with poor drainage
Associated Vegetation: Aciphylla, Erica lusitanucum, Rhacomitrium, Chionochloa rubra, Dracophyllum.
Altitude: 900m ABS
Map Reference:T19 0458:146
Slope: 0^{o}
Species collected: Cassinia vauvilliersii (NZ735-NZ739), Raoulia hookeri var. albo sericea, (NZ 833-836) Raoulia tenuicaulis (NZ 837, NZ 838)

PIR TE PIRIPIRI STREAM
Location: Tongariro National Park. Desert Rd side at sign post 690/13.97 ERP
Topography: Volcanic Plateau 200m on army side of road in dry stream bed
Substrate: Volcanic derived soils. Sand predominates
Associated Vegetation: Aciphylla, Erica lusitanucum, Rhacomitrium, Chionochloa rubra, Dracophyllum Euphrasia, Olearia, Senecio
Altitude: 1050m ABS
Map Reference:T19 0465:139
Slope: 15^{o}
Species collected: Cassinia vauvilliersii (NZ742-NZ746), Raoulia hookeri var. albo sericea, (NZ 846- 849) Raoulia tenuicaulis (NZ 843-845)

TUK TUKINO ROAD
Location: Tongariro National Park. Desert Rd side at sign post for Tukino Ski fields.
Topography: Volcanic Plateau 100m on army side of road
Substrate: Volcanic derived soils. poor drainage mostly sand
Associated Vegetation: Rhacomitrium, Chionochloa rubra, Monao Dracophyllum. Major shrubs in grassy Knolls
Altitude: 900m ABS
Map Reference:T19 0458:087
Slope: 0^{o}
Species collected: Cassinia vauvilliersii (NZ748-NZ752), Raoulia hookeri var. albo sericea, (NZ 852) Raoulia tenuicaulis (NZ 850, 851, 853-855)

RAN RANGIPO DESERT
Location: Tongariro National Park. Desert Rd side at sign post marking summit
Topography: Volcanic Plateau 100m on army side of road
Substrate: Volcanic derived soils. poor drainage
Associated Vegetation: Gaultheria, Erica, Rytidiosperma, Rhacomitrium, Chionochloa rubra, Monao Dracophyllum.
Altitude: 1074m ABS
Map Reference:T19 0477:095
Slope: 10°
Species collected: Cassinia vauvilliersii (NZ753 - NZ760), Raoulia hookeri var. albo sericea, (NZ 860-864) Raoulia australis (NZ 856-859)

WAI WAIHOHONU
Location: Tongariro National Park. Waihohonu Track 3/4 hr from Desert Road. Recent regeneration due to Fire in 1984
Topography: Volcanic Plateau
Substrate: Volcanic derived soils. poor drainage
Associated Vegetation: Erica lusitanucum, Olearia,Chionochloa rubra, Euphrasia Monao Dracophyllum.
Altitude: 1050m ABS
Map Reference:T19 0433:0174
Slope: 0°
Species collected: Cassinia vauvilliersii (NZ761-765), Raoulia hookeri var. albo sericea (NZ 865-870)

TAW TAWHAI TRACK
Location: Tongariro National Park. On Bruce Road 3km from Chateau
Topography: Lahaar Slope
Substrate: Volcanic derived soils.
Associated Vegetation: Mixed Mt Beech, Tanekaha, Manuka.
Altitude: 1050m ABS
Map Reference:T19 274:227
Slope: 0°
Species collected: Cassinia vauvilliersii (NZ 1431); Raoulia hookeri var. albo sericea (NZ 871)

WHA WHAKAPAPANUI
Location: Tongariro National Park. 400m from Park Headquarters
Topography: River bed
Substrate: Alluvial derived soils.
Associated Vegetation: Erica lusitanucum, Olearia, Nothofagus, Euphrasia Monao Dracophyllum.
Altitude: 1050m ABS
Map Reference:T19 293:194
Slope: 0o
Species collected: Cassinia vauvilliersii (NZ 1432-1435), Raoulia hookeri var. albo sericea (NZ 872, NZ 873) Raoulia australis (NZ 877-880); Raoulia tenulicaulis (NZ 881-883); Raoulia hookeri var. albo sericea (NZ 874-876); Helichrysum bellidioides

PUKE PUKEONAKE
Location: Andesite/basalt cone Tongariro National Park.
Topography: composite cinder cone
Substrate: volcanic derived soils
Associated Vegetation: Erica lusitanucum, Olearia, Nothofagus, Euphrasia Monao Dracophyllum.
Altitude: 1350m ABS
Map Reference:T19
Slope: 20^{o}
Species collected: Cassinia vauvilliersii (NZ 1436-1438), , Raoulia hookeri var. albo sericea (NZ 884, NZ 885); Raoulia australis,(NZ 887, NZ 889) Raoulia tenulicaulis, (NZ 888); Helichrysum bellidioides

POK POKAKA
Location: Railway Clearing on Main trunk rail line Tongariro National Park. north west of Bruce Road
Topography: River bed
Substrate: Alluvial derived soils.
Associated Vegetation: Erica lusitanucum, Olearia, Nothofagus, Euphrasia Monao Dracophyllum.
Altitude: 950m ABS
Map Reference:T19
Slope: 0^{o}
Species collected: Cassinia vauvilliersii (NZ 1439-1442), , Raoulia hookeri var. albo sericea (NZ 890-895); Raoulia australis (NZ 1600), Raoulia tenulicaulis (NZ 896-899), Raoulia hookeri var. albo sericea (NZ 1601, NZ1602), Helichrysum bellidioides

SIN SINCLAIR HEAD
Location: Sea front cliffs on Eastern side of Wellington Harbour
Topography: Eroding cliff.
Substrate: Loess on Yellow Brown Earths
Associated Vegetation: Chionochloa, introduced grasses, Hebe, Dracophyllum
Altitude: 20m ABS North facing
Map Reference: 41°19'47"S 174°45'15"
Slope: 60°
Species collected: Cassinia leptophylla (NZ 1443-1444), Raoulia hookeri var. hookeri (NZ 1604-1606), Raoulia australis (NZ 1607)

MATA WAINUIOMATA BEACH ROAD
Location: South facing beach front at Pencarrow head
Topography: Beach front.
Substrate: Loess on Yellow Brown Earths
Associated Vegetation: Chionochloa, introduced grasses, Hebe, Dracophyllum
Altitude: 20m ABS North facing
Map Reference: 651:991 NZMS 262/8
Slope: 60°
Species collected: Cassinia leptophylla (NZ 1445), Raoulia hookeri var. hookeri, (NZ 1608-1610) Raoulia australis (NZ 1611)

FERR LAKE FERRY ROAD
Location: South facing beach at the southern end of the Wairarapa Valley
Topography: Beach front.
Substrate: Loess on Yellow Brown Earths
Associated Vegetation: Chionochloa, introduced grasses, Hebe, Dracophyllum
Altitude: 20m ABS North facing
Map Reference:41°24'46"S 175°10'54"
Slope: 60°
Species collected: Cassinia leptophylla (NZ 1446), Raoulia hookeri var. hookeri (NZ 1612), Raoulia australis (NZ 1613)

SOUTH ISLAND
PP PORTER'S PASS
Location: Central Canterbury at Porter's stream 200m North of Lake Lyndon camp site on Highway 73
Topography: Mountain Pass through Southern alps from Canterbury to West Coast
Substrate: Aluvial soils dominated by Loess
Associated Vegetation: Hebe, Discaria toumatou, Aciphylla, Introduced grasses
Altitude: 939m ABS
Map Reference: 408:767 NZMS 262/13
Slope: 20°
Species collected: Cassinia fulvida var. fulvida (NZ 702, NZ770-774), Raoulia australis (NZ 1614-1616), Raoulia glabra (NZ 613), Raoulia tenuicaulis (NZ 1618)

FOG FOGGY PEAK
Location: Central Canterbury above Porter's stream 200m North of Lake Lyndon camp site on Highway 73
Topography: Mountain peak in Torless range
Substrate: Aluvial soils dominated by Loess
Associated Vegetation: Hebe, Discaria toumatou, Aciphylla, Introduced grasses
Altitude: 939m ABS
Map Reference: 402:769 NZMS 262/13
Slope: 20°
Species collected: Cassinia fulvida var. fulvida (NZ 781-NZ 786), Raoulia hookeri var. hookeri, (NZ 1617, 1619, 1620) Raoulia subsericea (NZ 1622), Raoulia australis (NZ1621), Raoulia tenuicaulis (NZ 1623-1625)

CAV CAVE STREAM
Location: Arthurs' Pass by road side clearing
Topography: Greywacke shingle Fan covered with Loess
Substrate: Greywacke derived soils. Loess soils
Associated Vegetation: Mt Beech, Hebe
Altitude: 830m ABS
Map Reference: 405:786 NZMS 262/13
Slope: 0°
Species collected: Cassinia fulvida var. montana (NZ775- NZ779), Raoulia australis (NZ 1626), Raoulia subsericea (NZ1627), Raoulia glabra, Helichrysum bellidioides (NZ913a- 920a, Helichrysum depressum (NZ901a-905a) Helichrysum intermedium (NZ905a-912a), Helichrysum selago (NZ 921a-925a)

DRY DRY STREAM
Location: Torless Range Central Canterbury,
Topography: Braided River bed on South facing **Slope**
Substrate: Greywacke derived soils. Loess dominated soil
Associated Vegetation: Discaria, Raoulia, Chionochloa rubra, Euphrasia, Monao Dracophyllum, Hebe, Pymelia
Altitude: 1400m ABS
Map Reference:402:773 NZMS 262/13
Slope: 20°
Species collected: Cassinia fulvida var. montana (NZ1401-NZ1410); Raoulia australis (NZ 1628-1630); Raoulia subsericea (NZ 1631); Raoulia glabra Helichrysum bellidioides (NZ 900-901 912-920), Helichrysum depressum (NZ 902-904,921-927) Helichrysum intermedium (NZ 905-911), Helichrysum selago (NZ 928-935)

CASS CASS RIVER
Location: Torless Range Central Canterbury,
Topography: Braided River bed on South facing Slope
Substrate: Greywacke derived soils. Loess dominated soil
Associated Vegetation: Discaria, Chionochloa rubra, Dracophyllum, Hebe, Pymelia
Altitude: 1400m ABS
Map Reference:402:773 NZMS 262/13
Slope: 0^{o}
Species collected: Cassinia fulvida var. montana (NZ1411-NZ1418), Raoulia glabra, Helichrysum depressum (NZ936-939) Helichrysum intermedium (NZ943-948), Helichrysum selago (NZ 940-942)

AP ARTHUR,S PASS
Location: Arthur's Pass by road side clearing by Park Headquarters
Topography: High alpine pass through the main divide
Substrate: Greywacke derived soils. Loess soils
Associated Vegetation: Mt Beech, Hebe
Altitude: 830m ABS
Map Reference: 405:786 nzms 262/13
Slope: 0^{o}
Species collected: Cassinia fulvida var. montana (NZ701), Raoulia hookeri var. hookeri (NZ 1632-1633) Raoulia subsericea (NZ 1635)

HUR HURUNUI
Location: 2.6km south of main Hurunui River mouth
Topography: River bank
Substrate: Aluvial soils
Associated Vegetation: Introduced Grasses
Altitude: 50m ABS
Map Reference:519:812 NZMS 262/11
Slope: 0^{o}
Species collected: c. f. Cassinia fulvida var. fulvida (NZ787- NZ 790), Raoulia australis (NZ 1634)

FYF MT FYFFE
Location: Kaikoura on Sandy Saddle/Kowhai Track. 2km from Hinau picnic ground above Kaikoura township
Topography: Very old River bank
Substrate: Aluvial soils
Associated Vegetation: Introduced Grasses, lavender, Pseudopanax, Manuka, Cyathodes
Altitude: 250m ABS
Map Reference: 561:878 NZMS 262/11 (173°38'E 42°18'S)
Slope: 0°
Species collected: Cassinia fulvida var. fulvida (NZ 791-NZ799, NZ1400-1405) Raoulia australis (NZ 1636); Raoulia hookerii var. apice-nigra (NZ 1637, NZ 1638)

BATH MT ST BATHANS RANGE
Location: central Otago
Topography: Very old River bank
Substrate: Aluvial soils
Associated Vegetation: Introduced Grasses, lavender, Pseudopanax, Manuka, Cyathodes
Altitude: 1450m ABS
Map Reference:44°46'S 169°47'E
Slope: 20°
Species collected: Cassinia fulvida var. montana, Raoulia australis, Raoulia petriensis (NZ600-NZ605) Leucogenes grandiceps (NZ 619-624)

OLD OLD MAN RANGE
Location: Lewis Pass on highway 7 2km west of Foleys bridge
Topography: Very old River bank
Substrate: Aluvial soils
Associated Vegetation: Introduced Grasses, lavender, Pseudopanax, Manuka, Cyathodes
Altitude: 250m ABS
Map Reference: 561:878 NZMS 262/11 (42°18'S 173°38'E)
Slope: 0°
Species collected: Cassinia fulvida var. montana (NZ 1450-1453); Raoulia australis, Raoulia glabra (NZ546-550) Leucogenes grandiceps (NZ613-618), Raoulia petriensis (NZ606-612)

AWA AWATERE RIVER
Location: River valley between Seaward and Inland Kaikoura Mountain Ranges
Topography: Braided river
Substrate: Aluvial soils
Associated Vegetation: Introduced Grasses, lavender, Pseudopanax, Manuka, Cyathodes
Altitude: 0-250m ABS
Map Reference:41°48'58"S 173°43'21"E
Slope: 0°
Species collected: Cassinia leptophylla (NZ 1454), Raoulia australis, Raoulia hookeri var. apice-nigra (NZ 1639) Cassinia fulvida var. fulvida,(NZ 1455-1458)

PICT PICTON
Location:
Topography: Pasture lying fallow 2knm south of borough limits
Substrate: Aluvial soils
Associated Vegetation: Introduced Grasses
Altitude: 0m ABS
Map Reference: 41°16'31"S 173°55'22"E
Slope: 0°
Species collected: Cassinia leptophylla (NZ 1459)

OTA OTARI NATIVE PLANT MUSEUM
Location: On Johnsonville Road in cultivated garden maintained by Wellington City Council.
Topography: Ridge top
Substrate: Loess thin stony soils on Yellow Brown Earths.
Associated Vegetation: Weeds growing in public carpark next to main gates
Altitude: 400m ABS
Map Reference: 656:992 NZMS 262/8
Slope: 10-25°
Species collected: Cassinia leptophylla (CLEP), Raoulia hookeri var. albo sericea (NZ 1640)
Collection number: Cassinia amoena NZ 1406 originally from Kerr Point, Cassinia leptophylla NZ 708 originally from Manawatu River; Cassinia vauvilliersii originally from Desert road; originally from Mt Holdsworth;

AUSTRALIA

1 RUSHWORTH ROAD
Location: Gully in Melbourne City next to land fill. Cleared land reverting to scrub
Topography: Ridge top and gully
Substrate: Loess thin stony soils with various human additions including vehicular remains
Associated Vegetation: Weeds growing in public carpark next to main gates
Altitude: 400m ABS
Map Reference: 37°40'06"S 145°10'56"
Slope: 10-25°
Species collected: Cassinia uncata (NGW 3420); Cassinia arcuata (NGW 3421,NGW 3422); Cassinia longifolia (NGW 3423); Ozothamnus ferruginea (NGW 3430); Ozothamnus obcordatum (NGW 3426); Hybrid C.uncata x O. obcordatum (NGW 3427)

2 GRANTS PICNIC GROUND

Location: Sherbrooke Forest, Dandenong Ranges 30km North East of Melbourne city centre
Topography: Ridge top and gully
Substrate: Loess thin stony soils overlain with alluvial derived debris
Associated Vegetation: Eucalyptus, Banksia, Melaleuca, Warratah
Altitude: 400m ABS
Map Reference: 37°54'24"S 144°31'39"E
Slope: 10-25°
Species collected: Cassinia aculeata (NGW 3424, NGW 3426); Cassinia trinerve (NGW 3425); Cassinia uncata (AR 3427-3430); Cassinia arcuata (AR 3437-3440); Cassinia longifolia (AR 3431-3434); Ozothamnus ferruginea (AR 2096, AR 2097); Ozothamnus rosmarinifolius (AR 2098-2104)

3 PORTLAND

Location: South west Victoria coastline
Topography: Forest on Ridge
Substrate: Uplifted sea bed calcicole thin stony soils
Associated Vegetation: Eucalyptus, Banksia, Melaleuca, Warratah
Altitude: 400m ABS
Map Reference: 37°50'15"S 141°08'54"E
Slope: 10-25°
Species collected: Cassinia rugata (NGW 3428 NGW 3429 NGW 2074 NGW 2075 NGW2076); Ozothamnus hookerii (JJE 2093); Ozothamnus rosmarinifolius (JJE 2094); Ozothamnus dendroideum (JJE 2095); Ozothamnus diosmifolius (BR 2385)

4 MAROOTA

Location: New South Wales Coast 10km south Maroota township
Topography: coastal forest dominated by Eucalyptus regnans
Substrate: Alluvial
Associated Vegetation: Eucalyptus, Banksia, Melaleuca, Warratah
Altitude:at sea level
Map Reference: 33°32"50"S 150°57'30"E
Slope: 10-25°
Species collected: Cassinia aculeata (RR 2386); Cassinia uncata (AR 3435-3436); Cassinia arcuata (AR 3441-3444); Ozothamnus ferruginea; Ozothamnus rosmarinifolius; Ozothamnus diosmifolius

5 MT FRANKLIN RD
Location: Brundabella Ra. ACT
Topography:Ridge top forest dominated by Eucalyptus regnans
Substrate: Alluvial
Associated Vegetation: Eucalyptus, Banksia
Altitude:1250m ABS
Map Reference: 35°23'S 148°41'E
Slope: 10-25°
Species collected: Cassinia aculeata (LGA 4121); Ozothamnus stirlingii (LGA 4122, LGA 4127-LGA 4135); Cassinia uncata (LGA 4123); Cassinia arcuata (LGA 4124); Ozothamnus rosmarinifolius (LGA 4125); Ozothamnus diosmifolius (LGA 4126).

6 WEE JASPERS
Location: South east Victoria Coast 50km from Portland
Topography: coastal forest dominated by Eucalyptus
Substrate: Alluvial
Associated Vegetation: Coastal Eucalyptus forest.
Altitude: at sea level
Map Reference: 37°44'52"S 140°46'52"
Slope: 10-25°
Species collected: Cassinia aculeata,(NGW 3316); Cassinia quinquefaria (NGW 3358); Cassinia uncata (NGW 3359); Ozothamnus ferruginea (NGW 3317); Ozothamnus rosmarinifolius (NGW 3318); O. diosmifolius (NGW 3319); Haeckeria ozothamnoides (NGW 3320)

7 DARLING DOWNS
Location: Queensland Coast 11.4km from New England Highway on Clifton Grafton Road
Topography: coastal forest dominated by Eucalyptus
Substrate: Alluvial
Associated Vegetation: Eucalyptus
Altitude:at sea level
Map Reference: 27°51'15"S 152°03'27"E
Slope: 15°
Species collected: Cassinia laevis (PGW 1262)

8 BUNGONIA HEIGHTS
Location: New South Wales south east of Sydney
Topography: coastal forest dominated by Eucalyptus
Substrate: Alluvial
Associated Vegetation: Eucalyptus, Banksia.
Altitude:at sea level
Map Reference: 34°54.97'S 149°53.01'E
Slope: 10-25°
Species collected: Cassinia aculeata (SJ 6144)

9 AUGUSTA
Location: Western Australia due south of Freemantle
Topography: Scrubland adjacent to Augusta Gun Club gates
Substrate: Alluvial soil on calcicole
Associated Vegetation: Malee scrub and introduced weeds
Altitude:200m ABS
Map Reference: 33°22'04"S 115°58'E
Slope: 10°
Species collected: Ozothamnus cordatum (RJC 8212, RJC 8213, RJC 8214)

10 GEELONG
Location: City park on outskirts of town 2 blocks south of the Wool Museum
Topography: city park
Substrate: Well maintained and fertilised soils, human manufactured habitat
Associated Vegetation: Eucalyptus, Banksia, Melaleuca, Warratah
Altitude: 400m ABS
Map Reference: 37°53'38"S 143°07'50"E
Slope: 10-25°
Species collected: Cassinia aculeata (AR 3440); Cassinia trinerve (AR 3441-3443); Cassinia longifolia (AR 3444)

11 BARWON RIVER VALLEY
Location: Above the river valley along the Geelong -Anglesey highway
Topography: Ridge top and gully
Substrate: Loess thin stony soils overlain with alluvial derived debris
Associated Vegetation: Eucalyptus, Banksia, Melaleuca, Warratah
Altitude: 400m ABS
Map Reference: 38°34'02S 143°47'29"E
Slope: 10-25°
Species collected: Cassinia aculeata (AR 3445-3447); Cassinia trinerve (AR 3450-3452); Cassinia uncata (AR 3448); Cassinia longifolia (AR 3449);

12 PALUMA
Location: Queensland; North Kennedy Paluma hideen valley road 84 km N.Townsville
Substrate: brown red earths
Associated Vegetation: Tropical rainforest
Altitude: 940m ABS
Map Reference: 19°01'S 146°09' E
Species collected: MEL2019336 Cassinia subtropica

13 MT BARNEY
Location: Queensland
Topography: Rock outcrops open forest
Substrate: Granitic
Altitude: 900m ABS
Map Reference: 28°17'S 152°41'E
Species collected: MEL713584 Cassinia subtropica c.2mtall

14 MORETON
Location: Queensland; Coomera falls McPherson Ranges, Moreton district
Associated Vegetation: wet sclerophyll
Altitude: 850m ABS
Map Reference: 28°13'S 153°11E
Species collected: MEL1582763 Cassinia subtropica c. 2m shrub

15 CAWLEY LOOKOUT
Location: Queensland State Forest # 652 at Cawley Lookout
Associated Vegetation: Eucalypt forest shrubby understorey
Altitude: 800m abs
Map Reference: 20°49'S 148°32'E
Species collected: MEL1598778 Cassinia subtropica shrub 1.5m

16 PINE MOUNTAIN
Location: Victoria, Pine Mt, 90km ENE of Wodonga
Map Reference: 37°02'37"S 146°48'05"E
Species collected: MEL92300 Haeckeria ozothamnoides

17 BOWENYA
Location: Victoria, Bowenya Fauna & Flora Reserve, Murray Valley study area sector 1 sub block 63A
Map Reference: 36°38'36"S 143°38'40"E
Species collected: MEL680822 Haeckeria ozothamnoides

18 KILLAWARRA
Location: Victoria, Murray River, North of Warby Ranges in Killawarra forest
Associated Vegetation: Eucalyptus sierxylon, Calytrix tetragona, Pultenaeae largi-florens
Map Reference: 36°13'S 146°10'E
Species collected: MEL604651 Haeckeria ozothamnoides; MEL226952 Haeckaria ozothamnoides c.2m

19 NETHERCOTE FALLS
Location: NSW, Nullica State Forest, Nethercote falls
Associated Vegetation: Open forest, Eucalyptus sieberi, Acacia obtusifolia, Casuarina littoralis Persoonia linearis
Map Reference:36°59' 45"s 149°48'45"E
Species collected: MEL675841 Ozothamnus ferrugineus shrub to 1.5m

20 MT WELLINGTON
Location: Tasmania Mt Wellington near Springs Hotel
Topography:
Substrate:
Map Reference: 42°54'S 147°14'E
Associated Vegetation: Eucalypt forest regenerating, Bedfordia salicina, Hakea spp Pomaderis apetala, Olearia phlogopappa
Species collected: MEL626535 Ozothamnus ferrugineus shrub c. 2m

21 DOVER ISLAND
Location: Tasmania, Dover Island, Bass Straight
Topography: windswept island ~ 5km^2
Substrate: granitic
Map Reference: 40°29'43"S 148°11'46"E
Species collected: MEL235449 Ozothamnus ferrugineus

22 CLARKE'S ISLAND
Location: Tasmania, Green Hill, Clarkes Island.
Map Reference: 40°00'17"S 148°11'46"E
Species collected: MEL529099 Ozothamnus ferrugineus (small leaf O. dendroideum)

23 MCLEANS BAY
Location: Tasmania, airstrip at McLeans Bay Clarkes Island.
Map Reference: 40°00'17"S 148°11'46"E
Species collected: MEL 529101 Ozothamnus ferrugineus (small leaf O. dendroideum)

24 WARRUMBUNGLE
Location: NSW, Coonabarbaran, Warrumbungle NP
Topography: in rock crevice
Map Reference: 30°38'32"S 150°01'54"E
Species collected: MEL1598551 MEL646158 Ozothamnus obcordatus 0.5m

25 MT LINDSAY
Location: NSW Mt Lindsay, northern table lands, Katipur National Park
Topography: NW Slope
Map Reference: 30°16'S 150°05'E
Species collected: MEL2014651 Ozothamnus obcordatus Compact shrub c.1m

26 EGAN PEAKS
Location: NSW Egan Peaks Nature Reserve
Topography: open woodland rocky terrain
Map Reference: 36° 59'40"S 149°40' 20"E
Associated Vegetation: Eucalyptus sieberi, Hakea macreana, Lepidosperma urophorum, Olearia indochroa, Beyeria lasiocarpa
Species collected: MEL673724 Ozothamnus obcordatus

27 HAYCOCK HILL
Location: NSW 0.4 km N of summit of Haycock hill
Topography: open woodland rocky terrain
Substrate:
Map Reference: 37°09'S 149°57'E
Associated Vegetation: Eucalyptus sieberi, Acacia obtusifolia, Casuarina littoralis, Persoonia linearis, Leucopogon lanceolatus, Banksia spinosa Indigofera australis
Species collected: MEL671568 Ozothamnus obcordatus

28 ROLLEYS FLAT
Location: ACT Rolleys Flat Upper Cotter Valley, Namadgi National Park
Topography: open woodland rocky terrain
Substrate: alluvial soils granitic spm
Altitude: 1120m abs
Map Reference: 33°42'30"S 148°50'30"E
Associated Vegetation: Eucalyptus stellulata, Olearis glandulosa, Carex gaudichaudiana, Poa labilardieri
Species collected: MEL1559634 Ozothamnus rosmarinifolius

29 WHITE ROCKS RIVER
Location: NSW southern table lands white rocks river
Topography: heath-sedge swamp in drainageline
Substrate: alluvial soils granitic spm
Altitude: 500m abs
Map Reference: 37°08'15"S 149°21'15"E
Associated Vegetation: Gahnia sieberiiana, Lepidospermum filliforme, L. neesii, L. tortuosum
Species collected: MEL689342 Ozothamnus rosmarinifolius rare c. 1.5m

30 TRIAL HARBOUR
Location:Tasmania, Trial Harbour, 5km WSW of Zeehan 4km E Mt Agnew
Topography: wide valley floor
Substrate: Thin soil over quartzite gravel
Altitude: 500m abs
Map Reference: 41°52'S 145°16'E
Associated Vegetation: Melaleuca and Leptospermum
Species collected: MEL235450 Ozothamnus rosmarinifolius

31 ARTHUR RIVER
Location:Tasmania, tamma road 22 km S of Arthur river
Topography: wide valley floor
Substrate: dark grey sands
Map Reference: 41°12'S 144°42'E
Associated Vegetation: low shrublands of Melaleuca and Leptospermum
Species collected: MEL1617273 Ozothamnus rosmarinifolius shrub c1.5m

32 CORRINA ROAD
Location:Tasmania, Corrinna Road 2km S of Waratah
Topography: wide valley floor
Substrate: dark loam
Map Reference: 41°27'S 145°32'E
Associated Vegetation: low shrublands of Melaleuca and Leptospermum
Species collected: MEL1606621 Ozothamnus rosmarinifolius shrub c 1.8m

33 MT GAMBIER
Location: South East South Australia state coastline 200km from Portland Victoria
Topography: Forest on Ridge
Substrate: Uplifted sea bed calcicole thin stony soils
Associated Vegetation: Eucalyptus, Banksia, Melaleuca, Warratah
Altitude: 400m ABS
Map Reference: 36°07'33"S 139°49'36"E
Slope: 10-25°
Species collected: Ozothamnus ferruginea (AR 3321); Ozothamnus rosmarinifolius (AR 3322); O. diosmifolius (AR 3323); Ozothamnus hookerii (NGW 3324).

Samples examined from herbarium specimens
The Herbarium, University of British Columbia Vancouver B.C. Canada

Species	Location	UBC Aquisition Number
C. theodorei	Gulgong NSW	70104
C. subtropica	Springbrook Qld	153078
C. laevis	Clarence SA	70690
C. longifolia	Lord Howe	74371, 70103
C. longifolia	Mt Buffalo NP Vict.	153077
C. longifolia	Como NSW	70102
C. quinquefaria	Jenolan Lakes NSW	70586
C. denticulata	Crosslands NSW	105457, 105456
C. denticulata	Galstin Gorge NSW	105455
C. aculeata	Mt. Victoria NSW	70101
C. aculeata	Deloraine Tas	153074
C. aculeata	Myall Lakes NSW	153073
C. aculeata	Muwillumbah NSW	153075
C. arcuata	Clarence SA	70685
C. fulvida	Beacon Hill Park, Victoria BC	v191529, 9864
C. fulvida	Vanduesen Gardens Vancouver	166404
vauvilliersiii var albida (?)	Vanduesen Gardens Vancouver	166403
vauvilliersii	Vanduesen Gardens Vancouver	195834

The Hugh D. Gordon Herbarium. University of Wellington, Wellington, New Zealand.

Species	Location	WELTU Aquisition number
C. amoena	Kerr Point	4917
O. depressus	Boulder Creek Marlborough	14549
	Molesworth, Canterbury	16027*
O. coralloides	Awatere Valley	16032*
Lawrencella bellidioides	Mt. Egmon, Statford side	8605
O. dimorphus	Broken River	5307

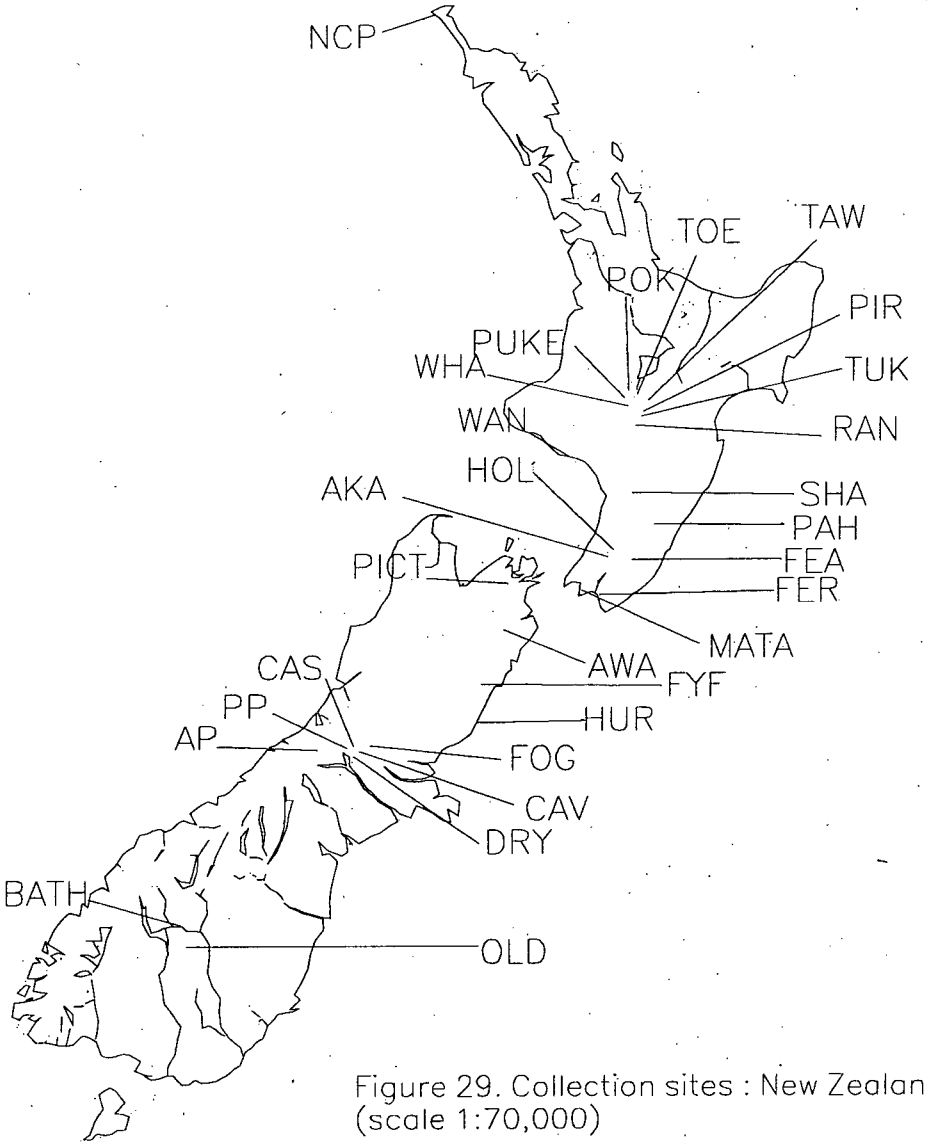

Figure 29. Collection sites : New Zealand
(scale 1:70,000)

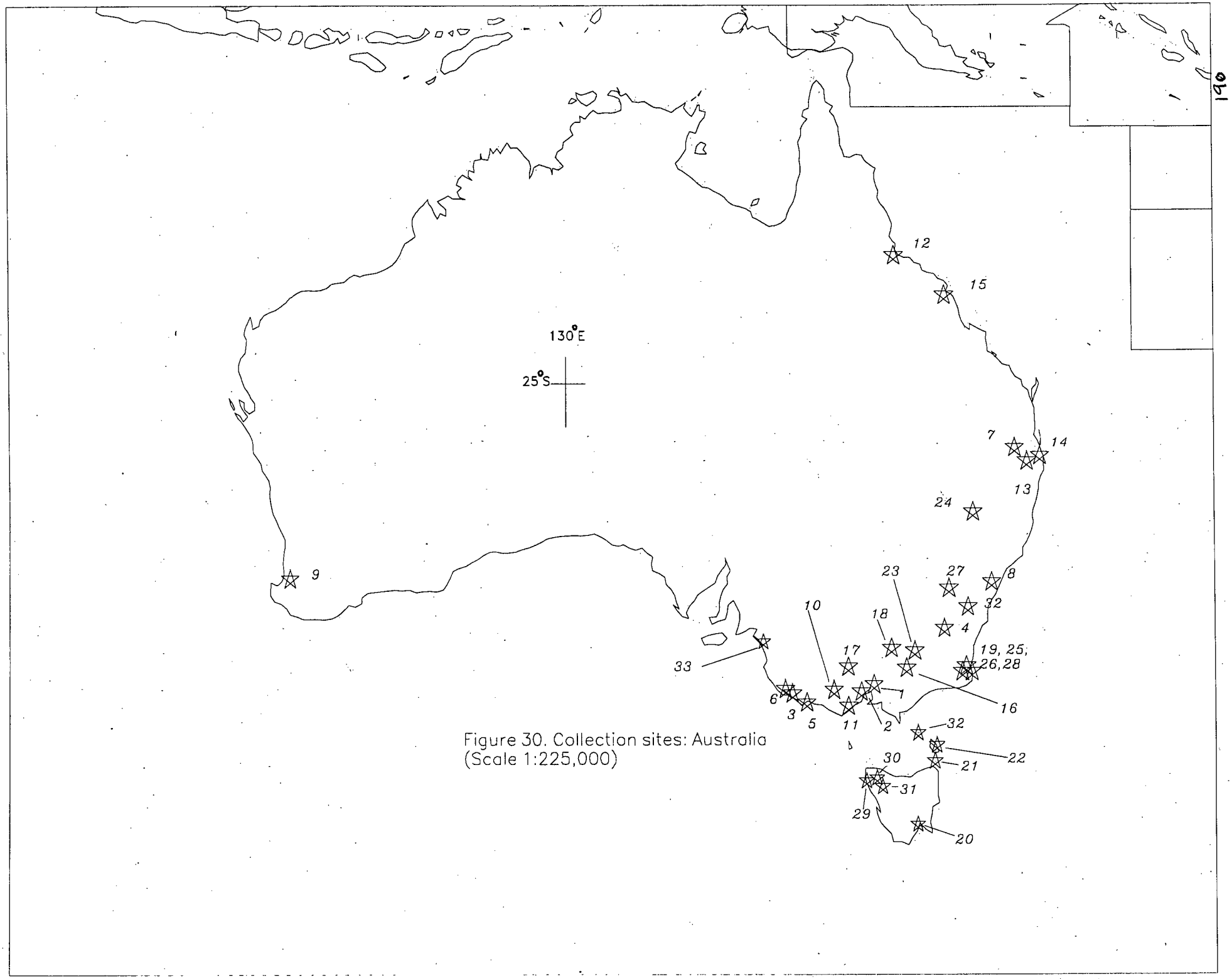

Figure 30. Collection sites: Australia
(Scale 1:225,000)

Appendix 2 Flavonoid spectral data: EXUDATE FLAVONOIDS

2'4' dihydroxy chalcone

Absorbs UV (366nm) and gives yellow brown colour with diphenylborate spray Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 291sh 330	chalcone indicated
Acetate: no shift	
Al^{+3}/HCl: noshift	
NaOMe: 50 nm shift, (330 -> 380) stable,	2' & 4'-OH indicated

2'hydroxy 4'methoxychalcone

Absorbs UV (366nm) and gives yellow brown colour with diphenylborate spray Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 252sh 317 342sh	chalcone indicated
Acetate: no shift 4'-OR indicated	
Al^{+3}/HCl : 52nm shift (342sh -> 408)	2'-OH indicated
Base: 42nm shift (342sh-> 408)	2' OH possible

2'4'6'4 tetrahydroxychalcone (chalconaringenin)

Yellow in UV (366nm), yellowish with NH3, yellow/orange colour with diphenylborate spray Naturstoff. Reag. A.). Orange with Vis light

UV wavelengths in CH_3OH: 289sh 346	chalcone indicated
Acetate: 54nm shift (346-> 400sh)	4-OH indicated
Al^{+3}/HCl : 52nm shift (346-> 398)	2'-OH indicated
Base: 39nm shift (346-> 395)	4'-OH indicated (+2' OH possible)

2'4'34 tetrahydroxychalcone (chalconaringenin)

Dark in UV (366nm), yellow with NH3, Yellow with diphenylborate spray Naturstoff. Reag. A)

UV wavelengths in CH_3OH: 290sh 330	chalcone indicated
Al^{+3} : 90nm shift (330-> 420)	B-ring ortho OH groups indicated
HCl: 50nm shift (330-> 380)	2' OH indicated
Acetate: 20nm shift (330-> 350)	4' + 4OH indicared
Borate: 20nm shift (330-> 350)	B-ring ortho OH groups indicated
Base: 39nm shift (330-> 369)	4'-OH indicated (+2' OH possible)

2'44' trihydroxy chalcone

Dark in UV (366nm), yellow with NH3, Yellow with diphenylborate spray Naturstoff. Reag. A)

UV wavelengths in CH_3OH: 258sh 298sh 367	chalcone indicated
Al^{+3}/HCl: 56nm shift (367 -> 423)	2' OH indicated

Acetate: shift to longer wavelength and shoulder ((443 and 476sh) 4OH and 4'OH indicated)

Base: 39nm shift with increased intensity (367-> 430) 4'-OH indicated (+2' OH possible)

57 dihydroxy flavanone (pinocembrin)

Yellow in UV (366nm), yellowish with NH3, green colour with diphenylborate spray Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 289, 330sh	flavonone indicated
Acetate: 40nm shift (289 -> 329)	5 & 7-OH indicated
Al^{+3}/HCl : 23nm shift (289 -> 379) acid stable	5-OH indicated
Base: no shift,	no 4'-OH indicated

4'57 trihydroxyflavanone (eriodictyol)

Dark in UV (366nm), dark with NH3, Red colour with diphenylborate spray Naturstoff. Reag. A) 2-3hrs after spray red with Vis light

UV wavelengths in CH_3OH: 289 326	flavanone indicated
Acetate: 42nm shift (289 -> 330sh)	7-OH with 5-OH indicated
BO3: Shifts acetate peaks back to MeOH wavelengths	
Al^{+3} : 28nm shift (289 -> 317) stable with HCl.	5-OH indicated
Base: 39nm shift (289 -> 326)	indicates 5,7 -OH flavanone

4'5 dihydroxy 7 methoxy flavanone (eriodictyol 7 methyl ether)

Dark in UV (366nm), dark with NH3, Red colour with diphenylborate spray Naturstoff. Reag. A) 2-3hrs after spray red with Vis light

UV wavelengths in CH_3OH: 289 326sh	flavanone indicated
Acetate: no shift	7-OR indicated
Al^{+3} : 28nm shift (289 -> 317) stable with HCl.	5-OH indicated
Base: 52nm shift (289 -> 323)	4'-OH indicated

573'4' tetrahydroxy flavanone (naringenin)

Yellow in UV (366nm), yellowish with NH3, yellow colour with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 289, 325sh	flavonone indicated
Acetate: 34nm shift (28 9-> 323)	7-OH indicated
Al^{+3} : 23nm shift (289 -> 312)	5-OH indicated
HCl: 15nm (289 -> 304)	B-ring ortho OH groups indicated
Base: 52nm shift (289 -> 323)	4'-OH indicated

kaempferol 3-methyl ether

Absorbs UV (366nm) and gives green colour with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 265, 350	flavonol indicated
Acetate: 7nm shift (265 -> 272)	7-OH indicated
Al^{+3}/HCl : 46 nm shift (350 -> 396) acid stable	5-OH indicated
NaOMe: 46 nm shift, stable	4'-OH indicated

MS M = 300 (C16H12O6) (flavone/flavonol; 3 OH 1 OMe)
M = 257 M - 43 indicates 3-OMe
M = 153 the A-ring fragment
M = 121 the B-ring fragment

These data are consistent with kaempferol 3-methyl ether.

quercetin 3 methyl ether

Absorbs UV (366nm) and gives yellow colour with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 258 267sh 348	flavonol indicated
Acetate: 10nm shift (258 -> 268)	7-OH indicated
Al^{+3}: 44 nm shift (348 -> 420)	5-OH indicated
HCl: 28nm shift (348 -> 376)	B-ring ortho OH groups indicated
NaOMe: 59 nm shift, stable,	4'-OH indicated

quercetin 7 methyl ether (rhamnetin)

Absorbs UV (366nm) and gives yellow colour with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 258 267sh 348	flavonol indicated
Acetate: no shift	no 7-OH indicated
Al^{+3}: 44 nm shift (348 -> 420)	5-OH indicated
HCl: 28nm shift (348 -> 376)	B-ring ortho OH groups indicated
NaOMe: 59 nm shift, stable,	4'-OH indicated

VACUOLAR FLAVONOIDS

kaempferol 3-O glucoside

Absorbs UV (366nm) and gives green colour with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 265, 350	flavonol indicated
Acetate: 7nm shift (265 -> 272)	7-OH indicated
Al^{+3}: 46 nm shift (350 -> 396) acid stable	5-OH indicated
NaOMe: 46 nm shift, stable,	4'-OH indicated

Acid hydrolysis (Ceska & Styles 1984, Kartnig and Wegschaider (1971)) produced glucose end product

kaempferol 3-rhamno-glucoside

Absorbs UV (366nm) and gives green colour with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 265, 350	flavonol indicated
Acetate: 7nm shift (265 -> 272)	7-OH indicated
Al^{+3}: 46 nm shift (350 -> 396) acid stable	5-OH indicated
NaOMe: 46 nm shift, stable,	4'-OH indicated

Acid hydrolysis (Ceska & Styles (1984), Kartnig and Wegschaider (1971) produced rhamnose and glucose end product

quercetin-3-O glucoside

Absorbs UV (366nm), yellowish with NH3, yellow colour with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 258, 269sh, 301sh, 363	flavonol indicated
Acetate: 16nm shift (258-> 274)	7-OH indicated
Al^{+3} : 47nm shift (363 -> 410)	5-OH indicated
HCl: 39nm relative to the MeOH	B-ring ortho OH groups indicated
Base: 47nm shift (363 -> 410)	4'-OH indicated

Acid hydrolysis (Ceska & Styles (1984), Kartnig and Wegschaider (1971)) produced glucose end product

quercetin-3-O rhamno-glucoside (rutin)

Absorbs UV (366nm), yellowish with NH3, yellow colour with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 261, 269sh, 301sh, 359	flavonol indicated
Acetate: 19 nm shift (261-> 270)	7-OH indicated
Al^{+3} : 51nm shift (359 -> 410)	5-OH indicated
HCl: 43nm relative to the MeOH	B-ring ortho OH groups indicated
Base: 51nm shift (363 -> 410)	4'-OH indicated

Acid hydrolysis (Ceska & Styles (1984), Kartnig and Wegschaider (1971) produced rhamnose and glucose end product

isorhamnetin-3-O glucoside

Absorbs UV (366nm), yellowish with NH3, yellow/green colour with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 251, 267sh, 299sh, 361	flavonol indicated
Acetate: 23nm shift (251-> 274)	7-OH indicated
Al^{+3} : 48nm shift (361-> 409) acid stable	5-OH indicated
Base: 52nm shift (363 -> 415)	4'-OH indicated

Acid hydrolysis (Ceska & Styles (1984), Kartnig and Wegschaider (1971)) produced glucose end product

5,7,4' trihydroxyflavone (apigenin)

Yellow in UV(366nm), yellow with NH3, green with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 267 296sh 336	(flavone indicated)
Al3+: 12 nm shift (336 -> 348)	5OH indicated acid stable
Acetate: 7nm shift (267 -> 274)	7 OH indicated
Borate: no shift	
Base:56nm shift (336 -> 392)	4'-OH indicated

573'4' tetrahydroxyflavone (luteolin)

Yellow in UV(366nm), yellow with NH3, yellow with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 242sh, 253, 267sh, 291sh, 349 (flavone indicated)

Al3+: 80nm shift (348 -> 428)	5 OH indicated
HCl: 41nm shift (348 -> 385)	B-ring Ortho OH indicated
Acetate: 16nm shift (253-269)	7 OH indicated
Borate: 21 nm shift (349 -> 370)	B-ring Ortho OH indicated
Base: 52nm shift (349 -> 401)	4'-OH indicated

357 trihydroxyflavone(galangin)

dull Yellow in UV(366nm), yellow with NH3, dull yellow with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 267 305sh 359	flavonol indicated
Al3+: 54nm shift (359 -> 413) acid stable	5 OH indicated no B-ring Ortho OH
Acetate: 6nm shift (267 -> 273)	7 OH indicated
Borate: no shift no	B-ring Ortho OH indicated

357 4' tetrahydroxyflavone (kaempferol)

Yellow in UV(366nm), yellow with NH3, green with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 253sh, 266, 294sh, 322sh, 367 flavonol indicated

Al3+: 57nm shift (367 -> 424) acid stable	5 OH indicated
Acetate: 8nm shift (266-274)	7 OH indicated
Borate: 5nm shift (367 -> 372)	B-ring Ortho OH indicated

Base: 49nm shift (367 -> 416) decomposes with time 4'-OH indicated

357 3'4' pentahydroxyflavone (quercetin)

Yellow in UV(366nm), yellow with NH3, yellow with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 255 269sh 301sh 370 flavonol indicated

Al3+: 88nm shift (370 -> 458)	5 OH indicated
HCl: 58nm shift (370 -> 428)	B-ring Ortho OH indicated
Acetate: 19nm shift (255 -> 274)	7 OH indicated decomposes with time
Borate: 18nm shift (370 -> 388)	B-ring Ortho OH indicated

Base: 46nm shift (370 -> 416) decomposes with time 4'-OH indicated

3574' tetrahydroxy dihydroflavonol (dihydrokaempferol)

yellow in UV (366nm) yellow with NH3, green colour with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 291 329sh

Al3+: 53nm shift (329 -> 382) acid stable	5 OH indicated
Acetate: 36nm shift (291 -> 327)	7 OH indicated decomposes with time
Borate: 7nm shift (329 -> 336)	B-ring Ortho OH indicated
Base: new band at 325nm	7 OH indicated

3573'4' pentahydroxy dihydroflavonol (dihydroquercetin, taxifolin)

yellow in UV (366nm) yellow with NH3, yellow colour with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 290 327sh

Al3+: 48nm shift (327 -> 375)	5 OH indicated
HCl: 29nm shift (327 -> 356)	B-ring Ortho OH indicated
Acetate: 36nm shift (290 -> 327)	7 OH indicated decomposes with time
Borate: 7nm shift (327 -> 336)	B-ring Ortho OH indicated
Base: new band at 325nm	7 OH indicated

3573'4' tetrahydroxy 6 methoxyflavonol (patuletin, quercetin 6 O-methyl ether)

dull yellow in UV(366nm), yellow with NH3, yellow with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 258 272sh 293sh 371 flavonol indicated

Al3+: 56nm shift (371 -> 427)	5 OH indicated
HCl: 20nm shift (374 -> 394)	B-ring Ortho OH indicated
Acetate: 9nm shift (258 -> 269)	7 OH indicated decomposes with time
Borate: 22nm shift (371 -> 393)	B-ring Ortho OH indicated

Base: 40nm shift (371 -> 411) decomposition with time 4'-OH

new band at 332nm 7 OH indicated

MS M = 332 ($C_{17}H_{12}O_8$) (flavone/flavonol; 5-OH's, 1 OCH_3)

M = 331 mass ion - H

M = 317 mass -15 loss of CH_3

M =183 the A-ring fragment

M = 134 the B-ring fragment

These data are consistent with patuletin, quercetin 6 O-methyl ether

573'4'5' hexahydroxyflavonol 3 O-glucoside (myricetin 3 O-glucoside)

Yellow in UV(366nm), yellow with NH3, yellow with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 254 272sh 301sh 374 flavonol indicated

Al3+: 76nm shift (374 -> 450)	5 OH indicated
HCl: 54nm shift (374 -> 428)	B-ring Ortho OH indicated
Acetate: 19nm shift (254 -> 269)	7 OH indicated decomposes with time
Borate: 18nm shift (374 -> 392)	B-ring Ortho OH indicated

Base: 46nm shift (374 -> 432) complete decomposition with time 4'-OH indicated and 3 adjacent OH groups on B-ring

Acid hydrolysis (Ceska & Styles (1984), Kartnig and Wegschaider (1971)) produced glucose end product

353'4' pentahydroxy flavonol 7-O rhamnoside (quercetin 7-O rhamnoside)

dark in UV(366nm), yellow with NH3, yellow with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 256 269sh 372	flavonol indicated
Al3+: 86nm shift (372 -> 458)	5 OH indicated
HCl: 54nm shift (372 -> 426)	B-ring Ortho OH indicated
Borate: 15nm shift (372 -> 387)	B-ring Ortho OH indicated

Base: 75nm shift (372 -> 457) decomposes with time 4'-OH indicated

Acid hydrolysis (Ceska & Styles (1984), Kartnig and Wegschaider (1971)) produced rhamnose end product

573'4' pentahydroxy flavonol 3-O galactoside (quercetin 3-O galactoside)

dark in UV(366nm), yellow with NH3, yellow with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 257 269sh 299sh 362 flavonol indicated

Al3+: 76nm shift (362 -> 438)	5 OH indicated
HCl: 43nm shift (362 -> 405)	B-ring Ortho OH indicated
Acetate: 17nm shift (257 -> 274)	7 OH indicated decomposes with time
Borate: 15nm shift (362 -> 377)	B-ring Ortho OH indicated
Base: 47nm shift (362 -> 409)	4'-OH indicated

Acid hydrolysis (Ceska & Styles (1984), Kartnig and Wegschaider (1971)) produced galactose end product

573'4' pentahydroxy flavonol 3-O rhamnoside (quercetin 3-O rhamnoside, quercetrin)

dark in UV(366nm), yellow with NH3, yellow with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 256 265sh 301sh 350 flavonol indicated

Al3+: 80nm shift (350 -> 430)	5 OH indicated
HCl: 55nm shift (350 -> 405)	B-ring Ortho OH indicated
Acetate: 15nm shift (256 -> 272)	7 OH indicated decomposes with time
Borate: 17nm shift (350 -> 367)	B-ring Ortho OH indicated
Base: 47nm shift (350 -> 393)	4'-OH indicated

Acid hydrolysis (Ceska & Styles (1984), Kartnig and Wegschaider (1971)) produced rhamnose end product

5673'4'penta hydroxyflavonol 3-O glucoside (quercetagetin 3-O glucoside)

Absorbs UV (366nm), yellowish with NH3, yellow/orange colour with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 258, 269sh, 301sh, 363 flavonol indicated

Acetate: 16nm shift (258-> 274)	7-OH indicated reduced intesity
Al^{+3} : 47nm shift (363 -> 410)	5-OH indicated
HCl: 39nm relative to the MeOH	B-ring ortho OH groups indicated
Base: 47nm shift (363 -> 410)	4'-OH indicated decomposes with time A ring ortho OH groups

MS M = 302 (C15H10O7) (flavone/flavonol; 5-OH's)

M = 301 mass ion -H

M = 168 the A-ring fragment

M = 134 the B-ring fragment

These data are consistent with quercetagetin 3-O glucoside.

Acid hydrolysis (Ceska & Styles (1984), Kartnig and Wegschaider (1971)) produced glucose end product

5 3'4' trihydroxy 7 methoxy flavonol 3-O glucoside (rhamnetin 3-O glucoside)

Absorbs UV (366nm), yellowish with NH3, yellow/orange colour with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 256 270sh 295sh 371 flavonol indicated

Acetate: no shift	7-OR indicated
Borate: 18nm shift (371 -> 389)	B-ring ortho OH groups indicated
Al^{+3} : 47nm shift (371 -> 418)	5-OH indicated
HCl: 39nm relative to the MeOH	B-ring ortho OH groups indicated
Base: 47nm shift (371 -> 432)	4'-OH indicated

Acid hydrolysis (Ceska & Styles (1984), Kartnig and Wegschaider (1971)) produced glucose end product

5 7 3' trihydroxy 4' methoxy flavonol 3-O glucoside (isorhamnetin 3-O glucoside)

Absorbs UV (366nm), yellowish with NH3, yellow/orange colour with diphenylborate spray (Naturstoff. Reag. A.)

UV wavelengths in CH_3OH: 253 267sh 306sh 326sh 370 flavonol indicated

Acetate: 21nm shift (253-> 274)	7-OH indicated
Al^{+3} : 47nm shift (370 -> 431) acid stable	5-OH indicated
Base: new band at 328nm	7-OH indicated

Acid hydrolysis (Ceska & Styles (1984), Kartnig and Wegschaider (1971)) produced glucose end product