Diversity in New Zealand Gnaphalieae

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ABSTRACT

New Zealand indigenous Gnaphalieae are examined for endemism, ecological and morphological diversity, hybridism and taxonomic difficulty. The *Raoulia* alliance, an almost endemic clade, is shown to be remarkably diverse in morphology but with some interconnections within this diversity. Similarities between *Leucogenes* and *Leontopodium*, *Anaphalioides* and *Anaphalis*, *Raoulia* and *Mniodes*, and *Ewartiothamnus* and *Ewartia* are hypothesized to be due to the independent acquisition of remarkably similar morphological adaptations.

Keywords: convergent evolution, endemism, hybridism, morphology, *Raoulia* alliance

OVERVIEW

Compositae/Asteraceae tribe Gnaphalieae Cass. ex Lecoq & Juill. comprises about 2,100 species in 178 genera (Smissen et al., 2020), of which 65 species in 11 genera are indigenous to New Zealand (Schönberger et al., 2020). Only species that have been formally described are included in this number and in the following account. Many species await description, particularly in *Craspedia* G.Forst. and *Raoulia* Hook.f. The New Zealand Gnaphalieae flora is noteworthy for its degree of endemism, ecological and morphological diversity, propensity for hybridization and taxonomic intractability.

The New Zealand seed plant flora as a whole has a remarkable degree of endemism, with 82% of its species not occurring elsewhere (Breitwieser et al., 2012). Gnaphalieae exceed even this figure, with 56 of the 65 species endemic (Schönberger et al., 2020). Four genera are endemic (*Ewartiothamnus* Anderb., *Leucogenes* Beauverd, *Rachelia* J.M.Ward & Breitw., and *Raoulia*), and this number is expected to rise when current revision work is published.

A wide range of ecological tolerance is apparent in New Zealand Gnaphalieae, with species found from seashore to mountain top and from bog to semi-desert. They inhabit coastal sands, braided river flood-plains, low tussock grasslands, rocky cliffs, scrub, forest margins, wet banks, arid grasslands, tall tussock grasslands, alpine rock faces, herbfield, fellfield, alpine bogs, snow hollows and mobile screes.

They are morphologically diverse, with forms ranging from tall shrubs (e.g., *Ozothamnus* R.Br.) through smaller shrubs (whipcord *Helichrysum* Mill., Figure 1), cushion shrubs (pulvinate *Raoulia*, Figure 2), and one liane (*Helichrysum dimorphum* Cockayne), to upright, decumbent or prostrate, often woody-based perennial herbs (e.g., *Ewartiothamnus*) and perennial mat-forming (mat-forming *Raoulia*, Figure 3) and rosette herbs (e.g., *Euchiton* Cass.), with or without stolons. Leaves range in length from less than 2 mm to more than 200 mm and may be petiolate, sessile, or with the lower part broad but non-photosynthetic and partly sheathing the stem. One species, *Helichrysum dimorphum*, even has two morphologically and anatomically different leaf types

Mountains Gandalf!

The country where Tolkien characters came to life harbors amazing scenary and otherworldy daisies. This blanket bog near the remote Lake Monk in Fiordland National Park is the habitat of an undescribed *Craspedia.*

Lake Monk in Fiordland National Park, South Island
Photo by Rainer Vogt

Figure 1. The small shrub *Helichrysum coralloides* (Hook.f.) Benth. & Hook.f. has an unusual whipcord growth form; Molesworth, South Island. Photo: R.W. Vogt.

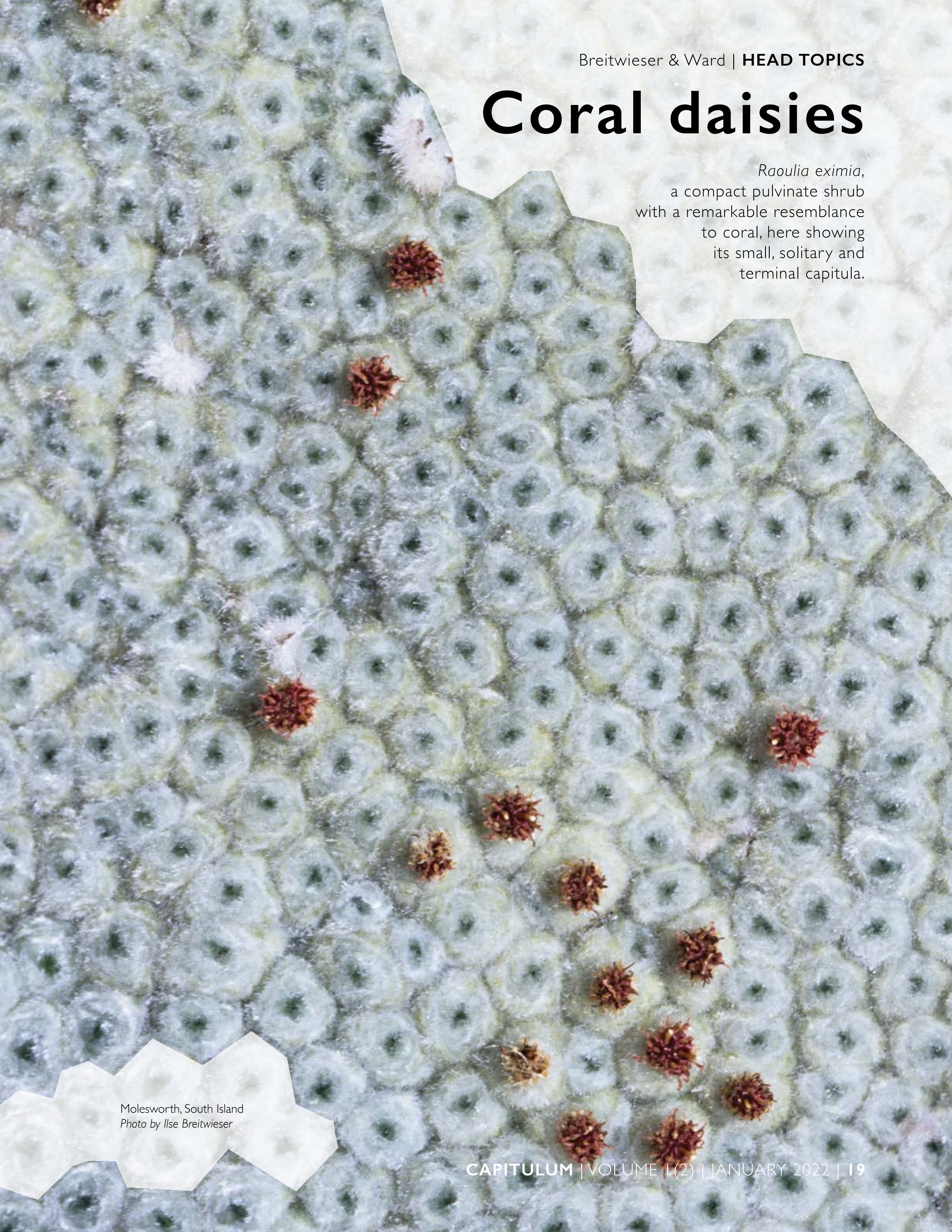
alternating in bands up the stem. Capitula are borne in lax to dense panicles (*Ewartiothamnus*, Figure 4A), in lax [e.g., *Anaphalioides* (Benth.) Kirp., Figure 4B] to very dense corymbs (*Leucogenes*, Figure 4C), in loose glomerules [*Helichrysum lanceolatum* (Buchanan) Kirk] or in densely glomerular secondary heads (*Craspedia*, Figure 5); frequently they are solitary, and then they may be terminal (e.g., *Raoulia*, Figure 3C) or lateral and sessile or scapose, or sessile at flowering and scapose at fruiting. Capitula range from homogamous to almost entirely female. Corollas may be white, yellow, red, greenish or colourless, opaque or translucent. Pappus is variable, ranging from a few broad, persistent hairs in a ring to several hundred very fine caducous hairs in several series. Inner involucral bracts may be shorter than the florets or more than twice their length, and range in colour from white through cream to yellow, and from pale translucent brown to almost black. Fruits vary in size, shape, epidermal cell configuration and twin hair type.

Interspecific hybrids are common in New Zealand (Cockayne & Allan, 1934; Connor, 1985), possibly reflecting the youth of much of the flora and the disturbed nature of the landscape, so the frequency of such hybrids in Gnaphalieae is not particularly surprising. More surprising and noteworthy are the hybrids that occur sporadically in the wild between species in different genera of Gnaphalieae (Allan, 1939, 1961; Ward, 1997).

Asteraceae in general and Gnaphalieae in particular are renowned for being taxonomically difficult. In New Zealand Gnaphalieae taxonomic problems occur at several levels. In *Craspedia* and *Ozothamnus* R.Br., for example, generic delimitation is clear but species delimitation is problematic, whereas

Coral daisies

Raoulia eximia,
a compact pulvinate shrub
with a remarkable resemblance
to coral, here showing
its small, solitary and
terminal capitula.



Molesworth, South Island
Photo by Ilse Breitwieser

Figure 2. Cushion shrub, *Raoulia rubra*, Round Lake, Kahurangi National Park, South Island. **A.** Habit. **B.** Close up of heads. Photos: K.A. Ford.

in *Raoulia*, species are clear-cut but the genus has defied satisfactory delimitation for over 150 years. A group of genera, including *Raoulia*, *Leucogenes*, *Anaphalioides*, *Ewartiothamnus*, *Rachelia*, and those species not yet transferred from *Helichrysum*, exhibits reticulate character distribution, in which one species may show features characteristic of several different genera. One result of this has been a great deal of horizontal reshuffling, with several species having been assigned at different times to three or four different genera.

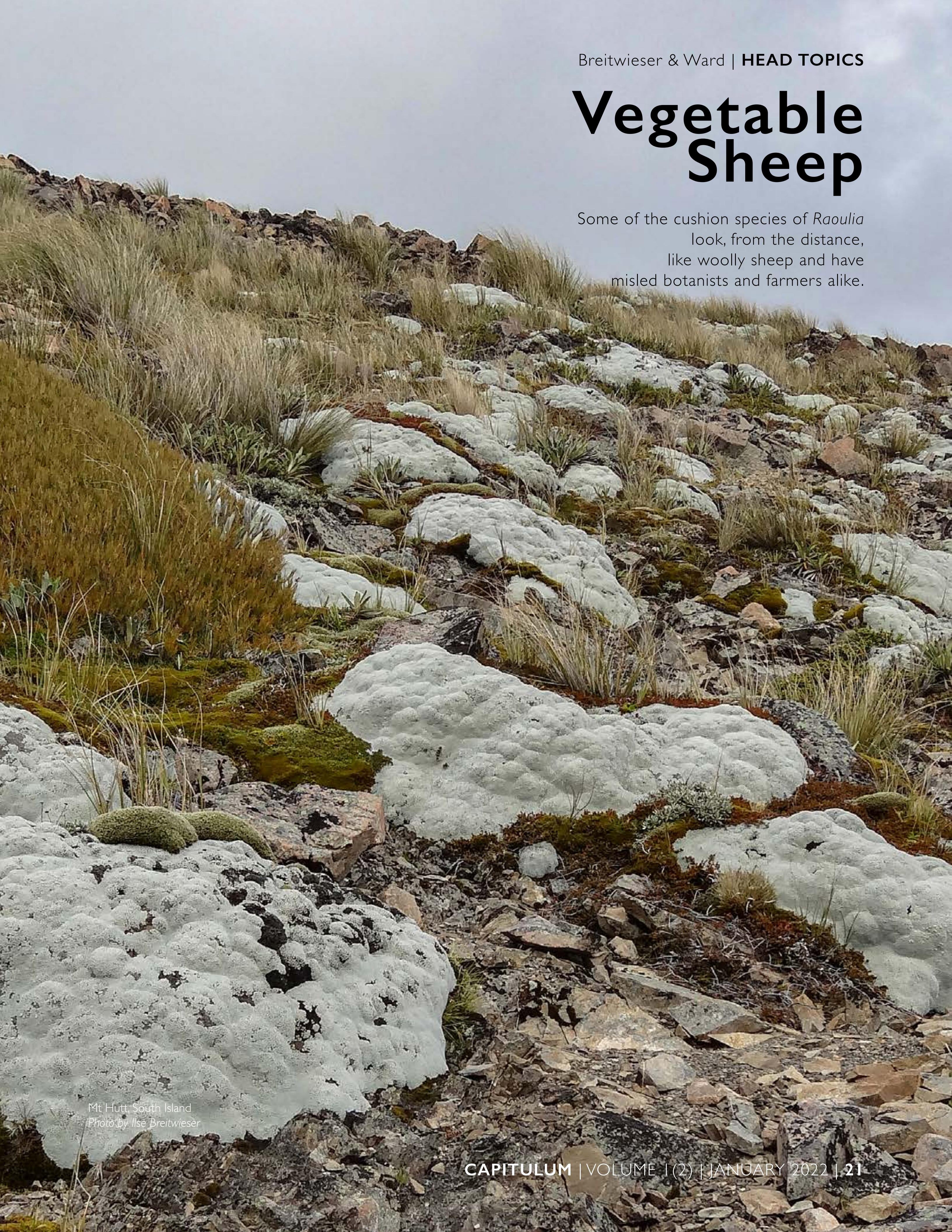
SUBTRIBES AND CLADES OF GNAPHALIEAE

In view of their degree of morphological diversity it is perhaps to be expected that the indigenous New Zealand Gnaphalieae will be taxonomically diverse. This appears to be borne out by the comprehensive classification of Gnaphalieae (Anderberg, 1991, 1994), in which they were distributed through four of the five subtribes (the fifth being almost endemic to Africa). However, based on recent advances in our understanding of their phylogenetics and evolution, a revised subtribal classification (Smissen et al., 2020) showed that, with the exception of *Pseudognaphalium* Kirp., all New Zealand Gnaphalieae belong to the "Australasian clade" within subtribe Gnaphaliinae Dumort. Schmidt-Lebuhn and Bovill's (2021) study of Australian Gnaphalieae, which included only those New Zealand genera also occurring in Australia, placed *Craspedia* in their "Angianthus clade", *Ozothamnus* in their "Cassinia clade", and *Euchiton* Cass. and *Argyrotegium* J.M.Ward & Breitw. in their "Euchiton clade", all falling within their "Australian clade".

The remaining six New Zealand genera (*Anaphalioides*, *Ewartiothamnus*, *Leucogenes*, *Rachelia*, *Raoulia*, and the species not yet transferred from *Helichrysum*) comprise the Raoulia alliance (e.g., Smissen et al., 2006). With 42 currently recognized species, the Raoulia alliance is endemic to New Zealand except for two species of *Anaphalioides* that are endemic to New Guinea. It has also been referred to as the New Zealand endemic clade (e.g. Breitwieser et al., 1999; Smissen et al., 2004). Data from natural and artificial hybridization suggest a close relationship among *Anaphalioides*, *Ewartiothamnus*, *Leucogenes*, *Raoulia*,

Vegetable Sheep

Some of the cushion species of *Raoulia* look, from the distance, like woolly sheep and have misled botanists and farmers alike.



Mt Hutt, South Island
Photo by Ilse Breitwieser

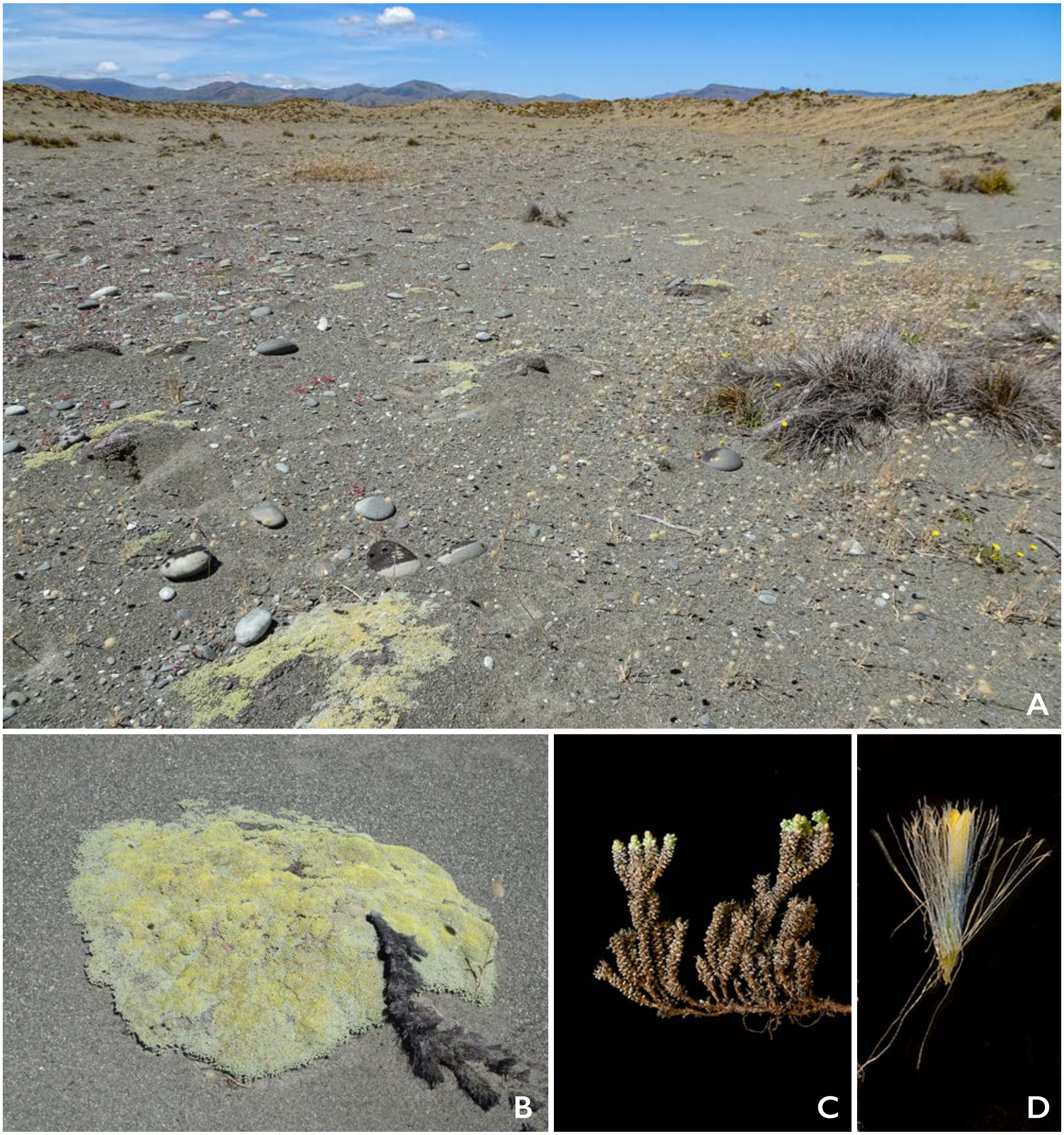


Figure 3. Mat-forming *Raoulia australis* Hook.f. ex Raoul at Kaitōrete Spit, near Christchurch, South Island. **A.** Habitat. **B.** Habit. **C.** Close up of branches, notice long and short shoots. **D.** Floret. Photos: A-B, R.W.Vogt; C-D, K.A. Ford.

and the species not yet transferred from *Helichrysum*. This is supported by morphological, anatomical, palynological and molecular data, which also support the inclusion of *Rachelia*. An ITS sequence analysis of a selection of Australasian Gnaphalieae (Breitwieser et al., 1999) retrieved a strongly supported clade comprising these six genera.

INTERGENERIC HYBRIDS IN THE RAOULIA ALLIANCE

Crosses between species in different genera are well known in the Raoulia alliance (e.g., Allan, 1961), but only some are well documented. Generally, they occur as isolated individuals, occasionally as very

Figure 4. A. *Ewartiothamnus sinclairii* Anderb. has capitula in lax to dense panicles; it is found only in Molesworth, South Island **B.** *Anaphalioides trinervis* (G.Forst.) Anderb. has a lax corymb; Arthur's Pass National Park, South Island. **C.** *Leucogenes grandiceps* (Hook.f.) Beauverd has a dense corymb; it grows here in a rock face in Molesworth, South Island. Photos: A-B, R.W. Vogt; C, J.D. Lovis.

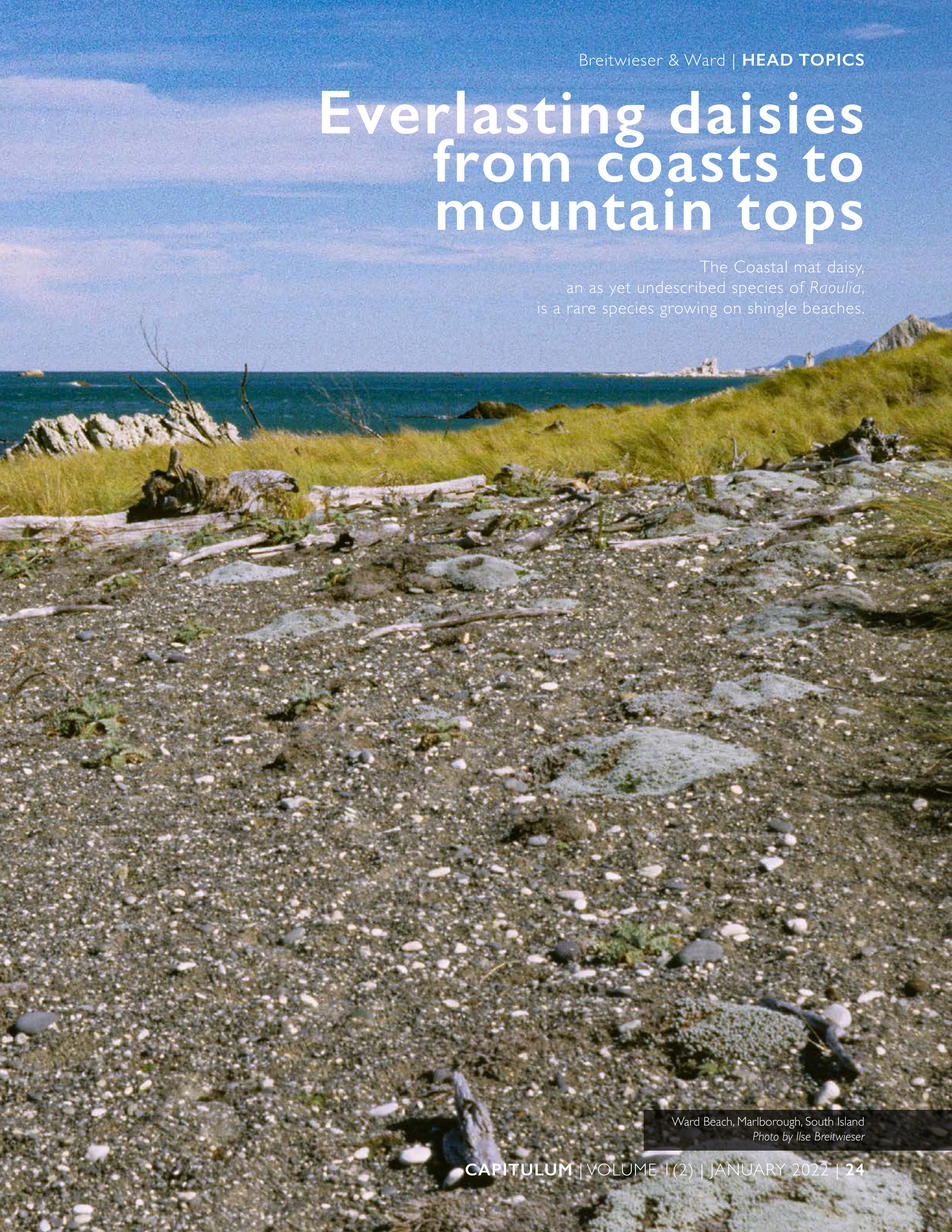
small populations, intermediate in form between the putative parents (Figure 6A) and usually in close proximity to one or both (Figure 6B). Within the Raoulia alliance five of the six genera are linked by wild hybrids to at least two of the other genera. The exception is *Rachelia*, which is monotypic, with a very limited distribution and a specialized alpine habitat on fine scree containing argillite. It does not grow in proximity to any other Gnaphalieae except *Raoulia bryoides* Hook.f., a cushion shrub that is adapted to a disparate alpine habitat on rock outcrops. Survival of offspring is rare even for these species, so would be very unlikely for hybrids.

Detailed study of hybrids between *Anaphalioides bellidioides* (G.Forst.) Glenny and *Ewartiothamnus sinclairii* (Hook.f.) Anderb. (McKenzie et al., 2004, 2008) has demonstrated fertility in the F1 generation and successful production of plants from seed of wild and artificial hybrids, with evidence of back-crossing to *A. bellidioides* and possible advanced-generation hybrids. By far the most commonly reported generic combination is between *Leucogenes* and the pulvinate shrub species of *Raoulia* subg. *Psychrophyton* Beauverd (e.g. Allan, 1939, 1961). This may be due in part to the ease of recognizing hybrids between two such morphologically different genera. There is no doubt the hybrids are common in the wild and found in most geographically feasible species combinations. Experimental crosses by McKenzie (2001) generally followed the wild hybrid pattern, except that the autogamous genus *Euchiton* was crossed successfully with *Anaphalioides*, *Ewartiothamnus*, *Helichrysum*, *Leucogenes* and *Raoulia* (but not *Ozothamnus* or *Pseudognaphalium*). Attempted crosses between *Leucogenes* and the similar looking but distantly related Eurasian *Leontopodium* were unsuccessful.

More recently we used DNA sequencing to confirm intergeneric hybridization between *Helichrysum lanceolatum* and *Anaphalioides bellidioides* (Smissen et al., 2007). Using DNA fingerprinting we found some evidence of reduced seed set in hybrids. Two wild back-crosses to *H. lanceolatum* were identified using AFLP profiles. Subsequent generations have been produced in the glasshouse, and some come close to recovering the morphology of *H. lanceolatum* (Smissen, unpubl.). However, F1 hybrids were far more common than second and later generation hybrids in nature, and introgression between the parental populations was not detected. Glasshouse-grown backcrosses to *A. bellidioides* show marked morphological variation, as would be expected in recombinant generations descended from a cross between two morphologically distinct species.

Everlasting daisies from coasts to mountain tops

The Coastal mat daisy,
an as yet undescribed species of *Raoulia*,
is a rare species growing on shingle beaches.



Ward Beach, Marlborough, South Island
Photo by Ilse Breitwieser

Figure 5. *Craspedia lanata* (Hook. f.) Allan from the Pisa Range, South Island. A. Habit. B. Close up of densely glomerular secondary head. Photos: R.W. Vogt.

With the help of analyses of nuclear rDNA ITS sequences and plastid *trn*K intron, we also confirmed that wild intergeneric hybrids occur between *Argyrotegium mackayi* (Buchanan) J.M.Ward & Breitw. and *Leucogenes leontopodium* (Hook.f.) Beauverd (Smissen et al., 2015). This is the only known instance of wild hybrids between species inside and outside the Raoulia alliance.

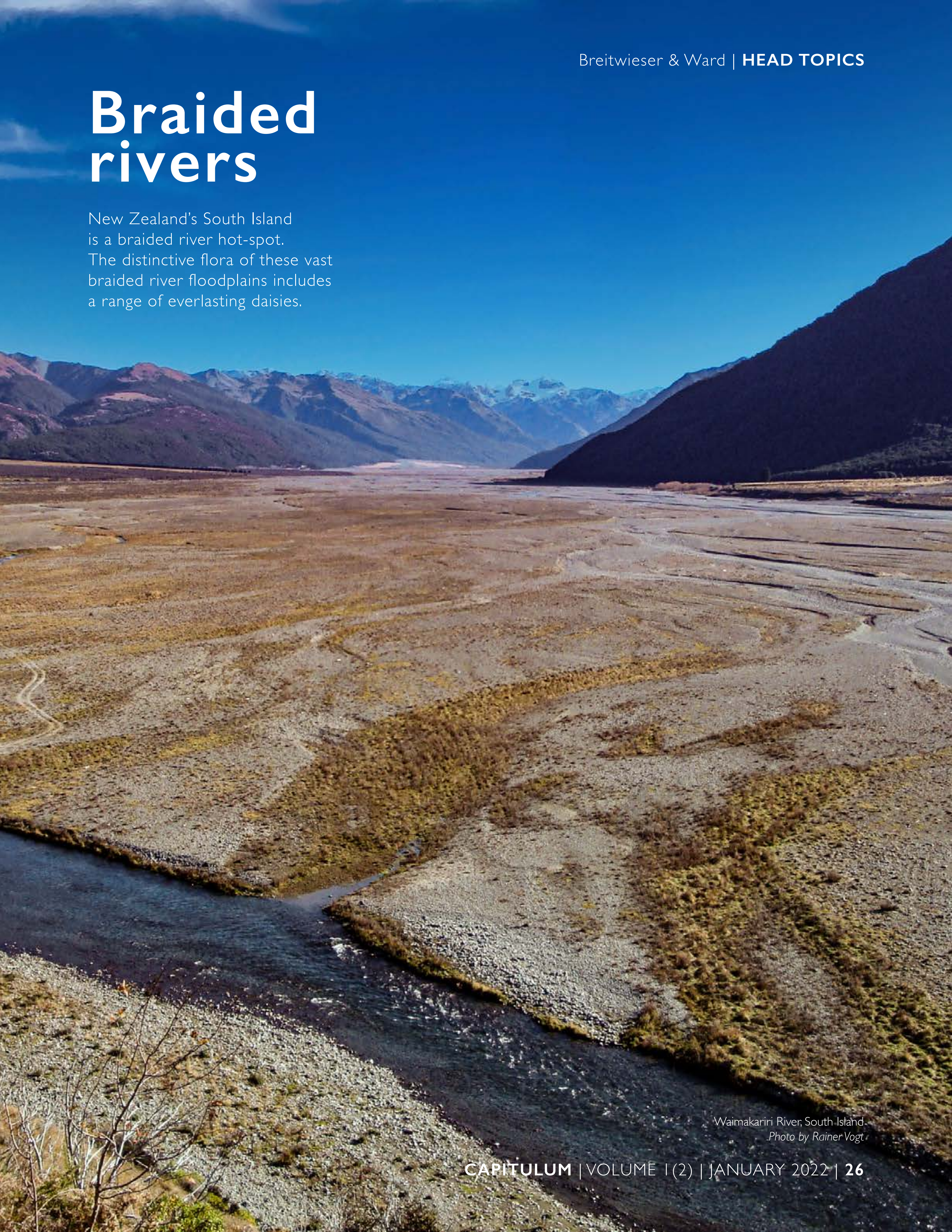
MORPHOLOGICAL DIVERSITY AND EVOLUTION OF THE RAOULIA ALLIANCE

The Raoulia alliance embraces most of the remarkable morphological and ecological variation described above for New Zealand Gnaphalieae, apart from conventional shrubs and rosette herbs. A close relationship among taxa with such diverse morphology may seem unlikely, but some connections between very different forms can be demonstrated. The distinctive condensed corymb of *Leucogenes* (Figure 7A), with its ring of showy, white-tomentose bracts, found elsewhere in the tribe only in *Leontopodium* (Pers.) R.Br. *ex* Cass., is very different from the small, solitary, terminal capitula nested among the uppermost leaves of a pulvinate *Raoulia* (Figure 7B). Yet a possible linking form can be seen in *Rachelia* (Figure 7C), in which the capitula are terminal and lateral in the axils of the uppermost leaves. These leaves are large, white-tomentose and very close-set, giving the appearance of a rosette. It would require only minor morphological adjustments to convert this to the inflorescence of a *Leucogenes*. Alternatively, loss of lateral capitula would result in the solitary, sessile, terminal capitulum of *Raoulia*. Isolated plants with solitary capitula, but otherwise conforming in all aspects to other plants in the population, have been observed at least twice in *Leucogenes* (Figure 7C), demonstrating that this transition is developmentally feasible.

The leaves of the whipcord species of *Helichrysum* (Figure 8 A-B) are scale-like, imbricate, appressed and abaxially glabrous, very different from the spreading, densely tomentose leaves found in other genera. However, the whipcord species are heteroblastic and their juvenile leaves are spreading and densely tomentose (Figure 8C).

Braided rivers

New Zealand's South Island is a braided river hot-spot. The distinctive flora of these vast braided river floodplains includes a range of everlasting daisies.



Waimakariri River, South Island
Photo by Rainer Vogt

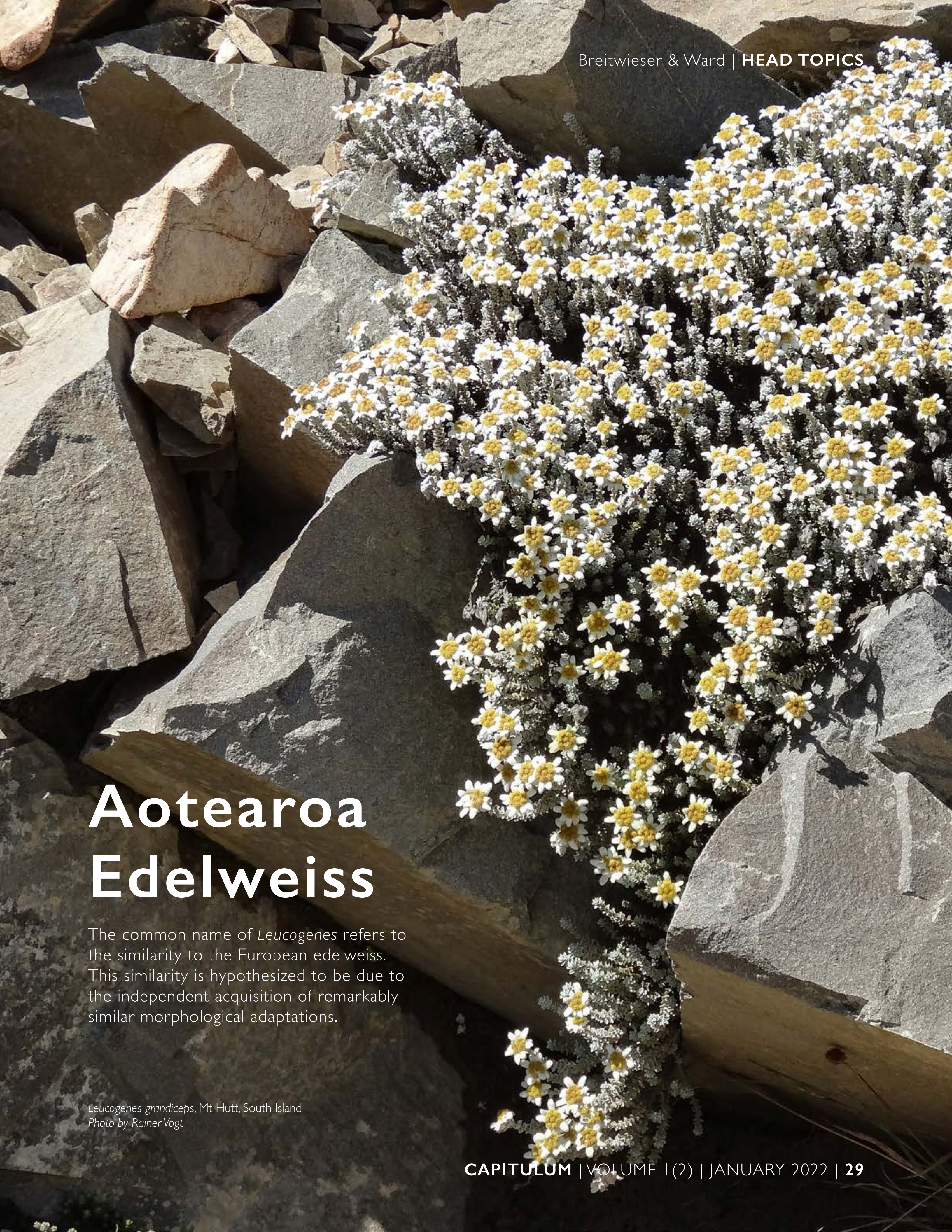
Figure 6. Intergeneric hybrid between *Raoulia* and *Leucogenes* at Mt Hutt, South Island. **A.** *Raoulia exima* surrounded by *Leucogenes grandiceps* with one plant of *Leucogenes* growing in the *Raoulia* cushion. **B.** Close up of putative hybrid. Photos: R.W.Vogt.

Figure 7. A. The distinctive condensed corymb of *Leucogenes*. **B.** Inflorescence of *Rachelia*, characterized by capitula that are terminal and lateral in the axils of the uppermost leaves. **C.** *Leucogenes* showing a solitary capitulum. Photos: A, C: R.W. Vogt; B: I. Breitwieser.

Hybrids are a well-documented source of intermediate and novel characters. We have shown (Smissen et al., 2004) that chloroplast lineages in the Raoulia alliance do not correspond to taxonomic units, with groups suggested by analysis of morphological characters, or with groups indicated by nuclear rDNA ITS sequences. This suggests complex inter-relationships among extant species and past reticulation among diverging populations. Hybridization may have played a significant role in producing the present-day diversity seen in the Raoulia alliance (see Smissen et al., 2011), as well as the reticulate character distribution that makes it so taxonomically intractable. The Raoulia alliance has radiated into a wide array of forms to colonize the myriad new habitats formed by Pliocene/Pleistocene mountain building and glacial/interglacial climate cycles (e.g., Breitwieser et al., 1999; Smissen et al., 2004).

GENERIC PARALLELISMS WITHIN GNAPHALIEAE

Evidence from hybridization and analyses from sequences of nrDNA spacers, cpDNA and low-copy nuclear markers support the existence of a morphologically and ecologically diverse mainly New Zealand lineage, the Raoulia alliance (Breitwieser et al., 1999; Smissen et al., 2011), and do not support Anderberg's (1991) classification based on phylogenetic analyses of morphological data and the purported close relationship between *Leucogenes* and *Leontopodium*, *Anaphalioides* and *Anaphalis* DC., or the cushion-forming species of *Raoulia* and other Gnaphalieae such as *Mniodes* (A.Gray) Cuatrec.; nor do they support the pairing of *Ewartiothamnus* with the Australian genus *Ewartia* Beauverd. This is surprising, because, with the possible exception of



Aotearoa Edelweiss

The common name of *Leucogenes* refers to the similarity to the European edelweiss. This similarity is hypothesized to be due to the independent acquisition of remarkably similar morphological adaptations.

Leucogenes grandiceps, Mt Hutt, South Island
Photo by Rainer Vogt

Leucogenes and *Leontopodium*, which have not been compared in detail, these pairs of genera show much more than superficial similarity. *Ewartiothamnus* and *Ewartia* (Ward, 1993), as well as *Anaphalioides* and *Anaphalis* (Breitwieser & Ward, 2003), show high levels of overall similarity. *Raoulia* and *Mniodes* have not been fully compared reproductively, although it is known that *Raoulia* is gynomonoecious to functionally monoecious and *Mniodes* is dioecious. However, the habit (Figure 9) and the unusual leaves of *Raoulia eximia* Hook. f. and *Mniodes andina* (A.Gray) Cautrec. are almost identical down to the smallest detail. This leads one to speculate how many cases exist where a true genetic relationship has been obscured by the independent acquisition of such remarkably similar adaptations.

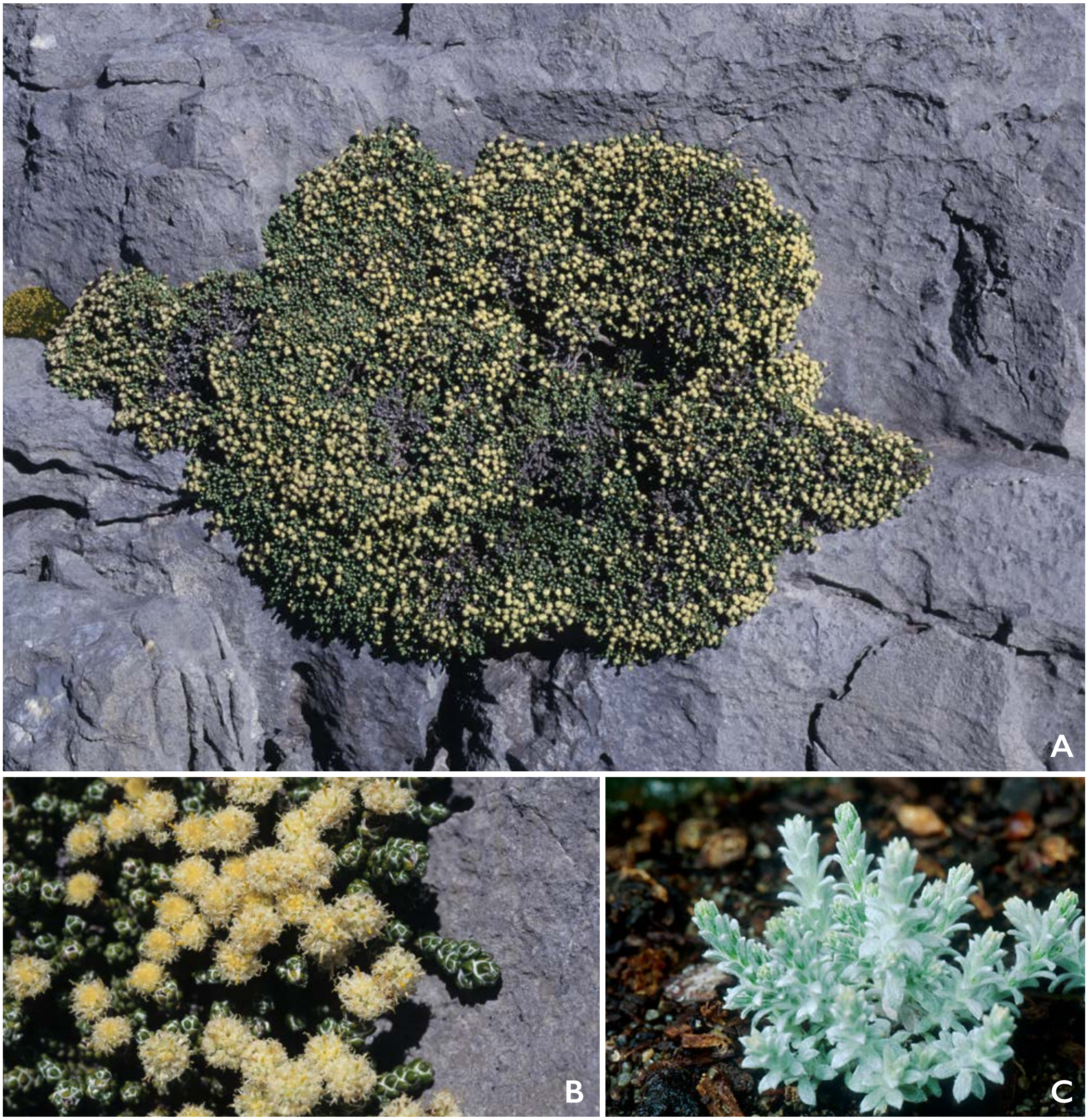


Figure 8. A. Adult form of *Helichrysum intermedium* G. Simpson has scale-like, imbricate, appressed and abaxially glabrous leaves **B.** Close up of heads and leaves. **C.** Juvenile form showing leaves spreading and densely tomentose. Photos: A-B: R.W. Vogt; C: J.M. Ward).

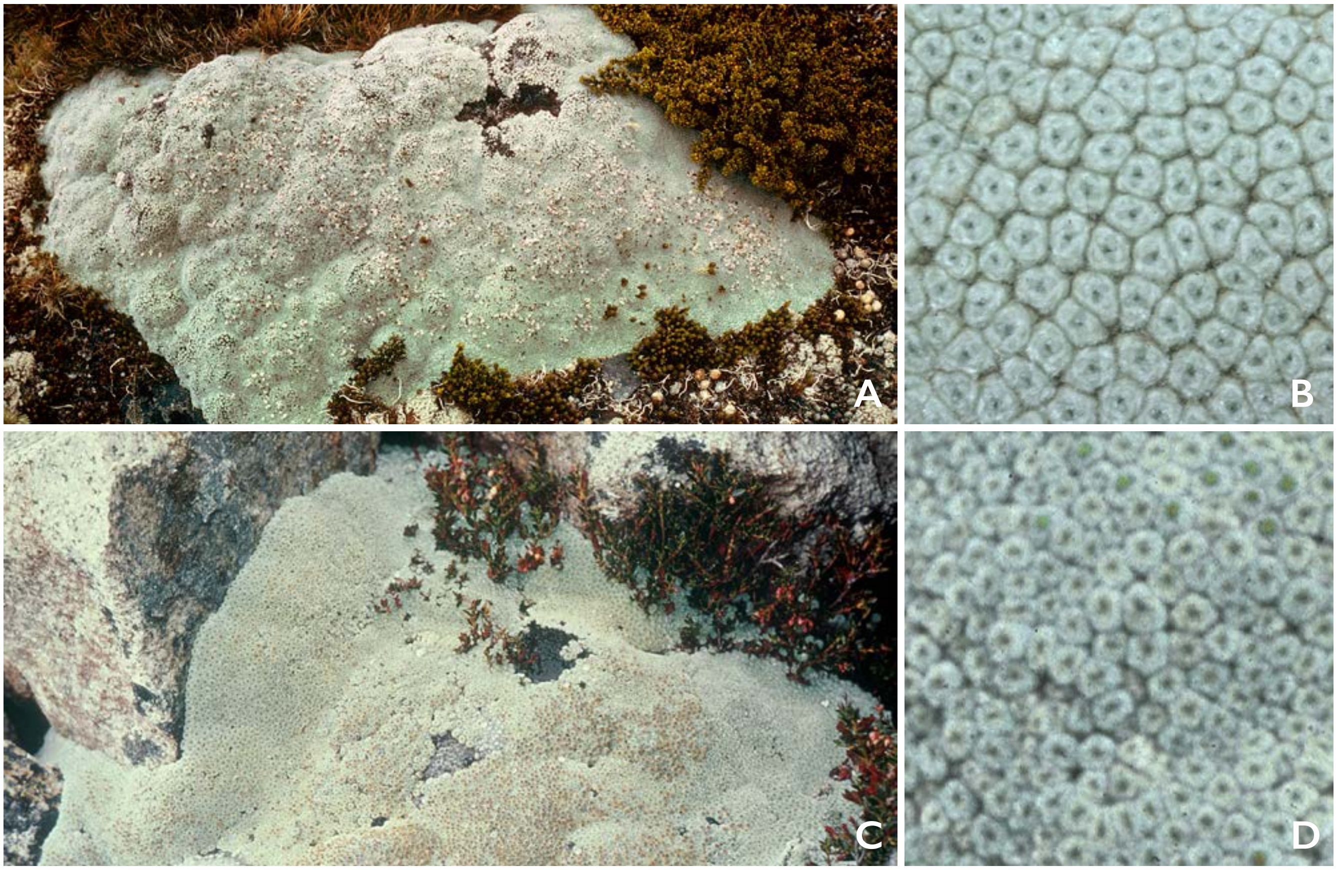


Figure 9. Startling morphological similarities in not closely related taxa. **A-B** *Raoulia eximia* (New Zealand). **C-D.** *Mniodes andina* (Peru). Photos: A-B: J.M. Ward; C-D: H. Wilson.

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LITERATURE CITED

Allan, H.H. 1939. Remarks on X *Leucoraoulia. Trans. Roy. Soc. New Zealand* 68: 457–461.

Allan, H.H. 1961. *Flora of New Zealand.* Vol. 1. Wellington, NZ: Government Printer.

Anderberg, A.A. 1991. Taxonomy and phylogeny of the tribe Gnaphalieae (Asteraceae). *Opera Bot.* 104: 1–195.

Anderberg, A.A. 1994. Tribe Gnaphalieae. In: Bremer, K. *Asteraceae: Cladistics and Classification.* Oregon: Timber Press.

Breitwieser, I., Brownsey, P.J., Garnock-Jones, P.J., Perrie, L.R. & Wilton, A. 2012. Phylum Tracheophyta — vascular plants. In Gordon, D. (ed.), *New Zealand Inventory of Biodiversity*. Vol. 3. Christchurch, NZ: Canterbury University Press, pp. 411–459

Breitwieser, I., Glenny, D.S., Thorne, A. & Wagstaff, S.J. 1999. Phylogenetic relationships in Australasian Gnaphalieae (Compositae) inferred from ITS sequences. *New Zealand J. Bot.* 37: 399–412.

Breitwieser, I. & Ward, J.M. 2003. Phylogenetic relationships and character evolution in New Zealand and selected Australian Gnaphalieae (Compositae) inferred from morphological and anatomical data. *Bot. J. Linn. Soc.* 141: 183–203.

Cockayne, L. & Allan, H.H. 1934. An annotated list of groups of wild hybrids in the New Zealand flora. *Ann. Bot. (Oxford)* 38: 1–55.

Connor, H.E. 1985. Biosystematics of higher plants in New Zealand 1965–1984. *New Zealand J. Bot.* 23: 613–644.

McKenzie, R.J. 2001. *Intergeneric hybridisation in New Zealand Gnaphalieae (Compositae)*. PhD thesis, University of Canterbury.

McKenzie, R.J., Ward, J.M. & Breitwieser, I. 2008. Hybridization beyond the F1 generation between the New Zealand endemic everlastings *Anaphalioides bellidioides* and *Ewartia sinclairii* (Asteraceae, Gnaphalieae). *Pl. Syst. Evol.* 273: 13–24.

McKenzie, R.J., Ward, J.M., Lovis, J.D. & Breitwieser, I. 2004. Morphological evidence for natural hybridization in the New Zealand Gnaphalieae (Compositae): *Anaphalioides bellidioides* × *Ewartia sinclairii*. *Bot. J. Linn. Soc.* 145: 59–75.

Schmidt-Lebuhn, A.N. & Bovill, J. 2021. Phylogenetic data reveal four major clades of Australian Gnaphalieae (Asteraceae). *Taxon* 70: 1020–1034.

Schönberger, I., Wilton, A.D., Boardman, K.F., Breitwieser, I., de Lange, P.J., de Pauw, B., Ford, K.A., Gibb, E.S., Glenny, D.S., Greer, P.A., Heenan, P.B., Korver, M.A., Novis, P.M., Prebble, J.M., Redmond, D.N., Smissen, R.D. & Tawiri, K. 2020. Checklist of the New Zealand Flora – Seed Plants. Lincoln, NZ: Manaaki Whenua-Landcare Research. http://dx.doi.org/10.26065/s3gg-v336

Smissen, R.D., Bayer, R.J., Bergh, N.G., Breitwieser, I., Freire, S.E., Galbany-Casals, M., Schmidt-Lebuhn, A.N. & Ward, J.M. 2020. A revised subtribal classification of Gnaphalieae (Asteraceae). *Taxon* 69: 778–806.

Smissen, R.D., Breitwieser, I. & Ward, J.M. 2004. Phylogenetic implications of trans-specific chloroplast DNA sequence polymorphism in New Zealand Gnaphalieae (Asteraceae). *Pl. Syst. Evol.* 249: 37–53.

Smissen, R.D., Breitwieser, I. & Ward, J.M. 2007. Genetic characterisation of hybridisation between the New Zealand everlastings *Helichrysum lanceolatum* and *Anaphalioides bellidioides* (Asteraceae: Gnaphalieae). *Bot. J. Linn. Soc.* 154: 89–98.

Smissen, R.D., Galbany-Casals, M. & Breitwieser, I. 2011. Ancient allopolyploidy in the everlasting daisies (Asteraceae: Gnaphalieae): Complex relationships among extant clades. *Taxon* 60: 649–662.

Smissen, R.D., Thorsen, M.J., Breitwieser, I. &Ward, J.M. 2015. DNA sequence analysis confirms the identity of the intergeneric hybrid *Argyrotegium mackayi* × *Leucogenes leontopodium* (Asteraceae: Gnaphalieae). *New Zealand J. Bot.* 53: 210–215.

Ward, J.M. 1993. Systematics of New Zealand Inuleae (Compositae-Asteraceae)-2. A numerical phenetic study of *Raoulia* and allied genera. *New Zealand J. Bot.* 31: 29–42.

Ward, J.M. 1997. *Raoulia* and its hybrids. Pp. 40–44 in: Sheppard J. S. (ed.) *Southern Alpines '96*. Christchurch, NZ: Southern Alpines.