An overview of Celmisiinae (Astereae):

A diverse endemic Australasian lineage

Patricio Saldivia[1,2] & **Duncan Alastair Nicol**[3]

[1] Biota Ltda. Av. Miguel Claro 1224, Providencia, Santiago, CHILE.
[2] Museo Regional de Aysén, Km 3 Camino a Coyhaique Alto, Coyhaique, CHILE.
[3] Department of Botany, University of Otago, PO Box 56, Dunedin 9054, NEW ZEALAND.

Author for correspondence: Patricio Saldivia, *patricio.saldivia.perez@gmail.com*

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ABSTRACT

Within the Australasian Astereae, the recently circumscribed Celmisiinae constitute a rich and morphologically diverse lineage centered in New Zealand but also significant in Australia and the tropical island of New Guinea. The taxonomic history of the subtribe goes back to the beginnings of the botanic exploration of New Zealand. However, it was only in the 1980s that the idea of closely related Australasian elements started to be discussed. Currently, the following genera are accepted within Celmisiinae: *Celmisia*, *Damnamenia*, *Macrolearia*, *Pachystegia*, *Pleurophyllum*, and *Olearia* pro parte. The latter, however, needs a new generic circumscription because its type, *O. tomentosa*, belongs to a different subtribe. The main morphological attributes defining Celmisiinae (shoot architecture, receptacle, androecium morphology, and leaf indumentum) are discussed in detail. The distribution patterns and richness are shown in the context of the most recent phylogeny of the subtribe. Finally, a brief account of habitat diversity and ecological interactions with invertebrate fauna is given.

Keywords: architecture, Asteraceae, *Celmisia* group, Compositae, diversity, endemism, *Shawia*, taxonomy.

FROM J.D. HOOKER TO G.L. NESOM AND THE CURRENT TAXONOMIC CONCEPT OF CELMISIINAE

The history of Celmisiinae Saldivia is linked to the botanic exploration of New Zealand. Johann Reinhold Forster and his son Georg (Forster & Forster, 1776), based on collections made during Captain James Cook's second voyage in 1773, described *Shawia paniculata* J.R.Forst. & G.Forst [≡*Olearia paniculata* (J.R.Forst. & G.Forst.) Druce], a small tree of unusual uniflorous capitula arranged in panicle-like capitulescences. Years later and based on collections from the same voyage, Georg Forster (1786) described four species belonging to Celmisiinae: *Arnica oporina* G.Forst. [≡ *Macrolearia oporina* (G.Forst.) Saldivia], *Aster coriaceus* G.Forst. [≡ *Celmisia coriacea* (G.Forst.) Hook.f.], *Aster holosericeus* G.Forst. [≡ *Celmisia holosericea* (G.Forst.) Hook.f.], and *Solidago arborescens* G.Forst. [≡ *Olearia arborescens* (G.Forst.) Cockayne & Laing], all endemic to New Zealand.

During the 1800s and beginnings of the 1900s, there were many important figures that greatly contributed to the taxonomic knowledge of the flora of New Zealand in general and to Celmisiinae in particular (e.g., L.C. Cockayne, W. Colenso, T.F. Cheeseman, and T. Kirk). However, Joseph D. Hooker was, undoubtedly, the most influential botanist of all in this context. Between 1844 and 1867, Hooker published in several books (e.g., 1864, 1867) the most complete taxonomic work of the flora of New Zealand of that time, authoring a formidable number of species new to science,

One flowered marvel

Olearia paniculata (J.R.Forst. & G.Forst.) Druce (≡ *Shawia paniculata* J.RForst & G.Forst.), a small tree endemic to New Zealand's North and South Islands, was the first species described of Celmisiinae in 1776 (Forster & Forster, 1776). Its anomalous uniflorous capitula probably led the authors to consider the proposal of a new genus. The genus *Shawia* J.RForst & G.Forst. holds the nomenclatural priority among the *Olearia* Moench species belonging to Celmisiinae.

Olearia paniculata, cultivated at Dunedin Botanic Garden, Dunedin, New Zealand. *Photo by Patricio Saldivia*

Figure 1. Nesom (1994a) proposed that *Pacifigeron*, a small endemic genus to Rapa Iti (Austral Islands in southern French Polynesia), was part of Celmisiinae (as *Celmisia* group). Nonetheless, a recent study (Saldivia et al., 2020) has shown that it is phylogenetically related to South American genera, distant from Celmisiinae. Morphologically, its terminal capitulescences and obtuse anther's bases confirm this phylogenetic finding. **A.** *P. rapensis* (F.Br.) G.L.Nesom, habit. **B.** *P. rapensis* (F.Br.) G.L.Nesom, terminal capitulescence. **C.** *P. indivisus* Saldivia, habit and terminal capitulescences. *Photos by:* **A** *Kenneth R. Wood,* **B-C.** *Jean-Yves Hiro Meyer.*

including over 20 *Celmisia* Cass. species and many in *Olearia* Moench (some within *Eurybia* Cass.) and forged most of the taxonomic concepts of genera belonging to Celmisiinae. Hooker (1844), in the description of the genus *Pleurophyllum* Hook.f. and *Celmisia vernicosa* Hook.f. [≡ *Damnamenia vernicosa* (Hook.f.) Given] wrote: "I may here mention another little-known New Zealand plant, originally discovered by Forster, and called by him *Arnica oporina* [≡ *Macrolearia oporina*]; it is nearly allied both to these [*Celmisia*] and the former genus *Pleurophyllum*." This comment, although not addressed further by subsequent authors (e.g., Archer, 1860; Kirk, 1891a, 1891b, 1899; Cheeseman, 1906, 1914, 1925; Allan, 1961), was the first insight into the close relationship among different elements of Celmisiinae (Saldivia et al., 2022).

The *Olearia* conundrum

Summarized phylogeny of Astereae by Brouillet et al. (2009). **Highlighted** subtribes follow Nesom (2020a)

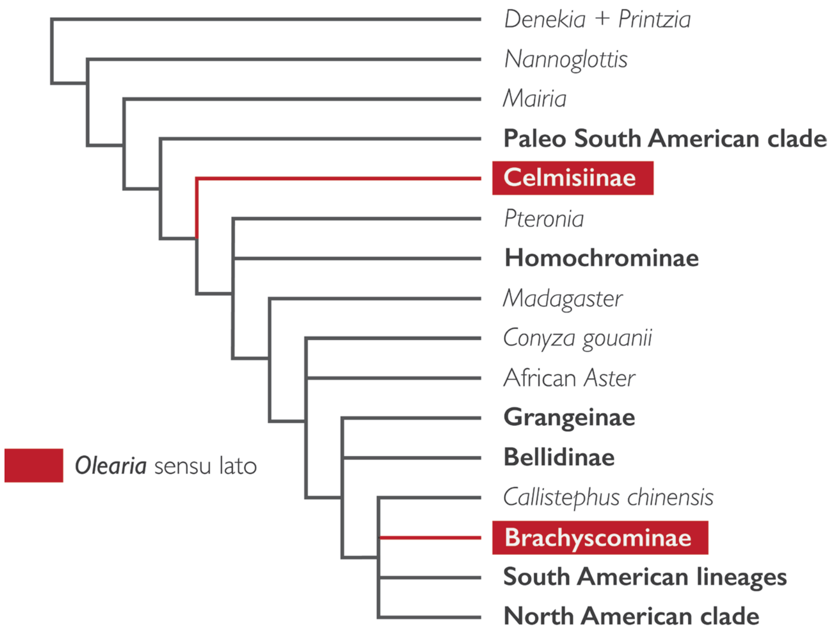


Figure 2. For over a century, *Olearia* has been regarded as the largest Australasian genus of Asteraceae, with ca. 180 spp. divided into five sections based on leaf trichome morphology (Archer, 1860; Bentham, 1867) plus one section based on shoot architecture (Heads, 1998). However, Nesom (1993, 1994a), based on chromosome numbers and morphology, suggested that *Olearia* was polyphyletic. Cross et al. (2002), Brouillet et al. (2009), and Saldivia et al. (2020) confirmed Nesom´s hypothesis. *Olearia* species belong to two lineages distantly related within Astereae (see highlighted subtribes in red). The recently expanded Brachyscominae (Nesom 2020a) is one lineage in which the type species, *O. tomentosa*, and ca. 90 other *Olearia* belong. These Australian endemic *Olearia* species do not form a monophyletic group, and, accordingly, Nesom (2020b) proposed ten new generic names for 29 of these species. The second lineage, Celmisiinae, includes ca. 78 species from New Zealand, New Guinea, and Australia, and new generic affiliations for these *Olearia* species are forthcoming (Nicol and Saldivia in prep.)

Given & Gray (1986) presented an overview of *Celmisia* and proposed the *Olearia-Celmisia* complex, which also includes *Damnamenia* Given, some *Erigeron* L. species that are currently recognized as *Pappochroma* Raf. (Nesom, 1998), the Polynesian genus *Pacifigeron* G.L.Nesom (Nesom 1994b, Figure 1), *Pachystegia* Cheeseman, and *Pleurophyllum* Hook. f. It is important to mention that Given & Gray (1986) included *Olearia* as a whole within the *Olearia-Celmisia* complex, including even *Olearia rapae* F.Br. which is endemic to Rapa Iti and currently recognized as the monotypic genus *Apostates* Lander (Lander, 1989) in the tribe Bahieae B.G.Baldwin (Baldwin & Wood, 2016). However, a thorough proposal, encompassing closely connected Australasian Astereae Cass. elements, was not recognized until the groundbreaking paper by G.L. Nesom "Subtribal classification of the Astereae (Asteraceae)" in 1994. Nesom (1994a) proposed the *Celmisia* group as follows: *Achnophora* F.Muell. (doubtfully), *Celmisia*, *Damnamenia*, *Olearia* pro parte (Figure 2), *Pachystegia*, *Pacifigeron* (Figure 1), and *Pleurophyllum*, highlighting that the members of the *Celmisia* group have high levels of polyploidy. Nesom (1994b) was less clear about the morphological circumscription, but based on scattered data from literature he did indicate that the *Celmisia* group: "[…] are characterized by a combination of subterete, multinerved, and eglandular achenes and parallel-veined leaves tomentose with simple hairs [trichomes] (branching hairs [trichomes] occur among Australian taxa of *Olearia*), as well as a mix of other characters that occur less regularly among the species: reduced ligules in *Pleurophyllum*; markedly

The key to *Olearia*

Original illustration of *Aster tomentosus* J.C.Wendl. (≡ *O. tomentosa* (J.C.Wendl) DC.), the type species of *Olearia* Moench, by Wendland (1798). Note the terminal capitulescences (see text, Morphology of Celmisiinae).

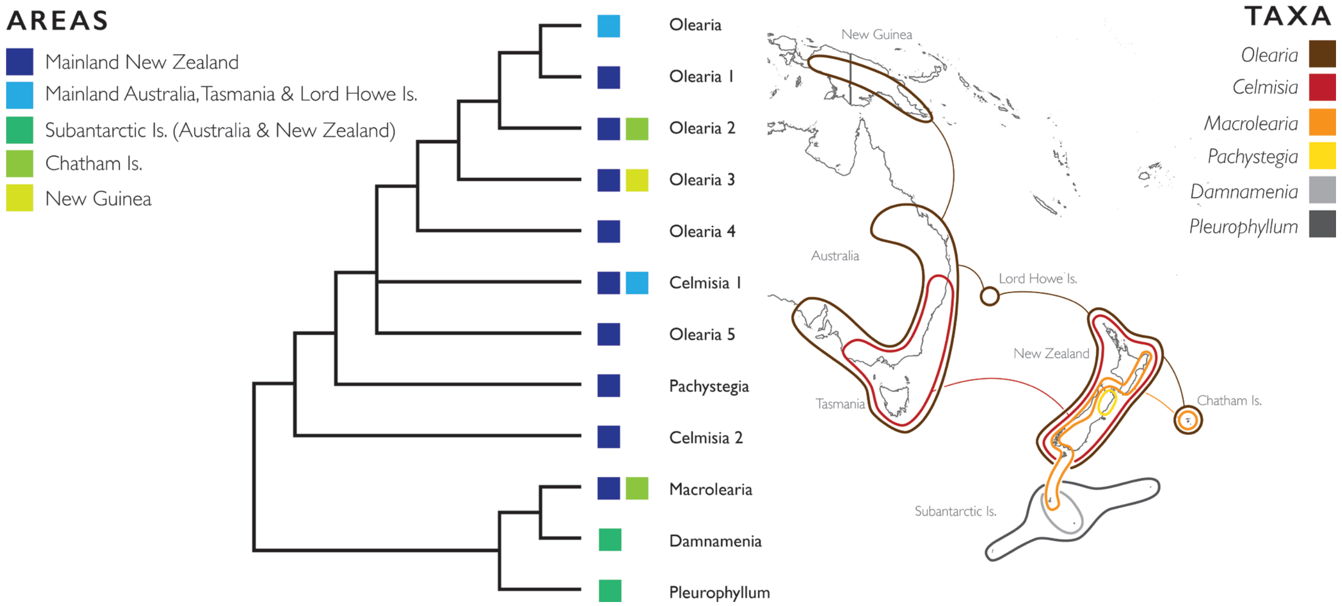


Figure 3. Phylogeny and distribution of Celmisiinae. Summarized phylogeny of Saldivia (2021). The *Olearia* pro parte species from New Zealand are divided as follows: *Olearia* 1 = *O. fragrantissima*, *Olearia* 2 = *O.* sect. *Divaricaster*, *Olearia* 3 = *O. arborescens* and allies, *Olearia* 4 = *O. paniculata* and allies, *Olearia* 5 = *O. furfuracea* complex. *Celmisia* is divided into two clades: *Celmisia* 1 = *C.* subg. *Celmisia* and *C.* subg. *Pelliculatae*, *Celmisia* 2 = *C.* subg. *Caespitosa*, *C.* subg. *Glandulosae*, and *C.* subg. *Lignosae*. The distribution of the recognized *Olearia* subgroups is provided in the section "Current genera in Celmisiinae".

short twin hairs [trichomes] on achenes of the *Olearia chathamica* Kirk group; and a subshrubby habit, with leaves produced in terminal clusters, in sect. *Lignosae* (Allan) Given of *Celmisia*".

Cross et al. (2002) and Brouillet et al. (2009) used nrITS sequences and provided the initial molecular insights regarding the phyletic nature of Nesom's *Celmisia* group. They found that elements such as *Achnophora* and many *Olearia* species (including its type, *O. tomentosa* (Wendl.) DC.) are part of a lineage only distantly related to the other proposed genera in the *Celmisia* group. However, in both studies species sampling was scarce. More recently, Saldivia et al. (2020) and Saldivia (2021), based on ITS and ETS sequence data, expanded the sampling to include representative taxa of all genera and infrageneric taxa of Nesom (1994a). This research proposed a new phylogenetic and morphological delimitation of the *Celmisia* group that included *Celmisia*, *Damnamenia*, *Pachystegia*, *Pleurophyllum*, and *Olearia* pro parte, and, on the other hand, excluded *Pacifigeron* (Figure 1) and about half of the *Olearia* species (Figure 2). Accordingly, Saldivia (2020) formally proposed this newly delimited group as the subtribe Celmisiinae, recognizing two main clades. The *Pleurophyllum* clade (Saldivia et al., 2022) including *Damnamenia*, *Macrolearia* Saldivia (formerly the macrocephalous *Olearia*; Kirk, 1891a), and *Pleurophyllum*, and the second clade includes *Celmisia*, *Olearia* pro parte, and *Pachystegia*. In the latter clade, eight major subclades plus the isolated *O. fragrantissima* Petrie were recognized, matching either previously recognized taxa or geographically delimited species groups (Figure 3).

MORPHOLOGY OF CELMISIINAE

Saldivia (2020) proposed the following morphological definition of Celmisiinae: Small trees rarely up to 18 m, erect or plagiotropic shrubs, subshrubs, or perennial herbs with large leaves; phyllotaxis alternate (2/5), subopposite or opposite, abaxial surface of the leaves covered by dense white to ferrugineous tomentum made up of long aseptate, T- or Y-shaped,

Far over the misty mountains

Looking up to cloud-covered Xenicus Peak at the head of Cobb Valley, Kahurangi National Park, Tasman, New Zealand. *Celmisia rupestris* Cheeseman is endemic to the Cobb Valley region. Rocky outcrops and tussock herb-fields are common habitats for many *Celmisia* Cass.

Xenicus Peak at the head of Cobb Valley, Kahurangi National Park, Tasman, New Zealand
Photo by Duncan Nicol

or lepidote-like trichomes in most of the species; shoots indeterminate with lateral capitulescences typically or plants with long shoots determinate by abortion rather than by floral development and brachyblasts bearing capitula and leaves; capitula radiate, or rarely disciform or discoid; capitulescences fasciculate, paniculate or corymbose, or capitula solitary; ray flowers pistillate, occasionally with staminodes; disc flowers perfect or functionally staminate only in some *Olearia* species from New Guinea; anthers caudate and with a conspicuous apical appendage; receptacles epaleate, alveolate; cypselae fusiform-cylindrical, obconic or rarely gibbous, 4–13-ribbed, often covered with twin trichomes. The ploidy level is mainly 12x (but also 10x, 24x, 32x, 36x, and 48x; Beuzenberg & Hair, 1984) in relation to the base number of Astereae x = 9 (Semple & Watanabe, 2009, Brouillet et al., 2009). Although most of the species in Celmisiinae have been reported as diploidised dodecaploids (2n = 108 = 12x), higher ploidy levels have also been described in particular species (e.g., 2n = ca. 432 for *Olearia angulata* Kirk). Currently, direct investigations are wanting (e.g., genomic or fluorescence in situ hybridisation experiments), therefore the specific chromosome history of polyploidisation attributed to degrees of allopolyploidy and aneuploidy cannot be determined [and interpretations to some extant remain speculative]. Saldivia et al. (2020, 2022) proposed the *Pleurophyllum* clade characterized by the combination of cyathiform and purple to dark red disc corollas, a morphological syndrome absent in the rest of Celmisiinae. The main morphological attributes are discussed next.

Shoot architecture. Celmisiinae have three main architectural features (Figure 4). Both plagiotropic *Celmisia* subshrubs and shrubs (Figure 5 A, B) and orthotropic *Olearia* trees or shrubs (Figure 5 C, D) have indeterminate shoots and axillary capitulescences. The same is true for *Damnamenia*, *Pachystegia*, and *Pleurophyllum*.

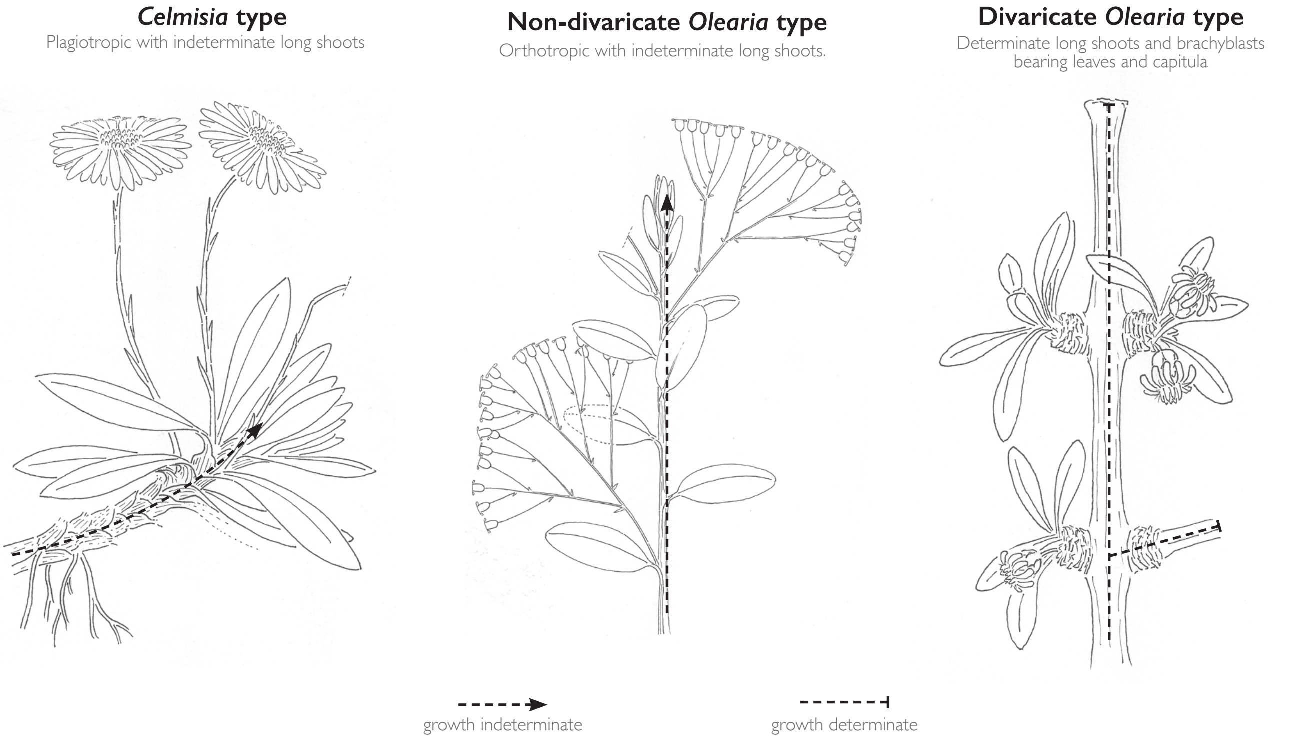
Olearia section *Divaricaster* Heads sensu stricto (Figure 5 E, F) is characterized by short shoots or brachyblasts bearing leaves and axillary capitula, long shoots with apical abortion, and at least a portion of their branches growing plagiotropically or even geotropically (i.e., Philipson's model; Heads, 2019). Section *Divaricaster* is the only element of Celmisiinae with determinate shoots by apical abortion rather than floral development. It should be noted that there are a few exceptions to capitulescence position in Celmisiinae (e.g., *Olearia pachyphylla* Cheeseman), and in several *Olearia* species the capitulescence position is often difficult to evaluate. Species with capitulescences longer than the shoot (Figure 5 C-D) can give the false appearance of a shoot with terminal capitulescences, especially when these are born near the apex. This attribute is relevant for differentiating between the Celmisiinae *Olearia* species with T- or Y-shaped leaf trichomes and the type species of *Olearia* in Brachyscominae Nesom, *O. tomentosa.* The former typically have axillary capitulescences, whereas *O. tomentosa* is the only *Olearia* outside Celmisiinae with T- or Y-shaped leaf trichomes but has terminal capitulescence (see page 5).

Alveolate and epaleate receptacles. In contrast to receptacles with a smooth surface typically seen in the South American Chiliotrichinae Bonifacino (putative sister of Celmisiinae; Saldivia et al., 2020), Celmisiinae have alveolate receptacles. However, there is variation in the height and margin of the ridges between the concavities (Figure 6 A, D, G, J). Regarding paleae subtending florets on the receptacle, *Olearia allomii* Kirk, an endemic restricted to Great Barrier Island of New Zealand, is the only species belonging to Celmisiinae which has these structures, although scattered.

Caudate anthers. In Celmisiinae the thecae bases are always projected in an acute appendage or tail. This appendage varies in length and can reach the bottom of the filament collar (Figure 6 B, E, H, K). Interestingly, this attribute has been pointed out as absent, rare, or anomalous within Astereae (Karis, 1993; Nesom, 1994a; Funk et al., 2009) or even for Asteroideae (Bremer, 1994).

Leaf indumentum. A dense layer of indumentum covers the abaxial surface of the leaves and obscures the epidermis in 94% of the species (Figure 6 C, F, I, L). Three species, *Celmisia lateralis* Buchanan, *C. sinclairii* Hook.f., and *C. glandulosa* Hook.f. do not possess such a layer but instead have glandular trichomes. The divaricate *Olearia gardneri* Heads possesses scattered T-shaped trichomes which rarely form a thin layer, and *Celmisia gibbsii* Cheeseman is sparsely covered by diminutive scurfy scales. Only *Celmisia bellidioides* Hook.f., *C. thomsonii* Cheeseman, *C. prorepens* Petrie, *C. mackaui* Raoul, and *Damnamenia vernicosa* have glabrous leaves.

Shoot architecture in Celmisiinae


***Celmisia* type**
Plagiotropic with indeterminate long shoots

Non-divaricate *Olearia* type
Orthotropic with indeterminate long shoots.

Divaricate *Olearia* type
Determinate long shoots and brachyblasts bearing leaves and capitula

Figure 4. Shoot architecture in Celmisiinae (modified from Saldivia, 2021). *Illustrations by Patricio Saldivia.*

The character states mentioned above allow a general representation of Celmisiinae, although they are not exclusive to it. Additionally, the species cited above as exceptions differ only in one of those characters. For example, although *Olearia pachyphylla* is exceptional regarding terminal capitulescence, its receptacles are epaleate and alveolate, its anther bases are caudate, and the abaxial surfaces of its leaves are densely covered by a layer of trichomes.

CURRENT GENERA IN CELMISIINAE

Celmisiinae comprise the following genera: *Celmisia, Damnamenia, Macrolearia, Pachystegia, Pleurophyllum*, and *Olearia* pro parte. As already mentioned, *Olearia* species belonging to Celmisiinae (i.e., *Olearia* pro parte) are not directly related to the type species, *Olearia tomentosa*, which belongs to Brachyscominae (Nesom, 2020a); therefore, they cannot be retained in *Olearia*.

Celmisia includes ca. 60 species endemic to New Zealand (Schönberger et al., 2021), six endemic to southeast mainland Australia, and two endemic to Tasmania (Given & Gray, 1986; de Salas & Baker, 2015). Its species range from subshrubs with herbaceous aerial structures arising from a woody hypogeous rhizome or short vertical stem to prostrate or procumbent cushion-like shrubs. It has axillary solitary capitula born on bracteate peduncles, with white and occasionally mauve pistillate ray florets and yellow perfect disc florets (Given 1969; Saldivia, 2023).

Pachystegia is a conspicuous element of the Marlborough region in the north-east South Island, one of the driest areas of New Zealand. There are four species recognized (Heenan & Molloy, 2022); however, morphological boundaries among the species are not clear. It includes stout, profusely branched shrubs 1–2 m high and axillary solitary capitula borne on almost ebracteate peduncles, with white pistillate ray florets and yellow perfect disc florets. Although morphologically distant

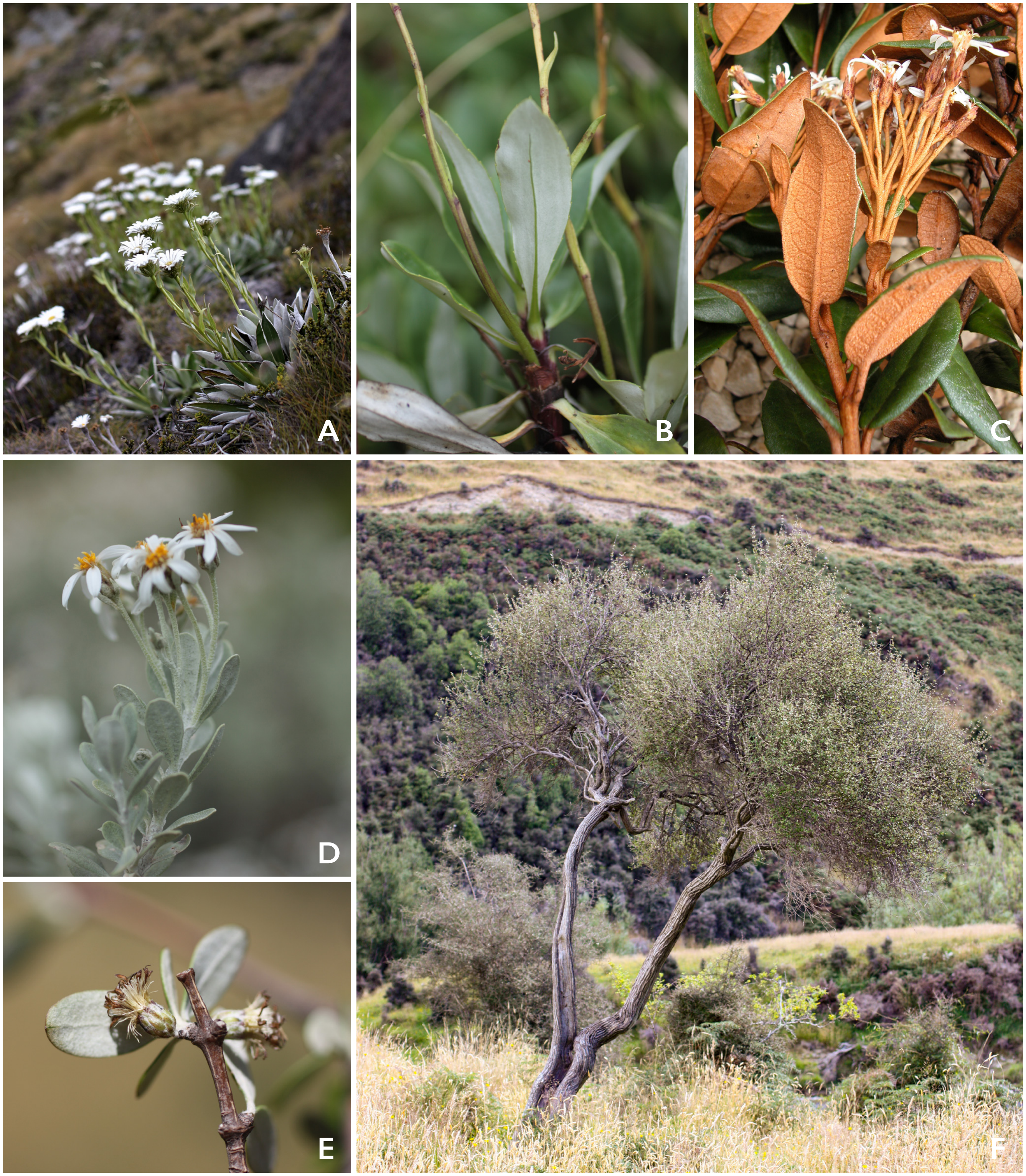


Figure 5. Main features of shoot architecture in Celmisiinae (modified from Saldivia, 2021). **A.** *Celmisia dallii* Buchanan, habit; **B.** *Celmisia bonplandii* (Buchanan) Allan, detail of axillary peduncle; **C.** *Olearia durifolia* J.Kost., axillary capitulescence; **D.** *Olearia moschata* Hook.f., axillary capitulescence; **E.** *Olearia fimbriata* Heads, detail of shoot abortion and brachyblasts; **F.** *O. fimbriata,* habit. *All the photos by Patricio Saldivia, except for F which is by Wayne Takeuchi.*

Figure 6. Main morphological features of Celmisiinae (modified from Saldivia, 2021). Receptacle: **A.** *Olearia spectabilis* J.Kost.; **D.** *O. erubescens* (DC.) Dippel; **G.** *Celmisia hieraciifolia* Hook.f.; **J.** *O. archeri* Lander. Anthers: **B.** *O. tasmanica* W.M.Curtis; **E.** *C. tomentella* M.Gray & Given; **H.** *O. velutina* J.Kost.; **K.** *O. traversiorum* (F.Muell.) Hook.f. Leaves: **C.** *C. bonplandii* (Buchanan) Allan; **F.** *O. rani* Druce; **I.** *O. avicenniifolia* (Raoul) Hook.f.; **L.** *C. discolor* Hook.f.. *All photos by Patricio Saldivia.*

Land of *Celmisia*

Celmisia sessiliflora Hook.f. is flowering during the 2018-2019 mast year. *C. discolor* Hook.f. is flowering just upslope. The marble-topped Mt. Arthur (New Zealand) is in the background.

Mt. Arthur (New Zealand)
Photo by Duncan Nicol

Eyre Mountains

Sharp ridges at the Eyre Mountains, Southland, New Zealand. This mountain range holds two narrow endemic *Celmisia* Cass. species, *C. philocremna* Given and *C. thomsonii* Cheeseman.

Eyre Mountains (New Zealand)
Photo by Patricio Saldivia

Amid the tussocks

Celmisia semicordata subsp. *aurigans* Given, a conspicuous element of subalpine tussock grasslands at Maungatua, Otago, New Zealand

Maungatua, Otago (New Zealand)
Photo by Patricio Saldivia

The wall

Celmisia lindsayi Hook.f. is a narrow endemic to the coastal cliffs of the Catlins, Otago, New Zealand. This is the sole shrubby *Celmisia* associated with this environment.

The Catlins, Otago (New Zealand)
Photo by Patricio Saldivia

Pachystegia

A *Pachystegia* shrub roots into the rocky crevices in the coastal Kaikoura mountains. Mt. Fyffe, New Zealand. Although *Pachystegia* has a narrow geographic range in the Marlborough and Kaikoura ranges, it is cultivated commonly throughout New Zealand.

Mt. Fyffe, Kaikoura (New Zealand)
Photo by Duncan Nicol

from other Celmisiinae taxa from New Zealand, it resembles some Australian Celmisiinae species such as *Olearia pannosa* Hook.f.

The *Olearia* species belonging to Celmisiinae comprise a diverse group distributed in Australia, New Zealand, and New Guinea. This group shows a wide range of morphological syndromes, ranging from compact ericoid shrubs to trees up to 18 m tall. According to the phylogeny shown in Figure 3, the following subgroups are recognized:

Australian species: 23 species from mainland Australia and Tasmania and one species from Lord Howe Island.

***Olearia fragrantissima*:** a fragrant peach-scented tree endemic to the South Island of New Zealand.

***Olearia* sect. *Divaricaster*:** 11 species endemic to mainland New Zealand with a remarkable divaricate architecture (Sect. *Divaricaster* sensu stricto; Heads, 1998) and two species endemic to the Chatham Islands with no divaricate architecture (Heenan et al., 2008).

***Olearia arborescens* and allies:** 14 species endemic to mainland New Zealand.

New Guinea species: 19 species, mostly alpine (Koster, 1966; van Royen, 1983).

***Olearia paniculata* and allies:** eight species endemic to mainland New Zealand.

***Olearia furfuracea* Hook.f. complex:** five species endemic to the North Island of New Zealand.

Damnamenia is a monotypic genus endemic to the subantarctic Campbell and Auckland Islands. The sole species, *D. vernicosa,* is a small, glabrous, stoloniferous mostly herbaceous plant, developing from a thick, woody, multicipital basal stock. It forms rosettes 4–15 cm diameter and a few centimetres high at tips of branchlets and leafy stolons. Like *Celmisia*, it develops solitary capitula borne on bracteate peduncles, with white pistillate ray florets, but, in contrast, *Damnamenia* has purple perfect disc florets (Given, 1973; Saldivia et al., 2022).

Macrolearia is a recent segregate of *Olearia* with six species and a hybrid all endemic to New Zealand. *Macrolearia* species are shrubs or small trees, 1–10 m high, profusely branched from the base or near the base, with the foliage developed at the end of the branches which are often covered with lanose-white indumentum. Capitula are solitary, or arranged in loose umbelliform or racemiform capitulescences, axillary or terminal, radiate, disciform, or discoid (Saldivia et al., 2022).

Pleurophyllum, like *Damnamenia*, is endemic to the subantarctic islands but with a wider range, extending north-east to the Antipodes Islands and south-west to Macquarie Island (Saldivia et al., 2022). *Pleurophyllum* species are rosette herbs up to 50 cm high and 100 cm wide. Most of the stem corresponds to a hypogeous rhizome, from which a single or a few short axes arise bearing the new growing leaves. Floral branches are axillary, stout, erect, arising from the bottom of the plant. Capitula are arranged in loose or dense racemiform or pseudocorymbiform capitulescences clustered towards the distal part of the floral branches, erect or nodding, radiate or disciform.

DISTRIBUTION AND ECOLOGY

The ca. 159 Celmisiinae species are distributed in Australasia as follows: the Australian-New Zealand subantarctic islands: five species (3%), mainland New Zealand: 103 species (65%) including four species on the Chatham Islands, southeast Australia, including Tasmania and Lord Howe Island: 32 species (20%), New Guinea: 19 species (12%).

The *Pleurophyllum* clade is confined mainly to the south of New Zealand's South Island, Stewart Island/Rakiura, Chatham Islands, and the subantarctic islands. Its distribution contrasts with the other members of Celmisiinae, which are absent from the subantarctic islands. The most interesting feature of the *Pleurophyllum* clade's distribution is the allopatry between *Macrolearia* and the subantarctic endemics *Pleurophyllum* and *Damnamenia* (Figure 3). Even if the presence of *M. lyallii* (Hook.f.) Saldivia in the Auckland Islands is considered natural, it is restricted to the

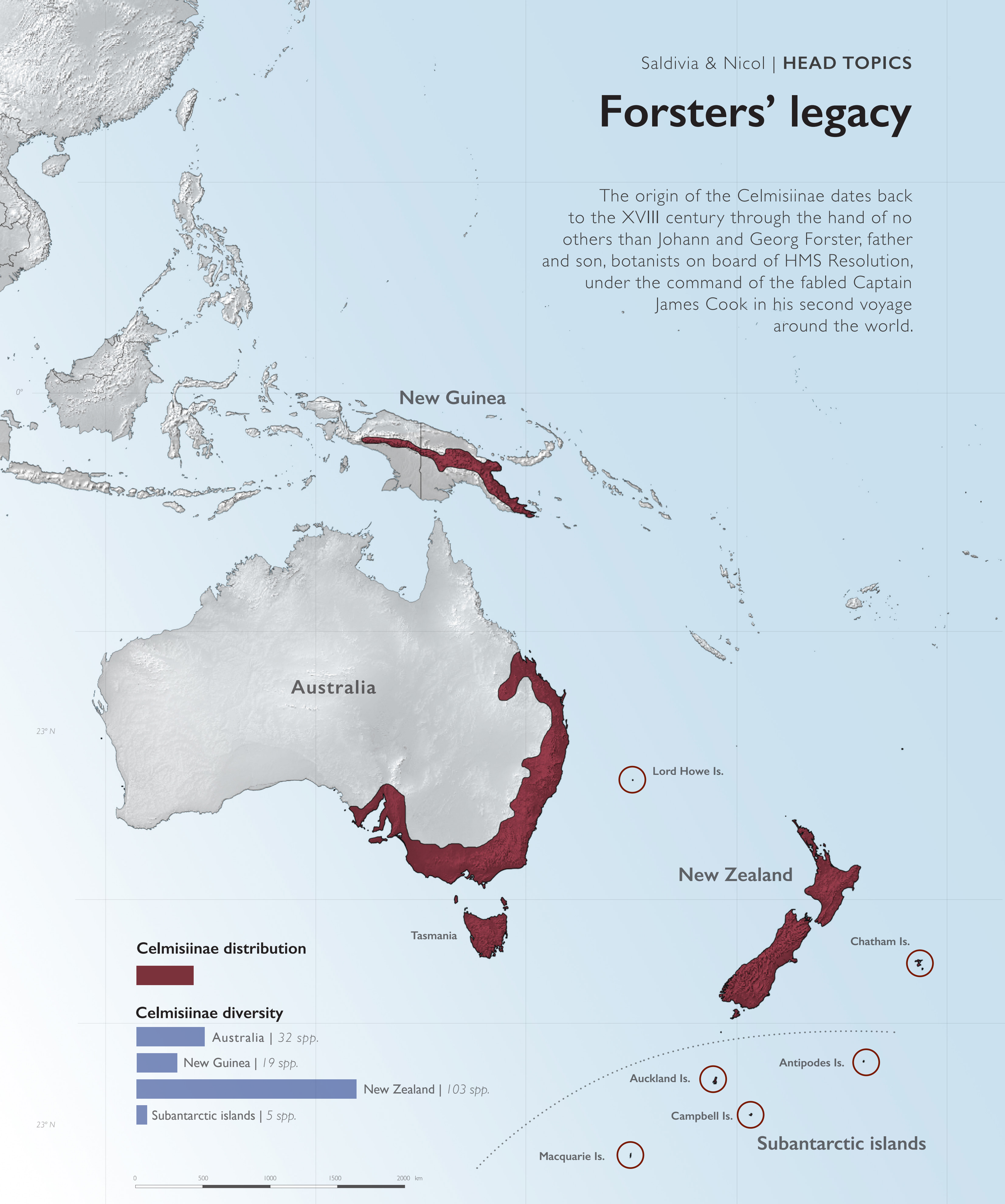
Fiordland

Fiordland tussock herb-field and shrubland hosts more than 20 Celmisiinae species. Although there is geographic overlap for many of these species, there is also ecological differentiation such as the ridge-lines, rocky outcrops, or swampy edges of alpine tarns, here, at Mt. Burns, Southland, New Zealand.

Mt. Burns (New Zealand)
Photo by Duncan Nicol

Forsters' legacy

The origin of the Celmisiinae dates back to the XVIII century through the hand of no others than Johann and Georg Forster, father and son, botanists on board of HMS Resolution, under the command of the fabled Captain James Cook in his second voyage around the world.



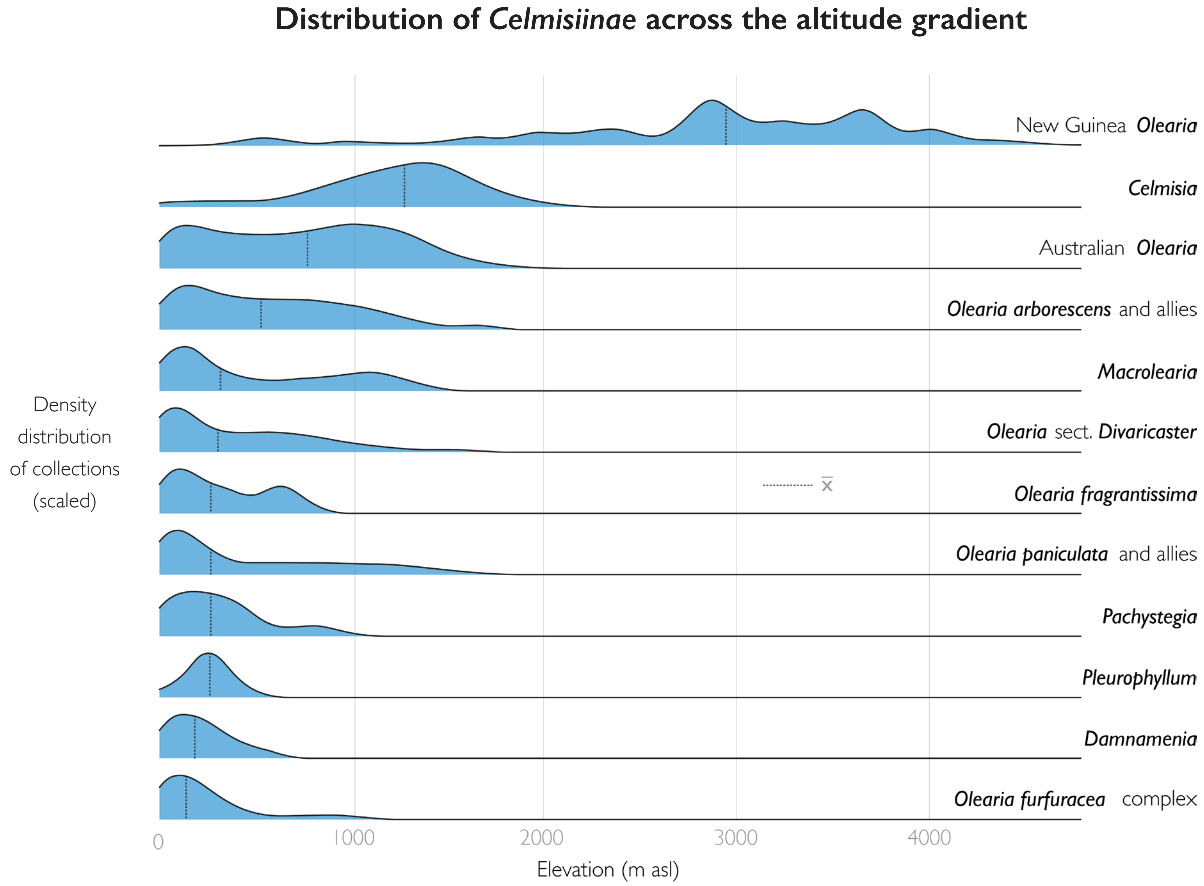


Figure 7. Elevation profiles for each genus and *Olearia* subgroups (modified from Nicol, 2023). Herbarium collections for species within each group were retrieved from GBIF (Global Biodiversity Information Facility) and studied from New Zealand herbaria for some groups (e.g., Saldivia, 2023). Elevation values were extracted from the georeferenced collections using SRTM (Shuttle Radar Topography Mission) data available from WordClim v2 (Fick & Hijmans, 2017).

north of Auckland Island and small islands around it (Enderby, Ocean, and Ewing Islands), forming coastal forest patches where *Pleurophyllum* species do not occur (Godley, 1965; Johnson & Campbell, 1975; Campbell & Rudge, 1976; Wilmshurst et al., 2015 Saldivia et al., 2022).

In contrast to the allopatry seen in the *Pleurophyllum* clade, many *Olearia* groups have overlapping distributions throughout the forests and shrublands of mainland New Zealand and southeast Australia, where hybridism sometimes occurs. There are also mountains which host more than nineteen species of *Celmisia*. However, within most Celmisiinae clades, there is a high degree of geographic separation between closely related species. In New Guinea, for example, *Olearia* species "have a remarkably restricted area, sometimes confined to one mountain" (Koster, 1966). This pattern of increased geographic overlap at higher taxonomic levels (or older cladogenetic events) is consistent with allopatric differentiation, followed by range expansion and overlap through time.

Genera or clades and species in Celmisiinae occupy a wide array of habitats and elevations (Figure 7). New Guinea *Olearia* occupy the highest sites with most localities being above 2,000 m, and the highest reaching around 4,000 m (Koster, 1966). *Celmisia*, commonly known as mountain daisies in New Zealand and snow daisies in Australia is the next highest group. Although the mountains in New Zealand reach a peak height of 3,724 m at Aoraki/ Mt. Cook, *Celmisia* occupies sites only as high as ca. 2,300 m. *Celmisia* lives in a diverse range of habitats, being found in swamps and bogs, well-drained grasslands and subalpine woodlands rocky outcrops, coastal cliffs, cushionfields, tussock-

Buckland

View northward from the Buckland Peaks, Paparoa Range, New Zealand. The Paparoa metamorphic core complex is an important biogeographic feature as many species are endemic to the area and many others have a distribution limit surrounding it (Heads, 2017). For example, in Celmisiinae, *Celmisia dubia* Cheeseman and *C. dallii* Buchanan have limits just to the north, and *C. morganii* Cheeseman is endemic to it.

Buckland Peaks, Paparoa Range (New Zealand)
Photo by Duncan Nicol

herbfields, scree slopes, scrub, and rock crevices. Some species such as *C. spectabilis* Hook.f. and *C. gracilenta* Hook.f. can be found in most of these habitats. Other species can have a much narrower habitat, such as *C. glandulosa* and *C. sericophylla* J.H.Willis found only in bogs, or *C. lindsayi* Hook.f. found only on coastal cliffs in the Catlins, Otago, New Zealand.

Some sub-alpine and montane *Olearia* in Australia and New Zealand are found above 1,000 m but most are below. Although the New Guinea *Olearia* occupy higher elevations than *Celmisia*, their habitat is similar to other *Olearia* from New Zealand and Australia. Most *Olearia* species are found in forests, forest margins, forest gullies, scrub, shrubland, and coastal cliffs. Some are found along streamsides, swampy sites, or exposed rock (Koster, 1966). The divaricate *Olearia* can occupy gorges, flood-prone valleys, frosty terraces, alluvial flats, poorly drained sites, rock bluffs, and hillslopes (Heads, 1998). *Pachystegia* tends to be found on coastal, hilly, or mountainous rocky sites. *Macrolearia* is found in forest, scrub, coastal cliffs, hillslopes, peaty ground and bogs, and *M. colensoi* (Hook.f.) Saldivia is one of the dominant species of the subalpine vegetation of New Zealand. There are few habitats in which Celmisiinae are not found.

Many species in *Celmisia*, and also *Macrolearia colensoi*, have a record of masting (i.e., the intermittent production of large fruit crops). Other species in tree genera such as *Nothofagus* Blume, *Dacrydium* Sol. ex G.Forst, and *Metrosideros* Banks ex Gaertn, also exhibit masting, and during a mast year en masse flowering occurs which can be spectacular (Dawson & Lucas, 2019).

Celmisiinae also have a diverse range of ecological interactions with invertebrate fauna. More than 40 endemic New Zealand moth species have been found on the divaricate *Olearia* and *O. fragrantissima* (Patrick, 2000). Seventeen of these are restricted feeders to this group. The moths feed on leaves, bark, foliage buds, flowers, and some scavenge other insects. Groves of divaricate *Olearia* host a range of algae, lichens, and mosses, all of which support a range of insect groups, such as Coleoptera, Diptera, and Hemiptera. In New Zealand other Celmisiinae associations include *Asterivora* (Lepidoptera) which feed within webbing on *Celmisia* and *Olearia*; the alpine weevil *Kuschelysius* (Coleoptera) has been found on *Celmisia,* and because of pollen found in the gut, it has been hypothesised as a pollinator (Brown & Leschen, 2018); *Macrolearia* and *Pleurophyllum* both provide larval food for both the owlet moth *Graphania erebia* (Noctuidae) and the tortrix moth *Apoctena syntona* (Tortricidae) (Patrick, 1994); *Celmisia* stems are specially eaten by the larvae of the diurnal tortrix moth *Gelophaula*; in the alpine zone the lygaeid bugs in the genus *Rhypodes* (Hemiptera) feed during day time on *Celmisia*; the larvae of the picture-winged flies *Trupanea longipennis* and *T. centralis* feed on the flowers of *Celmisia* and the adults are involved in pollination; and the nymph and adult of the wingless stonefly *Vesicaperla celmisia* (Plecoptera) feed on the leaves of *Celmisia haastii* Hook.f. (Patrick, 2021).

In Australia, most *Olearia* species included in ecological studies were part of the Australian lineage in Brachyscominae, such as *O. algida* N.A. Wakef. (Green, 2006) and *O. viscidula* Benth. (Bell, 1985), and there are few data on Australian *Celmisia*. Monophagous larvae of the leaf-rolling moths *Epiphyas* and *Technitis* (Tortricidae) have been observed on *O. phlogopappa* (Labill.) DC. and *O. ramulosa* Benth. (Brachyscominae), but also *O. tasmanica* (Hook. f.) W.M. Curtis and *O. argophylla* (Labill.) Benth. (Celmisiinae) (McQuillan, 1992; McDougall et al., 2018). In Charlotte Pass, Kosciuszko National Park, both dipterans and coleopterans were observed visiting inflorescenses of *O. algida* (Brachyscominae), and at the same site *Celmisia* sp. were visited by those two and also hymenopterans and lepidopterans (Goodwin et al., 2021). In the same national park, species of Tephritidae were found to predate on most if not all flower heads in *C. costiniana* M.Gray & Given, and out of 29 Asteraceae species observed, *Tephritis bushi* was found only on *C. costiniana* (Pickering, 2009). Additionally, a nectar and pollen bee review found that *Pachyprosopis* (Colletidae) and *Halictus* (Halictadae) are visitors of Australian *Celmisia* (Armstrong, 1979). The associations outlined above are not exhaustive, and similar studies of ecological interactions in New Guinea are, to our knowledge, lacking. However, what can be drawn is that Celmisiinae are an important habitat and an important part of the life cycle for a variety of invertebrate taxa in Australasia.

WHAT'S NEXT IN THE TAXONOMY OF CELMISIINAE: FUTURE TAXONOMIC RESEARCH.

The phylogenetic resolution using traditional markers has been insufficient to resolve the relationships among the main recognized clades. Therefore, a new generic taxonomic proposal solving mainly the generic affiliation of most of the *Olearia* species has remained elusive. Nonetheless, the target enrichment protocol Angiosperms353 and a broad species-sampling approach has recently provided robust phylogenetic evidence to propose new taxonomic arrangements in Celmisiinae, including new affiliations for *Olearia* pro parte (Nicol, 2023). New studies are forthcoming with formal taxonomic proposals which will provide a sound and hopefully stable generic circumscription of the subtribe (DN and PS in preparation).

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