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THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER

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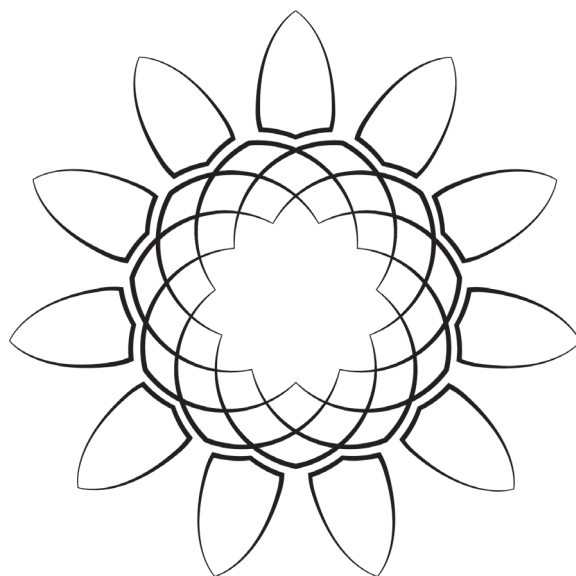THE INTERNATIONAL COMPOSITAE ALLIANCE

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CAPITULUM

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Cover photo: *Pleurophyllum speciosum* Hook.f. in flower in a megaherb field with *Bulbinella rossii* (Hook.f.) Mottet . In the distance are two pink inflorescences of *Anisotome lyallii* Hook.f. Col-Lyall Saddle, Campbell Island, New Zealand

Photo by Phil Garnock-Jones

Island Compositae: across the seven seas.

Island biota has long fascinated biologists and provided valuable contributions to our knowledge of biodiversity and evolution. Compositae on islands, in particular, are a fascinating study system. Not only is the family exceptionally diverse on islands, but Compositae also provides many remarkable examples of island adaptive radiations, such as the textbook Silversword alliance on the Hawaiian archipelago, and many cases of interesting trait evolution on islands, for example, the woody *Sonchus* alliance on the Canary Islands. In this special island issue, we bring you six articles featuring Compositae from archipelagos around the world.

Illustration by Lizzie Roeble
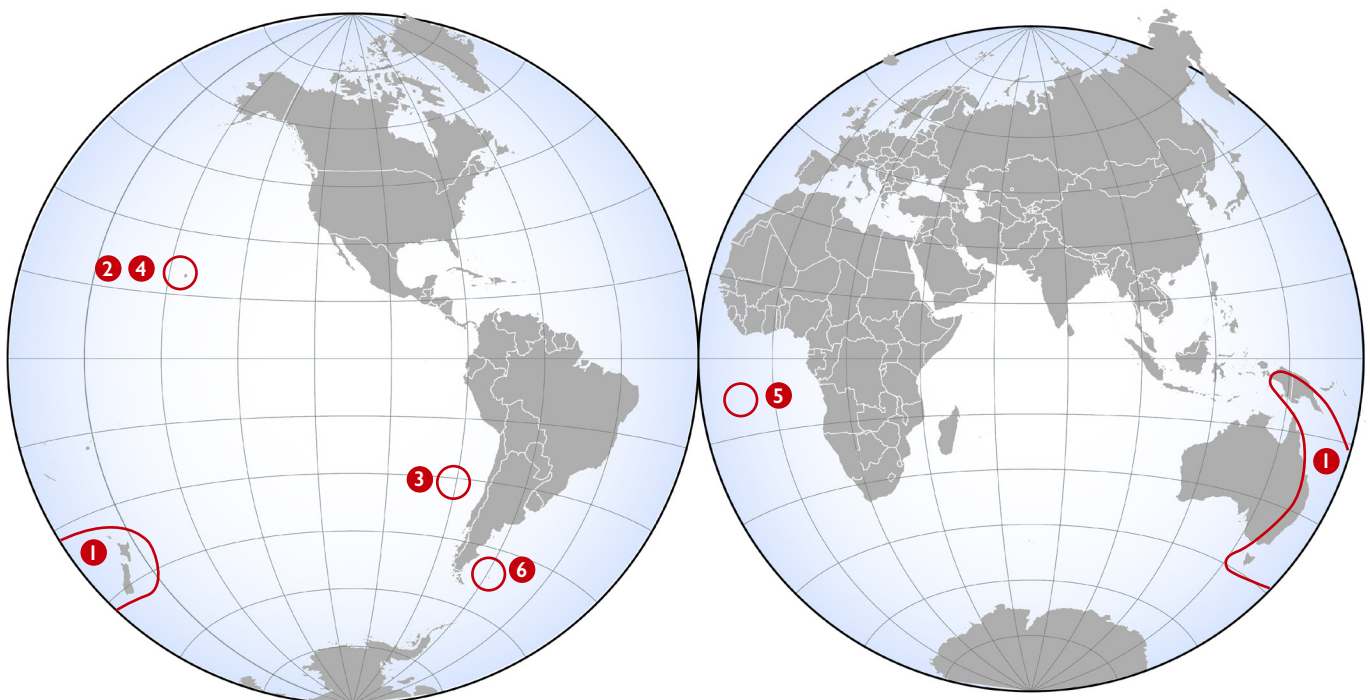
❶ Australasia
Patricio Saldivia and Duncan Alastair Nicol who explore the diverse Australasian Celmisiinae lineage which includes many charismatic island endemics such as Pleurophyllum on the Subantarctic islands. (see page **1**)

❷ Hawaiian Islands
We journey to Hawai'i with Susan Ching Harbin who presents us with an overview of the rare and critically endangered endemic Hesperomannia and gives an update on the current conservation status (see page **26**).

❸ Juan Fernández Islands
Tod Stuessy and Daniel Crawford discuss the history of the monospecific genus Yunquea, which grows only on the top of a single peak on Robinson Crusoe Island in the Juan Fernández Archipelago. (see page **43**)

❹ Hawai'i Island
Renee Bellinger gives a brief overview of genome sequencing methods and progress and then highlights recent work on the genome assembly of Bidens hawaiensis, a member of the Hawaiian Bidens adaptive radiation. (see page **50**)

❺ Saint Helena Island
A group led by Timothy Collins unravels the history of how an Australian paper daisy (Xerochrysum bracteatum) came to be naturalized on the island of St Helena during the time of Napoleón Bonaparte's exile. (see page **58**).

❻ Malvinas/Falkland Islands
A team led by Gisela Sancho takes us on a journey to the Malvinas/Falkland Archipelago in pursuit of a minuscule yet amazing Lagenophora. (see page **66**)

Be sure to check out the stunning images by Steve Wagstaff and Phil Garnock-Jones in the 'Style' section.
This issue finishes with a recap of the latest Composite news in the 'TICA Times' section.

An overview of Celmisiinae (Astereae):
A diverse endemic Australasian lineage

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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 paniculat*a (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)
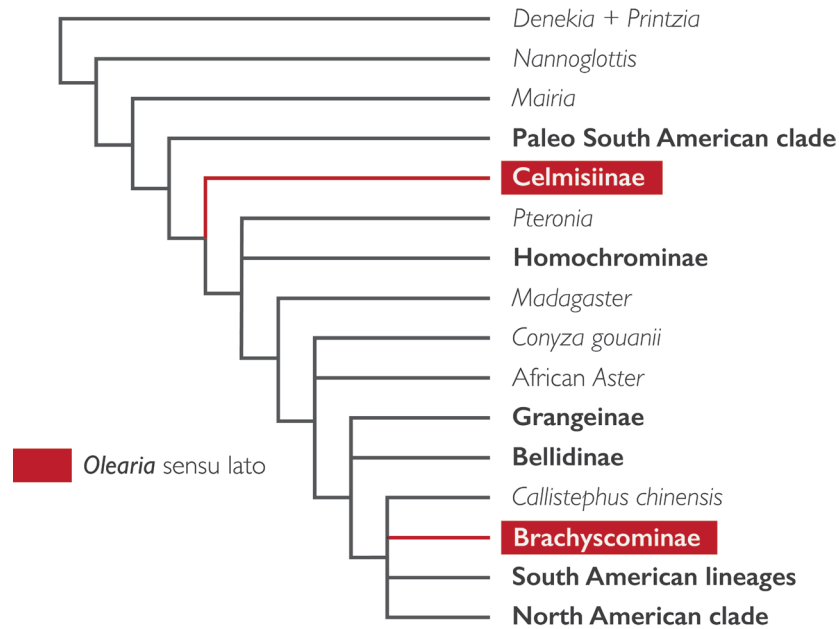
Figure 2. For over a century, *Olearia* has been regarded as the largest Australasian genus of Asteraceae, with ca. 180 spp. divided into five sections based on leaf trichome morphology (Archer, 1860; Bentham, 1867) plus one section based on shoot architecture (Heads, 1998). However, Nesom (1993, 1994a), 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*

Tab XXIIII

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).

Aster tomentosus
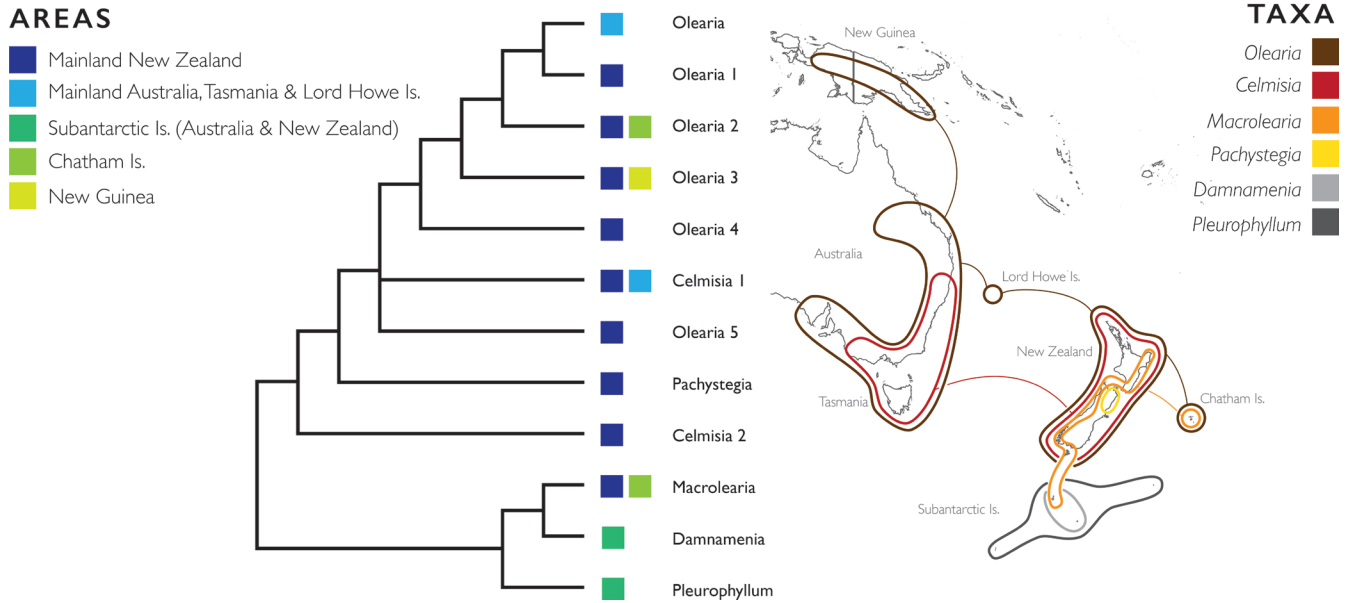
Figure 3. Phylogeny and distribution of Celmisiinae. Summarized phylogeny of Saldivia (2021). The *Olearia* pro parte species from New Zealand are divided as follows: *Olearia* 1 = *O. fragrantissima*, *Olearia* 2 = *O.* sect. *Divaricaster*, *Olearia* 3 = *O. arborescens* and allies, *Olearia* 4 = *O. 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	Non-divaricate *Olearia* type	Divaricate *Olearia* type
Plagiotropic with indeterminate long shoots	Orthotropic with indeterminate long shoots.	Determinate long shoots and brachyblasts bearing leaves and capitula

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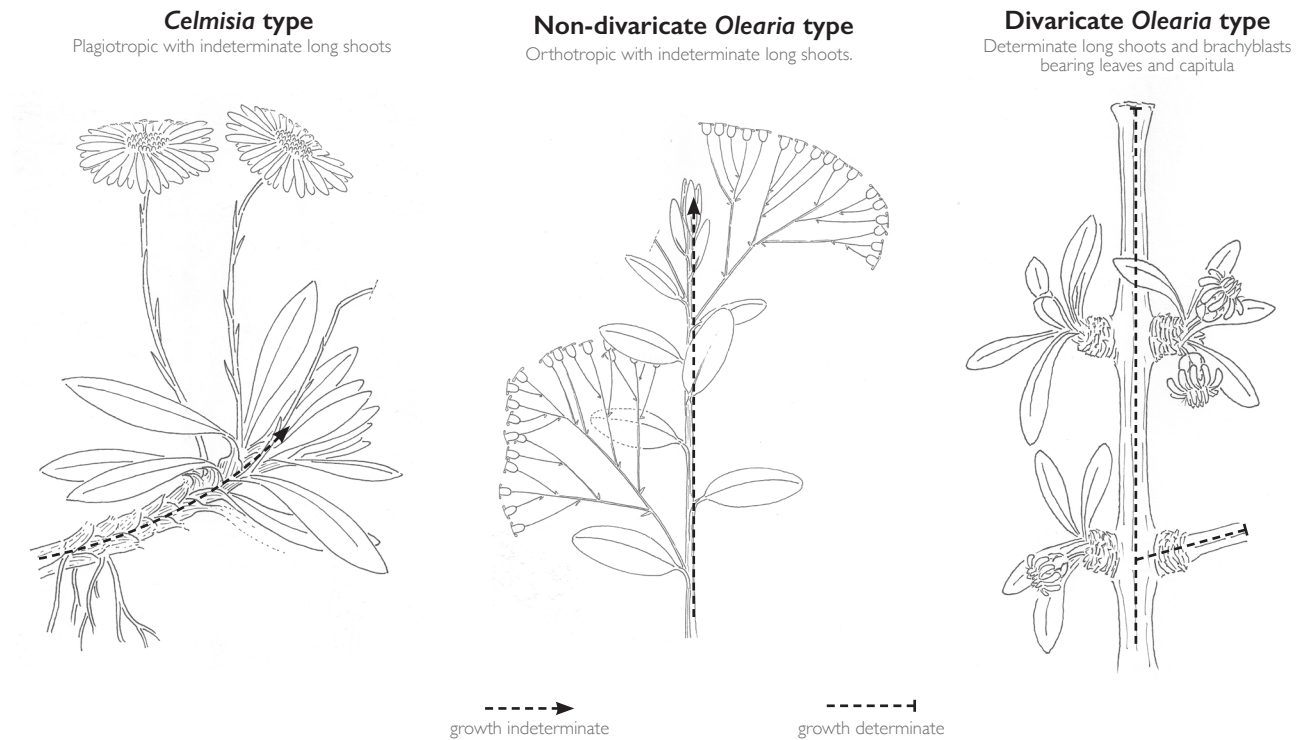
Figure 4. Shoot architecture in Celmisiinae (modified from Saldivia, 2021). *Illustrations by Patricio Saldivia.*

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
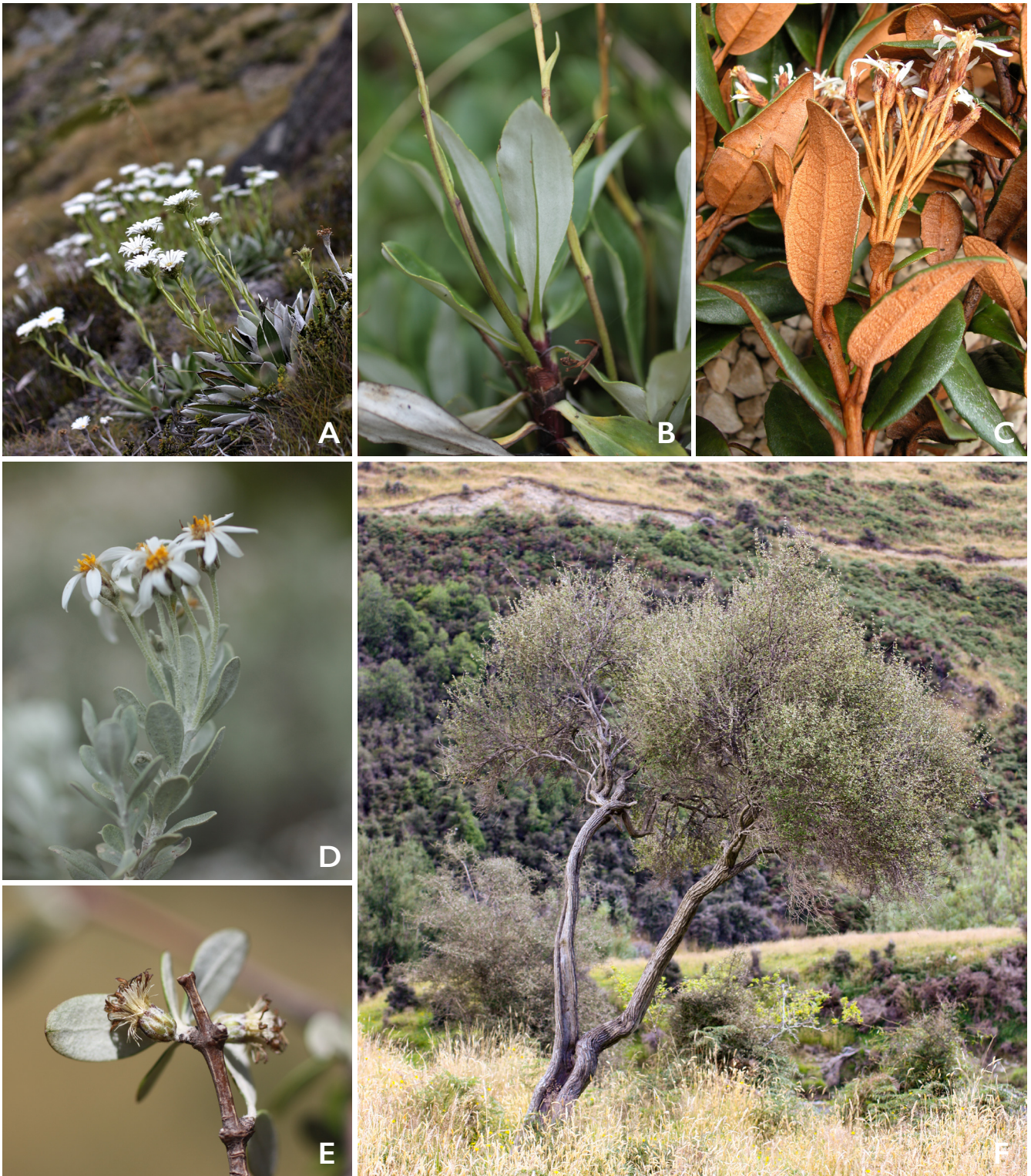
Figure 5. Main features of shoot architecture in Celmisiinae (modified from Saldivia, 2021). **A.** *Celmisia dallii* Buchanan, habit; **B.** *Celmisia bonplandii* (Buchanan) Allan, detail of axillary peduncle; **C.** *Olearia durifolia* J.Kost., axillary capitulescence; **D.** *Olearia moschata* Hook.f., 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.

New Guinea

Australia

0°

23° N

Lord Howe Is.

New Zealand

Tasmania

Chatham Is.

Celmisiinae distribution

Celmisiinae diversity

Australia | *32 spp.*

New Guinea | *19 spp.*

New Zealand | *103 spp.*

Subantarctic islands | *5 spp.*

23° N

Antipodes Is.

Auckland Is.

Campbell Is.

Subantarctic islands

Macquarie Is.

0   500   1000   1500   2000   km
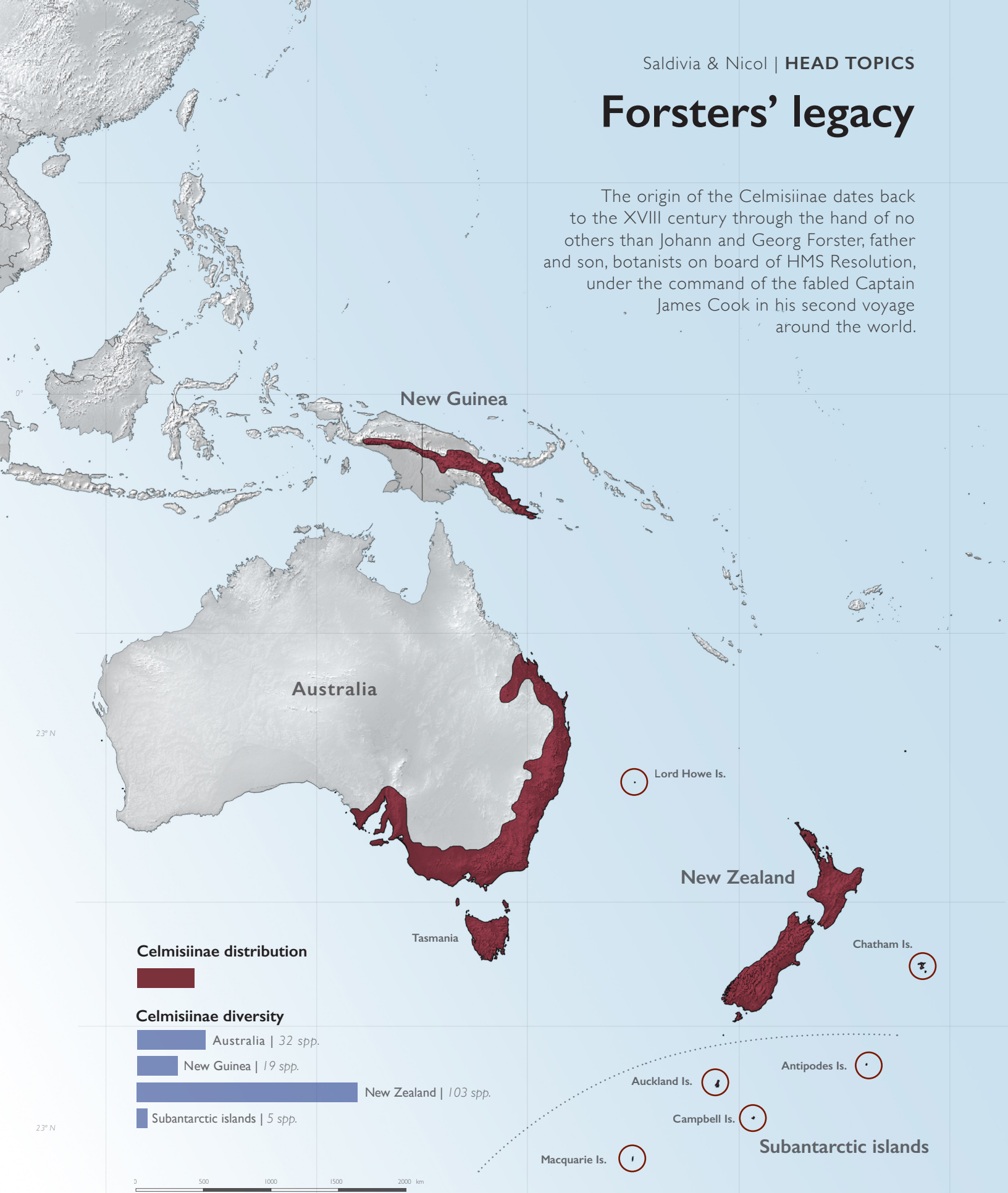
Distribution of *Celmisiinae* across the altitude gradient
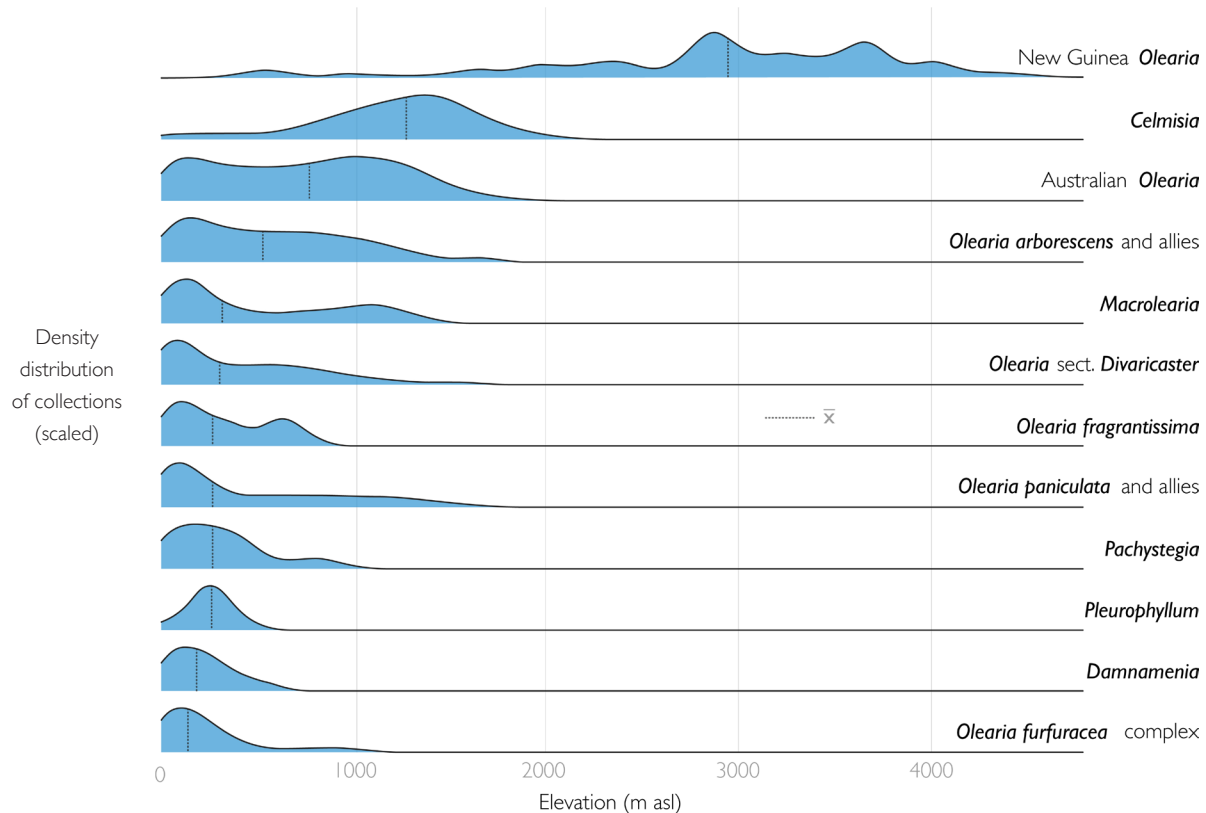
Figure 7. Elevation profiles for each genus and *Olearia* subgroups (modified from Nicol, 2023). Herbarium collections for species within each group were retrieved from GBIF (Global Biodiversity Information Facility) and studied from New Zealand herbaria for some groups (e.g., Saldivia, 2023). Elevation 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).

ACKNOWLEDGMENTS

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Hesperomannia A. Gray (Vernonieae):

Extreme rarity and conservation status of an endemic Hawaiian genus

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ABSTRACT

Hesperomannia, is a Hawaiian endemic genus of four species and is highly endangered throughout its range. The four species and their habitats are described and a conservation assessment for each species and the genus is provided. Each species is threatened by small population size, climate change, and non-native species- including rodents, ungulates, and invasive plants. Conservation measures such as ungulate fencing, weed control, rodent control, and hand pollination have proven effective but specific funding for these efforts is necessary to prevent the extinction of all four species.

Keywords: Asteraceae, Endangered species, climate change, Compositae, hand pollination, Hawaii, Hawaiian flora, invasive species.

INTRODUCTION

Hesperomannia A. Gray is endemic of the Hawaiian islands,and is comprised of four species: *H. arborescens* A. Gray, *H. lydgatei* C.N. Forbes, *H. oahuensis* (Hillebr.) O. Deg., and *H. swezeyi* O. Deg. (Morden & Ching Harbin 2013; Wagner et al. 2012). The genus was originally thought to have been most closely related to South American genus *Stifftia* J.C.Mikan, Subfamily Stifftidoideae (formerly Tribe Mutisieae), based on morphological characters (Funk and Wagner 1995), but more recently, genetic information placed the genus in the Tribe Vernonieae with closest known relatives in *Gymnanthemum* Cass. of the East Africa and Madagascar region (Kim et al., 1998; Keeley et al., 2007). This geographical distance is immense, 12,000 km, and is proposed as the result of dispersal via an extinct ancestor(s) (likely through Australia) to the Hawaiian Archipelago (Keely et al., 2021; Price & Wagner, 2018). Divergence from Madagascan *Gymnanthemum* is estimated at 17.19 Mya with diversification within the Hawaiian archipelago around 5.7 Mya. (Price & Clague, 2002; Keeley et al., 2007; Keeley et. al., 2021). Other Hawaiian plant radiations with African origins include *Kokia* Lewt., Malvaceae (Seelanan, 1997), and all Hawaiian Campanulaceae (Givnish, 2009; Steve Hunter, pers. comm. 2022).

Hawaii's floristic endemism is unmatched by any other archipelago at ~90% for vascular plants (Wagner et al. 1990, 2012). Driven by extreme isolation of high islands with varied biomes, the evolution of the Hawaiian flora is arguably one of the most fascinating. Unfortunately, this unique flora holds another distinction: one of the most endangered floras in the world (Sakai et al., 2002; Weisenberger & Keir, 2014; Rønsted et al., 2022). The Hawaiian *Hesperomannia*, is a prime example of both extraordinary evolutionary radiation from a long-distance dispersal event (Keeley et al. 2007, Kim et al. 1998) as well as acute rarity. In this paper we aim to provide a short taxonomic overview of this interesting genus and an update of its precarious conservation status.

TAXONOMIC OVERVIEW

Hesperomannia A.Gray, Proc. Amer. Acad. Arts 6: 554, 1865. Type species: Hesperomannia arborescens A.Gray.

Trees; leaves alternate. Capitula solitary or in clusters of 2-10, homogamous, discoid; involucre of 4 to 8 series of phyllaries, persistent; receptacle epaleate. Florets monoclinous, corollas actinomorphic, deeply 5-lobed, yellow; anthers tailed, apical appendage acute; style branches dorsally prorulose, scarcely separated at tip when receptive, with little stigmatic tissue. Achenes costate, glabrous. Pappus of scabrid setae, arranged in 2-3 series. Pollen tricolporate, minutely spiculiferous (n = 10). Hawaii. Four species.

KEY TO THE SPECIES OF *Hesperomannia* A.Gray

1a. Flowering heads nodding at anthesis; leaf blades glabrous; phyllaries white to pink or brown at anthesis; Kauai ....**H. lydgatei**

1b. Flowering heads erect to ascending at anthesis; leaf blades pubescent, sparsely puberulent, tomentose, densely tomentose, sparsely pubescent, or nearly glabrous; phyllaries green and magenta, magenta, or dusty pink at anthesis; other Hawaiian Islands, not Kauai.

    2a. Plants with lower leaf surfaces, petioles, and apical buds densely tomentose; leaf blades ovate to elliptic-ovate, upper surface tomentose to sparsely pubescent; innermost phyllaries 2.3–2.5 cm long; phyllaries green and magenta at anthesis; O'ahu (Waianae Mountains) ....**H. oahuensis**

    2b. Plants with lower leaf surfaces, petioles, and apical buds nearly glabrous or sparsely pubescent; leaf blades oblanceolate to obovate or broadly oblanceolate (sometimes elliptic), upper surface glabrous; innermost phyllaries 2.7–3.0 cm long; phyllaries dusty pink or magenta at anthesis; Maui, Molokai and Lanai or O'ahu (Koolau Mountains)

        3a. Leaf blades oblanceolate to obovate, lower surface sparsely puberulent, especially along lower 1/3–1/2 portion of midrib on young leaves, upper surface glabrous; petioles 1/7–1/4 of total leaf length; peduncles 8–13 mm long; phyllaries in 3rd to 5th series 4 –5 cm wide; phyllaries dusty pink at anthesis; West Maui, Molokai, Lanai...**H. arborescens**

        3b. Leaf blades oblanceolate to broadly oblanceolate, or sometimes elliptic, both surfaces glabrous or nearly so with lower leaf blade surface of young leaves sometimes sparsely pubescent along 1/2–1/3 of midrib; petioles 1/8–1/7 of leaf total length; peduncles 4–6 mm long; phyllaries in 3rd to 5th series 3–3.5 cm wide; involucre phyllaries magenta at anthesis; O'ahu (Koolau Mountains) ....**H. swezeyi**

Ku'u home 'o *Hesperomannia*

In Ōlelo Hawai'i, the archipelago's native tonge, Ku'u home 'o *Hesperomannia* means "the beloved home of *Hesperomannia*". The Hawaiian archipelago is home the endemic genus *Hesperomannia* A.Gray (Vernonieae). A genus composed of four species, all are critically endangered.

Ni'ihau

Kaua'i

O'ahu

Honolulu

Moloka'i

Maui

Lana'i

Kaho'olawe

Hawai'i

▲ *Mauna Kea*

▲ *Mauna Loa*

Hawaiian Archipelago

● *Hesperomannia*

0   20   40   60   80   100 km

Hesperomannia arborescens A.Gray, Proc. Amer. Acad. Arts 6: 554, 1865. Type: Summit of Lanai, *H. Mann & W. T. Brigham 357*, 1865 (holotype: GH! [00008996]; isotypes: BISH 1005806!, BISH 1005807!, US 00432531).

Hesperomannia arbuscula Hillebrand, Flora Hawaiian Islands, 232, 1888. Type: West Maui about 1,200 ft above Lahaina, *E. Bishop s. n.*, May 1871 (holotype: B [destroyed], fragment: BISH 1005809!; lectotype: GH 00008997!; isolectotype: BISH 1005808!).

Hesperomannia mauiensis St. John, Ann. Mo. Bot. Gard. 70:198, 1983. Type: Iao Valley, Makalaloa Stream, steep forest slope, West Maui, *Hobdy 859* (holotype: BISH 1005814!).

Trees 2– 4 m tall, young stems and apical buds pubescent. Leaves with petioles 1/7–1/4 of total leaf length, sparsely puberulent; leaf blades oblanceolate to obovate, lower leaf surfaces sparsely puberulent, especially along lower 1/3–1/2 portion of midrib on young leaves, upper leaf blade surface glabrous, margins entire or slightly crenate/ undulate. Heads on stout puberulent peduncles, 8–13 mm long, erect at anthesis; involucre in 6 or 7 series, phyllaries dusty pink at anthesis, inner phyllaries 2.7–2.9 cm; middle phyllaries 4 –5 cm wide. Corollas 2.5–3 cm long; pappus 2.2-2.5 cm long, elements tapering towards the apex, fimbriate at the base, scabrid all along, pale pink to light brown.

Distribution and ecology: Highly endangered in wet forest on West Maui; possibly extirpated from Molokai; extirpated from Lanai.

Additional specimens examined: United States. Hawaii. Lanai. *C.N. Forbes 322.L*, Sep 1917(BISH1022037); *W.B. Hillebrand s.n.*. s.d.(BISH1022036); *G.C. Munro 492*, Mar 1922(BISH1022032); *G.C. Munro 684*, Jun 1922(BISH1022039); *G.C. Munro 936*, 01 Nov 1929(BISH1022034); *G.C. Munro s.n.*, 1925(BISH1022040); *G.C. Munro 492*, Mar 1922(BISH1022033); *G.C. Munro 104*, 17 Jun 1927(BISH1022038). **Maui**. *R.W. Hobdy 3046*, 07 Jun 1989(BISH1022135); *R.W. Hobdy 758*, 20 Jan 1980(BISH1022136); *J. Lau 3231*, 21 Jan 1989(BISH1022043); *J. Lau 3230*, 21 Jan 1989(BISH1022044); *J.S. Meidell 126*, 22 Aug 1996(BISH1022041); *J.S. Meidell 141*, 29 Aug 1996(BISH1022045); *H.L. Oppenheimer H90612*, 13 Sep 2006(BISH1022042); *H.L. Oppenheimer H71302*, 24 Jul 2013(BISH1199205); *H.L. Oppenheimer H71410*, 30 Jul 2014(BISH1199204); *K.R. Wood 6106*, 26 Mar 1997(BISH1022046). **Molokai**. *C.N. Forbes 239.Mo*, Jul 1912(BISH1022050); *S.L. Montgomery s.n.*, 02 Sep 1976(BISH1022047); *S.L. Montgomery s.n.*, 02 Sep 1976(BISH1022048); *S. Perlman 10341*, 10 Mar 1989(BISH1022049).

Hesperomannia lydgatei C.N.Forbes, Occas. Pap. Bernice Pauahi Bishop Mus. 4: 220, 1909. Type: Wahiawä Mountains, Kauaʻi, *Lydgate s. n.*, May 1908 (holotype: BISH 1005813!).

Small trees 2–3 m tall, young stems glabrous. Leaves glabrous, petiole 1/10 –1/7 of total leaf length; leaf blades obovate-elliptic to broadly oblanceolate, margins entire. Heads on narrow glabrous peduncles, 23– 40 mm long, nodding at anthesis; involucre in 4 or 5 series, phyllaries white to pink or brown at anthesis, inner phyllaries 3.7– 4.5 cm long; middle phyllaries 2.6 – 3.4 cm wide. Corollas 2.3–2.5 cm long; pappus 1.5-1.7 cm long, elements tapering towards the apex, fimbriate at the base, scabrid all along, pink to light brown.

Distribution and ecology: Highly endangered in wet forest, Kauai.

Additional specimens examined: United States. Hawaii. Kauai. *S. Carlquist s.n*, Apr 1964 (BISH1022143); *C. Christensen 325*, 15 Oct 1977 (BISH1022156); *C.N. Forbes 190.K*, Aug 1909 (BISH1022159); *C.N. Forbes 189.K*, Aug 1909 (BISH1022158); *D.R. Herbst 2414*, 22 May 1972 (BISH1022153); *D.R. Herbst 2414*, 22 May 1972 (BISH1022154); *R.W. Hobdy 9*, Sep 1968 (BISH1022150); *R.W. Hobdy 99*, 09 Apr 1969 (BISH1022149); *C.H. Lamoureux 1512*, 25 Aug 1960 (BISH1022137); *C.H. Lamoureux 1513*, 25 Aug 1960 (BISH1022139); *C.H. Lamoureux 1511*, 25 Aug 1960 (BISH1022138); *C.R. Long 1639*, 25 Apr 1964 (BISH1022157); *J.M. Lydgate s.n.*, s.d.(BISH1022145); *S. Perlman s.n.*, 02 Jun 1979 (BISH1022142); *S. Perlman 477*, 13 Aug 1979 (BISH1022140); *S. Perlman 12448*, 30 Dec 1991 (BISH1022141); *S. Perlman 5969*, 20 Jun 1987 (BISH1022151); *S. Perlman 23081*, 31 Oct 2012 (BISH1020223); *S Perlman 23767*, 04 Dec 2013 (BISH1199265); *S. Perlman 23861*, 25 Feb 2014 (BISH1200255); *H.U. Stauffer 5912*, 24 Apr 1964 (BISH1022155); *N. Tangalin 2924*, 15 Dec 2011 (BISH1044844); *N. Tangalin 2181*, 14 Sep 2009 (BISH1200026); *W.L. Wagner 4996*, 27 Aug 1983 (BISH1022148); *W.L. Wagner 6298*, 21 Nov 1989 (BISH1022147); *W.L. Wagner 6015*, 07 Apr 1988 (BISH1022146); *K.R. Wood 1542*, 30 Dec 1991 (BISH1022144); *K.R. Wood 2047*, 08 Aug 1992 (BISH1022152); *K.R. Wood 14349*, 14 Oct 2010 (BISH1059057); *K.R. Wood 15755.00*, 04 Dec 2013 (BISH1067937).

Hahai nō ka ua i ka ululā'au

Hahai nō ka ua i ka ululā'au means "The rain follows the forest". The intact wet forests of West Maui are essential habitat for *H. arborescens* A.Gray. Native trees, ferns, and mosses allow water to slowly percolate into the ecosystem. Non native ungulates and weeds threaten this balance.

West Maui
Photo by Zach Pezzillo

A ʻai ka manu i luna

A ʻai ka manu i luna means "The birds feed above".
An attractive person is compared to a tree laden with
flowers that attracts birds. *H. lydgatei* C.N.Forbes is
hypothesized to have pendant flowers to be more
attractive to honey creepers (Drepanidae)

Kauaʻi, Oʻahu
Photo by Natalia Tangalin

Hesperomannia oahuensis (Hillebr.) O.Deg., Fl. Hawaiiensis [Degener] Fam. 344, 1938.

Hesperomannia arborescens subsp. *oahuensis* Hillebrand, Flora Hawaiian Islands, 232, 1888.

Hesperomannia arbuscula subsp. *oahuensis* (Hillebrand) Carlquist, Pac. Sci. 11:213, 1957. Type: Puakea, Mt. Kaala, Oahu, *Wawra s. n.* (lectotype (designated by Degener, 1938): B [destroyed]; syntype: Makaleka, Mt. Kaala, Oahu, *Lydgate sn.* BISH 1005805!). (See discussion by St. John [1978] on effective lectotypification by Degener.)

Hesperomannia arbuscula var. *pearsallii* St. John, Phytologia 40:241, 1978. Type: Southern Waianae, Oahu, *Pearsall 500-* (holotype: BISH 1005804!).

Small, sprawling trees/shrubs 2–3 m tall, young branches and apical buds densely tomentose. Leaves with petioles 1/4 −1/3 of total leaf length, tomentose; leaf blades ovate to elliptic-ovate, densely tomentose on lower surface, upper surface tomentose to sparsely pubescent, margins entire or dentate. Heads on stout, puberulent peduncles, 6 −8 mm long, erect at anthesis; involucre in 5–8 series, phyllaries green at bottom and magenta at top at anthesis; inner phyllaries 2.3–2.5 cm long; middle phyllaries 3–3.5 cm wide. Corollas 1.3 cm long; pappus 2.0-2.5 cm long, elements broadened towards the apex, fimbriate at the base and scabrid all along, pink to light purple.

Distribution and ecology: Highly endangered, restricted to mesic forests in the Waianae Mountain Range of Oahu.

Additional specimens examined: United States. Oahu. *B. Bishop s.n.*, 03 Aug 1963(BISH1022134); *S. Carlquist 640*, 26 Aug 1961(BISH1022116); *S. Carlquist 1720*, 03 Jul 1965(BISH1022115); *S. Carlquist 1910*, 02 Jul 1966(BISH1022117); *O. Degener 11200*, 11 Apr 1937(BISH1022106);*C.N.Forbes s.n.*,26 Apr 1912(BISH1022121); *C.N. Forbes 1591.O*, 27 Apr 1910(BISH1022119); *C.N. Forbes 1591.O*, 27 Apr 1910(BISH1022118); *C.N. Forbes 1829.O*, 26 Apr 1912(BISH1022120); *G.W. Gillett 1725*, 10 Apr 1965(BISH1022132); *D.R. Herbst 5047*, 21 Sep 1974(BISH1022113);*D.R.Herbst 1416*,02 Jun 1969(BISH1022112); *D.R. Herbst 1132*, 17 Jun 1968(BISH1022114); *P.C. Hutchison 7370*, 23 Jul 1967(BISH1022133); *J.K. Obata 77-310*, 27 Mar 1977(BISH1022127);*J.K.Obata 328*,01 Aug 1977(BISH1022130); *J.K.Obata 77-310*,27 Mar 1977(BISH1022129);*J.K.Obata 85-545*, 1985(BISH1022126);*J.K.Obata 375*,Apr 1978(BISH1022131);*G.A. Pearsall s.n.*.26 Mar 1960(BISH1022105); *S. Perlman 5466*, 24 Mar 1987(BISH1022107); *J. Rohrer s.n.*, 18 Oct 2007(BISH1199614); *John, H. St. John 13005*, 29 Mar 1933(BISH1022003); *B.C. Stone 2788*, 04 May 1959(BISH1022053); *B.C. Stone 3660*, Sep 1961(BISH1022052);*B.C.Stone 3450*,30 Apr 1960(BISH1022110); *B.C. Stone 3293*, 26 Mar 1960(BISH1022111); *W.N. Takeuchi 2118*, 31 Mar 1985(BISH1022122); *W.N. Takeuchi 2186*, May 1985(BISH1022125); *B. Tate 2*, May 1987(BISH1022108); *P. Welton 749*. 17 Jul 1991(BISH1022109).

Hesperomannia swezeyi O.Deg., Fl. Hawaiiensis [Degener] Fam. 344, 1935. Hesperomannia arborescens subsp. swezeyi (Degener) Carlquist, Pac. Sci. 11:214, 1957. Type: Pupukea-Kahuku region on Kahuku side, Oahu, in rain forest at crest just south of trail, O.Degener & O.Swezey 4398 (holotype: BISH 1005815!; isotypes: B †, NY 00007532).

Hesperomannia bushiana Degener, Flora Hawaiiensis, 1933. *Hesperomannia arborescens* subsp. *bushiana* (Degener) Carlquist, Pac. Sci. 11:214, 1957. Type: Along crest of middle Hawala Ridge about 2.5 mi. above makai boundary of Forest Reserve, Oahu, *O. Degener, W. Bush, C. Potter, K. Park 9981* (holotype: BISH 005810!; isotype: B 10 0088463 [3 sheets; ex GH], BISH 1005811!, M 0031144, MICH 1107453!, NY 00007529 [2sheets], WIS 0256899WIS);

Hesperomannia bushiana var. *fosbergii* Degener, 1933, Flora Hawaiiensis. Type: Kalawao Ridge, Koolau Mountains, Oahu, alt. 540 m, *Fosberg 9470* (holotype: BISH 1005812!; isotype: NY 00007531).

Trees 2–5 m tall, young stems and apical buds pubescent. Leaves with petioles 1/8–1/7 of total leaf length; leaf blades broadly oblanceolate to obovate, sometimes elliptic, glabrous or nearly so, with lower leaf surface of young leaves sometimes being sparsely pubescent along 1/2–1/3 of midrib, margins entire or sometimes crenate. Heads on stout sparsely puberulent peduncles 4 − 6 mm long, erect at anthesis; involucre in 5–8 series of phyllaries, phyllaries magenta at anthesis, inner phyllaries 2.7− 3.0 cm long; middle phyllaries 3.0 −3.5 cm wide. Corollas 2.0 cm long; pappus 2.5-3.0 cm long, elements tapering towards the apex, fimbriate at the base and scabrid all along, pink.

Distribution and ecology: Highly endangered in wet forest, mainly on the leeward side of the Koolau

He pua laha ʻole

He pua laha ʻole means "A rare flower".
The multiseriate involucre of *H. lydgatei* C.N.Forbes
has pale whitish pink phyllaries at anthesis. These
flowering heads are conspicuous in the dark green
wet forest of Kauaʻi.

Kauaʻi, Hawaiʻi
Photo by Scott Heintzman

Somewhere over the Rainbow

Although down to just 3 wild individuals,
H. oahuensis (Hillebr.) O.Deg. is starting to rebound
through efforts by the Army Natural Resources
Program, O'ahu. Their hand pollination efforts saved
this species from extinction.

Wai'anae Mountains, O'ahu
Photo by Ane Bakutis

The Law of Attraction

Open flowering heads of *H. swezeyi* O.Deg. produce copius nectar, and are pollinated by native honey creeper birds such as 'apapane (*Himatone sanguinea*) and 'amakihi (*Chlorodrepanis flava*). This species flowers synchronously with the dominant forest tree 'Ōhi'a lehua (*Metrosideros polymorpha* Gaudich., Myrtaceae) which is also visited by these bird species for nectar.

Ko'olau Mountains, O'ahu
Photo by Susan Ching Harbin

Mountain Range, Oahu. One population documented as extirpated from the windward Waianae Range, Oahu.

Additional specimens examined: United States. Oahu. *A.M. Adamson s.n.*, 29 Mar 1933 (BISH1022082); *H. Akiyama s.n.*, 13 May 1951 (BISH1022058); *B. Bishop s.n.*, 29 Apr 1962(BISH1022062); *E. H. Bryan Jr. 860*, 20 Nov 1934(BISH1022063); *E.L. Caum s.n.*, 12 Aug 1930(BISH1022026);*E.L.Caum s.n.*,14Aug1930(BISH1022025); *A.K. Chock 231*, 13 May 1951(BISH1022008); *A.K. Chock 231*, 13 May 1951(BISH1022009); *A.K. Chock 230*, 13 May 1951 (BISH1022010);*O. Degener 7447,*27 Mar 1933 (BISH1022066); *O. Degener 75482*, 19 Sep 1950 (BISH1022067); *O. Degener 10080*, 02 Jun 1935 (BISH1022074); *O. Degener 10081*, 29 Jul 1935 (BISH1022073); *O. Degener 10079*, 16 Jun 193 5(BISH1022065); *O. Degener 7445*, 31 Mar 1929 (BISH1022069); *O. Degener 3397*, 15 Feb 1928 (BISH1022068); *O. Degener 10007*, 02 Jun 1935(BISH1022072); *O. Degener 7446*, 06 Dec 1931 (BISH1022070); *O. Degener 10079*, 16 Jun 1935 (BISH1022064); *O. Degener 10008*, 25 Apr 1935 (BISH1022075);*O. Degener 10007*,02 Jun 1935 BISH1022071); *C.N. Forbes 2035.O*, 10 Feb 1915 (BISH1022088); *C.N. Forbes 1703.O*, 09 Apr 1911 (BISH1022089); *C.N. Forbes 2035.O*, 10 Feb 1913 (BISH1022087); *C.N. Forbes 2035.O*, 10 Feb 1913 (BISH1022086); *C.N. Forbes 2035.O*, 10 Feb 191 3 (BISH1022090);*F.R. Fosberg 9820,*08 Aug 1933 (BISH1022101); *F.R. Fosberg 9791*, 08 Aug 1933 (BISH1022102); *F.R. Fosberg 9419*, 15 Apr 1933 (BISH1022060); *D.W. Garber 283*, 07 Mar 1920 (BISH1022103); *D.W. Garber 202*, 01 Feb 1920 (BISH1022104);*M.L. Grant 7251*, 08 Aug 1934 (BISH1022023); *M.L. Grant 7251*, 08 Aug 1934(BISH1022024); *M.L. Grant 7251*, 08 Aug 1934 (BISH1022022); *M.L. Grant 7251*, 08 Aug 1934 (BISH1022020); *M.L. Grant 7146*, 01 Aug 1934(BISH1022021); *D.R. Herbst 1169*, 22 Jun 1968 (BISH1022059); *E.Y. Hosaka 619*, 04 Jul 1932 (BISH1022011); *E.Y. Hosaka 2036*, 08 May 1938 (BISH1022012);*Jr.,A.F. Judd Jr, 1244*,06 Jun 1925(BISH1022081); *Jr., A.F. Judd Jr. 1244*, 06 Jun 1925(BISH1022083); *H.L. Lyon s.n.*, 15 Sep 1926(BISH1022030); *H.L. Lyon s.n.*, 20 Apr 1934(BISH1022029);*H.L. Lyon s.n.*, 15 Sep 1926 (BISH1022031); *S. Miyake 97*, 1950 (BISH1022085); *J.K. Obata s.n.*, 20 Apr 1952(BISH1022057); *J.K. Obata s.n.*, Apr 1989(BISH1022076); *G.A. Pearsall s.n.*, 25 Apr 1948 (BISH1022014); *G.A. Pearsall s.n.*, 05 Jul 1958 (BISH1022015); *G.A. Pearsall s.n.*, 30 Oct 194 9(BISH1022013); *S. Perlman 6197*, 19 Jul 1987 (BISH1022078); *S. Perlman 6197*, 19 Jul 1987 (BISH1022077); *S. Perlman 23654*, 22 Aug 2013 (BISH1199539); *J.F.C. Rock 10301*, s.d. (BISH1022093);*J.F.C. Rock 25766,*03 Apr 1957 (BISH1022095); *J.F.C. Rock 16019*, Sep 1917 (BISH1022094); *J.F.C. Rock 10301*, s.d. (BISH1022091); *J.F.C. Rock 10301*, s.d. (BISH1022092); *C.J.F. Skottsberg s.n.*, 23 Oct 1922 (BISH1022027); *C.J.F. Skottsberg*

890, 25 Oct 1922 (BISH1022028); *John, H. St. John 11570*, 06 Mar 1932 (BISH1022002); *John, H. St. John 20188*, 16 Feb 1941 (BISH1022006);*John,H.St.John13005,*29Mar1933(BISH1022004); *John, H. St. John 20270*, 19 Oct 1941 (BISH1022016); *John, H. St. John 11570*, 06 Mar 1932 (BISH1022000); *John, H. St. John 13005*, 29 Mar 1933 (BISH1022005); *John, H. St. John 11547*, 14 Feb 1932 (BISH1022056); *John, H. St. John 11570*, 06 Mar 1932 (BISH1022001); *John, H. St. John 13116*, 30 Apr 1933 (BISH1022007); *John, H. St. John 20270*, 19 Oct 1941 (BISH1022018); *A. Suehiro s.n.*, Sep 1933 (BISH1022054); *O.H.*

Figure 1. Dried inflorescences of *Hesperomannia lydgatei* C.N.Forbes in wet forest habitat of Kauai, Hawaii. The dried achenes with pappus of scabrid setae are wind dispersed short distances within populations.

Ching Harbin | **BREVIA**

He ali'i ka 'āina; he kauwā ke kanaka

He ali'i ka 'āina; he kauwā ke kanaka means "The land is chief; man is its servant" The upland wet forest of Kaua'i is home to *H. lydgatei* C.N.Forbes. Due to introduced species, development, and climate change, the Hawaiian islands have less than 50% of native forest habitat remaining. In addition to direct work to preserve rare flora, the State of Hawaii with partners such as watershed partnerships are working to protect and restore essential habitat.
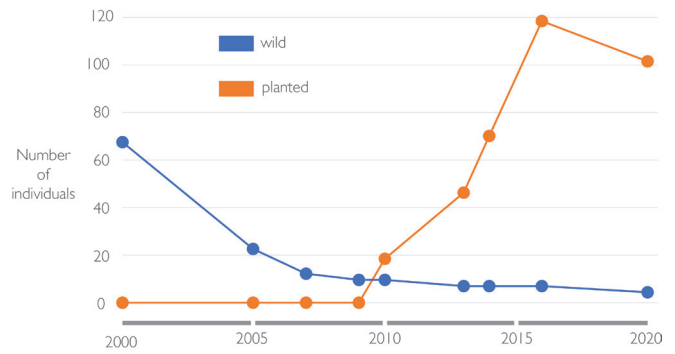
Kaua'i, Hawai'i
Photo by Scott Heintzelman

Swezey s.n., 26 Mar 1933 (BISH1022080); *O.H. Swezey s.n.*, 22 Aug 1920 (BISH1022055); *W.N. Takeuchi 2206*, 19 May 1985 (BISH1022019); *W.N.Takeuchi 2738,* Aug 1986 (BISH1022017); *G.L. Webster 1558*. 25 Apr 1948 (BISH1022079); *K.A. Wilson 124*, 06 Apr 1952 (BISH1022084)

Figure 2. Evolution of populations of *Hesperomannia oahuensis* (Hillebr.) O.Deg., wild mature individuals and restoration plantings (ANRPO 2021 data).

CURRENT CONSERVATION STATUS

The current conservation status of the genus is reflective of Hawaii's overall ecosystem crises. All currently accepted species are listed by the IUCN as Critically Endangered, CR (World Conservation Monitoring Centre, 1998; Bruegmann & Caraway, 2003; Walsh et al., 2020) as well as listed as Endangered by the USFWS (USFWS 1991a, 1991b, 1994 ONLY ONE OF 1991 CITED). Causes for this are numerous and include: feral ungulates, rats, mice, invasive plants, climate change, and over visitation by humans (Price & Toonen, 2017; Rønsted et al. 2022). Furthermore, with reduced abundance these species are now affected simply by small population sizes consisting of just 1-3 individuals (Kawelo et al. 2012). Low genetic diversity is evident in all four species (Ching Harbin, 2003).

Hesperommania is presumably bird pollinated, with large, brightly colored flowering heads that produce copious amounts of nectar at anthesis. The genus is also protandrous and assumed to be strongly self-incompatible. With the continued decline of Hawaiian nectivorous

birds (Paxton et al. 2018), small populations of bird pollinator dependent plant species could be effectively experiencing an Allee effect, where small populations are not attracting enough floral visitors to successfully move pollen amongst individuals. Forsyth (2003) found that in the Haleakala Silversword (*Argyroxiphium sandwicense* D.C. subsp. *macrocephalum* (A. Gray) Meyrat, Tribe Madieae) - a self-incompatible insect pollinated species - percent seed set was significantly correlated with the number of flowering plants in a population.

The floral morphology and pollination syndrome of this genus is also similar to the most common mesic and wet forest tree in Hawaii, Ohia lehua, *Metrosideros polymorpha* Gaudich. (Myrtaceae). Generalist nectivorous bird pollinators would visit both *Metrosideros* Banks ex Gaertn. and

Table 1. Conservation status of the endemic Hawaiian genus, *Hesperomannia* A.Gray. #s given as mature (immature) (S. Heinztman, H. Oppenheimer, A. Bakutis, S. Ching Harbin PEPP; T. Chambers Army Natural Resources Program, Oahu (ANRPO, pers. comm)).

Species	# Wild populations	# Wild individuals	# Conservation planting	Ex situ representation
H. arborescens A.Gray	8	88	0	<25 seeds (from 1 pop.)
H. lydgatei C.N.Forbes	1 (+ outlier individuals)	<30	1	<25 seeds (from 1 pop.)
H. oahuensis (Hillebr.) O.Deg	1	3	38 (64)	246 seeds (from 3 pops.)
H. swezeyi O.Deg	20	200 (181)	0	<50 seeds (from 4 pops.)

Ola I Ka Wai

Ola I Ka Wai means "Water is Life". *H. arborescens* A.Gray occurs in the steep, wet gulches of West Maui. This species once occurred on Lana'i and has not been seen on Moloka'i in recent years. This species is in need of seed collections representing all remaining populations and large scale ungulate fences.

West Maui, Hawai'i
Photo by Hank Oppenheimer

Table 2. Threat control summary by *Hesperomannia* A.Gray species.

Species	Ungulate fence	Rat Control	Slug control
H. arborescens A.Gray	1 population	0	0
H. lydgatei C.N.Forbes	0	0	0
H. oahuensis (Hillebr.) O.Deg	All wild/reintroduced fenced	100%	100%
H. swezeyi O.Deg	<10 individuals in 3 populations	1 pop	0

Hesperomannia, which generally have overlapping flowering times in the spring (Ching Harbin pers. Obs.). *Hesperomannia oahuensis* is known from mesic forest in the Waianae mountains of Oahu. The *Metrosideros* canopy cover in the mesic habitat unique to *H. oahuesnsis* has been reduced due to invasive species and climate change. Perhaps, as remaining *Hesperomannia* exist only as scattered populations of a few individuals, pollinators are no longer attracted in sufficient numbers to effectively cross pollinate individuals causing the observed low to absent seed set observed in wild populations of *H. oahuensis* (ANRPO, 2021). In contrast, medium sized populations of *H. swezeyi* have more demographic structure with seedlings and immatures and occurs in more intact *Metrosideros* forest on Oahu. This suggests that this species, although declining, continues to be successfully pollinated as a benefit from being within an Ohia dominated forest.

Hesperomannia oahuensis underwent a steep decline from 67 mature individuals in 2000 to just 3 remaining wild individuals in 2022. The Army Natural Resources Program Oahu (ANRPO) has been actively managing this species for the past 20+ years. A large effort to cross pollinate by hand was made to secure seed from the remaining plants beginning in 2007, with 12 wild matures in 6 populations. The efforts have been extremely successful with over 250 progeny planted into wild sites to date (Figure 2). ANRPO has shown that larger planted stands of mature *H. oahuensis* combined with synchronous flowering of the Ohia canopy are beginning to attract native honeycreeper pollinators such as the Oahu Amakihi, *Chlorodrepanis flava* A. Bloxam (Fringillidae). This has resulted in the observance of viable seeds and seedlings being produced without human pollination assistance, something that hasn't been seen in over 10 years (Figure 1).

The other three species *Hesperomannia arborescens, H. lydgatei,* and *H. swezeyi* have received much less in situ conservation work. All *H. oahuensis* are protected from feral ungulates and rats, while only a handful of individuals of *H. swezeyi* and *H. arborescens* are within ungulate fences. There is minimal rodent control for *H. swezeyi* and no ungulate or rodent control for *H. lydgatei* (Table 2). Recent work with a population of *H. swezeyi* showed, 90% of the flowering heads were eaten by rats until a rodent control grid was set up. With the continued decline of all of these species, unprotected populations face eventual extinction due to ungulate damage, reduced or no pollinations, and minimal recruitment potential.

Not only are all of the four species declining precipitously in the wild, the genus has little to no ex situ conservation collections to preserve these species from extinction. Fewer than 400 mature individuals exist in the entire genus and fewer than 100 seeds in storage (Table 1). A handful of seeds have been stored from *H. lydgatei* on Kauai (S. Heinzman PEPP, 2022 pers. comm.), *H. swezeyi* on Oahu (T. Chambers ANRPO, 2022 pers. comm.), and *H. arborescens* Maui only (H. Oppenheimer PEPP, 2022 pers. comm.). A few seedlings have been rescued from *H. arborescens* on Maui and Molokai, none are currently alive ex situ (H. Oppenheimer, A. Bakutis, PEPP 2022 pers. comm.). *Hesperomannia* seeds are orthodox, can withstand drying and cold storage conditions, with a storage life expectancy of at least 25+years (T. Chambers/M. Akiona, ANRPO pers. comm.). However, with the lack of refined storage and propagation techniques for the

genus, and few seeds available for germination, it is likely to result in fewer live plants than seeds, given the age of the collections and the varying degrees of seed viability.

LOOKING AHEAD

In situ threat control at every population and wild collections of each species in the genus need to begin immediately. As environmental conditions continue to deteriorate and change rapidly, each species and population are expected to continue contracting. Ex situ storage is needed to represent each species for long term preservation against extinction. Without immediate threat control for ungulates and rodents as well as hand pollination for some populations, the four species may not survive the next 100 years.

The Plant Extinction Prevention Program http://www.pepphi.org/ partnered with The State of Hawaii's Department of Land and Natural Resources https://dlnr.hawaii.gov/ecosystems/rare-plants/; The Army Natural Resources Program Oahu https://oanrp.weebly.com/; and National Tropical Botanical Gardens https://ntbg.org/, and The Hawaii Rare Plant Program https://manoa.hawaii.edu/lyon/research/hrpp/ are working together towards these goals (Werden et al., 2020).

For continued positive progress, funding specific to these species is necessary. Aside from ANRPO, the programs listed above do not receive funding directly for these taxa. Most of the sites are accessed by helicopter, ungulate fences are needed, and rodent control needs to be targeted during flowering/fruiting (Table 2). Many remaining populations are too small to attract sufficient pollinators. Therefore, hand pollination will be necessary in most cases. Propagation and wild introductions of all species is essential, and a task largely not begun. The cost of these actions is sometimes prohibitive. However, the efforts made to date prove this work can be successful if given these opportunities. The time to act is now before there is not enough habitat remaining or genetic variation available to successfully prevent extinction of this extraordinary example of long distance dispersal, adaptive radiation, and island evolution.

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The lure and intrigue of *Yunquea tenzii* Skottsb. (Cardueae: Centaureinae)

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ABSTRACT

We discuss the history of the monospecific genus *Yunquea*, which is endemic to the highly inaccessible peak El Yunque on Robinson Crusoe Island, Juan Fernández Archipelago. The allure of the genus rests largely on the difficulty of reaching the one known population; we trace the history of the few persons who succeeded in climbing to the summit where the genus occurs. The genus remains of interest to botanists because of the lack of flowering material, having been described only from leaves! During the near century since its description, *Yunquea tenzii* remains a mysterious species. Molecular phylogenetic studies identify the Juan Fernández endemic *Centaurodendron* and the continental genus *Plectocephalus* as closest relatives. However, resolution of relationships among the four genera has not been achieved, leaving biogeographic relationships unknown. Whether *Yunquea tenzii* evolved anagenetically from continental colonists or cladogenetically from a common ancestor with *Centaurodendron* remains a mystery. Viable seeds have been collected from the natural population, suggesting sporadic sexual reproduction, but lack of mature floral tissue precludes insights into the floral evolution and reproductive biology of *Yunquea*.

Keywords: Chile, conservation, evolution, island biology, Juan Fernández, Robinson Crusoe

Imagine a genus of Compositae that is nearly impossible to collect, virtually inaccessible, for which only poor specimens exist, and whose taxonomic affinities are still not entirely clear. This is the genus *Yunquea* Skottsb., with the single species *Y. tenzii* Skottsb. This reclusive taxon grows only on the top of El Yunque (Figure 1), the highest peak of the oceanic Robinson Crusoe Island in the Juan Fernández Archipelago, 667 kms west of continental Chile in the Pacific Ocean (insert map).

The history of attempts to collect *Yunquea tenzii* goes back to the first efforts to scale El Yunque (Woodward, 1969; Stuessy, 2020). In 1794 the

governor of the island, Fernando Amador de Amaya, wanted to inventory the plants on the island, including the tallest peak. To achieve this objective, he offered a cash incentive and even freedom to any convict who would be willing to attempt the climb and return with information. Two prisoners, Ramón Negrete and Francisco Clavel, responded to this challenge, and on 19 November they successfully scaled the peak, which measures 915 m elevation, up the ridge from El Camote. Although the height of El Yunque is child's play for any experienced mountaineer, the volcanic rock is friable, easily becoming dislodged, and this is what makes the ascent dangerous. Due to fog, the adventurers stayed overnight until visibility

Robinson Crusoe & Santa Clara Islands, Juan Fernández Archipelago

Large triangle shows the location of the single population of *Yunquea tenzii* Skottsb. on Cerro El Yunque on Robinson Crusoe Island in the Pacific. Smaller triangles indicate other prominent peaks on the island. The village of San Juan Bautista on Cumberland Bay is the only permanent settlement on the island, with some 900 residents (Stuessy, 2020).

Figure 1. El Yunque ("The Anvil"), the tallest peak on Robinson Crusoe Island, Juan Fernández Archipelago. **A.** View of El Yunque behind the village of San Juan Bautista. **B.** View from El Camote, at the base of the southern (and only) route up to the summit of El Yunque. From Stuessy (in press).

The first naturalist to attempt to scale El Yunque was Dr. Otto Tenz. He was from the Institut für allgemeine Botanik in Hamburg, Germany (Skottsberg, 1929), who came to Chile and made a trip to Robinson Crusoe Island, staying about 1.5 months in 1922. In the early decades of the 20th century, a number of the islanders had now scaled El Yunque as a physical challenge to gain prestige within the village of San Juan Bautista. Uberlindo Andauer was one of these adventurers, and he offered to escort Tenz to the top. Their climb began early on 7 February, arriving successfully at the summit, which provided time for observations and collections. Weather mandated staying on the peak until the following day, followed by a safe descent to the village.

Tenz had made the first botanical collections from the summit of El Yunque, and after his death these were sent for study to Carl Skottsberg, a Swedish botanist of long experience with the flora of the archipelago (Skottsberg, 1921). Among the collections were two large leaves, which Tenz had tentatively assigned to the endemic Compositae genus, *Dendroseris* D. Don (Cichorieae). Skottsberg realized that this referral was inaccurate, but dealing with only two leaves made assignation problematic. He noticed, however, that the leaves bore many shiny glandular trichomes on the upper surface, similar to what he had observed on leaves of another endemic genus of the archipelago, *Centaurodendron* Johow (Cardueae; Johow, 1896; Skottsberg, 1938). But the structure of the leaves of this enigmatic taxon--large (more than 30 cm long), ovate, and serrate-dentate at the margins--did not fit with the species of *Centaurodendron* known at that time (*C. dracaenoides*; a second species, *C. palmiforme* Skottsb., was described by Skottsberg in 1957, and a third, *C. schilleri* Penneck., N. Garcia & Susanna, has recently been described as new from the far island, Alejandro Selkirk, by Penneckamp et al., 2022). Skottsberg described it as a new genus, certainly Asteraceae, with a possible connection to *Centaurodendron*. Skottsberg's understanding of the flora was sufficiently expert that he had confidence in describing this new genus and species (Skottsberg, 1929), *Yunquea tenzii*, based on only two isolated leaves!

returned for a safe descent on the following day, but the fog had made it impossible to provide a suitable inventory for the governor. Hence, they were sent back on 24 November, this time with the soldiers Pedro José Gutiérrez and Marcel Boza, staying two days until returning on 26 November. They made observations on the vegetation and endemic flora (from Woodward, 1969: 97-98), noting the tree "cinamon" (= canelo; *Drimys confertifolia* Phil.), the robust herb "pangue" (*Gunnera bracteata* Steud. ex Benn.), plus ferns and grasses. To indicate to the townspeople and governor that they really had climbed to the summit, they set fire to the top, which supposedly burned for "eight days" (Woodward, 1969: 98). This was a beginning for understanding the botanical resources of El Yunque, but these early efforts provided only a sketch of the complete flora.

During Skottsberg's last trip to the Juan Fernández Archipelago in 1955 (he died in 1963; Peterson, 1964), a young German writer and botanist, Günther

Figure 2. One of the few herbarium specimens of *Yunquea tenzii* Skottsb., collected in 1957 by G. Kunkel, at Chile National Museum of Natural History herbarium (SGO). Image courtesy of SGO herbarium.

Kunkel, living on Robinson Crusoe Island, offered to make the ascent in the company of the local resident, Jorge Charpentier. This effort took place on 6 March and was more successful with regard to inventorying the flora (Kunkel, 1957) and also regarding *Yunquea*, from which they brought back a leaf and old inflorescences with fruits (Figure 2). Skottsberg successfully germinated some of these fruits in the Bergius Botanical Garden in Stockholm, but none of the seedlings survived to flowering stage. Based on the new, but scant material, Skottsberg (1958) confirmed the familial referral of *Yunquea*, and now armed with three leaves, portions of old stems, and several inflorescence stalks with very old heads (Figure 2), he provided an updated description of the genus and also emphasized the relationship with, but still generically distinct from, *Centaurodendron*. Material from both genera were sent by Skottsberg to Sherwin Carlquist at the Rancho Santa Botanic

Garden (now the California Botanical Garden), and he published on the vegetative and reproductive anatomy (Carlquist, 1958), concluding that the genera were related to each other, but generically distinct, and with general affinities with *Centaurea* L., *Plectocephalus* D. Don, and *Serratula* L.

These previous efforts stimulated us to attempt an ascent of El Yunque. The idea was to employ a professional rock climber to make the ascent and then use ropes and harnesses for us to struggle to the top. We submitted a proposal in 1983 to the National Geographic Society to obtain funding for the effort. The objectives were to complete the inventory of the vegetation on the summit of El Yunque, collect more rock samples for additional radiometric dating, and most importantly, to find, inventory, and collect *Yunquea*. The technical climber on the project was Timothy H. Jefferson, a Ph.D. in geology and paleobotany from Cambridge University. But one month after the proposal was submitted, the shocking news came that Tim had been killed on 12 September 1983 in an avalanche in Peru while on an expedition with the Institute of Polar Studies from Ohio State University (Holland, 1983). He was only 27 years old and just starting his academic career (and entire life). We worked to find a substitute climber, but this tragedy cast such an ominous shroud that we decided not to pursue the project further.

Two recent successful efforts to ascend El Yunque have taken place. Philippe Danton, a botanist from Grenoble, France, made the ascent on 15 February 1999 with the national park (CONAF: Corporación Nacional Forestal) guides Ramón Schiller, his son Rodrigo, Alfonso Andauer, and Oscar Chamorro. Again, the objective was to inventory the vegetation and flora of this peak, which at the summit has a sloping flat surface of 3 ha (7.4 acres; hence the name, "The Anvil" in Spanish). Danton (2000) did publish a good description of the vegetation with a list of the flora, including a photograph of a plant of *Yunquea*, with its rosette of ovate leaves (Figure 3), but it was once again a sterile individual, and it was not collected. In total, he observed 25 sterile adults and about 100 juveniles (*in litt.*). Another scaling of El Yunque occurred in 2015 by several CONAF guides (Alarcón, 2015), and several photographs of *Yunquea* were taken, again in sterile condition. These recent explorations document that *Yunquea tenzii* still survives on the top of El Yunque, but little still

Figure 3. Isolated individual of *Yunquea tenzii* Skottsb. showing rosette tree habit (copyright Ph. Danton, photo RC3612, Feb 1999)

is known about reproductive structures, pollination mechanisms, and flowering phenology.

Due to lack of detailed reproductive morphological information on *Yunquea*, investigations have turned to molecular phylogenetic analyses. Susanna et al. (2011) carried out a combined analysis of two nuclear (ITS, ETS) and three chloroplast (*trnL-trnL-F*, *rpl32-trnL*[UAG], *ndhF*) markers for genera of subtribe Centaureinae. Working with available herbarium material, they sampled only *Centaurodendron palmiforme*. They accepted the previous taxonomic viewpoints in Dittrich (1977), Bremer (1994), and Susanna and Garcia-Jacas (2007) that *Yunquea* belongs more properly in *Centaurodendron* as *C. tenzii*. The results demonstrated that *C. palmiforme* nests among species of *Centaurea* and *Plectocephalus*, with the limits between these other two genera unclear (Penneckamp et al., 2000, 2022). Susanna et al. (2011) and Herrando-Moraira et al. (2019) elected to continue to accept *Centaurodendron* as a distinct genus because of its morphological distinctions from continental South American taxa. Herrando-Moraira et al. (2019) using Hyb-Seq data have examined phylogeny among 76 representative species of Cardueae, including *Centaurodendron dracaenoides*, and of particular

interest is that *Centaurodendron* is hypothesized to have originated within *Plectocephalus* about 4 Mya, the age of Robinson Crusoe Island (Stuessy et al., 1984, 2022). Recent unpublished phylogenomic studies by Alfonso Susanna and colleagues (pers. comm.), which included all three species of *Centaurodendron* and species of *Plectocephalus*, have so far failed to resolve affinities among the taxa.

Resolution of phylogenetic relationships among species of *Plectocephalus, Centaurodendron* and *Yunquea* would provide the potential for interpreting the evolution of floral traits and reproductive biology in this fascinating group. The recently discovered *Centaurodendron schilleri* lacks both the peripheral staminate florets found in *C. palmiforme* and the large showy peripheral sterile florets of Chilean *Plectocephalus*, the latter presumably functioning to attract floral visitors. The hermaphroditic (monoclinous) central florets and the peripheral staminate florets with slightly curved tubular corollas in *C. palmiforme* (Skottsberg, 1957) make the plants andromonoecious, which is rare in Asteraceae (Burtt, 1977; Torices et al., 2011), and could promote outcrossing. Inadequate floral material of *Centaurodendron dracaenoides* and *Yunquea tenzii* precludes determination of the sexual expression of their peripheral florets.

The breeding systems of these endemic island species, e.g., whether plants are self-compatible or self-incompatible, remain unknown, but have important implications for sexual reproduction in the small populations. Field observations reveal one or very few, if any, plants with floral remains in populations, meaning there would be few or no mates for outcrossing when a self-incompatible plant flowers. By contrast, a single self-compatible plant could produce viable cypselae, especially if it were self-pollinating as well. Numerous small plants in one population (*Stuessy et al. 12094*; OS, CONC) of *Centaurodendron dracaenoiodes*, plants of different sizes in *Yunquea tenzii* (Danton, 2000; Alarcón, 2015), and the many plants in a population of *C. palmiforme* (*Stuessy et al. 15151*; OS, CONC) indicate periodic seedling recruitment within populations. As indicated above, cypselae from old inflorescences of *Yunquea* were germinated by Skottsberg but no plants survived to flowering

in the botanical garden in Stockholm. Many viable cypselae were found in the population (five plants) of *C. schilleri* and facilitated the establishment of seedlings in the Jardín Botánico Nacional, Viña del Mar, Chile (Penneckamp et al., 2022). Lastly, segregation of alleles at four of the 16 allozyme loci in 13 plants from one population of *C. palmiforme* (*Stuessy et al. 15151*) indicates sexual reproduction in that population (Crawford et al., unpubl.).

Regarding pollination, Brooke (1987) observed hummingbirds visiting *C. palmiforme* (cited by Bernardello et al., 2001); whether they effect pollen transfer is not known. As far as we are aware, there are no other reports of floral visitors to these insular taxa under discussion; this is not surprising given how rarely they flower and the paucity of floral visitors on Robinson Crusoe Island (Anderson et al., 2001; Bernardello et al., 2001). The purple to pink color of *Centaurodendron* flowers is common for bird-pollinated plants.

What is obviously needed are new samples of *Yunquea* that show all reproductive features, and from which more comprehensive molecular analyses can be completed. It will also be important to learn about the biology of the species, especially breeding system, genetic variation, and chromosome number (none yet recorded for *Centaurodendron* or *Yunquea*; Stuessy & Baeza, 2018), so as to establish more firmly its relationships and conservation status. There is no question that *Y. tenzii* is highly endangered, surviving only on the top of El Yunque, but more information is needed to take steps to ensure its survival in situ as well as ex situ in the botanical garden administered by CONAF on the island and perhaps also in the Jardín Botánico Nacional at Viña del Mar on the Chilean continent.

Historically, the lure of *Yunquea* has resided largely on it being a plant with huge leaves and no flowers that occurs exclusively on a highly inaccessible mountain top on an infrequently visited, generally unknown island. The observations made and materials collected from recent field expeditions raise questions and suggest evolutionary hypotheses about *Yunquea* and *Centaurodendron*, making them an intriguing group for further study.

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Genomes & islands & evolution: Oh my!

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ABSTRACT

A central question in evolutionary biology is how lineages quickly diversify to occupy different ecological niches, along with determining genomic factors that facilitate evolutionary change. Isolated, oceanic archipelagos are famous for adaptive radiations characterized by endemic, species-rich clades with substantial ecological variation, yet genome resources key to determining eco-evo processes are generally lacking. Here I present a comparison of the number of genome reference assemblies available (as of May 31, 2023) for three major eukaryotic lineages, briefly describe genome sequencing and benchmarking strategies, and highlight as a case study a genome assembly project for *Bidens hawaiensis* (Koʻokoʻolau, Asteraceae or Compositae; Coreopsidae), a member of a hexaploid Hawaiian plant adaptive radiation. The total number of plant genome references (1,394) was found to substantially lag the total number of genome references for animal (6,003) and fungi (4,400). Improvements to the quality of de novo assembled genomes are fueled by second- and third-generation long-read sequencing advancements, among other sequencing approaches. In conjunction, strategies to improve genome contiguity include optical maps, Hi-C chromatin capture, or trio binning. Continual improvements to genome sequencing and assembly algorithms have brought within reach telomere-to-telomere genome assemblies, albeit this level of sequencing has to date only been achieved in a few cases. With improvements in sequencing techniques and per-base pair costs that continue to trend downward, the number of high-quality genomes is anticipated to continue to increase, leading to the filling in of taxonomic gaps and sampling of groups of taxa from under sampled geographic areas. Increasing the number of plant genome resources available for the study of island endemism could help to shed light on genome-phenome relationships and genome characteristics that have produced the stunning biological diversity that we now observe across the globe.

Keywords: *Bidens*, Compositae, genome assembly, genome benchmarking, island endemism, next-generation sequencing platforms, repetitive content

INTRODUCTION

Plant genome assemblies are foundational to elucidating evolutionary histories, taxonomic boundaries, and genetic underpinnings to functional trait diversification and adaptive processes. The field of genomics is growing by leaps and bounds in concert with rapid advancements in sequencing technologies and computational power. In conjunction with those advances, the per-base cost for obtaining DNA sequences has plummeted and new tools are continually emerging to produce increasingly higher quality genomes, to the point that it is now possible to generate "telomere-to-telomere" (T2T) genome assemblies (McCartney et al., 2022).

STATUS OF REFERENCE GENOME ASSEMBLIES: PLANTS, ANIMALS, AND FUNGI

Although advancements in sequencing technologies have led to the rapid accumulation of reference genome assemblies -- defined as the highest quality genome sequence available for a single species -- the current number of genome assemblies available for green plants (Kingdom Viriplantitae), at 1,394 genomes, lags behind the number of genomes sequenced for other major Opisthokonta Kingdoms Metazoa (animals) and Fungi, at 6,003

Ko'oko'olau

The genus *Bidens* L. underwent extensive adaptive radiation on the Hawaiian Islands after a single colonization event by a hexaploid ancestor and is one of the largest lineages of Hawaiian flowering plants. A reference genome assembly for *Bidens hawaiensis* A.Gray is available to help deepen our understanding of ecological and evolutionary processes and for conservation genomics purposes.

Bidens hawaiensis (Ko'oko'olau) plant growing in Kalapana, Island of Hawai'i.
Photo by Erin Datlof

Cumulative number of reference genomes

Data obtained May 31, 2023, from NCBI
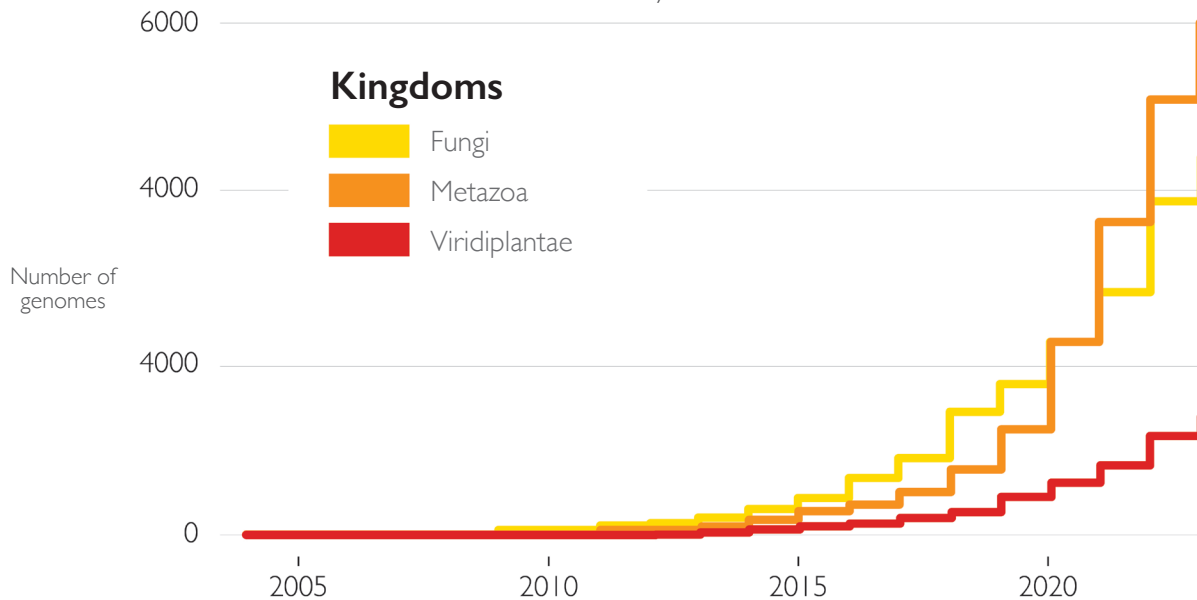
Figure 1. The cumulative number of reference genomes available by year for Kingdoms Metazoa (animals), Fungi, and Viriplantae (green plants). The reference genome is listed only once and is categorized by the most recent year of release.

and 4,400 genomes, respectively (Figure 2, download date May 31, 2023, data from the National Center for Biotechnology Information (NCBI). The gap between the cumulative number of plant and animal genomes has widened considerably over the past few years (Figure 1). Yet despite that gap, the proportion of green plants and animal genomes subjected to iterative genome improvements has remained similar between those two groups (Figure 2).

Particular to Asteraceae (or Compositae), the number of readily available reference genomes includes 43 species belonging to 29 genera (Figure 2; NCBI data download date May 31, 2023), which is a relatively small number considering the enormous size of this family, having 25,000+ named species and at least 1,700 genera (Mandel et al., 2019). The number of reference genomes available for Compositae has more than tripled since 2021, the point at which colleagues and I surveyed and benchmarked all publicly available (reasonably high-quality) Compositae genomes, n = 12, for comparison to a genome we assembled for ko'oko'olau, *Bidens hawaiensis* A. Gray (Bellinger et al., 2022), a single-island endemic and member of a

Hawaiian adaptive radiation. With the relatively low number of Compositae genome assemblies available it is unsurprising that few genomes of endemic island taxa have been sequenced (but see Bellinger et al., 2022 and Cerca et al., 2022), consistent with the assertion by Cerca et al., (2023) that the application of genomic tools to understand the evolution of oceanic island organisms is still in its infancy.
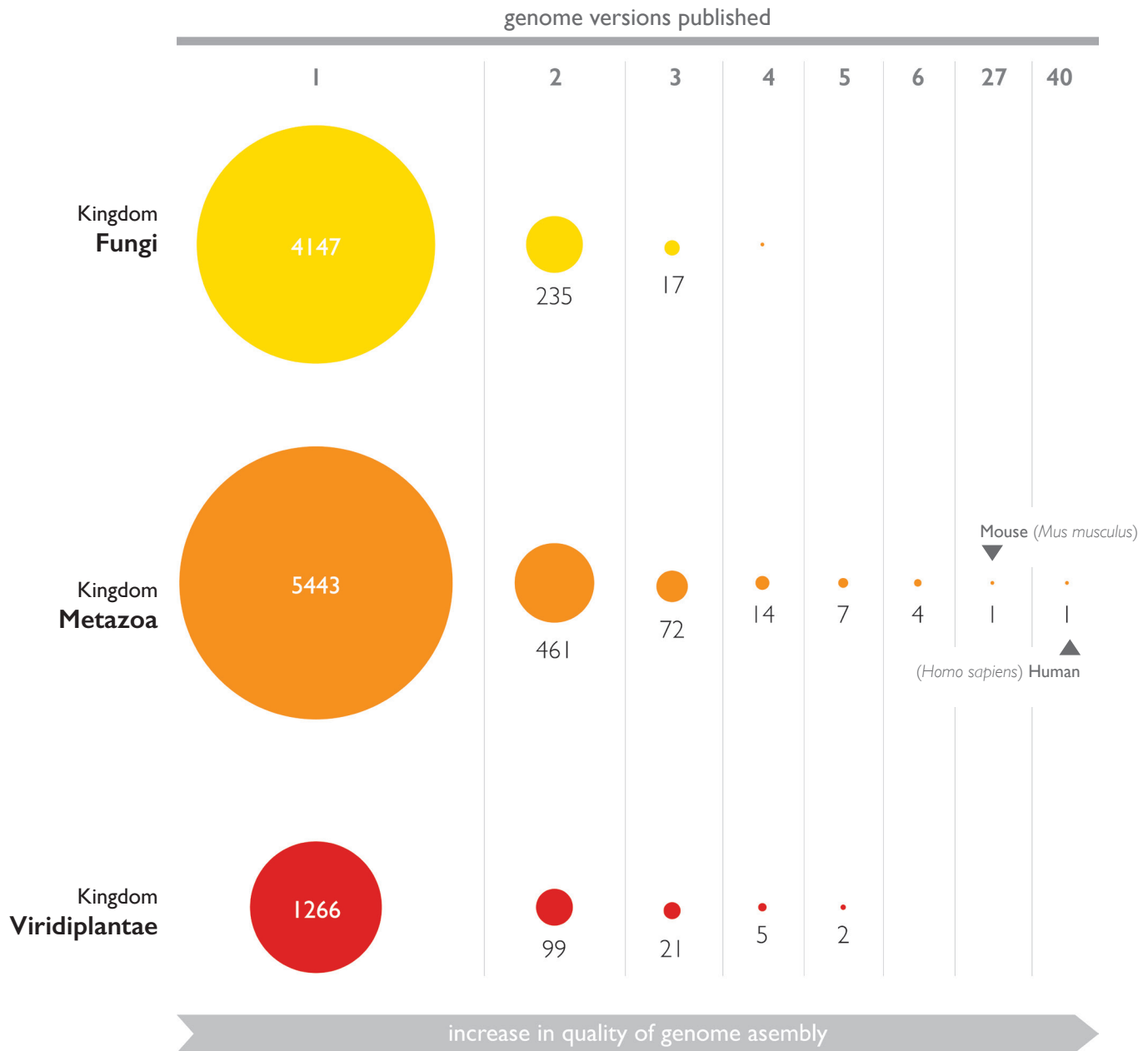
TOWARDS PRODUCING GENOME REFERENCE ASSEMBLIES

While embarking on a genome sequencing project one might vet the suitability of available approaches by surveying which technology is in widest use and reasons why, and powers and pitfalls of particular DNA sequencing platforms. Although there is no one-size fits all approach for genome sequencing, Pacific Biosystems (PacBio) high-fidelity (HiFi) and Oxford Nanopore Technologies (ONT) long-read sequencing platforms have recently been utilized to produce landmark T2T quality, gap-free genomes,

Number of published reference genomes

Data obtained May 31, 2023, from NCBI

genome versions published

	1	2	3	4	5	6	27	40
Kingdom **Fungi**	4147	235	17					
Kingdom **Metazoa**	5443	461	72	14	7	4	1	1
Kingdom **Viridiplantae**	1266	99	21	5	2			

Mouse (*Mus musculus*)

(*Homo sapiens*) **Human**

increase in quality of genome asembly

Figure 2. The number of published reference genomes available for Kingdom Viridiplantae, (green plants) and clade group Opisthokonta Cavalier-Smith 1987 Kingdom Metazoa (animals) and Kingdom Fungi. Data obtained May 31, 2023, from NCBI. The genome iteration column indicates how many genome versions have been published to date, which signals the level of polish and improvements to genome assembly quality. Also shown are the proportion of genomes by version.

especially when used in combination (McCartney et al., 2022, Rautiainen et al., 2023). The HiFi sequencing approach produces highly accurate reads (>99.5% accuracy), which overcomes a limitation inherent to PacBio noisy long-reads that are prone to high levels of sequencing error (up to 15%). The HiFi read accuracy is achieved by circularizing sheared DNA (length 15,000-20,000 bp), repeatedly sequencing the circularized DNA, and then performing a read-error correction step. Another notable advance in sequencing is the increase in ONT raw-read accuracy, having reached 99%, with an average long-read length of 100 Kb (Marx, 2023) on certain platforms and upper bound reported as 2.73 Mb (Payne et al., 2019). The use of long-reads in genome assembly can allow for reading through repetitive regions of chromosomes that would otherwise cause assembly fragmentation. Additionally, ONT and PacBio long-reads (but not HiFi reads) can provide information on methylation patterns that might be of interest to understanding epigenetic signals related to inheritance of functional traits.

Limitations to long-read sequencing protocols include the requirement of fresh-tissue for extraction of high-molecular weight (HMW) DNA, and some sequencing protocols require a relatively large amount of HMW DNA for library preparation. DNA sourced from dried specimens is not suitable for long-read sequencing because the drying and preservation process leads to DNA degradation and fragmentation (McAssey et al., 2023). With regards to DNA input amounts, the standard PacBio workflow requires at least 3 µg of DNA input per 1 Gb of genome length (PacBio, 2022). For some organisms, obtaining that amount of DNA from a single individual is not possible. However, advancements in workflows such as the low-DNA input HiFi library protocol enables generating long-read (~15 Kb) sequences from as little as 300 ng to 3 µg of DNA starting material, with a genome assembly size limit of 1 Gb per single molecule real time (SMRT) cell – noting that use of additional SMRT cells can scale to produce larger genome assemblies (PacBio, 2022). An alternative to long-read platforms is linked-read sequencing, typically performed on a short-read platform such as Illumina, which can be successfully applied to assemble long-reads from HMW DNA extracted from minimal tissue inputs and that performs relatively well even for highly heterozygous genomes (Helmkampf et al., 2019).

GENOME FEATURES AND ASSEMBLY BENCHMARKING

Several techniques can be utilized to evaluate genome features and benchmark the quality of a genome assembly. The assembled genome size can be compared to a haploid (or monoploid) size estimates from flow-cytometry (1C values) (e.g., Bellinger et al., 2022, Cerca et al., 2022) or through reference-free k-mer spectrum analysis (e.g., Ranallo-Benavidez et al., 2020). In simplest terms, kmer-spectrum analysis amounts to breaking DNA sequence data into short fragments (somewhere from 13 to 33 base pairs in length), tallying their frequencies, and modeling their complexity. The k-mer spectrum analysis can also be applied to estimate major genome characteristics such as heterozygosity and repeat content (Vurture et al., 2017), and can detect polyploid events, as was indicated for the hexaploid *B. hawaiensis* genome (Bellinger et al., 2022) using the polyploid-aware mixture model implemented in Genomescope v2 (Ranallo-Benavidez et al., 2020). Furthermore, k-mer spectrum analysis can be leveraged to identify subgenomes in cases where chromosome sequences are assigned to homeolog pairs, based on an approach developed by Cerca et al. (2022) for the tetraploid, critically endangered, Galápagos-endemic species *Scalesia atractyloides* Arnot. In that study, a hierarchical clustering algorithm grouped chromosomes into clusters (subgenomes) based on uneven representation of 'fossil transposable elements' that were actively replicating while the two subgenomes were separated, thus leading the authors to conclude the *Scalesia* Arn. ex Lindl. radiation is of allopolyploid origin. Another common approach for evaluating the quality of a genome assembly is to characterize the recovery of benchmarking universal single-copy orthologs (BUSCOs, Simão et al., 2015) through searches of genes contained within highly curated single-copy ortholog databases tailored to several major taxonomic lineages (OrthoDB, Kriventseva et al., 2019). Expectedly, genome assemblies reconstructed from HiFi and/or long reads tended to provide higher recovery of single-copy orthologs and have fewer missing or partial genes (Bellinger et al., 2022).

The gold-standard for producing a genome reference is to assemble an error-free, chromosome-level, gap free genome. Genome assembly contiguity is evaluated by the number and length of contiguous

assembled sequences (contigs) or scaffolds, the latter being contigs ordered by their locations on chromosomes, even if not assigned to chromosomes, *per se*. The quality of an assembly, even those described as "chromosome resolved," thus requires consideration of contig lengths and the number of NNNN breaks that denote sections of unresolved DNA sequences. Assembly contiguity can be hindered by the quality of the DNA inputs, sequencing technique (long- versus short-reads), assembly strategy, and the repetitive content of the genome (Bennetzen et al., 2014). Regarding the latter, plant genomes can possess extremely high or low repeat content, even within the same family. For example, the haploid-resolved 6.8 Gb genome assembly for *Glebionis coronaria* (L.) Tzvelev (crown daisy) shows a transposable element content of ~93% (Wang et al., 2022). In contrast, *Erigeron canadensis* L. (horseweed), with a much smaller genome (~426 Mb), shows an extremely low repeat content, at 6.25% (Peng et al., 2014). Repetitive elements can cause assembly fragmentation, especially when reads do not traverse genomic intervals that span the entire length of the repeat, leading to an assembly break. On the other hand, the contiguity of a genome assembly can be improved by incorporating optical mapping or high-throughput chromosome conformation capture "Hi-C" or "Omni-C" information (e.g., Yuan et al., 2020, Zhang et al., 2019). These approaches utilize varying combinations of restriction enzymes (or for Omni-C a sequence-independent endonuclease) and short-read sequencing strategies to map DNA reads that are in 3-dimensional proximity based on chromatin packing, which enables joining contigs that would otherwise go unplaced on scaffolds or chromosomes. An alternative, or additional, strategy to improve genome contiguity is to use trio-binning to assign reads to parental genomes and phase the genome into maternal and paternal haplotypes (Cheng et al., 2021).

CASE STUDY

The koʻokoʻolau (*Bidens hawaiensis* A.Gray) reference genome assembly recently produced by myself and colleagues was motivated by a desire to create a genomic resource for this Hawaiian endemic adaptive radiation, which may serve as a model system for understanding eco-morphological diversification and the evolutionary genomics of explosive plant diversifications within insular systems (Bellinger et al., 2022). We assembled the *B. hawaiensis* large (estimated 7.4 Gb) and highly complex, hexaploid genome (base number of 12 chromosomes, 2n = 6x = 72, Ballard 1986) using HiFi sequences obtained from only two PacBio flow cells sequenced on a PacBio Sequel II and high molecular weight (HMW) DNA extracts. Those two cells produced 9.4 million raw sequences (850 Gb raw data), which yielded 3.83 million HiFi sequences having an average size of 15.1 kb and N50 length of 13.5 kb. With only HiFi reads and modest sequencing depth (~15x per monoploid genome), our assembly was comparatively contiguous relative to all other Compositae genomes published at the time, despite the plant's hexaploid status, large genome size, and high repeat content, at ~70%. Additionally, among the Compositae genomes we quality benchmarked for completeness, the BUSCO recoveries were >90% for 8 of the 12 genomes, with *B. hawaiensis* at 96.6%, second only to lettuce (*Lactuca sativa*, haploid genome size of 2.1 Gb), at 97.2% (refer to Bellinger et al., 2022 for details). Further improvements to the *B. hawaiensis* genome can be achieved by polishing with long-reads, optical mapping, or Hi-C/Omni-C scaffolding protocols (Zhang et al., 2019, Gladman et al., 2023).

CONCLUSIONS

Although the total number of publicly available genome assemblies has markedly increased over the past decade, the number of plant genome reference assemblies lags the number of genome assemblies available for other major eukaryotic lineages. Relatively few plant genomes are available to serve as references for the study of island endemics belonging to adaptively radiated clades. Although few in number, the availability of Compositae genomes has more than tripled in just two years, an increase perhaps fueled by decreasing costs of sequencing and the now routine use of third generation, long-read sequencing platforms that are capable of sequencing large, highly complex genomes. To

help fill knowledge gaps, and for conservation purposes, colleagues and I recently published a *B. hawaiensis* genome assembly to contribute to the understanding of ecologically and evolutionarily driven morphological diversification within this highly polymorphic clade (Bellinger et al., 2022). This genome resource, along with others, can assist with determining the genetic basis of functional traits involved in eco-morphological diversification and processes that lead to high levels of island endemism.

METHODS

Genome statistics were obtained by extracting reference genome meta-data from the National Center for Biotechnology Information (NCBI) database using the Datasets and Dataformats command line tools v 15.1.0 (Sayers et al., 2021; download date: May 31, 2023). The taxonomic assignments of genomes followed the NCBI taxonomy database (Schoch et al., 2020).

DISCLAIMERS

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Napoleón's exile on St. Helena:
Everlasting love and Australian paper daisies

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ABSTRACT

The Australian and New Guinean everlasting paper daisy genus *Xerochrysum*, widely grown around the world as Strawflower, Everlasting or Immortelle, was recently revised. The first and type species, *Xerochrysum bracteatum*, was described in 1803 as *Xeranthemum bracteatum* from a plant cultivated in the Empress Joséphine's garden at Malmaison. During our project, we learned that *Xerochrysum* was naturalised in St. Helena, the place of Napoleón Bonaparte's last exile, and is presumed to have been introduced by him. We conducted genetic analyses to test the derivation of the St. Helena plants. Comparisons with some colourful hybrid cultivars and naturally occurring populations in Australia found the St. Helena plants to be most similar to *Xerochrysum bracteatum* s. str. of the Sydney Basin. The St. Helena plants were without admixture of another species as would be expected if they were more recently escaped ornamental cultivars. Our results support the conclusion that the St. Helena *Xerochrysum* were introduced during Napoleón's exile, likely as a reminder of his wife's garden.

Keywords: cultivars, Empress Joséphine, Gnaphalieae, history, Malmaison, *Xerochrysum*.

Picture the exiled former emperor Napoleón Bonaparte, imprisoned by the British on the remote island of St. Helena, gazing at daisies and remembering his wife, the Empress Joséphine, and a happier time. This vision is where our team of plant systematists found itself in a surprise twist in the discovery and documentation of Australia's stunning biodiversity.

Australia's plants and animals have a long history of admiration from around the world (Janick, 2007; Mabberley, 2020), yet today our unique biodiversity is still surprisingly poorly known and, in many instances, critically endangered (Taxonomy, 2018). Australia is a nation that exports raw products to the world. Currently it is iron ore and coal that top the list, but in the early days of the colony at Port

Jackson, it was our natural heritage in the form of seeds and plants (Mabberley, 2020).

We begin the story in 1803, when the French botanist Étienne Pierre Ventenat (1757–1808; https://www.biodiversitylibrary.org/bibliography/70396) was documenting the Empress Joséphine's garden at Malmaison, a manor house just outside Paris, and the large collections of exotic flora held in its orangery. A spectacular golden daisy with papery bracts attracted his eye. Like any good botanist, he tried to recognise this plant and recall its name, but it did not match anything known to him. Ventenat (1803) then described this plant as a new species, but we know it today as a popular Australian plant grown around the world: *Xerochrysum bracteatum* (Vent.) Tzvelev (syn. *Helichrysum bracteatum* (Vent.)

St. Helena, last home of Le Petit Caporal

St. Helena, one of the most remote islands in the world was picked by the British government as the exile location of Napoleón Bonaparte (affectionately called "le petit caporal" by his troops).

St. Helena

Jamestown

St. Helena

Tree fern thicket of St. Helena

The flora of St Helena includes 45 endangered endemic species of plants and there are ongoing programs to conserve and replant the great forest on the island.

Panoramic view of St. Helena
Photo by Jannas Du Plessis

Figure 1. Cultivar of *Xerochrysum* Tzvelev. Cultivars, including what are referred to as 'forms', 'varieties', and 'wild selections', have uncertain ancestry due to many growers use of and referral to a broadly defined *X. bracteatum* s. lat. *Photo by T.L. Collins.*

Andrews; *Bracteantha bracteata* (Vent.) Anderb. & Haegi), commonly known as the Immortelle, Straw Flower, or Golden Everlasting Paper Daisy (Figure 1).

Napoleón Bonaparte was exiled by the British to the island of St. Helena in the South Atlantic Ocean in 1815, where he remained until his death in 1821 (Brunyee, 2015). During Napoleón's six years of exile, parcels of food and books were sent to St. Helena, purportedly including 'seeds of everlasting daisies …to remind him of Joséphine's garden' (Hamilton, 1999).

Our research aimed to clarify and document the species diversity in *Xerochrysum*, which occupies widely varying habitats in Australasia. This type of research underpins the conservation of plants in the wild and can inform the horticultural

development of new cultivars and varieties (Figure 2). Horticulturists are inventive and industrious, and European growers had developed new colourful hybrid cultivars in the 1850's (Moore, 1861), and today the Immortelle continues to be improved and win awards at horticultural shows around the world in varying shades of yellow, pink, orange, purple and white (https://www.hortweek.com/xerochrysum-mnp-wins-ipm-essen-top-bedding-plant-prize/ornamentals/article/1523670; Figure 2).

We wanted to know where the daisies described by Ventenat at Malmaison came from and also: where did they go? A chance conversation in the university tearoom between then PhD student Tim Collins and Dr John Nevin revealed that *Xerochrysum* continues to grow wild on St. Helena and is thought to be plant-escapees from Napoleón's garden (Lambdon, 2013). Golden Everlastings and their cultivars are known to escape cultivation (Tropicos, 2020) and grow wild and weedy around the world. Sadly, Joséphine's Golden Everlastings can no longer be found in the garden at Malmaison (https://musees-nationaux-malmaison.fr/chateau-malmaison/le-parc-de-malmaison).

If we could compare the genetics of the St. Helena everlastings with naturally occurring populations in Australia, perhaps we could determine the location of the original 1790's collections that went to Europe and Joséphine's garden, and also confirm whether the naturalised plants on St. Helena are indeed from the time of Napoleón's garden or are more recently introduced cultivars. As the plant described by Ventenat from the Empress Joséphine's garden in Malmaison is the Type Specimen for the genus *Xerochrysum* (*X. bracteatum* (Vent.) Tzvelev, *Novosti Sist. Vyssh. Rast.* 27: 151 (1990)), it is the point of truth for defining what we mean when we refer to the genus.

When contacted by Tim, the good people at the St. Helena National Trust immediately grasped the excitement of this project. They thoughtfully collected samples and sent them to the University of New England in Armidale via Kew Gardens in London (Figure 2B).

We sequenced the DNA of the St. Helena samples, as well as some colourful hybrid cultivars and compared them with many different species and populations of

Gumwoods

The geographic isolation that made St Helena
an ideal prison for Napoleón also led to
the evolution of several endemic lineages of
Compositae, such as the rare
St Helena "gumwood"
Commidendrum robustum (Roxb.) DC.

Panoramic view of St. Helena with *Commidendrum robustum* in the foreground
Photo by Rebecca Cairns-Wick

Pierre-Joseph Redoute's masterpiece.

Painting of *Xerochrysum bracteatum* (Vent.) Tzvelev (syn. *Xeranthemum bracteatum* Vent.) by Pierre-Joseph Redouté published in the book *Jardin de la Malmaison*

Figure 2. **A.** Cultivar *Xerochrysum* 'Dwarf Mixed'. **B.** Capitulescence of *Xerochrysum bracteatum* (Vent.) Tzvelev grown from seed collected at Longwood, St. Helena. **C.** Capitulescence of *Xerochrysum macranthum (*Benth.) Paul G. Wilson growing in the wild, Western Australia. Photos, A-B, *T.L. Collins*, C, A.N. Schmidt-Lebuhn.

Xerochrysum that we collected from around Australia. The results showed us that the colourful hybrid cultivars originated from crossing *X. bracteatum* (Golden Everlasting) from populations growing naturally near Sydney with the Western Australian endemic, *X. macranthum* (Benth.) Paul G.Wilson (White Straw-flower; Figure 2C) .

The plants from St. Helena populations do not contain any White Straw-flower (*X. macranthum*) ancestry in their genome and are most similar to naturally occurring Golden Everlasting (*X. bracteatum*) populations in the Sydney Basin. Yet they have much lower genetic diversity, as could be expected after many generations of isolation on the island. Our results support the conclusion that St. Helena populations were introduced by or for Napoleón Bonaparte from the Sydney Basin (Collins et al., 2021).

The story of Napoleón and Joséphine's Paper Daisies has elements of a fairy-tale with daisies crossing oceans and centuries for the memories of lost love. The science behind this fairy-tale helps answer longstanding questions of the identity of the weedy plants on St. Helena and the origins of the colourful hybrid cultivars, but it has also illuminated species diversity in Australia. Based on this knowledge, we recently published 12 new species of *Xerochrysum* including some identified as Critically Endangered (Collins et al., 2022). But that is a story for another time.

ACKNOWLEDGMENTS

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Beyond the comfort zone:
Lagenophora Cass. (Astereae) in the Malvinas/Falkland Archipelago

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ABSTRACT

Lagenophora, a small genus within the Compositae family, captivates researchers with its intriguing characteristics. Its tiny size, lack of a pappus, and transpacific distribution on islands in the southern hemisphere are very unusual. Nowadays, *Lagenophora* comprises ca. 17 species, and its phylogenetic complexity hints at a more intricate evolutionary history. It inhabits Australia, New Zealand, Southeast Asia, India, and South America. Birds, due to sticky glands present on the fruits, may have aided in *Lagenophora*'s dispersal, although other vectors probably also played a role. The process of colonizing diverse habitats, especially remote islands, remains an enigma. Exploring continent-island biotic exchanges motivated a 2023 expedition to the Malvinas/Falkland Islands to collect insects, arachnids, and vascular plants. Support from FONCYT, Argentina, and a collaboration with SAERI were crucial for the success of this expedition. We found *L. nudicaulis* in dwarf shrub heath and montane vegetation. Although it is not a generalist plant, it has been also found in other habitats which unravels successful arrival and settling in the islands.

Keywords: Asteraceae, arachnids, biotic exchange, Compositae, islands

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INTRODUCTION

The Compositae family, which is the most species-rich among vascular plants, has developed various adaptive strategies throughout its evolution, leading to successful diversification. Doubtless, the traditional dispersal structure, the pappus, is one of them. A significant number of species within this family have successfully colonized diverse environments, thanks to the dispersal opportunities generated by the diversity of forms that the pappus has evolved into. However, there is a small group of genera that deviates from this rule: the species where the pappus is absent. These particular species have captivated researchers who have proposed different theories concerning their dispersal and current distribution, particularly on islands (e.g., Carlquist, 1967, 1983; Swenson & Bremer, 1997).

Lagenophora Cass., a small genus within the Astereae tribe, holds interest for researchers due to its characteristics. Made up of petite herbaceous plants, *Lagenophora* distinguishes itself by the absence of a pappus and sticky fruits. Adding to its uncommon nature, this genus showcases a transpacific distribution, predominantly inhabiting islands in the southern hemisphere.

These unusual features and, its affinity for remote islands, have piqued the curiosity of scientists, prompting them to explore the evolutionary history, adaptive strategies, and events that could have shaped its transoceanic distribution.

Phylogenetic studies on *Lagenophora* have revealed that the genus is paraphyletic, indicating its
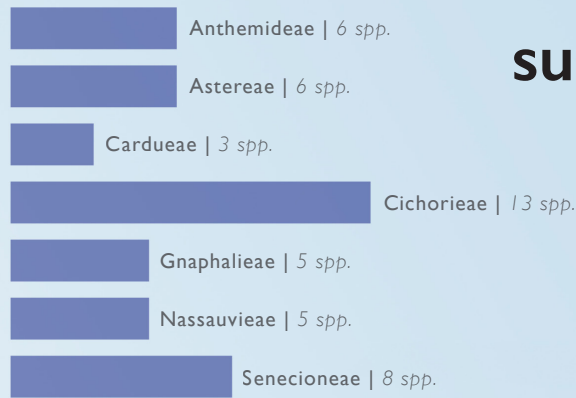
From Mount Williams to Mount Tumbledown

Climbing a mountain can always be a challenge. This time we also had to deal with deep emotions. The sound of the wind was not the only one echoing in our ears. Yes, the mind can be tricky... this time the sound of the wind was the only one up there.

Hike from Mt. Williams to Mt. Tumbledown, Isla Soledad/East Island
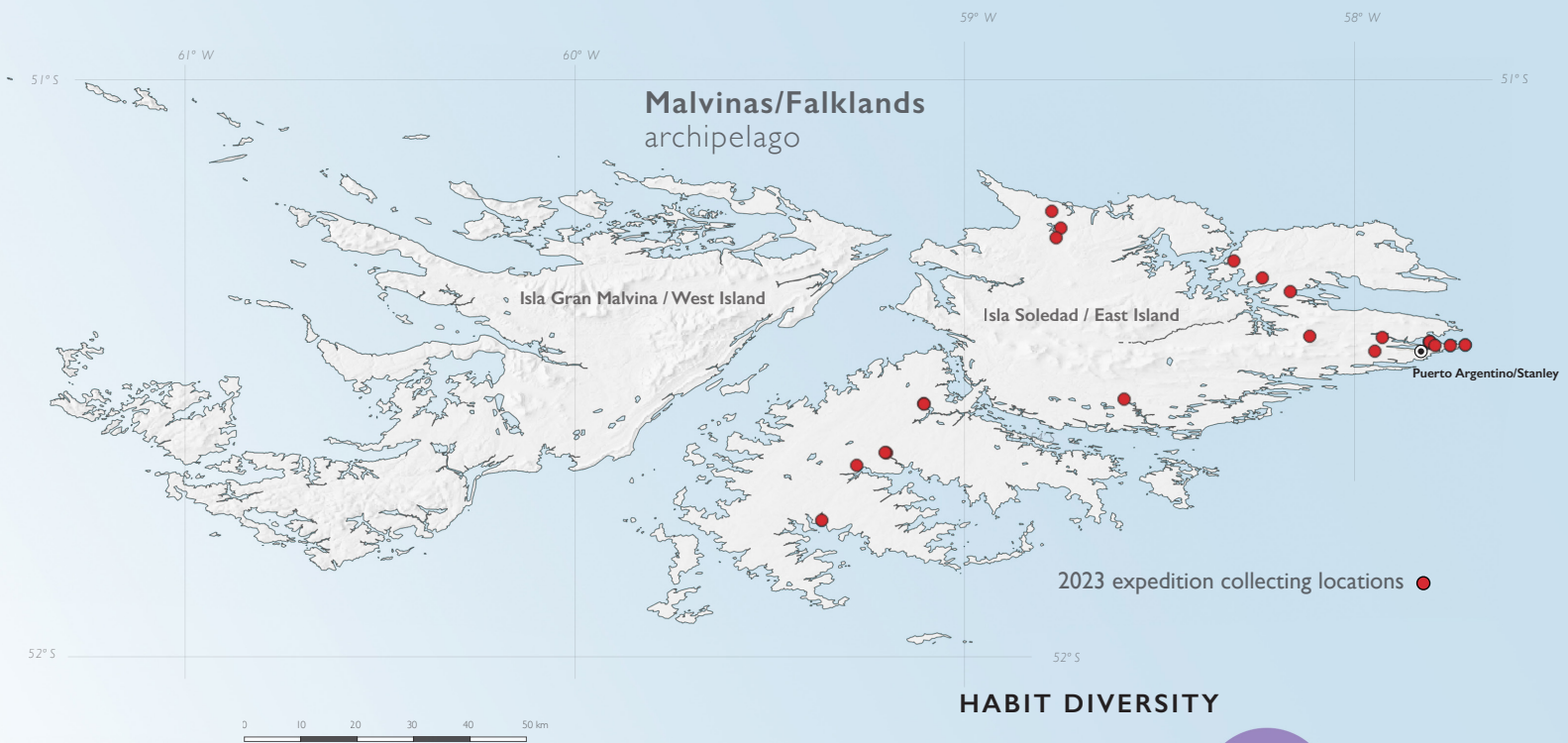*Photo by M. J. Ramírez.*

TAXONOMIC DIVERSITY

- Anthemideae | 6 spp.
- Astereae | 6 spp.
- Cardueae | 3 spp.
- Cichorieae | 13 spp.
- Gnaphalieae | 5 spp.
- Nassauvieae | 5 spp.
- Senecioneae | 8 spp.

Sancho et al. | **FROM THE FIELD**

Map of 2023 expedition & summary of the Compositae of the Malvinas/Falkland Archipelago.

Totalling 46 species between natives and introduced, the Compositae are the most species rich familiy in the archipelago. Out of a total of 14 endemic vascular plant species, the Compositae with 9 endemic species, account for 64 % of them.

Malvinas/Falklands archipelago

Isla Gran Malvina / West Island

Isla Soledad / East Island

Puerto Argentino/Stanley

2023 expedition collecting locations

Diversity data was extracted and processed from Heller et al. (2019)

Malvinas | Falklands Archipelago

HABIT DIVERSITY

| Annual herbs | Biennial herbs | Shrubs | Perennial herbs | Bushes |
| 8 spp. | 5 spp. | 2 spp. | 29 spp. | 2 spp. |

ORIGIN

Endemic
9 spp.

Native
25 spp.

Introduced
21 spp.
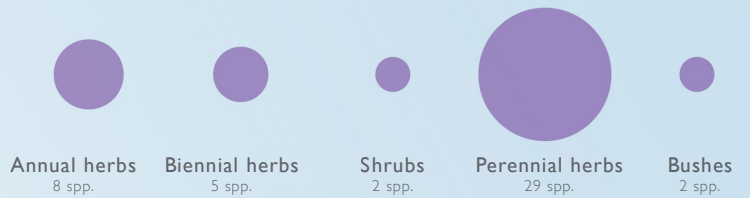
Occasional but not Invisible

Lagenophora nudicaulis (Comm. ex Lam.) Dusén, a beautiful, tiny plant emerging from the crowded *Sphagnum* surroundings. With its white capitula turning pink and even purple with time, this species has conquered some of the most beautiful environments in southern South America.

Gordon Island, Alberto de Agostini National Park, Chile.
Photo by Mauricio Bonifacino

Figure 1. Plant collecting in Mount Tumbledown. Understanding the community composition provides the context essential for uncovering the knowledge of the individual species we seek. *Photo: M. J. Ramírez.*

evolutionary relationships are more complex than initially thought (Nakamura et al., 2012; Sancho et al., 2015). This genus currently encompasses ca. 17 known species and inhabits various continents (Wang & Bean, 2016). The highest diversity of *Lagenophora* is found in New Zealand, yet it also lives in Australia. Moreover, a few species are scattered across Southeast Asia and India, highlighting their adaptability to different environmental conditions. *Lagenophora* also occurs in South America, where three species are currently documented. These three species form a monophyletic group with an estimated divergence time of around 4.6 ma (Sancho et al., 2015). These findings offer valuable insights into the historical biogeographic events that shaped *Lagenophora*'s distribution, especially because

Antarctica might have played a significant role in the dispersal of *Lagenophora* to South America before complete formation of the Antarctic ice shield. *Lagenophora's* South American species have a continental distribution, spanning regions in Chile and Argentina, as well as various islands, including Tierra del Fuego Archipelago, Isla de los Estados, Juan Fernández Archipelago, Malvinas/Falkland Archipelago, Tristan da Cunha and Gough Islands.

With their lack of pappus and their fruits equipped with sticky glands, birds have been suggested as potential dispersal vectors for *Lagenophora* (Cabrera, 1966), although other animals likely contribute to this process as well. Furthermore, Sancho et al. (2015) suggested that the secretion from the fruit

Table 1. Compositae of the Malvinas/Falkland Archipelago, extracted from Heller et al. (2019). AH: annual herb, B: bush, BH: Biennial herb, PH: perennial herb, S: shrub.

Tribe	Species	Status	Habit
Anthemideae	*Achillea millefolium* L.	Introduced	PH
	Leptinella scariosa Cass.	Native	PH
	Leucanthemum vulgare Lam.	Introduced	PH
	Matricaria discoidea DC.	Introduced	AH
	Tanacetum vulgare L.	Introduced	PH
	Tripleurospermum maritimum (L.) W.D.J.Koch	Introduced	PH
Astereae	*Baccharis tricuneata* (L. f.) Pers.	Native	S
	Bellis perennis L.	Native	PH
	Chiliotrichum diffusum (G. Forst.) Kuntze	Native	S
	Erigeron incertus (d'Urv.) Skottsb.	endemic	PH
	Lagenophora nudicaulis (Comm. ex Lam.) Dusén	Native	PH
	Symphyotrichum vahlii (Gaudich.) G.L.Nesom	Native	PH
Cardueae	*Carduus tenuiflorus* Curtis	Introduced	BH
	Cirsium arvense (L.) Scop.	Introduced	PH
	Cirsium vulgare (Savi) Ten.	Introduced	BH
Cichorieae	*Agoseris coronopifolium* (D'Urv.) Chambers ex D.M. Moore	Native	AH
	Crepis capillaris (L.) Wallr.	Introduced	AH
	Hieracium antarcticum d'Urv.	Native	PH
	Hieracium patagonicum Hook. f.	Native	PH
	Hypochaeris arenaria Gaudich.	Native	PH
	Hypochaeris radicata L.	Introduced	PH
	Leontodon hispidus L.	Introduced	PH
	Pilosella aurantiaca (L.) F.W.Schultz & Sch.Bip.	Introduced	PH
	Pilosella officinarum F.W.Schultz & Sch.Bip.	Introduced	PH
	Sonchus asper (L.) Hill	Introduced	AH
	Sonchus oleraceus L.	Introduced	AH
	Taraxacum gilliesii Hook. & Arn.	Native	PH
	Taraxacum officinale G. Weber ex F.H. Wigg.	Introduced	PH
Gnaphalieae	*Chevreulia lycopodioides* (D'Urv.) DC.	endemic	PH
	Gamochaeta americana (Mill.) Wedd.	Native	BH
	Gamochaeta antarctica (Hook. f.) Cabrera	endemic	BH
	Gamochaeta malvinensis (H. Koyama) T.R. Dudley	Native	PH
	Helichrysum luteoalbum (L.) Rchb.	Introduced	AH
Nassauvieae	*Leucheria suaveolens* (d'Urv.) Speg.	endemic	PH
	Nassauvia falklandica Upson, R. and Hind, D.J.N	endemic	B
	Nassauvia gaudichaudii (Cass.) Cass. ex Gaudich.	endemic	PH
	Nassauvia serpens d'Urv.	endemic	PH
	Perezia recurvata (Vahl) Less.	Native	B
Senecioneae	*Abrotanella emarginata* (Cass. ex Gaudich.) Cass.	Native	PH
	Senecio candidans DC.	Native	PH
	Senecio littoralis Gaudich.	endemic	PH
	Senecio squalidus L.	Introduced	PH
	Senecio sylvaticus L.	Introduced	AH
	Senecio vaginatus Hook. & Arn.	endemic	BH
	Senecio vulgaris L.	Introduced	AH
	Tussilago farfara L.	Introduced	PH

Kiting in the air

Spiders use silk threads to take lift in the wind and travel
long distances, colonizing even remote oceanic islands.
Is this the way many of them arrived here? Maybe the
sticky yellow traps will help us to get answers.

Puerto Argentino/Port Stanley surroundings, Isla Soledad/East Island
Photo by G. Sancho.

Figure 2. Reaching the summit. We looked for different environment searching for target species. The grasslands on the slopes gave way to rocky outcrops towards the top. *Photo: M. V. Lencinas.*

glands could aid in buoyancy, facilitating dispersal to new territories. These unique features have allowed *Lagenophora* species to successfully thrive in the understory of southern beech forests, while they also find a home in peat bogs or dwarf shrublands. According to Sancho et al. (2015), the ancestral habitat of *Lagenophora* species is the understory of beech forests, revealing a connection to its past environment.

Nonetheless, the process of colonization into diverse habitats, particularly remote islands, remains an enigma. Questions arise as to how *Lagenophora* in South America ventured away from its "comfort zone" of beech forests and managed to establish itself in other environments. Understanding the relationship between continental and island populations is a crucial aspect of *Lagenophora*'s biogeographic evolution. These inquiries served as strong motivations for ongoing research on the biogeography of *Lagenophora* in South America (Sancho et al., in prep.).

To figure out *Lagenophora*'s story, a thorough sampling across the whole distribution area seemed like the right approach and thus the collection of specimens from both continental and island populations of *Lagenophora* species started more than a decade ago. Through the collaborative efforts of various researchers led by G. Sancho and colleagues, including J. Mauricio Bonifacino, Laura Iharlegui, and Anabela Plos, among others, several collecting expeditions were planned. Contributions from other researchers, such as Andrea Raya Rey on Isla de los Estados and Rosa A. Scherson-Vicencio and Héctor Gutiérrez on Juan Fernández Archipelago, further enriched the sampling efforts. The remote and challenging conditions of Gough and Tristan da Cunha islands have made specimen collection an elusive endeavor. Nevertheless, near mainland southern South America, close islands crucial for comprehending the continent-island relationships in *Lagenophora*'s distribution remained unexplored: the Malvinas/Falkland Archipelago.

THE MALVINAS/FALKLAND EXPEDITION: IN THE BEGINNING

Among the three South American species of *Lagenophora*, namely *L. hariotii* Franch., *L. hirsuta* Poepp. ex Less., and *L. nudicaulis* (Lam.) Dusén,

Treasures among rocks

The rising rocks provide shelter to different communities of precious small plants and animals that we try to discover. The humid ground and shade provided by rocks show us a world of species escaping the full sun exposure.

Mt. Tumbledown, Isla Soledad/East Island
Photo by M. J. Ramírez.

Figure 3. Processing the treasures. At night, the work continues to register every detail of the long day. *Photo: M. J. Ramírez.*

only the latter is found on the Malvinas/Falkland Archipelago. An earlier attempt to collect this species during an enthralling previous trip in 2019, led by Rosa A. Scherson-Vicencio, Daniel Sziklai G., and Gisela Sancho, unfortunately proved unsuccessful. Adding to the complexity, the challenges posed by the Covid-19 pandemic further hindered access to materials collected by Stefanie Carter in the islands, underscoring the need for a new expedition to the archipelago.

This field trip held profound significance, not only for the biogeographic study of *Lagenophora* but also as an opportunity to better understand the evolution of the entire South American biota with continent-island distribution. María Vanessa Lencinas, Martín J. Ramírez, and Gisela Sancho, all of us researchers of Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), teamed up in planning an expedition to the Archipelago. With financial support by the Argentinean Ministerio de Ciencia, Tecnología e Innovación (MINCyT), we organized a comprehensive trip that focused on three fundamental objectives: 1) to collect insects

and arachnids, 2) to collect vascular plants, and 3) to analyze the plant communities at the collecting locations.

FROM THE FIELD

The expedition took place in January 2023 involving collections first in the Malvinas/Falkland Archipelago and later in southern Chile, around Punta Arenas.

While in the Islands, the success of the expedition would not have been possible without the collaboration of South Atlantic Environmental Research Institute (SAERI) and its director, Dr. Paul Brickle. SAERI played a pivotal role, as their helpful staff assisted us in planning the expedition. Given the challenging terrain, a 4x4 vehicle was needed, as the island roads were generally in good condition, but the topography posed its complexities. However, we faced restrictions, as the rented vehicles were prohibited from straying off the designated roads This limitation exists because all the remaining

Step by step, a succession of wonders

In Cape San Felipe/Pembroke, a succession of environments unfolds before us, stretching from the heart of the land to the vast expanse of the sea. From grasslands to peatbogs, all connected by meandrous creeks, to the sea and beyond.

Cape San Felipe/ Pembroke, Isla Soledad/East Island
Photo by M. J. Ramírez.

Figure 4. Pressing in the field saves time and mistakes. P*hoto: M. J. Ramírez.*

road infrastructure in the archipelago is exclusively reserved for residents living on the islands. Unfortunately, reaching Gran Malvina/ West Falkland Island demanded a different logistical approach and more time than our schedule allowed.

As is customary in any field trip, our daily activities started early, allowing us to maximize our time. The 4x4 vehicle quickly became our trusted ally, even though navigating on the left side of the road was not exempt of challenges for us. Departing the town of low houses and beautiful gardens, the immensity of the landscape overwhelmed our senses. On one side, the serene and chilly sea stretched as far as the eye could see, while on the other, the vast expanse of golden terrain with rolling hills seemed to continue endlessly to the horizon. The absence of trees did nothing to diminish the beauty of our surroundings. Throughout our journey, we encountered a diverse array of environments, often characterized by imposing rock formations that dramatically shaped the landscape (Figure 1). Some scenes before us were unlike any other, like the characteristic gray rock rivers flowing gracefully down the mountains, intermingling with the

golden grass (Figure 2) and green dark heathlands of dwarf shrubs and ferns (Figure 4). Some other places reminded us of the landscapes and biotic connections shared with other places like Tierra del Fuego (Figure 7). Setting foot on those hills evoked profound emotions within us.

We were impressed by the unusual characteristics of the ground that was draped in peat, making every step a challenge. Beneath the surface, inconspicuous streams meandered, concealed by the lush vegetation. Enigmatic circles of varying diameters, seemingly carved into the peat, form dark lagoons with depths that remained mysterious. The presence of vast fern expanses between the rocks served as a signature feature of the islands.

In other areas, the expansive prairie seemed to sway in harmony with the wind, its grasses displaying a vibrant range of colors from golden to crimson (Figure 5). Elsewhere, the striking contrast of the blue-green sea, fine white sands, and light green tussac grass dominated our view.

A sea of grass

Grasslands in Malvinas/ Falkland Islands encompass acid, neutral (including "Greens"), and improved and reseeded grasslands (Heller & al., 2019).

Horseshoe Farm, Isla Soledad/East Island
Photo by Gisela Sancho

The world of the minuscule: searching for the continental relatives

The answers not always are blowing in the wind. The ground offers a world of hints on the continental-island biota connections. With our collections from Malvinas/Falklands Islands in mind, here, we screen a peatbog in southern Chile.

Laguna El Parrillar Park, Punta Arenas, Región Magallanes, Chile.
Photo by G. Sancho.

White is not the absence of color

In Gypsy Cove, some landscapes of the islands are stunning by their contrasts. Here, the white sand intermediates between the sky and the sea.

Gypsy Cove, near Puerto Argentino/ Port Stanley, Isla Soledad/East Island
Photo: G. Sancho.

Figure 5. The blue sky in the islands can rapidly turn into gray sky indicating the work day is coming to a close. *Photo: G. Sancho.*

As usually we focused on the tiny wonders of plants and spiders, unaware of another world, of other beings that were unnoticed to us. These are the penguins with their gracious chicks nesting among the tussac grass. That's how we are, passionate about tiny things, so soon we looked at the ground again.

During the trip we realized something unusual, making the whole scene almost out of place, not in harmony with the landscape. This place should have been predominantly, if not entirely, moist, yet as we walked, instead of sinking our feet into soft ground, we felt a disheartening crunch underfoot. The past few years have been unusually dry, and the effects of climate change are becoming evident. Despite the hospitality of one resident, who drove us to cover much more ground with the vehicle than we could on foot, finding humid environments with *Lagenophora* was no longer a simple task. This unfortunate trend is mirrored in mainland southern South America, with growing concerns about its impact, for instance, on livestock. Whether due to climate phenomena, climate change, or a combination of factors, drought is wreaking havoc and reshaping the landscape.

Yet, amidst these somber reflections, the breathtaking red sunsets granted us a brief respite. Later, we had to process and preserve the precious specimens we had collected, cherishing them as invaluable treasures from our journey (Figure 3).

During our expedition to Isla Soledad / East Falkland Island, we visited a total of 28 locations (see map). In each of these sites, we collected specimens of

Nature's design

Nature, the master landscape designer, achieves in a single brushstroke wonders that humans can never replicate. This truth becomes evident as we immerse ourselves in the community of *Senecio candidans* DC.

Yorke Bay, Isla Soledad/East Island
Photo by M. Ramírez.

insects and arachnids, and in 22 of them, we also gathered vascular plants. At nine selected sites, we conducted environmental characterizations, considering impact types, ground and vegetation cover, and plant species richness.

To ensure the valuable specimens of vascular plants were well-documented and accessible for research, duplicates were distributed to several herbaria, including the Museo de La Plata (UNLP), Centro Austral de Investigaciones Científicas (CADIC, CONICET), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Falkland Conservation Institute, Instituto de la Patagonia, and the Government of Tierra del Fuego.

To gather arachnids and insects, we employed a variety of methods, including manual collection, Berlese funnels, and sticky traps. We are also collaborating with Alastair Lavery, a researcher that spent many years studying arachnids from the Islands. Currently, the collected organisms are being processed, ensuring that their scientific value is preserved and that they will contribute significantly to our research findings.

LAGENOPHORA NUDICAULIS: OCCASIONAL BUT NOT INVISIBLE

Spotting *Lagenophora* wasn't an easy task; its size doesn't exceed two centimeters in height (Figure 6). Nevertheless, there it was—occasional but not invisible—with its small heads of white or pinkish corollas, indicating the passage of time. After years of searching in the understory, identifying *L. nudicaulis* habitat in the Malvinas/Falkland Islands proved to be a challenge. However, certain characteristics remained consistent: moist areas with loose, organic-rich soil. As usually happens to botanists, once we gain sense of a search image, everything fell into place. Among the fourteen proposed habitat types for the islands (Heller & al., 2019), this plant thrives in inland rock, dwarf shrub heath, greens and natural grasslands, acid grasslands, and coastal cushion heath.

As one of the 34 native species of Compositae (Table 1) on the islands, *Lagenophora nudicaulis* offers a

Figure 6. Sterile *Lagenophora nudicaulis* (Comm. ex Lam.) Dusén is even more difficult to find than the blooming one, but a careful scrutiny of the ground reveals her among its companions (*Empetrum rubrum* Vahl ex Willd., *Pernettya pumila* (L. f.) Hook., *Blechnum penna-marina* (Poir.) Kuhn) in a heath community. *Photo: M. V. Lencinas.*

historical connection with mainland South America. Besides, many of the communities, with their familiar appearance and composition, mirror habitats found on the nearby continent. While some studies have explored these connections (e.g., Kopuchian & al., 2016; Baranzelli & al., 2018), we still need to uncover the how and when of the continent-island exchange for *Lagenophora* and the other organisms inhabiting

Figure 7. Not many tall shrubs rise from the ground in the islands. Here, *Chiliotrichum diffusum* (G. Forst.) Kuntze, another witness of the continent-island connections, seems to blend with the sea and the sky. Photo: G. Sancho.

the archipelago. The task is both challenging and enthralling, and we are committed to it. As we left the islands, we were saddened to say goodbye to a place so close and familiar, yet far away, taking with us inspiring memories of its majestic landscapes and marvelous biota.

journey possible. We also thank the director of SAERI, Paul Brickle, for his collaboration and support in organizing and planning the trip. Their staff, especially Amy Constantine, is also acknowledged as their assistance ensured the success of the expedition. We are very grateful to Stefanie Carter who collected *Lagenophora nudicaulis* in the islands for us. We deeply appreciate the willingness of the people living in the Malvinas/Falkland archipelago to collaborate in our work. We thank the reviewers for comments and suggestions.

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STYLE
Where art and science converge

RAYLESS

Closeup of the capitula of *Pleurophyllum criniferum* Hook.f., which lacks ray florets. The purple disk florets (rarely yellow) may be a synapomorphy uniting the subantarctic endemics genera *Pleurophyllum* Hook.f. and *Damnamenia* Given. Image taken in Campbell Island, New Zealand

Steve Wagstaff

MEGAHERBS

Pleurophyllum speciosum Hook.f. in flower in a
megaherb field with *Bulbinella rossii* (Hook.f.) Mottet.
Image taken in Campbell Island, New Zealand.

Phil Garnock-Jones

RAY BEARER

Close-up of the capitula of *Pleurophyllum speciosum* Hook.f showing colourful disk and ray florets. Vast meadows of *Pleurophyllum speciosum* are a stunning vista on Campbell Island. Colourful flowers are not a common occurrence in New Zealand, which is known for predominately white flowers. Image taken in Campbell Island, New Zealand

Steve Wagstaff

LIZZIE ROEBLE's ART GALLERY of Island COMPS

BIDENS COSMOIDES ▶

The spectacular *Bidens cosmoides* Sherff is a woody climber that is endemic to the high-elevation rainforests of Kaua´i Island on the Hawaiian archipelago. The capitula of this species are quite unique for the genus: the large pendent heads drop downward and have elongated styles that attract bird pollinators. Unfortunately, *Bidens cosmoides* is an endangered species.

Lizzie Roeble

◀ DISTEPHANUS POPULIFOLIUS

This woody shrub is endemic to Mauritius in the Indian Ocean, the species is rare and only found on a few mountaintops on the island. *Distephanus populifolius* (Lam.)Cass. is a striking plant notable for the dense silver, white tomentum covering the underside of the leaves and golden yellow corollas, a color unusual in Vernonieae

Lizzie Roeble

TICATIMES

selected Compositae news and updates from
THE INTERNATIONAL COMPOSITAE ALLIANCE

Edited by Jennifer R. Mandel

JULY 2023

IJPS SPECIAL ISSUE PUBLISHED HONORING VICKI A. FUNK

This July, a special issue was published in the International Journal of Plant Sciences: "A Botanist at the Extreme: Honoring the Great Contributions of Dr. Vicki A. Funk." This issue was guest edited by Jennifer R. Mandel (University of Memphis, USA), J. Mauricio Bonifacino (Universidad de la República, Uruguay), and Erika R. Moore (University of Memphis, USA). This issue was spurred by the symposium at the Botany Meeting in Alaska, 2022, that was hosted in Vicki's honor. Recognizing the achievements from a long and distinguished career by a pioneer in systematic botany, the issue brought together a diverse set of research topics made possible in Compositae through Vicki's generous and collaborative spirit: Biogeography, Collections, Genomics, Palynology, Phylogeny, and Systematics.
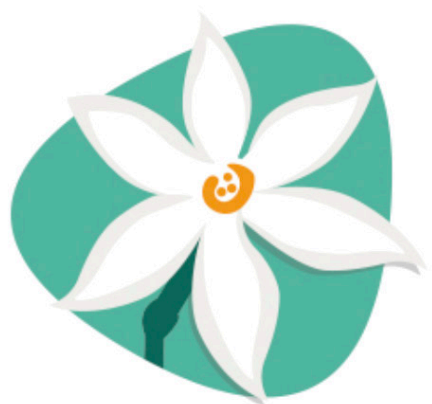
https://www.journals.uchicago.edu/doi/full/10.1086/725047

**TICA TO HOST SYMPOSIUM AT
IBC MADRID IN 2024**

In Madrid next year, TICA will host a symposium: "Synantherology reloaded: Recent advances and the future of evolutionary studies in Compositae." Organizers of the symposium are Jennifer R. Mandel (University of Memphis, USA) and J. Mauricio Bonifacino (Universidad de la República, Uruguay). Technological advances in high-throughput sequencing, large-scale phylogenomics, and improved database infrastructure have revolutionized the fields of plant systematics and evolution. The symposium will highlight the impact these technologies have had on our understanding of the biogeography, systematics, and evolution of the world's largest flowering plant family. Speakers will present major findings from the past decade including how new data have led to major changes in classification and have improved data accessibility and infrastructure. The symposium will address the future of studies in the family and what some of the newest technologies, e.g., highly accurate long-read sequencing, CRISPR/functional genetics, and single-cell/nuclei sequencing, will have to offer for further studying the evolution of this fascinating plant group. There are still a couple of slots left in the symposium, reach out to the organizers if you are interested in speaking. We will aim to maximize diversity of speakers and topics.

GUIDELINES FOR AUTHORS

Types of articles and editorial process

CAPITULUM accepts contributions matching the following sections, as long as they are relevant to the plant family Compositae (sunflower, daisy or aster family, a.k.a. Asteraceae). HEAD TOPICS & BREVIA: Section to showcase current research on Compositae. PIPET & PRESS: Articles about methods and techniques. THE HANDLENS: A close up look to a given species or morphological structure. THE CABINET: A window to the stories behind ancient or recent herbarium samples and the botanists behind them. FROM THE FIELD: The place where the bold and the adventurous share their latest finds in their eternal pursuit of the more recalcitrant comps. STYLE: Where science and art converge, artistic photography, botanical illustration or creative infographics. All is welcome if it comes with style. Manuscripts or photos intended for publication in CAPITULUM are to be submitted at www.compositae.org. Contributions will be sent to two external reviewers. Suggestions of suitable, qualified reviewers without conflicts of interest are encouraged.

General formatting and structure

Consult a recent issue of CAPITULUM and follow these instructions. Language for submission is English. Use Times New Roman/Arial typography size 12. Provide a title and if needed, a subtitle. Include names of all authors, their ORCIDs, their professional affiliations and emails. Include a list of 5–6 keywords in alphabetical order. Provide an abstract of up to 250 words. There is no set structure on how to organize your text; however most cases will adapt well to the classic I-M&M-R-D plus Acknowledgements and Literature Cited; Tables; Appendices; and Figure Legends. Monographic works should include proper citation of names including types. Morphological descriptions, notes when needed, additional specimens examined (country, political division, political subdivision, locality, collector, collector #, date, herbarium code). Keys should be indented. Each couplet should be numbered 1a and 1b, 2a and 2b, etc. All scientific names at the rank of tribe or inferior should include authorship the first time they appear in the text, following Brummitt & Powell, Authors of Plant Names (Kew, 1992; info included in the International Plant Names Index [IPNI]). In text, a single space must follow a period, colon, semi-colon, or comma. Molecular phylogenetic and systematic studies should clearly state the sampling strategy including all details related to the sequencing and data analysis. Phylogenetic trees should have support values plotted.

Tables and figures

Tables must be prepared using MS Excel, please include different tables as different spreadsheets on the same file. Figures should be provided in either TIFF format (for photos) or as vector graphics such as AI or EPS for diagrams, illustrations, or phylogenetic trees. Maps should be provided as SHP files when possible or as vector graphics. You may send the photos and other graphics ordered and arranged following your preference, but you are advised that we could edit them to adjust them to CAPITULUM style. All figures must be uploaded as individual original files. Photos should be at least 300 dpi in resolution. Literature citation: please check that all your references are cited and vice versa. For the style of references check a recent issue of CAPITULUM.

Data availability requirements

CAPITULUM requires all data sets to be archived in a permanent, publicly accessible location. To enable readers to locate archived data, include a "Data Availability" section before the Literature Cited section. This should list the database, digital object identifiers (DOIs), stable URLs, and the respective accession numbers for all data from the manuscript, as appropriate. Note that accession numbers provided in a supplementary table (voucher table) accompanying the article do not need to be duplicated here in the data availability statement.
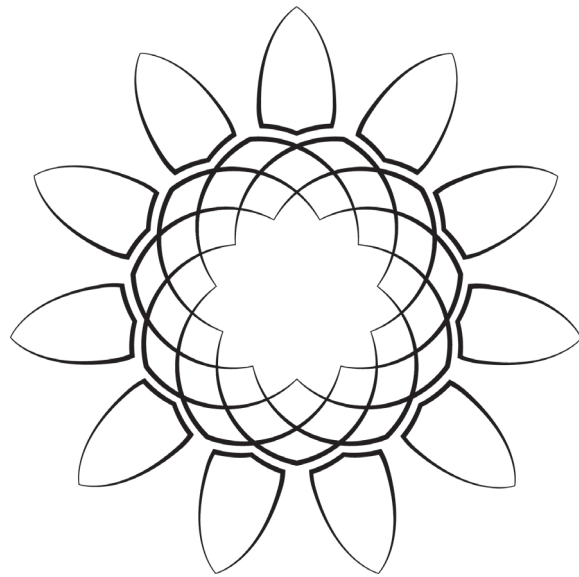
Magno amore in familiam Synantherearum captus
Lessing, 1829

TICA
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