

**REINSTATEMENT, BROADER CIRCUMSCRIPTION,
AND INFRAGENERIC CLASSIFICATION OF
SHAWIA (ASTEREAEE, CELMISIINAEE),
A LARGE WOODY GENUS ENDEMIC TO AUSTRALASIA**

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ABSTRACT

Recent phylogenomic studies have shown that more than half of the ca. 160 recognized species within subtribe Celmisiinae (Astereae) form a clade of shrubs and trees endemic to Australasia (Australia, New Zealand, and New Guinea). The architecturally and ecologically diverse species in this clade include part of the large polyphyletic genus *Olearia* and the small satellite and phylogenetically nested genus *Pachystegia*. This clade is also broken into seven well-supported subclades with distinctive morphology and distribution. However, the *Olearia* species belonging to Celmisiinae cannot be retained in it, because the type species, *Olearia tomentosa*, belongs to subtribe Brachyscominae. Based on phylogenetic and morphological evidence, new generic affiliation possibilities for the *Olearia* species of Celmisiinae were considered. One large genus versus the recognition of seven smaller genera (one for each main subclade) benefits nomenclatural stability. Accordingly, we propose the reinstatement of *Shawia*, the earliest validly published available name in this clade, to encompass all the *Olearia* species and infraspecific taxa (91 in total) in Celmisiinae plus *Pachystegia* (three species). Identification keys to Celmisiinae genera and to seven recognized *Shawia* sections are provided. For each section, morphology, distribution, and diversity are discussed. New combinations are proposed for 72 taxa, including 57 species, 1 subspecies, 6 varieties, and 8 hybrids.

Nesom's (1994a) seminal paper on the subtribal classification of Astereae set the modern taxonomic foundations upon which much research has been developed in the last three decades (e.g., Noyes & Rieseberg 1999; Bonifacino 2009; Bonifacino & Funk 2012; Karaman-Castro & Urbatsch 2009; Saldivia et al. 2020). One of the pillars of research has been the progressive clarification of the Australasian Astereae. In particular, Nesom (1994a) proposed the *Celmisia* Group and placed it within subtribe Hinterhuberinae, a chiefly southern hemisphere taxon broken into seven groups based mostly on morphology, chromosome number, and geographical distribution. However, Hinterhuberinae was found to be polyphyletic and needed reevaluation (Brouillet et al. 2009; Karaman-Castro & Urbatsch 2009).

Saldivia et al. (2020) and Saldivia (2021), based on morphological and phylogenetic evidence, proposed a new circumscription of the *Celmisia* Group with the following character states: indeterminate shoots or determinate by apical abortion (not by floral development) and axillary capitulescences, alveolate and epaleate receptacles, caudate anthers, and a dense layer of indumentum covering the abaxial surface of the leaves. Saldivia et al. (2020) also refined the original concept of the *Celmisia* Group by excluding *Pacifigeron* and *Achnophora*. This new delimitation was formally proposed as subtribe Celmisiinae Saldivia (Nesom 2020a). Additionally, karyotopic analyses indicated that members of Celmisiinae have high levels of ploidy, generally considered diploidized dodecaploids. The base Astereae chromosome number was inferred to be $x = 9$ (Nesom, 1994a; Brouillet et al. 2009; Semple & Watanabe 2009, 2023), whereas most species in Celmisiinae have ca. $2n = 108$ ($12x$) (Hair 1980; Beuzenberger & Hair 1984; Nicol et al. 2024).

Subtribe *Celmisiinae* are found in New Zealand, south and eastern Australia, and the island of New Guinea, inhabiting a wide array of habitats mainly associated to temperate climates from sea level up to ca. 4000 meters asl. *Celmisiinae* include some 160 species of small trees, erect or plagiotropic shrubs, subshrubs, and a few perennial herbs with large leaves distributed in the following genera: *Celmisia* Cass., *Pleurophyllum* Hook. f., *Damnomenia* Given, *Macrolearia* Saldivia, *Pachystegia* Cheeseman, and *Olearia* Moench in part (Saldivia & Nicol 2023; Saldivia 2024). *Olearia*, however, is still a matter of taxonomic confusion since it is not monophyletic and the type species, *Olearia tomentosa*, does not belong to *Celmisiinae*, and it is distantly related to it. Therefore, *Olearia* species belonging to *Celmisiinae* cannot be retained within this genus. This taxonomic issue requires special attention, and a detailed account is presented below.

Taxonomic history of *Olearia*

Olearia has a long, complex taxonomic history. Moench (1802) described the genus and provided a description with no clear diagnostic characters relative to several *Astereae* genera. Moench based *Olearia* on *O. dentata* (probably referring to *A. dentatus* Andrews) and placed *Aster tomentosus* J.C. Wendl. as a synonym. However, *A. tomentosus* had already been described in 1798 (Wendland, 1798; see Stafleu & Cowan 1985) and *A. dentatus* in 1799 (Andrews 1799; see Stafleu & Cowan 1976). Both names were accompanied by illustrations representing the same taxon.

Since the early works by Moench (1802) and de Candolle (1836), the current *Olearia* species have been treated in different genera. *Aster* has been considered congeneric (and prevalent by priority) with *Olearia* since the early stages of *Olearia*'s taxonomic history. Benthams (1867) doubtfully separated *Olearia* from *Aster*, while Mueller (e.g., 1865–6) was emphatic in keeping *Olearia* as part of the large genus *Aster*. Currently, *Aster* is considered a genus mainly from Eurasia and Africa, and absent from Australasia (Nesom & Robinson 2007).

Eurybia (Cass.) Cass. was the initial generic name for many of the Australian and New Zealand *Olearia* species before the establishment of the broader *Olearia* concept, which then included *Eurybia* as a synonym (Hooker 1864; Benthams 1867; Benthams & Hooker 1873). De Candolle (1836) and Sonder (1853) had treated most of the Australian species under *Eurybia*, and the New Zealand (Hooker 1847, 1853) and Tasmanian (Hooker 1860) species also had been treated the same way. The study by Archer (1860) on leaf trichome types of *Eurybia* and *Olearia* was fundamental for the taxonomic placement of the species currently treated under *Olearia*. Hooker (1864) and Benthams (1867) commented, based mainly on Archer's work, that *Olearia* and *Eurybia* were inseparable and adopted *Olearia* as the older name. The generic taxonomy of *Eurybia* is very complex. The original definitions of *Eurybia* by Cassini (1818, 1820, 1825) were inconsistent and ambiguous which led to early misinterpretations regarding the relationship between *Eurybia* and *Olearia*. Nesom (1994b) untangled this taxonomic problem and definitively regarded *Eurybia* as a genus from the USA, Canada, and northeastern Asia (Nesom & Robinson, 2007) and commented that "[...] the long association of *Eurybia* with *Olearia* is unjustified".

Sonder (1853) erected the genus *Steetzia* Sond. for four Australian species. These four species are currently synonyms of *Olearia pannosa* Hook. and *O. grandiflora* Hook., which are characterized by their axillary solitary capitula, a character suggesting a close relationship to New Zealand *Pachystegia* (Kirk, 1891). *Steetzia* is a *homonymum illegitimum* because the name had been previously validly published as a genus of liverworts of the family Pallaviciniaceae (*Steetzia* Lehm.) in 1846.

Don (1831) erected *Haxtonia* Caley ex G. Don and mentioned: "*Haxtonia* nomen *Asteri argophyllo* Billardieri primum imposuit b. Georgius Caley" and included another four Australian species, including the type species of *Olearia*, *Olearia tomentosa*. Further, the description is also a matter of confusion, since some of the given characters, such as leaf indumentum type and capitulescence arrangement, do not apply to all five species mentioned. Benthams & Hooker (1873) commented: "*Haxtonia* Caley ex Don is a generic name first proposed for *O.*

(*Dicerotriche*) *argophylla*, and extended to several species of *Olearia* by Don loc. cit., who distinguished it as a genus from *Aster*, but did not compare it with *Olearia*.” *Haxtonia* has not been followed by subsequent authors except for Cunningham (1839), who transferred *Aster furfuraceus* A. Rich. to *Haxtonia*.

De Candolle (1836) erected the genus *Steiractis* DC. (non *Steiractis* Raf., *hom. illeg.*) for segregating *Solidago arborescens* G. Forst. ($\equiv$ *Olearia arborescens* (G. Forst.) Cockayne & Laing) from *Solidago* L., a genus distributed mainly in North America and absent in Australasia (Nesom & Robinson 2007). *Steiractis* was not followed subsequently, and the genus was listed as a synonym of *Olearia* by Bentham & Hooker (1873).

The Forsters, father and son (Forster & Forster 1776), described *Shawia* based on *Shawia paniculata* J.R. Forst. & G. Forst. ($\equiv$ *Olearia paniculata* (J.R. Forst. & G. Forst.) Druce), a New Zealand species with uniflorous capitula and the first species described belonging to Celmsiinae. *Shawia* remained without use until the description of *Shawia avicenniifolia* Raoul (Raoul 1846), and then the treatment by Schultz-Bipontinus (1861). Schultz-Bipontinus placed most of the Australian and some New Zealand species of *Eurybia* ($=$ *Olearia*, see comments on *Eurybia* above) in *Shawia*, perhaps in consideration of its priority. However, such a decision was markedly rejected by Bentham (1867) who commented that “This is, however, a mistake. Forster considered the true *Olearias* as *Asters*, and founded *Shawia* on a plant characterized specially by solitary florets. It proved afterward that this was not a constant character, and this genus was suppressed, and the circumstance that this abnormal peculiarity occurs on some specimens of one species of *Olearia*, can surely be no reason for now transferring the name founded on it to a large genus where it has not been observed in any other species.” However, Kirk (1899) accepted *Shawia* as monotypic (*S. paniculata*) based on the uniflorous capitula character, arguing that under his experience of having examined numerous specimens from the whole area of the species, the character was constant. Cheeseman (1906, 1925) agreed with the observation about the constancy of the character, but he rejected *Shawia* and regarded it as a synonym of *Olearia*. Finally, *Olearia* Moench (1802) was conserved against *Shawia* J.R. Forst. & G. Forst. (1776) (Wiersema et al., 2018: Appendix III: E2).

Based on *Olearia insignis*, Cheeseman (1925) erected *Pachystegia*, a small genus endemic to the Marlborough region in the northeast of the South Island of New Zealand, which has remained accepted until today (further comments in the taxonomic treatment below).

Despite the mentioned classification attempts, the works by Hooker (1864, with additions and corrections in 1867) for New Zealand, and Bentham (1867) for Australia, are the main taxonomic references upon which *Olearia* became established as a widely accepted genus until recent years. Moreover, the taxonomic concept of *Olearia* was reasserted in the *Genera Plantarum* (Bentham & Hooker 1873). New species of *Olearia* in New Zealand have been described since the *Genera Plantarum*. Many were published in the treatments of the New Zealand flora subsequent to the works by J.D. Hooker (Kirk 1899; Cheeseman 1906, 1925; Allan 1961), but also in other works (e.g., Kirk 1891; Petrie 1911; Heads 1998; Heenan et al. 2008). All the descriptions followed Hooker and Bentham’s concept of *Olearia*. The situation for the genus in Australia has been similar, with many new species described under Hooker and Bentham’s generic concept (e.g., Wakefield 1956; Curtis 1970; Lander 1975, 1994, 1991; Albrecht et al. 2024).

The third main reference for *Olearia* is Koster (1966) who treated the Asteraceae of New Guinea. New Guinea species were not mentioned in early works because the first described species was *Aster kernotti* F. Muell. ($\equiv$ *Olearia kernotti* (F. Muell.) Mattf.) by Mueller (1889) with this comment “Had this been found in Australia, it would have been considered an *Olearia*, simply on phytogeographic account. It seems however preferable, to maintain the genus *Aster* in its ampler demarcation, though the abolishing or sustaining of *Olearia* as a genus remains optional.” Koster (1966) described 17 additional *Olearia* species for New Guinea. No attempt to change the generic placement of the New Guinea species has been undertaken so far.

Currently, *Olearia* is the most speciose Asteraceae genus in Australasia with some 180 species found in Australia, New Zealand, and New Guinea (Lander 1994; Cross et al. 2002; Nesom & Robinson 2007; Messina et al. 2014; Hind & Johns 2014; Schmidt-Lebuhn 2022a; Albrecht et al. 2024). However, given that the taxonomy at the specific rank has been unevenly assessed in different countries and that no complete taxonomic work has been done for the genus in modern times, the exact number of species remains unclear. There have been several attempts to define the genus morphologically, but all of them were unsatisfactory. Some of the characters used for delineating the genus and differentiating it from other Astereae genera include woody habit (as shrubs or trees), terete achenes, tailed anthers, radiate capitula, and dense indumentum of the abaxial surface of the leaves (Hooker 1864; Bentham 1873; Heads 1998; Cross et al. 2002; Hind & Johns 2014; Messina et al. 2014), but none of those characters is constant within *Olearia*. Bentham (1867) commented that “It [*Olearia*] is, however, very closely allied to the extensive genus *Aster* L., widely diffused over the temperate regions of the northern hemisphere, especially in America, not separated indeed from *Olearia* by any one definite character.” Bentham & Hooker (1873) separated *Aster* from *Olearia* based only on habit and geographic distribution.

Infrageneric classification of *Olearia*

Archer (1860), based on the trichome morphology of the leaf indumentum of many *Olearia* species (many at that time included *Eurybia*, see comments above) from Australia and some from New Zealand, proposed five sections: sect. *Olearia* [originally as *Dicerotriche*, see Saldivia et al. 2020], sect. *Asterotriche*, sect. *Eriotriche*, sect. *Adenotriche*, and sect. *Merismotriche*. However, these names were not validly published because epithets were not associated with a single genus (Messina et al. 2014; Turland et al. 2018; see ICN Art. 35.2). Bentham (1867) validated Archer’s sectional proposal.

Archer (1860) commented on the four New Zealand species placed in *Olearia* sect. *Eriotriche* as follows: “The best natural group, however, is that composed of *O. colensoi* and the three following species [*O. oporina*, *O. angustifolia*, *O. lyallii*], which would form a fair genus, and have large solitary or few heads, long villous achenia, subduplex rufescent pappus, and large, flat, denticulate, woolly-haired leaves.” Kirk (1891) coined the name ‘macrocephalous’ for this group, adding two species endemic to the Chatham Islands (*O. chathamica* and *O. semidentata* Decne.). Drury (1968) proposed a close relationship of the macrocephalous *Olearia* species with the subantarctic genus *Pleurophyllum*, rather than with the rest of the *Olearia* species.

Heads (1998) erected sect. *Divaricaster* Heads, the sixth section of *Olearia*. This section accommodated a group of New Zealand species characterized, by divaricate architecture, instead of by trichome morphology (further comments in the taxonomic treatment below).

The New Guinea *Olearia* species have not been classified according to the sectional scheme, although Moore (1916) mentioned *Olearia* (§ *Dicerotriche* [= sect. *Olearia*]) when he described *O. exilis* S. Moore. Archer’s classification was rejected by Mattfeld (1937), Koster (1966), and van Royen (1983) because in one species, *Olearia heterotricha* Mattf., the leaf indumentum is composed of three different types of trichomes: stellate-scale, fusiform, and T-shaped.

Recent advances in the systematics of *Olearia*

Nesom (1994a) concluded that a pressing issue in Astereae classification is the infrageneric organization of *Olearia* and its relationship among other Australian Hinterhuberinae. The same author (Nesom 1992, 1993a, 1993b, 1994c), based mainly on chromosome number, pointed out the non-monophyly of *Olearia*, stressing that the highly polyploid species should be removed from *Olearia* and, instead, be a part of the *Celmisia* group.

Subsequent molecular phylogenetic studies have proven Nesom’s hypothesis right (Cross et al. 2002; Brouillet et al. 2009; Saldivia et al. 2020). *Olearia* is polyphyletic with several well-supported clades not directly related to each other; still, *Olearia* species are part of two main clades distantly related within Astereae (Cross et al. 2002; Brouillet et al. 2009). One clade

corresponds to the “Australasian lineage” in Brouillet et al. (2009), which has a derived position in the tribal phylogeny; it contains mostly diploid species (Watanabe et al. 1996) and makes up the expanded concept of subtribe Brachyscominae by Nesom (2020a), endemic to Australia. The other clade, named the “New Zealand clade” by Brouillet et al. (2009) and equivalent to Celmisiinae, shows a relatively basal position in the tribe. The species in Celmisiinae, including *Olearia* and others, have high levels of ploidy (Hair 1980; Beuzenberger & Hair 1984; Semple & Watanabe 2009).

Nesom (2020a), based on taxonomic, morphological, and phylogenetic advances of the last 25 years, updated the subtribal classification of Astereae. For *Olearia* belonging to Brachyscominae, Nesom (2020b) segregated 10 new genera (29 species in total). However, his proposal has not yet been evaluated or found broad acceptance (Albrecht et al. 2024; Chen et al. 2024). In any case, considering the phylogenomic analyses by Chen et al. (2024), there are still major taxonomic arrangements that need to be made within Brachyscominae to appropriately accommodate the *Olearia* species from a phylogenetic and morphological perspective. So far, only sect. *Asterotriche* has been reviewed (Messina et al. 2014).

Regarding *Olearia* species belonging to Celmisiinae, Cross et al. (2002) confirmed their misplacement in *Olearia*. However, the lack of comprehensive studies and phylogenetic clarity has hampered the proposal of new taxonomic arrangements. The exception being the New Zealand endemic segregated genus *Macrolearia* (Saldivia et al. 2022) for the group of species previously known as the “macrocephalous Olearias” (Kirk 1891; see above).

The phylogenomic study by Nicol et al. (2024) used target enrichment sequencing with the Angiosperms353 bait set and provided systematic clarity of the inner organization of Celmisiinae. Three main clades were recovered: (i) *Celmisia*, (ii) the *Pleurophyllum* clade (including *Damnania*, *Macrolearia*, and *Pleurophyllum*), and (iii) all remaining *Olearia* species plus *Pachystegia*, which was nested within *Olearia* in all the analyses. Additionally, within the third clade, seven well-supported subclades were recovered, and most of them were morphologically and geographically distinct.

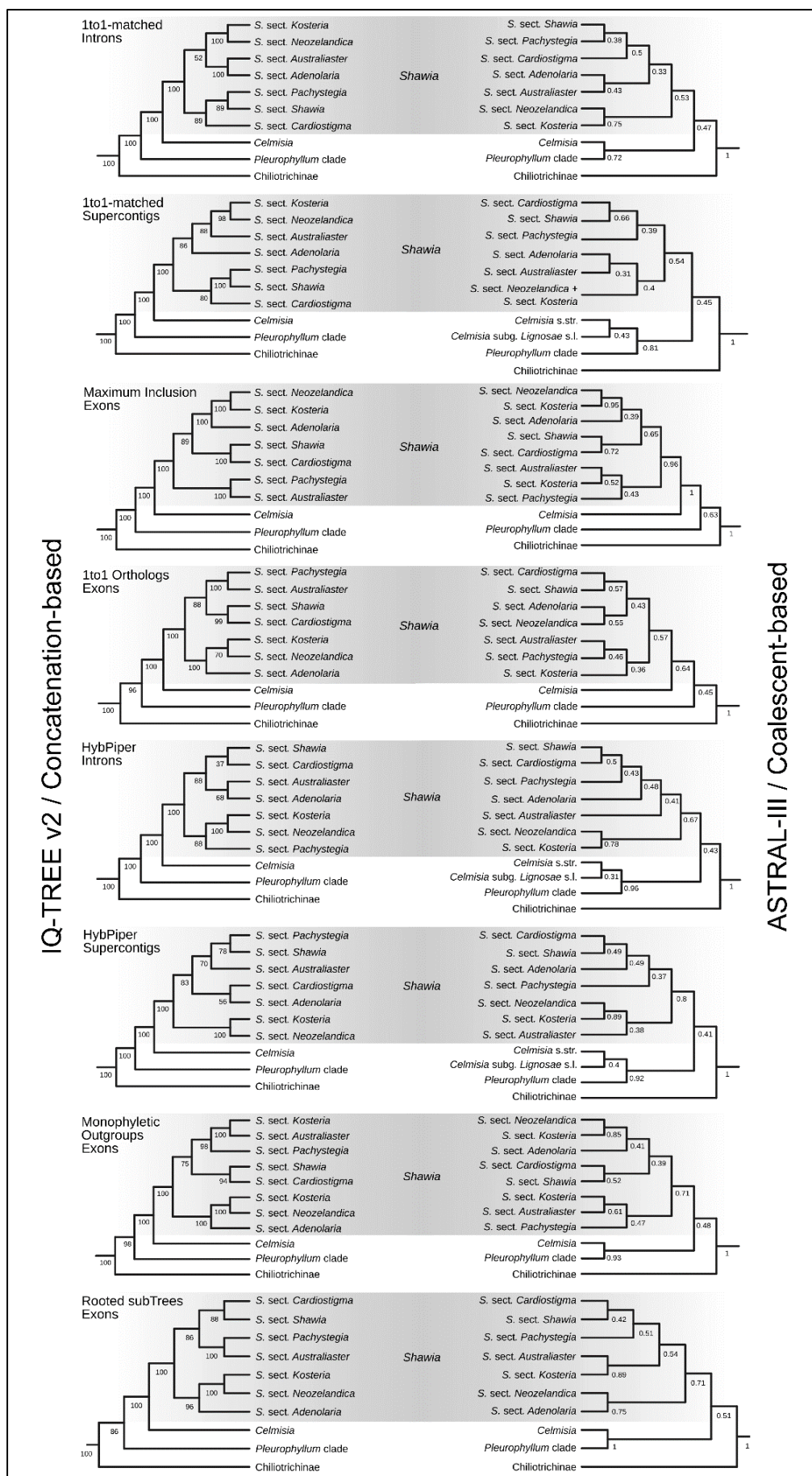
Here, we propose to rehabilitate *Shawia* to include all species in the clade *Olearia* pro parte + *Pachystegia*. Since this new generic concept would encompass over 90 taxa of varied morphology, ecology, and distribution grouped into seven well-supported clades, an infrageneric classification at sectional rank is also presented, as suggested by Nicol et al. (2024). For simplicity, some of the new proposed names will hereafter be used despite their formal taxonomic treatment in the final section.

METHODS

Phylogeny, morphology, and distributions

Our proposal is grounded in the findings of recent studies by the authors and collaborators. Phylogenetic relationships were informed by the analyses of targeted low-copy nuclear loci (Nicol et al. 2024; Fig. 1), and previous phylogenetic studies using traditional markers (Saldivia et al. 2020; Saldivia 2021) were also considered when proposing the sectional treatment. There are no detailed plastid genomic analyses of Celmisiinae, and across other families there are several studies that have found topological inconsistencies between nuclear-based and plastid-based phylogenies at shallow ranks but topological consistencies at deeper ranks (Villaverde et al. 2020; Lichter-Marck et al. 2020; Jin et al. 2023; McLay et al. 2023; Qin et al. 2024). This situation has been considered when structuring the infrageneric classification of *Shawia*.

Figure 1 (next page). Compilation of eight sets of comparisons between concatenation-based (IQ-TREE v2; left column) and coalescent-based (ASTRAL-III; right column) phylogenies. The *paragone-nf* containerized pipeline (Jackson et al., 2023) was utilized to extract eight sets of gene-families, which included four sets of putative orthologous gene-families from four tree-based analyses. Modified from Nicol et al. (2024: Fig. 3).



The morphology of Celmisiiinae, and particularly *Shawia* and its sections, is taken mainly from Saldivia (2021), and remarks are also found elsewhere (e.g., Heads 1998; Heenan 2005; Heenan et al. 2008; Heenan & Molloy 2022; Saldivia et al. 2020, 2022; Saldivia & Nicol 2023; Nicol & Saldivia 2025).

Herbarium collection localities were retrieved from GBIF (Global Biodiversity Information Facility) using the *gbif* function from the *dismo* package in R (Hijmans et al. 2024; R Core Team 2025). Only herbarium collections with geographic coordinates and locality descriptions were kept, gathering 8037 collections. With the aim of minimizing collection artefacts and errors, each species was mapped and reviewed individually. A series of checks were done: (1) Collections with coordinates in the ocean were moved according to the locality description: if the locality description was not specific or could not be verified, then the collection was removed entirely; (2) Collections with coordinates in or around urban centers were checked against their locality description in the same way as (1); (3) If the description included specific gardens or if the collection was potentially of horticultural origin, then these were also removed; (4) Outlying collections, such as collections separated from the main mass of species' collections by a disproportionate distance or by a geographic feature, were identified, checked, and potentially removed in the same way as (1); (5) Stacked localities, such as collections in the center of the state or province, were identified, checked, and potentially removed in the same way as (1). After all these checks were done for each species, 7296 collections remained.

Maps were designed with the verified *Shawia* localities, country borders, and a Digital Elevation Model (DEM). DEMs are photogrammetric measurements of the Earth's surface, and the DEM constructed from the Shuttle Radar Topography Mission (SRTM) (Jarvis et al. 2008) was retrieved from the WorldClim v2 data set (Fick & Hijmans, 2017). Country borders were retrieved using the *rnaturalearth* package (Massicotte & South 2023) which facilitates interaction with the Natural Earth public domain map dataset. The *sf* and *terra* packages (Pebesma 2018; Hijmans, 2023) were used to facilitate geospatial data management, and the maps were created using *ggplot2* (Wickham 2016) in R (R Core Team, 2025).

Taxonomic concepts and rationale

In Celmisiiinae all *Olearia* species plus *Pachystegia* form one of the three main clades (Nicol et al. 2024; Fig. 1 and Fig.S1). Within this clade, *Shawia* is the earliest available generic name; therefore, its reinstatement and stability are warranted by priority. *Shawia* J. R. Forst. & G. Forst. (1776) is a rejected earlier name in favor of *Olearia* Moench (1802). Nevertheless, Art. 14.6 of the ICN (Turland et al. 2018) allows the use of a rejected name for heterotypic names in the same range: “When a name of a taxon has been conserved against an earlier heterotypic synonym, the latter is to be restored, subject to Art. 11, if it is considered the name of a taxon at the same rank distinct from that of the conserved name.” The principles ruling the taxonomic scheme proposed here are explained next.

Recognition of monophyletic groups – Monophyly has become the leading and widely accepted principle in modern systematics, in which only monophyletic groups should be treated as taxa (Humphreys & Linder 2009; Linder & Hardy 2010; Global Carex Group 2015, 2021; Vilatersana et al. 2022; Zuccarello et al. 2022), at least above the species level (Slimp et al. 2021; Schmidt-Lebuhn 2022b; Wells et al. 2022; Nyamgerel et al. 2024; Turner 2024). *Shawia* and all recognized sections (see below) are well-supported clades (Nicol et al. 2024).

Nomenclatural stability – The genus is integral for communicating biodiversity, even beyond the scientific community (Drew et al. 2017). A generic taxonomy should seek nomenclatural stability (Camp 1940; Perrie et al. 2014), and natural classifications based on sound evidence will increase stability in the longer term (Garnock-Jones 2014). The phylogenomic study by Nicol et al. (2024) recovered, within the large “*Olearia* pro parte + *Pachystegia*” clade, seven well-supported subclades with different inter-clade topologies among them, depending on the parameters of the analyses. Therefore, the outcomes of that study present

two logical taxonomic alternatives, (1) treating the entire clade as a single genus or (2) recognizing each of its major subclades as distinct genera. The former option offers several benefits. (1) Fewest new combinations: there are already 22 species with validly published names in *Shawia* belonging to *Celmisiinae*, from which only 4 are part of the clade holding the type species *S. paniculata*. Therefore, maintaining one genus would require 72 new combinations. On the contrary, recognizing seven different genera (one for each main subclade) would require over 80 new combinations; only 4 names would be retained in *Shawia*, 3 names in *Pachystegia* (which would be retained at genus rank), and a few others if old generic names such as *Steiractis* were rehabilitated. (2) Historical coherence: almost all species in the clade have been recognized under one generic name, *Olearia*, for over a century; the exception being *Pachystegia*, which was also segregated from *Olearia* in 1925. Owing to this clade encompasses such a distinctive group of trees and shrubs with physiognomic, ecological, and conservation importance, its relevance goes far beyond the taxonomic community, reaching ecologists, conservationists, nurseries, and stakeholders in general — so, maintaining one generic name for the whole group will provide a smooth transition for understanding and recognition in a broad transversal audience. (3) Generic nomenclatural stability: since not all the subclades are morphologically distinctive and distributionally discrete, their recognition at any taxonomic rank is liable to further taxonomic changes with sufficient new evidence. In this situation, recognizing each subclade as a different genus would be vulnerable to nomenclatural instability. On the contrary, nomenclatural stability in the long term would be maintained with only one genus, since any taxonomic change at an infrageneric classification would not disturb the generic rank and thus, will not require scientific name changes.

Recognition of morphologically defined groups – Within the morphological boundaries of *Celmisiinae*, *Shawia*, as proposed here, is easily differentiated from *Celmisia* and the *Pleurophyllum* Clade by the trichome types of the abaxial surface indumentum and by the lack of leaf-sheaths. Within *Shawia*, most sections are also well-defined morphologically. Still, two problems remain: 1) sect. *Cardiostigma* needs the recognition of informal morphological groups, which is discussed in more detail in the treatment, and 2) there is a lack of diagnostic characters between sects. *Neozelandica* and *Australiaster*.

Regarding sects. *Neozelandica* and *Australiaster*, both are allopatric, the former endemic to New Zealand and the latter endemic to Australia. This is perhaps not surprising, for distributions have emerged as a critical character in modern systematics, and clades are frequently more closely related via geography than via morphological characters and traditional classifications. Accordingly, geographic distribution has explicitly been used as a criterion for delineating a new generic classification of the traditionally largest but highly polyphyletic araliaceous genus *Shefflera* (Lowry et al. 2017, 2019; Plunkett et al. 2020, 2021). However, cases that present a greater challenge for classifications are pairs of phylogenetically close but not sister clades without diagnostic characters and with varying levels of geographic overlap. For example, the pairs *Linochilos-Diplostegium* (Asteraceae) and *Senecio-Werneria* (Senecioneae) remain a challenge for morphological delineations, because they have phylogenetic support, but they are not distinct geographically nor do they have clear diagnostic characters. These pair-genera, as well as sects. *Neozelandica-Australiaster*, can be considered cryptic taxa (cf. Gagnon et al. 2015). Concerning diagnosability, Entwistle & Weston (2005) rejected the general guideline that ‘genera [or sections in this case] should be easy to recognize’, preferably in their vegetative state. That assertion is also here rejected. Diagnosability is here understood in the taxonomic context (Hassemer et al. 2020); that is, all members of a genus or infrageneric taxon should be identifiable based on one or a combination of morphological characters that define the taxon.

Accepted taxa and type specimens

Based on phylogenetic, morphological and karyotypic evidence, Saldivia (2021) listed all taxa that should be removed from *Olearia* to be transferred to other genera within *Celmisiinae*. The acceptance of taxa here included in *Shawia*, as well as their homotypic and main heterotypic synonyms, follows the relevant geographic authorities. The Australian accepted taxa follow the

Australian Plant Census (Council Heads of Australian Herbaria 2007); the New Zealand accepted taxa follow the Flora of New Zealand website (www.nzflora.info; Breitwieser et al. 2023) and Schönberger et al. (2021), unless otherwise mentioned in each section (e.g., Nicol & Saldivia 2025). Heenan et al. (2005) and Cockayne & Allan (1934) are the references followed for putative hybrids in New Zealand. The New Guinea accepted taxa follow Koster (1966), with a few additions by Hind & Johns (2014) and Hind (2024).

Regarding typification, this has been assessed for different sections or species' groups (e.g., Koster 1966; Lander 1989; Heads 1998; Heenan & Molloy 2022; Nicol & Saldivia 2025); yet many taxa need a thorough typification assessment. However, as many issues with old names have been identified in other *Celmisiinae* (cf. Saldivia 2023, Nicol & Saldivia 2025), we chose to leave typification to further taxonomic studies at species rank or below.

TAXONOMIC TREATMENT

Key to genera of subtribe *Celmisiinae*

1. Indumentum of the abaxial surface of the leaves made of T-shaped, Y-shaped, scutellate, or lepidote trichomes, exclusively or in combination, rarely glabrescent. Leaf-sheath absent **Shawia**

1. Indumentum of the abaxial surface of the leaves made primarily of long aseptate trichomes (sometimes present only at the margins or the base of the leaf); if absent (which is rare), the abaxial surface can be glabrous, or partially covered with stalked or non-stalked glandular trichomes or rarely diminutive scurfy scales. Leaf-sheath present or rarely absent.

2. Disc florets more or less tubular; narrow in lower part, wider but more or less parallel-sided from the filament insertion zone (throat); or with a short cylindrical tube and then open from the filament insertion zone (throat) with the lobes recurved; yellow **Celmisia**

2. Disc florets cyathiform; purple, dark red or bluish (*Pleurophyllum* clade).

3. Leaves glabrous. Stoloniferous herbs with woody basal stock **Damnania**

3. Leaves pubescent on both or only on the abaxial surface. Small trees, shrubs, or rosette non-stoloniferous herbs without woody basal stock.

4. Small trees or shrubs. Adaxial surface of the leaves glabrous or glabrescent, and abaxial surface densely covered exclusively by long aseptate trichomes. Staminodes present in the ray corolla tubes **Macrolearia**

4. Rosette herbs. Adaxial and abaxial surfaces of the leaves covered more or less densely by long aseptate trichomes and cylindrical moniliform trichomes. Staminodes not present in the ray corolla tubes **Pleurophyllum**

SHAWIA J.R. Forst. & G. Forst., Char. Gen. Pl., ed. 2. [95]. 1776. **TYPE: SHAWIA PANICULATA** J.R. Forst. & G. Forst.

Steiractis DC., Prodr. [A.P. de Candolle] 5: 345. 1837 – **TYPE: STEIRACTIS ARBORESCENS** (G. Forst.) DC.

Pachystegia Cheeseman, Man. New Zealand Fl., ed. 2. 910. 1925 – **TYPE: PACHYSTEGIA INSIGNIS** (Hook. f.) Cheeseman.

Haxtonia Caley ex G. Don, Edinburgh New Philos. J. 11(2): 272. 1831 (in part.), *nom. illeg.* – **TYPE: HAXTONIA ARGOPHYLLA** (Labill.) Caley ex D. Don.

Steetzia Sond., Linnaea 25: 450. 1853, *hom. illeg.* (non *Steetzia* Lehm. in Plantae Preissianae 2: 129. 1846) – **TYPE: STEETZIA PANNOSA** (Hook.) Sond.

Small trees (rarely up to 18 m) or shrubs; phyllotaxis alternate (2/5), leaves subopposite or opposite, mostly petiolate but also pseudopetiolate or rarely sessile, abaxial surface of the leaves covered by dense white to ferruginous tomentum (only a few species the tomentum is thin

leaving the epidermis exposed) made of non-glandular T- or Y-shaped, scutellate, or lepidote trichomes, glandular trichomes and resinosity are scattered across the genus, venation pinnate; shoots indeterminate with typically lateral flowering or plants with long shoots determinate by abortion (rather than by floral development) and short shoots (brachyblasts) bearing capitula and leaves; capitulescences fasciculate, paniculate-like, corymbose-like or capitula solitary; capitula radiate, or rarely disciform or discoid; involucre cylindrical, campanulate, infundibuliform, or cupuliform at anthesis; phyllaries arranged in 2–12 rows, often decreasing in length from the inner to the outer phyllaries; ray florets mostly white, arranged in 1–4 rows (rarely absent), pistillate or rarely with poorly developed staminodes; disc florets yellow or white (with mauve or green tinges in some species), 1–ca. 150, perfect or rarely functionally staminate (only in some species from New Guinea); corollas of both radial and disc florets often have non-glandular and (less frequently) diminutive glandular trichomes; anthers caudate and with a conspicuous apical appendage; receptacles epaleate (but see section *Adenolaria*), alveolate; pappus made of barbellate bristles arranged in 1–3 rows often reaching the corolla lobes and with an outer row of diminutive setae; cypselae fusiform-cylindrical (mostly) or obconic, 4–11 ribbed, often covered with twin trichomes and occasionally with presence of glandular trichomes or non-glandular trichomes as in the leaves; carpodium horizontal or oblique with a complete ring and shallow foramen.

Diversity and distribution: We accept 86 species, 1 subspecies, and 8 hybrids, broken into 7 sections (see below), and distributed in New Zealand, Australia, and New Guinea (Fig. 2). However, we believe that the number of taxa is liable to change if taxonomic research at the species level is developed.

Within the Compositae genera endemic to Australasia, the diversity of *Shawia* is only comparable to that of the herbaceous genus *Brachyscome* Cass, which is also distributed in New Zealand and New Guinea, but it is much more widespread in Australia (Short 2014; Schmidt-Lebuhn 2022a). There is one species described from Assam (India); nonetheless, it was excluded from *Brachyscome* by Short (2014). *Brachyscome* may hold around a hundred species, but a robust and well-sampled phylogenetic delimitation is lacking.

Etymology: After Thomas Shaw (1694-1751), English scholar and traveler.

Comments: The diversity of non-glandular leaf trichomes in *Shawia* requires special attention. Leaf trichome morphology was the key character employed in the initially proposed infrageneric classification of *Olearia* by Archer (1860). Although molecular studies have shown that Archer's classification is artificial (e.g., Cross et al. 2002), the morphology of non-glandular trichomes is still of great value within Celmisiinae. For instance, it allows the discrimination of *Shawia* from the remaining genera. Within *Shawia*, trichomes present several variations, from branched (Y-shaped or T-shaped) to scale-like (lepidote) (Fig. 3). However, all of them are here interpreted as different types of the same basic architecture: a uniseriate ≥ 2 -celled stalk with a (more or less) centered appending apical cell (head). There is a gradation in the general shape of the apical cell, from linear (which determine Y- or T-shaped trichomes) to fusiform (narrow scale-like trichomes) to almost orbicular (scutellate trichomes). In the scutellate trichomes, the margin of the apical cell can present slight undulation around the rim of the cell or can have indentations of varied depths dividing the cell into rays of different lengths and are perpendicular to the stalk. Taken to the extreme, *Shawia pallida* ($\equiv$ *Olearia pallida*) has rays of the apical cell reaching its center but each project at different angles from the stalk (stellate trichomes).

Besides, scale-like trichomes are of special interest because of their extreme paucity within Asteraceae. They are absent in the rest of Astereae, and within Asteraceae in general, they are probably found only in some genera of Vernonieae subtribes Piptocarphinae (e.g., *Piptocarpha*, Grokoviski et al. 2009) and Lychnophorinae (e.g., *Eremanthus*, Loeuille et al. 2019; Katinas 2025) and distributed mainly in South and Central America (Anderberg et al. 2007).

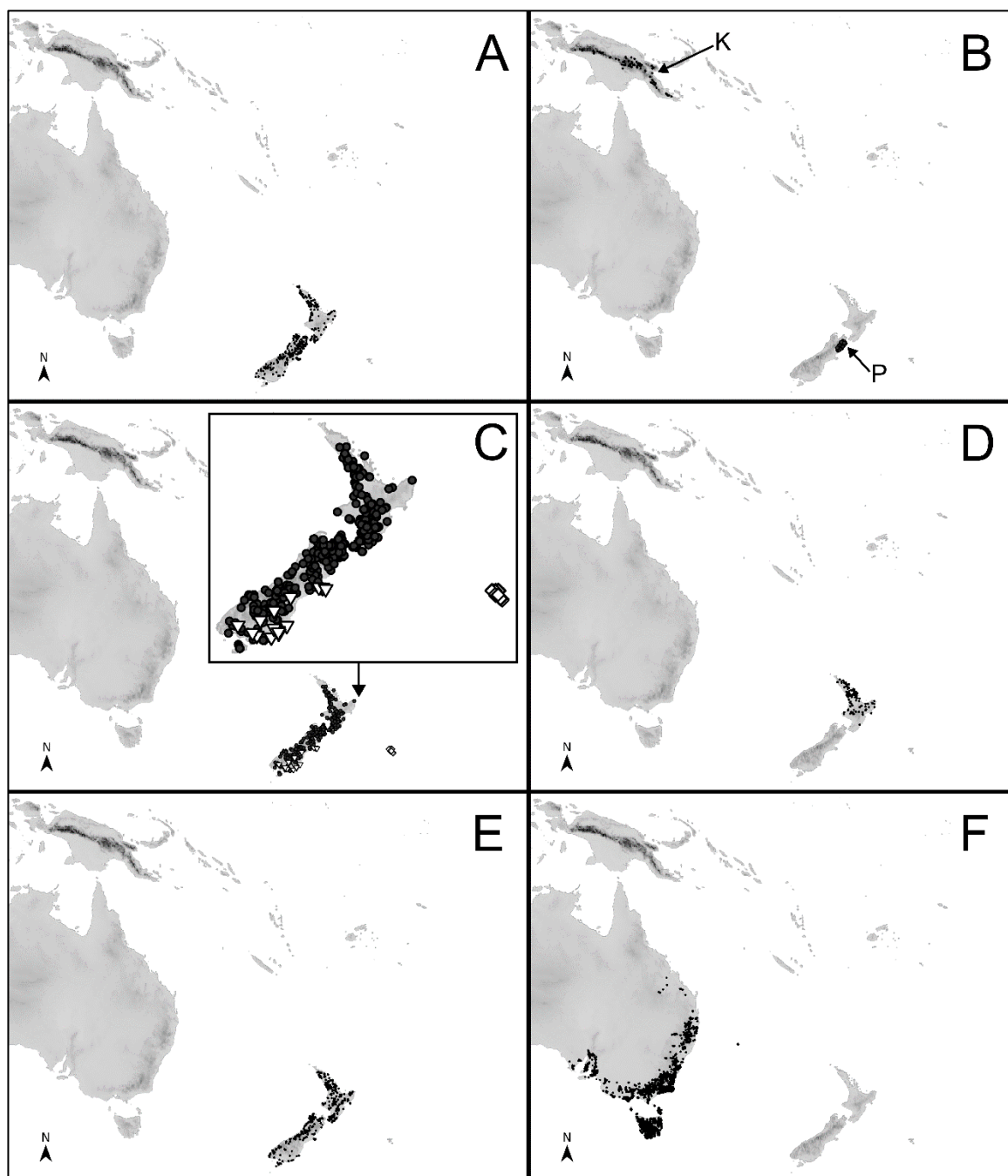


Figure 2. Geographic distribution of *Shawia* by sections. **A**, *S.* sect. *Shawia*; **B**, *S.* sect. *Kosteria* (K) and *S.* sect. *Pachystegia* (P); **C**, *S.* sect. *Cardistigma* (circles: *S. virgata* Group; triangles: *S. fragrantissima* Group; squares: *S. traversiorum* Group); **D**, *S.* sect. *Adenolaria*; **E**, *S.* sect. *Neozelandica*; **F**, *S.* sect. *Australiaster*.

Key to sections of *Shawia*

1. Indumentum of the abaxial surface of the leaves made of non-glandular lepidote, scutellate, or rarely by T-shaped or stellate long-stalked trichomes.

2. Indumentum of the abaxial surface of the leaves made of non-glandular short-stalked lepidote trichomes and unicellular apical cell. Rays of the apical cell (head) reach the center of the cell (area where the stalk is attached) and are perpendicular to the stalk. Disc florets perfect. Style branches exposure supinate (pronate only in *S. moschata*). Plants from the three main islands of New Zealand (North, South, and Stewart Island/Rakiura) **I. sect. *Shawia***

2. Indumentum of the abaxial surface of the leaves made of non-glandular long-stalked lepidote, scutellate, or T-shaped (in a few species) trichomes and unicellular head. Rays of the apical cell (head) of the lepidote and scutellate trichomes, when present, are perpendicular to the stalk and do not reach the center of the cell. If the rays reach the center of the apical cell, they are projected at different angles from the stalk. Disc florets perfect or functionally staminate. Style branches exposure pronate. Plants from New Guinea **II. sect. *Kosteria***

1. Indumentum of the abaxial surface of the leaves made of non-glandular T- or Y-shaped short-stalked trichomes.

3. Capitulescences glomeriform recemose. Florets with an intense peach-like scent **III.b. sect. *Cardiostigma* – *S. fragrantissima* Group**

3. Capitulescences corymbose, fasciculate, paniculate or solitary capitula. Florets without peach-like scent.

4. Brachyblasts (poorly developed in *S. solandri*) bearing leaves and capitula, long shoot abortion (often reduced in *S. lineata* and absent in *S. solandri*), and opposite phyllotaxis. Capitula short-pedunculate and arranged in loose fascicles or solitary **III.c. sect. *Cardiostigma* – *S. virgata* Group**

4. Brachyblasts and long shoot abortion absent, phyllotaxis alternate or rarely opposite. If brachyblast present, the phyllotaxis is alternate. Capitulescences paniculate or corymbose.

5. Styler branches ≤ 0.6 mm. Styler appendages truncate or clavate **III.a. sect. *Cardiostigma* – *S. traversiorum* Group**

5. Styler branches ≥ 1 mm. Styler appendages elongated, rounded, or deltoid.

6. Pappus made of two markedly different kinds of bristles, a longer set 8–12 mm long, and a shorter set 2–3 mm long. Capitula solitary **IV. sect. *Pachystegia***

6. Pappus not differentiated into two kinds. Bristles irregular to subequal. Capitula corymbose, solitary, or rarely paniculate.

7. Glandular trichomes present on the cypselae epidermis **V. sect. *Adenolaria***

7. Glandular trichomes absent on the cypselae epidermis.

8. Plants from New Zealand **VI. sect. *Neozelandica***

8. Plants from Australia **VII. sect. *Australiaster***

I. SHAWIA sect. SHAWIA

Diagnostic character states defining section *Shawia* are the abaxial surface of leaves covered by short-stalked lepidote trichomes with the rays of the apical cell reaching its center (Fig. 3A–C), and the supinate exposure of the style branches (Fig. 4A). However, style branch supination seems to be lacking in *S. moschata*.

Small trees or shrubs; phyllotaxis alternate; leaves petiolate, resinous in most of the species and occasionally with glandular trichomes, elliptic, oblong, oblong/orbicular, or obovate, 0.5–10 cm long, margin untoothed, blade plane, undulate or revolute; capitulescences corymbose-like, paniculate-like, or capitula solitary; involucre narrow-cylindrical at anthesis; phyllaries arranged in 4–6 rows with the inner phyllaries longer than the outer ones, resinous, glandular trichomes in some species; ray florets (when present) pistillate, ligulate, 1–8 arranged in one row; disc florets perfect, 1–6, the two species with paniculate-like capitulescences are remarkable as they have uniflorous discoid capitula; cypselae fusiform-cylindric or obconic, 5–10-ribbed, covered with twin, lepidote (as on leaves), or glandular trichomes.

Diversity, distribution, and ecology: Sect. *Shawia* includes eight species and two hybrids of small trees and shrubs endemic to the three main islands of New Zealand. A third hybrid, *Shawia* $\times$ *matthewsii* ($\equiv$ *Olearia* $\times$ *matthewsii*), is also listed here, which also is the only hybrid with putative parental species from different sections (sections *Shawia* and *Neozelandica*).

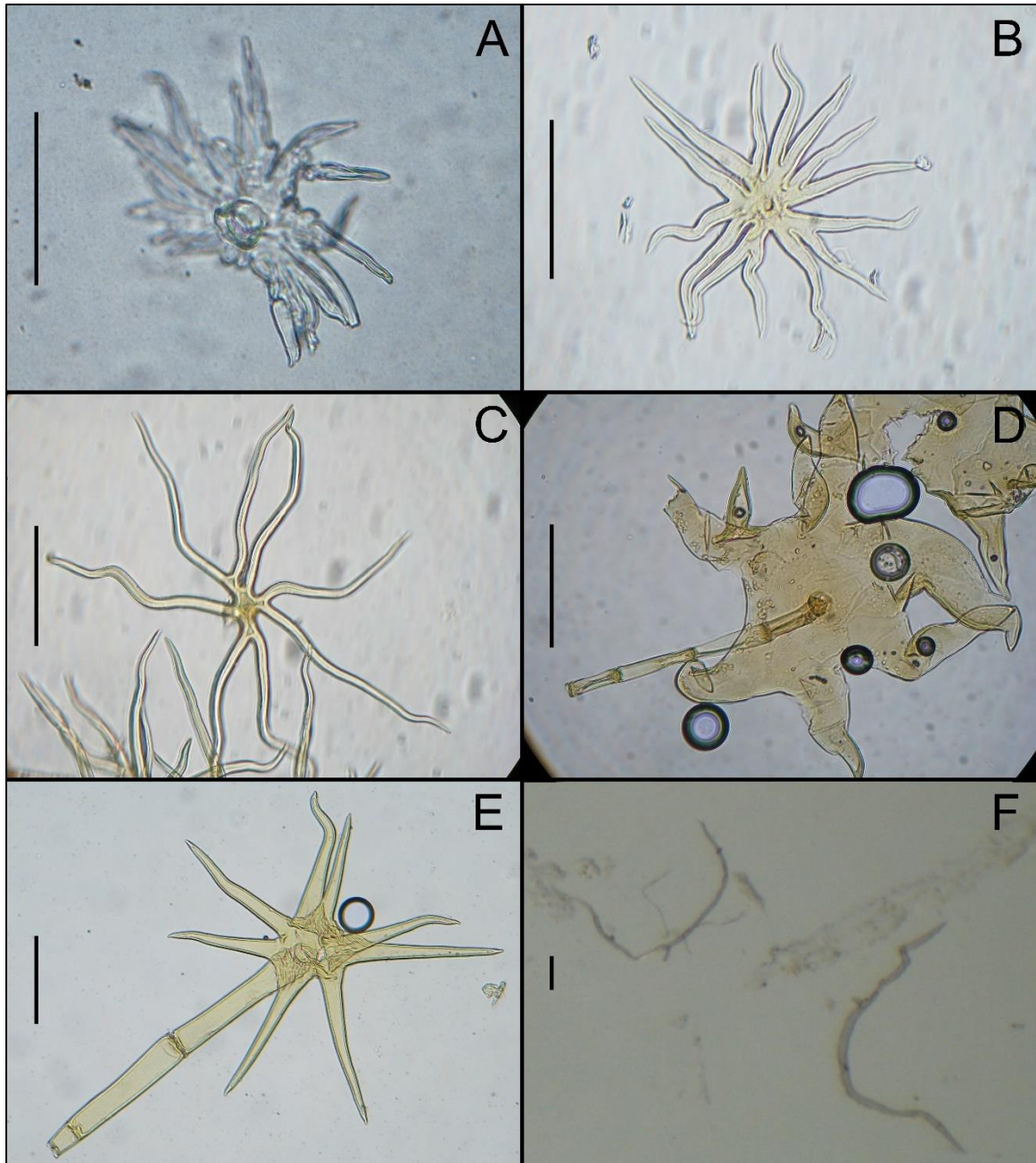


Figure 3. Diversity of non-glandular trichomes of leaves in *Shawia*. **A–C**, Short-stalked lepidote trichomes with the rays of the apical cell reaching its center in *S. sect. Shawia*; **D**, Long-stalked lepidote trichomes with the rays of the apical cell not reaching its center in *S. sect. Kosteria*; **E**, Long-stalked stellate trichomes with the rays of the apical cell projected at different angles from the stalk and reaching its center in *S. pallida* (*S. sect. Kosteria*); **F**, Short-stalked branched Y-shaped trichomes. (A: *S. albida* [CHR 477452]; B: *S. moschata* [OTA P. Saldivia-2571]; C: *S. cymbifolia* [OTA P. Saldivia-2549]; D: *S. rufa* [CANB 568462]; E: *S. pallida* [CANB 686711]; F: *S. insignis* [CHR 605973]). Scale bars: 100 μm . Photographs by P. Saldivia.

Sect. *Shawia* is found in disturbed and exposed habitats around coastal, lowland, montane, and sub-alpine shrub-lands, dune forests, and on forest margins (Allan 1961; Dawson & Lucas 2011; NZPCN 2025). Particular sites include rocky headlands, coastal cliff faces, rocky gorges, canopy gaps, post-fire landscapes, slips, and serpentine scrub-land. Most species are found below 500 m asl, but a few collections have been found above 1000 meters asl. Some species, especially *Shawia paniculata* ($\equiv$ *Olearia paniculata*), are widely used mainly as ornamental hedges.

Comments: Species in this section are clear-cut; however, different taxonomic approaches have been applied to the pairs *Shawia albida* ($\equiv$ *Olearia albida*)/*Shawia angulata* ($\equiv$ *Olearia angulata*) and *Shawia nummulariifolia* ($\equiv$ *Olearia nummulariifolia*)/*Shawia cymbifolia* ($\equiv$ *Olearia cymbifolia*).

Supinate exposure of the style branches is remarkable, since until recently supination has been considered absent in the whole tribe Astereae (Jones 1976; Karis 1993; Nesom & Robinson 2007). Nonetheless, supination may have been overlooked and could be more common within Astereae, as it has been shown to be present in some species within the *Pleurophyllum* Clade (Saldivia et al. 2022), it is clearly seen in the illustration accompanying the description of *Llerasia pascoensis* Sagást. & Dillon (Sagástegui-Alva & Dillon, 1988), and it is present in the photographs accompanying the description of *Diplostephium paposanum* S.T. Ibáñez & Muñoz-Schick (Ibáñez et al. 2022).

SHAWIA PANICULATA J.R. Forst. & G. Forst, Char. Gen. Pl., ed. 2: 96, t. 48. 1776. *Olearia paniculata* (J.R. Forst. & G. Forst.) Druce, Rep. Bot. Soc. Exch. Club Brit. Isles 4 (Suppl. 2): 638. 1917.

Eurybia forsteri Hook. f., Bot. Antarct. Voy. II. (Fl. Nov.–Zel.). 1: 119. 1853, *nom. superfl.*
Olearia forsteri (Hook. f.) Hook. f., Handb. New Zealand Fl.: 127. 1864, *nom. superfl.*

Olearia uniflora Colenso, Trans. & Proc. New Zealand Inst. 22: 469. 1889 [publ. in 1890].

Shawia paniculata var. *elliptica* Kirk, Stud. Fl. New Zealand: 277. 1899.

Shawia paniculata var. *obtusata* Kirk, Stud. Fl. New Zealand: 277. 1899.

Shawia paniculata var. *viscosa* G. Simpson, Trans. & Proc. Roy. Soc. N. Z. Inst. 75: 198. 1945.

Distribution: New Zealand: North and South Islands.

SHAWIA CORIACEA (Kirk) Saldivia & Nicol, **comb. nov.** *Olearia coriacea* Kirk, Stud. Fl. New Zealand 276: 1899.

Distribution: New Zealand: South Island.

SHAWIA NUMMULARIIFOLIA (Hook. f.) Sch.Bip., Jahresber. Pollichia 18–19: 175. 1861. *Eurybia nummulariifolia* Hook. f., Bot. Antarct. Voy. II. (Fl. Nov.–Zel.) 1: 118–119. 1852.
Olearia nummulariifolia (Hook. f.) Hook. f., Handb. New Zealand Fl.: 127. 1864. *Aster nummulariifolius* (Hook. f.) Kuntze, Revis. Gen. Pl. 1: 315. 1891.

Olearia hillii Colenso, Trans. & Proc. New Zealand Inst. 20: 194. 1887 [publ. in 1888].

Distribution: New Zealand: North and South Islands.

SHAWIA CYMBIFOLIA (Hook. f.) Saldivia & Nicol, **comb. nov.** *Olearia nummulariifolia* var. *cymbifolia* Hook. f., Handb. New Zealand Fl.: 732. 1867. *Olearia cymbifolia* (Hook. f.) Cheeseman, Trans. & Proc. New Zealand Inst. 39: 445. 1907.

Distribution: New Zealand: South Island.

SHAWIA MOSCHATA (Hook. f.) Saldivia & Nicol, **comb. nov.** *Olearia moschata* Hook. f., Handb. New Zealand Fl.: 127. 1864. *Aster moschatus* (Hook. f.) F.Muell., Fragm. (Mueller) 5(35): 85. 1865.

Distribution: New Zealand: South Island.

SHAWIA AVICENNIIFOLIA Raoul, Choix Pl. Nouv.–Zel.: 19. t. 13. 1846. *Eurybia avicenniifolia* (Raoul) Hook. f., Bot. Antarct. Voy. II. (Fl. Nov.–Zel.). 1: 120. 1853. *Olearia avicenniifolia* (Raoul) Hook. f., Handb. New Zealand Fl.: 127. 1864. *Aster avicenniifolius* (Raoul) F. Muell., Fragm. 5: 85. 1865.

Distribution: New Zealand: South and Stewart/Rakiura Islands.

SHAWIA ALBIDA (Hook. f.) Sch.Bip., Jahresber. Pollichia 18–19: 175. 1861. *Eurybia albida* Hook. f., Bot. Antarct. Voy. II. (Fl. Nov.–Zel.). 1: 118. 1852. *Olearia albida* (Hook. f.) Hook. f., Handb. New Zealand Fl.: 128. 1864. *Aster albidus* (Hook. f.) Kuntze, Revis. Gen. Pl. 1: 315. 1891.

Distribution: New Zealand: North Island.

SHAWIA ANGULATA (Kirk) Saldivia & Nicol, **comb. nov.** *Olearia angulata* Kirk, Trans. & Proc. New Zealand Inst. 13: 384. 1881. *Aster angulatus* (Kirk) Kuntze, Revis. Gen. Pl. 1: 317. 1891. *Olearia albida* var. *angulata* (Kirk) Allan, Fl. New Zealand I: 663. 1961.

Distribution: New Zealand: North Island.

SHAWIA × HAASTII (Hook. f.) Saldivia & Nicol, **comb. nov.** *Olearia × haastii* Hook. f., Handb. New Zealand Fl.: 126. 1864. *Aster × haastii* (Hook. f.) Kuntze, Revis. Gen. Pl. 1: 315. 1891. (= *Shawia avicenniifolia* × *S. moschata*).

Distribution: New Zealand: South Island.

SHAWIA × OLEIFOLIA (Kirk) Saldivia & Nicol, **comb. nov.** *Olearia × oleifolia* Kirk, Trans. N. Z. Inst. 11: 463. 1879. *Aster × oleifolius* (Kirk) Kuntze, Revis. Gen. Pl. 1: 315. 1891. *Olearia angustata* J.B.Armstr., Trans. & Proc. New Zealand Inst. 13: 337. 1881, *nom. illeg.* (= *Shawia avicenniifolia* × *S. nummulariifolia*).

Olearia willcoxii Petrie, Trans. & Proc. New Zealand Inst. 45: 266. 1912 [1913].

Distribution: New Zealand: South Island.

SHAWIA × MATTHEWSII (Heenan) Saldivia & Nicol, **comb. nov.** *Olearia × matthewsii* Heenan, Hort. New Zealand 2(2): 13. 1991. (= *Shawia moschata* × *S. ilicifolia*).

Distribution: New Zealand: South Island.

II. SHAWIA sect. KOSTERIA Saldivia & Nicol, **sect. nov.** **TYPE: SHAWIA DURIFOLIA** (J. Kost.) Saldivia & Nicol.

Diagnostic character states defining sect. *Kosteria* are the abaxial surface of leaves, phyllaries, and peduncles covered by a dense felt-like, and often floccose indumentum composed of long multi-celled stalked trichomes with the apical cell mostly lepidote and scutellate, rarely T-shaped or stellate (only in *Shawia pallida*, Fig. 3E). Of the 19 species, *Shawia heterotricha* (≡ *Olearia heterotricha*) has T-shaped and lepidote trichomes, 4 have T-shaped trichomes, and 14 have lepidote trichomes (Koster 1966; van Royen 1983; Hind & Johns 2014). Unlike sect. *Shawia*, the rays of the apical cell of the lepidote and scutellate trichomes, do not reach the center of the cell, or are absent (Fig. 3D).

Small trees or shrubs; phyllotaxis alternate, subopposite or opposite; leaves petiolate, non-resinous, glandular non-stalked trichomes present in some species, elliptic, elliptic-oblong, ovate-elliptic, ovate-oblong, obovate-elliptic, or linear (only in *Shawia kernotii* ≡ *Olearia kernotii*), 1.5–19 cm long, margin mostly untoothed, blade plane or revolute (only in *S. kernotii*); capitulescences corymbose-like; involucre cylindrical at anthesis; phyllaries arranged in 5–7 rows with the inner phyllaries longer than the outer ones, non-resinous, glandular trichomes in most of the species; ray florets pistillate (occasionally some florets present staminate), ligulate, 6–18 arranged in 1–2 rows; disc florets perfect or functionally staminate, 5–16; cypselae fusiform-cylindric, 4–9-ribbed, covered with twin trichomes.

Diversity, distribution, and ecology: Sect. *Kosteria* includes 19 species and 6 varieties of small trees and shrubs endemic to New Guinea (Indonesia/Papua New Guinea). The typical habitats for sect. *Kosteria* are in open grasslands and second growth moss forest (Koster 1966). However, these species have been recorded in a wide range of habitats, including in drained swamps, bog grasslands, depleted forests, at the edge of moss forest and sub-alpine forests, at the edge of montane cloud forest, in the canopy of low scrub moss forests, within montane and alpine shrub-lands and grasslands, in forest clearings, secondary growth on landslides, fire-induced shrub-lands and grasslands and fern-fields. Other sites include at the edge of *Podocarpus-Papuacedrus* forest, on narrow ridge crests, on steep rocky slopes in *Nothofagus* forest, among rocks on exposed mountain slopes, on granitic formations, in the cleft of exposed rock, on limestone ridges of mountain tracks, along cracks on stony soil and stony clay, on muddy organic soil, and along creeks, stream banks, and slopes in deep steep forested gullies. These species occupy the highest geography in *Shawia*, with some species found around 4000 meters asl, with most species found between 2000–3800 meters, and with few species below 1000 meters (Saldivia & Nicol 2023).

Etymology: Sect. *Kosteria* honors Dutch botanist Joséphine Thérèse Koster (1902–1986), who was the central figure in the Asteraceae taxonomy of New Guinea and described most of the species included in this section.

Comments: *Shawia* sect. *Kosteria* was represented by 3 of 19 species in the study by Nicol et al. (2024). The section was monophyletic in 12 of the 16 estimated phylogenies, the fewest recorded of the *Shawia* sections (Fig. 1). However, the non-monophyletic recoveries of this section were likely artificial. In sect. *Kosteria*, two of the three samples were of low quality (Nicol 2023; Nicol et al. 2024: Fig. S3). The type I (missing genes) and type II (fragmentation) missing data contributed to the sensitivity of many low quality samples in the study, and likely affected the recovery of sect. *Kosteria* (Nicol 2023). Because sect. *Kosteria* was recovered in 12 of the 16 phylogenies, and because of the distinct morphology and geographic distribution, sect. *Kosteria* is here supported as a taxonomic unit.

Species in this section are variable and difficult to identify. Taxonomic keys by Koster (1960) and van Royen (1983) are, most of the time, not easy to follow and require an accurate evaluation of the leaf trichomes (light microscopy often needed). Takeuchi (2007) mentioned that “Even when a specimen is carefully keyed out, the result often will not match the assigned name. The variation in certain species is either much wider than presently recognized, or there are more taxa in need of formal description.” This is illustrated by the confusion regarding the recently described *Olearia dibrachiata* Hind & Johns ($\equiv$ *Shawia dibrachiata*) by Hind & Johns (2014). The same leading author later realized that *O. dibrachiata* is conspecific with *Olearia exilis* var. *subacuta* J. Kost. (Hind 2024).

The gynoecial morphology of the New Guinea species is also of relevance. It is acknowledged that *Celmisiinae* genera have perfect disc florets (e.g., Allan 1961; Given 1969; Koster 1966). For example, this was the evidence upon which Cuatrecasas (1961, 1997) placed the South American *Celmisia* species with functionally male disc florets in the genus *Oritrophium* (Kunth) Cuatrec. (Saldivia 2024). In the New Guinea *Shawia* species (sect. *Kosteria*), however, sterility of the disc florets (which is found by observation that the stylar branches do not have stigmatic surface and thus are unable to be fertilized) was found in six species (Fig. 4E–F). In two species the stigmatic bands are reduced to 1/4 of the branch length; in two other species the stigmatic bands reach half the length of the branch (Fig. 4G); and in three additional species the stigmatic bands reach 3/4 or more of the stylar branch length (Fig. 4H), as in most of *Shawia* species. Additionally, Mueller (1889) in the description of *Aster kernotii* F. Muell. ($\equiv$ *Shawia kernotii*) mentioned that “The style of some of the central flowers remains often undivided.” Surprisingly, the sterility of the disc florets in some New Guinea species was overlooked by Koster (1966) and van Royen (1983). This phenomenon, found only in *Shawia* sect. *Kosteria* within *Celmisiinae*, is here interpreted as a trend of stigmatic band reduction, leading towards monoecy by the uni-sexualization of the disc florets.

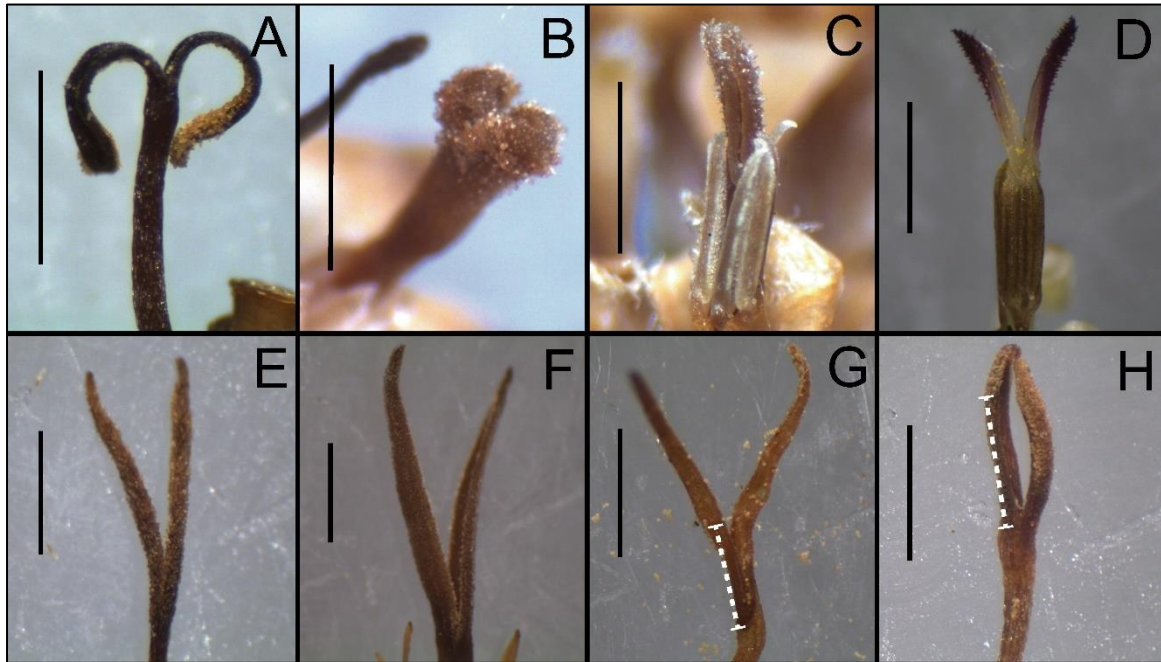


Figure 4. Key characters of styler morphology in *Shawia*. **A**, Supinate exposure of the styler branches in *S. sect. Shawia*; **B**, Short styler branches of *S. traversiorum* Group; **C**, Short papillae styler appendages in *S. fragrantissima* Group; **D**, Long and purple papillae styler appendages of *S. virgata* Group; **E–F**, Styler branches without stigmatic surface in *S. sect. Kosteria*; **G**, Styler branches with stigmatic bands (dashed line) reaching half of its length in *S. sect. Kosteria*; **H**, Styler branches with stigmatic bands (dashed line) reaching 3/4 of its length in *S. sect. Kosteria*. (A: *S. coriacea* [OTA P. Saldivia-2150]; B: *S. traversiorum* [OTA P. Saldivia-2495]; C: *S. fragrantissima* [OTA P. Saldivia-2488]; D: *S. gardneri* [OTA P. Saldivia-2518]; E: *S. lanata* [CANB 177937]; F: *S. velutina* [CANB 543548]; G: *S. kernotii* [NSW 833824]; H: *S. monticola* [CANB 83210]). Scale bars: 1 mm. Photographs by P. Saldivia.

SHAWIA DIBRACHIATA (Hind & Johns) Saldivia & Nicol, **comb. nov.** *Olearia dibrachiata* Hind & Johns, Kew Bull. 69(2)-9515:1. 2014.

Olearia exilis var. *subacuta* J. Kost., Nova Guinea, Bot. 24: 535. 1966.

Distribution: Indonesia: Mt Jaya (Carstensz) area.

SHAWIA DURIFOLIA (J. Kost.) Saldivia & Nicol, **comb. nov.** *Olearia durifolia* J. Kost., Nova Guinea, Bot. 24: 540–542. 1966.

Distribution: Indonesia: Mt Antares, Mt Wilhelm. Papua New Guinea: Mt. Kerewa, Star Mts. (boundary between Indonesia and Papua New Guinea).

SHAWIA EXILIS (S. Moore) Saldivia & Nicol, **comb. nov.** *Olearia exilis* S. Moore, Trans. Linn. Soc. London, Bot. 9(1): 81. 1916.

Distribution: Indonesia: Mt Jaya (Carstensz) area.

SHAWIA FLOCCOSA (J. Kost.) Saldivia & Nicol, **comb. nov.** *Olearia floccosa* J. Kost., Nova Guinea, Bot. 24: 545–546. 1966.

Distribution: Papua New Guinea: Mt Amungwiwa, Mt Otto, Mt Wilhelm, Kubor Ra., Mt Hagen, Mt Giluwe.

SHAWIA HETEROLEPIS (Mattf.) Saldivia & Nicol, **comb. nov.** *Olearia heterolepis* Mattf., Bot. Jahrb. Syst. 68: 253–254. 1937.

Distribution: Papua New Guinea: Wharton Ra.

SHAWIA HETEROTRICHA (Mattf.) Saldivia & Nicol, **comb. nov.** *Olearia heterotricha* Mattf., Bot. Jahrb. Syst. 68: 254–255. 1937.

Olearia crenifingens Mattf., Bot. Jahrb. Syst. 68: 255–256. 1937.

Distribution: Papua New Guinea: Wharton Ra., Main Owen Stanley Ra., Mt Knutsford, Mt Albert Edward, Mt Dickson.

SHAWIA HOOGLANDII (J. Kost.) Saldivia & Nicol, **comb. nov.** *Olearia hooglandii* J. Kost., Nova Guinea, Bot. 24: 542–543. 1966.

Distribution: Papua New Guinea: Sugarloaf complex.

SHAWIA KERNOTII (F. Muell.) Saldivia & Nicol, **comb. nov.** *Aster kernotii* F. Muell., Trans. Roy. Soc. Victoria n.s. 1(2): 10. 1889. *Olearia kernotii* (F. Muell.) Mattf., Bot. Jahrb. Syst. 62: 412. 1929.

Distribution: Papua New Guinea: Mt Victoria, Mt Albert Edward, Mt Musgrave, Owen Stanley Ra., Mt Knutsford.

SHAWIA LANATA (J. Kost.) Saldivia & Nicol, **comb. nov.** *Olearia lanata* J. Kost., Nova Guinea, Bot. 24: 536–537. 1966.

Distribution: Papua New Guinea: Mt Hagen, Mt Ambua (Doma Peaks).

SHAWIA LEPIDOTA (Mattf.) Saldivia & Nicol [var. *lepidota*], **comb. nov.** *Olearia lepidota* Mattf., Nova Guinea 14: 520. 1932.

Distribution: Indonesia: Mt. Hubrecht.

SHAWIA LEPIDOTA var. **SARAWAKETENSIS** (Mattf.) Saldivia & Nicol, **comb. nov.** *Olearia sarawaketensis* Mattf., Bot. Jahrb. Syst. 69: 284–285. 1938. *Olearia lepidota* var. *sarawaketensis* (Mattf.) J. Kost., Nova Guinea, Bot. 24: 552. 1966.

Distribution: Papua New Guinea: Rawlinson Ra., Mt Sarawaket.

SHAWIA LEPIDOTA var. **OPACA** (J. Kost.) Saldivia & Nicol, **comb. nov.** *Olearia lepidota* var. *opaca* J. Kost., Nova Guinea, Bot. 24: 552–553. 1966.

Distribution: Papua New Guinea: Mt Michael.

SHAWIA LEPTOCEPHALA (J. Kost.) Saldivia & Nicol, **comb. nov.** *Olearia leptocephala* J. Kost., Nova Guinea, Bot. 24: 550–551. 1966.

Distribution: Papua New Guinea: Asaro-Mairi Div., Mt Wilhelm, Toromambuno (Denglugu) mission, Pombameri – Mirima Track, Keglsugl – Kombugomambuno, Mt Hagen, Upper Ambum valley, Lagaip-Kandep valley, Sirunki, Mt Giluwe.

SHAWIA MONTICOLA (F.M.Bailey) Saldivia & Nicol [var. *monticola*], **comb. nov.** *Olearia monticola* F.M. Bailey, Dept. Agric. Brisbane Bot. Bull. 10: 39. 1895.

Distribution: Papua New Guinea: Mt Dayman, Maneao Ra., Mt Simpson, Mt Dickson.

SHAWIA MONTICOLA var. **GRANDIFOLIA** (J. Kost.) Saldivia & Nicol, **comb. nov.** *Olearia monticola* var. *grandifolia* J. Kost., Nova Guinea, Bot. 24: 532. 1966.

Distribution: Papua New Guinea: Mt Michael.

SHAWIA MONTICOLA var. **CUNEATA** (J. Kost.) Saldivia & Nicol, **comb. nov.** *Olearia monticola* var. *cuneata* J. Kost., Nova Guinea, Bot. 24: 532. 1966.

Distribution: Papua New Guinea: Mt Wilhelm, Marafunga.

SHAWIA PACHYCEPHALA (J. Kost.) Saldivia & Nicol, **comb. nov.** *Olearia pachycephala* J. Kost., Nova Guinea, Bot. 24: 532–533. 1966.

Distribution: Papua New Guinea: Mt Dayman, Maneao Ra.

SHAWIA PALLIDA (J. Kost.) Saldivia & Nicol, **comb. nov.** *Olearia pallida* J. Kost., Nova Guinea, Bot. 24: 537–539. 1966.

Distribution: Papua New Guinea: Sugarloaf complex, Mt Giluwe, Yobobos grassland area.

SHAWIA PLATYPHYLLA (Mattf.) Saldivia & Nicol [var. *platyphylla*], **comb. nov.** *Olearia platyphylla* Mattf., Nova Guinea 14: 519. 1932.

Olearia clemensiae Mattf., Bot. Jahrb. Syst. 69(2): 283–284. 1938.

Distribution: Indonesia: Lake Habbema area, Oranje Mts., Mt Hellwig. Papua New Guinea: Mt Sarawaket, Samanzing, Mt Michael, Mt Wilhelm, Wabab-Kubalis area – Lay valley.

Comment: Koster (1966: 554) mentioned that the type of *O. clemensiae* var. *pachylaena* Mattf. (Mt Sarawaket, c. 3600 m, *Clemens 7301* at B) is apparently lost, and she did not include it as a synonym at varietal rank.

SHAWIA PLATYPHYLLA var. **CINEREA** (Mattf.) Saldivia & Nicol, **comb. nov.** *Olearia cinerea* Mattf., Bot. Jahrb. Syst. 70(4): 471–472. 1940. *Olearia platyphylla* var. *cinerea* (Mattf.) J. Kost., Nova Guinea, Bot. 24: 554. 1966.

Distribution: Indonesia: Balim River valley. Papua New Guinea: Rawlinson Ra., Mt Sarawaket, Mt Otto, Marafunga – Upper Asaro valley, Nondugl, Kubor Ra, Tonga - Wapanamanda, Wabag, Yaki River valley, Yobobos grassland area.

SHAWIA PLATYPHYLLA var. **MICROCEPHALA** (J. Kost.) Saldivia & Nicol, **comb. nov.** *Olearia platyphylla* var. *microcephala* J. Kost., Nova Guinea, Bot. 24: 555. 1966.

Distribution: Papua New Guinea: Cromwell Mts., Sarawaket Ra., Mt Otto.

SHAWIA RUFA (J. Kost.) Saldivia & Nicol, **comb. nov.** *Olearia rufa* J. Kost., Nova Guinea, Bot. 24: 543–545. 1966.

Distribution: Papua New Guinea: Mt Sarawaket, Mt Enggom, Kubor Ra.

SHAWIA SPECTABILIS (J. Kost.) Saldivia & Nicol, **comb. nov.** *Olearia spectabilis* J. Kost., Nova Guinea, Bot. 24: 546, 548, 550. 1966.

Distribution: Papua New Guinea: Mt Amungwiwa, Mt Piora, Mt Otto, Kerigomna, Mt Wilhelm, Lake Piunde, Lake Aunde, Kubor Ra., Mt Giluwe, Mt Sugarloaf.

SHAWIA VELUTINA (J. Kost.) Saldivia & Nicol, **comb. nov.** *Olearia velutina* J. Kost., Nova Guinea, Bot. 24: 540. 1966.

Distribution: Indonesia: Lake Habbema, Mt Wilhelmna.

SHAWIA VERNONIIOIDES (White & Francis) Saldivia & Nicol, **comb. nov.** *Olearia vernonioides* White & Francis, Proc. Roy. Soc. Queensland 38: 260. 1927.

Olearia obovata Mattf., Bot. Jahrb. Syst. 68: 256–257. 1937.

Distribution: Papua New Guinea: Owen Stanley Ra., Mt Tafa, Mt Victoria.

III. SHAWIA sect. **CARDIOSTIGMA** (F. Muell.) Saldivia & Nicol, **comb. nov.** *Eurybia* sect. *Cardiostigma* F. Muell., Veg. Chatham–Isl.: 19, 21. 1864. **TYPE: SHAWIA TRAVERSIIORUM** (F. Muell.) Saldivia & Nicol.

Olearia sect. *Divaricaster* Heads, Bot. J. Linn. Soc. 127: 254. 1998. **TYPE: SHAWIA VIRGATA** (Hook. f.) Sch.Bip.

Most species present a divaricate morphological syndrome; however, two species differ markedly from the rest. Three morphological groups are recognized which are described below.

Etymology: Refers to the stylar morphology of the disc florets of the type species. Stylar branches are very short (the shortest in *Celmisiinae*), truncate to clavate apically, giving a heart shape.

Comments: Cross et al. (2002) and Saldivia et al. (2020), based on phylogenetic analyses of Internal Transcribed Spacer (ITS) and ITS + External Transcribed Spacer nuclear ribosomal regions, respectively, found *Shawia traversiorum* ($\equiv$ *Olearia traversiorum*) nested within sect. *Divaricaster* s. str. (Heads 1998). Saldivia et al. (2020) also recovered *Shawia fragrantissima* ($\equiv$ *Olearia fragrantissima*) as sister to a clade including all sampled Australian *Shawia* species (sect. *Australiaster*, see below). More recently, Nicol et al. (2024) based on nuclear phylogenomic analyses, recovered *S. traversiorum* and *S. fragrantissima* nested in sect. *Divaricaster*. Heenan (2005) suggested that sect. *Divaricaster* should be expanded to incorporate *S. traversiorum* based on the shared opposite phyllotaxis (Allan 1961), a previous ITS phylogenetic analysis (Cross et al. 2002), and leaf areolation patterns. Heenan et al. (2008) followed this suggestion and formally included *S. traversiorum* and their newly described *Shawia telmatica* ($\equiv$ *Olearia telmatica*, both similar species endemic to the Chatham Islands) in sect. *Divaricaster*. These results and proposals, however, are complicated to interpret morphologically. Sect. *Divaricaster* s. str., as described by Heads (1998), is a distinctive morphological group endemic to the three main islands of New Zealand, characterized by its divaricate syndrome or “Philipson’s Architectural Model” (Heads 1998, 2019; see description of *Shawia virgata* ($\equiv$ *Olearia virgata*) Group below). Conversely, *S. traversiorum* and *S. telmatica* do not have divaricate architecture but share the opposite phyllotaxis with sect. *Divaricaster*; yet strict opposite phyllotaxis is also found in seven species from sect. *Australiaster* and four from sect. *Kosteria*. Nonetheless, *S. traversiorum* and *S. telmatica* display a unique style morphology (Fig. 4B) with reduced stylar branches combined with clavate or truncate appendages, a character upon which Mueller (1864) erected *Eurybia* sect. *Cardiostigma*. It is worth mentioning that sect. *Cardiostigma* has so far been overlooked. When Heenan et al. (2008) included these two Chatham Islands endemics in sect. *Divaricaster*, by priority, sect. *Divaricaster* should have been treated as synonym of sect. *Cardiostigma*. This is formally done here.

The morphology and classification of *Shawia fragrantissima* also requires special attention. Heads (1998) wrote this: “*Olearia* sect. *Divaricaster* appears to be more closely related to *O. fragrantissima*. This species has a divaricate, deciduous habit with short shoots, and leaves which are alternate and acuminate but otherwise like those of *O. hectorii* Hook. f. It is distributed in the south-east of South Island (north to Banks Peninsula), like several species in *O. sect. Divaricaster*. However, the inflorescence differs in being almost racemose.” In the same way as *S. traversiorum* and *S. telmatica*, some critical architectural differences separate *S. fragrantissima* from sect. *Divaricaster* s. str. In *S. fragrantissima* the leaves are alternate and are arranged in both long shoots (Fig. 5C) and short-lived brachyblasts (vs. opposite leaves and brachyblasts in sect. *Divaricaster*, Fig. 5A–B). The brachyblasts represent only the first stage of shoot development, and usually last only one growing season. After the first season, the brachyblasts elongate, becoming long-shoots with no apical abortion (vs. apical abortion in sect. *Divaricaster* Fig. 5D,F). Another difference is that capitula in *O. sect. Divaricaster* are solitary or arranged in loose mostly umbelliform fascicles (Fig. 5D–H), whereas capitula in *S. fragrantissima* are glomeruliform racemes (Fig. 5I), a character unique within *Celmisiinae*. Style branch

appendages are consistently purple with long papillae (Fig. 4D) in *O.* sect. *Divaricaster*, markedly different from the yellow appendages with short papillae of *S. fragrantissima* (Fig. 4C). However, the most morphologically distant species included by Heads (1998) in sect. *Divaricaster*, *Shawia solandri* ($\equiv$ *Olearia solandri*), narrows the morphological gap between sect. *Divaricaster* and *S. fragrantissima* and *S. traversiorum* + *S. telmatica*, as *S. solandri* often lacks long shoot apical abortion and has poor development of brachyblasts (Fig. 5E).

In sum, *Shawia traversiorum* + *S. telmatica* and *S. fragrantissima* are morphologically different from sect. *Divaricaster*; still, both show different connections with it. *Shawia traversiorum* + *S. telmatica* share the strict opposite phyllotaxis and *S. fragrantissima* the general divaricate architecture. Additionally, the similar hosts assemblages of moth and other invertebrate communities between *S. fragrantissima* and sect. *Divaricaster* (Patrick 2000) strengthen the idea of a close phylogenetic affinity between them.

As explained above, the morphological heterogeneity of the species included in this section does not allow a uniform description. Instead, species in this section can be arranged in three morphologically homogeneous groups: *Shawia traversiorum* Group (*S. traversiorum* and *S. telmatica*), *Shawia fragrantissima* Group (*S. fragrantissima*), and *Shawia virgata* Group (*O.* sect. *Divaricaster* s. str.). A formal classification of these groups (e.g., sections, series) would go against the principle of monophyly, because phylogenetic evidence (Saldivia 2021; Saldivia et al. 2020; Nicol et al. 2024) indicates that *O.* sect. *Divaricaster* s. str. (Heads 1998) is paraphyletic with *S. traversiorum* and *S. fragrantissima* nested within it (Fig. S1).

a) SHAWIA TRAVERSIORUM Group

Diagnostic character states defining this group are the reduced stylar branches of the disc florets of 0.3–0.6 mm long with clavate or truncate appendages.

Trees up to 18 m tall, the tallest in *Celmisiinae*; phyllotaxis opposite; leaves petiolate, non-resinous, elliptic to obovate, 1.4–8 cm long, margin untoothed, blade plane; adaxial surface glabrescent, abaxial surface covered with a layer of indumentum made of non-glandular T-shaped trichomes; capitulescences paniculate-like; involucre cylindrical at anthesis; phyllaries arranged in 2 rows with the inner phyllaries longer than the outer ones, non-resinous; ray florets pistillate, short-ligulate, 3–5 arranged in one row; disc florets perfect, 3–7; cypselae fusiform-cylindric, 4–5-ribbed, sparsely covered with twin trichomes.

Diversity, distribution, and ecology: Two species endemic to the Chatham Islands, offshore east New Zealand. *Shawia traversiorum* is recorded from all the main Chatham Islands, and inhabits sand dunes, mixed forests, coastal cliffs, headlands, volcanic hills, and out-wash gravels and alluvium at river mouths. *Shawia telmatica* is recorded from Chatham Island and Pitt Island, and inhabits wetland sites, on lake margins, ponds, stream-banks, depressions, and seeps (Heenan et al. 2008; Dawson & Lucas 2011). Elevation reflects the low-lying Chatham Islands which reach a maximum height of ca. 300 meters asl.

SHAWIA TRAVERSIORUM (F. Muell.) Saldivia & Nicol, **comb. nov.** *Eurybia traversiorum* F. Muell., Veg. Chatham–Isl.: 19, t. 2. 1864. *Olearia traversiorum* (F. Muell.) Hook. f., Handb. New Zealand Fl.: 731. 1867. *Aster traversiorum* (F. Muell.) Kuntze, Revis. Gen. Pl. 1: 315. 1891.

SHAWIA TELMATICA (Heenan & de Lange) Saldivia & Nicol, **comb. nov.** *Olearia telmatica* Heenan & de Lange, New Zealand J. Bot. 46: 575–578. 2008.

b) SHAWIA FRAGRANTISSIMA Group

Diagnostic character states defining this group, which includes one species, are the sessile or subsessile florets arranged in glomeriform racemes. Additionally, the epithet “*fragrantissima*” refers to the strong peach-like scent of the florets at anthesis.

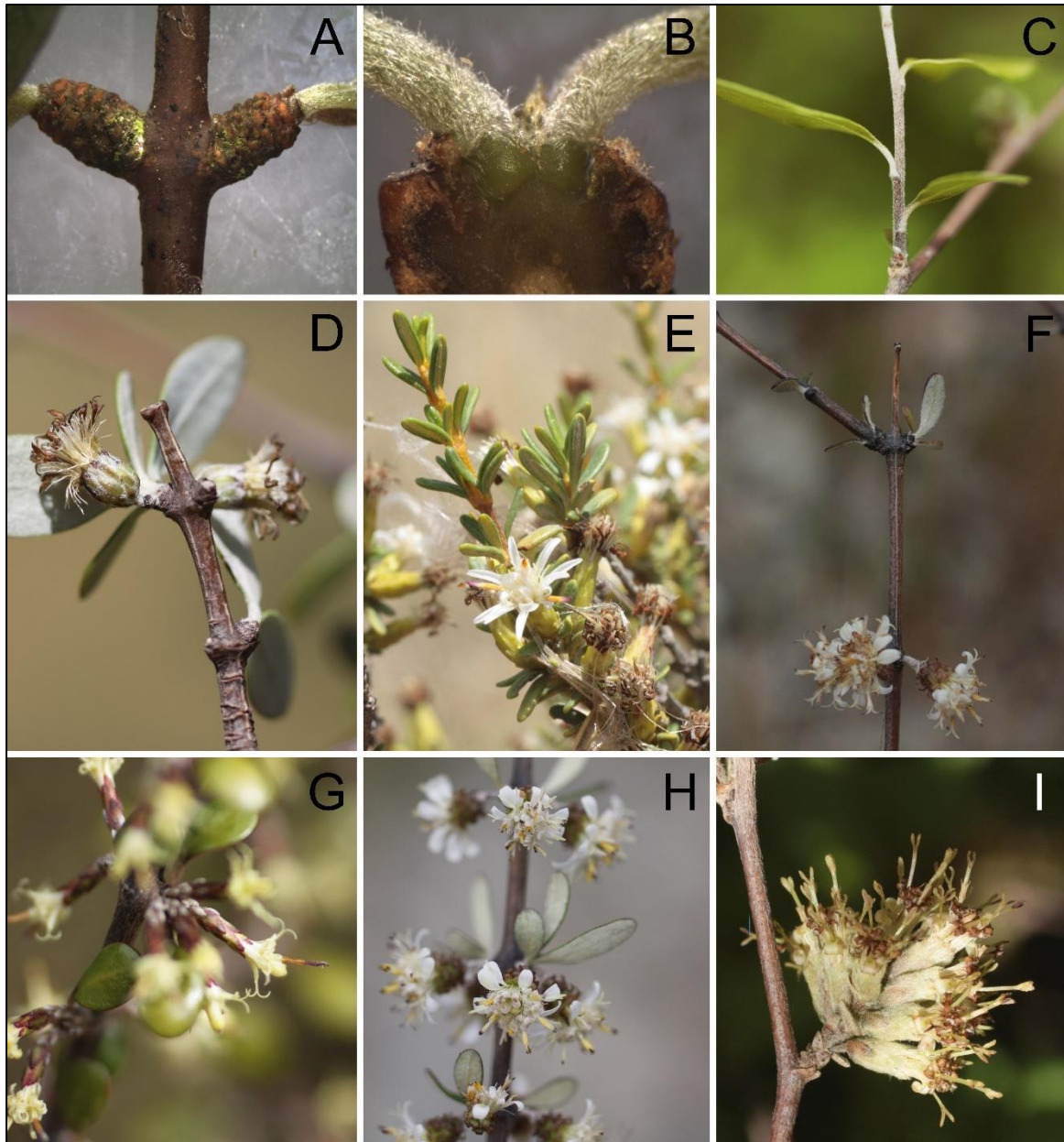


Figure 5. Phyllotaxis, shoot development, and capitulescences in *Shawia*. **A**, Opposite brachyblasts in *S. virgata* Group; **B**, Opposite leaves apically emerging from a brachyblast (only petioles visible) in *S. virgata* Group; **C**, Alternate phyllotaxis in *S. fragrantissima* Group; **D**, Shoot apical abortion in *S. virgata* Group; **E**, Shoot without apical abortion in *S. virgata* Group; **F**, Shoot apical abortion and brachyblast (top left) elongated into a long shoot in *S. virgata* Group; **G–H**, Capitula arranged in loose umbelliform fascicles in *S. virgata* Group; **I**, Capitula arranged in a glomeruliform raceme in *S. fragrantissima* Group. (**A–B**: *S. hectorii* [OTA P. Saldivia-2490]; **C–I**: *S. fragrantissima* [OTA P. Saldivia-2488]; **D**: *S. fimbriata* [OTA P. Saldivia-2507]; **E**: *S. solandri* [OTA P. Saldivia-2630]; **F–H**: *S. odorata* [OTA P. Saldivia-2584]; **G**: *S. polita* [OTA P. Saldivia-2491]). Photographs by P. Saldivia.

Small trees; phyllotaxis alternate; leaves arranged in both long shoots and short-lived brachyblasts, petiolate, non-resinous, mostly elliptic, 7.5–30 cm long, margin untoothed, blade plane; adaxial surface glabrescent or glabrous, abaxial surface covered with a layer of indumentum made of non-glandular T-shaped trichomes; involucre cylindrical at anthesis, phyllaries arranged in 4–5 rows with the inner phyllaries longer than the outer ones, non-resinous; ray florets pistillate, ligulate, 3–4 arranged in one row; disc florets perfect, 3–4; cypselae fusiform-cylindric, 5–6-ribbed, covered with twin trichomes.

Diversity, distribution, and ecology: One species endemic to the eastern flank of South Island of New Zealand, recorded from the Port Hills region of Banks Peninsula to Southland, inhabiting low-land dry forests and shrub-lands (Heads 1998; Dawson & Lucas 2011).

SHAWIA FRAGRANTISSIMA (Petrie) Saldivia & Nicol, **comb. nov.** *Olearia fragrantissima* Petrie, Trans. & Proc. New Zealand Inst. 23: 398–399. 1890 [publ. in 1891].

c) SHAWIA VIRGATA Group

Diagnostic character states defining this group are the divaricate syndrome (see some exceptions in the text), that is, long shoots apically aborted, brachyblasts (short shoots from aborted internodes) bearing leaves and florets, and at least a portion of their branches growing plagiotropically or even geotropically; and the style branch appendages consistently purple with long papillae.

Small trees or shrubs; phyllotaxis opposite; leaves arranged in brachyblasts (occasionally poorly developed or absent), sessile or pseudopetiolate, non or occasionally resinous, elliptic, elliptic-obovate, elliptic-orbicular, obovate, linear, linear-obovate, 2–40 mm long, margin untoothed, blade plane or revolute; adaxial surface glabrescent or glabrous, abaxial surface covered with a layer of indumentum made of non-glandular T-shaped trichomes and occasionally scattered glandular non-stalked trichomes; capitulescences umbelliform fasciculate or capitula solitary; involucre often narrow cylindrical at anthesis; phyllaries arranged in 2–6 rows with the inner phyllaries longer than the outer ones or subequal; ray florets pistillate, ligulate, 2–15 arranged in 1–2 rows; disc florets perfect, 1–25; cypselae fusiform-cylindric to obconic, 4–7-ribbed, covered with twin or glandular trichomes.

Diversity, distribution, and ecology: *Shawia virgata* Group includes 11 species of small trees and shrubs endemic to the three main islands of New Zealand (North, South, and Stewart Island/Rakiura). These species occupy a wide range of habitats, including sea cliffs, coastal shrublands, coastal dunes, sites with periodic flooding, coastal wetlands, near mangroves, in saltmarsh, on mudflats, beside estuaries, on alluvial deposits at creek mouths, along brackish creeks, on stream banks and river banks, in wetland shrublands, at edges of streams, seeps, lakes, tarns, swamps, and bogs, on valley floors, on river flats and terraces, in scrub filled creek beds, in gully wetlands and peatlands, in dune wetlands, at fixed dunes, in dune hollows, in open pastures, in tussock grasslands, in lowland- inland- montane- and subalpine-shrublands, in wetland forest, in open forest, in secondary forest, and at forest margins. Other sites include steep scrubby banks and hillsides, stony soils, mudstones, siltstones, and limestone, on broken rock outcrops and rock bluffs, terrace scarps, and avalanche fans (Heads 1998; Dawson & Lucas 2011). Reflecting the location of these habitats, some species are found up to and around 1000 meters, but most species in this group are recorded below 500 meters.

SHAWIA ADENOCARPA (Molloy & Heenan) Saldivia & Nicol, **comb. nov.** *Olearia adenocarpa* Molloy & Heenan, New Zealand J. Bot. 42(1): 22–24. 2004.

Distribution: New Zealand: South Island.

SHAWIA BULLATA (Wilson & Garn.–Jones) Saldivia & Nicol, **comb. nov.** *Olearia bullata* Wilson & Garn.–Jones, New Zealand J. Bot. 30(3): 365–366. 1992. *Olearia virgata* var. *rugosa* G.Simpson, Trans. Roy. Soc. New Zealand 75: 199. 1945

Distribution: New Zealand: South Island.

SHAWIA FIMBRIATA (Heads) Saldivia & Nicol, **comb. nov.** *Olearia fimbriata* Heads, Bot. J. Linn. Soc. 127(3): 271–273. 1998.

Distribution: New Zealand: South Island.

SHAWIA GARDNERI (Heads) Saldivia & Nicol, **comb. nov.** *Olearia gardneri* Heads, Bot. J. Linn. Soc. 127(3): 265–268. 1998.

Distribution: New Zealand: North Island.

SHAWIA HECTORII (Hook. f.) Saldivia & Nicol, **comb. nov.** *Olearia hectorii* Hook. f., Handb. New Zealand Fl: 128. 1864. *Aster hectorii* (Hook. f.) Kuntze in Revis. Gen. Pl. 1: 315. 1891.

Distribution: New Zealand: South Island.

SHAWIA LAXIFLORA (Kirk) Saldivia & Nicol, **comb. nov.** *Olearia laxiflora* Kirk, Stud. Fl. New Zealand: 275. 1899. *Olearia virgata* var. *laxiflora* (Kirk) Allan, Fl. New Zealand 1: 672. 1961.

Olearia divaricata Cockayne, Rep. Bot. Surv. Stewart Island 44. 1909. *Olearia virgata* var. *divaricata* (Cockayne) Allan, Fl. New Zealand 1: 671–672. 1961.

Distribution: New Zealand: South and Stewart/Rakiura Islands.

SHAWIA LINEATA (Cockayne) Saldivia & Nicol, **comb. nov.** *Olearia virgata* var. *lineata* Kirk, Stud. Fl. New Zealand: 276. 1899. *Olearia lineata* (Kirk) Cockayne, Trans. & Proc. New Zealand Inst. 43: 173. 1910 [publ. in 1911].

Distribution: New Zealand: South and Stewart/Rakiura Islands.

SHAWIA ODORATA (Petrie) Saldivia & Nicol, **comb. nov.** *Olearia odorata* Petrie, Trans. Proc. New Zealand Inst. 23: 399–400. 1890 [publ. in 1891].

Distribution: New Zealand: South Island.

SHAWIA POLITA (Wilson & Garn.–Jones) Saldivia & Nicol, **comb. nov.** *Olearia polita* Wilson & Garn.–Jones, New Zealand J. Bot. 30(3): 366–368. 1992.

Distribution: New Zealand: South Island.

SHAWIA SOLANDRI (Hook. f.) Sch.Bip., Jahresber. Pollichia 18–19: 175. 1861. *Eurybia solandri* Hook. f., Bot. Antarct. Voy. II. (Fl. Nov.–Zel.). 1: 119. 1852. *Olearia solandri* Hook. f., Handb. New Zealand Fl.: 128. 1864. *Aster solandri* (Hook. f.) F. Muell., Fragm. (Mueller) 5(35): 86. 1865.

Olearia fasciculifolia Colenso, Trans. & Proc. New Zealand Inst. 25: 330. 1892 [publ. in 1893].

Olearia consimilis Colenso, Trans. & Proc. New Zealand Inst. 28: 596. 1895 [publ. in 1896].

Olearia quinquefida Colenso, Trans. & Proc. New Zealand Inst. 28: 596. 1895 [publ. in 1896].

Distribution: New Zealand: North and South Islands.

SHAWIA VIRGATA (Hook. f.) Sch.Bip., Jahresber. Pollichia 18–19: 175. 1861. *Eurybia virgata* Hook. f., Bot. Antarct. Voy. II. (Fl. Nov.–Zel.). 1: 119. 1852. *Olearia virgata* (Hook. f.) Hook. f., Handb. New Zealand Fl.: 128. 1864.

Olearia ramuliflora Colenso, Trans. & Proc. New Zealand Inst. 22: 467. 1899 [publ. in 1890].

Olearia virgata var. *ramuliflora* (Colenso) Kirk in Stud. Fl. New Zealand: 276. 1899.

Olearia aggregata Colenso, Trans. Proc. New Zealand Inst. 28: 597. 1895 [publ. in 1896].

Olearia parvifolia Colenso, Trans. Proc. New Zealand Inst. 28: 598. 1895 [publ. in 1896].

Olearia virgata var. *implicita* G. Simpson, Trans. Roy. Soc. New Zealand 75: 199. 1945. *Olearia virgata* subsp. *implicita* (G. Simpson) Heads, Bot. J. Linn. Soc. 127: 275–277. 1998.

Olearia serpentina G. Simpson, Trans. Roy. Soc. New Zealand 75: 200. 1945. *Olearia virgata* var. *serpentina* (G. Simpson) Allan, Fl. New Zealand 1: 671. 1961. *Olearia virgata* subsp. *serpentina* (G. Simpson) Heads, Bot. J. Linn. Soc. 127: 277–278. 1998.

Olearia virgata subsp. *centralis* Heads, Bot. J. Linn. Soc. 127: 279–282. 1998.

Distribution: New Zealand: North and South Islands.

Comment: Heads (1998) recognized four allopatric subspecies within *S. virgata*, two from the South Island (subsp. *implicita* and subsp. *serpentina*) and two from the North Island (subsp. *centralis* and subsp. *virgata*) and mentioned that “In general the species of *Olearia* sect. *Divaricaster* are clear-cut and easily identified, at least with flowering material, but the subspecies of *O. virgata* are less distinct and would repay further study.” Heenan (2001) evaluated Heads’s subspecies based on six morphological features and found no differences among them and accordingly, merged them under a broader *O. virgata* concept without recognizing infraspecific taxa. However, as claimed by Heads (2003), Heenan did not investigate or use all the characters from Heads (1998), and two of the six characters used by Heenan (2001) (leaf width and number of leaves per brachyblast) were not used by Heads. Instead, architectural characters such as branch tropism, shoot abortion regularity, branch flexibility, etc., which were recognized as diagnostic by Heads (1998) were not analyzed by Heenan (2001). Whether or not these taxa are morphologically well supported, both Heads’s (1998) and Heenan’s (2001) works are not comparable, and an objective conclusion cannot be drawn. Genetic studies will be necessary to clarify the infraspecific variation and taxonomy of *Shawia virgata*.

IV. SHAWIA sect. **PACHYSTEGIA** (Cheeseman) Saldivia & Nicol, **comb. et stat. nov.** *Pachystegia* Cheeseman, Man. New Zealand Fl., ed. 2: 910. 1925. **TYPE:** *SHAWIA INSIGNIS* (Hook. f.) Saldivia & Nicol.

Diagnostic character states defining section *Pachystegia* are the combination of pappus made of two kinds of bristles (a longer set 8–12 mm long, and a shorter set 2–3 mm long, Fig. 6A–C) and phyllary rows 9–12.

Shrubs, robust, upright to spreading, up to 2 m tall; phyllotaxis alternate; leaves petiolate, clustered towards the distal part of the branchlets, non-resinous, coriaceous, obovate, elliptic, elliptic-oblong, or obovate-elliptic, rhomboid-elliptic, 5–19 cm long, margin entire, blade plane, adaxial surface often glabrescent, abaxial surface covered with a thick layer of indumentum made of non-glandular T-shaped trichomes; capitula solitary with few foliaceous bracts often arranged towards the distal portion of the peduncles, long exserted from the foliage; involucre wide campanulate, sub-globose or cupuliform at anthesis; phyllaries arranged in 9–12(–13) rows with the inner phyllaries longer than the outer ones, non-resinous; ray florets pistillate (occasionally some florets present staminodes), ligulate, ca. 30–90 arranged in 3–4 rows; disc florets perfect, ca. 100–500; cypselae fusiform-cylindric, 4–6-ribbed, densely covered with twin trichomes.

Diversity, distribution, and ecology: Sect. *Pachystegia* includes 3–4 species, which are endemic to and conspicuous elements of the Marlborough area in the South Island of New Zealand (Heenan & Molloy, 2022). The distribution of this section is flanked by the Wairau River in the north, and the Hurunui River in the south. These rupestral species are shrub-land associates and inhabit usually steep bluffs, greywacke rock bluffs, gorges, rock stream-sides, broken rock outcrops, rock faces, rock slopes, Pleistocene out-wash gravels, Oligocene age volcanics, and limestone. Sect. *Pachystegia* is found at sea level on the coast to inland sites reaching ca. 1000 meters asl.

Etymology: Probably referring to the thick (*pachys* in Greek), stout foliage covering (*tegia* in Latin) of the plants.

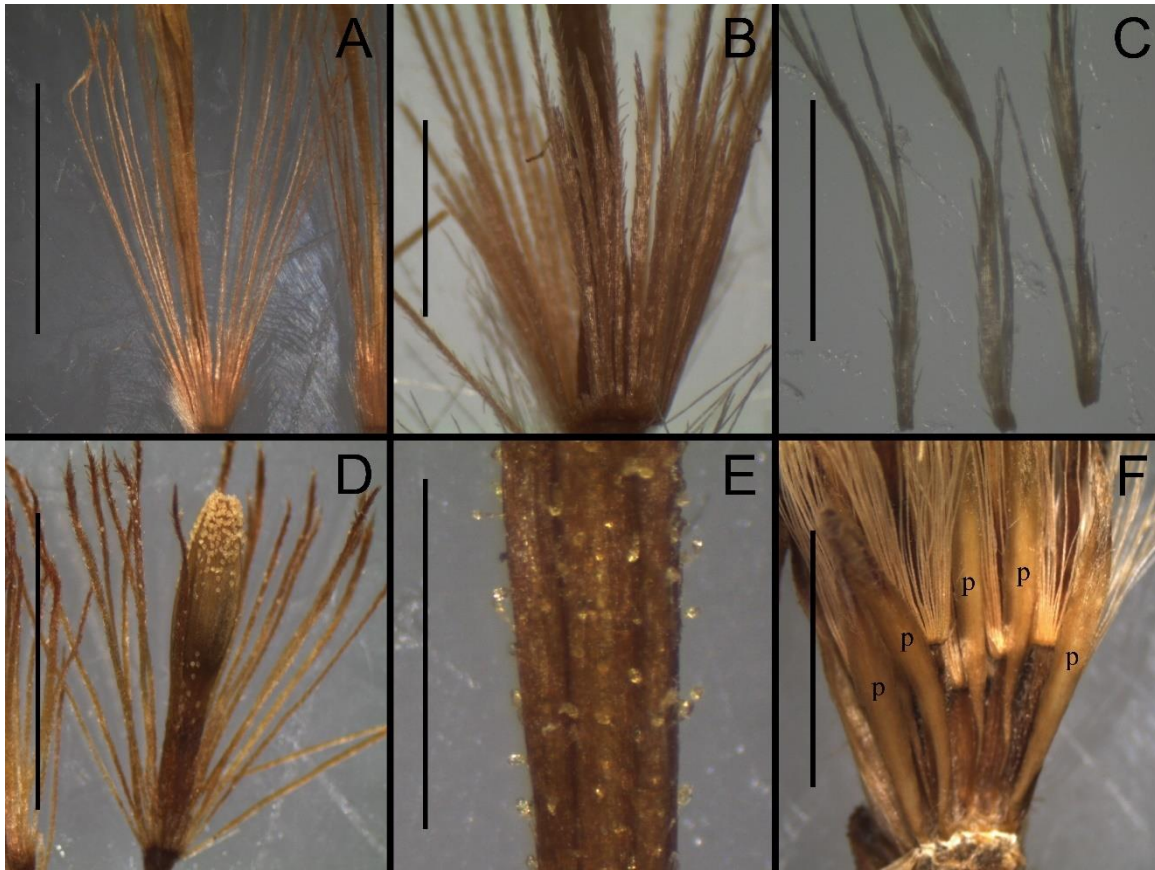


Figure 6. A–C, Bristles of two markedly lengths forming pappus in *S.* sect. *Pachystegia*; D, Typical pappus formed by bristles of subequal lengths in *Shawia* (except by *S.* sect. *Pachystegia*); E, Glandular trichomes on the cypselae surface of *S.* sect. *Adenolaria*; F, Receptacle paleae (p) in *S. allomii* (*S.* sect. *Adenolaria*). (A–B: *S. rufescens* [CHR 604522]; C: *S. insignis* [OTA PS-2632]; D: *S. mooneyi* [NWS 410643]; E: *S. pachyphylla* [NSW 833830]; F: *S. allomii* [CHR 503904]). Scale bars: 5 mm (A, D, F) and 1 mm (B, C, E). Photographs by P. Saldivia.

Comments: *Pachystegia* (sect. *Pachystegia* in this study) was segregated from *Olearia* (sensu Bentham & Hooker, 1873) based on two characters: “the great ovoid involucre with its multitudinous bracts [several phyllaries rows], and the uniseriate pappus, with its clubbed equal hairs” (Cheeseman 1925). However, this diagnosis has some issues. Firstly, the “great ovoid involucre” is not such in *Shawia minor* ($\equiv$ *Pachystegia minor*), in which the involucre is reduced and reaches the size of other *Shawia* species such as *Shawia pannosa* ($\equiv$ *Olearia pannosa*, sect. *Australiaster*). Secondly, the “multitudinous bracts” (phyllary rows) in sect. *Pachystegia* vary from 9–12, but *Shawia pachyphylla* (sect. *Adenolaria*) reaches 13 phyllary rows. Thirdly and most importantly, Cheeseman’s interpretation of the pappus, following Hooker (1889), is erroneous. Sect. *Pachystegia*, unlike all other *Shawia* species, has two markedly different kinds of bristles (Fig. 6A–C): a longer set 8–12 mm long and a shorter set 2–3 mm long, unlike the rest of the species in which the pappus is made up of bristles of subequal length (Fig. 6D). Unfortunately, the dimorphic bristle character has been overlooked, even though it is probably the best character for distinguishing sect. *Pachystegia* from the rest of *Shawia*.

Until recently, three taxa had been formally described and accepted in sect. *Pachystegia* (as genus, Schönberger et al. 2021). *Shawia insignis* ($\equiv$ *Pachystegia insignis*) is widely distributed across the Marlborough area of the South Island of New Zealand, and *S. minor* ($\equiv$ *P. minor*) and *S. rufescens* ($\equiv$ *P. rufa*) have smaller localized distributions surrounded by *S. insignis*. Hybrid specimens have been documented between *S. insignis* and the other two in the overlapping distributional areas (Heenan & Molloy 2022). Additionally, several tag names have also been proposed (Molloy & Simpson 1980). Still, morphological boundaries among them and with some accepted taxa are indistinct and based solely on continuous characters (e.g., length, size). In a

recent morphological work, Heenan & Molloy (2022) validated one of those tag names as a new species, *Pachystegia hesperia* Heenan & Molloy; however, all characters provided in the diagnosis, along with others used in their taxonomic key, overlap with those of *S. minor*. For instance, the leaf's general shape of *S. minor* was described as “rhomboid, rhomboid-elliptic, obovate to elliptic-obovate” vs. “usually obovate to elliptic-oblong, sometimes broadly elliptic but not rhomboid” for *P. hesperia*, but only two out of eleven of the specimens shown by Heenan & Molloy (2022: Fig. 4D,E) are slightly rhomboid in the shape variation of *S. minor*. Additionally, there is no difference in leaf shape between some examples of *S. minor* and *P. hesperia* (Heenan & Molloy 2022: Fig. 4H,I vs. Fig. 6). Floret amount is described as 90–200 in *S. minor* vs. 130–300 in *P. hesperia*, so there is overlap from 130–200. Heenan & Molloy (2022) described the peduncle length in *S. minor* up to 330 mm but no indication of the lower limit was given; however, the protologue in Cheeseman (1916) gave a total length of 76–130 mm. Therefore, the range of 76–330 mm of *S. minor* overlaps almost entirely with the 75–150 mm range described for *P. hesperia*. The adaxial surface of the leaves is described as “smooth with primary veins visible but secondary veins obscure” for *S. minor* vs. “usually reticulate with distinctive primary and secondary veins” in *P. hesperia*, but the secondary veins are obscured in two of the three *P. hesperia* leaf examples given by Heenan & Molloy (2022: Fig. 6C).

In sum, sect. *Pachystegia* is a well-supported section based on both molecular and morphological evidence; however, its internal classification needs to be evaluated statistically in both contexts. We are providing new combinations only for the three traditionally accepted species. As shown above, at least the most recently described species, *P. hesperia*, needs a more critical reevaluation.

SHAWIA INSIGNIS (Hook. f.) Saldivia & Nicol, **comb. nov.** *Olearia insignis* Hook. f., Bot. Antarct. Voy. II. (Fl. Nov.–Zel.). 2: 331. 1855. *Aster insignis* (Hook. f.) F. Muell., Fragm. (Mueller) 5(35): 86. 1865. *Pachystegia insignis* (Hook. f.) Cheeseman, Man. New Zealand Fl., ed. 2: 910. 1925.

Olearia marginata Colenso, Trans. & Proc. New Zealand Inst. 15: 321. 1883. *Aster neozelandicus* Kuntze, Revis. Gen. Pl. 1: 316. 1891, non *A. marginatus* Kunth, Nov. Gen. Sp. 4 (15): 71. 1818.

SHAWIA MINOR (Cheeseman) Saldivia & Nicol, **comb. nov.** *Olearia insignis* var. *minor* Cheeseman, Trans. & Proc. New Zealand Inst. 48: 210–211: 1915 [publ. in 1916]. *Pachystegia insignis* var. *minor* (Cheeseman) Cheeseman, Man. New Zealand Fl.: 911. 1925. *Pachystegia minor* (Cheeseman) Molloy, New Zealand J. Bot. 25: 144. 1987.

SHAWIA RUFESCENS Saldivia & Nicol, **nom. nov.** *Pachystegia rufa* Molloy, New Zealand J. Bot. 25: 144–145. 1987.

Comment: The name *Shawia rufa* (J. Kost.) Saldivia & Nicol has been used for *Olearia rufa* J. Kost. (see above in sect. *Kosteria*).

V. SHAWIA sect. **ADENOLEARIA** Saldivia & Nicol, **sect. nov.** **TYPE: SHAWIA FURFURACEA** (A. Rich.) Raoul.

Diagnostic character states defining section *Adenolaria* are the presence of glandular trichomes on the cypselae surface (Fig. 6E) along with the non-divaricate architecture (see section *Cardiostigma*) and the indumentum of the leaves made of T- or Y-shaped trichomes.

Small trees or shrubs; phyllotaxis alternate or subopposite; leaves petiolate, non-resinous, coriaceous, elliptic-ovate, ovate, oblong-ovate, elliptic-oblong to oblong-obovate, 2.5–13 cm long, margin untoothed to sinuate-dentate, blade plane to undulate, or slightly recurved; capitulescences corymbose-like; involucre cylindrical, turbinate, or campanulate at anthesis; phyllaries arranged in 2–13 rows with the inner phyllaries longer than the outer ones, non-resinous or with scattered non-stalked glandular trichomes; ray florets pistillate, ligulate, 2–11

arranged in 1 row; disc florets perfect, 3–12; cypselae fusiform-cylindric, (5–)6–12-ribbed, covered with twin and glandular trichomes.

Diversity, distribution, and ecology: Sect. *Adenolaria* includes three species endemic to the North Island of New Zealand. These species inhabit riparian and coastal banks, coastal scrub, ridges, scoria, broken rock outcrops, boulder fields, cliff-faces, exposed and covered shrub-lands and forests, and both mature and regenerating forests. (Nicol & Saldivia 2025).

Etymology: *Adeno-* (meaning “gland” in Greek) refers to the presence of glandular trichomes on the cypselae surface, and *Olearia* from which *Shawia* is reinstated and segregated.

Comments: Sect. *Adenolaria* (as the *Olearia furfuracea* complex) has been recently reviewed by Nicol & Saldivia (2025) who reduced the number of species from five to three. Two features that are unusual in Celmisiinae are expressed in sect. *Adenolaria*. One is that all three species present both axillary (as in the rest of Celmisiinae) and terminal flowering, and the second is that *S. allomii* develops (often poorly) receptacle paleae (Fig. 6F). Both features strengthen the hypothesis of the sister relationship between Celmisiinae and Chilotrichinae (Bonifacino & Funk 2012; Nicol et al. 2024; Zuntini et al. 2024), as both features are characteristics of the latter.

SHAWIA ALLOMII (Kirk) Nicol & Saldivia, Phytotaxa 687: 260. 2025 $\equiv$ *Olearia allomii* Kirk in Trans. Proc. New Zealand Inst. 3: 179. 1870 [publ. in 1871].

Distribution: New Zealand: Great Barrier Island, offshore North Island.

SHAWIA FURFURACEA (A. Rich.) Raoul, Choix Pl. Nouv.–Zél.: 45. 1846. *Aster furfuraceus* A. Rich., Essai Fl. Nouv.–Zél.: 246. 1832. *Eurybia furfuracea* (A. Rich.) DC., Prodr. [A.P. de Candolle] 5: 267. 1836. *Haxtonia furfuracea* (A. Rich.) A. Cunn., Ann. Nat. Hist. 2: 127. 1839. *Olearia furfuracea* Hook. f. in Handb. New Zealand Fl.: 125. 1864.

Olearia furfuracea var. *rubicunda* Kirk, Stud. Fl. New Zealand: 267. 1899.

Olearia furfuracea var. *angustata* Kirk, Stud. Fl. New Zealand: 268. 1899.

Olearia furfuracea subvar. *dubia* Kirk, Stud. Fl. New Zealand: 268. 1899.

Olearia townsonii Cheeseman, Man. New Zealand Fl., ed. 2: 917. 1925.

Olearia thomsonii Cheeseman, Man. New Zealand Fl., ed. 2: 918. 1925.

Distribution: New Zealand: quite widespread, especially towards the north of the North Island.

SHAWIA PACHYPHYLLA (Cheeseman) Nicol & Saldivia, Phytotaxa 687: 261. 2025. *Olearia pachyphylla* Cheeseman in Trans. New Zealand Inst. 42: 216. 1909 [publ. in 1910].

Distribution: New Zealand: North Island, Northeast Coromandel Peninsula; Bay of Plenty, Opape.

VI. SHAWIA sect. **NEOZELANDICA** (DC.) Saldivia & Nicol, **sect. nov.** **TYPE:** **SHAWIA ARBORESCENS** (G. Forst.) Raoul.

Small trees or shrubs, brachyblasts developed rarely (only in *Shawia quinquevulnera* $\equiv$ *Olearia quinquevulnera*); phyllotaxis alternate; leaves petiolate or occasionally pseudopetiolate, non-resinous or with glandular trichomes, elliptic, elliptic-oblong, elliptic-orbicular, obovate, obovate/orbicular, linear, or linear-ovate, 0.3–29 cm long, margin dentate or untoothed, blade plane, undulate or revolute; adaxial surface glabrescent or glabrous, abaxial surface covered with a layer of indumentum made of non-glandular T-shaped trichomes and occasionally scattered glandular non-stalked trichomes; capitulescences corymbose-like or paniculate-like; involucre cylindrical at anthesis, phyllaries arranged in 3–8 rows with the inner phyllaries longer than the outer ones, non-resinous, glandular trichomes infrequent; ray florets pistillate, ligulate, 2–15

arranged in 1–3 rows; disc florets perfect, 2–11; cypselae fusiform-cylindric, 5–7-ribbed, covered with twin trichomes.

Diversity, distribution, and ecology: Section *Neozelandica* includes eight morphologically diverse and clear-cut species and five hybrids endemic to the three main islands of New Zealand (North, South, and Stewart Island/Rakiura). These taxa inhabit lowland, montane, and subalpine shrublands, forest, forest margins, forest clearings, ridge lines in cloud forest, cliff faces, rocky river gorges, valley heads, sites of periodic flooding, stream edges, river flats, stream banks and river banks, and wetlands (Dawson & Lucas 2011; NZPCN 2025). Records in subalpine locations reach around 1500 meters but most species are found at or below 1000 meters.

Etymology: The epithet refers to the endemism of the section to the three main islands of New Zealand.

Comment: Sect. *Neozelandica* is morphologically distinct from all other sections above (sects. *Shawia*, *Kosteria*, *Cardiostigma*, *Pachystegia*, and *Adenolaria*). However, morphological characters that could discriminate sect. *Neozelandica* from all species endemic to Australia remain undiscovered (sect. *Australiaster*). Although both sections form well-supported clades, these were never recovered as sisters in the phylogenomic analyses of Nicol et al. (2024); therefore, both clades are recognized as different sections.

SHAWIA ARBORESCENS (G. Forst.) Raoul, Choix Pl. Nouv.–Zél.: 45. 1846. *Solidago arborescens* G. Forst., Fl. Ins. Austr.: 56. 1786. *Steiractis arborescens* (G. Forst.) DC., Prodr. [A.P. de Candolle] 5: 345. 1836. *Olearia arborescens* (G. Forst.) Cockayne & Laing, Trans. New Zealand Inst. 43: 367. 1910 [publ. in 1911].

Eurybia alpina Lindl. & Paxton, Paxton's Fl. Gard. 2: 84. 1851, *hom. illeg.*, non *Eurybia alpina* Hook. f. in London J. Bot. 6: 106. 1847.

Eurybia nitida Hook. f., Bot. Antarct. Voy. II. (Fl. Nov.–Zél.). 1: 117. 1852, *nom. superfl.* *Olearia nitida* (Hook. f.) Hook. f., Handb. New Zealand Fl.: 125. 1864, *nom. superfl.*

Olearia populifolia Colenso, Trans. & Proc. New Zealand Inst. 17: 243. 1885. *Aster populifolius* (Colenso) Kuntze, Revis. Gen. Pl. 1: 315. 1891.

Olearia suborbiculata Colenso, Trans. & Proc. New Zealand Inst. 18: 263. 1885 [publ. in 1886]. *Aster suborbiculatus* (Colenso) Kuntze, Revis. Gen. Pl. 1: 315. 1891.

Olearia erythropappa Colenso, Trans. & Proc. New Zealand Inst. 22: 468. 1889 [publ. in 1890].

Olearia multiflora Colenso, Trans. & Proc. New Zealand Inst. 27: 387. 1894 [publ. in 1895].

Olearia arborescens var. *cordatifolia* Kirk, Stud. Fl. New Zealand: 268. 1899.

Distribution: New Zealand: North, South, and Stewart/Rakiura Islands.

SHAWIA CHEESEMANNII (Cockayne & Allan) Saldivia & Nicol, **comb. nov.** *Olearia cheesemanii* Cockayne & Allan, Trans. & Proc. N. Z. Inst. 57: 57–58. 1927. *Olearia nitida* var. *angustifolia* Cheeseman, Man. New Zealand Fl.: 285. 1906.

Distribution: New Zealand: North and South Islands.

SHAWIA CREBRA (E.K.Cameron & Heenan) Saldivia & Nicol, **comb. nov.** *Olearia crebra* E.K.Cameron & Heenan, New Zealand J. Bot. 40: 535–538. 2002.

Distribution: New Zealand: North Island.

SHAWIA CROSBYSMITHIANA (Petrie) Saldivia & Nicol, **comb. nov.** *Olearia crosbysmithiana* Petrie, Trans. New Zealand Inst. 43: 254. 1911.

Distribution: New Zealand: South Island.

SHAWIA ILICIFOLIA (Hook. f.) Saldivia & Nicol, **comb. nov.** *Olearia ilicifolia* Hook. f., Handb. New Zealand Fl.: 126. 1864. *Eurybia dentata* var. β . *linearifolia* Hook. f., Bot. Antarct. Voy. II. (Fl. Nov.–Zel.) Part I: 118. 1853.

Olearia multibracteolata Colenso, Trans. & Proc. New Zealand Inst. 17: 242. 1885. *Aster multibracteolatus* (Colenso) Kuntze, Revis. Gen. Pl. 1: 315. 1891.

Distribution: New Zealand: North, South, and Stewart/Rakiura Islands.

Comment: Regarding *Olearia dentata* Hook. f. (1864), *hom. illeg.* [non *Olearia dentata* Moench (1802)], Hooker (1853) described *Eurybia dentata* and two varieties: α . *oblongifolia* and β . *linearifolia*. He cited types for α . and β ., but not specifically for *E. dentata*. Later, for the name *Olearia dentata*, Hooker (1864) gave *Eurybia dentata* α . in synonymy. For the name *Olearia ilicifolia*, Hooker (1864) based it on *Eurybia dentata* β . Both later taxonomic decisions support the contention that Hooker did not intend "*oblongifolia*" and "*linearifolia*" as part of the formal nomenclature. The nomenclatural problem with *O. dentata* sensu Hooker (1864) was pointed out by Baker (1884) who proposed the name *O. macrodonta* Baker, which is currently considered a hybrid (see below).

SHAWIA LACUNOSA (Hook. f.) Saldivia & Nicol, **comb. nov.** *Olearia lacunosa* Hook. f., Handb. New Zealand Fl.: 732. 1867. *Aster lacunosus* (Hook. f.) Kuntze, Revis. Gen. Pl. 1: 315. 1891.

Olearia alpina Buchanan, Trans. & Proc. New Zealand Inst. 19: 215. 1887 non *Olearia alpina* (Hook. f.) W.M. Curtis, Stud. Fl. Tasman. 2: 304, 463. 1963. *hom. illeg.*

Distribution: New Zealand: North and South Islands.

SHAWIA QUINQUEVULNERA (Heenan) Saldivia & Nicol, **comb. nov.** *Olearia quinquevulnera* Heenan, New Zealand J. Bot. 43(3): 757–760. 2005.

Distribution: New Zealand: North and South Islands.

SHAWIA RANI (A.Cunn.) Saldivia & Nicol, **comb. nov.** *Brachyglottis rani* A.Cunn., Ann. Nat. Hist. 2: 132. 1839. *Olearia rani* (A.Cunn.) Druce, Rep. Bot. Soc. Exch. Club Brit. Isles 4(Suppl. 2): 638. 1917.

Eurybia cunninghamii Hook. f., Bot. Antarct. Voy. II. (Fl. Nov.–Zel.) Part I: 117, t. 30. 1853, *nom. superfl.* *Shawia cunninghamii* (Hook. f.) Sch.Bip., Jahresber. Pollichia 18–19: 175. 1861, *nom. superfl.* *Olearia cunninghamii* (Hook. f.) Hook. f., Handb. New Zealand Fl.: 126. 1864, *nom. superfl.*

Olearia colorata Colenso, Trans. & Proc. New Zealand Inst. 12: 362. 1880. *Olearia cunninghamii* var. *colorata* (Colenso) Kirk, Stud. Fl. New Zealand: 269. 1899.

Olearia cunninghamii var. *miniata* Kirk, Stud. Fl. New Zealand: 270. 1899.

Distribution: New Zealand: North and South Islands.

Comment: Allan (1961: 669) did not accept infraspecific taxa within *Shawia rani* (as *Olearia rani*) and mentioned: “A somewhat polymorphic sp., the status of the different forms [not in the taxonomic meaning] not well understood”. Schönberger et al. (2021) accepted both of Kirk’s varieties (*colorata* and *miniata* [as *minuta*, following the misspelling by Allan 1961]). We follow Allan’s (1961) criterion because no taxonomic work validating these varieties has been done since.

SHAWIA × CAPILLARIS (Buchanan) Saldivia & Nicol, **comb. nov.** *Olearia* × *capillaris* Buchanan, Trans. Proc. New Zealand Inst. 3: 212. 1870 [publ. in 1871]. *Olearia nitida*

var. *capillaris* (Buchanan) Kirk, Stud. Fl.: 268. 1899. (= *Shawia quinquevulnera* × *S. arborescens*).

Distribution: New Zealand: South Island.

SHAWIA × **EXCORTICATA** (Buchanan) Saldivia & Nicol, **comb. nov.** *Olearia* × *excorticata* Buchanan, Trans. Proc. New Zealand Inst. 6: 241. 1873 [publ. in 1874]. *Aster* × *excorticatus* (Buchanan) Kuntze, Revis. Gen. Pl. 1: 315. 1891. (= *Shawia lacunosa* × *S. arborescens*).

Distribution: New Zealand: North Island.

SHAWIA × **MACRODONTA** (Baker) Saldivia & Nicol, **comb. nov.** *Olearia* × *macrodonta* Baker, Gard. Chron. n.s., 21(541): 604. 1884. *Eurybia dentata* var. *a. oblongifolia* Hook. f., Bot. Antarct. Voy. II. (Fl. Nov.–Zel.) Part I: 118. 1853. *Olearia* × *dentata* Hook. f., Handb. New Zealand Fl.: 126. 1864, *hom. illeg.* *Shawia* × *dentata* (Hook. f.) Sch.Bip., Jahresber. Pollichia 18-19: 175. 1861, *nom. illeg.* (= *Shawia ilicifolia* × *S. arborescens*).

Distribution: New Zealand: North and South Islands.

SHAWIA × **MOLLIS** (Kirk) Saldivia & Nicol, **comb. nov.** *Olearia ilicifolia* var. *mollis* Kirk, Stud. Fl. New Zealand: 269. 1899. *Olearia* × *mollis* (Kirk) Cockayne, Trans. Proc. New Zealand Inst. 43: 173. 1910 [publ. in 1911]. (= *Shawia ilicifolia* × *S. lacunosa*).

Distribution: New Zealand: South Island.

SHAWIA × **SUAVIS** (Cheeseman) Saldivia & Nicol, **comb. nov.** *Olearia* × *suavis* Cheeseman, Trans. Proc. New Zealand Inst. 24: 409. 1891 [publ. in 1892]. (= *Shawia lacunosa* × *S. quinquevulnera*).

Distribution: New Zealand: South Island.

VII. SHAWIA sect. **AUSTRALIASTER** Saldivia & Nicol, **sect. nov.** **TYPE: SHAWIA MYRSINOIDES** (Labill.) Sch.Bip.

Small trees or shrubs; phyllotaxis alternate or opposite; leaves petiolate or occasionally sessile, elliptic, elliptic-oblong, elliptic-ovate, linear, linear-elliptic, oblong, obovate, or ovate, 0.4–15 cm long, margin dentate or untoothed, blade plane or revolute; adaxial surface glabrous, resinous or non-resinous, with or without glandular trichomes, abaxial surface covered with a layer of indumentum made of non-glandular T-shaped trichomes and with scattered glandular non-stalked trichomes in most of the species; capitulescences corymbose-like or capitula solitary; involucre cylindrical or campanulate at anthesis; phyllaries arranged in 3–7 rows with the inner phyllaries longer than the outer ones, mostly non-resinous; ray florets pistillate (occasionally some florets present staminodes), ligulate (with a very short limb in *Shawia aglossa* ≡ *Olearia aglossa*), 1–25 arranged in 1–3 rows; disc florets perfect, 2–ca. 100; cypselae fusiform-cylindric, 5–11-ribbed, covered with twin trichomes in most of the species and occasionally with scattered T-shape trichomes.

Diversity, distribution, and ecology: Sect. *Australiaster* includes 24 morphologically diverse and mostly clear-cut species and one subspecies endemic to south and east mainland Australia, Tasmania, and Lord Howe Island. These species are found in wet and dry sclerophyll forest, in lowland and mountainous scrub and forest, in woodland, at rainforest margins, on stony hillsides, rocky sites, in sandy soil, arid mountains, open grassland, alpine sedgeland, and in a range of heath communities including bolster, deciduous, coniferous, and alpine.

Etymology: The epithet refers to the Australian endemicity of the section and to *Aster*, the genus under which many species were originally described.

SHAWIA AGLOSSA (Maiden & Betche) Saldivia & Nicol, **comb. nov.** *Olearia alpicola* var. *aglossa* Maiden & Betche, Proc. Linn. Soc. New South Wales 24: 147. 1899. *Olearia aglossa* (Maiden & Betche) Lander, Telopea 4(2): 146. 1991.

Distribution: Australia: New South Wales and Victoria.

SHAWIA ALPICOLA (F. Muell.) Saldivia & Nicol, **comb. nov.** *Eurybia alpicola* F. Muell., Papers and Proc. Roy. Soc. of Van Diemen's Land 3: 229–230. 1860. *Aster alpicola* (F. Muell.) F. Muell., Fragm. (Mueller) 5(34): 70. 1865. *Olearia alpicola* (F. Muell.) Benth. in Fl. Austral. 3: 468. 1867.

Distribution: Australia: New South Wales and Victoria.

SHAWIA ALPINA (Hook. f.) Sch.Bip., Jahresber. Pollichia 18–19: 174. 1861. *Eurybia alpina* Hook. f., London J. Bot. 6: 106. 1847. *Olearia persoonioides* var. *alpina* (Hook. f.) Benth., Fl. Austral. 3: 471. 1867. *Olearia tasmanica* W.M. Curtis, Vict. Naturalist 87: 251. 1970.

Distribution: Australia: Tasmania.

Comment: Curtis (1970) proposed the replacement name *Olearia tasmanica* when transferring *Eurybia alpina* to *Olearia*, because the combination in *Olearia* was already taken (*Olearia alpina* Buchanan = *Shawia lacunosa* (Hook. f.) Saldivia & Nicol).

SHAWIA ARCHERI (Lander) Saldivia & Nicol, **comb. nov.** *Olearia archeri* Lander, Muelleria 7: 117. 1989.

Distribution: Australia: Tasmania.

SHAWIA ARGOPHYLLA (Labill.) Sch.Bip., Jahresber. Pollichia 18–19: 173. 1861. *Aster argophyllus* Labill., Nov. Holl. Pl. 2: 52, t. 201. 1806. *Eurybia argophylla* (Labill.) Cass., Dict. Sci. Nat., ed. 2. [F. Cuvier] 37: 487. 1825. *Haxtonia argophylla* (Labill.) D. Don, Edinburgh New Philos. J. 1831: 272. 1831. *Olearia argophylla* (Labill.) Benth., Fl. Austral. 3: 470. 1867.

Distribution: Australia: New South Wales, Victoria, and Tasmania.

SHAWIA CHRYSOPHYLLA (DC.) Sch.Bip., Jahresber. Pollichia 18–19: 173. 1861. *Eurybia chrysophylla* DC., Prodr. [A.P. de Candolle] 5: 266. 1836. *Olearia chrysophylla* (DC.) Benth., Fl. Austral. 3: 468. 1867.

Distribution: Australia: New South Wales.

SHAWIA COVENYI (Lander) Saldivia & Nicol, **comb. nov.** *Olearia covenyi* Lander, Telopea 4: 152. 1991.

Distribution: Australia: New South Wales.

SHAWIA CYDONIIFOLIA (DC.) Sch.Bip., Jahresber. Pollichia 18–19: 173. 1861. *Eurybia cydoniifolia* DC., Prodr. [A.P. de Candolle] 5: 267. 1836. *Olearia cydoniifolia* (DC.) Benth., Fl. Austral. 3: 470. 1867.

Olearia argophylla var. *grandiflora* C.T. White, Proc. Roy. Soc. Queensland 47: 66. 1936.

Distribution: Australia: New South Wales and Queensland.

SHAWIA ERUBESCENS (Sieber ex Spreng.) Sch.Bip., Jahresber. Pollichia 18–19: 173. 1861. *Aster erubescens* Sieber ex Spreng., Syst. Veg. 16(3): 525. 1826. *Eurybia erubescens* (Sieber ex Spreng.) Sieber ex DC., Prodr. [A.P. de Candolle] 5: 267–268. 1836. *Olearia*

myrsinoides var. *erubescens* (Sieber ex Spreng.) Benth., Fl. Austral. 3: 471. 1867.
Olearia erubescens (Sieber ex Spreng.) Dippel, Handb. Laubholz. 1: 290. 1889.

Eurybia erubescens var. *ilicifolia* DC., Prodr. [A.P. de Candolle] 5: 268. 1836. *Shawia erubescens* var. *ilicifolia* (DC.) Sch.Bip., Jahresber. Pollichia 18–19: 173. 1861.

Eurybia myrsinoides var. *serrata* DC., Prodr. [A.P. de Candolle] 5: 268. 1836. *Olearia myrsinoides* var. *serrata* (DC.) Benth., Fl. Austral. 3: 471. 1867.

Distribution: Australia: New South Wales, South Australia, Victoria, and Tasmania.

SHAWIA GRANDIFLORA (Hook.) Saldivia & Nicol, **comb. nov.** *Olearia grandiflora* Hook., Icon. Pl. 9: t. 862. 1851. *Steetzia grandiflora* (Hook.) Sond., Linnaea 25(4): 452. 1853. *Aster sonderi* F.Muell., Fragm. 5: 83. 1865.

Distribution: Australia: South Australia.

SHAWIA LEDIFOLIA (DC.) Sch.Bip., Jahresber. Pollichia 18–19: 173. 1861. *Eurybia ledifolia* DC., Prodr. [A.P. de Candolle] 5: 269. 1836. *Olearia ledifolia* (DC.) Benth., Fl. Austral. 3: 472. 1867.

Distribution: Australia: Tasmania.

SHAWIA MEGALOPHYLLA (F. Muell.) Saldivia & Nicol, **comb. nov.** *Eurybia megalophylla* F. Muell., Proc. Roy. Soc. Tasm. 3: 228–229. 1859. *Aster megalophyllus* (F. Muell.) F. Muell., Fragm. (Mueller) 5: 70. 1865. *Olearia megalophylla* (F. Muell.) Benth., Fl. Austral. 3: 467–468. 1867.

Distribution: Australia: New South Wales and Victoria.

SHAWIA MOONEYI (F.Muell.) Saldivia & Nicol, **comb. nov.** *Aster mooneyi* F. Muell., Fragm. (Mueller) 8(65): 144. 1874. *Olearia mooneyi* (F. Muell.) Hemsl., Annals of Botany (London) 10: 239. 1896.

Distribution: Australia: Lord Howe Island.

SHAWIA MYRSINOIDES (Labill.) Sch.Bip., Jahresber. Pollichia 18–19: 173. 1861. *Aster myrsinoides* Labill., Nov. Holl. Pl. 2: 53, t. 202. 1806. *Eurybia myrsinoides* (Labill.) Nees, Gen. Sp. Aster: 146. 1832. *Olearia myrsinoides* (Labill.) Benth., Fl. Austral. 3: 470–471. 1867.

Distribution: Australia: New South Wales, Victoria, and Tasmania.

SHAWIA OBCORDATA (Hook. f.) Sch.Bip., Jahresber. Pollichia 18–19: 175. 1861. *Eurybia obcordata* Hook. f., London J. Bot. 6: 108. 1847. *Aster obcordatus* (Hook. f.) F. Muell., Fragm. (Mueller) 5: 69. 1865. *Olearia obcordata* (Hook. f.) Benth., Fl. Austral. 3: 471. 1867.

Distribution: Australia: Tasmania.

SHAWIA OLIGANTHEMA (F. Muell. ex Benth.) Saldivia & Nicol, **comb. nov.** *Olearia oliganthema* F. Muell. ex Benth., Fl. Austral. 3: 469–470. 1867. *Aster oliganthemus* (F. Muell. ex Benth.) F.Muell., Syst. Census Austral. Pl. 1: 78. 1882.

Distribution: Australia: New South Wales.

Comment: Presumed Extinct, last confirmed collection was in 1866 in the Blue Mtns. (NSW Flora Online, 2025).

SHAWIA OPPOSITIFOLIA (F.Muell.) Saldivia & Nicol, **comb. nov.** *Eurybia oppositifolia* F. Muell., *Fragm.* (Mueller) 2(13): 88–89. 1860. *Aster oppositifolius* (F. Muell.) F. Muell., *Fragm.* 5: 71. 1865. *Olearia oppositifolia* (F. Muell.) Lander, *Telopea* 4: 161. 1991.

Distribution: Australia: Queensland and New South Wales.

SHAWIA PANNOSA (Hook.) Saldivia & Nicol [subsp. *pannosa*], **comb. nov.** *Olearia pannosa* Hook., *Icon. Pl.* 9: sub t. 862. 1851. *Steetzia pannosa* (Hook) Sond., *Linnaea* 25: 451. 1853. *Aster pannosus* F. Muell., *Fragm.* (Mueller) 5(35): 83. 1865.

Distribution: Australia: South Australia.

SHAWIA PANNOSA subsp. **CARDIOPHYLLA** (F. Muell.) Saldivia & Nicol, **comb. nov.** *Eurybia cardiophylla* F. Muell., *Linnaea* 25: 398. 1853. *Olearia pannosa* subsp. *cardiophylla* (F. Muell.) D.A.Cooke, *Fl. S. Australia* 3: 1483. 1986.

Steetzia muelleri Sond., *Linnaea* 25: 453. 1853.

Steetzia ovata Sond., *Linnaea* 25: 452. 1853.

Distribution: Australia: New South Wales and South Australia.

SHAWIA PERSONIOIDES (DC.) Sch.Bip., *Jahresber. Pollichia* 18–19: 173. 1861. *Eurybia persoonioides* DC., *Prodr.* [A.P. de Candolle] 5: 267. 1836. *Aster persoonioides* (DC.) F. Muell., *Fragm.* (Mueller) 5: 69. 1865. *Olearia persoonioides* (DC.) Benth., *Fl. Austral.* 3: 471. 1867.

Eurybia persoonioides var. *lanceolata* Hook. f., *London J. Bot.* 6: 106. 1847.

Olearia persoonioides var. *lanceolata* Benth., *Fl. Austral.* 3: 471. 1867. *Olearia lanceolata* (Benth.) D.I. Morris, *Rec. Queen Victoria Mus. (Tasmania)* 55: 1. 1977.

Distribution: Australia: Tasmania.

SHAWIA PINIFOLIA (Hook. f.) Sch.Bip., *Jahresber. Pollichia* 18–19: 175. 1861. *Eurybia pinifolia* Hook. f., *London J. Bot.* 6: 108. 1847. *Olearia pinifolia* (Hook. f.) Benth., *Fl. Austral.* 3: 471. 1867.

Distribution: Australia: Tasmania.

SHAWIA ROSMARINIFOLIA (DC.) Sch.Bip., *Jahresber. Pollichia* 18–19: 173. 1861. *Eurybia rosmarinifolia* DC., *Prodr.* [A.P. de Candolle] 5: 268. 1836. *Olearia rosmarinifolia* (DC.) Benth., *Fl. Austral.* 3: 468. 1867.

Distribution: Australia: New South Wales and Queensland.

SHAWIA SPECIOSA (Hutch.) Saldivia & Nicol, **comb. nov.** *Olearia speciosa* Hutch., *Bot. Mag.* 133: t. 8118. 1907.

Distribution: Australia: Victoria.

SHAWIA STILWELLIAE (Blakely) Saldivia & Nicol, **comb. nov.** *Olearia stilwelliae* Blakely, *Proc. Linn. Soc. New South Wales* 50(203): 385–386. 1925.

Distribution: Australia: New South Wales.

SHAWIA VISCOSA (Labill.) Sch.Bip., *Jahresber. Pollichia* 18–19: 173. 1861. *Aster viscosus* Labill., *Nov. Holl. Pl.* 2 (20–21): 53, t. 203. 1806. *Eurybia viscosa* (Labill.) Cass., *Dict. Sci. Nat.*, ed. 2. [F. Cuvier] 16: 48. 1820. *Haxtonia viscosa* (Labill.) D. Don, *Edinburgh New Philos. J.* 1831: 272. 1831. *Olearia viscosa* (Labill.) Benth., *Fl. Austral.* 3: 468–469. 1867.

Olearia buchananii Kirk, Fl. New Zealand: 267. 1899.

Distribution: Australia: Victoria and Tasmania. There is one historical gathering from New Zealand upon which *O. buchananii* was described. See further details in Gardner et al. (2001).

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Supplementary Information

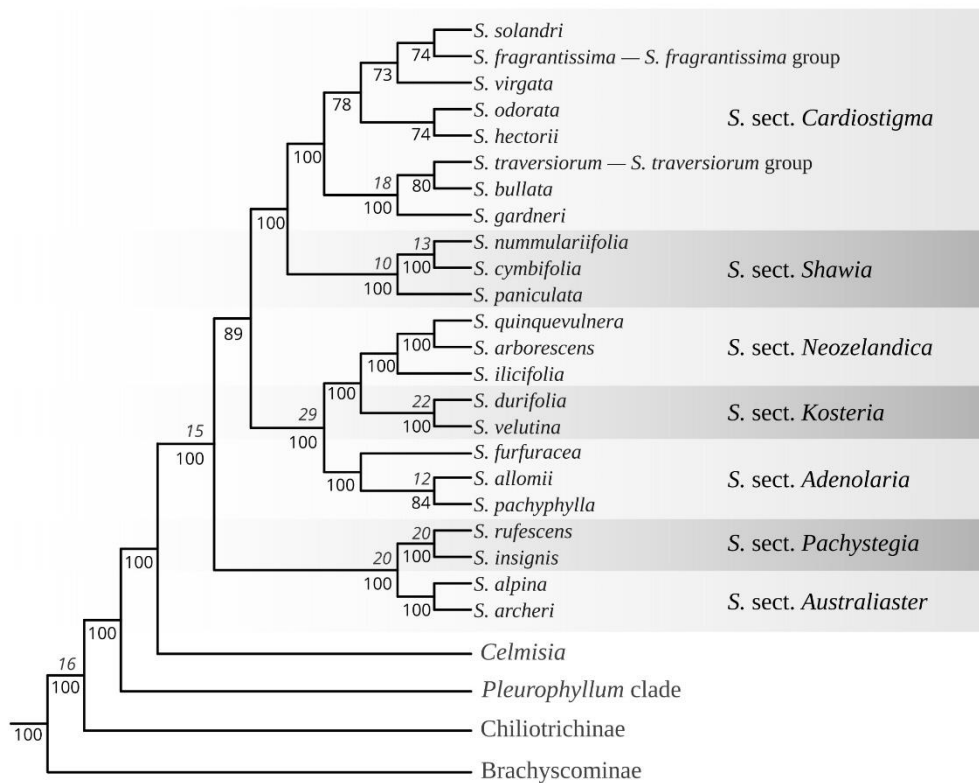


Figure S1. Simplified reconstructed phylogeny of Celmisiinae based on a filtered selection of 304 concatenated exon gene-families, estimated with IQ-TREE v2; maximum likelihood bootstrap support values shown below and behind nodes; gene concordance values 10 or greater shown above and behind in italics. Alternate shading for distinguishing easily between sections. *Shawia* sect. *Cardistigma* includes three groups (see text): *S. fragrantissima* group, *S. traversiorum* group, and the remaining tips all belong to *S. virgata* group. Modified from Nicol et al. (2024: Fig. 4).