Revision of subgeneric classification in *Astelia* Banks & Sol. ex R.Br. (Asteliaceae)

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Abstract

Systematic investigations and phylogenetic analyses (Birch 2011, Birch et al. 2012) have indicated that *Astelia*, as currently circumscribed (Skottsberg 1934), is paraphyletic, with *Collospermum* nested within it. Further, subgenus *Astelia* is polyphyletic, and subgenera *Asteliopsis* and *Tricella* are paraphyletic, as currently circumscribed (Skottsberg 1934). Revision of the subgeneric classification of *Astelia* is warranted to ensure classification accurately reflects the evolutionary history of these taxa. *Collospermum* is relegated to synonymy within *Astelia*. *Astelia* is dioecious or polygamodioecious, with a superior ovary, anthers dorsifixed or basifixed, pistillodes or pistils that have a single short or poorly defined style, a 3 lobed stigma, and fleshy unilocular or trilocular fruit with funicular hairs that are poorly to well developed. Subgenus *Collospermum* Birch is described. A key to *Astelia* sections is provided. Required nomenclatural revisions are presented including resurrection of *A. hastata* Colenso, *A. montana* Seem., and *A. microsperma* Colenso pro parte and the new combination *A. samōense* (Skottsb.) Birch comb. nov. is made.

Keywords: Asparagales; Asteliaceae; Austral; Australia, dioecy, New Zealand, Pacific
**Introduction**

*Astelia* Banks & Sol. ex R.Br. is the largest genus in Asteliaceae Dumort. containing twenty-six species and four subspecies with a Austral-Pacific distribution. *Astelia* species exhibit a range of growth forms including low, cushion-forming and tall, clustered habits. *Astelia* species grow in a diverse range of habitats including coastal, lowland wetlands, tropical and temperate lowland forests, tropical montane cloud forests, sub-alpine heath, alpine fellfields and grasslands, and bog habitats. Many *Astelia* species are facultatively epiphytic and three species are primarily epiphytic. *Collospermum* Skotts. includes four species that occur in lowland forests and in lowland and tropical montane cloud forests in New Zealand, the Independent State of Samoa and the Republics of Fiji and Vanuatu. All species exhibit a tall, clustered habit and are primarily epiphytic, although plants that fall to the ground can persist for long periods.

*Astelia* and *Collospermum* share many morphological characters (Bayer et al. 1998, Rudall et al. 1998). All Asteliaceae genera have branched hairs that are otherwise uncommon in the Liliaceae (Bayer et al. 1998) and those of *Astelia* and *Collospermum* are dense, at least in the young leaves of most species. The tomenta of *Astelia* and *Collospermum* consist of a multi-celled stalk, frayed unicellular filaments that form a basal wool adjacent to the stalk, and linear or ovate scales that are a single cell thick (McCarthy 1928, Skottsberg 1934, L. B. Moore 1980, Rudall et al. 1998). In *Astelia* the scales are linear, may be short or long, and the stalk is attached at the base of the scale. In *Collospermum*, the scales are ovate, short, and the stalk is peltate. Scales may be present on the adaxial and/or abaxial leaf surfaces, inflorescences, and flowers. On the leaves of *Astelia* species the scales may become fused to form a membranous pellicle over the leaf epidermis. *Astelia* and *Collospermum* have superior ovaries that are uni- or trilocular and trilocular, respectively. Published chromosome numbers for *Astelia* taxa range from 2n=60 to 2n=210 (Wheeler 1966, Dawson and Beuzenberg 2000, de Lange et al. 2004). Darlington and Wylie (1955) proposed a basic chromosome number for *Astelia* of n=8, but Wheeler (1966) considered the basic chromosome number to be n=5, 7, or 35. *Collospermum hastatum* and *C. microspermum* are the only *Collospermum* taxa for which chromosome numbers are known and both have a chromosome number of n=35.

Skottsberg (1934) segregated *Collospermum* from *Astelia* based on the presence of simple lateral racemes, dimorphism of staminate and pistillate plants, basifixed anthers, long style papillae, and mucilaginous seed hairs of the former, which differ from the predominantly paniculate lateral racemes, versatile anthers, and poorly developed mucilaginous seed hairs of the latter (Birch 2011, Birch et al. 2012). However, morphological (Bayer et al. 1998, Birch 2011), cytological (Wheeler 1966, Moore 1980), and molecular (Birch 2011, Birch et al. 2012) data suggested a close evolutionary relationship between these genera. Moore (1980) considered that a reevaluation of the circumscriptions of *Astelia* and *Collospermum* was warranted due to the production of viable progeny from intergeneric crosses. *Collospermum*, while monophyletic, was nested within *Astelia* in phylogenetic reconstructions based on combined chloroplast and nuclear sequence data applying Bayesian inference, maximum likelihood, and maximum parsimony criteria (Birch 2011, Birch et al. 2012). As a result, those authors recognized a broadly circumscribed *Astelia s.l.*, including *Collospermum*. 
Within *Astelia*, Skottsberg (1934) recognized three subgenera (*Astelia* Skottsb., *Asteliopsis* Skottsb., and *Tricella* Skottsb.) based on open or cushion-forming growth form, degree of tepal fusion, ovary division, and seed shape. Within these subgenera, he recognized seven sections (*Astelia* Skottsb., *Desmoneuron* Skottsb., *Isoneuron* Skottsb., *Micrastelia* Skottsb., *Palaeastelia* Skottsb., *Periastelia* Skottsb., and *Tricella* Skottsb.) based on leaf venation, pistillode size, seed surface features, and extent of funicle development. In phylogenetic analyses (Birch 2011, Birch et al. 2012), each of Skottsberg’s (1934) sections, except section *Tricella*, were monophyletic, subgenus *Astelia* and subgenus *Asteliopsis* were polyphyletic and subgenus *Tricella* was paraphyletic. A revised circumscription of *Astelia* subgenera is proposed that accurately reflects the evolutionary relationships within the genus. *Collospermum* is relegated to synonymy under *Astelia*. Skottsberg’s sections are retained as they are monophyletic and accurately capture the extensive morphological diversity that is present within the subgenera.

Revisions based on recognition of monophyletic taxa are proposed here. Multiple characters support the proposed circumscription of *Astelia*. All taxa are dioecious or polygamodioecious, with a superior ovary, dorsi- or basifixed anthers, pistillodes or pistils that have a single short or poorly defined style, a 3 lobed stigma, and fleshy uni- or trilocular fruit with funicular hairs that are poorly to well developed.

**Methods**

**Taxonomic Sampling**

All *Astelia* taxa, (twenty-six species and three non-nominotypical varieties) and all *Collospermum* (four species) were included in this study. Herbarium specimens were provided to the Joseph F. Rock Herbarium (HAW) on loan from the following herbaria: Auckland War Memorial Museum (AK), Herbarium Pacificum (BISH), Allan Herbarium (CHR), Harvard University (GH), Kew Royal Botanic Garden (K), National Herbarium of Victoria (MEL), Missouri Botanical Garden (MO), Herbar National de Paris (P), United States National Herbarium (US), and Museum of New Zealand Te Papa Tongarewa (WELT). Type specimens were examined from BISH, MEL, P, WELT and digital images of type specimens were examined from CHR and K (Herbarium abbreviations follow Index Herbariorum (Thiers continuously updated).

**Morphological Data and Analyses**

Morphological data were obtained for 410 herbarium specimens (Appendix 1). Data were obtained for ten specimens per species/subspecies/morphotypes, including five staminate and five pistillate specimens for species with unisexual flowers. For taxa in which subspecies/morphotypes are recognized data were obtained for six specimens per subspecies, including three staminate and three pistillate specimens for subspecies with unisexual flowers. If possible, five flowers were measured per specimen, and if fewer than five flowers were present on a specimen all were measured. Measurements and scores were averaged across all specimens to give a mean value for each taxon. Flower and fruit color data were obtained from multiple sources including field observations, specimen label data, and taxon descriptions in national floras (Drake del Castillo 1893, L. B. Moore and Edgar 1976, Coode 1978, D. M. Moore 1983, Williams 1987, Wagner et al. 1999).

Morphological characters that varied at or below the genus rank were measured or
scored for all *Astelia* and *Collospermum* taxa in the field and/or herbarium. Herbarium specimens were studied under a dissecting microscope and measurements obtained using digital calipers. Pollen and seed characters were examined directly from material obtained from herbarium specimens after coating with gold/palladium using a Hitachi S-4800 field emission scanning electron microscope (SEM) at the Biological Electron Microscope Facility, Pacific Biosciences Research Center of the University of Hawai‘i at Mānoa. Images were digitally processed and the final plates were prepared in Photoshop 10.0.
Taxonomic treatment


*Type:* *Astelia alpina*


Herbaceous perennials, terrestrial or epiphytic, often growing in clusters with three ramets in trigonal arrangement, some species turf-forming, rhizomatous, dioecious or polygamodioecious. Leaves: 3-ranked, caniculate, linear or ensiform; leaves usually keeled, margins erect or revolute; leaf sheath closed, with surface obscured by dense long white hairs; parallel venation, variously incrassate; tomentum composed of scales and lanate wool at base of scale stalk, scales with basal stalk or peltate. Inflorescence: a terminal panicle, sometimes reduced to a few flowers; lateral branches racemes of sub-panicles, subtended by foliaceous or membranous, linear or lanceolate spathes; peduncle tomentum composed of distinct, narrow scales with dense basal wool. Flowers: pedicillate; bracts membranous, linear or spathulate; perianth membranous or fleshy, 6 tepals in 2 series; connate at base into tube of variable length; outer tepals triangular to lanceolate, with three veins, scales present over entire surface; inner tepals linear with one midvein, scales present along midvein only. Staminate flowers: lobes recurved; stamens 6; filaments filamentous, adnate to tepals at base of tepal lobes; anthers elliptic or linear-hastate, dorsifixed and versatile or basifixed and immobile, latrorse; pistillode present, style undifferentiated or distinct; stigma not formed. Pistillate flowers: 6 reduced staminodes present, adnate to base of tepals, filament filamentous, anthers flattened, sterile; ovary superior, unilocular or trilocular, placentation parietal from three placentas or axile, with subapical placentas, ovules few to many; style distinct or undifferentiated, stigmas 3. Fruit: berry, stigma typically persistent. Seeds: black, obovoid, ellipsoid, fusiform, or polygonal; testa smooth or sculptured; funicle with mucilaginous funicular hairs poorly or well developed, funicle hairs surrounding the seeds either adhering or not.

Flowers with a very short perianth tube (0.1–0.8 mm); anthers dorsifixed, versatile; ovary unilocular; seeds ovoid; funicle long, curved, with mucilaginous funicular hairs poorly developed that surround but do not adhere to the seed. Typus: A. alpina R.Br.


Low, compact, growth form (including cushion or turf forming taxa); leaves caniculate, linear, or subcylindric; reduced inflorescences bearing few flowers; staminate flowers with short filaments (0.5–1.6 mm); pistillate flowers with long outer tepals (4.5–7.0 mm); ovary unilocular, ovary height long (4.3–8.3 mm); fruit ovoid or oblong; few or many seeds per fruit (<25); seeds short and narrow; (1.1–2.0 × 0.5–1.3 mm). Typus: A. alpina R.Br.


Habitat: lowland (low latitudes) to sub-alpine (mid and higher latitudes) herbfields particularly on wet substrates (seeps, swamps etc.).


Open growth form; leaves ensiform; large inflorescences bearing many flowers; staminate flowers with intermediate length filaments (1.7–4.6 mm); pistillate flowers with short outer tepals (2.3–4.4 mm); ovary unilocular, ovary height intermediate (3.2–4.2 mm); fruit ovoid, many seeds per fruit (<20); seed intermediate length and narrow (2.4–2.9 × 1.2–1.3 mm). Typus: A. hemichrysa (Lam.) Kunth designated here.

Species and Distribution: Mascarene Islands, Reunion Island. A. hemichrysa (Lam.) Kunth

Habitat: forest.

Remarks: Phylogenetic analyses indicate that subgenus Astelia, as circumscribed by Skottsberg (1934), is polyphyletic (Birch 2011, Birch et al. 2012). Subgenus Astelia is revised to include sections Palaeastelia and Asteliella, which form a clade. Section Desmoneuron is placed in a different clade and it is excluded from subg. Astelia.


Flowers with a short perianth tube (0.2–1.1 mm); anthers dorsifixed, versatile; ovary unilocular (sect. Desmoneuron) or trilocular (sect. Isoneuron); seeds obovoid, obovoid-reniform, or turbinate-polygonal; funicle ribbed, mucilaginous funicular hairs well developed that surround but do not adhere to the seed; Typus: A. trinervia Kirk designated here.

Open growth form; leaves ensiform with a group of three subequal lateral nerves
conspicuous in lower half; inflorescences bearing many flowers; staminate flowers
with short filaments (0.6–2.1 mm); pistillate flowers with short outer tepals (1.9–4.2 x
0.7–1.8 mm); ovary unilocular, short (1.3–2.8 mm); fruit ampulliform, many seeds
per fruit (8–32); seeds short and narrow (1.4–1.8 × 0.5–1.0 mm). *Typus: A. trinervia*
Kirk designated here.

Species and distribution: *New Zealand* *A. solandri* A.Cunn., *A. trinervia* Kirk.

1934.

Open growth form; leaves ensiform; inflorescences bearing many flowers; staminate
flowers with short filaments (0.6–1.9 mm); pistillate flowers with short outer tepals
(2.7–4.0 × 0.7–2.0 mm); ovary trilocular, intermediate length (2.2–4.4 mm); fruit
ovoid, many seeds per fruit (11–18); seeds small and narrow (1.3–2.2 × 0.8–1.4 mm).
*Typus: A. banksii* A.Cunn. designated here.


Habitat: Lowland coastal cliffs (*A. banksii*) and lowland tropical forest (*A.
neocaledonica*).

Remarks: Phylogenetic analyses indicate that subgenus *Asteliopsis*, as circumscribed
by Skottsberg (1934), is polyphyletic (Birch 2011, Birch et al. 2012). Subgenus
*Asteliopsis* is revised to include sections *Isoneuron* and *Desmoneuron*, which form a
clade. But, as sect. *Periastelia*, is placed in a different clade, it is excluded from subg.
*Asteliopsis*.

Astelia subgenus Collospermum (Skottsb.) Birch, stat. nov.

xiv. No. 2, 73. 1934. *Typus: Collospermum hastatum* Colenso [Lectotypified by
Moore and Edgar (1970)].

Open growth form; leaves ensiform with dark coloration at base and peltate branched
hairs; inflorescences bearing many flowers; flowers with a long perianth tube (1.3–3.1
mm); staminate flowers with long filaments (3.8–8.6 mm), anthers basifixed,
immobile; pistillate flowers with long outer tepals (1.5–6.2 × 0.9–1.6 mm); ovary
trilocular, intermediate length (2.1–4.8 mm); fruit globose or obpyriform, with many
seeds per fruit (1–22); seeds ellipsoid or ovoid; small and narrow (1.3–2.1 × 0.1–1.1
mm); funicle short, truncate, with well developed mucilaginous funicular hairs that
adhere to the seed.

Species and distribution: *New Zealand*: *A. hastata* Colenso, *A. microsperma* Colenso
pro parte. Republic of Fiji, Viti Levu, Vanua Levu, Kandavu; Republic of Vanuatu,
Espiritu Santo, Tanna, Aneityum: *A. montana* Seem. Independent State of Samoa,
Savai’i, Upolu; *A. samoëns* (Skottsb.) Birch.
Habitat: Lowland temperate forest (A. hastata and A. microsperma) and montane tropical cloud forest (A. montana and A. samoënse).

Remarks: Species belonging to Collospermum must be transferred as Astelia has nomenclatural priority. Synapomorphies recognized for the genus Collospermum (Skottsberg 1934) remain valid for subg. Collospermum.


Flowers with a short (sect. Periastelia) or long (sect. Tricella) perianth tube (0.3 – 3.5 mm); anthers dorsifixed, versatile; seeds ellipsoid, fusiform, or ovoid; funicle short, truncate, mucilaginous funicular hairs poorly developed; Typus: A. nervosa Banks & Sol. ex Hook.f. designated here.


Compact to open growth form; leaves ensiform; inflorescences bearing many flowers; staminate flowers with short or long filaments (0.9 – 2.8 mm); pistillate flowers with long outer tepals (2.3 – 5.3 × 1.2 – 2.6 mm); ovary trilocular, intermediate length (1.8 – 4.6 mm); fruit globose, few seeds per fruit (4 – 12); seeds long and narrow (1.8 – 3.6 × 0.7 – 1.6 mm). Typus: A. argyrocoma A.Heller & Skottsb., designated here.


Open growth form; leaves linear or ensiform; inflorescences bearing many flowers; staminate flowers with short or long filaments (0.9 – 2.8 mm); pistillate flowers with long outer tepals (2.3 – 5.3 × 1.2 – 2.6 mm); ovary trilocular, intermediate length (1.8 – 4.6 mm); fruit globose, few seeds per fruit (4 – 12); seeds long and narrow (1.8 – 3.6 × 0.7 – 1.6 mm). Typus: A. argyrocoma A.Heller & Skottsb., designated here.

Remarks: Subgenus *Tricella* is revised to include both sections *Tricella* and *Periastelia*, which form a well supported clade in phylogenetic analyses (Birch 2011, Birch et al. 2012). Section *Periastelia* is monophyletic, however section *Tricella* is present as a grade and relationships within each of these sections remain equivocal.

**Incertae sedis**


Low, compact, turf forming growth form; leaves caniculate; inflorescence bearing few flowers; staminate flowers with short filaments (0.6–1.9 mm); pistillate flowers with short outer tepals (2.6–3.8 × 0.8–1.3 mm); ovary trilocular, intermediate length (2.6–3.8 mm); fruit ellipsoid, many seeds per fruit (17–24); seeds short and narrow (1.1–1.7 × 0.5–0.8 mm). *Typus*: *A. pumila* (Forst.) Gaudich. designated here.

Species and distribution: Chile, Argentina, Falkland Islands: *A. pumila* (Forst.) Gaudich.

Habitat: lowland (low latitudes) to sub-alpine (mid and higher latitudes) herbfields particularly on wet substrates (seeps, swamps etc.).

Remarks: The relationships of section *Microastelia* are poorly resolved with alternate relationships with subgenus *Asteliopsis* and the clade containing subgenera *Tricella* and *Collospermum* (Birch 2011, Birch et al. 2012). Section *Microastelia* contains a single species, *Astelia pumila*, which is a compact, turf-forming plant and dominant component of Astelia moorland in Chile, Argentina, and the Falkland Islands. As a cushion-forming species, it is morphologically divergent from taxa in subg. *Asteliopsis*, which contains species with open, spreading growth form that are epiphytic or terrestrial and primarily found of the understory in lowland to montane forests. *Astelia pumila* does share morphological features with subgenera *Asteliopsis* (e.g. short pistillode or pistil) and, alternatively, with subgenera *Collospermum* and *Tricella* (e.g. seeds with a short, truncate funicle). The subgeneric placement of section *Microastelia* remains equivocal and the section is unplaced (*incertae sedis*).
1. Leaf tomentum with scales with stalk attached at base; anthers versatile; pollen densely echinate; ovary/pistillode with weakly to moderately-developed mucilaginous hairs that do not adhere to seed surface on drying .................. 2

Leaf tomentum with peltate scales; anthers immobile; pollen sparsely spinulous; ovary/pistillode with well-developed mucilaginous hairs that adhere to seed surface on drying .................................................. subg. Collospermum

2. Ovary or pistillode unilocular, placentation parietal ........................................ 3

Ovary or pistillode trilocular, placentation axile ........................................ 5

3. Plants <40 cm tall; leaves generally less than 30 cm long; compact growth form including cushion and turf forming plants; inflorescence 1–few flowered ............ sect. Astelia

Plants > 40 cm tall; leaves generally greater than 30 cm long; open growth form; inflorescence many flowered ................................................................. 4

4. Leaves with acute apex; outer staminate tepals lanceolate, 5.0–6.4 mm long; pistillode bottle-shaped (lageniform); ovary ovoid; funicle long and curved ........................................ sect. Palaeastelia

Leaves with long acuminate apex; outer staminate tepals ovate, 2.5–5.0 mm long; pistillode ovoid-conical; ovary ampulliform or obpyriform; funicle short and ribbed ................................................................. sect. Desmoneuron

5. Leaves generally <10 cm long; compact turf forming growth form; inflorescence 1-few flowered ................................................................. sect. Microstelia

Leaves generally >10 cm long; compact or open growth form, but not turf forming; inflorescence many flowered ................................................................. 6

6. Pistillode ampulliform, <1.2 mm long; pistillate flowers with short outer tepals (2.7–4.0 × 0.7–2.0 mm); fruit ovoid, white, pink or maroon; seeds 1.3–2.2 mm long, 11–18 seeds per fruit; funicle ribbed ........................................ sect. Isoneuron

Pistillode ovoid, >1.0 mm, long; pistillate flowers with long outer tepals (2.3–5.3 × 1.2–2.6 mm); fruit globose, orange; seeds 2.0–3.6 mm long, 4–12 seeds per fruit; funicle not ribbed ........................................ 7

7. Perianth tube 0.8-4.0 mm long; ovary 1.6–4.6 mm; seeds fusiform and narrow (0.7–1.6 cm) ................................................................. sect. Tricella

Perianth tube 0.1-0.7 mm long, ovary 2.9–6.8 mm; seeds ovate and wide (1.3–2.3 cm) ................................................................. sect. Periastelia
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References


Figure Legends

**Figure 1.** Scanning electron micrographs of *Astelia* seeds showing size, shape, and funicle characters. A. **Subgenus Astelia** section *Astelia* (*Astelia linearis* var. *linearis*; ovoid, funicle long), B. **Subgenus Tricella** section *Tricella* (*A. petriei*; ovoid, funicle short). C. **Subgenus Tricella** section *Tricella* (*A. chathamica*; ovoid, funicle short). D. **Subgenus Asteliopsis** section *Isoneuron* (*A. banksii*; polygonal-turbinate, funicle ribbed). E. Section *Micrastelia* (*A. pumila*; ovoid, funicle short). F. **Subgenus Asteliopsis** section *Desmoneuron* (*A. solandri*; obovoid-reniform, funicle ribbed). G. **Subgenus Asteliopsis** section *Isoneuron* (*A. neocaledonica*; obovoid, funicle ribbed). H. **Subgenus Tricella** section *Tricella* (*A. menziesiana*; fusiform, funicle short). Scale bars = 0.5 μm. SEM images created by J.L. Birch

Supplementary Data

**Appendix 1.** Specimens examined for generation of morphological data. Herbarium abbreviations follow Index Herbariorum (Thiers [continuously updated]). For each specimen, the following data are provided: sampled taxa, voucher specimen information [collection location, date, collector, collection number, herbarium, and herbarium accession number]
Appendix 1.


_A. alpina_ R.Br. var. _alpina_ - AUSTRALIA. Tasmania: 1844, _M. Verreaux s.n._ (P00614764); Table Mountain, _R. Brown 5652_ (K000524938); _R. Brown s.n._ (P00614768); Table Mountain, _R. Brown s.n._ (MEL727772); _R. Brown s.n._ (P00614766); _F. V. Mueller s.n._ (K000524934); Mt. Field National Park, _M. Verreaux s.n._ (P00614766); _F. V. Mueller s.n._ (K000524934); Mt. Field National Park, Mt Field East, 1876, _F. v. Mueller s.n._ (K000524936); 24 Jan 1983, _J. M. Lydgate_ (MEL1523734); 14 Feb 1989, _N. G. Walsh 2300_ (MEL1577414); Mt. Field National Park, Mt. Rodway tow, 8 Jan 2009, _J. L. Birch 369_ (HAW); Mt. Field National Park, Mt. Rodway tow, 8 Jan 2009, _J. L. Birch 370_ (HAW); Mt. Field National Park, Uraquat Trail, 8 Jan 2009, _J. L. Birch 372_ (HAW); Mt. Field National Park, Uraquat Trail, 8 Jan 2009, _J. L. Birch 373_ (HAW); Cradle Mountain-Lake St. Clair National Park, Marian’s Lookout trail, 11 Jan 2009, _J. L. Birch 379_ (HAW); Southwest National Park, Mt. Eliza Plateau, 13 Jan 2009, _J. L. Birch 387 and A. Buchanan_ (HAW); Tasmania: Southwest National Park, Mt. Eliza Plateau, 13 Jan 2009, _J. L. Birch 388A and A. Buchanan_ (HAW); Southwest National Park, Mt. Eliza Plateau, 13 Jan 2009, _J. L. Birch 389 and A. M. Buchanan_ (HAW); Southwest National Park, Mt. Eliza Plateau, 13 Jan 2009, _J. L. Birch 390 and A. M. Buchanan_ (HAW).


**A. chathamica** (Skottsb.) L.B.Moore - NEW ZEALAND. Chatham Islands: *J. D. Hector* M.D. s.n. (SP030867); Oct, *Travers 48* (MEL5298); *F. v. Mueller* (MEL5297); Chatham Island, *H. Travers* s.n. (SP034015A–B); *H. N. Travers* s.n. (SP033784); Chatham Islands source (cultivated at 17 Holmwood Road, Christchurch), 8 Apr 1966, *L. B. Moore* s.n. (CHR150989A–C); Chatham Islands source (cultivated at 17 Holmwood Road, Christchurch), 7 Nov 1967, *L. B Moore* s.n. (CHR181613A—D); *W. M. Martin* s.n. (SP080105A–B); Chatham Islands source (G. W. Ramsay) (cultivated in Botany division garden), 29 Feb 1972, *L. B. Moore* s.n. (CHR233293A–B). Chatham Island: 8 Sept 1966 (SP030867C,G,H); Tuku Valley, Timihunga, 19 Oct 1980, *A. M. Ringer* s.n. (AK170715). Pitt Island: Canister Cove, 5 Jan 1970, *N. C. Simpson* s.n. (SP0 42759).

**A. fragrans** Colenso - NEW ZEALAND. North Island: Bay of Islands County, Puketi Forest, side ridge south of Bramley’s Ridge, north of Waikape Stream, 12 Oct 1984, *P. J. Bellingham* s.n. (AK170933); Kahikatea bush, Elsthorpe Scenic Reserve, Hawkes Bay (near Otane), 28 Oct 1963, *I. M. Morice* 41 (CHR146207A–B); Egmont National Park, Curtis Falls Track, *J. L. Birch* 205 (HAW); Smith’s Creek, Kaitoke, 19 Oct 1964, *L. B. Moore* s.n. (CHR141163); South Auckland Land District, Ikawhenua


A. hastata Colenso - NEW ZEALAND. 1875, M. Filhol s.n. (P00614792). North Island: Atuanui State Forest, 6 Apr 1969, R. E and J. Beever 236 (CHR195414A–B); Auckland Ecological Region, Awhitu Ecological District, Pollok, S off Barthow Road, Craig’s Bush, lower part eastern end, 9 Jun 2005, P. A. Aspin s.n. (AK294016–7); Auckland Ecological Region, Hunua Ecological District, Hunua Range, Mangatangi Kauri area, 4 Feb 1971, I. L. Barton (AK208895); Egmont National Park, Stony River, May 1961, A. P. Druce s.n. (CHR129729); Rotorua County, Lake Rotoehu, 29 Jan 1963, R. Mason 100059 (CHR140253A–C); South Manukau, Mauku, Jun 1901 (AK222913); Tainui Ecological Region, Kawhia Ecological


Haleakala, upper Keanae valley, 19 Jul 1927, O. Degener 4057 (BISH121037); Hana District, Hana Forest Reserve, above N rim of Kipahulu, 1974, B. Harrison 395 (BISH49287); Hana District, E Haleakala, 2 mi N. E. of Paliku Cabin, N facing slope above Wai Anapanapa, J. Henrickson and R. Vogl 3556 (BISH35823); Rainforest SW of Kaunuoahu, 20 May 1982, J. Davis 759 (BISH657637); Ukulele, 1919, C. N. Forbes s.n. (BISH121031); West Maui: 20 Jul 1964, M. R. Crosby and W. R. Anderson 1864 (BISH121024); Puu Kukui Watershed Preserve, along boardwalk to summit at mile marker 2300, 31 Oct 2007, J. L. Birch 154, R. Bartlett, D. Cole, L. Dunn, and D. Tanaka (HAW); Puu Kukui Watershed Preserve, forest below bog, 31 Oct 2007, J. L. Birch 158, R. Bartlett, D. Cole, L. Dunn, and D. Tanaka (HAW); Puu Kukui Watershed Preserve, forest below bog, 31 Oct 2007, J. L. Birch 159, R. Bartlett, D. Cole, L. Dunn, and D. Tanaka (HAW); Molokai: Waikolu Valley, head of valley, 15 Mar 1952, O. Degener 22160 and C. Tousley (BISH10425); between Waikolu Valley and N. Puu Alii, 10 Apr 1928, O. Degener 4065 (BISH121013); Pepeopae Bog, 25 m after end of boardwalk through bog, 22 Jun 2007, J. L. Birch 149 and C. W. Morden (HAW); ridge E of Mapulehu Valley, 29 Dec 1932, H. St. John 12840 and F. Fosberg (BISH121017); Kawele, ridge to Pelekunu Pali, 17 Mar 1910, J. F. Rock 6095 (BISH121053); Oahu. Waianae Range: Mt. Kaala, 14 Sept 2007, J. L. Birch 179 (HAW); Mt. Kaala summit trail (Waianae access), 26 Sept 2009, J. L. Birch 393 (HAW); Mt. Kaala summit, 24 Nov 1929, H. St. John 10071 (BISH121055); Kuliouou Valley, summit, 23 Jun 1935, O. Degener 10471, K. Park, and D. Topping (HAW); N Kaaawa, 12 Apr 1931, E. P. Hume 189 (BISH121171); Kaimai Mamaku Forest Park, Mt. Te Aroha, 13 Dec 2007, J. L. Birch 244 and S. J. Birch (HAW); Mangonui County, Maungataniwha Range, Feb 1908, H. Carse 516/1 (CHR328214 A‒B); Mt. Egmont, near Punihou Hut, 20 Jan 1963, I. M. Morice s.n. (CHR132058); Ohakune, Mt. Road, 13–14 Dec 1962, J. M. Wheeler s.n. (CHR141652); Originally from Ruahine Range, west Tamaki River (cultivated in shade house at Lincoln), 2 Jan 1968, J. Clarke s.n. (CHR182141); Pureora State Forest Park, West Taupo, 26 Jan 1982, J. E. Braggins 97 (AK270463); Tararua Forest Park, trail to Mt. Holdsworth, 12 Jan 2008, J. L. Birch 244 and S. J. Birch (HAW); Tongariro National Park, road between Ohakune and Turoa, 17 Mar 1999, L. Perrie and L. Sheppard s.n. (SP083500).

A. microsperma Colenso - NEW ZEALAND. North Island: Auckland Ecological Region, Rodney Ecological District, Mt. Tamahunga, 28 Feb 1993, M. E. Young s.n. (AK212022); Blue Mountains, near Pinehaven, Hutt Valley, 1 Jan 1963, J. M. Morice s.n. (CHR132056A‒C); Kaimai Mamaku Forest Park, Mt. Te Aroha, 13 Dec 2007, J. L. Birch 248, C. Gemmill, E. Grove, and N. Wakefield (HAW); Maungataniwha Range, Feb 1908, H. Carse 516/1 (CHR328214 A‒B); Mt. Egmont, near Punihou Hut, 20 Jan 1963, I. M. Morice s.n. (CHR132058); Ohakune, Mt. Road, 13–14 Dec 1962, J. M. Wheeler s.n. (CHR141652); Originally from Ruahine Range, west Tamaki River (cultivated in shade house at Lincoln), 2 Jan 1968, J. Clarke s.n. (CHR182141); Pureora State Forest Park, West Taupo, 26 Jan 1982, J. E. Braggins 97 (AK270463); Tararua Forest Park, trail to Mt. Holdsworth, 12 Jan 2008, J. L. Birch 244 and S. J. Birch (HAW); Tongariro National Park, road between Ohakune and Turoa, 17 Mar 1999, L. Perrie and L. Sheppard s.n. (SP083500).


A. nervosa Banks & Sol. ex Hook.f. - NEW ZEALAND. North Island: Coromandel County, Moehau summit, 2 Nov 1980, R. O. Gardner 2763 (AK153040); Kokioanga Co., Waiima Forest, ridge between summit of Mount Misery and “highest point in Northland”, 16 Jan 1990, A. E. Wright 9684 (CHR192727); Egmont National Park, Ski field Road, 11 Dec 2007, J. L. Birch 207 (HAW); Kaimai Mamaku Forest Park, Mt. Te Aroha, Waikato, J. L. Birch 220, C. Gemmill, E. Grove, and N. Wakefield (HAW); Otorohanga County, Ranginui summit, Rangitoto Range, 16 Dec 1981, R. O. Gardner 3209 (AK158716); Table Mountain, Kauaeranga Valley, Coromandel Range, 10 Apr 1971, I. M. Morice 484B (CHR208245); Thames County, Lookout rocks, inland from Taran, 10 Dec 1986, R. O. Gardner 5049 (CHR484212); Tongariro (grown in cultivation at Lincoln), 10 Nov 1966, J. Clarke s.n. (CHR566443A–B); Waitemata County, Albany Scenic Reserve, valley lying east of Lonely Track Road, Wright's Road intersection, 6 Oct 1979, R. O. Gardner s.n. (AK150794); Wellington District, Tongariro National Park, ca. 1.5 km N. W. of Chateau Tongariro, nr. road to Chateau, Whakapapanui Track, 24 Mar 1970, P. J. Edwards 74 (AK129710). South Island: Marlborough Land District, Mt. Stokes, Marlborough Sounds, Mar 1977, A.P. Druce s.n. (CHR310138); Mt. Stokes, T. Kirk s.n. (SP030865); Mt. Stokes Scenic Reserve, Mt. Stokes summit, Marlborough Sounds, 14 Jan 2008, J. L. Birch 251 and
A. nivicola Cockayne ex Cheeseman var. nivicola - NEW ZEALAND. South Island:

A. nivicola Cockayne ex Cheeseman var. moriceae L.B.Moore - NEW ZEALAND.
Dec 1965, L. B. Moore, s.n., J. Clarke, and I. Robins (CHR168145A–C); On E side
15 minutes from Wilmot Pass, 14 Dec 1962, I. Morice s.n. (CHR133164A–C); Track
to Boulder Lake, The Pulpit, 6 Jan 1964, I. M. Morice 92 (CHR146984A–C); Nelson,

**A. papuana** Skottsb. - PAPUA NEW GUINEA. Central Highlands, Mt. Wilhelm, 25
province, Kainantu sub-province, Mt. Piora, 9 Jan 1975, *M. J. S. Sands* 92
(CHR133164A–C); Track to Boulder Lake, The Pulpit, 6 Jan 1964, I. M. Morice
92 (CHR146984A–C); Nelson, track to Mt. Arthur, 13 Apr 1963, I. M. Morice
12 (CHR 144249).

**A. petriei** Cockayne - NEW ZEALAND. South Island: Arthur’s Pass, Temple Basin,
8 Dec 1963, *B. H. MacMillan* 3 (CHR146933); Fiordland National Park, Gertrude
Saddle track, 23 Jan 2008, *J. L. Birch* 287 and *P. Michel* (HAW); Fiordland National
Park, Gertrude Saddle track, 23 Jan 2008, *J. L. Birch* 286 and *P. Michel* (HAW);
Fiordland National Park, Borland Saddle/Mt. Burns track, 24 Jan 2008, *J. L. Birch*
291 and *P. Michel* (HAW); Molesworth Ecological Region, Balaclava Ecological
District, Island Saddle just north of road summit, 4 Jan 2002, *E. K. Cameron* 10684
(ARK55636); *N. Canterbury, Upper Clarence Valley, Mt. St. Patrick, 14 Jan 1972
CHR228674; NW Nelson, Mt. Arthur, 15 Jan 2008, *J. L. Birch* 254, *S. Courtney,
Courtney, and R. Gaskill* (HAW); Otago Province, Lake Harris Saddle (cultivated in
Dunedin), 1923, *W. A. Thomson* s.n. (SP085977); Westland National Park, Fox

**A. psychrocharis** F.Muell. - AUSTRALIA. New South Wales: Mt. Kosciuszko, 19
Feb 1990, *M. G. Corrick* 10668 (MEL1578958); Mt. Kosciuszko, June 1901, *C. H.
Grove* s.n. (MEL 2213620); Kosciuszko National Park, Mt. Kosciuszko, 30 Dec 2008,
*J. L. Birch 359 and A. Beeshag* (HAW); Kosciuszko National Park, Mt. Kosciuszko,
30 Dec 2008, *J. L. Birch 360 and A. Beeshag* (HAW); Kosciuszko National Park, Mt.
Kosciuszko, 31 Dec 2008, *J. L. Birch 361 and A. Beeshag* (HAW); Kosciuszko National
Park, Mt. Kosciuszko, 31 Dec 2008, *J. L. Birch 362 and A. Beeshag* (HAW);
Kosciuszko National Park, Southern Tablelands, near end of Mt. Blue Cow,

**A. pumila** (Forst.) Gaudich. - ARGENTINA. Tierra del Fuego: Isla de los Estados,
Bahia San Antonio, Puerto Hoppner, 8 Nov 1971, *T. R. Dudley, R. N. P. Goodall, and
G. Crow* 1596 (MO2300439); Northwest side of Bahia Thetis, 14 Nov 1969, *R. N. P.
Goodall 2248 (US2626023). CHILE. Chiloé Island: River Toigoi, Chepu, 26 Oct
1958, *E. J. Godley* 349a (CHR 547077B); River Toigoi, Chepu, 26 Oct 1958, *E. J.
Godley 348 (CHR 55303). Magallenes y de la Antárctica Chilena: Churucuca, 30 Jan
1879, *Lud Savatier 189* (P00614743); Détroit de Magellan-Port Famine. *M. le
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