

A new species of *Roupala* (Proteaceae) from Central Brazil

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Academic editor: *Doug Soltis* | Received 8 February 2012 | Accepted 19 May 2012 | Published 28 May 2012

Citation: Prance GT (2012) A new species of *Roupala* (Proteaceae) from Central Brazil. *PhytoKeys* 13: 1–4. doi: 10.3897/phytokeys.13.2836

Abstract

A new species of *Roupala*, *R. gertii* from the endangered Atlantic coastal forests of Brazil is described and illustrated.

Keywords

Proteaceae, *Roupala*, Brazil, Atlantic rainforest

Introduction

The Neotropical representatives of the Proteaceae were monographed in 2007 (Prance et al. 2007) building on the earlier work of Sleumer (1954). The monograph included thirty-three species of *Roupala*. Since that time a collection has come to my attention that does not fit into any of the previously described taxa. This is presented here as *Roupala gertii*. It is currently only known from a single collection from the rather poorly collected Atlantic coastal forest of the State of Espírito Santo, Brazil a region from where novelties are to be expected.

Description

Roupala gertii Prance, sp. nov.

urn:lsid:ipni.org:names:77119674-1

http://species-id.net/wiki/Roupala_gertii

Fig. 1

Ab *R. paulensis* foliis minoribus acuminis 3–8 mm longis, petiolis 8–20 mm, rachidibus inflorescentiis tenuibus differt.

Type. Brazil. Espírito Santo, BR-262 road near junction to Laranja da Terra, Iúna Municipality, 7 Nov 1993 (fl), *G & M Hatchbach & J. M. Silva 59702* (holotype, MBM Curitiba; isotype, K).

Tree 6 m tall, young branches appressed-tomentose, not conspicuously lenticellate. Leaves simple, lamina chartaceous, drying reddish-brown, ovate, 4.5–8.5 × 2–4.4 cm, length:breadth ratio 1–2.2–2.7, semicraspedodromous: ferruginous-tomentose beneath, glabrous above except along midrib, the margins distinctly revolute, entire or slightly serrate, cuneate at base, equal or slightly unequal; apex acuminate, the acumen 3–8 mm long; primary veins 5–6 pairs, prominulous beneath, slightly prominulous above; midrib reaching apex of lamina, prominent beneath, plane above, tomentose, glabrescent; petioles 8–20 mm, tomentose when young, terete, lamina slightly confluent onto petiole for up to 5 mm. Inflorescence terminal or axillary; peduncle 3–10 mm × 1 mm thick; rachis 4.5–8.5 × 1 mm, ferruginous-tomentose; bracts few, 1 × 1 mm, tomentose; pedicels 1.5–2 mm, ferruginous-tomentose, free to base; flowers borne solitary or in pairs, 4–5 mm long, exterior ferruginous-tomentose.; tepals 4, reflexed and twisted when open; filaments adnate to upper half of tepals; anthers 1–1.2 mm long; nectary lobes 4, well separated, conspicuous; ovary erect, densely tomentose; style clavate. 3–4 mm long. Fruit not seen.

This species clearly belongs to the genus *Roupala* on account of its four hypogynous glands and bilocular ovary with pendulous ovules. It is near to *R. paulensis* Sleumer but differs in the thinner smaller leaves that dry brown above rather than green. The plants is far less robust, the petioles are shorter, the leaves more acuminate and the inflorescence rachis much thinner. It is a pleasure to name this species for Dr Gert Hatschbach who has done so much make the flora of south and central Brazil so much better known and who made the first collection of this species.



Figure 1. *Roupala gertii* Prance **A** habit **B** flower bud **C** open flower with two tepals removed **D** Ovary and style showing two of the nectary lobes **E** tepal and stamen. (drawn by Flora Bamford)

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Two new species of Gingers (Zingiberaceae) from Myanmar

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Academic editor: Sandra Knapp | Received 12 January 2012 | Accepted 28 May 2012 | Published 7 June 2012

Citation: Gowda V, Kress WJ, Htun T (2012) Two new species of Gingers (Zingiberaceae) from Myanmar. *PhytoKeys* 13: 5–14. doi: 10.3897/phytokeys.13.2670

Abstract

Two new species of gingers (Zingiberaceae), *Globba sherwoodiana* W.J. Kress & V. Gowda **sp. nov.**, and *Curcuma arracanensis* W.J. Kress & V. Gowda **sp. nov.**, from Myanmar are described. The new species of *Globba* is currently only known in cultivation and is commonly grown and sold in markets in Myanmar. In contrast *C. arracanensis* has been collected from a single restricted region in the cloud forests of the Rakhine Yoma above the Bay of Bengal in western Myanmar. Three-locus DNA barcodes were generated as aids for the identification of the two new species.

Keywords

Curcuma, endemic, *Globba*, Myanmar, new species, taxonomy, Zingiberaceae

Introduction

A recent surge of interest in the taxonomy and classification of the family Zingiberaceae (Kress et al. 2002, 2007) as well as significant efforts at field exploration in Southeast Asia have resulted in the discovery and description of a plethora of new species and genera of gingers (e.g., Kress et al. 2010, Leong-Škorničková et al. 2011). The abundance of gingers in the understory of evergreen and monsoonal forests and the common uses of gingers as spices, medicines, and ornamentals has led to new discoveries in both natural environments (Kress et al. 2010) as well as the marketplace (Kress

and Larsen 2001, Kress and Htun 2003). Here we describe two new species from Myanmar, one found on the top of a ridge in pristine cloud forest and the other as a common offering in Buddhist ceremonies and temples.

Methods

The morphology of both new species was analyzed using herbarium material and living plants cultivated in the Department of Botany Research Greenhouses at the Smithsonian (USBRG). Detailed morphological measurements were made using digital calipers and a calibrated eye piece under a dissecting microscope. Herbarium specimens to serve as types were taken from plants grown in cultivation when required (see Taxonomic Treatment).

DNA extraction, amplification and sequencing were carried out for three barcoding regions *rbcL*, *matK*, and the *trnH-psbA* spacer region using published primers under standard conditions (see Kress and Erickson 2007). Genbank accession numbers for all the sequences are listed in Table 1.

Table 1. Voucher information and Genbank accession numbers for *Globba sherwoodiana* and *Curcuma arracanensis*.

Species	Gene region	Genbank accession number	Voucher (Herbarium location)
<i>Globba sherwoodiana</i>	<i>rbcL</i>	1504642	WJK 00-6669 (US)
	<i>matK</i>	JQ480153	WJK 00-6669 (US)
	<i>trnH-psbA</i>	1504642	WJK 00-6669 (US)
<i>Curcuma arracanensis</i>	<i>rbcL</i>	1504641	WJK 03-061 (US)
	<i>matK</i>	JQ480152	WJK 03-061 (US)
	<i>trnH-psbA</i>	JX082290	WJK 03-061 (US)

Taxonomic treatment

Globba sherwoodiana W.J.Kress & V.Gowda, sp. nov.

urn:lsid:ipni.org:names:77119952-1

http://species-id.net/wiki/Globba_sherwoodiana

Fig. 1, Plate 1.

Diagnosis. A new species in the genus *Globba* Section *Globba* differing from other species in this section, such as *G. laeta* K.Larsen, *G. marantina* L., and *G. winitii* C.H.Wright by the combination of white, sharply reflexed and imbricate inflorescence bracts and soft, glabrous, bright green leaves.

Type. Myanmar: Mandalay Division: Pyin Oo Lwin, National Botanical Gardens, 69 km from Mandalay, 1000 m, 21°59'31"N, 96°28'09"E, *W. J. Kress, The Htun, and M. Bordelon s.n.* (only living plant collected for cultivation); Plants of this

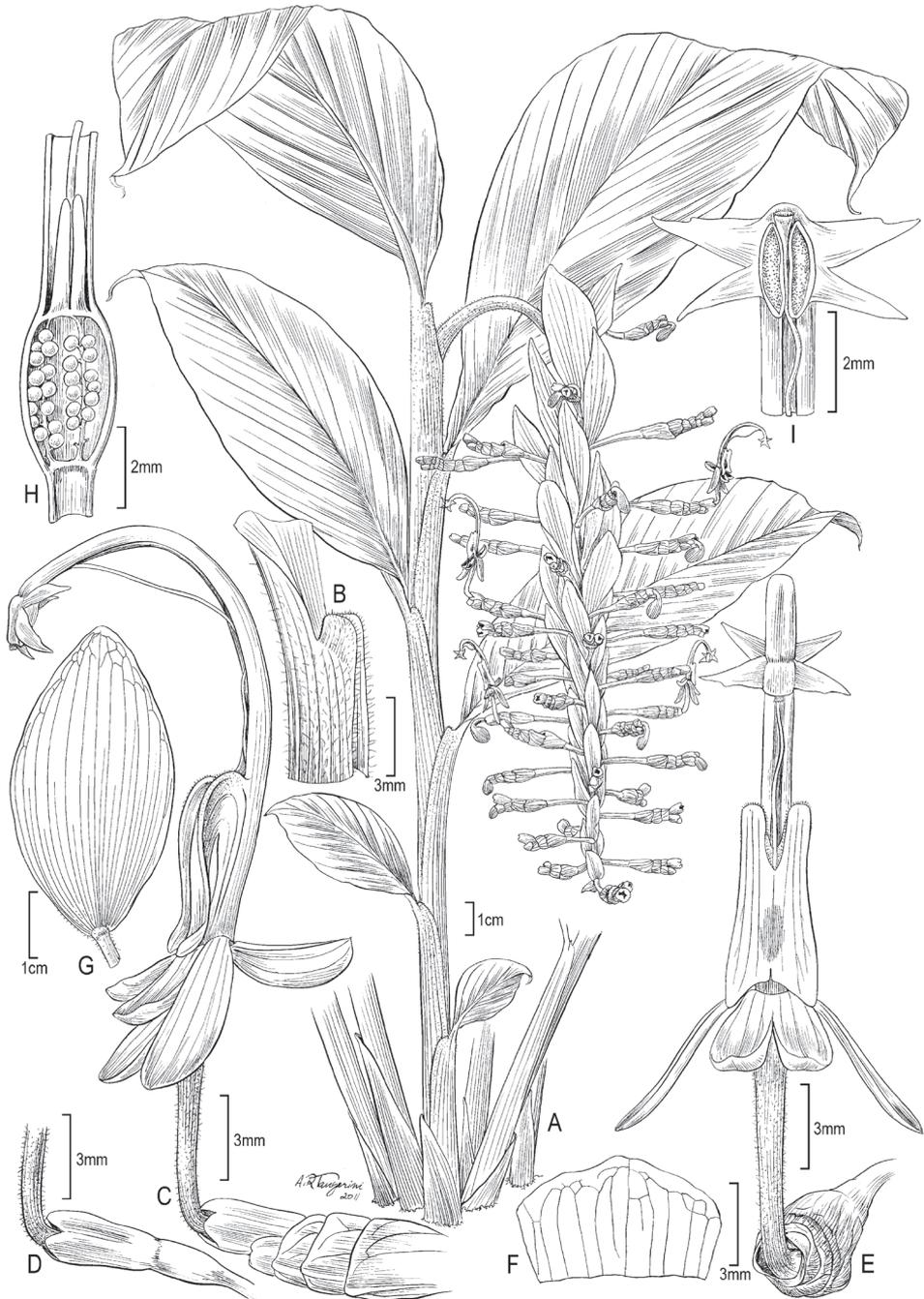


Figure 1. *Globba sherwoodiana* W.J.Kress & V.Gowda. **A** Habit of flowering plant **B** Apical part of leaf sheath showing ligule **C** Flower, lateral view showing bracteoles **D** Calyx with floral tube **E** Flower, frontal view **F** Bracteole **G** Inflorescence bract **H** Base of flower, cut-away view showing style, epigynous nectaries and placentation **I** Anthers with four appendages, style held in the ventral furrow of the filament with a cup-shaped stigma. WJK 11-8809 (US).



Figure 2. *Curcuma arracanensis* W.J.Kress & V.Gowda. **A** Habit of flowering plant **B** Tuberos rhizome **C** Ligule **D** Bracteole **E** Flower, lateral view **F** Flower, frontal view **G** Flower, cut-away view showing style and anthers **H** Base of flower, cut-away view showing style, epigynous nectaries and placentation **I** Placentation, cross section. WJK 03-7328 (US).

living collection cultivated at the Smithsonian Botany Research Greenhouses as US-BRG 1997–141, 29 September 2011, W. J. Kress, V. Gowda & M. Bordelon 11–8809 (holotype: US! [US 3635561, barcode 00940954; isotypes RAF!, E!).

Description. Small perennial herbs from 38–45 cm in height to the top of uppermost leaf sheath. Rhizomes compact, non-tuberulous, white with a light orange center internally. Leafy shoots densely clumped, 6 to 8-leaved, stems bright green in color, sparsely hirsute. Basal sheaths 5–7 × 1–2 cm, sparsely hirsute. Plane of distichy perpendicular to rhizome. Leaves glabrous and soft, only midvein of the ventral surface pubescent, lamina 17–20 × 5–8 cm elliptic bright green adaxially and pale green abaxially, margin entire, base attenuate, apex acuminate; petiole 0.5–0.7 × 0.3–0.4 cm, sparsely hirsute, green. Ligule small, 2–3 mm in length, hirsutulous, emarginate not becoming papery. Inflorescence terminal on leafy shoots, pendent 11–15 cm; peduncle 2.5–4 × 0.35–0.5 cm, hirsute, pale green; rachis hirsute, straight, visible; inflorescence bracts 25–30 per inflorescence, bracts decreasing in size from base to the tip, median bract 2.5–3.5 cm × 1.5–1.8 cm, spirally arranged, imbricate and widely separated, sharply reflexed 105–107° from vertical axis, glabrous, white. Cincinni ca. 1.4–2 cm long to the first flower, originating under the inflorescence bract, 2–8 mm apart on the rachis, one per bract containing 2–3 flowers; flowers maturing from base to apex of inflorescence; bracteoles tubular, basal and largest bracteole 2.6–3 × 3.5–5 mm, glabrous, light green. Flowers conspicuous; calyx tubular 4.5–5 mm long, reflexed at ca. 3–5 mm from base, tri-lobed, yellow green; corolla tube 1.1–1.4 cm long, sparsely puberulous, with lobes reflexed; lobes cucullate, ca. 4–6 mm × 2–3 mm; lateral staminodes 7–9 × 2.3–2.6 mm in length, elliptic, glabrous, orange; labelum 6.2–7.6 × 2.2–2.4 mm, triangular, bi-lobed, glabrous, orange with deep orange center; fertile stamen with filament 1.6–2.6 cm long, orange, glabrous, anther 2.2–2.6 mm long, thecae elliptic with four appendages, glabrous, crest not extended beyond thecae; style held in the ventral furrow of the filament; stigma cup-shaped, pubescent with ciliate margin; ovary uni-locular, 1.2–2 × 1.6–2.7 mm, glabrous, white, with parietal placentation. Epigynous (stylodial) nectaries 2, linear septal, 3–4 mm long, light orange. Fruit and seeds unknown. Bulbils not observed.

Distribution. At present this species is only known in cultivation in Myanmar where it is commonly sold in the markets and used as an offering in Buddhist ceremonies. However, it is suspected that wild populations are present in the border region between Myanmar and Thailand.

Ecology. The closest relatives of this species (see relationships) inhabit the understory of monsoon forests. We suspect that the same is true for *Globba sherwoodiana*.

Etymology. This splendid and magnificent species of *Globba* is named in honor of Dr. Shirley Sherwood, a great lover of plants and a patron of contemporary botanical art. Her support of botanical research in Myanmar is greatly appreciated.

Common name. The local name for this species, “Padein Gno,” means “weeping goldsmith” in the Burmese language. It is said that local goldsmiths in Myanmar weep when they see this flower because no matter how hard they try, they are unable to capture in gold metal the beauty and simplicity of the individual parts of the flower (see Kress 2009).

Conservation status. Because this species is commonly cultivated it is in no danger or threat of extinction. However, the lack of known natural populations may sug-

gest that this cultivated species may have low levels of genetic diversity. Genetic studies will provide a better understanding of the conservation status of this species.

Relationships. *Globba sherwoodiana* was included in the molecular phylogenetic analysis of Williams et al. (labeled as *Globba* “magnifica”; 2004). Using DNA sequence data from *matK* and ITS, they showed that this species is a member of Sect. *G. laeta* K.Larsen, *G. bulbifera* Roxb., *G. schomburgkii* Hook. f., *G. globulifera* Gagnep., *G. adhaerens* Gagnep., *G. marantina* L., and *G. winitii* C.H.Wright. Several species in this section have large conspicuous inflorescence bracts similar to those characterizing *G. sherwoodiana*.

Other specimens examined. Known from the type specimen and additional specimens of USBRG 97–141 in cultivation; WJK 00–6669; WJK 99–6533.

***Curcuma arracanensis* W.J.Kress & V.Gowda, sp. nov.**

urn:lsid:ipni.org:names:77119953-1

http://species-id.net/wiki/Curcuma_arracanensis

Fig 2; Plate 2.

Diagnosis. A new species in the genus *Curcuma* differing from other members of the genus known from Myanmar in the inflorescence borne well above the surface of the ground at the apex of a leafy shoot, deep maroon inflorescence bracts, and very conspicuous, bright orange flowers.

Type. Myanmar: Rakhine State: 57 miles from Taung-gok towards Pyay, steep hillsides of cloud forest in fine scree soil, 795 m, 18°38'15"N, 94°38'97"E, 20 June 2003, W. J. Kress, Aye Pe, Than Than Htay, Win Win Aung, and M. Bordelon 03–7328; living collection cultivated at the Smithsonian Botany Research Greenhouses as USBRG 2003–061, 20 June 2003. W. J. Kress 03–7328 (holotype: US! [US 3572390, barcode 00940953; isotypes RAF!; E!).

Description. Medium herb to 85 to 130 cm in height; rhizomes compact, yellow internally, with numerous white tubers (yellow internally). Leafy shoots loosely clumped, disarticulating during dry season, 3 to 5-leaved, with basal sheaths green with red speckles, glabrous, 20–22 × 4–5 cm. Plane of distichy parallel to rhizome. Leaves 60–70 cm in length, glabrous and coriaceous; petiole 19–23 0.7–0.8 cm, glabrous, green with small red speckles, deeply grooved in cross-section, margin entire, smooth; ligule medium-sized, 1.5–3.2 cm in length, bi-lobed, thin and translucent, pale yellow green, glabrous; blade 43–49 × 17–20 cm, narrowly ovate, midrib below green with sparse red speckles, glabrous, base cordate, subequal, apex caudate, adaxial surface dark green. Inflorescence terminal on relatively long leafy shoot, erect 19–25 cm in height; peduncle 2–5 cm in length, glabrous, green to deep maroon red; rachis short; inflorescence bracts 25–30 per inflorescence, 2.4–2.9 × 2.5–3.4 cm, spirally arranged and imbricate, each fused at base to adjacent members (“pouched”), 40–50° from vertical axis, glabrous, green basally to deep red maroon distally; no coma. Cincinni one per bract containing 3–4 flowers, maturing from base to apex of inflorescence; bracteoles not tubular, 13–15 × 4–6 mm, translucent,

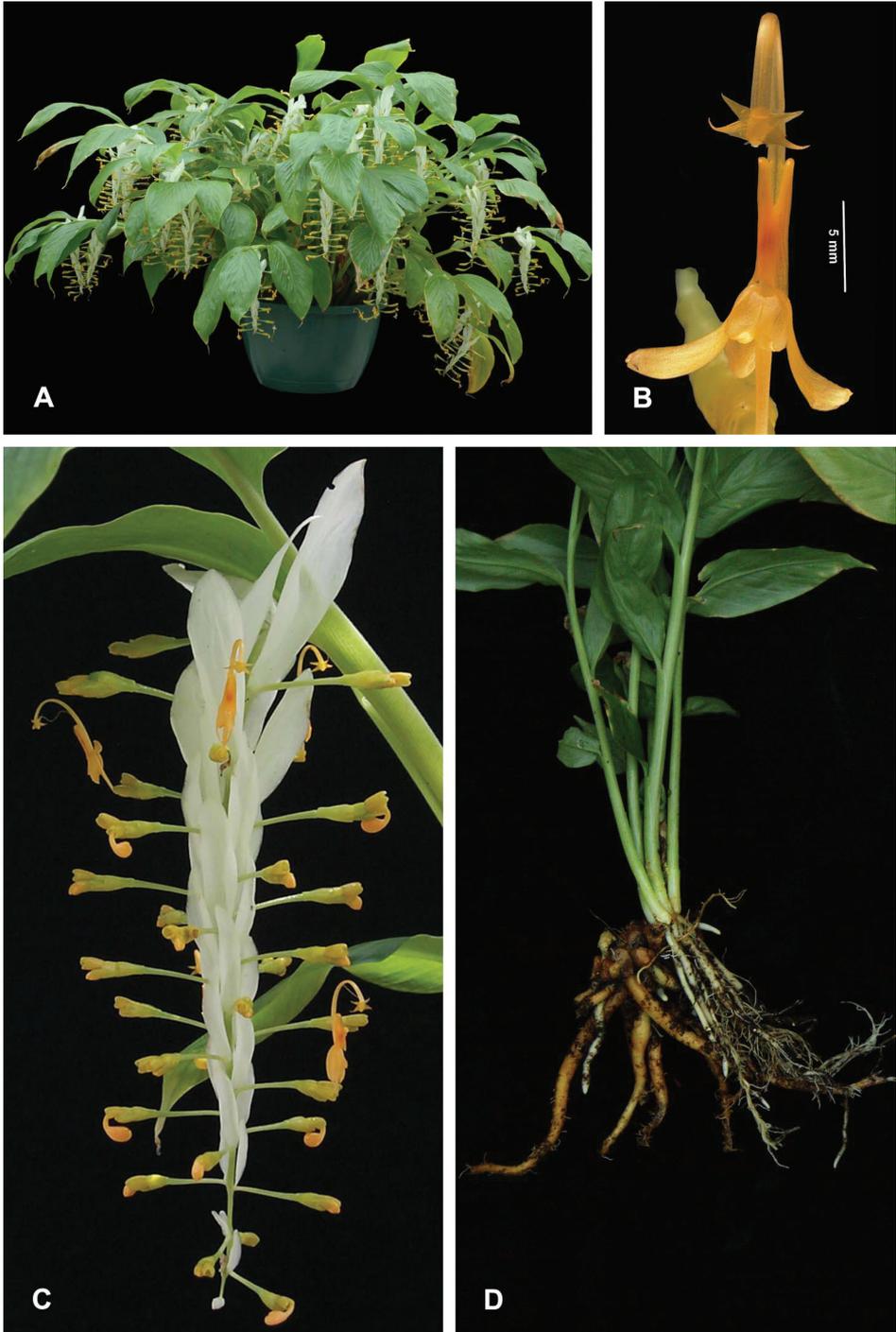


Plate I. *Globba sherwoodiana* W.J.Kress & V.Gowda. **A** Habit **B** Flower, front view showing two lateral staminodes, two petal lobes, labellum, and the four appendages of the anther **C** Inflorescence, lateral view **D** rhizome. WJK 97-141 (USBRG).



Plate 2. *Curcuma arracanensis* W.J.Kress & V.Gowda. **A** Habit **B** Flower, frontal view **C** Inflorescence **D** Rhizome. WJK 03-7328 (US).

glabrous, white with short red apex. Flowers with tubular calyx, 16–22 mm long, tri-lobed, sparsely hirsute with very short hairs, pale yellow orange; corolla tube 2.8–3.5 cm, orange to pale orange, glabrous, with lobes not reflexed, 19–22 mm in length; lateral staminodes fused to base of filament of fertile anther, 13–17 × 7–10 mm, bluntly acute, glabrous, orange; labellum 18–22 × 15–18 mm, spatulate, shallowly bi-lobed at apex, glabrous, yellow orange with deep orange central stripe and reddish margins, lobes not flared; fertile stamen with filament 7–9 mm long, 4–5 mm wide, glabrous, orange, anther versatile, 10–12 × 4.5 mm, thecae elongate with minute, blunt spurs, glabrous, orange, crest much reduced extended <1 mm beyond thecae; stigma shallowly cup-shaped, ovary tri-locular, 3–5 × 3–4 mm, glabrous, pale yellow or green, placentation axile. Epigynous (stylodial) nectaries 2, rounded, 2.4–2.8 mm long, with scattered minute hairs, pale orange to cream-colored; a collar of short hairs forming nectar chamber on inside of corolla tube 5 mm above apex of ovary. Fruit and seeds unknown.

Distribution. This species is known only from the area around the type locality in Rakhine State, Myanmar.

Ecology. Unlike many species of *Curcuma*, which are found in the understory of seasonally dry monsoonal forests, *C. arracanensis* inhabits open areas in evergreen cloud forest.

Etymology. This species is named for the region formerly known as Arrakan, an earlier name for today's Rakhine State in Myanmar.

Common name. The local name for this species is “Tauk tar phu” in the Burmese language.

Other specimens examined. Known only from the type specimen. Collections measured WJK 03–7328; USBRG 2003–061.

Conservation status. Because this species is only known from a single locality in Myanmar and the habitat in which it is found is steadily declining due to deforestation, we categorize it as critically endangered under criteria B and D following the IUCN guidelines (IUCN Standards and Petitions Subcommittee 2011).

Relationships. The relationship of *Curcuma arracanensis* to other members of the genus is not known at present. The anther shape is similar to that found in *C. petiolata* Roxb (distributed from India to Malaysia including Thailand) and may suggest evolutionary affinities to species allied to this taxon. Further molecular and morphological analyses are needed to determine more precise relationships.

Acknowledgments

We would like to acknowledge Mike Bordelon, Alice Tangerini, Jana Leong-Škorničková, Mark Newman, and Ida Lopez for discussion and assistance in preparing the manuscript, and colleagues in Myanmar, especially Daw Yin Yin Kyi, for assistance in the field and herbarium. We also thank the reviewers and Sandra Knapp for their comments and suggestions that have significantly improved this manuscript.

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A new species of *Cyanea* (Campanulaceae, Lobelioideae) from Maui, Hawaiian Islands

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Academic editor: Vicki Funk | Received 1 June 2012 | Accepted 15 June 2012 | Published 20 June 2012

Citation: Oppenheimer H, Lorence DH (2012) A new species of *Cyanea* (Campanulaceae, Lobelioideae) from Maui, Hawaiian Islands. *PhytoKeys* 13: 15–23. doi: 10.3897/phytokeys.13.3447

Abstract

Cyanea kauaulaensis H. Oppenheimer & Lorence, **sp. nov.**, a new, narrowly endemic species from Maui, Hawaiian Islands is described, illustrated with field photos, and its affinities and conservation status are discussed. It is currently known from 62 mature plants and is restricted to Kauaʻula and Waikapu valleys on leeward western Maui. It differs from all other species of *Cyanea* by its combination of many-branched habit; glabrous, unarmed, undivided leaves; small, narrow, glabrous corollas with small calyx lobes that do not persist in fruit; and bright orange, subglobose to obovoid fruits.

Keywords

Campanulaceae, conservation, *Cyanea*, Hawaiian Islands, IUCN Red List, Maui

Introduction

As currently circumscribed, the woody lobelioid genus *Cyanea* Gaudich. (including *Rollandia* Gaudich.) comprises 78 species (Lammers 2007), all endemic to the Hawaiian Islands where they occur in wet and mesic forests. The Hawaiian lobeliads are the largest plant clade restricted to any archipelago, with *Cyanea* being the largest genus within that clade. It is also the largest genus in Hawaiʻi, and originated 8–10 Mya (Givnish et al. 2008). *Cyanea* was first described by Gaudichaud-Beaupré (1824) based on the type species *C. grimesiana* Gaudich. The genus was later treated in Rock's (1919) monographic study of the Hawaiian Lobelioideae in which he recognized 52

species in 5 sections. Wimmer (1943) recognized only 3 sections in his monograph of Campanulaceae. Lammers (1990) revised the Hawaiian members and also recognized 52 species but stated relationships within *Cyanea* remained poorly understood and consequently did not recognize any formal sections. Recent exploration and collecting efforts in poorly explored, often rugged or remote regions in the Hawaiian Islands continue to yield undescribed species of *Cyanea* (Lammers 2004, Lammers and Lorence 1993). In 1989, during a botanical survey of lands then owned by Pioneer Mill Co. on West Maui (currently Makila Land Co.), about a dozen plants of an unusual Campanulaceae were found along the southern fork of the amphitheatre headwaters of Kaua`ula Valley (Fig. 1). The botanists on that excursion, Steve Perlman, Sam Gon, and Robert Hobdy, easily recognized the plants as belonging to the endemic Hawaiian genus *Cyanea*. However, these plants were misidentified and thought to represent *C. glabra* (F. Wimmer) St. John [based on *C. knudsenii* Rock var. *glabra* F. Wimmer], a species previously known to be endemic to wet forest of windward East Maui and possibly extinct. Recent research in the north fork of Kaua`ula Valley during 2008 and 2009 resulted in the discovery of additional plants. In July of 2011 a new population was discovered in Waikapu Valley nearly 5 km from the previously known plants and separated by several large valleys and canyon walls and ridges 700 m in height.

Critical study of these collections reveals that they are not *C. glabra* nor even closely related to it, and clearly represent an undescribed species. Based on the description in

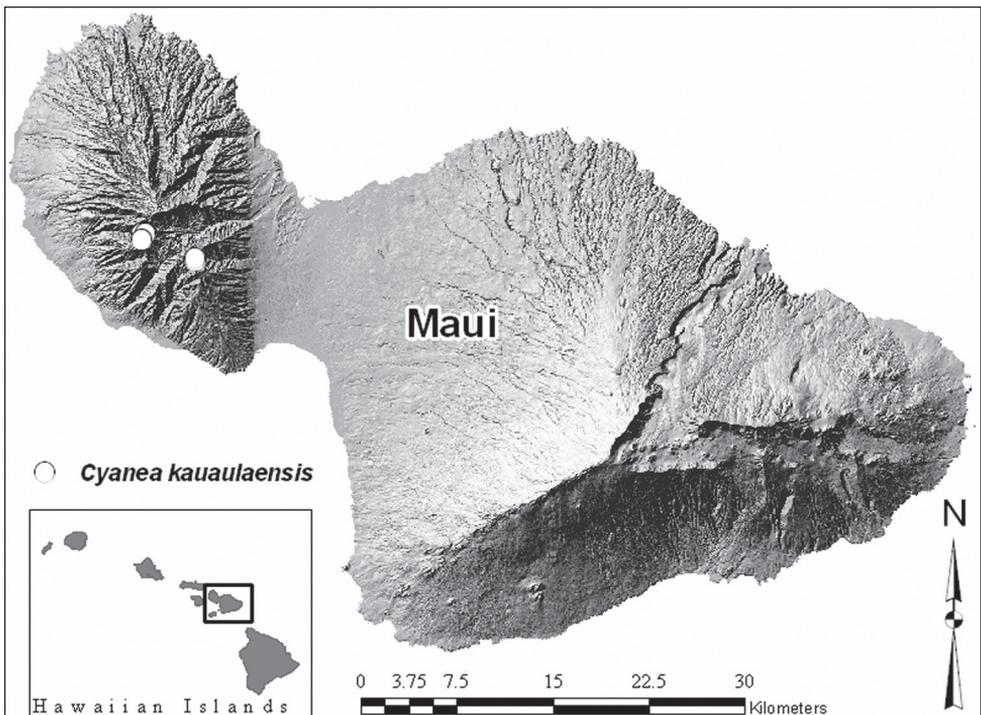


Figure 1. Distribution map of *Cyanea kauaulaensis* showing known localities on East Maui.

Lammers (1990) and examination of type collections at the BISH and W herbaria, *C. glabra* differs from this new species in having dimorphic leaves which are pinnatifid in juvenile plants with aculeate petioles and both surfaces of the midrib and veins, adult plants with 6–8-flowered inflorescences, flowers with larger hypanthium 7–10 mm long, larger calyx lobes 2–8 mm long, larger, often purple-tinged, strongly curved corollas 50–60 mm long, and somewhat larger, ellipsoid fruits 10–15 mm long crowned by the persistent calyx lobes. For consistency with other treatments and descriptions, measurements given below are based on dried herbarium specimens, although descriptions have been supplemented with pickled material and field photos.

Systematics

Cyanea kauaulaensis H. Oppenheimer & Lorence, sp. nov.

urn:lsid:ipni.org:names:77120339-1

http://species-id.net/wiki/Cyanea_kauaulaensis

Figures 2, 3

Species allied to Cyanea profuga C. Forbes, differs in its narrower leaves 5–7 cm wide, inflorescences with more numerous flowers (up to 20); flowers with smaller, lanceolate to linear calyx lobes 2–3 × 0.5–0.7 mm, apex acute to acuminate, shorter than the hypanthium, comparatively shorter corolla lobes 1/3–2/5 as long as the tube, and subglobose to obovoid orange fruits.

Type. USA. HAWAIIAN ISLANDS: West Maui: Lahaina District, N fork of Kaua`ula Valley, 910m (3000 ft), 2 Dec 2008, H. Oppenheimer & S. Perlman H120806 (Holotype PTBG-058138 [+ spirit collection]!; Isotypes BISH!, US!).

Description. *Unarmed shrubs* 2–4 m high, many-branched from the base with many basal shoots, stems light brown, erect to arching, up to 6m long, sometimes leaning on adjacent vegetation, often rooting where in contact with soil, leaf scars subcircular to broadly obovate-depressed; latex white. *Leaves* clustered near the end of the branches, when fresh light green on both surfaces, fleshy, the adaxial surface moderately glossy, drying membranaceous to chartaceous, glabrous on both surfaces, in juvenile plants occasionally minutely muricate adaxially along costa, elliptic, oblong, or elliptic-oblong, in adult plants blade 19–30 × 5–7 cm, base attenuate to cuneate, often asymmetrical, apex attenuate, acuminate, or cuspidate, margins entire to minutely serrulate-dentate, often undulate when fresh, sometimes coarsely serrate-dentate in juvenile plants; petioles 5–10 cm long, glabrous. *Inflorescences* axillary and on leafless nodes, developing along stems after leaves have fallen on well developed individuals, up to 30 per stem, mostly perpendicular to the stem, 5–20 flowered, peduncles 15–70 mm long, glabrous. *Flowers* on pedicels (4) 8–12 mm long, filiform, glabrous, subtended by caducous linear-subulate to linear bracts 12–20 × 3 mm, margins minutely serrulate, glabrous, pedicels with 2–3 glabrous subulate-oblong bracteoles 0.3–0.6 mm long; hypanthium 4–5 × 2.5–4 mm, broadly ellipsoid to obovoid-obconic; calyx lobes 2–3 × 0.5–0.7 mm, lanceolate to linear, apex acute to acuminate, caducous in fruit;

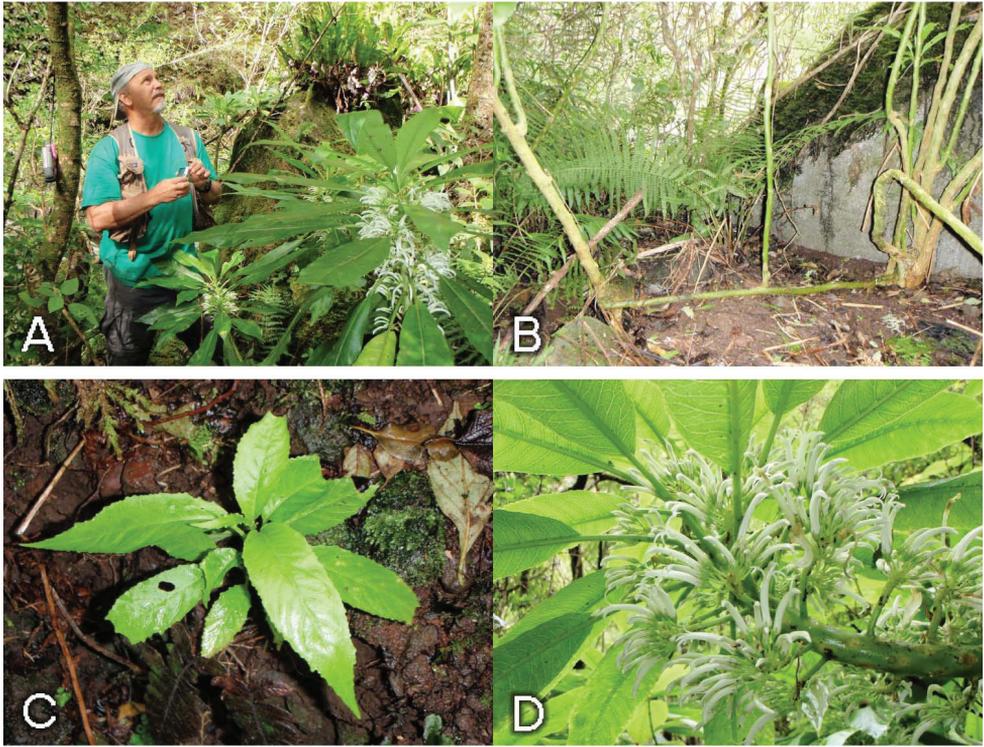


Figure 2. *Cyanea kauaulaensis*. **A** habit, with Steve Perlman (Oppenheimer & Perlman H120806) **B** base of plants showing new stems arising from decumbent branch (Oppenheimer & Perlman H120806) **C** juvenile plant (Oppenheimer & Wood H20928) **D** flowering stem (Oppenheimer & Perlman H120806); photos by H. Oppenheimer.

corolla white, tubular, round in cross section, gently curved to suberect, 28–35 × 3–4 mm, externally glabrous, internally minutely papillose, the tube 23–27 mm long, the lobes 5–10 mm × 0.5–0.9 mm medially, linear-subulate, reflexed, initially 1/3 to 2/5 as long as the tube but eventually splitting more deeply; staminal column glabrous, anthers 6–7 mm long, glabrous, the lower 2 with apical tufts of white hairs 3–4 mm long. *Fruits* bright orange when ripe, 8–10 mm in diameter, globose to obovoid, smooth, apex crowned by an apicular ring, calyx lobes caducous very early when fruits still small and green; old infructescences often producing leaves and continuing to develop as lateral shoots. *Seeds* numerous, embedded in translucent pulp, ovoid-ellipsoid, 0.5–0.6 × 0.35–0.4 mm, testa brown, shiny, smooth with faint striations.

Distribution. Known only from West Maui, Hawaiian Islands.

Habitat and ecology. *Cyanea kauaulaensis* occurs in riparian sites, on talus or basalt boulder-strewn slopes along perennial streams at elevations of 732 to 914 m. The plant community represents a *Metrosideros* Banks ex Gaertn. lowland wet forest. The most common associated woody elements are species of *Antidesma* L., *Boehmeria* Jacq., *Broussaisia* Gaud., *Cheiodendron* Nutt. ex Seem., *Clermontia* Gaud., *Coprosma*

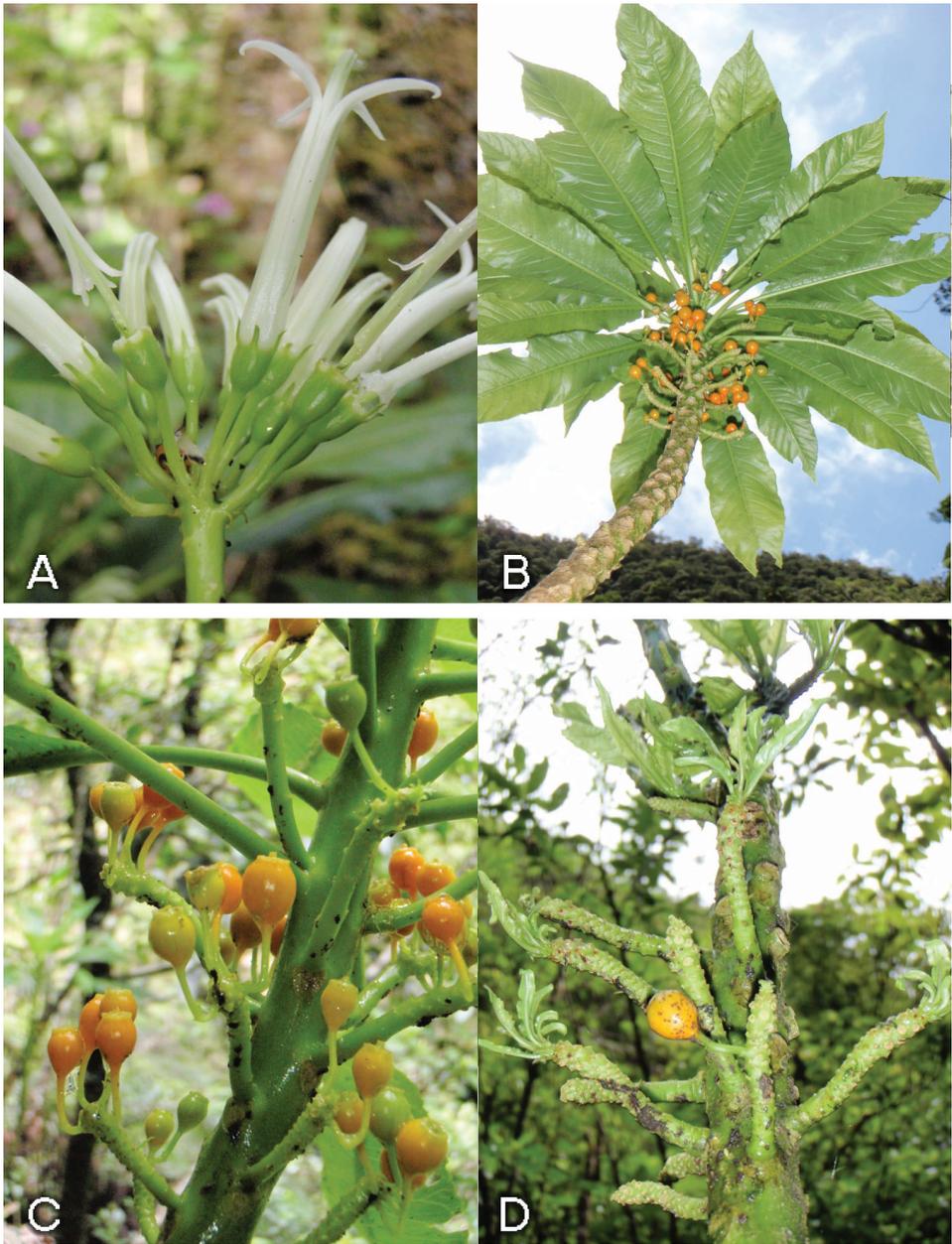


Figure 3. *Cyanea kauaulaensis*. **A** inflorescence (Oppenheimer & Perlman H120806) **B** fruiting stem (Oppenheimer et al. H40919) **C** infructescences (Oppenheimer et al. H40919) **D** old infructescences becoming lateral shoots (Oppenheimer & Wood H20928); photos by H. Oppenheimer.

J.R. Forst. & G. Forst., *Cyrtandra* J.R. Forst. & G. Forst., *Dodonaea* Mill., *Dubautia* Gaud., *Ilex* L., *Kadua* Cham. & Schldtl., *Perrottetia* Kunth, *Pipturus* Wedd., *Psychotria* L., *Urera* Gaud., and *Xylosma* G. Forst. Ferns including species of *Asplenium* L.,

Cibotium Kaulf., *Cyclosorus* Link, *Deparia* Hook. & Grev., *Diplazium* Sw., *Dryopteris* Adans., *Elaphoglossum* Schott ex J. Sm., *Microlepia* C. Presl, *Pteris* L., *Sadleria* Kaulf., *Tectaria* Cav., and *Vandenboschia* Copel. are prevalent. *Freycinetia arborea* Gaud. is a widespread liana, and several herbaceous species of *Peperomia* Ruiz & Pav. are also present. The sedge genera *Machaerina* Vahl. and *Rhynchospora* Vahl are also frequent. Soil is of typical basaltic origin. The average annual rainfall is approximately 3000 mm. Due to the steep canyon walls, often 700 m tall, direct sunlight is restricted to midday, and varies seasonally. Plants occur on both sides of the streams, with no apparent preference. Adult plants are clumped (Fig. 2A) and often many branched from the base, the decumbent branches often rooting when in contact with the ground and forming “runners”, often with erect shoots (Fig. 2B). Stems are erect to ascending or vine-like, to 6m long, often leaning on and tangled with adjacent vegetation, growing on lower talus slopes in riparian areas along perennial streams. On some stems old infructescences were observed to produce leaves and continue to grow as lateral shoots (Fig. 3D). This may represent a mechanism for producing lateral branches.

Phenology. *Cyanea kauaulaensis* has been observed flowering from late summer through January, followed by fruits maturing in March and April. Sporadically, some individuals may possess a few flowers or fruits earlier in summer.

Etymology. The specific name honors Kaua`ula Valley, a large, amphitheatre-headed valley on leeward Mauna Kahalawai (aka West Maui). *Lit.*, the red rain (Pukui et al. 1966), + Latin suffix *-ensis*, indicating a place of origin or growth. Kaua`ula Valley is an important site not only botanically, but economically (as a water source) as well as culturally and spiritually for Native Hawaiians.

Conservation status. *Cyanea kauaulaensis* should be considered Critically Endangered due to its limited range, low population numbers, lack of population structure and poor seedling recruitment, probable loss of most or all of its avian pollinators and dispersal agents, landslides, flooding, herbivory by alien slugs and rats, and competition with alien plants such as *Ageratina adenophora* (Sprengel) R.M. King & H. Rob., *Buddleia asiatica* Lour., *Coffea arabica* L., *Cortaderia jubata* (Lemoine ex Carrière) Stapf, *Erigeron karvinskianus* DC, *Macaranga tanarius* (L.) Müll. Arg., *Melinis minutiflora* P. Beauv., *Rubus rosifolius* Smith, *Setaria palmifolia* (J. König) Stapf. and *Toona ciliata* M. Roem. Approximately 45 plants plus four seedlings were observed during the recent visits in Kaua`ula Valleys north fork, three in the south fork, and 12 in Waikapu Valley. Recently, a new species of the endemic Hawaiian genus *Stenogyne* Bentham (Lamiaceae) was described from elsewhere in Kaua`ula Valley (Wood and Oppenheimer 2008). Additionally, an undescribed taxon in *Tetramolopium* Nees (Asteraceae) is also under study and is known from only Kaua`ula Valley and one additional site, also on West Maui.

When evaluated using the IUCN Red List criteria *Cyanea kauaulaensis* falls into the Critically Endangered (CR) category, a designation reserved for species facing the greatest risk of extinction in the wild, as it fulfills the following criteria: B) Extent of occurrence estimated to be less than 100 km² or area of occupancy estimated to be less than 10 km²; 2c) Continuing decline observed in area, extent and/or quality

of habitat; 2c(iv) Continuing decline observed in number of mature individuals; C) Population size estimated to number fewer than 250 mature individuals and C2a(1) no subpopulation estimated to contain more than 50 mature individuals. This species has a known range of less than 100 km², and an area of occupancy of less than 10 km² currently known from three populations, two in Kaua`ula Valley and one in Waikapu Valley, both on West Maui. Furthermore, *Cyanea kauaulaensis* should be considered by the US Fish & Wildlife Service as a Candidate for listing as Endangered under the Endangered Species Act of 1973, and a Recovery Plan written, funded, and implemented.

The Maui Invasive Species Committee (MISC) has been working to control the *Cortaderia* infestation in both valleys on the surrounding, vertical cliffs. The region has escaped the ravages of introduced feral ungulates due to the extremely rugged topography. This new species is a target of the Plant Extinction Prevention Program (PEPP), with efforts made to collect seeds from every individual plant, propagation of nursery stock, restoration outplanting into appropriate habitat, and *ex situ* seed storage. In April of 2009 seeds from 32 of the 45 plants in the north fork subpopulation were collected. The south fork subpopulation was sampled in 2004 and the population seemed stable with twelve plants. It was revisited in October 2010. Only three individuals remained, and the habitat had been significantly degraded by dense stands of *Coffea arabica*. Plants have been successfully grown at Lyon Arboretum, Honolulu, the National Tropical Botanical Garden, Kaua`i, and the Olinda Rare Plant Facility on Maui. In October 2010 84 plants from seeds collected in the north fork were planted in the south fork, in the hopes of augmenting the diminishing population there. In September of 2011, 16 plants from the north fork of Kaua`ula Valley were planted adjacent to the Waikapu population.

Specimens examined. USA. Hawaiian Islands. Maui [West Maui]: Lahaina District, AMFAC survey by TNCH, Kauaula Valley, back of valley near streambed, 27 Oct 1989, Perlman & Gon 10841 (F, BISH, PTBG, US); back of Kauaula Valley on west side, 866 m, 2 Dec 2008, Perlman & Oppenheimer 21284 (PTBG, BISH, NY, US), east side fork, 18 Jan. 1995, Perlman et al. 14626 (F, MO, NY, PTBG), 2700 ft. (823m), Perlman et al. 18875 (OSH, PTBG); Kaua`ula Valley, N fork, 3000 ft (914m), 6 Apr 2009 (fr), Oppenheimer et al. H40919 (BISH, PTBG [+ spirit coll.]), Kaua`ula Valley, N fork, 3000 ft (914m), 18 Feb 2009, Oppenheimer & Wood H20928 (PTBG), 2950 ft (899m), 1 July 2009, Oppenheimer & Perlman H70901 (PTBG); North fork headwaters, 2780 ft (847m), 26 Sep 2009, Oppenheimer & Kia 90914 (PTBG), Kauaula Valley, upper south fork below Helu, 2700 ft (823m), 18 Jan 1995, Wood et al. 3940 (PTBG); Wailuku District, Waikapu Valley, north fork, 2400 ft (732m), Jul 2011, Oppenheimer & Bustamente H71103 (BISH, PTBG).

Discussion. Several attempts have been made to divide *Cyanea* into sections (Hillebrand 1888; Rock 1919; Wimmer 1943; St. John 1969, Stone 1967, Lammers 1990), but none successfully arranges the genus into clear-cut phylogenetic entities. Givnish et al. (1995) divide the genus into two distinct clades: one with purple fruits and another with orange fruits. *Cyanea kauaulaensis* belongs to a lineage that previously has not been represented on Maui. Based on its glabrous leaves and similar floral

morphology, the new species appears to be most closely related to the rare *C. profuga* C. Forbes of Moloka`i, which was placed by Rock (1919) in his section *Genuinae*. The latter differs from the new species in having inflorescences with fewer (9–12) flowers, flowers with larger linear-elliptic or oblong calyx lobes 5–9 mm long and 1.2–2 mm wide, longer than the hypanthium, its comparatively longer corolla lobes $\frac{1}{4}$ to almost $\frac{1}{2}$ as long as the tube, and ellipsoid-cylindrical fruits which also ripen orange. Seedlings of both species grown together at the Olinda Rare Plant Facility are virtually indistinguishable from one another. The islands of Moloka`i, Lana`i, Kaho`olawe, and Maui were once a single, large land mass, referred to as Maui Nui, and their biota shares many components (Price and Elliott-Fisk 2004).

The following couplets can be inserted into the most recent revision of *Cyanea* (Lammers in Wagner et al. 1990) to separate *C. kauaulaensis* from *C. profuga*.

- 15(13) Leaf margins irregularly lobed or cleft; Mo **11** *C. dunbariae*
 15 Leaf margins callose-toothed, erose, entire or minutely serrulate (15')
 15'(15) Leaf margins entire or minutely serrulate; calyx lobes lanceolate to linear, apex acute to acuminate; M *C. kauaulaensis*
 15' Leaf margins callose-toothed or erose..... (16)
 16(15') Calyx lobes oblong, apex rounded and apiculate; Mo**38** *C. profuga*
 16 Calyx lobes dentiform or triangular, apex acute to acuminate (17)

Acknowledgements

The authors extend our deepest gratitude to Makila Land Co. and Wailuku Water Co. for permission to access Kaua`ula Valley and Waikapu Valley respectively; The West Maui Mountains Watershed Partnership for assistance in the field; Windward Aviation, Inc. for their skilled helicopter pilots; horticulturists Anna Palomino at the Olinda Rare Plant Facility, Bob Nishek at the National Tropical Botanical Garden (NTBG), and Nellie Sugii at the Lyon Arboretum; Alvin Yoshinaga and Tim Kroessig at the Lyon Arboretum Seed Storage Laboratory; botanists Steve Perlman and Ken Wood of NTBG for their assistance in the field as well as many helpful discussions; the Maui Invasive Species Committee for field assistance and *Cortaderia* grass control efforts. Clyde Imada at BISH was extremely helpful finding both Wimmers publication as well as C. N. Forbes' field notes, helping to clearly establish *C. kauaulaensis* as distinct from *C. glabra*. Michael Kiehn (Vienna University) assisted with providing information on the isotypes of *C. glabra* at WU. This manuscript was greatly improved by suggestions from Tom Lammers at University of Wisconsin at Oshkosh and anonymous reviewers. The Plant Extinction Prevention Program is funded in part by the U.S. Fish & Wildlife Service, and the State of Hawaii Dept. of Land & Natural Resources, Division of Forestry and Wildlife. We thank the curators of the Bernice P. Bishop Museum herbarium (BISH) and National Tropical Botanical Garden herbarium (PTBG) for access to specimens. The color plates were composed by Neil Brosnahan.

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Systematics of *Trigonochloa* (Poaceae, Chloridoideae, Chlorideae)

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Academic editor: Leonardo Versieux | Received 9 May 2012 | Accepted 16 June 2012 | Published 29 June 2012

Citation: Snow N, Peterson PM (2012) Systematics of *Trigonochloa* (Poaceae, Chloridoideae, Chlorideae). *PhytoKeys* 13: 25–38. doi: 10.3897/phytokeys.13.3355

Abstract

A systematic treatment including descriptions and a key for identification is provided for the two species of *Trigonochloa*, a genus recently segregated from the polyphyletic *Leptochloa* s.l. *Trigonochloa* ranges from southern Africa east to India and Sri Lanka, reflecting the widely ranging *T. uniflora*. *Trigonochloa rupestris* has a more limited distribution from East Africa to Yemen. *Trigonochloa* is diagnosable from other chloridoid grasses based on its unusually flaccid and membranous leaves that have uniquely enlarged lateral cells in the parenchyma sheath surrounding the vascular bundles in *T. uniflora* (unconfirmed for *T. rupestris* given limited material), primary and secondary vascular bundles that do not project above or below in fresh material, XyMS+ leaf anatomy, narrow spicate primary inflorescence branches, spikelets with one (or rarely two) florets, thinly membranous to hyaline lemmas, and a trigonous caryopses that bear a narrow but deep sulcus on the hilar side. Lectotypes are designated for *Agrostis montana* and *Cynodon gracilis*. The synonym *Leptochloa laurentii* De Wild. is confirmed for *T. uniflora*.

Keywords

Conservation, *Leptochloa*, leptotypification, Poaceae, systematics, taxonomy

Introduction

The generic boundaries of *Leptochloa* P. Beauv. have been contentious more or less continuously since the genus was first described in 1812 (Valls 1978; McNeill 1979; Phillips 1982; Snow 1997). Many previous discussions of generic boundaries focused

on whether *Diplachne* P. Beauv., often included in *Leptochloa*, could be recognized as a distinct genus (Phillips 1974; Jacobs 1987). A global monograph of *Leptochloa* (Snow 1997) based on morphology, lemmatal micromorphology (Snow 1996), anatomy of stems and leaves, and caryopsis morphology (Snow 1998) tested the monophyly of the genus in the context of a few putatively related genera. Preliminary results from cladistic studies using morphology were far from conclusive and at best suggested that *Diplachne* was not easily segregated from *Leptochloa* (Snow 1997). One noteworthy aspect of the cladistic studies (Snow 1997) was the consistent sister status of the *L. uniflora* Hochst. ex A. Rich. and *L. rupestris* C.E. Hubb. to other members of *Leptochloa* s.l., which was predictable since these two species share many morphological and anatomical characteristics absent in other members of *Leptochloa* s.l.

Leptochloa s.l. has been considered a diverse assemblage of C₄ (nicotinamide adenine dinucleotide co-factor malic enzyme [NAD-ME] and phosphoenolpyruvate carboxykinase [PCK]) grasses in the tribe Chlorideae (Clayton and Renvoize 1986; Watson and Dallwitz 1992; Soreng et al. 2012) with approximately 32 annual or perennial species (Snow 1997, 2003). The range of morphological variation within many species of *Leptochloa* is significant (Snow 1997, Peterson et al. 2012). However, *Leptochloa* s.l. is demonstrably polyphyletic when tested with molecular DNA markers (Columbus et al. 2007; Peterson et al. 2010, 2012). In a large phylogenetic study of the Chloridoideae based on seven DNA sequence markers the species of *Leptochloa* s.l. were found to form three separate lineages (Peterson et al. 2010), and more recently using six DNA markers these species were found to form five separate lineages, each treated as a separate genus: *Dinebra* Jacq., *Diplachne*, *Disakisperma* Steud., *Leptochloa* sensu strictu, and *Trigonochloa* P.M. Peterson & N. Snow (Peterson et al. 2012). Peterson et al. (2012) found that *Trigonochloa uniflora* (Hochst. ex A. Rich.) P.M. Peterson & N. Snow and *T. rupestris* (C.E. Hubb.) P.M. Peterson & N. Snow consistently resolved as a strongly supported clade (Peterson et al. 2012) outside of subtribe Elusiniinae.

Leptochloa uniflora was first described by Richard (1851). Chippindale (1955) later transferred this species to *Craspedorhachis* Benth., although her concept of *Craspedorhachis* was broader than that of other treatments (Clayton and Renvoize 1986; Gibbs-Russell et al. 1991; Watson and Dallwitz 1992). One current concept of *Craspedorhachis* includes three species that collectively occupy parts of sub-Saharan Africa and Madagascar (e.g., Simon et al. 2011).

Bentham (1882: 108) described two sections in *Leptochloa*, which he maintained distinct from *Diplachne*. In *L.* sect. *Pseudocynodon* Benth., characterized by spikelets having only one or two florets, Bentham ascribed *L. uniflora* and *L. neesii* (the latter of which included his concept of *L. polystachya* Benth.). The latter species, which is also characterized by one floret per spikelet (or in rare cases two), differs significantly from *Trigonochloa* by characters of leaf anatomy and has been transferred to *Dinebra* (Peterson et al. 2012).

The purpose of this paper is to present the systematics of *Trigonochloa* as the first step in revising *Leptochloa* s.l. into monophyletic genera.

Materials and methods

Approximately 110 collections were analyzed from the following 15 herbaria: B, BM, BRI, CANB, K, M, MO, NY, P, PRE, S, TAES, US, W, Z. A few specimens previously determined incorrectly as *L. uniflora* (Gould and Soderstrom 1974; Snow 1997) have been identified subsequently as *Leptochloa neesii* Benth. [= *Dinebra neesii* (Benth.) P.M. Peterson & N. Snow] (Peterson et al. 2012). Geographical ranges are summarized using Brummitt (2001) and herbarium acronyms follow Thiers (2012).

Fresh leaf samples of *Trigonochloa uniflora* and *Leptochloa* s.l. were studied for, but not summarized, in Snow (1997). The first author also viewed black and white anatomical photographs of *T. uniflora* taken by R. Ellis housed at PRE (Davidse & Ellis 5925, Ellis s.n., Ellis 3635, but see in particular Ellis 4534) and was able to confirm observations of *T. uniflora* made previously by Metcalfe (1960). Stems (culms) were hand-sectioned with fresh or rehydrated material. The sources of anatomical vouchers are mostly at MO: *T. rupestris*: Gilbert et al. 249, Pappi 2821; *T. uniflora*: Snow & Burgoyne 6978, Siame 581, Ellis 2780, Davidse et al. 6643. Lemmatal micromorphology of *Trigonochloa* and other species of chloridoid grasses was studied using scanning electron microscopy (Snow 1996), and caryopses were studied using simple light microscopy (Snow 1998).

Results and discussion

Trigonochloa uniflora and *T. rupestris* are highly similar in gross morphology (Phillips 1974, 1995), lemmatal micromorphology (Snow 1996), stem and leaf anatomy, and caryopsis morphology (Snow 1998; Peterson et al. 2012). The genus differs from *Lopholepis* Decne., *Mosdenia* Stent, *Perotis* Aiton, and *Toliara* Judziewicz by having several to numerous unilateral, secund racemes scattered along a central axis rather than a single raceme or false spike (Watson and Dallwitz 1992; Judziewicz 2009). Species placed in *Lopholepis*, *Perotis*, and *Toliara* have 1-nerved lemmas whereas both species of *Trigonochloa* they are 3-nerved (Watson and Dallwitz 1992).

Leaf anatomy. The transverse anatomical features of the leaves of these two species differ in several significant ways from the rest of *Leptochloa* s.l. The leaf blades of both species are quite thin (and flaccid) when fresh in *T. uniflora* and somewhat translucent. They also can be relatively broad basally and relatively short, thus appearing narrowly ovate.

Epidermal preparations of *T. uniflora* made separately by the first author (Davidse & Ellis 5925, MO; unpublished) and by Roger Ellis (Ellis 1928; photos on herbarium specimen; PRE) show the adaxial (more so) and abaxial (less so) surfaces (apart from areas above bulliform cells) to be covered with narrow rows of relatively small cells, virtually all of which are capped by a centrally located and prominent papilla (Snow, unpubl.). In addition, the cells of the leaf blade epidermis and lemma surface are not always clearly differentiated into short and long cells (Snow 1996).

Keels (areas of parenchyma in the middle of the leaf blade lacking vascular bundles) are absent, or if present then small, and if present then lacunae within the parenchyma are absent. Primary and secondary vascular bundles differed only slightly in size and in fresh material do not project adaxially or abaxially. Bulliform cells were noted between adjacent vascular bundles. Colorless cells were not observed between vascular bundles, but they do occur adaxially to the primary and secondary bundles, and may be the only cell layer between the epidermis and the secondary vascular bundles. As many as five successive colorless cells (in cross section) were observed adaxially to a secondary vascular bundle on *Ellis 4534*. Metcalfe (1960: 285) reported only a single bundle sheath in *Leptochloa uniflora* and first noted the significantly enlarged parenchyma sheath cells at 3 and 9 o'clock, which he termed *lateral cells*, which we confirmed for this species (see in particular images with *Ellis 4534* at PRE). The lateral cells often penetrate deeply into laterally adjacent mesophyll and are nearly completely filled by a large chloroplast. Enlarged lateral cells were not clearly evident in the single specimen of *T. rupestris* examined from limited rehydrated material so we cannot yet confidently confirm nor reject their presence in this species.

Hattersley and Watson (1976: 303) reported the species as being XyMS-, based on the implied lack of intervening cells between the metaxylem and PCR sheath given the results of Metcalfe (1960). Valls (1978: 73–74) reported the presence of a double sheath for *L. uniflora* and reported that walls of the inner sheath were “exceptionally thin-walled”. Valls (1978), however, may have used specimens incorrectly identified that in actuality were *Leptochloa neesii*. Specimens studied by Roger Ellis, and seen for this study, confirm the observations of Metcalfe (1960) of the enlarged lateral cells and the presence of a double sheath, supporting the XyMS+ condition. However, the “outer sheath” cells only occur on the distal edges of the enlarged lateral cells, such that colorless cells typically occur adaxially and abaxially to the proximal part of the lateral cell (i.e., that part adjacent to the vascular bundle), with smaller chloroplast-bearing cells bearing smaller and more diffuse chloroplasts adjacent to the part of the lateral cell that occurs closest to the intervacular region. With permission while on site at PRE in 1996, the first author took 35 mm SLR photographs of the original black and white images of *Ellis 4534*, which show the leaf anatomy clearly. However, photos of the original images did not reproduce at a high enough quality to include in this paper. Other images of the leaf anatomy of *Trigonochloa* are unknown to the present authors.

Stem anatomy. Both species have a solid culm. *Trigonochloa uniflora* has inner and outer sclerenchymatous rings, although an inner ring was absent for *T. rupestris*.

Lemmatal micromorphology. The two species share a unique combination of lemmatal micromorphological characters compared to other species of *Leptochloa* s.l. (Snow 1996). Cork cells and bicellular microhairs were present; macrohairs were terete (not crispate) and obtuse apically (not clavicorniculate; Snow 1996). Lemmatal characters in many species of *Leptochloa* s.l. but lacking in *Trigonochloa* included silica cells, and papillate long and papillate short cells (Snow 1996).

Caryopsis morphology. The caryopsis is trigonous in transverse section and possesses a narrow but deep hilar sulcus (=longitudinally grooved); the pericarp is tightly

adnate (Snow 1998). This combination of caryopsis characters is unique among genera of chloridoids (Peterson et al. 2012). In our earlier molecular study *Trigonochloa uniflora* is sister to the *Mosdenia-Toliara-Lopholepis-Perotis* clade that lies outside of the subtribe Eleusininae (Peterson et al. 2012). Species of *Mosdenia* and *Perotis* have longitudinally-grooved caryopses that are dorsally or laterally compressed but not trigonous.

Taxonomic treatment

Trigonochloa P.M. Peterson & N. Snow. Ann. Bot. 109: 1327. 2012.

<http://species-id.net/wiki/Trigonochloa>

Type species: *T. uniflora* (Chipp.) P.M. Peterson & N. Snow.

Description. Plants annual to short-lived perennial, sometimes rhizomatous or stoloniferous. Culms (15–)35–130 cm long, terete in cross section, solid, decumbent or clambering to erect; nodes glabrous. Leaf sheaths half as long to slightly longer than internodes, glabrous or ciliate apically along margins; ligules 1–3.5 mm long, membranous, irregularly lacerate with age; leaf blades 1–13(–17) cm long, 0.3–14(–19) mm wide, linear to broadly ovate, flat, typically thin and flaccid, apex acuminate to acute. Panicles 17–55 cm long, 2.0–8 cm wide, exerted at maturity, open, narrowly oblong to narrowly elliptic, composed of several to numerous unilateral, second spikes or spicate racemes scattered along a central axis; rachis semi-terete; branches (1.5–)2–7 cm long, ascending, straight or slightly drooping. Spikelets 1.9–2.8 mm long, 1 (rarely 2-flowered), laterally compressed, sessile, overlapping; disarticulation above the glumes; glumes 1.8–3.1 mm long, subequal, as long or longer than the floret, subequal, linear to narrowly ovate, 1-nerved, apex acute to acuminate, mucronate or emucronate; lemmas 1.2–2.6 mm long, ovate, 3-nerved, thinly membranous to hyaline, minutely hairy along the nerves, apex acute, entire, awnless; paleas 1.5–2.5 mm long, keels ciliolate. Stamens 3. Caryopses 1–1.2 mm long, narrowly elliptic, trigonous in cross section, narrowly but deeply sulcate on the hilar side; surface smooth to slightly rugose-striate, light brown, pericarp fused, tightly adherent to endosperm. $2n = 36$ for *T. uniflora* (Gould and Soderstrom 1974).

Comments. An appropriate common generic name to differentiate *Trigonochloa* from other members of *Leptochloa* is “triangle-seed grass”.

Key to species of *Trigonochloa*

- 1 Leaf blades 0.3–4.0 (–5.0) mm wide, more or less linear to narrowly ovate; leaf sheaths margins minutely ciliate towards the apex, the collar never pilose *Trigonochloa rupestris*
- Leaf blades 5–14 (–19) mm wide, ovate to broadly ovate; leaf sheaths glabrous or sparsely pilose near collar but not ciliate along upper margins *Trigonochloa uniflora*

Trigonochloa rupestris (C.E. Hubb.) P.M. Peterson & N. Snow. Ann. Bot. 109: 1328. 2012.

http://species-id.net/wiki/Trigonochloa_rupestris

Figure 1A–E

Leptochloa rupestris C.E. Hubb., Bull. Misc. Inform. Kew: 195. 1941.

Type. SOMALIA. Mt. Wobleh, J.B. Gillett 4981 (holotype: K!; isotype: K!)

Description. Plants perennial. Culms 35–85 cm tall, 0.7–1.4 mm wide at base, decumbent or sprawling-stoloniferous to erect, often arising from a thick root crown, branching (often profusely); internodes (0.7–)2.0–5.5(–8.5) cm long, soft to strongly lignified. Leaf sheaths longer or shorter than internodes, glabrous on sides but sometimes minutely papillate at high magnification, margins ciliate (trichomes <1 mm long); collar green; ligules 1.0–2.5 mm long, truncate or obtuse; blades 2.2–5.5(–10.7) cm long, 0.3–4.0(–5.0) mm wide, linear to narrowly ovate, glabrous above, glabrous below but sometimes densely minutely papillate, midrib prominent. Panicles 17–35 cm long, 2.0–4.5 cm wide with 13–66 branches, the branches (1.5–)2.0–4.5 cm long, minutely scabrous, the axils glabrous or at most scabrous and more or less short pilose on the exterior. Spikelets 2.0–2.8 mm long, 1-flowered, nearly sessile or with minute pedicels, more or less imbricate, callus area glabrous; lower glumes 2.4–3.1 mm long, membranous, lanceolate, midnerve scabrous, apex acute to acuminate; upper glumes, 2.2–2.8 mm long, otherwise like lower glumes; lemmas 1.2–2.1 mm long, ovate, light green or nearly white, the lateral nerves faint, sericeous along midnerve (use high magnification), the hair tips rounded, apex acute and awnless; paleas 1.6–2.0 mm long, hyaline, narrowly ovate, glabrous or sparsely sericeous near nerves, apex acute to obtuse; anthers 1.0–1.4 mm long, yellow to brownish green. Caryopses ca. 1.0 mm long and 0.4 mm wide, trigonous in cross section, the surface smooth.

Phenology. Flowering June through January.

Distribution. This species is found in Yemen and Eritrea south to Kenya in woodlands, hillsides, bushland and on damp rocks along streams; 900–1800 m. [Taxonomic Database Working Group (TDWG): 24: ERI, ETH, SOM; 25: KEN, UGA].

Conservation status. Since many parts of its range are presently inaccessible to botanists or still remain inadequately surveyed this species is data deficient. Additional observations and collections are highly desirable.

Etymology. The epithet *rupestris* is Latin for “of rocks”, presumably in reference to observations of the habitat of the type collection.

Vernacular name. Somalian triangle-seed grass.

Comments. This species closely resembles *T. uniflora*, with which it is morphologically similar. The best character to recognize *T. rupestris* from *T. uniflora* is leaf blade width. However, its sprawling, branching, and perennial growth form with narrow culms typically distinguish it from *T. uniflora*. The holotype and isotype are aberrant in their lack of ciliate sheath margins, but otherwise accord with the diagnostic characters. The observation of Phillips (1974) that *T. rupestris* has more widely divergent leaf blades than *T. uniflora* cannot be reliably applied to dried material. None of the specimens we

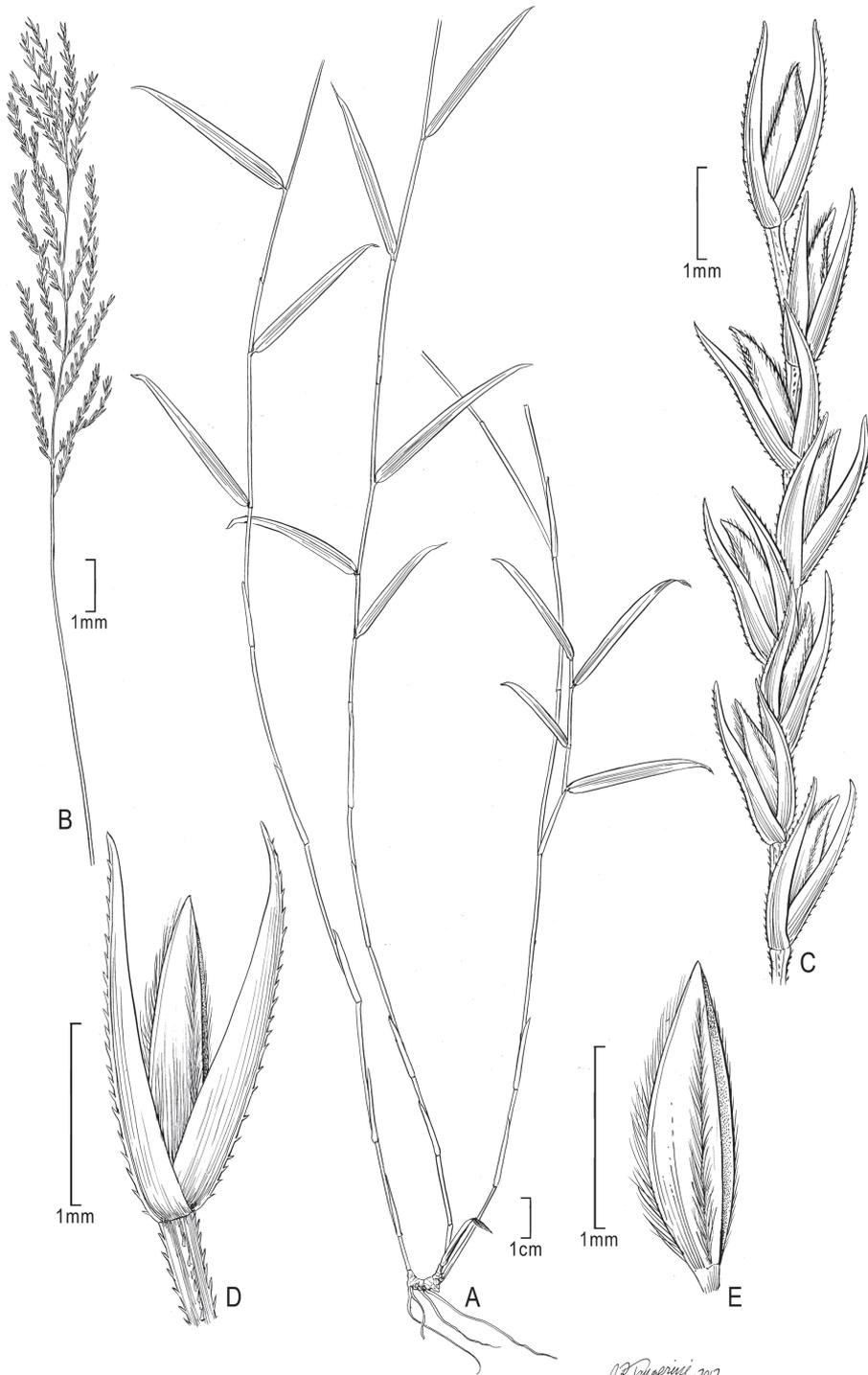


Figure 1. *Trigonochloa rupestris* (C.E. Hubb.) P.M. Peterson & N. Snow **A** Habit **B** Inflorescence **C** Portion of inflorescence branch **D** Spikelet **E** Floret. Drawn from Wood 2000.

have seen confirmed her observation (Phillips 1974) that *T. rupestris* is rhizomatous (i.e., culms within the soil), but the stems can be somewhat sprawling and stoloniferous.

Specimens examined. Eritrea. Donkollo, Schweinfurth 207 (P); Dongollo Presso Ghinda, Pappi 2821 (MO); Monte Dijot, Pappi 2940 (US). Ethiopia. Gamo Gofa: 44 km from Jinka on road to Konso, ca. 3 km E of K'ey Afer, Gilbert et al. 8954 (K); 13 km N of Lante, 29 km N of Arba Minch, Gilbert et al. 8874 (K). Arba Minch, Gilbert et al. 249 (K, MO). Harar: "Rock Valley", 36 km along the road from Harar to Jijiga, Amshoff 5520 (B, MO); Errer valley, 22 km SE of Harar on hwy to Djigdjigga, Burger 1162 (K); 7 km from Harar towards Jijiga, Gilbert & Gilbert 1443 (K). Sidamo: Between the Genale Doria bridge and the main road Kebre Mengist-Neghelle, on the Biderre track, Friis et al. 1034 (K). Kenya. Rift Valley: West Suk Reserve, 30 mi N of Kitale, Bogdan 3429 (K); West Suk Reserve, 10 mi W of Kapenguria, Suam Riv. Valley, Bogdan 289 (K); West Suk, Marech Pass, 40 mi N of Kapenguria, Bogdan 3844 (K); 30 mi N of Nakuru, Bogdan 4891 (K, US); Kenya Grassland Research Station, Bogdan AB3964 (P). Somalia. "WOGR near Sheikh", Wood S/72/95 (K); Jifa Uri, Gillett 4838 (K, US). Uganda. Northern: Moroto Mountains, Karamoja, Napper 1509 (K); Warr, Karamoja, Thomas 3176 (K). Yemen. Habash, Jebel Melhan, Wood 2848 (BM, K); 2 mi W of Mefhek, Wood Y/75/727 (BM); by Wadi Dur, Udayn, Wood 2000 (K, US).

Trigonochoa uniflora (Hochst. ex A. Rich.) P. M. Peterson & N. Snow. Ann. Bot. 109: 1328. 2012.

http://species-id.net/wiki/Trigonochoa_uniflora

Figure 2A–H

Leptochloa uniflora Hochst. ex A. Rich., Tent. Fl. Abyss. 2: 409. 1851.

Craspedorbachis uniflora (Hochst. ex A. Rich) Chippind., Grasses and Pastures of South Africa 205, f. 182. 1955.

Cynodon gracilis Nees ex Steud., Syn. Pl. Glumac. 1: 213. 1854. TYPE: India, Ab. loco. Wight Herbarium 8895 (lectotype: K! designated here, no specimen number given in the protologue; isotype: K!).

Agrostis montana Krock., Fl. Siles. 1: 110. 1787. *Agrostis montana* Rottl. ex Hook. f., Fl. Brit. Ind. 7: 298. 1896, nom. inval. TYPE: India, Tinnevely; at Palamcotta, 28 Nov 1895, Rottler s.n. (lectotype: K! designated here).

Craspedorbachis menyharthii Hack. ex Schinz, Bull. Herb. Boissier, ser. 2, 1: 770. 1901. TYPE: Mozambique, Boruma, Tanuar, L. Menyharth 665 (lectotype: Z!, designated by Phillips 1974: 277 [who did not include the collection number]; duplicate of lectotype: W!).

Leptochloa laurentii De Wild., Miss. Em. Laurent i. 207. 1906. TYPE: Democratic Republic of the Congo, Kiri, E. Laurent s.n. (holotype: BR! [seen digitally, June 2012; barcode BR0000008761873]).

Type: Ethiopia, In valle fluvii Tacaze, Schimper 1707 (holotype: P!; isotypes: B!, BM!, GH!, K!, MO!, PRE!, S!, W!, photo ex W!)

Description. Plants annual (or possibly weakly perennial). Culms (15–)45–130 cm tall, 0.6–2.0(3.0) mm wide at base, generally erect, sometimes geniculate below and stoloniferous by rooting at the nodes, sometimes branching, arising from fibrous roots or occasionally from a short knotted-rhizome; internodes 2–8 cm long, soft, solid. Leaf sheaths mostly shorter than internodes, glabrous throughout or rarely sparsely pilose near the collar, the margins glabrous; collars green; ligules 1.5–3.5 mm long, broadly obtuse, lacerate; blades 1–13(–17) cm long, 5–14(–19) mm wide, ovate to broadly ovate, glabrous above and below, midrib prominent or not. Panicles 25–55 cm long, 5–8 cm wide with 22–90 branches, the branches 2.5–7.0 cm long, minutely scabrous, the axils mostly glabrous internally but short pilose on external side. Spikelets 1.9–2.7 mm long, 1-flowered or rarely 2-flowered, but if so, only a few per plant, nearly sessile or with minute pedicels less than 0.3 mm long, somewhat imbricate, callus area glabrous; lower glumes 1.8–2.3 mm long, narrowly triangular, minutely scabrous on mid-nerve, apex acuminate to mucronate; upper glumes 2.2–2.6 mm long, otherwise like lower glumes; lemmas 1.6–2.6 mm long, ovate, whitish or light green, the lateral nerves very faint, sparsely pubescent along nerves, apex awnless; paleas 1.5–2.5 mm long, subequal to lemma, narrowly ovate, glabrous, apex obtuse or sometimes acute; anthers ca. 1 mm long, dark purple to pale olive green. Caryopses ca. 1.2 mm long and 0.4 mm wide, trigonous in cross section, the surface smooth to slightly rugose–striate. $2n = 36$.

Phenology. Flowering throughout the year when adequate moisture is available.

Distribution. This species is scattered through the eastern and southern portions of sub-Saharan Africa, rarely in India, most common in Sri Lanka in forests and shady areas on hillsides, well-drained and often sandy soils in disturbed and riparian areas; 0–1200 m. [TDWG: 22: GHA, NGR, ZAI (Dem. Rep. Congo); 25: KEN, TAN; 26: ANG, MLW, MOZ, ZIM; 27: BOT, NAM, NAT, TVL; 40: IND, SRL].

Conservation status. Since the species is widespread it is of least concern (IUCN 2010) given its widespread occurrence. However, the typical size of populations is undocumented. The thinly membranous leaves likely are sought after by grazers, although the relative nutrition content of the leaves is unstudied.

Etymology. The specific epithet is from the Latin *uniflora*, with reference to the single floret per spikelet.

Vernacular names. Common triangle-seed grass. Kenya: Mkuse - Digo (Magogo and Glover 477, W).

Comments. The species description and distribution differ from Snow (1997) because some specimens therein were incorrectly identified as *Leptochloa neesii*.

Trigonochloa uniflora individuals vary significantly in growth habit. Most specimens are relatively delicate, sprawling annuals, but some specimens have more erect, relatively stout culms that appear to be weakly perennial. The more erect forms typically occur in somewhat more open areas and have thicker leaves, whereas the more slender forms that frequently root at the lower nodes, typically occur in shade and have thinner leaves.

The glumes of *T. uniflora* typically are longer than the single floret and may be mucronate. The caryopsis is sometimes dispersed with a tightly adnate lemma and palea,



Figure 2. *Trigonochloa uniflora* (Hochst. ex A. Rich.) P.M. Peterson & N. Snow **A** Habit **B** Inflorescence **C** Portion of inflorescence branch **D** Spikelet **E** Floret **F** Caryopsis, dorsal view **G** Caryopsis, ventral view **H** Caryopsis, cross section. **A–C, F–G** drawn from *Ballard 1489*; **D, E** drawn from *Chare 4434*.

which may enhance water absorption prior to germination. The apex of the leaf sheath can sometimes be sparsely pilose, whereas in contrast nearly all specimens of *T. rupestris* have ciliate sheath margins. Many specimens of *T. uniflora* from Sri Lanka resemble *T. rupestris* based on thin, sprawling culms. Two culms on Exell et al. 1060 (BM) have a sparse covering of papillose hairs on the upper and lower surfaces of the leaf blades.

Two counts of $2n = 40$ ascribed to *Triglochloa* (as *Leptochloa*) *uniflora* by Gould and Soderstrom (1974) were misidentifications of *Leptochloa neesii* (vouchers at US!). We confirm the voucher with a polyploid count of $2n = 36$ based on $x = 9$ for *Triglochloa* (*Leptochloa*) *uniflora* (Soderstrom and Kulatunge 1753, US!). In contrast, the count of $n = 10$ by Olorode (1975) has not been confirmed with a voucher.

Specimens examined. Angola. Cuanza Norte: Cazengo, Welwitsch 2981 (BM, K); Cazengo, Gossweiler 4421 (BM, K); Granja de S. Luiz, Gossweiler 5200 (BM). Ab. loco, Gossweiler 2966 (K) and 5444 (BM). Botswana. North-West: Riparian woodland, near Kasane, Blair Rains 67 (K, US). Dem. Repub. Congo. Haut-Katanga: Kibula, Callens 4776 (PRE). Kivu: Entre Nyangwe et Malela, Lebrun 5971 (PRE). Kongo Central: Kisantu, Vanderyst s.n. (US 889080). Tshuapa: Mpangu, Delhay 440 (K). Province unknown: Gona, Vanderyst 5682 (US). Ghana. Ashanti: New Tafo, Lovi 3909 (K). Eastern: Aburi, Deighton 613 (BM). India. Kerala: "Palghat" [Palakkad], Madras Herbarium/South Indian Flora 16320 (US). Periakulam: Madurai, Matthew & Charles 51410 (K). Kenya. Coast: Longo Mwagandi Area, Shimba Hills, Magogo and Glover 477 (W); 50 mi SW of Mombasa, Shimba Hills, Bogdan AB3910 (P); Mombasa woodlands, Gibon s.n. (US 2954368); Kaya Muhaka, Luke 3405 (K); Forest between Umba and Mwena Rivers on Lungalunga-Msambweni Rd., Drummond & Hemsley 3787 (K, P). Malawi. Central: Dedza Distr., Mualivulezi Forest Reserve, Exell et al. 1060 (BM). Southern: Shire Valley, Hall-Martin 438 (MO); Lengwe Game Reserve, Hall-Martin 494 (K) and 582 (K); Lengwe Game Reserve, NE corner, Brummitt 8884 (K). Province Unknown: Mwenikumbila foothills, Jackson 1175 (MO). Mozambique. Manica: Maribane Forest, Chare 4434 (US); Amatongas Forest, near Gondola, Schweicherdt 272 (US). Sofala: Gorongosa N.P., Sangarassa Forest, 1 km W of Chitenga, Tinley 2497 (K); Amatongas Forest, Schweicherdt 2341 (K, US). Zambesia: Malema, Torre & Paiva 11192 (PRE); Arredores de Mocuba, Torre 4908 (K). Namibia. Province unconfirmed. Mpilia Island, Killich & Leistner 3347 (K). Nigeria. Ondo: Idanre, Brenan & Jones 8731 (K). South Africa. Kwazulu-Natal: Mkuze Game Reserve, Ellis 3635 (PRE); Mkuze Game Reserve, parking lot by Bube (Kubube) Hide, Snow et al. 6978 (MO, PRE); Tembe Elephant Park, Ward 1382 (PRE). Limpopo: Kruger N.P., Punda Milia area, Shipudza valley east of Punda Milia near Dongadziba, Ellis 3226 (K, PRE); Kruger N.P., ca. 12 km NW of Punda Milia, Davidse & Ellis 5925 (K, MO). Sri Lanka. Anuradhapura: Mihintale, Soderstrom & Kulatunge 1715 (CANB, K, TAES, US); Ritigala Strict Natural Reserve, ascent along eastern slope of Wannatikianda, Jayasuriya 1058 (K, US). Central: 54 miles N of Kandy toward Anuradhapura, trunk road A-9, marker 54/2, Gould 13250 (US); Dambulla, Trimens 28 (US); as previous, Ashton 998 (K, US); Ruhuna N.P., Block I, Cooray 69030805R (US); Ruhuna N.P.,

Block I, Patanagala Camp, Clayton 5924 (CANB, K, TAES, US); Kumbukkan Oya, ca. 2 mi above mouth, at Megahakanda Meda Duwa Block 2, M–d Plot, R 16, Fosberg 51099 (US); Ruhuna N.P., Rugamtota on Menik Ganga (Plot 31), Fosberg & Mueller-Dombois 50192 (US); Mennik Ganga (Riv.) 1 mile above Yalu Bungalow, Fosberg et al. 51045 (US); Ruhuna N.P., Patanagala, Cooray 69120212R (K, US); Ruhuna N.P., Block 2, Cooray 69010502R (K, US); Ruhuna N.P., Block I, Rugamtota, Mueller-Dombois 69030704 (US); Ruhuna N.P., Block I, next to Yala Camp site, Mueller-Dombois & Cooray 68013006 (US); Ruhuna N.P., Block 1, in plot R13 between Andunoruwa and Komawa Wawa, Mueller-Dombois 69010713 (US). Puttalam: Wilpattu N.P., Marai villu, Clayton 5597 (CANB, K, TAES, US). Trincomalee: Kantalai; road between Trincomalee and Kandy, Soderstrom & Kulantunge 1753 (CANB, K, TAES, US); Kantalai, 25 miles from Brincomalle on Kandy Rd., Ballard 1489 (US). Tanzania. Iringa Region: Ab. loco, Greenway et al. 14075 (MO). Lindi Region: 40 km W Lindi, Schlieben 5879 (B, BM, M, MO, S, US); Tendaguru, Migeod 104 (BM) and Migeod 126 (BM). Mahenge Region: Umgebung der Station Mahenge, Schlieben 1721 (BM, M, S). Morogoro Region: Uluguru-Gebirge, Schlieben 3630 (B, BM, G, M, S); 3 mi N Tunuguo, 30 mi SE Morogoro, Boaler 625 (B, US [2 sheets]). Province unknown. Rukwa Valley, Vuma Riv. near Zimba, Siame 581 (MO). Zambia. Central: Iolanda, N bank of R. Kafue, near Kafue town, Robinson 6440 (B, K, M); Kafue N.P., Musa-Kafue confluence, Mitchell 6/75 (K). Eastern: Chikwa, ca 50 mi NW of Lundazi in Luangwa Valley, Robinson 822 (K, M). Northern: M'fume Camp, Verboom 922 (BM, K); Mporokoso, Lake Mweru-Wantipa, Richards 9117 (K, NY). Southern: Siburu forest, Sekute Chieftancy, Bainbridge 709 (BM); Victoria Falls, Crook 52602 (K); Victoria Falls-Livingstone Island, Ellis 2780 (K, MO). Province unconfirmed. Kafue N.P., Mitchell 24/46 (B). Zimbabwe. Manicaland: Tanganda Tea Estate, Chipinga [now Chipinge], Brain 10615 (K). Mashonaland West: Eastern Urungwe [=Hurungwe], tributary of upper Mauora, Phipps 868 (K). Urungwe, Chirundu, Simon 706 (BM). Masvingo: Bikita, 5 km E of Moodie Pass, Davidse et al. 6643 (BRI, K, MO, US). Matabeleland North: Wankie [now Hwange], Kandahar Fishing Camp, Martin 87 (K). Midlands: Gokwe, Sengua Research Station, Guy 2391 (K).

Acknowledgements

This article derives from work done for a doctoral dissertation at Washington University in St. Louis (Snow 1997) and two Short-term visitor grants from the Smithsonian Institution in 1989 and 2007. The first author also was supported by National Science Foundation (BIR-9256779), The Explorer's Club, Grants-in-Aid of Research (Sigma Xi), Andrew W. Mellon Foundation, Missouri Botanical Garden, and American Society of Plant Taxonomists. Fieldwork in southern Africa was supported by the National Geographic Society; the first author thanks P. Burgoyne, M. Carranza, M.

Chatakuta, L. Cohen, J. Gumbi, R. Roux, and O. McKibbin for assistance. Cabelas Corporation of Sidney, Nebraska generously donated field equipment for a collecting trip to Africa and Australia in 1996. We thank the following herbaria for loans or permission to view specimens: B, BM, BRI, CANB, K, M, MO, NY, P, PRE, S, TAES, US, W, Z. Appreciation is extended to Alice R. Tangerini for providing excellent new drawings, and to Dr. L. Versieux and two anonymous reviewers for comments.

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Systematics and ecology of the Australasian genus *Empodisma* (Restionaceae) and description of a new species from peatlands in northern New Zealand

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Academic editor: L. Versieux | Received 20 April 2012 | Accepted 19 June 2012 | Published 3 July 2012

Citation: Wagstaff SJ, Clarkson BR (2012) Systematics and ecology of the Australasian genus *Empodisma* (Restionaceae) and description of a new species from peatlands in northern New Zealand. *PhytoKeys* 13: 39–79. doi: 10.3897/phytokeys.13.3259

Abstract

The genus *Empodisma* comprises two species that are ecologically important in wetland habitats. *Empodisma gracillimum* is restricted to south-western Australia, whereas *E. minus* is found in Tasmania, eastern Australia and New Zealand. We sequenced three cpDNA genes for 15 individuals of *Empodisma* sampled from throughout the range of the species. The results support an Australian origin for *Empodisma* sometime during the late Oligocene to early Miocene with more recent dispersal, colonization and diversification in New Zealand. We recovered six genetically distinct maternal lineages: three *E. gracillimum* haplotypes corresponding to the three accessions in our analysis, a wide-ranging *E. minus* haplotype found in eastern Australia and Tasmania, an *E. minus* haplotype found in New Zealand from Stewart Island to approximately 38° S latitude on the North Island, and a distinct haplotype restricted to the North Island of New Zealand north of 38° S latitude. The Eastern Australian and New Zealand haplotypes of *E. minus* were supported by only one cpDNA gene, and we felt the relatively minor morphological differences and the small amount of genetic divergence did not warrant taxonomic recognition. However, we recommend that the northern New Zealand haplotype should be recognized as the new species *Empodisma robustum* and provide descriptions and a key to the species of *Empodisma*. Monophyly of *E. robustum* is supported by all three cpDNA genes. *Empodisma robustum* can be distinguished from *E. gracillimum* and *E. minus* by its robust growth stature and distinct ecology. It is typically eliminated by fire and re-establishes by seed (seeder strategy), whereas *E. minus* and *E. gracillimum* regrow after fire (sprouter strategy).

Keywords

Restionaceae, *Empodisma*, taxonomy, new species, New Zealand

Introduction

As presently circumscribed, the genus *Empodisma* L.A.S.Johnson & D.F.Cutler (Restionaceae) comprises two species with a widely disjunct distribution in western Australia and south eastern Australia, Tasmania, and New Zealand. *Empodisma gracillimum* (F.Muell.) L.A.S.Johnson & D.F.Cutler is found on the coastal plain from Perth southwards, and along the south coast from Augusta to Albany (Fig. 1), while *E. minus* (Hook.f.) L.A.S.Johnson & D.F.Cutler is found in lowland to alpine zones from Queensland to South Australia, Tasmania and throughout most of New Zealand in New Zealand. They probably diversified in seasonally wet habitats, but exhibit adaptations to seasonal drought, fire and nutrient poor soils (Linder and Rudall 2005).

The species of *Empodisma* are plants of peatlands, particularly raised bogs, blanket bogs, fens, and wet heathlands (Meney and Pate 1999, Johnson and Brooke 1989, Johnson and Gerbeaux 2004). The scientific name is derived from the Greek word for obstacle or hindrance (Johnson and Cutler 1973), and because of their tendency to form dense masses of tangled culms they are also given the common name wire rush. They are rhizomatous perennials with evergreen culms. The horizontal roots branch profusely to form cluster roots (Lamont 1982), i.e. finely divided rootlets with persistent root hairs. The underlying peat is formed mainly from the remains of this densely branched root matrix, which binds litter and bryophytes into the peat (Campbell 1964). The cluster roots retain water like a sponge, up to 15 times their dry weight, and like *Sphagnum* they create acidic conditions (Campbell 1964, 1975, Agnew et al. 1993). In this type of environment incoming rainfall and atmospheric particulates are the major sources of nutrients, which are efficiently removed by the cluster roots of *Empodisma* at the bog surface (Clarkson et al. 2009).

Fire plays an important role in the development of restiad peat bogs in both Australia and New Zealand. For the most part, the species of *Empodisma* are “sprouters” (Pate et al. 1991, Meney et al. 1997, Meney and Pate 1999). In sprouters most of the carbon resources and nutrient elements are allocated towards maintenance and vegetative growth. The underground portions of individual plants are protected and survive fire, and regeneration occurs by the sprouting of new leafy shoots produced from the rhizome system. This contrasts with an obligate “seeder” strategy whereby the plants are killed by fire and re-establish from seed. Seeders generally produce more delicate, less extensive underground rhizome systems and have perennating buds higher in the soil, and without a requirement for nourishing the developing rhizomes, more resources can be allocated to seeds. However, this distinction is not as clear in habitats that experience waterlogged soils during the wet season but have a long intervening dry season, as occurs in much of Australia (Pate et al. 1999).

The taxonomic history of *Empodisma* is complex. The species of *Empodisma* were originally placed in *Calorophus* Labill or *Hypolaena* R.Br. by early taxonomists classifying Restionaceae (Labillardière 1806, Brown 1810, Hooker 1852–1853, Hooker 1857–58, Mueller 1872–1874, Bentham 1878, Cheeseman 1906, Cockayne 1958, Moore and Edgar 1970). The genus *Calorophus* Labill. was originally described by Labillardière (1806). When first de-

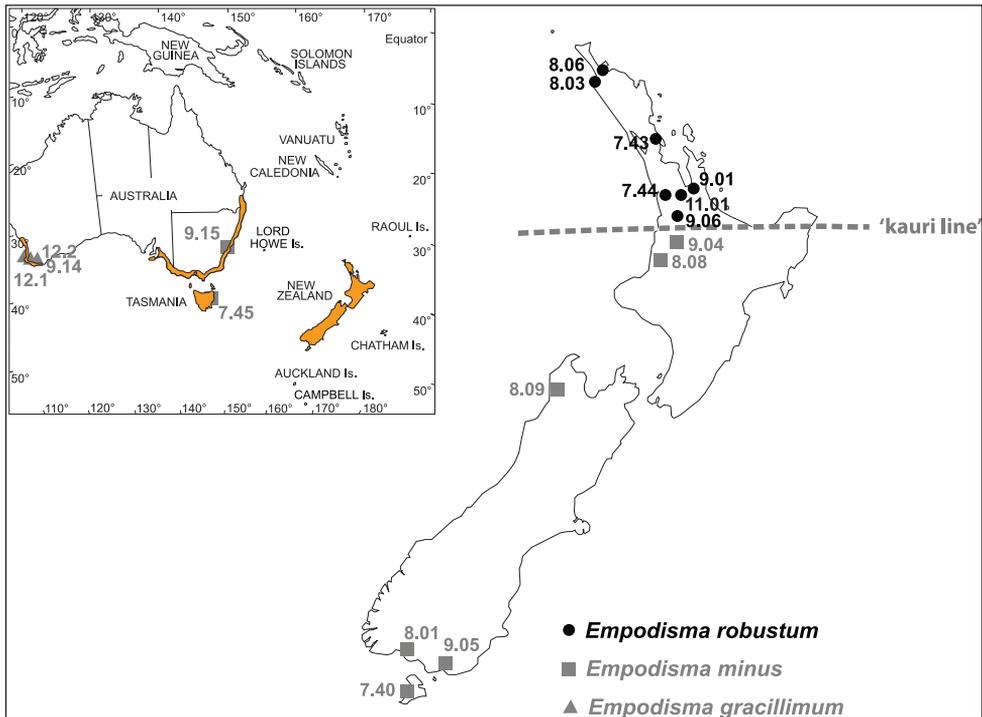


Figure 1. Map showing the generalized distribution of *Empodisma* in Australia and New Zealand and the collection localities of the DNA samples included in our study. The approximate position of the kauri line in New Zealand is shown with a dashed line.

scribed the Tasmanian species *C. elongatus* was the sole member of the genus and is the type. In his first treatment of the flora of New Zealand, Hooker (1853) described a new species of *Calorophus*, *C. minor* Hook.f., based upon Bidwell, Colenso and Lyall specimens. A specimen of *C. minor* collected on the South Island of New Zealand near Nelson by Bidwell was designated as the lectotype by Moore and Edgar (1970). However, in his treatment of the Flora of Tasmania, Hooker (1859) relegated *C. minor* Hook.f. as the variety *C. elongatus* var. *minor* (Hook.f.) Hook.f. Mueller (1872–74) distinguished the plants from western Australia as the distinct species *C. gracillimus* F. Muell., but in *Flora Australiensis* Bentham (1878) followed Brown's (1810) earlier treatment, which reduced *Calorophus* to sectional rank within the genus *Hypolaena*. Bentham's treatment was subsequently followed by Cheeseman (1906) and Cockayne (1958) who recognized the New Zealand plants as *Hypolaena lateriflora* var. *minor* (Hook.f.) Cheesem. However, Moore and Edgar (1970) followed Hooker's (1859) treatment, adopting the name *Calorophus minor* Hook.f. in their treatment of the Flora of New Zealand, Vol. II. Based on anatomical, morphological and cytological differences among the species of *Calorophus*, Johnson and Cutler (1973) subsequently erected the genus *Empodisma* L.A.S.Johnson & D.F.Cutler to accommodate *E. gracillimum* and *E. minus*.

The specimen upon which Hooker based the name *Calorophus minor* is a small slender plant characteristic of alpine regions found in South Island and Stewart Island

of New Zealand. Moore and Edgar (1970) noted that plants at lower elevation in the lowland bogs near Cambridge in the Waikato, northern North Island, were larger and more robust, but based upon study of herbarium specimens they felt the variation was continuous from low to high elevation. We provide evidence for an alternative taxonomic interpretation. The lowland populations of *Empodisma* north of the “kauri line” (the southern limit of *Agathis australis* (D. Don) Lindl. ex Loudon is approximately 38° S latitude in New Zealand) comprise a distinct evolutionary lineage that we here recognize as *Empodisma robustum* S.J. Wagstaff & B.R. Clarkson, sp. nov.

Methods

Study group

We conducted a global analysis of 48 members of the Restionaceae to test monophyly of *Empodisma* and its relationships to *Calorophus* and *Hypoleana*. Three genera of Anarthriaceae (*Anarthria* R. Br., *Hopkinsia* W. Fitzg. and *Lyginia* R. Br.) were selected as outgroups. Intraspecific variation within *Empodisma* was assessed by comparing DNA sequences from 18 accessions collected from throughout the range of these species (Fig. 1).

Data resources

Voucher specimens with their collection locality and GenBank accession numbers are listed in Appendix 1. The aligned data matrices have been submitted in Nexus format to TreeBase matrix accession number <http://purl.org/phylo/treebase/phylovs/study/TB2:S12748> and the Dryad repository: doi: 10.5061/dryad.94710.

Morphological analyses

A single set of morphological measurements were taken from each of 76 dried herbarium specimens on loan from AK, CHR, WAIK, WELT and PERTH (abbreviations follow Index Herbariorum). The morphological measurements describe the growth habit and floral structures of *Empodisma* and were confirmed with additional observations from field collections. Because *Empodisma* is dioecious, floral attributes of female flowers were coded as missing on male plants. Also very few specimens had mature fruits, and this attribute was also coded as missing from many specimens. We used GenStat version 8.1.0.152 (supplied by VSN International Ltd., www.vsn-int.com) to illustrate patterns of variation among the characters (listed in Fig. 6) using BOXPLOTS and PRINCIPAL COORDINATES ANALYSIS (PCoA). Principal coordinates analysis depicts relationships among the 91 Operational Taxonomic Units (OTU's) that comprised our sample. We initially generated

a similarity matrix of Euclidean distances then created a two-dimensional ordination. The first axis accounted most of the variation with less variation described by the second axis.

To test the influence of environmental conditions on growth form, we set up a common garden experiment by transplanting individuals ($n=3$) from New Zealand sites representing populations of both large (*E. robustum*) and small (*E. minus*) growth forms to Hamilton, North Island (37°47'S latitude). The sites selected were Torehape (37°18'S), Kopuatai (37°24'S), and Moanatuatua (37°55'S) for the large growth form, and Tongariro (39°16'S), Rangipo (39°22'S), and Awarua (46°33'S) for the small form. Ecological information was summarized from the published literature and unpublished data of BRC.

DNA extraction, amplification and sequencing

We extracted total DNA from either freshly collected plants or plants dried using silica gel, using a Qiagen DNeasy extraction kit (QIAGEN Pty Inc., Clifton Hill, Victoria, Australia) following the manufacturer's directions. Three chloroplast-encoded DNA regions were sequenced: *rbcl*, *matK* and *trnL*. These regions were selected as they have been used previously to resolve relationships within the Restionaceae (Briggs et al. 2000, 2010, Linder et al. 2003, Hardy and Linder 2005, Moline and Linder 2005, Givnish et al. 2010). The genes *rbcl* and *matK* encode functional proteins, whereas *trnL* encodes part of the gene for Phe-tRNA along with the intervening intron. With very few exceptions chloroplast genes are maternally inherited in flowering plants, so sequence differences correspond to unique haplotypes.

Our PCR amplification and sequencing procedures generally followed those described by Linder et al. (2003) and Hardy and Linder (2005). Excess primers and unincorporated nucleotides were removed from PCR products by a Shrimp Alkaline Phosphatase (GE Healthcare, Global Headquarters, Calfont St Giles, UK)/Exonuclease I (Fermentase International Inc, Burlington, ON, Canada) treatment. Sequencing reactions were run on an ABI3730 sequencer (Applied Biosystems, Foster City, CA, USA) by the Allan Wilson Centre Genome Service at Massey University, Palmerston North, New Zealand. In all instances we sequenced both the forward and reverse DNA strands. The sequence contigs were edited using Sequencher 4.8 (Gene Codes Corporation, Ann Arbor, MI, USA).

Sequence alignment

We used ClustalX (Thompson et al. 1997) to facilitate alignment of the sequences. The sequence alignments for *matK* and *rbcl* were easily achieved as there no gaps in the *rbcl* and only two gaps in the *matK* matrix. The gaps in *matK* occurred in multiples of three and were positioned so as not to disrupt the codon reading frame. The *trnL* sequence alignment across the Restionaceae was more complex, so we used a modification of the sequence profile alignment procedure described by Morrison (2006).

Closely related sequences were initially aligned using the multiple alignment settings, a gap opening penalty of 5, a gap extension penalty of 5, and a delay-divergent-sequences setting of 97%. These ClustalX penalties favour opening gaps rather than substitutions, and they delayed adding the most distantly related taxa in our study. We identified low-scoring segments and exceptional residues, using the quality settings in ClustalX, and reconciled alternative alignments of these short DNA stretches. The final alignments were then visually inspected, and minor adjustments were made manually before conducting the phylogenetic analyses.

Some of the outgroup sequences were not available from GenBank (e.g. a *matK* sequence was missing for *Chordifex hookeri* (D.I.Morris) B.G.Briggs, but both an *rbcL* and *trnL* sequence were available from GenBank for this taxon). Rather than excluding these taxa, the incomplete data partitions were coded as missing. Many recent empirical and simulated studies suggest that it is possible to include taxa with large amounts of missing data without compromising phylogenetic accuracy. Indeed, increasing both the number of taxa and characters can improve the accuracy of phylogenetic inferences (Weins and Morrill 2011).

Parsimony and median network analyses

We conducted both parsimony and network analyses of the sequence data sets, using PAUP* 4.0b10 (Swofford 2002) and SplitsTree version 4.8 (Huson 1998, Huson and Bryant 2006). For the parsimony searches we used the settings TBR branch swapping, MULPARS in effect, and RANDOM ADDITION with 1000 replicates. The parsimony characters were unordered and equally weighted. Duplicate trees were eliminated using the “condense trees” option collapsing branches with a maximum length of zero. Congruence of the data partitions was assessed using the Incongruence Length Difference (ILD) test (Farris et al. 1994, 1995) with 100 data partition replicates excluding uninformative sites as suggested by Hipp et al. (2004) and Ramirez (2006). Taxa that were missing one or more of the data partitions were excluded from the ILD test. In the absence of significant conflict, we combined the sequence data sets. Support for clades was estimated by bootstrap (Felsenstein 1985, 1988) with 1000 replications excluding uninformative sites; starting trees were obtained by RANDOM ADDITION with one replication for each bootstrap replicate, TBR branch swapping, and MULPARS in effect. Median networks were constructed using the options add all trivial characters and a minimum support value of 1.

Bayesian analysis and divergence estimates

Each gene partition was tested for the best substitution model using jModelTest (Posada 2008) with default settings based on the Bayesian Information Criterion (BIC) (Posada

and Buckley 2004), averaging over all included parameters in order avoid a bias towards parameter-rich models. The jModelTest comparisons selected TrN + I + G as the best fit model for *rbcL*, TPM1 for *matK* and TIM1ef for *trnL*. Because the genes *rbcL* and *matK* encode functional enzymes, we unlinked the substitution rate parameters and the base frequencies across codon positions (1+2), 3. Most of the synonymous mutations occur in the third codon position. The aligned matrices were then prepared as output files for analysis in BEAUti 1.6.1 (part of the BEAST package) and analyzed in BEAST 1.6.1 (Drummond and Rambaut 2007). A Yule prior (Yule 1924) was set for the tree model, together with unlinked relaxed lognormal clock models on the substitution rates for each locus. The MCMC chains were set to run for 90 million generations, logging parameters every 1000 generations. Chain mixing and convergences were checked in Tracer v1.5 (Rambaut and Drummond 2007) with all parameters showing ESS values of > 200. A maximum clade credibility trees was calculated using TreeAnnotator 1.6.1 (Drummond and Rambaut 2007) and a summary with 95% highest posterior density intervals of divergence time estimates was prepared using FigTree v1.3.1 (Rambaut 2009).

Incorporating uncertainty associated with the fossil record

The earliest verifiable fossils of Poales are from the early Cretaceous (Maastrichtian) deposits dated approximately 115 million years ago (Herendeen and Crane 1995). The Restionaceae are nested within the Poales, so it is unlikely that the age of the restiad lineage is older than 115 million years. The earliest restiad microfossils appear in late Cretaceous deposits in South Africa dated between 64 and 71 million years ago (Scholz 1985) with fossils appearing in progressively younger deposits in Antarctica, Australia, New Zealand and South America (Truswell and MacPhail 2009, Barreda and Palazzesi 2007, MacPhail 1997, Scholz 1985, Mildenhall 1980). We attempted to incorporate uncertainty associated with these fossil calibrations by applying a lognormal prior with an offset of 115, a log mean = 2 and a log (Sdev) = 0.5 applied to the root and an offset of 64, a log (mean) = 2 and a log (Sdev) = 0.5 to the node separating the Anarthriaceae from the Restionaceae. These settings provide broad probability distributions between 117.8–134.7 and 66.8–83.7.5, with median values of 118.2 and 71.4 respectively for these calibration points.

Results

The combined sequence data set comprised three data partitions with a total of 4267 characters; approximately 23% of the total data matrix was comprised of gap or missing data. An ILD test of the three data partitions failed to find significant conflict ($p = 1-82/100 = 0.18$). A heuristic search with parsimony as the optimality criterion recovered a single island of 180 trees of 2226 steps (Consistency Index (CI) = 0.607 (excluding uninformative characters); Retention Index = 0.788); a strict consensus is shown in Fig. 2. The three

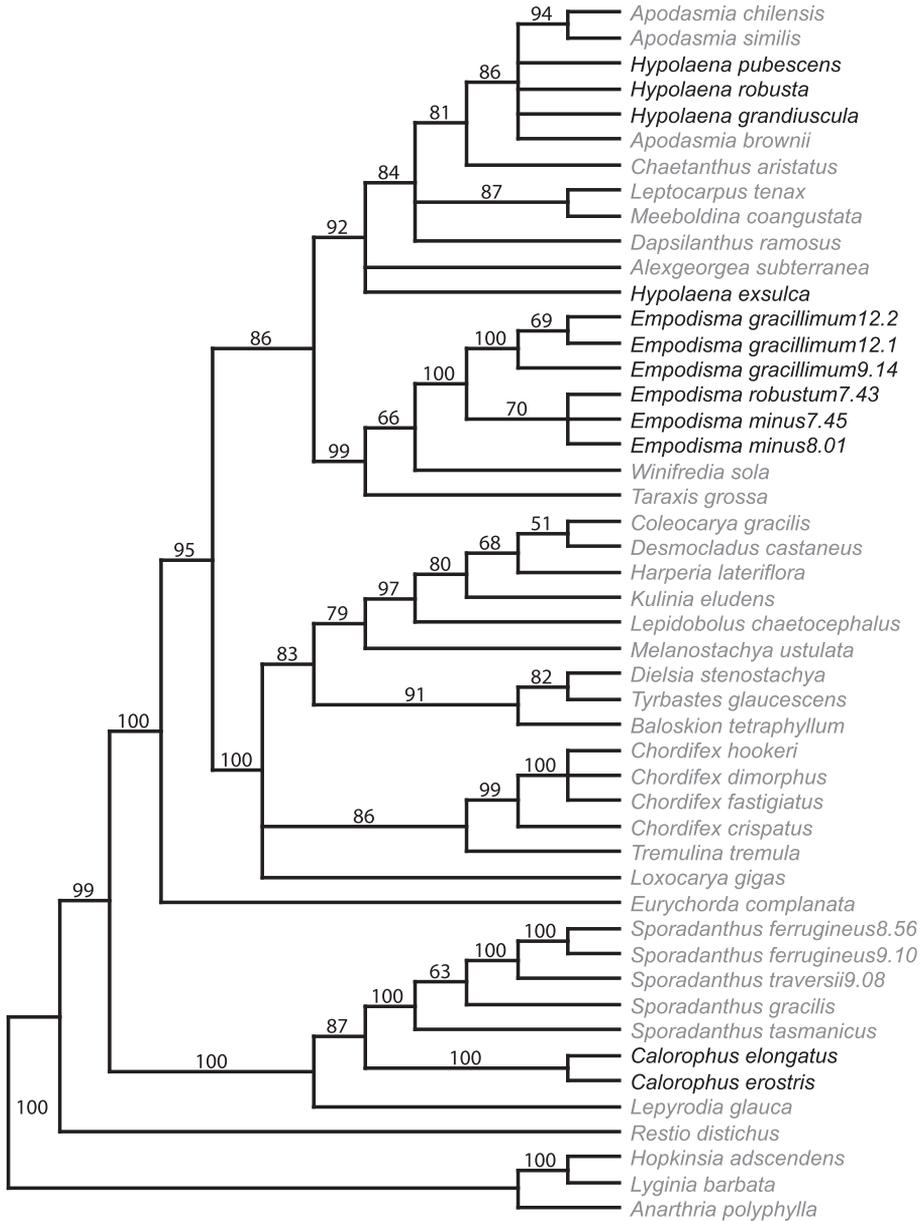


Figure 2. Strict consensus tree. The three species of *Empodisma* (highlighted in bold) emerge as a well-supported clade distinct from *Calorophus* and *Hypolaena*. They were placed in these latter two genera by Moore and Edgar (1970) and Cheeseman (1906). Bootstrap values are provided above the branches

gene regions differed in length, the number of variable characters, and the degree to which they resolved and supported phylogenetic relationships.

The strict consensus tree (Fig. 2) agrees with the subfamilial classification of Briggs and Linder (2009). *Restio distichus* is the only representative of Restionioideae (Afri-

can); *Calorophus*, *Sporadanthus* and *Lepyrodia* (Australian) make up Sporadanthoideae, while the remainder are representative of Leptocarpoideae. In our analysis the three species of *Empodisma* form a well-supported clade (100% bootstrap) with *E. gracillimum* emerging as sister to *E. minus* and *E. robustum*. *Winifredia sola* is weakly supported as sister to *Empodisma*, and *Taraxis grossa* emerges as sister to the *Empodisma* *Winifredia* clade (99% bootstrap). The two species of *Calorophus* also form a well-supported clade (100% bootstrap), but are distantly related to *Empodisma*, instead emerging as sister (100% bootstrap) to *Sporadanthus*. Likewise *Hypolaena* is also distinct from *Empodisma*. The species of *Hypolaena* are nested within a large clade (92% bootstrap) that includes *Apodasmia* and *Alexgeorgea subterranean* Carlquist.

The maximum parsimony and Bayesian analyses converged on trees with essentially the same topology, which suggested that the sequence data are robust to the different assumptions associated with these two approaches. Notably, the Bayesian posterior probability values were generally higher than the bootstrap support values, and the chronogram was better resolved (Fig. 3). The 95% highest posterior density estimates revealed substantial uncertainty associated with the divergence estimates, so our results should be viewed as preliminary. The results suggest *Empodisma* diverged from its most closely related ancestor (MCRA), *Winifredia sola* L.A.S. Johnson & B.G. Briggs approximately 21.8 (15.9–28.2) million years ago (mya). *Empodisma gracillimum* diverged at about 8.8 (5.4–12.9) mya and *E. robustum* split from *E. minus* approximately 2.0 (0.8–3.8) mya. Even though the algorithm for dating divergence times was different, the estimates presented here are similar to those obtained by Linder et al. (2003).

A comparison of median networks assessing levels of intraspecific variation in the three species of *Empodisma* is shown in Fig. 4. In each instance only a single parsimony tree was recovered. The *trnL* sequences were the shortest but the most variable. They were 953 nucleotides in length, and of these, 18 substitutions were parsimony informative. Fourteen substitutions supported the *Empodisma gracillimum* lineage with two unique parsimony uninformative substitutions distinguishing *E. gracillimum* 9.14 from the other species. One *trnL* character supported the eight accessions of *E. minus* (bootstrap 63%). The split between the Australian (*E. minus* 7.45 and *E. minus* 9.15) and the New Zealand specimens (*E. minus* 8.09, *E. minus* 9.05), was supported by one *trnL* character but again with low support (65% bootstrap). Two informative substitutions supported the split between the robust northern New Zealand specimens of *Empodisma* (e.g. *E. robustum* 9.06 and *E. robustum* 7.44) highlighted in bold and the other specimens of *Empodisma* in our data set (Fig. 4). Further support for this split comes from a 23-base duplication that is absent from *E. robustum* but present in *E. minus* and *E. gracillimum*. This split received 86% bootstrap support in our analysis. The sequences were identical within the seven accessions of *E. robustum*.

The *rbcL* sequences were 1401 nucleotides long; of these, eight characters were parsimony informative and 1393 were constant. The informative characters support four splits in the data (Fig. 4). Five substitutions support *E. gracillimum* with one substitution supporting *E. gracillimum* 12.1 and *E. gracillimum* 12.2. The third split sup-

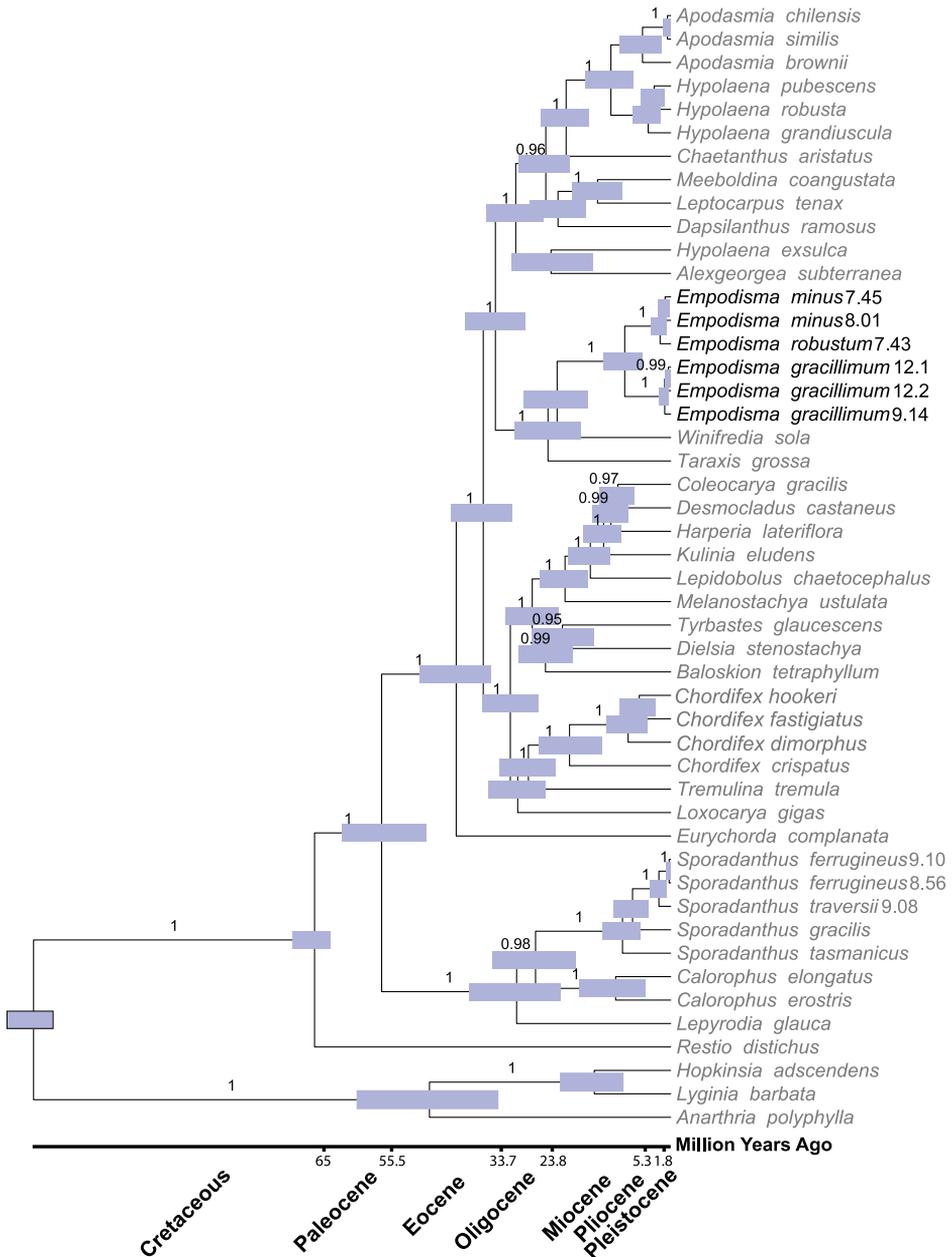


Figure 3. Bayesian chronogram with estimated divergence times. Node error bars are provided in blue showing the 95% highest probability density for the divergence estimates. Posterior probability support values > 97% are given above the branches. A geological time scale is shown at the base of the tree.

ports only the diminutive accessions of *E. minus* from New Zealand (65% bootstrap), and one substitution supports the fourth split separating the large lowland form of *Empodisma* (e.g. *E. robustum*7.43 highlighted in bold (68% bootstrap).

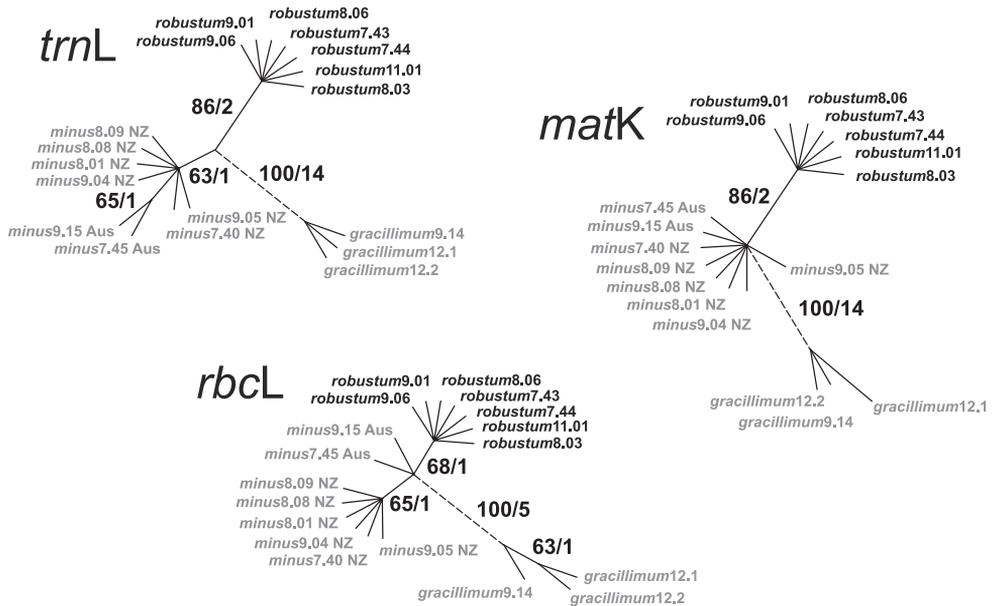


Figure 4. Comparison of median networks from independent analyses of *trnL*, *rbcL* and *matK* sequences. Bootstrap values / the number of mutations distinguishing each haplotype, are shown beside the branches. The accessions of *Empodisma minus* from New Zealand and Australia Aus.

By comparison, the *matK* sequences were 1469 nucleotides long, and of these 16 characters were parsimony informative, 3 variable characters were parsimony uninformative, and 1450 were constant. The informative characters again provided strong support for the split between *E. gracillimum* and the remaining samples in our data (14 substitutions/100% bootstrap) (Fig. 4). *E. gracillimum*12.1 was supported by two unique substitutions and *E. gracillimum*9.14 by one. The split between specimens of *E. robustum* from northern New Zealand and *E. minus* was supported by 2 substitutions / 86% bootstrap. The sequences within these latter two groups were identical.

The Incongruence Length Difference test failed to reveal significant incongruence ($p = 1 - 1/100 = 1.00$) among the three independent data sets, so we pooled them. An analysis of the combined data recovered a single maximum parsimony tree; an unrooted phylogram is shown in Fig. 5 (Consistency Index, excluding uninformative characters = 1.00, Retention Index = 1.00). The combined analysis provided strong support for clades corresponding to the western Australian endemic, *Empodisma gracillimum* (33 substitutions / 100% bootstrap) and the robust northern New Zealand plants (e.g. *E. robustum*9.06 and *E. robustum*9.01 (five substitutions / 100% bootstrap), but weak support for *E. minus* (1 substitution / 63% bootstrap).

We distinguished six distinct cpDNA haplotypes within the three species of *Empodisma*. Each accession of *E. gracillimum* was distinguished by one or more substitutions and constituted three unique haplotypes. The two sequences of *E. minus* from eastern Australia and Tasmania were identical and comprised the fourth haplotype (see also

Combined

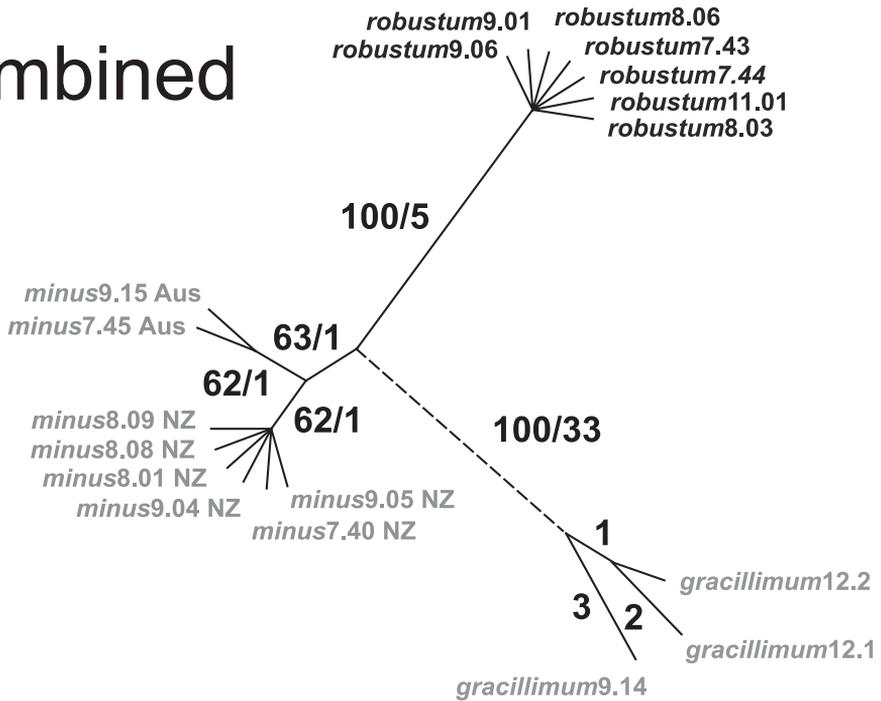


Figure 5. Unrooted parsimony tree from a combined analysis of the three sequence partitions. Six distinct cpDNA haplotypes are supported. Bootstrap values / the number of mutations distinguishing each haplotype are shown beside the branches. The accessions of *Empodisma minus* from New Zealand are indicated NZ and Australia Aus.

Figure 1). These were distinguished from a fifth haplotype comprising the *E. minus* accessions from New Zealand ranging from Stewart Island to approximately 38° S latitude on the North Island. The sequences of *E. robustum* restricted to the North Island of New Zealand north of 38° S latitude comprised a sixth haplotype.

We observed also a substantial degree phenotypic variation within the species of *Empodisma* especially in those characters that describe growth habit, e.g. culm height, internode distance, sheath length and leaf length. However, when grown together in common garden experiments in Hamilton, the two New Zealand species, *E. robustum* and *E. minus*, retained their distinctive growth forms, which suggests there is a genetic component to the pattern of morphological variation.

Empodisma robustum is generally a larger more robust plant, which ranges in height from 0.4 to over 1.3 m even taller in supporting vegetation, whereas *E. minus* approaches 0.8 m in lowland bogs in Queensland, but in southern latitudes and alpine environments the plants are dwarfed, barely reaching 0.3 m (Fig. 6). *Empodisma gracillimum* is similar in height to *E. robustum*, but the culms are light green in colour and more delicate; usually they are less than 0.7 mm in diameter. The culms of *E. robustum* are dark green and broader, in some individuals approaching 2.2 mm in diameter.

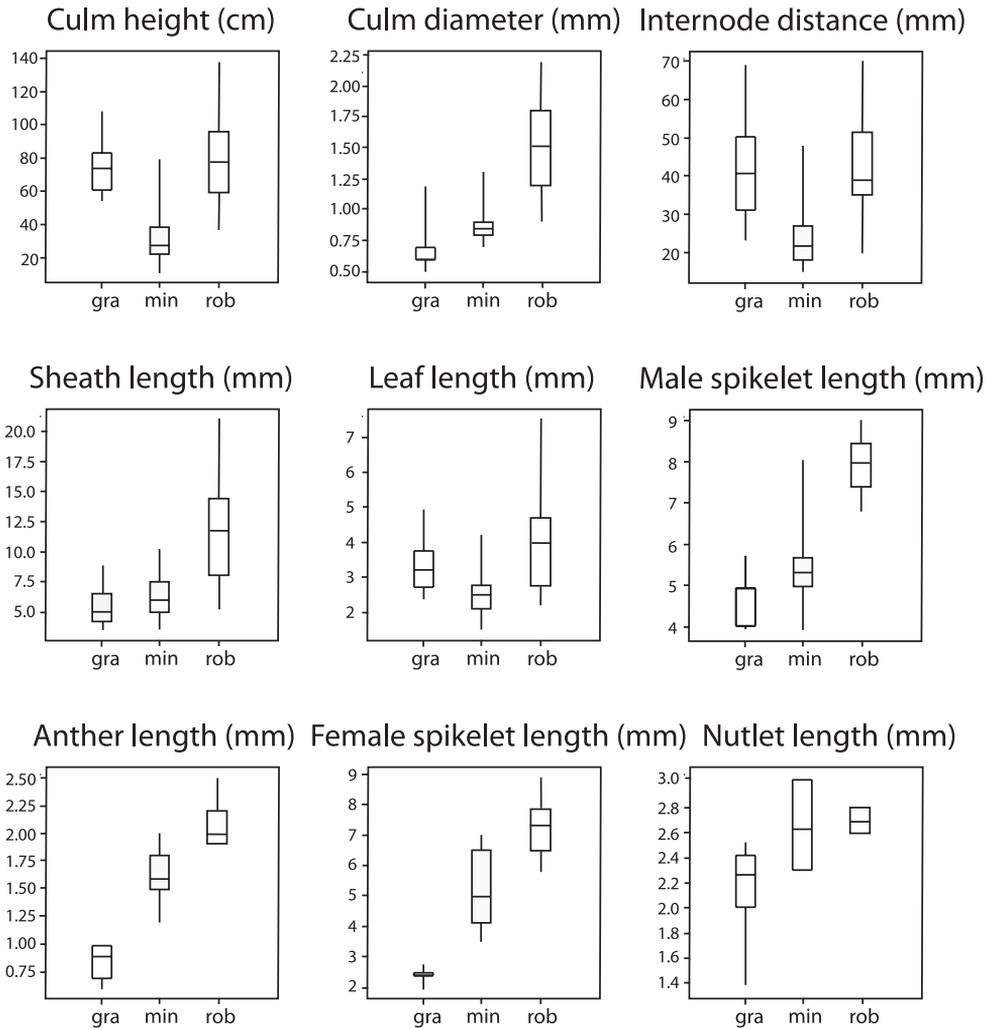


Figure 6. Box plots illustrating patterns of morphological variation among the species of *Empodisma*. The box spans the interquartile range of the values in the variate. The middle 50% of the data lie within the box, with a line showing the median. The whiskers extend beyond the ends of the box as far as the minimum and maximum values.

The culms of *E. minus* are also dark green, but they are seldom greater than 1.0 mm in diameter. Internode distances also vary substantially among the three species; the distances are greater in *E. robustum* and *E. gracillimum* ranging from 20.0 to 70.0 mm in *E. robustum* and from 25.0 to 80.0 in *E. gracillimum* in contrast to *E. minus* which ranges from 15.0 to 48.0 mm (Fig. 6). The leaf sheaths of *E. robustum* also tend to be longer, ranging from 5.2 to 21.0 mm, whereas the leaf sheaths of *E. gracillimum* range from 3.5 to 9.3 mm in length and from 3.5 to 10.2 mm in *E. minus*. The leaves of *E. robustum* are also longer, ranging from 2.2 to 7.55 mm, while the leaves range in length

from 2.4 to 5.0 mm in *E. gracillimum* and from 1.5 to 4.2 mm in *E. minus*. The floral structures of *E. robustum* are substantially longer than those of *E. minus*. In contrast, the inflorescences of *E. gracillimum* are smaller and more delicate than either *E. robustum* or *E. minus* (Fig. 6). The male spikelet of *Empodisma robustum* ranges from 6.8 to 9.0 mm in length, whereas *E. minus* ranges from 3.9 to 8.0 mm and *E. gracillimum* from 4.0 to 5.8 mm. The anthers in *E. robustum* range from 1.9 to 2.5 mm in length, 1.2 to 2.0 in *E. minus*, and 0.6 to 1.0 mm in *E. gracillimum*. The female spikelets in *Empodisma robustum* range from 5.8 to 8.9 mm in length, 3.5 to 7.0 mm in *E. minus* and 1.5 to 2.4 mm in *E. gracillimum*. While few of the herbarium specimens that we examined had mature fruits, fruits from *E. robustum* ranged from 2.6 to 2.8 mm in length, 2.3 to 3.0 mm in *E. minus*, and 1.4 to 2.5 mm in *E. gracillimum*.

The first PCoA axis accounted for 52.4 % of the variation in our sample and the second 23.4% (Fig. 7). The PCoA ordination separated *Empodisma gracillimum* primarily on the second axis but there was some overlap among the outliers of *E. robustum* and *E. minus* on the first axis. The greatest spread among the OTU's was observed in *E. robustum* and *E. gracillimum*; this might reflect their taller more scrambling growth habit. With the exception of one outlier from Queensland, specimens of *E. minus* are more tightly grouped. Several of the specimens of *E. minus* were collected in the high mountains or in lowland bogs at more southerly latitudes. The stature of these plants may be more constrained by the harsh environments that they inhabit.

Discussion

DeQueiroz (2007) proposed a unified species concept based on the single common element of most contemporary species definitions. He suggested that species are separately evolving metapopulation lineages. A metapopulation is a series of connected populations. A lineage implies an ancestor–descendant relationship. Species have a number of emergent biological properties, but these often arise at different times during the speciation process, and taxonomists may place a different emphasis on the biological properties that are used to define species. Incipient species may occupy a new adaptive zone, but this frequently precedes reproductive isolation and fixed morphological differences. The lowland plants of *Empodisma* from northern New Zealand exhibit many of these emergent properties. We feel the evidence is sufficient to justify recognizing the northern New Zealand plants as a distinct species and propose the name *E. robustum* S.J.Wagstaff & B.R.Clarkson sp. nov., which reflects its robust stature.

There is considerable uncertainty associated with estimating divergence times in Restionaceae. The fossil calibrations rely entirely upon microfossils and their affinities to extant genera are not clear. The divergence estimates presented here will undoubtedly be refined as more complete fossils are discovered. Nonetheless our preliminary findings suggest that *Empodisma* evolved in Australia during the mid Oligocene / early Miocene between 28–16 mya (Fig. 3). This was a time of warm, equitable environmental conditions. Crisp and Cook (2007) suggest members of the Restionaceae may

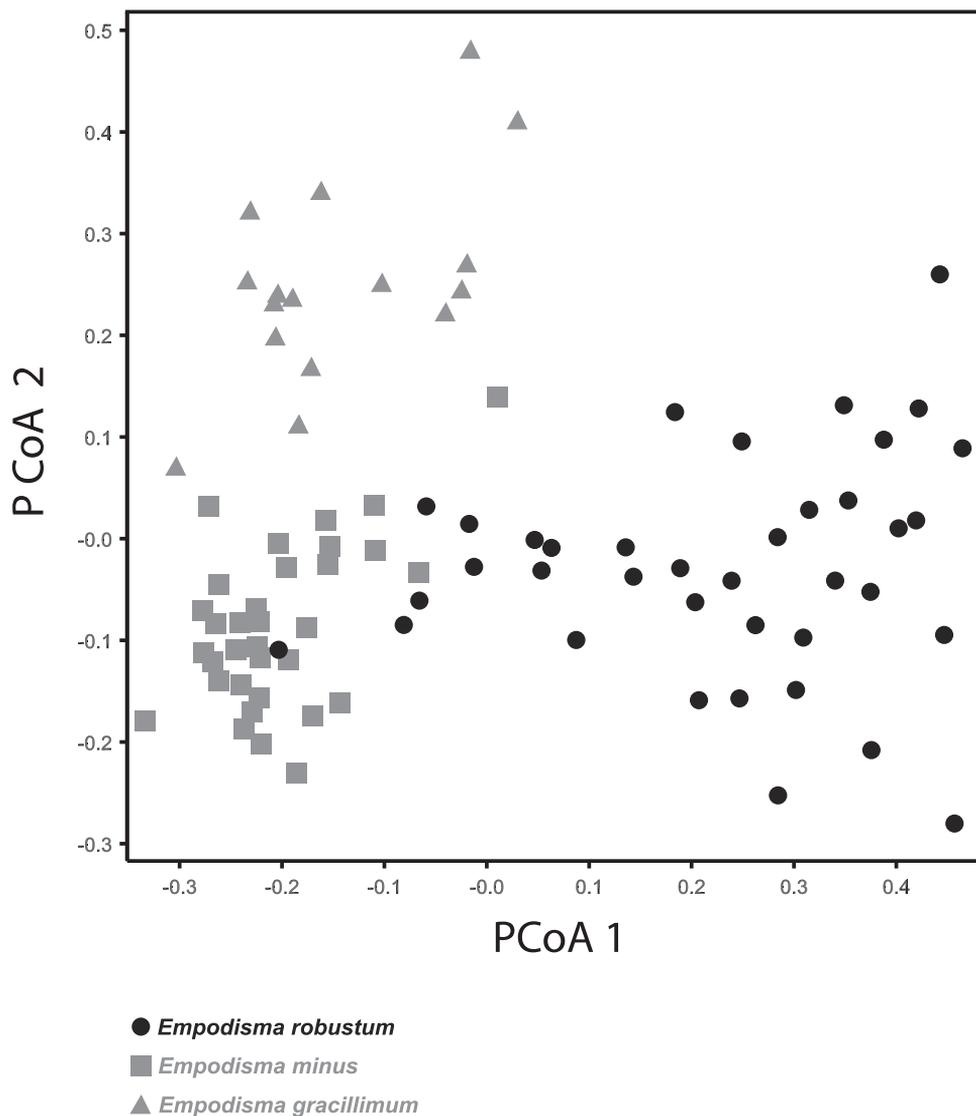


Figure 7. Principal coordinates ordination depicting patterns of overall similarity among the 74 OTEs that comprised our morphological sample. The first PC axis accounted for 58.3% of the variation in our sample and the second PC axis accounted for 23.4% of the variation.

have at one time been more widely distributed in Australia, but a rapid succession of marine incursions, the onset of aridity and the origin of the Nullarbor Plain during the Miocene beginning about 13–14 mya created climatic and edaphic barriers that isolated lineages in the southwestern and southeastern sclerophyll biomes in Australia. The split between *Empodisma gracillimum* and *E. minus* (13–5 mya) roughly coincided with these environmental changes. Colonization and diversification in New Zealand occurred more recently and was perhaps induced by uplift of the Southern Alps during

the Pliocene and episodes of glaciation during the Pleistocene. The split between *E. minus* and *E. robustum* (4–0.8 mya) spans this time frame.

The sequencing results also differentiate the populations of *Empodisma robustum* from northern New Zealand from the Australian or New Zealand populations of *E. minus* (Fig. 1), and this split was independently supported by each of the chloroplast DNA regions that we surveyed (Fig. 4). *Empodisma robustum* comprises a distinct evolutionary lineage united by six synapomorphies (Fig. 5). In contrast, the plants from mainland Australia and Tasmania are very similar to the diminutive lowland plants of *E. minus* from southern New Zealand, each haplotype is distinguished only by a single mutation and the plants are found in similar habitats. The three genes that we sequenced were encoded in the chloroplast and are probably maternally inherited. Interestingly, there is no homoplasy in the data. Nonetheless, it is conceivable that the chloroplast gene tree is not compatible with the species tree. Gene convergence, introgression hybridization and/or incomplete lineage sorting could result in incompatible phylogenetic signals. A degree of reproductive isolation is necessary for these mutations to become fixed, which suggests *E. robustum* and *E. minus* have been reproductively isolated, perhaps since the Pleistocene. Within the northern haplotype, the sequences are identical. Although the sample is small, the absence of unique mutations (autapomorphies) suggests gene flow is unrestricted among the northern populations of *E. robustum*. Historical rates of gene flow have traditionally been estimated indirectly from the number of fixed alleles in subpopulations relative to the total population (Sork et al. 1999, Slatkin and Maddison 1981).

Contrary to the observations of Moore and Edgar (1970), our results show that in New Zealand the pattern of morphological variation in *Empodisma minus* is not continuous from low to high elevation; rather two morphologically distinct New Zealand species can be readily distinguished. This interpretation is based upon recent collections from throughout the range of the species. *Empodisma robustum* differs by its more robust growth habit. The stature of *E. minus* diminishes with increasing latitude and altitude. Though they have distinct haplotypes, the diminutive plants of *E. minus* from New Zealand are morphologically very similar to plants from Tasmania, though plants from 0.4 to 1 m tall are noted from eastern Australia. We examined a specimen from Queensland that was 0.8 m tall. The culm diameter of 0.8 mm placed it within the range of the New Zealand accessions, but this plant was an outlier in the PCoA ordination (Fig. 7).

Hooker (1859) stated that the New Zealand plants could be distinguished from the Australian plants by their more woolly sheaths with erect apices. After close inspection we felt this was a relatively minor morphological difference, and considering the low bootstrap support and the small amount of genetic divergence, we did not consider these differences worthy of taxonomic recognition. *Empodisma gracillimum* emerges as sister to *E. minus* and *E. robustum* and is separated by 36 unique nucleotide substitutions. With its delicate light green culms, unbranched multicellular hairs on the rhizome, and pedicellate female flowers, *E. gracillimum* is morphologically very distinct from *E. robustum* and *E. minus*.

The three species of *Empodisma* also have distinct ecological and distributional differences.

Ecology of *Empodisma robustum*

Empodisma robustum is restricted to the region north of 38° S latitude on the North Island of New Zealand. This phytogeographical boundary has long been recognized by New Zealand ecologists and marks the southernmost range of many species, most notably *Agathis australis*, but also bog associates such as *Sporadanthus ferrugineus* de Lange, Heenan & B.D.Clarkson, *Dianella haemata* Heenan & de Lange, *Dracophyllum lessonianum* A.Rich., *Anzybas carsei* (Cheeseman) D.L.Jones & M.A.Clem., and *Lycopodiella serpentina* (Kunze) B.Øllg. This region is the warmest in New Zealand and is rich in endemic species (McGlone 1985). The pre-European vegetation in this part of New Zealand consisted primarily of warm-temperate forests and restiad peatlands.

Empodisma robustum is a mid- to late-successional species of restiad raised bogs in the lowland zone of northern North Island (Clarkson et al. 2004b). In the oldest bogs it forms a dense layer of sprawling, intertwined wiry stems 1–1.8 m in height, overtopped by swards of the bamboo-like *Sporadanthus ferrugineus* (also Restionaceae) up to 2.5 m tall (de Lange et al. 1999). Other canopy associates include the heath shrubs *Leptospermum scoparium* J.R.Forst. & G.Forst., *Epacris pauciflora* A.Rich., and *Dracophyllum lessonianum*, the sedges *Baumea teretifolia* (R.Br.) Palla and *Schoenus brevifolius* R.Br., and the fern *Gleichenia dicarpa* R.Br. *Sphagnum cristatum* Hampe is also present, but does not thrive in the shade of the taller restiads. These bogs were initiated in the post-glacial period (after 14 000 years BP; Newnham et al. 1995, McGlone 2009), and typically formed extensive domes covering up to 15 000 ha, with peat 10–12 m deep (Cranwell 1939). However, widespread drainage and development into pasture in the early to mid-1900s has confined the *Sporadanthus*–*Empodisma robustum* association to three sites in the Waikato: Torehape, Kopuatai, and Moanatuatua (de Lange et al. 1999, Clarkson 2002). Elsewhere in the northern North Island, *E. robustum* occurs in fens and young restiad bogs (Johnson and Brooke 1989, Johnson and Gerbeaux 2004, Hodges and Rapson 2011), and gumland heaths (Clarkson et al. 2011). Apart from *S. ferrugineus*, the species associated in these younger/shallower peat systems are similar to those listed above.

Empodisma robustum is the key species in the fen–bog transition (Clarkson et al. 2004b, Hodges and Rapson 2011) during the development of restiad raised bogs north of 38° S latitude. It is tolerant of a wide environmental range, establishing early in relatively fertile fens (dominated by *Gleichenia dicarpa*, sedges and heath shrubs) to initiate raised-bog development, and persists in significant amounts in low-nutrient, late-successional phases. It is the main peat former, with its dense surface layer of cluster roots that have high water-holding capacity (Campbell 1964), high resistance to decay (Kuder et al. 1998), and similar base-exchange properties to *Sphagnum* (Agnew et al. 1993). The presence of an initial *E. robustum* phase has been shown to be a precursor to the establishment of *Sporadanthus ferrugineus*, which becomes the physiognomic dominant in late-successional restiad raised bogs (Clarkson et al. 2004a).

The development of raised bogs is constrained by a delicate water balance. They typically form in regions with moderate to high rainfall, cool summers, poor drainage,

and isolation from flowing water (McGlone 2009). The warm-climate northern North Island lowlands thus appear unsuitable for raised bogs, having frequent dry summers with extended water deficits and a negative annual water balance (McGlone 2009). However, bogs with dense *Empodisma robustum* canopies have much lower evaporation rates than other wetland plant communities (Thompson et al. 1999). This is likely due to the high water-use-efficiency properties of *E. robustum*, namely reducing water loss by physiological controls of stomatal opening, having reduced scale-like leaves, and a dense mulch of decay-resistant culms, which protects the thick water-retaining root matrix at the bog surface (Campbell and Williamson 1997).

Because the raised-bog surface is isolated from the influence of groundwater and surface runoff, plants receive their water and nutrients from rainfall. They typically have very low levels of plant nutrients, particularly of nitrogen and phosphorus (Damman 1978, Clarkson et al. 2005). It has been shown that *E. robustum* is able to co-exist with the less nutrient demanding late-successional species *Sporadanthus ferrugineus*, by occupying different root zones (Clarkson et al. 2009). *Empodisma robustum* forms a thick layer of cluster roots that overlie the deeper roots of *Sporadanthus ferrugineus*, allowing preferential access to dissolved nutrients in rainfall.

Despite their saturated substrates, naturally occurring fires have been well documented in New Zealand peatlands (Newnham et al. 1995, McGlone 2009), and the frequency of fires has increased dramatically in recent times owing to land clearance by Polynesians and more widely by European settlers. Clarkson (1997) studied recovery from fire in two restiad raised bogs characterised by *E. robustum* at Whangamarino and Moanatuatua in Waikato. The populations of *E. robustum* were eliminated by fire and had to re-establish from seed, taking 4 years to achieve dominance at the two sites. Some minor resprouting was observed in localised pockets at Whangamarino (R.M. Irving, pers. comm., 1993) but recovery after fire is mostly via seed. *Empodisma robustum* has an erect rhizome, and its roots spread horizontally just below the surface of the bog, so its root system is susceptible to fire damage. Those species with rhizomes that penetrated deeply into the substrate, e.g. sedges, resprouted rapidly after fire and dominated in the first few years post-fire, before the restiads resumed pre-fire height and cover (*E. robustum* within 6 years and, where present, *Sporadanthus ferrugineus* within 12 years).

Ecology of *Empodisma minus*

Empodisma minus in New Zealand is also a mid- to late-successional wetland species. It dominates fens, blanket bogs, raised bogs, and pakihi heaths in coastal to alpine areas between 38° S latitude in the North Island and 48° S on Stewart Island, being particularly common in Westland and Southland. It is absent from Chatham Island. The vegetation is typically a dense, springy carpet of *E. minus*, averaging 40 cm tall, associated with heath shrubs (*Leptospermum scoparium*, *Dracophyllum oliveri* Du Rietz, *D. prostratum* Kirk), sedges (*Baumea teretifolia*, *B. tenax* (Hook.f.) S.T.Blake), the ferns

Gleichenia dicarpa and *G. microphylla* R.Br., the tussock grass *Chionochloa rubra* Zotov, sundews (*Drosera* spp.), and *Sphagnum cristatum* moss.

Many of the ecological properties of *E. robustum* also apply to *E. minus*. For example, *E. minus* forms peat via its cluster roots, although these are smaller and less dense than in *E. robustum*. It is also a key species in the fen–bog transition, particularly *C. rubra*-dominated fens (Hodges and Rapson 2011), and is the major peat former, except in very wet areas favoured by *Sphagnum* mosses (Rigg 1962, Burrows and Dobson 1972, Mark and Smith 1975, Whinam and Kirkpatrick 1995).

Empodisma minus resprouts after fire (Timmins 1992, Johnson 2001), and has probably become more common at the expense of woody species, because of land-clearance fires (McGlone 2009). Studies in vegetation recovery after fire in the far south of New Zealand at Eweburn Bog (Timmins 1992) and Awarua Bog (Johnson 2001) first noted resprouting (and some seed establishment) a few months after fire, but recovery was extremely slow and *E. minus* cover was still increasing after 4.5 years at Eweburn and 10 years at Awarua. However, after 40 years there was little difference observed in the cover of *E. minus* in the burnt and unburnt areas in a south Westland mire (Merton 1986). The magnitude of vegetation damage (and hence recovery) is determined by the intensity of the fire, which is influenced by site conditions such as water table depth, fuel build-up and climate (Timmins 1992, Clarkson 1997). In cooler, wetter regions, e.g. southern South Island, fires are likely to be less intense than fires in the northern North Island, which may favour the sprouter recovery strategy over the seeder strategy.

In Australia, *Empodisma minus* occurs in all states apart from Western Australia and Northern Territory, being concentrated in south-eastern Australia. It grows in similar habitats to New Zealand, i.e. fens and bogs, and seasonally or permanently inundated heaths, swamps and stream margins (Campbell 1983, Meney and Pate 1999, Whinam and Hope 2005) from sea level to alpine areas. *Empodisma minus* is most abundant at higher elevations, e.g. eastern Victoria highlands, and in cooler, wetter climates, e.g. Tasmania. Common associates include heath shrubs (*Richea continentis* B.L.Burt, *Baeckea gunniana* Schauer, *Leptospermum lanigerum* Sol. ex Aiton) Sm., *Epacris* spp.), sedges (*Carex gaudichaudiana* Kunth, *Carpha alpina* R.Br.), ferns (*Gleichenia alpina* R.Br., *G. dicarpa*), restiads, e.g. *Baloskion australe* (R.Br.) B.G.Briggs & L.A.S.Johnson, the monocotyledonous herb *Astelia alpina* R.Br., and *Sphagnum cristatum* moss. In lowland zones on the Australian mainland, e.g. eastern Australia, the more arid climate is not conducive to the formation of extensive raised peat bogs characteristic of lowland New Zealand (Campbell 1995). Conditions are suitable for *Empodisma* root growth and peat accumulation only during the wet season (usually winter). Dry conditions during the remainder of the year check root production and accelerate decomposition, resulting in only shallow deposits of peat. Associates in these warmer areas include the grass tree *Xanthorrhoea fulva* (A.T.Lee) D.J.Bedford, and heath and heath-like shrubs including *Sprengelia sprengelioides* (R.Br.) Druce, *Persoonia virgata* R.Br. and *Boronia falcifolia* A.Cunn. ex Endl. Recovery of *Empodisma minus* after fire is rapid. In the Victoria highlands, abundant resprouted plants were noted within a few weeks

of being burnt (Walsh and McDougall 2004), with new shoots from basal resprouts being several centimetres long within a month (McDougall 2007). *Empodisma minus* cover had returned to prefire levels within two years of burning and had continued to increase considerably by 17 years post-fire (Wahren and Walsh 2000). However, recovery of community composition to pre-fire levels may take many years because competition from *Empodisma* may impede the establishment and growth of more fire-sensitive species such as *Richea continentis* and *Epacris* spp.

Ecology of *Empodisma gracillimum*

Empodisma gracillimum is endemic to Australia. It is restricted to the coastal plain from Perth southwards, and along the south coast from Augusta to Albany (Meney and Pate 1999). This region receives the greatest amount of rainfall in the Southwest Australian Floristic Region (Hopper and Gioia 2004). *Empodisma gracillimum* inhabits seasonally or permanently inundated swamps, woodlands and stream margins on nutrient poor, peat or sandy peat soils (Meney and Pate 1999). It is locally abundant, forming dense masses up to 1.5 m high, is often associated with *Beaufortia sparsa* R.Br., *Leptocarpus* sp., and *Baumea rubiginosa* (Sol. ex G.Forst.) Boeckeler, and is often surrounded by tall shrubs such as *Agonis linearifolia* (DC.) Sweet, *A. parviceps* Schauer, *Homalospermum firmum* Schauer, *Hakea linearis* R.Br., *Callistemon glaucus* Sweet, and the woodland species *Eucalyptus marginata* D.Don ex Sm. and *E. calophylla* Lindl. Flowering occurs in the spring and summer with a prolonged seed maturation of 10 to 12 months. The vegetation of the Southwest Australia Floristic region is subject to frequent fires, and *Empodisma gracillimum* employs a sprouter recovery strategy following a fire (Meney et al. 1997).

Conclusions

The three species of *Empodisma* form a well-supported clade. The clade diverged during the early Miocene, which was a period of equitable environmental conditions in Australia. A rapid succession of marine incursions, the onset of aridity in Australia, and origin of the Nullarbor Plain during the mid to late Miocene created barriers that isolated the southwest Australian endemic *E. gracillimum* from the southeastern Australian *E. minus*. Dispersal, colonization and speciation in New Zealand occurred more recently, coinciding with the uplift of the Southern Alps during the Pliocene and episodes of glaciation during the Pleistocene. Genetic, morphological and ecological evidence supports the separation of *Empodisma minus* into two species, *E. minus* and *E. robustum*. The split between *E. minus* and *E. robustum* is unambiguous and independently supported by the three cpDNA regions that we surveyed. *Empodisma robustum* is distinguished by six unique nucleotide substitutions and a 23-base duplication. It is a taller, more robust plant that is typically killed by fire and confined to lowland regions

north of 38° S, whereas *E. minus* is smaller, resprouts after fire, and occurs in alpine and lowland areas south of 38° S. The western Australian species *E. gracillimum* emerges as sister to *E. minus* and *E. robustum*. It is geographically isolated and can be readily distinguished by its fine light green culms, shorter leaf sheaths and pedicellate female flowers. This last character appears to be a distinctive feature of the species.

Taxonomy

Empodisma L.A.S.Johnson & D.F.Cutler

<http://species-id.net/wiki/Empodisma>

Type species. *Empodisma minus* (Hook.f.) L.A.S.Johnson & D.F.Cutler

Description. Perennial herbs forming dense tangled masses, dioecious. Rhizomes stout up to 8.0 mm diam., covered with light brown, imbricate, scale-like sheaths and very thick tufts of brown hairs. Roots crowded, densely covered with persistent root hairs. Culms evergreen, hollow, dark to light green, profusely branching. Lamina reduced, awl-shaped, persistent, light green when young maturing dark brown, strongly reflexed from the leaf sheath. Leaf sheaths open, but overlapping and closely appressed, borne at short intervals, straw-coloured early in the season maturing dark brown, mouth ciliate with a tuft of woolly white hairs. Spikelets unisexual, borne in ultimate branch systems produced in second or third year, sessile or on short pedicels. Glumes imbricate; bracteoles lacking. Perianth segments 6, narrowly ovate almost hyaline. Male spikelets with 1–6 flowers, sessile to shortly pedicellate. Stamens 3, exerted beyond the perianth segments; filaments uniform; anthers linear oblong, dorsifixed, 1-celled, dehiscence along longitudinal slits, straw-coloured. Female spikelets solitary, each spikelet with 1– rarely 2 – flowers sessile to pedicillate. Ovary 1-celled; style branches 2 or 3, filiform, deciduous. Ovule solitary, pendulous. Fruit 1-seeded nut, ovoid with a thick and swollen base. 2n = 24. Fruit development is protracted with the seeds maturing in the following winter or early spring.

Key to species of *Empodisma*

- 1 Robust plants forming dense tangled thickets; culms > 1 mm in diameter at base of the plant; sheaths mostly >7.5 mm long; spikelets > 6.0 mm long..... *E. robustum*
- Slender and/or diminutive plants; culms mostly < 1 mm in diameter, sheaths mostly < 7.5 mm long; spikelets generally < 6.0 mm2.
- 2 Culms dark green, 18–80 cm in height (some plants rarely to 1.2 m in Eastern Australia); female spikelets sessile to shortly pedicellate.....2. *E. minus*
- Culms light green, 55–130 cm in height; spikelets borne on pedicels up to 20 mm long.....3. *E. gracillimum*

1. *Empodisma robustum* Wagstaff & B.R. Clarkson, sp. nov.

urn:lsid:ipni.org:names:77120446-1

http://species-id.net/wiki/Empodisma_robustum

Holotype. (Fig. 8) New Zealand, Waikato, Hoe-O-Tainui, R. Mason, N.T. Moar 6750, 6/12/1958, CHR11159.

Etymology. *robustum* describes the robust stature of *E. robustum*.

Description. Culms dark green, 38–139 cm in height (reportedly > 200 cm when supported by associated shrubs), 0.9–2.2 mm in diameter at the base, branching profusely. Leaf sheaths open, closely appressed, 5.2–21.0 mm in length, borne at intervals of 20.0–70.0 mm, light green to light brown early in the season maturing dark brown; mouth ciliate with a tuft of woolly white hairs. Lamina strongly reflexed from leaf sheath, 2.2–7.5 mm long, light green when young maturing dark brown. Spikelets brown; male spikelet 6.8–9.0 mm long, anthers 1.9–2.5 mm; female spikelet 5.8–8.9 mm; nutlets dark brown approximately 2.7 mm long. Flowering Aug.–Oct. See Figure 9.

Comments. Many herbarium specimens of *E. robustum* include only the upper portion of the plant. These specimens may be difficult to distinguish from the larger specimens of *E. minus*. Quality specimens should include a rhizome and the base of the culms, from which the distinguishing measurements are taken. Most collections of *E. robustum* are either sterile or male, and the few females generally lack mature fruits. A chromosome count of $2n=24$ was reported from plants collected at Moanatuatua Bog (Briggs 1966, Johnson and Cutler 1973).

Representative specimens. New Zealand, Lake Tangonge, H. Carse, H.B. Mathews, 25 Oct 1920, CHR295186; New Zealand, Moanatuatua Bog, W.F. Harris, 20 Nov 1951, CHR85625; New Zealand, Motutangi Swamp, T. Seymour, 15 July 1976, CHR287072; New Zealand, Tauhei, H. Carse, Aug 1925, CHR295191; New Zealand, Opuatia Bog, immature ♀ flowers J.T. Taylor, 27 July 1987, WAI8520; New Zealand, Torehape, not flowering, R.H. Chitty, WAI3280; New Zealand, Moanatuatua Bog, not flowering, R. Thompson, 3/77, WAI2099; New Zealand, Moanatuatua Bog, immature flower buds, H. Beaton 3/77, WAI2098; New Zealand, Kopouatai Peat Dome, immature flower buds, P.J. de Lange, 14 Mar 1988, WAI9008; New Zealand, ♂ in flower, R. Irving, M. Skinner, 12 Oct. 1983, WAI 422; New Zealand, Tairua Ecological District, not flowering, B.R. Clarkson, 3 Feb 1998, WAI 16755; New Zealand, Moanatuatua Bog, not flowering, H.J. Beaton, 16 Aug 1976, WAI 1100; New Zealand, Moanatuatua Bog, not flowering, K. Thompson 3/77, WAI 2100; New Zealand, Kaitaia, not flowering, W.F.B. Oliver, 26 Feb 1929, WELT19806; New Zealand, Ohaupo Swamp, ♂ flowers, T.F. Cheeseman, WELT19805; New Zealand, Ohaupo Swamp, not flowering, W. Petrie, WELT19804; New Zealand, Ohaupo Swamp, ♂ in flower, W. Petrie, WELT19803; New Zealand, Ohaupo Swamp, ♂ flowers, W. Petrie, WELT19802; New Zealand, Maitahi shrubland, not flowering, A.R. Jamieson, AK231291; New Zealand, Rukuhia Swamp ♂ and ♀ plants in flower, L.M. Cranwell 18/34, AK109372; New Zealand, Lake Ohia, ♂ flowers, R. Cooper, R. Mason, N. Moar 1 Aug 1949, AK35820; New Zealand, Torehape Peat Dome ♂ flowers, A.E. Wright 10576, AK215859; New Zealand, Whangamarino



Figure 8. Type of *Empodisma robustum*, N56 R. Mason, N.T. Moar 6750, 6/12/1958, CHR11159.

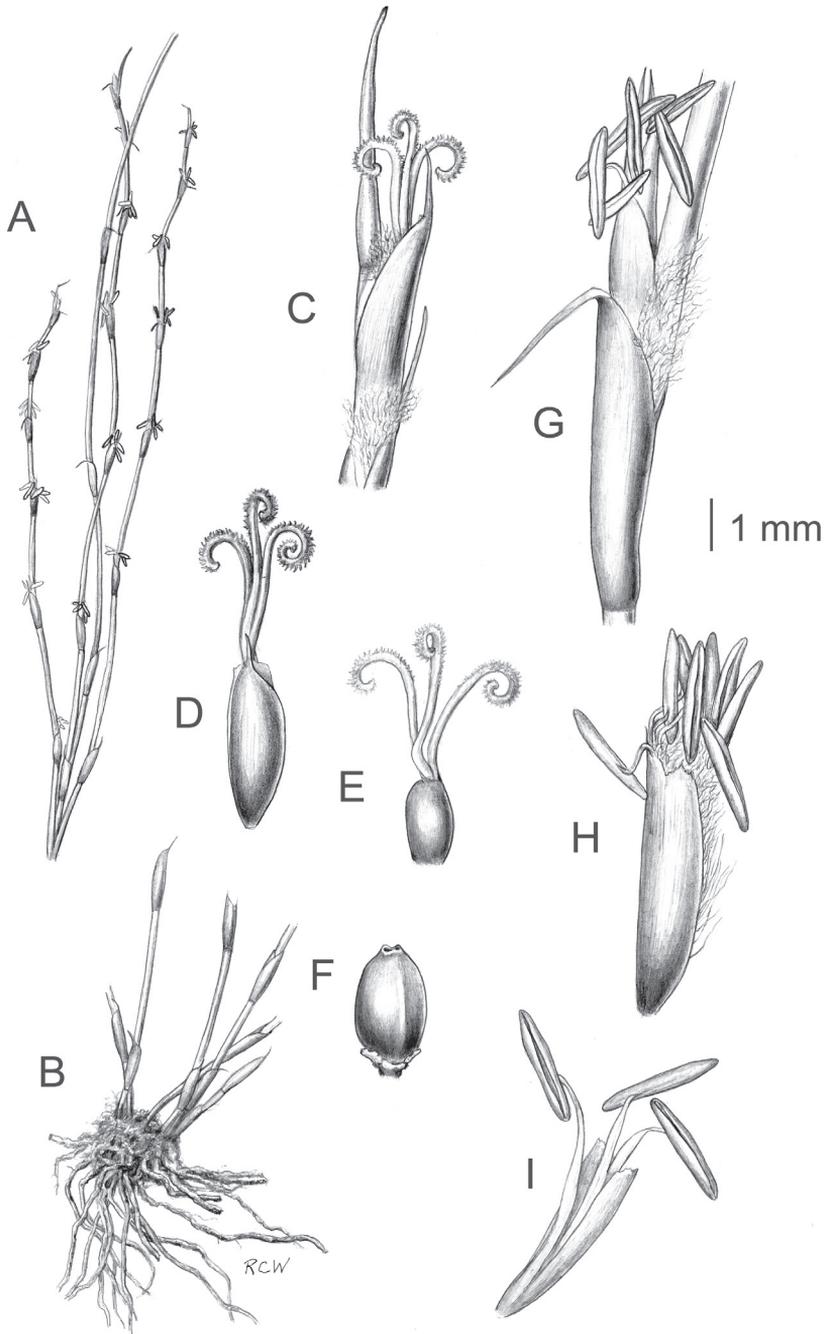


Figure 9. Morphological characteristics of *Empodisma robustum*. **A** Vegetative shoot with attached leaves and flowers (actual size) **B** Rhizomes with emerging vegetative shoots (2.5× actual size) **C** Vegetative shoot with attached pistillate flower **D** Pistillate flower with attached bracts **E** Gynoecium **F** Mature nut **G** Vegetative shoot with attached staminate spikelet **H** Staminate flower with attached bracts **I** Staminate flower. Scale bar = 1 mm.

Swamp, ♂ flowers, plants up to 1.2 m tall, E.K. Cameron 8839; AK234026; New Zealand, Kaihu Valley, ♂ flowers, A.R. Jamieson 30 Oct 1999, AK286616; New Zealand, Tomarata Lakes, not flowering, M.E. Young 20 March 2007, AK299780; New Zealand, Moanatuatua Peat Reserve, Rukuhia, ♂ flowers, F.J. Newhook July 1979, AK304253; New Zealand, Rukuhia Swamp, separate plants with ♂ and ♀ flowers, L.M. Cranwell 18/34, AK109373; New Zealand, Mangawhai Black Swamp, immature ♀ flowers, M.E. Young 18 July 1999, AK239846; New Zealand, Mercer Swamp, P. Hynes 15 Feb 1964, AK101004; New Zealand, Tomarata Lakes, with few ♀ flowers, M.E. Young 20 March 2007, AK299780; New Zealand, Lake Ohia, ♂ flowers, A.E. Wright 10554, AK232056; New Zealand, Lake Ohia, ♀ flowers and fruits, A.E. Wright 10555, AK232055; New Zealand, Tokerau Beach, M.E. Young, L.J. Forester 17 Oct 2006, AK306920; New Zealand, Lake Ohia, ♂ flowers, J.E. Braggins 87/87A, AK304249.

The acronym for the University of Waikato herbarium was recently changed from WAI to WAIK. We cited the older WAI acronym which appeared on specimen labels that we studied.

Distribution. New Zealand endemic ranging from North Cape southwards to approximately 38° S latitude.

Habitat. *Empodisma robustum* is restricted to ombrotrophic raised peat bogs where it often coexists with *Sporadanthus ferrugineus*, fens and gumland heathland peats. Locally abundant, but populations becoming fragmented by intensive land use.

Conservation status. Widespread drainage and conversion to pasture has dramatically reduced the extent of raised peat bogs in Northland and Waikato. This unique ecosystem is severely fragmented and provides habitat for a number of rare plant species such as *Sporadanthus ferrugineus* (de Lange et al. 1999) and *Dianella haemata* (Heenan and de Lange 2007). However, *E. robustum* is still relatively common in shallower/younger peat systems, and probably does not yet qualify as a threatened species. We recommend that its conservation status be regularly reviewed.

2. *Empodisma minus* (Hook.f.) L.A.S. Johnson & D.F. Cutler, *Kew Bull.* **28**, 383 (1973)

http://species-id.net/wiki/Empodisma_minus

≡ *Calorophus minor* Hook.f., *Fl. Nov. Zel.* **1**, 267 (1852–1853).

≡ *Calorophus elongatus* var. *minor* (Hook.f.) Hook.f., *Fl. Tas.* **II**, 75 (1858–1859).

≡ *Hypolaena lateriflora* var. *minor* (Hook.f.) Cheeseman, *Manual N.Z. Flora* ed. 1, 762 (1906)

Lectotype. New Zealand, near Nelson, Bidwell no. 84, K000441989; (Fig. 10; designated by Moore and Edgar 1970, pg 89).

Etymology. *minus* describes the small stature of *Empodisma minus*.

Description. Culms dark green, 12–81 cm in height, 0.7–1.3 mm in diameter, branching profusely. Leaf sheaths closely appressed, 3.5–10.2 mm in length, borne at



Figure 10. High resolution photograph of the lectotype of *Empodisma minus* (Hook.f.) L.A.S. Johnson & D.F.Cutler. Reproduced with the consent of the Royal Botanic Gardens, Kew, © The Board of Trustees of the Royal Botanic Gardens. Hooker (1853) described the new species *Calorophus minor* Hook.f. based upon Bidwell, Colenso and Lyall specimens. A specimen collected near Nelson by Bidwell, no. 84, K000441989, was chosen as the lectotype by Moore and Edgar (1970).

short intervals 15.0–48.0 mm; light green to light brown early in the season maturing dark brown; mouth ciliate with a prominent tuft of woolly white hairs in New Zealand specimens, sparse or lacking in Australian specimens. Lamina strongly reflexed from leaf sheath, 1.5–4.2 mm long, persistent light green when young maturing dark brown. Spikelets brown, male spikelet 3.9–8 mm long, anthers 1.2–2.0 mm long; female spikelet 3.5–7.0 mm long; nutlets dark brown approximately 2.6 mm long. $2n = 24$. Flowering Aug.–Apr. [Fig. 11; see also illustration in Meney and Pate (1999)].

Comments. Morphologically similar to small forms of *Empodisma robustum* distinguished by its smaller stature (though plants from 0.4 to 1 m tall are noted from eastern Australia), more delicate culms and smaller spikelets. Most collections are sterile or male, and the few females generally lack mature fruits. Chromosome counts of $2n=24$ were reported from plants collected from the NW slope of Mt. Ruapehu and three counts from NSW (Briggs 1966, Johnson and Cutler 1973).

Representative specimens. Australia, Tasmania, near Margate, ♂ flowers, D.A. & A. Ratkowsky 1474, CHR303032, Australia, Queensland, Moreton Island, ♂ flowers, L. Durrington 1114 & S. Levine, CHR272564, Australia, Tasmania, Newdegate Pass, not in flower, T. Dobson 77107, CHR313744; New Zealand, S. Westland, ♂ flowers, G.C. Kelly, Oct 1966, CHR177206; New Zealand, Rahu Saddle, with few ♀ flowers, E.J. Godley, 1 July 1958, CHR108315; New Zealand, Bell Hill Plains, ♂ flowers, J. Clarke 1 Feb 1969, CHR189013; New Zealand, Ngamatea, ♂ flowers, N.J. Moar, 12 Jan 1949, CHR70144; New Zealand, Waikareiti, ♂ flowers, A.P. Druce, Feb 1968, CHR180674; New Zealand, Silica Springs Track, ♂ flowers G. Rennison, A61/36, , CHR535708; New Zealand, Makerikeri tarns, ♂ flowers, A.P. Druce, Nov 1973, CHR260376; New Zealand, Tussock Creek, ♂ flowers, L.B. Moore, 28 July 1968, CHR188099; New Zealand, Mokoreta, with few ♀ flowers, W.R. Sykes 41/94, CHR497058; New Zealand, Bayswater Bog, not flowering, B.R. Clarkson 19 Feb .2009, CHR605146; New Zealand, Awarua Bay, not flowering, P.N. Johnson 653, CHR437892; New Zealand, West Cape, A.F. Mark, 5 Feb 1972, CHR218694; New Zealand, Coal Creek, ♂ flowers; I. Payton, 13 Sept 1976, CHR520808; New Zealand, Mt. Rockport, not flowering, I.A. McNew, 31 July 1942, CHR35234; New Zealand, Lake Sylvester, ♂ flowers, R. Melville 5915, CHR142781; New Zealand, Lake Sylvester, ♀ flowers, R. Mason & N. Moar 4658, CHR95709; New Zealand, Bealey spur, with immature ♀ flowers, P. Douglas 26 Nov 1979, CHR362302; New Zealand, Lake Tennyson, ♂ flowers, M.J.A. Simpson 6315, CHR22759; New Zealand, Patterson Inlet, ♂ flowers, L.J. Dumbleton & E. Edgar, CHR182509; New Zealand, ♂ flowers, Fosberg, Feb 1949; CHR30378; New Zealand, Kaitangata, plants with ♀ and ♂ flowers, R. Mason & N.T. Moar 953, CHR 75833; New Zealand, Kapuka, ♀ flowers, W.H. Harbond 20 Nov 1968, CHR183615.

Distribution. Widely distributed in Tasmania and all mainland Australian States except Western Australia and the Northern Territory; in New Zealand extending north to approximately 38°S latitude.

Habitat. Locally abundant in seasonally or permanently inundated wetlands, heathlands, fens and peat bogs from sea level to alpine

Conservation status. Not threatened.

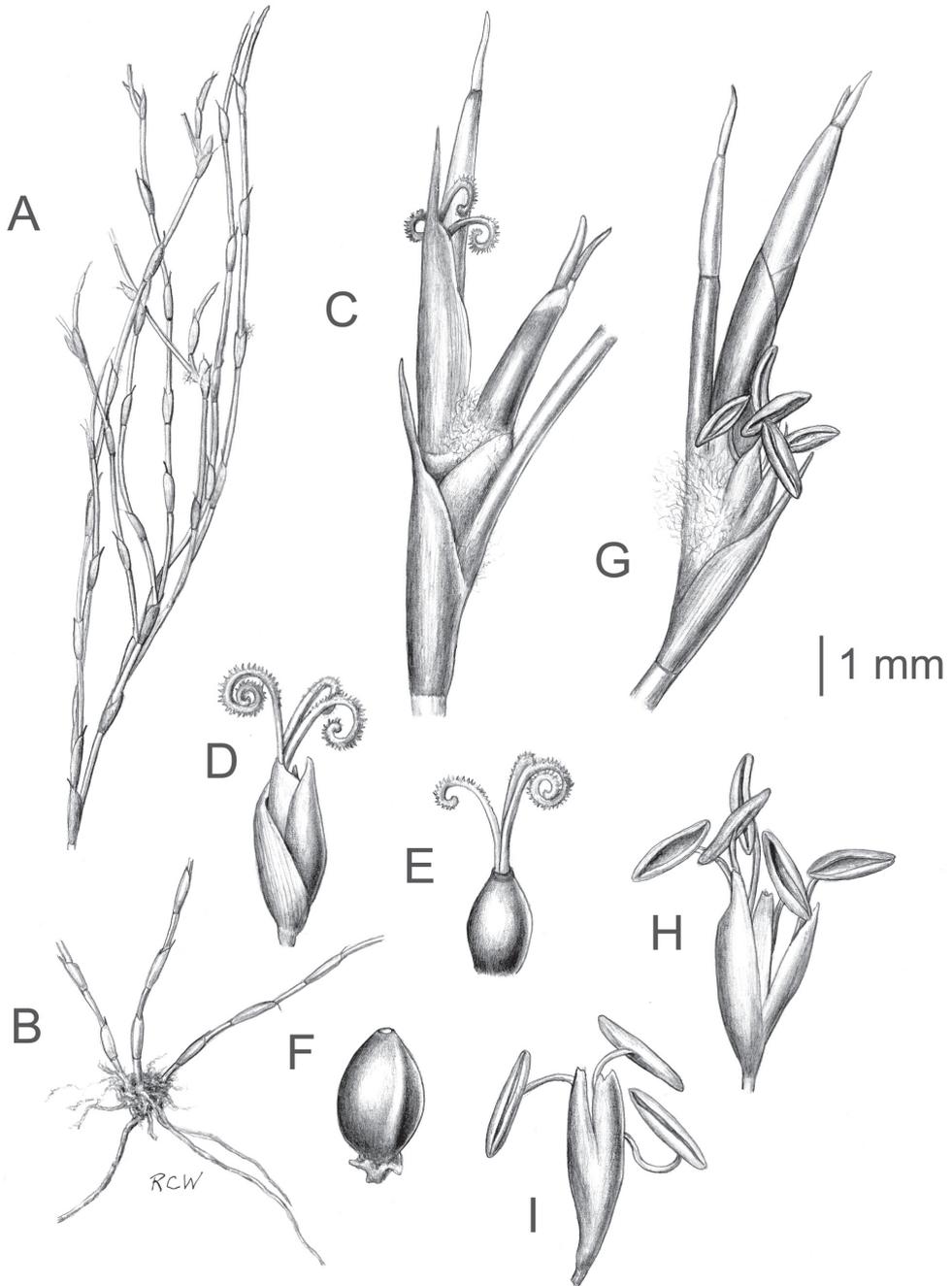


Figure 11. Morphological characteristics of *Empodisma minus*. **A** Vegetative shoot with attached leaves and flowers (2.5× actual size) **B** Rhizomes with emerging vegetative shoots (2.5× actual size) **C** Vegetative shoot with attached pistillate flower **D** Pistillate flower with attached bracts **E** Gynoecium **F** Mature nut **G** Vegetative shoot with attached staminate spikelet **H** Staminate flower with attached bracts **I** Staminate flower. Scale bar = 1 mm.

3. *Empodisma gracillimum* (F.Muell.) L.A.S. Johnson & D.F.Cutler Kew Bull. 28: 383 (1973)

http://species-id.net/wiki/Empodisma_gracillimum

- ≡ *Calorophus gracillimus* F. Muell., *Fragm. Phytogr. Australiae* 8, 88 (1872–74) as ‘*Calostrophus*’
 ≡ *Hypolaena gracillima* (F.Muell.) Benth., *Fl. Austral.* 7, 239 (1878).

Syntypes. (Fig. 12; *vide* BG Briggs xi.1998), Nouvelle-Hollande, Riv. des cygnes, Preiss JA 1711, 1843. P00748711; Nouvelle-Hollande, Riv. des cygnes, Preiss JA 1714, 1843. P00748712.

Etymology. *gracillimum* describes the slender culms of *Empodisma gracillimum*.

Description. (illustrated in Meneilly and Pate 1999). Culms delicate light green, 55–110 cm in height, 0.5–1.2 mm in diameter, branching profusely. Leaf sheaths, open, closely appressed, 3.5–9.0 mm in length, borne at intervals 25.0–80.0 mm; lamina strongly reflexed from leaf sheath, 2.4–5.0 mm, persistent, light green when young becoming straw coloured. Spikelets light brown, male spikelet 4–5.8 mm, anthers 0.6–1.0 mm long; female spikelet 1.5–2.4 mm long borne on pedicels up to 20 mm long; nutlets approximately 1.4–2.5 mm long straw-coloured. $2n = 24$. Flowering Aug.–Apr.

Comments. Though it approaches *Empodisma robustum* in height, *E. gracillimum* is readily distinguished by its more delicate light green culms and shorter leaf sheaths. The male and female spikelets of *Empodisma gracillimum* are smaller than either *E. robustum* or *E. minus*. The female spikelets are solitary and distinctly pedicellate; this character may be a synapomorphy for the species.

Representative specimens. Western Australia, Denmark, ♂ and ♀ flowers, B.G. Briggs 8449 & L.A.S. Johnson, CHR525963; Western Australia, 4.4 km east Watershed Road, ♂ flowers, A.R. Annels, R.W. Hearn 5112, PERTH04219031; Australia, 4.4 km east Watershed Road, fruits, A.R. Annels, R.W. Hearn 5111, PERTH04128567; Western Australia, Denmark, ♀ flowers, B.G. Briggs 8449 & L.A.S. Johnson, PERTH01586645; Western Australia, S. of junction with Brockman Highway, ♀ flowers D. Bright, C. Godden & T. Annels SC72.9 PERTH04723732; Western Australia, London Forest Block, 2 km S of Mountain Road along Renzo Road, ♂ flowers, R.J. Cranfield & B.G. Ward WFM53, PERTH07102399; Western Australia, Torndirrup National Park, ♂ flowers, G.J. Keighery 8805, PERTH02182831; Western Australia, Darling, ♂ flowers, B.G. Briggs 9330, PERTH06173853; Western Australia, 800 m E along O’Byrne Road from intersection of Commonage Road, ♂ flowers, N. Casson & T. Annels SC32.9, PERTH04741110; Western Australia, Walpole-Nornalup National Park, ♀ flowers, A.R. Annels ARA1580, PERTH05466172; Western Australia, Walpole, R.J. Cranfield 10897, PERTH04638530; Western Australia, 600 m S of Brockman Highway on Beck Road, ♂ flowers, N. Casson, P. Ellery & C. McChesney SC74.8, PERTH04723775; Western Australia, 400 m E of Blackwood and Great North Road, ♂ flowers, R. Davis 7680, PERTH05139317; Western Australia, WA, N. Casson & D. Bright SC106.2, PERTH04749677; Western Australia, S.E. Witch-

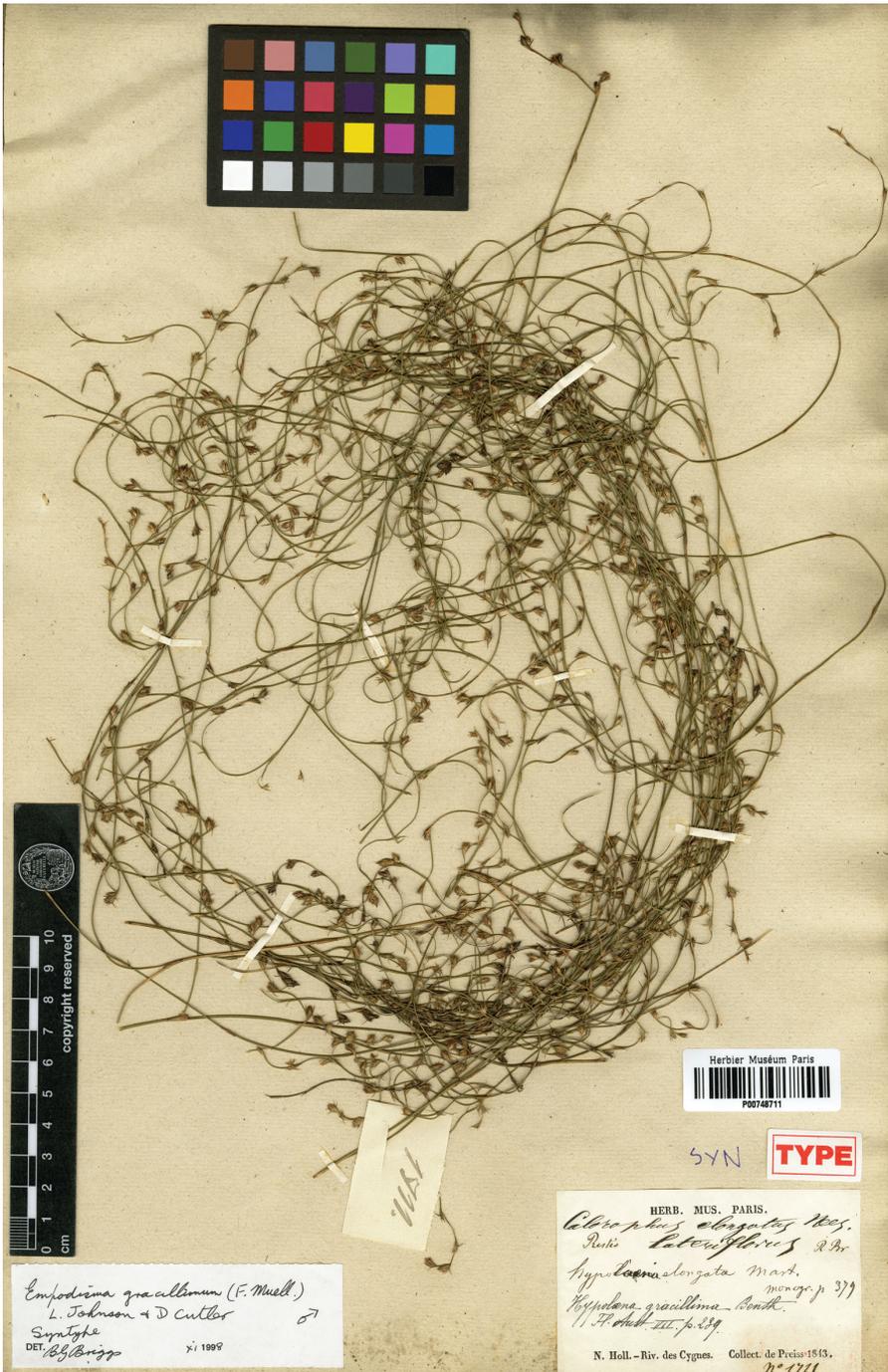


Figure 12. High resolution photograph of a syntype of *Empodisma gracillimum* (F. Muell.) L.A.S. Johnson & D.F. Cutler. Mueller (1872–74) originally described the plant as *Calorophus gracillimus* F. Muell. The specimen, Nouvelle-Hollande, Riv. des cygnes, Preiss JA 1711, 1843, P00748711 is held at HERBARIUM MUSEI PARIENSIS. The syntype was designated by BG Briggs xi.1998.

cliff, ♂ flowers, G.J. Keighery 16277, PERTH06330266; Western Australia, NE of Albany, E.M. Sandiford & D.A. Rathbone 1372, PERTH07926855.

Distribution. Endemic to western Australia on the coastal plain south of Perth extending along the south coast from Augusta to Albany.

Habitat. Grows on peat or sandy nutrient-poor soils. Locally abundant in seasonally or permanently inundated wetlands, swamps and stream margins.

Acknowledgements

We thank the curators of the Western Australia Herbarium (PERTH), Auckland Museum (AK), Te Papa-The National Museum of New Zealand (WELT), Waikato University Herbarium (WAIK) and Allan Herbarium (CHR) for the assistance with loans. The type of *Empodisma minus* was reproduced with the consent of the Royal Botanic Gardens, Kew, © The Board of Trustees of the Royal Botanic Gardens and *E. gracilimum* the Muséum National d'Histoire Naturelle (MNHN). Rebecca Wagstaff provided the beautifully rendered illustrations of *Empodisma minus* and *E. robustum*. Scott Bartlam and Jane Cruickshank helped with field and technical assistance. Earlier versions of this manuscript benefited greatly from the constructive suggestions provided by Ilse Breitwieser, David Glenny, Peter Heenan, Peter Linder and an anonymous reviewer. We would also like to acknowledge the careful editing of Christine Bezar and Anne Austin. This research was supported by the Ministry of Science and Innovation through the *Defining New Zealand's Land Biota* and the *Restoring Wetlands* contracts.

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Appendix I

Voucher specimens listing country of origin, literature citations, Allan Herbarium accession numbers for new sequences, their collection locality, DNA accession number, and GenBank accession numbers.

Specie	Country	Literature citation	Locality	Herbarium accession	DNA accession	<i>matK</i>	<i>rbcL</i>	<i>trnL</i>
<i>Alexeogeorgea subterranean</i> Carlquist	Australia	Briggs et al. (2010)		NSW 437369		GQ409034	GQ408918	GQ408988
<i>Anarthria polyphylla</i> Nees	Australia	Briggs et al. (2000, 2010)		NSW 391527		DQ257498	AF148760	AF148720
<i>Apodasmia brownii</i> (Hook.f.) B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2010)		NSW 494422		—	GQ408919	—
<i>Apodasmia chilensis</i> (Gay) B.G.Briggs & L.A.S.Johnson	Chile	Wardle et al. (2001)	Los Lagos, Mehuin	CHR513924		JX154568	AF307923	JX154570
<i>Apodasmia similis</i> (Edgar) B.G.Briggs & L.A.S.Johnson	New Zealand	Wardle et al. (2001)	Westland, Wanganui River	CHR517317		JX154569	AF307924	JX154571
<i>Baloskion tetraphyllum</i> (Labill.) B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW365050		DQ257501	AF148761	AF148721
<i>Calorophus elongatus</i> Labill.	Australia	Briggs et al. (2000, 2010)		NSW 264835		GQ409036	DQ257502	AF148725
<i>Calorophus erosus</i> (C.B. Clarke) L.A.S.Johnson & B.G.Briggs	Australia	Briggs et al. (2000, 2010)		NSW 264698		GQ409036	GQ408930	GQ408999
<i>Chaetanthus aristatus</i> (R.Br.) B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW 261929		DQ257508	AF148782	AF148743
<i>Chordifex crispatus</i> (R.Br.) B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010); Briggs and Johnson (2004)		NSW 401500		DQ257510	GQ408923	GQ408922
<i>Chordifex dimorphus</i> (R.Br.) B.G.Briggs	Australia	Briggs et al. (2000, 2010); Briggs and Johnson (2004)		NSW 270162		—	AF148763	AF148723
<i>Chordifex fastigiatus</i> (R.Br.) B.G.Briggs	Australia	Briggs et al. (2000, 2010); Briggs and Johnson (2004)		NSW 270160		—	AF148791	AF148752

Specie	Country	Literature citation	Locality	Herbarium accession	DNA accession	matK	rbcl	rnl
<i>Chordifex hookeri</i> (D.I.Morris) B.G.Briggs,	Australia	Briggs et al. (2000); Briggs and Johnson (2004)		NSW 264839		—	AF148762	AF148722
<i>Coleocarya gracilis</i> S.T.Blake	Australia	Briggs et al. (2000, 2010)		NSW 401500		GQ409023	AF148769	AF148730
<i>Dapsilanthus ramosus</i> (R.Br.) B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW 338881		—	AF148780	AF148741
<i>Desmodadus castaneus</i> B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW 423447		DQ257511	AF148770	AF148731
<i>Dielsia stenostachya</i> (W.Fitzg.) B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW 391321		—	AF148771	AF148732
<i>Empodisma gracillimum</i> (F.Muell.) L.A.S. Johnson & D.F.Cutler	Australia	This paper	Western Australia, Denmark	CHR 525963	9.14	JX129074	JX129095	JX129133
<i>Empodisma gracillimum</i> (F.Muell.) L.A.S. Johnson & D.F.Cutler	Australia	This paper	Western Australia, Caldyannup land system	PERTH 07102399	12.1	JX129076	JX129095	JX129132
<i>Empodisma gracillimum</i> (F.Muell.) L.A.S. Johnson & D.F.Cutler	Australia	This paper	Western Australia, NE of Albany	PERTH 046385330	12.2	JX129075	JX129097	JX129131
<i>Empodisma minus</i> (Hook.f.) L.A.S.Johnson & D.F.Cutler	Australia	This paper	Tasmania, Central Plateau, second lagoon	CHR 585759	7.45	JX129080	JX129101	JX129116
<i>Empodisma minus</i> (Hook.f.) L.A.S.Johnson & D.F.Cutler	Australia	This paper	Victoria, Mt. Buffalo	CHR 607930	9.15	JX129090	JX129111	JX129117
<i>Empodisma minus</i> (Hook.f.) L.A.S.Johnson & D.F.Cutler	New Zealand	This paper	Waipapa EA, Pureora	CHR 605145	9.04	JX129087	JX129108	JX129119
<i>Empodisma minus</i> (Hook.f.) L.A.S.Johnson & D.F.Cutler	New Zealand	This paper	Lookout Range	CHR 605066	8.09	JX129085	JX129106	JX129120
<i>Empodisma minus</i> (Hook.f.) L.A.S.Johnson & D.F.Cutler	New Zealand	This paper	Herangi Range, top	CHR 596548	8.08	JX129084	JX129105	JX129121

Specie	Country	Literature citation	Locality	Herbarium accession	DNA accession	matK	rbcl	rnl
<i>Empodisma minus</i> (Hook.f.) L.A.S.Johnson & D.F.Cutler	New Zealand	This paper	Taramoa	CHR 605065	8.01	JX129081	JX129102	JX129122
<i>Empodisma minus</i> (Hook.f.) L.A.S.Johnson & D.F.Cutler	New Zealand	This paper	Stewart Island, Mason Bay	CHR 605074	7.40	JX129077	JX129098	JX129123
<i>Empodisma minus</i> (Hook.f.) L.A.S.Johnson & D.F.Cutler	New Zealand	This paper	Pukerau Red Tussock Reserve	CHR 605847	9.05	JX129088	JX129109	JX129118
<i>Empodisma robustum</i> Wagstaff & Clarkson sp. nov.	New Zealand	This paper	Whangamarino	CHR 605067	11.01	JX129091	JX129112	JX129124
<i>Empodisma robustum</i> Wagstaff & Clarkson sp. nov.	New Zealand	This paper	Opuatia	CHR 605068	7.44	JX129079	JX129100	JX129129
<i>Empodisma robustum</i> Wagstaff & Clarkson sp. nov.	New Zealand	This paper	Moanatuatua Swamp	CHR 605165	9.06	JX129089	JX129110	JX129125
<i>Empodisma robustum</i> Wagstaff & Clarkson sp. nov.	New Zealand	This paper	Northland, Tangonge	CHR 605064	8.03	JX129082	JX129103	JX129128
<i>Empodisma robustum</i> Wagstaff & Clarkson sp. nov.	New Zealand	This paper	Lake Tomarata	CHR 605069	7.43	JX129078	JX129099	JX129130
<i>Empodisma robustum</i> Wagstaff & Clarkson sp. nov.	New Zealand	This paper	Kaimaumu	CHR 605063	8.06	JX129083	JX129104	JX129127
<i>Empodisma robustum</i> Wagstaff & Clarkson sp. nov.	New Zealand	This paper	Torehape Bog	CHR 605167	9.01	JX129086	JX129107	JX129126
<i>Eurychora complanata</i> (R.Br.) B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW 264949		DQ257514	AF148790	AF148751
<i>Harperia lateriflora</i> W.Fitzg.	Australia	Briggs et al. (2000, 2010)		NSW 423455		GQ409020	AF148776	AF148737
<i>Hopkinsia adscendens</i> B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW 364372		DQ257519	AF148727	AF148738
<i>Hypolaena exsulca</i> R.Br.	Australia	Briggs et al. (2000, 2010)		NSW 364832		—	GQQ408927	—
<i>Hypolaena grandisculula</i> F.Muell.	Australia	Briggs et al. (2000, 2010)		NSW 714757		—	—	GQ408962
<i>Hypolaena pubescens</i> (R.Br.) Nees	Australia	Briggs et al. (2000, 2010)		NSW 714454		GQ409046	—	GQ409963
<i>Hypolaena robusta</i> Meney & Pate	Australia	Briggs et al. (2000, 2010)		NSW 714451		—	—	GQ408964

Specie	Country	Literature citation	Locality	Herbarium accession	DNA accession	matK	ribL	rml
<i>Kulinia eludens</i> B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW 391535		—	AF148778	AF148739
<i>Lepidobolus chaetoccephalus</i> Benth.	Australia	Briggs et al. (2000, 2010)		NSW 364813		—	AF148779	AF148740
<i>Leptocarpus tenax</i> (Labill.) R.Br.	Australia	Briggs et al. (2000, 2010)		NSW 264954		GQ409039	AF148781	AF148742
<i>Lepyrodia glauca</i> (Nees) F.Muell.	Australia	Briggs et al. (2000, 2010)		NSW 423726		—	AF148785	AF148746
<i>Loxocarya gigas</i> B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW 364738		—	AF148786	AF148747
<i>Lyginia barbata</i> R.Br.	Australia	Briggs et al. (2000, 2010)		NSW 391339		DQ257523	AF148787	AF148748
<i>Meeboldina coangustata</i> (Nees) B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW 261610		GQ409043	AF148284	AF148745
<i>Melanostachya ustulata</i> (F.Muell. ex Ewart & Sharman) B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW 232599		GQ409035	AF148788	AF148749
<i>Restio distichus</i> Rottb.	Africa	Moline and Linder (2005)		Linder, Hardy and Moline 7327		AY881540	AY881467	AY881613
<i>Sporadanthus ferrugineus</i> de Lange, Heenan & B.D.Clarkson	New Zealand	This paper	South Auckland; Moanatuata Swamp	CHR 605163	9.10	JX129093	JX129114	JX129135
<i>Sporadanthus ferrugineus</i> de Lange, Heenan & B.D.Clarkson	New Zealand	This paper	South Auckland; Kupuati	CHR 604580	8.56	JX129092	JX129113	JX129134
<i>Sporadanthus gracilis</i> (R.Br.) B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW 270154		GQ409027	DQ257526	GQ409013
<i>Sporadanthus tasmanicus</i> (Hook.f.) B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW 264956		GQ409028	AF148793	AF148754
<i>Sporadanthus traversii</i> F.Muell.	New Zealand	This paper	Chatham Islands; Rakauroahi	CHR 605164	9.08	JX129094	JX129115	JX129136
<i>Tanais grossa</i> B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW 270154		GQ409027	DQ257526	GQ409013

Specie	Country	Literature citation	Locality	Herbarium accession	DNA accession	matK	rbcL	trnL
<i>Tremulina tremula</i> B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW 264956		GQ409028	AF148793	AF148754
<i>Tyrbastes glaucescens</i> B.G.Briggs & L.A.S.Johnson	Australia	Briggs et al. (2000, 2010)		NSW 261641		GQ409037	AF148795	AF148756
<i>Winifredia sola</i> L.A.S.Johnson & B.G.Briggs	Australia	Briggs et al. (2000, 2010)		NSW 713239		GQ409021	AF148796	AF148758

