A systematic revision of the *Carex nardina* complex (Cyperaceae)

Une révision systématique du complèxe *Carex nardina* (Cyperaceae)

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Abstract

The *Carex nardina* complex is a group of one to three species (*C. nardina*, *C. hepburnii*, *C. stantonensis*) and six taxa of unispicate sedges (Cyperaceae) whose taxonomy has been controversial since the 1800s. As initial DNA phylogenies suggested that the complex was nested within *Carex* section *Filifoliae* and sister to *C. elynoides*, a species often confused with *C. nardina* and sympatric with it in the western North American Cordillera, analyses were conducted to determine whether *C. hepburnii*, *C. stantonensis* and other infraspecific taxa could be the result of hybridization. Morphometric and molecular analyses found no substantial evidence for hybridization and supported the recognition of no taxon beyond *C. nardina*. Consequently, this study concludes that the complex comprises a single variable species, *Carex nardina*, distributed throughout arctic North America south through the western Cordillera to New Mexico with a minor portion of its range in northeastern Russia, northwestern Scandinavia and Iceland.

Résumé

Le complèxe *Carex nardina* comprend une à trois espèces (*C. nardina*, *C. hepburnii*, *C. stantonensis*) et six taxa de laîche (Cyperaceae) dont la taxonomie est contestée depuis le 19^{e} siècle. Des phylogénies ADN préliminaires ont suggéré que le complèxe est emboîté dans la section *Filifoliae* de *Carex* et que c'est soeur à *C. elynoides*, une espèce sympatrique souvent identifiée comme *C. nardina* dans la Cordillère Occidentale de l'Amérique du Nord; donc, *C. hepburnii*, *C. stantonensis* et d'autres taxa infraspécifiques pourraient être resultats de l'hybridisation. Cependant, l'analyse morphométrique et

moléculaire n’a trouvé aucune preuve ni de l’hybridisation ni d’un autre taxon à part de *C. nardina*. En conséquence, d’après cet étude le complèxe comprend une seule espèce variable, *Carex nardina*, répandue dans l’arctique nord-américain et au sud à travers la Cordillère Occidentale au Nouveau Méxique et en populations au nord-est de la Russie, de la Scandinavie nord-ouest et de l’Islande.

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INTRODUCTION

Cyperaceae is one of the most taxonomically challenging (Starr and Ford 2001) families of angiosperms due to its cosmopolitan distribution, enormous range of biogeographical patterns (Gondwanan to amphiatlantic; Ball 1990; Croizat 1952) and high species diversity (ca. 5000). The family is distinguished by 3-ranked leaves with closed sheaths, reduced flowers in which the gynoecium is subtended by a single, bract-like scale and fruits that are achenes (Figs. 1 and 2; Goetghebeur 1998). Many authors (e.g. Reznicek 1990; Starr *et al.* 2004; Ford *et al.* 2006) have noted the exceptional significance of the tribe Cariceae Kunth ex Dumortier (ca. 2 100 spp) as it accounts for almost half the species in the family. Cariceae itself is cosmopolitan and occurs in a broad range of habitats (tundra to rainforests; Starr *et al.* 2008) and has considerable cytological diversity (n = 6-56; Davies 1956). This tribe of herbaceous, mostly anemophilic, perennial plants is distinguished by its unisexual flowers in which the naked gynoecium is surrounded by a flask-like prophyll (Figs. 1 and 2) called a perigynium or utricle (Starr and Ford 2009).

Although the tribe is monophyletic, its reduced floral morphology, wide distribution and considerable species diversity create difficulties for reconstructing evolutionary patterns among its taxa (Waterway and Starr 2007; Starr and Ford 2009). Disagreement among taxonomists on the number of genera (five, Reznicek 1990; six, Bruhl 1995) has recently been resolved by ETS 1f (External Transcribed Spacer) and ITS (Internal Transcribed Spacer) sequence data that found four clades, although generic interrelationships remain contentious (Starr *et al.* 2004). Cariceae genera have traditionally been differentiated on the basis of morphological differences in the perigynium and

rachilla (a pistillate spikelet often interpreted as an extension of the axis bearing a single female flower; Fig. 1) (Starr and Ford 2009).

The largest genus of the tribe, *Carex* L. (ca. 2 000 species; Goetghebeur 1986), is distinguished from the other genera by a closed perigynium fused to the apex and its reduced, unhooked rachillae (Reznicek, 1990). Most *Carex* species are differentiated only by minor variations in the size, shape, venation and texture of the perigynium (Nelmes 1951). Despite over two centuries of scientific study, the evolutionary relationships among *Carex* species remain poorly understood (Naczi *et al.* 1998) due to the close morphological similarity between many species, transitional species (Starr *et al.* 2004), hybridization among species of certain sections (Cayouette and Catling 1992), frequent inflorescence reduction and proliferation (Starr and Ford 2009), and successive instances of parallelism and reversal (Starr *et al*. 1999). The development of a phylogeny of all *Carex* taxa has been further hindered by homology problems caused by a lack of ontogenetic data (Alexeev 1988; Starr *et al*. 1999).

Carex Subgenus *Psyllophora* (Degl.) Peterm. (= subg. *Primocarex* Kük. 1909), one of four subgenera in the genus, is a small group (60-70 species) that is crucial to resolving the complicated taxonomy of the genus (Starr and Ford 2009). *Psyllophora* is characterized by extremely reduced, androgynous, unispicate inflorescences (Starr and Ford 2009). *Psyllophora* has been largely responsible for obscuring the divisions between *Carex* subgenera and between *Cariceae* genera (Starr *et al.* 2004). As a result, *Psyllophora* has been called "the most difficult problem in *Carex*" (Reznicek 1990). Authors have debated whether *Psyllophora* is derived or plesiomorphic within *Carex* (e.g. Kükenthal 1909; Kreczetovicz 1936; Savile and Calder 1953). Some have postulated the rachilla-bearing

members as a separate taxon from those lacking a rachilla (e.g. Nelmes 1952). Nuclear ribosomal DNA, or nrDNA (ITS and ETS 1f; Starr *et al.* 2004), chloroplast DNA, or cpDNA (*ndhF*, *trnL* intron; Yen and Olmstead 2000) and combined nrDNA/cpDNA (Roalson *et al.* 2001) evidence has shown that the subgenus is polyphyletic and that its species represent derived elements within *Carex* (Starr and Ford 2009).

Given the cosmopolitan distribution and high species diversity of *Carex* most studies focus on a small number of taxa of limited geographic distribution (Starr *et al.* 2004). Relatively few studies consider phylogenetic relationships below the sectional level (Crins 1990). Yet, examining small, relatively well circumscribed taxa can help clarify the systematics of large, complex groups because the challenges of adequate sample size and reliable circumscription can be more easily overcome and results can be corroborated by gathering different types of data for the same set of specimens (Starr and Ford 2001). Of the 14 sections of *Psyllophora*, *Nardinae* (Tuckerman) Mackenzie is particularly notable because of the taxonomic uncertainty surrounding it since 1840 when the first segregate, *C. hepburnii* Boott was described (see Table 1 for full taxonomy).

Carex nardina Fries is a widespread, unispicate species with an Arctic-alpine distribution (Hulten 1958, Murray 2002) limited to rocky, xeric, windy habitats with poor soils (Cronquist *et al.* 1977). *Carex nardina* and *C. hepburnii* are the only taxa in the complex that occur in the western Cordillera of North America (W Cordillera), far eastern Siberia, the Canadian Arctic archipelago and coast, Greenland, Iceland and northern Scandinavia. They bear a close morphological resemblance to each other (Porsild 1943; Egorova 1999), grow in similar habitats (Mackenzie 1935), and represent the most crucial problem in the complex. The present study will therefore focus on these two taxa.

Murray (2002) described section *Nardinae* as having two or three stigmas, glabrous perigynia with distally marginal prickle hairs, and pistillate scales < 5 mm long (slightly shorter than the perigynium) with broad, hyaline margins (Figs. 2 and 3). Murray (2002) also specified *C. nardina* as having an ovate perigynium 1.4 – 1.6 mm wide with a gradually formed beak 0.5 mm long and a distinct stipe 0.5 – 1.0 mm long, occurring in calcareous, gravelly soils on dry slopes. *Carex hepburnii* is distinguished by a glabrous, elliptical perigynium 1.5 – 2.0 mm wide with an obscure beak < 0.4 mm long and obscure stipe < 0.2 mm long, occurring in similar habitats (Murray 2002).

For over 170 years botanists have debated whether the *C. nardina* complex constitutes one or several species. A total of six taxa have been proposed in the literature (Fries 1839; Boott 1840; Kükenthal 1909, 1910; Jones 1910; Porsild 1943) and conflicting descriptions, synonyms, mixed herbarium sheets and misidentified specimens are common (pers. obs.). Such a high number of similar taxa is plausible since field survey has revealed high species richness in *Carex* (e.g. Brunton 2005) and the examination of small taxa in *Carex* research often reveals substantial variability (e.g. Ford ***et al.*** 1998).

The *C. nardina* complex consists of *C. nardina*, *C. hepburnii*, *C. nardina* var. *atriceps* Kükenthal, *C. nardina* var. *hepburnii* Kükenthal, *C. stantonensis* Jones, *C. elynaeformis* AE Porsild and *C. nardina* subsp. *hepburnii* Jones, Jones and Kapoor. *Carex nardina* var. *atriceps* is confined to the eastern Canadian Arctic and Greenland. *Carex nardina* var. *hepburnii* has been described as occurring only in the W Cordillera (Kükenthal 1909). *Carex stantonensis* is represented by a single collection from Montana. *Carex elynaeformis* is limited to the northwestern Northwest Territories and high elevation

peaks in Colorado. Since Love *et al.* (1971) provided no protologue, *C. nardina* subsp. *hepburnii* was not considered.

No previous study alone has assessed the taxonomy of the complex by taking into consideration specimens from all parts of its distribution despite the compelling need to do so (Murray 2002). Also, the evolutionary sequence within Cariceae requires resolution (Naczi *et al.* 1998; Starr *et al.* 2004) and several authors (e.g. Mackenzie 1935; Savile and Calder 1953) have postulated a key position for section *Nardinae*. Furthermore, *C. nardina* holds promise for biogeographical comparisons with similar species that could, for example, help explain the origin of the Arctic-alpine distribution pattern. Generally, however, ambiguous synonyms pose a significant barrier to the study of species distributions (Culham and Yesson (2011) and artificial taxa undermine phylogenetic analysis by obscuring trends and confusing similarities (Page and Holmes 1998). Therefore, the taxonomic problems of the *C. nardina* complex outlined above must first be settled before such questions can be addressed.

Traditionally, botanists have noted that *C. nardina* bears a superficial resemblance to section *Filifoliae* (Cronquist *et al.* 1977; Mastrogiuseppe 2002), which is differentiated by the presence of three stigmas and dense pubescence on the perigynium body and is limited in distribution to the W Cordillera of North America. In particular, the *C. nardina* complex has been confused with *C. elynoides* Holm (section *Filifoliae*) as evidenced by an individual of *C. elynoides* that appears on the type specimen sheet for *C. hepburnii* created by Boott (1840). *Carex elynoides* is differentiated by having three stigmas, an elongated staminate spike, negligible marginal prickle hairs on the perigynium, two perigynial nerves and distally rounded pistillate scales with a pale midvein. The type specimens for *C.*

hepburnii and *C. stantonensis* were collected in the southwestern Cordillera. Perhaps not coincidentally, *C. elynoides* is only known from this area, which has been postulated as a Pleistocene glacial refugium (Holder 1999) during the last glacial maximum (LGM) ca. 10 000 BP (Knowles 2001; Marr *et al.* 2008; Pruett and Winker 2008). Glacial refugia are thought to have acted as sites of hybridization for many groups of organisms, e.g., Salicaceae (Fussi *et al.* 2010), Onagraceae (Lexer and van Loo 2006), Bovidae (Lorenzen *et al.* 2007) and Oscines (Krosby and Rohwer 2009).

If *C. hepburnii* represents hybridization between *C. nardina* and either *C. elynoides* or another member of section *Filifoliae* it would explain the morphological variation that has historically created confusion within the *C. nardina* complex. Natural hybridization (crossbreeding of two different taxa) is considered to be a cause of taxonomic confusion in a number of species complexes (Joly and Bruneau 2007). Hybridization is a common (Rieseberg and Soltis 1991; Okuyama *et al.* 2005) and evolutionarily important (Doyle *et al.* 2003) occurrence in some plant taxa, although it is known in only a few sections of North American sedges, and many *Carex* hybrids are represented by a single specimen each (Cayouette and Catling 1992). There are 843 species of *Carex* in North America (Ball and Reznicek, 2002), from which 180 hybrids are known (Cayouette and Catling 1992), although the largest proportion of hybrids by far is known from *Carex* subgenus *Carex* (Cayouette and Catling 1992).

Field observations suggest that hybridization with section *Filifoliae* is a possible explanation for the segregation of *C. hepburnii* and other taxa from *C. nardina*. *Carex elynoides* grows at elevations up to 3 800 m (Mastrogiuseppe 2002) and can occur in mixed populations with *C. nardina* (Jones 1910; 2010 field collections at Gray's Peak,

Colorado: *C. nardina*, *Starr 100211* and *C. elynoides*, *Starr 100221*, and at Union Peak, Wyoming: *C. nardina*, *Starr 100391* and *C. elynoides*, uncollected). Furthermore, although *C. elynoides* is tristigmatic it has a previously unrecognized habit of occasionally aborting the third stigma (pers. obs. of herbarium vouchers corroborated by field collections that had one brown and two fresh, white stigmas). It is therefore more likely to be confused with *C. hepburnii*, which has been described as either distigmatic or tristigmatic (Boott 1867, Kükenthal 1909; Egorova 1999), than with *C. nardina*, which is distigmatic according to its protologue (Fries 1839) and subsequent descriptions (Kükenthal 1909; Mackenzie 1935; Murray 2002). Many voucher labels support this prediction (pers. obs.).

Molecular results offer similar support. *Carex filifolia* was shown to be sister to *C. nardina* in the combined ITS and ETS 1f parsimony analysis of Starr *et al.* (2008), and *C. elynoides* was sister to *C. nardina* in the combined *trnL-F* and *rps16* Bayesian phylogeny of Gehrke *et al.* (2010). Also, preliminary sequencing with limited sampling in the present study suggested that the *C. nardina* complex was nested within section *Filifoliae*. Furthermore, preliminary morphological study has revealed characters derived from protologues that distinguish *C. nardina* from section *Filifoliae* and that are intermediate in *C. hepburnii*. These consist of staminate spike length, culm straightness and length, perigynium pubescence and stigma number. Only one of these characters, culm straightness and length, consistently segregated a plausible group of possible hybrids, which were straight and long like *C. elynoides* but otherwise resemble *C. nardina*. Perigynium pubescence could not segregate a putative hybrid group because extremely few specimens were completely glabrous and could thus be classified as *C. nardina*, while far more had moderate pubescence and would be classified using this character as the putative

hybrid. Similarly, stigma number varied on most specimens, meaning that extremely few specimens had two stigmas on every perigynium, as required by the *C. nardina* protologue. Staminate spike length was not used to segregate a putative hybrid group because no published description gave a guideline for what an average value should be for *C. nardina*.

Introgressive hybridization is the recombination of DNA from two compatible, but not necessarily closely related (Wells 1979) parent species, which often leads to greater morphological variation than existed in the parent species (Arnold 1994). morphological character states in hybrids are On average intermediate to those of the parents. However, hybrids may display intermediate or parental character states and the vast majority of hybrids develop novel or extreme characters, particularly after the first generation (Rieseberg and Ellstrand 1993; Linder and Rieseberg 2004; Guggisberg *et al.* 2009); nevertheless, most hybrids tend to resemble one parent or another in each character possibly due to positive assortative hybrid-parent back crossing (Arnold 1994).

Hybridization can be tested in a number of ways. Morphologically or anatomically diagnostic characters with intermediate values between the putative parents can be identified as evidence of possible hybridization (Arnold 1994; Joly and Bruneau 2007). Phylogenetically, a putative hybrid is expected to group together with one of the putative parents in a nrDNA tree and with the other putative parent in a cpDNA tree because the nuclear genome is inherited biparentally and evidence strongly suggests that the chloroplast genome is inherited uniparentally (Soltis *et al*. 1991). In the vast majority of a large sampling of plant families (65 out of 80) tested by Corriveau and Coleman (1988) plastid DNA was not detected in the generative or sperm cells of pollen. No Cyperaceae species were tested, however, leaving paternal plastid inheritance as a possibility.

If no hybridization evidence can be found, it must be determined whether *C. hepburnii* and the minor taxa within the *C. nardina* complex constitute separate species. The concept of a species can be defined in many ways. Fourteen leading species concepts are described in deQueiroz (2007) and many more have been proposed in the literature, although none is universally applicable. The biological species concept is most commonly used but rests on the concept of reproductive isolation (Mayr 1992), which is problematic in plant groups that hybridize and is inapplicable to asexually reproducing organisms. The evolutionary species concept rests on the idea of a lineage with a distinct evolutionary role and is suitable mostly for microbial organisms (Simpson 1951; Wiley 1978). The morphological species concept is defined by consistent phenotypic differences between groups of organisms and is often used in the absence of a well estimated phylogeny (Sokal and Crovello 1970). It is difficult to apply to *Carex* species since they are often distinguished by only subtle morphological differences.

The unified species concept (deQueiroz 2007) postulates species as separately evolving metapopulation lineages. Under this approach, all of the species concepts proposed in the literature constitute criteria for differentiating lineages and thus are all equally valid. The present study aims to use those criteria that can be readily tested in *Carex* species. Thus, separate species are here defined as groups or organisms that possess a unique character, be it molecular, morphological, anatomical or micromorphological, that is shared by all individuals in some populations but is absent in all remaining populations. This approach has been defined as the phylogenetic species concept (Donoghue 1985), and, since morphological characters can be used to construct a phylogeny, encompasses the morphological species concept as well. A similar approach was taken by Lehnebach (2011)

in resolving the taxonomy of a species complex in *Uncinia* section *Compactae* (Cyperaceae). In a phylogenetic tree, one would expect to find long branches between different species and short branches between individuals of the same species.

Objectives

A large sampling of specimens from the entire distribution of the complex was subjected to molecular, morphometric, anatomical and micromorphological analysis in order to find differences between putative taxa and/or a putative hybrid. Together, the goals of these analyses were 1) to determine the relationship between *C. nardina* and members of section *Filifoliae*, 2) to determine whether *C. hepburnii* could represent hybridization between *C. nardina* and members of section *Filifoliae*, with the result being *C. hepburnii*, and 3) to test the hypothesis that the two most important members of the complex, *C. nardina* and *C. hepburnii*, as defined by three authors (Boott 1840, 1867; Mackenzie 1935; Egorova 1999) who claimed an ability to differentiate the two, do not differ consistently and should therefore be considered one species.

Most of the same types of evidence (molecular, morphological, anatomical, micromorphological) can be used to evaluate the second and third questions, although silica body micromorphology has never produced any published instances of intermediate character states between species and is only applicable to the third objective. The first objective can be achieved using DNA evidence alone.

Disagreement between groups of specimens based on morphology and groups based on anatomical or micromorphological evidence in past studies has been deemed

indicative of homoplasy, leading some authors to conclude that anatomical (Standley 1987, 1990) and micromorphological (Rettig 1986; Waterway 1990) characters are ineffective for determining evolutionary relationships. However, these studies have focused on poorly circumscribed taxa for which phylogenetic analysis is lacking (Starr and Ford 2001).

Systematic background

Sectional classification

Tuckerman (1843) published section *Nardinae* consisting of *C. nardina* and *C. hepburnii*. The section was distinguished by the presence of two or three stigmas, an ovate spike, rounded pistillate scales and a mostly glabrous, ovate-lanceolate or elliptical perigynia with distally marginal prickle hairs. Shortly afterwards, Tuckerman (1843) also described section *Filifoliae*, the type species of which was *C. filifolia*. Mackenzie (1917) moved both sections to subgenus *Psyllophora*.

Carex nardina complex

Carex nardina (Fries) was described in 1839 based on a specimen from northern Sweden. *Carex hepburnii* (Boott) was published early in 1840 based on a specimen from the W Cordillera with a very similar description. Boott's (1840) protologue also mentions a specimen from Greenland. Debate began immediately whether they were one or two species. Drejer (1841) concluded that they were so similar that only one species existed. In 1848, Boott agreed with Drejer's (1841) conclusion, as indicated by Boott's annotation of collection 243 by Prescott (pers. obs.) and later publication of the two putative taxa as

synonymous (Boott 1867). No set of diagnostic characters has ever earned consensus among researchers. The protologues, however, indicate that *C. nardina* is distinguished by two stigmas, ovate-lanceolate perigynia and short, curved leaves and culm, while *C. hepburnii* has two or three stigmas, elliptical perigynia, and long, straight leaves and culm.

Kükenthal (1909) revived the name *hepburnii* and described it as a variety of *C. nardina* found in the W Cordillera and distinguished from C. nardina by its long, straight leaves and culms, three stigmas and short, abruptly contracted beak. Tengwall (1916) and Gorodkov (1927) described *C. hepburnii* as a valid species limited to Scandinavia and eastern Siberia respectively, yet very few authors have claimed an ability to differentiate *C. hepburnii* from *C. nardina*. Mackenzie (1935) did so, claiming that *C. nardina* had a tapering leaf sheath, ovoid-orbicular spike, two stigmas, ovate-orbicular or obtuse pistillate scale, lenticular achenes and a gradually tapering, membranaceous beak, while *C. hepburnii* had an abruptly contracted leaf sheath, oblong spike, three stigmas, triangular achenes and an abruptly tapering, hyaline beak. However, his conclusions have not been universally accepted among botanists and debate has continued whether the species complex comprises one or many taxa. Egorova (1999) published *C. nardina* and *C. hepburnii* as two good species (with *C. nardina* confined to parts of Scandinavia), while shortly afterwards Murray (2002) published the complex as one species.

Kükenthal (1910) also described a regional variety *C. nardina* var. *atriceps* supposedly distinguished by long, straight culms and leaves in the same year that Jones (1910) described *C. stantonensis* as occurring in Montana. Only a single specimen of *C. stantonensis* was ever collected and Jones (1910) speculated that it could be synonymous with *C. hepburnii*. Porsild (1943) described *C. elynaeformis* as a new species that was

supposedly distinguished by long, lanceolate achenes and a "bicentric" distribution. However, the protologue of *C. nardina* includes the lanceolate achene character and only one verified specimen of *C. elynaeformis* has ever been collected (in the Northwest Territories, Canada). Porsild redetermined three specimens of *C. hepburnii* from Colorado as *C. elynaeformis* but later changed his determination to *C. elynoides* (pers. obs.).

In order to avoid the confusion created by later descriptions, the present study will use only the protologue of each taxon considered and the descriptions of authors who claimed to be able to differentiate *C. nardina* and *C. hepburnii*, namely Boott (1840, 1867), Mackenzie (1935) and Egorova (1999). Also, type specimens will be examined wherever possible. However, another reason why the *C. nardina* complex has historically been difficult to define is that the type material for neither *C. nardina* nor *C. hepburnii* was ever designated as a holotype (Shetler *et al.* 1973; Koopman 2011). Type material was obtained for all taxa of the *C. nardina* complex except *C. nardina* var. *atriceps*

TABLE 1 Members of the *C. nardina* complex that were treated taxonomically in the present study.

Binomial	Author	Year	Section	Author	Year
Carex nardina	Fries	1839	*Nardinae*	(Tuckerman) Mackenzie	(1843) 1935
Carex hepburnii	Boott	1840	*Nardinae*	(Tuckerman) Mackenzie	(1843) 1935
Carex nardina var. *hepburnii*	Kükenthal	1909	*Nardinae*	(Tuckerman) Mackenzie	(1843) 1935
Carex nardina var. *atriceps*	Kükenthal	1910	*Nardinae*	(Tuckerman) Mackenzie	(1843) 1935
Carex stantonensis	Jones	1910	*Nardinae*	(Tuckerman) Mackenzie	(1843) 1935
Carex elynaeformis	Porsild	1943	*Nardinae*	(Tuckerman) Mackenzie	(1843) 1935
Carex nardina subsp. *hepburnii*	Love, Love and Kapoor	1971	*Nardinae*	(Tuckerman) Mackenzie	(1843) 1935

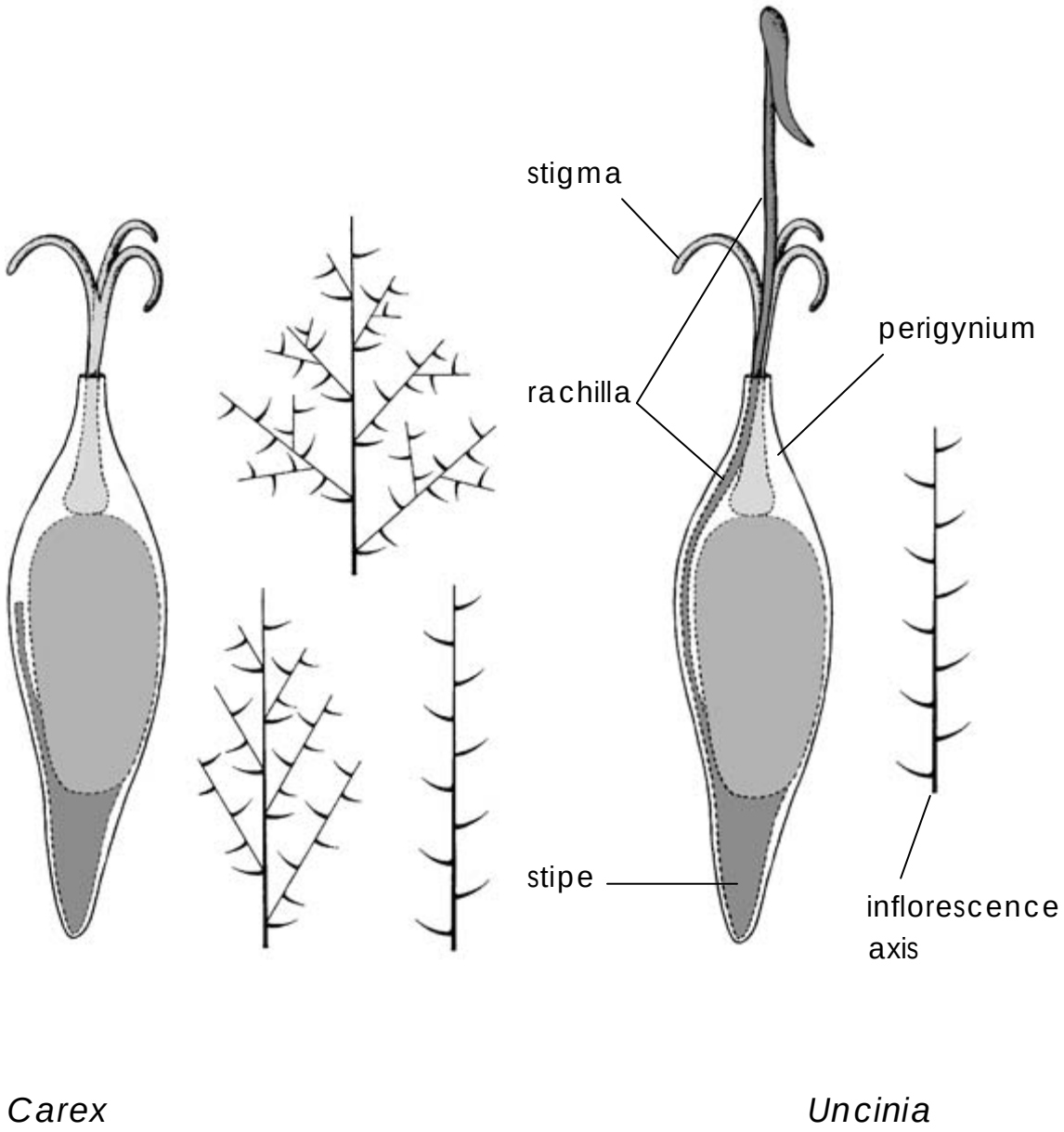


FIG. 1 Schematic diagram of the typical perigynium morphology and inflorescence axis structure in two genera of tribe *Cariceae*, *Carex* and *Uncinia* (from Starr and Ford 2009).

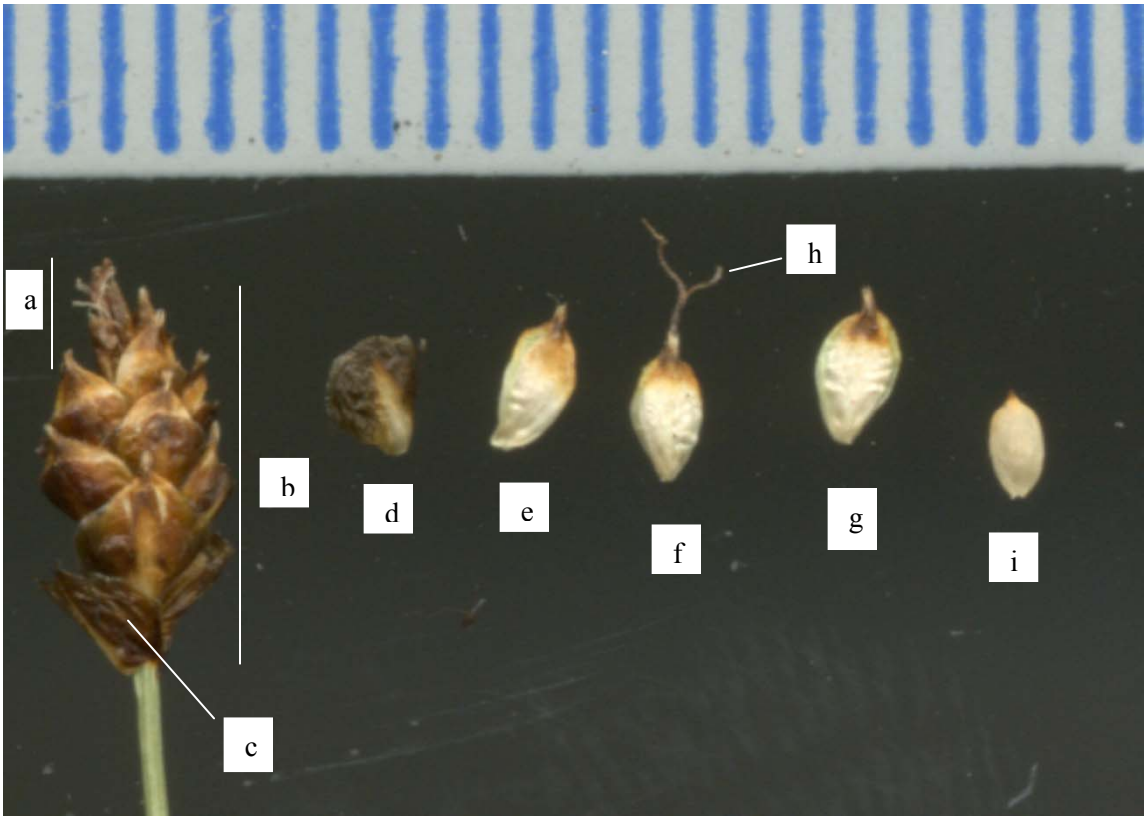


FIG. 2 *Carex nardina* Fries (photograph). Left to right: a) spike including staminate (male) spike, b) pistillate (female) spike, c) pistillate scale, d) pistillate scale, e-g) three perigynia, h) stigmas on exserted style, i) achene. Collection: *Carex nardina* Fries, *Moseley 2626*, ID109336. Scale in mm shown above.

FIG. 3 *Carex nardina* Fries. Collection by Fertig 11670 (RM) 592023. Scale in mm appears on the left.

MATERIALS AND METHODS

Specimens used – Herbarium loans and field collections

A total of 1063 voucher specimens were obtained for all taxa to be analyzed for DNA, morphology, anatomy, micromorphology and pollen stainability. Similar to Naczi *et al.* (1998) only mature, complete, ample specimens were chosen for analysis. These specimens were obtained on loan from the following herbaria (abbreviations follow Holmgren *et al.* 1981): MEXU, CAN, ASU, BRY, COLO, DAO, NY, IDS, MONTU, RM, UTC, WTU, SD, ALA, HUH, ICEL, KMN, LD, MO, OSC, OHN, S, U, UVSC and WIN.

In order to supplement the geographic sampling provided by herbarium specimens, fieldwork was conducted in the summer of 2010 in some areas currently underrepresented in herbaria. Five states of the W Cordillera (Colorado, Wyoming, Montana, Utah and Washington) were visited for the purpose of collecting populations of *C. nardina* and *C. elynoides* . Leaf material from 96 individuals from six populations of *C. nardina* and 74 individuals from eight populations of *C. elynoides* were placed in silica gel to preserve the tissue for DNA extraction. From each population, a minimum of 15 and maximum of 30 individuals were collected in order to achieve whole population sampling for the purpose of studying population genetics in the present or future studies of the *C. nardina* complex. Three voucher specimens for each population were obtained and will be deposited at CAN and DAO. The DNA sequences produced will be deposited in Genbank (http://ncbi.nlm.nih.gov/genbank).

The geographic locations of specimens were plotted on maps created in ArcView GIS 10.0 (ESRI 2011) (Figs. 4 - 6). Co-ordinates were obtained directly from the label data on herbarium sheets or indirectly by determining co-ordinates using Topo USA (DelOrme 2007) and the collection location description on the label. GPS co-ordinates were taken for specimens collected during the 2010 fieldwork season. Voucher label and field collection information on habitat and geographical location was entered into a database in order to detect whether any geographic or ecological differences might correspond to molecular, morphological, anatomical or micromorphological differences uncovered during analysis.

All specimens of *C. nardina* Fries and *C. hepburnii* Boott were initially identified using their protologues. Specimens of *C. nardina* var. *hepburnii* and *C. nardina* ssp. *hepburnii* were categorized as *C. hepburnii* for the purpose of analysis. The protologues for *C. stantonensis*, and *C. nardina* var. *atriceps* were not used because any characters in them that differed from the protologue for *C. nardina* were also contained in the protologue for *C. hepburnii*. The protologue for *C. elynaeformis* provided a single character (achene length/shape) that was said to differentiate the species from *C. hepburnii* (Porsild 1943). *Carex stantonensis*, *C. elynaeformis* and *C. nardina* var. *atriceps* do not appear in the phylogenetic analysis because either their voucher specimens were too yellow or physically degraded or DNA amplification was unsuccessful.

Genetic sequencing and phylogenetic analysis

In order to discover which species are most closely related to the *C. nardina* complex and would therefore be the best outgroup species, expanded sequencing of section

Filifoliae (*C. filifolia*, *C. elynoides* and *C. oreocharis*, *C. arsenii*) was conducted. Nuclear ribosomal and chloroplast regions of a representative sample from all parts of the known distribution of the *C. nardina* complex were sequenced and analyzed phylogenetically.

DNA marker selection

Although molecular analysis can help resolve longstanding taxonomic problems in *Carex* (Roalson and Friar 2004; Starr *et al.* 2004; Ford *et al.* 2006; Starr and Ford 2009), the choice of DNA marker depends on the question being asked, and in order to gain a clear picture of the evolution of phylogenetic lineages in plants, multiple analyses using both cpDNA and nrDNA data are generally necessary (Guggisberg *et al.* 2009). Avise (2004) explains the problems in interpretation of phylogenetic results arising from reliance on a single genetic marker. Using only cpDNA sequences is insufficient because the chloroplast genome evolves slowly (Wolfe *et al.* 1987) and in some families is inherited biparentally (Corriveau and Coleman 1988), possibly making phylogenetic interpretation complicated. Using only nrDNA sequences can be problematic because if paralogues are sequenced unintentionally existing genetic variability may go undetected (Avise 2004).

Sequencing in the present study began with the plant DNA barcoding gene *matK* (BOLD, Guelph University), which has been successfully sequenced in *Carex* species (e.g. Starr *et al.* 2009; LeClerc-Blain *et al.* 2010). Other cpDNA non-coding regions (*rps16*, *psbKI* and *atpFH*, *trnTLF*(a-d, c-f, and a-b), *trnV2*^{UAC}*/ndhC*, and *psbJ/petA*) were also sequenced in order to corroborate any variability that might be found in the *matK* region.

For the nuclear genome, the ETS 1f was sequenced using the same specimens. The nuclear ribosomal genome, with thousands of copies in every cell and much more non-

coding DNA, evolves much faster than the single copy chloroplast genome (Wolfe *et al.* 1997). The ETS 1f gene family consists of repeated units each consisting of coding RNA exons separated by larger non-coding sequences (Fig. 7). This repetitiveness is maintained by unequal crossing over and gene conversion (Elder *et al*. 1995; Gangloff *et al*. 1996). Thus, any new mutation in one part of the non-coding spacer that does not affect the fitness of the organism will be quickly transferred to all repeated subunits, leading to greater infraspecific than interspecific similarity (Page and Holmes 1998; Liao 1999). Also ETS is easy to amplify due to its high copy number and the availability of universal primers for Cyperaceae (Starr *et al.* 2003).

Also for the nuclear genome, the ITS region was selected for sequencing. Finally, 13 single copy microsatellite nuclear regions (*S082*, *S175*, *S180*, *S181*, *S245*, *CM01*, *CM25*, *CM27*, *Cko1-11*, *Cko1-47*, *Cko2-56*, *Cko2-112* and *Cko2-118*) (MacPhail 2009, unpubl.) were chosen in order to avoid the possibility of paralogues. These small flanking regions were established as single copy regions by following the experimental conditions of Ohsako and Yamane (2007), King and Roalson (2009) and Hipp *et al.* (2009).

Outgroup selection

The most effective outgroup for polarizing characters is the sister group to the ingroup (Colless 1985). However, when the preliminary analysis was conducted, the sister group was unknown. In order to determine whether the *C. nardina* complex might be sister to the *Filifoliae*, initial analyses used *C. rupestris* (section *Rupestres*) and *C. capitata* (section *Capituligerae*) as the outgroup because *C. rupestris* and *C. capitata* have been shown in previous phylogenetic analyses to be relatively closely related to *nardina* and the

Filifoliae, although they did not appear in the same clade as *C. nardina* and the *Filifoliae* (Ford *et al.* 2006; Starr and Ford 2009). The following taxa from section *Filifoliae* were included as part of the ingroup in the present phylogenetic analyses: *C. elynoides*, *C. filifolia* var. *filifolia*, *C. filifolia* var. *erostrata*, *C. oreocharis* and *C. arsenii*.

DNA extraction

Leaf samples were removed from herbarium specimens and from plants collected and pressed in the field. Total genomic DNA was extracted from leaves of 52 herbarium specimens and silica gel-dried field collections and one loan sample (*C. arsenii*, MEXU) using the silica-column-based method of Alexander *et al.* (2007) as modified by Starr *et al.* (2008). Approximately four green leaves (the equivalent of roughly 20 mg) were removed from each specimen in order to obtain undegraded DNA. More recently collected vouchers were sampled preferentially, although no maximum age threshold was applied. In some cases it was necessary to use vouchers > 50 years old in order to represent a certain taxon or geographic region in the sampling.

For each leaf sample, 20 mg of tissue was ground for 45 s in a BioSpec Mini Beadbeater-96 (BioSpec, Oklahoma). The powdery product was then suspended in a mixture of 320 µL homogenization buffer (0.1 M NaCl, 0.2 M sucrose, 0.01 M EDTA, 0.03 M Tris-HCl pH 8.0), 80 µL lysis buffer (0.25 M EDTA, 2.5% SDS, 0.5 M Tris-HCl pH 9.2), and 4 µL (100 mg/mL) RNase A. The samples were then incubated at 65°C for 30 min. Potassium acetate (130 µL, pH4.7, 3M) was then added, and each sample was stored in a -20°C freezer for five min then spun for ten min at 15 000 rpm in an Eppendorf 5424 centrifuge. The supernatant was transferred to a 1.5 µL tube containing 600 µL of plant

binding buffer (7M guanidine hydrochloride, 95% EtOH), and incubated at room temperature (20°C) for five min. Individual samples were then transferred to a silica membrane spin column (Epoch Biolabs, Texas) and spun for one min at 14 000 rpm to collect the DNA. The DNA bound to the silica gel columns was washed in a solution of 1 mL of 70% EtOH (14 000 rpm, 1 min) in order to remove residual salts then eluted by incubation in 150 µL of warm (55°C) THE Buffer (10 mM Tris-HCl pH 8.0, 0.5 mM EDTA) for 5 min before spinning the columns for 1 min at 14 000 rpm. DNA quality was evaluated by running 4 µL of each extraction on a 1.25 % agarose gel stained with Ethidium Bromide and visualized on a fluorescent light table.

DNA amplification and sequencing

Primers used to amplify DNA using polymerase chain reaction (PCR) and to sequence the extracted samples for each gene region are listed, with references, in Table 2. Each genetic region was amplified individually on an Eppendorf Mastercycler epgradient-S thermal cycler, and reaction success was verified by running PCR products out on a 1.25% agarose gel stained and visualized as above. Each PCR reaction consisted of 1X reaction Buffer (Sigma Aldrich, Ontario), 2.5 mM $MgCl_2$ (Sigma Aldrich), 0.2 mM of each deoxynucleotide (dATP, dCTP, dTTP, and dGTTP), 0.25 µM of each primer (Alpha DNA, Montreal), 1.0 µg Bovine Serum Albumin, BSA (BioShop Canada), 50 U Hot Start (HS) Taq DNA Polymerase (BioShop Canada) and 20-30 ng genomic DNA, adjusted to an end volume of 15 µL using nuclease-free ddH_2O. The thermal cycler conditions were set as follows: 94°C for 3 min, followed by 40 cycles each consisting of i) DNA denaturation at 94°C for 30 s, ii) primer annealing at 46°C for 30 s, and iii) DNA extension at 68°C for 2

min 30 s with iv) a final extension step at 72°C for 5 min. Ramping at 75% was used between the annealing and extension steps. Table 3 shows final concentrations of $MgCl_2$ (Sigma Aldrich) and annealing temperatures (T_A) for all other regions amplified.

Minor adjustments were made to the above reaction and cycling conditions depending on extracted DNA quality and the specific primer pair used to amplify a given region. However, in all cases, DNA amplification products were purified by adding 13 U Exonuclease I and 1.3 U Shrimp Alkaline Phosphatase (MJS Biolynx, Ontario) to successful reactions. This process removed any excess dNTPs and primers so that only double-stranded PCR product remained, thus ensuring that the subsequent sequencing reaction could proceed without interference.

The subsequent sequencing reaction contained 1.5 µL 5X ABI buffer, 0.5 µL primer, 0.4 µL BigDye Terminator v3.1 Ready Reaction (RR) mix, and 0.5 µL purified cycle sequencing product diluted to 10 µL using nuclease-free ddH_2O. The RR mix contained dNTPs, ddNTPs (dideoxynucleotides) fluorescently labelled according to the nucleotide base, and polymerase. During cycle sequencing, replication of DNA strands was randomly interrupted by the incorporation of ddNTPs, thus inhibiting any further addition of dNTPs to the strand. The end result of multiple cycles is a mixture of fragments of all lengths of the DNA of interest.

A final purification step involved 125mM EDTA, 3M Sodium acetate (Na-OAc), 99% and 70% EtOH and HIDI Formamide (Applied Biosystems). Samples were then incubated at 37°C (at which temperature the enzymes are active) for 30 min, followed by 90°C (in order to destroy the enzymes after use) for 10 min on a thermal cycler. Purified cycle sequencing products were read on a 3130xl Genetic Analyser using BigDye v3.1

chemistry (Applied Biosystems, California). As fragments pass through the automated sequencer capillaries and past the sensory laser, the ddNTPs were detected, thus ensuring that the entire DNA sequence is read.

Sequence data analysis

Sequences were assembled and base-calls were checked visually in Sequencher v.4.9 (Gene Codes Corp., Michigan). Only specimens (n = 53) for which clean sequences were obtained for all variable regions (*matK*, *psbKI* and ETS 1f) were retained in the analysis in order that parallel phylogenetic trees could be created and compared. Modified sequences were initially aligned using Clustal X 2.0.10 (Larkin *et al.* 2007) and then adjusted in PAUP*4.0B10 (Swofford 2003) using parsimony as an objective criterion to choose between alternative alignments (Starr *et al.* 2004). Indels (insertions or deletions) were scored using GapCoder (Young & Healy, 2003) according to the simple indel coding method of Simmons and Ochoterena (2000).

Maximum parsimony (MP) analysis was conducted in PAUP*4.0b10 (Swofford 2003) with heuristic searches on equally weighted characters for 10 000 random addition sequence (ADDSEQ = RANDOM) replicates in order to produce a bifurcating tree involving the fewest changes. All minimal trees (MULTREES = yes) were saved at each step to a maximum of 1 000 trees (MAXTREES = 1 000) and the tree-bisection-reconnection (TBR) method of branch swapping was used. Bootstrap analyses (Felsenstein 1985) were performed for 10 000 replicates using heuristic searches that implemented the TBR method with ADDSEQ = SIMPLE and MAXTREES = 1 000 in order to estimate support for the branches found in the strict consensus of MP trees. The BASEFREQ

command in PAUP*4.0b10 (Swofford 2003) was used to determine primary sequence lengths and CHGLST was used to find the numbers of mutations along tree branches.

Congruence between first the two cpDNA matrices and then between the nrDNA and cpDNA matrices was evaluated using the incongruence length difference (ILD) test (Farris *et al.* 1994, 1995) for 2 000 random addition sequence replicates (MULTREES = yes) with a maximum of 1 000 trees saved at each step as implemented in PAUP*4.0b10 (Swofford 2003). The ILD test evaluates the null hypothesis that characters comprising the data partitions are taken randomly from a single population of characters that reflect a single phylogeny (Farris *et al.* 1995)

Model selection for Bayesian analysis

Upon testing 24 models of nucleotide substitution, MrModeltest2.3 recommended models of nucleotide substitution that had the lowest cumulative Akaike, or AIC weights (Akaike 1974), which are given in parentheses: K80 (0.33) and K80+I (0.45) for *matK*; K80 (0.37) and K80+I (0.50) for *psbKI*; K80 (0.27) and HKY (0.45) for *matK*/*psbKI*; GTR (0.43) and GTR+I (0.59) for ETS 1f; and K80 (0.33) and K80+I (0.45) for the expanded *matK* data set matrix (i.e. with four additional *C. filifolia* var. *ersotrata* sequences). Generally, the lower the cumulative AIC weight the better the model will fit the data. Thus, AIC was used because it provided an objective criterion for choosing one model over another unlike other indices, such as the hierarchical likelihood ration test.

For ETS 1f, the first model (GTR) was chosen for Bayesian analysis because it had a far higher Akaike weight than the second. MrModeltest2.3 indicated that the K80 model was most appropriate for the *matK*/*psbKI* and the expanded *matK* data sets. Although there

appeared to be a higher proportion of transversions than transitions in the cpDNA data, the K80 model was chosen because it is the simplest model and reflects the extremely low amount of variability in the data set. MrModeltest2.3 results that showed many models with relatively low cumulative AIC weights, with none much lower than any of the others. This lack of variability suggests that regardless of the model the resulting topology would have been identical.

Phylogenetic analysis

The following terms used to assess the strength of clade support in trees are derived from simulation studies performed by Hillis and Bull (1993): strong(ly) (95-100% BS); very good or very well (85-94% BS); good or well (75-84% BS); moderate(ly) (65-74% BS); weak(ly) (55-64% BS); and very weak(ly) (<55% BS). Trees were visualized in TreeviewX (Page 2000) and annotated in Illustrator CS2 12.0 (Adobe 1987-2005).

In order to discover possible clades not found in the strict consensus MP analysis, a Bayesian analysis was performed, in which a model of nucleotide substitution was used. Bayesian analysis accounts for unseen changes (multiple changes at a single site over time) that necessarily occur over thousands of years, whereas MP does not. In order to estimate the posterior tree distribution, four Markov Monte Carlo Chains (MCMC) chains were run simultaneously for 5 000 000 generations with trees sampled every 500 generations from the one “cold” chain. For the cpDNA data set a K80 model of evolution was enforced during the running of the chain, while for the nrDNA data set a GTR (General Time Reversible) model (default settings) was used. These models were selected by running MrModeltest 2.2 (Nylander JAA, Uppsala University, 2004), a simplified version of

Modeltest (Posada and Crandall 1998) that tests 24 models of nucleotide substitution (the models common to PAUP*4.0B10, Swofford 2003, and MrBayes 3.0b4, Huelsenbeck and Ronquist 2001) to choose the most appropriate model for each locus based on the Akaike Information Criterion, or AIC (Akaike 1974). Following Bruneau *et al.* (2007) run parameters were plotted against the number of generations to identify the point at which the chain reached a plateau and started fluctuating around a stable value. This "burn-in" procedure led to the elimination of the first 50 000 generations from the analyses performed. Since the number of replicates was 10 000, the remaining 9 900 trees after burn-in were summarized in a majority rule consensus tree with clade support indicated by posterior probability (PP) values above the branches at the branch nodes. BS values were added to the Bayesian tree below all branch nodes except those that did not appear in the MP tree. Only BS values were used to evaluate results since they are more conservative than PP values (Erixon *et al.* 2003).

Abiotic habitat parameters

In order to determine the likelihood of hybridization between the *C. nardina* complex and either *C. elynoides* or *C. filifolia* var. *filifolia* approximate pairwise comparisons of their habitats were carried out. If two wind pollinated species do not grow in geographical proximity and at comparable elevation, cross pollination and hybridization are not likely (Stehlik *et al.* 2008; Vandepitte *et al.* 2009). In order to grow in close proximity both putative parents in a hybridization event must have similar habitat tolerances. Soil samples can be compared as a rough approximation of soil type. Elevation,

when considered over a scale of hundreds of meters, is also correlated with habitat type (Patterson *et al.* 1990; Axmacher and Fiedler 2008) and will therefore be compared based on data obtained either during fieldwork using GPS or from herbarium specimen labels.

Soil pH comparative analysis

Soil samples were taken during the 2010 collection trip to six western states in the U.S.A. An attempt was made to recover as much soil as possible from around the roots of collected specimens. The pH level of individual samples was determined using a Cornell Wide Range pH Test Kit (Ithaca, New York). In total samples were taken for seven *C. elynoides* and five *C. nardina* complex collections and for no other species examined. The mean pH level of the soil in which these two taxa grow was compared. The non-parametric (MW) test was used because of the small sample sizes.

Elevation-latitude correlation

The mean elevations of the two pairs of taxa most likely to hybridize were compared in geographic regions where elevation was not correlated with latitude. Only in regions where no correlation with latitude existed could mean elevation be inferred to be characteristic of a given species. *Carex elynoides* and the *C. nardina* complex were compared first over the entire geographic range of *C. elynoides* and then south of 42°N, where the distributions of *C. elynoides* and the *C. nardina* complex overlap. *Carex filifolia* var. *filifolia* and the *C. nardina* complex were compared in Beringia. Elevational data taken from herbarium labels and from GPS readings taken during fieldwork were entered

in an Excel spreadsheet along with the latitude for each specimen. The correlation between elevation and latitude was computed for each group using PAST (Hammer *et al.* 2001).

In geographic regions where no significant correlation between elevation and latitude was detected by a normal probability plot, the elevational data of pairs of taxa were compared with a parametric T-test. The elevational data were log10 transformed when necessary and rechecked for normality before performing the T-test or, when not normal, the MW test. Power analysis was then performed for significant results using GPower (Buchner *et al.* 1997) to measure effect size.

Spatial distribution of putative hybrids

The logic of dispersal would suggest that any hybrid would be more common in the geographic area where hybridization occurred in the past than it would be farther away. In order to assess the likelihood of hybridization, putative hybrids as a percentage of total specimens was calculated for each major region in the range of the *C. nardina* complex.

Palynological analysis

Pollen morphology is generally not taxonomically useful for differentiating *Carex* taxa below the level of subgenus (Wronska-Pilarek *et al.* 2010). Instead, the inability to absorb cotton blue stain (Jensen *et al.* 1968; Agarwal *et al.* 1998; Lyra 2011) and abnormal morphology (Tsukamoto and Matsubar 1968; Lyra *et al.* 2011) are thought to be roughly indicative of inviability, which one can use to assess the likelihood of hybridization (Wells 1979; Cayouette and Catling 1992; Ford *et al.* 1993).

Pollen grains were sampled from putative parent and putative hybrid specimens no older than 50 years (Cayouette, pers. comm.). In total, pollen was sampled from five specimens of *C. nardina*, six *C. elynoides*, two *C. filifolia* var. *filifolia* and 10 putative hybrids. All anthers were removed from the spike with the longest culm of each specimen sampled. When possible, anthers were preferentially taken from specimens that had also been measured for morphology but since such specimens were mature they typically lacked anthers with sufficient pollen for analysis.

The pollen staining procedure followed Bell's (1974) lactophenol - cotton blue dye protocol. A single drop of dye was placed on a cover slip. Anthers were placed in the drop of dye and teased apart with tweezers to liberate the pollen grains and capture them within the dye. On average, 541 grains were extracted from each of the 23 specimens sampled, exceeding the minimum used by Long (1959). A cover slip was then placed over the pollen. Slides were examined under a light microscope after 24 h (Cayouette 1987).

The percentage of stained pollen grains was calculated by dividing the number of stained pollen grains by the total number of pollen grains counted. Pollen grains were counted as stained if the cell was round, the walls of the cell were smooth and the majority of the cytoplasm was stained dark blue (Cayouette 1987; Lyra *et al.* 2011). Pollen grains were counted as unstained if the cell was irregularly shaped, the cell walls were uneven (Hauser and Morrison 1964) and the staining of the cytoplasm was either pale, absent or unevenly distributed in the cell (Lyra *et al.* 2011). Samples were classified as unviable or viable if the percentage of unstained pollen was below or above the threshold values calculated from the results of Cayouette (1986). Therefore, samples with > 63% unstained pollen were considered unviable and those with < 29% were considered viable.

Morphological analysis

The likelihood of hybridization and the differences between putative taxa of the *C. nardina* complex were investigated using morphological comparison. Morphological analysis has been used in numerous studies to resolve taxonomic relationships among *Carex* taxa (e.g. Cayouette 1987; Catling *et al.* 1989; Ford and Ball 1992; Naczi *et al.* 2002). In particular, any clades that emerged from the phylogenetic analysis were labeled in the morphological study to compare results following the approach taken in previous studies, notably Naczi *et al.* (1998) and Yeung and Ruzzo (2001).

In addition to molecular phylogenetic analysis, evidence for hybridization can be gained from morphological analysis (Cayouette and Catling 1992). Usually, hybrid individuals morphologically resemble either one parent or the other but on average morphological character states are generally intermediate between the two parents (Arnold 1994). Any of the putative clades within the *C. nardina* complex clade in the phylogenetic analysis above might possibly represent a hybrid, which in turn could be the cause of the morphological variability that led to the creation and continuation of *C. hepburnii*. PCA was therefore conducted between pairs of putative parents and a putative hybrid group that was segregated based on diagnostic characters from protologues of putative parent species.

In order to achieve a minimal sample size for multivariate statistical analysis, at least 30 specimens per taxon were obtained with sample sizes approximately equal between taxa, except that only 12 specimens were obtained for *C. filifolia* var. *erostrata*. A total of 184 voucher specimens (Appendix 1), including all those used in the above phylogenetic analysis, were examined for morphological variation using the most

diagnostic characters (Table 4) used to describe and circumscribe each taxon in its protologue (Nuttall 1818; Fries 1839; Boott 1840; Holm 1900; Kükenthal 1909). Diagnostic characters used in later descriptions by Boott (1867), Mackenzie (1935) and Egorova (1999) were also measured. Aside from stigma number, qualitative characters were not used because those contained in the above protologues were either too vague or could not be measured as continuous characters, which are conducive to statistical analysis.

Within the *C. nardina* complex and *C. filifolia* several examples were chosen of var. *atriceps* and var. *erostrata* respectively, including specimens that had been re-determined by Porsild and Mackenzie respectively. Several *C. nardina* and *C. hepburnii* specimens from Montana, the type location of *C. stantonensis*, were included. Specimens of the *C. nardina* complex were chosen roughly equally from the three main parts of its geographic range in case there exist geographically based morphotypes.

Putative hybrid identification

Specimens were examined visually to identify characters that appear in the protologue for *C. hepburnii*, which may represent a hybrid, and could segregate specimens from the putative parent species *C. nardina*, *C. elynoides* and *C. filifolia* var. *filifolia*. Three potentially suitable characters were identified. One obvious difference between the protologues of *C. nardina* and *C. hepburnii* is culm length and straightness. *Carex hepburnii*, as described by Boott (1840), is much taller and straighter than *C. nardina* and resembles *C. elynoides* and *C. filifolia* var. *filifolia* in this regard. A large group of specimens were thus segregated as a putative hybrid taxon. Based on the average culm

length given in Boott's (1840) protologue, 10 cm was chosen as the threshold value of culm length between specimens of the *C. nardina* complex and the putative hybrid.

Secondly, Boott's (1867) description mentions the occasional occurrence of three stigmas in *C. hepburnii* in contrast to the strictly distigmatic state in the protologue. Since *C. elynoides* is tristigmatic, it is possible that *C. hepburnii* could have obtained this trait through hybridization with *C. elynoides*. Excessive variation in stigma number among specimens on individual herbarium sheets and the prevalence of herbarium specimens that had lost all stigmas through post-collection mechanical damage precluded segregating a group of putative hybrids on this basis.

Thirdly, in addition to culm length and straightness an obvious and unique character that distinguishes the *C. nardina* complex from *C. filifolia* var. *filifolia* is perigynium pubescence. A group of *C. nardina* complex specimens with at least some hairs on the adaxial surface (as opposed to the prickle hairs on the margins) was identified. This trait was relatively rare but occurred in specimens from throughout the geographic range of the *C. nardina* complex. Therefore, this group was not considered a likely candidate for a separate putative hybrid.

Character measurement

Almost all relevant characters were measured as continuous characters to enable the use of multivariate statistical techniques. For example, instead of scoring the presence or absence of hairs on the adaxial surface of the perigynium, the number of hairs was counted. A total of 22 continuous characters (Table 4) were measured and the categorical character of stigma number was scored for all 184 specimens. Measurements were taken of these

characters under an Olympus SZX12 light microscope using a micrometer or a ruler for large-scale measurements. The longest culm was used to measure culm length and the longest leaf associated with it was chosen to measure leaf length. All characters within either the staminate or pistillate spike were measured on the spike of the longest culm. The most basal perigynium with a mature achene was chosen for all measurements involving the perigynium, scale and achene (Starr and Ford 2001). The pistillate scale of the most distal mature perigynium was used to measure awn length Boott (1840).

Data transformation

Morphometric analysis of the resultant matrix involved several steps. Missing data was scored as "?". Similar to Naczi *et al.* (1998), in order to avoid weighting characters, possibly genetically redundant characters were identified by performing pairwise correlation and removed if the Pearson correlation coefficient (r-value) was high (> 0.7). For $r < 0.7$ the amount of variance shared between pairs of characters would be < 50%, which has been cited as insignificant (Weisstein 2012). Following Naczi *et al.* (1998), the data were standardized by subtracting each specimen's measurement from the mean value of the character and dividing the difference by the standard deviation (SD). In this way, the effect of specimen size was eliminated in multivariate statistical analysis.

Cluster analysis

Cluster analysis (CA) was applied to the morphological measurements using PAST (Hammer *et al.* 2001). CA was designed to estimate quantitatively the structure in data sets of continuously measured morphological characters involving several taxa (Sokal and

Rohlf 1962; Lehnebach 2011). The output of cluster analysis consists of a dendrogram and a value for the cophenetic correlation coefficient (CCC).

The CCC is a linear correlation coefficient measuring of how closely the cophenetic distances derived from the dendrogram fit similarity matrices based on random data (Rohlf and Fisher 1968; Lehnebach 2011). Rohlf and Fisher (1968) computed a test criterion based on taxonomic data for ≤ 200 taxa in order to help future studies distinguish between hierarchic phenetic relationships and randomness among data points. Interpolating from the negative relationship between CCC value and number of taxa found in Rohlf and Fisher (1968), the present CA, which treated less than five taxa, used 0.75 as a minimum value to determine whether morphological data point clustering was non-random.

Various algorithms (e.g. paired group, single linkage, Ward's) and similarity indices (e.g. Euclidean, Gower, correlation, Simpson) are available for use in CA. Romesburg (1984) states that the average linkage (UPGMA; unweighted paired group method with arithmetic mean) algorithm is most commonly used. However, a comparison of the four most common methods (Blashfield 1976) showed that the minimum variance (Ward's) algorithm, which is based on Euclidean distances, gives the most accurate results by far. Milligan (1981) specifies that when clusters are overlapping, Ward's method is preferable. Therefore, in the current study Ward's method was used.

Principal components analysis

Principal components analysis (PCA) is among the commonest and simplest methods used to assess multivariate data (Jackson 1993). Many *Carex* species are distinguished only by an accumulation of minor quantitative differences in a large number

of characters (Catling *et al.* 1990). Therefore, PCA is suitable for morphometric analysis of *Carex* species because it can manage a large number of variables at once.

Using the same sets of specimens and morphological characters as used in CA, PCA was conducted on the correlation matrix of the character measurements using PAST (Hammer *et al.* 2001) to assess the naturally occurring relationships in multivariate space that might exist between the morphologically defined groups of specimens identified above. The correlation matrix, not the variance-covariance matrix, was used because not all variables were measured in the same units (Hammer *et al.* 2001).

Hybridization is evident in a PCA scatterplot that has four features (Archibald *et al.* 2004). The scatters of the two putative parent groups appear on either side of the putative hybrid group. There is distinct separation between the three point scatters. The three scatters are roughly aligned parallel to one of the orthogonal axes. There is slight but not complete overlap between the putative hybrid scatter and each of the putative parents.

A significant difference between groups would ideally be indicated by non-overlapping scatters of points aligned with one of the orthogonal axes representing the principal components (PCs; Naczi *et al.* 1998). In order to find the smallest number of significant PCs, i.e. those that explain the largest amount of variance in the dataset, the scree plot method published by Cattell (1966) was used. In a plot of each successive eigenvalue on the y-axis against the number of PCs the point along the x-axis at which the graph becomes straight, not necessarily horizontal, indicates the first non-significant PC to discard as opposed to the last significant PC to retain (Cattell 1966; Jackson 1993; Jolliffe 2002). In order to remove the element of subjectivity in identifying this point, a null model (Horn 1965), e.g. broken stick (Hammer *et al.* 2001) can be superimposed on the graph and

the point where the two lines intersect corresponds to the first non-significant PC (Horn 1965; Jackson 1993). Following the above procedure results in accurate estimates of the number of significant PCs for relatively uncorrelated data sets while avoiding the confusion of choosing a cut-off point of 0.7 (Jolliffe 1986) or 1.0 (Guttman 1954) for eigenvalues, which is the basis of the most common approach (Kaiser-Guttman; (Jackson 1993). After Naczi *et al.* (1998), only the characters with loadings > 0.6 on the significant PCs were deemed diagnostic and retained for subsequent PCA.

If PCA results suggested a morphological difference between groups, then either T-tests (for 2-taxa analyses) or one-way analysis of variance (ANOVA, for analyses between more than two taxa) were applied to each character individually using PAST in order to estimate the extent to which those groups differed (Naczi *et al.* 1998). Any pairwise PCA that found a difference in given character between two groups was checked by applying a T-test to the unstandardized data. If unequal variance (indicated by an F-test) or a non-normal distribution (evaluated by a normal probability plot) was found in at least one character then the measurement data for all characters were transformed by natural logarithm (ln) and the T-tests were performed again. If unequal variance or non-normality was still evident in at least one character then the MW test was performed on all characters. Barring any significant difference between the three taxonomic groups for any given characters that character was removed from the analysis and PCA was performed again.

In cases where PCA involving three groups (e.g. testing for hybridization) indicated morphological separation between groups, one-way ANOVA was performed on the non-standardized measurements of each character to verify that the means of the groups compared were not all equal (Naczi *et al.* 1998). If ANOVA results showed the residuals

for at least one character to be heteroscedastic or not normally distributed then the measurement data for all character measurements were ln transformed and ANOVA was performed again. If the residuals were still heteroscedastic or non-normally distributed, then the non-parametric KW test was performed. Characters for which ANOVA found no significant difference between group means were removed and PCA was performed again.

Given that, phylogenetically, *C. filifolia* var. *erostrata* appeared in a clade with *C. elynoides* rather than with *C. filifolia* var. *filifolia*, morphological analysis was also conducted on these three taxa in a similar manner as described above. All characters from Table 4 were used, except MARGHAIRN, SERRL and BEAKTEETHN because both varieties of *C. filifolia* lack marginal prickle hairs. CHESTHAIRN was retained in the analysis to account for the hairs on the adaxial surface, which, upon examination under a light microscope, were determined to be anatomically different than the marginal prickle hairs. This comparison was intended to clarify which taxa most closely resemble each other rather than to assess the likelihood of hybridization.

For each PCA, a scatterplot of the significant PCs was displayed with a convex hull drawn around the outer perimeter of the points to enhance visual differentiation of each group, as well as supporting data. Supporting data consist of eigenvalues, percentage of variance accounted for by each PC and the loadings of each variable for the significant PCs (Appendices 2 and 3). A box plot was created for each uncorrelated character in each comparison above, except the one between *C. filifolia* var. *filifolia*, *C. elynoides* and *C. filifolia* var. *erostrata*, to demonstrate possible intermediacy (Appendices 4 and 5).

Anatomical analysis

Metcalfe (1971) showed that conserved characters can be found in the leaf and culm anatomy of many sedge taxa, including *Carex*, and numerous subsequent studies (Toivonen and Timonen, 1976; Menapace and Wujek 1987; Standley 1987; Crins and Ball 1988; Standley 1990; Ford and Ball 1992; Saarela and Ford 2001; Starr and Ford 2001) succeeded in adequately circumscribing species. Therefore, continuous anatomical characters were measured morphometrically and compared using box plots, while categorical characters were scored and compared qualitatively.

Ten specimens from each of the five morphotypes examined in the morphological analysis above (*C. nardina*, *C. elynoides*, *C. filifolia* var. *filifolia*, *C. filifolia* var. *erostrata* and the putative hybrid of *C. nardina* and *C. elynoides*) were selected for cross-sectional examination of the leaf and culm. From each specimen, a 2 cm section was removed from the medial portion of the longest culm and from the medial portion of a leaf associated with the longest culm and both were boiled in ddH_2O for 5 min in order to re-hydrate the leaf material (Radford *et al.* 1974; Standley 1987; Starr and Ford 2001). Boiled samples were then stored overnight in formalin acetic acid, or FAA (Formaldehyde [37-40%], ddH_2O and Glacial Acetic Acid in a 2:18:1 ratio) to prevent degradation (Radford *et al.* 1974; Standley 1987; Saarela and Ford 2001). Each sample was then thin sectioned with a razor blade using a dense foam matrix to support the tissue during cuts. The sections were then subjected to an ethanol (EtOH) dehydration series as follows: 70% EtOH (15 min), 70% EtOH (15 min), 70% EtOH (15 min), 80% EtOH (15 min), 85 % EtOH (15 min), 90 % EtOH (15 min), 95 % EtOH (15 min), 100 % EtOH (15 min), then stained in 2%

Toluidine blue "O" dye in 100% EtOH base, followed by clarification in 100 % EtOH (5 min), 100 % EtOH-Histoclear® 1:1 (15 min) and then 100% Histoclear (15 min) (Saarela and Ford 2001). Stained sections were then mounted in Permount on glass slides.

A camera lucida mounted on a Leica DM2000 compound microscope was used to draw the mounted sections by hand. Pencilled drawings were then traced in ink, photocopied at a larger scale and scanned (Saarela and Ford 2001; Starr and Ford 2001). Using a micrometer, measurements were taken of 12 continuous anatomical characters (Table 5) of the mounted leaf sections, which were placed under an Olympus SZX12 light microscope. Eight categorical characters of the leaf sections were scored visually (Table 5). Ten continuous characters of mounted culm sections were also measured (Table 6), while three of the categorical culm characters were relevant to score (Table 6). T-tests were used to compare means. Apart from size, all characters and descriptive terminology followed Metcalfe (1971) and Starr and Ford (2001).

Micromorphology of fruit epidermal silica deposits

Several researchers have found fruit epidermal silica body micromorphology useful in delimiting sedge species (Toivonen and Timonen, 1976; Menapace *et al.* 1986; Wujek and Menapace 1986; Standley 1987; Crins and Ball 1988; Standley 1990; Saarela and Ford 2001; Starr and Ford 2001; Bouchenak-Khelladi 2010), although some note a high degree of infraspecific variability and recommend examining other types of evidence as well (Salo *et al.* 1994; Starr and Ford 2001). No previous studies have detected hybridization in silica body micromorphology. The limited number of potentially diagnostic characters makes it

unlikely that intermediate character states will appear. Therefore, micromorphology was used to detect possible differences between *C. nardina* and *C. hepburnii* rather than to search for signs of hybridization.

An initial test was performed on 17 specimens representative of the geographic range of the *C. nardina* complex using categorical characters derived from Schuyler (1971). Two achenes sampled per herbarium specimen were prepared using the protocol in Starr and Ford (2001) prior to SEM imaging. The lowermost mature perigynium from each of two terminal spikes was removed from each specimen. The perigynium surrounding the achene was dissected away. The achenes were then acetolyzed in a 1:9 sulfuric acid – acetic anhydride solution (Tallent and Wujek 1983; Starr and Ford 2001). To help remove digested pieces of cell wall from the silica body surfaces, the tubes containing the achenes were shaken vigorously by hand intermittently for 5 min, then left in solution for 24 h; at the end of this period, the tubes were shaken vigorously by hand intermittently for 5 min, then removed and placed in a tube of ddH_2O before being shaken vigorously intermittently for a final 5 min for cleaning (Starr and Ford 2001).

If any achenes showed visible signs of remaining cell walls under a light microscope they were sonicated in ddH_2O at maximum probe intensity for 1 min 30 s using a Rapidograph Ultrasonic cleaner 3069 USC3 (Koh-I-Noor Rapidograph). The achenes were then dried overnight at 50°C, mounted on adhesive aluminum stubs and coated with 20–25 nm of a gold–palladium alloy in a Denton Vacuum Desk II Sputter Coater. Micrographs were taken in high vacuum mode along the median portion of the achenes in a Philips XL30 ESEM with 10 kV accelerating voltage and using XL Control. Images were

examined visually for micromorphological differences. Silica body morphology was described using the terminology of Schuyler (1971).

Limitations to materials and methods

No attempt was made to determine chromosome number in the putative parents or putative hybrid as a way of investigating possible hybridization because it is often a deceptive metric of analysis of *Carex* taxa. Possession of diffuse centromeres, a common trait in Cyperaceae species (Ball *et al.* 2002) can lead to chromosome fragmentation (Grant 1981; Hakansson 2010) or fusion (Faulkner 1972; Whitkus 1988; Reznicek 1990) during meiosis. Chromosome counting is therefore difficult in *Carex* species. Furthermore, chromosome count is often correlated with habitat type (Bell 1982; Crins and Ball 1988; Whitkus 1988; Hoshino and Waterway 1994), which draws into question its usefulness for inferring evolutionary relationships (Starr 1997). An additional obstacle is that polyploidy is extremely rare in *Carex*, with only one documented example (autotetraploidy in *C. siderosticta* Hance; Cayouette and Catling 1992).

Furthermore, sampling for chromosomes is very complicated because live, flowering specimens with anthers are required and in order obtain a useful image they must be sampled at precisely the start of metaphase, which is difficult to predict. The *C. nardina* complex occurs only in very remote locations. Live specimens were obtained during the sole collection trip (2010). However, being a perennial species, no individuals flowered in over two years of greenhouse growth. It is unknown how many years might be required for these species to flower. As a result, crossing experiments to detect hybridization were not

performed. Even if it had been possible, the windy, desolate environmental conditions in which the *C. nardina* complex grows would be difficult to replicate in a greenhouse. Therefore, if specimens of the *C. nardina* complex were to cross with specimens of section *Filifoliae* in a greenhouse the results may not reflect the probability of crossing in the wild.

TABLE 2 Primers used in PCR and DNA sequencing. Letters used are either the four nucleotide bases (A,C,T,G) or the ambiguity codes proposed by the Nomenclature Committee of the International Union of Biochemistry (K, Y, W, S, R, M, B, D, H, V, N; 1985).

Primer	Sequence (5' to 3')	Reference
cpDNA		
KIM_3F	CGTACAGTACTTTTGTGTTTACGAG	Ki-Joong Kim in Fazekas *et al.* 2008
KIM_1R	ACCCAGTCCATCTGGAAATCTTGGTTC	Ki-Joong Kim in Fazekas *et al.* 2008
matK_1-F	CGTCAACAACAATGCTTATATCC	designed by Starr JR, unpubl.
matK_2.5F	TCAATGCTGGRTCCAAGATA	designed by Starr JR, unpubl.
matK_5-R	TTTATGTTTACGAGCCAAAG	designed by Starr JR, unpubl.
psbK	TTAGCCTTTGTTTGGCAAG	Ki-Joong Kim in Fazekas *et al.* 2008
psbI	AGAGTTTGAGAGTAAGCAT	Ki-Joong Kim in Fazekas *et al.* 2008
atpF	ACTCGCACACACTCCCTTTCC	Ki-Joong Kim in Fazekas *et al.* 2008
atpH	GCTTTTATGGAAGCTTTAACAAT	Ki-Joong Kim in Fazekas *et al.* 2008
psbJ	ATAGGTACTGTARCYGGATT	Shaw *et al.* 2007
petA	AACARTTYGARAAGGTTCAATT	Shaw *et al.* 2007
trnT^{UGU}F	CATTACAAATGCGATGCTCT	Taberlet *et al.* 1991
5trnL^{UAA}R	TCTACCGATTTCGCCATATC	Taberlet *et al.* 1991
trnL5^{UAA}F	CGAAATCGGTAGACGCTACG	Taberlet *et al.* 1991
trnL^{UAA}R	GGGGATAGAGGGACTTGAAC	Taberlet *et al.* 1991
trnL^{UAA}F	GGTTCAAGTCCCTCTATCCC	Taberlet *et al.* 1991
trnF^{GAA}	ATTTGAACTGGTGACACGAG	Taberlet *et al.* 1991
rps16_F	AAACGATGTGGTAGAAAGCAAC	Oxelman *et al.* 1997
rps16_R	AACATCAATTGCAACGATTCGATA	Oxelman *et al.*1997
trnV^{UAC}x2	GTCTACGGTTCGARTCCGTA	Shaw *et al.* 2007
ndhC	TATTATTAGAAATGYCCARAAAATATCATATTC	Shaw *et al.* 2007
nrDNA spacer		
ETS1-F	CTGTGGCGTCGCATGAGTTG	Starr *et al*. 2003
18S-R	AGACAAGCATATGACTACTGGCAGG	Starr *et al*. 2003
ITS-L	TCGTAACAAGGTTTCCGTAGGTG	Hsiao *et al*. 1994
ITS-4	TCCTCCGCTTATTGATATGC	White *et al*. 1990

TABLE 2 (Cont'd) Primers used in DNA sequencing.

Primer	Sequence (5' to 3')	Reference
nrDNA microsatellite		
S082_F	TGAGAACCCTAGGCAGATGG	Hipp *et al*. 2009
S082_R	GGGGAAACAAGGTCGTTTAGA	Hipp *et al*. 2009
S175_F	TATTGGGTGTGCGATTGAGA	Hipp *et al*. 2009
S175_R	TCAGATCAGCCAAGTCATCG	Hipp *et al*. 2009
S180_F	ACATGATTGTGGACGACAGG	Hipp *et al*. 2009
S180_R	TCACCAAAGTCCTGAAAATCAA	Hipp *et al*. 2009
S181_F	CCAACTTGCCCTTGTTCATT	Hipp *et al*. 2009
S181_R	CGTTTGCACGCTTTGTAGAT	Hipp *et al*. 2009
S245_F	GAAACAAAGGTGCCCCACT	Hipp *et al*. 2009
S245_R	GTTGCAAGCGGGTCTAATTC	Hipp *et al*. 2009
CM01_F	CAAAGGAGAGAAATTCTCTG	King and Roalson 2009
CM01_R	GATCAGGTCATACCAAGTAT	King and Roalson 2009
CM25_F	CGGTGTTTGGTGGGCTGATA	King and Roalson 2009
CM25_R	CGCTTCTCCGTTTCTTTTGT	King and Roalson 2009
CM27_F	GATTTAGTACAGCCCCACAG	King and Roalson 2009
CM27_R	ACCAACCAGTCAGCCTCTCA	King and Roalson 2009
Cko1-11_F	TGGATGGATGTGTACGATTATGA	Ohsako and Yamane 2007
Cko1-11_R	GTAGGTGCATAGTTGTTGCCTCT	Ohsako and Yamane 2007
Cko1-47_F	CCATCCATGGTATTTGACAGATT	Ohsako and Yamane 2007
Cko1-47_R	ACAGGCGCTATAACAGACAAAAG	Ohsako and Yamane 2007
Cko2-56_F	TCCAACCTGATTTCCTTTTTGTA	Ohsako and Yamane 2007
Cko2-56_R	CAATCTTTTGAGGAAGTGCAATC	Ohsako and Yamane 2007
Cko2-112_F	CCTTTGCATTATCTCTCTGGAAA	Ohsako and Yamane 2007
Cko2-112_R	AAGCACAAGATCGCAGTTTATGT	Ohsako and Yamane 2007
Cko2-118_F	ATCCCACCAGCACTACTACCAT	Ohsako and Yamane 2007
Cko2-118_R	AAAATCAAAACCCAGAAACTGGT	Ohsako and Yamane 2007

TABLE 3 Adjustments in volume of $MgCl_2$ [25mM] and annealing temperature (T_A) for PCR amplification.

Gene region	[$MgCl_2$] (mM)	T_{A1}: cycle 1-33 (°C)	T_{A2}: cycle 34-43 (°C)
nrDNA microsatellites			
Cdo2-56	25	58	53
Cko1-11	35	56	53
Cko1-47	20	58	53
Cko2-112	15	55	53
Cko2-118	25	56	53
CM01	25	55	53
CM25	25	58	53
CM27	30	50	50
S082	25	57	53
S175	20	58	53
S180	25	59	53
S181	20	48	48
S245	25	59	53
nrDNA spacers			
ETS	25	48	48
ITS	25	62	58
cpDNA			
atpFH	35	55	55
matK1-F/KIM3-F	20	47	47
psbKI	15	46	46
psbJ/petA	30	47	47
trnL-F(a-f)	15	46	46
trnVx2/ndhC	30	47	47

TABLE 4 Diagnostic continuous morphological characters from descriptions of Boott 1840, Mackenzie 1935 and Holm 1900, measured for PCA (all in mm, except counted characters BEAKTEETHN, CHESTHAIRN, MARGHAIRN and NERVEN).

Character	Description
AWNL	Awn length from emergence from distal end of scale to distal end of awn
ACHENEL	Length of achene from base of stipe to apex of achene
BEAKL	Length of perigynium beak from point where margins become parallel to apex teeth
BEAKTEETHN	Number of prickle hairs on beak margin of perigynium
CHESTHAIRN	Number of hairs on adaxial face of perigynium
CULML	Length of longest culm from base of sheath to apex of distal scale of perigynium
HYALINW	Least width of hyaline margin on female scale subtending distal mature perigynium
LEAFL	Length of longest leaf associated with longest culm from base of sheath to tip of leaf
MARGHAIRN	Number of prickle hairs on perigynium margins
MIDRIBL	Length of midrib of pistillate scale
MIDRIBW	Width of midrib of pistillate scale
NERVEN	Number of nerves on adaxial face of perigynium
PERIGL	Length of perigynium from base of stipe to apex of beak teeth
PERIGW	Width of perigynium at widest point
SCALEL	Length of pistillate scale subtending most proximal mature perigynium from base of scale to apex
SERRL	Length of perigynium margin serrulate – longest of the two margins
SHAPEPE	Distance from distal end of beak to widest point of perigynium
SHOULDER	Depth of concave curve from shoulder to beak of perigynium
SPIKEL	Length of entire spike from base of proximal scale to apex of distal scale
STAML	Length of staminate spike from base of proximal scale to apex of distal scale
STIPEL	Length of perigynium stipe from base to point where margins no longer parallel
STYLEXL	Length of style from emergence from apex of beak teeth to base of stigmas

TABLE 5 Anatomical leaf characters (considered diagnostic in sedges by Metcalfe (1971) examined. All continuous characters measured in mm except counted characters BEAKTEETHN, CHESTHAIRN, MARGHAIRN and NERVEN.

Continuous character	Description
ABORTL	Length difference between shortest and longest lamina
ABEPICHLORD	Diameter of largest abaxial epidermal cell over chlorenchyma
ADEPICHLORD	Diameter of largest adaxial epidermal cell over chlorenchyma
ADEPISCLERD	Diameter of largest epidermal cell over prominent sclerenchyma girders
ABSTOMAN	Number of abaxial stomata
ADSTOMAN	Number of adaxial stomata
MAJVBD	Diameter of largest major vascular bundle
MAJVBN	Number of major vascular bundles
MINVBD	Diameter of largest minor vascular bundle
MINVBN	Number of minor vascular bundles

Categorical or binary character	Description
AIR	Air spaces in chlorenchyma present (1) or not (0)
GIRDSH	Shape of sclerenchyma girder: increasing (1), straight/decreasing (2), bell (3)
KEELP	Keel present (1) or not (0)
KEELPROM	Keel prominent (1) or not (0)
KEELSH	Keel shape, if prominent (0=rounded, 1=acute)
LAMFUSE	Laminae fused (1) or not (0)
LEAFSH	Leaf shape (0=rounded, 1=folded)
TIPS	Tips of laminae sclerified (1) or not (0)
VBPERIPH	Vascular bundles peripheral only (0) or protruding into cortex (1)

TABLE 6 Anatomical culm characters considered diagnostic in sedges by Metcalfe (1971) examined. All continuous characters were measured in mm except counted characters.

Continuous character	Description
ADEPISCLERD	Diameter of largest epidermal cell over prominent sclerenchyma girders
ADEPICHLORD	Diameter of largest adaxial epidermal cell over chlorenchyma
MAJVBN	Number of major vascular bundles
MINVBN	Number of minor vascular bundles
MAJVBD	Diameter of largest major vascular bundle
MINVBD	Diameter of largest minor vascular bundle
STOMAN	Number of stomata

Categorical or binary characters	Description
AIR	Air spaces present within chlorenchyma (1) or not (0)
GIRDSH	Shape of sclerenchyma girder: increasing (1), straight/decreasing (2), bell (3)
VBPERIPH	Vascular bundles peripheral only (0) or protruding into cortex (1)

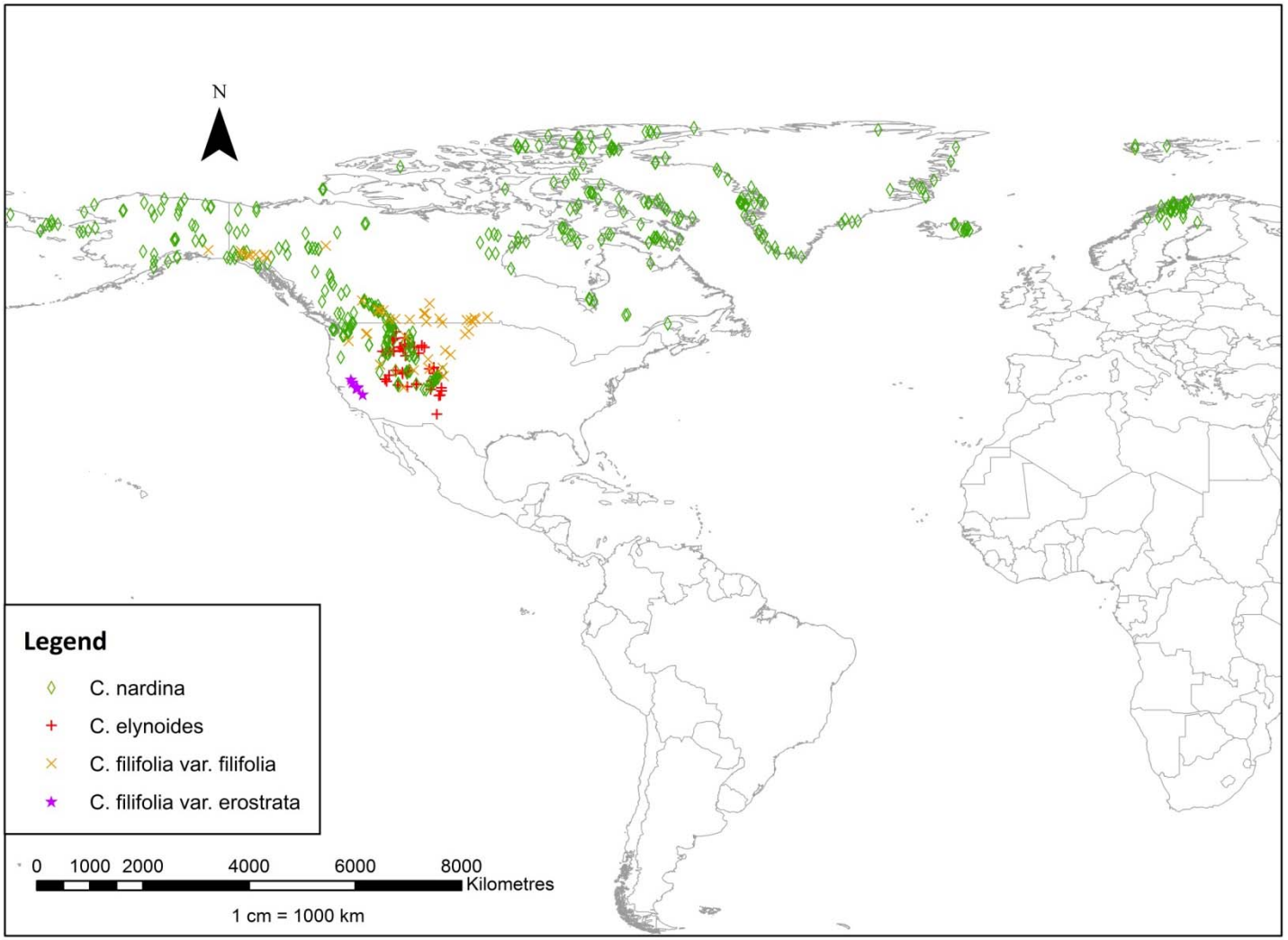


FIG. 4 Distribution of specimens examined for the *C. nardina* complex, *C. elynoides*, *C. filifolia* var. *filifolia* and *C. filifolia* var. *erostrata*.

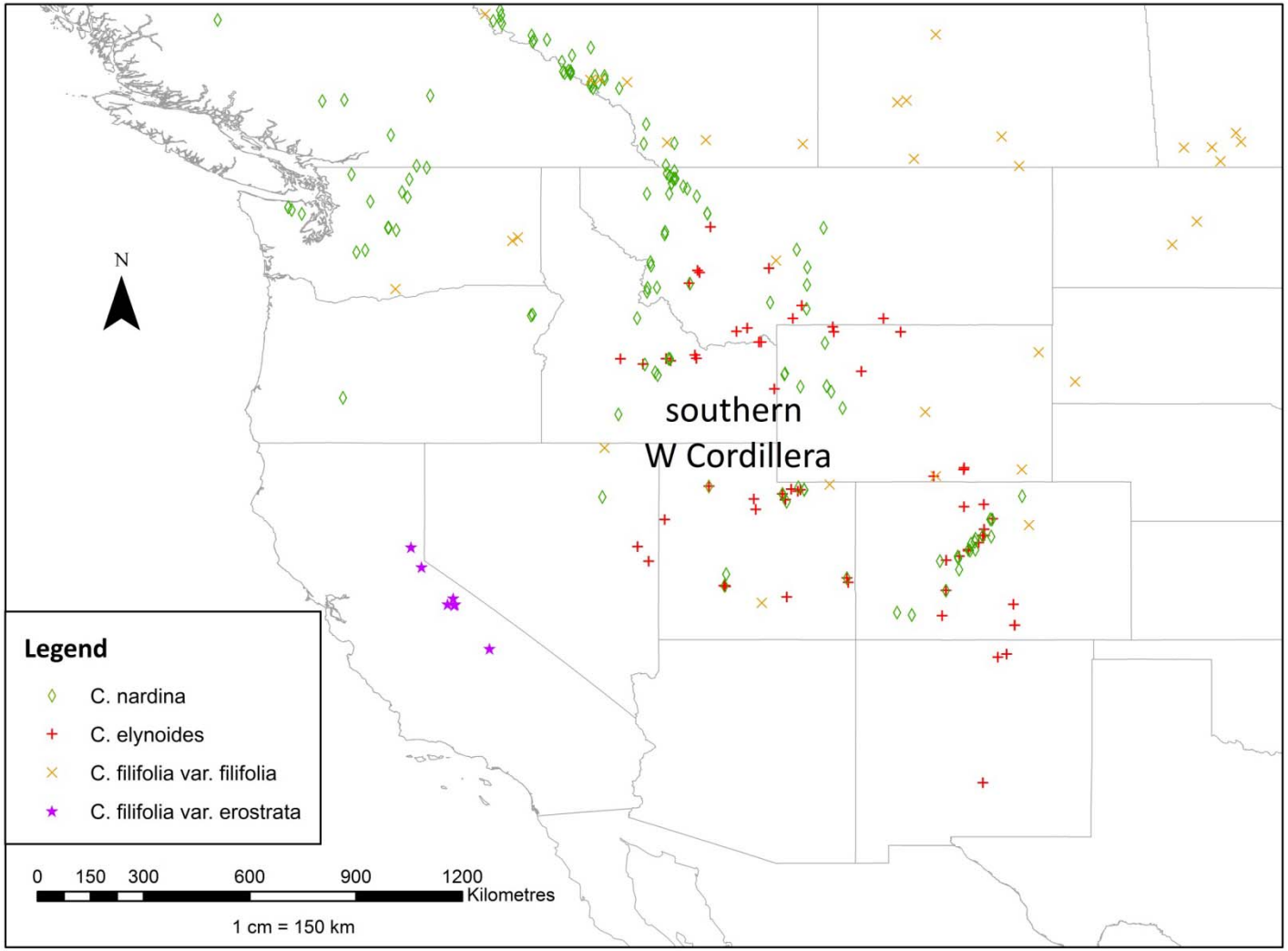


FIG. 5 Distribution of specimens examined for the *C. nardina* complex, *C. elynoides*, *C. filifolia* var. *filifolia* and *C. filifolia* var. *erostrata* in southern part of western Cordillera.

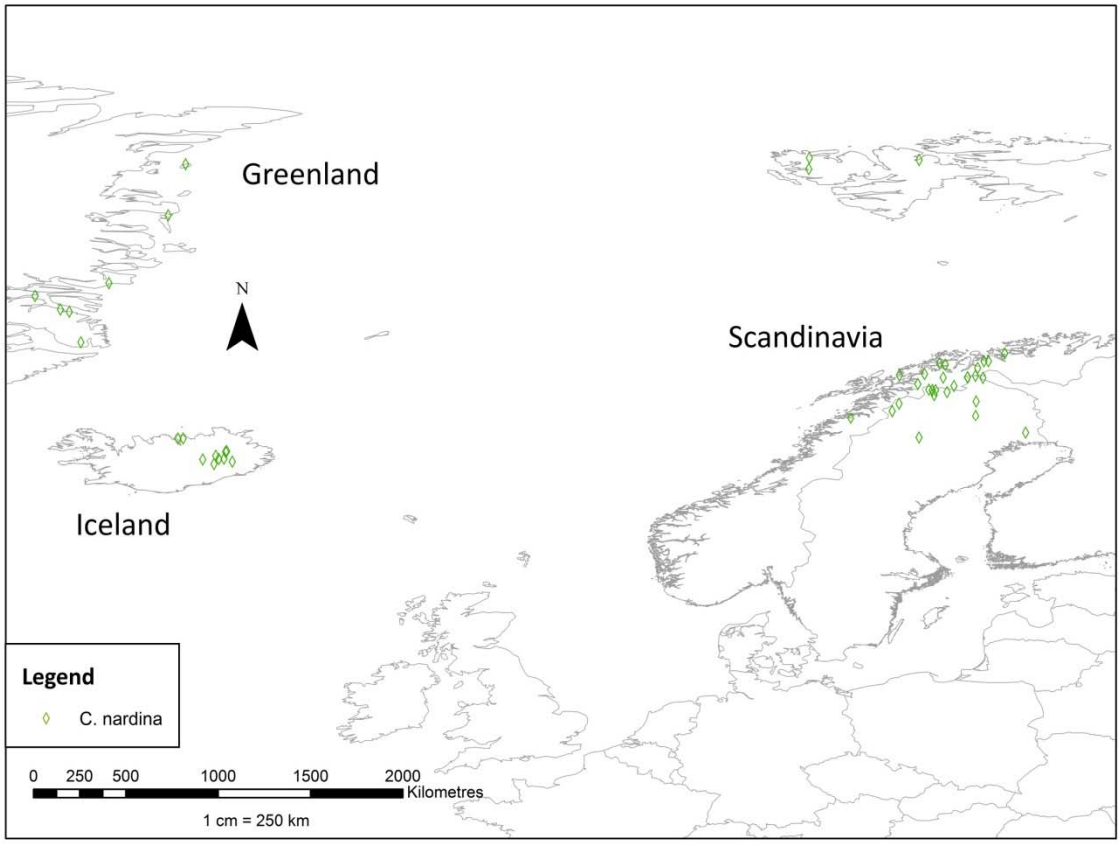


FIG. 6 Distribution of specimens examined for the *C. nardina* complex in Scandinavia, Iceland and eastern Greenland.

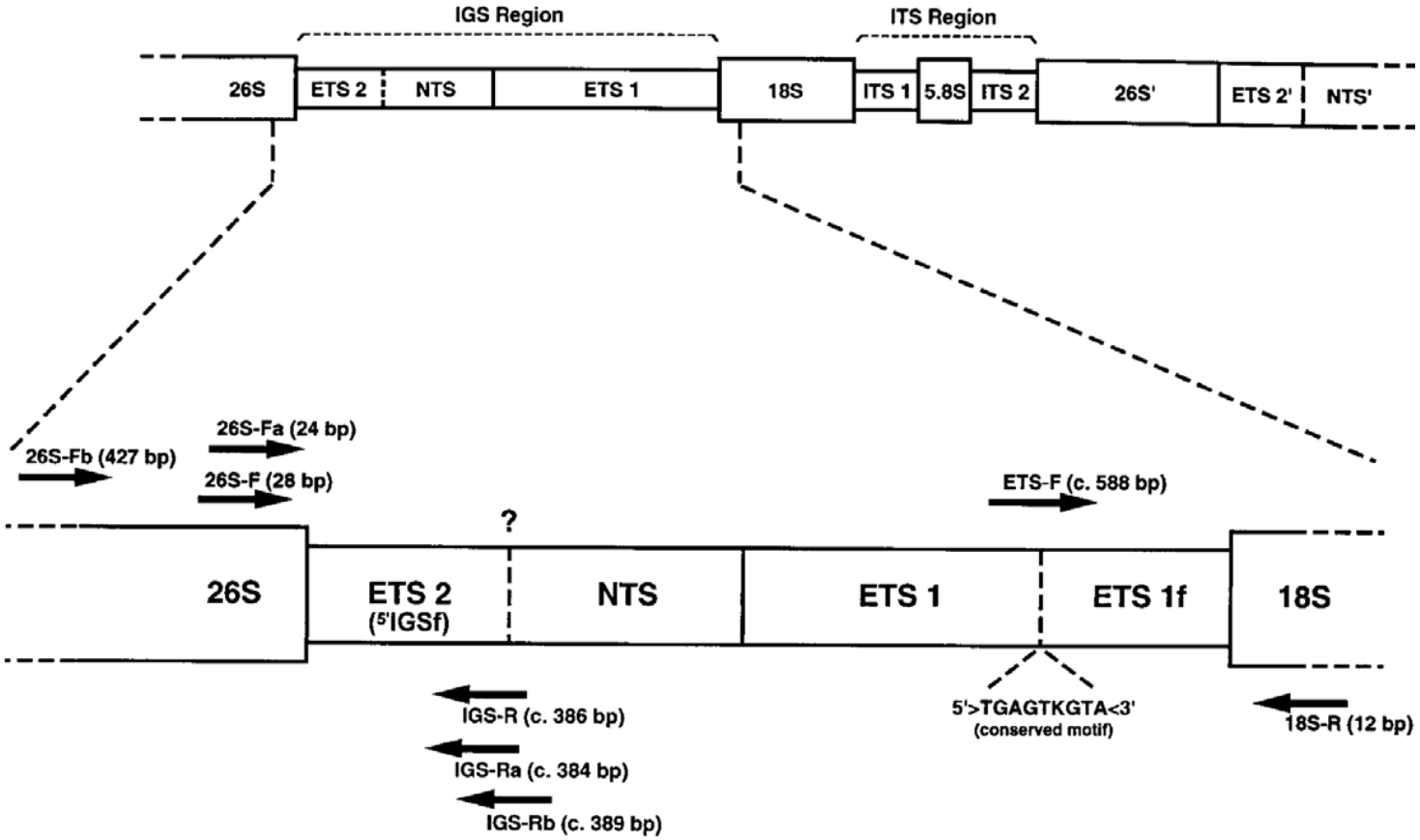


FIG. 7 The ETS 1f region is a 3' ETS1 fragment located between the 18S gene and a conserved sequence motif 5'TGAGTKGTA3' (Bena *et al*. 1998). ETS 1 is part of the larger intergenic spacer (IGS) region between the 18S and 26S genes. (Figure from Starr *et al*. 2003)

RESULTS

Character selection

In order to test the possibility of hybridization, specimens were divided into putative taxonomic groups, including the putative hybrid group, using 22 diagnostic characters (Table 4) derived from the protologues of the putative parents by Boott 1840 (*C. hepburnii*), Nuttall 1818 (*C. filifolia* var. *filifolia*) and Holm 1900 (*C. elynoides*) and Mackenzie's (1935) description of *C. nardina*. The putative hybrid group consisted of 39 specimens that the collector had identified as a member of the *C. nardina* complex but had tall (> 10 cm), straight culms. Redetermination of the *C. filifolia* var. *filifolia* specimens available resulted in California not being represented in the current sampling. Nevertheless, this species is known from California where its distribution overlaps with that of *C. filifolia* var. *erostrata* (Mastrogiuseppe 2002).

To test for phylogenetic differences between *C. nardina* and *C. hepburnii*, the specimens of the *C. nardina* complex were classified and analyzed as either *C. nardina* or *C. hepburnii* according to the protologue of Boott (1840), then again according to the description of Egorova (1999) and again according to the description of Mackenzie (1935).

Sequencing results

Of the 23 genetic markers assayed, only *matK*, *psbKI* and ETS 1f provided characters that displayed patterns of variability shared among multiple specimens.

Sequencing of cpDNA produced matrices of *matK* (aligned length 837 bp) and *psbKI* (aligned length 372 bp) that each included the same 52 taxa. The *matK* matrix contained a C at bp 689 in five *C. nardina* complex specimens from Beringia while all others, displayed a G at this position. The *psbKI* matrix contained a G at bp 179 in the same five specimens while all others displayed a C at this position, and there was a large (13 bp) insertion at bp 73 in all specimens except six from the Arctic and Scandinavia.

nrDNA sequencing

ETS 1f analysis of the same individuals used in the cpDNA analyses produced an aligned matrix of 626 bp. A total of 22 indels of one, two or six bp each were found throughout the sequence. A large number of transversions throughout the sequence distinguished the outgroup taxa *C. capitata* and *C. rupestris* from the ingroup taxa. A group of Beringian *C. nardina* complex specimens shared a G, T, A and C at bps 195, 268, 330 and 360, while all other specimens had C, A, T and G respectively at these positions. Membership in the ETS 1f Beringian group was only partly shared with the cpDNA Beringian group. A larger group of *C. nardina* complex specimens across the Arctic and in Scandinavia displayed a C at bp 470, while all other specimens had a G at this position.

Data partitioning – incongruence length difference test

For the *matK* and *psbKI* matrices, a statistically insignificant p-value of 1.0 was obtained, meaning that one cannot reject the null hypothesis of congruence. Therefore, as expected, there is no basis for concluding that these two chloroplast regions evolved separately and the two matrices can be concatenated and treated as one region for the

purpose of phylogenetic analysis. However, an ILD test performed on the ETS 1f and combined *matK*/*psbKI* matrices resulted in a statistically significant p-value of 0.0001, meaning that one must reject the null hypothesis of congruence. The cpDNA and nrDNA data sets were therefore separately analyzed during phylogenetic analysis.

The source of the incongruence between the cpDNA and nrDNA data sets was investigated. The *C. nardina* complex specimens (1545, 1562, 1565, 1566, 1567 and 1855) that appeared in the Beringian clades of both the cpDNA and nrDNA phylogenies as well as specimens that appeared alone on separate branches (*C. nardina* 1597 from Washington and *C. filifolia* 1833 from Utah in phylogenetic analysis) were removed from the data sets. The ILD test was performed again on the reduced data sets and led to a different result ($p = 0.99$) than with the full data sets. Therefore, the incongruence between the cpDNA and nrDNA data sets may be attributable to the above specimens.

Bayesian and MP analysis

For each Bayesian phylogeny presented, the values derived from the BS analysis of the MP tree are given below the branches at the nodes (Figs. 8 - 11). In cases where the Bayesian and MP phylogeny differ, branches in the Bayesian tree that did not appear in the MP tree are marked with arrows.

Bayesian analysis of nrDNA

Bayesian analysis of the ETS 1f data produced a majority rule consensus shown in Fig. 8. Bayesian analysis recovered a clade of two *C. oreocharis* specimens on a weakly

supported branch as well as a putative clade of *C. nardina* specimens from Scandinavia, neither of which appear in the MP tree. Morphologically distinct taxa (the *C. nardina* complex, *C. elynoides*, *C. filifolia* var. *filifolia*, *filifolia* var. *erostrata* and *C. oreocharis*) fell out together within one large polytomy. Sister to that polytomy was a weakly BS supported clade of *C. nardina* complex specimens from Beringia (Beringia I: specimens 1545, 1562, 1565 and 1566), which represented a change of 17 mutations. Within the large polytomy there are three small, putative clades of *C. nardina* complex specimens, two of which are regionally based (Scandinavia and W Cordillera) and the other of which is pan-Arctic. The putative Scandinavian clade consisted of 1573, 1848, 1854 and 1859; the W Cordillera putative clade consisted of 1592 and 1594; and the pan-Arctic putative clade consisted of 1537, 1554, 1555 and 1569. However, there is no relationship evident between these putative clades and they all have very weak BS support.

The *C. nardina* complex specimens in the ETS 1f Bayesian consensus in Fig. 8 were categorized using Boott's (1840) protologue. The analysis was performed again after reclassifying the *C. nardina* complex specimens using the descriptions of Egorova (1999) and then Mackenzie (1935). Under each author, *C. nardina* and *C. hepburnii* co-occur in the pan-Arctic, Scandinavian, W Cordilleran and Beringian putative clades, with two exceptions. Using Egorova's (1999) description only, the two-member W Cordillera putative clade consisted entirely of *C. nardina* specimens. The two *Carex oreocharis* specimens appeared in a weakly supported clade with no evident relationship to the other specimens within the larger polytomy.

Bayesian analysis of *matK* and *psbKI* (cpDNA)

Bayesian analysis of the combined cpDNA matrix resulted in a majority rule consensus (Fig. 9). The topology was identical to that of the MP tree and the results of the BS analysis of the MP tree indicated that all branches were weakly or very weakly supported. Only one weakly supported clade of *C. nardina* complex specimens was recovered showing *C. nardina* and *C. hepburnii* specimens co-occurring in the clade.

Four putative clades were found in the Bayesian consensus and correspond to *C. oreocharis*, *C. filifolia* var. *filifolia*, *C. elynoides*/*C. filifolia* var. *erostrata* and the *C. nardina* complex. One specimen of *C. filifolia* var. *filifolia* (1833 from Mt. Bald, Utah) appeared separate, albeit on a very weakly BS supported branch as its convarietal specimens, making the taxon polyphyletic. The monophyletic *C. nardina* complex fell out in the same clade as the *Filifoliae* (*C. filifolia* var. *filifolia*, *C. filifolia* var. *erostrata*, *C. elynoides* and *C. oreocharis*). No phylogenetic relationships between these taxa were evident. *Carex elynoides* was paraphyletic since *C. filifolia* var. *erostrata* (1824 from California) grouped with it instead of with the *C. filifolia* var. *filifolia* clade.

The very weak BS support for the branches in the MP tree justified the choice of the simplest model of nucleotide substitution (K80) for Bayesian analysis. Even if another model had produced a different topology any additional branches found would also not have been significantly BS supported and thus would not have indicated reliable clades.

Bayesian analysis of *matK* with expanded sampling

In order to corroborate the appearance of the lone *C. filifolia* var. *erostrata* specimen (1824) that grouped with *C. elynoides* in the cpDNA Bayesian consensus (Fig.

10), four additional specimens of *C. filifolia* var. *erostrata*, for which only *matK* sequences were available on Genbank (Chouinard *et al.* 2009; http://ncbi.nlm.nih.gov/genbank), were added to the cpDNA analysis. The resulting Bayesian consensus of 837 base pairs and 56 taxa was identical in topology to the MP phylogeny.

The *matK* consensus with expanded sampling showed *C. filifolia* var. *erostrata* grouping together with *C. elynoides*. *Carex filifolia* var. *filifolia* was polyphyletic since although most specimens appeared in a weakly BS supported clade, 1833 (from Utah) appeared alone on another branch. All branches had weak or very weak BS support. Within the *C. nardina* complex clade there was a weakly supported putative clade (Beringia II) of five specimens (1545, 1562, 1565, 1567 and 1855), three of which also appeared in the ETS 1f Beringian I clade. Whether using the description of either Boott (1840), Egorova (1999) or Mackenzie (1935) to classify the *C. nardina* complex specimens, *C. nardina* and *C. hepburnii* co-occurred in the putative Beringia II clade. The two *C. oreocharis* specimens form a weakly BS supported clade that fell out with the *C. filifolia* var. *filifolia* clade, although no relationship was evident between the two clades.

MP analysis of combined cpDNA and nrDNA

When the causes of incongruence between the cpDNA and nrDNA data sets (Beringian *C. nardina* complex specimens 1545, 1562, 1855, 1567, 1565 and 1566; *C. hepburnii* 1597; *C. filifolia* var. *filifolia* 1833) were removed, a combined strict consensus MP tree was created (Fig. 11). All branches had very weakly BS support. The *C. nardina* complex, *C. filifolia* var. *filifolia*, and *C. oroecharis* were all monophyletic, although *C. elynoides* was paraphyletic since the *C. filifolia* var. *erostrata* specimen grouped with it.

The *C. nardina* complex appeared deeply nested within section *Filifoliae* and sister to the *C. elynoides*/*C. filifolia* var. *erostrata* group. Within the *C. nardina* complex clade there was a small pan-Arctic clade of *C. nardina* and *C. hepburnii* specimens.

Abiotic habitat parameters

Habitat comparison - soil pH

Soil samples were available for seven *C. elynoides* and three *C. nardina* vouchers from collection sites in the southern W Cordillera. Mean pH values were compared using the MW test because of small sample size. No significant difference was found ($p = 0.87$). Mean soil pH was 6.2 ± 0.49 (SD) for *C. elynoides* and 6.4 ± 0.68 (SD) for *C. nardina*.

No soil pH data were obtained for *C. filifolia* var. *filifolia* but voucher label information indicated that in Beringia the taxon grows on limestone substrate, suggesting that it could possibly grow in soils of the same pH as those in which *C. nardina* is found.

Determination of putative contact zones using elevation data

Carex nardina complex and *C. elynoides*

The southwestern Cordillera south of Canada, a putative glacial refugium, is the only area where the distributions of *C. elynoides* and the *C. nardina* complex overlap and where hybridization between them would be possible. However, elevation was highly and significantly correlated with latitude (Table 7) for both the *C. nardina* complex ($r=-0.94$, $p=2.49E-16$) and *C. elynoides* ($r=-0.81$, $p=3.19E-15$) in the entire region. This strong

correlation means that any comparison of mean elevation between these two taxa in this region would not reliably indicate whether both grow at comparable elevations in the same locations, a key requirement for hybridization to occur. However, south of 42° N the correlation was not significant. In this region, for the *C. nardina* complex elevation was slightly but insignificantly correlated with latitude (r=-0.47, p=0.06) and for *C. elynoides* it was uncorrelated (r=-0.17, p=0.36).

South of 42° N the T-test performed on the elevation data showed a statistically significant difference (p=2.94E-6) between *C. elynoides* (3437 m ± 34 m) and the *C. nardina* complex (3745 m ± 48 m). A normal probability plot showed that the elevation data were not normally distributed. Therefore, the MW test was performed and yielded a statistically significant result (p=2.40E-5). The effect size was computed to be 1.55 using GPower. Therefore, there is a statistically significant difference of 226 m between the confidence intervals (CIs) based on standard errors for the two taxa. The elevations of these putative parents are shown in (Fig. 12).

In wind pollinated plants, such as *Carex* (Friedman and Barrett 2009) most pollen is typically deposited close to its source with deposition rapidly decreasing with distance (Stehlik *et al*. 2008; Vandepitte *et al*. 2009). Eppley and Pannell (2007) found that distance from the source of pollen had a significantly negative effect on seed set in the wind pollinated herb *Mercurialis annua*, with a 15% decrease over a distance of 2m. Therefore, the mean difference in elevation of 226 m between the *C. nardina* complex and *C. elynoides* makes hybridization unlikely. However, since these two taxa do grow in mixed populations at least occasionally (pers. obs.) hybridization remains a possibility. Therefore,

PCA was performed between the putative hybrid and its putative parents in the southern W Cordillera south of 42° N.

Carex nardina complex and *C. filifolia* var. *filifolia*

Latitude and elevation were also tested for correlation in *C. nardina* and *C. filifolia* var. *filifolia* in the region where their geographic distributions overlap (west of the prairies from the southern W Cordillera to Alaska) (Fig. 4). However, the Pearson correlation coefficient between latitude and elevation for *C. filifolia* var. *filifolia* was -0.80 (p = 4.1E-6), indicating a strong, significant correlation (see Table 7 for full results). For *C. nardina* also, latitude correlated strongly and significantly with elevation (r = -0.95, p = 1.6E-27).

Therefore, the analysis was restricted to the putative glacial refugium of Beringia, where both taxa occur. For this region, only three specimens of *C. filifolia* var. *filifolia* had elevation, latitude and longitude data and occurred in the extreme southeastern part of the ice-free refugium area, barely overlapping with the range of the *C. nardina* complex. The correlation between latitude and elevation was not significant for either *C. filifolia* var. *filifolia* (r = 0.97, p=0.14) or *C. nardina* (r = -0.59, p = 0.055; Fig. 13). The possibility of correlation between longitude and elevation was also investigated. For *C. filifolia* var. *filifolia* there was a strong but insignificant correlation (r = -0.97, p = 0.16). For *C. nardina* there was a moderate but insignificant correlation (r = 0.57, p = 0.067).

Therefore, testing for elevation differences was relevant in Beringia. The MW test produced a difference in mean elevation between *C. filifolia* var. *filifolia* and *C. nardina* that was statistically significant (p = 0.013). The respective mean values were 663 m ± 137 (SD) and 1651 m ± 415 (SD), creating a difference between CIs of 436m. Since, these two

taxa have never been reported growing in mixed populations, hybridization is therefore an extremely remote possibility.

Spatial analysis of the putative hybrid

Putative hybrid specimens were found throughout the entire range of the *C. nardina* complex often in higher concentration than in the most likely sites of hybridization, the southern W Cordillera and Beringia. Only 8% of the individuals from the southern W Cordillera and 19% from Beringia could be classified as putative hybrids. Only a small proportion of individuals collected in Scandinavia (4%) were classified as putative hybrids, but a large proportion from Greenland/eastern Canadian Arctic (25%) were categorized as putative hybrids (Fig. 14). Scandinavia and the eastern Canadian Arctic are very far from the regions where the two most likely possibilities, *C. elynoides* and *C. filifolia* var. *filifolia*, could have crossbred with the *C. nardina* complex.

Palynological analysis

Pollen was recovered from five *C. nardina*, six *C. elynoides*, two *C. filifolia* var. *filifolia* and 10 putative hybrid specimens. Figure 15 shows the percentage of unstainable pollen in each specimen. For *C. nardina*, two specimens were stainable and three were not. For *C. elynoides*, five specimens were stainable and one was not. Both specimens of *C. filifolia* var. *filifolia* were stainable. For the putative hybrid, five specimens were stainable

and five were not. Most slides contained a large proportion of indeterminate pollen grains (shrivelled and partially stained, or round and entire but unstained).

Multivariate analysis of morphology

Putative hybrid identification

Incongruence between cpDNA and nrDNA data sets can be indicative of several phenomena, including hybridization (Doyle *et al.* 2003; Hipp *et al.* 2004; Edwards *et al.* 2006). However, the only group of *C. nardina* complex specimens for which preliminary PCA results suggested hybridization was the tall (≥ 10 cm), straight group postulated above. This group consisted of specimens having straight culms and leaves like *C. hepburnii* and *C. elynoides* but resembling *C. nardina* in terms of staminate spike length, beak length and serrulation of the distal margins of the perigynium. Specimens of the putative hybrid group were either glabrous or had a moderately pubescent perigynium (< 40 hairs compared to as many as 480 in *C. filifolia* var. *filifolia*), and frequently had at least one tristigmatic perigynium.

Character selection – correlation analysis

For each of the morphological comparisons outlined above, the measurements of continuous characters listed in Table 4 were tested for correlation. Very few characters overall were found to be significantly correlated. LEAFL and CULML were excluded in order to eliminate the effect of size. The resulting matrices of r-values are presented in

Appendices 6-9. Only uncorrelated characters were retained for PCA. In all comparisons below, the r-values of uncorrelated characters were statistically significant ($p < 0.05$).

In each of the three comparisons between *C. nardina* and *C. hepburnii* using the descriptions of Boott (1840), Mackenzie (1935) and Egorova (1999) respectively, the same 18 characters (ACHENEL, AWNL, BEAKL, BEAKTEETHN, CHESTHAIRN, HYALINW, MARGHAIRN, MIDRIBW, NERVEN, PERIGL, PERIGW, SCALEL, SERRL, SHOULDER, SPIKEL, STAML, STIPEL and STYLEXL) were uncorrelated.

Comparing the *C. nardina* complex, *C. elynoides* and the putative hybrid, the 16 uncorrelated characters were ACHENEL, AWNL, BEAKL, BEAKTEETHN, CHESTHAIRN, HYALINW, MARGHAIRN, MIDRIBW, NERVEN, PERIGL, PERIGW, SCALEL, SERRL, STAML, STIPEL and STYLEXL. For the *C. nardina* complex-*C. filifolia* var. *filifolia*-putative hybrid comparison, the results were the same as the *C. nardina*–putative hybrid-*C. elynoides* comparison except that ACHENEL, BEAKTEETHN, CHESTHAIRN, MARGHAIRN, SERRL and STAML, were correlated while SHAPEPE and SHOULDER were uncorrelated. For the comparison between *C. filifolia* var. *filifolia*, *C. elynoides* and *C. filifolia* var. *erostrata*, the results were the same as the *C. nardina* complex-*C. filifolia*-putative hybrid comparison, except that PERIGL was correlated and SERRL and STAML and SPIKEL were uncorrelated.

For all PCAs involving *C. filifolia* var. *filifolia* the characters CHESTHAIRN was not used because the hairs on the perigynium body in this species are different anatomically than the prickle hairs on *C. elynoides* and the *C. nardina* complex.

Cluster analysis

Comparing *C. nardina* to *C. hepburnii* following Egorova's (1999) description using the 18 uncorrelated characters identified above, CA found two discernible clusters (Fig. 16) although with several specimens overlapping between groupings. A non-significant CCC value of 0.54 (< 0.75) was returned.

Similarly, CA failed to differentiate *C. hepburnii* from *C. nardina* using either Boott's (1840) or Mackenzie's (1935) descriptions. Under Boott's (1840) protologue, the CCC value was not significant (0.35) and more than two discernible clusters with many overlapping specimens were evident (Fig. 17). Under Mackenzie's (1935) description, more than two discernible clusters were evident with many overlapping specimens (Fig. 18) and the CCC value was not significant (0.49).

CA between the *C. nardina* complex, *C. elynoides* and the putative hybrid using six uncorrelated characters (ACHENEL, BEAKL, HYALINW, MARGHAIRN, NERVEN and STAML) resulted in four discernible clusters with many overlapping specimens between them. Only one specimen overlapped between the *C. elynoides* grouping and one of the *C. nardina* complex groupings. CA produced a significant CCC value of 0.77 (Fig. 19). The *C. nardina* var. *atriceps* specimens (not marked) did not cluster together. However, the significant CCC value can be attributed to the *C. elynoides* grouping because when it was removed from the data set and CA was performed again on only the *C. nardina* complex specimens the CCC value was non-significant (0.45) and four clusters of points with overlapping membership were discernible (Fig. 20).

CA between the *C. nardina* complex, *C. filifolia* var. *filifolia* and the putative hybrid using five uncorrelated characters (HYALINW, MIDRIBW, NERVEN, PERIGW

and STAML) produced a non-significant CCC value of 0.70 (Fig. 21). *Carex filifolia* var. *filifolia* was mostly separated from the *C. nardina* complex but there was overlapping membership between *C. nardina* and the putative hybrid. Similarly, CA conducted only on the same *C. nardina* and putative hybrid specimens as in Fig. 21 resulted in a non-significant CCC value of 0.54 and overlap (16 specimens) between the two putative taxa.

CA between *C. filifolia* var. *filifolia*, *C. elynoides* and *C. filifolia* var. *erostrata* the putative hybrid using 7 uncorrelated characters (ACHENEL, BEAKL, SCALEL, SERRL, SHAPEPE, SPIKEL and STAML) revealed overlapping membership between three discernible groupings and produced a non-significant CCC value of 0.48 (Fig. 22).

PCA results

The results of PCA (Figs. 23 - 30) conducted on 22 continuous morphological characters are shown in Table 8. Points in the PCA plots in Figs. 24, 26, 28 and 30 are labelled with clade numbers (1=Beringian I in the cpDNA tree, 2=W Cordilleran, 3=Scandinavian, 4=pan-Arctic, 5=Beringian II in the nrDNA tree) or "N" (specimens in the *C. nardina* complex clade not found in any of putative clades 1 - 5) from the phylogenetic analyses in Figs. 8 - 11. The holotypes for *C. nardina*, *C. hepburnii*, *C. stantonensis*, *C. elynaeformis* and *C. elynoides* are labelled "NARD", "HEP", "ST", "ELYNA" and "ELY" respectively. The syntype of *C. nardina* var. *hepburnii* is labeled "H". The topotype of C. *filifolia* var. *erostrata* is labeled "EROS". Specimens of *C. nardina* var. *atriceps* are labelled "A". The Colorado vouchers that AE Porsild had originally annotated as resembling *C. elynaeformis* are labelled "E". The loadings for each

character, or variable, in each PCA are given in Appendices 2 and 3. Table 8 shows the percentage of variance accounted for by each PC.

PCAs between pairs of putative taxa were verified, character by character, using T-tests, while the results of each PCA between three putative taxa were similarly verified using one-way ANOVA. The ANOVA and T-test results appear in Appendices 10 and 11.

Carex nardina, C. elynoides and the putative hybrid

Using the uncorrelated characters identified above, box plots (Appendices 4 and 5) of the character measurements identified six characters that were clearly not intermediate between *C. nardina* and *C. elynoides*. In the initial PC performed on the remaining ten characters, the scree plot (Fig. 31) indicated that one PC should be retained. On the first PC, the loadings of ACHENEL, AWNL, BEAKL, BEAKTEETHN, CHESTHAIRN, HYALINW, MIDRIBW, NERVEN, SCALEL and STAML were > 0.6 (Appendix 2) and were retained for subsequent PCA (Figs. 23 and 24), in which PC 1 accounted for 65.9% of the variance and PC 2 accounted for 11.9%. The three scatterplots are not aligned along the axis of either PC. The scatterplot of *C. elynoides* is separated from the *C. nardina* scatterplot and those of the putative hybrid are in between. However, the putative hybrid points overlap with those of *C. nardina*.

There was substantial overlap between points representing the various putative clades (numbered 1 - 5) and the rest of the *C. nardina* complex specimens that appear in the Bayesian analyses (Figs. 8 - 10). Furthermore, four of the *C. elynaeformis* specimens lay clearly within the scatter of *C. elynoides* points, while the type specimen of *C. elynaeformis* appeared almost adjacent to the *C. nardina* scatter. The type specimens of *C.*

nardina, *C. hepburnii* and *C. stantonensis* and all seven specimens of *C. nardina* var. *atriceps* determined by AE Porsild lay in the overlap area between the scatterplot of *C. nardina* and the putative hybrid. The type specimen of *C. elynoides* appeared on the edge of the *C. elynoides* scatterplot nearest to the putative hybrid scatterplot.

The characters used in PCA were verified by one-way ANOVA. The residuals for at least one character were shown by the Shapiro-Wilk (SW) test not to be normally distributed. The data were ln transformed, and ANOVA was performed again on each character. Again, SW tests showed the residuals not to be normally distributed, and Levene's test showed the residuals to be homoscedastic. Therefore, a non-parametric test (KW test) was applied. It showed that all characters used in the final PCA were significantly different between at least two of the three putative taxa being compared (*C. elynoides*, *C. nardina* and the putative hybrid).

Carex nardina, C. filifolia var. *filifolia* and the putative hybrid

Using the 12 uncorrelated characters identified above, box plots (Appendices 4 and 5) of the character measurements identified four characters that were clearly not intermediate between *C. nardina* and *C. filifolia* var. *filifolia*.

In the initial PCA using the remaining eight characters, the scree plot in Fig. 32 indicated that only the first PC should be retained. Only HYALINW, MIDRIBW, NERVEN, PERIGW and STAML had loadings > 0.6 on PC1 and were retained. Figs. 25 and 26 show the subsequent PCA. Table 8 shows that the first PC was significant and explained 57.1% of the variance. Appendix 3 gives the loadings of each variable. The three

scatters of points are aligned roughly horizontally along the axis of PC 1. The scatters of *C. filifolia* var. *filifolia* and *C. nardina* complex points are almost completely separate and those of the putative hybrid are in between but overlap those of *C. nardina*.

There was substantial overlap between points representing the various putative clades (numbered 1 - 5) and the rest of the *C. nardina* complex specimens that appeared in the Bayesian analyses (Figs. 8 - 10). The type specimens of *C. nardina* and *C. stantonensis* lay just outside the scatter of putative hybrid points. The type specimens for *C. stantonensis*, *C. hepburnii* and *C. elynaeformis*, as well as all seven *C. nardina* var. *atriceps* specimens appeared in the overlap between the *C. nardina* and *C. filifolia* var. *filifolia* scatterplots. Specimen 1833 (*C. filifolia* var. *filifolia*) appeared on the periphery of the *C. filifolia* var. *filifolia* scatterplot.

ANOVA was used to verify the characters used in PCA. Levene's test showed the residuals not to be normally distributed for at least one character for either the raw or ln transformed data. Hence, a non-parametric test (KW test) was applied to each character. The KW test of all characters used in the final PCA showed a significant difference between at least two of *C. filifolia* var. *filifolia*, *C. nardina* and the putative hybrid.

Carex nardina and *C. hepburnii*

Using each of the three main authors' descriptions in turn, preliminary PCA on the 18 uncorrelated characters followed by MW tests were performed. Using Egorova's (1999) description six characters (ACHENEL, PERIGW, SCALEL, SERRL, SPIKEL and STAML) had loadings > 0.6 (Appendices 2 and 3). Initial PCA results showed almost complete overlap between the scatterplots of each putative taxon (Figs. 27 and 28). Table 8

shows that the first PC was significant and explained 48.6% of the variance. Appendix 3 gives the loadings of each variable. The type specimens of *C. nardina* and *C. elynaeformis* lay outside the overlap zone between the two scatterplots. The type specimens for *C. hepburnii* and *C. stantonensis* lay within the overlap zone. Roughly half the *C. nardina* var. *atriceps* specimens lay in the overlap and half were outside. There was substantial overlap between points representing the various putative clades (numbered 1 - 5) and the rest of the *C. nardina* complex specimens that appeared in the Bayesian analyses.

ANOVA was used to verify the characters used in PCA. In the comparison between *C. nardina* and *C. hepburnii* the data for at least one character were found by F-test to be heteroscedastic even when ln transformed. Also, the data for at least one character were found not to be normally distributed using SW tests, so the ln transformation was applied. However, F-tests revealed that the transformed data were heteroscedastic. Therefore, for all three descriptions, non-parametric MW tests were performed on the transformed data.

Using the description of Egorova (1999) MW tests showed significant differences between all characters used in the final PCA except SERRL. Therefore, SERRL was dropped from the analysis and ACHENEL, PERIGW, SCALEL, SPIKEL and STAML were retained.

Using the protologue of Boott (1840) the PCA plot showed nearly complete overlap between the *C. hepburnii* specimens and half of the *C. nardina* specimens. MW tests revealed no difference in means only for any character. Similarly, the PCA plot for Mackenzie's description showed only minor overlap between the *C. nardina* and *C. hepburnii* scatterplots, yet MW tests revealed a difference in means only for SCALEL.

Since PCA requires at least three variables with significantly different means (Naczi *et al.* 1998; Hammer *et al.* 2001) it could not be performed in either case.

Carex filifolia* var. *filifolia*, *C. elynoides* and *C. filifolia* var. *erostrata

Initial PCA using these characters produced a scree plot (Fig. 34) indicating that two PCs were significant. Only ACHENEL, BEAKL, SCALEL, SHAPEPE, SERRL, SPIKEL and STAML had loadings > 0.6 on PC1 to PC 6 (Appendix 3). Figs. 29 and 30 show the results of the subsequent PCA using only these characters. PCs 1 and 2 accounted for 41.3% and 26.2% of the variance respectively. The three scatters of points are not aligned along either axis. The scatterplots of *C. filifolia* var. *erostrata* and *C. elynoides* are separate from each other but each slightly overlaps the scatterplot of *C. filifolia* var. *filifolia*. The type specimens of *C. elynoides* and *C. filifolia* var. *erostrata* lay just within the *C. filifolia* var. *filifolia* scatterplot. Specimen 1824 appeared much closer to the *C. elynoides* scatterplot (reflecting the cpDNA phylogenetic results) than to the *C. filifolia* var. *erostrata* scatterplot. Specimen 1833 lies on the periphery of the *C. filifolia* var. *filifolia* scatterplot.

For the PCA between *C. filifolia* var. *filifolia*, *C. elynoides* and *C. filifolia* var. *erostrata* the residuals were shown by SW tests to be heteroscedastic for at least one character. The data were ln transformed and ANOVA was performed again on each character. Again, Levene's tests demonstrated the residuals to be heteroscedastic. Therefore, a non-parametric KW test was applied to each character. The characters that showed a significant difference between at least two of *C. filifolia* var. *filifolia*, *C. elynoides* and *C. filifolia* var. *erostrata* in KW tests were ACHENEL, BEAKL, SCALEL, SERRL, SHAPEPE, SPIKEL and STAML.

Anatomical analysis

A consistent difference was found in only one aspect of the leaf anatomy for the putative taxa examined. Leaf laminae were fused in 12 of the 14 *C. elynoides* specimens sampled, but the same character was only seen in two of the 11 *C. nardina* complex specimens observed (Fig. 35 b and a). Of the 14 putative hybrids sampled, seven had fused leaf laminae (Fig. 35 c and d). The difference in length between the two leaf laminae (ABORTL) seemed to vary between *C. nardina* and *C. hepburnii* specimens regardless of which of the three main authors' descriptions were used; however, T-tests returned a non-significant p-value (< 0.05) in each case (Appendix 12).

A consistent difference was found in only one aspect of the culm anatomy of the putative taxa sampled. As shown in Fig. 36 a-d, vascular bundles protrude into the cortex of *C. filifolia* var. *filifolia* consistently, whereas in *C. nardina* this was never seen and in the putative hybrid only rarely (2 of 12 cases). Similarly, vascular bundles were found always to protrude into the central cortex in *C. filifolia* var. *filifolia*, never in *C. elynoides* and sometimes (7 of 10 specimens) in *C. filifolia* var. *erostrata*. Appendices 12 - 21 summarize the results of the anatomical analysis.

In all of the continuous characters measured, there was nearly total overlap between the CIs (mean ± SD) for all comparisons between taxa considered. Therefore, no significant differences were found among any character examined.

Micromorphology of fruit epidermal silica bodies

Acid digestion of the achene cell walls was excessive to the point that the cell wall bases were damaged, making interpretation difficult. Also, clear images were not obtained because sonication or rinsing was unable to remove much of the debris from the acid digestion step. None of the epidermal silica deposits were prominent and the only observable variation concerned the number of silica bodies and the shape of the silica base in the cell. Some had one silica body on a hexagonal base and others had two silica bodies on an elongated base (Fig. 37 a - d). When the specimens were classified as either *C. nardina* or *C. hepburnii* according to Boott (1840), Mackenzie (1935) and Egorova (1999) the above two silica body morphotypes did not correspond to these two taxa. For each author's description, in one or both morphological groups *C. nardina* and *C. hepburnii* co-occurred. Furthermore, some specimens of the second type contained cells resembling the first type. No further achene sampling was performed because of the technical difficulties in obtaining high quality images and the relative lack of observable micromorphological complexity and variability, despite geographically broad sampling.

TABLE 7 Results of elevation vs. latitude linear correlation among the *C. nardina* complex, *C. elynoides*, *C. filifolia* var. *filifolia*, *C. filifolia* var. *erostrata* and the potential hybrid in various geographic regions.

Region	Taxon	r	p	Significant
entire range	*C. nardina*	-0.90	3.0E-91	Yes
W Cordillera S. of Canada	*C. nardina*	-0.94	2.5E-16	Yes
W Cordillera S. of Canada	*C. elynoides*	-0.81	3.2E-15	Yes
W Cordillera S. of Canada	potential hybrid	-0.93	2.2E-07	Yes
W Cordillera S. of 42°N	*C. nardina*	-0.47	0.06	No
W Cordillera S. of 42°N	*C. elynoides*	-0.17	0.33	No
W Cordillera S. of 42°N	potential hybrid	-0.46	0.43	No
Beringia	*C. nardina*	0.57	0.07	No
Beringia	*C. filifolia* var. *filifolia*	-0.97	0.16	No
Beringia	*C. nardina*	-0.59	0.06	No
Beringia	*C. filifolia* var. *filifolia*	0.97	0.14	No

TABLE 8 Statistical results of principal components analyses. Significant PCs in bold.

Taxa	PC	Eigenvalue	% variance
C. nardina, C. hepburnii (Egorova protologue)	**1**	**2.914**	**48.6**
(n = 84)	2	0.881	14.7
	3	0.774	12.9
	4	0.656	10.9
	5	0.532	8.9
	6	0.243	4.1
C. elynoides, C. nardina, putative hybrid	**1**	**3.297**	**65.9**
(n = 120)	2	0.595	11.9
	3	0.523	10.5
	4	0.317	6.3
	5	0.268	5.4
C. filifolia var. *filifolia,*	**1**	**2.855**	**57.1**
C. nardina, putative hybrid	2	0.759	15.2
(n = 135)	3	0.633	12.7
	4	0.435	8.7
	5	0.318	6.4
C. filifolia var. *filifolia, C. elynoides,*	**1**	**3.077**	**51.3**
C. filifolia var. *erostrata*	**2**	**1.358**	**22.6**
(n = 99)	3	0.665	11.1
	4	0.398	6.6
	5	0.335	5.6
	6	0.167	2.8

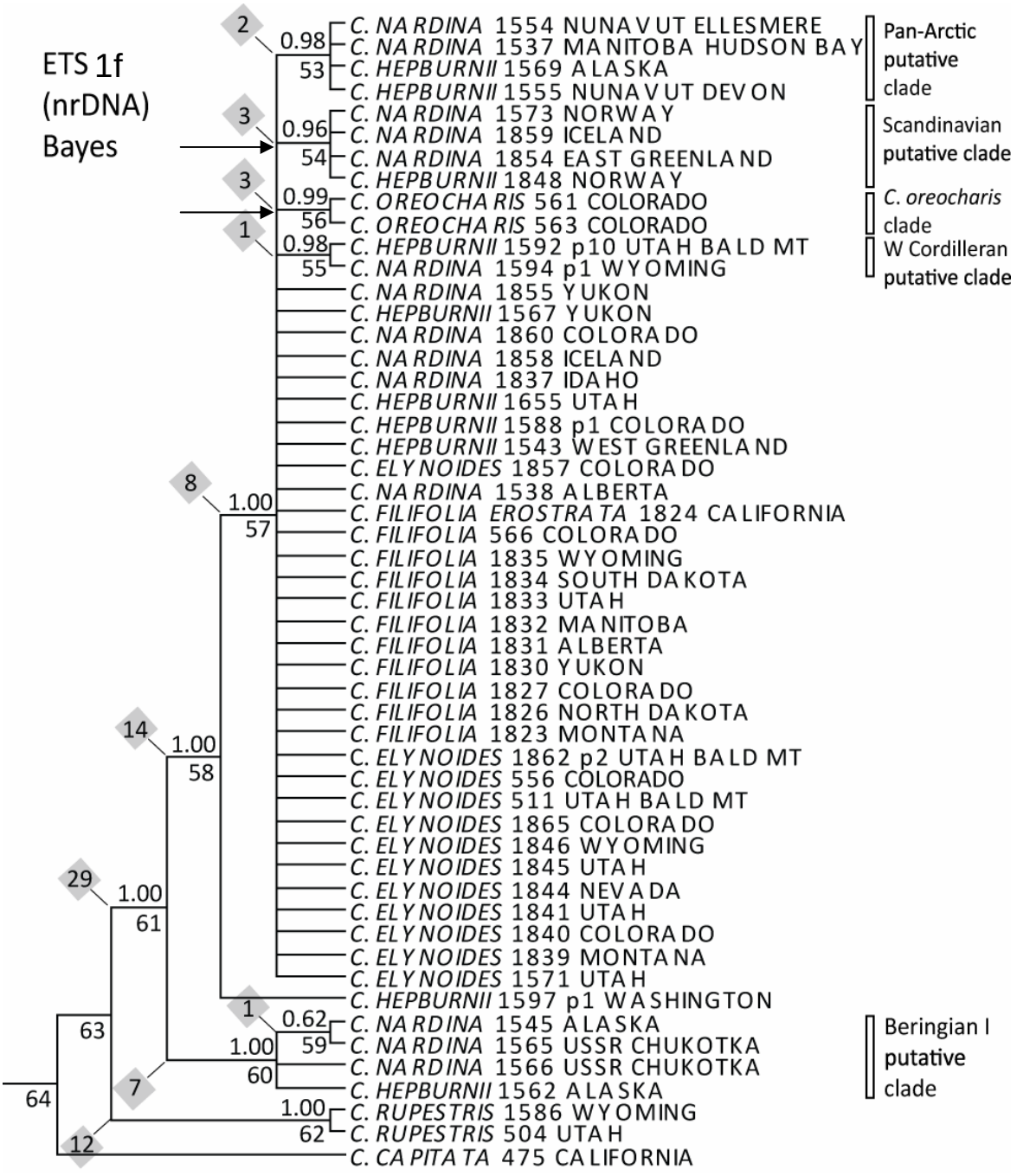


FIG. 8 Bayesian 50% majority-rule consensus of all compatible groups of 9 900 trees sampled from the posterior distribution under a GTR model of evolution for the ETS 1f nrDNA region. PP values given above branches. Number of mutations along branches given in diamonds. BS values ≥ 50% are given below branches. The genus *Carex* is abbreviated as "*C.*" to the right of the tree followed by the specific epithet, DNA number and sample locality. Boott's (1840) protologue used to name *C. nardina* complex specimens. Bars on right indicate putative clades. Arrows indicate branches that do not appear in MP analysis, n = 52.

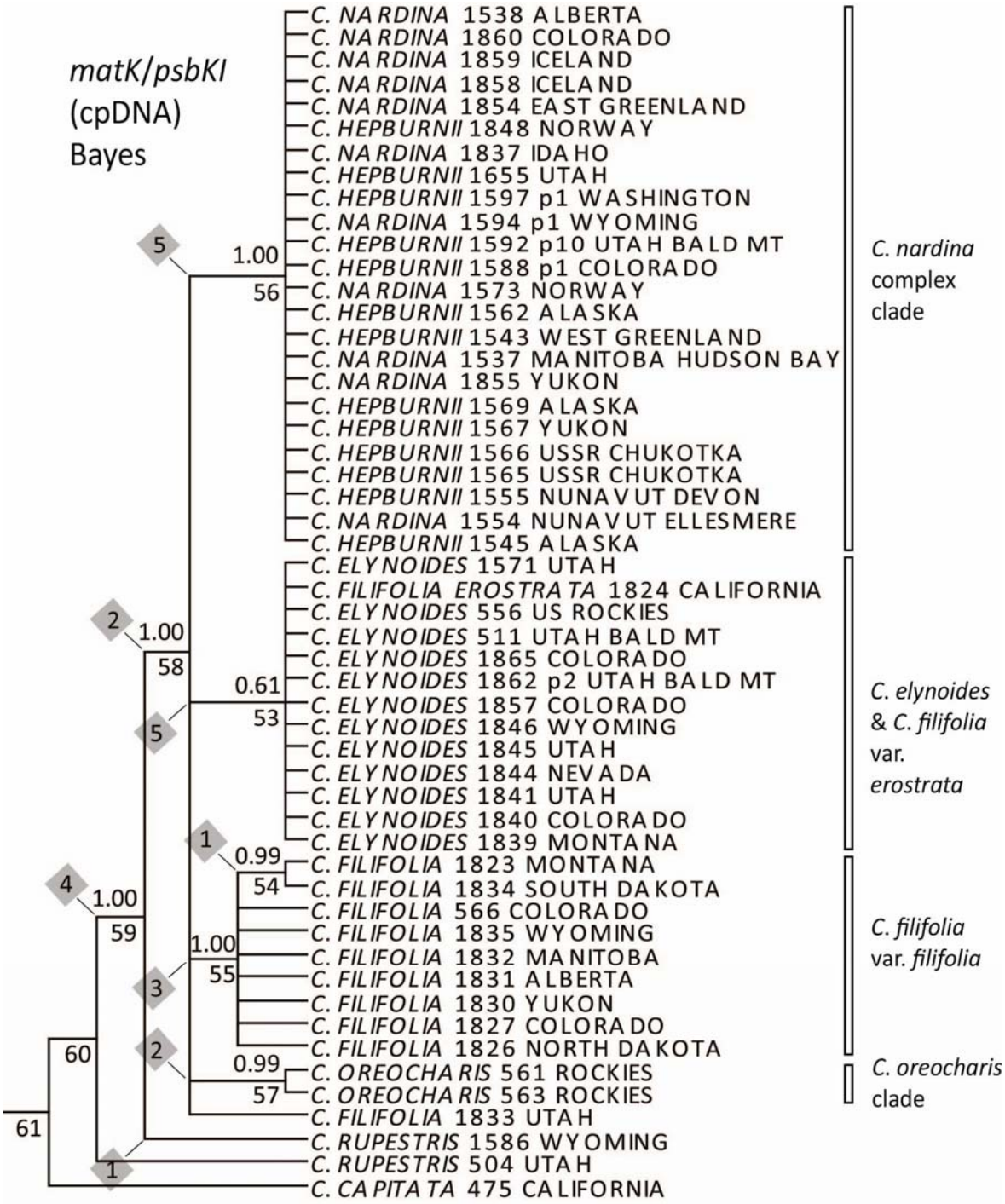


FIG. 9 Bayesian 50% majority-rule consensus of all compatible groups of 9 900 trees sampled from the posterior distribution under a K80 model of evolution for the combined *matK*/*psbKI* regions. PP values are given above branches. Number of mutations along branches is given in diamonds. BS values ≥ 50% are given below branches. PP values are given above branches. The genus *Carex* is abbreviated as "*C.*" to the right of the tree followed by the specific epithet, DNA number and sample locality. Bars on right putative apparent clades. Arrows indicate branches that do not appear in MP analysis, n = 52.

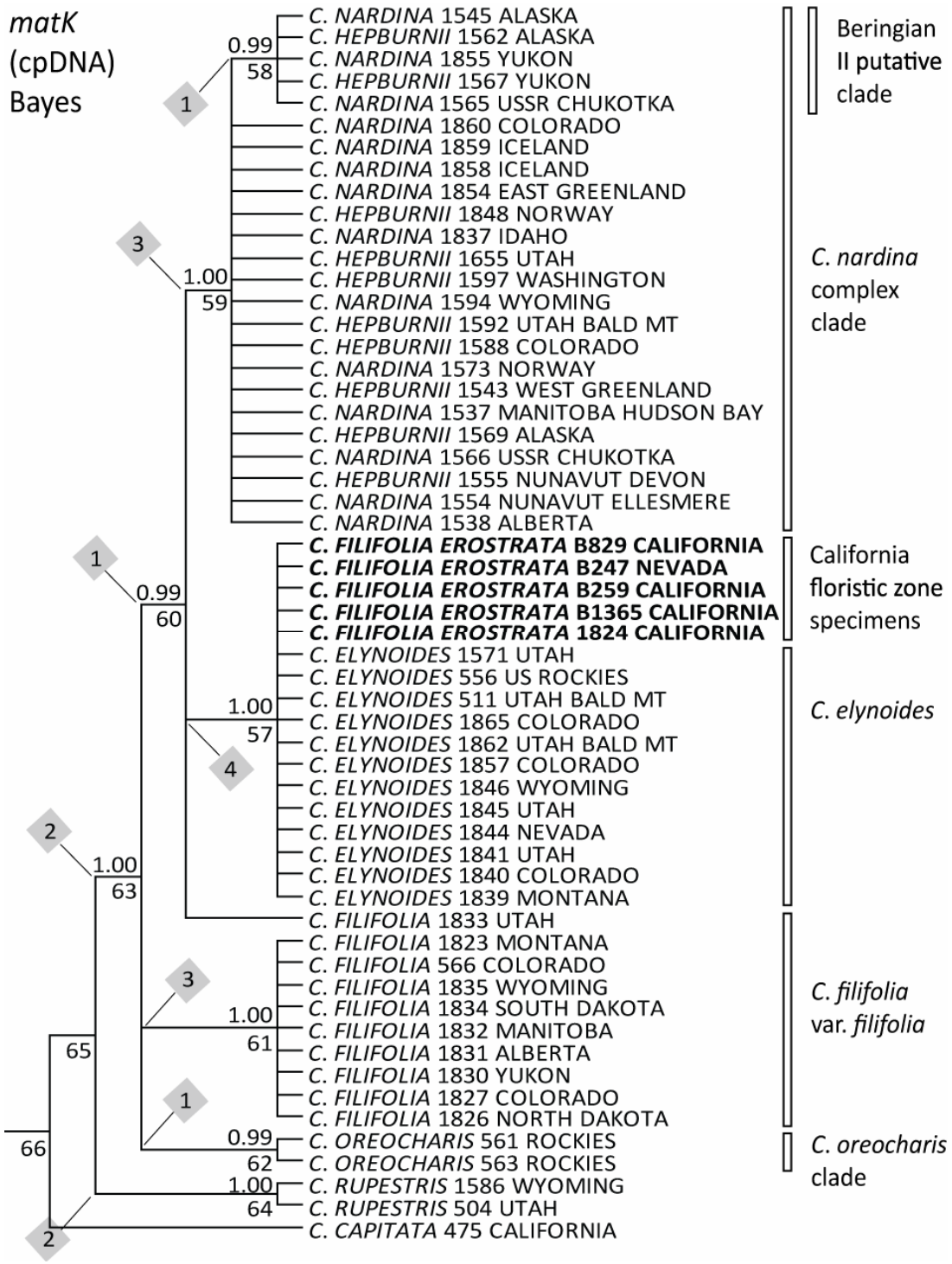


FIG. 10 Bayesian 50% majority-rule consensus of all compatible groups of 9 900 trees sampled from the posterior distribution under a K80 model of evolution for the *matK* region. PP values are given above branches. The numbers of mutations along branches are given in diamonds. BS values ≥ 50% are given below branches. PP values are given above branches. The genus *Carex* is abbreviated as "*C.*" to the right of the tree followed by the specific epithet, DNA number and sample locality. Bars on right putative apparent clades. No differences with MP tree, n =56.

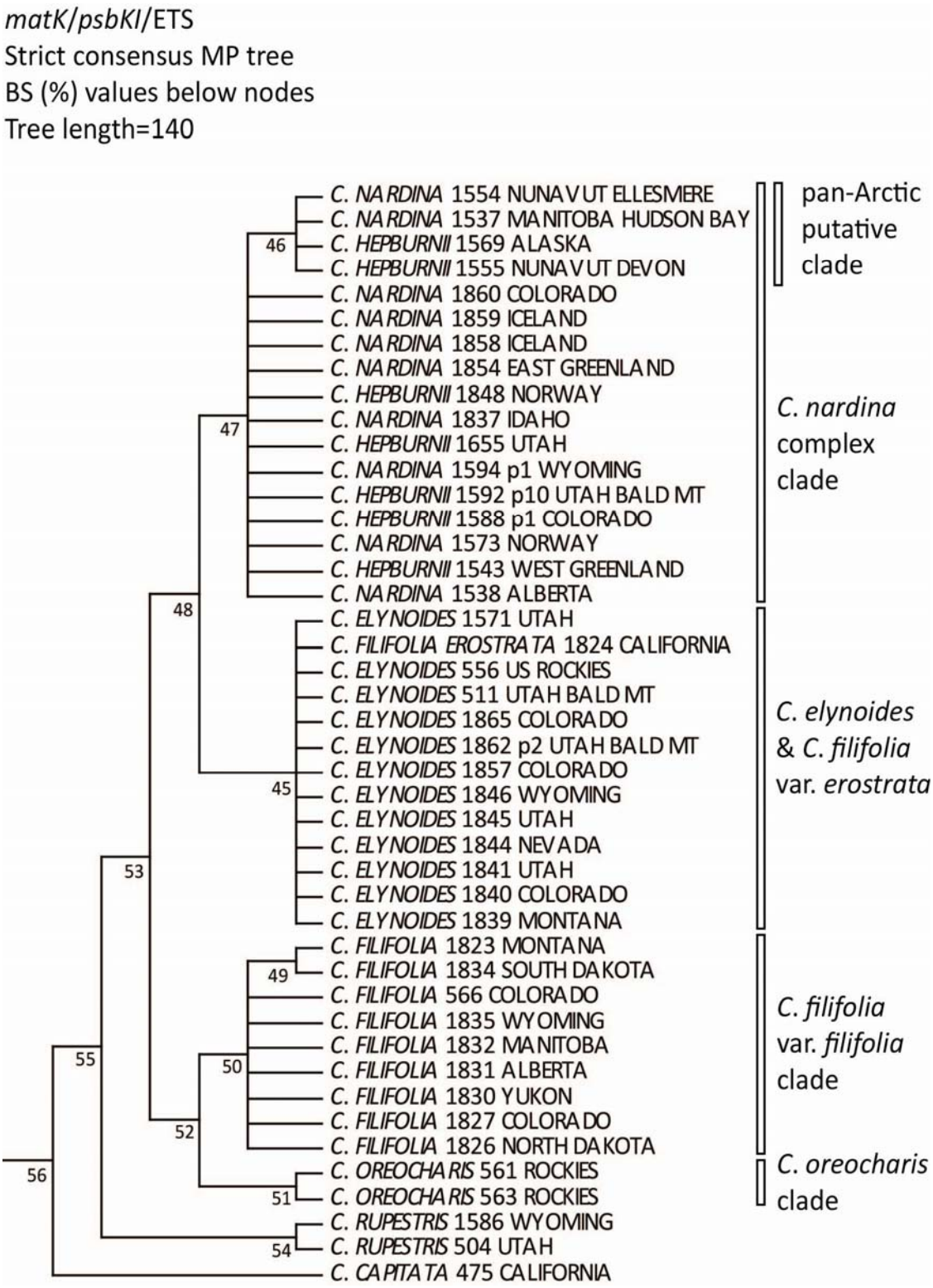


FIG. 11 Strict consensus tree of the 1000 most parsimonious trees resulting from heuristic searches of concatenated *matK*, *psbKI* and ETS sequences. Tree length = 140. CI = 0.74. HI = 0.89. The genus *Carex* is abbreviated as "*C.*" to the right of the tree followed by the specific epithet, DNA number and sample locality. Bars on right putative apparent clades, n = 44.

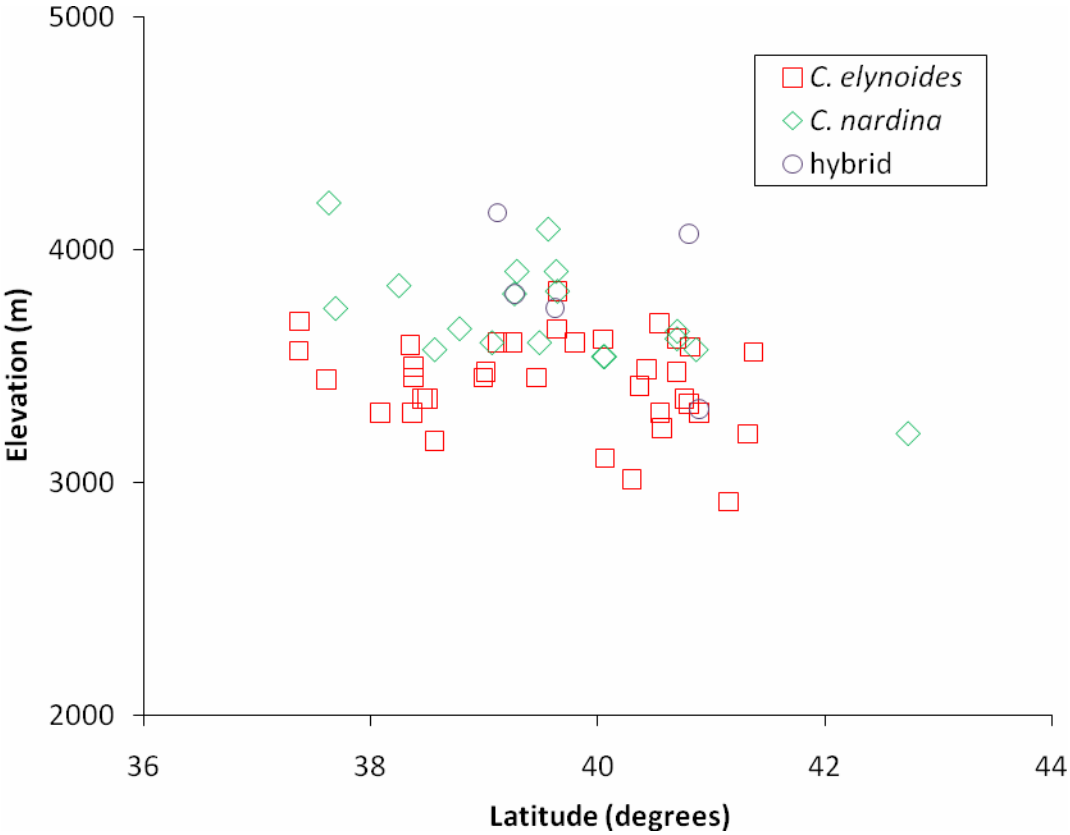


FIG. 12 Elevation vs. latitude for *C. elynoides*, *C. nardina* and the putative hybrid in the southwestern Cordillera, n = 60.

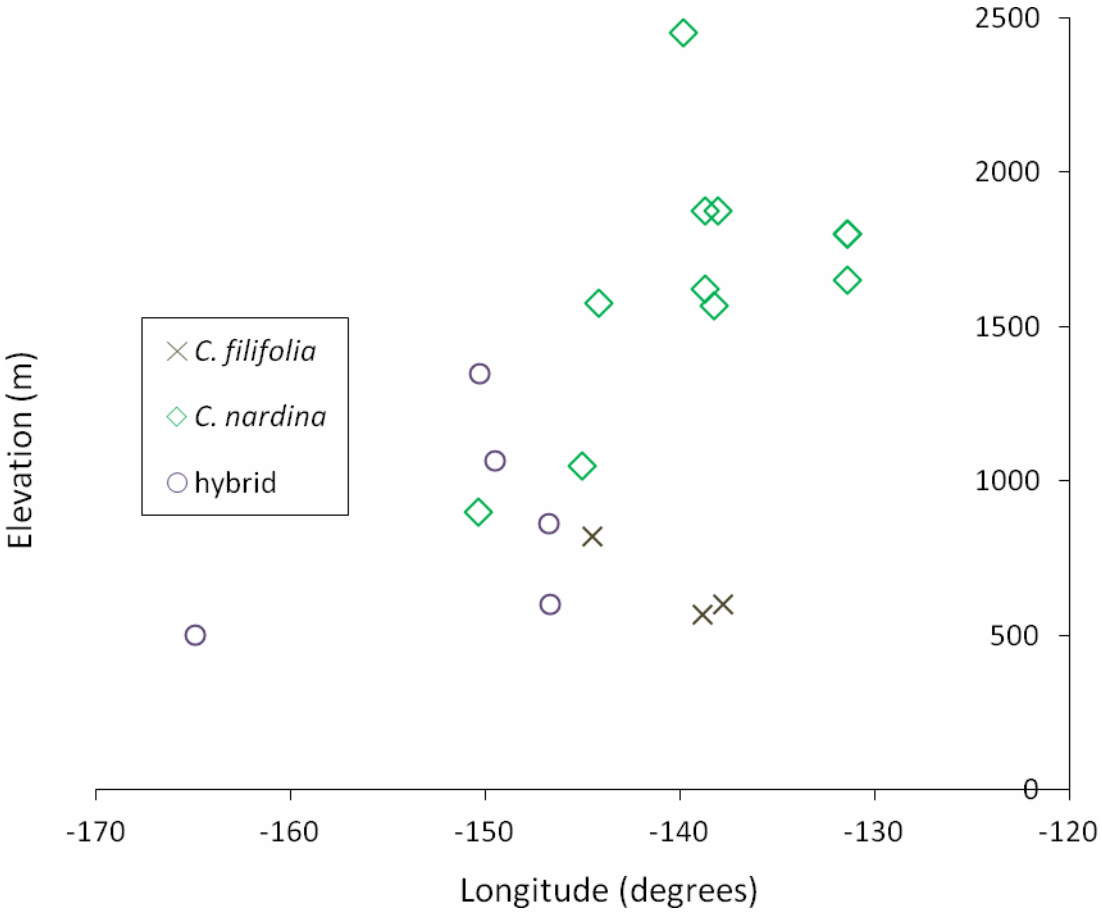


FIG. 13 Elevation vs. longitude for *C. filifolia* var. *filifolia*, *C. nardina* and the putative hybrid in Beringia, n = 21.

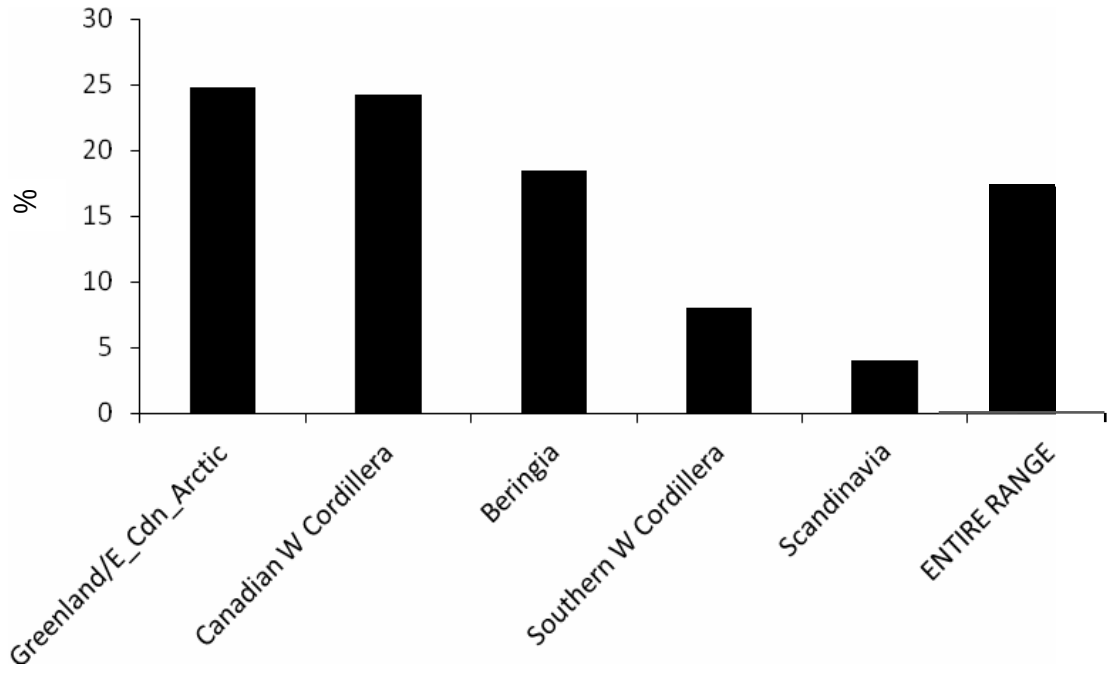


FIG. 14 Individual hybrid specimens as a percentage of total individual specimens examined by geographic region within the range of the *C. nardina* complex: Greenland/eastern Canadian Arctic, Canadian W Cordillera, Beringia, W Cordillera south of Canadian border, Scandinavia including Svalbard, and the entire range, n = 2699.

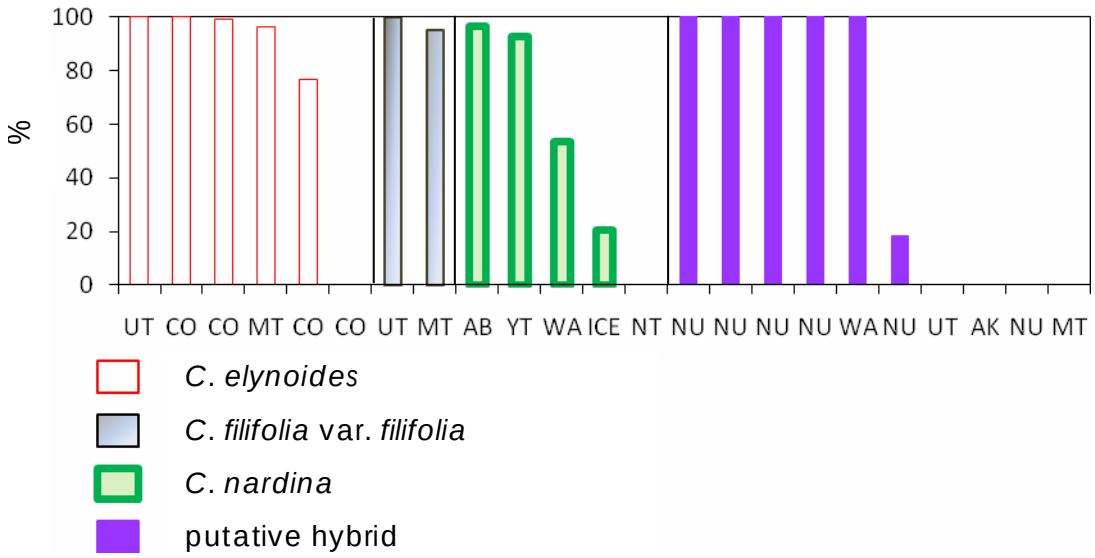


FIG. 15 Percentage of viable pollen found in each specimen of *C. elynoides*, *C. filifolia* var. *filifolia*, the *C. nardina* complex and the putative hybrid. Canadian province and US state abbreviations on x-axis, "ICE" = Iceland, n = 23.

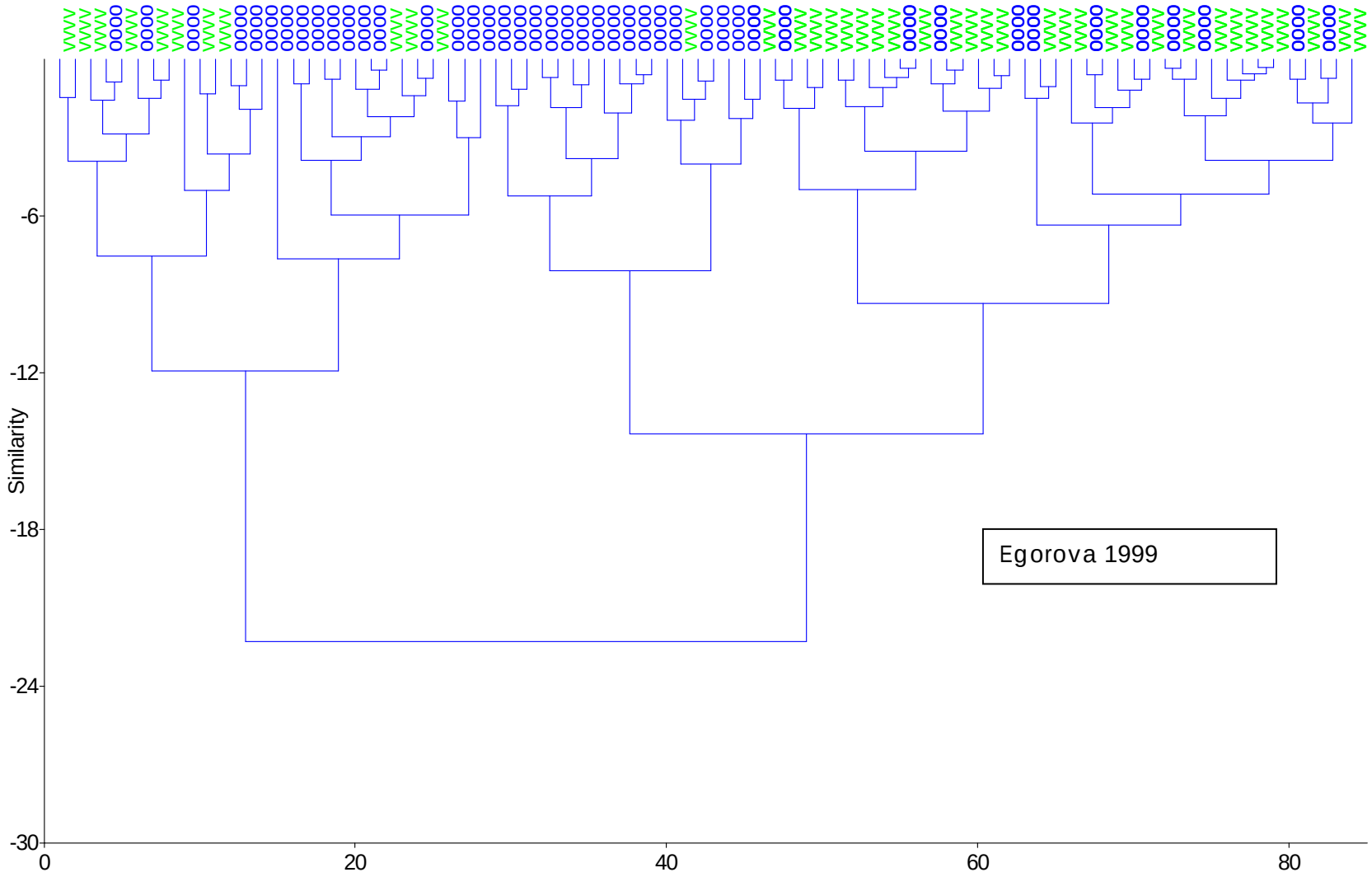


FIG. 16 CA dendrogram using Ward's algorithm (Blashfield 1976) for *C. nardina* (vvvv) and *C. hepburnii* (oooo) categorized according to Egorova (1999) using characters ACHENEL, PERIGW, SCALEL, SERRL, SPIKEL and STAML. CCC = 0.54, n = 84.

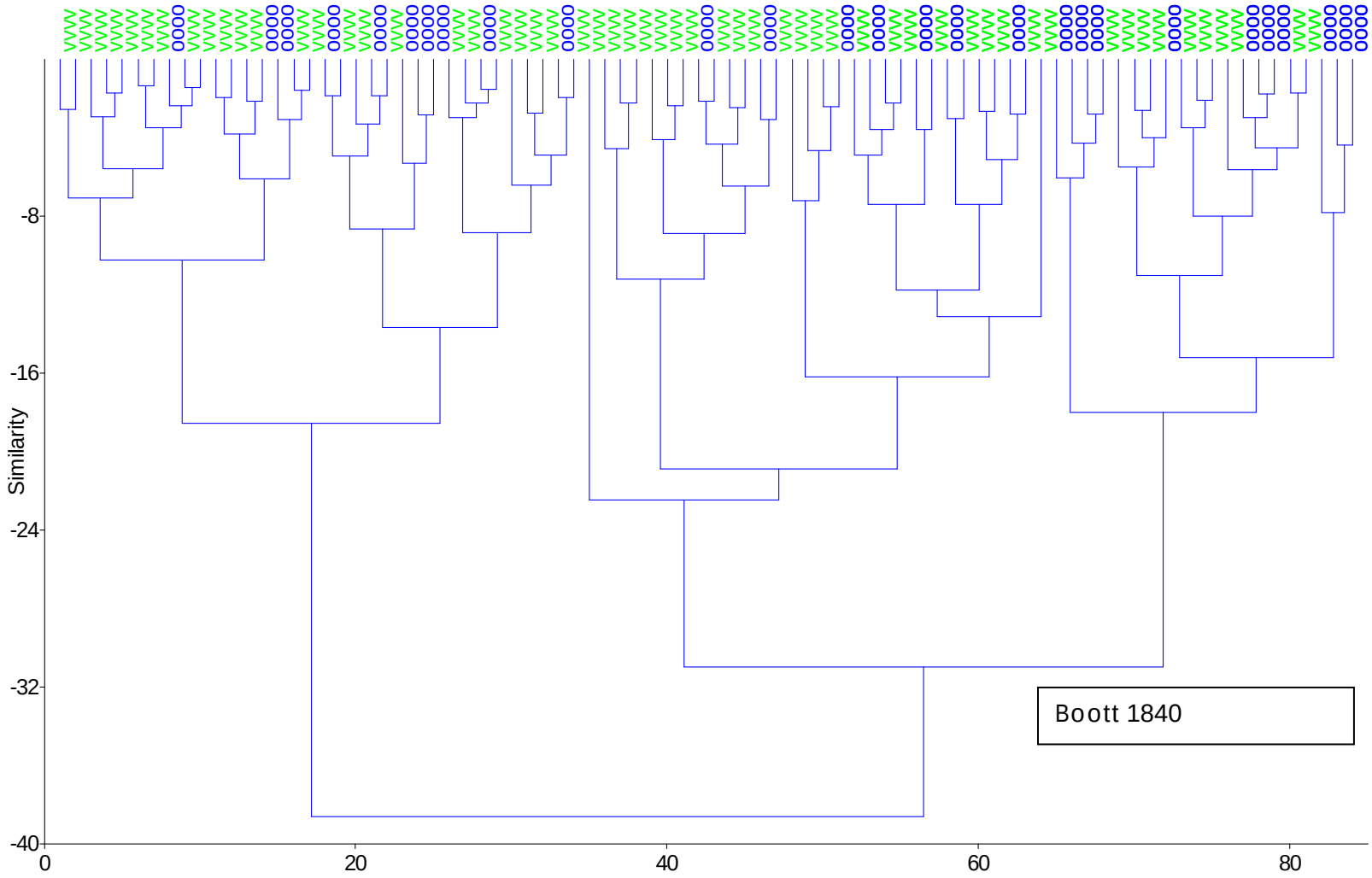


FIG. 17 CA dendrogram of *C. nardina* (vvvv) and *C. hepburnii* (oooo) specimens classified according to Boott (1840) using 18 uncorrelated characters (ACHENEL, AWNL, BEAKL, BEAKTEETHN, CHESTHAIRN, HYALINW, MARGHAIRN, MIDRIBW, NERVEN, PERIGL, PERIGW, SCALEL, SERRL, SHOULDER, SPIKEL, STAML, STIPEL and STYLEXL). Ward's algorithm. CCC = 0.35, n = 84.

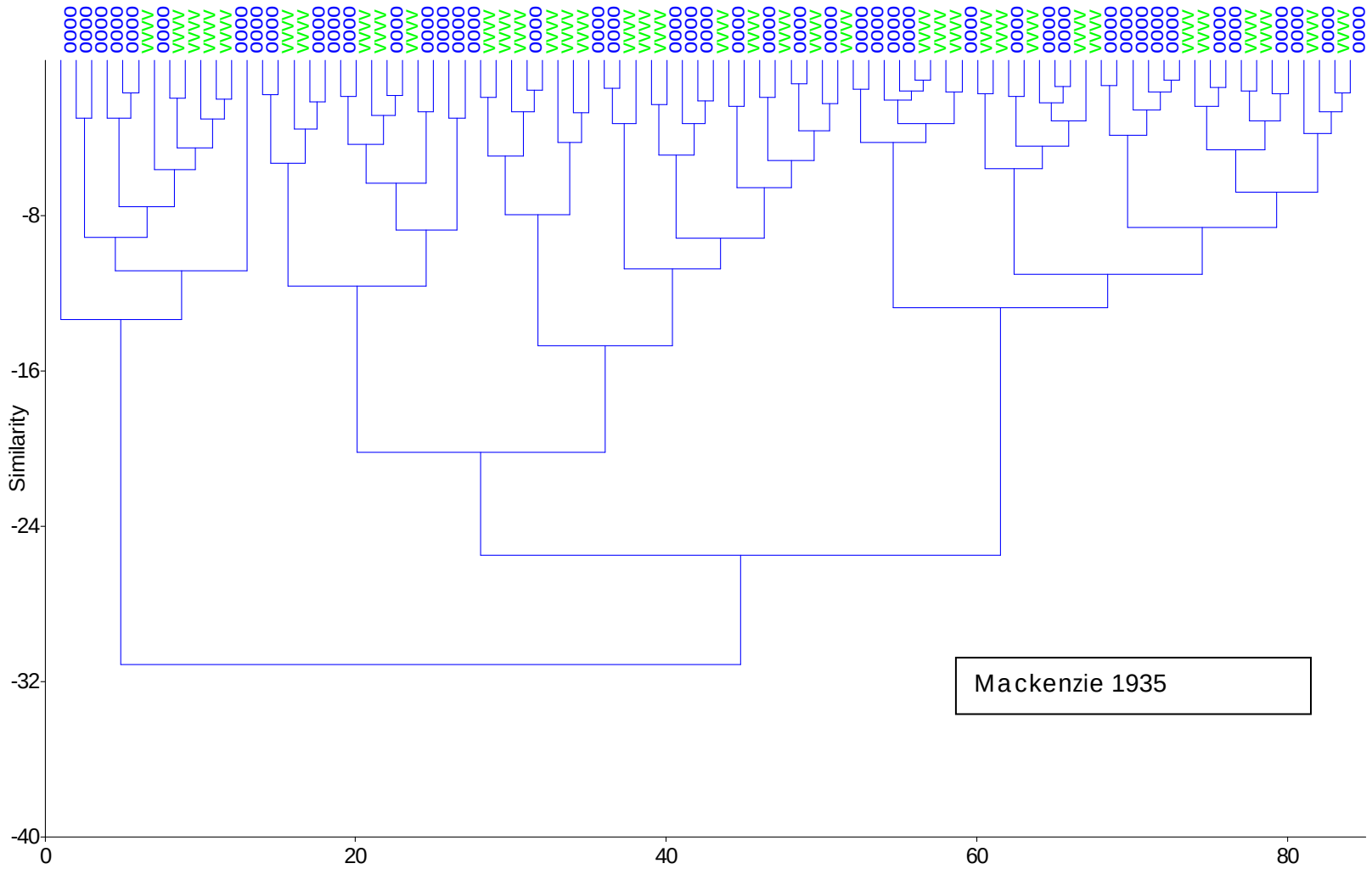


FIG. 18 CA dendrogram of *C. nardina* (vvvv) and *C. hepburnii* (oooo) specimens classified according to Mackenzie (1935) using 18 uncorrelated characters ACHENEL, AWNL, BEAKL, BEAKTEETHN, CHESTHAIRN, HYALINW, MARGHAIRN, MIDRIBW, NERVEN, PERIGW, SCALEL, SERRL, SHOULDER, SPIKEL, STAML, STIPEL and STYLEXL. Ward's algorithm. CCC = 0.49, n = 84.

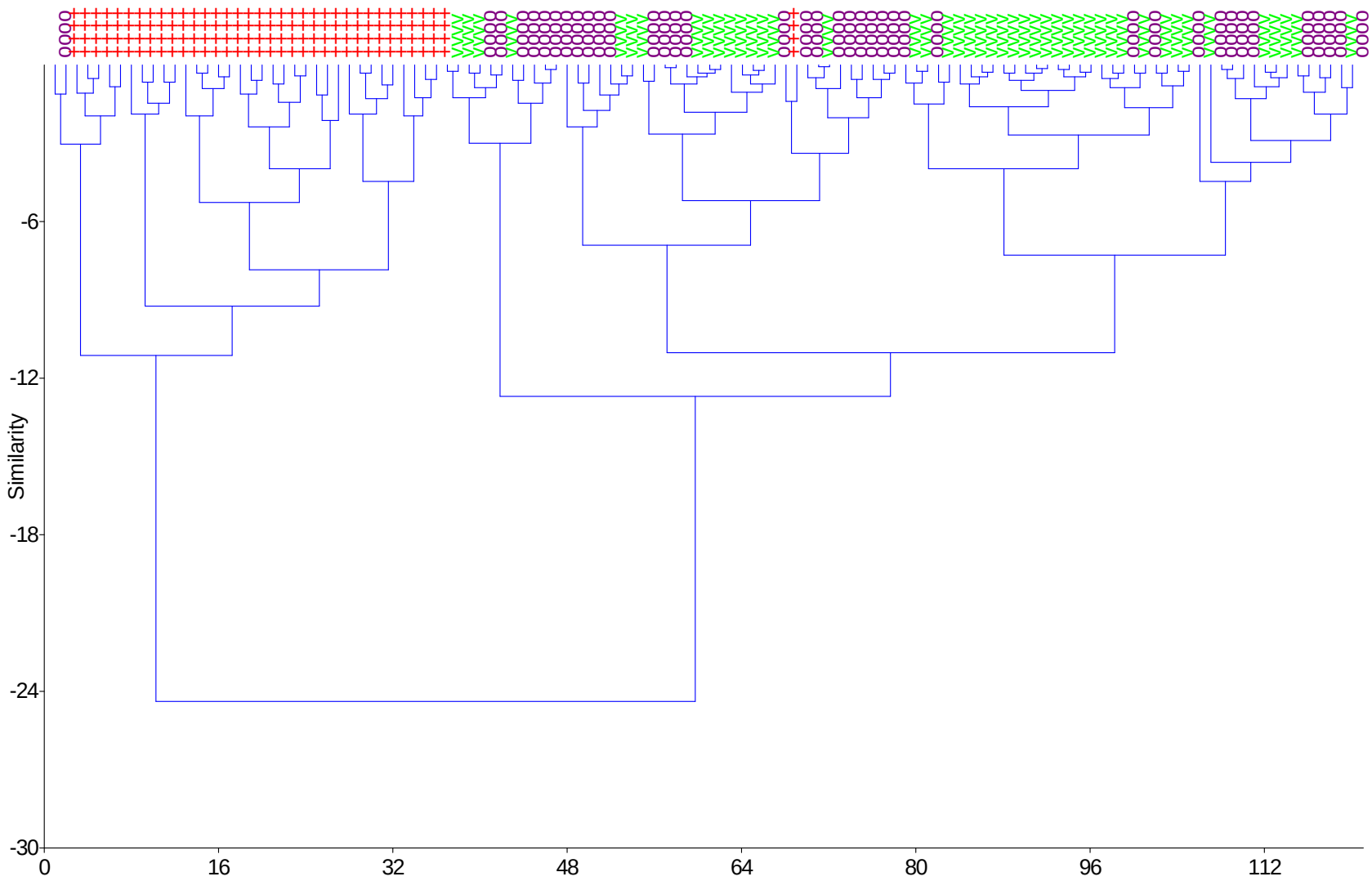


FIG. 19 CA dendrogram using Ward's algorithm for *C. nardina* (vvvv), *C. elynoides* (++++) and putative hybrid (oooo) using ACHENEL, BEAKL, HYALINW, NERVEN and STAML. CCC = 0.77, n = 120.

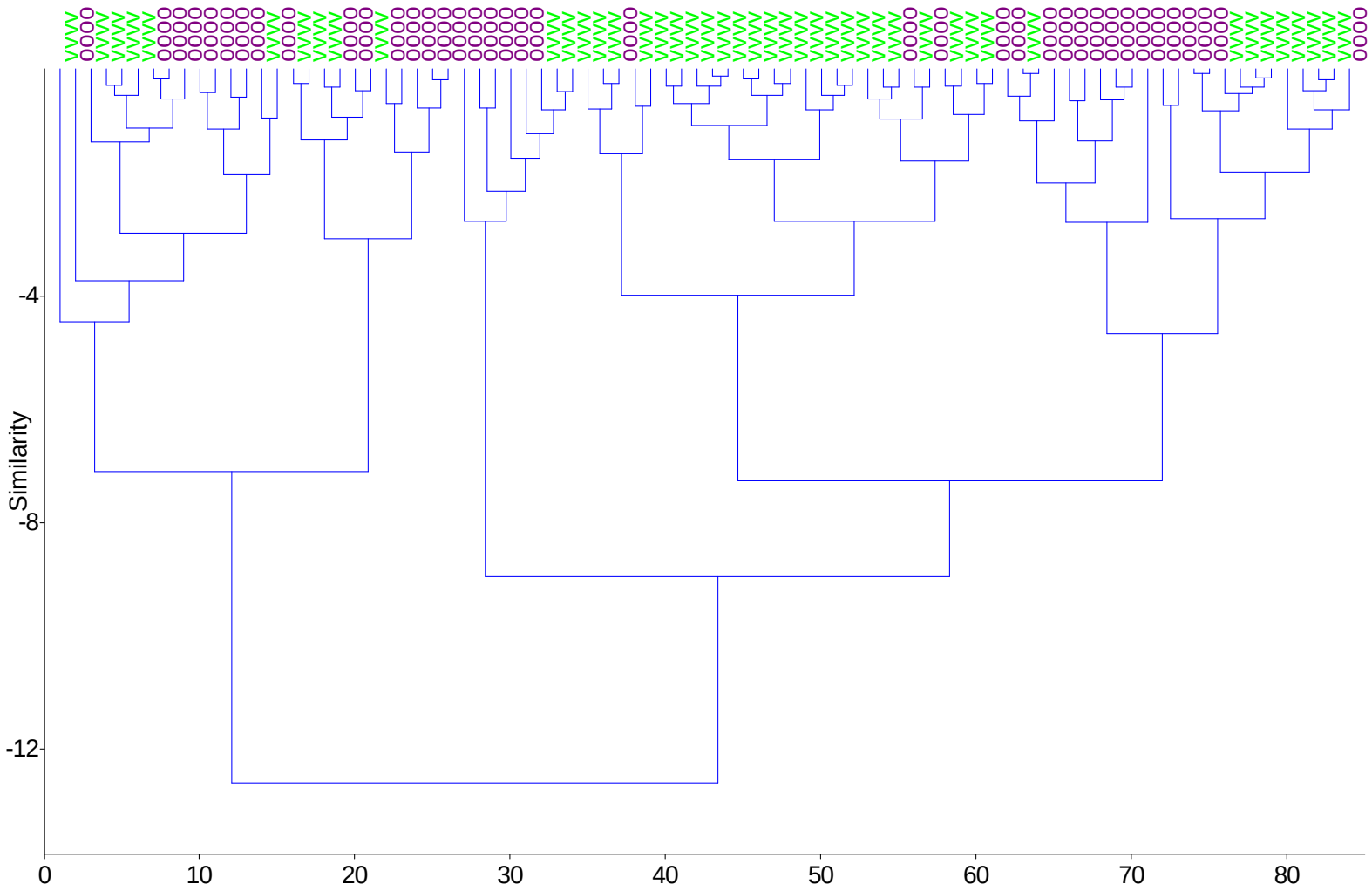


FIG. 20 CA dendrogram using Ward's algorithm for *C. nardina* (vvvv) and the putative hybrid (oooo) using ACHENEL, BEAKL, HYALINW, NERVEN and STAML. CCC = 0.45, n = 84.

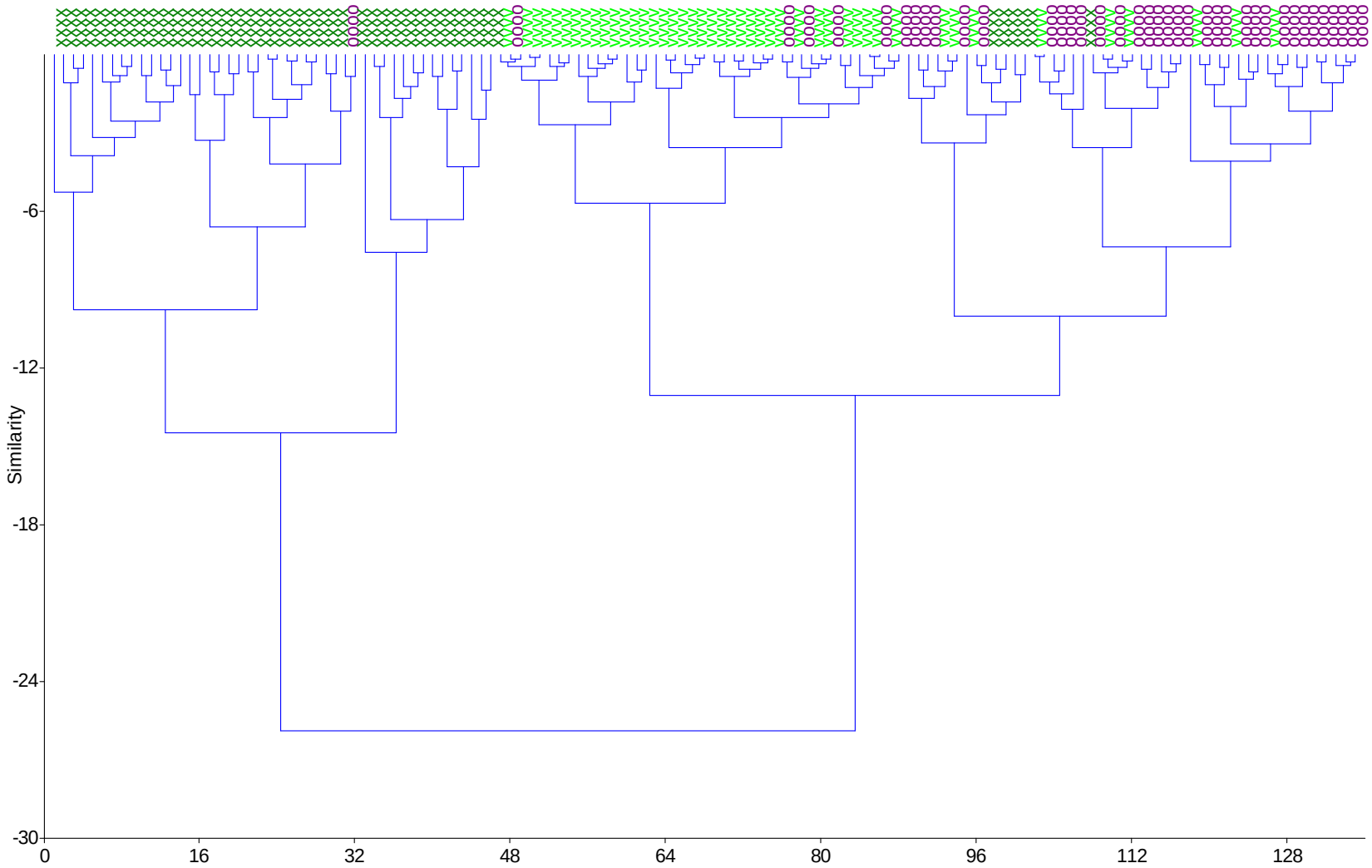


FIG. 21 CA dendrogram of the *C. nardina* complex (www), *C. filifolia* var. *filifolia* (xxxx) and the putative hybrid (oooo) using HYALINW, MIDRIBW, NERVEN, PERIGW and STAML using Ward's algorithm. CCC = 0.70, n = 135.

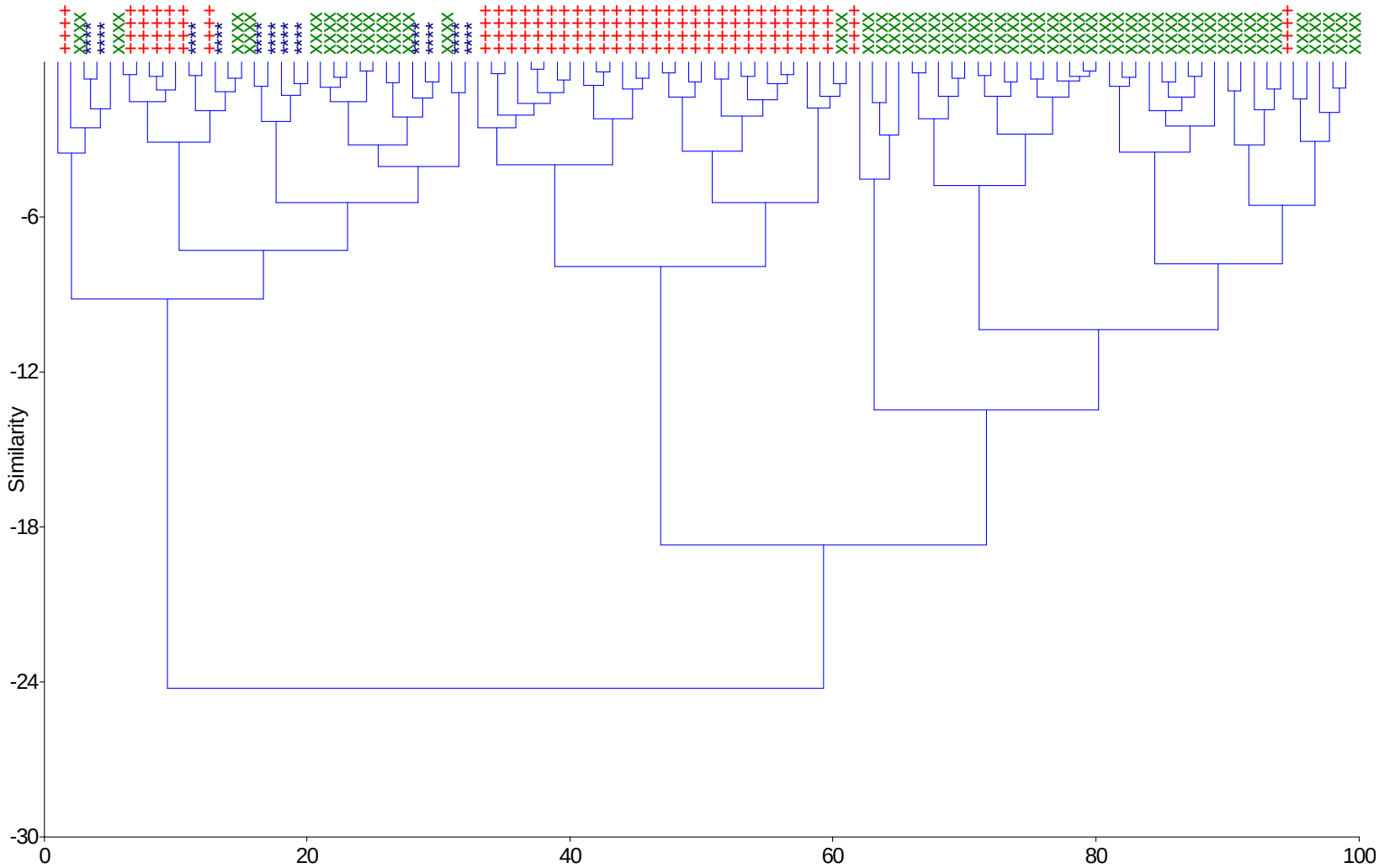


FIG. 22 CA dendrogram of *C. filifolia* var. *filifolia* (xxxx), *C. elynoides* (++++) and *C. filifolia* var. *erostrata* (****) using ACHENEL, BEAKL, SCALEL, SERRL, SHAPEPE, SPIKEL and STAML using Ward's algorithm. CCC = 0.48, n = 99.

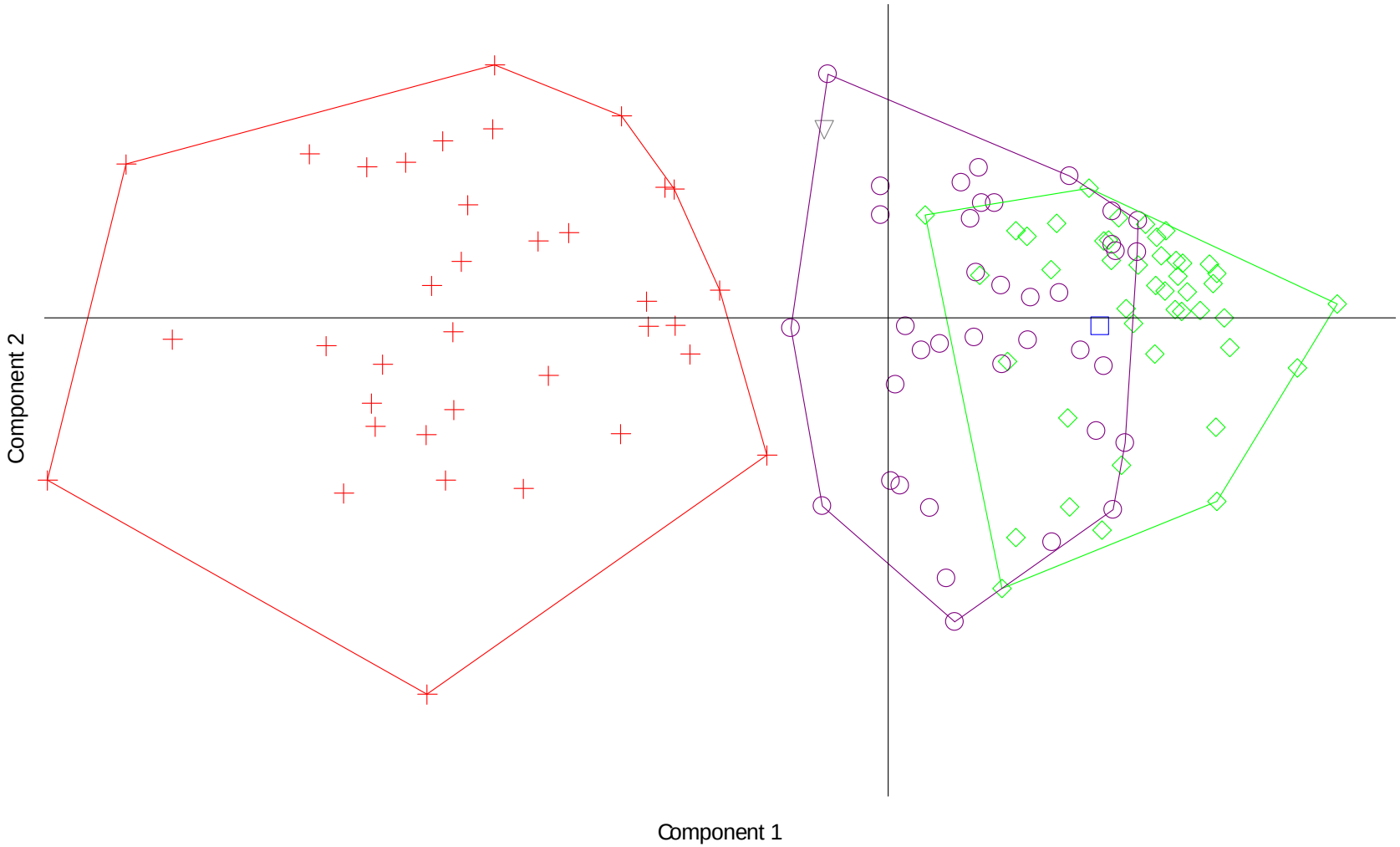


FIG. 23 PCA plot of *C. elynoides* (crosses), putative hybrid (circles) and *C. nardina* (diamonds) using uncorrelated, intermediate, significantly different morphological characters ACHENEL, BEAKL, HYALINW, NERVEN and STAML. PC 1 accounted for 65.9% of variance, n = 120.

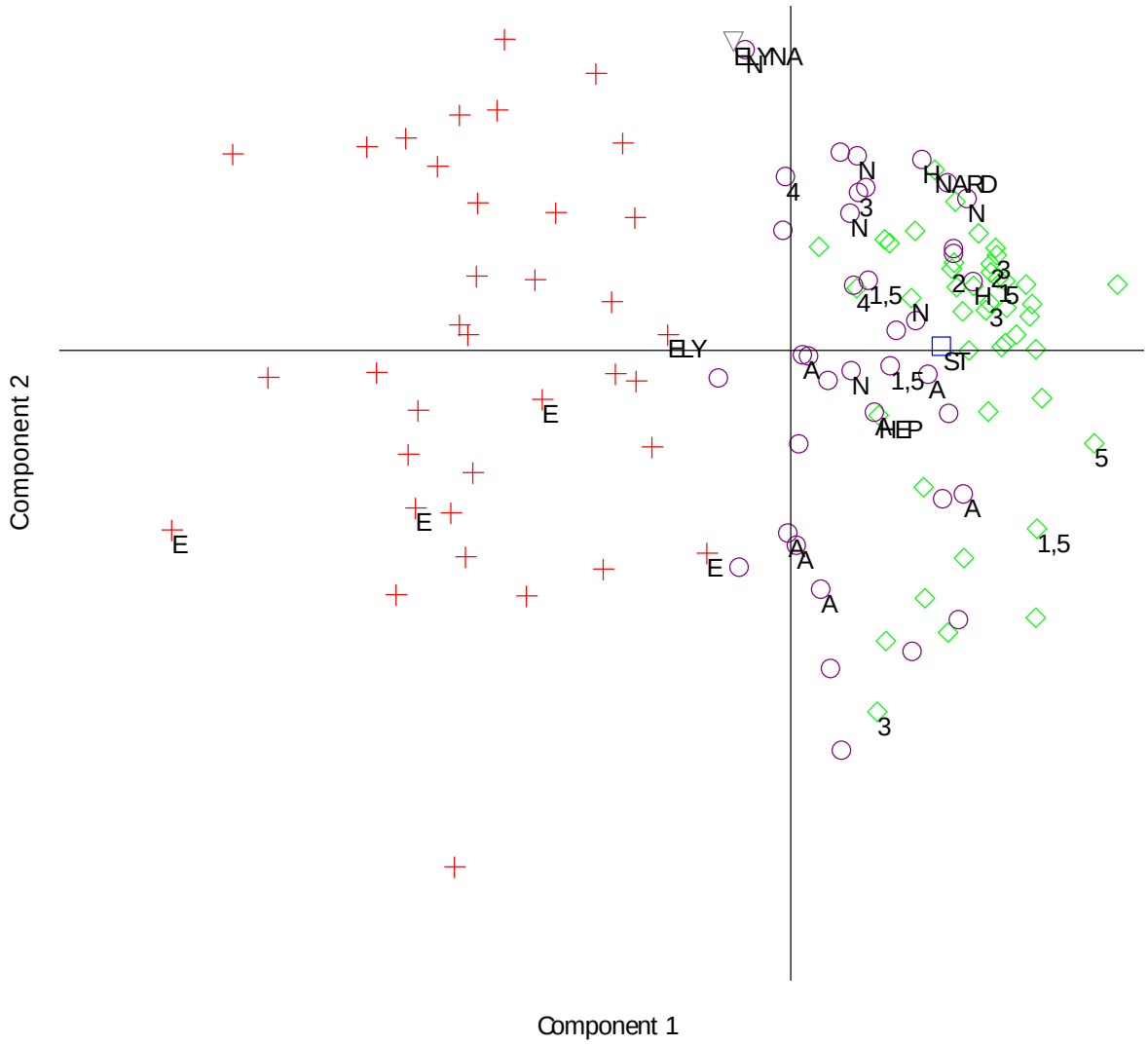


FIG. 24 PCA plot of *C. elynoides* (crosses), putative hybrid (circles) and *C. nardina* (diamonds) using five uncorrelated, significantly different morphological characters, ACHENEL, BEAKL, HYALINW, NERVEN and STAML. PC1 accounted for 65.9% of variance. Specimens appearing in Bayesian cp and nrDNA analyses are labelled (1=Beringian I in cpDNA, 2=W Cordilleran, 3=Scandinavian, 4=pan-Arctic, 5=Beringian II in nrDNA and N=*C. nardina* complex). NARD=*C. nardina* holotype, HEP=*C. hepburnii* holotype, ELYNA=*C. elynaeformis* holotype, ST=*C. stantonensis* holotype, H=*C. hepburnii* syntype, A=*C. nardina* var. *atriceps*, n = 120.

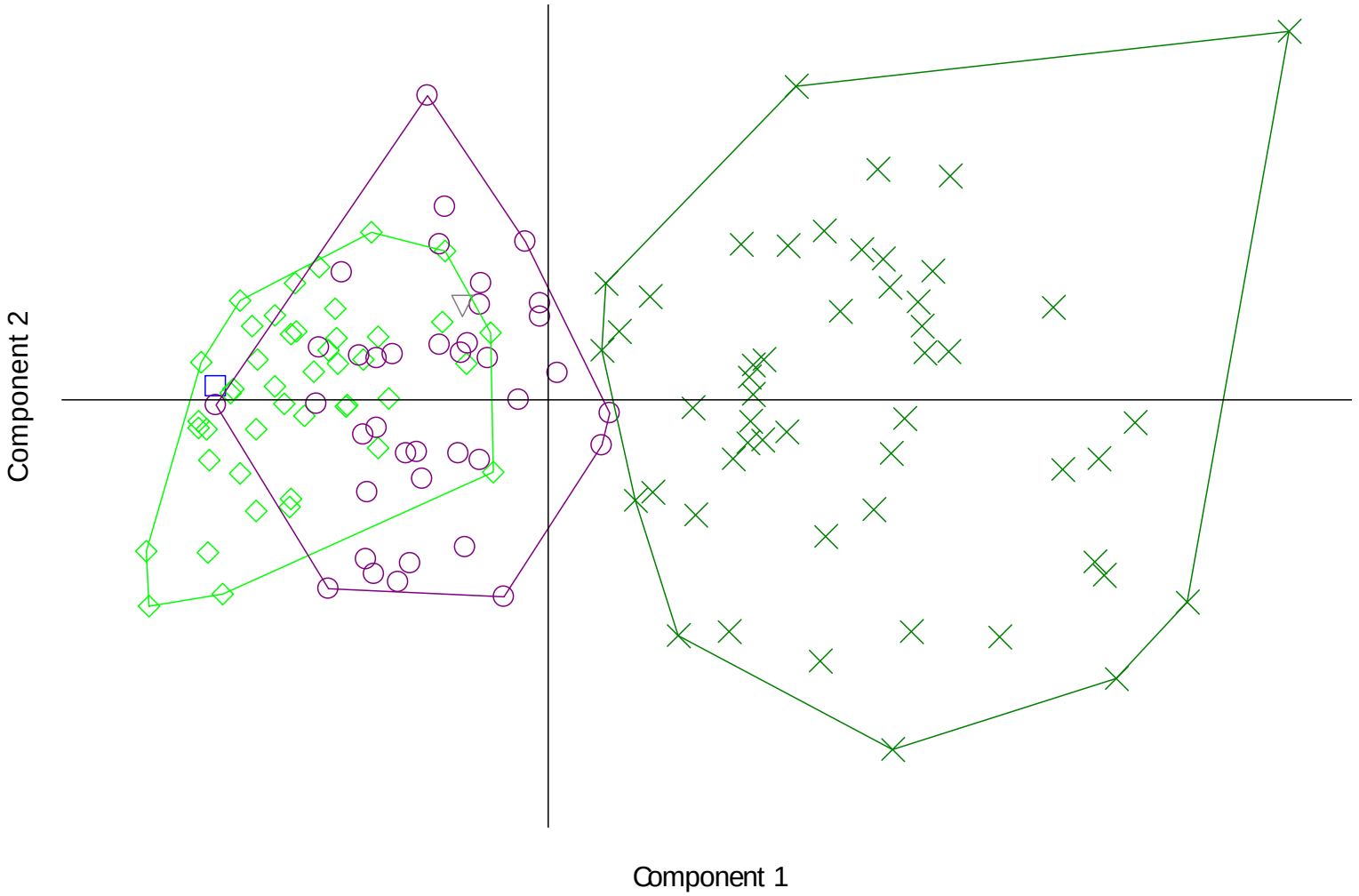


FIG. 25 PCA plot of *C. nardina* (diamonds), putative hybrid (circles) and *C. filifolia* var. *filifolia* (Xs) specimens. PC1 vs. PC2 for four uncorrelated, intermediate, significantly different characters using HYALINW, MIDRIBW, NERVEN, PERIGW and STAML. PC1 accounted for 57.1% of total variance, n = 135.

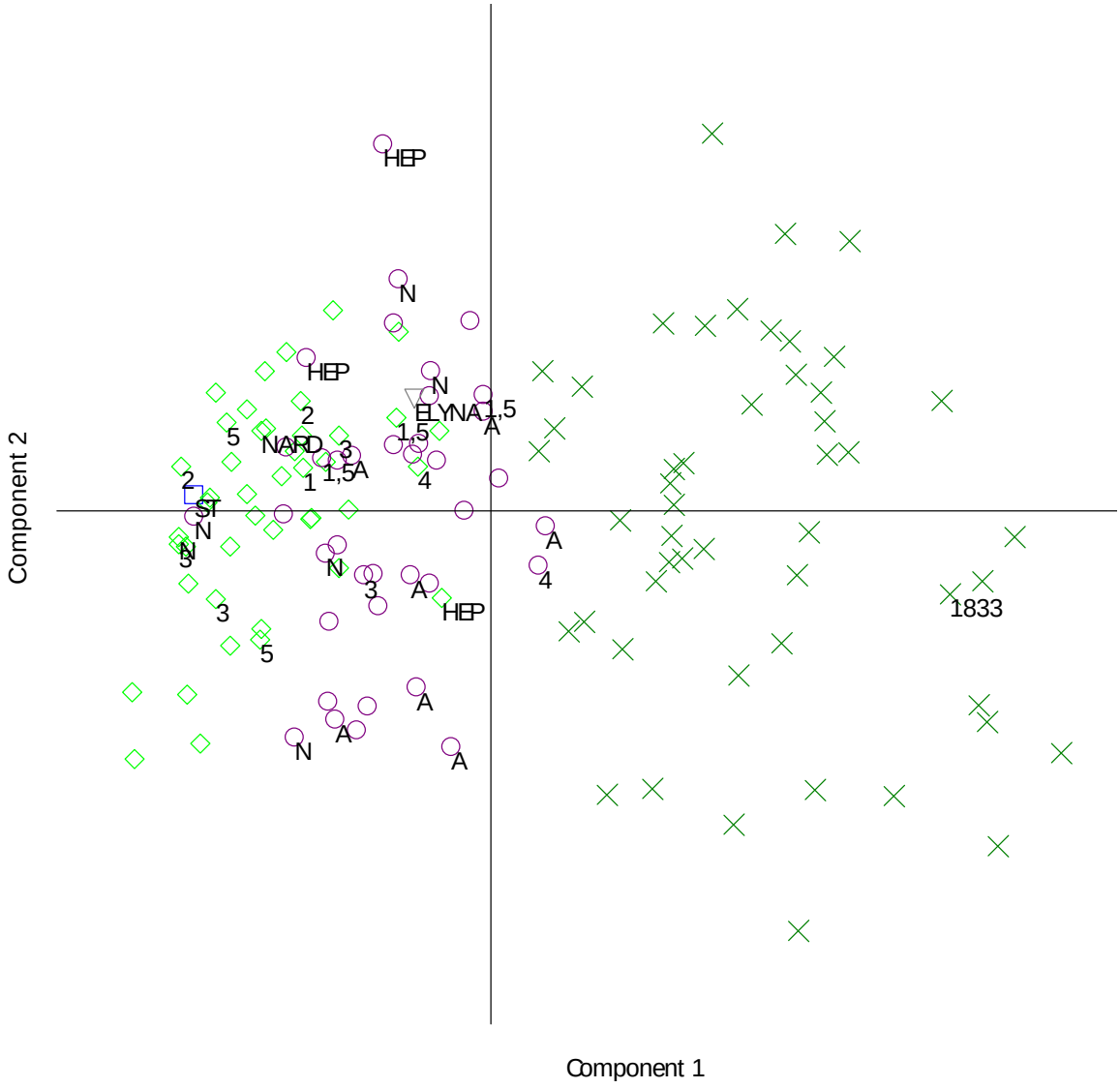


FIG. 26 PCA plot of *C. nardina* (diamonds), the putative hybrid (circles) and *C. filifolia* var. *filifolia* (Xs) specimens. PC1 vs. PC2 for four uncorrelated, significantly different characters HYALINW, MIDRIBW, NERVEN, PERIGW and STAML. PC1 accounted for 57.1% of total variance. Specimens appearing in Bayesian cp and nrDNA analyses are labelled (1=Beringian I in cpDNA, 2=W Cordilleran, 3=Scandinavian, 4=pan-Arctic, 5=Beringian II in nrDNA and N=*C. nardina* complex). NARD=*C. nardina* holotype, HEP=*C. hepburnii* holotype, ELYNA=*C. elynaeformis* holotype, ST=*C. stantonensis* holotype, H=*C. hepburnii* syntype, A=*C. nardina* var. *atriceps*, 1833: see Figs. 15 and 16), n = 135.

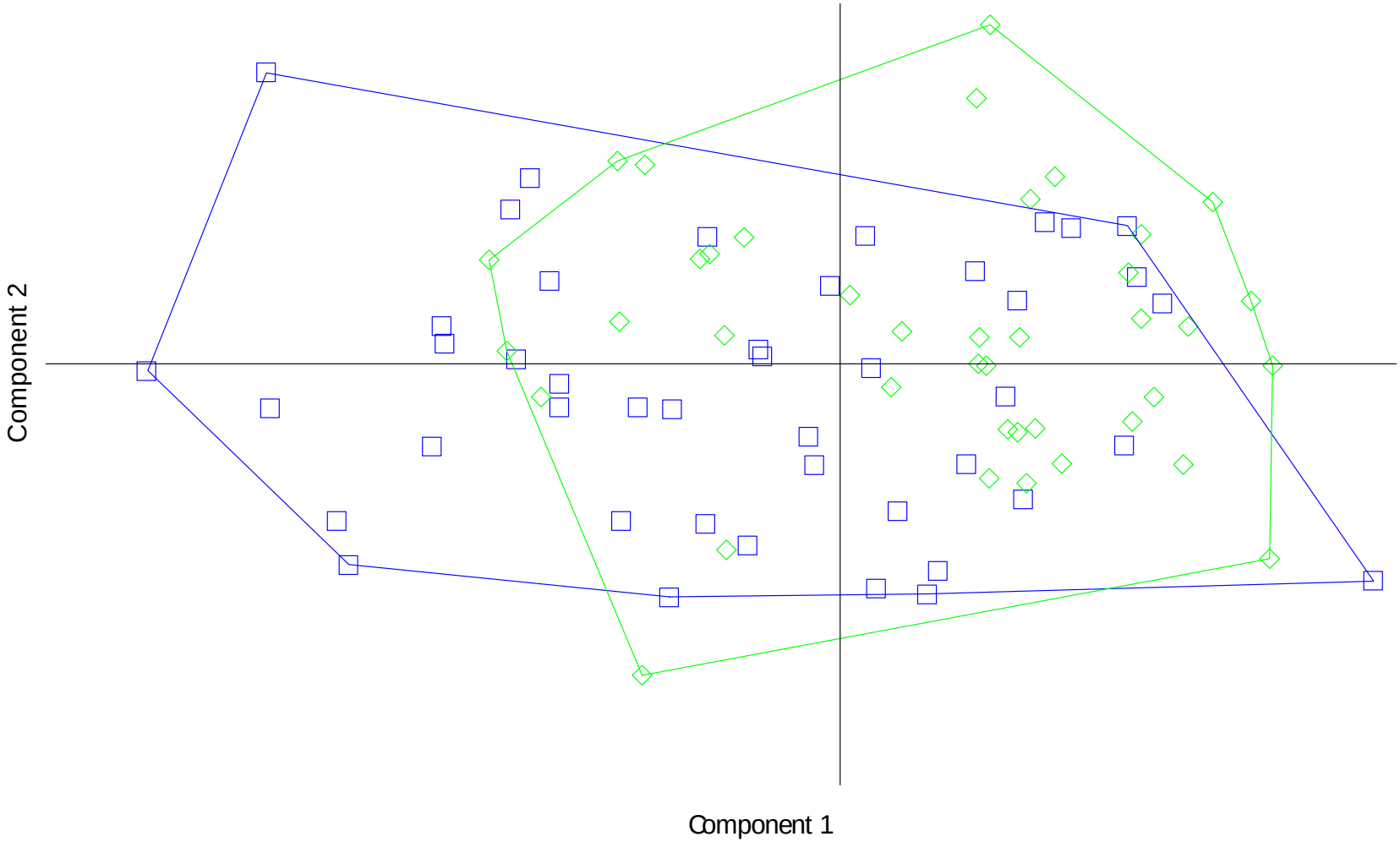


FIG. 27 PCA plot of *C. nardina* (diamonds) and *C. hepburnii* (squares) specimens according to Egorova (1999). PC1 vs. PC2 for six uncorrelated, significantly different characters (ACHENEL, PERIGW, SCALEL, SPIKEL and STAML). PC1 accounted for 48.6% of total variance, n = 84.

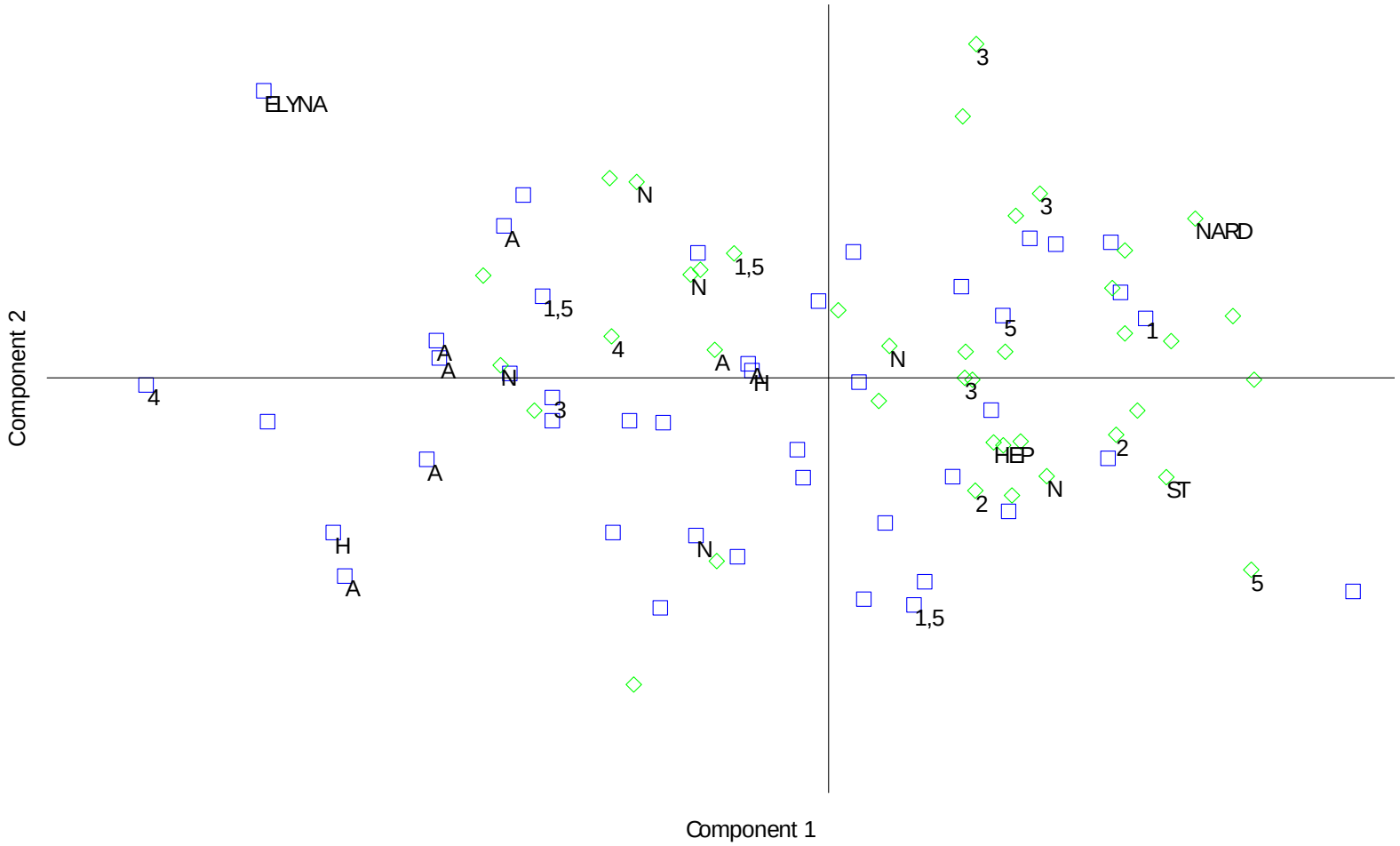


FIG. 28 PCA plot of *C. nardina* (diamonds) and *C. hepburnii* (squares) specimens according to Egorova (1999). PC1 vs. PC2 for five uncorrelated, significantly different characters (ACHENEL, PERIGW, SCALEL, SPIKEL and STAML). PC1 accounted for 48.6% of total variance. Specimens appearing in Bayesian cpDNA and nrDNA analyses labelled (1=Beringian I in cpDNA, 2=W Cordilleran, 3=Scandinavian, 4=pan-Arctic, 5=Beringian II in nrDNA, N=*C. nardina* complex). NARD=*C. nardina* holotype, HEP=*C. hepburnii* holotype, ELYNA=*C. elynaeformis* holotype, ST=*C. stantonensis* holotype, H=*C. hepburnii* syntype, A=*C. nardina* var. *atriceps*, n = 84.

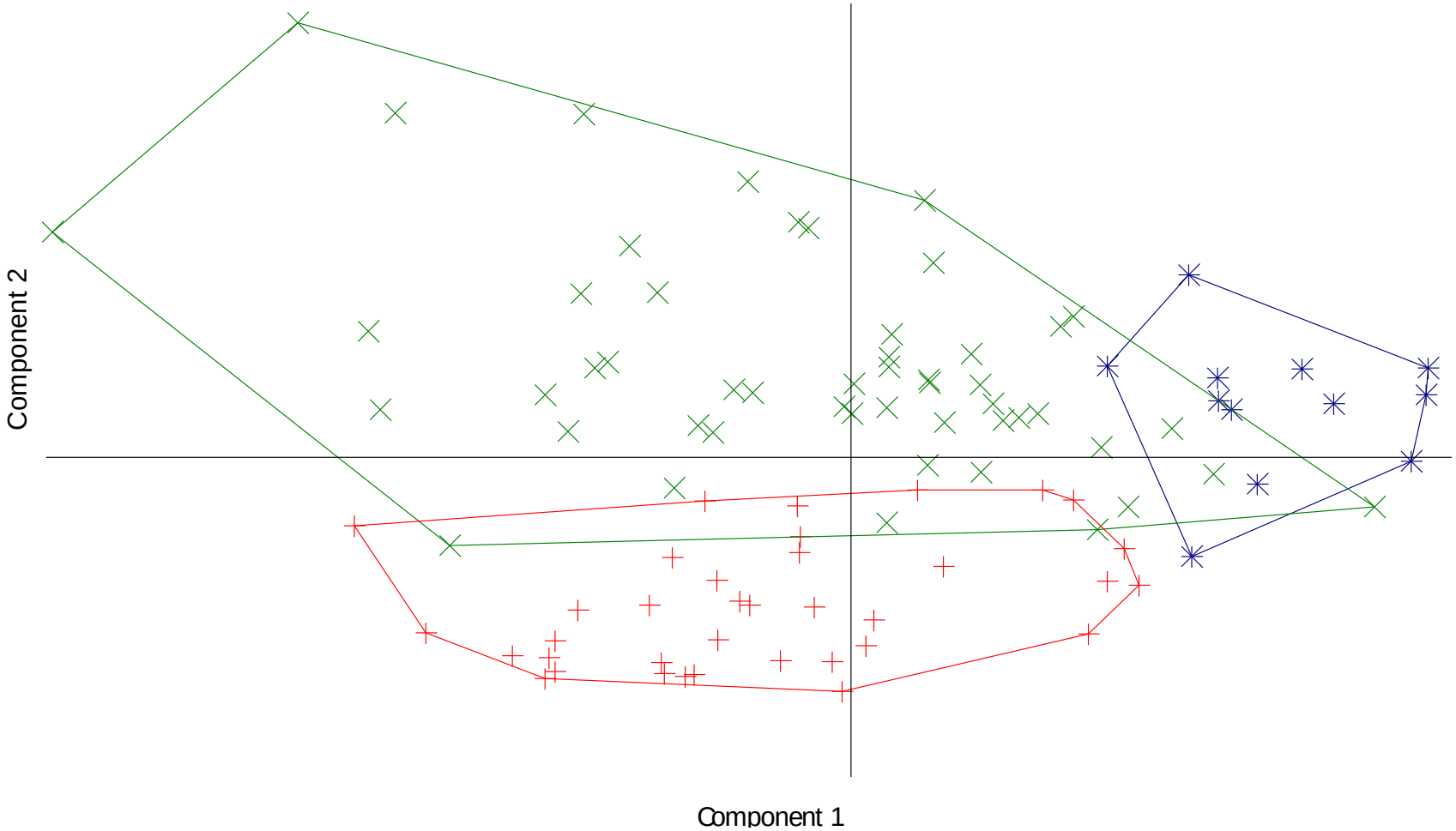


FIG. 29 PCA plot of *C. elynoides* (+), *C. filifolia* var. *erostrata* (*) and *C. filifolia* var. *filifolia* (X) specimens. PC1 vs. PC2 for 6 uncorrelated, significantly different characters (ACHENEL, BEAKL, SCALEL, SERRL, SHAPEPE, SPIKEL and STAML. PCs 1 and 2 accounted for 41.3% and 26.2% of total variance respectively, n = 99.

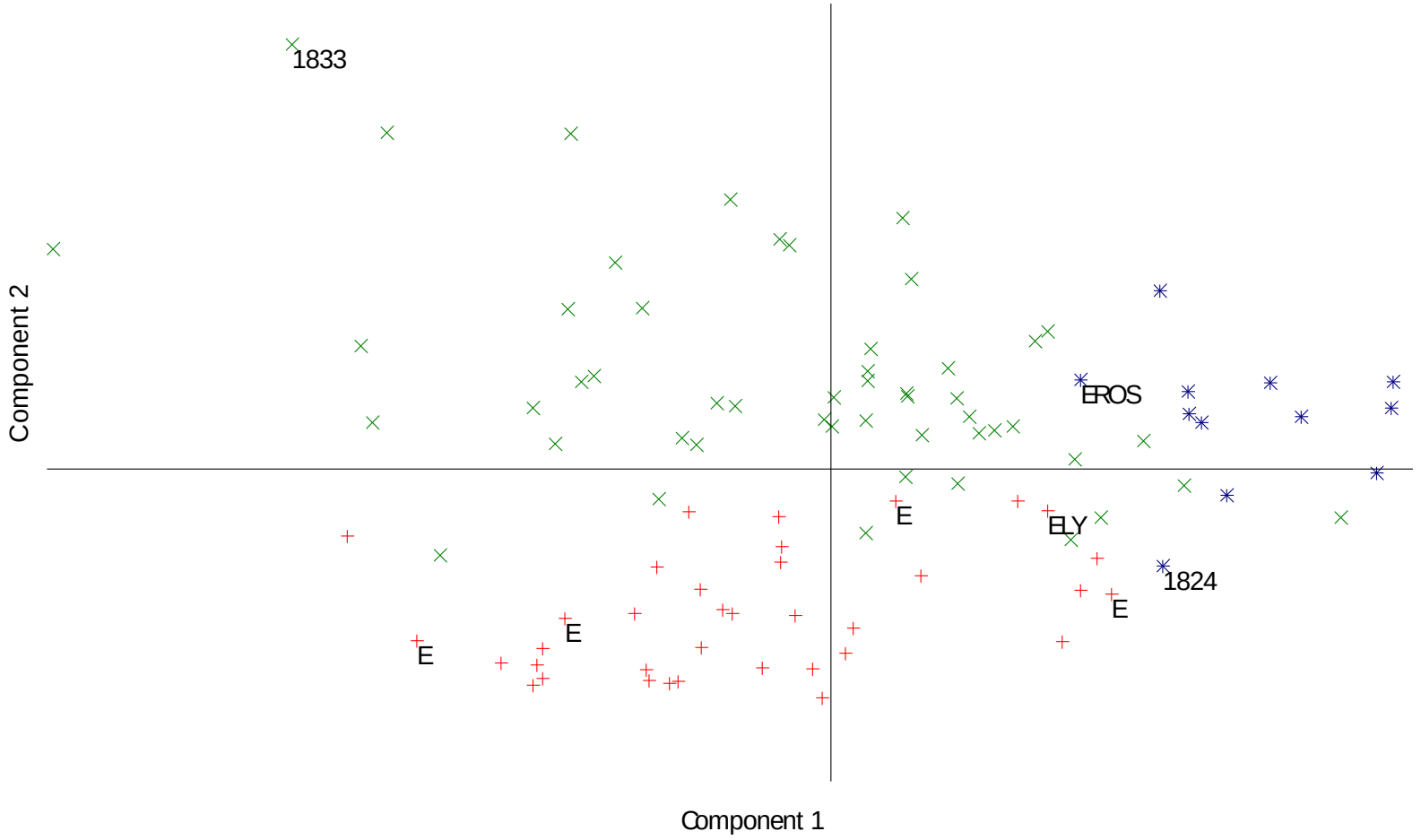


FIG. 30 PCA plot of *C. elynoides* (+), *C. filifolia* var. *erostrata* (*) and *C. filifolia* var. *filifolia* (X) specimens. PC1 vs. PC2 for 7 uncorrelated, significantly different characters (ACHENEL, BEAKL, SCALEL, SHAPEPE, SERRL, SPIKEL and STAML. PCs 1 and 2 accounted for 41.3% and 26.2% of total variance respectively. ELY=*C. elynoides* holotype, EROS=*C. filifolia* var. *erostrata* holotype, E=*C. elynaeformis*, n = 99.

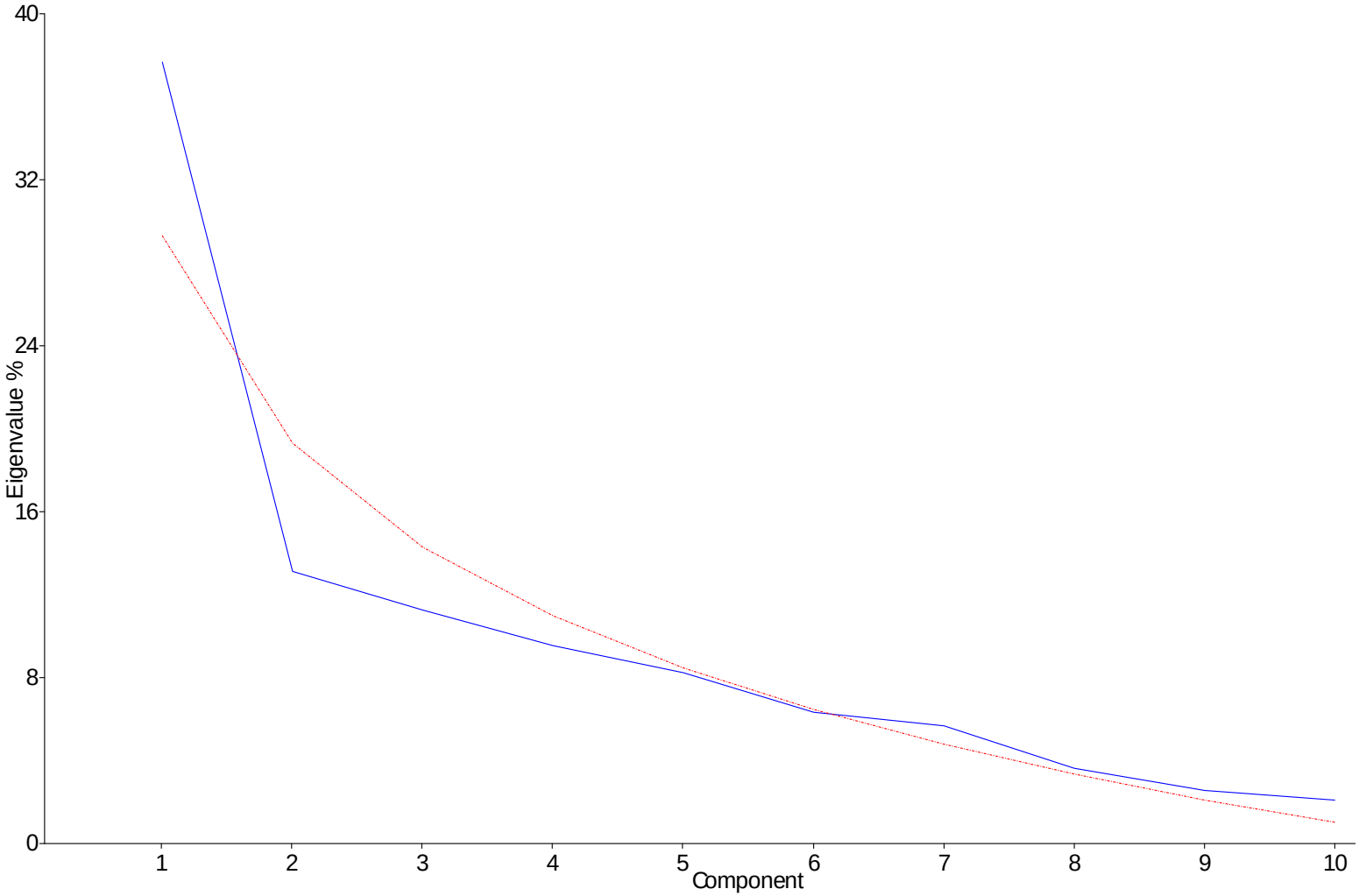


FIG. 31 Scree plot of eignenvalues against PCs (solid line) with broken stick model (dotted line) superimposed for PCA of *C. nardina* complex, *C. elynoides* and putative hybrid using uncorrelated characters ACHENEL, AWNL, BEAKL, BEAKTEETHN, CHESTHAIRN, HYALINW, MIDRIBW, NERVEN, SCALEL and STAML. Intersection of graphs indicates 1 significant PC, n = 120.

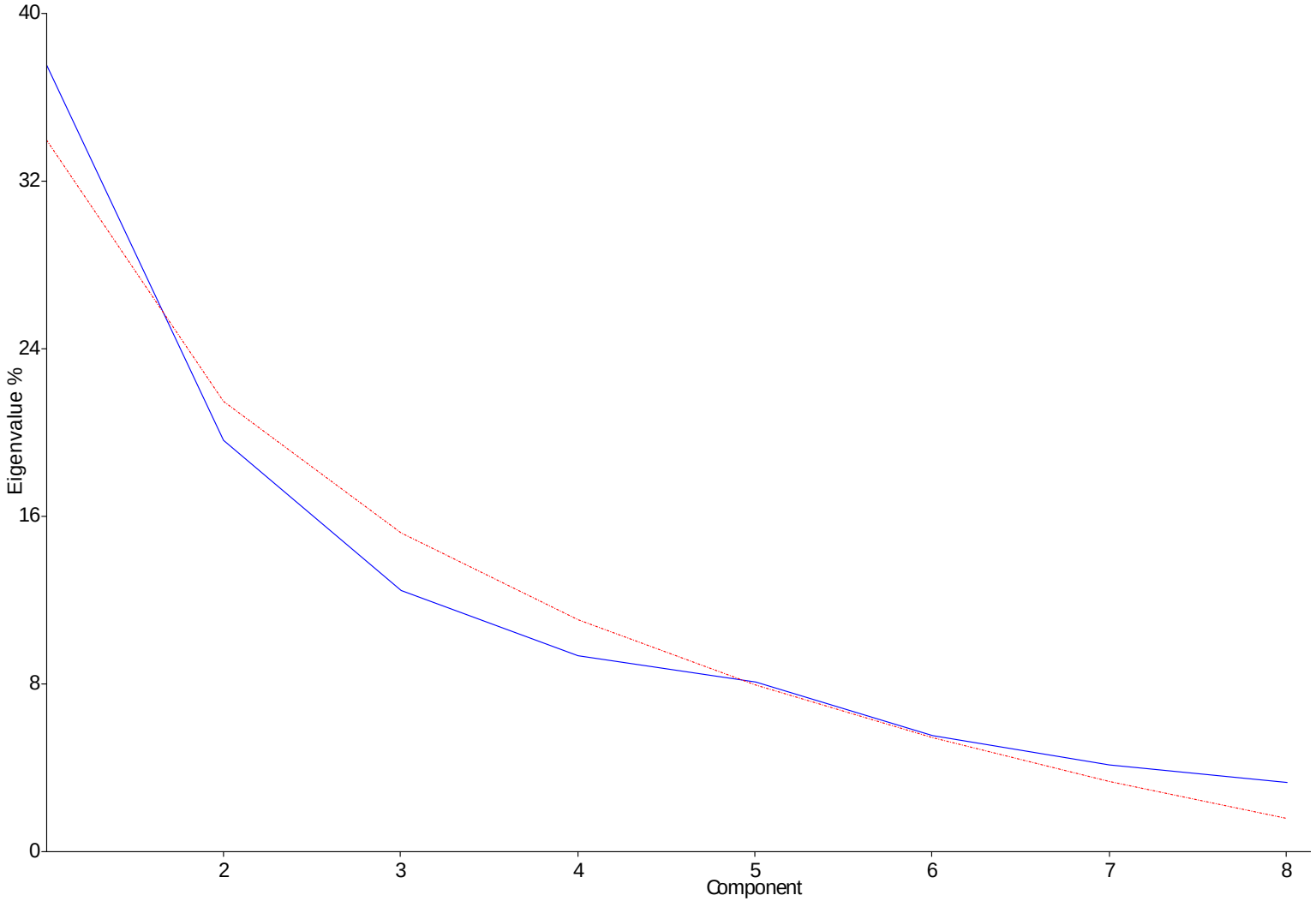


FIG. 32 Scree plot of eignenvalues against PCs (solid line) with broken stick model (dotted line) superimposed for PCA of *C. nardina* complex, *C. filifolia* var. *filifolia* putative hybrid using uncorrelated characters AWNL, BEAKL, HYALINW, MIDRIBW, NERVEN, PERIGW, SHOULDER and STAML. Intersection of graphs indicates 1 significant PC, n = 135.

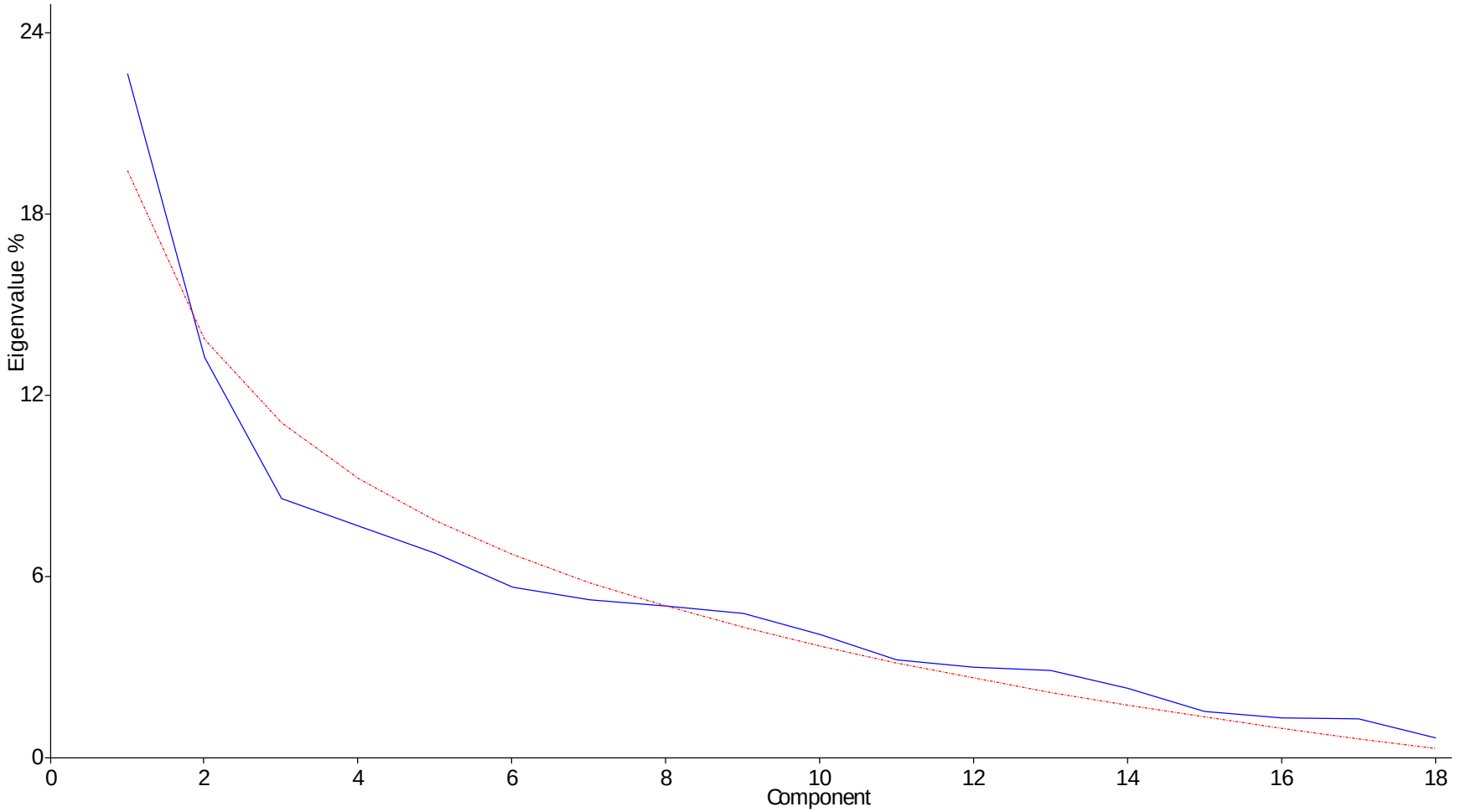


FIG. 33 Scree plot of eignenvalues against PCs (solid line) with broken stick model (dotted line) superimposed for PCA of *C. nardina* and *C. hepburnii* using uncorrelated characters ACHENEL, AWNL, BEAKL, BEAKTEETHN, CHESTHAIRN, HYALINW, MARGHAIRN, MIDRIBW, NERVEN, PERIGW, SCALEL, SERRL, SHAPEPE, SHOULDER, SPIKEL, STAML, STIPEL and STYLEXL. Egorova 1999 protologue used. Intersection of graphs indicates one significant PC, n = 84.

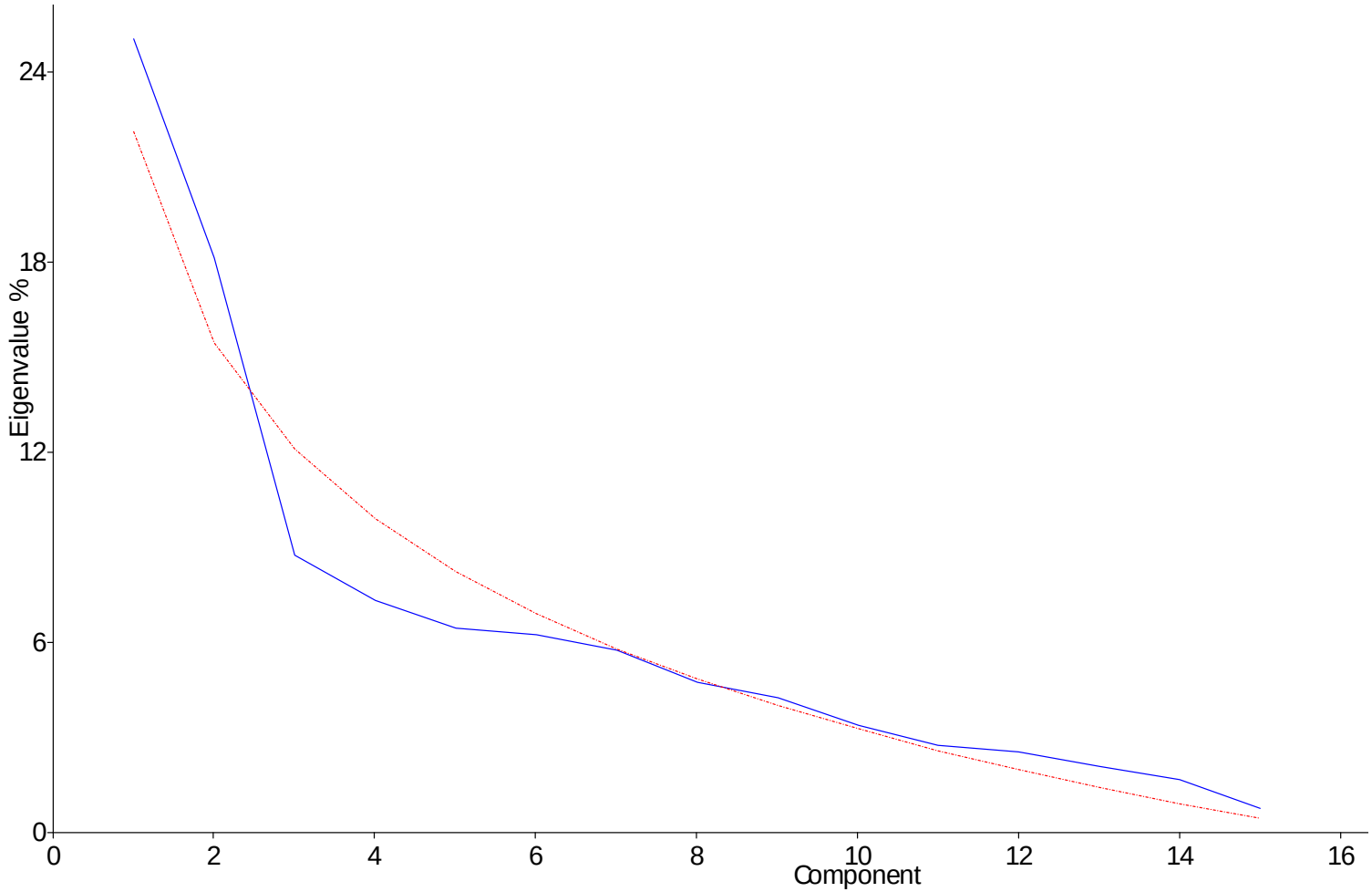


FIG. 34 Scree plot of eignenvalues against PCs (solid line) with broken stick model (dotted line) superimposed for PCA of *C. filifolia* var. *filifolia*, *C. elynoides* and *C. filifolia* var. *erostrata* using 15 uncorrelated characters ACHENEL, AWNL, BEAKL, HYALINW, MIDRIBW, NERVEN, PERIGW, SCALEL, SERRL, SHPAPE, SHOULDER, SPIKEL, STAML, STIPEL and STYLEXL. Intersection of graphs indicates 2 significant PCs, n = 99.

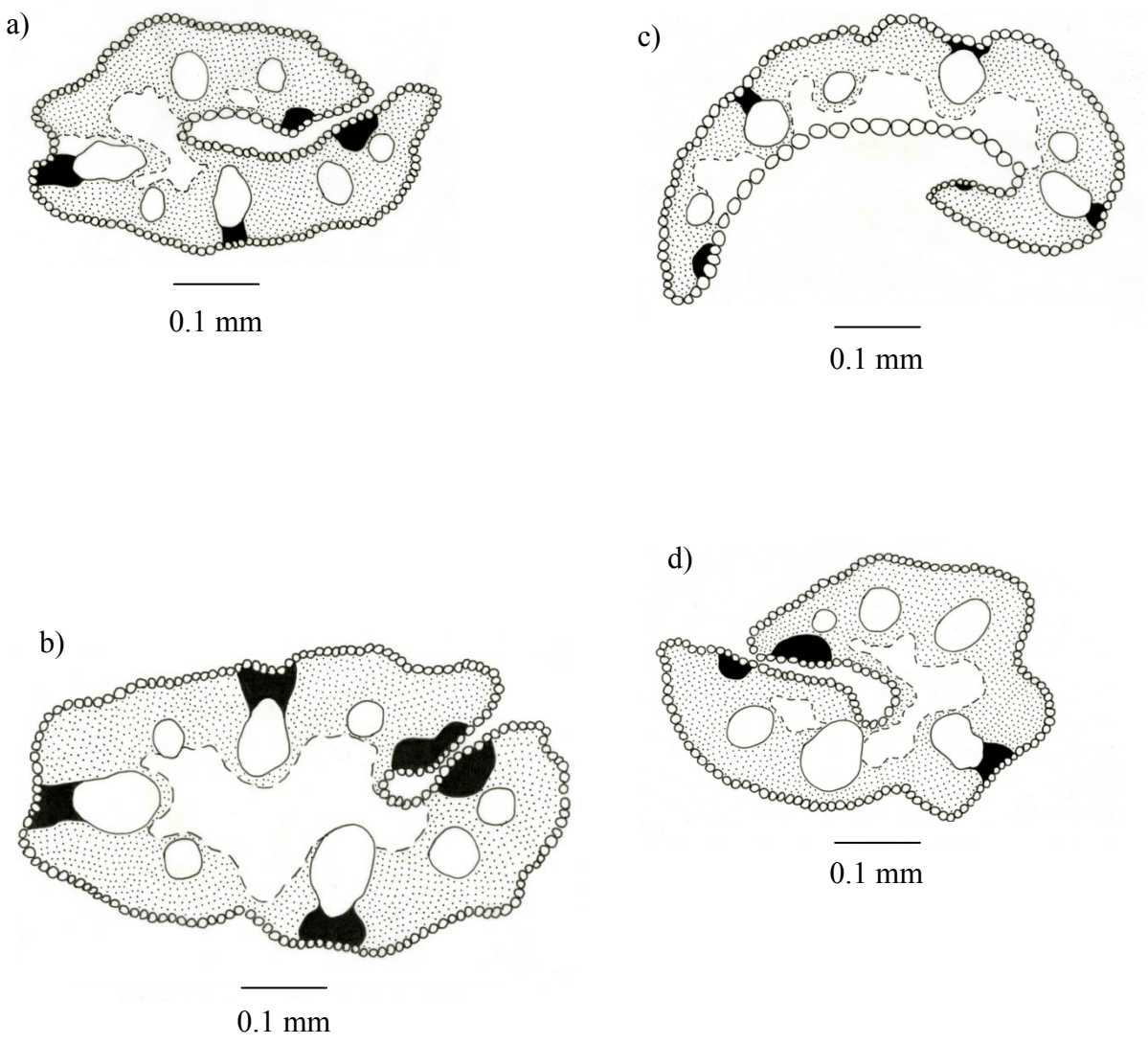
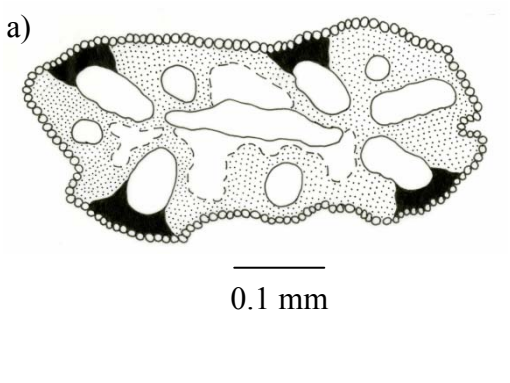
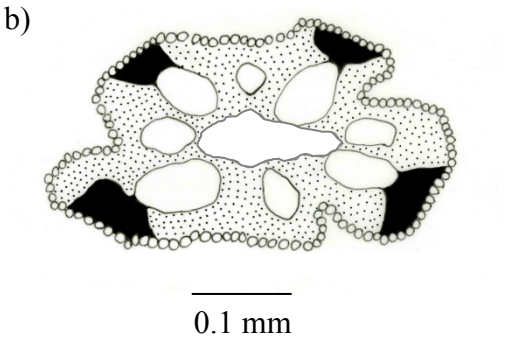
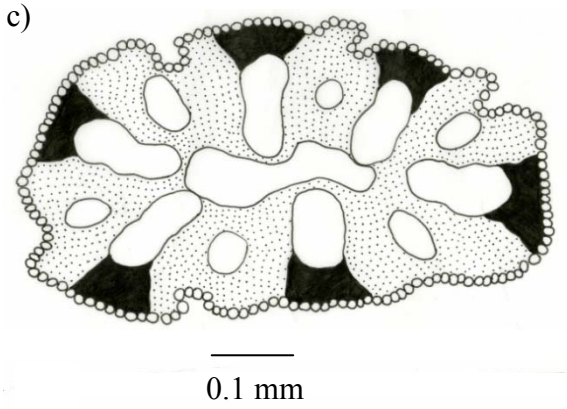


FIG. 35 Leaf sections of a) *C. nardina*, *McIsaac* 1231, CAN465805; b) *C. elynoides*, *Taye* 2552, CAN515863; c) the putative hybrid, *Kelso* 84277, ALA79127; and d) the putative hybrid, *Aiken* 86375, CAN518256. Solid dark areas are sclerenchyma, white areas bounded by solid lines are vascular bundles, stippled areas are chlorenchyma and white areas bounded by dashed lines are air spaces







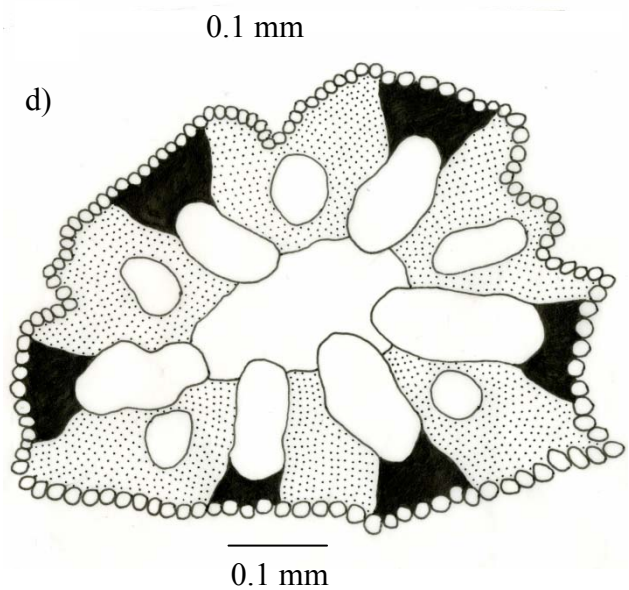


FIG. 36 Culm sections of a) *C. nardina*, *McIsaac* 1231, CAN465805; b) *C. nardina*, *Maguire* 591, UTC2309; c) the putative hybrid, *Aiken* 86375, CAN518256; and d) *C. filifolia* var. *filifolia*, *Nagy* 1179, CAN339443. Solid dark areas are sclerenchyma, white areas bounded by solid lines are vascular bundles, stippled areas are chlorenchyma and white areas bounded by dashed lines are air spaces.

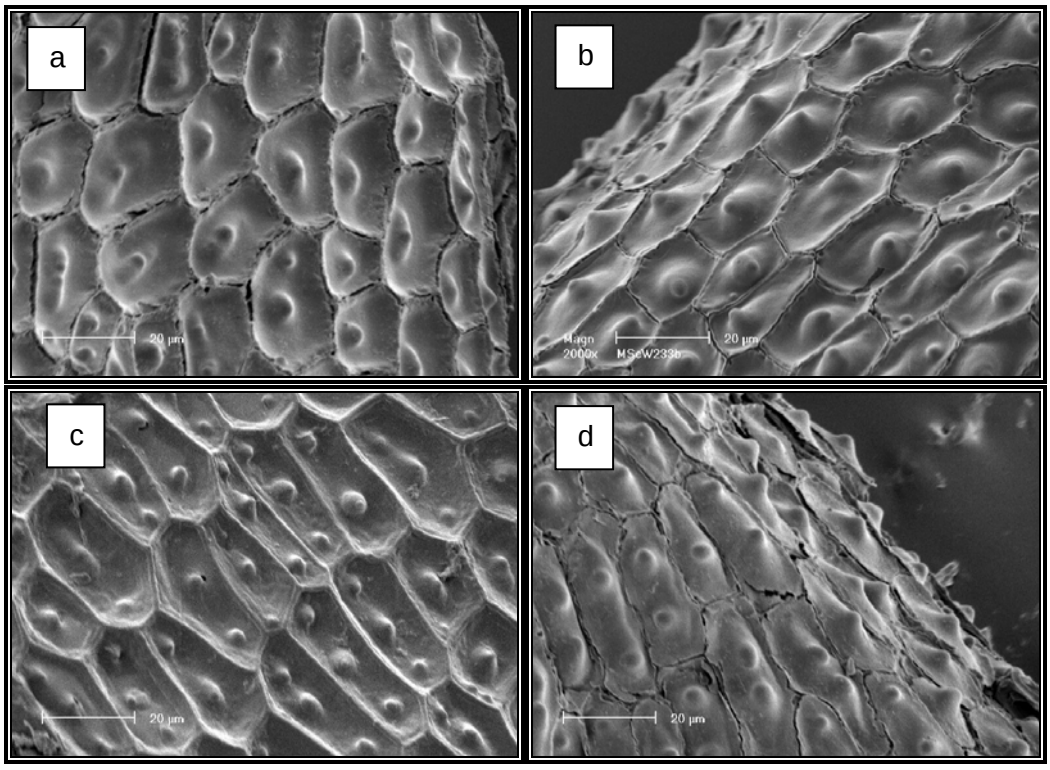


FIG. 37 Scanning electron micrographs of silica deposits in achene epidermal cells in the *C. nardina* complex specimens: a) *C. nardina*, *Tengwall*, CAN135231; b) *C. hepburnii*, *Viereck* 1480, ALA11539; c) *C. nardina*, *Berg* 39, ALA113036; and d) *C. nardina*, *Weber* 2438, CAN17320. Taxonomic classifications follow Egorova (1999). The variation displayed comprises all that is seen in the *C. nardina* complex.

DISCUSSION

Relationship between the *C. nardina* complex and section *Filifoliae*

The phylogenetic results confirm, with broader sampling, the close relationship between the *C. nardina* complex (section *Nardinae*) and members of section *Filifoliae* published in previous studies. The present phylogenetic analysis was the most complete to date because it included all members taxa of section *Filifoliae* (*C. filifolia* var. *filifolia*, *C. filifolia* var. *erostrata*, *C. elynoides*, *C. oreocharis*), except a few minor taxa limited to Mexico. Phylogenetic analysis of the cpDNA data showed that section *Nardinae* is monophyletic and therefore constitutes a natural group. PCA confirmed that it is morphologically distinct from *C. elynoides* and *C. filifolia*. The species of section *Filifoliae* unexpectedly appeared allied with section *Nardinae* in the cpDNA phylogeny (Fig. 9) and *C. filifolia* var. *filifolia* was polyphyletic. Further research will therefore be required to resolve the taxonomy of *C. filifolia*. Additionally, most specimens of the two sections appeared in a polytomy in the nrDNA tree (Fig. 8), affirming their close phylogenetic relationship. Therefore, these two sections as currently described may have to be combined into one section once future research has better specified the relationships between all the taxa involved. The combined section would be named *Nardinae* because although both it and *Filifoliae* were published in 1843 by Tuckerman, *Nardinae* appeared first, several months before *Filifoliae* (International Association for Plant Taxonomy 2007)

Questions remain concerning the evolutionary and biogeographic history of the species in these groups. Significant incongruence was found between the cpDNA and

nrDNA data sets. When the taxa responsible for the incongruence were removed from the analysis, a combined cpDNA/nrDNA MP analysis (Fig. 10) showed that section *Nardinae* is sister to *C. elynoides* and is nested deeply within section *Filifoliae*. Since the distribution of *Nardinae* is more expansive and northerly than that of all *Filifoliae* taxa, an ancient and southerly origin for the putative combined section is suggested.

Assessment of hybridization

The idea that hybridization between *C. nardina* and a member of the closely related section *Filifoliae* might account for the morphological variability that led to the segregation of *C. hepburnii*, *C. stantonensis* and several minor taxa was not supported by the results. The possibility that *C. hepburnii* represented a hybridization event was suggested by the incongruence between the cpDNA and nrDNA data sets. *Carex hepburnii* appeared allied with one putative parent (*C. nardina*) in the cpDNA tree, as one would predict if hybridization had occurred. However, although *C. hepburnii* appeared with the other putative parent (*C. elynoides*) in the nrDNA tree, neither *C. elynoides* nor any of the other taxa in the tree were resolved as separate species. All appeared in a large polytomy.

The possibility of hybridization with section *Filifoliae* was found to be limited to cases in which *C. nardina* and *C. elynoides* would be the putative parent species. Only this species pair overlapped geographically and was found to occur at overlapping elevations within their common range area, south of 42° N in the W Cordillera (fig. 12). By contrast, specimens of *C. filifolia* var. *filifolia* and the *C. nardina* complex co-occurred in only a very geographically restricted portion of southeastern Yukon. Within that zone the

elevations of the specimens of each species did not overlap (fig. 13). Therefore, for the present sampling, the probability of hybridization between *C. filifolia* var. *filifolia* and *C. nardina* is remote. Sampling of *C. filifolia* var. *filifolia* was not comprehensive for the present study since it did not bear directly on the original research problem of the *C. nardina* complex. However, unlike *C. elynoides*, *C. filifolia* var. *filifolia* has never been observed growing in mixed populations with the *C. nardina* complex. Therefore, the possibility of hybridization was investigated only for the *C. elynoides*-*C. nardina* pair.

Unlike the phylogenetic results, the results of all other types of analyses were inconsistent with the predictions of hybridization. In the PCA analysis of the morphometric data, the putative hybrid overlapped with *C. nardina*. In CA, there was overlapping membership between the *C. nardina* grouping and the putative hybrid grouping, and furthermore the CCC index was non-significant. These results suggest that the character used to segregate the putative hybrid group (straightness and length of leaves and culm) did not correspond to any other morphological differences between specimens.

Variability in specimen length can often be attributed to physical environmental differences, which are known to affect plant morphology (Joly and Bruneau 2007). Generally, the habitat of *C. nardina* is harsh, but some areas may have drier microclimates than others or may have a longer growing season than other areas because of less shading from surrounding mountains. No significant differences in soil pH were found between the putative parents, although sampling was very limited. Other physical environmental variables were not sufficiently documented on the herbarium labels of the specimens examined to enable comparisons. Overall, the observed variability in plant length can be more plausibly attributed to environmental conditions than to hybridization.

The test of pollen viability was inconclusive and can be used neither to support nor refute the possibility of hybridization. The fact that some of the putative parent specimens had predominantly unstainable pollen indicated that the staining procedure used was not an accurate test of viability. Unviable pollen grains are generally sticky and remain in the anther long after dehiscence (Ford *et al.* 1993) and may therefore be overrepresented in anthers of individuals that are collected too long after fruiting. However, *C. nardina* has not been observed to fruit before July (Murray 2002), and the unstainable specimens were collected between early July and early August. Therefore, it is unlikely that they were collected after the loss of presumably stainable pollen.

Examination of both the culm and leaf sections revealed no anatomical character that consistently differentiated *C. nardina* from either *C. elynoides* or *C. filifolia* and was intermediate in the putative hybrid. The only variation observed was in terms of fusion of the leaf laminae. Although it was intermediate in the putative hybrid, this character was not consistent in *C. nardina*.

The putative hybrid group provisionally segregated may have been the best candidate morphologically but not biogeographically. One would expect a much lower proportion of hybrids in distant regions to which putative hybrids would have dispersed than in the putative hybridization zone. However, the putative hybrid was found to be far less common in the most likely geographic areas of hybridization than in very distant regions, such as Greenland.

Therefore, considering all the types of evidence examined, the tentative explanation of the variability within the *C. nardina* complex as being the result of hybridization was either refuted or not supported by the above analyses that were performed. Similar

investigations of hybridization in other plant groups have led to similar conclusions. For example, in species of the genus *Quercus*, frequent variability in trivial characters has traditionally led researchers to believe erroneously that hybridization is more common than it is (Muller 1952). Hybridization between *Carex* species is confined to a small number of sections, none of which are androgynous, North American members of subgenus *Psyllophora* (Cayouette and Catling 1992). Therefore, previously unrecognized morphological variability is more likely than hybridization as the reason why additional taxa historically were segregated from *C. nardina*, creating a species complex.

Evaluation of *C. nardina* segregates

In the absence of evidence that *C. hepburnii* or any of the segregates within the *C. nardina* complex represented a hybrid, it was ascertained that no putative taxa within the complex should be segregated from *C. nardina*. All segregates were included in the present study, although *C. nardina* var. *atriceps* and *C. stantonensis* could not be included in the phylogenetic analysis due to a lack of success in DNA amplification. None of the types of evidence considered in the present study upheld the existence of more than one taxon in the *C. nardina* complex. Phylogenetically, all specimens of the complex grouped together in the same clade in the combined cpDNA/nrDNA analysis. There was one small, pan-Arctic clade within the *C. nardina* complex clade, but it contained both *C. nardina* and *C. hepburnii* specimens and did not correspond to any consistent morphological, anatomical, micromorphological, geographical or ecological differences with respect to the rest of the *C. nardina* complex. Similarly, in separate cpDNA and nrDNA analyses, *C. hepburnii* and

C. nardina specimens co-occurred in all putative clades regardless of which author's description was used to classify the specimens as either *C. hepburnii* or *C. nardina*. Although some putative ETS 1f clades were regionally based, all were small and none corresponded to any consistent differences in the other data types gathered with respect to the rest of the complex.

Other analyses produced results consistent with the phylogenetic results. Cluster analysis of *C. nardina* and *C. hepburnii* morphology showed overlapping membership between apparent groups of specimens and an insignificant CCC index. PCA revealed no apparent groupings of specimens of the complex. Only minor, inconsistent anatomical or micromorphological differences were observed among specimens and did not correspond to the taxonomic division between *C. nardina* and *C. hepburnii*. In comparison to Starr and Ford (2001), who found well differentiated and morphologically complex fruit epidermal silica body types indicating different species within *Carex* section *Phyllostachyae*, the silica body deposits of the present study showed no consistent differences.

Specimens were divided into either *C. nardina* or *C. hepburnii* using successively the description of each of the three authors, Boott (1840), Mackenzie (1935), Egorova (1999) who claimed to know the difference between the two putative taxa. Thus, the above analyses were each performed three times on the same set of specimens, and the same negative result was obtained in each case. This procedure discounted the possibility that previous authors had simply made errors in their circumscriptions of the two putative taxa. Therefore, the null hypothesis that the *C. nardina* complex represents a single species could not be rejected. This result was unexpected, given the widespread, arctic-alpine distribution of the complex and large number of segregates described over the course of

more than 170 years and contrasts with similar studies of Cariceae complexes (e.g. Naczi et al. 2002; Lehnebach 2011) that found multiple species.

Incongruence of cpDNA and nrDNA data

The fact that the *C. nardina* complex appeared allied in a polytomy with all specimens of section *Filifoliae* sequenced for the ETS 1f region was unexpected and remains unexplained. Not only was this result incongruent with the cpDNA results but also with the existence of diagnostic morphological characters that distinguish the *C. nardina* complex from these species. No evidence exists to support the possibility of hybridization as an explanation of the ETS 1f results. Other possible explanations (e.g. incomplete lineage sorting, ancient polymorphisms, paralogues) remain speculative.

If ancient introgression events had occurred between *C. nardina* and section *Filifoliae* then perhaps the process of coalescence was slow and never led to the formation of distinct hybrid species. Measuring this phenomenon would require the application of a coalescent model (Barraclough *et al.* 2009). In the present case there is no direct evidence for ancient introgression, but it would be consistent with the recurrence of ancestral characters, such as three stigmas, observed frequently in the *C. nardina* complex. Several authors (Moran and Kornfield 1993; Avise 2004; Doyle *et al.* 2004) warn that the same indications of introgressive hybridization that are involved in reticulate evolution (intermediate characters, sharing of diverse genetic polymorphisms) could also be evidence of incomplete lineage sorting and the retention of ancestral polymorphisms. The most effective way to discern the true cause is to sequence multiple nuclear loci (Moran and

Kornfield 1993), yet in the present study even this approach failed to uncover sufficient variability to resolve the issue.

Conclusion

The most parsimonious conclusion that fits the data is that the *C. nardina* complex consists of one highly variable species, namely *C. nardina*, which the present results suggest may in the future have to be made part of the same section as the species of section *Filifoliae*. The segregation of multiple taxa within the *C. nardina* complex is attributable to previously unrecognized morphological variability rather than to hybridization. This explanation is consistent with the early taxonomic history of the *C. nardina* complex. Soon after Boott (1840) named the first segregate, a third author (Drejer 1841) synonymized the two putative taxa. More importantly, Boott (1867) retracted the name *C. hepburnii* and published a description of *C. nardina* that was more detailed than the protologue of *C. nardina* and included more measurements that accounted for the higher morphological variability among specimens of the complex than either he or Fries (1839) had initially recognized. Later segregates by other authors thus represent a failure to take into account Boott's (1867) account of this variability. This failure can be attributed to regionally focused sampling and reliance on a single type of evidence. The present study reinforces the importance of conducting substantial sampling from the entire known distributions of the taxa under consideration, of sequencing regions within both the chloroplast and nuclear genomes and of examining multiple lines of evidence concurrently when attempting to resolve complicated, longstanding taxonomic problems.

Taxonomic treatment

Other relationships within the *C. nardina* complex

Porsild (1943) stated that *C. elynaeformis* closely resembled *C. nardina*. In fact, *C. elynaeformis* is most likely synonymous with *C. nardina* since the holotype of *C. elynaeformis* grouped with the *C. nardina* complex in PCA and was collected at low elevation within the range of *C. nardina* thousands of kilometres north of the range of *C. elynoides*. In 1944, Porsild redetermined the four other *C. elynaeformis* specimens used in the current study as *C. elynoides* (pers. obs. of herbarium sheets). Their redetermination as *C. elynoides* is most likely correct since they grouped with *C. elynoides* in PCA and were collected at high elevation in the southern W Cordillera (Colorado), and the only one of the four that was sequenced (extraction 1840) grouped with *C. elynoides* phylogenetically,.

PCA results strongly suggest that *C. nardina* var. *atriceps* is synonymous with *C. nardina.* Two specimens of *C. nardina* var. *atriceps* were within the *C. nardina* complex scatter and the other five were close to but separate from the *C. elynoides* scatter (Fig. 23). The *C. nardina* var. *atriceps* scatter was not a tight cluster on its own and, if integrated with the *C. nardina* complex, would form a coherent cluster separate from *C. elynoides*.

The lone specimen of *C. stantonensis* examined appeared near the centre of the PCA plot and on the edge of the scatterplot of putative hybrids (Fig. 23), indicating that it is morphologically intermediate between *C. nardina* and *C. elynoides* and is close to what has been known as *C. hepburnii*. This result explains why *C. stantonensis* was described as a new species despite the fact that the above PCA results strongly suggest synonymy with *C. nardina*. Examination of the type specimen found no differences with *C. nardina*.

Relationships within section *Filifoliae*

Carex filifolia var. *erostrata* was expected to group together phylogenetically and morphometrically with its convarietal taxon but in each analysis was clearly separate. Furthermore, it unexpectedly fell out with *C. elynoides* in the cpDNA and cpDNA/nrDNA trees. This finding is inconsistent with the PCA results showing *C. filifolia* var. *erostrata* segregated from *C. elynoides* (Figs. 29 and 30). The geographic distributions of these two taxa do not overlap, being separated by the Nevada Desert at the southern limit of the W Cordillera. Some taxonomic controversy has surrounded *C. filifolia* var. *erostrata*, since Mackenzie (1915) described it as a species and named it *C. exserta*. The small sample size makes it impossible to draw any firm taxonomic conclusions, but the present analysis suggests *C. filifolia* var. *erostrata* may warrant species status and should be studied further.

An additional conclusion of the present study is that the geographic range of *C. elynoides* Holm does not extend into Canada, contrary to Macoun's (1895) claim as reported by Porsild (1942). The only collection from Canada (*Macoun 10762*, CAN17302) was redetermined as *C. nardina* Fries. This means that the northern extent of the species is now 45°10' N latitude, almost 4° south of the previous extent, based on a collection by *Lesica 8160*, MONT125731) from the Absaroka Mountains in Park County.

Taxonomic conclusions

Specimens of *C. hepburnii*, *C. nardina* var. *atriceps*, *C. stantonensis*, and *C. elynaeformis* were shown to be indistinguishable molecularly, morphologically, anatomically and micromorphologically from *C. nardina*. The position of *C. nardina* var. *atriceps*, *C. stantonensis*, and *C. elynaeformis* in PCA (fig. 23) suggests that they were

erroneously segregated from *C. nardina* because of their resemblance to *C. elynoides*. These segregate taxa are symptomatic of the greater variability within *C. nardina* that early botanists failed to recognize. Therefore, the names *C. hepburnii*, *C. stantonensis*, *C. nardina* var. *atriceps*, *C. nardina* var. *hepburnii* and *C. nardina* ssp. *hepburnii* are considered here to be synonymous with *C. nardina*.

The occasional confusion among botanists between *C. nardina* and *C. elynoides* was found to be attributable almost entirely to misidentification of *C. nardina* specimens rather than of *C. elynoides* specimens. Of the 79 specimens of *C. elynoides* examined in the present study, 22 (roughly 28%) had been originally misidentified as a member of the *C. nardina* complex. Conversely, of the 609 specimens of *C. nardina* examined, only four (roughly 1%) had been originally misidentified as *C. elynoides*. Therefore, this confusion is attributable to the previously unrecognized large amount of morphological variability of *C. nardina*. Hence, until future researchers decide whether sections *Nardinae* and *Filifoliae* should be merged, the descriptions of *C. nardina* and its section, *Nardinae*, should be altered to account for this variation. The following descriptions are proposed:

Sectional description

CAREX L. sect. ***Nardinae*** (Tuckerman) Mackenzie in N.L. Britton *et al.*, North American Flora 18:21. 1935. - *Carex* (unranked) *Nardinae* (Tuckerman) Mackenzie, Enum. Meth. Caric., 8, 1844. – TYPE SPECIES: *C. nardina* Fries.

Plants caespitose to short-rhizomatous. **Culms** yellow-brown at base. **Leaves** with basal sheaths not or slightly fibrous, long-persistent; sheath fronts membranous; blades filiform, glabrous. **Inflorescence** a single spike; bracts absent; spike androgynous. **Staminate spike** oblong, 0.1 - 4.2 mm. **Pistillate scales** brown, ovate, 2.1 - 4.9 mm, shorter or longer than perigynium, midvein slightly raised, distal margins thinly or broadly hyaline, apex obtuse to subacute. **Perigynia** erect or ascending, green becoming light brown at maturity, obscurely or prominently 6-veined, obovate, oblong or elliptical, plano-convex or trigonous, 2. 1- 4.9 mm x 1.0 - 2.0 mm, distal margins serrulate or occasionally glabrous, perigynium surface glabrous or scarcely pubescent, apex gradually or abruptly beaked. **Beak** (when present) 0.1 - 0.7 mm, with abaxial suture, emarginate or entire, apex brown or hyaline, margins glabrous or serrulate. **Stigmas** 2(-3). **Achenes** biconvex or trigonous, 1.4 - 2.7 mm; **style** deciduous, exserted or unexserted.

Range Iceland, Svalbard, Norway, Sweden, Greenland, North America (north of 37°N), Russian far east (east of 178°W). In Scandinavia, excluding Iceland, occurrence is limited to north of 67 °N. Elevation: 1 – 1350 m in the North American Arctic Archipelago, Greenland and coastal areas of Alaska and the Arctic Ocean coast of Canada; 725 - 4 200 m in the Western Cordillera of North America from Colorado north to Alaska; 490 – 1 000 m in Iceland; 40 – 1 400 m in Scandinavia including Svalbard.

Identification key

Given the similarity of *C. nardina* to *C. elynoides*, the following revisions to sectional key A of the Flora of North America v.23 (FNA Committee 2002) are proposed

as an aid to collectors in the southwestern Cordillera of North America, where these species co-occur:

28. Perigynia with veins on faces, ± distinct at least over achene.

    29. Perigynia rounded at apex.

        30. Perigynia beakless …..… 26mmm. *Carex* section *Leptocephalae*, p. 565

        30. Perigynia with beak 0.4–1.0 mm …….....…….……..

            …….....…....… 26nnn. *Carex* section *Filifoliae*, p. 566

    29. Perigynia tapering to apex, beaked.

        31. Perigynia 3-4 mm, 1.5-2.5 times as long as wide; proximal pistillate scales obtuse to subacute …….....…….....……

            …….....……. 26ooo. *Carex* sect. *Nardinae* (in part), p. 568

        31. Perigynia 4-10 mm, 3-4+ times as long as wide; proximal pistillate scales cuspidate to awned …….....……

            …….....…..… 26yy *Carex* sect. *Circinatae* (in part), p. 528

28. Perigynia with 0 or 2 marginal veins, or very faint proximal veins.

    32. Perigynia 3-5 mm, proximal somewhat reflexed at maturity.

        33. Pistillate scales deciduous before perigynia …….....……..

            …….....….. 26zz. *Carex* sect. *Dornera*, p. 528

        33. Pistillate scales persistent ..... 26nnn. *Carex* sect. *Filifoliae*, p. 566

    32. Perigynia (4-)4.5-10 mm, ascending to spreading; pistillate scales.

Carex nardina species description

Carex nardina Fries, Novit. Fl. Suec. Mant. 2:55. 1839. - TYPE: Sweden, Lule Lappmark, Virihaure 08/1837, *Angstrom 2626*, V121286 (holotype: at U).

Carex hepburnii Boott, in Hooker, Flora Boreali Americana. Vol. 1: 209. 1840. - TYPE: USA, Rocky Mountains, *Drummond s.n.*, K0003094449 (holotype: at K).

Carex stantonensis Jones, Montana Bulletin 15(20):19-20. 1910. - TYPE: USA, Montana, Flathead Co., mountain above Stanton Lake, *Williams RS s.n.* (holotype: at NY).

Carex elynaeformis Porsild, Sargentia Vol. 4: 15-17. 1943. – TYPE: *Carex hepburnii*, Canada, Northwest Territories, Great Bear Lake, Olmsted Bay, N shore of Smith Arm, 16/07/1928, AE Porsild *5057*, CAN20702 (holotype: at CAN).

Carex nardina var. *atriceps* Kükenthal, Repert. Species Novae Regni Veg. 8(7): 7. 1910. - TYPE: Greenland, West Greenland, Godhavn. Rikli (holotype: at ZT).

Carex nardina var. *hepburnii* (Boott) Kükenthal, Cyperaceae - Caricoideae in Engler, Das Pflanzenreich, IV. 20 (Heft 38):70. 1909. - TYPES: USA, Washington, Cascade Mtns., *Elmer 1128*; Canada, AB, Kicking Horse Pass, *J Macoun 16496*, CAN17300; USA, Washington, Cascade Mtns., Mt. Paddo, *Suksdorf 4172*, WTU6500 (holotypes: *J Macoun 16496*, *Suksdorf 4172* at CAN).

Carex nardina subsp. *hepburnii* (Boott) A. Love, D. Love and B.M. Kapoor, Arctic and Alpine Research 3(2):144. 1971. - TYPE: USA, Colorado, Summit Co., Hoosier Pass summit, *Defler and Snyder 13451*.

Plants caespitose to short-rhizomatous. **Culms** yellow-brown at base 22 - 250 mm. **Leaves**: basal sheaths not or slightly fibrous, long-persistent 37 – 250 mm; sheath fronts membranous; blades filiform, glabrous. **Inflorescence** a single androgynous spike; bracts absent. **Staminate scales** red-brown, oblong-ovate, apex obtuse. **Pistillate scales** brown, ovate, 2.1 - 4.9 mm, shorter or longer than perigynium, midvein slightly raised, distal margins thinly or broadly hyaline, apex obtuse to subacute. **Perigynia** erect or ascending, green becoming light brown at maturity, obscurely or prominently veined, substipitate to stipitate, obovate or oblong, plano-convex or trigonous, 2.1-4.9 mm x 1.0-2.0 mm, base ± tapering, distal margins serrulate or occasionally glabrous, margins acutely angled, apex gradually or abruptly beaked, glabrous or scarcely pubescent; **Beak** (when present) 0.1-0.7 mm, with abaxial suture, emarginate, tip brown or hyaline. **Stigmas** 2(-3). **Achenes** biconvex or trigonous, 1.4-2.7 mm; **Style** deciduous, exserted or unexserted. 2n = 68. Follows the same range and has the same elevation as the section.

Habitat description

Carex nardina occurs in dry, exposed, windswept, sparsely vegetated areas. In the W Cordillera of North America south of Canada, the most common substrate on which it grows is gravel or thin, basic, sandy silt in the crevices between rocks on slopes. In the Arctic (the Canadian Arctic Archipelago, the Arctic coast of Canada and Alaska, Greenland, Iceland and northernmost Scandinavia) it occurs on sand beaches, but is most common on rocky, gravelly areas with a calcareous substrate. *Carex nardina* generally has

very few vascular plant associates, and with increasing elevation, other members of family Cyperaceae are less likely to be found in association with this species.

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APPENDIX 1 Classification and voucher information for all field collections and herbarium loans examined. Herbarium abbreviations follow *Index Herbariorum* (Holmgren *et al*. 1981); collector identifications redetermined as *C. nardina*: * denotes *hepburnii*, ** *atriceps*, *** *stantonensis* and **** *elynaeformis*. "Indeterminate" specimens were too incomplete to identify reliably.

Carex L. subgenus *Psyllophora* (Peterm.) Degl. section *Nardinae* (Tuckerm.) Mackenzie						
Species	Collector	Number	Country, province/state, county/quadrant/island	Institute	Catalogue Number	Extraction Number
nardina Fries	*Huber*	2334	USA, Utah, Duchesne Co.	UTC	216175	
nardina Fries*	*Murray*	10309	Canada, NU, Ellesmere I.	CAN	582854	1548
nardina Fries*	*Sekretareva*	s.n.	USSR, Chukotka	COLO	323051	1534
nardina Fries*	*Cronquist*	7941	USA, MT, Missoula Co.	WTU	162409	
nardina Fries*	*Caswell*	259	Canada, YT, Mt. St. Elias Quad	ALA	132838	1532
nardina Fries*	*Vaage*	s.n.	Greenland, Greenland, Tunu	CAN	17247	
nardina Fries*	*AE Porsild*	399	USA, AK	CAN	17331	
nardina Fries*	*JM Macoun*	98081	Canada, AB	CAN	17321	
nardina Fries*	*Scoggan*	16446	Canada, AB	CAN	307869	1538
nardina Fries*	*Harvey*	7125	USA, MT, Glacier Co.	DAO	242737	
nardina Fries*	*Pemble*	302	USA, MT, Ravalli Co.	DAO	242636	
nardina Fries*	*Sekretareva*	s.n.	USSR, Chukotka	DAO	273381	
nardina Fries*	*Gorbunova*	s.n.	USSR, Chukotka	DAO	139862	1535
nardina Fries*	*Kozhevnikov*	s.n.	USSR, Chukotka	DAO	139877	
nardina Fries*	*Sekretareva*	s.n.	USSR, Chukotka	DAO	139878	1533
nardina Fries*	*Hitchcock*	7730	Canada, AB	DAO	257325	
nardina Fries*	*Bailey*	4936	USA, WY, Teton Co.	RM	252820	
nardina Fries*	*Gorbunova*	s.n.	USSR, Chukotka	CAN	386517	
nardina Fries*	*Maksimenko*	s.n.	USSR, Chukotka	CAN	386513	
nardina Fries*	*Sekretareva*	s.n.	USSR, Chukotka	CAN	386520	
nardina Fries*	*Sekretareva*	s.n.	USSR, Chukotka	CAN	386493	
nardina Fries*	*Kozhevnikov*	s.n.	USSR, Chukotka	CAN	408342	

Species	Collector	Number	Country, province/state, county/quadrant/island	Institute	Catalogue Number	Extraction Number
nardina Fries*	*Tengwall*	s.n.	Sweden, Lule Lappmark	U	325409	
nardina Fries*	*Hitchcock*	10956	USA, ID, Custer Co.	UTC	68482	
nardina Fries*	*ME Lewis*	274	USA, UT, Summitt Co.	UTC	89573	
nardina Fries*	*ME Lewis*	349	USA, UT, Grand Co.	UTC	90234	
nardina Fries*	*ME Lewis*	475	USA, UT, Beaver Co.	UTC	92856	
nardina Fries*	*Anderson*	532	USA, WY, Teton Co.	UTC	92152	
nardina Fries	*Simmons*	300	Canada, NU, Ellesmere I.	CAN	17276	
nardina Fries	*McIsaac*	1231	Canada, AB	CAN	465805	
nardina Fries*	*J Macoun*	31495	Canada, BC	CAN	17310	
nardina Fries*	*J Macoun*	31496	Canada, BC	CAN	17309	
nardina Fries	*Argus*	8923	Canada, BC, Peace R. Dist.	CAN	372357	
nardina Fries*	*HM Raup*	3916	Canada, BC	CAN	17326	
nardina Fries	*Argus*	10270	Canada, BC, Peace R. Dist.	CAN	411006	
nardina Fries	*Argus*	10304	Canada, BC, Peace R. Dist.	CAN	411040	
nardina Fries	*Gillett*	17789	Canada, BC	CAN	412156	
nardina Fries	*AE Porsild*	5563	Canada, NU	CAN	17292	
nardina Fries	*Talbot*	614515	Canada, NT, MacKenzie Dist.	CAN	479642	
nardina Fries	*Talbot*	601524	Canada, NT, MacKenzie Dist.	CAN	479646	
nardina Fries	*Talbot*	62528	Canada, NT, MacKenzie Dist.	CAN	479644	
nardina Fries	*Talbot*	600115	Canada, NT, MacKenzie Dist.	CAN	479645	
nardina Fries	*HM Raup*	9605	Canada, NT	CAN	268407	1570
nardina Fries	*HM Raup*	9604	Canada, NT	CAN	268408	1516
nardina Fries	*HM Raup*	9394	Canada, NT	CAN	268409	1515
nardina Fries	*AE Porsild*	5760	Canada, NU	CAN	17293	1522
nardina Fries	*AE Porsild*	5635	Canada, NU	CAN	17291	
nardina Fries	*Brunton*	10470	Canada, NU	CAN	565232	
nardina Fries	*AE Porsild*	5880	Canada, NU, Coats I.	CAN	17290	

Species	Collector	Number	Country, province/state, county/quadrant/island	Institute	Catalogue Number	Extraction Number
nardina Fries	*Gillett*	16717	Canada, NU, Coats I.	CAN	393647	
nardina Fries	*Gillett*	16833	Canada, NU, Coats I.	CAN	409238	
nardina Fries	*Malte*	s.n.	Canada, NU, Baffin I.	CAN	17267	
nardina Fries	*Malte*	s.n.	Canada, NU, Baffin I.	CAN	17273	
nardina Fries	*Malte*	s.n.	Canada, NU, Baffin I.	CAN	17274	
nardina Fries**	*Welch*	65	Canada, NU, Baffin I.	CAN	274112	
nardina Fries	*Aiken*	4055	Canada, NU, Baffin I.	CAN	586524	
nardina Fries	*Wynne-Edwards*	7380	Canada, NU, Baffin I.	CAN	17254	
nardina Fries	*Malte*	s.n.	Canada, NU	CAN	17286	1523
nardina Fries	*Malte*	s.n.	Canada, NU	CAN	17288	
nardina Fries	*Brown*	903	Canada, NU	CAN	258618	
nardina Fries	*JM Macoun*	16497	Canada, NU, Nottingham I.	CAN	17283	
nardina Fries	*Bell*	16498	Canada, NU	CAN	17284	
nardina Fries**	*Wynne-Edwards*	9228	Canada, NU, Baffin I.	CAN	205070	
nardina Fries**	*AE Porsild*	21515	Canada, NU, Baffin I.	CAN	259398	
nardina Fries	*Gillett*	19048	Canada, NU, Baffin I.	CAN	466229	
nardina Fries	*Gillett*	19108	Canada, NU, Baffin I.	CAN	466285	
nardina Fries	*Gillett*	19132	Canada, NU, Baffin I.	CAN	466308	
nardina Fries	*Aiken*	86313	Canada, NU, Baffin I.	CAN	518180	
nardina Fries**	*Aiken*	86375	Canada, NU, Baffin I.	CAN	518256	
nardina Fries	*Aiken*	86487	Canada, NU, Baffin I.	CAN	518373	
nardina Fries	*Brunton*	9922	Canada, NU, Baffin I.	CAN	549915	
nardina Fries	*Brunton*	9931	Canada, NU, Baffin I.	CAN	549918	
nardina Fries	*Brunton*	9818	Canada, NU, Baffin I.	CAN	549996	
nardina Fries	*Aiken*	97003	Canada, NU, Baffin I.	CAN	579660	
nardina Fries	*Aiken*	97040	Canada, NU, Baffin I.	CAN	579661	
nardina Fries	*Aiken*	97041	Canada, NU, Baffin I.	CAN	579662	

Species	Collector	Number	Country, province/state, county/quadrant/island	Institute	Catalogue Number	Extraction Number
nardina Fries**	*McLaren*	118	Canada, NU, Baffin I.	CAN	283976	
nardina Fries*	*AE Porsild*	11829	Canada, NT	CAN	17329	
nardina Fries*	*AE Porsild*	11789	Canada, NT	CAN	17330	
nardina Fries	*AE Porsild*	6112	Canada, NU	CAN	17289	
nardina Fries	*Brown*	486	Canada, NU	CAN	258619	
nardina Fries**	*AE Porsild*	21708	Canada, NU	CAN	259397	
nardina Fries	*Malte*	s.n.	Canada, NU	CAN	17258	
nardina Fries*	*Malte*	s.n.	Canada, NU	CAN	17260	
nardina Fries	*Malte*	s.n.	Canada, NU	CAN	17261	
nardina Fries	*Dutilly*	980	Canada, NU, Baffin I.	CAN	200474	1509
nardina Fries	*Brown*	1701	Canada, NU	CAN	262102	
nardina Fries**	*NG Smith*	147	Canada, NU	CAN	282082	
nardina Fries	*Aiken*	86210	Canada, NU, Baffin I.	CAN	518060	
nardina Fries*	*Shacklette*	2912	Canada, NT	CAN	199979	1524
nardina Fries**	*Lindsey*	486	Canada, NT	CAN	216065	
nardina Fries	*Welsh*	12041	Canada, NT	CAN	383325	
nardina Fries	*MC Lewis*	s.n.	Canada, NU	CAN	437718	
nardina Fries**	*Baldwin*	1971	Canada, NU	CAN	203377	1521
nardina Fries**	*Baldwin*	1966	Canada, NU	CAN	582963	1508
nardina Fries**	*NG Smith*	7061	Canada, NU, Baffin I.	CAN	282083	
nardina Fries	*MC Lewis*	s.n.	Canada, NU, Igloolik	CAN	437719	
nardina Fries**	*Wynne-Edwards*	8801	Canada, NU, Baffin I.	CAN	204804	
nardina Fries**	*Wynne-Edwards*	8953	Canada, NU, Baffin I.	CAN	204806	
nardina Fries**	*Hainault*	3719	Canada, NU, Baffin I.	CAN	301907	
nardina Fries**	*Hainault*	4056	Canada, NU, Baffin I.	CAN	301908	
nardina Fries	*Webber*	451	Canada, NU, Baffin I.	CAN	295782	
nardina Fries	*Malte*	s.n.	Canada, NU, Baffin I.	CAN	17272	

Species	Collector	Number	Country, province/state, county/quadrant/island	Institute	Catalogue Number	Extraction Number
nardina Fries	*Gillett*	18813	Canada, NT, Banks I.	CAN	464408	
nardina Fries	*Polunin*	858	Canada, NU, Ellesmere I.	CAN	17257	
nardina Fries**	*Polunin*	2581	Canada, NU, Baffin I.	CAN	17255	1520
nardina Fries	*Malte*	s.n.	Canada, NU, Devon I.	CAN	17266	1575
nardina Fries	*Malte*	s.n.	Canada, NU, Devon I.	CAN	17269	
nardina Fries	*Malte*	s.n.	Canada, NU, Devon I.	CAN	17270	
nardina Fries	*Malte*	s.n.	Canada, NU	CAN	17263	
nardina Fries	*Edlund*	57	Canada, NU, Melville I.	CAN	496768	1549
nardina Fries	*Blachut*	18	Canada, NU, Ellesmere I.	CAN	472876	
nardina Fries	*Gillett*	18294	Canada, NU, Ellesmere I.	CAN	453988	
nardina Fries	*Gillett*	18157	Canada, NU, Ellesmere I.	CAN	453885	
nardina Fries	*Gillett*	18171	Canada, NU, Ellesmere I.	CAN	453897	
nardina Fries**	*Beschel*	11382	Canada, NU, Axel Heiberg I.	CAN	267544	
nardina Fries	*Kuc*	423	Canada, NU, Axel Heiberg I.	CAN	330600	
nardina Fries**	*AE Porsild*	18645	Canada, NU, Axel Heiberg I.	CAN	223323	
nardina Fries	*Edlund*	178	Canada, NU, Ellesmere I.	CAN	532458	
nardina Fries	*Edlund*	20	Canada, NU, Ellesmere I.	CAN	533005	
nardina Fries**	*Cooper*	247	Canada, NU, Melville I.	CAN	235148	
nardina Fries	*Malte*	s.n.	Canada, NU, Ellesmere I.	CAN	17264	
nardina Fries	*Malte*	s.n.	Canada, NU, Ellesmere I.	CAN	17268	
nardina Fries	*Malte*	s.n.	Canada, NU, Ellesmere I.	CAN	17271	
nardina Fries	*Gillett*	18227	Canada, NU, Ellesmere I.	CAN	453936	
nardina Fries	*Gillett*	18242	Canada, NU, Ellesmere I.	CAN	453943	
nardina Fries**	*Meiklejohn*	102	Canada, NU, Ellesmere I.	CAN	556031	
nardina Fries**	*Brassard*	3034	Canada, NU, Ellesmere I.	CAN	320130	
nardina Fries**	*Brassard*	1889	Canada, NU, Ellesmere I.	CAN	296252	
nardina Fries	*Murray*	10019	Canada, NU, Ellesmere I.	CAN	582793	

Species	Collector	Number	Country, province/state, county/quadrant/island	Institute	Catalogue Number	Extraction Number
nardina Fries**	*Harington*	361	Canada, NU, Ellesmere I.	CAN	270816	
nardina Fries**	*Beschel*	13105	Canada, NU, Axel Heiberg I.	CAN	295449	
nardina Fries	*Soper*	8043	Canada, NU, Ellesmere I.	CAN	483462	
nardina Fries**	*Powell*	62	Canada, NU, Ellesmere I.	CAN	483463	
nardina Fries**	*Soper*	8058	Canada, NU, Ellesmere I.	CAN	483464	
nardina Fries**	*Soper*	8164	Canada, NU, Ellesmere I.	CAN	483465	
nardina Fries**	*Powell*	588	Canada, NU, Ellesmere I.	CAN	483466	
nardina Fries**	*Soper*	8259	Canada, NU, Ellesmere I.	CAN	483467	
nardina Fries**	*Harington*	32	Canada, NU, Ellesmere I.	CAN	261563	
nardina Fries	*Ford*	4216	Canada, AB	WIN	70895	
nardina Fries	*Thompson*	393	Canada, BC	WTU	17378	
nardina Fries	*Lubin*	74	Canada, BC	ALA	75385	
nardina Fries*	*Komarkova*	s.n.	USA, CO, Boulder Co.	COLO	262795	1648
nardina Fries*	*Matthews*	594	USA, CO, Pitkin/Gunnison Co.	COLO	431988	1649
nardina Fries*	*Komarkova*	s.n.	USA, CO, Summit Co.	COLO	274376	1650
nardina Fries*	*Michener*	643	USA, CO, La Plata Co.	COLO	190927	1651
nardina Fries	*Clokey*	s.n.	USA, CO,	WTU	59668	
nardina Fries	*Gillett*	18270	Canada, NU, Ellesmere I.	COLO	396857	
nardina Fries	*LaFarge*	140	Canada, NU, Baffin I.	COLO	280943	
nardina Fries	*Fredskild*	660	Greenland	COLO	354560	
nardina Fries**	*MP Porsild*	s.n.	Greenland	RM	144870	
nardina Fries*	*Hartman*	13786	USA, ID, Custer Co.	RM		1531
nardina Fries	*Moseley*	2194	USA, ID, Custer Co.	IDS	107772	
nardina Fries	*Moseley*	1904	USA, ID, Lehmi Co.	IDS	107327	
nardina Fries*	*Thompson*	13540	USA, ID, Blaine Co.	WTU	3101	
nardina Fries*	*Hitchcock*	10956	USA, ID, Custer Co.	WTU	93928	
nardina Fries	*Ford*	2230	Canada, MB	WIN	71029	1527

Species	Collector	Number	Country, province/state, county/quadrant/island	Institute	Catalogue Number	Extraction Number
nardina Fries	*Ford*	2230	Canada, MB	WIN	70257	1537
nardina Fries**	*Soper*	8043	Canada, NU, Ellesmere I.	WIN	40971	
nardina Fries**	*Soper*	8058	Canada, NU, Ellesmere I.	WIN	40972	
nardina Fries**	*Soper*	8164	Canada, NU, Ellesmere I.	WIN	40973	
nardina Fries**	*Powell*	274	Canada, NU, Ellesmere I.	WIN	40974	
nardina Fries	*Blondeau*	93231	Canada, QC	WIN	53976	
nardina Fries	*Longton*	1834	Canada, NU, Ellesmere I.	WIN	34016	
nardina Fries	*Longton*	1585	Canada, NU, Ellesmere I.	WIN	34041	
nardina Fries	*Stickney*	1722	USA, MT, Lake Co.	RM	431189	
nardina Fries	*Evert*	19617	USA, MT, Carbon Co.	RM	619509	
nardina Fries	*Evert*	18439	USA, MT, Sweet Grass Co.	RM	579305	
nardina Fries	*Lackschewitz*	3234	USA, MT, Ravalli Co.	WTU	257691	
nardina Fries	*Harvey*	7125	USA, MT, Glacier Co.	WTU	231330	
nardina Fries	*Hitchcock*	14804	USA, MT, Deerlodge Co.	WTU	107636	
nardina Fries	*Lackschewitz*	2913	USA, MT, Ravalli Co.	MONT	68340	
nardina Fries	*Lackschewitz*	9772	USA, MT, Park Co.	MONT	7071	
nardina Fries	*Lackschewitz*	2984	USA, MT, Ravalli Co.	MONT	68339	
nardina Fries	*Lesica*	1821	USA, MT, Madison Co.	MONT	87418	
nardina Fries	*Lesica*	2443	USA, MT, Flathead Co.	MONT	91458	
nardina Fries	*Lesica*	7376	USA, MT, Flathead Co.	MONT	121634	
nardina Fries	*Lesica*	6385	USA, MT, Glacier Co.	MONT	119463	
nardina Fries	*Lesica*	5270	USA, MT, Flathead Co.	MONT	114347	
nardina Fries	*Lesica*	7310	USA, MT, Glacier Co.	MONT	121753	
nardina Fries	*DeBolt*	3197	USA, MT, Glacier Co.	MONT	94486	
nardina Fries	*Lesica*	6227	USA, MT, Flathead Co.	MONT	118874	
nardina Fries	*Harvey*	7000	USA, MT, Glacier Co.	MONT	54257	
nardina Fries	*McMullen*	1162	USA, MT, Glacier Co.	MONT	88779	

Species	Collector	Number	Country, province/state, county/quadrant/island	Institute	Catalogue Number	Extraction Number
nardina Fries	*Lesica*	4081	USA, MT, Pondera Co.	MONT	104377	
nardina Fries	*Lesica*	4057	USA, MT, Teton Co.	MONT	104383	
nardina Fries	*Lackschewitz*	9608	USA, MT, Teton Co.	MONT	14416	
nardina Fries	*Lackschewitz*	3120	USA, MT, Ravalli Co.	MONT	68337	
nardina Fries	*Lesica*	5569	USA, MT, Madison Co.	MONT	115198	
nardina Fries	*Hanna*	7793	USA, MT, Glacier Co.	MONT	133232	
nardina Fries	*Lesica*	8720	USA, MT, Flathead Co.	MONT	129635	
nardina Fries	*Lesica*	8317	USA, MT, Flathead Co.	MONT	126565	
nardina Fries	*AE Porsild*	10110	Canada, YT	CAN	17318	
nardina Fries	*Grulke*	61	USA, AK	WTU	305188	
nardina Fries*	*Komarkova*	342	USA, AK	WTU	271756	
nardina Fries	*Murie*	2138	USA, Alaska, Denali Co.	RM	640648	
nardina Fries	*Jansen*	2138	USA, Alaska, Afognak Quad	ALA	143297	
nardina Fries	*Parker*	9697	USA, Alaska, Skagway Quad	ALA	130445	
nardina Fries	*Parker*	6311	USA, Alaska, Charley R. Quad	ALA	122099	
nardina Fries	*Parker*	12709	USA, Alaska, Chandler L. Quad	ALA	140614	
nardina Fries	*Parker*	4922	USA, Alaska, Livengood, Quad	ALA	117069	
nardina Fries*	*Khokhryakov*	6618	USA, Alaska, Philip Smith Mts Quad	ALA	69621	1530
nardina Fries	*Walker*	83122	USA, Alaska, Beechey Pt. Quad	ALA	99497	
nardina Fries	*Murray*	6646	USA, Alaska, Harrison Bay Quad	ALA	78758	
nardina Fries*	*Viereck*	1480	USA, AK	ALA	11539	1529
nardina Fries	*Peterson*	13240	USA, AK	ALA	123191	
nardina Fries**	*Tengwall*	s.n.	Sweden, Lule Lappmark	CAN	135231	
nardina Fries	*Parker*	16708	USA, Alaska, Mt St Elias Quad	ALA	157989	
nardina Fries	*Parker*	10721	USA, Alaska, Misheguk Mt Quad	ALA	134665	
nardina Fries	*Johnson*	211	USA, Alaska, Bering Strait Quad	ALA	9016	
nardina Fries	*Parker*	10654	USA, Alaska, Howard Pass Quad	ALA	134600	

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nardina Fries	*Parker*	13153	USA, Alaska, killik R. Quad	ALA	139539	
nardina Fries	*Batten*	2368	USA, Alaska, Iliamna Quad	ALA	142069	
nardina Fries	*Batten*	7894	USA, Alaska, Mt Hayes Quad	ALA	82866	
nardina Fries*	*Solstad*	s.n.	USA, AK	ALA	154754	
nardina Fries	*Klein*	176	USA, AK	ALA	23038	
nardina Fries	*Murray*	6277	USA, Alaska, Chandler L. Quad	ALA	79853	
nardina Fries	*Kelso*	84277	USA, Alaska, Solomon Quad	ALA	79127	1536
nardina Fries	*Murray*	11590	USA, Alaska, Bendeleben Quad	ALA	114328	
nardina Fries	*Bosworth*	119	USA, Alaska, Mt Fairweather Quad	ALA	150970	
nardina Fries	*Lipkin*	3223	USA, Alaska, Seward Quad	ALA	152631	
nardina Fries	*Malte*	120509	Canada, NU	WTU	188895	
nardina Fries	*Dyring*	s.n.	Norway	RM	108109	
nardina Fries	*LaFarge*	140	Canada, NU, Baffin I.	WTU	277416	
nardina Fries	*Engelskjon*	s.n.	Norway, Troms, Troms	COLO	234892	1848
nardina Fries	*Zika*	10953	USA, OR, Wallowa Co.	OSC	173259	
nardina Fries	*York*	2881	USA, OR, Douglas Co.	OSC	209161	
nardina Fries	*Zika*	10970	USA, OR, Wallowa Co.	OSC	173257	
nardina Fries	*Lundstrom*	s.n.	Norway, Svalbard	RM	142542	
nardina Fries	*Smith*	689	Sweden, Lappmark, Karesuando	RM	213419	
nardina Fries	*Tengwall*	329	Sweden, Lappmark, Jokkmokk	COLO	133176	
nardina Fries	*Huber*	2387	USA, Utah, Duchesne Co.	BRY	375434	1654
nardina Fries	*Huber*	409	USA, Utah, Duchesne Co.	BRY	368546	1655
nardina Fries	*Arnot*	s.n.	USA, WA, Okanogan Co.	WTU	335395	
nardina Fries	*Thompson*	9518	USA, WA, Chelan Co.	WTU	390	
nardina Fries	*Thompson*	9578	USA, WA, Chelan Co.	WTU	390	
nardina Fries	*Thompson*	7810	USA, WA, Kittitas Co.	WTU	390	
nardina Fries	*Potash*	12	USA, WA, Chelan Co.	WTU	366394	

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nardina Fries	*Ramsden*	704	USA, WA, Pierce Co.	WTU	367219	
nardina Fries	*Thompson*	11057	USA, WA, Jefferson Co.	WTU	1057	
nardina Fries	*Bliss*	4	USA, WA, Clallam Co.	WTU	336733	
nardina Fries	*Thompson*	8408	USA, WA, Clallam Co.	WTU	394	
nardina Fries	*Thompson*	7447	USA, WA, Clallam Co.	WTU	394	
nardina Fries**	*RT Porsild*	509	Canada, YT	WTU	229332	
nardina Fries	*Welsh*	10375	Canada, YT	ALA	44162	
nardina Fries	*Clokey*	3404	USA, CO,	CAN	163726	
nardina Fries	*Mauby*	31493	USA, MT	CAN	163724	
nardina Fries*	*Allen*	173	USA, WA, Pierce Co.	CAN	163727	
nardina Fries*	*Weber*	11126	USA, CO, Summit Co.	CAN	269102	
nardina Fries	*Norman*	s.n.	Norway	CAN	238987	1526
nardina Fries	*Blytt*	s.n.	Norway, Troms	CAN	241586	1850
nardina Fries	*Norman*	s.n.	Norway, Troms	CAN	234974	
nardina Fries	*Wange*	s.n.	Norway, Troms	CAN	218015	
nardina Fries	*Jorgenesen*	59233	Norway	CAN	135232	
nardina Fries	*Dyring*	s.n.	Norway	CAN	135230	
nardina Fries	*Dyring*	s.n.	Norway	CAN	135229	
nardina Fries	*Smith*	328	Sweden, Lappland, Jukkasjarvi	CAN	135226	1525
nardina Fries	*Svensson*	s.n.	Sweden, Troms	CAN	135228	
nardina Fries	*Caswell*	96183	USA, Alaska, Clarke L. Quad	ALA	126563	1544
nardina Fries**	*Tengwall*	329	Sweden, Lappland	CAN	135227	1568
nardina Fries	*Andersen*	4458	Greenland, Alangordlia, Sioralik Dist.	CAN	434103	1543
nardina Fries	*Andersen*	4458	Greenland, Alangordlia, Sioralik Dist.	CAN	434023	
nardina Fries	*Yngvar*	s.n.	Norway, Troms, Kvaenangen	CAN	381814	
nardina Fries**	*Johannes*	s.n.	Norway, Svalbard	CAN	241563	
nardina Fries	*Hanfgarn*	398	Greenland	CAN	488210	

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nardina Fries	*Fredskild*	1	Greenland	CAN	488211	
nardina Fries	*Bay*	7852	Greenland	CAN	488212	
nardina Fries	*AE Porsild*	8808	Greenland	CAN	17229	
nardina Fries	*AE Porsild*	8571	Greenland, Bjome I.	CAN	17230	
nardina Fries	*AE Porsild*	8854	Greenland, Proven I.	CAN	17231	
nardina Fries**	*Halliday*	453	Greenland, N Scoresby I.	CAN	284102	
nardina Fries**	*Scholander*	s.n.	Greenland	CAN	241211	
nardina Fries	*Termometerfjeld*	447	Greenland	CAN	17250	
nardina Fries	*Gunn*	29	Greenland, Thule I.	CAN	205428	1517
nardina Fries	*MP Porsild*	s.n.	Greenland	CAN	26808	1518
nardina Fries	*AE Porsild*	8742	Greenland	CAN	17232	
nardina Fries	*AE Porsild*	8528	Greenland, Godthaab Dist.	CAN	17233	
nardina Fries	*MP Porsild*	8385	Greenland, Godthaab Dist.	CAN	17234	
nardina Fries	*MP Porsild*	s.n.	Greenland	CAN	17235	1561
nardina Fries	*MP Porsild*	s.n.	Greenland	CAN	17236	
nardina Fries	*MP Porsild*	s.n.	Greenland	CAN	17237	
nardina Fries	*MP Porsild*	s.n.	Greenland	CAN	17238	
nardina Fries	*MP Porsild*	s.n.	Greenland	CAN	17239	
nardina Fries	*MP Porsild*	s.n.	Greenland	CAN	17240	
nardina Fries	*AE Porsild*	365	Greenland, Disko I.	CAN	17241	
nardina Fries	*Anderson*	49700	Greenland	CAN	17242	
nardina Fries	*Fredskild*	660	Greenland, Melville Bugt	CAN	462421	
nardina Fries	*Jorgensen*	661608	Greenland	CAN	311367	
nardina Fries	*Holmen*	146	Greenland	CAN	282510	1541
nardina Fries	*Holmen*	28	Greenland, Charcots Land	CAN	263213	1542
nardina Fries	*LG Raup*	773	Greenland	CAN	308803	
nardina Fries	*Holmen*	397	Greenland, Angmagssalik Dist	CAN	344345	

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nardina Fries	*Hansen*	1497	Greenland	CAN	318834	
nardina Fries	*Swainson*	6	Greenland	CAN	311667	
nardina Fries	*Elsley*	67114	Greenland	CAN	311668	
nardina Fries	*Jensen*	s.n.	Greenland, Disko I.	CAN	17245	
nardina Fries	*MP Porsild*	s.n.	Greenland, Disko I.	CAN	17244	
nardina Fries	*Sorensen*	3163	Greenland, Ella I.	CAN	17246	
nardina Fries**	*Bridgland*	720	Canada, NU, Ellesmere I.	CAN	455113	
nardina Fries	*Gillespie*	4301	Canada, NU, Ellesmere I.	CAN	588978	
nardina Fries	*Gillespie*	4283	Canada, NU, Ellesmere I.	CAN	589066	
nardina Fries	*Gillespie*	4280	Canada, NU, Ellesmere I.	CAN	589065	
nardina Fries	*Edlund*	285	Canada, NU, Ellesmere I.	CAN	535397	
nardina Fries	*Kuc*	422	Canada, NU, Ellesmere I.	CAN	118512	
nardina Fries	*Kuc*	422	Canada, NU, Axel Heiberg I.	CAN	330611	
nardina Fries**	*Beschel*	10764	Canada, NU, Axel Heiberg I.	CAN	267534	
nardina Fries	*Kuc*	421	Canada, NU, Axel Heiberg I.	CAN	330594	
nardina Fries**	*RT Porsild*	509	Canada, YT	CAN	303346	
nardina Fries	*Murray*	649	Canada, YT	CAN	454183	
nardina Fries**	*RT Porsild*	386	Canada, YT	CAN	303598	
nardina Fries	*Murray*	74	Canada, YT	CAN	306814	
nardina Fries**	*Murray*	1404	Canada, YT	CAN	324079	
nardina Fries*	*HM Raup*	11322	Canada, YT	CAN	276659	
nardina Fries	*AE Porsild*	10053	Canada, YT	CAN	17316	
nardina Fries	*AE Porsild*	10882	Canada, YT	CAN	17315	
nardina Fries	*AE Porsild*	10109	Canada, YT	CAN	17317	
nardina Fries	*AE Porsild*	9909	Canada, YT	CAN	17319	
nardina Fries	*Murray*	637	Canada, YT	CAN	454636	
nardina Fries	*Murray*	1602	Canada, YT	CAN	454639	

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nardina Fries	*Murray*	6646	USA, Alaska, Harrison Bay Quad	CAN	454401	
nardina Fries	*Hettinger*	647	USA, AK	CAN	370876	
nardina Fries	*Argus*	5457	USA, AK	CAN	327842	
nardina Fries	*Argus*	5458	USA, AK	CAN	327843	
nardina Fries	*Spetzman*	1767	USA, AK	CAN	262949	
nardina Fries	*Spetzman*	1688	USA, AK	CAN	262948	
nardina Fries**	*Gjaerevoll*	532	USA, Alaska,	CAN	225264	
nardina Fries	*Spetzman*	957	USA, AK	CAN	211595	1503
nardina Fries	*Spetzman*	620	USA, AK	CAN	211596	1504
nardina Fries	*Johansen*	309	Canada, QC, James Bay	CAN	17281	
nardina Fries**	*Baldwin*	1699	Canada, QC, James Bay	CAN	203378	1505
nardina Fries	*AE Porsild*	4212	Canada, QC, James Bay	CAN	17282	1506
nardina Fries	*Pease*	25505	Canada, QC, Matane Co.	CAN	17280	1540
nardina Fries	*Dutilly*	11599	Canada, QC, James Bay	CAN	17277	1507
nardina Fries*	*AE Porsild*	13229	Canada, AB	CAN	243934	1510
nardina Fries	*Packer*	61	Canada, AB	CAN	370060	
nardina Fries*	*AE Porsild*	22514	Canada, AB	CAN	266090	
nardina Fries*	*AE Porsild*	14880	Canada, AB	CAN	243924	
nardina Fries*	*AE Porsild*	14582	Canada, AB	CAN	243923	1512
nardina Fries*	*AE Porsild*	20609	Canada, AB	CAN	290013	
nardina Fries*	*AE Porsild*	14539	Canada, AB	CAN	243925	1513
nardina Fries	*Macoun*	25520	Canada, AB	CAN	17307	
nardina Fries	*Dawson*	31494	Canada, AB	CAN	17295	
nardina Fries	*Macoun*	s.n.	Canada, AB	CAN	17294	
nardina Fries	*Macoun*	64014	Canada, AB	CAN	17297	
nardina Fries	*Macoun*	64015	Canada, AB	CAN	17296	
nardina Fries	*Macoun*	10762	Canada, AB	CAN	17302	

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nardina Fries	*Pellvet*	289	Canada, AB	CAN	17301	
nardina Fries	*Macoun*	s.n.	Canada, AB	CAN	17298	
nardina Fries	*Macoun*	16495	Canada, AB	CAN	17299	
nardina Fries	*Macoun*	14048	Canada, AB	CAN	17306	
nardina Fries	*Macoun*	14048	Canada, AB	CAN	17305	
nardina Fries	*Macoun*	14048	Canada, AB	CAN	17304	
nardina Fries	*Weber*	2438	Canada, AB	CAN	17320	1514
nardina Fries*	*AE Porsild*	13154	Canada, AB	CAN	243932	
nardina Fries*	*AE Porsild*	13964	Canada, AB	CAN	243929	
nardina Fries*	*AE Porsild*	15843	Canada, AB	CAN	243926	
nardina Fries	*Argus*	8823	Canada, BC, Pine Pass Quad.	CAN	372259	
nardina Fries*	*Elven*	3474	Canada, NU, Baffin I.	CAN	583250	
nardina Fries*	*Elven*	3546	Canada, NU, Baffin I.	CAN	583251	
nardina Fries*	*Elven*	3315	Canada, NU, Devon I.	CAN	583247	
nardina Fries*	*Elven*	3371	Canada, NU, Devon I.	CAN	583248	1547
nardina Fries	*Spetzman*	81	Canada, YT	CAN	274572	
nardina Fries*	*RT Porsild*	1081	Canada, YT	CAN	312644	1546
nardina Fries*	*Macoun*	25547	Canada, AB	CAN	17323	
nardina Fries*	*Kujala*	s.n.	Canada, BC	CAN	393784	
nardina Fries*	*Scamman*	6587	Canada, AB	CAN	245512	
nardina Fries	*JM Macoun*	98085	Canada, BC	CAN	17324	
nardina Fries	*Beamish*	60968	Canada, BC	CAN	304151	
nardina Fries	*Spreadborough*	20845	Canada, BC	CAN	17303	
nardina Fries	*Spreadborough*	78162	Canada, BC	CAN	17314	
nardina Fries	*Spreadborough*	78163	Canada, BC	CAN	17313	
nardina Fries	*JM Macoun*	98086	Canada, BC	CAN	17312	
nardina Fries	*JM Macoun*	98084	Canada, BC	CAN	17311	

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nardina Fries	*Ramsden*	187	USA, MT, Lake Co.	DAO	465083	
nardina Fries	*Ronning*	s.n.	Norway, Nordland, Beiam	DAO	257348	
nardina Fries	*Hasselrot*	s.n.	Sweden, Torne Lappmark, Karesuando	DAO	257350	
nardina Fries	*Raymond*	61	Sweden, Lappland	DAO	257351	1563
nardina Fries	*Yngvar*	s.n.	Norway, Troms, Kvaenangen	DAO	286019	1551
nardina Fries	*Gjaerevoll*	s.n.	Norway, Troms, Nordreisa	DAO	257343	
nardina Fries	*Dutilly*	11514	Canada, QC	DAO	257309	1856
nardina Fries	*Hudson*	3832	Canada, AB	DAO	333632	
nardina Fries	*Lee*	481	Canada, AB	DAO	332707	
nardina Fries	*Argus*	17094	Canada, AB	DAO	614827	
nardina Fries*	*Boivin*	5062	Canada, AB	DAO	121602	
nardina Fries	*Hainault*	7720	Canada, BC	DAO	840548	
nardina Fries	*Taylor*	5880	Canada, BC	DAO	199437	
nardina Fries	*Dutilly*	4232	Canada, NU	DAO	844472	
nardina Fries**	*Manning*	s.n.	Canada, NU, James Bay	DAO	653303	
nardina Fries	*Dutilly*	6225	Canada, NU, Hudson Bay	DAO	652513	
nardina Fries	*Loewen*	93052	Canada, NT	DAO	670150	
nardina Fries	*Krajina*	s.n.	Canada, YT	DAO	201129	
nardina Fries	*Rosie*	1562	Canada, YT	DAO	404756	
nardina Fries	*Webber*	298	Canada, NU, Baffin I.	CAN	295781	
nardina Fries	*Blouin*	550	Canada, NU, Baffin I.	CAN	392190	
nardina Fries**	*Malte*	s.n.	Canada, NU, Baffin I.	CAN	17259	
nardina Fries**	*Wynne-Edwards*	9165	Canada, NU, Baffin I.	CAN	204999	
nardina Fries	*Calder*	37171	Canada, AB	DAO	257326	
nardina Fries	*Parker*	s.n.	Canada, NU	DAO	612103	
nardina Fries	*Dutilly*	1035	Canada, NU, Franklin Dist.	DAO	655639	
nardina Fries	*Hudson*	2798	Canada, AB	DAO	688647	

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nardina Fries	*Douglas*	4174	USA, WA, Chelan Co.	DAO	621357	
nardina Fries	*Douglas*	3800	USA, WA, Okanogan Co.	DAO	621343	
nardina Fries	*Thacker*	4	Canada, NU, Baffin I.	CAN	17253	1519
nardina Fries	*Norman*	s.n.	Norway, Troms, Troms	DAO	257354	
nardina Fries	*Lackschewitz*	3234	USA, MT, Ravalli Co.	WTU	68334	
nardina Fries*	*AE Porsild*	20925	Canada, AB	CAN	290011	
nardina Fries	*Malte*	s.n.	Canada, NU, Baffin I.	CAN	17275	
nardina Fries	*Starr*	100261	USA, CO, Park Co.			1588
nardina Fries	*Starr*	100265	USA, CO, Clear Creek Co.			1589
nardina Fries	*Starr*	1002610	USA, CO, Clear Creek Co.			1590
nardina Fries	*Starr*	100515	USA, UT, Summitt Co.			1591
nardina Fries	*Starr*	1005110	USA, UT, Summitt Co.			1592
nardina Fries	*Starr*	1005120	USA, UT, Summitt Co.			1593
nardina Fries	*Starr*	100391	USA, WY, Sublette Co.			1594
nardina Fries	*Starr*	1003910	USA, WY, Sublette Co.			1595
nardina Fries	*Starr*	1003920	USA, WY, Sublette Co.			1596
nardina Fries	*Starr*	100581	USA, WA, Whatcom Co.			1597
nardina Fries	*Starr*	1005810	USA, WA, Whatcom Co.			1598
nardina Fries	*Starr*	100585	USA, WA, Whatcom Co.			1599
nardina Fries*	*Komarkova*	s.n.	USA, CO, Park Co.	COLO	274473	
nardina Fries	*Hartman*	7923	USA, CO, Lake Co.	COLO	469229	
nardina Fries*	*RA Nelson*	7872	USA, CO, Pitkin Co.	COLO	194327	
nardina Fries*	*Michener*	646	USA, CO, La Plata Co.	COLO	187619	
nardina Fries*	*Mauby*	343	USA, MT	HUH		
nardina Fries*		s.n.	USA	HUH	27258	
nardina Fries	*Harris*	1767	Greenland	UVSC	23	
nardina Fries	*Cusick*	3336	USA, OR	OSC	17013	

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nardina Fries*	*Prescott*	243	USA	NY		
nardina Fries	*Zika*	10970	USA, OR, Wallowa Co.	WTU	372305	
nardina Fries	*Denton*	4173	USA, WA, Okanogan Co.	WTU	271916	
nardina Fries	*Selander*	s.n.	Sweden, Lule Lappmark, Jokkmokk	S	6053	
nardina Fries	*Bjorkman*	s.n.	Sweden, Lule Lappmark, Jokkmokk	S	6063	
nardina Fries	*Selander*	s.n.	Sweden, Lule Lappmark, Jokkmokk	S	6069	
nardina Fries	*Bjorkman*	s.n.	Sweden, Lule Lappmark, Jokkmokk	S	6085	
nardina Fries	*Asplund*	s.n.	Sweden, Torne Lappmark, Jukkasjarvi	S	6109	
nardina Fries	*Arwidsson*	s.n.	Sweden, Pite Lappmark, Arjeplog	S	6030	
nardina Fries	*Selander*	s.n.	Sweden, Lule Lappmark, Jokkmokk	S	6050	
nardina Fries	*Dahlbeck*	s.n.	Sweden, Lule Lappmark, Jokkmokk	S	6046	
nardina Fries	*Harpen*	s.n.	Sweden, Lule Lappmark, Jokkmokk	S	6043	
nardina Fries	*Karlsson*	s.n.	Sweden, Lule Lappmark, Karesuando	S	138285	
nardina Fries	*Karlsson*	s.n.	Sweden, Lule Lappmark, Karesuando	S	592506	
nardina Fries	*Damsgaard*	s.n.	Norway, Troms, Jloyfjellet	KMN	19991	
nardina Fries	*Svendsen*	s.n.	Norway, Troms, Nordreisa	KMN	19990	
nardina Fries	*Jorgensen*	2799	Greenland	MO	2384955	
nardina Fries	*Fredskild*	413	Greenland, Qingaussarssuaq	MO	3628753	
nardina Fries	*Anderson*	4796	Greenland, Alangordlia	MO	2774075	
nardina Fries	*Fredskild*	1087	Greenland, Depothavn	MO	5099642	
nardina Fries	*Fredskild*	2746	Greenland, Disko I.	MO	3654655	
nardina Fries	*H Smith*	s.n.	Sweden, Torne Lappmark, Karesuando	LD	1149657	
nardina Fries	*Anderson*	s.n.	Sweden	LD	1150512	
nardina Fries		s.n.	Norway, Troms	LD	150210	
nardina Fries	*H Smith*	328	Sweden, Lappland, Jukkasjarvi	LD	135230	
nardina Fries	*Hasslerot*	s.n.	Sweden, Lule Lappmark	OHN	123813	
nardina Fries	*Gergson*	s.n.	Sweden, Torne Lappmark	OHN	85178	

Species	Collector	Number	Country, province/state, county/quadrant/island	Institute	Catalogue Number	Extraction Number
nardina Fries	*Einarsson*	s.n.	Iceland	ICEL	5760	
nardina Fries	*Jonsdottir*	s.n.	Iceland, Finnungsstor	ICEL	44515	
nardina Fries	*Davidsson*	s.n.	Iceland	ICEL	5768	
nardina Fries	*Einarsson*	s.n.	Iceland	ICEL	5757	
nardina Fries	*Guttormsson*	s.n.	Iceland	ICEL	42901	
nardina Fries	*Kristinsson*	7383	Iceland, Finnungsstor	ICEL	10902	
nardina Fries	*Hallgrimsson*	1589	Iceland, Finnungsstor	ICEL	10900	1858
nardina Fries	*Kristinsson*	19967	Iceland, Finnungsstor	ICEL	15450	
nardina Fries	*Kristinsson*	14143	Iceland, Finnungsstor	ICEL	10898	
nardina Fries	*Kristinsson*	20644	Iceland, Finnungsstor	ICEL	15972	
nardina Fries	*Kristinsson*	7393	Iceland, Finnungsstor	ICEL	10903	1859
nardina Fries*	*Tengwall*	s.n.	Sweden	RM	107914	
nardina Fries*	*AE Porsild*	15691	Canada, AB	RM	529696	
nardina Fries	*Alm*	2740	Sweden, Torne Lappmark, Jukkasjarvi	RM	253248	
nardina Fries	*Starr*	100211	USA, CO, Clear Creek Co.			1860
nardina Fries	*Starr*	100215	USA, CO, Clear Creek Co.			
nardina Fries	*Starr*	1002110	USA, CO, Clear Creek Co.			
nardina Fries	*Starr*	100522	USA, UT, Summitt Co.			1862
nardina Fries	*Starr*	100523	USA, UT, Summitt Co.			
nardina Fries	*Starr*	100524	USA, UT, Summitt Co.			1863
nardina Fries	*Guldberg*	s.n.	Sweden, Nordlands, Salten	RM	127267	
nardina Fries	*Swales*	s.n.	Canada, NU	RM	304168	
nardina Fries	*Senn*	4037	Canada, NU, Baffin I.	RM	216048	
nardina Fries	*Lackschewitz*	10526	USA, MT, Teton Co.	RM	395046	
nardina Fries	*Fertig*	12049	USA, WY, Sublette Co.	RM	593140	
nardina Fries	*Hartman*	48370	USA, WY, Teton Co.	RM	625588	
nardina Fries	*Hartman*	7923	USA, CO, Lake Co.	RM	621335	

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nardina Fries	*Moore*	8677	USA, CO, Dolores Co.	RM	716371	
nardina Fries	*alm*	s.n.	Sweden, Torne Lappmark, Jukkasjarvi	U	121310	
nardina Fries	*Norman*	s.n.	Norway, Troms	U	223329	
nardina Fries	*Svedberg*	s.n.	Sweden, Torne Lappmark, Jukkasjarvi	U	180010	
nardina Fries	*Bjorkman*	s.n.	Sweden, Lule Lappmark, Jokkmokk	U	121283	
nardina Fries	*Frisendahl*	s.n.	Sweden, Lule Lappmark, Jokkmokk	U	224346	
nardina Fries	*Bjorkman*	s.n.	Sweden, Lule Lappmark, Jokkmokk	U	224352	
nardina Fries	*VF Holm*	s.n.	Sweden, Pite Lappmark, Jukkasjarvi	U	224360	
nardina Fries	*Lars-Gunnar*	s.n.	Sweden, Lule Lappmark, Gallivare	U	390807	
nardina Fries	*Lars-Gunnar*	s.n.	Sweden, Lule Lappmark, Jokkmokk	U	390804	
nardina Fries*	*Simmons*	2523	Canada, NU, Ellesmere I.	U	510903	
nardina Fries*	*Bjorling*	s.n.	Greenland	U	510904	
nardina Fries*	*Hart*	s.n.	Canada, NU	U	510906	
nardina Fries*	*Rink*	s.n.	Greenland	U	510908	
nardina Fries*	*Kornerup*	25	Greenland	U	510909	
nardina Fries*	*Fries*	s.n.	Greenland	U	510910	
nardina Fries*	*Fries*	s.n.	Greenland	U	510912	
nardina Fries	*Fries*	s.n.	Greenland	U	510914	
nardina Fries	*Fries*	s.n.	Greenland	U	510913	
nardina Fries*	*Fries*	s.n.	Greenland	U	510915	
nardina Fries	*Berlin*	s.n.	Greenland	U	510916	
nardina Fries		s.n.	Greenland	U	510917	
nardina Fries*	*L Holm*	650	Canada, BC	U	510918	
nardina Fries*	*Weber*	11126	USA, CO, Summit Co.	U	510919	
nardina Fries*	*Malmgren*	s.n.	Norway, Svalbard	U	510932	
nardina Fries*	*Fries*	s.n.	Norway, Svalbard	U	510931	
nardina Fries	*Arnell*	s.n.	Norway, Svalbard	U	510933	

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nardina Fries	*Nannfeldt*	s.n.	Norway, Troms, Nordreisa	U	510934	
nardina Fries	*Norman*	s.n.	Norway, Troms, Lavangen	U	510935	
nardina Fries	*Klinger*	3	Norway, Svalbard	COLO	430792	
nardina Fries*	*Komarkova*	s.n.	USA, CO, Summit Co.	COLO	274362	
nardina Fries*	*Michener*	742	USA, CO, La Plata Co.	COLO	187628	
nardina Fries	*H Smith*	328	Sweden, Lappland, Jukkasjarvi	COLO	133175	
nardina Fries*	*Maguire*	591	USA, MT	UTC	2309	
nardina Fries	*Neely*	3165	USA, CO, Chaffee Co.	UTC	193300	
nardina Fries	*Presho*	45	Norway, Svalbard			
nardina Fries	*Westergaard*	28	Greenland, Qeqertarsuaq			
nardina Fries	*Westergaard*	47	Norway, Svalbard			
nardina Fries	*Westergaard*	41	Greenland, Narsarsuaq			
nardina Fries	*Westergaard*	48	Norway, Svalbard			
nardina Fries	*Westergaard*	4637	Greenland, Qaanaaq			
nardina Fries	*Westergaard*	4655	Canada, NU			
nardina Fries	*Neely*	3132	USA, CO, Park Co.	UTC	193447	
nardina Fries*	*Malte*	s.n.	Canada, NU, Baffin I.	UTC	30115	
nardina Fries	*Malte*	s.n.	Canada, NU, Ellesmere I.	UTC	30128	
nardina Fries	*Burt*	s.n.	Canada, NU, Baffin I.	CAN	594178	
nardina Fries	*Burt*	s.n.	Canada, NU, Baffin I.	CAN	594166	
nardina Fries	*Burt*	s.n.	Canada, NU, Baffin I.	CAN	594202	
nardina Fries	*Burt*	s.n.	Canada, NU, Baffin I.	CAN	594396	
nardina Fries	*Burt*	s.n.	Canada, NU, Baffin I.	CAN	594212	
nardina Fries*	*Komarkova*	s.n.	USA, CO, Boulder Co.	UTC	137187	
nardina Fries	*Starr*	100263	USA, CO, Clear Creek Co.			
nardina Fries	*Starr*	100393	USA, WY, Sublette Co.			
nardina Fries	*Starr*	100392	USA, WY, Sublette Co.			

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nardina Fries	*J Macoun*	10762	Canada, AB	CAN	20703	1866
nardina Fries	*B Moseley*	2626	USA, ID, Blaine Co.	ID	109336	1837
nardina Fries	*B Moseley*	2626	USA, ID, Blaine Co.	ID	109336	1838
nardina Fries	*Maguire*	22602	USA, NV, Elko Co.	UTC	55897	
nardina Fries***	*RS Williams*	s.n.	USA, MT, Flathead Co.	NY		
nardina Fries	*R Jones*	666	USA, WY, Fremont Co.	RM	541743	
nardina Fries	*MP Porsild*	s.n.	Greenland, Disko I.	CAN	17228	
nardina Fries	*Blouin*	922	Canada, NU, Baffin I.	CAN	392202	
nardina Fries	*Aiken*	s.n.	Canada, NU, Baffin I.	CAN	586602	
nardina Fries	*Aiken*	s.n.	Canada, NU, Baffin I.	CAN	517973	
nardina Fries	*Edlund*	s.n.	Canada, NT, Victoria I.	CAN	486648	
nardina Fries**	*AE Porsild*	s.n.	Canada, NT, Victoria I.	CAN	127567	
nardina Fries	*Aiken*	s.n.	Canada, NU, Ellesmere I.	CAN	566172	
nardina Fries	*Gillett*	s.n.	Canada, NU, Ellesmere I.	CAN	453966	
nardina Fries	*Aiken*	s.n.	Canada, NU, Ellesmere I.	CAN	581898	
nardina Fries*	*Franklin*	s.n.	USA, CO, Summit Co.	COLO	269102	
nardina Fries	*Macoun*	25520	Canada, AB	CAN	100540	
nardina Fries	*JM Macoun*	98080	Canada, AB	CAN	17322	
nardina Fries	*McIsaac*	1008	Canada, AB	CAN	465750	
nardina Fries*	*HM Raup*	3780	Canada, BC	CAN	17327	
nardina Fries*	*HM Raup*	3904	Canada, BC	CAN	17328	
nardina Fries*	*HM Raup*	3918	Canada, BC	CAN	26809	1501
nardina Fries	*Argus*	11002	Canada, BC, Peace R. Dist.	CAN	410598	
nardina Fries	*Argus*	10065	Canada, BC, Peace R. Dist.	CAN	410800	
nardina Fries	*Talbot*	620425	Canada, NT, MacKenzie Dist.	CAN	479643	
nardina Fries	*Edlund*	354	Canada, NU	CAN	495649	
nardina Fries**	*Wynne-Edwards*	8908	Canada, NU, Baffin I.	CAN	204805	

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nardina Fries**	*Hainault*	3877	Canada, NU, Baffin I.	CAN	301906	
nardina Fries**	*Lambert*	s.n.	Canada, NT, Banks I.	CAN	535883	
nardina Fries	*Malte*	s.n.	Canada, NU, Baffin I.	CAN	17265	
nardina Fries	*Polunin*	732	Canada, NU, Baffin I.	CAN	17256	
nardina Fries	*Blachut*	15	Canada, NU, Ellesmere I.	CAN	472875	
nardina Fries	*Kuc*	470	Canada, NU, Axel Heiberg I.	CAN	330596	
nardina Fries	*Waterston*	72124	Canada, NU, Ellesmere I.	CAN	370924	
nardina Fries	*Gillett*	18085	Canada, NU, Ellesmere I.	CAN	453836	
nardina Fries**	*Meiklejohn*	7	Canada, NU, Ellesmere I.	CAN	556062	
nardina Fries	*Ebersole*	332	USA, AK	COLO	379589	
nardina Fries	*Parker*	8891	USA, Alaska, Lime Hills Quad	ALA	128201	
nardina Fries	*Berg*	39	USA, Alaska, Seldovia Quad	ALA	113036	
nardina Fries	*Parker*	16704	USA, Alaska, Bering Glacier Quad	ALA	157992	
nardina Fries	*Parker*	15956	USA, Alaska, Nome Quad	ALA	155061	
nardina Fries	*Duffy*	131	USA, Alaska, Mt McKinley Quad	ALA	147768	
nardina Fries	*Galland*	s.n.	Canada, NU, Devon I.	WTU	313703	
nardina Fries	*Thompson*	14330	USA, WA, Snohomish Co.	WTU	17672	
nardina Fries	*Murray*	1706	Canada, YT, Kluane Lake Quad	ALA	81002	
nardina Fries	*Huber*	409	USA, UT, Duchesne Co.	CAN	568113	
nardina Fries*	*Wulff*	s.n.	Greenland, Greenland, Tunu	CAN	241210	1539
nardina Fries	*Seidenfaden*	1580	Greenland, Norske I.	CAN	17248	
nardina Fries	*Holmen*	6683	Greenland, Heilprin Land	CAN	256670	
nardina Fries*	*Nygaard*	s.n.	Greenland, Inglifield Land	CAN	17249	1560
nardina Fries	*Kuc*	s.n.	Canada, NU, Axel Heiberg I.	CAN	330605	
nardina Fries	*Kuc*	s.n.	Canada, NU, Axel Heiberg I.	CAN	330632	
nardina Fries	*Murray*	509	Canada, YT, Mt. St. Elias Quad	CAN	454136	
nardina Fries*	*AE Porsild*	22592	Canada, AB	CAN	266089	

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nardina Fries*	*AE Porsild*	15691	Canada, AB	CAN	243922	1511
nardina Fries	*Macoun*	16496	Canada, AB	CAN	17300	
nardina Fries*	*AE Porsild*	13228	Canada, AB	CAN	243931	
nardina Fries*	*AE Porsild*	13463	Canada, AB	CAN	243930	
nardina Fries*	*AE Porsild*	14095	Canada, AB	CAN	243928	
nardina Fries*	*AE Porsild*	14213	Canada, AB	CAN	243927	
nardina Fries*	*AE Porsild*	13032	Canada, AB	CAN	243933	
nardina Fries*	*AE Porsild*	12546	Canada, AB	CAN	243935	
nardina Fries	*JM Macoun*	33689	Canada, BC	CAN	17308	
nardina Fries*	*Ledingham*	s.n.	Canada, AB	DAO	257329	
nardina Fries*	*Komarkova*	s.n.	USA, CO, Summit Co.	COLO	274435	
nardina Fries*	*Evert*	6326	USA, WY, Park Co.	RM	531211	
nardina Fries*	*T Holm*	s.n.	Greenland	U	510905	
nardina Fries*	*Fries*	s.n.	Greenland	U	510911	
nardina Fries	*ME Lewis*	475	USA, UT, Beaver Co.	COLO	306915	
nardina Fries*	*Matthews*	1949	USA, CO, Pitkin Co.	COLO	434178	
nardina Fries*	*Viereck*	1398	USA, AK	COLO	119708	
nardina Fries*	*Viereck*	1398	USA, AK	COLO	119692	
nardina Fries	*Beckett*	s.n.	Canada, NU	CAN	299863	
nardina Fries	*Malte*	s.n.	Canada, NU	CAN	17262	
nardina Fries	*Duman*	2127	Canada, NU, Melville Peninsula	CAN	200473	
nardina Fries*	*Freuchen*	12	Canada, NU, Melville Peninsula	CAN	17287	
nardina Fries	*Gillett*	18399	Canada, NU	CAN	454068	
nardina Fries**	*Hattersley-Smith*	s.n.	Canada, NU, Ellesmere I.	CAN	296042	
nardina Fries	*Soper*	8035	Canada, NU, Ellesmere I.	CAN	483461	
nardina Fries	*Christie*	38	Canada, NU	CAN	234210	
nardina Fries	*Murray*	2066	USA, Alaska, McCarthy, Quad	CAN	454628	1502

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nardina Fries	*Gjaerevoll*	1526	USA, AK	CAN	225265	
nardina Fries*	*AE Porsild*	20693	Canada, AB	CAN	290012	
nardina Fries	*Beder*	s.n.	Canada, BC	CAN	364239	
nardina Fries*	*Elven*	3120	Canada, NU, Ellesmere I.	CAN	583246	
nardina Fries*	*Suksdorf*	4172	USA, WA, Yakima Co.	WTU	6500	
nardina Fries	*AE Porsild*	3480	Canada, NT	CAN	17285	
nardina Fries****	*AE Porsild*	5087	Canada, NT, Great Bear L.	CAN	20702	
nardina Fries	*Suksdorf*	4172	USA, WA, Yakima Co.	WTU	6500	
nardina Fries	*Fertig*	11670	USA, Wyoming, Sublette Co.	RM	592023	
Carex L. subgenus *Psyllophora* section *Filifoliae* (Tuckerman) Mackenzie						
arsenii Kükenthal		47023	Mexico, Michoacan, Morelia	MEXU		1940
elynoides Holm	*Johnson*	572	USA, CO, Clear Creek Co.	RM	430600	
elynoides Holm	*Hitchcock*	16135	USA, MT, Judith Basin Co.	CAN	163104	
elynoides Holm	*Maguire*	16467	USA, UT, Grand Co.	CAN	163108	
elynoides Holm	*Rydberg*	7218	USA, UT	CAN	163725	
elynoides Holm	*Bowland*	16729	USA, UT, Salt L. Co.	COLO	215258	
elynoides Holm	*Cronquist*	9446	USA, UT, Garfield Co.	DAO	257340	1657
elynoides Holm	*Parker*	5876	USA, WY, Park Co.	DAO	257337	1658
elynoides Holm	*Willard*	6263	USA, CO, Pitkin Co.	DAO	257334	1550
elynoides Holm	*Clokey*	3403	USA, CO, Denver Co.	CAN	163106	1840
elynoides Holm	*Clokey*	3402	USA, CO, Lake Co.	CAN	163107	
elynoides Holm	*Clokey*	4022	USA, CO, Grand Co.	CAN	163098	
elynoides Holm	*Weber*	15172	USA, MT, Deerlodge Co.	COLO	288762	
elynoides Holm	*Willard*	6263	USA, CO, Pitkin Co.	WTU	220207	1652
elynoides Holm	*Henderson*	3309	USA, ID, Clark Co.	WTU	359261	
elynoides Holm	*Lesica*	4040	USA, MT, Lewis & Clark Co.	MONT	104369	

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elynoides Holm	*Franklin*	6737	USA, UT, Summitt Co.	RM	561691	1653
elynoides Holm	*Huber*	2334	USA, Utah, Duchesne Co.	RM	740885	1528
elynoides Holm	*Huber*	2334	USA, Utah, Duchesne Co.	BRY	375486	1656
elynoides Holm	*Goodrich*	s.n.	USA, UT, Summitt Co.	BRY	425947	
elynoides Holm	*WA Weber*	17375	USA, CO, Park Co.	CAN	499689	
elynoides Holm	*Olmsted*	s.n.	USA, WY, Albany Co.	COLO	280664	
elynoides Holm	*Kelso*	6864	USA, CO,	DAO	257341	
elynoides Holm	*Starr*	7090	USA, UT			511
elynoides Holm	*Starr*	7091	USA, UT			512
elynoides Holm	*Goodrich*	24618	USA, Utah, Duchesne Co.	UTC	216205	
elynoides Holm	*Starr*	100521	USA, UT, Summitt Co.			1861
elynoides Holm	*Starr*	100525	USA, UT, Summitt Co.			
elynoides Holm	*Starr*	100526	USA, UT, Summitt Co.			
elynoides Holm	*Starr*	100221	USA, CO, Clear Creek Co.			1865
elynoides Holm	*Goodrich*	24618	USA, Utah, Duchesne Co.	RM	740864	
elynoides Holm	*Starr*	100441	USA, WY, Big Horn Co.			1864
elynoides Holm	*Starr*	100444	USA, WY, Big Horn Co.			
elynoides Holm	*Lesica*	8882	USA, MT, Beaverhead Co.	MONTU	129969	1839
elynoides Holm	*Maguire*	16670	USA, UT, Grand Co.	CAN	163110	1841
elynoides Holm	*Soreng*	2017	USA, NM, Lincoln Co.	COLO	383974	1843
elynoides Holm	*Tiehm*	9849	USA, NV, White Pine Co.	COLO	417605	1844
elynoides Holm	*Taye*	2552	USA, UT, Beaver Co.	CAN	515863	1845
elynoides Holm	*Fertig*	16723	USA, WY, Carbon Co.	CAN	703094	1846
elynoides Holm	*Clokey*	3699	USA, CO, Clear Creek Co.	CAN	163105	
elynoides Holm	*Clokey*	3655	USA, CO, Clear Creek Co.	CAN	163099	
elynoides Holm	*Maguire*	19687	USA, UT, Beaver Co.	CAN	163103	
elynoides Holm	*Lesica*	5029	USA, MT, Madison Co.	CAN	112916	

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elynoides Holm	*Lesica*	785	USA, MT, Broadwater Co.	MONT	85176	
elynoides Holm	*Lesica*	4933	USA, MT, Madison Co.	MONTU	113392	
elynoides Holm	*Lesica*	6174	USA, MT, Carbon Co.	MONTU	120135	
elynoides Holm	*Markow*	8981	USA, ID, Fremont Co.	RM	694232	
elynoides Holm	*ME Lewis*	348	USA, UT, Grand Co.	RM	368033	
elynoides Holm	*Taye*	5238	USA, UT, Beaver Co.	BRY	372953	
elynoides Holm	*Gierisch*	3044	USA, WY, Albany Co.	COLO	202896	
elynoides Holm	*RK Moseley*	418	USA, ID, Butte Co.	RM	361637	
elynoides Holm	*Evert*	19987	USA, MT, Park Co.	RM	621589	
elynoides Holm	*Lackschewitz*	3062	USA, MT, Deerlodge Co.	MONTU	68136	
elynoides Holm	*Hartman*	2217	USA, NM, Colfax Co.	RM	299687	
elynoides Holm	*Yeatts*	5054	USA, UT, Beaver Co.	COLO	524238	
elynoides Holm	*Lackschewitz*	4621	USA, MT, Deerlodge Co.	MONTU	73091	
elynoides Holm	*Mancuso*	2801	USA, ID, Custer Co.	ID	138737	
elynoides Holm	*BE Nelson*	54047	USA, CO, Jackson Co.	COLO	521879	
elynoides Holm	*Hermann*	24062	USA, CO, Boulder Co.	USFS	430604	
elynoides Holm	*Flaig*	555	USA, CO, Mineral Co.	RM	795889	
elynoides Holm	*Brown*	351	USA, UT, Summitt Co.	BRY	478889	
elynoides Holm	*Bjork*	6604	USA, ID, Bonneville Co.	ID	121834	
elynoides Holm	*ME Lewis*	465	USA, UT, Beaver Co.	CAN	515056	
elynoides Holm	*Johnson*	612	USA, UT, Utah Co.	PROVO	383337	
elynoides Holm	*RK Moseley*	636	USA, ID, Custer Co.	ID	395637	
elynoides Holm	*Lesica*	7461	USA, MT, Glacier Co.	MONTU	122958	
elynoides Holm	*Clokey*	3700	USA, CO, Teller Co.	CAN	163101	
elynoides Holm	*Starr*	100062	USA, NM, Taos Co.			
elynoides Holm	*Starr*	100152	USA, CO, La Veta Co.			
elynoides Holm	*Starr*	100181	USA, CO, Huerfano Co.			

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elynoides Holm	*Starr*	100221	USA, CO, Clear Creek Co.			
elynoides Holm	*Starr*	100141	USA, CO, La Veta Co.			
elynoides Holm	*Maguire*	21150	USA, NV, White Pine Co.	CAN	163102	
elynoides Holm	*Franklin*	2049	USA, UT, San Juan Co.	CAN	515612	
elynoides Holm	*Lesica*	7407	USA, MT, Glacier Co.	MONTU	122475	
elynoides Holm	*Hitchcock*	11143	USA, ID, Custer Co.	CAN	163100	
elynoides Holm	*AE Porsild*	22737	USA, WY	CAN	266465	
elynoides Holm	*Franklin*	2049	USA, UT, San Juan Co.	RM	368717	
elynoides Holm	*Starr*	7186	USA, CO, Clear Creek Co.			556
elynoides Holm	*Wellner*	4306	USA, ID, Custer Co.	IDS	100772	
elynoides Holm	*Lesica*	8160	USA, MT, Park Co.	MONT	125731	
elynoides Holm	*Franklin*	6756	USA, UT	CAN	555200	
elynoides Holm	*Kelso*	6774	USA, CO,	DAO	257338	
elynoides Holm	*Mosquin*	4816	USA, WY, Park Co.	DAO	257335	1659
elynoides Holm	*Weber*	4982	USA, CO, Boulder Co.	DAO	293442	
filifolia Nuttall var. *erostrata* Kuk.	*Grant*	7716	USA, CA, El Dorado Co.	CAN	272092	
filifolia Nuttall var. *erostrata* Kuk.	*Turesson*	603	USA, CA, Tuolumne Co.	CAN	163123	
filifolia Nuttall var. *erostrata* Kuk.	*Howell*	20224	USA, CA, Mono Co.	CAN	163124	
filifolia Nuttall var. *erostrata* Kuk.	*Stacey*	12451	USA, CA, Lassen Co.	MONTU	25904	
filifolia Nuttall var. *erostrata* Kuk.	*Starr*	7012	USA, CA, Fresno Co.	CAN		
filifolia Nuttall var. *erostrata* Kuk.	*Starr*	7051	USA, CA, El Dorado Co.	CAN		
filifolia Nuttall var. *erostrata* Kuk.	*Starr*	7050	USA, CA, El Dorado Co.	CAN		
filifolia Nuttall var. *erostrata* Kuk.	*Starr*	7014	USA, CA	CAN		
filifolia Nuttall var. *erostrata* Kuk.	*Beetle*	3960	USA, CA, El Dorado Co.	DAO	293458	
filifolia Nuttall var. *filifolia*	*Reveal*	2325	USA, CA, Mono Co.	SD	103885	
filifolia Nuttall var. *filifolia*	*Sharsmith*	2608	USA, CA, Tuolumne Co.	CAN	163189	1824
filifolia Nuttall var. *filifolia*	*Sandberg*	81	USA, WA, Spokane Co.	CAN	163182	

Species	Collector	Number	Country, province/state, county/quadrant/island	Institute	Catalogue Number	Extraction Number
filifolia Nuttall var. *filifolia*	*Pearson*	29	Canada, YT	CAN	316738	
filifolia Nuttall var. *filifolia*	*Porter*	6874	USA, WY, Platte Co.	UTC	93815	
filifolia Nuttall var. *filifolia*	*Neely*	2762	USA, WY, Laramie Co.	UTC	192352	
filifolia Nuttall var. *filifolia*	*Goodrich*	5815	USA, UT, Daggett Co.	UTC	146948	
filifolia Nuttall var. *filifolia*	*ME Lewis*	3132	USA, NV, Elko Co.	UTC	139176	
filifolia Nuttall var. *filifolia*	*Schofield*	7399	Canada, YT	CAN	270251	
filifolia Nuttall var. *filifolia*	*HM Raup*	13169	Canada, YT	CAN	280747	
filifolia Nuttall var. *filifolia*	*AE Porsild*	22356	Canada, AB	CAN	266081	
filifolia Nuttall var. *filifolia*	*AE Porsild*	12262	Canada, AB	CAN	243955	
filifolia Nuttall var. *filifolia*	*Macoun*	14031	Canada, AB	CAN	20691	
filifolia Nuttall var. *filifolia*	*AE Porsild*	13128	Canada, AB	CAN	243953	
filifolia Nuttall var. *filifolia*	*Macoun*	7395	Canada, AB	CAN	20689	
filifolia Nuttall var. *filifolia*	*Skoglund*	s.n.	Canada, SK, Moosejaw-Watrous Quad	CAN	344528	
filifolia Nuttall var. *filifolia*	*Scoggan*	7165	Canada, MB	CAN	201518	
filifolia Nuttall var. *filifolia*	*Scoggan*	7129	Canada, MB	CAN	201520	
filifolia Nuttall var. *filifolia*	*Clarke*	146	Canada, YT	CAN	20700	
filifolia Nuttall var. *filifolia*	*AE Porsild*	18423	Canada, YT	CAN	208651	
filifolia Nuttall var. *filifolia*	*Scoggan*	10891	Canada, MB	CAN	224809	
filifolia Nuttall var. *filifolia*	*Hitchcock*	16181	USA, MT, Meagher Co.	CAN	163186	1823
filifolia Nuttall var. *filifolia*	*Suksdorf*	31067	USA, WA, W. Klickitat Co.	CAN	163190	1825
filifolia Nuttall var. *filifolia*	*Turesson*	319	USA, ND, Burleigh Co.	CAN	163192	1826
filifolia Nuttall var. *filifolia*	*Clokey*	3064	USA, CO, Denver Co.	CAN	163193	1827
filifolia Nuttall var. *filifolia*	*Spetzman*	1629	USA, Alaska, Valdez-Cordova Co.	CAN	262933	1829
filifolia Nuttall var. *filifolia*	*Spetzman*	79	Canada, YT	CAN	274576	1830
filifolia Nuttall var. *filifolia*	*Nagy*	1179	Canada, AB	CAN	339443	1831
filifolia Nuttall var. *filifolia*	*Baldwin*	10856	Canada, MB	CAN	437539	1832
filifolia Nuttall var. *filifolia*	*Welsh*	24723	USA, SD, Custer Co.	CAN	563843	1834

Species	Collector	Number	Country, province/state, county/quadrant/island	Institute	Catalogue Number	Extraction Number
filifolia Nuttall var. *filifolia*	*Welsh*	24753	USA, WY, Crook Co.	CAN	563836	1835
filifolia Nuttall var. *filifolia*		s.n.			580404	
filifolia Nuttall var. *filifolia*	*Shchepaned*	8994	Canada, SK	CAN	580247	1836
filifolia Nuttall var. *filifolia*	*Scoggan*	7311	Canada, MB	CAN	201519	
filifolia Nuttall var. *filifolia*	*Campbell-Snelling*	468	Canada, AB	CAN	477315	
filifolia Nuttall var. *filifolia*	*Shchepaned*	9150	Canada, SK	CAN	580404	
filifolia Nuttall var. *filifolia*	*Stevens*	1886	USA, ND, Sheridan Co.	CAN	261485	
filifolia Nuttall var. *filifolia*	*Anderson*	10013	Canada, YT	CAN	20701	
filifolia Nuttall var. *filifolia*	*Fraser*	s.n.	Canada, SK	CAN	20684	
filifolia Nuttall var. *filifolia*	*AE Porsild*	22382	Canada, AB	CAN	266080	
filifolia Nuttall var. *filifolia*	*A Nelson*	4007	USA, WY, Carbon Co.	UTC	174899	
filifolia Nuttall var. *filifolia*		s.n.	USA, WY, Natrona Co.	UTC	201667	
filifolia Nuttall var. *filifolia*	*Constance*	1538	USA, WA, Whitman Co.	UTC	23059	
filifolia Nuttall var. *filifolia*	*ME Lewis*	5763	USA, UT, Wayne Co.	UTC	165308	
filifolia Nuttall var. *filifolia*	*Howell*	s.n.	USA, OR, Harvey Co.	UTC	97156	
filifolia Nuttall var. *filifolia*	*AE Porsild*	s.n.	Canada, YT	CAN	20698	
filifolia Nuttall var. *filifolia*	*Spetzman*	82	Canada, YT	CAN	274579	
filifolia Nuttall var. *filifolia*	*Macoun*	13384	Canada, MB	CAN	20681	
filifolia Nuttall var. *filifolia*	*Macoun*	31071	Canada, SK	CAN	20682	
filifolia Nuttall var. *filifolia*	*JM Macoun*	39	Canada, AB	CAN	20688	
filifolia Nuttall var. *filifolia*	*Anderson*	9529	Canada, YT	CAN	20699	
filifolia Nuttall var. *filifolia*	*Brayshaw*	s.n.	Canada, SK	CAN	569889	
filifolia Nuttall var. *filifolia*	*Macoun*	10718	Canada, AB	CAN	20692	
filifolia Nuttall var. *filifolia*	*Saarela*	377	Canada, SK	CAN	591343	
filifolia Nuttall var. *filifolia*	*G Lewis*	789	Canada, AB	CAN	432875	
filifolia Nuttall var. *filifolia*	*AE Porsild*	9707	Canada, YT	CAN	20694	
filifolia Nuttall var. *filifolia*	*Malte*	633	Canada, AB	CAN	26923	

Species	Collector	Number	Country, province/state, county/quadrant/island	Institute	Catalogue Number	Extraction Number
filifolia Nuttall var. *filifolia*	*Franklin*	6135	USA, UT, Wayne Co.	CAN	551170	1833
filifolia Nuttall var. *filifolia*	*AE Porsild*	16657	Canada, NT	CAN	20693	1828
filifolia Nuttall var. *filifolia*	*Starr*	7209	USA, CO,			566
oreocharis Holm	*Landrum*	7126	USA, AZ, Apache Co.	ASU	177390	1842
oreocharis Holm	*Starr*	s.n.	USA			559
oreocharis Holm	*Starr*	s.n.	USA			561
oreocharis Holm	*Starr*	s.n.	USA			563
Carex L. subgenus *Psyllophora* section *Capituligerae* Kükenthal						
capitata Linnaeus	*Starr*	7054	USA, CA			475
Section *Chordorrhizae* (Heuffel) Meinhausen						
chordorrhiza Erhart ex Linnaeus f.	*Brayshaw*	28759	Canada, AB	CAN	569904	
Section *Obtusatae* (Tuckerman) MacKenzie						
obtusata Liljeblad	*Neatby*	s.n.	Canada, MB	DAO	257317	
Section *Rupestres* (Tuckerman) Meinhausen						
rupestris Allioni	*Starr*	100415	USA, WY			1586
rupestris Allioni	*Starr*	7083	USA, UT			504
Section *Dornera* Heuffel						
nigricans Meyer	*Cronquist*	1891	USA, ID, Fremont Co.	UTC	32906	
nigricans Meyer	*French*	241	USA, WA, King Co.	WTU	364720	
nigricans Meyer	*Davis*	266	USA, WY, Albany Co.	UTC	178294	

Species	Collector	Number	Country, province/state, county/quadrant/island	Institute	Catalogue Number	Extraction Number
micropoda Meyer	*Arnett*	6119	USA, CO, Hinsdale Co.	RM	749006	
micropoda Meyer	*Lesica*	6385	USA, MT, Glacier Co.	MONT	119476	
micropoda Meyer	*Langston*	3398	USA, MT, Ravalli Co.	RM	736066	
micropoda Meyer	*Kennedy*	56	Canada, BC	DAO	668308	
Kobresia Willdenow						
myosuroides (Villars) Fiori	*Lambert*	s.n.	Canada, NT, MacKenzie Dist.	CAN	535877	
myosuroides (Villars) Fiori	*Edlund*	267	Canada, NU, Melville I.	CAN	499911	
myosuroides (Villars) Fiori	*Edlund*	381	Canada, NU, Melville I.	CAN	489120	
myosuroides (Villars) Fiori	*Aiken*	280	Canada, NU, Melville I.	CAN	499880	
myosuroides (Villars) Fiori	*Spellenberg*	5679	Canada, AB	CAN	457664	
myosuroides (Villars) Fiori	*Packer*	3195	Canada, AB	DAO	638698	
myosuroides (Villars) Fiori	*Weber*	7144	USA, CO, Park Co.	DAO	257342	
myosuroides (Villars) Fiori	*HM Raup*	3916	Canada, BC	CAN	17325	
myosuroides (Villars) Fiori	*Komarkova*	s.n.	USA, CO, Boulder Co.	UTC	137113	
myosuroides (Villars) Fiori	*Pogson*	468	USA, OR, Harney Co.		152374	
myosuroides (Villars) Fiori	*Cusick*	2456	USA, OR		18724	
myosuroides (Villars) Fiori	*Allen*	768	Canada, AB	CAN	465704	
indeterminate	*Kozhevnikov*	s.n.	USSR, Chukotka	CAN	408304	
indeterminate	*Christie*	122	Canada, NU, Ellesmere I.	CAN	264248	
indeterminate	*Duffy*	4160	USA, Alaska, Talkeetna B5 Quad	ALA	133649	
indeterminate	*Holmen*	49699	Greenland	CAN	17243	
indeterminate	*Kristinsson*	14144	Iceland, Finnungsstor	ICEL	10899	
indeterminate		s.n.	USA	HUH		

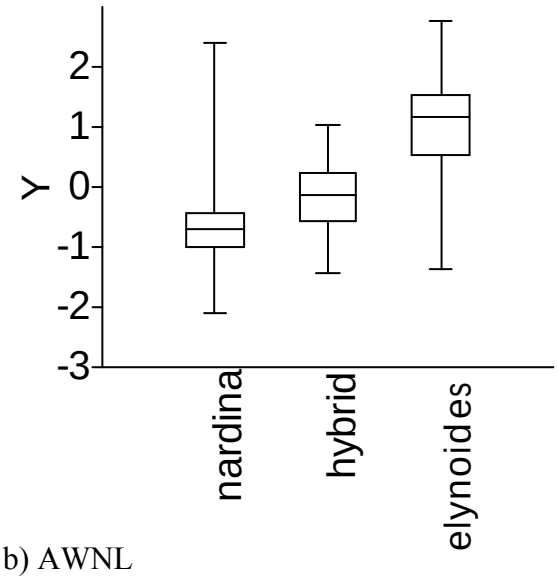
APPENDIX 2 PCA loadings of uncorrelated characters used in comparing a) *C. hepburnii* and *C. nardina* classified using Egorova (1999), n = 84, and b) the *C. nardina* complex, *C. elynoides* and the putative hybrid (n = 114). Significant loadings (< - 0.6 or > 0.6) are in bold.

Morphological character	PC1
a) *C. hepburnii*, *C. nardina*	
ACHENEL	**-0.626**
AWNL	0.0585
BEAKL	-0.238
BEAKTEETHN	-0.140
CHESTHAIRN	-0.504
HYALINW	-0.178
MARGHAIRN	-0.505
MIDRIBW	-0.355
NERVEN	0.0428
PERIGW	**-0.604**
SCALEL	**-0.748**
SERRL	**-0.604**
SHAPEPE	-0.526
SHOULDER	-0.449
SPIKEL	**-0.779**
STAML	**-0.643**
STIPEL	-0.382
STYLEXL	-0.0471
b) *C. nardina*, *C. elynoides*, putative hybrid	
ACHENEL	**-0.768**
AWNL	-0.335
BEAKL	**-0.862**
BEAKTEETHN	0.231
CHESTHAIRN	0.0666
HYALINW	**-0.678**
MIDRIBW	-0.398
NERVEN	**0.802**
SCALEL	-0.565
STAML	**-0.826**

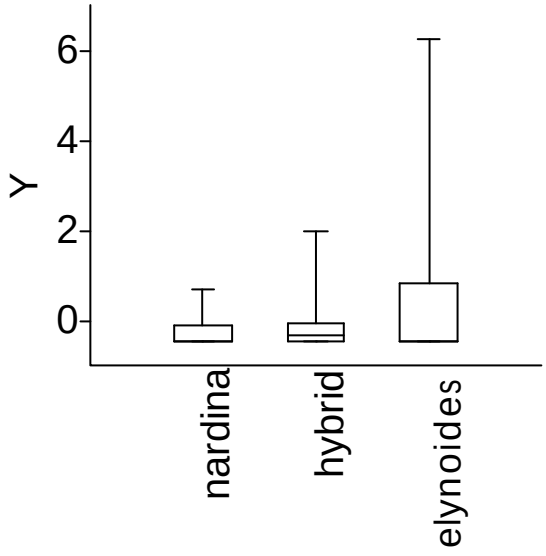
APPENDIX 3 PCA loadings of uncorrelated characters used in comparing a) the *C. nardina* complex, *C. filifolia* var. *filifolia* and the putative hybrid (n = 135) and b) *C. filifolia* var. *filifolia*, *C. elynoides* and *C. filifolia* var. *erostrata* (n = 101). Significant loadings (< - 0.6 or > 0.6) are in bold.

Morphological character	PC1	PC2
a) *C. nardina*, *C. filifolia* var. *filifolia*, putative hybrid		
AWNL	-0.0250	
BEAKL	-0.400	
HYALINW	**-0.649**	
MIDRIBW	**-0.639**	
NERVEN	**0.809**	
PERIGW	**-0.702**	
SHOULDER	-0.370	
STAML	**-0.853**	
b) *C. filifolia* var. *filifolia*, *C. elynoides*, *C. filifolia* var. *erostrata*		
ACHENEL	**-0.602**	0.398
AWNL	-0.137	-0.361
BEAKL	**-0.608**	**0.681**
HYALINW	-0.222	0.385
MIDRIBW	-0.453	0.281
NERVEN	-0.166	-0.242
PERIGW	-0.430	0.518
SCALEL	**-0.813**	-0.121
SERRL	-0.0433	**-0.740**
SHAPEPE	**-0.774**	-0.288
SHOULDER	**-0.620**	**-0.613**
SPIKEL	**-0.603**	0.374
STAML	-0.598	0.428
STIPEL	-0.403	0.0982
STYLEXL	-0.0921	-0.249

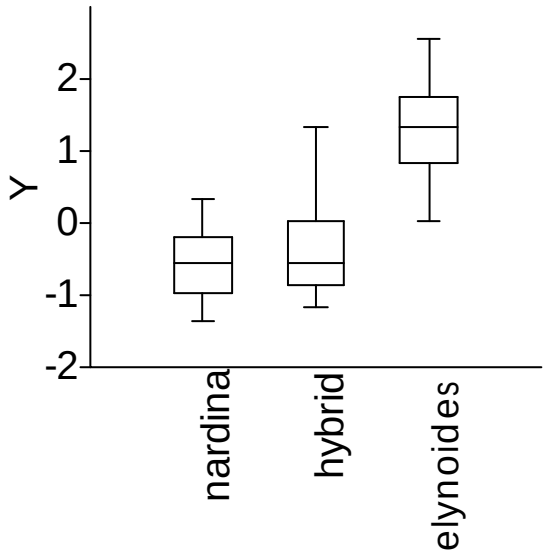
a) ACHENEL



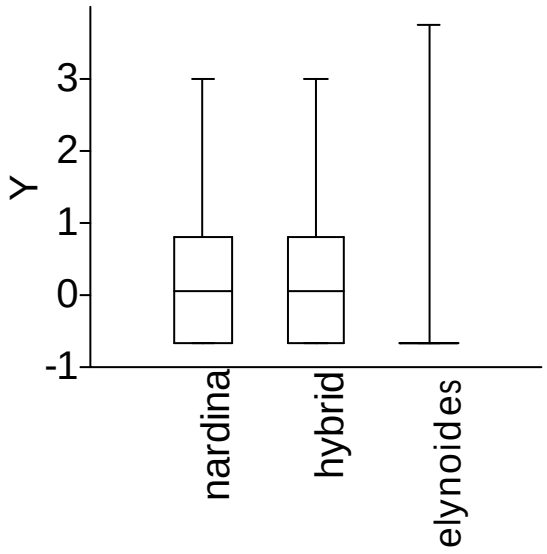
b) AWNL



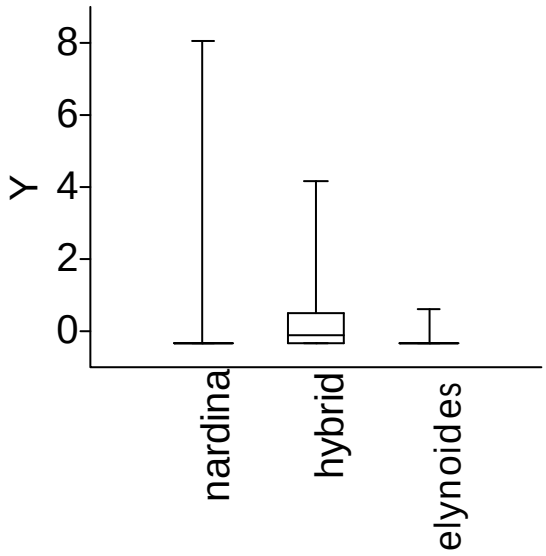
c) BEAKL



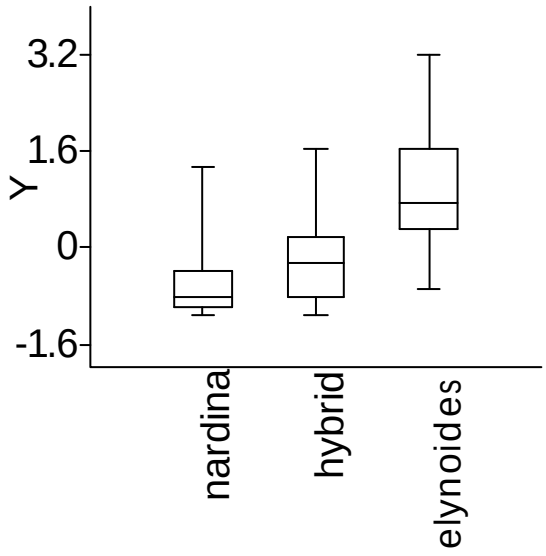
d) BEAKTEETHN



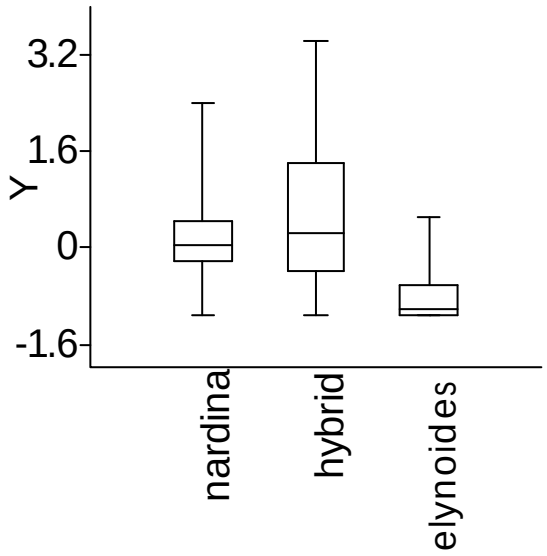
e) CHESTHAIRN



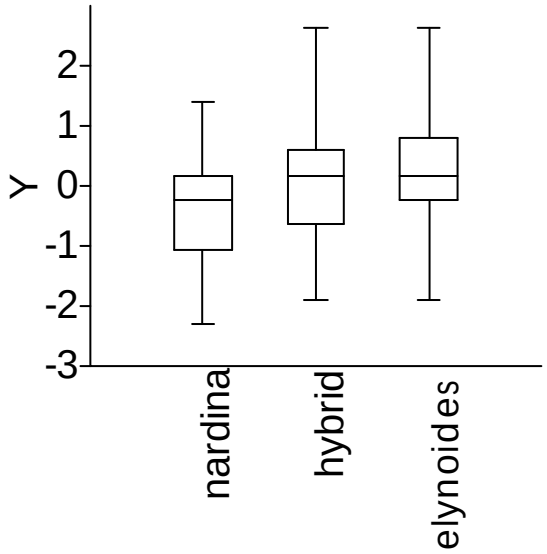
f) HYALINW



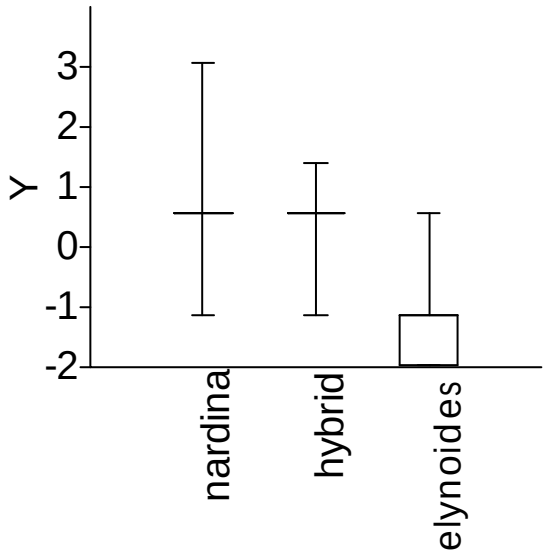
g) MARGHAIRN



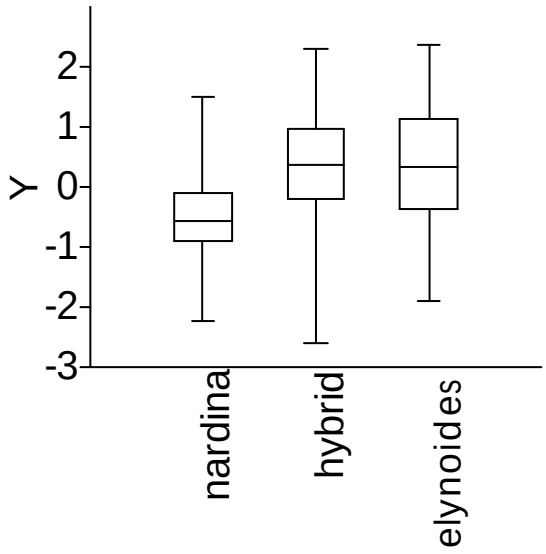
h) MIDRIBW



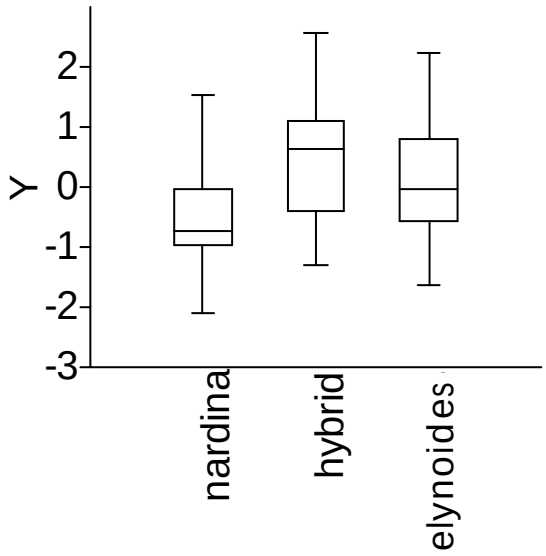
i) NERVEN



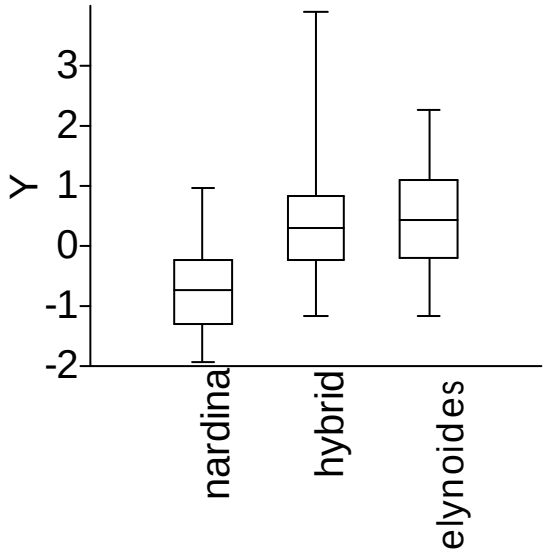
j) PERIGL



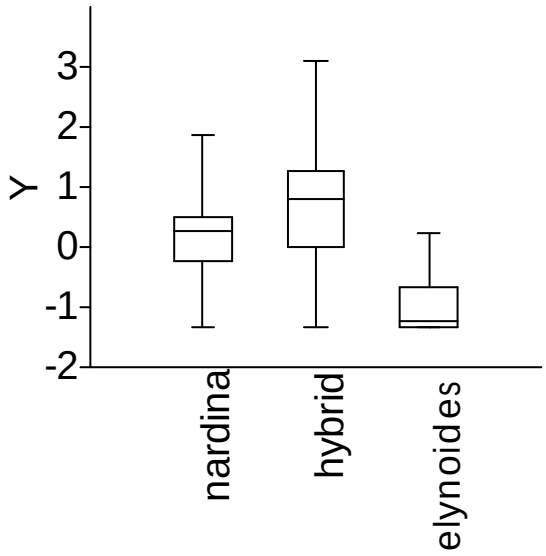
k) PERIGW



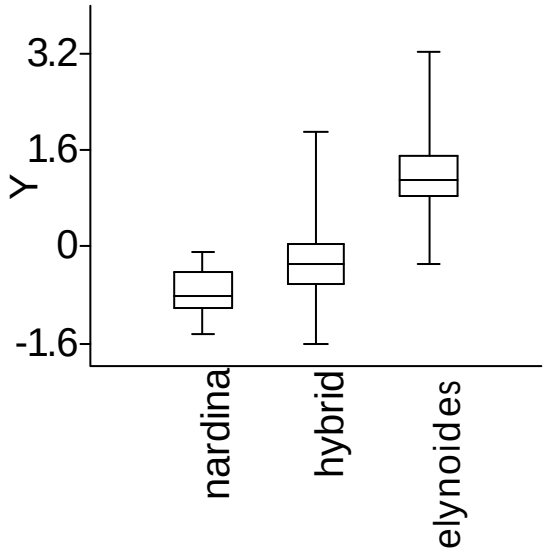
l) SCALEL



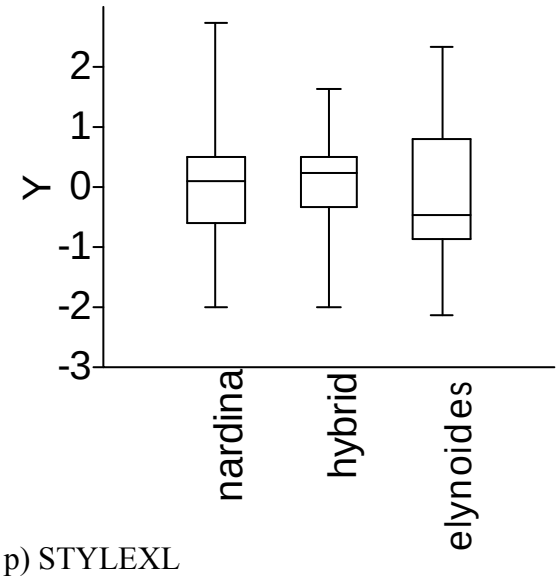
m) SERRL



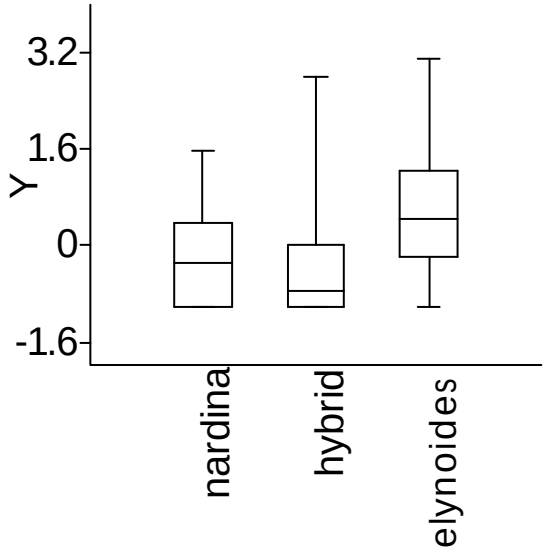
n) STAML



o) STIPEL

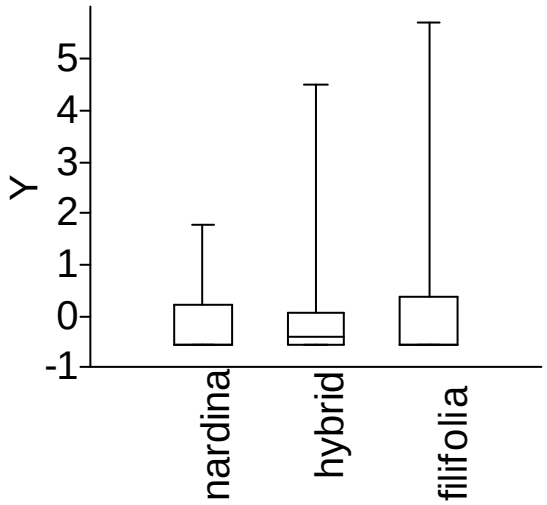


p) STYLEXL

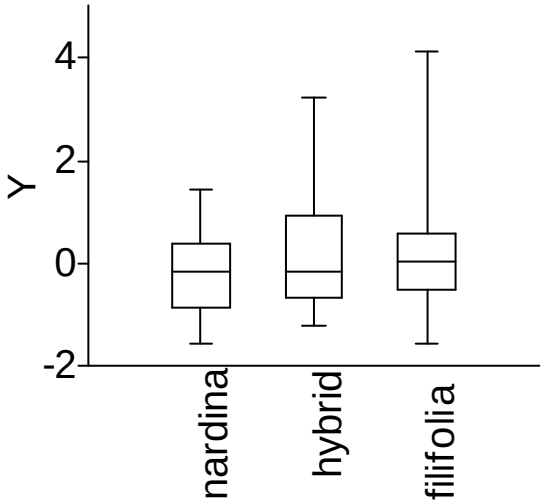


APPENDIX 4 Box plots of uncorrelated morphological character measurements for *C. nardina*, the putative hybrid and *C. elynoides*. a) ACHENEL*, b) AWNL*, c) BEAKL*, d) BEAKTEETHN*, e) CHESTHAIRN*, f) HYALINW*, g) MARGHAIRN, h) MIDRIBW, i) NERVEN*, j) PERIGL, k) PERIGW, l) SCALEL*, m) SERRL, n) STAML*, o) STIPEL, p) STYLEXL. * = apparently intermediate, n = 120.

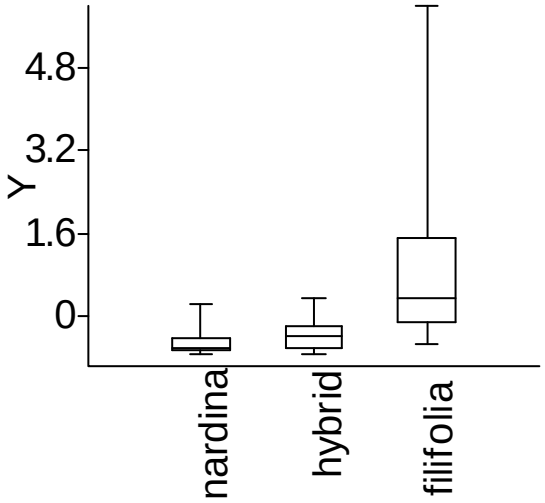
a) AWNL



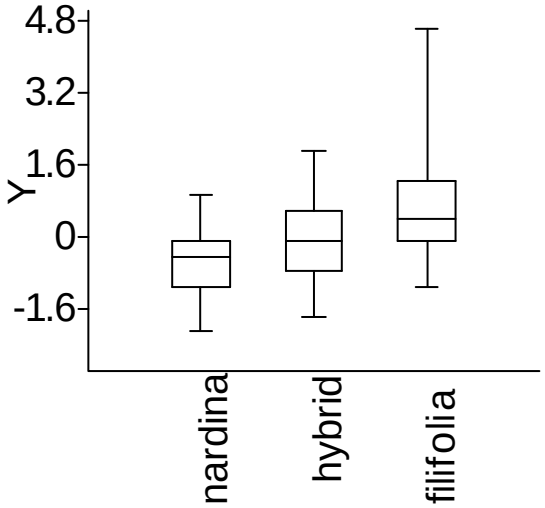
b) BEAKL



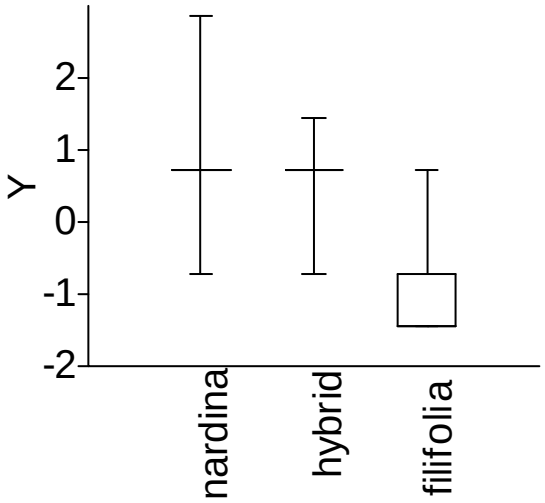
c) HYALINW



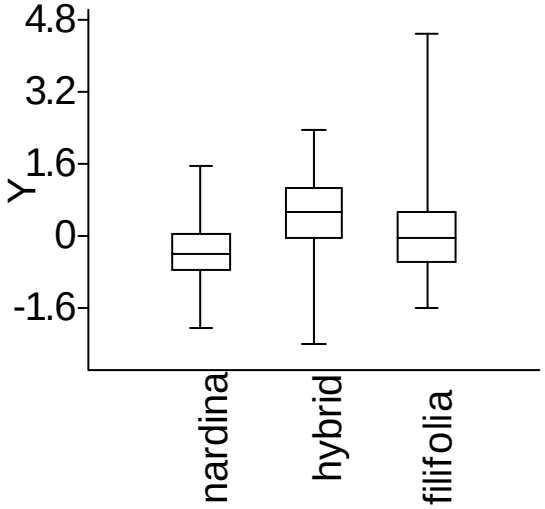
d) MIDRIBW



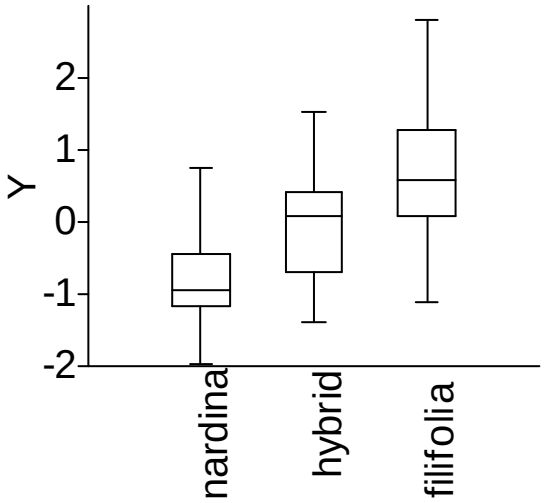
e) NERVEN



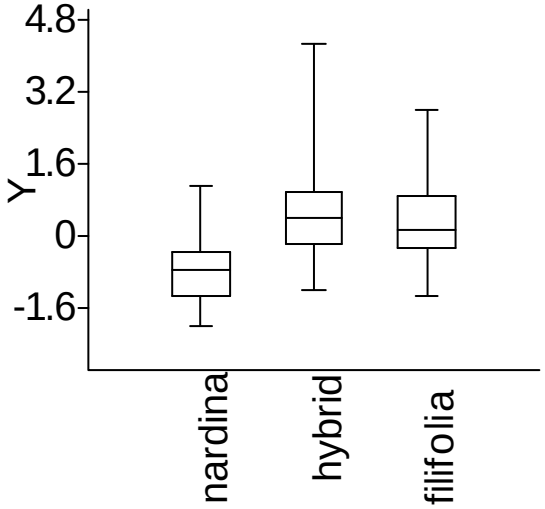
f) PERIGL



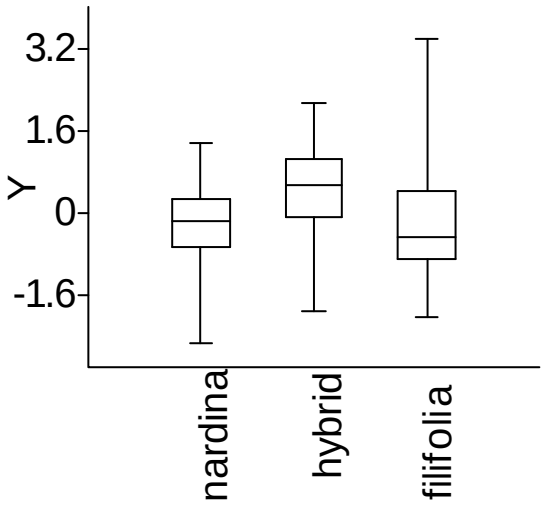
g) PERIGW



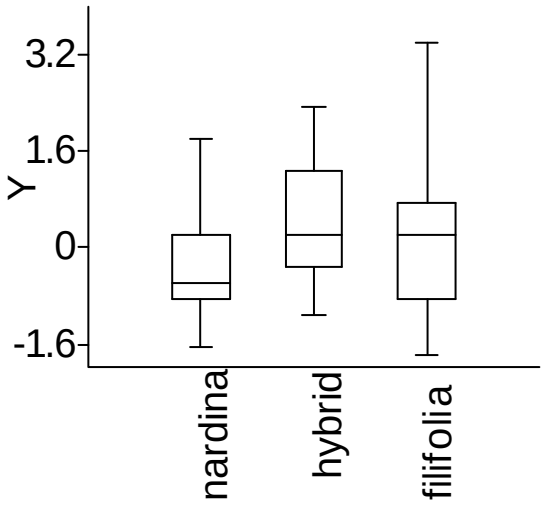
h) SCALEL



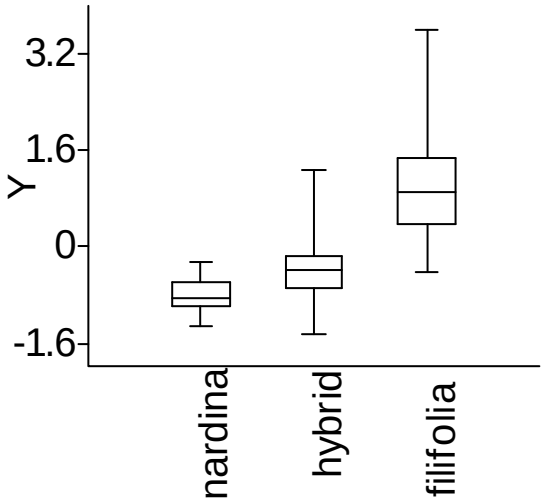
i) SHAPEPE



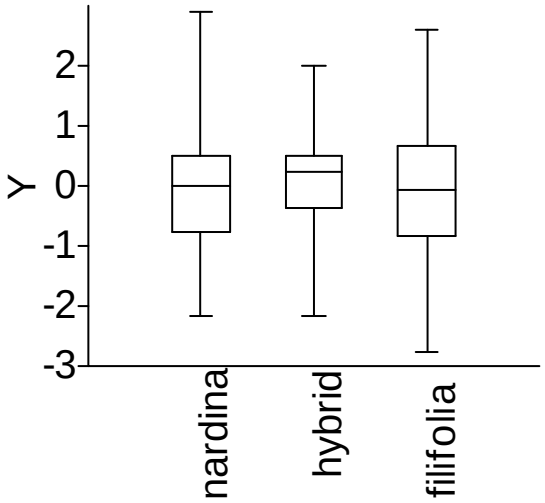
j) SHOULDER



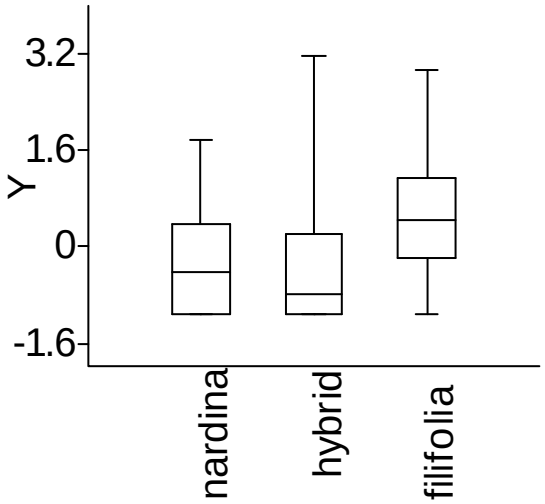
k) STAML



l) STIPEL



m) STYLEXL



APPENDIX 5 Box plots of uncorrelated morphological character measurements for *C. nardina*, the putative hybrid and *C. filifolia* var. *filifolia*. Means and quartiles are shown. a) AWNL*, b) BEAKL*, c) HYALINW*, d) MIDRIBW*, e) NERVEN*, f) PERIGL, g) PERIGW*, h) SCALEL, i) SHAPEPE, j) SHOULDER*, k) STAML*, l) STIPEL and m) STYLEXL. * = apparently intermediate, n = 135.

APPENDIX 6 Linear correlation matrix with r-values and p-values (r*p*) for 20 morphological characters for *C. nardina* and *C. hepburnii*. Significant correlations (|r| ≥ 7.0E-01) are in bold, n = 84.

	ACHENEL	AWNL	BEAKL	BEAKTEETHN	CHESTHAIRN	HYALINW	MARGHAIRN	MIDRIBL	MIDRIBW	NERVEN
ACHENEL	-	2.99E-01	4.70E-01	3.44E-01	2.17E-05	5.26E-01	1.04E-01	5.07E-03	8.17E-01	9.92E-01
AWNL	1.15E-01	-	9.21E-02	4.57E-01	1.69E-01	6.89E-02	3.08E-01	4.68E-01	6.73E-01	3.71E-01
BEAKL	7.99E-02	1.85E-01	-	8.04E-01	8.63E-01	2.07E-01	8.87E-02	9.13E-01	4.54E-02	1.13E-04
BEAKTEETHN	1.05E-01	-8.22E-02	2.74E-02	-	3.66E-01	3.38E-01	1.30E-01	1.58E-01	3.79E-01	2.39E-01
CHESTHAIRN	4.46E-01	-1.52E-01	-1.91E-02	9.99E-02	-	2.79E-01	4.22E-05	9.94E-02	1.22E-01	8.40E-01
HYALINW	7.02E-02	1.99E-01	-1.39E-01	1.06E-01	1.20E-01	-	7.30E-01	2.04E-01	5.94E-01	9.28E-01
MARGHAIRN	1.79E-01	-1.12E-01	-1.87E-01	1.66E-01	4.31E-01	3.82E-02	-	2.20E-02	4.87E-01	1.38E-02
MIDRIBL	3.03E-01	8.02E-02	1.22E-02	-1.55E-01	1.81E-01	1.40E-01	2.50E-01	-	6.45E-05	9.32E-01
MIDRIBW	2.56E-02	-4.67E-02	2.19E-01	-9.72E-02	1.70E-01	5.90E-02	7.70E-02	4.22E-01	-	3.73E-02
NERVEN	-1.08E-03	-9.89E-02	-4.09E-01	1.30E-01	2.24E-02	9.97E-03	2.68E-01	-9.44E-03	-2.28E-01	-
PERIGL	4.48E-01	-2.14E-02	1.01E-01	1.43E-01	2.09E-01	-1.01E-01	3.89E-01	3.96E-01	1.88E-01	-1.08E-02
PERIGW	4.39E-01	-9.97E-02	-1.38E-01	1.42E-01	2.10E-01	2.17E-01	3.52E-01	3.13E-01	1.15E-01	5.79E-02
SCALEL	3.03E-01	6.68E-02	1.09E-01	-2.37E-02	1.70E-01	1.19E-01	3.13E-01	**8.13E-01**	4.70E-01	-1.30E-02
SERRL	3.82E-01	3.61E-02	1.44E-01	1.63E-01	1.92E-01	-3.29E-02	4.04E-01	3.43E-01	2.18E-01	1.55E-01
SHAPEPE	3.79E-01	-1.27E-01	2.34E-01	3.00E-02	9.44E-02	-2.41E-01	1.90E-01	3.00E-01	7.53E-02	-1.41E-02
SHOULDER	1.88E-01	1.99E-01	6.27E-01	1.14E-01	6.01E-02	1.02E-01	-1.05E-01	1.98E-01	1.97E-01	-2.50E-01
SPIKEL	3.91E-01	1.93E-01	2.69E-01	6.37E-03	3.31E-01	2.26E-01	2.02E-01	5.53E-01	2.17E-01	-1.59E-01
STAML	2.71E-01	-1.55E-03	6.72E-02	4.03E-02	3.13E-01	1.41E-01	3.48E-01	3.31E-01	-4.98E-03	-1.39E-02
STIPEL	1.66E-01	-8.68E-03	-1.27E-01	-2.48E-02	1.85E-01	7.42E-02	2.88E-01	2.67E-01	1.19E-01	4.44E-02
STYLEXL	3.02E-02	1.20E-01	1.75E-01	-1.17E-01	-5.25E-02	-5.28E-02	-1.13E-01	6.53E-02	6.52E-02	6.91E-02

APPENDIX 6 (Cont'd) Linear correlation matrix with r-values and p-values (r*p*) for 20 morphological characters for *C. nardina* and *C. hepburnii*, n = 84. Significant correlations (|r| ≥ 7.0E-01) are in bold.

	PERIGL	PERIGW	SCALEL	SERRL	SHAPEPE	SHOULDER	SPIKEL	STAML	STIPEL	STYLEXL
ACHENEL	1.93E-05	2.99E-05	5.13E-03	3.36E-04	3.74E-04	8.73E-02	2.37E-04	1.25E-02	1.32E-01	7.85E-01
AWNL	8.47E-01	3.67E-01	5.46E-01	7.44E-01	2.50E-01	6.99E-02	7.83E-02	9.89E-01	9.38E-01	2.75E-01
BEAKL	3.59E-01	2.11E-01	3.25E-01	1.91E-01	3.21E-02	1.70E-10	1.34E-02	5.44E-01	2.49E-01	1.11E-01
BEAKTEETHN	1.93E-01	1.97E-01	8.30E-01	1.38E-01	7.86E-01	3.01E-01	9.54E-01	7.16E-01	8.23E-01	2.91E-01
CHESTHAIRN	5.61E-02	5.50E-02	1.22E-01	7.94E-02	3.93E-01	5.87E-01	2.12E-03	3.73E-03	9.21E-02	6.35E-01
HYALINW	3.59E-01	4.73E-02	2.81E-01	7.67E-01	2.73E-02	3.54E-01	3.87E-02	2.01E-01	5.02E-01	6.34E-01
MARGHAIRN	2.57E-04	1.03E-03	3.74E-03	1.36E-04	8.28E-02	3.40E-01	6.47E-02	1.19E-03	7.90E-03	3.05E-01
MIDRIBL	1.91E-04	3.73E-03	5.64E-21	1.43E-03	5.49E-03	7.04E-02	5.05E-08	2.11E-03	1.39E-02	5.55E-01
MIDRIBW	8.69E-02	2.96E-01	6.51E-06	4.61E-02	4.96E-01	7.28E-02	4.70E-02	9.64E-01	2.83E-01	5.56E-01
NERVEN	9.22E-01	6.01E-01	9.07E-01	1.60E-01	8.99E-01	2.18E-02	1.49E-01	9.00E-01	6.89E-01	5.32E-01
PERIGL	-	2.25E-03	4.02E-07	5.78E-09	6.19E-16	4.71E-01	4.24E-05	1.70E-02	3.88E-04	9.76E-01
PERIGW	3.29E-01	-	3.24E-04	3.92E-02	1.33E-01	1.39E-01	2.64E-04	3.09E-04	6.28E-03	4.67E-01
SCALEL	5.20E-01	3.83E-01	-	7.94E-04	1.12E-03	1.23E-02	3.29E-11	1.13E-03	3.65E-05	2.89E-01
SERRL	5.83E-01	2.25E-01	3.59E-01	-	2.06E-06	3.08E-01	1.92E-02	3.12E-03	6.72E-02	8.88E-01
SHAPEPE	**7.43E-01**	1.65E-01	3.50E-01	4.92E-01	-	2.07E-01	1.14E-03	3.56E-02	1.66E-01	5.18E-01
SHOULDER	7.98E-02	1.63E-01	2.72E-01	1.13E-01	1.39E-01	-	2.58E-06	3.88E-03	6.80E-01	3.75E-01
SPIKEL	4.31E-01	3.88E-01	6.46E-01	2.55E-01	3.49E-01	4.87E-01	-	9.78E-09	4.78E-01	2.07E-01
STAML	2.60E-01	3.84E-01	3.49E-01	3.19E-01	2.30E-01	3.12E-01	5.76E-01	-	3.45E-01	2.71E-01
STIPEL	3.78E-01	2.96E-01	4.34E-01	2.01E-01	1.52E-01	-4.56E-02	7.85E-02	1.04E-01	-	8.88E-01
STYLEXL	3.40E-03	-8.04E-02	1.17E-01	1.56E-02	7.15E-02	9.81E-02	1.39E-01	-1.21E-01	1.57E-02	-

APPENDIX 7 Linear correlation matrix with r-values and p-values (r*p*) for 20 morphological characters for the *C. nardina* complex, *C. elynoides* and the putative hybrid. Significant correlations (|r| ≥ 7.0E-01) are in bold, n = 120.

	ACHENEL	AWNL	BEAKL	BEAKTEETHN	CHESTHAIRN	HYALINW	MARGHAIRN	MIDRIBL	MIDRIBW	NERVEN
ACHENEL	-	*1.79E-02*	*2.25E-15*	*4.70E-01*	*1.40E-01*	*1.93E-07*	*2.66E-03*	*1.40E-05*	*9.98E-02*	*4.12E-08*
AWNL	2.16E-01	-	*4.73E-03*	*4.62E-01*	*2.81E-01*	*5.58E-02*	*9.72E-02*	*1.49E-01*	*8.35E-01*	*2.10E-03*
BEAKL	6.44E-01	2.56E-01	-	*1.16E-01*	*8.37E-02*	*5.55E-08*	*4.86E-10*	*3.17E-03*	*2.00E-03*	*3.28E-17*
BEAKTEETHN	-6.66E-02	-6.77E-02	-1.44E-01	-	*1.09E-01*	*6.48E-01*	*1.91E-03*	*5.38E-02*	*2.04E-01*	*9.74E-03*
CHESTHAIRN	1.35E-01	-9.92E-02	-1.59E-01	1.47E-01	-	*5.32E-01*	*3.42E-07*	*3.75E-01*	*3.39E-01*	*9.33E-02*
HYALINW	4.54E-01	1.75E-01	4.71E-01	-4.21E-02	-5.76E-02	-	*3.22E-04*	*3.87E-03*	*1.34E-01*	*8.79E-09*
MARGHAIRN	-2.72E-01	-1.52E-01	-5.30E-01	2.81E-01	4.45E-01	-3.23E-01	-	*8.64E-01*	*7.38E-01*	*9.61E-09*
MIDRIBL	3.85E-01	1.33E-01	2.67E-01	-1.77E-01	8.18E-02	2.62E-01	1.58E-02	-	*1.34E-06*	*3.82E-02*
MIDRIBW	1.51E-01	1.92E-02	2.79E-01	-1.17E-01	8.80E-02	1.38E-01	-3.09E-02	4.25E-01	-	*1.04E-03*
NERVEN	-4.75E-01	-2.78E-01	-6.74E-01	2.35E-01	1.54E-01	-4.95E-01	4.94E-01	-1.89E-01	-2.96E-01	-
PERIGL	5.37E-01	8.43E-02	2.97E-01	1.12E-01	1.34E-01	8.77E-02	1.51E-01	4.18E-01	1.98E-01	-5.11E-02
PERIGW	3.73E-01	-1.22E-02	8.92E-02	1.20E-01	1.74E-01	1.51E-01	1.82E-01	2.74E-01	1.36E-01	-2.81E-02
SCALEL	4.27E-01	1.70E-01	3.80E-01	-7.16E-02	7.10E-02	2.60E-01	2.13E-02	**8.19E-01**	4.62E-01	-2.23E-01
SERRL	-2.63E-01	-1.21E-01	-4.95E-01	3.03E-01	2.56E-01	-4.10E-01	6.28E-01	3.16E-02	1.30E-02	5.42E-01
SHAPEPE	4.99E-01	-1.14E-02	4.24E-01	1.77E-02	2.61E-02	7.58E-02	-5.43E-02	3.15E-01	1.32E-01	-1.02E-01
SHOULDER	5.47E-01	3.02E-01	**8.10E-01**	-6.09E-02	-9.49E-02	4.79E-01	-4.50E-01	3.32E-01	2.16E-01	-6.26E-01
SPIKEL	6.43E-01	3.34E-01	**7.25E-01**	-1.47E-01	5.73E-02	5.52E-01	-2.95E-01	4.90E-01	3.04E-01	-6.40E-01
STAML	6.05E-01	8.85E-02	6.97E-01	-1.53E-01	4.13E-03	5.44E-01	-2.91E-01	3.33E-01	1.51E-01	-6.48E-01
STIPEL	1.00E-01	2.01E-02	-5.75E-02	-3.74E-02	1.48E-01	-2.14E-02	2.02E-01	1.89E-01	5.19E-02	1.27E-01
STYLEXL	2.55E-01	2.12E-01	3.64E-01	-2.10E-01	-9.92E-02	1.78E-01	-2.98E-01	1.05E-01	4.75E-02	-3.48E-01

APPENDIX 7 (Cont'd) Linear correlation matrix with r-values and p-values (r*p*) for 20 morphological characters for the *C. nardina* complex, *C. elynoides* and the putative hybrid. Significant correlations (|r| ≥ 7.0E-01) are in bold, n = 120.

	PERIGL	PERIGW	SCALEL	SERRL	SHAPEPE	SHOULDER	SPIKEL	STAML	STIPEL	STYLEXL
ACHENEL	*2.48E-10*	*2.75E-05*	*1.16E-06*	*3.67E-03*	*6.75E-09*	*9.84E-11*	*2.53E-15*	*2.49E-13*	*2.75E-01*	*5.02E-03*
AWNL	*3.60E-01*	*8.95E-01*	*6.38E-02*	*1.90E-01*	*9.02E-01*	*7.86E-04*	*1.92E-04*	*3.36E-01*	*8.28E-01*	*2.01E-02*
BEAKL	*9.74E-04*	*3.33E-01*	*1.89E-05*	*9.33E-09*	*1.36E-06*	*4.34E-29*	*7.61E-21*	*9.94E-19*	*5.32E-01*	*4.45E-05*
BEAKTEETHN	*2.22E-01*	*1.93E-01*	*4.37E-01*	*7.77E-04*	*8.48E-01*	*5.09E-01*	*1.09E-01*	*9.53E-02*	*6.85E-01*	*2.13E-02*
CHESTHAIRN	*1.45E-01*	*5.71E-02*	*4.41E-01*	*4.81E-03*	*7.78E-01*	*3.03E-01*	*5.34E-01*	*9.64E-01*	*1.06E-01*	*2.81E-01*
HYALINW	*3.41E-01*	*1.00E-01*	*4.17E-03*	*3.25E-06*	*4.11E-01*	*3.12E-08*	*6.16E-11*	*1.35E-10*	*8.16E-01*	*5.24E-02*
MARGHAIRN	*9.98E-02*	*4.65E-02*	*8.17E-01*	*1.66E-14*	*5.56E-01*	*2.51E-07*	*1.09E-03*	*1.26E-03*	*2.73E-02*	*9.42E-04*
MIDRIBL	*1.99E-06*	*2.47E-03*	*2.74E-30*	*7.32E-01*	*4.61E-04*	*2.11E-04*	*1.39E-08*	*2.01E-04*	*3.83E-02*	*2.52E-01*
MIDRIBW	*3.05E-02*	*1.37E-01*	*1.10E-07*	*8.88E-01*	*1.51E-01*	*1.79E-02*	*7.42E-04*	*9.88E-02*	*5.74E-01*	*6.07E-01*
NERVEN	5.80E-01	7.61E-01	1.42E-02	1.65E-10	2.67E-01	2.15E-14	3.46E-15	1.22E-15	1.67E-01	9.90E-05
PERIGL	-	*7.22E-04*	*6.35E-11*	*1.21E-02*	*9.74E-24*	*3.60E-02*	*9.41E-06*	*9.40E-03*	*3.90E-04*	*6.43E-01*
PERIGW	3.04E-01	-	*3.59E-05*	*6.58E-01*	*3.29E-02*	*1.26E-02*	*9.00E-04*	*3.81E-03*	*4.57E-03*	*7.38E-01*
SCALEL	5.52E-01	3.68E-01	-	*9.55E-01*	*2.74E-06*	*1.84E-06*	*8.83E-14*	*5.19E-05*	*1.50E-03*	*3.02E-02*
SERRL	2.28E-01	4.08E-02	5.19E-03	-	*2.91E-01*	*3.45E-06*	*6.85E-05*	*5.60E-06*	*9.76E-02*	*3.57E-03*
SHAPEPE	**7.59E-01**	1.95E-01	4.13E-01	9.73E-02	-	*1.27E-03*	*3.73E-06*	*9.45E-04*	*6.86E-02*	*9.27E-02*
SHOULDER	1.92E-01	2.27E-01	4.20E-01	-4.09E-01	2.91E-01	-	*1.02E-20*	*8.09E-15*	*4.66E-01*	*3.76E-05*
SPIKEL	3.92E-01	2.99E-01	6.14E-01	-3.55E-01	4.08E-01	**7.24E-01**	-	*6.62E-25*	*8.14E-01*	*4.70E-05*
STAML	2.36E-01	2.62E-01	3.61E-01	-4.01E-01	2.98E-01	6.34E-01	**7.71E-01**	-	*8.53E-01*	*8.89E-03*
STIPEL	3.19E-01	2.57E-01	2.87E-01	1.52E-01	1.67E-01	-6.72E-02	2.17E-02	1.71E-02	-	*7.19E-02*
STYLEXL	4.28E-02	3.08E-02	1.98E-01	-2.64E-01	1.54E-01	3.67E-01	3.63E-01	2.38E-01	1.65E-01	-

APPENDIX 8 Linear correlation matrix with r-values and p-values (r\p) for 20 morphological characters for the *C. nardina* complex, *C. filifolia* var. *filifolia* the putative hybrid. Significant correlations (|r| ≥ 7.0E-01) are in bold, n = 135.

	ACHENEL	AWNL	BEAKL	HYALINW	MIDRIBL	MIDRIBW	NERVEN	PERIGL	PERIGW	SCALEL
ACHENEL	-	5.17E-01	1.34E-02	7.24E-10	9.64E-08	5.62E-05	3.38E-14	7.40E-07	1.47E-15	2.58E-06
AWNL	5.63E-02	-	2.64E-01	5.42E-01	3.72E-01	9.91E-01	8.18E-01	9.82E-01	7.09E-01	7.35E-01
BEAKL	2.12E-01	9.68E-02	-	4.12E-01	3.17E-02	1.52E-02	2.08E-02	6.59E-03	8.99E-01	5.49E-03
HYALINW	4.99E-01	5.29E-02	7.11E-02	-	2.86E-03	1.78E-03	5.14E-10	8.99E-01	1.88E-06	3.17E-02
MIDRIBL	4.40E-01	7.74E-02	1.85E-01	2.55E-01	-	7.59E-07	1.21E-03	2.27E-07	2.65E-05	3.38E-35
MIDRIBW	3.40E-01	-9.65E-04	2.09E-01	2.67E-01	4.11E-01	-	1.62E-09	1.28E-01	1.72E-04	7.63E-06
NERVEN	-5.93E-01	2.00E-02	-1.99E-01	-5.03E-01	-2.76E-01	-4.90E-01	-	9.83E-01	1.65E-08	1.34E-02
PERIGL	4.11E-01	2.01E-03	2.33E-01	1.11E-02	4.28E-01	1.32E-01	-1.90E-03	-	5.88E-04	2.15E-12
PERIGW	6.18E-01	-3.24E-02	-1.10E-02	3.97E-01	3.53E-01	3.18E-01	-4.62E-01	2.92E-01	-	2.70E-05
SCALEL	3.92E-01	2.94E-02	2.38E-01	1.85E-01	**8.28E-01**	3.75E-01	-2.12E-01	5.58E-01	3.53E-01	-
SHAPEPE	1.33E-01	-8.51E-02	2.47E-01	-1.04E-01	2.77E-01	1.01E-02	8.18E-02	6.82E-01	1.27E-01	3.96E-01
SHOULDER	1.97E-01	7.36E-02	6.44E-01	1.26E-02	2.50E-01	1.45E-01	-1.10E-01	2.37E-01	1.33E-01	3.21E-01
SPIKEL	7.00E-01	1.20E-01	2.56E-01	5.18E-01	5.09E-01	4.23E-01	-6.75E-01	2.09E-01	5.88E-01	4.87E-01
STAML	**7.42E-01**	-1.26E-02	2.67E-01	4.79E-01	4.38E-01	4.10E-01	-6.27E-01	2.62E-01	6.17E-01	4.08E-01
STIPEL	2.27E-01	-8.65E-02	1.86E-02	-3.10E-03	2.28E-01	1.28E-01	-9.49E-03	4.28E-01	1.54E-01	3.64E-01
STYLEXL	1.12E-01	5.56E-02	6.10E-02	1.50E-01	1.06E-01	3.67E-01	-3.01E-01	-9.30E-02	9.69E-02	9.26E-02

APPENDIX 8 (Cont'd) Linear correlation matrix with r-values and p-values (r*p*) for 20 morphological characters for the *C. nardina* complex, *C. filifolia* var. *filifolia* the putative hybrid. Significant correlations (|r| ≥ 7.0E-01) are in bold, n = 135.

	SHAPEPE	SHOULDER	SPIKEL	STAML	STIPEL	STYLEXL
ACHENEL	1.24E-01	2.20E-02	3.63E-21	7.93E-25	8.20E-03	1.94E-01
AWNL	3.27E-01	3.96E-01	1.67E-01	8.85E-01	3.19E-01	5.22E-01
BEAKL	3.87E-03	3.47E-17	2.76E-03	1.72E-03	8.30E-01	4.82E-01
HYALINW	2.32E-01	8.85E-01	1.21E-10	4.12E-09	9.72E-01	8.31E-02
MIDRIBL	1.17E-03	3.47E-03	2.88E-10	1.04E-07	7.85E-03	2.19E-01
MIDRIBW	9.08E-01	9.23E-02	3.28E-07	7.68E-07	1.38E-01	1.22E-05
NERVEN	3.45E-01	2.04E-01	2.85E-19	3.95E-16	9.13E-01	3.81E-04
PERIGL	8.05E-20	5.60E-03	1.48E-02	2.12E-03	2.19E-07	2.83E-01
PERIGW	1.43E-01	1.25E-01	6.41E-14	1.51E-15	7.51E-02	2.63E-01
SCALEL	2.02E-06	1.46E-04	2.09E-09	8.79E-07	1.43E-05	2.85E-01
SHAPEPE	-	1.17E-02	6.49E-01	5.96E-01	1.20E-01	4.43E-01
SHOULDER	2.16E-01	-	3.40E-03	6.82E-03	2.13E-01	9.30E-01
SPIKEL	3.96E-02	2.50E-01	-	4.14E-38	7.30E-01	8.76E-04
STAML	4.60E-02	2.32E-01	**8.46E-01**	-	1.82E-01	5.69E-02
STIPEL	1.34E-01	1.08E-01	3.00E-02	1.16E-01	-	7.20E-01
STYLEXL	-6.66E-02	7.59E-03	2.83E-01	1.64E-01	-3.11E-02	-

APPENDIX 9 Linear correlation matrix with r-values and p-values (r*p*) for 20 morphological characters for *C. filifolia* var. *filifolia*, *C. elynoides* and *C. filifolia* var. *erostrata*. Significant correlations (|r| ≥ 7.0E-01) are in bold, n = 99.

	ACHENEL	AWNL	BEAKL	HYALINW	NERVEN	PERIGL	PERIGW	MIDRIBL	MIDRIBW	SCALEL
ACHENEL	-	*7.20E-01*	*5.27E-01*	*2.82E-03*	*5.91E-01*	*5.97E-13*	*2.01E-04*	*2.91E-05*	*2.57E-02*	*3.03E-05*
AWNL	-3.64E-02	-	*2.72E-02*	*5.30E-01*	*6.91E-01*	*1.73E-01*	*3.78E-01*	*2.56E-01*	*8.29E-01*	*1.15E-01*
BEAKL	6.43E-02	2.22E-01	-	*3.26E-01*	*7.10E-03*	*3.96E-09*	*1.78E-01*	*8.26E-05*	*4.01E-01*	*6.12E-08*
HYALINW	2.97E-01	-6.39E-02	-9.97E-02	-	*6.35E-01*	*2.04E-01*	*1.86E-02*	*4.16E-02*	*9.02E-02*	*2.13E-01*
NERVEN	5.47E-02	4.05E-02	2.69E-01	-4.83E-02	-	*5.10E-02*	*6.97E-01*	*2.90E-01*	*1.32E-01*	*3.22E-01*
PERIGL	6.45E-01	1.38E-01	5.49E-01	1.29E-01	1.97E-01	-	*2.61E-04*	*1.31E-10*	*4.84E-03*	*9.99E-16*
PERIGW	3.65E-01	-8.95E-02	-1.36E-01	2.36E-01	3.96E-02	3.59E-01	-	*2.28E-02*	*3.02E-03*	*2.01E-02*
MIDRIBL	4.07E-01	1.15E-01	3.85E-01	2.05E-01	1.08E-01	5.90E-01	2.29E-01	-	*1.21E-05*	*1.84E-29*
MIDRIBW	2.24E-01	-2.20E-02	8.53E-02	1.71E-01	-1.52E-01	2.81E-01	2.95E-01	4.24E-01	-	*4.25E-04*
SCALEL	4.06E-01	1.59E-01	5.12E-01	1.26E-01	1.01E-01	6.98E-01	2.33E-01	**8.55E-01**	3.48E-01	-
SERRL	2.30E-01	-1.52E-01	-4.20E-01	1.06E-01	-7.17E-02	4.28E-02	3.51E-01	2.78E-02	2.49E-01	-4.26E-02
SHOULDER	1.01E-01	2.46E-01	**8.23E-01**	-9.65E-02	1.80E-01	5.25E-01	-5.38E-04	4.04E-01	9.86E-02	5.07E-01
SPIKEL	3.49E-01	1.18E-01	7.88E-02	2.43E-01	2.69E-03	3.64E-01	3.65E-01	3.64E-01	3.03E-01	4.39E-01
STAML	4.49E-01	-1.74E-01	1.77E-01	1.40E-01	-1.64E-02	4.22E-01	3.35E-01	3.08E-01	2.20E-01	3.36E-01
STIPEL	3.83E-01	5.27E-03	1.16E-01	7.36E-03	8.71E-02	3.99E-01	1.36E-01	1.90E-01	1.54E-01	2.15E-01
STYLEXL	-1.81E-01	1.36E-01	1.00E-01	-7.30E-02	-4.85E-02	1.42E-02	-4.35E-03	-8.27E-03	2.08E-01	4.19E-02

APPENDIX 9 (Cont'd) Linear correlation matrix with r-values and p-values (r*p*) for 20 morphological characters for *C. filifolia* var. *filifolia*, *C. elynoides* and *C. filifolia* var. *erostrata*. Significant correlations (|r| ≥ 7.0E-01) are in bold, n = 99.

	SERRL	SHOULDER	SPIKEL	STAML	STIPEL	STYLEXL
ACHENEL	*2.21E-02*	*3.19E-01*	*4.07E-04*	*3.15E-06*	*8.93E-05*	*7.29E-02*
AWNL	*1.34E-01*	*1.41E-02*	*2.46E-01*	*8.49E-02*	*9.59E-01*	*1.80E-01*
BEAKL	*1.51E-05*	*1.40E-25*	*4.38E-01*	*7.98E-02*	*2.53E-01*	*3.23E-01*
HYALINW	*2.97E-01*	*3.42E-01*	*1.54E-02*	*1.66E-01*	*9.42E-01*	*4.73E-01*
NERVEN	*4.81E-01*	*7.44E-02*	*9.79E-01*	*8.72E-01*	*3.91E-01*	*6.34E-01*
PERIGL	*6.74E-01*	*2.38E-08*	*2.15E-04*	*1.34E-05*	*4.36E-05*	*8.89E-01*
PERIGW	*3.74E-04*	*9.96E-01*	*2.00E-04*	*7.07E-04*	*1.78E-01*	*9.66E-01*
MIDRIBL	*7.84E-01*	*3.29E-05*	*2.17E-04*	*1.93E-03*	*5.92E-02*	*9.35E-01*
MIDRIBW	*1.28E-02*	*3.32E-01*	*2.30E-03*	*2.84E-02*	*1.29E-01*	*3.91E-02*
SCALEL	*6.75E-01*	*8.59E-08*	*5.42E-06*	*6.62E-04*	*3.25E-02*	*6.81E-01*
SERRL	-	*1.38E-03*	*2.47E-02*	*6.18E-04*	*2.73E-01*	*1.81E-01*
SHOULDER	-3.17E-01	-	*3.05E-01*	*1.93E-01*	*1.26E-01*	*8.83E-02*
SPIKEL	2.26E-01	1.04E-01	-	*2.24E-10*	*2.29E-01*	*9.39E-01*
STAML	3.38E-01	1.32E-01	5.84E-01	-	*1.99E-02*	*1.75E-01*
STIPEL	1.11E-01	1.55E-01	1.22E-01	2.34E-01	-	*6.06E-02*
STYLEXL	-1.36E-01	1.72E-01	7.83E-03	-1.37E-01	1.89E-01	-

APPENDIX 10 Means and Kruskal-Wallis results by character for a) the *C. nardina* complex, the putative hybrid and *C. elynoides* (n = 120), b) the *C. nardina* complex, the putative hybrid and *C. filifolia* var. *filifolia* (n = 135), and c) *C. elynoides*, *C. filifolia* var. *erostrata* and *C. filifolia* var. *filifolia* (n = 99), using uncorrelated morphological characters. Means are shown for each taxon. Significant values (p < 5.00E-02) are in bold.

a)	*C. nardina*	putative hybrid	*C. elynoides*	H	p
ACHENEL	1.97	2.27	2.68	51.24	**7.46E-12**
BEAKL	0.215	0.256	0.684	68.65	**1.24E-15**
HYALINW	0.118	0.189	0.386	47.52	**4.81E-11**
NERVEN	6.00	5.73	1.89	51.49	**6.59E-12**
STAML	3.74	5.11	8.47	80.66	**3.05E-18**

b)	*C. nardina*	putative hybrid	*C. filifolia* var. *filifolia*	H	p
HYALINW	0.118	0.189	0.685	66.85	**3.05E-15**
MIDRIBW	0.438	0.500	0.608	32.52	**8.67E-08**
NERVEN	6.00	5.73	1.06	76.27	**2.74E-17**
PERIGW	1.34	1.57	1.80	59.37	**1.28E-13**
STAML	3.74	5.11	9.22	95.45	**1.87E-21**

c)	*C. elynoides*	*C. filifolia* var. *erostrata*	*C. filifolia* var. *filifolia*	H	p
ACHENEL	2.68	2.10	3.04	22.67	**1.19E-05**
BEAKL	0.684	0.0937	0.270	65.86	**4.99E-15**
SCALEL	3.68	2.58	3.50	25.98	**2.29E-06**
SERRL	0.197	1.24	1.45	35.23	**2.24E-08**
SHAPEPE	1.84	1.08	1.57	30.77	**2.08E-07**
SPIKEL	14.20	11.71	16.39	25.11	**3.54E-06**
STAML	8.47	6.95	9.22	9.59	**8.28E-03**

APPENDIX 11 Means and Mann-Whitney test results by character for *C. hepburnii* and *C. nardina* specimens categorized by a) Egorova (1999), b) Boott (1840), and c) Mackenzie (1935) using uncorrelated morphological characters, n = 84. Means are shown for each taxon. Significant values (p < 5.00E-02) are in bold.

a) Egorova (1999)	*C. hepburnii*	*C. nardina*	U	p
ACHENEL	2.07	2.14	600	2.07E-01
PERIGW	1.32	1.57	310.5	**5.42E-07**
SCALEL	3.06	3.37	655	**4.15E-02**
SERRL	1.08	1.01	780.5	4.71E-01
SPIKEL	8.13	9.49	596.5	**1.12E-02**
STAML	4.00	4.69	594	**1.62E-02**
b) Boott (1840)				
ACHENEL	2.12	2.10	583.5	5.53E-01
PERIGW	1.46	1.44	704	7.20E-01
SCALEL	3.28	3.18	717	6.18E-01
SERRL	1.01	1.06	703	6.10E-01
SPIKEL	9.56	8.5	586	7.95E-02
STAML	4.43	4.34	695	6.55E-01
c) Mackenzie (1935)				
ACHENEL	2.09	2.12	646	4.58E-01
PERIGW	1.43	1.46	804	6.70E-01
SCALEL	3.12	3.35	643.5	**3.86E-02**
SERRL	1.09	0.991	765.5	4.36E-01
SPIKEL	8.68	9.04	788	4.42E-01
STAML	4.38	4.35	641.5	5.86E-01

APPENDIX 12 Anatomical measurements (mean ± SD) using continuous leaf characters for taxonomic comparisons. Specimens were classified as either *C. nardina* or *C. hepburnii* using Boott (1840), Egorova (1999) or Mackenzie (1935).

	n	ABORTL	ABEPI-CHLORD	ADEP-CHLORD	ADEP-SCLERD	AB-STOMAN	AD-STOMAN	MAJVBN	MINVBN	MAJVBD	MINVBD
Boott (1840)											
C. hepburnii	7	142.6 ± 82.5	17.8 ± 4.1	14.8 ± 2.4	14.0 ± 3.0	0.3 ± 0.3	1.4 ± 1.3	2.0 ± 2.0	4.4 ± 1.0	69.3 ± 8.7	54.2 ± 17.6
C. nardina	14	118.2 ± 87.7	16.7 ± 4.2	15.3 ± 2.9	13.2 ± 3.1	0.0 ± 0.0	0.5 ± 0.5	1.7 ± 0.9	4.3 ± 2.0	66.0 ± 12.5	49.1 ± 16
Egorova (1999)											
C. hepburnii	11	138.4 ± 78.4	17.2 ± 4.3	15.6 ± 2.7	12.8 ± 1.7	0.1 ± 0.4	1.3 ± 1.3	2.0 ± 2.0	4.7 ± 1.3	67.4 ± 9.4	52.7 ± 18.6
C. nardina	10	113.1 ± 85.7	17.0 ± 4.1	14.6 ± 2.6	14.0 ± 3.4	0.1 ± 0.3	0.3 ± 0.7	1.6 ± 1.6	3.9 ± 1.9	66.8 ± 12.4	48.7 ± 15.9
Mackenzie (1935)											
C. hepburnii	12	103.7 ± 71.1	16.7 ± 4.4	15.6 ± 2.6	13.9 ± 2.8	0.2 ± 0.4	0.6 ± 0.8	1.8 ± 0.9	4.0 ± 1.9	68.0 ± 12.2	47.6 ± 16.1
C. nardina	9	156.6 ± 95.9	17.6 ± 3.9	14.5 ± 2.8	12.8 ± 3.4	0.0 ± 0.0	1.1 ± 1.2	1.8 ± 2.0	4.8 ± 1.4	65.8 ± 10.4	55.1 ± 16.6
C. nardina complex	11	117.6 ± 76.3	16.4 ± 4.5	14.6 ± 2.8	14.4 ± 3.3	0.2 ± 0.4	0.4 ± 0.7	1.8 ± 0.9	3.4 ± 1.0	65.8 ± 9.0	42.6 ± 11.1
C. elynoides	14	89.0 ± 100.2	14.6 ± 1.9	13.9 ± 1.6	12.4 ± 1.8	0.2 ± 0.4	0.6 ± 0.9	2.8 ± 0.7	5.4 ± 1.6	72.8 ± 12.7	45.0 ± 10.9
putative hybrid	14	146.0 ± 89.1	17.9 ± 3.9	15.1 ± 2.6	12.1 ± 2.4	0.0 ± 0.0	1.1 ± 1.0	1.9 ± 1.9	5.3 ± 1.9	70.3 ± 14.9	56.1 ± 16.0
C. filifolia var. *filifolia*	14	136.3 ± 75.6	22.3 ± 5.8	17.7 ± 3.0	20.4 ± 5.0	0.6 ± 0.9	0.1 ± 0.4	4.1 ± 0.8	5.8 ± 1.9	85.1 ± 7.9	51.1 ± 11.0
C. filifolia var. *erostrata*	10	110.5 ± 92.9	14.3 ± 4.6	11.2 ± 2.2	13.2 ± 2.2	0.3 ± 0.5	0.7 ± 0.7	4.0 ± 0.7	5.5 ± 1.8	75.3 ± 12.9	47.0 ± 7.9

APPENDIX 13 Anatomical measurements (mean ± SD) using continuous culm characters for taxonomic comparisons. Specimens were classified as either *C. nardina* or *C. hepburnii* using Boott (1840), Egorova (1999) or Mackenzie (1935).

	n	ADEPICHLORD	ADEPISCLERD	MAJVBN	MAJVBD	MINVBN	MINVBD	STOMAN
Boott (1840)								
C. hepburnii	7	15.0 ± 3.1	12.5 ± 3.3	6.6 ± 1.1	77.1 ± 8.9	4.3 ± 1.1	41.9 ± 6.3	2.3 ± 1.1
C. nardina	14	15.8 ± 3.5	14.9 ± 3.5	6.0 ± 0.8	82.2 ± 27.6	4.4 ± 1.3	48.5 ± 17.1	2.5 ± 1.3
Egorova (1999)								
C. hepburnii	11	14.8 ± 2.5	13.2 ± 3.0	6.5 ± 0.9	75.5 ± 13.0	4.6 ± 1.4	48.5 ± 16.9	2.5 ± 1.2
C. nardina	10	16.4 ± 4.0	15.0 ± 3.9	5.9 ± 0.9	86.0 ± 30.3	4.1 ± 1.1	43.9 ± 11.9	2.4 ± 1.3
Mackenzie (1935)								
C. hepburnii	12	15.7 ± 3.6	14.8 ± 3.8	5.8 ± 1.0	83.0 ± 29.8	4.0 ± 1.4	45.7 ± 17.8	2.4 ± 1.1
C. nardina	9	15.4 ± 3.3	13.2 ± 3.4	6.7 ± 0.5	77.2 ± 12.9	4.9 ± 0.9	47.1 ± 10.9	2.4 ± 1.4
C. nardina complex	11	15.0 ± 3.6	13.7 ± 4.1	5.4 ± 0.8	83.4 ± 29.5	4.0 ± 1.3	42.6 ± 10.9	2.4 ± 1.0
C. elynoides	14	13.8 ± 3.4	13.0 ± 17.0	6.5 ± 1.2	87.1 ± 28.1	5.4 ± 0.9	53.6 ± 17.6	3.0 ± 1.7
putative hybrid	12	15.8 ± 3.1	14.4 ± 3.1	6.7 ± 0.8	80.5 ± 14.3	4.9 ± 1.1	47.3 ± 17.5	2.5 ± 1.4
C. filifolia var. *filifolia*	15	17.7 ± 3.2	18.0 ± 3.6	6.3 ± 1.1	101.1 ± 20.1	6.4 ± 1.5	60.4 ± 14.1	1.5 ± 1.2
C. filifolia var. *erostrata*	10	11.6 ± 1.7	12.9 ± 2.7	7.9 ± 1.7	107.9 ± 14.4	7.0 ± 1.8	56.2 ± 15.7	3.4 ± 1.8

APPENDIX 14 Anatomical measurements (mean ± SD) using categorical and binary leaf and culm characters for *C. nardina* and *C. hepburnii*. Specimens were classified as either *C. nardina* or *C. hepburnii* using Boott (1840), n = 21.

	Leaf characters									Culm characters		
	LEAFSH	**TIPS**	**GIRDSH**	**KEELSH**	**KEELPROM**	**KEELP**	**VBPERIPH**	**AIR**	**LAMFUSE**	**AIR**	**VBPERIPH**	**GIRDSH**
C. hepburnii	0	1	1	-	-	0	0	1	1	1	0	1 and 3
	0	1	3	-	-	0	0	1	1	1	0	1
	0	1	1	-	-	0	0	1	0	1	0	1
	1	0	1	0	1	1	0	1	1	1	1	2
	0	1	3	-	-	0	0	1	0	1	0	1
	0	1	3	-	-	0	0	1	0	1	0	1
	1	1	1	-	-	0	0	1	0	1	0	1 and 3
C. nardina	0	1	3	-	-	0	0	0	0	0	0	1
	1 and 2	1	2 and 3	-	-	0	0	1	0	1	1	1
	0	1	1	-	-	0	0	1	0	1	0	2
	0	1	1	-	-	0	0	1	0	1	0	-
	0	1	1	-	-	0	0	1	0	1	0	1
	1	1	3	-	-	0	0	0	0	1	0	1
	0	1	1	-	-	0	0	1	0	1	0	1
	0	1	1	-	-	0	0	1	0	0	0	3
	0	1	1	-	-	0	0	1	0	1	0	1
	0	1	1 and 3	-	-	0	0	1	1	1	0	1 and 3
	0	1	1	-	-	0	1	1	1	1	0	1
	1	1	1	-	-	0	0	1	1	1	0	1
	1	1	3	0	0	1	1	0	1	1	0	1
	0	1	3	-	-	0	0	1	0	0	0	1 and 3

APPENDIX 15 Anatomical measurements (mean ± SD) using categorical and binary leaf and culm characters for *C. nardina* and *C. hepburnii* Specimens were classified as either *C. nardina* or *C. hepburnii* using Egorova (1999), n = 21.

	Leaf characters									Culm characters		
	LEAFSH	**TIPS**	**GIRDSH**	**KEELSH**	**KEELPROM**	**KEELP**	**VBPERIPH**	**AIR**	**LAMFUSE**	**AIR**	**VBPERIPH**	**GIRDSH**
C. hepburnii	0	1	1	-	-	0	0	1	1	1	0	1 and 3
	0	1	3	-	-	0	0	1	1	1	0	1
	1	0	1	0	1	1	0	1	1	1	1	2
	0	1	3	-	-	0	0	1	0	1	0	1
	0	1	3	-	-	0	0	1	0	1	0	1
	0	1	3	-	-	0	0	0	0	0	0	1
	1 and 2	1	2 and 3	-	-	0	0	1	0	1	1	1
	0	1	1	-	-	0	0	1	0	1	0	2
	0	1	1 and 3	-	-	0	0	1	1	1	0	1 and 3
	0	1	1	-	-	0	1	1	1	1	0	1
	1	1	1	-	-	0	0	1	1	1	0	1
C. nardina	0	1	1	-	-	0	0	1	0	1	0	1
	1	1	1	-	-	0	0	1	0	1	0	1 and 3
	0	1	1	-	-	0	0	1	0	1	0	-
	0	1	1	-	-	0	0	1	0	1	0	1
	1	1	3	-	-	0	0	0	0	1	0	1
	0	1	1	-	-	0	0	1	0	1	0	1
	0	1	1	-	-	0	0	1	0	0	0	3
	0	1	1	-	-	0	0	1	0	1	0	1
	1	1	3	0	0	1	1	0	1	1	0	1
	0	1	3	-	-	0	0	1	0	0	0	1 and 3

APPENDIX 16 Anatomical measurements (mean ± SD) using categorical and binary leaf and culm characters for *C. nardina* and *C. hepburnii* Specimens were classified as either *C. nardina* or *C. hepburnii* using Mackenzie (1935), n = 21.

	Leaf characters									Culm characters		
	LEAFSH	**TIPS**	**GIRDSH**	**KEELSH**	**KEELPROM**	**KEELP**	**VBPERIPH**	**AIR**	**LAMFUSE**	**AIR**	**VBPERIPH**	**GIRDSH**
C. hepburnii	0	1	1	-	-	0	0	1	1	1	0	1 and 3
	0	1	3	-	-	0	0	1	1	1	0	1
	0	1	3	-	-	0	0	0	0	0	0	1
	1 and 2	1	2 and 3	-	-	0	0	1	0	1	1	1
	0	1	1	-	-	0	0	1	0	1	0	2
	0	1	1	-	-	0	0	1	0	1	0	1
	0	1	1	-	-	0	0	1	0	1	0	?
	0	1	1	-	-	0	0	1	0	1	0	1
	1	1	3	-	-	0	0		0	1	0	1
	0	1	1	-	-	0	0	1	0	1	0	1
	0	1	1	-	-	0	0	1	0	0	0	3
	0	1	1	-	-	0	0	1	0	1	0	1
C. nardina	1	0	1	0	1	1	0	1	1	1	1	2
	0	1	3	-	-	0	0	1	0	1	0	1
	0	1	3	-	-	0	0	1	0	1	0	1
	0	1	1 and 3	-	-	0	0	1	1	1	0	1 and 3
	0	1	1	-	-	0	1	1	1	1	0	1
	1	1	1	-	-	0	0	1	1	1	0	1
	1	1	1	-	-	0	0	1	0	1	0	1 and 3
	1	1	3	0	0	1	1	0	1	1	0	1
	0	1	3	-	-	0	0	1	0	0	0	1 and 3

APPENDIX 17 Anatomical measurements (mean ± SD) for categorical and binary leaf and culm characters for *C. nardina* complex, n = 11.

	Leaf characters									Culm characters		
	LEAFSH	**TIPS**	**GIRDSH**	**KEELSH**	**KEELPROM**	**KEELP**	**VBPERIPH**	**AIR**	**LAMFUSE**	**AIR**	**VBPERIPH**	**GIRDSH**
C. nardina complex	1	1	1	-	-	0	0	1	0	1	0	1 and 3
	0	1	1	-	-	0	0	1	0	1	0	-
	0	1	1 and 3	-	-	0	0	1	1	1	0	1 and 3
	0	1	3	-	-	0	0	0	0	0	0	1
	0	1	-	-	-	0	0	1	0	1	0	1
	0	1	1	-	-	0	0	1	0	1	0	1
	1	1	3	-	-	0	0	0	0	1	0	1
	0	1	1	-	-	0	0	1	0	1	0	1
	0	1	1	-	-	0	0	1	1	1	0	1 and 3
	0	1	1	-	-	0	0	1	0	1	0	1
	0	1	1	-	-	0	0	1	0	0	0	3

APPENDIX 18 Anatomical measurements (mean ± SD) for categorical and binary leaf and culm characters for *C. elynoides*, n = 14.

	Leaf characters									Culm characters		
	LEAFSH	**TIPS**	**GIRDSH**	**KEELSH**	**KEELPROM**	**KEELP**	**VBPERIPH**	**AIR**	**LAMFUSE**	**AIR**	**VBPERIPH**	**GIRDSH**
C. elynoides	0	1	1 and 3	-	-	0	0	1	1	1	0	1
	0	1	1 and 3	0	0	1	0	1	1	1	0	1
	0	1	1 and 3	-	-	0	0	1	1	1	0	1
	1	1	1	-	-	0	0	1	1	0	0	1 and 2
	1	1	1 and 3	-	-	0	0	1	1	1	0	1
	0	1	1 and 3	-	-	0	0	1	1	0	0	1
	0	1	1	-	-	0	0	1	1	0	0	1
	1	1	3	-	-	0	0	1	0	0	0	1
	0	1	1	-	-	0	0	1	1	1	0	1
	0	1	1 and 3	-	-	0	0	1	1	0	0	1
	-	1	1	0	1	1	0	1	1	-	0	
	0	1	1	-	-	0	0	1	1	1	0	1 and 3
	0	1	1	-	-	0	0	1	0	1	0	1 and 2
	0	1	1	-	-	0	0	1	1	0	0	1

APPENDIX 19 Anatomical measurements (mean ± SD) for categorical and binary leaf and culm characters for putative hybrid, n = 14.

	Leaf characters									Culm characters		
	LEAFSH	**TIPS**	**GIRDSH**	**KEELSH**	**KEELPROM**	**KEELP**	**VBPERIPH**	**AIR**	**LAMFUSE**	**AIR**	**VBPERIPH**	**GIRDSH**
putative hybrid	0	1	1	-	-	0	0	1	0	1	0	1
	1	1	3	0	0	1	1	0	1	1	0	1
	1	0	1	0	1	1	0	1	1	1	1	2
	0	1	3	-	-	0	0	1	0	1	0	1
	1 and 2	1	2 and 3	-	-	0	0	1	0	1	1	1
	0	1	1	-	-	0	1	1	1	1	0	1
	0	1	1	-	-	0	0	1	0	1	0	2
	0	?	1	-	-	0	0	1	1	1	0	2
	1	1	1	-	-	0	0	1	1	1	0	1
	0	1	3	-	-	0	0	1	0	0	0	1 and 3
	0	1	3	-	-	0	0	1	0	1	0	1
	1	1	1	-	-	0	0	1	0	-	-	-
	0	1	1	-	-	0	0	1	1	-	-	-
	0	1	3	-	-	0	0	1	1	1	0	1

APPENDIX 20 Anatomical measurements (mean ± SD) using categorical and binary leaf and culm characters for *C. filifolia* var. *filifolia*, n =16.

	Leaf characters									Culm characters		
	LEAFSH	**TIPS**	**GIRDSH**	**KEELSH**	**KEELPROM**	**KEELP**	**VBPERIPH**	**AIR**	**LAMFUSE**	**AIR**	**VBPERIPH**	**GIRDSH**
C. filifolia var. *filifolia*	0	1	1	-	-	0	0	1	0	1	1	3
	0	1	1 and 3	0	1	1	0	1	0	0	1	1
	0	1	1	-	0	1	0	1	0	1	1	1
	0	1	1 and 3	0	1	1	0	1	0	1	1	1 and 3
	1	1	1	-	-	0	0	1	0	0	1	2
	0	1	1	0	0	1	0	1	0	0	1	1
	1	1	1	-	-	0	0	1	0	1	1	2
	1	1	1	0	1	1	0	1	0	1	1	1
	1	1	1	-	-	0	0	1	0	1	1	3
	1	1	1 and 3	0	0	1	0	1	0	1	1	1 and 3
	1	1	3	-	0	1	0	1	0	0	1	1 and 3
	-	-	-	-	-	-	-	-	-	0	-	1 and 3
	0	1	1 and 3	0	1	1	0	1	0	0	1	1
	0	1	1	-	-	0	0	1	0	?	1	1
	1	1	3	0	1	1	0	1	0	0	0	1
	-	-	-	-	-	-	-	-	-	1	0	1

APPENDIX 21 Anatomical measurements (mean ± SD) using categorical and binary leaf and culm characters for *C. filifolia* var. *erostrata*, n = 10.

	Leaf characters									Culm characters		
	LEAFSH	**TIPS**	**GIRDSH**	**KEELSH**	**KEELPROM**	**KEELP**	**VBPERIPH**	**AIR**	**LAMFUSE**	**AIR**	**VBPERIPH**	**GIRDSH**
C. filifolia var. *erostrata*	0	1	3	0	1	1	0	1	1	1	1	1
	0	1	3	-	-	0	0	1	1	0	0	1
	0	1	3	-	0	1	0	1	1	0	0	1 and 2
	0	1	1 and 3	-	0	0	0	1	1	1	1	1
	0	1	1 and 3	-	-	0	0	1	0	0	1	1
	0	1	1 and 3	-	0	1	0	1	1	0	1	1
	1	1	1 and 3	0	1	1	1	1	1	1	1	1
	1	1	1 and 3	-	-	0	0	1	0	1	-	1
	0	1	1 and 3	-	-	0	0	1	0	1	1	1
	0	1	3	0	1	1	0	1	0	0	1	1