Systematics and phylogeography of the *Carex capitata* complex (Cyperaceae)

by

Tamara Villaverde Hidalgo

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Faculty of Science
University of Ottawa

Supervisor:

Dr. Julian R. Starr

Committee members:

Dr. Stéphane Aris-Brosou

Dr. Lynn Gillespie

Dr. Simon Joly

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Abstract

Only thirty known species have populations at high latitudes in both hemispheres, this is, a bipolar distribution. Five of them belong to the genus *Carex*. Before attempting to elucidate the origins of such distributions, we need to resolve taxonomical problems that are typically encountered in such species. We focus on the *Carex capitata* complex, which includes *Carex arctogena* as a bipolar species, in world-wide scope sampling. A morphometric study and phylogenetic analyses based on maximum parsimony, Bayesian inference and Statistical Parsimony have revealed: a) *C. capitata* and *C. arctogena* are different species; b) *C. anctarctogena* is a synonym of *C. arctogena* and c) a great biodiversity previously undetected in western North America that could lead to the description of three new taxa (*"Carex cayouetteana"*, *Carex sp. nov. 1* and *2*) comprised in the so called *"C. cayouetteana"* lineage. More studies are needed in some *C. capitata* samples from Russia that appears in the molecular analyses in a strongly supported clade.

Résumé

Seulement trente espèces connues sont dans des populations dans les hautes latitudes des deux hémisphères, c'est, une distribution bipolaire. Cinq d'entre eux appartiennent à la genre *Carex.* Avant de tenter d'élucider les origines de ces distributions, nous avons besoin pour résoudre les problèmes taxonomiques qui sont généralement rencontrés dans ces espèces. Nous nous concentrons sur le complexe *Carex capitata*, qui comprend *Carex arctogena* comme une espèce bipolaire, sur laquelle était fait une échantillonnage de portée mondiale. Une étude morphométrique et analyse phylogénétique basée sur la parcimonie maximale, l'inférence bayésienne et parsimonie statistique ont révélé: a) *C. capitata* et *C. arctogena* sont des espèces différentes; b) *C. anctarctogena* est un synonyme de *C. arctogena*; et c) une grande biodiversité précédemment détectés dans l'ouest de l'Amérique du Nord qui pourrait conduire à la description de trois nouveaux taxons (*"Carex cayouetteana"*, *Carex sp. nov. 1* et *2*), comprise dans soi-disant *"C. cayouetteana"* lignée. D'autres études sont nécessaires dans certains échantillons *C. capitata* de la Russie qui apparaissent dans les analyses moléculaires dans un clade fortement soutenue.

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Chapter 1

Introduction

1.1 Taxonomic background

The Cyperaceae Juss., or the sedge family, is among the largest families of flowering plants, occurring on all continents, except Antarctica. The family comprises approximately 104 genera, 14 tribes and 5,400 species (Goetghebeur 1996) making it the 7th or 8th largest angiosperm family and the third largest monocot family after orchids (Orchidaceae) and grasses (Poaceae). Its species occur in a great diversity of habitats, ranging from deserts to rainforests (Reznicek 2011), although they are predominantly found in wetland habitats such as littoral communities, peatlands and wet meadows. Although its economic significance is often at a regional or local level (Simpson & Inglis 2001), approximately 10% of its species are used by humanity for food (Chinese water chestnut, *Eleocharis dulcis* (Burm.) f. Trin. ex Henschel, or the yellow nut sedge, *Cyperus esculentus* L.); for pasture (*Carex lyngbyei* Hornem.); for construction (*Schoenoplectus californicus* (C.A. Mey) Palla); as an elixir (*Carex arenaria* L.); and even for making paper (*Cyperus papyrus* L.), whereas other sedge species, such as *Cyperus rotundus* L., *C. esculentus* L., *C. difformis* L. or *Fimbristylis miliacea* L. are considered to be serious weeds due to their negative effect on agriculture (Brayson & Carter 2008).

Sedge flowers are small and evolutionally highly reduced in size with the perianth typically lacking or reduced to either bristles or scales. In some species, a modified bract in the female flower surrounds the naked gynoecium, enclosing the pistil and later the achene, in a sac-like structure (Blaser 1944) known as utricle or perigynium. The flowers are arranged in structures known as spikelets with the inflorescence consisting of one or many spikelets in one or more axes.

Approximately forty percent of all sedge species (ca. 2100 spp.) are grouped in the cosmopolitan tribe *Cariceae* Kunth ex. Dumort. based on two main characters: strict unisexual flowers and presence of perigynium (Starr & Ford 2009). The division of the tribe into four genera (*Carex* L., *Uncinia* Pers., *Kobresia* Willd., *Schoenoxiphium* Nees) is based upon spikelet morphology, the distribution of sexes in the spikelet (bisexual vs. unisexual) and the degree of fusion of the perigynium (open vs. closed to apex) (Starr & Ford 2009, see Figure 1.1 1.1).

The largest genus in the tribe and family is the cosmopolitan genus *Carex* L. (ca. 2000 species) which is also one of the most taxonomically difficult and morphologically challenging genera (Starr & Ford 2009) due to its extremely reduced morphology. Its relatively rapid radiation (Magallón & Sanderson 2001) combined with its high dispersal capability and high cytogenetic variation (Hipp 2007), have been proposed to contribute to the extraordinary diversity of *Carex.* In the last 20 years, the discovery rate of new *Carex* species in North America has been, on average, two per year (Ford et al. 2009), which seems to be a trend that has not yet reached a plateau.

Carex is divided into four subgenera, *Carex* L., *Vignea* (P. Beauv. ex Lestib. f.) Peterm., *Vigneastra* (Tuck.) Kük. and *Psyllophora* (Degl.) Peterm. (Starr & Ford 2009), and 70 sections (Mackenzie 1935). To understand the morphological variation within *Carex* and the *Cariceae*, special attention must be paid to inflorescence and floral structures. Differences between taxa are largely based on characters related to the morphology of the inflorescence (unispicate vs. multispicate), the sexuality of spikes (bisexual vs. unisexual), the presence/absence of peduncles and of tubular (cladoprophylls) or utricle-like prophylls (inflorescence prophylls sensu Reznicek (1990), see Figure 1.2 1.2).

1.2 The *Carex capitata* complex

All *Carex* subgenera have taxonomic problems, including *Carex* subgen. *Psyllophora* Degl. Peterm. (= subgen. *Primocarex* Kük.), which remains as an unnatural group in the latest phylogeny of the tribe *Cariceae* (Starr & Ford 2009). It comprises species that are characterized by unispicate inflorescences (typically androgynous), and the absence of cladoprophylls or inflorescence prophylls (Starr & Ford 2009, see Figures 1.1 and 1.2). It is divided into approximately 25 sections and 75 species distributed worldwide mostly in extratropical, alpine or arctic habitats (Egorova 1999). Section *Capituligerae* Kük. (=*Capitatae* Christ.) is distinguished from other sections in *Psyllophora* by their densely capitate unispicate androgynous inflorescences, caespitose or loosely caespitose habit and filiform leaves (see Figure 1.3). It is a small group of two to four arctic-alpine, alpine, circumpolar or bipolar species that are distributed in the boreal area of the North Hemisphere and in Patagonia, South America. The section has two traditionally recognizable species: *C. capitata* L. a circumboreal species and *C. oreophila* C. A. Mey, an alpine species endemic to the eastern mountains of Turkey and the Caucasus (Kükenthal 1900). Although the circumscription of *C. oreophila* has never been in doubt, the circumscription of *C. capitata* and its segregates, *C. arctogena* Harry Sm. and *C. antarctogena* Roivanen has been controversial. Thus, even this small section presents taxonomic problems.

Carex capitata is first named by Linnaeus (1759) from a specimen collected by Solander from Sweden. Its circumscription was not in doubt for nearly two centuries (181 years) until H. Smith (1940) described *C. arctogena* also from Sweden, claiming that it could be separated from *C. capitata* by both morphological (pistillate scales longer and wider than the perigynium in *C. arctogena* vs. shorter and narrower *C. capitata*; scabrid peryginia vs. smooth) and ecological differences (often in alpine and dry areas vs. subalpine and wet areas). However, these variations were only based in populations from Scandinavia. A few years later, Roivanen (1954) noticed that populations of *C. arctogena* collected in South America had longer staminate portions of the spikes and a greater number of teeth than *C. arctogena* from Eurasia, which led him to segregate *C. antarctogena* from *C. arctogena*.

The taxonomy of *C. capitata* had been interweaved with *C. arctogena* and*C. antarctogena*, often treated as subspecies (Hiitonen 1944), varieties (Hultén 1958; Moore & Chater 1971; Scoggan 1978; Hultén & Fries 1986), or forms (Raymond 1949). Even though some authors have found morphological (Smith 1940; Egorova 1999; Reinhammar & Bele 2001), ecological (Gjaerevoll 1990; Nilson 1991; Reinhammar & Bele 2001, Table 2.1 in Chapter 2).) and even genetic differences (Reinhammar 1999) between *C. capitata* and *C. arctogena* in specimens from Scandinavia, the most recent treatment in the Flora of North America (Murray 2002) and the most important online plant names databases (e.g. Tropicos, http://www.tropicos.org/; The Plant list, http://www.theplantlist.org; The Monocot Checklist, http://www.kew.org/) treat both, *C. capitata* and *C. arctogena*, species as synonymous.

Therefore, the morphological variability within the taxa in the *C. capitata* complex and the different types of habitats in which these taxa can occur, suggest not only that *C. capitata* and *C. arctogena* may be poorly circumscribed, but that more than two taxa may exist within the complex. Consequently, it seems desirable to study in depth the taxonomy of this species complex to establish the taxon limits more confidently. *Carex capitata* may form a complex of three or more taxa whose limits need to be resolved.

1.3 Bipolar biogeography

After solving the complex taxonomic problems, it is possible to study their biogeography and evolutionary relationships. Beyond its distinctive morphology, the *C. capitata* complex is also exceptional because it possesses a bipolar distribution. Moore & Chater (1971) defined bipolar species as those taxa in the northern Hemisphere that reached latitudes as high as Alaska or the European Arctic, and south to the Straits of Magellan in the southern Hemisphere, irrespective of their occurrences elsewhere. Such a distribution is displayed by a few plant species but from thirteen different plant families. So far, only 30 species (Moore & Chater (1971)) present such distributions, and six of them (20%) belong to the genus *Carex* (*C. maritima* Gunn., *C. macloviana* D'Urv., *C. canescens* L. from the subgenus *Vigena* (P. Beauv. ex T. Lestib.) Peterm.; *C. microglochin* Wahlenb. and *C. arctogena* Harry Sm. from the subgenus *Psyllophora* (Degl.) Peterm.; *C. magellanica* Lam. from the subgenus *Carex*).

The origin of bipolar disjunctions, which may be seen as the largest and most challenging disjunctions, has captivated scientists such as Darwin, who devoted two chapters in *The Origin of the Species* (Darwin 1872) to biogeography, emphasizing the importance of the past and present geographic distribution of the organisms to his entire argument on evolution. Darwin tried to explain bipolar distributions as a species migration, in response to climate changes alternations; glacial period in one hemisphere would correspond to an interglacial period in the other (Darwin 1872). During cold periods in the northern Hemisphere, cold-adapted species would move South due to the advance of the ice-sheet; higher temperatures afterwards would have pushed these organisms to northern latitudes or to higher elevations in order to reach suitable habitats.

Bipolar biogeography is still the focus of numerous studies since Darwin's first approach based on organism migrations (e.g., Du Rietz 1940; Smith 1986; Vollan et al. 2006; Escudero et al. 2010). In total, four main hypotheses have been proposed to explain such distributions: long-distance dispersal (Van Steenis 1962; Raven 1963), mountain-hopping (Moore & Chater 1971; Vollan et al. 2006), parallelism and convergence (Humboldt 1817). Almost all bipolar species present taxonomical problems (e.g. *C. microglochin* Wahlenb., Wheeler & Guaglianone 2003; *Armeria maritima* Willd., Baumbach & Hellwig 2007; *Osmorhiza berteroi* DC., Wen et al. 2002) that should be resolved previously to determine whether bipolar species even really exist before an interpretation of the origins of bipolar distributions could be attempted.

Escudero et al. (2010) sampled five of the bipolar *Carex* species (*C. capitata* was not included) using a molecular approach and suggested long-distance dispersal as the most plausible cause of bipolar disjunctions. Although alternative dispersal hypotheses, such as mountain hopping, could not be tested due to the sampling, haplotype genealogical relationships indicated a southwards direction of dispersal in three species (*C. macloviana*, *C. magellanica* and *C. canescens*; Escudero et al. 2010). North-South colonization hypothesis was also suggested for bipolar *Empetrum* species (Popp et al. 2011); in this case, a long-distance dispersal event was suggested to have occurred in a single step by bird dispersal.

1.4 Objectives

Hence, the main purpose of this thesis is to gain a better understanding of the circumscription and phylogeographic relationships of members of the *C. capitata* complex. A multidisciplinary approach to this problem, combining both taxonomic and molecular analyses, is made throughout two different chapters.

The first study (Chapter 2) tries to resolve taxonomic problems within the *C. capitata* complex, especially in relation to the status of the different taxa described within this complex. Morphological, micromorphological, ecological and geographical analyses are conducted using more than 450 herbarium specimens. The second study (Chapter 3) uses chloroplast (cpDNA) and nuclear DNA (nDNA), to gain an insight into the phylogenetic and biogeographical relationships between the members of the complex. Infraspecific genetic variation and areas of endemism are pointed out, particularly in western North America where a high degree of endemism has already been recognized in several organisms as the result of Pleistocene periglacial fragmentation and refugial isolation of populations in this region (e.g., Brunsfeld et al. 2001; Hewitt 2003).

1.5 Supporting Figures

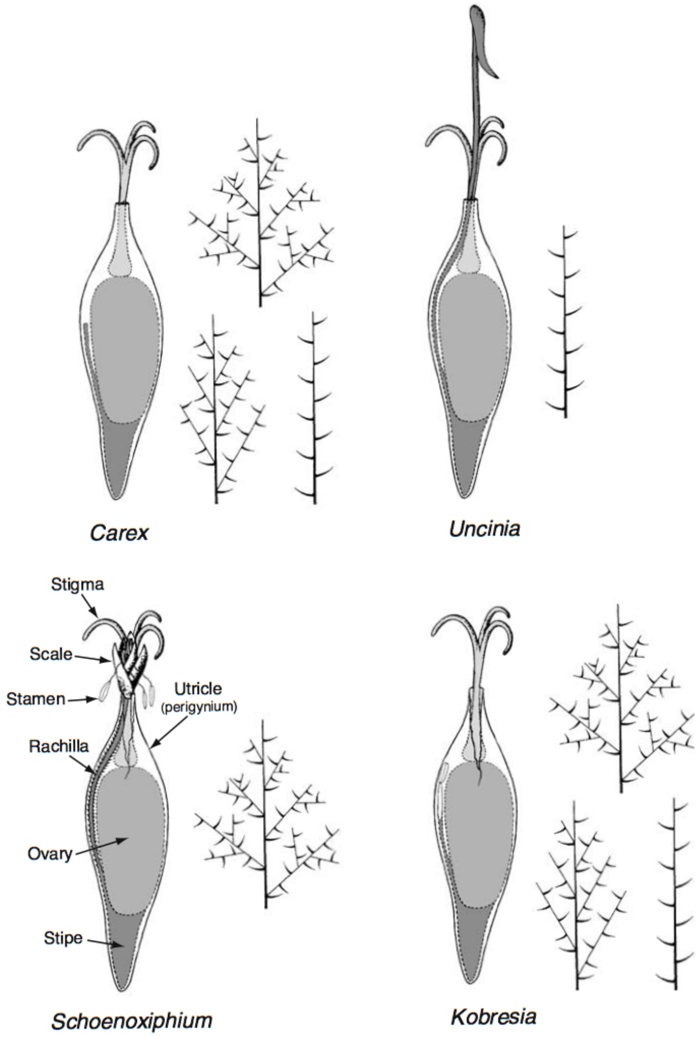


Figure 1.1: Spikelet morphologies for each genus in tribe *Cariceae* with a stylized representation of typical inflorescences: unispicate, multispicate (one lateral axis) and highly compound (two or more lateral axis) (from Starr et al. 2008).

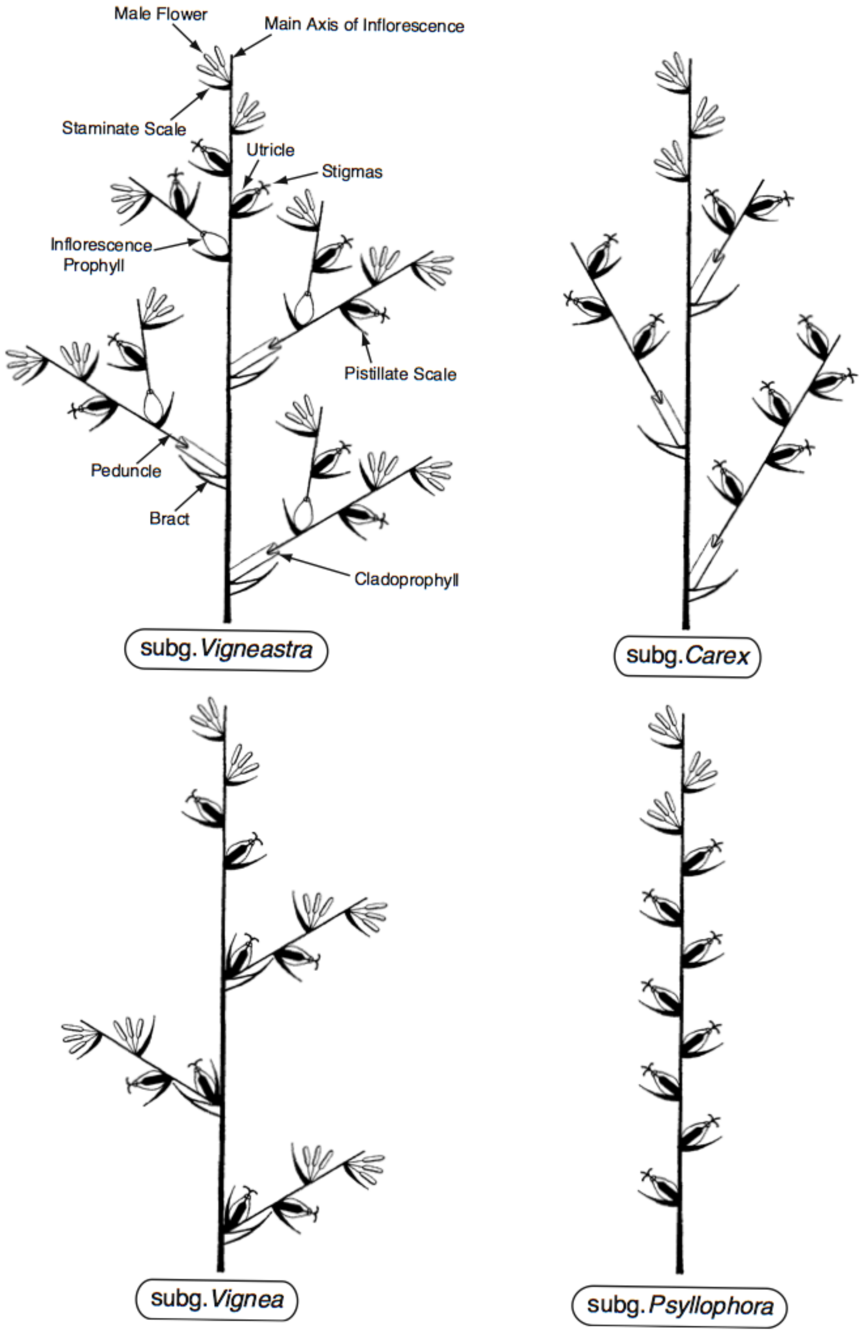


Figure 1.2: Comparison of typical inflorescence structures for the four subgenera of *Carex*. Subgenus *Vigneastra* is distinguished from all other subgenera by the presence of peduncled, bisexual spikes (androgynous) with cladoprophylls and inflorescence prophylls; subgen. *Carex* by peduncled, predominant unisexual spikes (lateral females, terminal males) with cladoprophylls; subgen. *Vignea* by typically sessile, bisexual spikes (androgynous or gynaecandrous), two stigmas, and the absence of cladoprophylls, and subgen. *Psyllophora* by a unispicate inflorescence (from Starr et al. 2008).

Figure 1.3: *Carex arctogena* from the section *Capituligerae* Kük. (=*Capitatae* Christ.) which is distinguished from other sections in subgenus *Psyllophora* by their densely capitate unispicate androgynous inflorescences, caespitose or loosely caespitose habitat and filiform leaves.

Chapter 2

Taxonomy of the *Carex capitata* complex

2.1 Introduction

Carex subgenus *Psyllophora* consists of ca. 25 sections and 75 species (Egorova 1999). Section *Capituligerae* Kük. (=*Capitatae* Christ.) is distinguished by their densely capitate, androgynous inflorescences, caespitose habit and filiform leaves (see Figure 1.3). It comprises two to four taxa, *C. oreophila* C. A. Mey, an alpine species found in the mountains of southwestern Asia Egorova 1999), *C. capitata* a circumboreal species and *C. arctogena* Harry Sm., an arctic-alpine species in North America, South America and Eurasia, which has been treated as synonym of *C. antarctogena* by Egorova (1999) and Moore & Chater (1971). Despite its small size, the section is characterized by several taxonomic problems concerning the circumscription of its species. Although *C. capitata* and *C. arctogena* are recognized as separate species in some taxonomical treatments (e.g. Egorova 1999), they are considered conspecific by other authors (e.g. Murray 2002) and in important online plant names databases (e.g. http://www.tropicos.org; http://www.kew.org; http://www.emplantbase.org).

Authors supporting the independent status of both species argue that *C. capitata* is distinguished from *C. arctogena* for having longer inflorescences, bigger achenes, shorter pistillate scales and perigynia with smooth margins, for forming looser tussocks and for occurring in soils with high water content (Table 2.1). *Carex arctogena*'s distribution in Europe is less widespread (Figure 2.1), occurring only in Scandinavian countries. In North America, where it occurs from Greenland to Mexico along the Rocky Mountains, it presents a considerable morphological and ecological variability, particularly in western North America. Some authors (Smith 1940; Egorova 1999; Cayouette 2007) stated the necessity of more studies including specimens from North America to clarify the taxonomic status of *C. capitata* and *C. arctogena*. Moreover, populations of *C. arctogena* from South America, were described as a distinct species, *C. antarctogena* Roivanen (1954). As stressed by Reinhammar & Bele (2001), a comprehensive worldwide study of the species complex using morphological, genetic and ecological data could help to elucidate its systematics.

In this study, we use morphological data with the following aims: (1) to clarify the taxonomy of *C. capitata* complex and propose the necessary taxonomic decisions; and (2) to characterize the different taxa morphologically, ecologically and geographically.

2.2 Materials and methods

2.2.1 Sampled material

Four hundred and forty six herbarium specimens were examined on loan, in person or by photograph from the following herbaria (acronyms follow Index Herbariorum hosted online by the New York Botanical's Garden, http://sweetgum.nybg.org/ih/): A, ALA, BAA, BRY, C, CAN, CAS, CCO, CHSC, COLO, DAO, GH, H, ICEL, M, MICH, MONTU, O, OSC, RM, RMS, UBC, UNM, UTEP, WIN and

WTU. Owing to the scarceness of herbarium specimens of *Carex capitata* s.l. from South America and the western USA, two expeditions were made to collect fresh material: one to Patagonia (January-February 2010) and a second to the western United States (July-August 2010). Samples were collected for a total of 12 populations (7 in South America and 5 in North America), covering the distributional range of the species in those regions. Vouchers of field collections (see Tables 2.2, 2.3 and 2.4) were deposited at CAN, SI, and UPOS. The isotype of *C. arctogena* was obtained on loan from DAO (Ottawa) and included in the morphological study, whereas high resolution scans of the holotype and lectotype of *C. capitata* and *C. antarctogena* were obtained from LINN and from H, respectively. Type material was included in the study to check the diagnostic morphological characters. Due to the limitations with measurements taken from photographs, these specimens were not included in the morphological study.

2.2.2 Morphological study

Specimens for morphometric analysis were selected to represent the full morphological and geographical range of each putative taxon (see Table A.9 in Appendix). The characters selected to be measured (Table 2.5) were those important for the taxonomy of the sect. *Capituligerae*, including some of those previously used by Reinhammar & Bele (2001) to differentiate *C. capitata* from *C. arctogena* (number of teeth along the margins of the perigynium, culm length, and length and width of the spike and achene).

All specimens available (see Figures A.10, A.9 and A.11 in Appendix for their distribution maps) were carefully examined. Morphometric studies were based on a subset of mature and complete specimens (see Figure 2.2 for a distribution map of those specimens used for morphometric analyses). Specimens from South America representing *C. antarctogena* were initially separated and then the rest of the specimens were placed into two groups according to Egorova (1999). She considered the whole distribution in the northern Hemisphere, and separated *C. capitata* and *C. arctogena* based on teeth number in the margins of the perigynia (smooth margins in *C. capitata* vs. sparsely scabrid margins in *C. arctogena*), on the shape of the pistillate scale (twice shorter and narrower than the perigynia in *C. capitata* vs. shorter than the perigynia and almost equal in width in *C. arctogena*) and on the shape of the perigynia (ovate in *C. capitata* vs. orbicular-ovate or broadly elliptical in *C. arctogena*). Plants that could not easily fit into these three groups, *C. capitata*, *C. arctogena* and *C. antarctogena*, were separated as unclassified using characters from a pilot analysis that suggested that the length of the staminate portion of the inflorescence, the length of the hyaline margin of the pistillate scale, the inflorescence shape and the length of the longest culm provided consistent characters.

Vegetative characters were measured using a standard ruler for parts longer than 10 cm whereas all other quantitative characters were measured to the nearest 0.1 of a millimeter using a stereoscopic binocular Nikon microscope Olympus SZX12 and a micrometer. Qualitative states were scored by eye. Twenty nine morphological characters (28 quantitative, one qualitative; see Table 2.5), were measured on a total of 147 specimens (*C. capitata*, N=43; *C. arctogena*, N=34, *C. antarctogena*, N=6); unclassified specimens N= 63). All measurements were compiled in an spreadsheet. Summary statistics for all characters including means, standard deviations and ranges were calculated for each group in R (http://www.r-project.org/).

2.2.3 Micromorphological study

Silica bodies are phytoliths produced by some plant species when soluble silica from the ground water is absorbed by the roots and carried to different parts of the plant through the vascular system. In sedges, they are found in the achene and leaf epidermal layers (Toivonen & Timonen 1976). Micromorphology has been used to discriminate macromorphologically similar taxa (Stuessy 1990). Silica bodies were studied because they can sometimes show significant interspecific variation among closely related species (Starr & Ford 2001; Zhang 2006). However, some silica bodies micromorphology studies did not help to differentiate between closely related species in some other *Carex* species groups (Standley 1987; Rothrock 1997).

The lowermost, mature achene was removed from the terminal spikes of representative samples of each group (*C. capitata*, *C. arctogena*, *C. antarctogena* and unclassified specimens). The perigynium surrounding the achene was dissected away and the cell wall of the epidermal layer of achenes was removed using a 9:1 sulfuric acid - acetic anhydride solution in order to expose the silica bodies (Starr & Ford 2001). Scanning Electron Microscopy (SEM) was then employed to search for taxonomically diagnostic micromorphological characters on the silica deposit surfaces. Samples were mounted onto aluminum stubs with conductive carbon adhesive discs, sputter coated with a 20-25 nm layer of a gold/palladium alloy and photographed in high vacuum mode using a Philips XL-30 ESEM with a 10kV accelerating voltage. Silica body morphology was described according to the terminology of Schulyer (1971).

2.2.4 Statistical Analysis

Statistical analyses were aimed at identifying groups. Statistical analyses were also used to identify the most informative morphological characters that could differentiate taxa and to test if the individuals studied formed different groups correlated with the different taxa traditionally recognized within the *C. capitata* complex and whether these groups were significantly different or received statistical support.

Histograms showing interspecific frequency differences between groups were made for the six discrete variables. Quantitative variables for the five putative taxa were explored using box and whisker plots. The Shapiro Wilk normality test conducted in the data set showed that most of the variables were not normally distributed within the putative taxa, thus intertaxon variation was analyzed using a Kruskal-Wallis one-way ANOVA. A post-hoc Mann-Whitney U pairwise test was also performed to assess whether differences were significant between groups. These analyses were run in R (http://www.r-project.org/).

Principal component analyses (PCA) were performed to detect groups among all specimens. In order to assess visually if taxonomic concepts corresponded to morphologically distinct entities, coloured symbols and convex hulls for each putative taxon were included in the resulting scatterplots made using eingenvalues for group's mean. These analyses were carried out using PAST (Hammer et al. 2001), where missing values are corrected by column average substitution.

A first PCA was conducted using specimens of *C. capitata*, *C. arctogena* and *C. antarctogena* and all 22 continuous variables. The analysis was repeated in the same dataset using a subset of 12 quantitative variables (denoted by asterisks in Table 2.5) that included the characters employed by Egorova (1999) to differentiate between *C. capitata* and *C. arctogena* and those determined in a pilot analysis to set apart three groups within the unclassified specimens. A correlation matrix was studied in order to discard highly correlated variables (> 0.8) within the subset (see Tables A.2 and A.3 in Appendix). Although the length of the inflorescence and length of the staminate portion were highly correlated (0.9), both were retained in the PCA because this correlation was observed to be inconsistent in *C. capitata.* PCA is primarily used for structure detection and its purpose is to examine the underlying relationships between groups. Therefore, consecutive PCA were performed removing *C. capitata* and *C. arctogena* samples, as these species can be easily recognized within all specimens (Jiménez-Mejías & Cabezas 2009).

2.2.5 Geography

All studied specimens were geo-referenced to determine the geographic ranges for each putative taxon and to reveal whether taxa occur in sympatry or allopatry. Distribution maps (from Olson et al. 2001 for world maps, and North American Commission for Environmental Cooperation for North American maps) of all the putative taxa in the complex were made in ESRI ArcGIS v. 9.2, using all the specimens examined. The acronyms used for species distributions follows Brummitt (2001).

2.2.6 Ecology

For the three populations collected in North America, soil pH measurements using Cornell pH Test Kit Wide Range (Ithaca, New York) were taken to characterize habitat conditions. A list of vascular plants associated with the complex (observed within 10 m of a plant of *C. capitata* complex) was noted. Habitat characterization of all the putative taxa in the *C. capitata* complex was made from field work observations and voucher label information, unless otherwise noted.

2.3 Results

Summary statistics from all specimen measurements is available in Appendix A. All the specimens' measurements and label information studied are gathered in a Botanical Research and Herbarium Management System database (www.brahmsonline.com) that is available upon request from the author (see Figure 2.2).

During the study of the North American specimens, substantial variation in the morphological features (length of the culm, length of staminate portion of the inflorescence, length of hyaline margin of the pistillate scale), ecological requirements (habitat conditions) and geographical distribution revealed the existence of three different groups. Therefore, the unclassified specimens were divided in three groups: *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2.*

2.3.1 Univariate analysis

Measurements for each continuous character are reported as the mean ± one standard deviation, with observed ranges included in parenthesis (Table 2.6). Specimens of *C. arctogena* from South America (=*C. antarctogena*) and northern hemisphere were compared in a Kruskall Wallis one-way ANOVA test (see Table 2.8) resulting in statistically significant differences for length and with of inflorescences, length of the staminate and pistillate portions, width of pistillate scales and length of perigynia (see Table 2.7). These differences were assessed in a post-hoc Mann-Whitney U pairwise test (see Table 2.8), supporting only the width of the inflorescence, length of pistillate and staminate portions and the length of the perigynia. *Carex arctogena* samples from South America (N=6) have higher values for the significant variables than *C. arctogena* samples from the northern hemisphere; these differences are in average of a 10% higher of the mean values, except for the variable length of the staminate portion (39%) but whose standard deviation for the South American samples is of the same order of magnitude as the mean. Therefore, as these differences are not considered by the author as enough to discriminate between specimens from the southern hemisphere, those samples were included in the *C. arctogena* group.

Despite some overlap in the measurements for many characters, all taxa present significant differences between taxa for some variables (Table 2.9). Based on Mann-Whitney pairwise comparisons between taxa in the complex, whose null hypothesis is that two samples come from the same population, revealed the following critical diagnostic characters for differentiating between species within the complex (Table 2.9): length of the longest culm overwintered (CLHMT) or from the present year (CLMH), length of the staminate portion of the inflorescence (MSPL), leaf length (LEAFL), length of the spike (INFLOL), width of the perigynium (PERIGW), width of the spike (INFLOW) and length of the narrowest hyaline margin in the pistillate scale (GLUMHC).

Although discrete characters do not present statistically significant differences between putative taxa (Figure A.1 in Appendix), *C. arctogena* usually possesses more teeth (3-7) along the edges of the perigynium than what it is seen in the other taxa in the complex. *Carex capitata* and *Carex sp. nov. 1* have smooth (no teeth) perigynia or possess only a few teeth, generally no more than three, on perigynium margins. In general, *Carex sp. nov. 2* also possesses smooth perigynia (0-2), but at least one specimen presented 16 teeth along its margins.

2.3.2 Multivariate analyses

During the analyses of morphological traits, one qualitative character, colour of the culm sheath, was discarded as it could not be reliably scored. Box plots for each of twenty two continuous variables (Figures A.2 and A.3 in Appendix) show differences between putative taxa. Only two characters (achene and leaf width) were not significantly different among members of the complex (Table A.1 in Appendix).

A scatter plot of the two first components in a PCA using *C. arctogena* specimens from North America and Europe and *C. antarctogena* specimens and the 12 variables selected showed that there is not a geographical pattern within the samples (see Figure 2.8). *Carex arctogena* specimens from South America seem to be placed in one side of the plot (there are small significant differences as it has been shown above), and close to other samples of *C. arctogena.* Therefore, *C. antarctogena* specimens were labelled afterwards as *C. arctogena.*

PCA of the five groups (*C. capitata*, *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2*) graphically summarized the phenetic differences among individuals (see Figure 2.10). Two PCA were made, one using all 22 variables and a second using only 12 quantitative variables. Principal components scores were always higher when only 12 variables are used (Table 2.10). Therefore, only scatter plots from the PCA with the 12 variables are shown. Similar results are obtained when using the 22 continuous variables measured (results are not shown).

When comparing all specimens of *C. capitata* with other groups, there is some overlap between them. *Carex capitata* can be easily separated from the other taxa by the teeth character; *C. capitata* has a smooth perigynia (discrete character not included in the PCA). Therefore, if only *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2* are used; there is a clear separation of all the putative taxa (Figure 2.11).

Then, if *C. arctogena* is removed from the analysis, there is a clear increase in the split of *"C. cayouetteana"* from *Carex sp. nov. 1* and *Carex sp. nov. 2* (Figure 2.12).

The first two principal components axes in PCA using 12 continuous variables, accounted for 71.76% and 18.07% of the total variance. The third and the fourth principal component accounted for 5.99% and 4.17%.

All taxa can be identified by a unique set of characters. Specimens with the longest culms, leaves, inflorescence and staminate flowers portion were referable to *Carex sp. nov. 1* (Figure 2.3). Specimens with short culms and leaves and the narrowest inflorescence were referable to *Carex sp. nov. 2* (Figure 2.4). Specimens with medium-size culms, the longest pistillate scale and the widest perigynia were referable to *"C. cayouetteana"* (Figure 2.5). Specimens with short culms, small staminate flowers portion, long hyaline margins, narrow perigynia and with the smallest staminate scales were referable to *C. arctogena*, being in consistence with both its holotype and *C. antarctogena* holotype (Figures 2.6, A.7 and A.8 in Appendix). Finally, specimens with long culms and leaves, the widest inflorescence, the narrowest pistillate scales and the longest perigynia were referable to *C. capitata* (Figure 2.7).

2.3.3 Micromorphological characters

Silica bodies presented no significant differences between or within putative taxa in the complex, with all the members possessing a single, circular central body in the middle of a concave silica platform. Epidermal cell walls were commonly linear, isodiametric and six-sided (Figure 2.13).

2.3.4 Geographical distribution

All the following geographical information was taken from herbarium specimens, unless otherwise noted. *Carex capitata* presents a polar-boreal-alpine distribution and it occurs in Eurasia and in North America (Figure 2.14). In Europe, it occurs in Iceland, Norway, Sweden, Finland, Germany, Austria, Switzerland and Italy. In Asia, it occurs in Russia from Kola Peninsula to Chukotka peninsula, occurring south to 50°N in central eastern Russia. Raymond (1949) also noted that it occurs in northern Mongolia, but no specimen from this region was examined during this study. In North America, it occurs in Alaska, the Yukon Territory, the Northwest Territories, British Columbia (South to ca. 50°N), Alberta, Saskatchewan (South to ca. 52°N), northern Manitoba, northern Ontario and Greenland (North to ca. 72°N).

Carex arctogena has a bipolar and amphi-Atlantic distribution with stations in northern Europe (Scandinavia), North America and South America (Figure 2.1). In North America, it occurs in British Columbia (South to ca. 50°N), northern Saskatchewan, Manitoba (South to 52°N), northern Ontario, northern Québec, Newfoundland and Labrador (South to ca. 52°N), Nunavut (until South of Victoria Island and Baffin Island, 63.5N), New Hampshire (White Mountains and Mt. Washington, 4450°N; Steele & Hodgon (1973) reported to occur in Mt. Cardigan but that material was not examined) and its northernmost latitude occurs in Greenland (North to ca. 68°N). In South America, it occurs in Argentinian and Chilean Patagonia, from Tierra del Fuego (Argentina) to Neuquén province (38°S, Argentina).

"Carex cayouetteana", *Carex sp. nov. 1* and *Carex sp. nov. 2* are endemic to North America (Figure A.10 in Appendix). *Carex cayouetteana* occurs only in western North America with stations in Colorado, Utah, Montana, Wyoming, Nevada, California, Washington, Alberta and British Columbia (North to ca. 49°N). *Carex sp. nov. 1* occurs only in northern California and southern Oregon (Deschutes, Jackson and Lake Counties). *Carex sp. nov. 2* is a Californian endemic, restricted to high elevations in the Sierra Nevada (Inyo, Mono, Tulare and Tuolumne Counties).

2.3.5 Ecological requirements

All ecological data have been taken from label information and fieldwork studies, unless otherwise noted. Hybrids involving different members of the *C. capitata* complex have never been reported and were not discovered during this study.

Carex capitata is an alpine species. In northern latitudes such as Alaska or the European Arctic, it is found in tundra and taiga (boreal forest) environments whereas in southern latitudes, such as central Europe or western Canada, it is found in alpine or subalpine areas. It occurs in rich and calcareous fens, mires, peat-bog margins, meadows, wet tundra and other humid or moist habitats, sometimes with moss as also noticed by Smith (1940). In Alaska, it is also found in marshes and poplar forest from lowlands (400 m) to at least 800 meters. In northeastern North America, it is mainly found in areas adjacent to Hudson Bay, rare or local in alpine summits towards South. *Carex capitata* elevational occurrence in Italy is at 1900 - 1980 m (in the South Tyrols). It has been reported to be strictly a calciphile or calciphilous (Smith 1940; Nilson 1991; Cayouette 2007), but such information was not taken from the label data from the specimens examined for this study.

Carex arctogena is an arctic-alpine species. It generally occurs in wind-exposed alpine heaths, often dominated by *Empetrum* (Ericaceae) and also in cliffs, ridges, summits and in dry areas often dominated by rocky or gravelly soil. In northeastern North America it is found locally in New Hampshire (Alpine Garden and Mt. Cardigan) at 1900 m, one of the highest elevations within its entire distribution together with its southernmost localities in British Columbia (ca. 2000 m). Similarly, it occurs near this altitude in northern Patagonia (Neuquén). In southern South America, it occurs in humid areas such as bogs, wet meadows and eutrophic marshes at low elevations, often in areas of high floral diversity (Table 2.2). In the southernmost region of Patagonia, Tierra del Fuego, *C. arctogena* was found in a semi-humid grassland, dominated by tufted grasses interspersed with *Empetrum rubrum* at low elevations (Table 2.2). It has been reported to grow in either calciphile, peridotite, gneiss, granite or serpentine soils (Smith 1940; Nilson 1991) but such information is generally missing in voucher specimens.

Carex cayouetteana generally occurs in acidic and rocky soils (see Table 2.3), in wind-exposed, alpine moist tundra areas and sometimes in dry meadows. It is found from ca. 2000 m in Washington and California to at least 3500 m in Colorado and Utah, where it can grow on quartzite soils.

Carex sp. nov. 1 may occur in acidic-neutral pH soils (see Table 2.4), in wet meadows or mires surrounded by woods. In northern California (Tehama, Plumas and Butte Counties) and southern Oregon (Lake and Jackson Counties), it occurs at unusual elevations for the complex at this latitude (ca. 1400 m). In Sierra and El Dorado Counties, it occurs in wet marshy meadows and in open *Pinus contorta* forests at ca. 1980- 2300 m where it reaches its highest elevation.

Carex sp. nov. 2 is restricted to the highest elevations in California. It occurs in non-glaciated plateaus and wet banks. On the North side of Mount Humphries ("Humphries Plateau", Inyo Co.) it grows at 3900 m and also at 3600 m at Mono Mesa (Inyo Co.); in northeastern Tulare Co., in wet banks at ca. 3400 m. It is found in Tuolumne Co., in soil formed from metamorphic rocks, in non glaciated areas at ca. 3800 m. Only 8 herbarium specimens where observed during the course of this study. Giving the extreme elevation at which this species occurs, this might indicate that *Carex sp. nov. 2* is rare or that the habitat in which it occurs has been under collected.

2.4 Discussion

2.4.1 Species concept in *C. capitata* complex

Owing to the diversity and complexity of life, no universal species concept has yet been accepted (Balakrishnan 2005). However, in order to be clear on what criteria were deemed necessary to recognize species in this study, the species concept employed is defined as follows: the smallest aggregation of populations diagnosable by a unique combination of characteristics (morphological, genetic, ecological and geographical) in comparable individuals, supported by phylogenetic analyses. Plant taxonomists, such as Henderson (2006), has suggested the phylogenetic species concept to be appropriate for plant systematists. The phylogenetic species concept can be divided into two approaches: character-based and lineage-based (Baum & Donoghue 1995). The character-based species concept defines species as the “smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (Nixon & Wheeler 1990). The lineage-based phylogenetic species concept, views species as a “temporal series of populations connecting two speciation events (Willmann & Meier 2000). One of the problems in the phylogenetic species concept is the validity of a phylogenetic approach to units at and below the species level (Willmann & Meier 2000). Therefore, morphological, ecological and geographical differences among individuals are needed to be consistent with lineages in order to describe new species.

2.4.2 *Carex capitata* complex

Our results suggest that five species should be recognized within the *C. capitata* complex on the basis of morphological data: *C. capitata*, *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2*.

Each taxon presents distinctive morphological, geographical and ecological characteristics that are unique to it. Morphologically, a combination of characters is needed to distinguish the different taxa in the complex. The best diagnostic characters to recognize these species are length of the culm, length of the staminate portion in the inflorescence, length of the pistillate scale and length of the shortest hyaline margin.

Geographically, *C. capitata* presents a circumboreal distribution whereas *C. arctogena* presents a bipolar distribution. *Carex cayouettena* is only found in western North America from 37°N until 50°N; *Carex sp. nov. 1* is restricted to southern Oregon and northern California (Sierra, El Dorado, Nevada, Lake, Jackson and Deschustes counties); and *Carex sp. nov. 2* occurs locally at high elevations (3400 - 3900 m) in California (Tuolumne, Inyo and Tulare counties). *Carex sp. nov. 2* small representation in herbarium specimens gathered for this study could reflect both its narrow distribution, restricted to high Sierras of northern California, or an undercollected area.

Ecologically, *C. capitata* grows in low alpine or wet tundra areas, in rich, calcareous and moist habitats (e.g. fens, mires, bogs, meadows); *C. arctogena* grows in arctic, high alpine or dry tundra areas in North America and Europe whereas in southern South America, it grows in bogs, wet meadows and even in grasslands at low elevations (60 - 730 m) and at higher elevations in northern Patagonia (ca. 2300 m); *"C. cayouetteana"* grows in alpine, moist tundra areas, but also in meadows and rocky soils, from 2000 to 3800 m; *Carex sp. nov. 1* grows in wet meadows, mires, fens and open marshes from low elevations (ca. 1400 - 2300) m; *Carex sp. nov. 2* grows in non-glaciated plateaus and wet banks at high elevations (3400 -

3900 m).

Although *C. antarctogena* specimens from South America displayed statistically significant morphological differences regarding to northern hemisphere specimens in some variables, the author do not consider them as enough to differentiate between northern and southern specimens. These differences are of a 10% in average and for one variable, length of the staminate portion, is of 38% (but this variable has an standard deviation of the same order of magnitude as the mean). Thus, *C. antarctogena* and *C. arctogena* are treated as synonyms in this study, which is consistent with the previous morphological analysis by Moore & Chater (1971). In congruence, in Chapter 3, molecular analyses of three chloroplast regions (*matK*, *atpF*-*atpH* and *rps16*; 2297 characters) and five nuclear loci (CM25, S082, S180, Cko1-47 and CM01; 861 characters), show no genetic differences between *C. arctogena* from the northern vs. southern Hemisphere.

On the other hand, some variability was found within *C. capitata* specimens from Russia, Austria, Ontario and Alberta, which have culms longer than 41 cm long. This plasticity within *C. capitata* was also remarked by Raymond (1949) in some specimens collected in Québec (Lac De l'Ours). However, in our opinion, this appears to be no more than a regional trend and it is not correlated with other morphological characters, so it might not deserve taxonomical recognition.

All taxa in the *C. capitata* complex are long-lived perennials, wind-pollinated and reproduce sexually. Hybrids between members of the complex have not been reported. Nonetheless, more studies are needed to fully understand their reproduction biology (e.g. self-pollination or self-compatible) (Reinhammar & Bele 2001).

A large number of new species has been described over the last few decades in North America North of Mexico (Ertter 2000). This is especially true for the genus *Carex* (Naczi 1993; Naczi et al. 1998; Naczi & Ford 2001; Saarela & Ford 2001), with an average of two taxa described per year over the last 20 years (Ertter 2000). This rich biodiversity in North America could be possibly due to ecological diversity and historical environmental transformations during the last 18000 thousand years due to paleoclimatic changes as it has been highlighted in many intensive Flora studies (e.g. Ball et al. 2002; Hickman 1993), and should continue to be the focus of research interests in order to better understand species distributions.

All five species of the *C. capitata* complex occur in North America and the three new taxa are endemic to North America, which provides further evidence of the taxonomic richness that exists within North American *Carex*. Some other examples include *C. maritima* Gunn. species complex, a bipolar species widely distributed in North America, whose ecological and morphological variability led Kreczetowitcz (1932) to described twelve different species and some other botanists to describe new taxa (e.g. *C. incurviformis* Mack. varieties, *C. maritima* var.*setina* (Christ) Fernald or *C. maritima* var. *misera* (Kük.) Fernald); and forms (e.g. *C. maritima* f. *inflata* (Simmons) Polunin). It is also remarkable studies made by Naczi et al. (2002) who described seven new *Carex* species from North America (*C. acidicola* Naczi, *C. calcifugens* Naczi, *C. paeninsulae* Naczi, E. L. Bridges & Orzell, *C. thornei* Naczi, *C. kraliana* Naczi & Bryson, *C. gholsonii* Naczi & Cochrane and *C. infirminervia* Naczi).

2.4.3 Taxonomic treatment

The following key helps to identify the species of *C. capitata* complex recognized in this study. Mature, complete and ample specimens are necessary for correct identifications.

1. Tallest culm (8.3)9-12(14) cm long; pistillate scales (1.5)1.9-2 mm long; leaves curled at the tip . . . . ***Carex sp. nov. 2***

1. Tallest culm longer than (12.6)20.4-35.4(54) cm; pistillate scales (1.7)2-2.4(2.7) mm long; leaves straight at the tip **2**

2. Tallest culm 17-42(54) cm; perigynium margin smooth or with 1-3 teeth; pistillate scales light coloured **3**

3. Inflorescence (5.5)6.3-8.7(10.3) mm long and (3.3)4-5(5.4) mm wide, with staminate portion (0.8)1.3-2.5(3.5) mm long; perigynium (1.8)2.5-3.4(3.6) mm long, generally spreading and lowermost sometimes even descending; scales twice shorter and narrower than the perigynium .... ***C. capitata***

3. IInflorescence (6.8)11-13(16.9) mm long and (3.2)3.6-4.2(4.6) mm wide, with staminate portion (2)5-7(10) mm long; perigynium (1.5)2.3-2.8(3.1) mm long, generally ascending; scales as long or slightly shorter than the perigynium, and as wide or slightly narrower than the perigynium .... ***Carex sp. nov. 1***

2. Tallest culm (12)15-21cm; perigynium margins with (1)3-16 teeth; pistillate scales dark coloured **4**

4. Pistillate scales (0.8)1.2-1.6(1.8) mm wide; perigynium margin smooth or with 1-2 teeth; pistillate scales light coloured; lowermost perigynia descending .***C. capitata***

4. Pistillate scales (1)1.4-2(2.6) mm wide; perigynium margins almost always scabrous with (1)3-16 teeth; pistillate scales dark coloured; lowermost perigynia horizontally orientated **5**

5. Inflorescence (3.5)3.8-5(6.1) mm wide, with staminate portion (0.9)1.8-4.6(6.6) mm long; pistillate scales with no hyaline margin or 0.07-0.4(0.5) mm in the central portion and 0.17-1 mm along the edges; staminate portion of the spike with cone shape; hyaline margins on the pistillate scales drawing in an inverted V shape .... ***"C. cayouetteana"***

5. Inflorescence (2.9)3.4-4.2(4.7) mm wide, with staminate portion (1.2)1.4-2.8(3.7) mm long; pistillate scales with hyaline margins (0.1)0.2-0.6(1) mm in the central portion and (0.4)0.5-1.4(2.6) mm along the edges; staminate portion generally cylindrical; hyaline margins on the pistillate scales with in a triangular shape .... ***C. arctogena***

2.4.4 Species descriptions

Carex capitata L., Syst. Nat. (1759) 10th ed., 2:1261. Type: Sweden, Lapponia. Leg. Solander. Stockholm Linnean Herbarium 378.13 (S-LINN: IDC 378.13) photo!

Herb forming loose to dense tussocks. **Roots** dark yellow, light brown, yellow or greyish-yellow. **Culms** 12-49 cm high and 0.6-1.0 mm wide at the middle, slender, wiry, more or less dentate on the margins and mainly near the apex. **Leaves** usually 3-5 per culm, old leaves persistent, most often shorter than the culm; **Leaf sheaths** dark orange-brown, dark brown-red or dark brown at the base, sparingly filamentose; **blades** 11.5-36 cm long and 0.4-1.5 mm wide in the middle, filiform, stiff, erect or recurving, truncate mouth; **ligule** very short, obtuse. **Spike** solitary, androgynous, globose, ovoid or trigonal, with staminate portions covering 15 % to 34 %, fairly densely packed, of 5.5-10.3 mm long and 3.3-5.4 mm wide, staminate portions from 0.8-3.5 x 0.5-1.3 mm, 5-15 staminate flowers, 12-27 pistillate flowers; **bract** absent or rarely present; **staminate scales** erect, obovate or ovate, the body orange, dark yellow-orange or brown-yellow with hyaline margins located in the distal 1/3 and 0.1-0.2 mm wide, often folded, glabrous, 1.6-2.9 x 0.6-1.5 mm, incomplete veins, acute apex; **stamen** with anthers 1.0-1.5 mm long; **pistillate scales** ovate or broadly ovate, the body orange, dark orange or brown, hyaline margins absent or 0.1-0.5 mm in the central portion and 0.1-2.25 mm along the edges, central nerve rarely present, glabrous, 1.5-2.5 x 0.8-1.8 mm, shorter than the perigynium body and reaching 1/2 of perigynia body length, narrower than the perigynia and sometimes not reaching 3/4 of perigynia width; distal **perigynia** erect or ascending, mostly spreading or the lowermost descending or retracted in the proximal part, the body greenish-light yellow in proximal half, yellow to yellow-grayish or brown with some redness in the distal half, surface often shiny with some red dots, 1.8-3.6 x 1.3-2.2 mm, margins sometimes winged especially in the 1/3 proximal and 0.1-0.2 mm wide, smooth (rarely 0-5 teeth), round bases, apex acute, contracting gradually into a beak; **beaks** brown or orange-brown, apex orange or hyaline, 0.8-1.7 mm long x 0.2-0.3 mm wide at the base, straight; **gynoecium** with 2 stigmas; **rachilla** often visible in relief on the side of abaxial perigynia, setaceous, as long or slightly longer than achenes; **achenes** ellipsoid, broadly ellipsoid or almost orbicular, the body light yellow, yellow-greenish, non-glossy surface, 1.1-2.1 x 1.0-1.5 mm, filling more than 2/3 to 3/4 of the perigynium, broadly cuneate or rounded at the base, apex acute, obtuse or truncated; style bases absent or persistent by the bottom of the style.

Notes: *C. capitata* is easily differentiated from other members of the complex by its spreading perigynia with the lowermost sometimes even descending, similar to the morphological condition separating the species pair *C. typhina* Michaux and *C. squarrosa* L. It can also be easily recognized from all other members of the complex by its pistillate scales, shorter and narrower than the perigynia; its small staminate portion; the presence of some redness in the perigynia and glabrous perigynia.

Distribution: Europe (ICE, NOR, SWE, FIN, GER, AUT, SWI, ITA); N Russia; N North America (ASK, YUK, NWT, BRC, ABT, SAS, MAN, ONT, GNL).

Ecology: Tundra, taiga (boreal forest) and alpine and subalpine areas, in various humid soils (fens, mires, meadows).

Specimens examined:

Austria, Innsbruck, Seefeld, 1180 m, HöllerJ. s.n., 26.7.1958, (M, 0151923). Tirol, Seiser Alp, 2000 m, Görz s.n., 27.7.1914, (GH). Canada, Alberta, Ft. Fitzgerald, Cody, W.J. 4533 and Loan, C.C., 19.7.1950, (RM, 228683). British Columbia, Bluster Mt., 2133 m, Thompson, J. s.n. and Thompson, M., 14.7.1938, (WTU, 17326). British Columbia, Mt. Tinsdale, 2133 m, Krajina, J. s.n. and Pojar, J., 13.8.1974, (UBC, 149191). British Columbia, Mount Apex, 2164 m, Calder, J. 11795 and Savile, O., 11.8.1953, (WTU, 170234). British Columbia, Anahim Lake, 1219 m, Calder, J. 18578, Parmelee, J.A.; Taylor, R.L., 9.7.1956, (WTU, 197744). British Columbia, Anahim Lake, 1219 m, Calder, J. s.n., Parmelee, J.A.; Taylor, R.L., 9.7.1956, (COLO, 158463). British Columbia, Summit Pass, Raup, H.M. 10788 and Correll, D.S., 24.7.1948, (RM, 272042). Manitoba, Fort Churchill, Ritchie, J. 2104, 5.8.1956, (WIN, 22433). Manitoba, Wapusk National Park, 10 m, Punter, E. 03-509 and Piercey-Normore, M., 19.7.2003, (WIN, 71429). Manitoba, Twin Lakes, Ford, A. 02379, Piercey-Normore, M.; Punter, E.; Punter, D., 25.7.2002, (WIN, 71024). Manitoba, Fort Churchill, Johnson, K. J73-402, 26.8.1973, (WIN, 33557). Manitoba, Fort Churchill, Shay, J. 59-924a, 9.7.1959, (WIN, 64354). Manitoba, Fort Churchill, Shay, J. 83-60, 11.7.1983, (WIN, 40808). Manitoba, Fort Churchill, Zbigniewicz, M. 83-237, 5.8.1983, (WIN, 40839). Manitoba, Wapusk National Park, 15 m, Ford, A. 02-330, Piercey-Normore, M.; Punter, D.; Punter, E., 21.7.2002, (WIN, 70209). Manitoba, Wapusk National Park, 23 m, Ford, A. 02-306, Piercey-Normore, M.; Punter, D.; Punter, E., 20.7.2002, (WIN, 70255). Manitoba, Vicinity of Churchill, Schofield, W. 6862 and Crum, H., 21.7.1956, (CAN, 247332). Manitoba, Fort Churchill, Ritchie, J. 2104, 5.8.1956, (CAN, 248387). Manitoba, Open coastal plain 3 miles East of camp, McFarlane, D.M. 239 and Irvine, B.R., 7.8.1953, (CAN, 322733). Manitoba, Fort Churchill, Brown, D.K. 733, 12.7.1951, (CAN, 263696). Manitoba, Fort Churchill, Argus, G.W. 425-58, 4.8.1958, (CAN, 281144). Manitoba, Fort Churchill, Rossbach, G.B. 7073, 5.8.1965, (CAN, 329753). Manitoba, Fort Churchill, s.n., 30.7.1910, (CAN, 17340). Northwest Territories, Aubry Lake, Riewe, R. 225 and Marsh, J., 17.7.1976, (WIN, 32000). Northwest Territories, Aubry Lake, Riewe, R. 336 and Marsh, J., 4.8.1976, (WIN, 31438). Northwest Territories, Aubry Lake, Riewe, R. 225 and Marsh, G. .M., 17.7.1976, (CAN, 433230). Northwest Territories, Kakisa river, Thieret, J.W. MM3 and Reich, R.J., 18.6.1959, (CAN, 298045). Northwest Territories, Sawmill Bay, Shacklette, H.T. 2970, 13.7.1948, (CAN, 199991). Ontario, Fort Severn, Hustich, I. 1296, 13.7.1956, (CAN, 242845). Ontario, Winisk, Lundsden, H. s.n., (COLO, 448829). Ontario, Kenora District, Riley, J.L. 5848, 23.8.1976, (CAN, 409561). Ontario, Lake River, Dutilly, A. 16550-16807 and Lepage, E., 12.9.1946, (CAN, 17332). Quebec, Fort Chimo, Calder, J. 2316, 2.8.1948, (RM, 216050). Saskatchewan, Hwy #2 Waskesim, Hudson, J. 5063, 31.7.1992, (CAN, 565528). Yukon, Mile 85 on road from Whitehorse to Dawson, 579 m, Calder, J. 25796 and Gillett, J., 22.6.1960, (ALA, 1124987). Yukon, Kluane Lake Quad, 1036 m, Scotter, W. 20992 (Y-18), 2.8.1972, (ALA, 1124986). Yukon, Francis Lake, Duman, G. 70-805, 28.7.1970, (ALA, 1124985). Yukon, Ogilvie Mountains, Porsild, A.E. 1462, Porsild, R., 28.6.1968, (CAN, 318349). Yukon, Alaska Highway at milepost 1149, Welsh, S.L. 7921, Moore, G., 5.7.1968, (BRY, 71334). Yukon, Rink Rapids, Macoun, 7922, 9.7.1902, (CAN, 17356). Yukon Territory, Dempster Highway, Porsild, R. 1593, 17.7.1968, (CAN, 318505).Finland, Enontekiö Lapland, Lake Raittijrvi, 545 m, Väre, H. 11643, 8.8.2001, (H, 737942). Enontekiön Lappi, Enontekiö, 520 m, Piirainen, M. 2118 and Piirainen, P., 19.7.1991, (H, 668357). Enontekiön Lappi, Enontekiö, 600 m, Väre, H. 14955, 1.8.2003, (H, 746021). Enontekin Lappi, Goaskinjörvi, Kulmala, H. 83/02, 8.8.2001, (H, 744865). Inari Lapland, Kevo Research Station, Sulkinoja, M. s.n., 12.9.1967, (M, 0151936). Inarin Lappi, Kietsimäjoki, Kulmala, H. 8/97, 27.7.1997, (H, 720181). Kainuu, Yli-Näljänkä, 230 m, Ohenoja, M. 11, 8.8.1990, (H, 696101). Karesuando, Karesuando, Honkell, J.s.n., 9.8.1923, (M, 0151934). Kemi Lapland, Vesmajärvi, 210 m, Kurtto, A. 1778, Vuokko, S., 10.8.1978, (O, 660352). Kittilä, Mustavaara, 202 m, Ulvinen, T. s.n., Vilpa, E.; Seitapuro, H., 10.7.1997, (H, 720622). Kuusamo, Liikasenvaara, Ulvinen, T. s.n., 9.8.1962, (O, 539355). Kuusamo, Liikasenvaara, Ulvinen, T. s.n., 9.8.1962, (M, 0151946). Kuusamo, Lake Paanajrvi, Laurila, M. s.n., 9.7.1938, (H, 272411). Kuusamo, Liikasenvaara, Kukkonen, I. s.n., 30.8.1966, (RMS, 284390). Kuusamo, Liikasenvaara, Ulvinen, T. s.n., 9.8.1962, (CAN, 276804). Kuusamo, NE-section, Paanajärv, Savola, J. s.n., 28.7.1985, (H, 616973). Länsi-Suomen Lääni, Frösön, Mickstrm s.n., Lagerheim, C.; Sjögren, G., .8.1844, (GH). Lapland, Upper Kemi-river, Ulvinen, T. s.n., 12.8.1961, (C). Lapland, Poroeno, 540 m, Väre, H. 11651, 9.8.2001, (H, 737950). Lapland, Kivijärvi, 460 m, Väre, H. 11515, 29.7.2001, (H, 737814). Lapland, Upper Kemi-river, Ulvinen, T. s.n., 12.8.1961, (H, 328698). Lapland, Tulppio district, Vuokko, S. 8, 29.7.1975, (H, 449415). Lapponia, Muornis, Montell, I. s.n., 17.7.14, (GH). Lapponia, Euvntekiensis, Montell, I. s.n., 9.8.1923, (M, 0151944). Lapponia, Shishe, Montell, I. s.n., 11.7.1909, (M, 0151913). Lapponia, Kouda, Brotherus, V.F. s.n. and Brotherus, A.H., .8.1872, (H, 244602). Lapponia orientalis, Tjavauga, Brenner, M. s.n., 4.7.1863, (H, 1037144). Lapponia Varsug, Kihlman, A.O. s.n., 19.8.1889, (H, 328709). Petsamo, Primmanki, Saxn, U. s.n., 13.7.1930, (H, 328729). Pohjanmaa, Ylitornio, Mellakoski, 137 m, Ulvinen, T. s.n., 24.7.1980, (COLO, 394339). Pohjois-Pohjanmaa, Pessalompolo, 140 m, Ulvinen, T. s.n., Karjalahti, T., 30.7.1976, (H, 457472). Sompion Lappi, Petkula, Ohenoja, E. s.n., Melamies, H., 26.7.1996, (H, 722418). Tulijoki, Kainuu, Lehtonen, L. s.n., 18.7.1933, (DAO, 257434). Tulijoki, Kainuu, Lehtonen, L. s.n., 18.7.1933, (DAO, 257433). Tuntsa, Ylitornio, Mellakoski, Kämäräinen, H. 1999-215, 16.7.1999, (H, 732554). Vaskojoki, Kihlman, A.O. s.n., .8.87, (GH). Germany, Bavaria, Monacho Bavaria, Brügger, C. s.n., 29.6.1873, (GH, 2275). Bavaria, Mikalum, Buccarini s.n., (GH). Bavaria, Oberbayern, Seurs 2053, 27.5.1949, (M, 0151919). Bavaria, Oberbayern, Seurs s.n., 22.5.1851, (M, 0151916). Bavaria, Oberbayern, Leuvs s.n., Seuvnad, 9.6.1851, (M, 0151915). Bavaria, Deining, Brügger, C. 2275, 29.6.1873, (H, 1093339). Oberbayern, Haspelmoor, Holler s.n., 6.1872, (M, 0151918). Oberbayern, Deininger Fliz, Ohmüller s.n., 5.1867, (M, 0151920). Spitzel, V. 379, 1960, (O, 135). Oberschwaben, Schánzle 5.1880, 5.1880, (M, 0151921). Fleischer 18-1900, 1900, (H, 1226126). Greenland, Vestgrønland, Sydostbugten, 80 m, Mller, M. 1156, 15.7.1981, (C).Vestgrønland, Akuliarusikavsak, Jakobsen, K. 12291, 11.8.1956, (C). Iceland, Akureyrense, Skjóldalsárgil, Hg, H. 1529, 20.6.1965, (H, 1226120). Akureyri, Løgumshlid, Grøntved, J. s.n., 24.7.1928, (GH). Árnessýsla, Votamýri, 60 m, Löve, A. A095, Löve, D., 25.9.1949, (GH, 095). Belgsá, Fnjóskadal, Kristinnsson, H. 5143, 27.7.1973, (DAO, 288690). Borgarnes, Borgarnes Fjöfdur, Scamman, E. 1260, 22.8.1938, (GH, 1260). Dalfjall, Mývatnssvei, 460 m, Einarsson, E. E6042, 21.8.1974, (ICEL, 04073). Egilsstadir, Héradi, 80 m, Meyer, Dr. med. G 7146, 27.8.1932, (ICEL, 04083). Egilsstadir, Vopnafirdi, Stefánsson I, S. 256, 4.8.1895, (ICEL, 04088). Finnsstadir, Eida?inghá, Lagarfljótsrannsóknir 7145, 24.7.1975, (ICEL, 04082). Hallormsstadur, Egilsstadir, Gøtzsche, H.F. 81.37, 22.7.1981, (C, 8). Hrísey, Eyjafirdi, Gardarsson, A. s.n., 12.8.1967, (ICEL, 04078). Hrísey, Eyjafirdi, Gardarsson, A. s.n., 8.8.1967, (ICEL, 04077). Hvalfjördur, Ingimarsson, Ó. s.n., 11.8.1951, (DAO, 257458). Lagarfoss, Hróarstungu, Lagarfljótsrannsknir s.n., 26.6.1976, (ICEL, 04080). Lagarfoss, Fljótsdals, Magnússon, S.H. s.n., 26.6.1976, (ICEL, 47380). Lagarfoss, Hróarstungu, Lagarfljótsrannsóknir s.n., 26.6.1976, (ICEL, 04081). Moldhaugar, Kraeklingahlíd, Óskarsson, I. 935, 22.8.1926, (ICEL, 04052). Nes, Höfdahverfi, Óskarsson, I. 681, 30.6.1926, (ICEL, 46472). Öraefi, Baejarstadarskógur Örfum, Björnsson, H. 9633, 16.10.1947, (ICEL, 04074). Öraefi, Fagurhólsmýri Örfum, Björnsson, H. 9638, 7.1947, (ICEL, 04075). Örfi, Skaftafell Örfum, Björnsson, H. 9624, 15.6.1946, (ICEL, 04076). Reykjahlid, Lake Mývatn, 280 m, Seberg, O. 427, 14.8.1976, (C, 7). Sellátur, Reydarfirdi, Óskarsson, I. s.n., 14.7.1927, (ICEL, 04051). Skagafjord, Valnsfjall, Sørensen, T.H. 31/7, 31.7.1930, (O, 539367). Vaglaskógur, Fnjóskadal, Óskarsson, I. 1295, 7.8.1927, (ICEL, 04055). Vesturdalur, Bachufer, Lang, W. s.n., 29.7.1987, (M, 0151937). s.n., 9.7.87, (GH). 285 m, Lid, J. s.n., 14.7.1937, (O, 539360). Italy, South Tirol, Seiser Alm, 1860 m, Bestand, G. s.n., 17.7.1958, (M, 0151928). South Tirol, 1100 m, Hoock, G. s.n., 3.8.1908, (M, 0151922). South Tirol, Seisseralpe, , Koch, J. s.n., 7.7.1955, (M, 0151914). South Tirol, Seiser Alm, 1900 m, Hertel, H. 4324, 27.6.1964, (M, 0151927). South Tirol, Dolomiten, 2370 m, s.n., 15.7.1958, (M, 0151924). South Tirol, Seisseralpe, 1980 m, Roessler, H. 2519, 25.7.1959, (M, 0151925). South Tirol, Seiser Alm, 2000 m, Dietrich, W. 3283, 28.6.1964, (M, 0151930). South Tirol, Bozen, 1950 m, Dietrich, W. 1963-66, 28.6.1964, (M, 0151929). Südtirol, Feuchstelle, 2200 m, Angerer, O. s.n., 23.7.1976, (M, 0151926). Norway, Finnmark, Veinesbukt, Skifte, O. s.n., Stellander, O., 6.8.1967, (C). Finnmark, Kautokeino, 340 m, Kautokeino, N. s.n., Mieron, N.; Moor, 23.8.1967, (M, 0151938). Finnmark, Bugöynes, 20 m, Toivonen, H. s.n., 3.8.1977, (H, 1471327). Finnmark, Bugöynes, 20 m, Toivonen, H. s.n., 3.7.1977, (H, 1471326).

Finnmark, Bugöynes, 25 m, Toivonen, H. s.n., 3.8.1977, (H, 1468929). Finnmark, Billefjord, 5 m, Toivonen, H. s.n., 1.8.1972, (H, 1470511). Hamar, Jerkim, Conradi, F.E. s.n., 15.7.1887, (GH). Hedmark, Gammelsetran, 860 m, Vileid, M. s.n., 18.8.1998, (O, 235091). Hedmark, Jogåsmyra, 630 m, Kielland-Lund, J. s.n., 9.7.1967, (O, 176158). Hedmark, Os, 780 m, Elven, R. s.n., (O, 4689). Hedmark, Folldal, 840 m, Buttle 8066, Gauhl, 19.8.1965, (M, 0151912). Hjerkinn, Stanley Pease, A. s.n., 21.7.1930, (GH, 20740). Hordaland, Eidfjord, 100 m, Lid, J. s.n., 26.7.1936, (O, 414980). Kongsvold, Dovrefjeld, Nilsson, S.J. s.n., .8.1898, (GH). Nordland county, Srfold, Apold, W. s.n., Brodal, G.; Skifte, O., 8.8.1954, (H, 1013890). Norland, Nordland fylke, , Notø, A. s.n., 6.7.1932, (M, 0151945). Oppland, Espedal, Berg, R.Y. s.n., 11.8.1973, (O, 260563). Oppland, Lom, 940 m, Berg, R.Y. s.n., 10.8.1994, (O, 174746). Oppland, Grimsdalen, 900 m, Bratli, H. s.n., 28.7.1994, (O, 114994). Sör-Tröndelag, Opdal herred, Kongsvoll, , Nilsson, S.J. s.n., .7.1883, (DAO, 257470). Sör-Tröndelag, Oppdal, Near Kongsvoll, Wendelbo, P. s.n., 17.7.1948, (COLO, 100223). Troms, Stordalen, 250 m, Engelskjøn, T. s.n., 24.7.1962, (C). Troms, Lulleborg, 360 m, Lye, K.A. 18728, Berg, T., 1.9.1992, (O, 75397). Troms, Fossbakken, Svendsen, S. s.n., 31.7.1967, (O, 92610). Tromsö, Ringvatso Island, 30 m, Notø, A. s.n., 10.7.1896, (GH). Russia, Chita region, Between the rivers Nerchei and Kuengoi, Sukatschew, W. s.n., 10.7.1911, (DAO, 142005). Chukotka national district, Anui upland region, Zimarskaja, E.V. s.n., Korobkov, A.A.; Yurtsev, B.A., 12.7.1967, (DAO, 139880). Chukotka national district, Rauchua river, Yurtsev, B.P. s.n., 12.7.1967, (BRY, 122530). Chukotski peninsula, river Utaveem, Kozhevnikov, U.P. s.n., Nechaev, A.A.; Yurtsev, B.A., 27.7.1970, (COLO, 323093). Irkutsk, Balagansk region, Maltsev, I. s.n., 19.6.1905, (GH). Kamchatka region, Olyutorsky area, Harkevich, S. s.n., 9.8.1975, (GH). Komi Republic, Syktyvkar, Andreev, V.D. s.n., 21.6.1909, (H, 1037137). Magadan region, North Even, Hohrjakov, A.P. s.n., 2.8.1976, (CAN, 455497). Republic of Karelia, Karelia onegensis (Kon), Ruuhijärvi, R. 40/02, 9.7.2002, (H, 744530). Republic of Karelia, Belomorskiy District, 10 m, Kravchenko, A. s.n., 21.8.2002, (H, 742280). Republic of Karelia, Karelia pomorica orientalis, Piirainen, M. 5376, 19.8.2004, (H, 807345). Republic of Karelia, Karelia pomorica orientalis, 20 m, Piirainen, M. 5027, 22.8.2002, (H, 741569). Sakha Republic, Bulunsk region, Yurtsev, B.A. s.n., 25.6.1960, (DAO, 257437). Taymyr, River Pyasina, Kozhevnikov, U.P. s.n., 21.8.1982, (CAN, 490439). Between the rivers Nerchei and Kuengoi, Sukachev, V. s.n., 27.7.1970, (DAO, 139887). Kihlman, A.O. s.n., 18.8.1891, (H, 1226124). Chersky, Kozhevnikov, U.P. 714, 24.7.1977, (CAN, 455526). Sweden, Dalecarlia, Morngen, Kllstrm, S. s.n., 7.1887, (GH). Dalecarlia, Fries s.n., (GH). Härjedalen, Valmåsen, Dusn, K. s.n., 11.8.1879, (DAO, 363985). Jämtland, Paroecia Frösö, Asplund, E. s.n., 2.6.1925, (GH). Jämtland, Paroecia

Frösö, Asplund, E. s.n., (C). Jämtland, Nyhem, 280 m, s.n., 4.7.1977, (M, 0151939). Jämtland, Häggenås, 400 m, s.n., 3.7.1977, (M, 0151940). Jämtland, Mosjön, 305 m, s.n., 5.7.1977, (M, 0151941). Jämtland Ås, Ahlqvist, A. s.n., 28.6.1902, (GH). Kilpisjärvi, Saana, 50 m, Roivainen, L. s.n., 14.7.1958, (DAO, 257436). Lule Lappmark, Avvakko-tunturi, 500 m, Hertel, H. 7248b, 21.7.1967, (M, 0151935). Scandinavia, s.n., 1887, (M, 0151938). Sverige, Torne Lappmark, Pederson, T.M. 5615, 15.7.1960, (O, 314293). Torne Lappmark, Torne Träsk, Torlöf, A. s.n., 12.8.1958, (GH). Torne Lappmark, Låktatjakko, 700 m, Alm, G. 449, 11.8.1935, (GH, 449). Torne Lappmark, Jukkasjärvi, 333 m, Alm, G. s.n., 8.8.1935, (GH, 442). Torne Lappmark, Abisko, Selander, S. s.n., 9.7.1905, (GH). Torne Lappmark, Lake Torneträsk District, 450 m, Alm, G. s.n., 9.8.1958, (O, 539346). Torne Lappmark, Abisko, Hertel, H. 22918, 8.8.1980, (M, 0151931). Torne Lappmark, Abisko, s.n., 13..8, (M, 0151947). Torne Lappmark, Abisko, Hiitonen, I. s.n., 22.7.1950, (H, 1693670). Torne Lappmark, Abisko, 400 m, Alm, G. s.n., 6.8.1958, (H, 1226056). USA, Alaska, Old John Lake Area, Holmen, K. 61-1227, 13.7.1961, (C, 61-1227). Alaska, Wiseman, Anderson, J.F. 5970, Gasser, G.W., 3.8.1939, (ALA, 1125027). Alaska, Shaw Creek Flats, Elven, R. s.n., Solstad, H., 28.7.2001, (ALA, 1125006). Alaska, Euchre Moutain, 3868 ft, Bennett, B. 194/13273, Loomis, P., 20.6.2003, (ALA, 1125007). Alaska, Smith Lake, Parker, C.L. 15339, 7.8.2003, (ALA, 1125008). Alaska, Central Noatak R. Valley, 100 m, Parker, C.L. 15128, Elven, R.; Solstad, H., 23.7.2003, (ALA, 1124990). Alaska, Kilikmak Cr., 8 m, Parker, C.L. 14722, Elven, R.; Solstad, H., 13.7.2003, (ALA, 1124991). Alaska, Mt. Hayes, 419 m, Duffy, M. 98-201, 15.7.1998, (ALA, 1124993). Alaska, Endicott Mountains, 900 m, Parker, C.L. 12108, Elven, R.; Solstad, H.; Bennett, B.A., 19.7.2002, (ALA, 1124994). Alaska, Neacola Moutains, Caswell, P. 96-205, 19.6.1996, (ALA, 1124995). Alaska, Mt. Michelson, 861 m, Batten, A. 686, 26.7.1973, (ALA, 1124996). Alaska, Howard Pass, 700 m, Parker, C.L. 7648, , 27.7.1997, (ALA, 1124998). Alaska, Table Mountain, 622 m, Mouton, M.A. MM79279, 30.6.1979, (ALA, 1125000). Alaska, Imiaknikpak Lake, 581 m, Murray, D.F. 4314, 27.7.1973, (ALA, 1124970). Alaska, Baird Mountains, 85 m, Parker, C.L. 15299, Elven, R.; Solstad, H., 29.7.2003, (ALA, 1124972). Alaska, Charley River, 850 ft, Larsen, A. 02-2430, Batten, A., 25.7.2002, (ALA, 1124973). Alaska, Bering Land Bridge NPreserve, 250 m, Kelso, T. 87-319, 7.7.1987, (ALA, 1124975). Alaska, McKinley River, 1900 ft, Viereck, L.A. 1613, 30.7.1956, (ALA, 1124982). Alaska, Arctic National Wildlife Range, 430 m, Murray, D.F. 3350, 26.7.1970, (ALA, 1124984). Alaska, Alaska Range, 750 m, Duffy, M. MD02-240, 16.8.2002, (ALA, 1125011). Alaska, Alaska Range, 725 m, Roland, C. 4519, Batten, A.; Goeking, S., 7.1.2000, (ALA, 1125012). Alaska, Solomon, 85 m, s.n., 14.7.2000, (ALA, 1125013). Alaska, Seward Peninsula, 37 m, Murray, D.F. 11077, Yurtsev, B.A.; Kelso, T., 26.7.1992, (ALA, 1125015). Alaska, Kokrine Hills, 275 m, Foote, J. JF4208, 24.6.1980, (ALA, 1125016). Alaska, Fort Wainwright Military Reservation, 115 m, Duffy, M. 95-624, Lipkin, R., 10.7.1995, (ALA, 1125017). Alaska, Jago Lake, Cantlon, J.E. 57-1613, Gillis, W.T., 28.7.1957, (ALA, 1125021). Alaska, Tanana River, Spetzman, L. 11868, 7.8.1957, (ALA, 1125022). Alaska, Bendeleben Quad, 100 m, Kelso, T. 82-190, 10.8.1982, (COLO, 387320). Alaska, Mt. Mckinley Natl. Park Teklanika River, 792 m, Viereck, L.A. 7427, 3.8.1964, (ALA, 1125025). Alaska, Mt. Mckinley Natl. Park Teklanika River, 792 m, Viereck, L.A. 7427, 3.8.1964, (RMS, 430206). Alaska, Mt. Mckinley Natl. Park Teklanika River, 792 m, Viereck, L.A. 7427, 3.8.1964, (CAN, 362141).

Carex arctogena Harry Sm., Acta Phytogeogr. Suecica (1940), 13:193. Type: Sweden, Torne Lappmark, karesuando, Moskana ca. 1000 m.s.m. 26/7 1933, Harry Sm. (UPS Holotype) photo! (Fig. A.7 in Appendix)

C. capitata L. ssp. *arctogena* (Harry Sm.) Hiit., Luonnon Ystävä 48: 52-64. (H) photo! (= *C. capitata* L. ssp. *arctogena* (Harry Sm.) Böcher, in Medd. om Grønl.147(9), 1952. Isonym)

C. capitata L. var. *arctogena* (Harry Sm.) Hultén, Kungl. Sv. Vet. Ak. Handl. (1958), 4 (7):38. Uppsala. Type: Sweden, Torne Lappmark, Karesuando, Moskana ca. 1000 m.s.m. 26/7 1933, H. Smith. (UPS) photo!

C. capitata f. *arctogena* Raymond, Contrib. bot. Univ. Montral (1949), 64:38.

C. capitata f. *alpicola* Andersson, Bot. Not. (1849), 2.

Carex antarctogena Roiv., Ann. Soc. Zool. Bot. Fenn. Vanamo (1954), 28 (2): 197-198. Type: Estancia Vicuña, in palude. H. Roivanen (H Holotype) photo!

Carex rahuiensis Kurtz. ex. Kükenth., Bot. Jahrb. (1900), 27:495 - nomen nudum, according to Smith (1940).

Kurtz based *Carex rahuiensis* on plants he collected in Argentina (Kükenthal 1900). According to Smith (1940) it is nomen nudum, although he did not see any specimen from Kurtz's collections. *Carex antarctogena* was described by Roivanen on the basis of Argentinian specimens which he considered to be more robust in structure and to have a greater number of staminate flowers and perigynial teeth than *C. arctogena* from the northern Hemisphere. The present morphological study does not support these observations since specimens from South America are not statistically significant bigger than the North American or European specimens (Table 2.7). Both species will therefore be considered as synonyms here. In Chapter 3, molecular analyses shows no genetic differences between *C. arctogena* samples from the northern vs. southern Hemisphere in the three chloroplast regions and five nuclear loci studied.

Herb forming loose to dense tussocks. **Roots** sometimes short-creeping, yellow or reddish. **Culms** 10-33 cm tall and 0.5-1.1 mm wide in diameter at the middle, slender, wiry, more or less dentate on the margins and dense towards the apex. **Leaves** erect, 3-5 per culm, old leaves persistent, shorter or as long as the culm; **Leaf sheaths** dark red or brown at the base, sparingly filamentose; **blades** 9-29 cm and 0.4-1.0 mm wide at the middle, filiform, stiff, erect or recurving, truncate mouth; **ligule** very short, obtuse or nearly truncate. **Spike** solitary, androgynous, globose, ovoid or trigonal, with staminate portions covering 20 % to 37 %, fairly densely packed, 5.2-9.8 mm long x 2.9-4.7 mm wide, staminate flower portion 1.2-3.7 mm long x 0.5-1.3 mm wide, pistillate flowers portion 3.5-6 mm long, 5-26 staminate flowers, 9-32 pistillate flowers; **bract** absent, rarely present; **staminate scales** erect, obovate, broadly obovate or ovate, the body yellow or olive-brown with hyaline margins located in the distal 1/3, 0.1-0.2 mm wide, often folded, glabrous, 1.0 to 2.8 mm long x 0.7 to 1.6 mm wide, with 1-3 veins, apex acute; **stamens** with anthers 0.6-1.4 mm long; **pistillate scales** ovate or broadly ovate, the body yellow, orange-brown or dark brown with hyaline margins rarely absent and typically occupying the proximal and distal portions, length of 0.1-1.0 mm in the central portion and 0.4-2.6 mm along the edges in a triangular shape, no nerve or one, incomplete, glabrous, 1.0-2.6 x 1.4-3.0 mm shorter than the perigynia and reaching 3/4 of perigynia body length or until the base of the beak, wider or little narrower than perigynia; distal **perigynia** erect or ascending, proximal mostly spreading, the body greenish or yellow on the proximal half and dark grayish, yellow-green or brownish green in the distal half, surface glossy, 1.5-3.2 x 1.0-2.0 mm, 0.8-1.4 mm, margins sometimes winged especially in the proximal half and 0.1-0.3 mm wide, almost always scabrous (1-16 teeth), cuneiform base, abruptly contracted into a beak; **beak** brown, dark-brown or olive-brown, apex orange or hyaline, 0.3-0.9 mm long and 0.2-0.3 mm wide at base, mostly straight, bifid; **gynoecium** with 2 stigmas; **rachilla** often visible in relief on the side of abaxial perigynia, setaceous, as long or slightly longer than the achene; **achenes** ellipsoid, broadly ellipsoid or almost orbicular, the body grayish, yellow or dark, non-glossy surface, 1.4-1.9 mm long x 0.7-1.7 mm wide, filling more than 3/4 of the perigynium, broadly cuneate or rounded at the base, apex obtuse or truncated; style bases absent or persistent by the bottom of the style.

Notes: *C. arctogena* is differentiated from all other members of the complex by its pistillate scales, broader and as long or longer than the perigynia; its scabrous perigynia; and its hyaline margins along pistillate scales, which have a triangular shape and which can cover up to half of the surface of the scale. It is most similar to *"C. cayouetteana"* and *Carex sp. nov. 2* but they can be easily separated by the character mentioned above.

Distribution: Europe (NOR, SWE, FIN); N Russia; N North America (NUN, BRC, SAS, MAN, ONT, QUE, NFL, GNL, NWH) and S South America (AGS, CLC).

Ecology: Arctic-alpine areas and wind-exposed alpine heaths, in soils with low water content.

Specimens examined:

Argentina, Chubut, Los Alerces National Park, Soriano, A., 30.3.1952, (BAA). Dept. Chos Malal, 2300 m, Boelcke, O., Correa, M.N.; Bacigalupo, N.M., 30.1.1964, (BAA, 11368). Mendoza, Cordillera del Rio Barrancas, Kurtz, F., 16.11.1888, (MICH). Canada, Alberta, Mercoal, Rousseau, J., 18.7.1947, (COLO, 13811). Alberta, Mercoal, 4300 ft, Malte, M.O., Watson, W.R., 8.8.1925, (RM, 280606). British Columbia, Pine Pass, 1402 m, Argus, G.W., 12.7.1973, (CAN, 372267). British Columbia, 7228 ft, Calder, J., 149035, Parmelee, J.A.; Taylor, R.L., 8.8.1956, (COLO, 149035). British Columbia, Mount Apex, 7100 ft, Calder, J., Savile, O., 11.8.1953, (RM, 252249). Manitoba, Fort Chimo, Rousseau, J., 14.8.1951, (WIN, 22355). Manitoba, Baralzon Lake, Scoggan, H.J., 22434, Baldwin, W.K.W., 28.7.1950, (WIN, 22434). Manitoba, Hudsons Bay Co., Duck Lake, Scoggan, H.J., Baldwin, W.K.W., 10.8.1950, (WIN, 22435). Manitoba, Fort Chimo, Legault, A., 22.7.1963, (COLO, 491481). Manitoba, Hudsons Bay Co., Duck Lake, Scoggan, H.J., Baldwin, W.K.W., 10.8.1950, (CAN, 201506). Manitoba, Baralzon Lake, Scoggan, H.J., Baldwin, W.K.W., 30.7.1950, (CAN, 202500). Manitoba, Nueltin Lake, Baldwin, W.K.W., 26.7.1951, (CAN, 212816). Manitoba, Cochrane River, Baldwin, W.K.W., 3.7.1951, (CAN, 212817). Manitoba, Cochrane River, Baldwin, W.K.W., 3.7.1951, (CAN, 212817). Manitoba, Baralzon Lake, Scoggan, H.J.,Baldwin, W.K.W., 28.7.1950, (CAN, 201507). Newfoundland-Labrador, Esker area, Mäkinen, Y., Kankainen, E. 21.7.1967, (CAN, 314758). Newfoundland-Labrador, Esker area, 838 m, Mäkinen, Y.Kankainen, E.21.7.1967, (CAN, 314758). Newfoundland-Labrador, Twin Falls, Hustich, I., 6.7.1967, (CAN, 313311). Nunavut, Upper Hood River, Gould, W., 7.1995, (COLO, 475773). Ontario, Kenora District, Patricia PortionRiley, J.L., 12.8.1980, (CAN). Ontario, Hudson Bay Lowlands, Porsild, A.E., Baldwin, W.K.W.4.7.1957, (CAN, 278707). Quebec, Fort Chimo, Srensen, T.H., 17.8.1959, (C). Quebec, Baie dUngava, Blondeau, M., 1.8.1993, (WIN, 53902). Quebec, Baie d'Ungava, Rousseau, J., 23.7.1951, (WIN, 22356). Quebec,Lac Jaucourt Region Lichteneger Lake,487 m Argus, G.W., 16.7.1974, (CAN, 3779977). Quebec, Boatswain Bay, Baldwin, W.K.W., 17333, Hustich, I.; Kucyniak, J.; Tuomikoski, R., 8.7.1947, (CAN, 17333). Quebec, Lac Payne, Legault, A., 23398, 2.8.1965, (CCO, 23398). Quebec, Northern QuebecLake Payne, Legault, A.,Brisson, S. 2.8.1965, (COLO, 210789). Quebec, Ungava, Husons Bay, Dutilly, A., Lepage, E., 21.3.1945, (RM, 233644). Quebec, Fort Chimo, Calder, J., 31.7.1948, (RM, 255325). Quebec,Hudson Bay Cairn Island, Abbe, E.C.,Abbe, L.B.; Marr, J. 30.7.1939, (RM, 252521). Quebec, Hudson Bay,Great Whale River Calder, J.Savile, O.; Kukkonen, I., 8.8.1959, (RM, 260486). Quebec, Lac Kopeteokash, Rousseau, J., 18.7.1947, (RM, 228636). Saskatchewan, Vicinity of Patterson Lake, Argus, G.W., 20.7.1963, (CAN, 282691). Saskatchewan, Vicinity of Patterson Lake, Argus, G.W., 20.7.1963, (CAN, 282691). Saskatchewan, Northeastern Saskatchewan, Patterson Lake , Argus, G.W., 20.7.1963, (RM, 277437). Enontekiö, KilpisjärviSaana, 750 m, Roivainen, L., 8.7.1935, (H, 127310). Enontekiö, KilpisjärviSaana, 750 m, Väre, H., 29.7.2004, (H, 805587). Enontekiö Lapland, 825 m, Väre, H., 17.7.2006, (H, 809948). Inari, Vätsäri Wilderness Area, Kulmala, H., 27.7.1996, (H, 717201). Lapponia Imandrae, Lindén, J., 18.7.1891, (H, 325665). Lapponia Imandrae, Axelson, W.M., Borg, V., 24.7.1901, (H, 325667). Finland, Lapponia murmanica, 550 m, Brotherus, V.F., 8.1887, (H, 325639). PetsamoCajander, A., 10.7.1927, (H, 325644). Porojärvet, Toskalhar, 950 m, Roivainen, H.Ollila, L. 15.7.1955, (H, 127313). Porojärvet, Toskalhar, 910 m, Roivainen, H., 15.7.1966, (H, 179889). Foutell, C.W., Jalan, M.J., 10.8.1899, (H, 325657). Altevatn, 500 m, 17.8.1967, (M, 0151943). Groenlandia meridionalis, Kangerdluarssuk, Hansen, C. 282521,Hansen, K.; Petersen, M. 4.7.1962, (CAN).Nigerdleq, Jørgensen, L.B. 15.7.1966, (CAN, 311369). Greenland, Vestgrønland, Pingorssuaq Kitdleq, 400 m, Hanfgarn, S., 11.8.1983, (C). Tugtilik Lake, 10 m, Elsley, J.E. 15.8.1967, (M, 0151948). Lagerkranz, J., 2.8.1936, (RMS, 153944). Finnmark, Sör-Varanger Bugöynes, Toivonen, H., 30.7.1971, (H, 1081734). Finnmark, Sör-Varanger, Bugynes, Toivonen, H., 1081733, 30.7.1971, (H, 1081733). Nordland, Narvik hd., Skjomen, Skifte, O., Raff, G.; Spjelkavik, S., 11.8.1973 (H). Norland, Sulitjelma, Skifte, O. 1.8.1962, (DAO, 285800). Sverige, Abisko, Paddas, Lid, J., 2.8.1950, (H, 1300264). Norway, Troms, Bardu, Leinavatn, 498 mEngelskjn, T.,Engelskjøn, E.M. 7.7.1977, (C). Troms, Bardu, Altevatn, 580 m, 18.8.1967, (M, 0151942). Troms, Bardu, Kampaksla 780 m, Engelskjn, T.,Skifte, O. 9.8.1978, (H, 1685049). Petsamo, Petchenga Vouvatusjärvi, Piirainen, M., 27.7.1995, (H, 1682990). Sweden, Torne Lappmark, Karesuando, 1000 m, Smith, H., 26.7.1933, (DAO, 257429). Torne Lappmark, Karesuando, 1000 m, Smith, H., 26.7.1993, (H, 1652844). Torne Lappmark, Jukkasjrvi parish, 550 m, Alm, G., Smith, H. 23.7.1939, (H, 1300259). New Hampshire, Coos Co., Mt. Washington, Hodgon, A.R., Gale, M., 30.6.1950, (DAO, 257427). New Hampshire, White Mountains, Mt. Washington, Forbes, F., 9.8.1902, (RMS, 242089). New Hampshire, Alpine Garden, Mt. Washington, Sargent, F.H., 5.7.1942, (BRY, 143916). New Hampshire, Alpine Garden, Mt. Washington,5000 ft Löve, A., Löve, D. 27.7.1958, (COLO, 288736). New Hampshire, Alpine Garden, Mt. Washington, Löve, A. ,Löve, D. 3.7.1960, (COLO, 295019). New Hampshire, White MountainsMt. Washington, Forbes, F., 9.8.1902, (RM, 50212).

Carex cayouetteana sp. nov.

Holotype: Canada, Alberta: Banff National Park, Snow Creek Pass, A.E. Porsild 22673 (CAN-266077).

Herb forming loose tussocks. **Roots** light brown to yellowish. **Culms** 11-26 cm tall and 0.6-1.1 mm in diameter at the middle, slender, wiry, more or less dentate on the margins and dense towards the apex. **Leaves** 3-6(7) per culm, old leaves persistent, shorter than culm; **Leaf sheaths** yellow or light brown at the base, sparingly filamentose. **blades**11-19 cm long and 0.4-0.9 mm wide in the middle; **ligules** obtuse or nearly truncate. **Spike** solitary, androgynous, trigonal to ovoid, lanceolate, with staminate portions wider at the bottom and covering 50 % to 60 %, densely packed, of 6.1-12.8 mm long x 3.5-6.1 mm wide, staminate portions from 0.9- 6.7 x 1.5-2.9 mm, pistillate 3.9-6.4 mm long, 15-26 staminate flowers, 17-32 pistillate flowers; **bract** absent or rarely when present; **staminate scales** erect, broadly obovate or ovate, the body dark brown or yellowish, central bands are not clearly delineated with hyaline margins located in the 1/3 distal and 0.1-0.15 mm wide, often folded, glabrous, 1.8-3.0 x 0.6-1.9 mm, with 1-2 veins, apex acute, subacute or rounded; **pistillate scales** ovate or broadly ovate, the body dark brown, hyaline margins absent or occupying the distal portions, length of 0.1-1 mm in the central portion and 0.1-0.5 mm crossing the edges, one nerve clearly marked and surrounded by light brown or light yellow, glabrous, 1.5-3.4 x 1.2-2.5 mm shorter than the perigynia and reaching full or 3/4 of body length perigynia, wider or as wide as perigynia, apex rounded, truncated or obtuse; **perigynia** distal erect or ascending, most proximal spreading, the body greenish-yellow in proximal part, dark brown to brown in the half distal until top of the achene, surface gloss with some redness, 1.5-3.4 x 1.2-2.5 mm, 0.6-1.5 mm, margins sometimes with nerves, almost scabrous (0-5(7) teeth), obtuse angle at the bottom, acute apex contracted smoothly into a beak; **beak** dark brown, apex orange or hyaline, long of 0.9-1.9 mm, mostly straight, teeth acuminate, bifid, smooth; **gynoecium** with 2 stigmas;

rachilla often visible in relief on the side of abaxial perigynia, setaceous, as long as or slightly surpassing; **achenes** ellipsoid, broadly ellipsoid, the body dark yellow to light brown, glossy surface, 1.0-2.3 x 0.6-1.8 mm, covering over 3/4 volume perigynia, broadly cuneate, rounded or rotund at the base, apex obtuse or truncated, wrinkled; beaks marked by the straight base of the style.

Notes: *"C. cayouetteana"* can be identified by its staminate portion, as longer as the pistillate portion, presenting a cone shape; pistillate scales, broader and as long as the perigynium beak, or longer than the perigynia; its scabrous perigynia, usually with 2-3 teeth; its hyaline margins in the pistillate scales, which are around 1 mm wide and go around the edges of the scale, drawing an inverted V shape; its brown perigynia beak and green perigynia body. *Carex arctogena* can be easily separated from *"C. cayouetteana"* by its staminate portion, shorter and cylindrical in *C. arctogena*; its hyaline margin with triangular shape; for having more teeth in the margins of the perigynium and less number of perigynia in the spike.

Distribution: North American endemic (COL, UTA, WYO, NEV, CAL, WAS, ALB, BRC).

Ecology: Tundra and alpine areas, in dry, acidic and rocky soils. 2000 - 3500 m.

Etymology: This taxon is named after Jacques Cayouette, a passionated botanist who has spent his life working extensively in North American sedges and particularly in Quebéc.

Specimens examined (paratypes):

Canada, Alberta, Snow Creek Pass, 2133 m, Porsild, A.E. 22673, 29.7.1960, (CAN, 266077). Alberta, Snow Creek Pass, 7400 ft, Calder, J. 23957, 24.7.1959, (COLO, 148926). Alberta, Snow Creek Pass, 7000 ft, Porsild, A.E. 22673, 29.7.1960, (RM, 529780). British Columbia, Bluster Mt., 2133 m, Thompson, J. s.n., Thompson, M., 14.7.1938, (WTU, 48964). British Columbia, Chipuin Mt., 1828 m, Thompson, J. s.n., Thompson, M., 21.7.1938, (WTU, 17893). British Columbia, Quiniscoe Lake, 2316 m, Calder, J. 19594, Parmelee, J.A.; Taylor, D., 2.8.1956, (WTU, 199618). British Columbia, 7100 ft, Calder, J. 11795, Savile, O., 11.8.1953, (COLO, 118024). British Columbia, Ashnola Range, 7600 ft, Calder, J. 19594, Parmelee, J.A.; Taylor, R.L., 2.8.1958, (RM, 260491). Mexico, Pacheco, Chihuahua, Hartman, C.V. s.n., 10.6.1891, (MICH, 1132452). USA, California, Anderson Mdw., 1950 m, Gierisch, R. 3493, Esplin, D., 25.6.1969, (RMS, 430207). California, Anderson Mdw., 6400 ft, Gierisch, R. 3493, Esplin, D., 25.6.1969, (COLO, 246761). California, Anderson Mdw., Gierisch, R. 3493, Esplin, D., 25.6.1969, (CAS, 690732). California, South Warner Mountains, 9000 ft, Otting, N. NAD27, Lytjen, D., 2.9.2004, (OSC, 219450). Colorado, Clear Creek Co., Loch Lomond, W.A. Weber, T. Koponen & P. Nelson s.n. (CAN-374041). Colorado, Lake Co., San Isabel National Forest, J. Starr 10S-030, W. Sawtell & T. Villaverde. Colorado, Hinsdale Co., Gunnison National Forest, J. Starr 10S-033, W. Sawtell & T. Villaverde. Colorado, Bill Moore Lake, 3627 m, Lederer, N. 4257, 31.8.1993, (COLO, 00263731). Colorado, Loch Lomond, 3395 m, Weber, W.A. s.n., Koponen, T.; Nelson, P., 8.8.1972, (CAN, 374041). Colorado, San Juan National Forest, 11900 ft, Rink, G. 3668, 25.7.4, (BRY, 467234). Colorado, Loch Lomond, 11140 ft, Weber, W.A. s.n., Koponen, T.; Nelson, P., 8.8.1972, (COLO, 259883). Colorado, Hagerman Pass, 11980 ft, Hartman, E.L. 6718, Rottman, M.L., 29.8.1986, (COLO, 428741). Colorado, Fraser Exp. Forest, 12000 ft, Weber, W. 8621, Dahl, E., 31.7.1953, (COLO, 76204). Colorado, Mesa Seco, 12300 ft, Johnson, K. J64-117, (COLO, 232659). Montana, Carbon Co., Custer National Forest, Absaroka-Beartooth Wilderness, J. Starr 10S-047A, W. Sawtell & T. Villaverde. Montana, Sweet Grass County, 2956 m, Lesica, P. 7663, 27.7.1998, (MONTU, 122991). Montana, Sweet Grass County, 2743 m, Lesica, P. 7362, 10.8.1996, (MONTU, 122399). Montana, Sweet Grass County, 2743 m, Lackshewitz, H. 9909, 15.8.1981, (MONTU, 86558). Montana, Carbon County, 2999 m, Ramsden, J. 1625, 10.7.1987, (MONTU, 118978). Montana, Carbon County, 2987 m, Lesica, P. 5583, 15.8.1991, (MONTU, 115081). Montana, Carbon County, 3048 m, Lesica, P. 4483, 11.8.1987, (MONTU, 108435). Montana, Park County, Ramsden, J. 85542, 9.7.1980, (MONTU, 85542). Montana, Carbon County, 3017 m, Lackshewitz, H. 7790, 11.8.1977, (MONTU, 78793). Montana, Sweet Grass County, 2743 m, Lackshewitz, H. s.n., 15.8.1981, (COLO, 355226). Montana, Stillwater County, 2767 m, Evert, E. 24076, 27.7.1992, (RMS, 780026). Montana, Carbon County, 3048 m, Evert, E. 19835, 23.7.1990, (RMS, 619855). Montana, Carbon County, 2987 m, Lackshewitz, H. 7000, 14.9.1976, (WTU, 272540). Montana, Carbon County, 3017 m, Lackshewitz, H. 7790, 11.8.1977, (WTU, 288770). Montana, 9800 ft, Lackschewitz, K.H. 7035, 15.9.1976, (RM, 367206). Montana, Beartooth Pass, 11000 ft, Hermann, F.J. 20079, 20.7.1965, (RMS, 430211). Montana, 9000 ft, Evert, E. 18434, 9.8.1989, (RM, 579301). Montana, Lackschewitz, K.H. 9909, 15.8.1981, (RM, 521779). Montana, 9900 ft, Lackschewitz, K.H. 7790, 11.8.1977, (RM, 367094). Montana, Sweet Grass County, 9000 ft, Lackschewitz, K.H. s.n., 15.8.1981, (GH). Nevada, Browns Cr., 2590 m, Lewis, E. 448, 17.7.1955, (RMS, 390545). Nevada, Browns Cr., 2590 m, Lewis, E. 17.7.1955, (CAN, 550536). Utah, Uinta Mountains, Lewis, E. 512, 15.8.1955, (RMS, 368032). Utah, Gilbert Bench, 3505 m, Goodrich, S. 25583, Huber, A.; Prescott, D., 20.8.1996, (BRY, 392186). Utah, Gilbert Creek, 3493 m, Huber, A. 440, Goodrich, S., 25.8.1993, (BRY, 368578). Utah, Uinta Mountains, Lewis, E. 512, 15.8.1955, (CAN, 515168). Utah, Gilbert Bench, 12100 ft, Goodrich, S. 26303, Huber, A.; Frandsen, J.; Bartlett, F., 9.8.2000, (BRY, 437123). Utah, Ridge saddle, 12600 ft, Huber, A. 4134, 3.8.1999, (BRY, 426752). Utah, Ashley Forest, 11850 ft, Goodrich, S. 23530, Bartlett, F.; Atwood, D.; Nelson, D., 19.8.1991, (BRY, 350794). Washington, Whatcom Co., Baker-Snoqualmie National Forest, J. Starr 10S-061, W. Sawtell & T. Villaverde. Washington, Chowder Ridge, 6800 ft, Douglas, G. 4345, Douglas, G., 3.8.1972, (DAO, 621358). Washington, Rocky Mt., 2365 m, Douglas, G. 2887, 19.7.1971, (RMS, 430209). Wyoming, 10700 ft, Mosquin, T. 4817, 2.8.1962, (DAO, 257425). Wyoming, 3279 m, Mellmann-Brown, S. 2575, 7.8.1996, (RMS, 644114). Wyoming, Elk Peak, 3566 m, Hartman, L. 24223, Poll, T., 9.8.1988, (RMS, 533361). Wyoming, 3474 m, Hartman, L. 31265, 19.8.1991, (RMS, 589096). Wyoming, Neely, B. 2435, 18.8.1984, (COLO, 399492). Wyoming, Beartooth Plateau, 3300 m, Weber, W. s.n., 18.8.1973, (COLO, 270915). Wyoming, Beartooth Plateau, 9800 ft, Lackshewitz, H. s.n., 14.9.1976, (COLO, 306544). Wyoming, Cascade Creek, 10300 ft, Evert, E. 18305, 3.8.1989, (COLO, 449077). Wyoming, Lamar River, 10300 ft, Nelson, B.E. 12725, Hartman, R.L., 22.7.1985, (RM, 482304). Wyoming, Beartooth Plateau, 9800 ft, Lackschewitz, K.H. 7000, 14.9.1976, (RM, 367209). Wyoming, Beartooth Plateau, 9800 ft, Dorn, R.D. 3590, 12.8.1980, (RM, 330260). Wyoming, Francs Fork, 11150 ft, Hartman, L. 16805, 14.8.1983, (RM, 558454). Wyoming, Beartooth Plateau, 10800 ft, Mellmann-Brown, S. 2470, 22.7.1996, (RM, 612812). Wyoming, Eastern Wind River Range, 10240 ft, Mills, S. 232a, 18.8.1995, (RM, 603492). Wyoming, Head Elk Creek, 11500 ft, Johnson, W.M. 140, 29.8.1961, (RMS, 401425). Wyoming, Northern Wind River Range, 10240 ft, Mills, S. 230b, 18.8.1995, (RM, 603491). Wyoming, Bug Creek Pass, Absarokas, 11000 ft, Johnson, W.M. 270, 8.8.1962, (RM, 189438-s). Wyoming, Bug Creek Pass, Absarokas, 11000 ft, Johnson, W.M. 270, 8.8.1962, (RMS, 401298). Wyoming, Absaroka Mountains, 10000 ft, Kirkpatrick, R.S. 5901, Kirkpatrick, R.E.B., 14.8.1984, (RM, 558456). Wyoming, Cascade Creek, 10300 ft, Evert, E. 18305, 3.8.1989, (RM, 579204). Wyoming, Absaroka

Mountains, 11150 ft, Kirkpatrick, R.S. 5910, Kirkpatrick, R.E.B., 21.8.1984, (RM, 558455). Wyoming, Absaroka Mountains, 10200 ft, Evert, E. 18249, 3.8.1989, (RM, 579080). Wyoming, Absaroka Mountains, 9800 ft, Evert, E. 9608, 20.8.1985, (RM, 623052). Wyoming, Absaroka Mountains, 10000 ft, Hartman, R.L. 19105, 21.8.1984, (RM, 558453). Wyoming, Absaroka Mountains, 11750 ft, Hartman, R.L. 19289, 22.8.1984, (RM, 558452). Wyoming, Absaroka Mountains, 10700 ft, Hartman, R.L. 23927, Poll, T., 5.7.1988, (RM, 536641). Wyoming, West Slope Wind River Range, 10400 ft, Hartman, R.L. 31278, 19.8.1991, (RM, 589095). Wyoming, Absaroka Mountains, 10500 ft, 4416, 20.7.1984, (RM, 558457). Wyoming, Beartooth Plateau, 9570 ft, Fertig, W. 15202, 23.7.1994, (RM, 602345). Wyoming, Beartooth Mountanis, 10000 ft, Fertig, W. 17194, Mellmann-Brown, S., 24.8.1996, (RM, 615036). Wyoming, Park Co., Shoshone National Forest, Beartooth Plateau, J. Starr 10S-047B, W. Sawtell & T. Villaverde.

Carex sp. nov. 1

Holotype: USA, California: Butte Co., near Cherry Hill Campground, Lassen National Forest, J. Starr 10S-054 & T. Villaverde.

Herb densely caespitose. **Roots** light brown, orange or dark yellow. **Culms** 19-54 cm tall and 0.7-1.0 mm at the middle, slender greenish or yellowish at the base. **Leaves** 3-5 per culm; **Leaf sheaths** dark brown to light brown at the base, sparingly filamentose. **blades** 13-27 cm long and 0.5-0.9 mm wide in the middle; **ligules**, acute, obtuse or nearly truncate. **Spike** solitary, androgynous, trigonal, slender, with staminate portions covering 50 % to 70 %, loosely packed, of 6.8-16.9 mm x 3.2-4.6 mm, staminate portions 2- 10.5 x 1-1.5 mm, pistillate 3.5-6 mm long, 30-37 staminate flowers, 8-15(30) pistillate flowers; **bract** absent or rarely when present; **staminate scales** erect, obovate, broadly obovate or ovate, the body light brown to light yellow in the middle portion, central bands are clearly delineated, hyaline margins located in the 1/3 distal and 0.1-0.25 mm wide, often folded, glabrous, 1.6-2.9 x 0.8-1.8 mm, 1 vein, apex truncate or rounded; **stamen** with anthers 2-2.6 mm long; **pistillate scales** ovate or broadly ovate, the body brown to light brown, orange towards the edges with hyaline margins absent or occupying the proximal and distal portions, length of 0.1-0.3 mm in the central portion and 0.1-1.8 mm crossing the edges, one nerve marked, glabrous, 1.2-2.7 x 1.4-2.2 mm longer, sometimes as long as or shorter than the perigynia, reaching 3/4 of body length perigynia, wider and the bottom, a little narrower or about the same width as perigynia in the distal portion; **perigynia** distal erect or ascending, proximal spreading, the body greenish yellow in 1/2 proximal, dark brown or light brown in the half distal surface, gloss stinks, 1.5-3.1 x 1-2 mm, 1.2-2.2 mm body length perigynia, almost always smooth (0-3 teeth), base subacute or rounded, apex contracted smoothly into a beak; **beak** brown to dark brown, apex orange or hyaline, mostly straight, teeth acuminate, bifid; **gynoecium** with 2 stigmas; **rachilla** often visible in relief on the side of abaxial perigynia, setaceous, as long as or slightly surpassing, 1.2-1.9 x 1 mm; **achenes** ovoid or almost orbicular, the body light brown, glossy surface, 1-2 x 0.5-1.4 mm, covering over 3/4 volume perigynia, rounded at base, apex obtuse or truncated; beaks absent or marked by the straight base of the style.

Notes: *Carex sp. nov. 1* is easily differentiated by its staminate portion, usually longer than the pistillate portion; its perigynia ascending, loosely packed; its long culms, much longer than the leaves. It occurs in wet meadows at low elevations in California.

Distribution: Western North American endemic (CAL, ORG).

Ecology: Wet meadows in boreal areas, in soils with high water content. 1400 - 2300 m.

Specimens examined (paratypes): USA: California, El Dorado Co., Lake Tahoe Basin Management Unit, J.R. Starr & J. Thibeault 07-44 (CAN). California, Sierra County, Tahoe National Forest, J.R. Starr

& J. Thibeault 07-52 (CAN). California: Butte Co., Lassen National Forest, Forest Ranch, Cheery Hill meadows, near Cherry Hill campsite. J.R. Starr & J. Thibeault 06016 (CAN). California: Sierra Co., Yuba Pass-Weber Lake Road, V.H. Oswald & L. Ahart 8221 (CHSC-66824). California: Tehama Co., L. Ahart 13.051 (CHSC-94326). Oregon, Deschutes Co., Deschutes National Forest, J. Starr 10S-057 & T. Villaverde. Oregon: Deschutes Co., C. Halpern 600 & T. Magge (OSC-159046). California, El Dorado Co., Echo Summit, Howell, J.T. 257424, 1.9.1946, (DAO, 257424). California, El Dorado Co., El Dorado National Forest, 2350 m, Toivonen, H. 661914, Norris, D.H.; Pykälä, J., 23.7.1987, (DAO, 661914). California, El Dorado Co., El Dorado National Forest, 2350 m, Pykälä, J. 6, Norris, D.H.; Toivonen, H., 23.7.1987, (C). California, El Dorado Co., Freel Peak quad, 2292m, Janeway, L. 73322, Schroder, E., 2.9.1998, (CHSC, 73322). California, Plumas County, Blucks Lake quad, 481 m, Janeway, L. 78722, 7.7.2000, (CHSC, 78722). California, Tehama County, Yellow Pine Forest, 1540 m, Ahart, L. 94326, 19.7.2006, (CHSC, 94326). California, Sierra County, Yuba Pass- Weber Lake Rd., 2194 m, Oswald, H. 66824, Ahart, L., 19.8.1996, (CHSC, 66824). California, Nevada County, University of California Trout Lab, 6500 ft, Langenheim, J. 272099, 19.7.1957, (CAN, 272099). California, Nevada County, University of California Trout Lab, 6500 ft, Nisbet, W.A. 272091, 20.7.1957, (CAN, 272091). California, Nevada County, Sagehen Creek, 6300 ft, True, G.H. 845706, Howell, J.T., 29.8.1966, (CAS, 845706). California, Nevada County, University of California Trout Lab, 6500 ft, Langenheim, J. 845707, 19.7.1957, (CAS, 845707). California, Lassen Volcanic National Park, Badger Flat, 6275 ft, Leschke, H. 136120, 10.8.1960, (OSC, 136120). California, Nevada County, Truckee, 2035 m, Naczi, R.F.C., 3.8.2006, (NY). California, Nevada County, Truckee, 1980 m, Naczi, R.F.C., 4.8.2006, (NY). California, Tulare County, Kaweah Meadows, Howell, J.T. 17724, 5.8.1942, (GH, 17724). Oregon, Lake County, Sycan Marsh, 1524 m, Christy, A. 188302, 23.8.1980, (OSC, 188302). Oregon, Deschutes County, 1981 m, Wilson, B. 178855, 9.8.1990, (OSC, 178855). Oregon, Jackson County, Cascade Mountains, 1636 m, Otting, N. 210656, 28.6.2001, (OSC, 210656). Oregon, Deschutes County, 1926 m, Halpern, C. 159046, Magee, T., 30.8.1982, (OSC, 159046).

Carex sp. nov. 2

Holotype: USA, California: Tulare Co., Sierra Nevada, Army Pass, J.T. Howell s.n. (DAO-257423).

Herb forming loose to dense tussocks, caespitose. **Roots** light yellow or light brown. **Culms** 8-20 cm tall and 0.7-1.0 mm in diameter at the middle. **Leaves** 3-4(7) per culm, 90-290 x 0.4-1.0 mm; **Leaf sheaths** brown-dark red or orange, sparingly filamentose. **blades** 8-14 cm long and 0.4-0.9 mm wide in the middle; **ligules**, acute, obtuse or nearly truncate. **Spike** solitary, androgynous, ovoid or trigonal, with staminate portions covering 35 % to 60 %, densely packed, of 6.2-8.5 mm x and 2.5-4.0 mm, staminate portions from 2.2-4.9 x 1.2-1.7 mm, pistillate 2.0-4.2 mm long, 26-30 staminate flowers, 14-16 pistillate flowers; **bract** absent or rarely when present; **staminate scales** erect, obovate, broadly obovate or ovate, the body pale yellow, light brown to dark brown, central bands are clearly delineated with hyaline margins located in the 1/3 distal and 0.1-0.2 mm wide, often folded, glabrous, 1.9-2.5 x 0.9-1.2 mm, with 1 vein, apex acute to subacute; **pistillate scales** the body dark brown, light brown to orange towards the edges, hyaline margins occupying the proximal and distal portions, length of 0.1-0.5 mm in the central portion and 0.1-2.0 mm crossing the edges, central nerve rarely present, ovate or broadly ovate, glabrous, 1.8-2.1 x 1.15-2.0 mm, as long as or shorter than the perigynia and reaching 3/4 of body length perigynia until the base of the beak, wider or as wide as perigynia in the bottom and narrower than perigynia in the distal part, subacute apex, scarbid; **perigynia** erect or ascending in the distal part, mostly spreading in the proximal part, the body greenish or light yellow in 1/2 proximal part with some redness, dark brown in the half distal portion, not very gloss surface, 2.0-3.8 x 1.1-1.9 mm, 1.4-2.2 mm body length perigynia, almost always smooth (0-1(16) teeth), rounded to subacute base, beak often abruptly or subacutely contracted; **beaks** brown to dark brown, apex orange or hyaline, mostly straight, teeth truncate, smooth, bifid; **gynoecium** with 2 stigmas; **rachilla** often visible in relief on the side of abaxial perigynia, setaceous, as long as or slightly surpassing; **achenes** ellipsoid, broadly ellipsoid, lenticular or almost orbicular, the body grayish to light brown, non-glossy surface, 1.4-2.6 x 1.0-1.9 mm, covering over 3/4 volume perigynia, at base broadly truncated or rounded, apex obtuse or truncated; beaks absent or marked by the straight base of the style.

Notes: *Carex sp. nov. 2* can be differentiated by its short culms, as long as the leaves; its staminate portion, as long as or slightly longer than the pistillate portion, presenting a cone shape; its pistillate portion, densely packed. It occurs in high elevations in California. *Carex arctogena* can be easily separated from *Carex sp. nov. 2* for having longer culms, longer spikes, straight tip leaves and for having its lowermost perigynia horizontally orientated.

Distribution: Southwestern North American endemic (CAL).

Ecology: Non-glaciated plateaus and wet banks. 3400 - 3900 m.

Specimens examined (paratypes):

USA, California: Inyo Co., Mono Mesa, J.T. Howell 22750 (WTU-137524). California: Northeastern Tulare Co., Sierra Nevada, Central Basin, Lower lake, P.A. Munz 12669 (WTU-133536). California, Tulare Co., Sierra Nevada, 12000 ft, Howell, J.T. s.n., 5.8.1949, (DAO, 257423). California, Inyo County, Mount Humphreys, 12880 ft, Sharsmith, C.W. 3116, 11.8.1937, (DAO, 257428). California, Inyo County, Mono Mesa, 3657 m, Howell, J.T. s.n., 26.7.1946, (WTU, 137524). California, Mono County, Mt. Dana Plateau, 3505 m, Taylor, D. 7550, 25.7.1979, (COLO, 330874). California, Sierra Nevada, Central Basin, 3444 m, Munz, A. 12669, 26.7.1948, (WTU, 133536). California, Tuolumne County, Kuna Peak, 12500 ft, Sharsmith, C.W. 2681, 21.7.1937, (CAN, 162869). California, Mono County, White Mountains, 11800 ft, Morefield, J.D. 4829, Perala, C., 27.7.1988, (MICH). California, Mono County, Dunderberg Peak, 11800 ft, Taylor, D. 5291, 27.7.1975, (CAS, 856994). California, Fresno County, 11192 ft, Quibell, C.H. 4162, 7.8.1954, (OSC, 96143). California, Inyo County, Mono Mesa, 12000 ft, Howell, J.T. s.n., 26.7.1946, (GH, 12750).

2.5 Supporting Tables

Table 2.1: Diagnostic morphological characteristics used by Smith (1940) and Nilson (1991) to differentiate *C. capitata* from *C. arctogena* (taken from Reinhammar 1999).

Character	***Carex capitata***	***Carex arctogena***
Spike size	6-9 mm long, light brownish-green	3-6 mm long, dark brownish-green
Achene size	On average 2.5 mm long and 1.8 mm wide	On average 1.9 mm long and 1.5 mm wide
Achene shape	Pear-shaped, with a beak about ?- 1/5 of the total length; smooth in the upper part	More rounded, with a beak about 1/3 of the total length; provided with 3-5 small, sharp, teeth in the upper part
Pistillate scale length	Shorter than the achenes	As long as the achenes
Beak length	On average 0.4 mm	On average 0.6 mm; achene more abruptly contracted into a beak
Leaf length	Leaves shorter than culms	Leaves as long or longer than the culms
Tussock density	Loose tussocks	Dense tussocks
Habitat demands	In rich mires, and along riverlets; calciphilous; lowlands subalpine-lowalpine	Wind-exposed heaths in rather dry habitats; weakly calciphilous, also on serpentine; mostly alpine, but occurs rarely in subalpine habitats

Table 2.2: Species associated of *C. arctogena* in South America

Locality	**Collection No.**	**Elevation (m)**	**Associates**
Argentina:Tierra del Fuego, Rio Grande	J. Starr 10015 & T. Villaverde	60	*Erigeron myosotis*, *Phleum alpinum*, *Caltha sagittata*, *Cerastium arvense*, *Carex macloviana* and *C. canescens*
Argentina: Santa Cruz, Los Glaciares National Park	J. Starr 10020 & T. Villaverde	732	*Nothofagus antartica*, *Marsippospermum grandiflorum*, *Chiliotrichum diffusum*, *Escallonia* sp., *Carex microglochin*, *C. banksii*, *C. atropicta*, *C. canescens*,*C. decidua*, *Gaultheria pumila*, *Empetrum rubrum*, *Rostkovia magellanica*
Argentina: Santa Cruz, Los Glaciares National Park	J. Starr 10023 & T. Villaverde	449	*Carex microglochin*, *C. magellanica*, *C. canescens*, *C. barrosii*, *Schoenus andinus*, *Tetroncium magellanicum*, *Escallonia sp.*, *Empetrum rubrum*, *Juncus sp.*, *Rubus sp.*, *Chiliotrichum diffusum*, *Blechnum penna-marina*, *Gaultheria pumila*, *Gavilea sp.*

Table 2.3: Species associates of *"C. cayouetteana"*

Locality	**Collection No.**	**Elevation (m)**	**pH**	**Associates**
U.S.A.: Colorado, Lake Co., San Isabel National Forest	J. Starr 10S-030, W. Sawtell & T. Villaverde	3602	5	*Rhodiola sp.*, *Castilleja sp.*, *Potentilla sp.*, *Salix spp.Bistorta sp.*,*Caltha leptosepala*,*Pedicularis groenlandicum*,*Carex spp.*
U.S.A.: Colorado, Hinsdale Co., Gunnison National Forest	J. Starr 10S-033, W. Sawtell & T. Villaverde	3834	-	*Kobresia myosuroides*
U.S.A.: Montana, Carbon Co., Custer National Forest, Absaroka-Beartooth Wilderness	J. Starr 10S-047A, W. Sawtell & T. Villaverde	3137	5.4	*Carex scirpoidea* and *Kobresia myosuroides.* It has also been reported to occur with *Cassiope mertensiana*, *Siebbaldia procumbens* and *Stellaria* spp.
U.S.A.: Wyoming, Park Co., Shoshone National Forest, Beartooth Plateau	J. Starr 10S-047B, W. Sawtell & T. Villaverde	3291	-	
U.S.A.: Washington, Whatcom Co., Baker-Snoqualmie National Forest	J. Starr 10S-061, W. Sawtell & T. Villaverde	1984	5	*Phyllodoce empetriformis*

Table 2.4: Associates of *Carex sp. nov. 1*

Locality	**Collection No.**	**Elevation (m)**	**pH**	**Associates**
U.S.A.: California, Butte Co., near Cherry Hill Campground, Lassen National Forest	J. Starr 10S-054 & T. Villaverde	1441	7.7	*Calocedrus decurrens*, *Pseudotsuga menziesii*, *Pinus ponderosa*, *Abies magnifica*, *Darlingtonia californica*, *Drosera anglica*, and *Spiranthes* sp.
U.S.A.: Oregon, Deschutes Co., Deschutes National Forest	J. Starr 10S-057 & T. Villaverde	1927	5.8	*Kobresia myosuroides*

Table 2.5: Morphological characters studied. Continuous characters used by Egorova (1999) to differentiate between *C. capitata* and *C. arctogena* and those used in a pilot study to differentiate between *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2* are denoted by asterisks.

Character	**Definition**	**Description**
Continuous variables		
CLMHT	Culm length	distance from the base of the culm to the base of the spike for the longest culm present (current and previous years)
CLMH*	Culm length	same as CLMHT but present year growth only
CULMW	Culm width	width of the longest culm in the medial portion
LEAFL	Leaf length	longest leaf from the base of the pseudoculm to the tip
LEAFW	Leaf width	width of the longest leaf in the medial portion
INFLOL*	Inflorescence length	maximum length from base of the spike to the bottom of the uppermost perigynium beak (=PERBKL)
INFLOW*	Inflorescence width	maximum width of the spike from the base of the perigynium beak (=PERBKL)
MSPL*	Inflorescence staminate portion length	distance from the top of the proximal staminate scale to the apex
FPPL*	Inflorescence pistillate portion length	distance from the base of the spike to the base of the most distance pistillate beak (=PERBKL)
GLUMH*	Length of the pistillate scale hyaline margin	longest hyaline margin from the distal point of the proximal pistillate scale
GLUMHC*	Length of the pistillate scale hyaline margin	narrowest hyaline margin from the distal point of the proximal pistillate scale
FSCL*	Length of the pistillate scale	maximum scale length of the proximal perigynium
FSCW*	Pistillate scale width	maximum scale width of the proximal perigynium
FSCWL	Maximum pistillate scale width length	distance from FSCW to the base of the scale
PERIGL*	Perigynium length	maximum length of the perigynium including the beak
PERBKL	Beak length	distance from distal point of the perigynium to the distal point of the achene
PERIGW*	Perigynium width	maximum width of the perigynium
PERIWD	Maximum perigynium width length	distance from PERIGW to the base of the perigynium
ACHL	Achene length	maximum achene length
ACHW	Achene width	maximum achene width
MSCL*	Staminate scale length	maximum scale length at the medial part of the staminate portion of the inflorescence
MSCW	Staminate scale width	maximum scale width at the medial point of the staminate portion of the inflorescence
Discrete variables		
LEAFN	Leaf number	along the longest culm
PSA	Angle of the distal edge of the pistillate scale	less than or greater than 45°
PERIGA	Perigynium beak inclination	straight or bent
PERIGBo	Perigynium angle	less than or greater than 45°
TEETHN	Perigynium teeth number	along the margins of the perigynium
CULMD	Culm teeth number	number within the distal 1mm of the culm
Qualitative variable		
CULMC	Culm sheath colour	brown, red-brown, red-purple or purple-brown

Table 2.6: Mean ±1 SD and ranges for 22 morphological characters measured for the *C. capitata* complex. Character abbreviations correspond to those described in Table 2.5. All measurements are in millimeters. N = sample size.

Character	*C. capitata* (N=38)	*C. arctogena* (N=35)	*“C. cayouetteana”* (N=28)	*Carex sp. nov. 1* (N=24)	*Carex sp. nov. 2* (N=6)
CLMHT	296.45±70.5	204.03±52.1	204.90±30.44	354.27±72.37	158.03±24.75
	(150-490)	(125.9-335)	(142-260)	(225-540)	(140-205)
CLMH	272.10±82.3	168.89±44.74	178.29±39.83	347.73±75.68	110.78±22.56
	(120-490)	(100-280)	(116-260)	(193-540)	(83-140)
LEAFL	205.92±50.0	154.64±47.9	157.49±21.11	206.97±41.68	113.08±19.27
	(115-360)	(90-298)	(115-195)	(133-270)	(85-140)
CULMW	0.75±0.09	0.78±0.15	0.89±0.12	0.88±0.08	0.83±0.12
	(0.6-1)	(0.5-1.1)	(0.6-1.1)	(0.7-1)	(0.7-1)
LEAFW	0.59±0.19	0.62±0.12	0.64±0.13	0.65±0.12	0.58±0.17
	(0.4-1.5)	(0.4-1)	(0.4-0.9)	(0.5-0.9)	(0.4-0.9)
INFLOW	4.41±0.48	3.83±0.39	4.44±0.61	3.86±0.43	3.07±0.69
	(3.3-5.4)	(2.9-4.7)	(3.5-6.1)	(3.2-4.6)	(2.5-4)
MSPL	1.95±0.65	2.12±0.68	3.22±1.40	5.36±2.00	3.05±1.03
	(0.8-3.5)	(1.2-3.7)	(0.9-6.65)	(2-10.5)	(2.2-4.9)
GLUMH	0.56±0.62	0.97±0.49	0.53±0.36	0.39±0.52	1.35±0.74
	(0.01-2.25)	(0.4-2.6)	(0-1)	(0.01-1.8)	(0.01-2)
GLUMHC	0.19±0.15	0.40±0.17	0.23±0.16	0.09±0.10	0.27±0.18
	(0.01-0.5)	(0.1-1)	(0-0.5)	(0.01-0.3)	(0.01-0.5)
INFLOL	7.52±1.20	7.34±1.16	9.11±1.63	11.25±2.33	7.65±0.87
	(5.5-10.3)	(5.2-9.8)	(6.1-12.8)	(6.8-16.9)	(6.2-8.5)
FPPL	4.78±0.89	4.46±0.64	5.00±0.80	5.08±0.83	3.70±0.84
	(2.7-7.2)	(3.5-6)	(3.9-6.4)	3.9-6.9)	(2-4.2)
FSCL	2.12±0.25	2.18±0.29	2.43±0.24	2.18±0.33	1.93±0.12
	(1.5-2.5)	(1.4-3)	(1.9-3)	(1.2-2.7)	(1.8-2.1)
FSCW	1.43±0.21	1.77±0.34	1.73±0.27	1.74±0.24	1.53±0.35
	(0.8-1.8)	(1-2.6)	(1.1-2.4)	(1.4-2.2)	(1.15-2)
FSCWL	0.61±0.16	0.68±0.29	0.77±0.25	0.65±0.24	0.60±0.13
	(0.3-1)	(0.1-1.7)	(0.1-1.3)	(0.2-1)	(0.4-0.8)
PERIGL	2.99±0.45	2.65±0.45	2.80±0.38	2.35±0.45	2.55±0.64
	(1.8-3.6)	(1.5-3.2)	(1.5-3.4)	(1.5-3.1)	(2-3.8)
PERBKL	1.28±0.24	1.13±0.23	1.23±0.22	1.01±0.22	0.97±0.35
	(0.8-1.7)	(0.7-1.8)	(0.9-1.9)	(0.7-1.4)	(0.6-1.6)
PERIGW	1.79±0.21	1.50±0.19	1.96±0.31	1.66±0.17	1.50±0.26
	(1.3-2.2)	(1-2)	(1.2-2.5)	(1.2-2.2)	(1.1-1.9)
PERIWD	0.94±0.20	0.82±0.19	0.81±0.29	0.77±0.18	0.75±0.14
	(0.5-1.3)	(0.5-1.3)	(0.3-1.8)	(0.4-1)	(0.5-0.9)
ACHW	1.21±0.13	1.18±0.18	1.23±0.22	1.16±0.16	1.23±0.35
	(1-1.5)	(0.7-1.7)	(0.6-1.8)	(0.5-1.4)	(1-1.9)
ACHL	1.72±0.21	1.61±0.15	1.59±0.24	1.55±0.23	1.82±0.43
	(1.1-2.1)	(1.4-1.9)	(1-2.3)	(1-2)	(1.4-2.6)
MSCL	2.19±0.26	1.86±0.35	2.28±0.30	2.24±0.29	2.20±0.20
	(1.6-2.9)	(1-2.8)	(1.8-3)	(1.6-2.9)	(1.9-2.5)
MSCW	1.02±0.23	1.12±0.21	1.16±0.27	1.23±0.24	1.04±0.10
	(0.6-1.5)	(0.7-1.6)	(0.6-1.9)	(0.8-1.8)	(0.9-1.2)

Table 2.7: Mean ±1 SD and ranges for morphological characters measured for *C. arctogena* from South America vs. North America and Europe. Character abbreviations correspond to those described in Table 2.5. All measurements are in millimeters. N = sample size.

Character	*C. arctogena* from Europe (N=10)	*C. arctogena* from North America (N=23)	*C. arctogena* from South America (N=6)
CLMHT	179.52±32.28	217.54± 58.46	221.28± 77.22
CULMW	7.70 ±1.64	8.02 ±1.47	8.00 ± 2.10
CLMH	153.10 ±34.37	72.52 ±50.73	195.99 ± 65.20
LEAFL	130.72 ±29.53	60.61 ±45.73	94.31± 70.21
LEAFW	6.00 ± 0.67	6.24 ±1.35	6.83 ± 1.47
INFLOW	36.30 ± 3.68	38.43 ±3.82	43.17 ± 2.79
INFLOL	72.80 ±13.85	71.48 ±9.76	93.50 ± 20.54
MSPL	20.60 ± 7.76	20.04 ±6.11	33.17 ± 13.09
FPPL	42.20 ± 6.71	44.96 ±6.53	51.50 ± 5.47
GLUMH	8.90 ±1.73	9.35 ±5.36	12.33 ± 4.80
GLUMHC	4.40 ±0.97	4.13 ±1.98	4.00 ± 1.79
FSCL	22.00 ±2.16	21.04 ±2.48	24.67 ± 4.46
FSCW	17.40 ±3.17	16.52 ±3.10	22.67 ± 2.66
FSCWL	6.50 ±2.59	7.26 ±3.08	6.50 ± 3.39
PERIGL	25.20 ±3.05	25.87 ±4.98	30.50 ± 2.59
PERBKL	11.67 ±3.24	10.95 ±2.08	13.00 ± 1.55
PERIGW	14.70 ±1.25	14.83 ±2.04	16.83 ± 2.48
PERIWD	6.80 ±1.69	8.91 ±2.56	9.00 ± 3.16
ACHW	11.89 ±1.54	11.41 ±2.02	12.67 ± 1.51
ACHL	15.78 ±1.56	16.36 ±1.36	15.83 ± 1.72
MSCL	18.50 ±3.69	18.22 ±2.52	23.67 ± 5.68
MSCW	11.20 ±2.66	10.89 ±1.35	12.83 ± 3.19
CULMD	5.70 ±3.13	8.30 ±4.34	7.50 ± 5.01

Table 2.8: Mann-Whitney significance for pairwise comparisons of each significant variable from the Kruskal-Wallis test for *C. arctogena* from North America (NA), South America (SA) and Europe (E). Percentage of length difference for significant variables are shown.

Variables	Kruskal Wallis p-value	Mann-Whitney p-value NA vs SA	Mann-Whitney p-value E vs SA	% of difference
CULMH	0.2797			
CLMHT	0.6026			
CULMW	0.7452			
LEAFL	0.1610			
LEAFW	0.1600			
INFLOW	0.0033	0.006	0.008879	11.62
INFLOL	0.0032	0.002	0.05072	
MPSL	0.0039	0.0059	0.01646	39
FPPL	0.0054	0.012	0.01029	13.7
GLUMH	0.7162			
GLUMHC	0.7882			
FSCL	0.0434	0.03481	0.1868	
FSCW	0.0005	0.0008573	0.0043	22.3
FSCWL	0.9838			
PERIGL	0.0099	0.0255	0.0098	16.6
PERBKL	0.4757	20.644	16.055	
PERIGW	0.0831			
PERIWD	0.5136			
ACHW	0.6009			
ACHL	0.4971			
MSCL	0.0239	0.0319	0.063	
MSCW	0.0571			

Table 2.9: Mann-Whitney significance for pairwise comparisons of each significant variable from the Kruskal-Wallis test, ordered by its utility to significantly differentiate between taxa. N denotes no significance, Y denotes significance with $p < 0.05$ and Y* denotes significance with $p < 0.01$. Variables in bold were included in the Principal Component Analysis. *Carex capitata* (C), *C. arctogena* (A), *"C. cayouetteana"* (Y), *Carex sp. nov. 1* (Y2) and *Carex sp. nov. 2* (Y3).

Variable	Y3-Y2	Y3-Y	Y3-A	Y3-C	Y2-Y	Y2-A	Y2-C	Y-A	Y-C	A-C
CLMH	Y	Y	Y	Y	Y*	Y*	Y	N	Y*	Y*
CLMHT	Y	N	Y	Y	Y*	Y*	Y	N	Y*	Y*
MSPL	N	Y	Y	Y	Y	Y*	Y*	Y	Y	N
LEAFL	Y	Y	N	Y	Y*	Y*	N	N	Y*	Y*
INFLOL	Y	N	N	N	Y	Y*	Y*	Y*	Y	N
PERIGW	N	N	N	N	Y	Y	Y	Y*	Y	Y*
GLUMHC	N	N	N	N	Y	Y*	Y	Y	N	Y*
INFLOW	N	Y	N	N	Y*	N	Y*	Y*	N	Y*
FSCL	N	Y	N	N	Y	N	N	Y*	Y*	N
MSCW	N	N	N	N	N	Y	Y	N	Y*	Y
FSCW	N	N	N	N	N	N	Y*	N	Y*	Y*
MSCL	N	N	N	N	N	Y*	N	Y*	N	Y
CULMW	N	N	N	N	N	N	Y*	Y	Y*	N
GLUMH	N	N	N	N	N	Y*	N	Y	N	Y
ACHL	N	N	N	N	N	N	Y	N	Y	Y
FPPL	Y	N	N	N	N	Y	N	Y	N	N
PERIBKL	N	N	N	N	Y	N	Y	N	N	Y
PERIGL	N	N	N	N	Y	N	Y	N	N	Y
FSCWL	N	N	N	N	N	N	N	N	Y	N
PERIWD	N	N	N	N	N	N	Y	N	N	N

Table 2.10: Percentage of the total variance explained by principal component scores of the variables included in different PCAs. PC = Ordered principal Component.

PC	All variables	12 variables
1	19,401	28,53
2	12,4	16,709
3	10,989	12,48
4	7,6767	10,307
5	6,7801	7,8787
6	6,0676	6,4935
7	5,2372	5,0133
8	4,3777	4,467
9	3,8413	3,0117
10	3,4106	2,774
11	3,0812	2,1061
12	2,899	0,23034
13	2,7171	
14	2,2072	
15	1,9515	
16	1,7454	
17	1,3808	
18	1,347	
19	1,1537	
20	1,0073	
21	0,21384	
22	0,1153	
	100	100

2.6 Supporting Figures

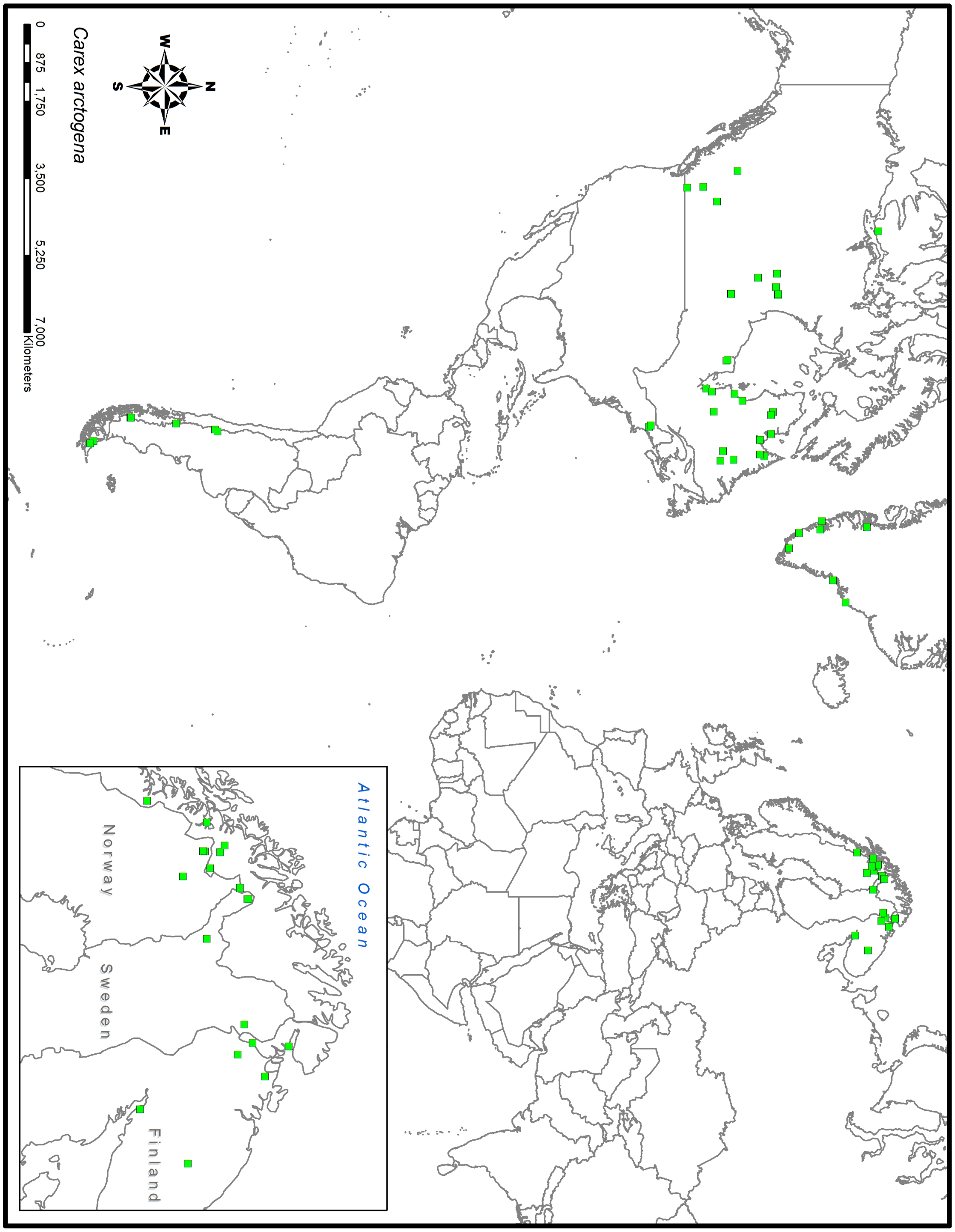


Figure 2.1: The distribution of *C. arctogena* based on all the herbarium specimens examined in this study. Elongated box represents the distribution in Scandinavia.

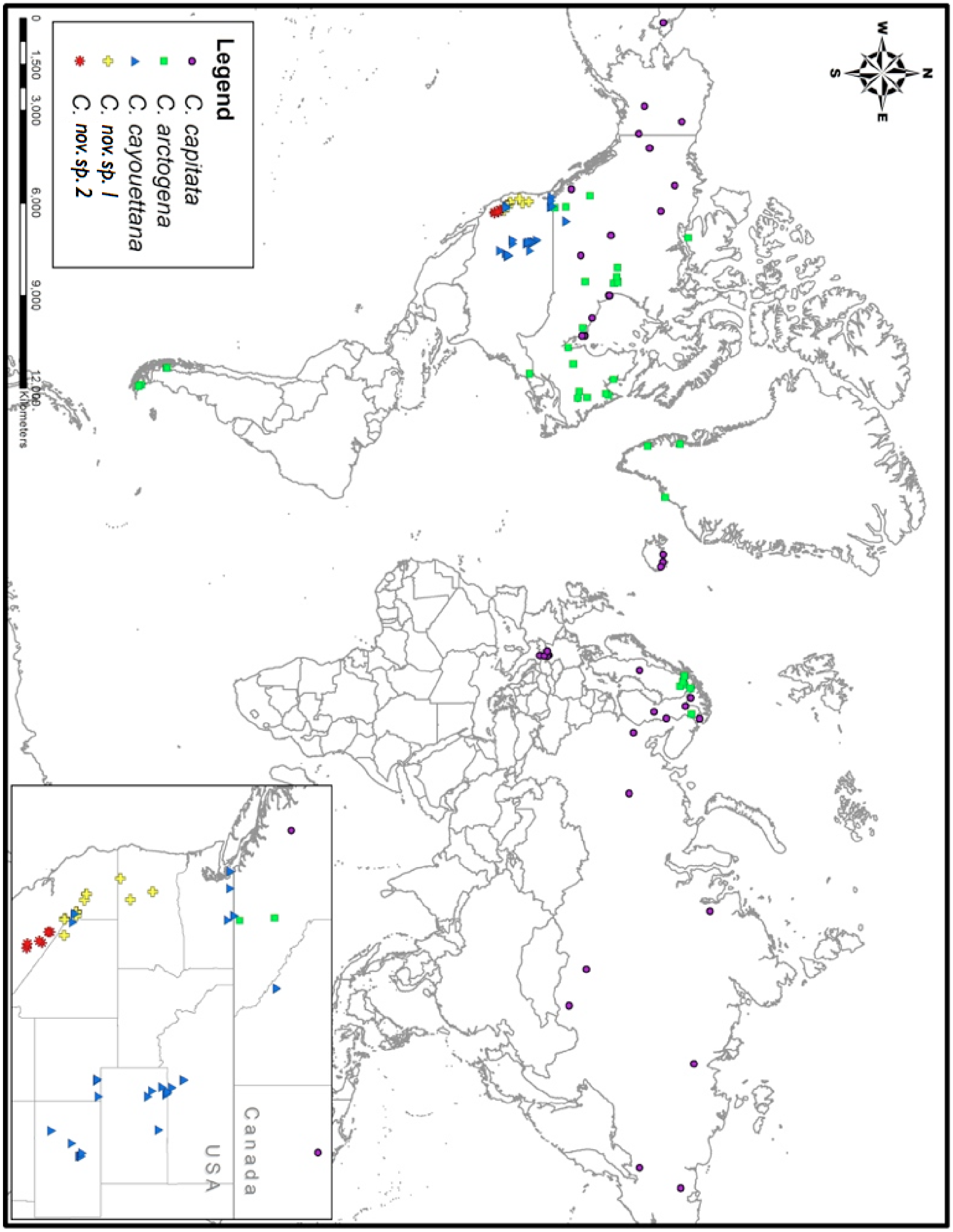
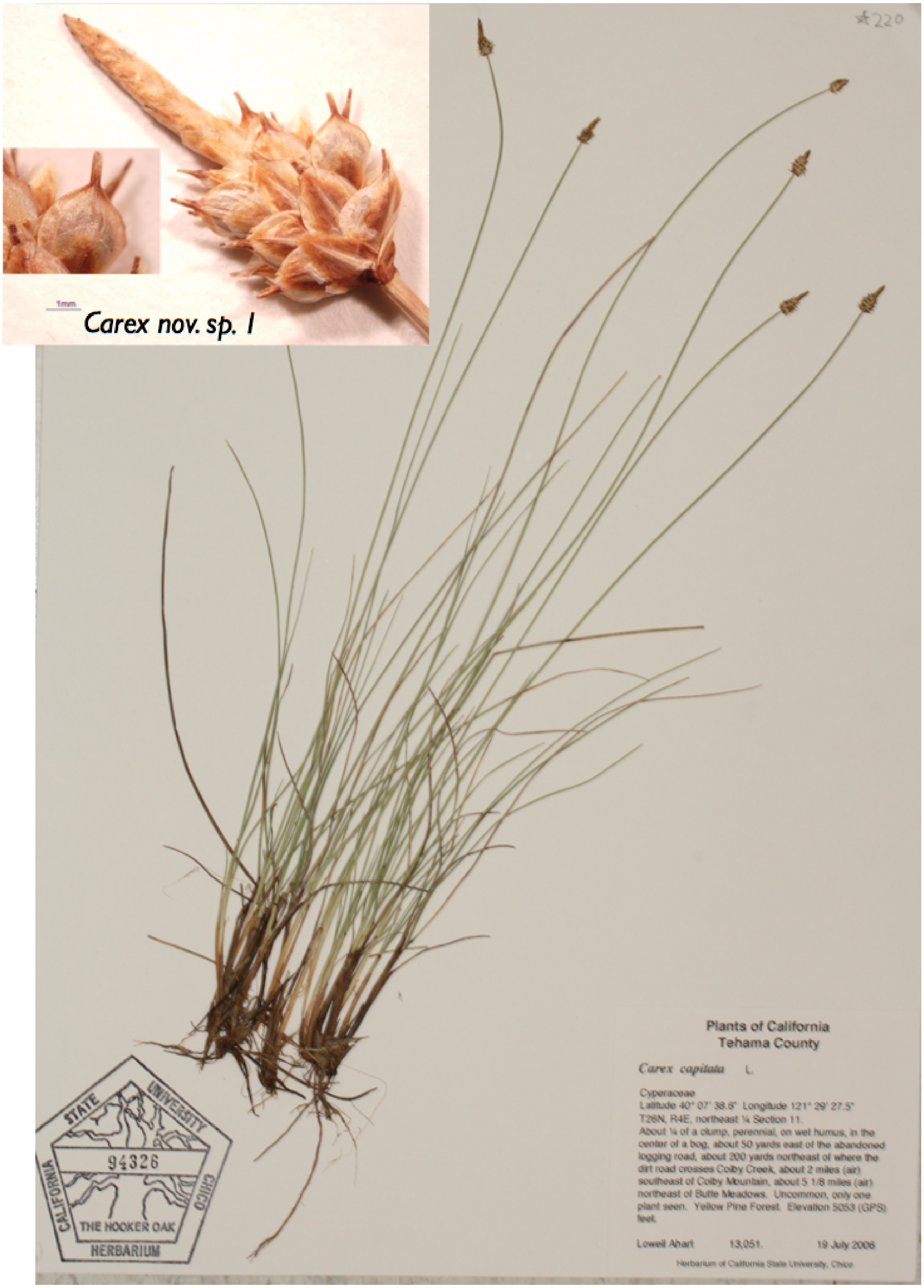


Figure 2.2: Distribution of *C. capitata*, *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2* herbarium specimens used in the morphological study.



Plants of California
Tehama County

Carex capitata L.

Cyperaceae
Latitude 40° 07' 38.6" Longitude 121° 29' 27.5"
T26N, R4E, northeast ¼ Section 11.
About ¼ of a clump, perennial, on wet humus, in the center of a bog, about 50 yards east of the abandoned logging road, about 200 yards northeast of where the dirt road crosses Colby Creek, about 2 miles (air) southeast of Colby Mountain, about 5 1/8 miles (air) northeast of Butte Meadows. Uncommon, only one plant seen. Yellow Pine Forest. Elevation 5053 (GPS) feet.

Lowell Ahart 13,051. 19 July 2006

Herbarium of California State University, Chico

Figure 2.3: Photographs of herbarium sheets of *Carex sp. nov. 1* identified as *C. capitata* from CHSC. Elongated box shows spike and perigynium details.

Figure 2.4: Photographs of herbarium sheets of *Carex sp. nov. 2* identified as *C. arctogena* from CAL. Elongated box shows spike and perigynium details.

COLORADO, U. S. A.

14522. CAREX ARCTOGENA H. Smith

CLEAR CREEK CO.: Loch Lomond, 11,140 ft. alt., between Mount Bancroft and James Peak; upper limit of krummholz, willow bogs just below the dam ; forming a solid stand about 50 feet diam. on the west edge of the bog

8 August 1972 W. A. Weber, T. Koponen, P. Nelson

ex herb. COLO

Figure 2.5: Photographs of herbarium sheets of *"C. cayouetteana"* identified as *C. arctogena* from COLO. Elongated box shows spike and perigynium details.

Figure 2.6: Photographs of herbarium sheets of *C. arctogena* form H. Elongated box shows spike and perigynium details.

MUSEUM BOTANICUM UNIVERSITATIS, HELSINKI (H)
PLANTAE FENNICAE

Carex capitata

ENONTEKIÖ LAPLAND (EnL/Le). Enontekiö. Vanaseana
(Venemaa) between lakes Skádjajávri and Vancajávri.
Minerotrophic polygons at subalpine belt. Rare.
1 dupl.

Grid 27°E: 7685394:279029 Alt. 600 m a.s.l.
01.VIII.2003 Väre, Henry 14955
(H 746021)

Figure 2.7: Photographs of a herbarium sheet of *C. capitata* from H. Elongated box shows spike and perigynium details.

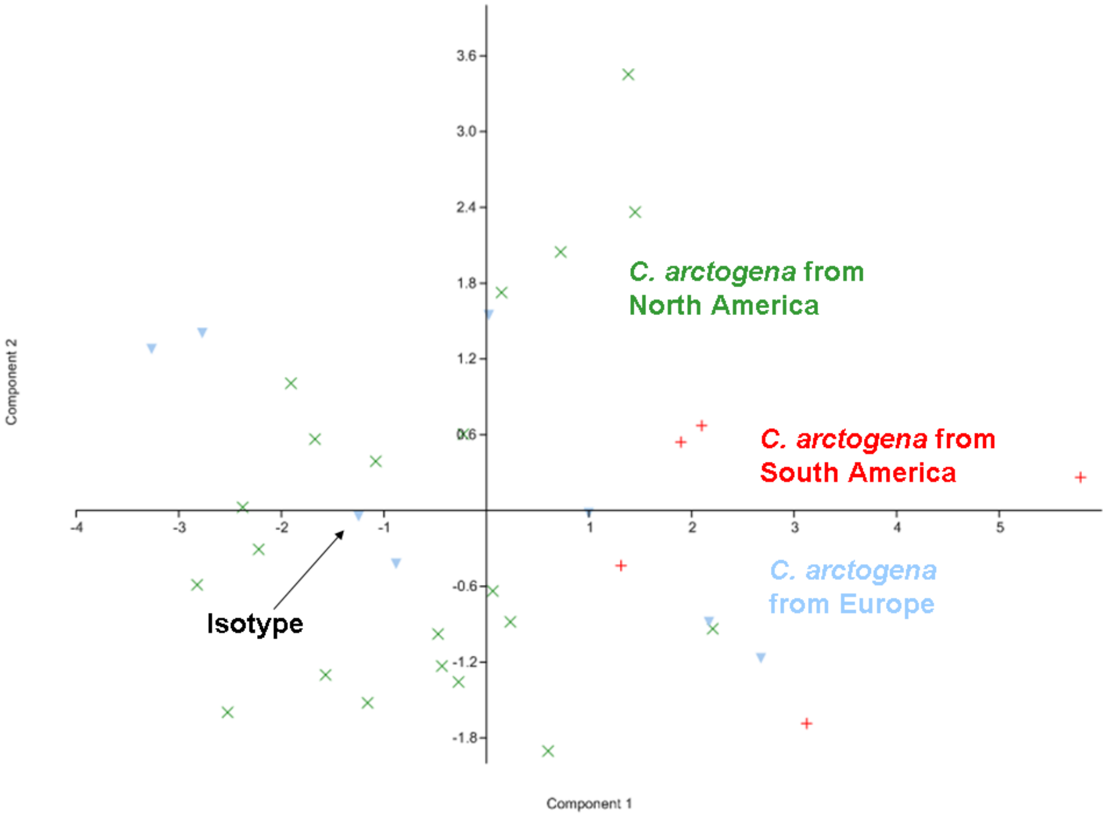


Figure 2.8: PCA scatter plot of the first two principal component using *C. arctogena* specimens from North America (green diamonds), South American (red cross) and European (blue triangles) and 12 quantitative variables. The isotype of *C. arctogena* is indicated.

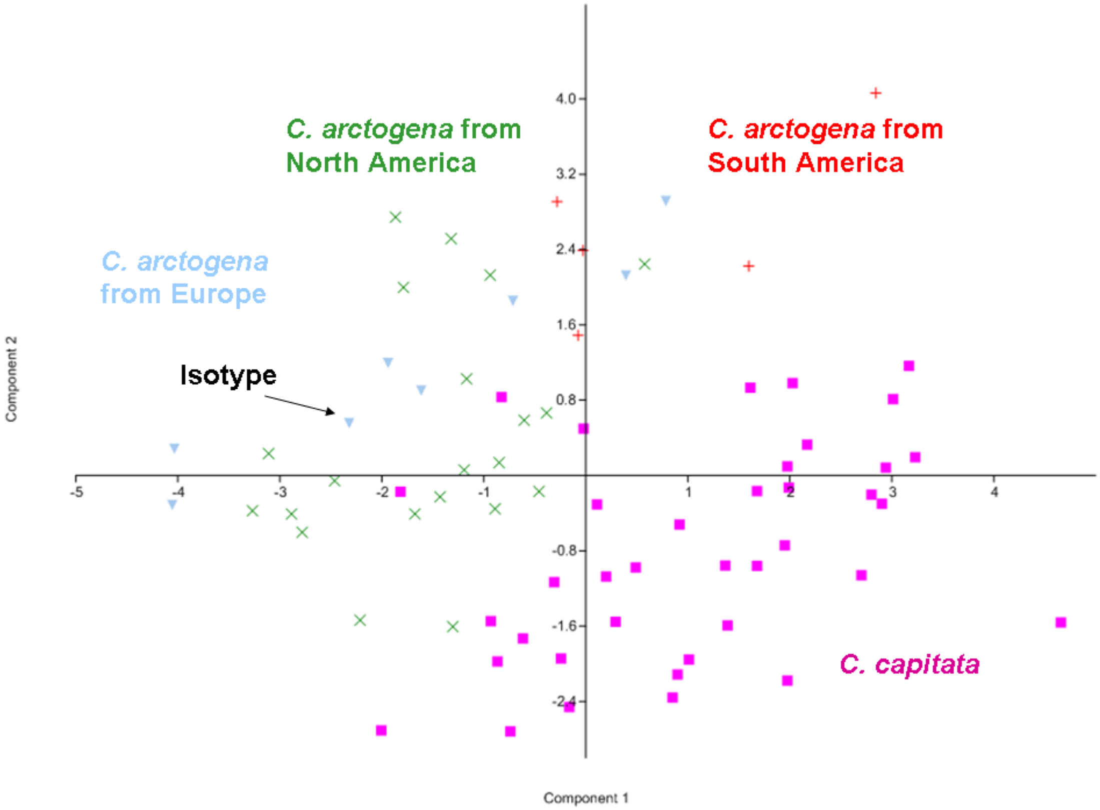


Figure 2.9: PCA scatter plot of the first two components using all *C. arctogena* and *C. capitata* specimens studied and 12 quantitative variables. Coloured symbols represent *C. arctogena* from North America and Europe (green diamond); *C. arctogena* from South America (red cross); and *C. capitata* (pink squares). The isotype of *C. arctogena* is indicated.

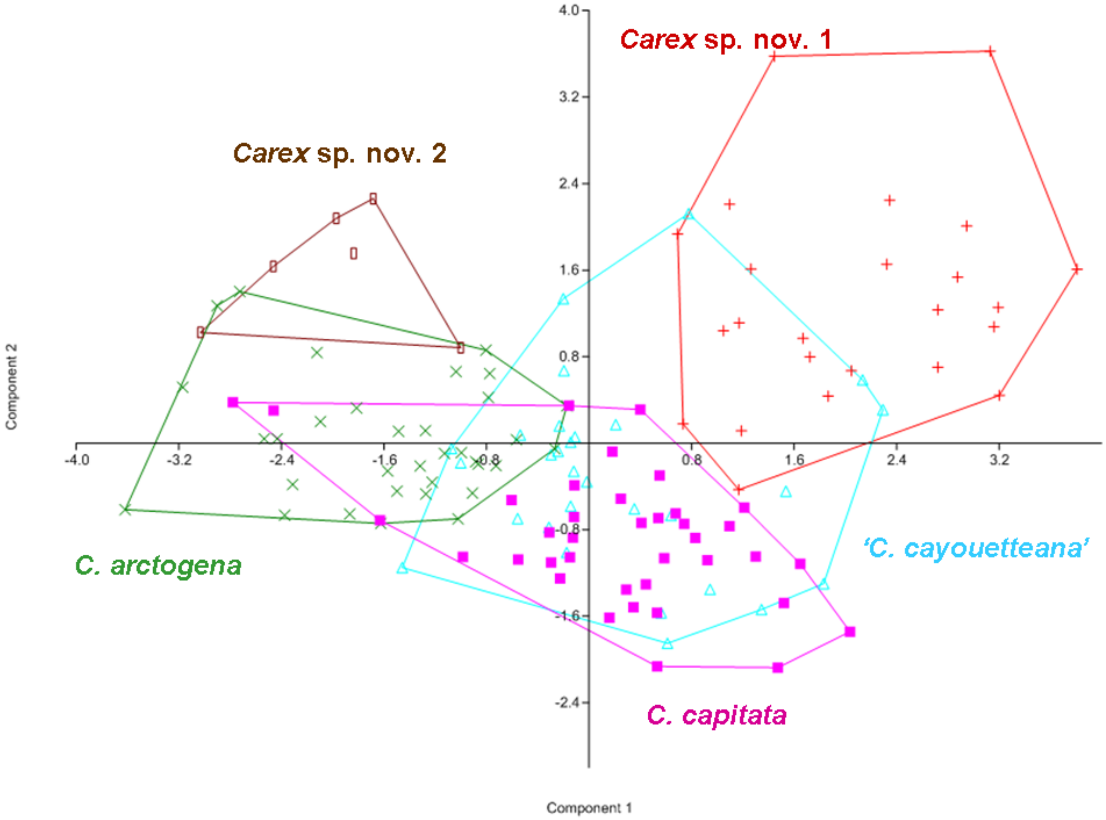


Figure 2.10: PCA scatter plot of the first two components using all specimens studied of *C. capitata*, *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2* and 12 quantitative variables. Each convex hull represents the follow taxa: pink, *C. capitata*, green, *C. arctogena*; blue, *"C. cayouetteana"*; yellow, *Carex sp. nov. 1*; brown, *Carex sp. nov. 2*.

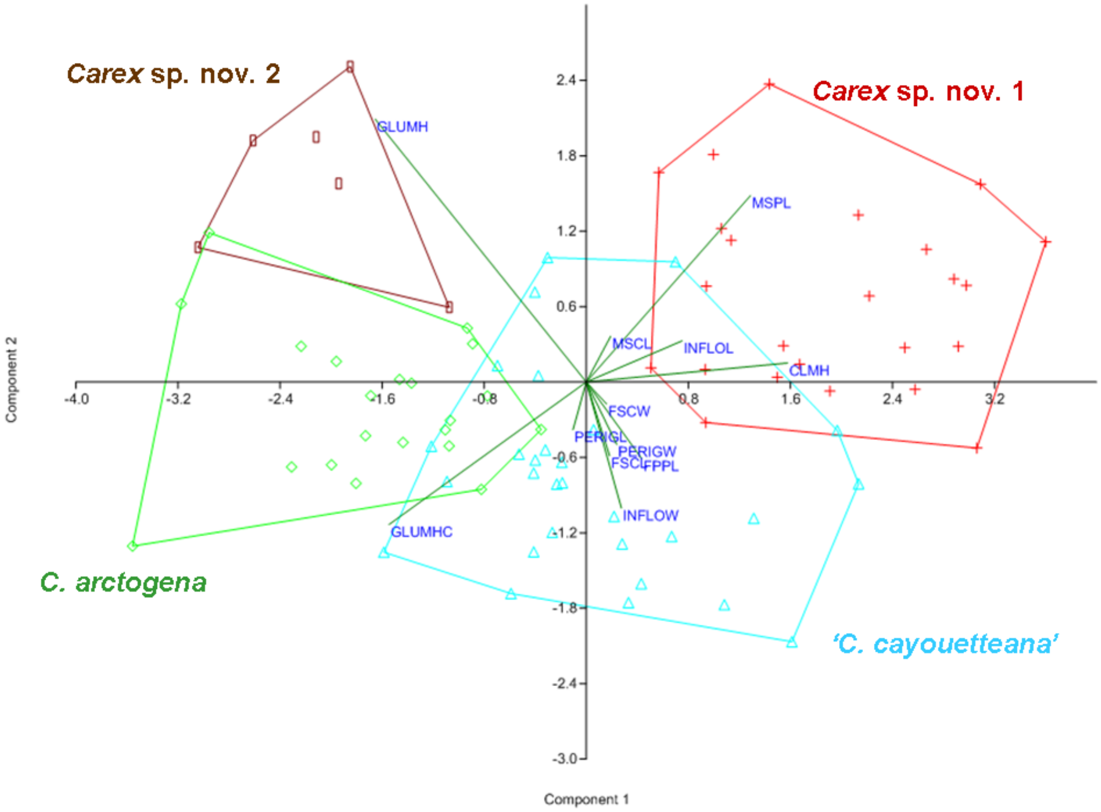


Figure 2.11: PCA scatter plot of the first two components using all specimens of *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2* and 12 quantitative variables. Each convex hull represents the follow taxa: green, *C. arctogena*; blue, *"C. cayouetteana"*; red, *Carex sp. nov. 1* brown, *Carex sp. nov. 2*. A biplot of the variables used in the PCA is included.

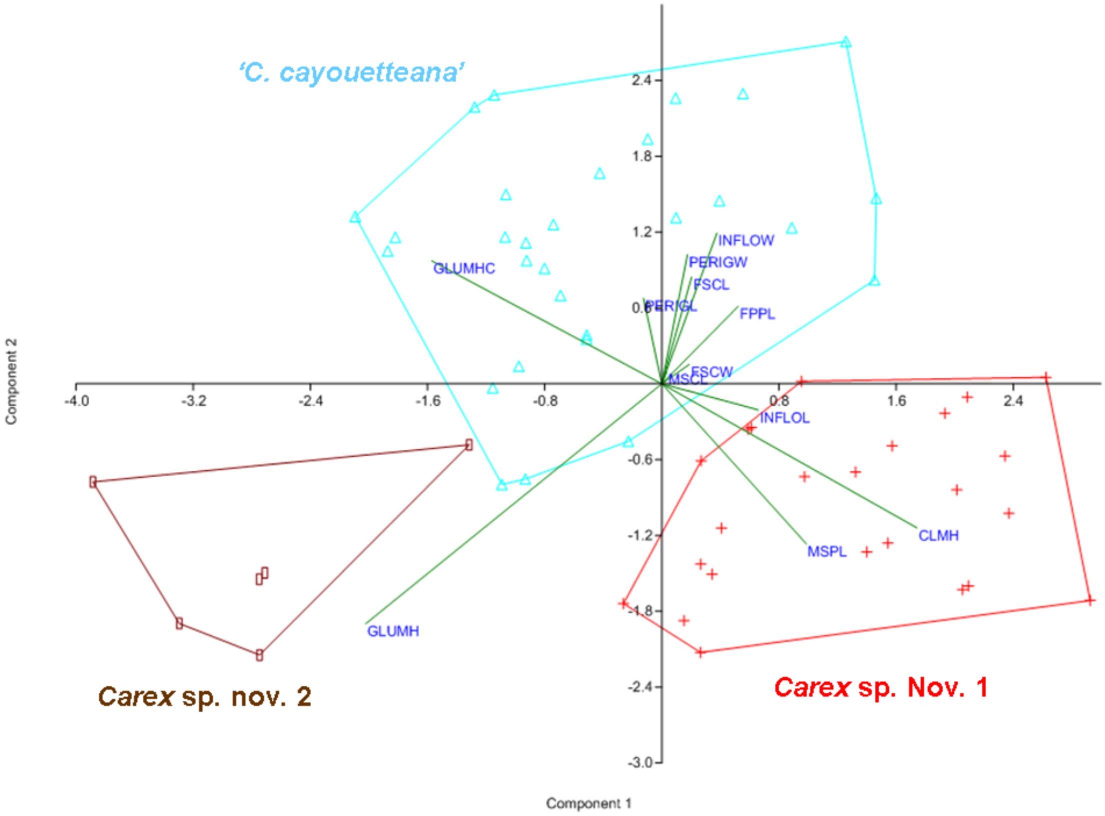


Figure 2.12: PCA scatter plot of the first two components using *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2* specimens and 12 quantitative variables. Each convex hull represents the follow taxa: blue, *"C. cayouetteana"*, red *Carex sp. nov. 1* and brown, *Carex sp. nov. 2.*

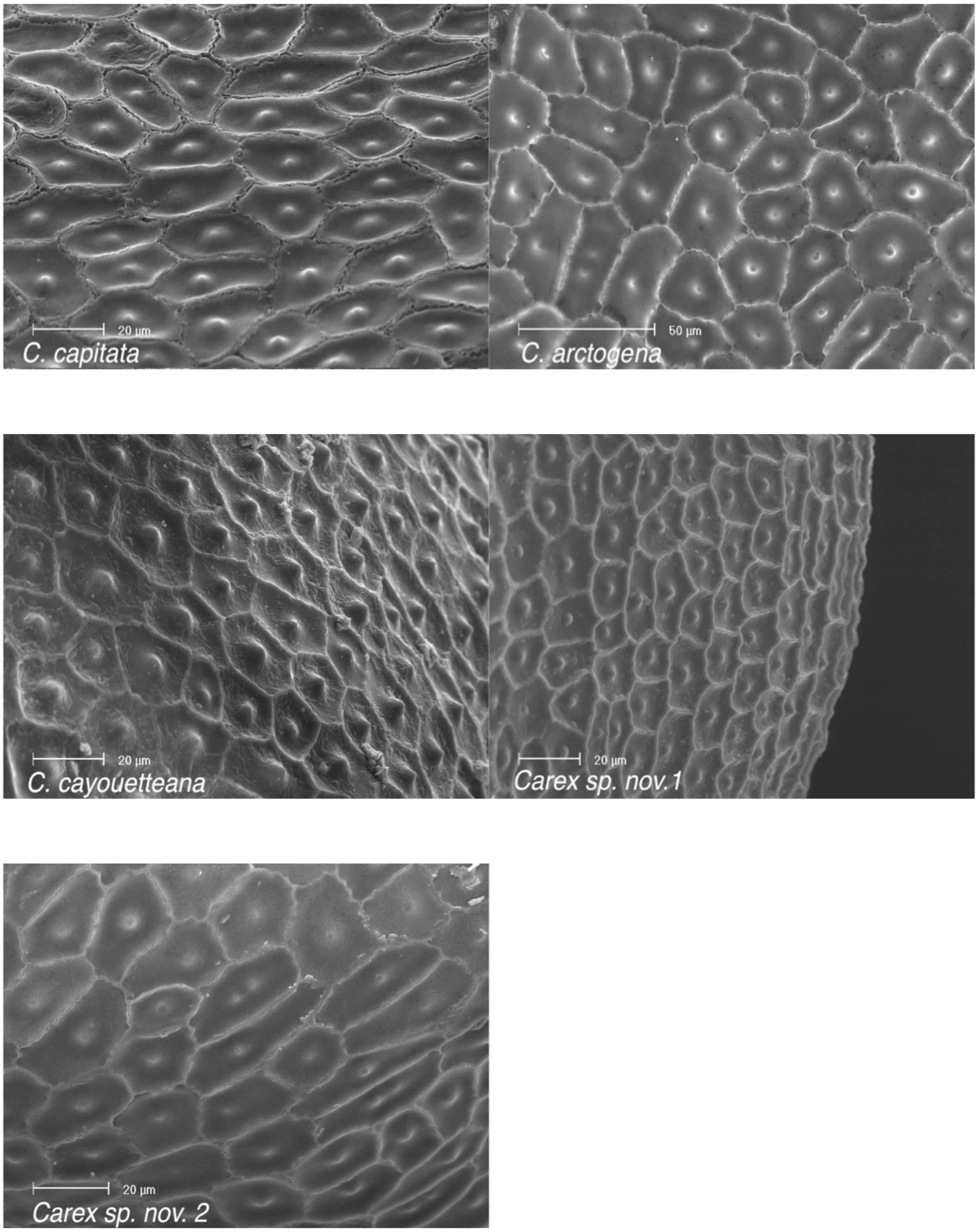


Figure 2.13: Scanning electron photographs of silica bodies of all putative taxa in the *C. capitata* complex. *Carex capitata*, A. Dutilly & E. Lepage 16761 (CAN-17332) from Ontario; *C. arctogena*, J. Starr 10023 & T. Villaverde (CAN) from Argentina; *"C. cayouetteana"*, K. H. Lackschewitz 9909 (MONTU-86558) from Montana; *Carex sp. nov. 1*, J. Starr & J. Thibeault 07-44 from California (CAN); *Carex sp. nov. 2*, C. W. Sharsmith 2681 (CAN-162869). See Table A.9 for additional specimen voucher information.

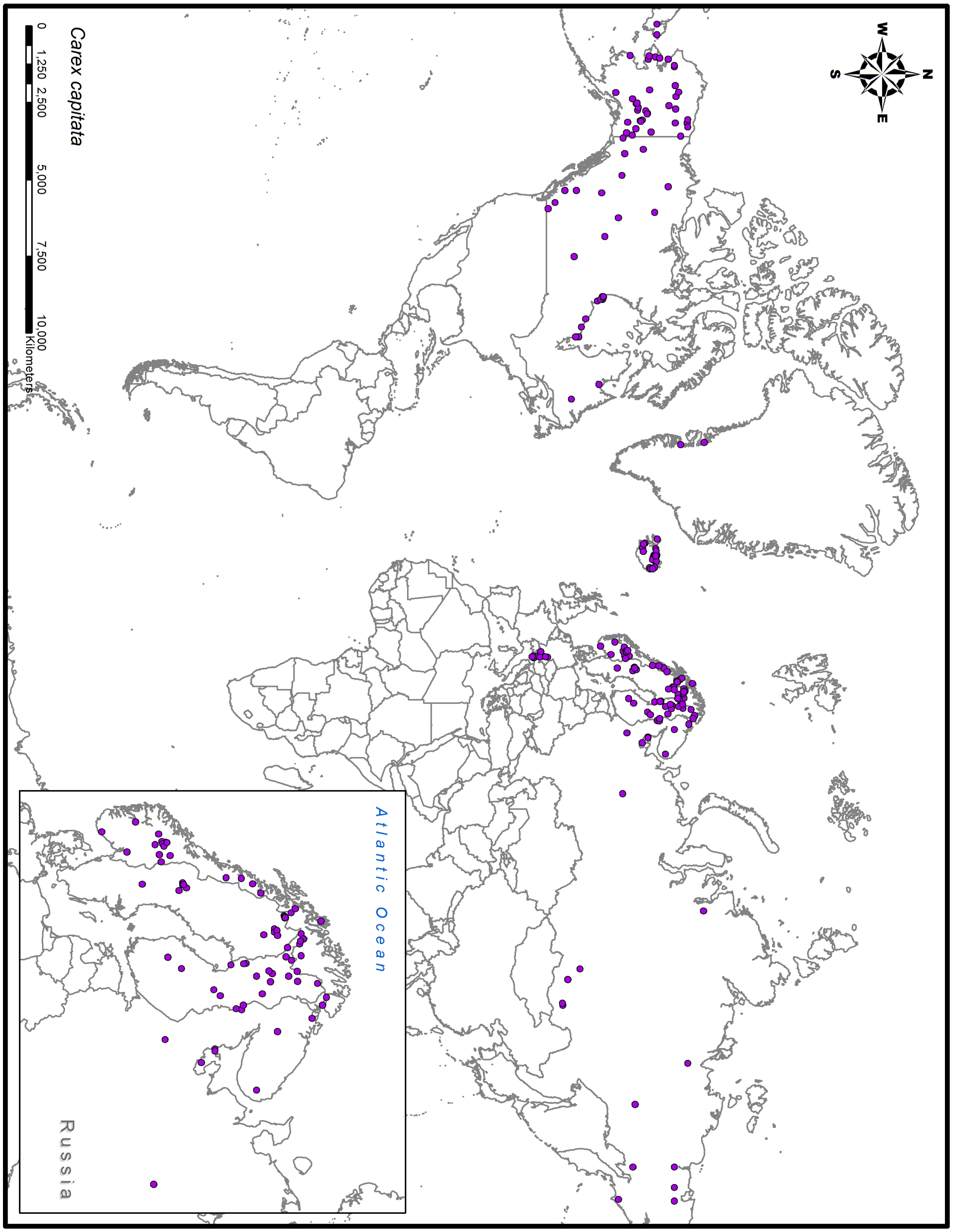


Figure 2.14: The distribution of *C. capitata* based on all the herbarium specimens examined in this study. Inset represents the distribution in Scandinavia.

Chapter 3

Phylogeny of the *C. capitata* complex

3.1 Introduction

A taxonomical study based on morphological data conducted in Chapter 2 in the *C. capitata* complex has revealed the existence of three new species from North America: *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2*. In addition, our results support the identity of *C. capitata* and *C. arctogena* as distinct species and the inclusion of *C. antarctogena* under *C. arctogena*.

The value of a multi-pronged approach, as suggested by Ford et al. (2009), lies in confirming the taxonomic status of species using molecular techniques, and in inferring potentially phylogenetic relationships among closely related taxa. The distribution pattern of the species in the *C. capitata* complex is remarkably different: amphi-Atlantic (*C. capitata*), bipolar (*C. arctogena*) and endemic of different areas of western North America (*"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2*). The reasons why this species complex has such biogeography could be better understood by investigating the evolutionary relationships between them, through a phylogeographical approach

The word ‘Phylogeography’ was used first by Avise (1986) to study the relationship between geography and mitochondrial DNA in animals. Phylogeography is a discipline that emerged in a multidisciplinary context and it incorporates methods and concepts from genetics of populations (microevolution) and systematics (macroevolution). Chloroplasts in plants are analogous to mitochondria in animals in phylogenetic studies and it can be used to study species dispersion. In contrast to nuclear DNA, the chloroplast genome is maternally inherited, with little or no crossing over, which allows the investigation of geographical migration patterns due to seed dispersal (McCauley 1995). It has also a reduced effective population size due to its haploid nature, a feature that results in an increased effect of genetic drift, reflected in a greater genetic differentiation of fragmented populations. Therefore, plastid regions may retain longer phylogeographic signals of past migrations, range fragmentation and dispersal events (Schaal et al. 1998; Hudson & Coyne 2002; Rendell & Ennos 2003; Kadereit et al. 2005; Petit et al. 2005). On the other hand, nuclear DNA might help to test for species reproductive isolation or hybridization due to its biparental inheritance. Therefore, variation in both, nuclear and chloroplast DNA, within plant species might elucidate evolutionary processes and reveal species’ histories (Soltis et al. 1997). The distribution and composition of the Arctic flora have been severely influenced by different glaciation periods in the Quaternary (ca. 2 Ma until present), when the advance and retreat of the ice sheet produced major shifts in the range of plant species; some populations could have survived in ice-free areas, from where they could have started a recolonization during interglacial periods (Hewitt 2003). Some of those refugia have been located in the Beringian land bridge, the High Arctic archipelago, the eastern Arctic or the high mountains in the southern Rocky Mountains (Murray 1995; Hultén 1937; Tremblay & Schoen 1999), from where plants could have migrated towards the Arctic following different paths. Molecular footprints, such as high levels of genetic diversity, are expected to be harbored in populations that have survived over the long term in such glacial refugia, relative to the populations that have occupied deglaciated regions (Hewitt 2000) due to the successive founder effects during the recolonization in interglacial periods. Thus, migrants contain only a subsample of the overall genetic diversity found in a species population (Widmer & Lexer 2001).

The lack of information on the origin of arctic plants in Asia, such as *C. capitata*, and in the southern Hemisphere, such as *C. arctogena*,, is even more striking (Hewitt 2004). The bipolar distribution presented by *C. arctogena* is known to occur only in 29 other plant species (Moore & Chater 1971) (e.g. *Armeria maritima*, Plumbaginaceae; *Osmorhiza chilensis*, Apiaceae) five of which are from the genus *Carex*: *C. canescens* L., *C. microglochin* Wahlenb., *C. macloviana* D'Urv., *C. magellanica* Lam. and *C. maritima* Gunn.). Unravelling the evolutionary history of those bipolar taxa is challenging due to the scale of their distribution, the different hypotheses that could be tested and the fact that their taxonomy is often unresolved. Phylogenetic relationships studied in all bipolar *Carex* species but *C. arctogena* showed a low level of genetic differentiation among northern-southern populations and suggested long-distance dispersal as the most plausible cause of the bipolar disjunction for the five sampled species (Escudero et al. 2010).

In this chapter, four hypotheses are tested for the large biogeographical disjunct distribution displayed by *C. arctogena*. First, the mountain-hopping hypothesis (Ball 1990), that relies on the idea that species have slowly migrated from one chain of mountains to the next to achieve such distribution (Moore & Chater 1971), could be rejected if nearby populations are genetically closer than to distant populations. Second, the long-distance dispersal hypothesis, which implies a dispersal vector such as birds, could be rejected if genetic similarities are found between disjunct populations but not between close populations. The third and the fourth hypotheses are parallelism and vicariance hypotheses, historically proposed to be the most plausible causes for such a distribution (Du Rietz 1940). The vicariance hypothesis implies a previous continuous species distribution and a subsequent disruption in northern and southern populations. The parallelism hypothesis implies the accumulation of evolutionary steps in the same fashion in northern and southern populations. Both hypotheses could be rejected if disjunct populations are genetically identical.

Therefore, the aim of this study is to provide molecular support to the status of the different taxa in the complex and analyze the phylogenetic relationship between them.

3.2 Materials and methods

For the delimitation of the study group, we consider that *C. capitata* complex includes five species (*C. capitata*, *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2*) recognized in a previous taxonomic study based on morphological data (see Chapter 2).

3.2.1 Species studied

Carex capitata complex includes five species *Carex* species (*C. capitata*, *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2*). As outgroup taxon, *C. hepburnii* Boot. from section *Nardinae* was selected based on previous phylogenetic studies that showed this taxon as sister species to section *Capituligerae*. (Roalson et al. 2001; Starr et al. 2004, 2008) and taxonomical treatment (Egorova 1999). *Carex oreophila*, the sixth species in the *Capituligerae* section, was not included in any of the analyses since the extraction procedure from the single specimen we could obtain failed to produce good DNA quality, probably due to the old age of the voucher. A similar situation occurred with *C. monostachya* Schur from section *Longespicate*, a sister species to the complex (Starr et al. 2004).

3.2.2 Sampled material

As mentioned in Chapter 2, two expeditions were organized to Patagonia and western USA, where fresh plant material was collected and used for DNA analysis. Leaf material was dried in silica gel for DNA extractions and vouchers of each population were deposited in CAN, SI and UPOS. DNA from herbarium specimens was also extracted (see Table A.2) in order to represent the entire distribution of each taxon and to cover the morphological variation in the complex (Figure 3.1). Vouchers are deposited in CAN, UPOS and SI. DNA sequences will be deposited in GenBank (http://ncbi.nlm.nih.gov/genbank).

3.2.3 Molecular methods

All specimens were extracted following the protocol of Alexander et al. 2007 (Alexander et al., 2007) as modified by Clerc-Blain et al. (2010).

Chloroplast DNA

A pilot study was performed with 29 samples of three species (*C. capitata*, *C. arctogena* and *"C. cayouetteana"*) for five chloroplast regions (*rps16* gene intron, *matK* gene and the intergenic spacers *psbA*-*trnH*, *atpF*-*atpH* and *psbK*-*psbI*) to test their molecular variability within the study group. Results showed that *matK*, *atpF*-*atpH* and *rps16* were the most variable and therefore they were amplified.

Each PCR amplification contained the following reagents dissolved in a final volume of 15μl: 1x PCR buffer (10x), 10mM of each dNTP, 10μM of each primer, 0.5 mM $MgCl_2$, 1μg of bovine serum albumin (BSA), 1μl DNA and 50U of *Taq* DNA polymerase. The following PCR conditions were performed for all regions: 30 cycles of DNA denaturation at 95°C for 45s, primer annealing at 45°C for 45s, and DNA strand extension at 72°C for 90s, with a pre-treatment at 95°C for 60s before cycling. The PCR was terminated by a final extension step of 72°C for 3 min. Minor adjustments (e.g., reagent concentrations, annealing temperature) were sometimes necessary to obtain suitable amplification products, which often depended on DNA extract quality and the primer-pair used for amplification.

Nuclear DNA

Recent studies in *Carex* have characterized 54 microsatellite loci for three different species of *Carex* (Ohsako & Yamane 2008; Hipp et al. 2009; King & Roalson 2009). Cross amplification assays have identified 13 of these loci (Cko1-11, Cko1-47, Cko-2-118, Cko2-112, CM25, CM01, CM27, S245, S082, S180, S175 and S181) that will amplify easily for *C. capitata* (MacPhail 2009). A pilot study with 7 samples of three species (*C. capitata*, *C. arctogena* and *"C. cayouetteana"*) showed that five of them (CM25, S082, S180, Cko1-47 and CM01) were the most variable and were amplified.

The following PCR conditions were used to amplify all these loci: 43 cycles of DNA denaturation at 94°C for 30s, primer annealing at 58°C for 30s, and DNA strand extension at 72°C for 45s, with a pre-treatment at 94°C for 3 min before cycling. The PCR was terminated by a final extension step of 72°C for 5 min. A ramping of 25% was applied between the annealing and extension phases to increase binding efficacy and thus increase the reproducibility of the results. The last 10 cycles were run at an annealing temperature of 53°C to increase the specificty of primer binding. Minor adjustments (e.g. reagent concentrations, presence of bovine serum albumin (BSA), annealing temperature) were sometimes necessary to obtain suitable amplification products, which often depended on DNA extract quality and the primer-pair used for amplification.

A sample of 3μl from both chloroplast and nuclear PCRs reaction was run on 1.25% agarose gels stained with ethidium bromide to check for the success of the amplification. Successfully amplified products were purified using the following reagents dissolved in a final volume of 200μl: 1/μl of Exonuclease (10U/μl, MJ Biolynx Inc.), 10/μl of Shrimp Alkaline Phosphatase (1U/μl, MJ Biolynx Inc.). Then, they were amplified with an ABI PRISM®Big Dye™Terminator Cycle Sequencing Ready Reaction Mix (Applied Biosystems) following the manufacturer's protocols and repurified using the following reagents: EDTA 125mM, sodium acetate (NaOAc) 3M, ethanol 99% and 70% and HIDI formalmide (Applied Biosystems). Finally, they were run in the automated sequencer ABI 3130xl DNA analyzer (Applied Biosystems). Sequenced data were assembled and edited using the program Sequencher 4.7 (Gene Codes Corporation, Ann Arbor, MI, USA).

3.3 Molecular analyses

3.3.1 Phylogenetic analysis

Two different matrices were prepared for each type of nucleotide information, nuclear DNA vs. chloroplast DNA. The three amplified chloroplast regions selected in the pilot study (*matK*, *atpF-atpH* and *rps16*) were combined in a single matrix, containing 86 sequences. In the nuclear matrix, the five different amplified microsatellites regions selected in the pilot study were combined, resulting in a matrix with 18 samples. Nucleotide repetitions (Poly A - Poly T) were eliminated (Table 3.5), treating the rest of the sequence as a single copy region. Both matrices were aligned using CLUSTAL X (Thompson et al. 1997) and revised manually with subsequent minor adjustments based on the most parsimonious alignment.

For each data matrix, heuristic searches under the criterion of maximum parsimony (MP) were conducted in PAUP* 4.0b10 (Swofford 2002) using 10,000 random addition-sequence replicates with tree-bisection-reconnection (TBR) branch-swapping and multiple trees saved for each replicate off (MULTREES=no). Clade support was determined using bootstrap (BS) analysis with 10,000 replicates. DeBry & Olmstead (2000) have shown that when the MULTRESS option is off bootstrap proportions are similar to the values produced when the MULTREES option is on. Based on simulation studies of Starr et al. (2004) and Hillis & Bull (1993), we used the following terms to describe the strength of clades support: strongly supported 95-100%, BS; very well supported 85-94%, BS; well supported 75-84%, BS; moderately supported 65-74%; weakly supported 55-64%, BS; and very weakly supported <55% BS.

A Bayesian analysis was also performed for the chloroplast data set using MrBayes v. 3.0b4 (Ronquist 2003) and including the parameters for the model of evolution that best fit each locus. Model selection for each locus was conducted on the basis of the Akaike Information Criterion (AIC) (Akaike 1974) using MrModeltest v2 (Nylander 2004). Nucleotide substitution models resulted in a Felsenstein 1981 (F81) for *matK*, a General Time Reversible (GTR) for *atpF-atpH*, and GTR + Γ for *rps16*. Two independent runs of four Markov Monte Carlo Chains were run simultaneously in each Bayesian analysis for 5,000,000 generations with trees saved every 1,000 generations. Tree likelihood from the analyses were evaluated over generations, discarding (burn-in) those trees that did not reach the stationary likelihood. They were summarized in a 50% majority rule consensus tree; posterior probabilities (PP) were used for clade support.

3.3.2 Statistical Parsimony

To explore the phylogeographic history in the complex and to look for ancestral haplotypes that could help to understand the relationships between individuals, statistical parsimony analyses were conducted in the chloroplast dataset (*C. capitata*, 26 samples; *C. arctogena*, 15 samples; *"C. cayouetteana"*, 17 samples; *Carex sp. nov. 1*, 7 samples and *Carex sp. nov. 2*, 2 samples) using the method of Templeton et al. (1992) as implemented in TCS (Clement et al. 2000). Based on the coalescence theory (Hudson 1989; Templeton et al. 1992), the algorithm calculates the probability that two DNA sequences share a parsimonious relationship without multiple substitutions underlying any single nucleotide difference. Sequences are collapsed into haplotypes whose frequencies are calculated. Pairwise comparisons of haplotypes, gathered in a distance matrix, are used to calculate the most parsimonious network (above 95% probability, analogous to 0.05 from statistical hypothesis testing) for mutational steps. Missing intermediates, extinct or not sampled haplotypes, are shown in the network. All the analyses were run without missing data as Joly et al. (2007) demonstrated that it could make a sequence look identical to different haplotypes and reduce network resolution. Gaps due to mononucleotide repeat units (poly-T and poly-A), which are considered to be highly homoplasic (Kelchner 2000) were coded as missing data.

3.4 Results

3.4.1 Phylogenetic analyses

Chloroplast DNA analyses

Phylogenetic reconstruction of maximum parsimony (MP) analysis of the chloroplast matrix (aligned length 2,252 bp: 605 bp *atpF* - *atpH*, 790 bp *matK* and 857 bp *rps16*, 84 taxa; see Table 3.2) produced a consensus tree from 51,200 most parsimonious trees found in the heuristic search (C.I. =1, R.I.= 1; Figure 3.2). In the Bayesian analysis of the combined chloroplast matrix the first 16,500 trees were discarded since they did not reach the stationary Likelihood of the analysis. The Bayesian majority rule consensus tree obtained from the analyses of the chloroplast matrix is consistent with the strict consensus tree of MP analysis. When combining the three genes, four clades were detected. First, a very well supported monophyletic group (Clade A: 86% BS, 1 PP) comprising all *C. arctogena* samples from Europe and North and South America. Secondly, a very well supported clade (Clade B: 89% BS, 1 PP) comprising *C. capitata* samples from Eurasia and North America, which contains a subclade (78% PP) comprising samples from Saskatchewan and The Northwest Territories. Thirdly, a very well supported clade (Clade C: 93% BS, 1 PP) that comprises *"C. cayouetteana"* samples and two subclades, one comprising all *Carex sp. nov. 1* samples in a weakly supported subclade (64% BS, 0.65 PP) and another very well supported (94% BS, 1 PP) clade, comprising *Carex sp. nov. 2* samples. This lineage will be referred as ' *"C. cayouetteana"* complex'. Finally, a fourth well supported clade comprising some *C. capitata* samples from Russia (Clade D: 82% BS, 1PP). *C. arctogena*, *Carex sp. nov. 1* and *Carex sp. nov. 2* were returned as monophyletic species, whereas the remaining taxa within the complex appeared as paraphyletic (Figure 3.2). *Carex capitata* was formed of two different lineages (Eurasia-North America and Russia) while *"C. cayouetteana"* also included *Carex sp. nov. 1* and *Carex sp. nov. 2*.

Nuclear DNA analyses

Maximum parsimony analysis of the nuclear matrix (aligned length 861 bp: 97 bp CM25, 119 bp Ck01-47, 128 bp S245, 182 bp CM01 and 335 bp S082, 18 samples; see Table 3.4) produced an unrooted tree (Figure 3.3). The heuristic search found six most parsimonious trees (C.I.= 0.94, R.I.= 0.0556). Gaps due to mononucleotide repeat units (poly-T and poly-A) were coded as missing data. No outgroups were included due to the failure to produce good quality sequences from their DNA. Thus, the MP analysis yield an unrooted phylogram (Figure 3.3). In the Bayesian analysis of the combined nuclear matrix, the first 1,500 trees were discarded since they did not have the stationary likelihood of the analysis. The topology retained in the most parsimonious tree is congruent with the Bayesian Inference analyses. A very well supported (94% BS, 1 PP) split comprises *C. capitata* samples from Europe and North America and, in a polytomy, a weakly supported (62% BS, 0.55 PP) clade comprising samples from Saskatchewan and the Northwest Territories. A second weakly supported (57% BS) split comprises *Carex sp. nov. 1* and *Carex sp. nov. 2* samples in a polytomy and another split consisting on *C. capitata* samples from Russia. Then, *C. arctogena* samples are not resolved in the tree. *"Carex cayouetteana"* appears in a separate linage from all the other samples, in a weakly supported (63%, 0.63 PP) split.

3.4.2 Sequence variation and haplotype analysis

Statistical parsimony analysis of the three chloroplast regions yielded one simple network with no loops (ambiguities in the network reconstruction). The matrix included 68 samples and 1916 bp. Twenty one sites were variable within the dataset and seven different haplotypes were detected (H1 - H7; Figure 3.4 and Table 3.6). The haplotype 1 (H1) comprises all the samples of *C. arctogena* (15) from Europe and North and South America; a second haplotype (H2) was exclusive to four *C. capitata* samples from Russia; a third haplotype (H3) comprises only samples of *C. cayouettena*; a fourth haplotype (H4), which differs from H3 by a single point mutation, comprises all *Carex sp. nov. 1* samples; a fifth haplotype (H5) comprises 20 samples for *C. capitata* from both Eurasia and North America; a six haplotype (H6) comprises three *C. capitata* samples from Saskachetwan and Northwest Territories; and finally, a seventh haplotype (H7), comprises all samples of *Carex sp. nov. 2* (7). The haplotypes with the greatest amount of differences are H6 (*C. capitata*) and H7 (*Carex sp. nov. 2*), separated by 16 point mutations. Haplotype 1 and 2 are separated by the same numbers of point mutations from the rest of the network, being separated by four base pairs differences from each other.

3.5 Discussion

3.5.1 *Carex arctogena*

The bipolar taxon, *C. arctogena*, is shown to be a monophyletic species, presenting no genetic differences among the samples from northern and southern America despite sampling three chloroplast regions (coding *matK*, *atp*, and non coding, *rsp16*) and five microsatellite nuclear loci. More samples for the nuclear regions as well as different regions of the nuclear genome could be investigated in future work to look for differences between northern and southern populations. In addition, in Chapter 2, no statistically significant morphological differences were found between the populations from the northern vs. the southern Hemisphere. This is consistent with both, the molecular analysis herein and the conclusions of Moore & Chater (1971), based on morphology, that *C. antarctogena* from South America cannot be separated from *C. arctogena* from the Northern Hemisphere. The lack of genetic variation throughout the entire range of *C. arctogena* suggests that it might have undergone a genetic bottleneck in a refugium during the Quaternary glaciations, from which it subsequently recolonized during interglacial periods. The Canadian Arctic Archipelago, Greenland or the Beringia region might have served as a refugium for *C. arctogena* as these regions have been proposed as refugia for other arctic-alpine species such as *Saxifraga oppositifolia* (Abbott et al. 2000) or *Dryas integrifolia* (Tremblay & Schoen 1999).

Raven (1963) suggested that many of the disjunct patterns, such as a bipolar or amphi-Atlantic distribution, correspond with migration routes of birds. Some arctic birds are able to travel from high latitudes in the northern Hemisphere to the southernmost region in the southern Hemisphere in days or weeks, such as Hudsonian Gotwit (*Limosa haemastica*, Elphick & Klima 2002), Red Knot (*Calidris canutus*, Harrington 2001), White-rumped Sandpiper (*Calidris fuscicollis*, Parmelee 1992), Baird's Sandpiper (*C. bairdii*, Moskoff & Montgomerie 2002), Sanderling (*C. alba*), Pectoral Sandpiper (*C. melanotos*), Lesser Yellowlegs (*Tringa flavipes*) or Semipalmated Plover (*Charadius semipalmatus*, Nol & Blanken 1999). Most of these birds make some stopovers before getting to southern South America (e.g Baird's Sandpiper, Moskoff & Montgomerie 2002; White-rumped Sandpiper, Parmelee 1992; Lesser Yellowlegs, Tibbitts & Moskoff 1999; Pectoral Sandpiper, Holmes & Pitelka 1998 or Red Knot, Harrington 2001), eat preferentially insects rather than seeds before departing (e.g. Sanderling, Macwhirter et al. 2002) or are mostly coastal (e.g. Semipalmated Plover, Nol & Blanken 1999; Sanderling, Macwhirter et al. 2002; Red Knot, Harrington 2001) a habitat not suitable to *C. arctogena*. However, the Hudsonian Gotwits appear to be perfect candidates as a vector of transportation not only because they make a non-stop flight of several thousands miles from northern North America to Tierra del Fuego, where half of the world's population winters (Elphick & Klima 2002), but also because they eat sedge seeds to embark on their long migratory flight (Alexander 1994). Besides, indigested sedge seeds were found in the anterior portion of gastrointestinal tracts (gizzards), suggesting they might have been eaten to help grind other food (Alexander et al. 1996). Moreover, Hudsonian Godwits place their nests on dry tops of hummocks where the 90% of the vegetation correspond to sedges (Elphick & Klima 2002) or in tussocks of sedge-tundra marsh (Hagar 1966) which is the optimal habitat of *C. arctogena*.

Bird migration routes to South America almost invariably begin in North America, with a few exceptions such as Europe (M. Gosselin, personal communication). *Carex arctogena* seeds lack mechanisms to facilitate seed transportation attached to animals (epizoochory), but seed dispersal could occur via ingestion (endozoochory). Before departing, birds fill their gizzards, a secondary stomach used to grind their food before digestion, with seeds that will be eaten during the flight (Alexander et al. 1996). Bird's gizzards must also be filled with small stones to facilitate food grinding (Alexander et al. 1996). *Carex* fruits are full of silica bodies which make them as hard as rocks but they are still lighter than pebbles. Therefore, birds could use them for both grinding and food. Fridriksson & Sigurdsson (1969) have demonstrated that some *Carex* seeds retain their ability to germinate after passing through the gut of a bird, Snow Bunting (*Plectrophenax nivalis*), that migrate from the British Isles, via Iceland, to Greenland. This feature may permit seed dispersal and successful colonization over short and possibly long distances.

Carex arctogena is a scarce taxon in Patagonia since no more than seven herbarium sheets are kept in Argentinian and Chilean major herbaria from the southernmost region of South America (Table 3.7). Besides, during the expedition made in January-February 2010, it was quite difficult to find *C. arctogena* populations, mostly due to habitat loss (e.g. some populations seem to be lost due to recent changes in field hydrology). An alternative hypothesis to the long-distant dispersal could be anthropogenic dispersal, this is, transported by humans. One of the first collections of *C. arctogena* in South America is from the northernmost region of Patagonia (Neuquén) in a plateau elevated ca. 2000 m. It is unlikely, due to the difficulty of reaching this remote plateau, that *C. arctogena* could have been transported there, willfully or unintentionally, by humans. *Carex arctogena* occupies undisturbed habitats and it does not match the expected pattern for most introduced species, which are usually generalist and become widespread in disturbed habitats (Liston et al. 1989; Martin-Bravo 2009).

Two other hypotheses have been proposed to explain *C. arctogena* staggering disjunct pattern; the mountain hopping hypothesis (Ball 1990), which suggests a migration through mountain chains, can be rejected since the populations found in Patagonia are genetically identical to the populations from the northern Hemisphere. Likewise, parallelism and convergence hypotheses can be also can be ruled out due to the monophyly of the taxon.

3.5.2 *Carex capitata*

Phylogenetic results have revealed some degree of differentiation within *C. capitata*, resulting in two different lineages. *Carex capitata* samples are grouped in two strongly supported clades; one comprising some *C. capitata* samples from Russia, all of them above 65°N (100% PP, 82% BS, see Figure 3.1); and another one comprising *C. capitata* samples from Eurasia and North America (100% PP, 88% BS).

The author could not find any morphological trait to differentiate these samples from other *C. capitata* specimens. The disparity between genetic and morphological traits could be due to the species history during the Quaternary cold periods, which had a remarkable influence on plants occurring in temperate regions (Hewitt 1993, 1996), forcing them to remain in southern refugia (Taberlet et al. 1998) or in unglaciated areas located within glaciers (nunataks). Plant species were forced then to contract their geographical distribution (Hewitt 1996) which could have plunged their genetic variability. Those populations would initially maintain a restricted subset of parental genetic variability that could be lost under genetic drift (Vanderpoorten & Shaw 2010). During interglacial periods, plant species could have accomplished their continuous distribution from those refugia, exhibiting now a geographically structured genetic diversity (Soltis et al. 1997). Lineages B and D could have originated in the northern part of Beringia, an area that was mainly unglaciated throughout the Quaternary (Andersen & Borns 1997), where it might have persisted for a long period. This region has been already highlighted for preserving biodiversity insofar as other plant species and animals (Alsos et al. 2005, Hewitt 2004). Nevertheless, only 22 specimens of *C. capitata* from the Beringia area were available for both studies and thus a wider sampling in those areas at a fine scale (e.g. population genetics, increasing the molecular regions studied) and further studies from other approaches, such as anatomical, are needed.

On the other hand, some genetic differentiation, based on single nucleotide character, is also found within the rest of *C. capitata* samples from Eurasia and North America, particularly in samples from Saskatchewan and The North West Territories. Again, the author could not find any morphological traits to differentiate between these samples from other *C. capitata* samples. Statistical parsimony analysis suggests that these samples (H6) are derived from other *C. capitata* samples (H5) from Europe and North America, inferred as ancestral. Those samples could have reached some refugia in the high Arctic Archipelago during the Quaternary, when its population size could have decreased dramatically. These conditions could have helped to acquire its genetic variability by genetic drift.

3.5.3 *"Carex cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2*

These three taxa are comprised in a strongly supported clade (100%PP, 92% BS,"C. cayouetteana" complex) in chloroplast analyses, with *Carex sp. nov. 1* and *Carex sp. nov. 2* each forming subclades within a polytomy (Figure 3.2). In Maximum Parsimony analysis, all *Carex sp. nov. 1* and *Carex sp. nov. 2* samples are grouped in a clade within *"C. cayouetteana"* , which is consistent with the results from statistical parsimony that suggest that both taxa are derived from *"C. cayouetteana"* as the coalescent theory predicts a derived condition for tip haplotypes and an ancestral condition for central haplotypes (Templeton et al. 1992). The three of them have unique morphological, geographical, ecological (see Chapter 2) and genetic traits (each of the species display an exclusive haplotype, *"C. cayouetteana"* , H3; *Carex sp. nov. 1* H4 and *Carex sp. nov. 2*, H7) that suggest that the Quaternary glaciations may have affected these taxa but not in an identical fashion. *Carex cayouetteana* and *Carex sp. nov. 2* are alpine taxa whilst *Carex sp. nov. 1* is boreal. During Pleistocene glaciations, the advance of the ice sheet might have isolated *"C. cayouetteana"* in separated refugia south of the glacial maximum, different from where *Carex sp. nov. 1* and *Carex sp. nov. 2* might have evolved. Some refugia in western North America have been suggested (Soltis et al. 1997) such as the Siskiyou-Klamath Mountains of northern California and southern Oregon (Whittaker 1961, Smith & Sawyer 1988). *Carex sp. nov. 1* has accumulated small nucleotide sequence differences in the loci investigated (e.g. 1 nucleotide change in chloroplast regions with respect to *"C. cayouetteana"*) whilst presents a great morphological, ecological and geographical differentiation. These could be due to a recent divergence that have been insufficient for a wider genetic differentiation. Such reduced genetic variation has been also related to strong directional selection, genetic drift and/or the founder effect in other plant species (Karron 1987). Moreover, some lineages could accumulate morphological traits faster than others not due to accumulated mutations in multiple genes, but based on one or few point mutations (Hedenäs & Eldenäs 2008) or even changes in the mechanism of gene regulation.

Similarly, *Carex sp. nov. 2* has high interspecific genetic variability (3 nucleotide changes from *"C. cayouetteana"*) and it is also readily distinguished by morphological traits. Due to a small effective population size during the Pleistocene glaciations, morphological traits could have been acquired faster (Vanderpoorten & Shaw 2010). In the western side of the Rocky Mountains, genotypes of *Carex sp. nov. 1* and *Carex sp. nov. 2* may have been better adapted to two different isolated portions of the species' geographic range, northern vs. southern California, during glaciation. A continuous geographic range was reestablished, albeit with the genetic discontinuity now present, reflecting glacial history (Soltis et al. 1997). Although *Carex sp. nov. 1* and *Carex sp. nov. 2* are not resolved in the nuclear analysis, their ecological requirements (boreal vs. alpine habitats) and allopatric distribution appear unbridgeable for an interbreeding.

Glaciations during the Quaternary had a major impact on the genetic architecture of plants and animals on western North America (Marr et al. 2008). The geographical distribution of *Carex sp. nov. 1* and *Carex sp. nov. 2* represents a disjunction between southern Oregon-northern California and Sierra Nevada-southern California (Figure 3.1), that is common to many closely related plant species with different life histories from herbaceous perennials to shrubs and trees (Soltis et al. 1997). The small distribution of *Carex sp. nov. 1* and *Carex sp. nov. 2* might be due to a process of adaptation to a specific successional stage, community or habitat type that restricts them to those ecologically appropriate areas (Purdy et al. 1994). *Carex sp. nov. 1* grows at low elevations for such latitude and *Carex sp. nov. 2* grows at high elevations in the southernmost latitude for the complex. Our analyses suggest that both species are derived from *"C. cayouetteana"* which grows between these ranges of latitude and altitude. Therefore, *Carex sp. nov. 1* and *Carex sp. nov. 2* could be considered taxa that had been adapted to new habitats.

3.5.4 Conclusions

As a result of the combined evidence derived from Chapters 2 and 3, the *C. capitata* complex is composed of five distinctive species. Likewise, the multidisciplinary study of the *C. backii* complex (sect. *Phyllostachyae*), has revealed that it was composed by three different species (Saarela & Ford 2001), *C. saximontana* Mack., *C. cordillerana* Saarela & Ford and *C. latebracteata* Waterf. Although all quantitative characters measured in the morphological study of *C. saximontana*, *C. cordillerana* overlapped, anatomic, micromorphologic and phytogeographic characters showed enough differences to recognise the three taxa at the species level which was later supported by molecular studies (Ford et al. 2009). Therefore, a multidisciplinary strategy is strongly suggested to avoid results' misinterpretations produced by relying exclusively on one type of data; taxonomic problems must be solved in the first place before conducting genetic analyses.

Finally, molecular results in the *C. capitata* complex could give some insights on plant species identification based on DNA barcoding, a useful tool for identifying animals that it is now being adapted for use in plants. Chouinard (2010) has developed a reference barcode database for the Cariceae of North America, north of Mexico, using the chloroplast gene *matK*. Two more regions, one coding (*atpF* - *atpH*) and one non-coding (*rsp16*), were also used for the phylogenetic analysis of the *C. capitata* complex, resulting in a complete resolution of its five species when combining it with morphological data. Further molecular studies, including the sixth species in the sect. *Capituligerae*, *C. oreophila*, and sister species, such as *C. obtusata*, should be conducted to test for the monophyly of the section.

3.6 Supporting Tables

Table 3.1: Primers used to PCR amplify and sequence the studied chloroplast regions used in phylogenetic analyses of the *C. capitata* complex, including the pilot study.

Region	Primer sequence (5'-3')	**Reference**
rps16_F	AAACGATGTGGTAGAAAGCAAC	Oxelman et al. 1997
rps16_R	AACATCAATTGCAACGATTCGATA	Oxelman et al. 1997
matK_2.1f_J	CCTGTCCATTTTGAAATCTTAG	(PWG)
matK_5r_J	GTTTTAGCACACGAAAGTCG	(PWG)
trnH_f	ACTGCCTTGATCCACTTGGC	Tate & Simpson 2003
psbA	CGAAGCTCCATCTACAAATGG	Tate & Simpson 2003
atpF	ACTCGCACACACTCCCTTTCC	Ki-Joong Kim, See Fazekas et al. 2008
atpH	GCTTTTATGGAAGCTTTAACAAT	Ki-Joong Kim, See Fazekas et al. 2008
psbK	TTAGCCTTTGTTTGGCAAG	Ki-Joong Kim, See Fazekas et al. 2008
psbI	AGAGTTTGAGAGTAAGCAT	Ki-Joong Kim, See Fazekas et al. 2008

Table 3.2: Summary of phylogenetics results obtained form the analyses of *rsp16*, *matK* and *atpF* - *atpH* sequences of the *C. capitata* complex, once outgroup sequences were excluded.

Chloroplast matrix	***rsp16***	***matK***	***atpF* - *atpH***
Length range bp	775-857	730-790	558-605
Aligned length bp	857	790	605
Number of variable sites	7	9	8
Informative indels	0	0	0

Number of variable vs. informative characters in the matrix 27/24

Table 3.3: Primers used to PCR amplify and sequence those nuclear regions used in phylogenetic analyses of the *C. capitata* complex.

Region	**Primer sequence (5'-3')**	**Reference**
Cko1-47	F: CCATCCATGGTATTTGACAGATT	Ohsako & Yamane (2008)
	R: ACAGGCGCTATAACAGACAAAAG	Ohsako & Yamane (2008)
CM25	F: CGGTGTTTGGTGGGCTGATA	King & Roalson (2009)
	R: CGCTTCTCCGTTTCTTTTGT	King & Roalson (2009)
CM01	F: CAAAGGAGAGAAATTCTCTG	King & Roalson (2009)
	R: GATCAGGTCATACCAAGTAT	King & Roalson (2009)
S245	F: GAAACAAAGGTGCCCCACT	Hipp et al. (2009)
	R: GTTGCAAGCGGGTCTAATTC	Hipp et al. (2009)
S082	F: TGAGAACCCTAGGCAGATGG	Hipp et al. (2009)
	R: GGGGAAACAAGGTCGTTTAGA	Hipp et al. (2009)

Table 3.4: Summary of phylogenetics results obtained from the analyses of CM25, Cko1-47, CM01, S082 and S245 sequences of the *C. capitata* complex.

Nuclear matrix	**CM25**	**Cko1-47**	**CM01**	**S082**	**S245**
Length range bp	61-97	119-125	198-228	345	128-147
Aligned length bp	97	125	228	345	147
Number of variables sites	2	3	3	7	2
Informative indels	0	0	1	3	0
Number of nucleotide additivities	0	0	0	0	0
Number of variable vs. informative characters in the matrix 12/5					

Table 3.5: Nucleotide positions deleted from the microsatellite sequences for the phylogenetic analyses of the *C. capitata* complex.

Region	**Positions removed**	**Characteristic**	**Total length**
CM01	82-97	Size differences in the nucleotide repetitions	345
	198-228	Missing data	
S082	211-216	Size differences in the nucleotide repetitions	228
Ck01-47	1-6	Missing data	125
S245	128-147	Missing data	147

Table 3.6: Haplotypes detected in statistical parsimony analyses of combined chloroplast regions of 68 samples of five species (*C. capitata*, *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1*, *Carex sp. nov. 2*) in the *C. capitata* complex. No missing data or outgroups were included in the analysis. The frequency of each haplotype (N) and point mutations for each chloroplast region are shown.

			Position																				
			atp					***matK***											***rps16***				
Samples	Haplotype	N	33	141	226	238	244	269	571	669	713	716	887	927	932	962	1080	1125	1249	1328	1337	1762	1834
C. arctogena	H1	15	C	G	G	A	C	C	A	A	A	G	C	T	T	G	A	A	C	G	C	T	G
C. capitata (Russia)	H2	3	C	G	T	G	C	T	A	C	C	G	C	G	T	A	G	G	C	G	C	C	G
"C. cayouetteana"	H3	17	C	G	G	A	T	C	A	A	C	G	C	G	C	G	A	A	C	G	C	T	G
Carex sp. nov. 1	H4	7	C	G	G	A	C	C	A	A	A	G	C	T	T	G	A	A	C	G	C	T	G
C. capitata (Europe + North America)	H5	20	A	G	G	A	C	C	T	A	C	A	C	G	T	G	A	A	C	T	G	T	G
C. capitata (Canada)	H6	3	A	G	G	A	C	C	T	A	C	A	C	G	T	G	A	A	T	T	G	T	G
Carex sp. nov. 2	H7	2	A	A	G	A	C	C	T	A	C	A	T	G	T	G	A	A	C	T	G	T	C

Table 3.7: Number of *C. capitata* specimens found in Argentinian major herbaria and Chilean from the southernmost region of South America. Number of specimens housed in each herbarium according to Index Herbariorum (http://sweetgum.nybg.org/ih/) is shown.

Herbarium acronyms	**No. of specimens in collection**	**No. *C. capitata* specimens**
BA	153.000	1
BAA	200.000	1
BAB	480.000	1
BCRU	20.000	0
HIP	20.000	2
SI	650.000	2
Total	**ca. 1.5 Million**	**7**

3.7 Supporting Figures

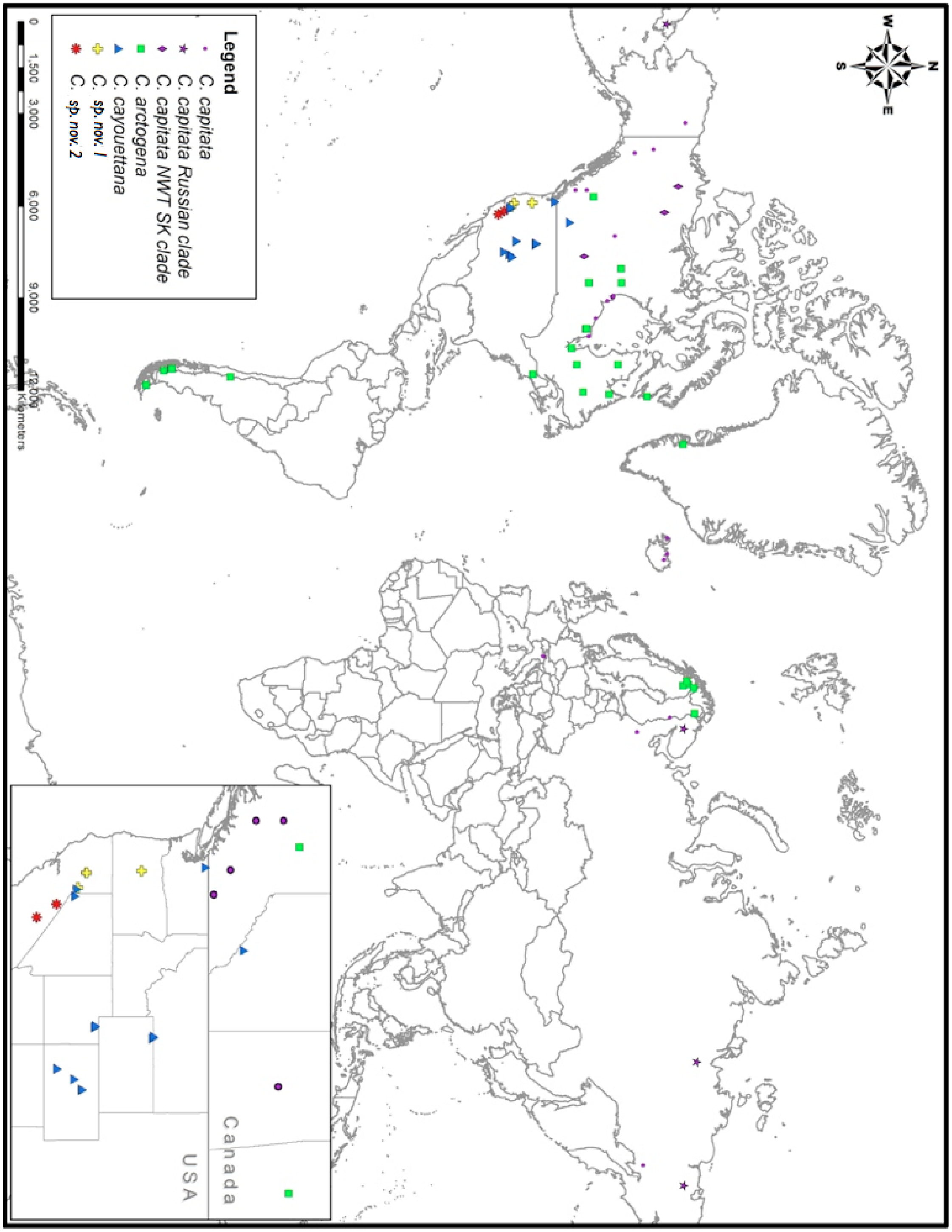


Figure 3.1: Distribution of *C. capitata*, *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2* herbarium specimens based on molecular data used in the phylogenetic analyses.

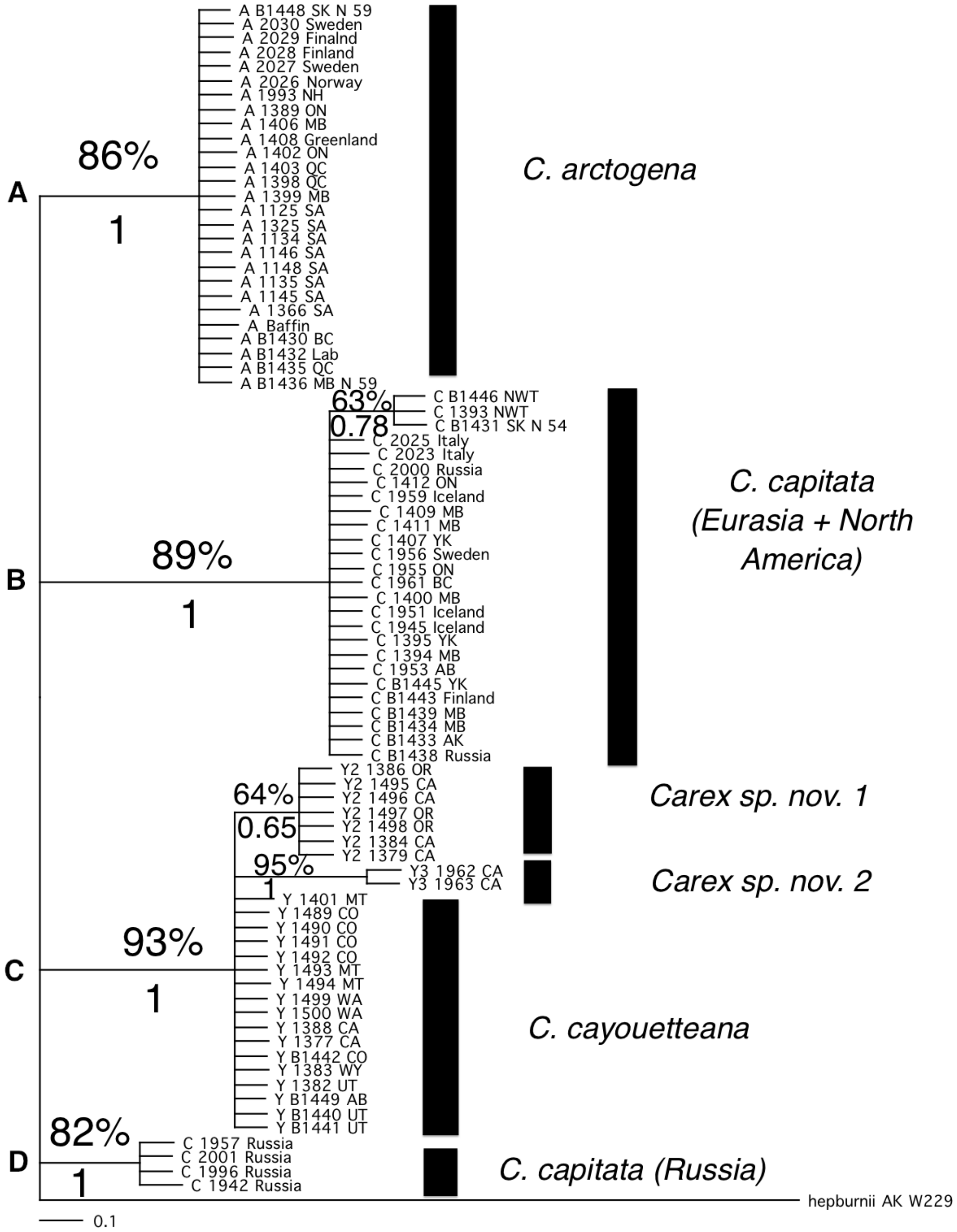


Figure 3.2: Majority rule consensus tree from the Bayesian analysis of three chloroplast regions (*matk*, *atpF* - *atpH* and *rsp16*), 84 samples of *C. capitata*, *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2* and *C. hepburnii* as outgroup. Vertical bars assemble samples from the same species and/or geographic area. Bootstrap values are given above branches and Posterior probabilities values below branches.

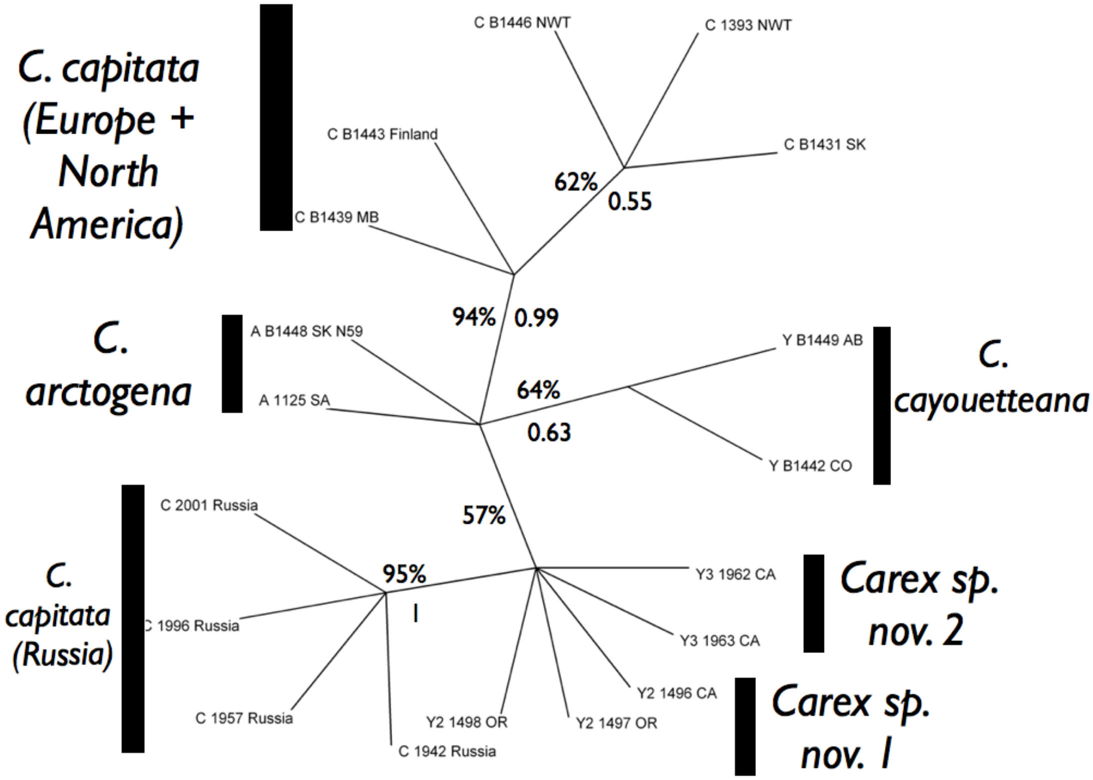


Figure 3.3: Majority rule consensus tree of the combined Bayesian analysis of five microsatellite loci and 18 individuals representing *C. capitata*, *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2*. Vertical bars assemble samples from the same species and/or geographic area. Bootstrap values are given above branches and Posterior probability values below branches..

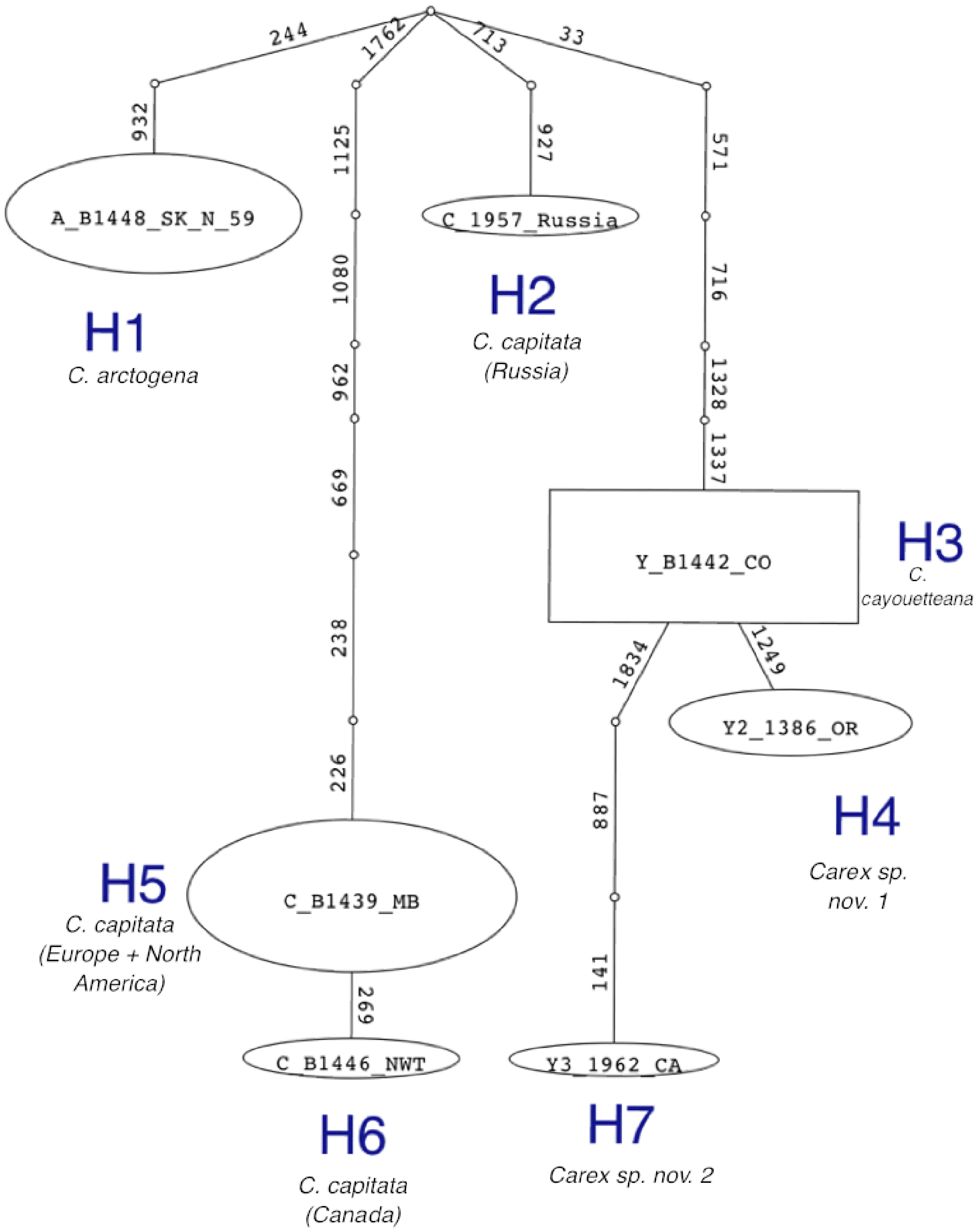


Figure 3.4: Parsimony network of 68 samples of *C. capitata*, *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2* for three combined chloroplast regions (*atp*F - *atp*H, *matk* and *rps16*). A 95% probability of parsimony was used. Gaps were treated as missing data. Bars represent single mutations between haplotypes whereas empty circles represent unsampled or extinct haplotypes. Haplotypes are displayed as ovals and squares, which correspond to haplotype frequency, calculated as the square root of the sample size.

Chapter 4

Conclusions

Given the extraordinary diversity in *Carex*, a multidisciplinary approach based on morphological and genetic studies, as well as a broad taxonomical sampling across the entire range of distribution when conducting systematics studies in sedges, are strongly suggested to understand the taxonomy in the family and to potentially reconstruct the origins of its species. Resolving its numerous taxonomical problems, firstly at a sectional level, would avoid result misinterpretations. Herein, two different studies, taxonomical and phylogeographical, were conducted in the *C. capitata* complex, both of them covering the whole distribution of the complex.

In Chapter 2, five species were revealed in the *C. capitata* complex: *C. capitata*, *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2*. Each taxon has unique morphological, ecological and geographical traits. Morphologically, a combination of characters is need to distinguish the different taxa in the complex which is typical for most sections in the genus (e.g. sect. *Phyllostachyae*, Ford et al. 2009; sect. *Phacocystis*, Standley et al. 2002). The best diagnostic characters to recognize these species are culm length, length of the staminate portion, pistillate scale length and shortest hyaline margin length. Geographically, *C. capitata* presents a circumpolar distribution whereas *C. arctogena* presents a bipolar distribution. *Carex cayouettena* is found in western North America until 50°N; *Carex sp. nov. 1* is restricted to southern Oregon and northern California; and *Carex sp. nov. 2* is a narrow endemic that occurs locally at high elevations in southern California. Ecologically, *C. capitata* grows in low alpine or wet tundra areas, in rich, calcareous and moist habitats such as fens, mires, bogs or meadows throughout its distribution; *C. arctogena* grows in arctic, high alpine or dry tundra areas in North America and Europe whereas in South America, it grows in bogs, wet meadows and in grasslands at low elevations (ca. 60 m) in the southernmost localities and at high elevation (ca. 2000 m) in the northern Patagonia; *"C. cayouetteana"* grows in alpine, moist tundra areas but also in meadows and rocky soils (from 2000 - 3800 m) in western North America; *Carex sp. nov. 1* grows in wet habitats such as meadows, mires, fens and open marshes at low elevations (ca. 1400 - 2300 m) throughout its distribution; *Carex sp. nov. 2* grows in unglaciated plateaus and wet banks at very high elevations (3400 - 3900 m) in southern California.

In Chapter 3, molecular analyses of the *C. capitata* complex are consistent with the results from Chapter 2, when five different taxa were revealed in the complex, being new species three of them. However, four main lineages appear in the complex: *C. arctogena*, some *C. capitata* samples from Russia (above 65°N), *C. capitata* s.l. and the ' *"C. cayouetteana"* ' complex. The lack of haplotype inferred as missing intermediates between the four main lineages in the statistical parsimony analysis (Figure 3.4), suggests that the split of the lineages is old. Therefore, it is believed that the four main lineages were affected to a certain extent independently by all major Pleistocene glaciations, as suggested for other species such as *Vaccinium uliginosum* (Alsos et al. 2005), *Saxifraga oppositifolia* (Abbott et al. 2000), *Dryas intgrifolia* (Tremblay & Schoen 1999) and other plant and animal species (Hewitt 2004).

As in other *Carex* sections, such as sect. *Phyllostachyae* (Ford et al. 2009) or sect. *Spirostachyae* (Escudero 2009), taxonomical studies and the analyses of multiple datasets have revealed previous unrecognised diversity, as discovered in *C. capitata* complex. Although the flora of North America, North of Mexico, is one of the best world known floras, the rate of ongoing floristics discoveries does not seem to taper off (Ertter 2000). Ford et al. (2009) predicted an increase in *Carex* species discovery, particularly in western North America, which had a discovery rate of two new species per year in the past twenty years.

Present-day distribution of the taxa in the complex not only reflect their habitat preferences and the outcome of competition, but also the consequences of their postglaciation recolonization process as suggested by Koch et al. 2006. *Carex capitata* s.l. presents a circumpolar distribution, occurring throughout northern North America, Russia, and northern and central Europe, whereas *C. arcotgena* present an amphi-Atlantic distribution in the northern Hemisphere. Their low genetic diversity suggests that these taxa have migrated recently across the Atlantic, even if they lack of a seemingly obvious mechanism to promote long-distance dispersal, as it is suggested for other arctic plants (Dahl 1963; Brochmann 2003; Alsos et al. 2007; Schönswetter et al. 2008). Amphi-Atlantic disjuctions could be explained by different causes such as drifting ice, icebergs (Nordal 1987) or birds (Fridriksson & Sigurdsson 1969), such dispersal vectors that could facilitate plant colonization. This trans-Atlantic distribution pattern is repeated in various species such as *Cerastium nigrescens* (Hagen et al. 2001), *Lychnis alpina* (Haraldsen & Wesenberg 1993), *Phippsia algida* (Aares et al. 2000) or *Carex bigellowii* Torr. ex Schwein. (Schönswetter et al. 2008).

Although in the morphometric study conducted in Chapter 2, any morphological differences were found between the two main lineages of *C. capitata* found in Chapter 3, it can be due to the lack of specimens from that region as well as the characters currently used. Different morphometric studies using more characters, and other kind of studies, such as an anatomical one, might reveal that both lineages correspond to separate species.

The Quaternary glaciations may have affected severely arctic species distributions, reducing their population sizes and imposing genetic bottlenecks, leading to the capture of different genotypes in respective isolated pockets (Soltis et al. 1997) such as Beringia, High Arctic Archipelago or Greenland. Arctic plant species might have expanded their ranges as the climate warmed rapidly after the Last Glacial Maximum, 24-18 thousand years ago (Hewitt 2004), recolonizing once-glaciated areas and exhibiting now a geographically structured genetic diversity (Alsos et al. 2005). *Carex capitata* samples from the Alps present no morphological or genetic differences from those found further North, supporting the hypothesis of a recent colonization as well. Other studies in *Carex* species from the Alps, such as *C. atrofusca* (Schönswetter et al. 2006) also suggested migration as the origin for alpine populations.

Carex arctogena samples from South America present no statistically significant morphological differences with those in the northern Hemisphere, contrary to what was stated by Roivanen (1954) when he described *C. antarctogena*. The molecular data support the synonymy of both taxa and suggest a recent dispersal by a direct jump from the northern Hemisphere. Popp et al. (2011) have also suggested a single dispersal event by bird to explain the distribution of crowberries (*Empetrum*) in South America.

Taxonomical and molecular analyses have revealed that *Carex sp. nov. 1* and *Carex sp. nov. 2* are two endemic species to the western North America. Statistical parsimony results suggest a pattern of diversification of both taxa from *"C. cayouetteana"*, into a region with heterogeneous habitats such as western North America (Smith & Sawyer 1988).

Contrary to what might have happened with the *C. capitata* and *C. arctogena* populations in Europe where mountain chains are East- West oriented, the advance and the retreat of the ice sheet during glacial periods could have had a less severe effect shifting species latitudinally during climate changes, due to the continuous mountains chains in a North-South direction (Albach et al. 2006) and to the vast area available below the ice sheet in North America. *Carex sp. nov. 1* might have adapted to boreal habitats while *Carex sp. nov. 2* might have been isolated in tundra habitats in southern California. Population fragmentation during glacial periods may have led to the formation of new species (Abbott & Brochmann 2003) and their small population sizes could have led to the acquisition of morphological traits at a faster rate than in large populations (Vanderpoorten & Shaw 2010). A similar pattern appears to have occurred in the *C. aquatilis* Wahlenb. - *C. lenticularis* Michx. group (section *Phagocystis*, Dragon & Barrington 2009) where species ecological specialization and the Quaternary geological history of North America, had split the group in different lineages.

Although *"C. cayouetteana"* appears in a polytomy in the results from phylogenetic analyses using cpDNA, microsatellite loci and morphological characters gives enough evidence to consider this taxon as unique and monophyletic, being genetically isolated form *Carex sp. nov. 1* and *Carex sp. nov. 2*. The lack of unique characters in chloroplast data set of *"C. cayouetteana"* could be due to e.g. insufficient phylogenetic signal or incomplete lineage sorting, as suggested for other *Carex* species (e.g. Hipp et al. 2006; Roalson & Friar 2008; King & Roalson 2008).

Other phylogeographical studies conducted in *Carex* species have shown different phylogeographical patterns, to what it has been seen in the *C. capitata* complex. The distribution of the coastal *C. macrocephala* Willd. ex Spreng. was not disrupted by glacial events during the Quaternary (King et al. 2009), and it has therefore not undergone through any significant bottleneck since then, unlike arctic-alpine species where geographical isolation and recolonization of once-glaciated areas after the retreat of the ice sheet, have genetically affected these taxa.

The two avenues of research presented here, a taxonomical study first, and phylogenetic analyses later, are suggested to truly understand phylogeographical relationships in *Carex*. Morphological convergence and parallelism in *Carex* species (Starr & Ford 2009) as well as a regionally species sampling, rather than a global perspective, have hampered the reconstruction of its evolutionary lineages and the understanding of how a single genus has become so diverse (Dragon & Barrington 2009).

Once the taxonomy of a species group is solved and accurate phylogenies are made, estimation of lineages divergence could be inferred. Although fossil evidence in *Carex* is scarce (Smith et al. 2009), attempts to date speciation events such as that conducted by Dragon & Barrington (2009) could facilitated the understanding of evolutionary processes in the genus.

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Appendix A

Table A.1: Kruskal-Wallis test. Chi-square value, degrees of freedom (df) and P-value are shown for each variable.

Variable	Kruskal-Wallis chi-square	df	p- value
CLMHT	76.238	4	1.090e-15
CLMH	78.0187	4	4.577e-16
LEAFL	44.7911	4	4.394e-09
CULMW	29.9697	4	4.964e-06
LEAFW	6.9523	4	0.1384
INFLOW	44.2021	4	5.825e-09
MSPL	59.2884	4	4.093e-12
GLUMH	28.639	4	9.255e-06
GLUMHC	45.1364	4	3.725e-09
INFLOL	54.9027	4	3.405e-11
FPPL	17.9482	4	0.001263
FSCL	28.635	4	9.272e-06
FSCW	33.4419	4	9.698e-07
FSCWL	10.4719	4	0.03319
PERIGL	32.1547	4	1.779e-06
PERBKL	23.7847	4	8.822e-05
PERIGW	53.2796	4	7.448e-11
PERIWD	13.2667	4	0.01004
ACHW	3.1064	4	0.5402
ACHL	14.5449	4	0.005745
MSCL	30.7368	4	3.464e-06
MSCW	12.7065	4	0.01280

Table A.2: Correlation matrix for 22 continuous variables used in the morphometric study.

	CLMHT	CLMH	LEAFL	CULMW	LEAFW	INFLOW	MSPL	GLUMH	GLUMHC	INFLOL	FPPL
CLMHT	1,000	0,948	0,750	0,037	0,010	0,055	0,341	0,185	0,342	0,373	0,170
CLMH	0,948	1,000	0,731	0,014	0,007	0,076	0,385	0,172	0,337	0,400	0,177
LEAFL	0,750	0,731	1,000	0,051	0,067	0,217	0,190	0,056	0,203	0,266	0,238
CULMW	0,037	0,014	0,051	1,000	0,210	0,103	0,264	0,183	0,059	0,349	0,210
LEAFW	0,010	0,007	0,067	0,210	1,000	0,106	0,096	0,120	0,037	0,142	0,108
INFLOW	0,055	0,076	0,217	0,103	0,106	1,000	0,016	0,127	0,108	0,192	0,482
MSPL	0,341	0,385	0,190	0,264	0,096	0,016	1,000	0,089	0,227	0,910	0,215
GLUMH	0,185	0,172	0,056	0,183	0,120	0,127	0,089	1,000	0,566	0,147	0,202
GLUMHC	0,342	0,337	0,203	0,059	0,037	0,108	0,227	0,566	1,000	0,224	0,135
INFLOL	0,373	0,400	0,266	0,349	0,142	0,192	0,910	0,147	0,224	1,000	0,521
FPPL	0,170	0,177	0,238	0,210	0,108	0,482	0,215	0,202	0,135	0,521	1,000
FSCL	0,015	0,033	0,063	0,335	0,124	0,274	0,175	0,007	0,130	0,263	0,214
FSCW	0,096	0,033	0,017	0,168	0,137	0,059	0,293	0,171	0,133	0,303	0,180
FSCWL	0,007	0,029	0,028	0,226	0,022	0,020	0,171	0,013	0,093	0,187	0,011
PERIGL	0,043	0,053	0,099	0,151	0,156	0,375	0,067	0,120	0,058	0,060	0,080
PERBKL	0,044	0,017	0,106	0,035	0,033	0,470	0,149	0,018	0,029	0,059	0,177
PERIGW	0,065	0,078	0,131	0,173	0,088	0,469	0,127	0,193	0,237	0,208	0,165
PERIWD	0,027	0,050	0,032	0,076	0,058	0,145	0,202	0,083	0,020	0,163	0,063
ACHW	0,062	0,026	0,052	0,069	0,102	0,227	0,034	0,104	0,122	0,045	0,015
ACHL	0,002	0,008	0,024	0,003	0,143	0,100	0,037	0,121	0,034	0,000	0,009
MSCL	0,218	0,245	0,234	0,073	0,109	0,351	0,271	0,054	0,190	0,378	0,292
MSCW	0,079	0,142	0,065	0,191	0,139	0,027	0,369	0,094	0,001	0,359	0,009

Table A.3: Correlation matrix for 22 continuous variables used in the morphometric study (continuation)

	FSCL	FSCW	FSCWL	PERIGL	PERBKL	PERIGW	PERIWD	ACHW	ACHL	MSCL	MSCW
CLMHT	0,015	0,096	0,007	0,043	0,044	0,065	0,027	0,062	0,002	0,218	0,079
CLMH	0,033	0,033	0,029	0,053	0,017	0,078	0,050	0,026	0,008	0,245	0,142
LEAFL	0,063	0,017	0,028	0,099	0,106	0,131	0,032	0,052	0,024	0,234	0,065
CULMW	0,335	0,168	0,226	0,151	0,035	0,173	0,076	0,069	0,003	0,073	0,191
LEAFW	0,124	0,137	0,022	0,156	0,033	0,088	0,058	0,102	0,143	0,109	0,139
INFLOW	0,274	0,059	0,020	0,375	0,470	0,469	0,145	0,227	0,100	0,351	0,027
MSPL	0,175	0,293	0,171	0,067	0,149	0,127	0,202	0,034	0,037	0,271	0,369
GLUMH	0,007	0,171	0,013	0,120	0,018	0,193	0,083	0,104	0,121	0,054	0,094
GLUMHC	0,130	0,133	0,093	0,058	0,029	0,237	0,020	0,122	0,034	0,190	0,001
INFLOL	0,263	0,303	0,187	0,060	0,059	0,208	0,163	0,045	0,000	0,378	0,359
FPPL	0,214	0,180	0,011	0,080	0,177	0,165	0,063	0,015	0,009	0,292	0,009
FSCL	1,000	0,402	0,376	0,138	0,172	0,292	0,079	0,109	0,045	0,150	0,159
FSCW	0,402	1,000	0,222	0,059	0,086	0,011	0,130	0,008	0,129	0,120	0,280
FSCWL	0,376	0,222	1,000	0,240	0,011	0,159	0,114	0,113	0,077	0,011	0,223
PERIGL	0,138	0,059	0,240	1,000	0,512	0,406	0,218	0,334	0,173	0,210	0,057
PERBKL	0,172	0,086	0,011	0,512	1,000	0,325	0,142	0,183	0,147	0,142	0,114
PERIGW	0,292	0,011	0,159	0,406	0,325	1,000	0,039	0,324	0,064	0,438	0,063
PERIWD	0,079	0,130	0,114	0,218	0,142	0,039	1,000	0,090	0,047	0,045	0,057
ACHW	0,109	0,008	0,113	0,334	0,183	0,324	0,090	1,000	0,487	0,227	0,074
ACHL	0,045	0,129	0,077	0,173	0,147	0,064	0,047	0,487	1,000	0,095	0,001
MSCL	0,150	0,120	0,011	0,210	0,142	0,438	0,045	0,227	0,095	1,000	0,231
MSCW	0,159	0,280	0,223	0,057	0,114	0,063	0,057	0,074	0,001	0,231	1,000

Table A.4: Summary statistics for the morphometric analysis of *C. arctogena*. Abbreviations: n = sample size; sd = standard deviation; mad = median absolute deviation; se= standard error.

Variable	n	mean	sd	median	trimmed	mad	min	max	range	skew	kurtosis	se
CLMHT	35	204.03	52.16	190.5	200.03	45.29	125.9	335.05	209.15	0.68	-0.29	8.82
CLMH	35	168.89	44.74	169.0	165.20	38.62	100.7	280.05	179.35	0.64	-0.09	7.56
LEAFL	35	154.64	47.90	145.5	150.61	52.34	90.5	298.70	208.20	0.87	0.32	8.10
CULMW	35	0.78	0.15	0.8	0.78	0.15	0.5	1.10	0.60	0.03	-0.97	0.03
LEAFW	35	0.62	0.12	0.6	0.61	0.15	0.4	1.00	0.60	0.65	0.98	0.02
INFLOW	35	3.83	0.39	3.8	3.83	0.44	2.9	4.70	1.80	-0.02	-0.46	0.07
MSPL	35	2.12	0.68	2.0	2.09	0.74	1.2	3.70	2.50	0.46	-0.95	0.12
GLUMH	35	0.97	0.49	0.9	0.88	0.30	0.4	2.60	2.20	1.70	2.56	0.08
GLUMHC	35	0.40	0.17	0.4	0.40	0.15	0.1	1.00	0.90	0.98	2.64	0.03
INFLOL	35	7.34	1.16	7.4	7.30	1.19	5.2	9.80	4.60	0.41	-0.64	0.20
FPPL	35	4.46	0.64	4.5	4.43	0.74	3.5	6.00	2.50	0.34	-0.51	0.11
FSCL	35	2.18	0.29	2.1	2.17	0.15	1.4	3.00	1.60	0.43	1.15	0.05
FSCW	35	1.77	0.34	1.8	1.77	0.30	1.0	2.60	1.60	0.11	0.04	0.06
FSCWL	35	0.68	0.29	0.6	0.66	0.15	0.1	1.70	1.60	1.22	2.79	0.05
PERIGL	35	2.65	0.45	2.7	2.72	0.44	1.5	3.20	1.70	-1.19	0.81	0.08
PERBKL	35	1.13	0.23	1.2	1.12	0.30	0.7	1.80	1.10	0.50	0.80	0.04
PERIGW	35	1.50	0.19	1.5	1.50	0.15	1.0	2.00	1.00	-0.03	0.58	0.03
PERIWD	35	0.82	0.19	0.8	0.82	0.15	0.5	1.30	0.80	0.26	-0.41	0.03
ACHW	35	1.18	0.18	1.2	1.18	0.15	0.7	1.70	1.00	0.07	1.34	0.03
ACHL	35	1.61	0.15	1.6	1.60	0.15	1.4	1.90	0.50	0.61	-0.55	0.03
MSCL	35	1.86	0.35	1.8	1.86	0.30	1.0	2.80	1.80	0.17	0.41	0.06
MSCW	35	1.12	0.21	1.1	1.11	0.15	0.7	1.60	0.90	0.40	-0.36	0.04

Table A.5: Summary statistics for the morphometric analysis of *C. capitata*. Abbreviations: n = sample size; sd = standard deviation; mad = median absolute deviation; se= standard error.

Variable	n	mean	sd	median	trimmed	mad	min	max	range	skew	kurtosis	se
CLMHT	38	296.45	70.50	290.05	293.55	70.42	150.05	490.05	340.00	0.49	0.12	11.44
CLMH	38	272.10	82.37	270.70	268.12	66.72	120.05	490.05	370.00	0.53	-0.14	13.36
LEAFL	38	205.92	50.00	210.38	203.87	43.70	115.05	360.05	245.00	0.64	0.70	8.11
CULMW	38	0.75	0.09	0.70	0.74	0.15	0.60	1.00	0.40	0.45	0.46	0.01
LEAFW	38	0.59	0.19	0.60	0.57	0.15	0.40	1.50	1.10	2.78	10.06	0.03
INFLOW	38	4.41	0.48	4.45	4.43	0.52	3.30	5.40	2.10	-0.14	-0.50	0.08
MSPL	38	1.95	0.65	1.85	1.93	0.74	0.80	3.50	2.70	0.25	-0.77	0.11
GLUMH	38	0.56	0.62	0.50	0.46	0.59	0.01	2.25	2.24	1.39	1.24	0.10
GLUMHC	38	0.19	0.15	0.15	0.18	0.21	0.01	0.50	0.49	0.21	-1.44	0.02
INFLOL	38	7.52	1.20	7.40	7.51	1.33	5.50	10.30	4.80	0.16	-0.90	0.19
FPPL	38	4.78	0.89	4.60	4.71	0.67	2.70	7.20	4.50	0.74	0.92	0.14
FSCL	38	2.12	0.25	2.20	2.14	0.22	1.50	2.50	1.00	-0.72	0.03	0.04
FSCW	38	1.43	0.21	1.40	1.43	0.15	0.80	1.80	1.00	-0.49	0.60	0.03
FSCWL	38	0.61	0.16	0.60	0.60	0.15	0.30	1.00	0.70	0.16	-0.28	0.03
PERIGL	38	2.99	0.45	3.10	3.04	0.30	1.80	3.60	1.80	-1.09	0.69	0.07
PERBKL	38	1.28	0.24	1.30	1.29	0.30	0.80	1.70	0.90	-0.39	-0.74	0.04
PERIGW	38	1.79	0.21	1.80	1.79	0.30	1.30	2.20	0.90	-0.30	-0.52	0.03
PERIWD	38	0.94	0.20	1.00	0.94	0.22	0.50	1.30	0.80	-0.26	-0.86	0.03
ACHW	38	1.21	0.13	1.20	1.21	0.15	1.00	1.50	0.50	0.08	-0.69	0.02
ACHL	38	1.72	0.21	1.70	1.73	0.15	1.10	2.10	1.00	-0.86	0.82	0.03
MSCL	38	2.19	0.26	2.20	2.19	0.15	1.60	2.90	1.30	0.17	0.46	0.04
MSCW	38	1.02	0.23	1.00	1.02	0.30	0.60	1.50	0.90	0.16	-0.81	0.04

Table A.6: Summary statistics for the morphometric analysis of *“C. cayouetteana”*. Abbreviations: n = sample size; sd = standard deviation; mad = median absolute deviation; se= standard error.

Variable	n	mean	sd	median	trimmed	mad	min	max	range	skew	kurtosis	se
CLMHT	28	204.90	30.44	205.23	205.15	22.24	142.72	260.50	117.78	-0.09	-0.25	5.75
CLMH	28	178.29	39.83	182.12	177.94	51.32	116.00	260.05	144.05	-0.04	-1.16	7.53
LEAFL	28	157.49	21.11	160.05	157.93	25.39	115.05	195.70	80.65	-0.15	-1.00	3.99
CULMW	28	0.89	0.12	0.90	0.89	0.15	0.60	1.10	0.50	-0.33	-0.34	0.02
LEAFW	28	0.64	0.13	0.60	0.63	0.15	0.40	0.90	0.50	0.29	-0.62	0.02
INFLOW	28	4.44	0.61	4.35	4.39	0.52	3.50	6.10	2.60	1.07	0.61	0.11
MSPL	28	3.22	1.40	3.25	3.13	1.11	0.90	6.65	5.75	0.50	0.05	0.27
GLUMH	28	0.53	0.36	0.50	0.53	0.52	0.00	1.00	1.00	-0.08	-1.43	0.07
GLUMHC	28	0.23	0.16	0.25	0.23	0.22	0.00	0.50	0.50	0.07	-1.27	0.03
INFLOL	28	9.11	1.63	9.40	9.09	1.56	6.10	12.80	6.70	0.04	-0.63	0.31
FPPL	28	5.00	0.80	5.00	4.97	0.96	3.90	6.40	2.50	0.23	-1.34	0.15
FSCL	28	2.43	0.24	2.45	2.42	0.22	1.90	3.00	1.10	0.09	0.27	0.05
FSCW	28	1.73	0.27	1.65	1.72	0.22	1.10	2.42	1.32	0.27	0.09	0.05
FSCWL	28	0.77	0.25	0.77	0.78	0.22	0.10	1.30	1.20	-0.17	0.38	0.05
PERIGL	28	2.80	0.38	2.90	2.84	0.30	1.50	3.40	1.90	-1.45	2.98	0.07
PERBKL	28	1.23	0.22	1.20	1.20	0.15	0.90	1.90	1.00	1.44	1.95	0.04
PERIGW	28	1.96	0.31	1.90	1.99	0.30	1.20	2.50	1.30	-0.59	0.34	0.06
PERIWD	28	0.81	0.29	0.75	0.80	0.37	0.30	1.80	1.50	1.13	2.59	0.05
ACHW	28	1.23	0.22	1.20	1.22	0.15	0.60	1.80	1.20	0.16	2.34	0.04
ACHL	28	1.59	0.24	1.60	1.59	0.15	1.00	2.30	1.30	0.32	1.38	0.05
MSCL	28	2.28	0.30	2.20	2.26	0.30	1.80	3.00	1.20	0.47	-0.31	0.06
MSCW	28	1.16	0.27	1.13	1.16	0.19	0.60	1.90	1.30	0.28	0.75	0.05

Table A.7: Summary statistics for the morphometric analysis of *Carex sp. nov. 1.* Abbreviations: n = sample size; sd = standard deviation; mad = median absolute deviation; se= standard error.

Variable	n	mean	sd	median	trimmed	mad	min	max	range	skew	kurtosis	se
CLMHT	24	354.27	72.37	355.30	353.44	68.13	225.50	540.0	314.50	0.22	0.03	14.77
CLMH	24	347.73	75.68	353.50	347.85	70.79	193.05	540.0	346.95	0.10	0.16	15.45
LEAFL	24	206.97	41.68	210.05	208.14	58.93	133.05	270.2	137.15	-0.15	-1.36	8.51
CULMW	24	0.88	0.08	0.90	0.88	0.15	0.70	1.0	0.30	0.05	-1.02	0.02
LEAFW	24	0.65	0.12	0.60	0.64	0.15	0.50	0.9	0.40	0.65	-0.63	0.02
INFLOW	24	3.86	0.43	3.90	3.85	0.52	3.20	4.6	1.40	0.09	-1.27	0.09
MSPL	24	5.36	2.00	5.40	5.24	1.63	2.00	10.5	8.50	0.48	-0.02	0.41
GLUMH	24	0.39	0.52	0.10	0.31	0.13	0.01	1.8	1.79	1.11	0.00	0.11
GLUMHC	24	0.09	0.10	0.10	0.08	0.13	0.01	0.3	0.29	0.82	-0.56	0.02
INFLOL	24	11.25	2.33	11.04	11.15	2.23	6.80	16.9	10.10	0.34	-0.15	0.48
FPPL	24	5.08	0.83	5.30	5.04	0.82	3.90	6.9	3.00	0.18	-0.91	0.17
FSCL	24	2.18	0.33	2.20	2.20	0.22	1.20	2.7	1.50	-0.83	1.25	0.07
FSCW	24	1.74	0.24	1.75	1.73	0.30	1.40	2.2	0.80	0.11	-1.23	0.05
FSCWL	24	0.65	0.24	0.60	0.66	0.15	0.20	1.0	0.80	-0.12	-0.86	0.05
PERIGL	24	2.35	0.45	2.35	2.37	0.52	1.50	3.1	1.60	-0.30	-0.92	0.09
PERBKL	24	1.01	0.22	1.00	1.01	0.30	0.70	1.4	0.70	0.11	-1.09	0.04
PERIGW	24	1.66	0.17	1.70	1.66	0.15	1.20	2.2	1.00	0.42	3.04	0.04
PERIWD	24	0.77	0.18	0.75	0.78	0.22	0.40	1.0	0.60	-0.08	-1.20	0.04
ACHW	24	1.16	0.16	1.20	1.18	0.07	0.50	1.4	0.90	-2.52	8.14	0.03
ACHL	24	1.55	0.23	1.55	1.56	0.22	1.00	2.0	1.00	-0.17	-0.27	0.05
MSCL	24	2.24	0.29	2.20	2.24	0.15	1.60	2.9	1.30	0.22	0.08	0.06
MSCW	24	1.23	0.24	1.20	1.22	0.30	0.80	1.8	1.00	0.43	-0.17	0.05

Table A.8: Summary statistics for the morphometric analysis of *Carex sp. nov. 2*. Abbreviations: n = sample size; sd = standard deviation; mad = median absolute deviation; se= standard error.

Variable	n	mean	sd	median	trimmed	mad	min	max	range	skew	kurtosis	se
CLMHT	6	158.03	24.75	147.53	158.03	9.25	140.50	205.05	64.55	1.01	-0.74	10.10
CLMH	6	110.78	22.56	112.53	110.78	26.39	83.97	140.05	56.08	0.03	-2.01	9.21
LEAFL	6	113.08	19.27	114.03	113.08	18.35	85.00	140.05	55.05	-0.07	-1.55	7.87
CULMW	6	0.83	0.12	0.85	0.83	0.15	0.70	1.00	0.30	0.04	-1.88	0.05
LEAFW	6	0.58	0.17	0.55	0.58	0.07	0.40	0.90	0.50	0.80	-0.86	0.07
INFLOW	6	3.07	0.69	2.70	3.07	0.22	2.50	4.00	1.50	0.51	-1.94	0.28
MSPL	6	3.05	1.03	2.85	3.05	0.82	2.20	4.90	2.70	0.77	-1.06	0.42
GLUMH	6	1.35	0.74	1.45	1.35	0.59	0.01	2.00	1.99	-0.77	-0.99	0.30
GLUMHC	6	0.27	0.18	0.30	0.27	0.22	0.01	0.50	0.49	-0.20	-1.76	0.07
INFLOL	6	7.65	0.87	8.00	7.65	0.52	6.20	8.50	2.30	-0.62	-1.48	0.36
FPPL	6	3.70	0.84	4.00	3.70	0.00	2.00	4.20	2.20	-1.33	-0.13	0.34
FSCL	6	1.93	0.12	1.95	1.93	0.15	1.80	2.10	0.30	0.04	-1.88	0.05
FSCW	6	1.53	0.35	1.46	1.53	0.43	1.15	2.00	0.85	0.23	-1.94	0.14
FSCWL	6	0.60	0.13	0.60	0.60	0.00	0.40	0.80	0.40	0.00	-0.92	0.05
PERIGL	6	2.55	0.64	2.40	2.55	0.22	2.00	3.80	1.80	1.09	-0.48	0.26
PERBKL	6	0.97	0.35	0.95	0.97	0.22	0.60	1.60	1.00	0.72	-0.96	0.14
PERIGW	6	1.50	0.26	1.50	1.50	0.15	1.10	1.90	0.80	0.00	-1.15	0.11
PERIWD	6	0.75	0.14	0.80	0.75	0.07	0.50	0.90	0.40	-0.76	-0.95	0.06
ACHW	6	1.23	0.35	1.10	1.23	0.15	1.00	1.90	0.90	1.05	-0.63	0.14
ACHL	6	1.82	0.43	1.75	1.82	0.30	1.40	2.60	1.20	0.81	-0.89	0.17
MSCL	6	2.20	0.20	2.20	2.20	0.15	1.90	2.50	0.60	0.00	-1.29	0.08
MSCW	6	1.04	0.10	1.04	1.04	0.07	0.90	1.20	0.30	0.10	-1.45	0.04

A.1 Studied specimens used in Chapter 2

Table A.10: Voucher data for all *C. capitata* (C), *C. arctogena* (A), *"C. cayouetteana"* (Y), *Carex sp. nov. 1* (Y2) and *Carex sp. nov. 2* (Y3) specimens used in the morphological analysis. DNA number associated with each specimen is indicated when applicable. Specimens used for micromorphology are in bold.

DNA No.	**Sheet No.**	**Sp.**	**Locality**	**Coor.**	**Elev.**	**Coll. date**	**Voucher specimen**
	T038	C	Russia: Chita region, between the rivers Nerchei and Kuengoi, near the river Gorbitsa, at the mouth of the river Gorbichikana	ca. 52.0591666667, 113.573611111		10 July 1911	V. Sukachev s.n. (DAO-142005)
1942	T034	C	Russia: Yakutia (presently named Sakha Republic). Bulunsk region. Severnoe Verhojané. Mouth of river Kusagan-Uu, confluent of river Altan, upstream of frazil.	ca. 69°25'N 130°40'E		25 June 1960	B. Yurtsev s.n. (DAO-257437)
1957	T037	C	Russia: Eastern part of Chukotski peninsula, middle branch of the river Utaveem (left bank) and its confluent, the river Yararmoveem, gentle south-west slope of flood-land terrace.	ca. 66°N 171°E		27 July 1970	U.P. Kozhevnikov, A.A. Nechaev, B.A. Yurtsev s.n. (DAO-139887)
	T444	C	Russia: Taymyr, river Pyasina, 6km higher of Kungudajar, grassy tundra, bottom part of gully slope	ca. 71°N 86°E		21 August 1982	U.P. Kozhevnikov s.n. (CAN-490439)
	T450	C	Russia: Vologodsk (presently Komi Republic), Ust-Sisol'sk (presently named Syktyvkar) region, peat bog near Poztykeres village	ca. 61°34'N 51°32'E		21 June 1909	V.D. Andreev s.n. (H-1037137)
	T448	C	Russia: Irkutsk, Balagansk region, peat bog near Bazheevsky village	ca. 55°N, 103°E		19 June 1905	I. Maltsev s.n. (GH-2386)
	T095	C	Iceland: Egilsstair Vopnafiri			4 August 1895	S. Stefnsson I 256 (ICEL-VR-04088)
1951	T084	C	Iceland: Dalfjall Mývatnssveit	ca. 65.657, -16.815	460 m	21 August 1974	E. Einarsson s.n. (ICEL-VR-04073)
1945	T085	C	Iceland: Hrísey Eyjafirø	ca. 66.000000, -18.383333		12 August 1967	A. Garøarsson s.n. (VR-04078)
	T130	C	Finland: Lapponia enontekiensis	ca. 68.5°N, 26°W		9 August 1923	I. Montell s.n. (M-0151944)
	T048	C	Finland: Tulijoki, Puolanka, Kainuu	ca. 64.868611111, 27.6711111		18 July 1933	L. Lahtonen s.n. (DAO-257434)
B1443	T315	C	Finland: Fennia, Ls. Kuusamo, Liikasenvaara	ca. 66.36667, 29.5333		9 August 1962	T. Ulvinen s.n. (CAN-276804)

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DNA No.	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
	T124	C	Norway: Finnmark, Kautokeino-N, Mieron-N, Moor	69.5°N, 23.5°W	340 m	23 August 1967	(M-0151938)
	T162	C	Norway: Finnmark, Sr-Varanger, Bugynes, ca. 2.5 km W of Bugynes-Vaer	ca. 69.9727778, 29.5727778	ca. 20 m	3 August 1977	H. Toivonen s.n. (H-1471326)
	T125	C	Sweden: Jämtland, Östersund-SE, Nyhem NW Röringen Ufer	63°0'N, 15°30'W	280 m	4 July 1977	(M-0151939)
1956	T168	C	Sweden, Torne Lappmark: Jukkasjärvi parish, Lake Torneträsk District, Abisko, marshy ground south of the railway station	68° - 68°34'N, 18° - 20°30'E	400 m	6 August 1958	C.G. Alm s.n. (H-1226056)
	T131	C	Germany: Bayern, Oberbayern, Frstenfeldbruck, Haspelmoor	ca. 48.2225, 11.09388889		June 1872	Hller s.n. (M-0151918)
	T132	C	Germany: Bayern, Oberbayern, Wolfratshausen, Deininger Moor	ca. 47.9166667, 11.4166667		May 1867	Ohmller s.n. (M-0151920)
	T149	C	Germany: Oberschwaben, Wurzachen Ried	ca. 47.9, 9.866667		May 1880	Schänzle s.n. (M-0151921)
	T138	C	Italy: South Tyrol, Seiseralpe, ca. 300 m NNW of Giogo-Joches	ca. 46.4305556, 11.1688889	1980 m	25 July 1959	H. Roessler 2519 (M-0151925)
	T142	C	Austria: Tyrol, Innsbruck-N, Seefeld i.T.	ca. 47.306667, 11.29416667	1180 m	26 July 1958	(M-0151923)
	T267	C	Canada, Northwest Territories: Aubry Lake, District of Mackenzie, N warm, west side, at junction of two seismic lines	67°20'N, 126°25'W		17 July 1976	R.R. Riewe 225 & J. Marsh (WIN-32000)
	T334	C	Canada: Churchill, Hudson Bay	ca. 58.75527778, -94.1125		30 July 1910	(CAN-17340)
	T357	C	Canada, Yukon Territory: Black spruce muskeg, at milepost 1149, Alaska Highway	ca. 53.55959444, -64.10782778		5 July 1968	S.L. Welsh 7921 & G. Moore (BRY-71334)
	T395	C	Canada, Ontario: Lake River (Nakitawisagi)	ca. 54.3333, -82.4029944		12 September 1946	A. Dutilly & E. Lepage 16761 (CAN-17332)
1412	T329	C	Canada, Ontario: Fort Severn, near H.B.C. post	56-00N, 87-38W		13 July 1956	I. Hustich 1296 (CAN-242845)
1955	T394	C	Canada, Ontario: Kenora District, Patricia Portion, Runway 415, south of Cape Henrietta Maria	54°48'N. 82°23'W.		23 August 1976	J.L. Riley 5848 (CAN-409561)
	T359	C	USA, Alaska: Black spruce muskeg, at Deadman Lake Campground, ca. 1 mile south of milepost 1150, Alaska Highway	ca. 62.8875, -141.5375		7 July 1968	S.L. Welsh 8009 & G. Moore (BRY-71488)
	T311	C	USA, Alaska: Healy Quadrangle, Mt. McKinley National Park, Teklanika River	63°40'N, 149°35'W	2600 ft	3 August 1964	L.A. Viereck 7427 (CAN-362141)
B1431	T316	C	Canada, Saskatchewan: Highway no.2 Waskesim Road, south side of bridge	54°04'40"N, 105°56'25"W		31 July 1992	J.H. Hudson 5063 (CAN-565528)

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DNA No.	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
1954	T371	C	Canada, British Columbia: Anahim Lake	ca. 52°28'N 125°19'W	ca. 4000 ft	9 July 1956	J.A. Calder 18578, J. A. Parmelee & R. L. Taylor (COLO-158463)
B1434	T318	C	Canada, Manitoba: Fort Churchill	ca. 58.75527778, -94.0788889		5 July 1956	J.C. Ritchie 2104 (CAN-248387)
B1439	T313	C	Canada, Manitoba, Vicinity of Churchill	58°46'N, 94°10'W		21 July 1956	W.B. Schofield & H.A. Crum 6862 (CAN-247332)
1948	**T276**	C	Canada, Manitoba: Churchill, south of Fort	ca. 58.635, -94.13		26 August 1973	K. Johnson J73-402 (WIN-33557)
B1445	T314	C	Canada, Yukon Territory: Ogilvie Mountians, along Dempster Highway near Mile 81 calcareous flats along Blackstone Road	ca. 64.366667, -137.266667		28 June 1968	R.T. Porsild 1462 & A.E. Porsild (CAN-318349)
1395	T337	C	Canada, Yukon Territory: Ogilvie Mountians, along Dempster Highway near Mile 68	ca. 64.366667, -137.266667		17 July 1968	R.T. Porsild 1593 (CAN-318505)
1393	T336	C	Canada, Northwest Territories: Sawmill Bay, Neast tip of Leith Peninsula, Great Bear Lake	ca. 65.717, -118.833		13 July 1948	H.T. Shacklette 2970 (CAN-199991)
B1446	T312	C	Canada, Northwest Territories: District Mackenzie, Aubry Lake, N arm, west side, at junction of two seismic lines	67°20'N, 126°25'W		14 July 1976	R.R. Riewe & J. Marsh 225 (CAN-433230)
1953	T393	C	Canada, Alberta: 12 miles N of Fort Fitzgerald	58°59'N, 111°50'W		19 July 1950	W.J. Cody 4533 & C.C. Loan (RM-228683)
B1433	T317	C	USA, Alaska: Old John Lake	68°08'N, 145°W	600 m	13 July 1961	K. Holmen (CAN-271116)
	T358	A	USA, New Hampshire: Alpine Garden, Mount Washington, sup-alpine slopes	ca. 44.271944444, -71.30111111		5 July 1942	(BRY-143916)
	P11-2	A	Argentina: Tierra del Fuego, Departamento Rio Grande, left bank of the Arroyo Damajuana, on the east side of Ruta D, 600 m south of the intersection of Ruta B and D at point where a small road leads to a house ca. 600 m west of Ruta D	53°55'56.3" S, 68°05'20.2" W	60m (±4m)	13 January 2010	J. Starr 10015 & T. Villaverde
	P11-2	A	Argentina: Tierra del Fuego, Departamento Rio Grande, left bank of the Arroyo Damajuana, on the east side of Ruta D, 600 m south of the intersection of Ruta B and D at point where a small road leads to a house ca. 600 m west of Ruta D	53°55'56.3" S, 68°05'20.2" W	60m (±4m)	13 January 2010	J. Starr 10015 & T. Villaverde

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DNA No.	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
	P11-5	A	Argentina: Tierra del Fuego, Departamento Rio Grande, left bank of the Arroyo Damajuana, on the east side of Ruta D, 600 m south of the intersection of Ruta B and D at point where a small road leads to a house ca. 600 m west of Ruta D	53°55’56.3” S, 68°05’20.2” W	60m (±4m)	13 January 2010	J. Starr 10015 & T. Villaverde
	P16-1	A	Argentina: Provincia Santa Cruz, Los Glaciares National Park, near El Chaltén, pathway (sendero) to Monte FitzRoy, 760 m south of the point where the path splits leading to either Laguna de Los Tres or to Lagunas Hija and Madre (via sendero Madre e Hija)	49°17’22.0” S, 72°56’57.1” W	732m (±6m)	21 January 2010	J. Starr 10020 & T. Villaverde
	P18A-11	A	Argentina: Provincia Santa Cruz, Los Glaciares National Park, near El Chaltén, east side of Ruta Nacional 23 leading to Lago del Desierto, ca. 800 m north of Laguna La Pava and 14 km south of the Prefectura Naval Argentina (P.N.A) on the south end of Lago del Desierto	49°10’43.1” S, 72°56’51.0” W	732m (±7m)	22 January 2010	J. Starr 10023 & T. Villaverde
	P18A-6	A	Argentina: Provincia Santa Cruz, Los Glaciares National Park, near El Chaltén, east side of Ruta Nacional 23 leading to Lago del Desierto, ca. 800 m north of Laguna La Pava and 14 km south of the Prefectura Naval Argentina (P.N.A) on the south end of Lago del Desierto	49°10’43.1” S, 72°56’51.0” W	732m (±7m)	22 January 2010	J. Starr 10023 & T. Villaverde
	40SMB10(40)	A	Argentina: Tierra de Fuego, entre Tolhuin y Río Grande, entre la Estancia Indiana y la Estancia Rivadavia. Pastizales mesófilos venteados	54°21’7” S, 67°27’3” W	80 m	12 January 2010	S. Martín-Bravo 40SMB10, P. Vargas, M. González & M. Luceño
	T158	A	Norway: XR NW Nordland, Narvik hd., Skjomen, N of E end of Kjørisvatn	ca. 68.383333, 17.25		11 August 1973	O. Skifte, G. Graff & S. Spjelkavik s.n. (H-1679404)
	T051	A	Sweden: Torne Lappmark	ca. 67.9°N, 20.2°W		27 July 1933	H. Smith s.n. (DAO-714568)
	T069	A	West Greenland: Pingorssuaq, near point 490 NW of	64°03’N, 50°03’W	400 m	11 August 1983	S. Hanfgarn 83-175 (C-17-2009-3)
	T151	A	South-East Greenland: north side of Tugtilik lake from west bank of inflow river to Nigertussoq Fjord	66.22°N, 35.08°W	10 m	15 August 1967	J.E. Elsley 163/67 (M-0151948)

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DNA No.	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
2026	T075	A	Norway: Troms, Bardu hd., Leinavatn, Havgaluokta W-side	ca. 68.456111, 19.768611	498 m	7 July 1977	E.M. Engelskjøn & T. Engelskjøn s.n. (C-15-2009-1)
2027	T174	A	Sweden, Torne Lappmark: Karesuando parish, Moskana	ca. 67.9, 20.2	ca. 1000 m	26 July 1933	H. Smith s.n. (H-1652844)
2030	T196	A	Sweden, Torne Lappmark: Jukkasjärviparish, between Mt. Paddos and Mt. Nissontjærro, dry boggy ground	ca. 68.309561, 18.809477	550 m	23 July 1939	C.G. Alm & H. Smith s.n. (H-1300259)
2029	**T199**	A	Finland: NW-Le, W-Saana, in devilitate saxosa humida	ca. 69.043843, 20.828667	750 m	7 August 1935	L. Roivainen s.n. (H-127310)
2028	T207	A	Finland: Inarin Lappi (InL/Li), Inari, Vätsäri, Rovipää	ca. 69.133333, 28.35000		27 July 1996	H. Kulmala s.n. (H-717201)
1408	T294	A	Greenland: West Greenland, Arfersiorflk, Itjvdljarssuk	67°54'N, 50°35'W	75 m	19 July 1987	B. Fredskild & V. Dalgaard s.n. (COLO-456814)
1406	T296	A	Canada, Manitoba: Baralzon Lake	60-00N, 98-10W		18 July 1950	H.J. Scoggan 8201 & W.K.W. Baldwin (WIN-22434)
1399	T304	A	Canada, Manitoba: Fort-Chimo, Nouveau-Québec	58°07'N, 58°23'W		22 July 1963	A. Legault 6782 (COLO-491481)
B1436	T324	A	Canada, Manitoba: Duck Lake (southeast arm of Nejanllini Lake), sand-gravel knoll at Hudson's Bay Co. post	59-22 N, 97-46 W		19 August 1950	H.J. Scoggan 8288 & W.H.W. Baldwin (CAN-201506)
	T268	A	Canada, Québec (Nunavik): Ungava Bay (west side), Hopes Advance Bay, surrounding Aupaluk	59°18'N, 69°36'W		1 August 1993	M. Blondeau AU-93079 (WIN-53902)
	T272	A	Canada, Québec: Korok River, 3 mi. NE of Ungava	ca. 58.583333, -65		23 July 1951	J. Rousseau 543 (WIN-22356)
	T373	A	Canada, Québec: George River, the esker of Kopeteokash Lake	ca. 55.15, -64.33333		18 July.1947	J. Rousseau 152 (COLO-13811)
B1432	T323	A	Canada, Newfoundland-Labrador: Esker area, 2 miles south of the 3049 ft. summit	51-53 N, 66-03 W	2750 ft	21 July 1967	Y. Mäkinen 67-925 (CAN-314758)
B1448	T325	A	Canada, Saskatchewan: Northeastern Corner, Vicinity of Patterson Lake	59°55'N, 102°20'W		20 July 1963	G.W. Argus s.n. (CAN-282691)
B1430	T326	A	Canada, British Columbia: Pine Pass Quad, unnamed peak at mile 4.5 on finaly forks road	55°37'N, 123°21'W	4600 ft	12 July 1973	G.W. Argus 8831 (CAN 372267)
B1435	T327	A	Canada, Québec: Lichteneger Lake Quad, Lac Jaucourt Region, ca. 5 Mi. East of CAN. Forestry SV	52°45'N, 74°07'W	1600 ft	16 July 1974	G.W. Argus 9221 (CAN 3779977)
1403	**T348**	A	Canada, Québec: East Coast of James Bay, Boatswain Bay, rocky granite shore	ca. 51.83, -78.87		8 July 1947	W. Baldwin 406, I. Hustich, J. Kucyniak & R. Tuomikoski (CAN-17333)

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DNA No.	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
1402	T343	A	Canada, Ontario: Hudson Bay Lowlands, diabase cliffs and ridges west of narrows between Hawley and Sutton Lakes	ca. 54.41530000, -84.69185556		4 July 1957	A.E. Porsild, W.K.W. Baldwin, H. & G. Sjors 19898 (CAN-278707)
1389*	T310	A	Canada, Ontario: Kenora District, Patricia Portion, Sutton ridges, summit of westernmost of pair of prominent 'cuestas', 3 mi. east of south central portion of Aquatuk Lake	54°19'N, 84°32'W		12 August 1980	J.L. Riley 11856 (CAN-462937)
	T392	A	Canada, British Columbia: Mount Apex southwest of Penticton, near summit	ca. 49.36, -119.910125	ca. 7100 ft	11 August 1953	J.A. Calder 11795 & D.B.O. Savile (RM-252249)
1993	T399	A	USA, New Hampshire: Alpine Garden, Mt. Washington	ca. 44.27083333, -71.30555556		29 July 1899	W.W. Eggleston 1681 (RM-23379)
	T303	A	Canada, Nunavut: Upper Hood River, low arctic tundra vegetation along the upper Hood River valley, between the headwaters and Wilderforce Falls within the Bear Slave Uplands	66°47'N, 111°00'W	100-400 m	June-July 1995	W. Gould s.n. (COLO-475773)
	T339	A	Canada, Keewatin: Baralzon Lake	60°00'N, 98°10'W		30 July 1950	H.J. Scoggan 8387 & W.K.W. Baldwin (CAN-202500)
	T340	A	Canada, Newfoundland-Labrador: Twin Falls, near the Churchill airstrip	ca. 53.559594444, -64.107827778		6 July 1967	I. Hustich 220 (CAN-313311)
	T341	A	Canada, Manitoba: Nueltin Lake, southern part of lake	59°48'N, 99°39'W		26 July 1951	W.K.W. Baldwin 2303 (CAN-212816)
	T389	A	Canada, Saskatchewan: Northeastern Corner, vicinity of Patterson Lake, on glacier hill west of lake	59°55'N, 102°20'W		20 July 1963	G.W. Argus 372-63 (RM-277437)
	T374	A	Canada, British Columbia: Baldy Mtn. about 7.5 miles ENE of Littlefort	51°27'N, 120°03'W	7228 ft	8 August 1956	J.A. Calder 19846, J.A. Parmelee & R.L. Taylor (COLO-149035)
	T386	Y	USA, Colorado: Grand Co., moist tundra slope, head of Fool Creek, Fraser Exp. Forest, S.W. of Fraser	ca. 39.904166667, -105.88194444	12 000 ft	31 July 1953	W.A. Weber 8621 & E. Dahl (COLO-76204)
	P33-1	Y	USA, Colorado: Hinsdale Co., Gunnison National Forest, N east base of the southern and lower peak of Mesa Seco, along trail to Cannibal Plateau (ATV road), reached via Co. Road 50 and State Road 149 (Thread Byway). Alpine tundra ca. 300 m from the summit and 50 m lower in elevation.	38°01'31.7"N, 107°14'24.3"W	3834 m (±5m)	26 July 2010	J. Starr 10S-033 & T. Villaverde

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DNA No.	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
	T369	Y	USA, Colorado: Clear Creek Co., Loch Lomond, between Mount Bancroft and James Peak	ca. 39.84305556, -105.6894444	11140 ft	8 August 1972	W.A. Weber 14522, T. Koponen, P. Nelson (COLO-259883)
1489	P30-1	Y	USA, Colorado: Lake Co., San Isabel National Forest, reached via Co. Road 4 beginning at Leadville. Wet meadow ca. 350 m N east of Hagerman Pass. Cirque below pass.	39°15'55.0" N, 106°28'45.6" W	3602 m (±5m)	25 July 2010	J. Starr 10S-030 & T. Villaverde
B1442	T321	Y	USA, Colorado: Clear Creek Co., Loch Lomond, between Mount Bancroft and James Peak	ca. 39.83472222, -105.678889	11140 ft	8 August 1972	W.A. Weber, T. Koponen & P. Nelson s.n. (CAN-374041)
	P47-A-2	Y	USA, Montana: Carbon Co., Custer National Forest, Absaroka-Beartooth Wilderness, Hellroaring Plateau, reached via Forest Route 421 which begins at US 212 (road to Greenough Lake, Limber Pine and Parkside Campgrounds). ca. 1 km sotuh east of Snowbank Lake. Dense alpine tundra ca. 200 m N of trail.	45°01'55.3"N, 109°29'06.1"W	3137 m (±7m)	31 July 2010	J. Starr 10S-047A & T. Villaverde
	T259	Y	USA, Montana: Sweet Grass Co., Crazy Mountains, common in moist turf among boulders on the ridge between Crazy Peak and Blue Lake	ca. 46.0244, -110.28361111	9000 ft	10 August 1996	P. Lesica 7362 (MONTU-122399)
	T260	Y	USA, Montana: Sweet Grass Co., Crazy Mountains, N-slope of mountain S. of Blue Lake	ca. 46.0272222, -110.28527778	ca. 9000 ft	15 August 1981	K.H. Lackschewitz 9909 (MONTU-86558)
	T277	Y	USA, Montana: Stillwater Co., Beartooth Mountains, N. end of the Stillwater Plateau (The Golf Course), Custer National Forest, 6 mi. S. of Nye	ca. 45.320219444, -109.83712222	9080 ft	27 July 1992	E. Evert 24076 (RM-780026)
	T279	Y	USA, Montana: Carbon Co., Beartooth Plateau, alpine tundra W. of Hwy 212	ca. 45.04277778, -109.5813889	9800 - 10000 ft	14 September 1976	K.H. Lackschewitz 7000 (WTU-272540)
	T256	Y	USA, Nevada: Head of Browns Cr. (meadows)	ca. 39.3309448, -119.8649597	8500 ft	17 July 1955	M.E. Lewis 448 (RM-390545)
	T319	Y	USA, Nevada: Head of Browns Cr. (meadows)	ca. 39.3383333, -119.7922222	8500 ft	17 July 1955	M.E. Lewis 448 (CAN-550536)
	T285	Y	USA, Utah: Duchesne Co., Uinta Mountains, N of Painter Basin	ca. 40.7875, -110.3341667		15 August 1955	M.E. Lewis 512 (RM-368032)
B1441	**T286**	Y	USA, Utah: Duchesne Co., Ashley National Forest, Uinta Mtns., Uinta drainage, Gilbert Bench	ca. 39.338333, -119.79222	11500 ft	20 August 1996	S. Goodrich 25583, A. Huber & D. Prescott (BRY-392186)

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DNA No.	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
B1440	T320	Y	USA, Utah: Duchesne Co., Uinta Mountains, North of Painter Basin	ca. 40.81111, -110.331944		15 August 1955	M.E. Lewis 512 (CAN-515168)
1382	T287	Y	USA, Utah: Duchesne Co., N edge of lake on Gilbert Creek, Gilbert Creek Basin, Uinta Drain., Uintah Mtns.	ca. 40.77805556, -110.23722	11460 ft	25 August 1993	A. Huber & S. Goodrich 440 (BRY-368578)
	T361	Y	USA, Utah: Summit Co., Uinta Mountains, Ridge saddle 0.4 miles east of Gilbert Peak, saddle separating West Fork Beaver Creek and Gilbert Creek Basin	ca. 40.823509, -110.331982	12600 ft	3 August 1999	A. Huber 4134 (BRY-426752)
	P47-B-8	Y	USA, Wyoming: Park Co., Shoshone National Forest, Beartooth Plateau, reached via US 212. Wet to mesic tundra on flat or gentle slopes growing in boulder field ca. 500 m east of a sharp hairpin turn in the road near the summit of the Beartooth Pass and 750 m N east of Christmas Lake. Near summit of peak immediately to the N east of Christmas Lake	44°58'17.1"N, 109°25'14.6"W	3291 m (±6m)	31 July 2010	J. Starr 10S-047B & T. Villaverde
	P61-19	Y	USA, Washington: Whatcom Co., Baker-Snoqualmie National Forest, N side of Mt. Baker. On summit of ridge leading to Chowder Ridge along Skyline Divide Trail reached via National Forest Develop Road 37 and Mount Baker Hwy. (SR 542) which passes through Glacier.	48°50'32.4"N, 121°51'27.9"W	1984 m (±6m)	11 August 2010	J. Starr 10S-061 & T. Villaverde
	T238	Y	USA, Washington: Okanogan Co., Rock Mountain, ca. 21 mi. NE of Winthrop	ca. 48.69, -119.9169444	7760 ft	19 July 1971	G.W. Douglas 2887 (RM-430209)
	T251	Y	USA, California: Sierra Co., Tahoe, Anderson Mdw.	ca. 39.4783333, -120.2927778	6400 ft	25 June 1969	R.K. Gierisch 3493 & D.H. Esplin (RM-430207)
	T289	Y	USA, Wyoming: Johson Co., Big Horn Moutains, Elk Peak, ca 3 air mi SW of Dome Lake reservoir	ca. 44.50472222, -107.2819444	10500 - 11000 ft	9 August 1988	R.L. Hartman 24223 & T.J. Poll (RM-533361)
	T290	Y	USA, Wyoming: Sublette Co., West Slope Wind River Range, peak 1.5 air mi WSW of Temple Peak, 3 air mi N of Independence Mountain	ca. 39.7242527778, -105.68614444	10400 - 11800 ft	19 August 1991	R.L. Hartman 31265 (RM-589096)
	T383	Y	USA, Wyoming: Park Co., Absaroka Mountains, along E side of Cascade Creek ca. 1-2 mi. S of Kerwin, ca. 24-25 mi. SW of Meeteetse	ca. 43.852177778, -109.296394444	10300 - 10800 ft	3 August 1989	E. Evert 18305 (COLO-449077)

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DNA No.	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
	T391	Y	USA, Wyoming: Park Co., Yellowstone National Park, Northern Absarokas and above Hoodoo Basin at the head of Lamar River between Lamar Mountain and Hoodoo Peak, ca 41 air mi. WNW of Cody	ca. 44.7063889, -109.85129444	10200 - 10400 ft	22 July 1985	B.E. Nelson 12725 (RM-482304)
	T430	Y	USA, Wyoming: Park Co., Southwestern Absarokas, Ishawooa Mesa, ca 40 mi SW of Cody	ca. 44.1129167, -109.6268771	9800 - 10200 ft	20 August 1985	E.F. Evert 9608 (RM-623052)
1383	T291	Y	USA, Wyoming: Park Co., Beartooth Plateau, 1/4 mile east of Twin Lakes, below Highway 212	ca. 45.05194444, -109.57416667		18 August 1984	B. Neely 2435 (COLO-399492)
	T043	Y	USA, Washington: Whatcom Co., Chowder Ridge, ca. 7 mi. SE of Glacier	ca. 48.8162462, -121.832199	6800 ft	3 August 1972	G.W. Douglas 4345 & G.G. Douglas (DAO-621358)
	T388	Y	Canada, Alberta: Banff National Park, Snow Creek Pass, alpine tundra and hillsides west of pass	ca. 51.61055556, -115.82138889	7000 ft	29 July 1960	A.E. Porsild 22673 (RM-529780)
B1449	T322	Y	Canada, Alberta: Banff National Park, Snow Creek Pass, alpine tundra and hillsides west of pass	ca. 51.61055556, -115.82138889	7000 ft	29 July 1960	A.E. Porsild 22673 (CAN-266077)
	T390	Y	Canada, British Columbia: Near west end of Quiniscoe Lake in the Ashnola Range	ca. 49°04'N, 120°12'W	7600 ft	2 August 1956	J.A. Calder 19594, J.A. Parmelee & R.L. Taylor (RM-260491)
	07-044	Y2	USA, California: El Dorado County, Lake Tahoe Basin Management Unit, ca. 17 km southeast of Pope Beach (southern shore of Lake Tahoe) and 200 m southwest of State Road 89 (Luther Pass Rd.) ca. 5.5km from its junction with SR 88 (Carson Pass National Scenic Byway). Quaking bog about 200 m east of Grass Lake	38.79330 N, 119.95767 W	2349 m	16 July 2007	J.R. Starr & J. Thibeault 07-44 (CAN)
	07-045	Y2	USA, California: El Dorado County, Lake Tahoe Basin Management Unit, ca. 17 km southeast of Pope Beach (southern shore of Lake Tahoe) and 200 m southwest of State Road 89 (Luther Pass Rd.) ca. 5.5km from its junction with SR 88 (Carson Pass National Scenic Byway). QUaking bog about 200 m east of Grass Lake	38.79330 N, 119.95767 W	2349 m	16 July 2007	J.R. Starr & J. Thibeault 07-45 (CAN)

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DNA No.	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
	07-052	Y2	USA, California: Sierra County, Tahoe National Forest, ca. 10 km southeast of Sierraville and 5 km northwest of Webber Lake. Open wet meadow on the south side of Yuba Pass Road (Forest Route 12) reached via hwy 89 and Henness Pass Rd.	39.52153 N, 120.44292 W	2257 m	19 July 2007	J.R. Starr & J. Thibeault 07-52 (CAN)
	07-053	Y2	USA, California: Sierra County, Tahoe National Forest, ca. 10 km southeast of Sierraville and 5 km northwest of Webber Lake. Open wet meadow on the south side of Yuba Pass Road (Forest Route 12) reached via hwy 89 and Henness Pass Rd.	39.52153 N, 120.44292 W	2257 m	19 July 2007	J.R. Starr & J. Thibeault 07-53 (CAN)
	JS06016	Y2	USA, California: Butte Co., Lassen National Forest, Forest Ranch, Cheery Hill meadows, near Cherry Hill campsite. Take hwy 32 from Chico for ca. 42 km to Lomo where Humboldt Rd begins, then 10 km along road to site. ca. 200 m due N of the point where Humboldt Rd. crosses Butte Creek.	40°06'08.0"N, 121°30'03.0"W	1428 m	3 August 2006	J.R. Starr & J. Thibeault 06016 (CAN)
	JS06019	Y2	USA, California: Butte Co., Lassen National Forest, Forest Ranch, Cheery Hill meadows, near Cherry Hill campsite. Take hwy 32 from Chico for ca. 42 km to Lomo where Humboldt Rd begins, then 10 km along road to site. ca. 200 m due N of the point where Humboldt Rd. crosses Butte Creek.	40°06'08.0"N, 121°30'03.0"W	1428 m	3 August 2006	J.R. Starr & J. Thibeault 06019 (CAN)
	P54-18	Y2	USA, California: Butte Co., near Cherry Hill Campground, Lassen National Forest, ca. 250 m N west of the point where Humboldt Road crosses Butte Creek.	40°06'09.1"N, 121°30'03.0"W	1441 m (±7m)	6 August 2010	J. Starr 10S-054 & T. Villaverde
	P54-19	Y2	USA, California: Butte Co., near Cherry Hill Campground, Lassen National Forest, ca. 250 m N west of the point where Humboldt Road crosses Butte Creek.	40°06'09.1"N, 121°30'03.0"W	1441 m (±7m)	6 August 2010	J. Starr 10S-054 & T. Villaverde
	T246	Y2	USA, California: Eldorado Co., Freel Peak quad, Big Meadow, about 1.5 mi east of Upper Truckee River and 0.6 mi south of Hwy 50.	38°46'40"N, 119°00'04"W	7520 ft	2 September 1998	L.P. Janeway 6253 & E. Schroder (CHSC-73322)

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DNA No.	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
	T247	Y2	USA, California: Plumas Co., Bucks Lake quad, Northern High Sierra Nevada, at Kanaka Flat, on N side of Maple Flat, upper drainage of Spanish Creek	39°59’17”N, 121°07’40”W	1579 m	7 July 2000	L.P. Janeway 6891 (CHSC-78722)
	T071	Y2	USA, California: El Dorado Co., El Dorado National Forest, along road 89, W-side of Grass lake	38°47.5’N, 119°57.5’W	7700 ft = 2350 m	23 July 1987	J. Pykää 2900, D.H. Norris & H. Toivonen (C-15-2009-6)
	T047	Y2	USA, California: El Dorado Co., El Dorado National Forest, along road 89, W-side of Grass lake	38°47.5’N, 119°57.5’W	7700 ft = 2350 m	23 July 1987	J. Pykää 2900, D.H. Norris & H. Toivonen (DAO-661914)
	T039	Y2	USA, California: Sierra Nevada, El Dorado Co., Echo Summit	ca. 38.813056, -120.030278		1 September 1946	J.T. Howell 22959 (DAO-257424)
1384	T248	Y2	USA, California: Tehama Co., about 50 yards east of the abandoned logging road, about 200 yards norteast of where the dirt road crosses Colby Creek, about 2 miles (air) Neast of Colby Mountain, about 5 1/8 miles (air) Neast of Butte Meadows	40°07’38.6”N, 121°29’27.5”W	5053 ft	19 July 2006	L. Ahart 13.051 (CHSC-94326)
1377	T249	Y2	USA, California: Sierra Co., Yuba Pass-Weber Lake Road (Forest Rt. 12) 1.5 mi S of the road to Haypress Valley	ca. 39.495205, -120.411133	ca. 7200 ft	19 August 1996	V.H. Oswald & L. Ahart 8221 (CHSC-66824)
	T442	Y2	USA, California: Sierra Nevada, peat meadow back of stream, one mile west of University of California Trout Laboratory (12 miles N of Truckee)	ca. 39.501912, -120.1832542	ca. 6500 ft	20 July 1957	W.A. Nisbet 45 (CAN-272091)
	T441	Y2	USA, California: Nevada Co., along edge of western part of main bog, near Lodgepole Pine seedlings, Sage Hen Creek, University of California Trout Laboratory	ca. 39.501912, -120.1832542	ca. 6500 ft	19 July 1957	J. Langenheim 4429 (CAN-272099)
1386	**T284**	Y2	USA, Oregon: Deschutes Co., W edge of wet meadow c.a. 1 mile N of Three Creeks Lake-near parking lot where Snow Creek flows through meadow	ca. 44.114444, -121.622500	1926 m	30 August 1982	C. Halpern 600 & T. Magge (OSC-159046)
	P57-21	Y2	USA, Oregon: Deschutes Co., Deschutes National Forest, at the entrance to Three Creek Campground, reached via National Forest Develop Road 16 and Three Creek Lake Road, which starts in Sisters. Light sloping wet meadow traversed by Three Creek adjacent to road. Along small tributaries and seeps leading to creek.	44°06’52.8”N, 121°37’26.6”W	1927 m (±5m)	9 August 2010	J. Starr 10S-057 & T. Villaverde

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DNA No.	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
	P57-22	Y2	USA, Oregon: Deschutes Co., Deschutes National Forest, at the entrance to Three Creek Campground, reached via National Forest Develop Road 16 and Three Creek Lake Road, which starts in Sisters. Light sloping wet meadow traversed by Three Creek adjacent to road. Along small tributaries and seeps leading to creek.	44°06’52.8”N, 121°37’26.6”W	1927 m (±5m)	9 August 2010	J. Starr 10S-057 & T. Villaverde
	T282	Y2	USA, Oregon: Deschutes Co., entrance to 3-creek meadow campground near Three-Creek Lake, gravel edge of road near meadow	ca. 44.1122222, -121.6225	6500 ft	9 August 1990	B. Wilson 4176 (OSC-178855)
	T281	Y2	USA, Oregon: Lake Co., Sycan Marsh, 40 km S of Silver Lake. On high bog hummocks in open marsh NW of Brattons Bog	ca. 42.76583333, -121.155	1524 m	23 August 1980	J.A. Christy s.n. (OSC-188302)
	T283	Y2	USA, Oregon: Jackson Co., Cascade Moutains, southeast slopes of Chinquapin Mountain, 13 air miles east of Ashland	42°8.998’N, 122°25.419’W	5370 ft	28 June 2001	N. Otting 312 (OSC-210656)
	T250	Y3	USA, California: Inyo Co., Mono Mesa	ca. 37.454276, -118.758326	ca. 12000 ft	26 July 1946	J.T. Howell 22750 (WTU-137524)
1963	T040	Y3	USA, California: Tulare Co., Sierra Nevada, Army Pass	ca. 36.49957222, -118.248300	12000 ft	5 August 1949	J.T. Howell s.n. (DAO-257423)
1962	T252	Y3	USA, California: Mono Co., Mt. Dana Plateau	ca. 37.92166667, -119.2147222	11500 ft	25 July 1979	D. Taylor 7550 (COLO-330874)
	T438	Y3	USA, California: Tuolumne Co., Sierra Nevada, in metamorphics of unglaciated plateau on south slope of Kuna Peak	ca. 37.812706, -119.2076454	12500 ft	21 July 1937	C.W. Sharsmith 2681 (CAN-162869)
	T046	Y3	USA, California: Inyo Co., Sierra Nevada, unglaciated plateau on N side of Mount Humphreys (”Humphreys Plateau”)	ca. 37.283386, -118.662705	12880 ft	11 August 1937	C.W. Sharsmith 3116 (DAO-257428)
	T253	Y3	USA, California: Northeastern Tulare Co., Sierra Nevada, Central Basin, lower lake	ca. 36.548889, -118.51916667	11300 ft	26 July 1948	P.A. Munz 12669 (WTU-133536)

A.2 Studied specimens used in Chapter 3

Table A.12: Voucher data for all *C. capitata* (C), *C. arctogena* (A), *"C. cayouetteana"* (Y), *Carex sp. nov. 1* (Y2) and *Carex sp. nov. 2* (Y3) specimens sampled for the phylogenetic analyses. Asterisks denote specimens used also for the morphological study.

DNA	**Sheet No.**	**Sp.**	**Locality**	**Coord.**	**Elev.**	**Coll. date**	**Voucher specimen**
1942*	T034	C	Russia: Yakutia (presently named Sakha Republic). Bulunsk region. Severnoe Verhojané. Mouth of river Kusagan-Uu, confluent of river Altan, upstream of frazil.	ca. 69°25'N 130°40'E		25 June 1960	B. Yurtsev s.n. (DAO-257437)
1996	T033	C	Russia: Western Chukotka, N part of Anui upland region, upper reaches of river Erguveem (left confluent of river Rau-Chau)	ca. 68°N, 167°E		12 July 1967	E.V. Zimarskaja, A.A. Korobkov & B.A. Yurtsev s.n. (DAO-139880)
2001	T362	C	Russia: Western Chukotka, N part of Anui upland region, upper reaches of river Erguveem (left confluent of river Rau-Chau)	ca. 68°N 167°E		12 July 1967	E.V. Zimarskaja, A.A. Korobkov & B.A. Yurtsev s.n. (BRY-122530)
1957*	T037	C	Russia: Eastern part of Chukotski peninsula, middle branch of the river Utaveem (left bank) and its confluent, the river Yararmoveem, gentle south-west slope of flood-land terrace.	ca. 66°N 171°E		27 July 1970	U.P. Kozhevnikov, A.A. Nechaev, B.A. Yurtsev s.n. (DAO-139887)
2000	T173	C	Russia: Republic of Karelia, Karelia onegensis (Kon)	ca. 62°12'N, 33°47'E		9 July 2002	R. Ruuhijärvi40/02 (H-744530)
B1438	T446	C	Russia: Magadan region, North Even area, basin of river Kegali, valley of river Pravie Ishljaki	ca. 63°N, 161°E		2 August 1976	A.P. Hohrjakov s.n. (CAN-455497)
B1443*	T315	C	Finland: Fennia, Ls. Kuusamo, Liikasenvaara	ca. 66.366667, 29.533333		9 August 1962	T. Ulvinen s.n. (CAN-276804)
1956*	T168	C	Sweden, Torne Lappmark: Jukkasjärvi parish, Lake Torneträsk District, Abisko, marshy ground south of the railway station	68° - 68°34' N, 18° - 20°30' E	400 m	6 August 1958	C.G. Alm s.n. (H-1226056)
2025	T144	C	Italy: South Tyrol	ca. 46.212155, 11.456657	2200 m	23 July 1976	O. Angerer s.n. (M-0151926)
2023	T136	C	Italy: Dolomites, Seiser Alm	ca. 46.541111, 11.644722	ca. 1900m	27 June 1964	H. Hertel 4324 (M-0151927)
1959	T098	C	Iceland: Lagarfoss Hróarstungu	ca. 66.050000, -23.13333333		26 June 1976	Lagarfljótsrannsóknir s.n. (ICEL-VR-04081)

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DNA	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
1951*	T084	C	Iceland: Dalfjall Mývatnssveit	ca. 65.657, -16.815	460 m	21 August 1974	E. Einarsson s.n. (ICEL-VR-04073)
1945*	T085	C	Iceland: Hrísey Eyjafirø	ca. 66.000000, -18.383333		12 August 1967	A. Garøarsson s.n. (VR-04078)
B1431*	T316	C	Canada, Saskatchewan: Highway no.2 Waskesim Road, south side of bridge	54° 04' 40"N, 105° 56' 25"W		31 July 1992	J.H. Hudson 5063 (CAN-565528)
1954*	T371	C	Canada, British Columbia: Anahim Lake	ca. 52°28'N 125°19'W	ca. 4000 ft	9 July 1956	J.A. Calder 18578, J. A. Parmelee & R. L. Taylor (COLO-158463)
1961	T244	C	Canada, British Columbia: Anahim Lake, rare in area but locally common in moist depression in open Lodgepole Pine woods	approx. 52° 28'N, 125° 19'W	ca. 4000 ft	9 July 1956	J.A. Calder 18578, J. A. Parmelee & R. L. Taylor (WTU-197744)
1955*	T394	C	Canada, Ontario: Kenora District, Patricia Portion, Runway 415, south of Cape Henrietta Maria	54°48' N. 82°23'W.		23 August 1976	J.L. Riley 5848 (CAN-409561)
1412*	T329	C	Canada, Ontario: Fort Severn, near H.B.C. post	56-00 N, 87-38 W		13 July 1956	I. Hustich 1296 (CAN-242845)
1409	T273	C	Canada, Manitoba: Wapusk National Park, N side of the Owl River, about 4 km inland, near cabin, 130 km SE of Churchill, pond east of cabin, just below the 10 m a.s.l.	57°49'46.1"N, 92°48'09.3"W		19 July 2003	E. Punter 03-509 & M. Piercey-Normore (WIN-71429)
1400	T271	C	Canada, Manitoba: Fort Churchill	ca. 58.75527778, -94.07888889		5 July 1956	J.C. Ritchie 2104 (WIN-22433)
B1434*	T318	C	Canada, Manitoba: Fort Churchill	ca. 58.75527778, -94.07888889		5 July 1956	J.C. Ritchie 2104 (CAN-248387)
B1439*	T313	C	Canada, Manitoba, Vicinity of Churchill	58°46'N, 94°10'W		21 July 1956	W.B. Schofield & H.A. Crum 6862 (CAN-247332)
1411	T274	C	Canada, Manitoba: Twin Lakes Road, 2 km N of Twin Lakes	58°38'14"N, 93°49'22"W		25 July 2002	B.A. Ford 02379, M. Piercey-Normore, E. & D. Punter (WIN-71024)
1394	T297	C	Canada, Manitoba: Churchill	58°47'N, 94°11'W		11 July 1983	J.M. Shay 83-60 (WIN-40808)
1948*	T276	C	Canada, Manitoba: Churchill, south of Fort	ca. 58.635, -94.13		26 August 1973	K. Johnson J73-402 (WIN-33557)
B1445*	T314	C	Canada, Yukon Territory: Ogilvie Mountians, along Dempster Highway near Mile 81 calcareous flats along Blackstone Road	ca. 64.36666667, -137.26666667		28 June 1968	R.T. Porsild 1462 & A.E. Porsild (CAN-318349)

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DNA	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
1395*	T337	C	Canada, Yukon Territory: Ogilvie Mountians, along Dempster Highway near Mile 68	ca. 64.36666667, -137.26666667		17 July 1968	R.T. Porsild 1593 (CAN-318505)
1393*	T336	C	Canada, Northwest Territories: Sawmill Bay, Neast tip of Leith Peninsula, Great Bear Lake	ca. 65.717, -118.833		13 July 1948	H.T. Shacklette 2970 (CAN-199991)
B1446*	T312	C	Canada, Northwest Territories: District Mackenzie, Aubry Lake, N arm, west side, at junction of two seismic lines	67° 20’N, 126° 25’W		14 July 1976	R.R. Riewe & J. Marsh 225 (CAN-433230)
1953	T393	C	Canada, Alberta: 12 miles N of Fort Fitzgerald	58°59’N, 111°50’W		19 July 1950	W.J. Cody 4533 & C.C. Loan (RM-228683)
1407	T307	C	Canada, Yukon Territory: Mile 85 on road from Whitehorse to Dawson, south of Carmacks	61°52’N, 136°07’W	1900 ft	22 June 1960	J.A. Calder 25796 & J.M. Gillet (ALA-43436)
B1433*	T317	C	USA, Alaska: Old John Lake	68° 08’N, 145° W	600 m	13 July 1961	K. Holmen (CAN-271116)
2026*	T075	A	Norway: Troms, Bardu hd., Leinavatn, Havgaluokta W-side	ca. 68.456111, 19.768611	498 m	7 July 1977	E.M. Engelskjøn & T. Engelskjøn s.n. (C-15-2009-1)
2027*	T174	A	Sweden, Torne Lappmark: Karesuando parish, Moskana	ca. 67.9, 20.2	ca. 1000 m	26 July 1933	H. Smith s.n. (H-1652844)
2030*	T196	A	Sweden, Torne Lappmark: Jukkasjärviparish, between Mt. Paddos and Mt. Nissontjærro, dry boggy ground	ca. 68.309561, 18.809477	550 m	23 July 1939	C.G. Alm & H. Smith s.n. (H-1300259)
2029*	T199	A	Finland: NW-Le, W-Saana, in devilitate saxosa humida	ca. 69.043843, 20.828667	750 m	7 August 1935	L. Roivainen s.n. (H-127310)
2028*	T207	A	Finland: Inarin Lappi (InL/Li), Inari, Vätsäri, Rovipää	ca. 69.133333, 28.35000		27 July 1996	H. Kulmala s.n. (H-717201)
1408*	T294	A	Greenland: West Greenland, Arfersiorflk, Itjvdljarssuk	67°54’N, 50°35’W	75 m	19 July 1987	B. Fredskild & V. Dalgaard s.n. (COLO-456814)
A Baffin		A	Canada, Nunavut: Baffin Island, Beekman Peninsula	66.55 N, 64.67 W		22 August 1964	I.A. McLaren 153 (CAN-283963)
1406*	T296	A	Canada, Manitoba: Baralzon Lake	60-00 N, 98-10 W		18 July 1950	H.J. Scoggan 8201 & W.K.W. Baldwin (WIN-22434)
1399*	T304	A	Canada, Manitoba: Fort-Chimo, Nouveau-Québec	58°07’N, 58°23’W		22 July 1963	A. Legault 6782 (COLO-491481)
B1436*	T324	A	Canada, Manitoba: Duck Lake (southeast arm of Nejanllini Lake), sand-gravel knoll at Hudson’s Bay Co. post	59-22 N, 97-46 W		19 August 1950	H.J. Scoggan 8288 & W.H.W. Baldwin (CAN-201506)
B1432*	T323	A	Canada, Newfoundland-Labrador: Esker area, 2 miles south of the 3049 ft. summit	51-53 N, 66-03 W	2750 ft	21 July 1967	Y. Mäkinen 67-925 (CAN-314758)
B1448*	T325	A	Canada, Saskatchewan: Northeastern Corner, Vicinity of Patterson Lake	59 55’N, 102 20’W		20 July 1963	G.W. Argus s.n. (CAN-282691)

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DNA	**Sheet No.**	**Sp.**	**Locality**	**Coord.**	**Elev.**	**Coll. date**	**Voucher specimen**
B1430*	T326	A	Canada, British Columbia: Pine Pass Quad, unnamed peak at mile 4.5 on finaly forks road	55°37'N, 123°21'W	4600 ft	12 July 1973	G.W. Argus 8831 (CAN 372267)
B1435*	T327	A	Canada, Québec: Lichteneger Lake Quad, Lac Jaucourt Region, ca. 5 Mi. East of CAN. Forestry SV	52°45'N, 74°07'W	1600 ft	16 July 1974	G.W. Argus 9221 (CAN 3779977)
1403*	T348	A	Canada, Québec: East Coast of James Bay, Boatswain Bay, rocky granite shore	ca. 51.83, -78.87		8 July 1947	W. Baldwin 406, I. Hustich, J. Kucyniak & R. Tuomikoski (CAN-17333)
1398	T356	A	Canada, Québec: Lac Payne	Circa 59°16' N, 73°25' W.		2 August 1965	A. Legault 7849 & S. Brisson (CCO-23398)
1402*	T343	A	Canada, Ontario: Hudson Bay Lowlands, diabase cliffs and ridges west of narrows between Hawley and Sutton Lakes	ca. 54.41530000, -84.69185556		4 July 1957	A.E. Porsild, W.K.W. Baldwin, H. & G. Sjors 19898 (CAN-278707)
1389*	T310	A	Canada, Ontario: Kenora District, Patricia Portion, Sutton ridges, summit of westernmost of pair of prominent 'cuestas', 3 mi. east of south central portion of Aquatuk Lake	54°19'N, 84°32'W		12 August 1980	J.L. Riley 11856 (CAN-462937)
1993	T399	A	USA, New Hampshire: Alpine Garden, Mt. Washington	ca. 44.27083333, -71.30555556		29 July 1899	W.W. Eggleston 1681 (RM-23379)
1145	P16-20	A	Argentina: Provincia Santa Cruz, Los Glaciares National Park, near El Chaltén, pathway (sendero) to Monte FitzRoy, 760 m south of the point where the path splits leading to either Laguna de Los Tres or to Lagunas Hija and Madre (via sendero Madre e Hija)	49°17'22.0" S, 72°56'57.1" W	732m (±6m)	21 January 2010	J. Starr 10020 & T. Villaverde
1146	P18A-1	A	Argentina: Provincia Santa Cruz, Los Glaciares National Park, near El Chaltén, east side of Ruta Nacional 23 leading to Lago del Desierto, ca. 800 m N of Laguna La Pava and 14 km south of the Prefectura Naval Argentina (P.N.A) on the south end of Lago del Desierto	49°10'43.1" S, 72°56'51.0" W	732m (±7m)	22 January 2010	J. Starr 10023 & T. Villaverde

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DNA	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
1125	P11-1	A	Argentina: Tierra del Fuego, Departamento Rio Grande, left bank of the Arroyo Damajuana, on the east side of Ruta D, 600 m south of the intersection of Ruta B and D at point where a small road leads to a house ca. 600 m west of Ruta D	53°55'56.3" S, 68°05'20.2" W	60m (±4m)	13 January 2010	J. Starr 10015 & T. Villaverde
1366	T081	A	Argentina: Neuquén, Dep Chos Mala, NW end of the Pampa Ferraina	36°43'S, 70°28'W	2300 m	30 January 1964	O.Boelcke, M.N.Correa, N.M.Bacigalupo et al., s.n. (BAA-11368)
1134	P11-10	A	Argentina: Tierra del Fuego, Departamento Rio Grande, left bank of the Arroyo Damajuana, on the east side of Ruta D, 600 m south of the intersection of Ruta B and D at point where a small road leads to a house ca. 600 m west of Ruta D	53°55'56.3" S, 68°05'20.2" W	60m (±4m)	13 January 2010	J. Starr 10015 & T. Villaverde
1135	P16-1	A	Argentina: Provincia Santa Cruz, Los Glaciares National Park, near El Chaltén, pathway (sendero) to Monte FitzRoy, 760 m south of the point where the path splits leading to either Laguna de Los Tres or to Lagunas Hija and Madre (via sendero Madre e Hija)	49°17'22.0" S, 72°56'57.1" W	732m (±6m)	21 January 2010	J. Starr 10020 & T. Villaverde
1325		A	Argentina, Sierra Baguales: Between Co. St. Lucia and the confluence of the rivers Baguales and mandolin	50°44'S, 72°20'W		16 January 1985	M.K. Arroyo 85201 (HIP-10500)
1148	P18A-20	A	Argentina: Provincia Santa Cruz, Los Glaciares National Park, near El Chaltén, east side of Ruta Nacional 23 leading to Lago del Desierto, ca. 800 m N of Laguna La Pava and 14 km south of the Prefectura Naval Argentina (P.N.A) on the south end of Lago del Desierto	49°10'43.1" S, 72°56'51.0" W	732m (±7m)	22 January 2010	J. Starr 10023 & T. Villaverde
B1442*	T321	Y	USA, Colorado: Clear Creek Co., Loch Lomond, between Mount Bancroft and James Peak	ca. 39.83472222, -105.67888889	11140 ft	8 August 1972	W.A. Weber, T. Koponen & P. Nelson s.n. (CAN-374041)
1489*	P30-1	Y	USA, Colorado: Lake Co., San Isabel National Forest, reached via Co. Road 4 beginning at Leadville. Wet meadow ca. 350 m N east of Hagerman Pass. Cirque below pass.	39°15'55.0" N, 106°28'45.6" W	3602 m (±5m)	25 July 2010	J. Starr 10S-030 & T. Villaverde

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DNA	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
1490	P30-2	Y	USA, Colorado: Lake Co., San Isabel National Forest, reached via Co. Road 4 beginning at Leadville. Wet meadow ca. 350 m N east of Hagerman Pass. Cirque below pass.	39°15’55.0” N, 106°28’45.6” W	3602 m (±5m)	25 July 2010	J. Starr 10S-030 & T. Villaverde
1491	P33-17	Y	USA, Colorado: Hinsdale Co., Gunnison National Forest, N east base of the southern and lower peak of Mesa Seco, along trail to Cannibal Plateau (ATV road), reached via Co. Road 50 and State Road 149 (Thread Byway). Alpine tundra ca. 300 m from the summit and 50 m lower in elevation.	38°01’31.7” N, 107°14’24.3” W	3834 m (±5m)	26 July 2010	J. Starr 10S-033 & T. Villaverde
1492	P33-22	Y	USA, Colorado: Hinsdale Co., Gunnison National Forest, N east base of the southern and lower peak of Mesa Seco, along trail to Cannibal Plateau (ATV road), reached via Co. Road 50 and State Road 149 (Thread Byway). Alpine tundra ca. 300 m from the summit and 50 m lower in elevation.	38°01’31.7” N, 107°14’24.3” W	3834 m (±5m)	26 July 2010	J. Starr 10S-033 & T. Villaverde
1493	P47A-22	Y	USA, Montana: Carbon Co., Custer National Forest, Absaroka-Beartooth Wilderness, Hellroaring Plateau, reached via Forest Route 421 which begins at US 212 (road to Greenough Lake, Limber Pine and Parkside Campgrounds). ca. 1 km SE of Snowbank Lake. Dense alpine tundra ca. 200 m N of trail.	45°01’55.3” N, 109°29’06.1” W	3137 m (±7m)	31 July 2010	J. Starr 10S-047A & T. Villaverde
1401	T280	Y	USA, Montana: Carbon Co., Beartooth Mountains, Hell Roaring Plateau	ca. 45.05883350, -109.47682970	9900 ft	11 August 1977	K.H. Lackshewitz 7790 (WTU-288770)
B1440*	T320	Y	USA, Utah: Duchesne Co., Uinta Mountains, North of Painter Basin	ca. 40.81111111, -110.33194444		15 August 1955	M.E. Lewis 512 (CAN-515168)
B1441*	T286	Y	USA, Utah: Duchesne Co., Ashley National Forest, Uinta Mtns., Uinta drainage, Gilbert Bench	ca. 39.33833333, -119.79222222	11500 ft	20 August 1996	S. Goodrich 25583, A. Huber & D. Prescott (BRY-392186)
1382*	T287	Y	USA, Utah: Duchesne Co., N edge of lake on Gilbert Creek, Gilbert Creek Basin, Uinta Drain., Uintah Mtns.	ca. 40.77805556, -110.23722222	11460 ft	25 August 1993	A. Huber & S. Goodrich 440 (BRY-368578)
1494	P47B-4	Y	USA, Wyoming: Park Co., Shoshone National Forest, Beartooth Plateau, reached via US 212. Wet to mesic tundra on flat or gentle slopes growing in boulder field ca. 500 m east of a sharp hairpin turn in the road near the summit of the Beartooth Pass and 750 m N east of Christmas Lake. Near summit of peak immediately to the N east of Christmas Lake	44°58’17.1” N, 109°25’14.6” W	3291 m (±6m)	31 July 2010	J. Starr 10S-047B & T. Villaverde

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DNA	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
1383*	T291	Y	USA, Wyoming: Park Co., Beartooth Plateau, 1/4 mile east of Twin Lakes, below Highway 212	ca. 45.05194444, -109.57416667		18 August 1984	B. Neely 2435 (COLO-399492)
B1449*	T322	Y	Canada, Alberta: Banff National Park, Snow Creek Pass, alpine tundra and hillsides west of pass	ca. 51.61055556, -115.82138889	7000 ft	29 July 1960	A.E. Porsild 22673 (CAN-266077)
1499	P61-5	Y	USA, Washington: Whatcom Co., Baker-Snoqualmie National Forest, N side of Mt. Baker. On summit of ridge leading to Chowder Ridge along Skyline Divide Trail reached via National Forest Develop Road 37 and Mount Baker Hwy. (SR 542) which passes through Glacier.	48°50’32.4” N, 121°51’27.9” W	1984 m (±6m)	11 August 2010	J. Starr 10S-061 & T. Villaverde
1500	P61-20	Y	USA, Washington: Whatcom Co., Baker-Snoqualmie National Forest, N side of Mt. Baker. On summit of ridge leading to Chowder Ridge along Skyline Divide Trail reached via National Forest Develop Road 37 and Mount Baker Hwy. (SR 542) which passes through Glacier.	48°50’32.4” N, 121°51’27.9” W	1984 m (±6m)	11 August 2010	J. Starr 10S-061 & T. Villaverde
1388	T251	Y	USA, California: Sierra Co., Tahoe, Anderson Mdw.	ca. 39.47833333, -120.29277778		25 June 1969	R.K. Gierisch & D.H. Esplin 3493 (RM-246761)
1495	P54-15	Y2	USA, California: Butte Co., near Cherry Hill Campground, Lassen National Forest, ca. 250 m N west of the point where Humboldt Road crosses Butte Creek.	40°06’09.1” N, 121°30’03.0” W	1441 m (±7m)	6 August 2010	J. Starr 10S-054 & T. Villaverde
1496	P54-5	Y2	USA, California: Butte Co., near Cherry Hill Campground, Lassen National Forest, ca. 250 m N west of the point where Humboldt Road crosses Butte Creek.	40°06’09.1” N, 121°30’03.0” W	1441 m (±7m)	6 August 2010	J. Starr 10S-054 & T. Villaverde
1379	JS06018	Y2	USA, California: Butte Co., Lassen National Forest, Forest Ranch, Cheery Hill meadows, near Cherry Hill campsite. Take Hwy 32 from Chico for ca. 42 km to Lomo where Humboldt Rd regins, then 10 km along road to site. ca. 200 m due N of the point where Humboldt Rd. crosses Butte Creek.	40°06’08.0” S, 121°30’03.0” W	1428 m	3 August 2006	J.R. Starr & J. Thibeault 06018 (CAN)

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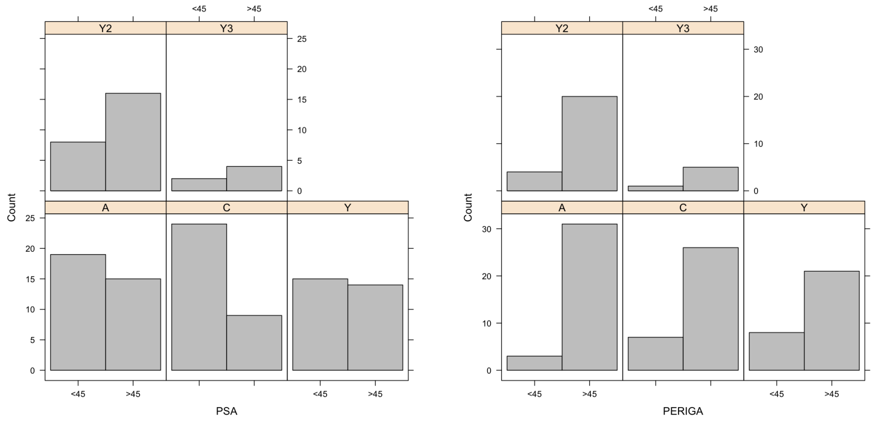
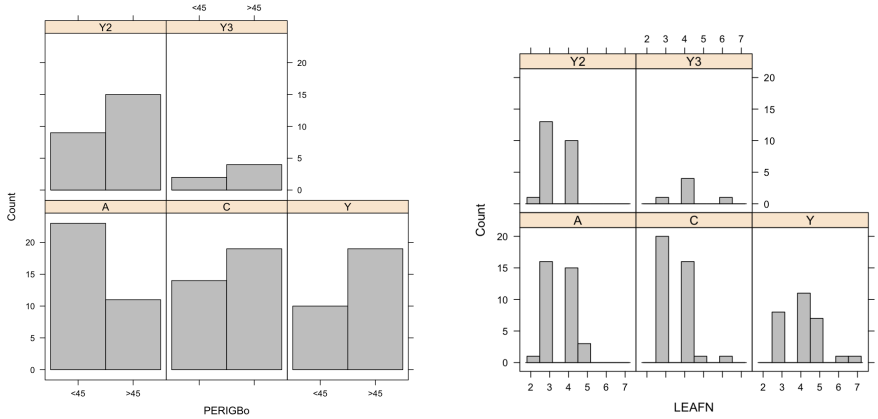
DNA	Sheet No.	Sp.	Locality	Coord.	Elev.	Coll. date	Voucher specimen
1384*	T248	Y2	USA, California: Tehama Co., about 50 yards east of the abandoned logging road, about 200 yards norteast of where the dirt road crosses Colby Creek, about 2 miles (air) Neast of Colby Mountain, about 5 1/8 miles (air) Neast of Butte Meadows	40°07'38.6"N, 121°29'27.5" W	5053 ft	19 July 2006	L. Ahart 13.051 (CHSC-94326)
1377*	T249	Y2	USA, California: Sierra Co., Yuba Pass-Weber Lake Road (Forest Rt. 12) 1.5 mi S of the road to Haypress Valley	ca. 39.495205, -120.411133	ca. 7200 ft	19 August 1996	V.H. Oswald & L. Ahart 8221 (CHSC-66824)
1386*	T284	Y2	USA, Oregon: Deschutes Co., W edge of wet meadow c.a. 1 mile N of Three Creeks Lake-near parking lot where Snow Creek flows through meadow	ca. 44.11444444, -121.62250000	1926 m	30 August 1982	C. Halpern 600 & T. Magge (OSC-159046)
1498	P57-11	Y2	USA, Oregon: Deschutes Co., Deschutes National Forest, at the entrance to Three Creek Campground, reached via National Forest Develop Road 16 and Three Creek Lake Road, which starts in Sisters. Light sloping wet meadow traversed by Three Creek adjacent to road. Along small tributaries and seeps leading to creek.	44°06'52.8" N, 121°37'26.6" W	1927 m (±5m)	9 August 2010	J. Starr 10S-057 & T. Villaverde
1497	P57-9	Y2	USA, Oregon: Deschutes Co., Deschutes National Forest, at the entrance to Three Creek Campground, reached via National Forest Develop Road 16 and Three Creek Lake Road, which starts in Sisters. Light sloping wet meadow traversed by Three Creek adjacent to road. Along small tributaries and seeps leading to creek.	44°06'52.8" N, 121°37'26.6" W	1927 m (±5m)	9 August 2010	J. Starr 10S-057 & T. Villaverde
1963*	T040	Y3	USA, California: Tulare Co., Sierra Nevada, Army Pass	ca. 36.49957222, -118.24830000	12000 ft	5 August 1949	J.T. Howell s.n. (DAO-257423)
1962*	T252	Y3	USA, California: Mono Co., Mt. Dana Plateau	ca. 37.92166667, -119.21472222	11500 ft	25 July 1979	D. Taylor 7550 (COLO-330874)

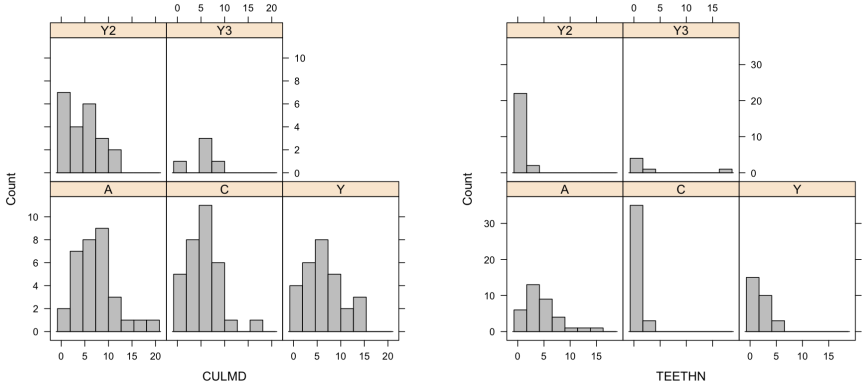
A.3 Supplementary material for Chapter 2



(a) Top angle of the pistillate scale (b) Perigynium beak inclination: Straight or bended



(c) Perigynium bottom angle (d) Leaf number



(e) Number of teeth under the spike (f) Teeth number

Figure A.1: Histograms of the six discrete variables scored for the morphometric study. *C. capitata* (C), *C. arctogena* (A), *"C. cayouetteana"* (Y), *Carex sp. nov. 1* (Y2) and *Carex sp. nov. 2* (Y3). X axis represents the measurements and Y axis the number of specimens.

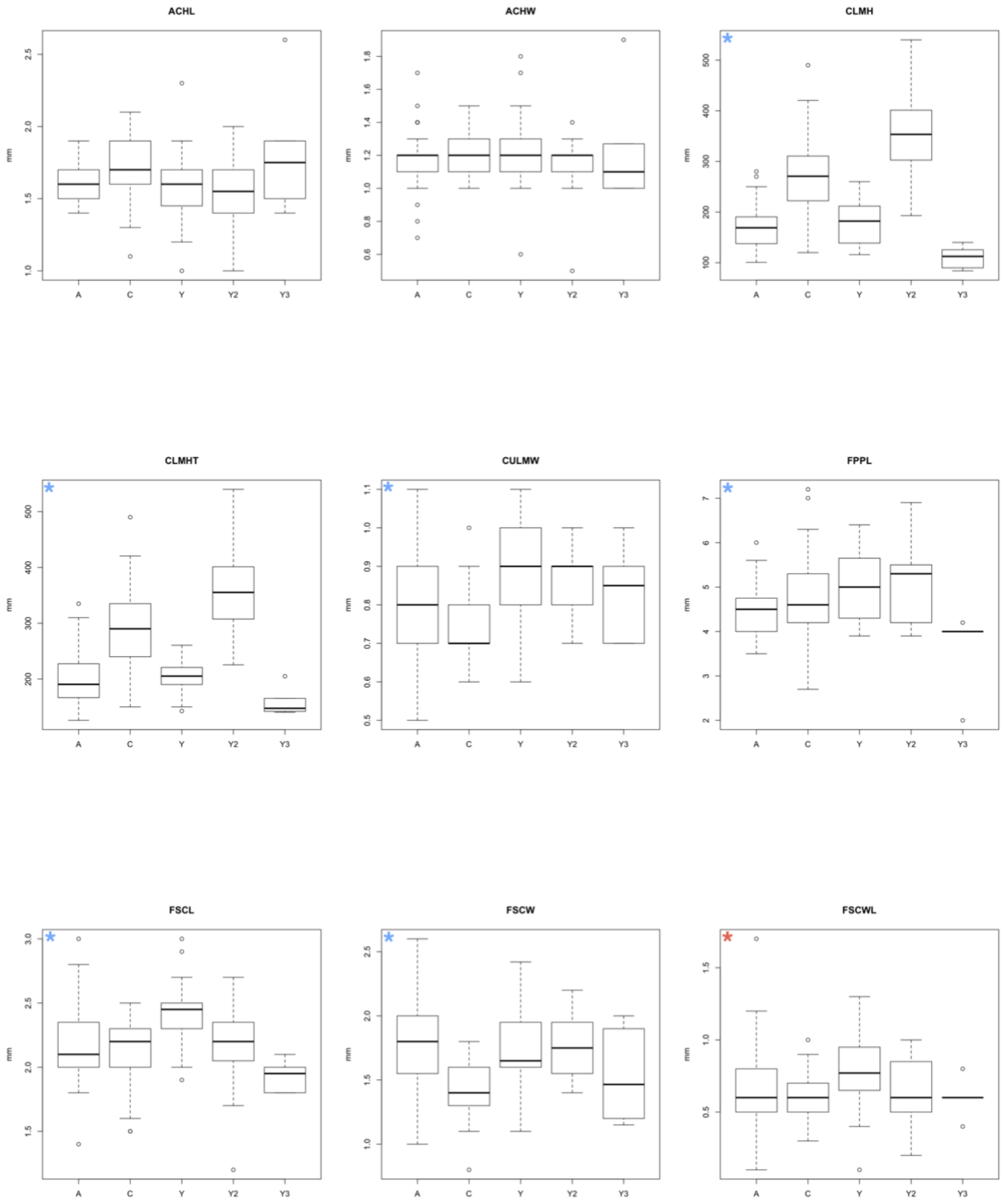


Figure A.2: Box plots showing mean interspecific differences between *C. capitata* (C), *C. arctogena* (A), *"C. cayouetteana"* (Y), *Carex sp. nov. 1* (Y2) and *Carex sp. nov. 2* (Y3) for twenty two quantitative and continuous variables. Asterisks to the left of each box denote level of statistical significance based on a Kruskal-Wallis ANOVA. Blue denotes $P<0.01$ and red $P<0.05$. Characters are alphabetically arranged. A full description of the characters is given in Table 2.5.

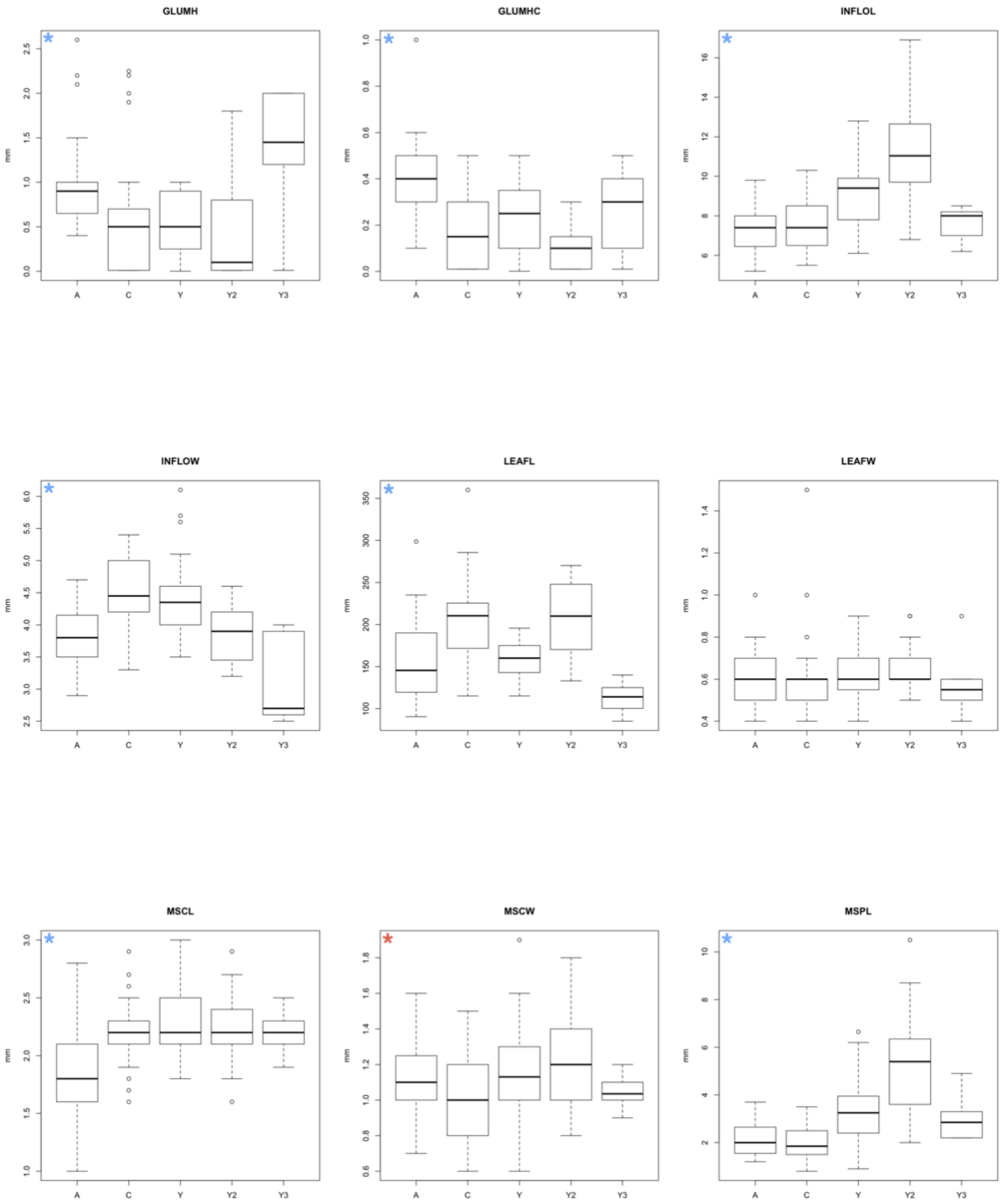


Figure A.3: (Continued) Box plots showing mean interspecific differences between *C. capitata* (C), *C. arctogena* (A), *"C. cayouetteana"* (Y), *Carex sp. nov. 1* (Y2) and *Carex sp. nov. 2* (Y3) for twenty two quantitative and continuous variables. Asterisks to the left of each box denote level of statistical significance based on a Kruskal-Wallis ANOVA. Blue denotes P<0.01 and red P<0.05. Characters are alphabetically arranged. A full description of the characters is given in Table 2.5.

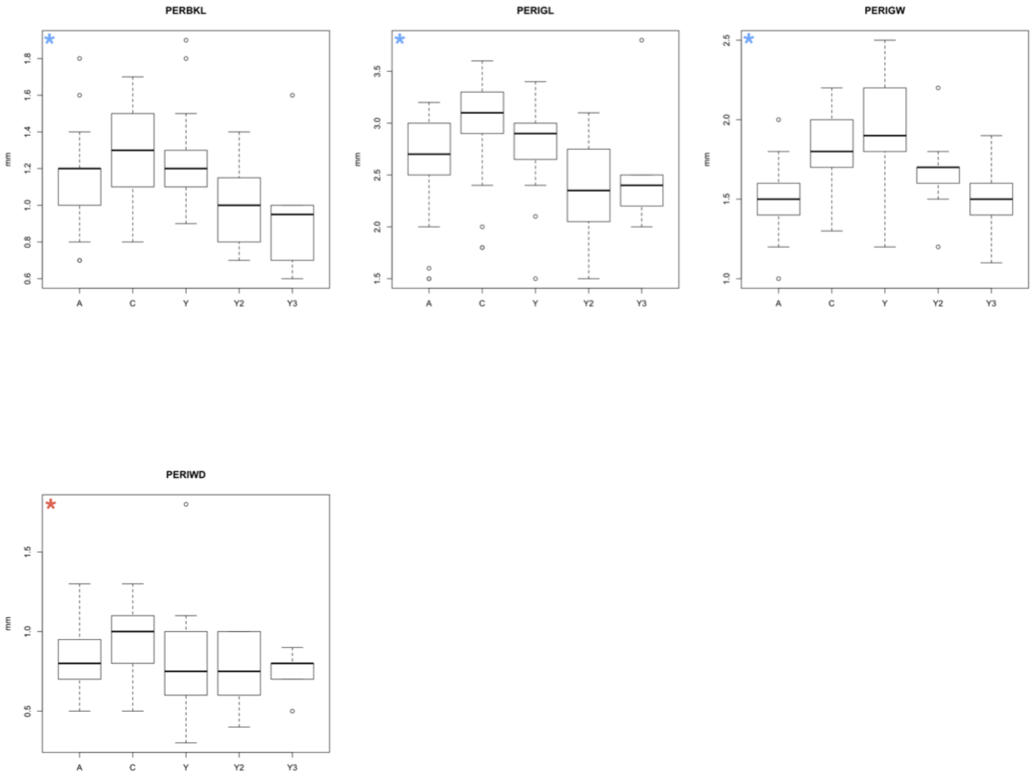


Figure A.4: (Continued) Box plots showing mean interspecific differences between *C. capitata* (C), *C. arctogena* (A), *"C. cayouetteana"* (Y), *Carex sp. nov. 1* (Y2) and *Carex sp. nov. 2* (Y3) for twenty two quantitative and continuous variables. Asterisks to the left of each box denote level of statistical significance based on a Kruskal-Wallis ANOVA. Blue denotes P<0.01 and red P<0.05. Characters are alphabetically arranged. A full description of the characters is given in Table 2.5.

Figure A.5: Pistillate scales (above) and periginia (below) of *C. capitata* (C), *C. arctogena* (A), *"C. cayouetteana"* (Y), *Carex sp. nov. 1* (Y2) and *Carex sp. nov. 2* (Y3).

Figure A.6: Holotype of *C. capitata* L. at LINN.

TYPUS

PLANTAE SUECICAE

№

Carex arctogena H. Sm.

Torne Lappmark: par. Karesuando, Moskana, södra delen mot Peldsavagge på vindskuren moränås intill snölägekärr.

Ca 1000 m s. m. 26. 7. 19~~48~~ 33

HARRY SMITH

Figure A.7: Holotype of *C. arctogena* Harry Sm. at DAO

Figure A.8: Holotype of *C. antarctogena* Roivanen at H.

A.4 Supplementary maps for Chapter 2

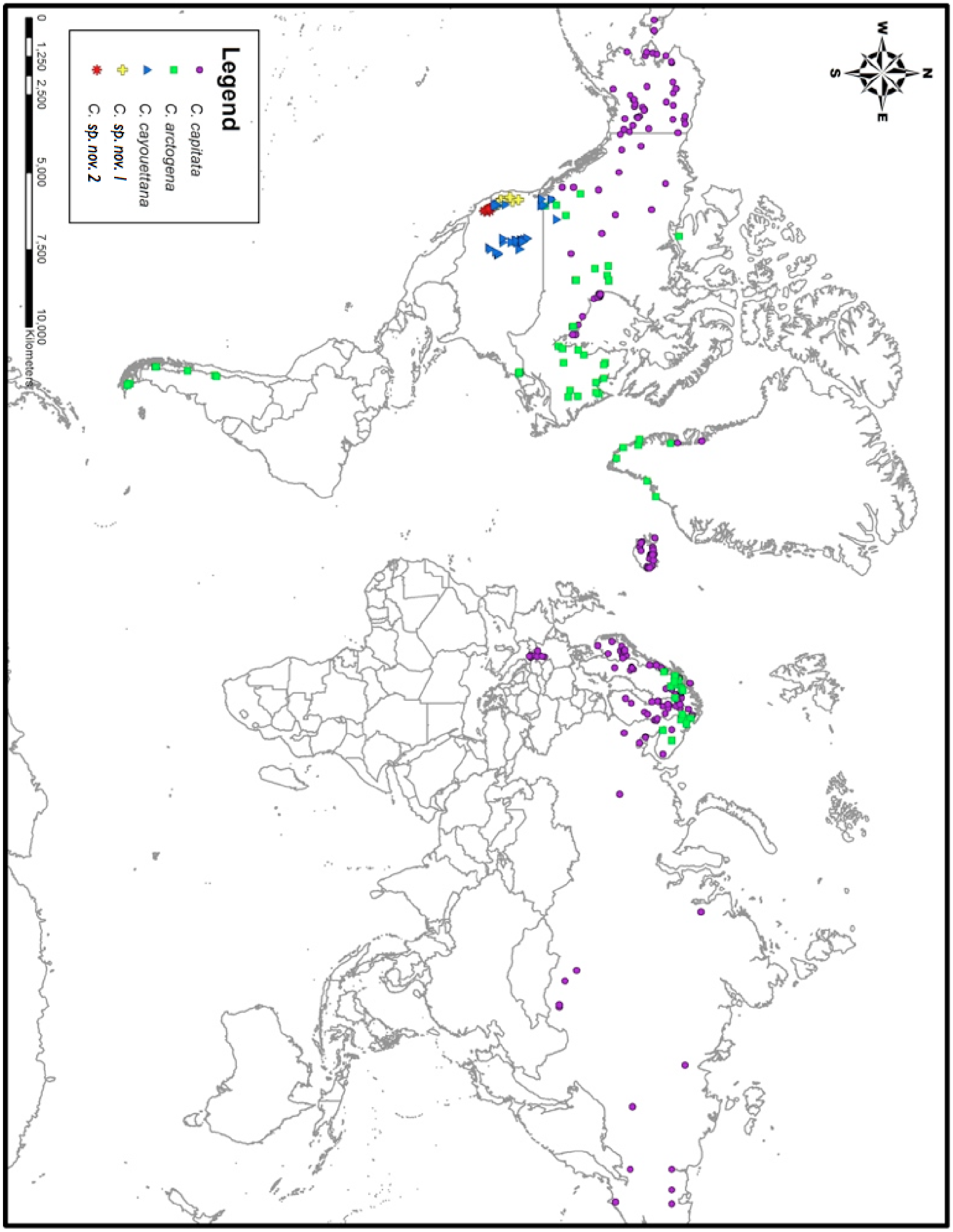


Figure A.9: The distribution of *C. capitata*, *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2* based on all the herbarium specimens examined in this study.

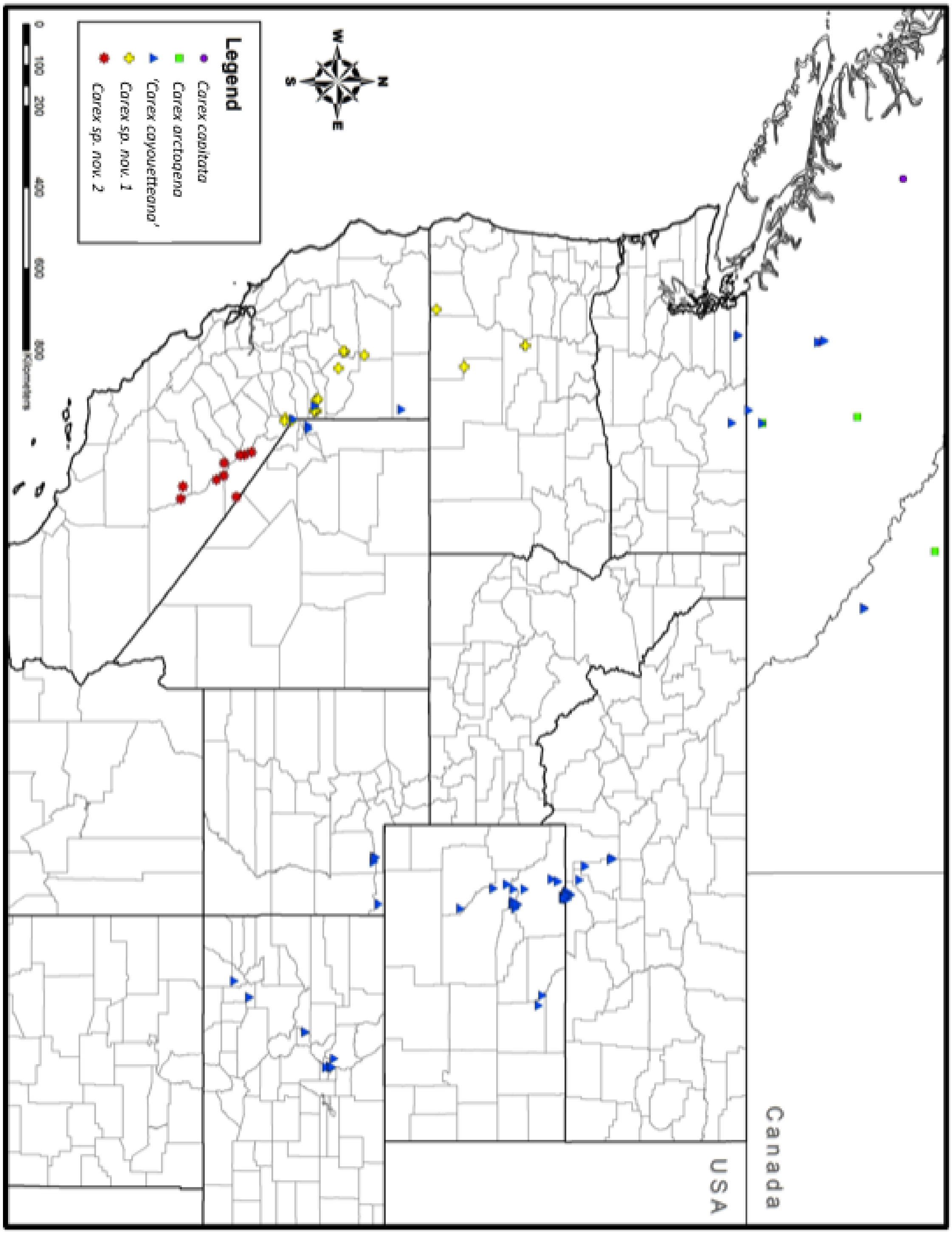


Figure A.10: The distribution of *C. capitata*, *C. arctogena*, *"C. cayouetteana"*, *Carex sp. nov. 1* and *Carex sp. nov. 2* in North America based on all the herbarium specimens examined in this study.

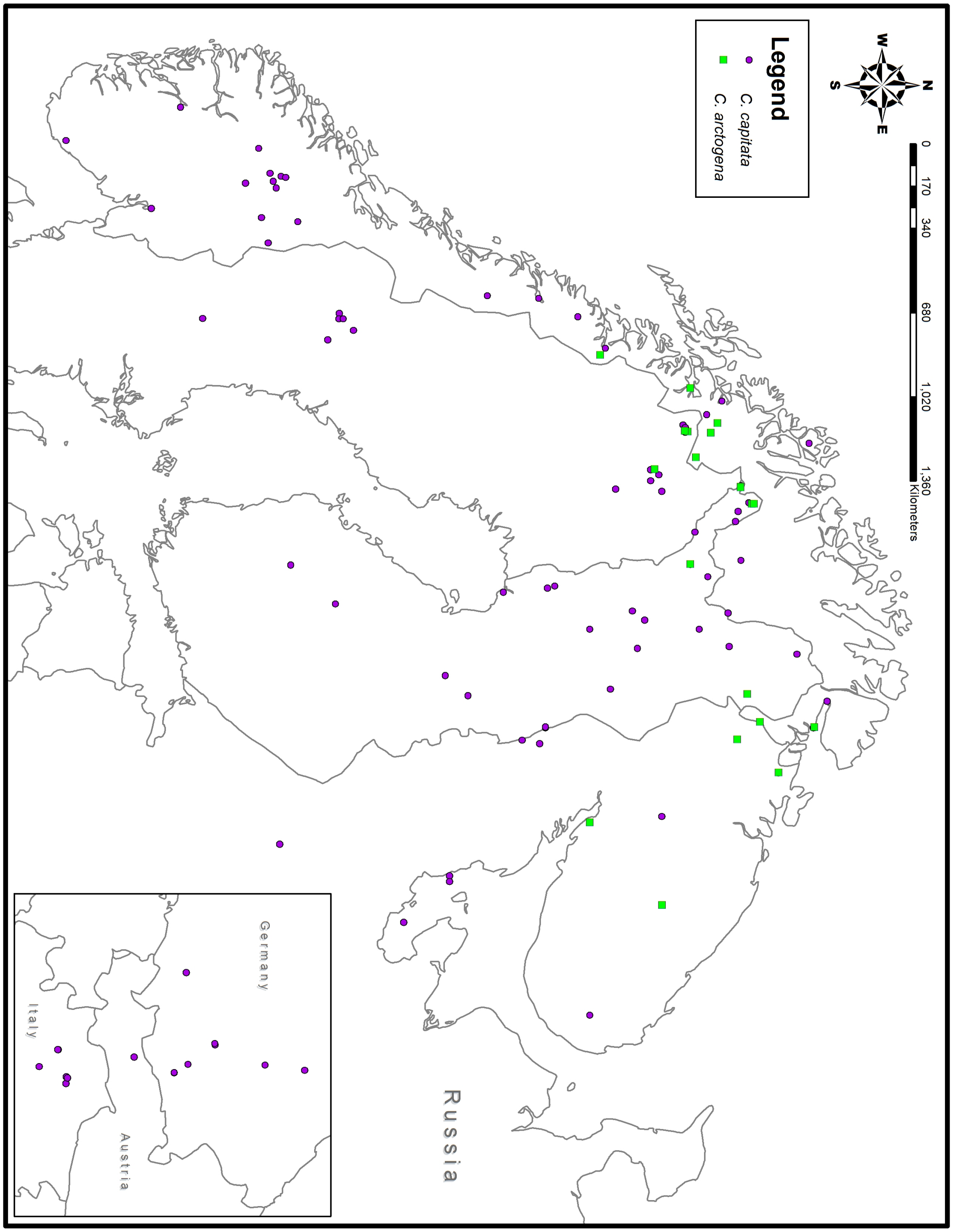


Figure A.11: The distribution of *Carex capitata* and *C. arctogena* in Europe based on all specimens examined in this study.

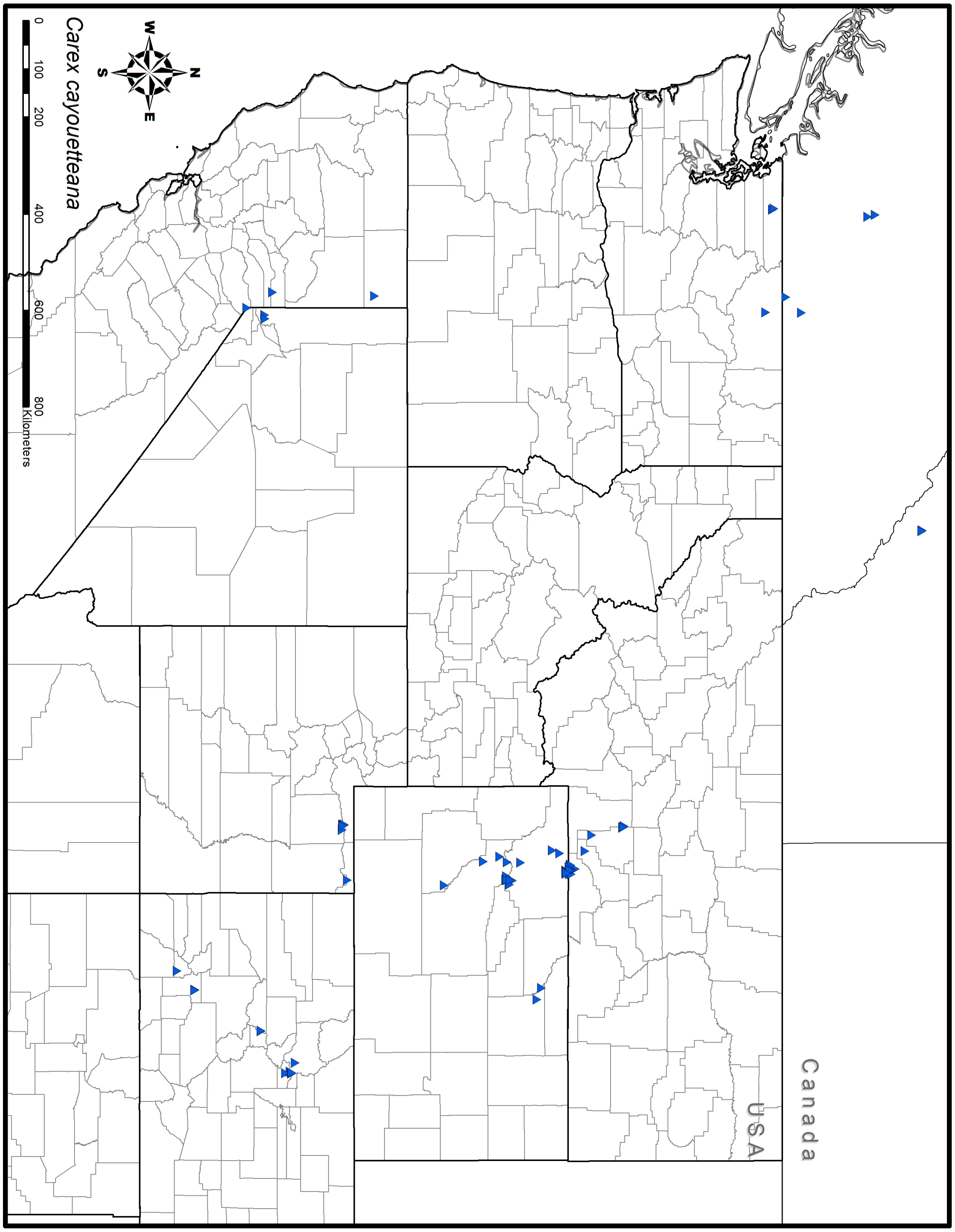


Figure A.12: The distribution of *"C. cayouetteana"* based on all the herbarium specimens examined in this study.

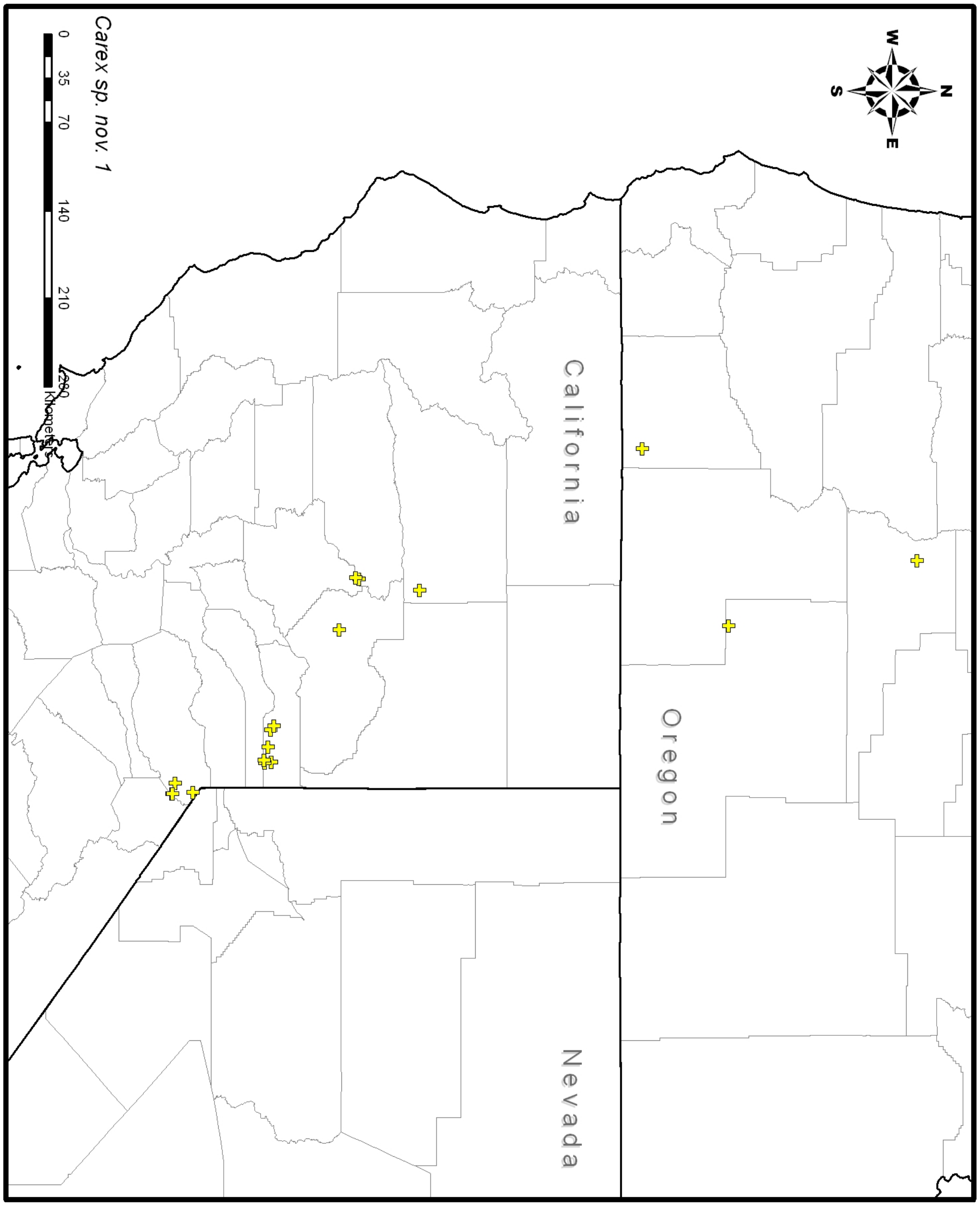


Figure A.13: The distribution of *Carex sp. nov. 1* based on all the herbarium specimens examined in this study.