

Chapter 11



Carex Sect. *Phyllostachyae*: The Value of a Multidisciplinary Approach in Conducting Systematics Studies in Sedges

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ABSTRACT Over the past 20 years, taxonomic novelties within *Carex* L. have been discovered at an unprecedented rate. For the most part, discovery has been a gradual process involving the analysis of existing specimens and the use of a variety of data sources. Our studies of *Carex* sect. *Phyllostachyae* Tuck. ex Kük. serve as a striking example of this recent pattern of discovery. A detailed examination of herbarium specimens and extensive fieldwork alerted us to the presence of significant taxonomic variation. Macro- and micromorphologic, anatomic, genetic, and phytogeographic data were then used to test our initial taxonomic hypotheses. As a result of our research, the number of species now recognized in section *Phyllostachyae* doubled over a 10-year period. Our clarified understanding of species limits allowed the generation of phylogenetic hypotheses that were unencumbered by a poorly resolved taxonomy. Cladistic analyses of sequences from the internal and external transcribed spacer regions of nuclear ribosomal DNA, plus morphologic data, have shown that section *Phyllostachyae* is monophyletic and is composed of three clades. Scales that do not conceal the perigynia, filiform stigmas, and relatively large numbers of staminate flowers characterize the narrow-scaled clade (*C. basiantha* Steud., *C. jamesii* Schwein., *C. juniperorum* Catling, Reznicek & Crins, *C. superata* Naczi, Reznicek & B. A. Ford, *C. timida* Naczi & B. A. Ford, *C. willdenowii* Willd.), while species in the wide-scaled clade (*C. backii* Boott in Hook., *C. cordillerana* Saarela & B. A. Ford, *C. saximontana* Mack.) are distinguished by pistillate scales that conceal the perigynia, thick stigmas, and relatively small numbers of staminate flowers. *Carex latebracteata* Waterf., with its much larger perigynia, absence of lateral spikes, and tightly coiled stigmas, is sister to both the wide- and narrow-scaled clades. Our studies emphasize the benefits of a sectional-level investigation and the advantage of a multidisciplinary approach to systematics studies in sedges. Our research also provides suggestions for future systematics research on *Carex*.

KEY WORDS *Carex* sect. *Phyllostachyae*, multidisciplinary research, new species, phylogeny, systematics.

The genus *Carex* L. offers exceptional challenges for systematics research. The large number of species (ca. 2000), the uncertainty of infrageneric relationships, the reduced reproductive structures, and the existence of many species-level taxonomic problems have hindered efforts to delimit taxa and to understand their phylogenetic relationships (Crins & Ball, 1988; Crins, 1990; Ball & Reznicek, 2002). While recent higher-level phylogenetic studies have provided novel hypotheses regarding infrageneric relationships (Starr et al., 1999, 2004, 2008; Yen & Olmstead, 2000; Roalson et al., 2001), many of the most persistent problems in *Carex* revolve around the circumscription of species and sections (e.g., Reznicek & Ball, 1980; Reznicek, 1986; Crins & Ball, 1988; Naczi, 1992, 2002; Crins & Rettig, 2002; Waterway, 2002). Significant advancements in terms of the discovery of new taxa and in understanding phylogenetic relationships can be achieved through a sectional-level approach to systematics. The reasons for this are many. First, the relatively small size of most sections (< 30 species) allows for the in-depth study of interspecific and intraspecific variation and the resolution of taxonomic problems. Second, the accuracy of results can be practically assessed through the examination of multiple data sets. Third, the phylogenetic position of sections can be determined through a comparison with representatives from putatively related sections. Finally, it allows systematists to relatively easily test the monophyly of sections and clarify sectional limits. As a result of these investigations, sampling strategies can be refined for higher-level phylogenetic studies of both *Carex* and the Cariceae Kunth ex Dumort.

With this philosophy in mind, we have been studying *Carex* sect. *Phyllostachyae* Tuck. ex Kük., a small, well-defined group of woodland carices endemic to North America (see Naczi and Ford [2001] for a discussion of sectional nomenclature). This is one of the most clearly marked groups of sedges, with species characterized by reduced staminate portions of the inflorescences, large, foliaceous pistillate scales, and culms that are strongly dilated at their apices. Several factors favored the selection of section *Phyllostachyae* for our research. These included (1) a clear delimitation from other sections; (2) tractability in terms of number of species and availability of specimens; (3) high levels of intraspe-

Table 1. Comparison of the taxonomy of *Carex* sect. *Phyllostachyae* in 1992 versus 2008. Question mark indicates the controversial taxonomic status of *C. saximontana* prior to the studies by Starr and Ford (2001) and Saarela and Ford (2001).

1992 (4–5 species)	2008 (10 species)
<i>C. backii</i> <i>C. saximontana?</i> →	<i>C. backii</i> Boott in Hook., 1839 <i>C. saximontana</i> Mack., 1906 <i>C. cordillerana</i> Saarela & B. A. Ford, 2001
<i>C. latebracteata</i> →	<i>C. latebracteata</i> Waterf., 1954
<i>C. jamesii</i> →	<i>C. jamesii</i> Schwein., 1824 <i>C. juniperorum</i> Catling, Reznicek & Crins, 1993 <i>C. timida</i> Naczi & B. A. Ford, 2001
<i>C. willdenowii</i> →	<i>C. willdenowii</i> Willd., 1805 <i>C. superata</i> Naczi, Reznicek & B. A. Ford, 1998 <i>C. basiantha</i> Steud., 1855

cific variation suggesting the presence of additional taxa; and (4) a highly reduced and unusual inflorescence morphology that had led to wide speculation concerning the origin of the section and its systematic position within the genus.

This paper presents an overview of aspects of our research conducted on section *Phyllostachyae* over the past decade (Ford et al., 1998a, b, c; Naczi et al., 1998; Starr et al., 1999; Ford & Naczi, 2001; Naczi & Ford, 2001; Saarela & Ford, 2001; Starr & Ford, 2001; Starr & Ford, unpubl. data). Here we provide a synopsis of our systematic research highlighting a much larger trend of taxonomic discovery in *Carex*. We also examine the phylogenetic position of section *Phyllostachyae* in the genus and the relationships among its species. Our studies emphasize the benefits of a sectional-level investigation and the advantage of a multidisciplinary approach to systematics studies in sedges.

TAXONOMY OF CAREX SECT. PHYLLOSTACHYAE

One of the most unexpected findings of our research has been the discovery of a proportionately large number of previously undetected or undescribed species in section *Phyllostachyae*. The number of species now recognized doubled over a

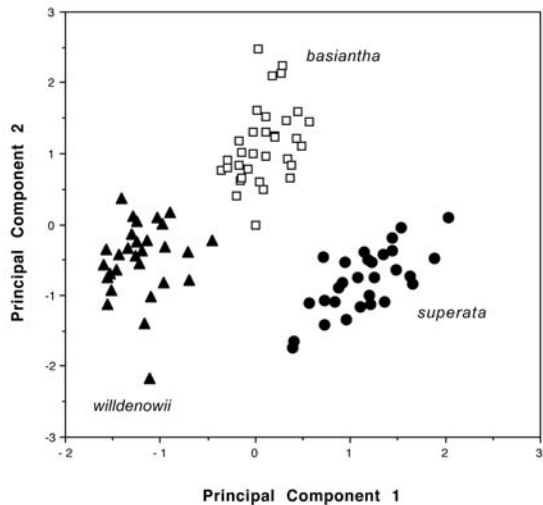


Figure 1. Scatter plot of the scores from Principal Components 1 and 2 for 92 specimens representative of the *Carex willdenowii* complex (Naczi et al., 1998). Reproduced with permission; copyright Botanical Society of America.

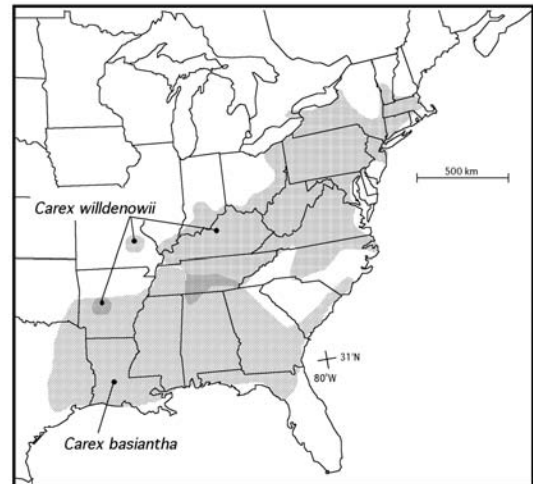


Figure 2. Geographic distribution of *Carex basiantha* and *C. willdenowii* (based on Naczi et al., 1998).

10-year period (Table 1). In all cases these new species turned out to be members of widespread species complexes that were masquerading under a single name (*Carex willdenowii* Willd., *C. jamesii* Schwein., or *C. backii* Boott in Hook.). It was only after the examination of herbarium specimens and extensive fieldwork, especially becoming familiar with regional variation and syntopy of different taxa, that we were alerted to the presence of significant taxonomic variation within each taxon. Macro- and micromorphologic, anatomic, genetic, and phytogeographic data were invaluable in substantiating our taxonomic hypotheses. The following summarizes the findings from our taxonomic investigations.

CAREX WILLDENOWII COMPLEX

Carex willdenowii s.l. is a distinctive taxon that can be distinguished from other species in section *Phyllostachyae* by the combination of nonconcealing, hyaline-margined pistillate scales, perigynia with gradually tapering beaks, obtuse staminate scales, filiform stigmas, and relatively large numbers of staminate flowers. This taxon and *C. jamesii* s.l. make up the narrow-scaled clade of section *Phyllostachyae* (see section entitled “Phylogeny of *Carex* sect. *Phyllostachyae*”).

Carex willdenowii s. str. was described very early in the history of North American botanical exploration (Willdenow, 1805), and is a species that is universally recognized in the floras of eastern North America. *Carex basiantha* Steud. (Steudel, 1855) and *C. willdenowii* var. *megarrhyncha* F. J. Herm. (Hermann, 1954), on the other hand, are names that either languished in obscurity as synonyms of *C. willdenowii* (Kükenthal, 1909; Mackenzie, 1935) or were ignored (e.g., Radford et al., 1968; Jones & Coile, 1988; Wofford & Kral, 1993; Smith, 1994). Extensive fieldwork and an examination of herbarium material revealed that these names were in fact correlated with three distinctive morphologies: each found in a particular region of North America and each worthy of recognition at the species level.

A principal components analysis based on eight continuous macromorphologic characters, measured on 92 specimens, along with the construction of voucher-based distribution maps, confirmed our initial observations (Figs. 1–3) (Naczi et al., 1998). *Carex willdenowii* s. str. is widespread across the northeastern United States and is the smallest member of the complex. This sedge is characterized by short staminate portions in the inflorescence (usually 4.9–8.6 mm long), short perigynia (usually 4.5–5.7 mm long), and culms that are on average two thirds the length of plant height. The other two species,

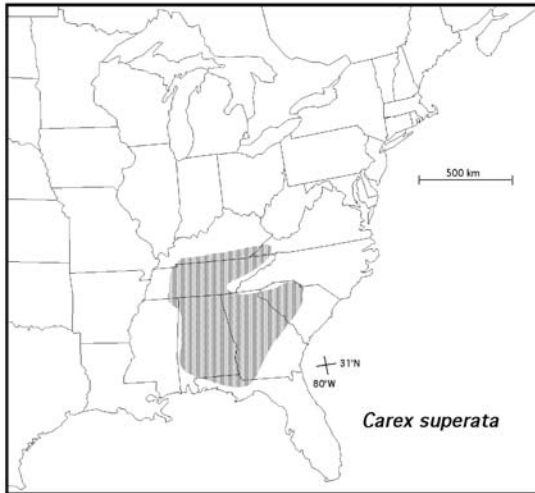


Figure 3. Geographic distribution of *Carex superata* (based on Naczi et al., 1998).

C. basiantha and *C. superata* Naczi, Reznicek & B. A. Ford (= *C. willdenowii* var. *megarrhyncha*), are found in the southeastern and south-central United States and are recognized by their longer staminate portions of terminal spikes (12.7–25.6 mm, 9.6–20.1 mm, respectively) and longer perigynia (5.8–8.0 mm, 7.5–10.8 mm, respectively). *Carex superata* is found in scattered locations throughout the Southeast and is easily distinguished from *C. basiantha* by its short culms, which are greatly exceeded by the foliage, and longer perigynia. In contrast, *C. basiantha* is identified by its tallest culms being on average two thirds the height of the plant and by its shorter perigynia. This species is widespread throughout the southeastern and south-central United States.

A wide body of other evidence also supported the recognition of three species in the *Carex willdenowii* complex. Though few differences could be found in leaf and culm anatomy, distinctive patterns were seen in the silica deposits in achene epidermal cells (Starr & Ford, 2001). In *C. basiantha*, the central platform is ruminant and flat, while in *C. superata* the surface is smooth and rises continuously to the top of the central body (Fig. 4). In contrast, *C. willdenowii* uniquely possesses a central platform with well-developed satellite bodies (Fig. 4).

Isozyme analysis also fully corroborated our morphologic and phytogeographic data (Ford et al.,

1998a). A cluster analysis of 14 populations, representing all three species, using Nei's (1978) unbiased genetic identity values, showed the presence of three distinct groups, with a close association evident between *Carex basiantha* and *C. superata* (Fig. 5). Interestingly, this same pattern of relationship was also recovered in a molecular phylogenetic study of section *Phyllostachyae* that showed *C. basiantha* and *C. superata* to be sister species (see section entitled "Phylogeny of *Carex* sect. *Phyllostachyae*").

Ecological trends were also apparent. While all three species inhabit deciduous forests, *Carex basiantha*, *C. superata*, and *C. willdenowii*, respectively, were found to track an environmental gradient related to increasing elevation on slopes and lower pH, moisture, and calcium levels in the soil (Naczi et al., 1998).

The combined evidence from our morphologic, phytogeographic, enzymatic, and ecologic studies clearly supported the recognition of three species in the *Carex willdenowii* complex.

CAREX JAMESII COMPLEX

Since the mid-1980s one of us (RFCN) had been aware of the presence of unusual populations of sedges in the southeastern and central United States that looked similar to *Carex jamesii* but differed in a number of key features. It was not until we had carried out morphologic, phylogenetic, and isozyme studies of section *Phyllostachyae*, and conducted extensive fieldwork throughout the eastern United States that we were able to determine both the taxonomic status of these populations and circumscribe the *C. jamesii* complex (Ford et al., 1998c; Ford & Naczi, 2001; Naczi & Ford, 2001). Based on our findings, the *C. jamesii* complex is composed of three species: *C. jamesii* s. str., *C. juniperorum* Catling, Reznicek & Crins, and *C. timida* Naczi & B. A. Ford. Morphologically and phylogenetically, this complex is closest to the *C. willdenowii* complex, but it can be distinguished by perigynium bodies that are abruptly contracted to beaks and truncate staminate scales. All three species of the *C. jamesii* complex share identical internal transcribed spacer (ITS) sequences (Starr, 1997; Starr et al., 1999; Starr & Ford, unpubl. data).

Principal components analysis based on nine continuous macromorphologic characters measured on 74 specimens, as well as micromorphologic studies, showed the presence of three distinct taxa (Figs.

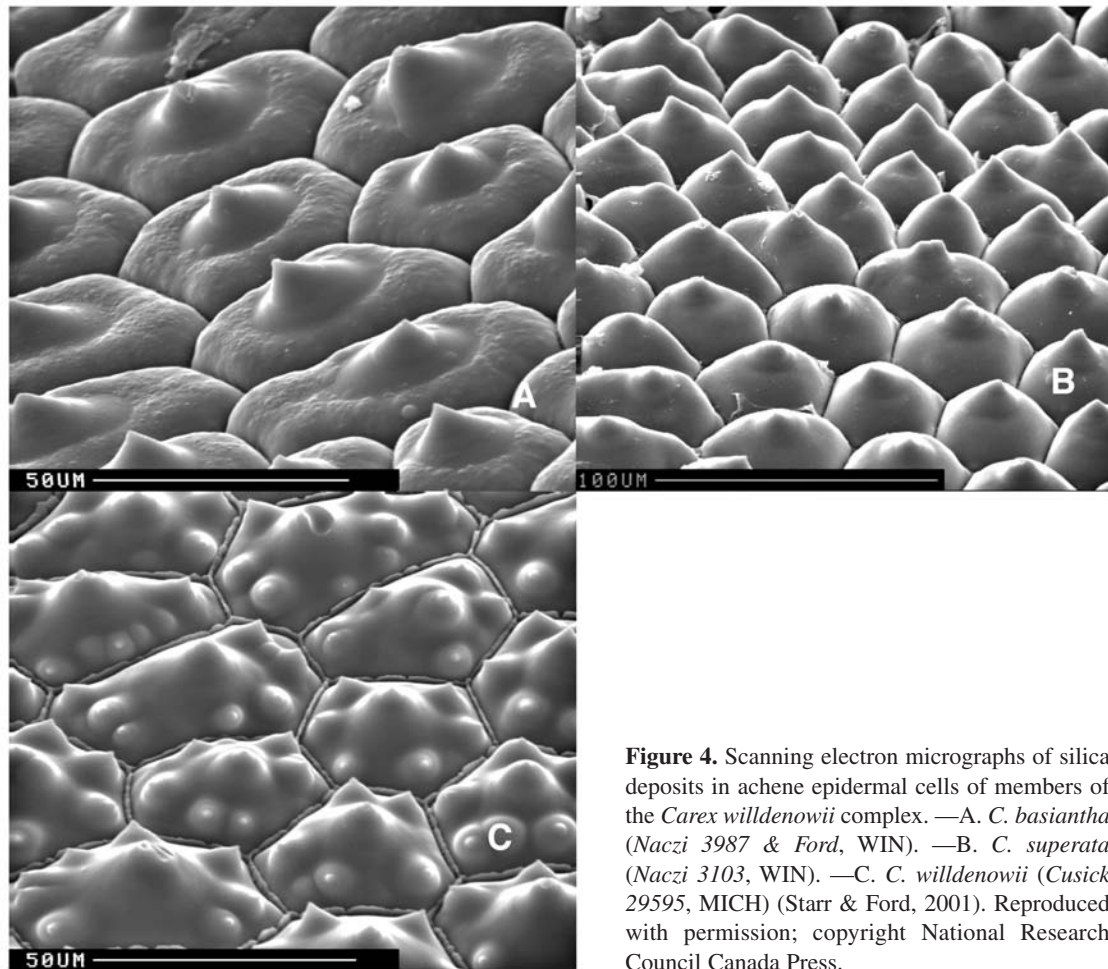


Figure 4. Scanning electron micrographs of silica deposits in achene epidermal cells of members of the *Carex willdenowii* complex. —A. *C. basiantha* (Naczi 3987 & Ford, WIN). —B. *C. superata* (Naczi 3103, WIN). —C. *C. willdenowii* (Cusick 29595, MICH) (Starr & Ford, 2001). Reproduced with permission; copyright National Research Council Canada Press.

6, 7) worthy of recognition at the species level. *Carex juniperorum* is the most divergent member of this complex and is distinguished by its short culms and lack of hyaline margins on the pistillate scales, five or more perigynia in an inflorescence, and red-purple cataphylls with bulging epidermal cells. *Carex jamesii* and *C. timida* possess elongate culms and pistillate scales with conspicuously hyaline margins, and one to three perigynia per inflorescence. Both species are morphologically very similar. However, *C. jamesii* has brown cataphylls with sunken epidermal cells, while the cataphyll morphology in *C. timida* is similar to that found in *C. juniperorum*. In addition, *C. timida* has very short staminate portions to the inflorescence relative to *C. jamesii* (usually 3.4–5.6 mm vs. 5.8–13.5 mm) and longer proximal staminate scales (usually 2.1–3.3 mm vs. 1.1–1.8 mm).

All three species are sympatrically distributed (Figs. 8, 9). *Carex jamesii* is found throughout much of the eastern and central United States and in southern Ontario, Canada. *Carex juniperorum* is much more localized, occurring in three disjunct areas: southeastern Ontario, southwestern Virginia, and the southern Ohio/northeastern Kentucky region. *Carex timida* is known from only 20 counties scattered between southwestern Ohio and easternmost Oklahoma. All three species inhabit mesic, calcareous, deciduous woodlands, with *C. juniperorum* and *C. timida* often found in habitats with a significant red juniper (*Juniperus virginiana* L.) component.

Isozyme data supported the recognition of three species in the *Carex jamesii* complex, although the distinction between species was not as clear as that found in our study of the *C. willdenowii* complex. Furthermore, the relationships implied in the cluster

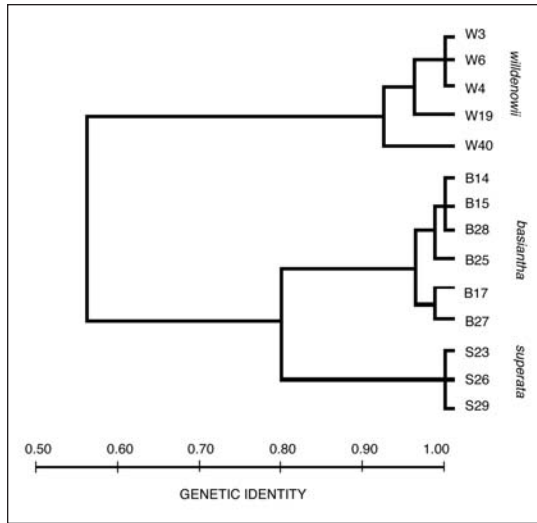


Figure 5. Dendrogram of 14 populations of the *Carex willdenowii* complex using Nei's (1978) unbiased genetic identities and unweighted pair group method with arithmetic averages (UPGMA) cluster analysis (Ford et al., 1998a). Reproduced with permission; copyright Botanical Society of America.

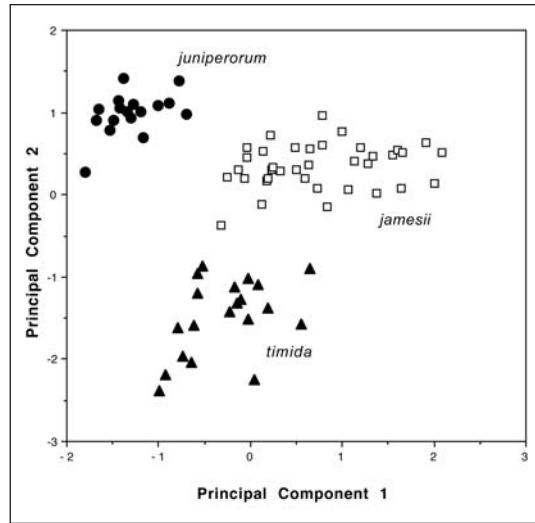


Figure 6. Scatter plot of the scores from Principal Components 1 and 2 for 74 specimens representative of the *Carex jamesii* complex (Naczi & Ford, 2001). Reproduced with permission; copyright Botanical Research Institute of Texas.

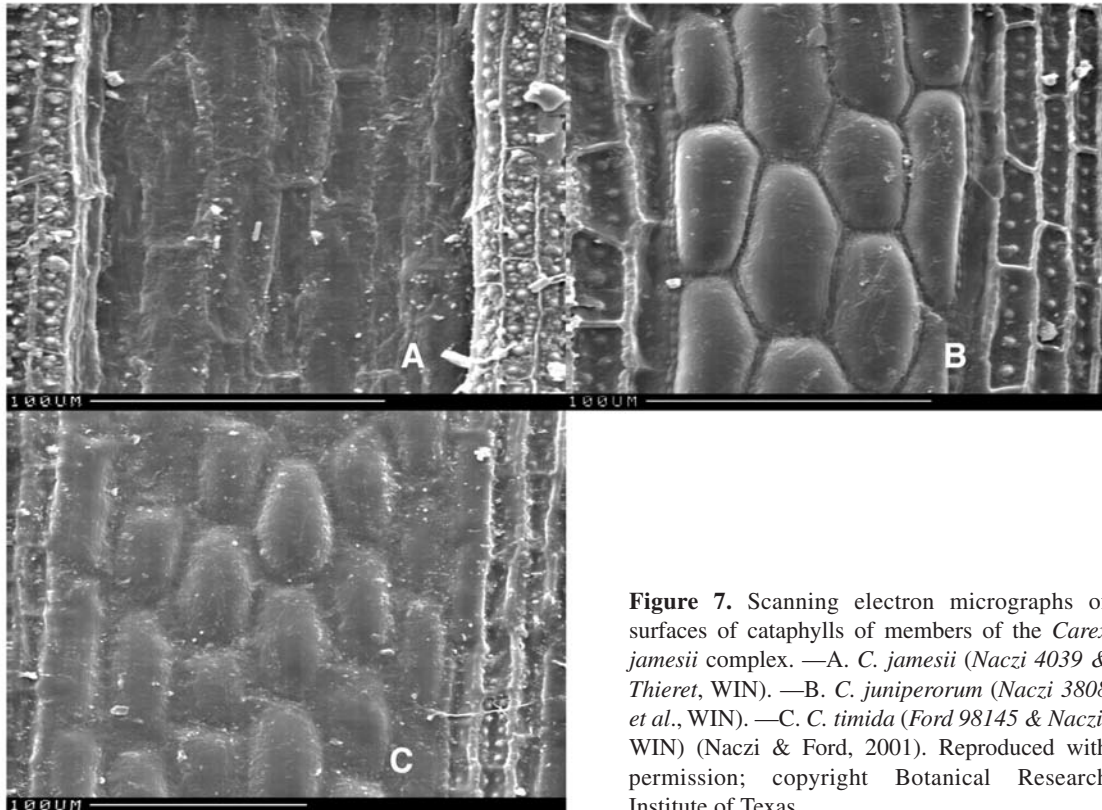


Figure 7. Scanning electron micrographs of surfaces of cataphylls of members of the *Carex jamesii* complex. —A. *C. jamesii* (Naczi 4039 & Thieret, WIN). —B. *C. juniperorum* (Naczi 3808 et al., WIN). —C. *C. timida* (Ford 98145 & Naczi, WIN) (Naczi & Ford, 2001). Reproduced with permission; copyright Botanical Research Institute of Texas.

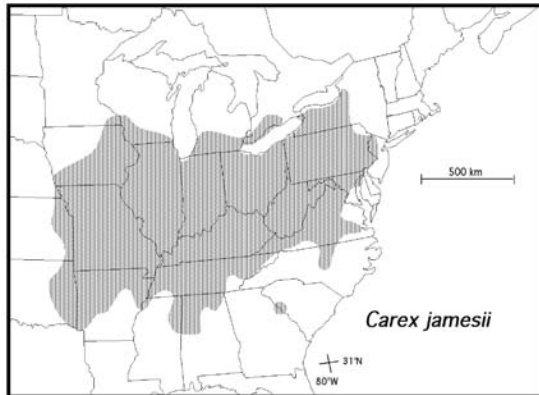


Figure 8. Geographic distribution of *Carex jamesii* (based on Naczi & Ford, 2001).

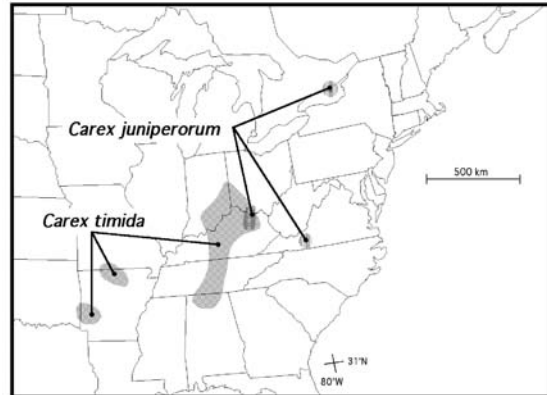


Figure 9. Geographic distribution of *Carex juniperorum* and *C. timida* (based on Naczi & Ford, 2001).

analysis of these data were not those intuitively expected based on our morphologic observations. For example, *C. jamesii* and *C. timida* were clearly separated from one another, despite their morphologic similarity (Fig. 10). On the other hand, *C. timida* and *C. juniperorum*, which are highly distinctive morphologically, were shown to be genetically similar. Interestingly, this close association is congruous with our phylogenetic studies (Naczi & Ford, 2001; see section entitled: “Phylogeny of *Carex* sect. *Phyllostachyae*”) that showed *C. juniperorum* and *C. timida* to be sister species. Populations from the Ouachita Mountains of Arkansas, which are genetically intermediate between the two species (populations 16 and 20, Fig. 10), were intriguing because morphologically these plants are clearly *C. timida*. These intermediate populations suggest that *C. timida* and *C. juniperorum* may have originated in the Ouachita Mountains. Alternatively, *C. juniperorum* may have originated from populations or a population of *C. timida* similar to those found in western Arkansas.

As was found in our study of *Carex willdenowii* s.l., micro- and macromorphologic characters, along with phylogeographic and isozyme data, supported the recognition of three species in the *C. jamesii* complex.

CAREX BACKII COMPLEX

Carex backii s.l. (*C. backii* s. str., *C. saximontana* Mack., and *C. cordillerana* Saarela & B. A. Ford = the wide-scaled clade—see section entitled “Phylogeny of *Carex* sect. *Phyllostachyae*”) is a distinctive taxon

that can be distinguished from other species in the section by a combination of characters, including thick stigmas, wide pistillate scales that conceal the perigynia, and extremely short staminate portions of the inflorescences. This species complex has had a rather checkered taxonomic past with various opinions expressed regarding both the number and rank of the taxa within this group. While some authors have chosen to recognize a single polymorphic species (*C. backii* s.l.), others recognize plants from the Great Plains as being distinct from *C. backii* s. str. [*C. saximontana* = *C. backii* var. *subrostrata* (Bates) Dorn]. Our research revealed that *C. backii* and *C. saximontana* are distinct species and that variability within *C. saximontana* includes a third taxon (*C. cordillerana*) (Saarela & Ford, 2001; Starr & Ford, 2001).

A discriminant functions analysis based on nine continuous macromorphologic characters measured on 79 specimens, along with anatomic, micromorphologic, and phylogeographic data, clearly showed the presence of three species within the *Carex backii* complex (Figs. 11–16). *Carex backii* s. str. is the most distinctive taxon in this group and is easily identified by its long perigynia (4.8–6.6 mm) with smooth surfaces, and long, smooth beaks (1.9–2.9 mm). Marginal sclerenchyma deposits, confined to the adaxial surface of the leaf, are also diagnostic. This is the most widely distributed species in the *C. backii* complex and is found throughout temperate and boreal regions of Canada and the adjacent United States, with disjunct populations found in western North America as far south as Colorado.

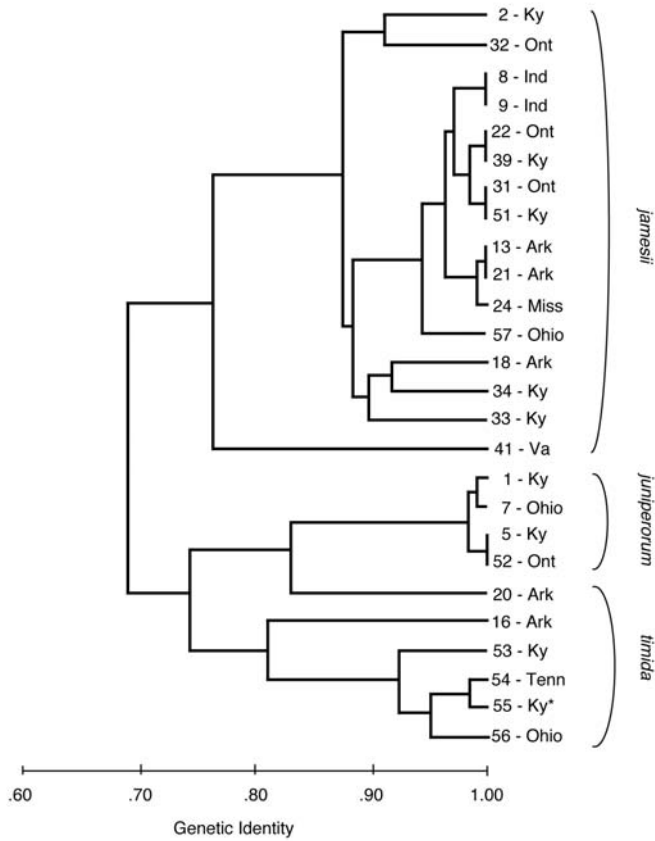


Figure 10. Dendrogram of 26 populations of the *Carex jamesii* complex using Nei's (1978) unbiased genetic identity values and UPGMA cluster analysis (Ford & Naczi, 2001). Reproduced with permission; copyright Botanical Research Institute of Texas.

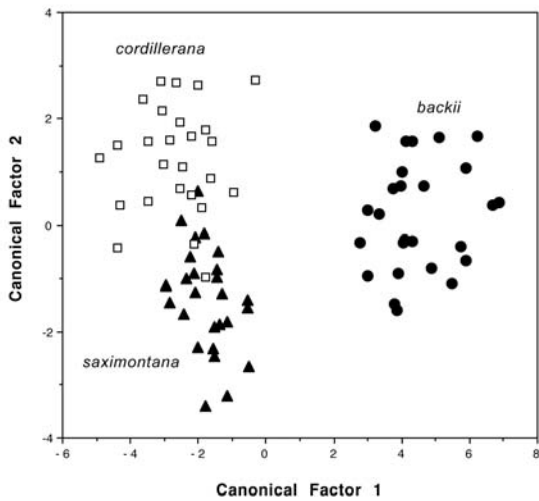


Figure 11. Scatter plot of the scores from Canonical Variates 1 and 2 for 79 specimens representative of the *Carex backii* complex (Saarela & Ford, 2001).

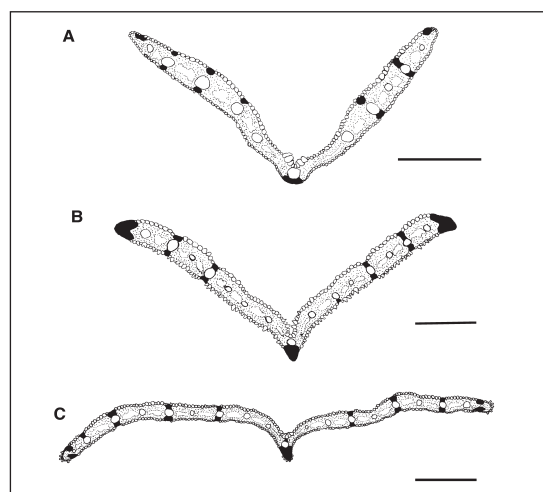


Figure 12. Leaf cross sections. —A. *Carex backii* (Ford *et al.* 94191, WIN). —B. *C. saximontana* (Ford 9526 & Starr, WIN). —C. *C. cordillerana* (Crofts 91-108, WS). Scale bars represent 0.5 mm. Darkened areas = sclerenchyma, stippled areas = chlorenchyma, stipple-bordered ellipses = air cavities, continuous circles between upper and lower surfaces = vascular bundles (Saarela & Ford, 2001).

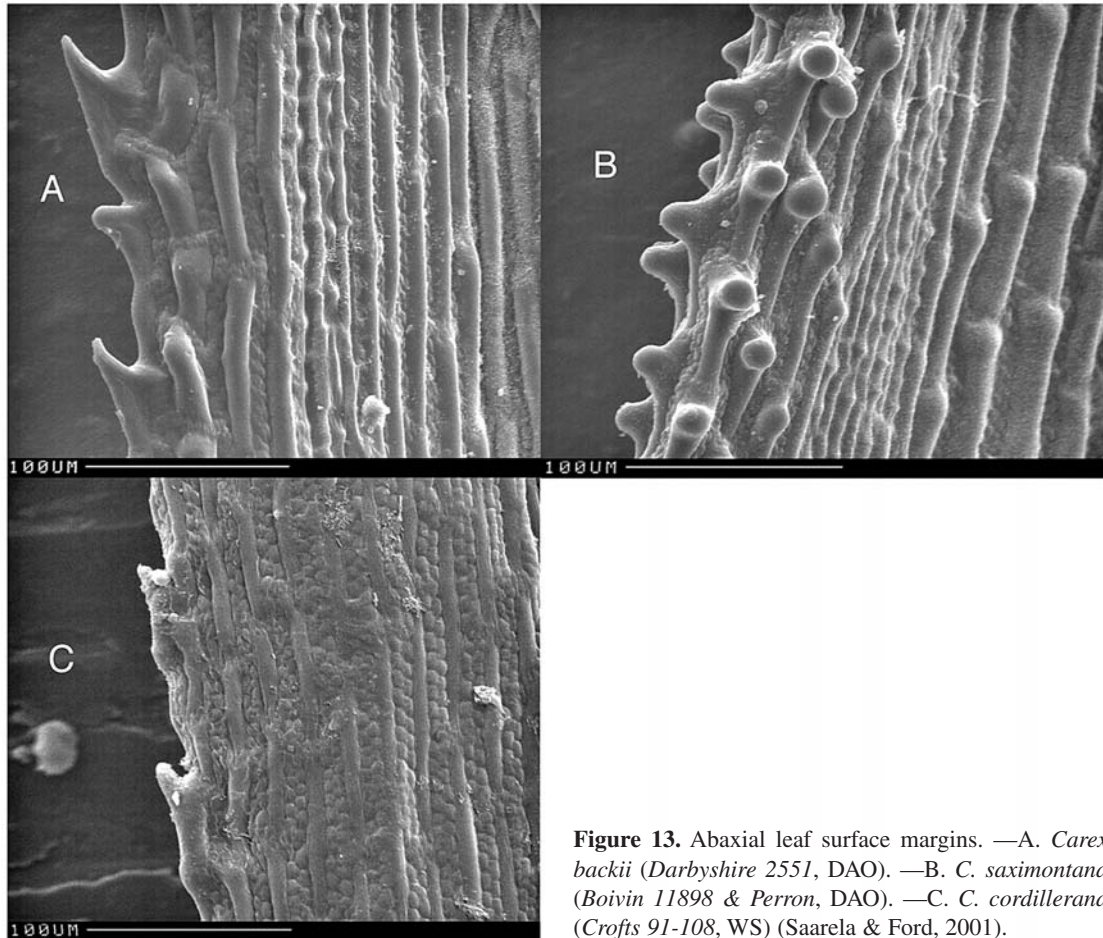


Figure 13. Abaxial leaf surface margins. —A. *Carex backii* (Darbyshire 2551, DAO). —B. *C. saximontana* (Boivin 11898 & Perron, DAO). —C. *C. cordillerana* (Crofts 91-108, WS) (Saarela & Ford, 2001).

Carex saximontana and *C. cordillerana* overlap in all quantitative characters measured, and as a result were incompletely separated in the discriminant functions analysis (Fig. 11). However, anatomic, micro-morphologic, and phytogeographic characters show a number of discontinuities supporting the recognition of these taxa at the species level (Figs. 12–14, 16). *Carex saximontana* is restricted to the Great Plains region of North America and is distinguished by its papillose perigynia and leaves that are greenish glaucous to dark herbage green (as described using the color charts of Rayner, 1970) with completely sclerified, hyaline margins. *Carex cordillerana*, on the other hand, has dull green to yellow-green leaves with green, densely papillate leaf margins that have sclerenchyma deposits found adjacent to the adaxial and abaxial surfaces. The perigynium surface appears smooth when examined with a dissecting microscope.

However, the epidermal cells have a distinctive convex morphology when viewed under higher magnification. *Carex cordillerana* is completely allopatric with *C. saximontana* and occurs from central British Columbia to northern Utah.

Isozyme studies have demonstrated that *Carex backii* and *C. saximontana* are distinct species despite the fact that they often occur together in mixed populations (see Ford et al., 1998c). Isozyme variation has not been examined in *C. cordillerana*. However, molecular phylogenetic studies have shown that this species, as well as others in the section, can be distinguished by one or more autapomorphies (see section entitled “Phylogeny of *Carex* sect. *Phyllostachyae*”).

The combined evidence demonstrated that *Carex backii* s.l. is composed of three distinct species. As with the other complexes previously

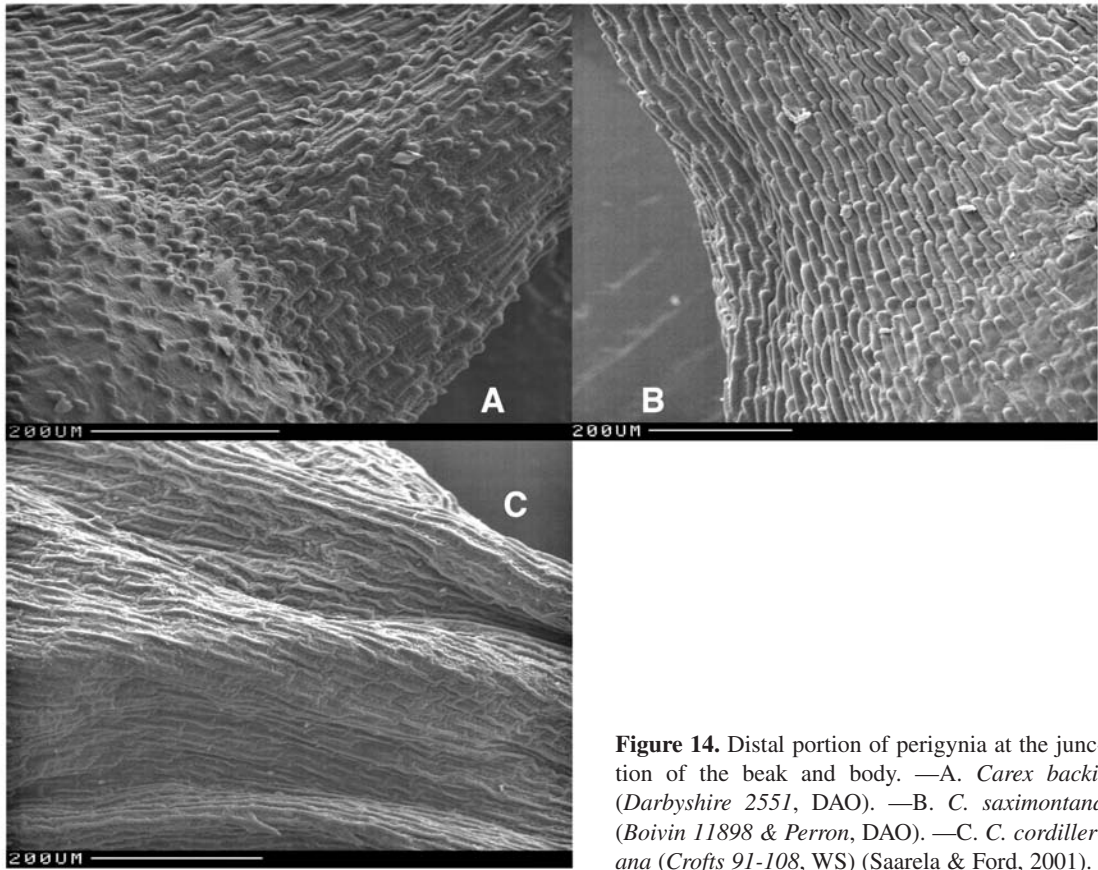


Figure 14. Distal portion of perigynia at the junction of the beak and body. —A. *Carex backii* (Darbyshire 2551, DAO). —B. *C. saximontana* (Boivin 11898 & Perron, DAO). —C. *C. cordillerana* (Crofts 91-108, WS) (Saarela & Ford, 2001).

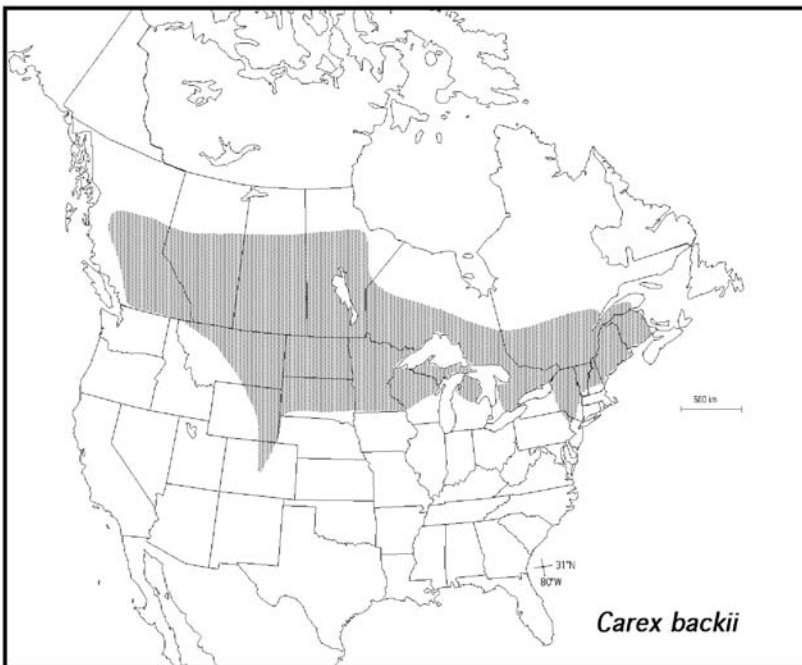


Figure 15. Geographic distribution of *Carex backii* (Saarela & Ford, 2001).

Carex backii

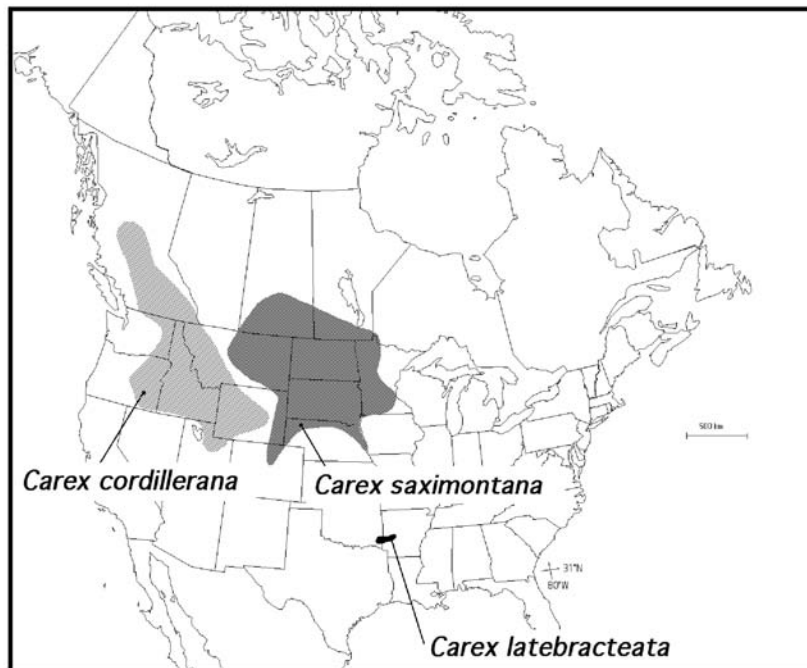


Figure 16. Geographic distribution of *Carex saximontana*, *C. cordillerana*, and *C. latebracteata* (Saarela & Ford, 2001).

described, this study has shown the value of delineating taxa through the integration of evidence from macromorphology, micromorphology, anatomy, phylogeography, and genetics.

CAREX LATEBRACTEATA

Carex latebracteata Waterf. is a narrow endemic from the Ouachita Mountains of Arkansas and eastern Oklahoma (Fig. 16) and is the only species in section *Phyllostachyae* that was found to contain no “hidden” taxa (Naczi & Ford, unpubl. data). *Carex latebracteata* is one of the most distinctive species in the genus. In the field it looks superficially more like an *Iris* L. than a *Carex*! Surprisingly, this species escaped detection until the 1950s when it was first described by Waterfall (1954). *Carex latebracteata* shares a number of features with *C. backii* and its allies (thickened stigmas, wide pistillate scales that conceal the perigynia, and extremely short staminate portions of the inflorescences) but is easily distinguished by its taller stature, much longer perigynia, absence of lateral spikes, and tightly coiled stigmas. Achene silica bodies that possess convex versus concave platforms and persistent outer periclinal walls are also diagnostic (Starr & Ford, 2001) (Fig. 17).

Until recently, we regarded *Carex latebracteata* as part of the wide-scaled clade but now understand that this clade includes only *C. backii* and its allies. *Carex latebracteata* is likely primitive within the section and sister to both the wide- and narrow-scaled clades (see section entitled “Phylogeny of *Carex* sect. *Phyllostachyae*”). A synopsis of the revised taxonomy of *Carex* sect. *Phyllostachyae*, including a key to all its species, appears in Crins et al. (2002).

TAXONOMIC CONCLUSIONS

Our taxonomic work on *Carex* sect. *Phyllostachyae* highlights two important points with respect to systematics work on *Carex*.

1. *The Carex flora of North America is not fully known.* The discovery of new species in *Carex* sect. *Phyllostachyae* is part of a larger trend of taxonomic discovery in *Carex* in general. On average two new taxa of *Carex* per year over the past 20 years have been described from North America: the vast majority of these being from the southeastern United States and western North America (Hartman & Nelson, 1998; Naczi et al., 1998, 2002; Ertter, 2000; Saarela & Ford, 2001). In recent years the rate of dis-

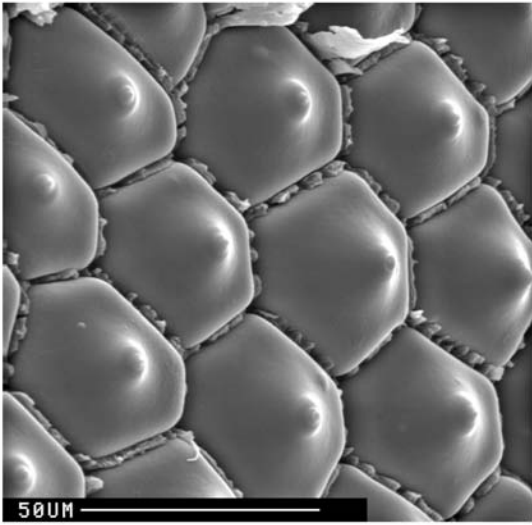


Figure 17. Scanning electron micrographs of silica deposits in achene epidermal cells of *Carex latebracteata* (Naczi 3953 & Ford, WIN).

covery has been even more dramatic. Twelve taxa were formally described in North American *Carex* between 2001 and 2002 (Naczi & Ford, unpubl. data). We predict that southeastern and western North America will continue to yield a proportionately large number of new sedge taxa. In particular, collections from known areas of endemism such as the Klamath (sensu Smith & Sawyer, 1988), Cascades, Sierra Nevada, Blue Ridge, and Ouachita Mountains, and the Queen Charlotte Islands should be carefully examined and compared with specimens from elsewhere in North America. Clearly the answer to such a basic question as “How many species of *Carex* occur in North America?” is far from answered.

2. *A multidisciplinary approach is critical in taxonomic studies of Carex.* The parsing of species diversity in section *Phyllostachyae* has not been a straightforward process involving the discovery of overtly distinct taxa in the field. Rather our “wholesale rethinking of the existing taxonomic framework” (Ertter, 2000: 95) has been a gradual process involving the comparison and analysis of existing specimens using a variety of data sources. Field observations, analyses of live material, and phyto-geographic studies have been critical to our research.

PHYLOGENY OF *CAREX* SECT. *PHYLLOSTACHYAE*

Molecular phylogenetic studies of *Carex* and the Cariceae by Starr et al. (1999, 2004, 2008), Yen and Olmstead (2000), and Roalson et al. (2001) have revolutionized our ideas regarding the evolution of *Carex*. These studies, while different in some aspects, show that all the genera within the Cariceae must be included within a more broadly circumscribed *Carex*. Within this more widely defined view of the genus, three main clades can be distinguished: (1) a compound clade, comprised largely of multispicate species traditionally placed in subgenus *Vigneastra* (Tuck.) Kük. [= *Indocarex* (Baill.) Kük. in Engl.], *Psyllophora* (Degl.) Peterm. (= *Primocarex* Kük in Engl.), and a portion of subgenus *Carex*; (2) a reduced clade made up predominantly of unispicate species traditionally placed in part of subgenus *Carex*, *Psyllophora*, plus all other genera in the Cariceae (*Cymophyllus* Mack., *Kobresia* Willd., *Uncinia* Pers., *Schoenoxiphium* Nees); and (3) subgenus *Vignea* (P. Beauv. ex T. Lestib.) Peterm. Sequence data from the ITS and external transcribed spacer (ETS) regions of nuclear ribosomal DNA (nrDNA) (ITS-1, ITS-2, ETS 1f) showed *Carex* sect. *Phyllostachyae* to be monophyletic and part of the reduced clade (Starr et al., 1999, 2004, 2008) with unispicate species in *Carex* sections *Firmiculmes* Kük. and *Filifoliae* (Tuck.) Mack., and *Cymophyllus fraserianus* (Ker Gawl.) Kartesz & Gandhi being sister to the *Phyllostachyae* (Starr et al., 1999, 2008; Starr & Ford, unpubl. data).

While phylogenetic relationships within section *Phyllostachyae* were explored by Starr et al. (1999), patterns of relationships were not fully resolved because of the limited data set (ITS data only). The research presented here incorporates both ITS and ETS 1f sequence data plus a suite of 20 morphologic characters. For our study we included all 10 species from section *Phyllostachyae* plus three outgroup taxa: *Carex filifolia* Nutt. (sect. *Filifoliae*), *C. geyeri* Boott (sect. *Firmiculmes*), and *Cymophyllus fraserianus*. Outgroup taxa were chosen on the basis of previous studies that had hypothesized that these species might be closely related to section *Phyllostachyae* (Starr et al., 1999, 2004, 2008; Starr & Ford, unpubl. data).

Maximum parsimony analysis yielded two most parsimonious trees with the strict consensus shown in Figure 18. The same topology is also recovered

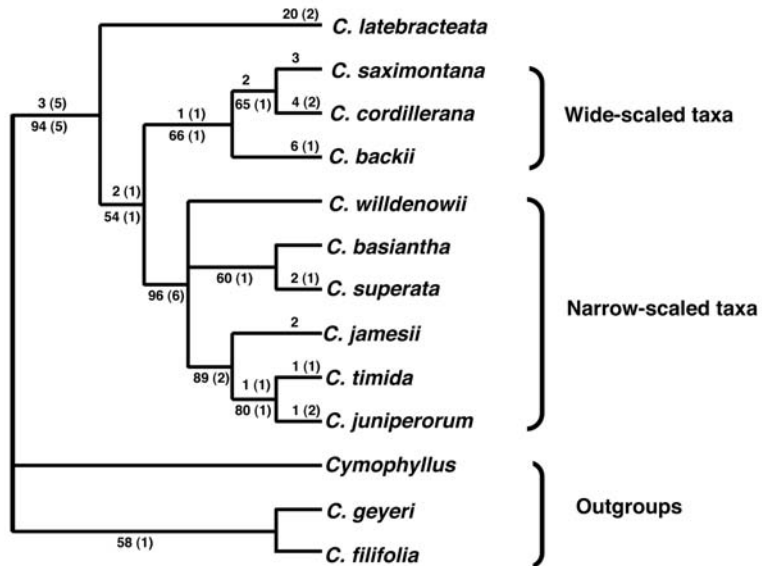


Figure 18. The strict consensus of two most parsimonious trees resulting from the phylogenetic analysis of *Carex* sect. *Phyllostachyae* using ITS, ETS 1f, and morphological data. Bootstrap and decay indices (in parentheses) are given below the branch. Molecular and morphological (in parentheses) apomorphies for the ingroup are given above the branch. Consistency index (CI) excluding uninformative characters = 0.65, retention index (RI) = 0.68.

using maximum likelihood. Analyses that excluded the morphologic data yielded identical results to a study based entirely on the combined data set (Starr & Ford, unpubl. data).

Our findings indicate that section *Phyllostachyae* is composed of three monophyletic groups. The narrow-scaled clade (*Carex basiantha*, *C. jamesii*, *C. juniperorum*, *C. superata*, *C. timida*, *C. willdenowii*) is characterized by scales that do not conceal the perigynia, filiform stigmas, and relatively large numbers of staminate flowers. In contrast, species in the wide-scaled clade (*C. backii*, *C. cordillerana*, *C. saximontana*) are distinguished by pistillate scales that conceal the perigynia, thick stigmas, and relatively small numbers of staminate flowers. *Carex latebracteata* is sister to both the wide- and narrow-scaled clades. Interestingly, it is not closely related to the members of the *C. backii* complex with which it had been previously associated (see Ford et al., 1998c). However, this relationship is consistent with the macro- and micromorphologic differences that have been noted in this taxon (see above). Bootstrap and decay values indicate at least moderate support for most clades, with the narrow-scaled clade and the *C. jamesii* complex having the highest values.

The relationships shown within the various species complexes are comparable to those hypothesized in previous isozyme studies (see Ford et al.,

1998a, c; Ford & Naczi, 2001) and cladistic analysis of molecular and morphologic data (Starr et al., 1999; Naczi & Ford, 2001). However, a couple of these relationships are worth commenting on further. *Carex willdenowii* remains an enigmatic taxon whose relationship is still unclear. The equivocal positioning of *C. willdenowii* was evident in a previous isozyme study of the section (see Ford et al., 1998c) and in the molecular phylogeny presented here. The combined evidence suggests that even if the *C. willdenowii* complex is monophyletic, *C. willdenowii* is highly divergent from both *C. basiantha* and *C. superata*.

A previous phylogenetic analysis of the *Carex jamesii* complex based on 13 morphologic characters supported the sister-group relationship for *C. juniperorum* and *C. timida* (Naczi & Ford, 2001). Our molecular phylogeny provides strong independent support for this relationship.

A previous isozyme study of the *Carex backii* complex did not include *C. cordillerana* in the analysis. Our results indicate that the *C. backii* complex is monophyletic and that *C. saximontana* and *C. cordillerana* are sister species. The close relationship between the latter two species is not unexpected since these two species have been shown to be close phenetically. Most herbarium collections of *C. cordillerana* were originally identified as *C. saximontana*.

While molecular data are most often used for phylogenetic studies, it is important to note that most species are characterized by at least one molecular autapomorphy (Starr et al., 1999, 2008; Starr & Ford, unpubl. data). Thus, molecular data provided further evidence in support of our revised taxonomy of this section.

FUTURE RESEARCH ON CAREX SECT. PHYLLOSTACHYAE

While section *Phyllostachyae* has become one of the most studied sections of *Carex*, there are a number of opportunities for future research.

Quantitative ecological studies of this section have not been conducted but could provide insights into niche partitioning in *Carex* and a better understanding of evolutionary processes in sympatric anemophilous species. Studies such as that by Bayer et al. (1991) could serve as an example for such research.

Chromosome number variation has been studied extensively in many *Carex* sections, with chromosome number known to vary between species within a section, populations within a species, and even between individuals within a population (see references cited in Naczi, 1999). While chromosome number may vary randomly within a species or species complex, it is often correlated with the macromorphologic characters used to delimit morphologically similar taxa (see Naczi, 1992). There may also be a correlation between geographic distribution, ecology, and/or phylogenetic relatedness (see Crins & Ball, 1988; Crins, 1990; Naczi, 1992, 1999; Hoshino & Okamura, 1994; Hoshino & Waterway, 1994). Chromosome numbers are known for half the species in section *Phyllostachyae* (*C. willdenowii*: $2n = 62, 78$; *C. jamesii*: $2n = 66, 70$; *C. saximontana*: $2n = 64$; *C. backii*: $2n = 66$; *C. latebracteata*: $2n = 98$; Crins et al., 2002). While chromosome number appears to have no correlation with phylogenetic relationships in section *Phyllostachyae*, trends related to interspecific variation (especially in taxa such as *C. jamesii*), species distribution, and ecology may be present.

Phylogeographic studies (see Avise, 2000) have not been conducted on any group of sedges to date. Localized endemics such as *Carex latebracteata*, which is confined to river and stream systems in the

Ouachita Mountains of Arkansas and Oklahoma, are ideally suited to the study of the geographic distribution of lineages within a species.

CONCLUSIONS

Our studies of *Carex* sect. *Phyllostachyae* have allowed us to gain insights into the systematics of this taxon. Our findings also have wider implications in terms of future directions for systematics studies of the genus. Our research suggests the following:

1. *Species diversity in many Carex sections is greater than previously realized.* We suspect that section *Phyllostachyae* is just the tip of the iceberg. Other sections in North America may prove, or have proven, to be rich sources of taxonomic novelties. These include sections *Acrocystis* Dumort., *Careyanae* Tuck. ex Kük., *Griseae* (L. H. Bailey) Kük., *Laxiflorae* (Kunth) Mack., and *Ovales* Kunth. Regions such as temperate South America and eastern Asia, which are also known to have diverse sedge floras, probably represent even greater potential for previously unsuspected diversity. Integrating numerous sources of evidence (macromorphology, micromorphology, anatomy, phytogeography, molecular) will be critical to resolving many of these taxonomically complex sections and understanding the *Carex* flora in various regions of the globe.

2. *A detailed phylogeny of Carex at the sectional level is an attainable goal.* Indeed, efforts toward the completion of this task have already taken place (e.g., Ford et al., 2006; Waterway & Starr, 2007). A concerted effort among caricologists focused on phylogenetic reconstruction using nrDNA and chloroplast DNA (cpDNA) markers will allow for a detailed picture of evolutionary relationships.

These two avenues of research represent the overarching initiatives of most systematics research: the parsing of taxonomic diversity and understanding phylogenetic relationships. *Carex* serves as a striking reminder of the necessity for both avenues of research in understanding global biodiversity.

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LITERATURE CITED

- Avise, J. C. 2000. *Phylogeography: The History and Formation of Species*. Harvard Univ. Press, Cambridge.
- Ball, P. W. & A. A. Reznicek. 2002. *Carex*. Pp. 254–273 in *Flora of North America Editorial Committee (editors), Flora of North America North of Mexico, Vol. 23: Magnoliophyta: Commelinidae (in part): Cyperaceae*. Oxford Univ. Press, New York.
- Bayer, R. J., B. G. Purdy & D. G. Lebedyk. 1991. Niche differentiation among eight sexual species of *Antennaria* Gaertner (Asteraceae: Inuleae) and *A. rosea*, their allopolyploid derivative. *Evol. Trends Pl.* 5: 109–123.
- Crins, W. J. 1990. Phylogenetic considerations below the sectional level in *Carex*. *Canad. J. Bot.* 68: 1433–1440.
- & P. W. Ball. 1988. Sectional limits and phylogenetic considerations in *Carex* sect. *Ceratocystis* (Cyperaceae). *Brittonia* 40: 38–47.
- & J. H. Rettig. 2002. *Carex* sect. *Acrocystis*. Pp. 532–545 in *Flora of North America Editorial Committee (editors), Flora of North America North of Mexico, Vol. 23: Magnoliophyta: Commelinidae (in part): Cyperaceae*. Oxford Univ. Press, New York.
- , R. F. C. Naczi, A. A. Reznicek & B. A. Ford. 2002. *Carex* sect. *Phyllostachyae*. Pp. 558–563 in *Flora of North America Editorial Committee (editors), Flora of North America North of Mexico, Vol. 23: Magnoliophyta: Commelinidae (in part): Cyperaceae*. Oxford Univ. Press, New York.
- Erterter, B. 2000. Floristic surprises in North America north of Mexico. *Ann. Missouri Bot. Gard.* 87: 81–209.
- Ford, B. A. & R. F. C. Naczi. 2001. Genetic diversity in the *Carex jamesii* complex (Cyperaceae: sect. *Phyllostachyae*) with insights into the evolution and origin of the newly described species *Carex timida*. *Sida* 19: 885–897.
- , D. A. R. McQueen, R. F. C. Naczi & A. A. Reznicek. 1998a. Allozyme variation and genetic relationships among species in the *Carex willdenowii* complex (Cyperaceae). *Amer. J. Bot.* 85: 546–552.
- , D. A. R. McQueen, J. R. Starr & R. F. C. Naczi. 1998b. The impact of species-specific traits and phylogenetic relatedness on allozyme diversity in *Carex* sect. *Phyllostachys* (Cyperaceae). *Pl. Syst. Evol.* 212: 13–29.
- , J. R. Starr, D. A. R. McQueen & R. F. C. Naczi. 1998c. Relationships among species in *Carex* sect. *Phyllostachys* (Cyperaceae) based on allozyme divergence. *Pl. Syst. Evol.* 212: 31–51.
- , M. Iranpour, R. F. C. Naczi, J. R. Starr & C. A. Jerome. 2006. Phylogeny of *Carex* subg. *Vignea* (Cyperaceae) based on non-coding nrDNA sequence data. *Syst. Bot.* 31: 70–82.
- Hartman, R. L. & B. E. Nelson. 1998. Taxonomic Novelties from North America North of Mexico: A 20-Year Vascular Plant Diversity Baseline. *Monogr. Syst. Bot. Missouri Bot. Gard.* 67: 1–59.
- Hermann, F. J. 1954. Addenda to North American carices. *Amer. Midl. Naturalist* 51: 265–286.
- Hoshino, T. & K. Okamura. 1994. Cytological studies on meiotic configurations of intraspecific aneuploids of *Carex blepharicarpa* (Cyperaceae) in Japan. *J. Plant Res.* 107: 1–8.
- & M. J. Waterway. 1994. Cytogeography and meiotic chromosome configurations of six intraspecific aneuploids of *Carex conica* Boott (Cyperaceae) in Japan. *J. Plant Res.* 107: 131–138.
- Jones, S. B. & N. C. Coile. 1988. *The Distribution of the Vascular Flora of Georgia*. Department of Botany, Univ. of Georgia, Athens.
- Kükenthal, G. 1909. Cyperaceae–Caricoideae. Pp. 1–824 in A. Engler (editor), *Das Pflanzenreich IV, 20 (Heft 38)*. Wilhelm Englemann, Leipzig.
- Mackenzie, K. K. 1935. Cyperaceae–Cariceae. *N. Amer. Fl.* 18: 169–478.
- Naczi, R. F. C. 1992. *Systematics of Carex* sect. *Griseae* (Cyperaceae). Ph.D. Dissertation, Univ. of Michigan, Ann Arbor.
- , 1999. Chromosome numbers of some eastern North American species of *Carex* and *Eleocharis* (Cyperaceae). *Contr. Univ. Michigan Herb.* 22: 105–119.
- , 2002. *Carex* sect. *Deweyanae*. Pp. 321–325 in *Flora of North America Editorial Committee (editors), Flora of North America North of Mexico, Vol. 23: Magnoliophyta: Commelinidae (in part): Cyperaceae*. Oxford Univ. Press, New York.
- & B. A. Ford. 2001. Systematics of the *Carex jamesii* complex (Cyperaceae: *Phyllostachyae*). *Sida* 19: 853–884.
- , A. A. Reznicek & B. A. Ford. 1998. Morphological, geographical, and ecological differentiation in the *Carex willdenowii* complex (Cyperaceae). *Amer. J. Bot.* 85: 434–447.
- , C. T. Bryson & T. S. Cochrane. 2002. Seven new species and one new combination in *Carex* (Cyperaceae) from North America. *Novon* 12: 508–532.
- Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89: 583–590.

- Radford, A. E., H. E. Ahles & C. R. Bell. 1968. Manual of the Vascular Flora of the Carolinas. Univ. of North Carolina Press, Chapel Hill.
- Rayner, R. W. 1970. A Mycological Colour Chart. Commonwealth Mycological Institute and British Mycological Society, Kew, Surrey.
- Reznicek, A. A. 1986. The taxonomy of *Carex* sect. *Hymenochlaenae* (Cyperaceae) in Mexico and Central America. *Syst. Bot.* 11: 56–87.
- & P. W. Ball. 1980. The taxonomy of *Carex* sect. *Stellulatae* in North America north of Mexico. *Contr. Univ. Michigan Herb.* 14: 153–203.
- Roalson, E. H., J. T. Columbus & E. A. Friar. 2001. Phylogenetic relationships in Cariceae (Cyperaceae) based on ITS (nrDNA) and *trnT-L-F* (cpDNA) region sequences: Assessment of subgeneric and sectional relationships in *Carex* with emphasis on section *Acrocystis*. *Syst. Bot.* 26: 318–341.
- Saarela, J. M. & B. A. Ford. 2001. Taxonomy of the *Carex backii* complex (sect. *Phyllostachyae*, Cyperaceae). *Syst. Bot.* 26: 704–721.
- Smith, E. B. 1994. Keys to the Flora of Arkansas. Univ. of Arkansas Press, Fayetteville.
- Smith, J. P. & J. O. Sawyer. 1988. Endemic vascular plants of northwestern California and southwestern Oregon. *Madroño* 35: 54–69.
- Starr, J. R. 1997. The Origin and Phylogenetic Position of *Carex* sect. *Phyllostachys* in the Genus *Carex* (Cyperaceae). M.A. Thesis, Univ. of Manitoba, Winnipeg.
- & B. A. Ford. 2001. The taxonomic and phylogenetic utility of vegetative anatomy and fruit epidermal silica bodies in *Carex* sect. *Phyllostachys* (Cyperaceae). *Canad. J. Bot.* 79: 362–379.
- , R. J. Bayer & B. A. Ford. 1999. The phylogenetic position of *Carex* sect. *Phyllostachys* and its implications for phylogeny and subgeneric circumscription in *Carex* (Cyperaceae). *Amer. J. Bot.* 86: 563–577.
- , — & —. 2004. Phylogeny of the unispicate taxa in Cyperaceae tribe Cariceae I. Generic relationships and evolutionary scenarios. *Syst. Bot.* 29: 528–544.
- , S. A. Harris & D. A. Simpson. 2008. Phylogeny of the unispicate taxa in Cyperaceae tribe Cariceae II: The limits of *Uncinia*. Pp. 243–268 in R. F. C. Naczi & B. A. Ford (editors), *Sedges: Uses, Diversity, and Systematics of the Cyperaceae*. *Monogr. Syst. Bot. Missouri Bot. Gard.* 108.
- Steudel, E. G. 1855. *Synopsis Plantarum Cyperacearum*. J. B. Metzler, Stuttgart.
- Waterfall, U. T. 1954. A new species of *Carex* (section *Phyllostachyae*) from Oklahoma. *Rhodora* 56: 21–23.
- Waterway, M. J. 2002. *Carex* sect. *Hymenochlaenae*. Pp. 461–475 in *Flora of North America* Editorial Committee (editors), *Flora of North America North of Mexico*, Vol. 23: Magnoliophyta: Commelinidae (in part): Cyperaceae. Oxford Univ. Press, New York.
- & J. R. Starr. 2007. Phylogenetic relationships in tribe Cariceae (Cyperaceae) based on nested analyses of four molecular data sets. In J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince & M. G. Simpson (editors), *Monocots: Comparative Biology and Evolution—Poales*. Rancho Santa Ana Botanic Garden, Claremont, California.
- Willdenow, C. L. 1805. *Species Plantarum*, Vol. 4. G. C. Nauk, Berlin.
- Wofford, B. E. & R. Kral. 1993. Checklist of the vascular plants of Tennessee. *Sida Bot. Misc.* 10: 1–66.
- Yen, A. C. & R. G. Olmstead. 2000. Molecular systematics of Cyperaceae tribe Cariceae based on two chloroplast DNA regions: *ndhF* and *trnL* intron-intergenic spacer. *Syst. Bot.* 25: 479–494.