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CHROMOSOME NUMBERS OF SOME EASTERN NORTH AMERICAN SPECIES OF CAREX AND ELEOCHARIS (CYPERACEAE)

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INTRODUCTION

In the sedges (Cyperaceae), chromosome numbers are best known from species of the large, cosmopolitan *Carex* and *Eleocharis*. Within these genera, variation in chromosome number is quite extensive. Chromosome numbers often differ among species within a genus (Wahl 1940; Strandhede 1967; Harms 1968, 1972; Schuyler 1977; Hoshino 1981; Standley 1985), populations within a species (Wahl 1940; Strandhede 1967; Harms 1968, 1972; Hoshino 1981; Standley 1985; Whitkus 1991; Hoshino 1992; Hoshino & Okamura 1994; Hoshino & Onimatsu 1994; Waterway 1996), and individuals within a population (Strandhede 1967; Hoshino 1981; Standley 1985; Luceño & Castroviejo 1991; Whitkus 1991; Hoshino & Okamura 1994; Hoshino & Onimatsu 1994).

The reason for the extreme variability of chromosome number in sedges is incompletely understood. The most likely explanation is the possession of holokinetic chromosomes by sedges (Strandhede 1965; Faulkner 1972; Wrensch, Kethley & Norton 1994). Holokinetic chromosomes have diffuse centromere activity; they act as if the spindle attachment is not localized (Wrensch, Kethley & Norton 1994). If holokinetic chromosomes fragment, the fragments are retained in successive nuclear and cell divisions. Also, the opposite can happen—chromosomes can fuse. Especially pertinent for sedges is Wrensch, Kethley, and Norton's comment (1994, p. 326), "As a labile system for karyotype evolution, holokinetic chromosomes appear superior to monocentric chromosomes..."

Knowledge of chromosome number variation is useful for several reasons. First, different chromosome numbers can be useful in distinguishing morphologically similar species and infraspecific taxa (Strandhede 1967; Harms 1972; Manhart 1986a). Second, chromosome number variation may correlate with geography and ecology, suggesting that particular combinations of alleles may be adaptive in certain environments (Hoshino & Okamoto 1979; Cayouette & Morisset 1986; Luceño & Castroviejo 1991; Hoshino 1992; Hoshino & Waterway 1994). Third, since chromosome number can correlate with phylogeny, evaluating chromosome number variation in light of phylogenetic hypotheses can increase understanding of sedge speciation (Crins 1990; Naczi 1997).

Variation in chromosome arrangement is valuable, too, especially in the detection of hybridization and polyploidy. During meiosis, *Carex* and *Eleocharis* hybrids have many nonbivalent associations, particularly univalents and trivalents, and the associations vary from cell to cell within the same individual (Strandhede 1965; Cayouette & Catling 1992). *Carex* polyploids, which appear to be quite rare

in the genus, also exhibit a relatively large number of nonbivalent associations during meiosis (Faulkner 1972; Cayouette & Catling 1992; Luceño 1994).

Because chromosome numbers and arrangements are so variable in *Carex* and *Eleocharis*, the extent of variation must be documented prior to using numbers and arrangements in taxonomic, ecologic, and evolutionary studies. Chromosome numbers and arrangements are still unknown or incompletely known for most species in the Cyperaceae. To increase knowledge and improve understanding of sedge chromosomes, in this paper I report chromosome numbers and arrangements for various species of *Carex* and *Eleocharis* native to eastern North America. My specific goals are to provide first counts for previously unstudied taxa, provide counts from new populations of previously studied taxa, and review literature and vouchers for previously studied taxa. The groups of sedges whose chromosomes I have investigated are those subject to ongoing systematics research by co-workers and me.

MATERIALS AND METHODS

Since meiotic figures are more informative and easier to interpret than mitotic ones (Faulkner 1972), I studied the number and arrangement of chromosomes during meiosis of pollen mother cells. Plants of selected taxa of *Carex* and *Eleocharis* for these studies originated in various locations in eastern Canada and eastern U.S.A. (Appendices 1–7). I transplanted most of these plants from the field to greenhouses at the University of Michigan Matthaei Botanical Gardens (Ann Arbor, Michigan) or Northern Kentucky University Department of Biological Sciences (Highland Heights, Kentucky). Growing sedges in greenhouses minimizes difficulties associated with collecting meiotic material from them (rapid meiosis that is usually synchronized within spikes and occurs mostly in the morning and, for *Carex*, often before the spikes emerge from subtending bract and leaf sheaths). The few chromosome preparations of *Carex* obtained from material not grown in a greenhouse originated from spikes collected and fixed in the field or from plants transplanted from the field to the gardens of Anton A. Reznicek (Ann Arbor, Michigan) or Robert Naczi (Independence, Kentucky).

To detect the chromosomes, I collected immature spikes containing developing anthers from plants that appeared to be within a few days of shedding pollen. I fixed the spikes in a solution of three parts (by volume) absolute ethanol and one part glacial acetic acid at room temperature for 6–12 hours. Any material not studied within 12 hours of fixation I transferred to 70% ethanol for storage at 2°C. Next, I dissected several anthers from a spike into a drop of 45% acetic acid and then placed them into a drop of Snow's stain (Snow 1963) for 5–15 minutes. I placed the stained anthers in a drop of a solution of equal parts (by volume) Hoyer's mounting medium (Beeks 1955) and 45% acetic acid on a microscope slide, split each anther to release the pollen mother cells, and covered the drop with a cover slip. I squashed the pollen mother cells by covering the slide with a piece of blotting paper and applying as much pressure as possible on the cover slip with my thumb. For the determination of chromosome number, I sketched the metaphase I chromosome complement of at least 5 cells per individual plant and counted the sketched chromosomes. To make the sketches, I used a drawing tube and phase contrast optics at 1000× magnification.

In the appendices, I report chromosome numbers with their arrangements at metaphase I, where I = univalent, II = bivalent, III = trivalent, and IV = quadrivalent. I vouchered all plants whose chromosomes I studied, except the plant of *Carex*

crawei from Mackinac County, Michigan, which died shortly after collection of staminate spikes from it and before it produced mature infructescences for vouchering. Voucher specimens for new counts are deposited at MICH, with duplicates of most at KNK [herbarium abbreviations follow Holmgren et al. (1990)]. For the taxa with new counts, I attempted to locate and examine the vouchers for previously published counts. Counts reported by Wahl (1940), Whitkus (1981), and Manhart (1987) are from pollen mother cell meioses and those of Löve and Löve (1981) are mitotic, apparently from root tips. Only Wahl (1940) includes chromosome arrangements with the counts.

RESULTS AND DISCUSSION

In this paper, I report 46 new chromosome counts for 26 taxa of Cyperaceae. Apparently, these are the first counts for 10 of these taxa. In addition, I located and examined vouchers for 26 previously reported counts from 14 taxa.

Carex Section Careyanae Tuckerman ex Kükenthal (Appendix 1)

Members of this section of eight species are endemic to eastern North America and usually inhabit mesic deciduous forests. Most recent authors (e.g., Mackenzie 1935; Fernald 1950; Bryson 1980; Manhart 1986b; Gleason & Cronquist 1991) include this section in *Carex* sect. *Laxiflorae*; however, phylogenetic analyses reveal that sect. *Careyanae* and sect. *Laxiflorae* s.s. are not each other's sister groups and thus are best treated as separate sections (Naczi 1989, 1992). In addition, molecular evidence supports the separation of sect. *Careyanae* and sect. *Laxiflorae* (Starr et al. 1997).

Carex abscondita Mackenzie. My count of 24 II appears to be the first report of a chromosome number for this species, which inhabits floodplains, swamps, and moist, wooded slopes. It ranges throughout the southeastern U.S.A. and north to eastern Massachusetts along the Atlantic coast.

Carex austrocaroliniana L. H. Bailey. This species has a small range in the mesic forests of the southern Appalachian Mountains in northeastern Alabama, northern Georgia, eastern Tennessee, western South Carolina, western North Carolina, and southeastern Kentucky. It is variable in chromosome number, with haploid numbers of 28 II, 29 II, and 30 [II]. Chromosome number appears to form a cline in this species, with an increase in chromosome number southward (Fig. 1).

Carex careyana Torrey in Dewey. The count I obtained from an eastern Tennessee plant (34 II) agrees with the count Wahl (1940) reports from a southern New York plant. *Carex careyana* is widespread in interior eastern North America in calcareous, nutrient-rich, mesic deciduous forests.

Carex digitalis Willdenow. Three varieties constitute the very wide-ranging, forest-dwelling *C. digitalis* (Fernald 1950; Bryson 1980): var. *asymmetrica* Fernald, var. *digitalis*, and var. *macropoda* Fernald. The chromosome number of var. *asymmetrica* is unknown. The count I report for var. *digitalis* from northern Kentucky (24 II) is the same as Wahl (1940) reports from central Pennsylvania. My count of 24 II for var. *macropoda*, apparently the first for this variety, is the same as that known for var. *digitalis*.

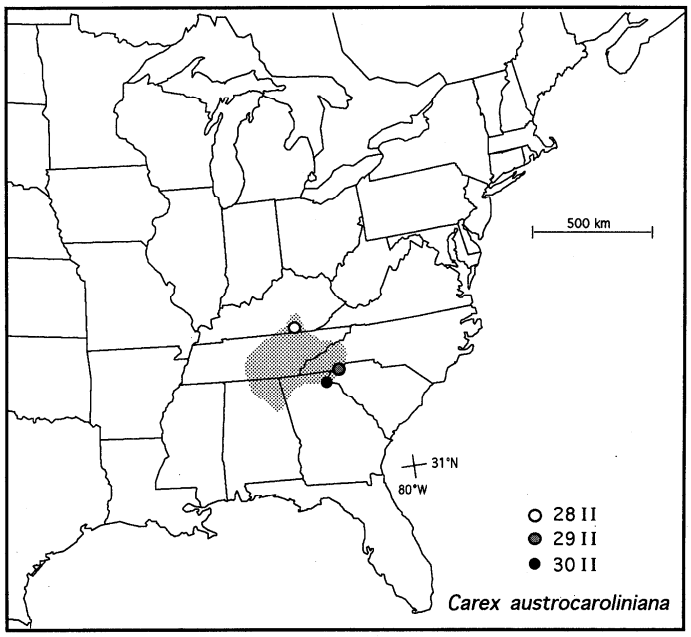

FIG. 1. Cytogeography of *Carex austrocaroliniana*. Each symbol represents a locality for a plant with a particular chromosome number. Shading depicts the range of the species (modified from Bryson, 1980).

Carex laxiculmis Schweinitz. This species, widespread in eastern North American mesic deciduous forests, includes var. *copulata* (L. H. Bailey) Fernald and var. *laxiculmis*. The taxonomy of var. *copulata* is controversial. Mackenzie (1935) treated it as a species, *C. copulata* (L. H. Bailey) Mackenzie. Fernald (1906) first considered it a variety. Later, he treated it as a hybrid between *C. digitalis* and *C. laxiculmis* (Fernald 1942, 1950).

Each of the varieties of *C. laxiculmis* is cytologically variable. My counts for var. *copulata* are 23 II from a southeastern Michigan plant, 24 II from a southern Ohio plant, and 24 II from a southern West Virginia plant. These counts are apparently the first for this variety, Wahl's (1940) report of a count from *C. copulata* notwithstanding (his voucher is *C. laxiculmis* var. *laxiculmis*). Previous counts for var. *laxiculmis* are 22 II from southern New York and 23 II from central Pennsylvania (Wahl 1940). I add 25 II from central North Carolina. Chromosome number is apparently clinal in *C. laxiculmis* (Fig. 2), with higher chromosome numbers southward. Interestingly, both varieties of *C. laxiculmis* follow this pattern.

Chromosome numbers support the treatment of *C. laxiculmis* var. *copulata* as a variety, since its numbers overlap those of var. *laxiculmis*. However, overlapping

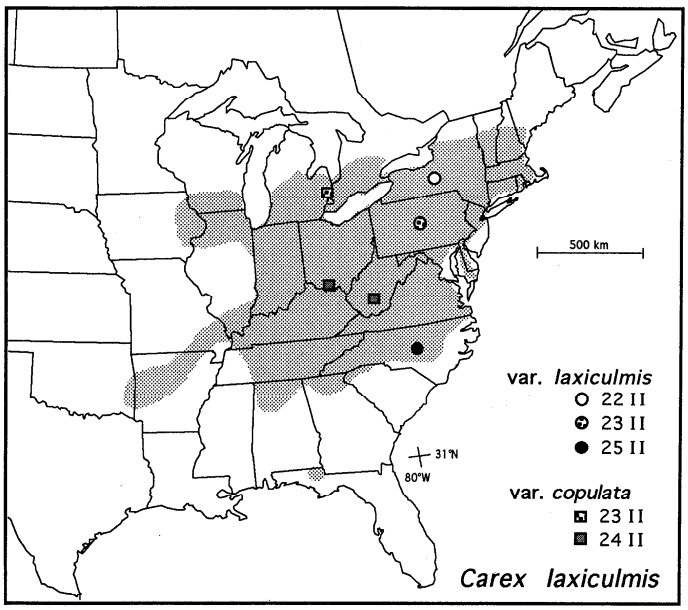

FIG. 2. Cytogeography of *Carex laxiculmis*. Each symbol represents a locality for a plant of *C. laxiculmis* var. *laxiculmis* or *C. laxiculmis* var. *copulata* with a particular chromosome number. Shading depicts the range of the species (Bryson 1980; Naczi & Bryson 1990), including the disjunction in northern Florida (Mitchell 1963).

chromosome numbers do not negate species status for var. *copulata*, since different (but closely related) species sometimes have the same chromosome number (e.g., *C. abscondita* and *C. digitalis*). One hypothesis that can be falsified by the cytologic data is the origin of *C. laxiculmis* var. *copulata* through hybridization, since all three individuals studied have regular pairing during metaphase I.

Carex platyphylla Carey. This species ranges through much of the northeastern United States and adjacent southeastern Canada, usually in mesic deciduous and deciduous-coniferous forests. Cytologically, it is the best known of *Carex* sect. *Careyanae*, with a total of eight counts reported by Wahl (1940) and me. It is variable in both chromosome number and arrangement. In fact, *C. platyphylla* is the only member of the section from which nonbivalent associations are known—both trivalents and quadrivalents. The plant I studied from southeastern Michigan, with 35 II, has the same number and arrangement of chromosomes as a plant Wahl (1940) studied from Pennsylvania. Wahl reports counts from two plants whose vouchers I could not locate (*Wahl 3418* and *Wahl 3435*), but these reports are identical to others whose vouchers I did find.

CAREX SECTION DEWEYANAE (TUCKERMAN EX MACKENZIE) MACKENZIE (APPENDIX 2)

Six or seven species belong to *Carex* sect. *Deweyanae*, a section of primarily woodland sedges of most of North America and eastern Asia.

Carex bromoides Willdenow. *Carex bromoides* includes two subspecies, subsp. *bromoides* and subsp. *montana* Naczi. Both subspecies inhabit a diversity of wet habitats, usually in forests (occasionally in open sites). *Carex bromoides* subsp. *bromoides* is widespread through eastern North America and subsp. *montana* is narrowly endemic to southwestern Virginia, western North Carolina, and western South Carolina. Both subspecies are cytologically variable. In *C. bromoides* subsp. *bromoides*, known chromosome numbers and arrangements are 32 II, 31 II + 1 IV, 33 II, and 34 II. The most frequent and geographically widespread configuration appears to be 33 II. Though Wahl (1940) detected a quadrivalent in the one plant he studied, I observed only bivalents in the five I studied. In *C. bromoides* subsp. *montana*, chromosome numbers and arrangements are 30 II and 31 II, the first counts for the subspecies. In *C. bromoides*, the non-overlapping chromosome numbers for the two subspecies support the recognition of the recently described subsp. *montana* (Naczi 1990). The wide span of chromosome numbers for *C. bromoides* makes it one of the more cytologically variable species known for eastern North America.

Carex deweyana Schweinitz var. **deweyana**. This variety is widespread in northern North American forests and forest openings, ranging from Newfoundland to Alaska south to the northern United States and further south in the Rocky Mountains. Despite its wider range, it appears to be much less variable chromosomally than *C. bromoides*. My counts of 27 II from northern Michigan and northern Pennsylvania are identical with those reported from northern Pennsylvania (Wahl 1940) and (as 2n = 54) from southern Manitoba (Löve & Löve 1981). Additionally, Packer and Whitkus (1982) report 27 [II] for *C. deweyana* (without variety identified) from eastern British Columbia, whose voucher I could not locate. The only count reported for *C. deweyana* that differs from these others is one count of 28 [II] from eastern British Columbia (Packer & Whitkus 1982). Since Packer and Whitkus did not identify the variety and I have not seen the voucher, it is possible this count is from a taxon other than *C. deweyana* var. *deweyana*.

CAREX SECTION GRANULARES (O. LANG) MACKENZIE (APPENDIX 3)

Carex sect. *Granulares* contains six species of North and Central American meadows, prairies, and forests.

Carex crawei Dewey. This species ranges through most of northern North America (and south in scattered localities to Alabama, Arkansas, and Utah) in wet, calcareous prairies, meadows, and lake shores. The counts I obtained from northern Michigan (30 II) and southeastern Wisconsin (28 II + 1 III) are nearly identical, but quite different from the one previous report of 2n = 38 from Manitoba (Löve & Löve 1981), whose voucher I could not locate. More plants of *C. crawei* from throughout its range should be studied before reaching a conclusion about the range of chromosome numbers of this species.

Carex granularis Muhlenberg ex Willdenow. This species ranges widely (most of eastern North America west to Saskatchewan, Wyoming, and Texas), grows in a diverse array of habitats, such as meadows, wooded floodplains, roadside ditches, and seepy openings in upland forests, and exhibits a large amount of morphologic variation. Some authors (e.g., Mackenzie 1935) believe some of this morphologic variation can be partitioned among segregate taxa: *C. haleana* Olney [*C. granularis* var. *haleana* (Olney) Porter] and *C. rectior* Mackenzie (*C. granularis* var. *recta* Dewey); however, preliminary results of taxonomic investigation of *C. granularis* show its morphologic variation to be continuous. Among the plants studied cytologically are variants encompassed by the segregate taxa.

Correlated with the geographic, ecologic, and morphologic variability of *C. granularis* is great cytologic variability. *Carex granularis* varies in both chromosome numbers and arrangements. The chromosome number obtained by Wahl (1940) from a central Pennsylvania plant (16 II + 1 IV) is lower than, but close to, the numbers I observed in specimens from northern Michigan (19 II), northern Alabama (13 II + 3 IV), northern Arkansas (14 II + 3 IV), western Mississippi (18 II + 1 IV in two individuals), northeastern Texas (18 II + 1 IV), and southernmost Ontario (17 II + 2 IV). The count of 2n = 42 reported from southern Manitoba (Löve & Löve 1981), whose voucher I could not locate, matches the count I obtained from Ontario. Especially noteworthy is the very high proportion of plants of *C. granularis* with quadrivalents during metaphase I. All but one plant studied during meiosis possessed at least one quadrivalent, including the plant studied by Wahl (1940). When present, the number of quadrivalents per cell varied from one to three. The presence of quadrivalents is unusual, but the presence of more than one per cell is particularly rare in *Carex* species.

Underscoring the striking plasticity of chromosome numbers and arrangements in *C. granularis* is the apparent lack of correlation between geography and either chromosome number or arrangement. As well, I did not detect any correlation between morphologic variation and cytologic variation in *C. granularis*. Thus, I found no cytologic support for recognition of the segregate taxa of *C. granularis*.

Carex microdonta Torrey & Hooker. This species inhabits prairies in the southern United States, from northern Florida west to southeastern Arizona. The counts I obtained, apparently the first for this species, are the same for a plant from southwestern Arkansas and another from eastern Mississippi: 32 II. *Carex microdonta* is morphologically very similar to *C. crawei*. The few counts available indicate different numbers characterize the two species. Obviously, the chromosomes of more plants of both species should be studied, especially of *C. crawei* from the southern United States, before concluding that chromosome number distinguishes *C. microdonta* and *C. crawei*.

Carex Section Laxiflorae Kunth (Appendix 4)

This section contains about 23 species of North America, Central America, and Eurasia (Naczi 1989). Most of the species of the section inhabit mesic forests.

Carex albursina Sheldon. This species inhabits calcareous, nutrient-rich, mesic deciduous forests in much of eastern North America. My count of 22 II from Ohio is identical with the one Wahl (1940) reported from Pennsylvania.

Carex blanda Dewey. *Carex blanda* is a very common, widespread, and morphologically variable sedge of eastern North American mesic forests and forest openings. My counts of 15 II and 16 II from Mississippi are lower than the 18 [II] and 15 II + 1 IV reported from New Jersey and Pennsylvania, respectively (Wahl 1940; Whitkus 1981). Löve and Löve (1981) reported 2n = 38 for *C. blanda* from Manitoba, an area from which *C. blanda* is unknown. The morphologically similar *C. leptonervia* (Fernald) Fernald occurs in the area from which the counted plant originated and is likely the basis for the Löves' report (B. A. Ford, pers. comm.).

The voucher for one of Wahl's (1940) counts of *C. blanda* (*Wahl 125135*, NCU!, PAC!) is actually *C. gracilescens*. Vouchers for two counts that Wahl reports for *C. blanda* from central Pennsylvania (*Wahl 2536*, NCU!, PAC! and *Wahl 4175*, NCU!, PAC!) are hybrids. Characteristic of hybrids, both have aborted achenes and anthers included in (rather than exserted from) their subtending scales. Their morphology indicates that both of these hybrids are likely *C. blanda* × *C. laxiflora* Lam. var. *laxiflora*. Wahl reported only approximate counts for them ("ca. 38/2" and "ca. 40/2, " respectively), because they had many nonbivalent associations in each cell and, in *Wahl 2536*, an inconstant chromosome number from cell to cell. Both the high number of nonbivalent arrangements and variability in number within an individual are diagnostic of hybrids. Though he noted the chromosomal similarity of these plants to hybrids, Wahl (1940: 464) stated, "Number 2536 is considered by the writer to be typical *C. blanda*, but 4175 has wider leaves and suggests a slight trend toward *C. laxiflora*..."

Carex gracilescens Steudel. A widespread and morphologically variable inhabitant of eastern North American mesic forests, *C. gracilescens* is variable in both chromosome number and arrangement. My count of 15 II + 1 III from Michigan is lower than any of the numbers observed by Wahl (1940) from New York (20 II) and Pennsylvania (15 II + 2 IV and 20 II) plants. I was unable to locate a voucher for one of the plants of *C. gracilescens* studied by Wahl (*Wahl 2516*), whose chromosome configuration he reports as identical to those from two other plants he studied (20 II).

Carex radfordii Gaddy. This recently described, narrow endemic of northeastern Georgia, western North Carolina, and western South Carolina grows in mesic forests (Gaddy 1995). *Carex radfordii* and its sister species, *C. purpurifera* Mackenzie, are unique among North American members of section *Laxiflorae* in possessing the synapomorphy of overwintered leaf blades densely papillate on the abaxial surfaces. The count of 23 II for *C. radfordii* (the first for this species) appears to distinguish it cytologically from *C. purpurifera* Mackenzie, with chromosome numbers of 17 [II], 18 [II], and 19 [II] (Manhart 1986a). Since so few plants have been studied, more chromosome counts are necessary for both species before one can conclude they have non-overlapping numbers.

Carex striatula Michaux. This species of mesic and dry-mesic forests occurs in the southeastern United States and, along the Atlantic coast, north to Connecticut. *Carex striatula* is often difficult to distinguish from *C. laxiflora* Lam. Consequently, some authors lump *C. striatula* with the earlier-described *C. laxiflora* or suggest they should be lumped (Hermann 1940; Manhart 1986b; Gleason & Cronquist 1991). The counts of 18 II and 20 II, the first for *C. striatula*, indicate cytologic overlap with

C. laxiflora. Wahl (1940) reported counts of 20 II for *C. laxiflora* from both a New York plant (*Wahl 24208*, PAC!) and a Pennsylvania plant (*Wahl 34146*, PAC!). Thus, chromosome numbers fail to clarify the taxonomic status of *C. striatula*.

Carex Section Paniceae G. Don (Appendix 5)

Eleven species belong to *Carex* sect. *Paniceae*, an especially wide-ranging section (North America, Central America, South America, and Eurasia) of prairies, meadows, fens, and forests.

Carex meadii Dewey. This species grows in prairies, meadows, and forest edges over much of eastern North America. The count of 28 II from Wisconsin agrees with the report of 2n = 56 by Löve and Löve (1981) from Manitoba, whose voucher I could not locate.

Carex woodii Dewey. This woodland species ranges from New York west to Minnesota and south to northern Georgia. My count of 22 II for *C. woodii* from Michigan is identical with Wahl's (1940) count from a New York plant. Wahl's other count of 26 II (from a Pennsylvania plant) indicates *C. woodii* is cytologically variable. Though Löve and Löve (1981) report a count of 2n = 44 for *C. woodii* from Manitoba (whose voucher I could not locate), *C. woodii* is unknown there (B. A. Ford, pers. comm.; A. A. Reznicek, pers. comm.). This report probably applies to *C. tetanica* Schkuhr, a species morphologically similar to *C. woodii* and known from the area of Manitoba from which the counted plant originated (B. A. Ford, pers. comm.).

Carex Section Phyllostachys (J. Carey) L. H. Bailey (Appendix 6)

Carex sect. *Phyllostachys* is endemic to North American forests and forest openings, and contains eight species. This section has been the focus of much recent taxonomic, genetic, and phylogenetic research (Crins 1990; Catling et al. 1993; Starr et al. 1997; Ford et al. 1998a, 1998b, 1998c; Naczi & Ford 1998; Naczi et al. 1998).

Carex jamesii Schweinitz. *Carex jamesii* inhabits calcareous, mesic deciduous forests of much of eastern North America. Not surprisingly for a widespread and morphologically variable species (Naczi & Ford 1998), the count reported here from Kentucky (33 II) differs from the one previous report by Wahl (1940) from Pennsylvania (35 II).

Carex latebracteata Waterfall. This narrow endemic inhabits mesic and dry-mesic deciduous forests of the Ouachita Mountains of western Arkansas and eastern Oklahoma. It is the tallest member of sect. *Phyllostachys* and has the widest leaves of any member of the section. As well, it is the only member of sect. *Phyllostachys* that has strongly glaucous leaves. Furthermore, it does not produce lateral spikes, unlike all other members of the section. As with morphology, its chromosome number is divergent from the rest of the members of its section. Its chromosome number of 49 II, the first reported for the species, is much higher than the numbers reported for all of the other members of the section, which range from 31 II to 39 II (Crins 1990; reports in this paper).

Carex willdenowii Willdenow. This species grows in acidic, calcium-poor, dry-mesic deciduous forests throughout much of the northeastern U.S.A. and immediately adjacent Canada. The newly reported chromosome count of 39 II from two plants from the same population in Kentucky is quite different from the previous report of 31 II from one population in Pennsylvania (Wahl 1940). The rather high degree of genetic and morphologic variability possessed by *C. willdenowii* (Ford et al. 1998a; Naczi et al. 1998) may account for its wide span of chromosome numbers.

Eleocharis (Appendix 7)

Eleocharis brittonii Svenson and **E. microcarpa** Torrey. Both of these spike-rushes inhabit sunny, wet, acidic habitats in eastern North America. Because they are morphologically very similar, the taxonomic merit of the later-described *E. brittonii* has been controversial. Small (1933), Fernald (1950), and Svenson (1957) all recognize *E. brittonii* as a species distinct from *E. microcarpa*; however, most recent authors combine them (Radford, Ahles & Bell 1968; Godfrey & Wooten 1979; Gleason & Cronquist 1991). The intermediate position of treating *E. brittonii* as *E. microcarpa* var. *brittonii* (Svenson) Svenson was advocated by Svenson (1937). Unfortunately, chromosomes do not clarify the taxonomy of *E. brittonii*, since it and *E. microcarpa* have the same number and arrangement (5 II). Apparently, these chromosome counts are the first reported for both *E. brittonii* and *E. microcarpa*.

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APPENDIX 1

Chromosome Numbers and Arrangements of Some Species of Carex sect. Careyanae

C. abscondita
24 II; Alabama. Winston Co.: N of Double Springs, *Naczi 2964.*

C. austrocaroliniana
28 II; Kentucky. McCreary Co.: NE of Hill Top, *Naczi 7114.*
29 II; South Carolina. Pickens Co.: N of Rocky Bottom, *Naczi 2308.*
30 [II]; Georgia. Stephens Co.: Toccoa, *Manhart 179* (GA!); Manhart 1987.

C. careyana
34 II; Tennessee. Carter Co.: SW of Butler, *Naczi 2313.*
34 II; New York. Tompkins Co.: Ithaca, *Wahl 33288* (PAC!);Wahl 1940.

C. digitalis var. *digitalis*
24 II; Kentucky. Harrison Co.: NE of Sunrise, *Naczi 6611.*
24 II; Pennsylvania. Centre Co.: State College, *Wahl 32175* (PAC!), *Wahl 85116* (NCU!); Wahl 1940.

C. digitalis var. *macropoda*
24 II; Alabama. Monroe Co.: N of Midway, *Naczi 2972.*

C. laxiculmis var. *copulata*
23 II; Michigan. St. Clair Co.: WNW of Blaine, *Naczi 2760.*
24 II; Ohio. Adams Co.: Blue Creek, *Naczi 2941.*
24 II; West Virginia. Fayette Co.: W of Prince, *Naczi 2761.*

C. laxiculmis var. *laxiculmis*
22 II; New York. Tompkins Co.: near Ithaca, *Wahl 15298* (NCU!, PAC!); Wahl 1940.
23 II; Pennsylvania. Centre Co.: E of Coburn, *Wahl 95115* (NCU!); Wahl 1940.

23 II; PENNSYLVANIA. [origin not stated on voucher label, though state mentioned in Wahl (1940); county unknown, but probably Centre Co.], *Wahl 1556* (NCU!, PAC!); reported as *C. copulata* by Wahl (1940).
25 II; NORTH CAROLINA. Lee Co.: NE of Colon, *Naczi 2973.*

C. platyphylla
32 II + 1 III; PENNSYLVANIA. Centre Co.: [no additional locality data on voucher label], *Wahl 54198* (PAC!); Wahl 1940.
33 II + 1 III; NEW YORK. Tompkins Co.: Ithaca, *Wahl 63288* (PAC!); Wahl 1940.
34 II; PENNSYLVANIA. Centre Co.: [no additional locality data on voucher label], *Wahl 34148* (PAC!).
35 II; MICHIGAN. Van Buren Co.: SW of Covert, *Reznicek 7153.*
35 II; PENNSYLVANIA. Centre Co.: E of Coburn, *Wahl 44146* (NCU!, PAC!); Wahl 1940.
33 II + 1 IV; NEW YORK. Tompkins Co.: Ithaca, *Wahl 13248* (NCU!, PAC!); Wahl 1940.

APPENDIX 2

CHROMOSOME NUMBERS AND ARRANGEMENTS OF SOME SPECIES OF CAREX SECT. DEWEYANAE

C. bromoides subsp. *bromoides*
31 II + 1 IV; PENNSYLVANIA. Centre Co.: E of Coburn, *Wahl 4205* (NCU!, PAC!); Wahl 1940.
32 II; MISSISSIPPI. Washington Co.: E of Helm, *Naczi 2309.*
33 II; ARKANSAS. Garland Co.: SW of Crystal Springs, *Naczi 2728.*
33 II; PENNSYLVANIA. Bradford Co.: NW of Franklindale, *Naczi 2724.*
33 II; SOUTH CAROLINA. Berkeley Co.: N of Goose Creek, *Naczi 2726.*
34 II; TENNESSEE. Marion Co.: SSE of Jasper, *Naczi 2725.*

C. bromoides subsp. *montana*
30 II; SOUTH CAROLINA. Pickens Co.: N of Rocky Bottom, *Naczi 2723.*
31 II; VIRGINIA. Grayson Co.: Whitetop Mountain, *Naczi 2333.*

C. deweyana var. *deweyana*
27 II; MICHIGAN. Emmet Co.: SE of Conway, *Naczi 2310.*
27 II; PENNSYLVANIA. Bradford Co.: NW of Franklindale, *Naczi 2722.* Potter Co.: near Cross Fork, *Wahl 14146* (NCU!, PAC!); Wahl 1940.
2n = 54; CANADA: MANITOBA. Camp Morton, *Löve & Löve 5711* (US!, WIN!); Löve & Löve 1981.

APPENDIX 3

CHROMOSOME NUMBERS AND ARRANGEMENTS OF SOME SPECIES OF CAREX SECT. GRANULARES

C. crawei
28 II + 1 III; WISCONSIN. Kenosha Co.: S of Kenosha, *Naczi 2746.*
30 II; MICHIGAN. Mackinac Co.: NW of St. Ignace, Pointe aux Chenes, no voucher collected.

C. granularis
19 II; MICHIGAN. Cheboygan Co.: E of Cheboygan, *Naczi 2250.*
13 II + 3 IV; ALABAMA. Madison Co.: E of Huntsville, *Naczi 2242.*
14 II + 3 IV; ARKANSAS. Marion Co.: Snow, *Naczi 2975.*
16 II + 1 IV; PENNSYLVANIA. Centre Co.: [no additional locality data on voucher label], *Wahl 55315* (NCU!, PAC!); Wahl 1940.
18 II + 1 IV; MISSISSIPPI. Washington Co.: W of Hollandale, *Naczi 2056, 2057.*
18 II + 1 IV; TEXAS. Red River Co.: SE of Johntown, *Naczi 2058.*
17 II + 2 IV; CANADA: ONTARIO. Essex Co.: S of McGregor, *Naczi 2262.*

C. microdonta
32 II; ARKANSAS. Little River Co.: SW of Foreman, *Naczi 2341.*
32 II; MISSISSIPPI. Lowndes Co.: S of Artesia, *Naczi 2342.*

APPENDIX 4

CHROMOSOME NUMBERS AND ARRANGEMENTS OF SOME SPECIES OF CAREX SECT. LAXIFLORAE

C. albursina
22 II; OHIO. Adams Co.: Blue Creek, *Naczi 2976*.
22 II; PENNSYLVANIA. Centre Co.: W of Woodward, *Wahl 45136* (PAC!); Wahl 1940.

C. blanda
15 II; MISSISSIPPI. Bolivar Co.: NE of Benoit, *Naczi 2729*.
15 II + 1 IV; PENNSYLVANIA. Centre Co.: [no additional locality data on voucher label], *Wahl 2556* (NCU!, PAC!); Wahl 1940.
16 II; MISSISSIPPI. Washington Co.: E of Helm, *Naczi 2730*.
18 [II]; NEW JERSEY. Sussex Co.: Stockholm, *Whitkus 221* (NY!); Whitkus 1981.

C. gracilescens
15 II + 1 III; MICHIGAN. Saginaw Co.: S of Saginaw, *Reznicek 8802*.
15 II + 2 IV; PENNSYLVANIA. Centre Co.: [no additional locality data on voucher label], *Wahl 125135* (NCU!, PAC!); reported as *C. blanda* by Wahl (1940).
20 II; NEW YORK. Tompkins Co.: [no additional locality data on voucher label], *Wahl 1478* (NCU!, PAC!); Wahl 1940.
20 II; PENNSYLVANIA. Centre Co.: E of Coburn, *Wahl 74208* (NCU!, PAC!); Wahl 1940.

C. radfordii
23 II; SOUTH CAROLINA. Pickens Co.: N of Rocky Bottom, *Naczi 2311*.

C. striatula
18 II; MISSISSIPPI. Montgomery Co.: W of Winona, *Bryson 8725*.
20 II; GEORGIA. Screven Co.: Blue Springs, *Naczi 2968*.

APPENDIX 5

CHROMOSOME NUMBERS AND ARRANGEMENTS OF SOME SPECIES OF CAREX SECT. PANICEAE

C. meadii
28 II; WISCONSIN. Kenosha Co.: S of Kenosha, *Naczi 2745*.

C. woodii
22 II; MICHIGAN. Wayne Co.: E of Belleville, *Naczi 2755*.
22 II; NEW YORK. Tompkins Co.: Ithaca, *Wahl 55288* (PAC!); Wahl 1940.
26 II; PENNSYLVANIA. Centre Co.: E of Coburn, *Wahl 45845* (PAC!); Wahl 1940.

APPENDIX 6

CHROMOSOME NUMBERS AND ARRANGEMENTS OF SOME SPECIES OF CAREX SECT. PHYLLOSTACHYS

C. jamesii
33 II; KENTUCKY. Campbell Co.: Highland Heights, *Naczi 3825*.
35 II; PENNSYLVANIA. Centre Co.: Woodward, *Wahl 5599* (NCU!, PAC!); Wahl 1940.

C. latebracteata
49 II; ARKANSAS. Howard Co.: E of Wickes, *Reznicek 8792*.

C. willdenowii
31 II; PENNSYLVANIA. Centre Co.: State College, *Wahl 1285* (PAC!); Wahl 1940.
39 II; KENTUCKY. Campbell Co.: E of Persimmon Grove, *Naczi 3819, 3820*.

APPENDIX 7

Chromosome Numbers and Arrangements of Some Species of Eleocharis

E. brittonii
5 II; Mississippi. Jackson Co.: Ocean Springs, *Naczi 2331*.
E. microcarpa
5 II; Michigan. Allegan Co.: SE of Fennville, *Naczi 2332*.