

Chapter 9



Phylogeny and Patterns of Convergence in *Carex* Sect. *Ovales* (Cyperaceae): Evidence from ITS and 5.8S Sequences

Andrew L. Hipp

ABSTRACT *Carex* L. sect. *Ovales* Kunth, with approximately 85 species worldwide, is one of the largest sections in the genus and the largest in *Carex* subg. *Vignea* (P. Beauv. ex T. Lestib.) Peterm. (ca. 400 species). Sequence data from the internal transcribed spacer (ITS) region and 5.8S gene of nuclear ribosomal DNA (nrDNA) demonstrate that section *Ovales* is monophyletic, including the East Asian *C. maackii* Maxim. and the two species of section *Cyperoideae* G. Don, but excluding *C. illota* L. H. Bailey. The two main synapomorphies that define section *Ovales*—winged perigynia and true vegetative culms—have each evolved independently in at least one other lineage in the genus. Moreover, the traditional infrasectional taxonomy of section *Ovales* is based on morphological characters that are for the most part homoplastic. The majority of eastern North American species in section *Ovales* form a single lineage (“ENA Clade I”) that derives from a poorly resolved western North American group.

KEY WORDS *Carex*, Cyperaceae, ITS phylogeny, nrDNA, section *Cyperoideae*, section *Ovales*, subgenus *Vignea*.

Section *Ovales* Kunth is one of the largest sections in *Carex* L. subg. *Vignea* (P. Beauv. ex T. Lestib.) Peterm. The section contains 72 North American species (Mastrogioseppe et al., 2002), 10 additional species of South and Central America, and three species that are confined to the Old World, for a total of ca. 85 species worldwide (Reznicek, 1993; Mastrogioseppe et al., 2002). The section ranges from floodplain forests to alpine tundra, encompassing much of the ecological diversity of the entire genus (Wheeler & Ownbey, 1984; Hipp, 1998). Regionally endemic species complexes account for much of the section's diversity and raise the question of whether speciation rate is elevated within section *Ovales* (Hermann, 1970; Raven & Axelrod, 1978; Whitkus & Packer, 1984; Whitkus, 1988; Reznicek & Rothrock, 1997; Rothrock & Reznicek, 2001).

Section *Ovales* is distinguished by the presence of winged perigynia borne on gynecandrous spikes, a caespitose growth form with very short rhizomes in all but a few species, and true vegetative culms, which may become elongate and root at the nodes late in the season (Reznicek & Catling, 1986; Reznicek, 1993). This combination of characters makes the section easily recognizable even if distinguishing species poses difficulties. Mackenzie (1935) recognized 11 informally named species groups within section *Ovales* based on characters of the perigynia, pistillate scales, leaf sheaths, and vegetative culms. Although a few of these species groups have strong ecological, geographical, and morphological homogeneity (e.g., the *Tribuloideae* and *Alatae*), Mackenzie's species groups are generally considered to be unnatural (Reznicek, 1993).

Two issues stand out regarding the circumscription of section *Ovales*. The first is the status of section *Cyperoideae* G. Don [= *Schellhammeria* (Moench) Kunth]. While the two species of section *Cyperoideae* sensu Tuckerman possess winged perigynia and gynecandrous spikes, their extremely elongate perigynia and unique inflorescence structure (Fig. 1) make them highly distinctive relative to the other members of section *Ovales*. Consequently, treatments in *Flora Europaea* (Chater, 1980), *The Sedges (Carex L.) of Russia and Adjacent States* (Egorova, 1999), and the *Flora of North America* (Mastrogioseppe et al., 2002) treat the *Cyperoideae* as a separate section. Mackenzie (1935), however, recognized section *Cyperoideae* as a species group

within *Ovales*. Many North American taxonomists follow Mackenzie's lead on this (e.g., Hermann, 1970; Gleason & Cronquist, 1991).

The second issue is the position of *Carex illota* L. H. Bailey, a gynecandrous species with unwinged perigynia that Kükenthal (1909) placed into section *Elongatae* Kunth. This section has subsequently been divided into sections *Deweyanae* Tuck., *Stellulatae* Kunth, and *Heleonastes* Kunth (in part), and *C. illota* might be expected to fall most naturally among one of those sections (Whitkus, 1988). Mackenzie (1935: p. 131), however, argued of *C. illota* that "its true relationship seems to be with the *Ovales*, of which it may be regarded as one of the most primitive species." The issue has not been addressed formally since Mackenzie.

While subgenus *Vignea* is known to be monophyletic (Reznicek, 1990; Starr et al., 1999, 2004, 2008; Yen & Olmstead, 2000; Roalson et al., 2001), relationships between and within most of its sections, including *Ovales*, have been examined in detail using molecular data by only a few workers (e.g., Hendrichs et al., 2004). This study uses sequence data from the internal transcribed spacer regions (ITS 1 and ITS 2) and the 5.8S gene of nuclear ribosomal DNA (nrDNA) to address the circumscription of section *Ovales*, the position of section *Ovales* within subgenus *Vignea*, and homoplasy in the characters that define section *Ovales* and the species groups that Mackenzie recognized within it.

MATERIALS AND METHODS

TAXON SAMPLING

Subgenus *Vignea* outside of section *Ovales* was represented by 28 species from 15 sections (Table 1), including all species known to produce true vegetative culms (*Carex sartwellii* Dewey, *C. chordorrhiza* Ehrh. ex L. f., *C. pseudocuraica* F. Schmidt, along with the species of section *Ovales*) as well as species outside of section *Ovales* with obviously winged perigynia (*C. planata* Franch. & Sav., *C. brizoides* L., and *C. siccata* Dewey). Efforts to amplify *C. inversa* R. Br. of section *Inversae* Kük. and *C. curvula* All. of section *Curvulae* Tuck. were unsuccessful. Three outgroups were included from subgenus *Carex* and one from subgenus *Psyllophora* (Degl.) Peterm. [= *Primocarex* Kük.] based on their placement in prior studies (Roalson et al., 2001; Starr et



Figure 1. Inflorescences and perigynia of selected species. *Carex maackii*: —a. Inflorescence. —b. Perigynium, ventral face. —c. Perigynium, dorsal face (Kan 8031). *C. illota*: —d. Habit. —e. Perigynium, ventral face (Hipp 700). *C. athrostachya*: —f. Inflorescence (Hipp 794). —g. Perigynium (Goodrich 22,204). *C. sychnocephala*: —h. Inflorescence (Iltis 13,453). —i. Perigynium, ventral face (Wedemeyer 135). *C. bohemica*: —j. Inflorescence. —k. Perigynium, ventral face (Wallnoffer 13755). Scale bar = 3 mm (perigynia only; inflorescences not to scale).

al., 2004). Ninety accessions sampled from section *Ovales* represent 79 of the ca. 85 species recognized in the section. The placement of *C. chondorrhiza*, *C. illota*, and 29 other species was confirmed using sequences from two or more individuals of each species (Table 1). All sequences except for vulpinoidea1294, macrorrhiza, macrocephala, and ovalis24872 were generated for this study and are deposited in GenBank (numbers AY779064 to AY779182).

DNA EXTRACTION, POLYMERASE CHAIN REACTION, AND SEQUENCING

DNA was extracted from live, silica-dried, frozen, and herbarium tissue of single individuals using a modified 6× CTAB method (Doyle & Doyle, 1987) or DNEasy Plant Mini Kits (Qiagen, Valencia, California). The ITS region was amplified using the primers ITS-I (Urbatsch et al., 2000) and ITS-4 (White et al., 1990) in 50- μ l reactions containing 5 μ l MgCl₂ at 25 μ M, 5 μ l 10× MgCl₂-free *Taq* buffer, 0.5 μ l 100× bovine serum albumin (BSA), 1.5 μ l dimethyl sulfoxide (DMSO), 0.5 μ l of each primer at 20 μ M, 0.25 μ l *Taq* DNA polymerase (1.25 units), and 29.75 μ l ultrapure deionized water. Amplification was conducted in 30 polymerase chain reaction (PCR) cycles of DNA denaturation at 94°C for 30 seconds, primer annealing at 48°C for one minute, and extension at 72°C for one and a half minutes, ending with a single seven-minute extension at 72°C. Double-stranded PCR products were quantified on 0.8% ethidium bromide-stained agarose gels and cleaned using spin columns, QIAQuick (Qiagen, Valencia, California), or magnetic beads.

Cleaned PCR products were cycle-sequenced in half-reactions (10 μ l) using BigDye reaction kits and the ITS-I and ITS-4 primers, with additional sequences using internal primers ITS-2 (White et al., 1990) and ITS-3B (Baum & Sytsma, 1994) for taxa in which ITS-I and ITS-4 sequences did not provide double coverage. Cycle sequencing products were precipitated in 75% ethanol or cleaned with magnetic beads and sequenced on Applied Biosystems (ABI) 377 or ABI 3100 automated sequencers at the University of Wisconsin–Madison Biotechnology Center's DNA Facility.

PHYLOGENETIC ANALYSIS

Sequences were edited and assembled in Sequencher 3.0 (GeneCodes Co., 1991–1995) and aligned manually in BioEdit 5.0.9 (Hall, 1999). Sequence alignments were unambiguous except for a few single base-pair indels. Alternate alignments at these points made no difference in topology or support for final trees. Indels were coded as present (1) or absent (0) and included in all parsimony analyses, which were performed in PAUP* 4.0b10 (Swofford, 1998). Heuristic parsimony searches were performed on equally weighted characters in 100 replicates of random sequence addition to detect multiple islands of most parsimonious (MP) trees (Maddison, 1991), with 1000 MP trees saved for each replicate (MULTREES = yes) and tree bisection-reconnection (TBR) branch swapping on all MP trees. Nonparametric bootstrap analysis (Felsenstein, 1985) was conducted using 500 heuristic bootstrap replicates of 100 random addition sequence replicates each, with one tree held at each step during stepwise addition (MULTREES = no) and TBR branch swapping (DeBry & Olmstead, 2000). Percent sequence divergence was calculated in PAUP* using the general time-reversible (GTR) model with other distance parameters at default settings.

Data were also analyzed using Metropolis-coupled Markov chain Monte Carlo (MCMC) in MrBayes v. 2.01 (Huelsenbeck & Ronquist, 2001). The GTR + I + G model was selected using a hierarchical likelihood ratio test of 24 sequence evolution models as implemented in MrModeltest 1.1b (Nylander, 2002). Prior probabilities were set at program defaults: topologies equiprobable; gamma distribution shape parameter uniform on the interval (0.05, 50.0); nucleotide frequencies and substitution rates uniform on the dirichlet distribution. Four parallel MCMC chains were run with heating parameter set at 0.2. Chains were run for 1,000,000 generations and trees sampled every 100 generations. Tree likelihood was graphed against generation number in Excel and the burn-in was visually determined to be confined to the initial 300,000 generations. Trees from these generations were eliminated prior to analysis. A second independent run was conducted to verify that trees were sampled from the correct distribution.

Monophyly of several sections and of species groups within section *Ovales* was tested using the Wilcoxon signed rank (WSR) test (Templeton, 1983) as implemented in PAUP*. Heuristic parsimony searches of 100 random addition replicates with TBR branch swapping on a single tree at each replicate were performed with the trees constrained to be monophyletic for each group in turn. Constrained MP trees were compared with an unconstrained MP tree for a total of 16 comparisons. One-tailed *P* values are reported and Bonferroni-corrected when significant (Buckley et al., 2001).

RESULTS

ITS DATA MATRIX

The aligned ITS data matrix is 634 nucleotide positions in length, which includes all of ITS 1, 5.8S, and ITS 2, with the exclusion of the first three nucleotides at the 5' end of ITS 1 for all taxa and 19 nucleotides at the 3' end of ITS 2 in *Carex sartwellii* only. ITS 1 ranges from 216 to 222 nucleotides in length (excluding the first three nucleotides), ITS 2 from 219 to 227 nucleotides. One-hundred fifty-four nucleotide positions are parsimony-informative across the entire data set, 139 within subgenus *Vignea*, and 54 within section *Ovales* excluding *C. illota*. Maximum pairwise sequence divergence (GTR distances) among all taxa is 12.8%, 10.3% within subgenus *Vignea*, 4.1% within section *Ovales* excluding *C. illota*. Three single-nucleotide synapomorphies are found within the 5.8S region: a synapomorphy for the clade that includes section *Ovales* plus *C. illota* and *C. chordorrhiza*, a synapomorphy for *C. davyi* Mack. and *C. constanceana* Stacey, and a shared polymorphism between *C. planata* and *C. pennsylvanica* Lam. Thirteen indels are potentially informative across all taxa included in this study, five within *Ovales*.

PHYLOGENETIC RESULTS

Heuristic searches of the combined data recovered 90,791 MP trees (Fig. 2). As this search was limited to swapping on 1000 trees at each random addition replicate, more MP trees are certain to exist. Addition of indels supports only one clade not recovered using nucleotide data alone: a clade composed of the core of Mackenzie's Tribuloideae (*Carex projecta* Mack., *C. tribuloides* Wahlenb., and *C.*

crystalata Britton) plus *C. crawfordii* Fernald is supported by a single, homoplastic insertion that maps onto the tree with six or seven steps (depending on whether *C. cristatella* resolves with the other core Tribuloideae). The topology recovered in Bayesian analysis (Figs. 3 and 4) is slightly more resolved than the 50% majority rule consensus of MP trees (not shown) and significantly more resolved than the strict consensus (Fig. 2).

Monophyly of section *Ovales* with the exclusion of *Carex illota* is supported with posterior probability (PP) of 0.93 and parsimony bootstrap (PB) of 70%. *Carex chordorrhiza* and *C. pseudocuraica* form a strongly supported clade that is weakly supported as sister to section *Ovales* (PP = 0.75, PB = 44%). Within section *Ovales*, many small clades are recovered with moderate to weak support (Fig. 4). The largest clade recovered within the section is composed of the majority of eastern North American species in the section (eastern North America [ENA] Clade I; Figs. 2 and 4). The remainder of the tree is largely unresolved and composed of mostly western North American species. The East Asian *C. maackii* is resolved as sister to the rest of section *Ovales* (PP = 0.96, PB = 47%). The branch supporting this placement collapses in the strict consensus but is present in 97% of MP trees. The species of section *Cyperoideae* are embedded within section *Ovales*, but trees constrained such that sections *Ovales* and *Cyperoideae* are reciprocally monophyletic cannot be rejected (WSR test *P* = 0.11 before Bonferroni correction). Based on WSR test results, none of Mackenzie's named species groups are strongly rejected using ITS data alone.

Within the remainder of subgenus *Vignea*, two clades are supported with bootstrap support of 70% or higher (Fig. 3): one composed of section *Holarrrhenae* (Doell.) Pax, the western North American *Phaestoglochin* Dumort. sampled, and the only member of section *Ammoglochin* Dumort. native to North America, and a second composed of the capitate eastern North American *Phaestoglochin* sampled, two sections with compound inflorescences (sections *Vulpinae* (Heuffel) Christ and *Multiflorae* (J. Carey) Kük.), and *C. vernacula* L. H. Bailey (section *Foetidae* (Tuck. ex L. H. Bailey) Kük.). Monophyly of section *Phaestoglochin* is strongly rejected (WSR *P* < 0.0016 with Bonferroni correction).

Table 1. Taxa included in study. Taxa for which two or more individuals were sequenced are marked with an asterisk (*). Sectional assignments follow Ball and Reznicek (2002) for most North American taxa, Egorova (1999) for most Old World taxa. Assignment to species group within section *Ovales* follows Mackenzie (1935) and Hermann (1970), with remaining species assigned according to morphology where feasible.

Carex species	Locality	Voucher	GenBank
SUBGENUS CAREX L.			
Sect. <i>Acrocystis</i> Dumort.			
<i>C. pensylvanica</i> Lam.	U.S.A., Wisconsin	Hipp 513 (WIS)	AY779137
Sect. <i>Hymenochlaenae</i> Drej. ex L. H. Bailey			
<i>C. gracillima</i> Schwein.	U.S.A., Wisconsin	Hipp 505 (WIS)	AY779103
Sect. <i>Phacocystis</i> Dumort.			
<i>C. haydenii</i> Dewey	U.S.A., Wisconsin	Hipp 501 (WIS)	AY779106
SUBGENUS PSYLLOPHORA (DEGL.) PETERM. [= SUBG. PRIMOCAREX KÜK.]			
Sect. <i>Capituligeræ</i> Kük.			
* <i>C. capitata</i> L.	U.S.A., Colorado	Hipp & Hartman 1507 (WIS)	AY779079
SUBGENUS VIGNEA (P. BEAUV. EX T. LESTIB.) PETERM.—EXCLUDING SECT. OVALES			
Sect. <i>Ammoglochin</i> Dumort.			
<i>C. brizoides</i> L.	Czechoslovakia	Bohuslavek 694 (MICH)	AY779076
<i>C. siccata</i> Dewey	U.S.A., Wisconsin	McNeilus 89-307 (WIS)	AY779158
Sect. <i>Chordorrhizae</i> Meinsh.			
* <i>C. chordorrhiza</i> Ehrh. ex L. f.	U.S.A., Wisconsin	Judziewicz 11790 (WIS)	AY779087
<i>C. pseudocuraica</i> F. Schmidt	China	Lin 668 (MO)	AY779148
Sect. <i>Deweyanae</i> Tuck.			
* <i>C. deweyana</i> Schwein. subsp. <i>deweyana</i>	U.S.A., Wisconsin	DeJooode 1543 (WIS)	AY779094
Sect. <i>Divisæ</i> Christ ex Kük.			
<i>C. macrorrhiza</i> Boeck.	Argentina, Santa Cruz	Roivainen 2630 (RSA)	AF285018
<i>C. praegracilis</i> W. Boott	U.S.A., California	Hipp 216 (WIS)	AY779143
Sect. <i>Foetidae</i> (Tuck. ex L. H. Bailey) Kük.			
* <i>C. vernacula</i> L. H. Bailey	U.S.A., California	Hipp & Clifton 680 (WIS)	AY779178

Phylogeny and Patterns of Convergence in *Carex* Sect. *Ovales* (Cyperaceae)

203

Sect. <i>Glareosae</i> G. Don				
* <i>C. canescens</i> L.	U.S.A., Wisconsin	<i>Hipp et al. 587</i> (WIS)		AY779078
Sect. <i>Heleoglochin</i> Dumort.				
<i>C. prairea</i> Dewey ex A. W. Wood	U.S.A., Wisconsin	<i>Hipp & Zimmerman 602</i> (WIS)		AY779144
Sect. <i>Holarrhenae</i> (Doell.) Pax				
<i>C. sartwellii</i> Dewey	U.S.A., Wisconsin	<i>Hipp 515</i> (WIS)		AY779154
* <i>C. curauca</i> Kunth	Russia, Siberia	<i>Krasnoborov et al. s.n.</i> (MO)		AY779092
Sect. <i>Macrocephalae</i> Kük.				
<i>C. macrocephala</i> Willd. ex Spreng.	U.S.A., Oregon	<i>Halse 1543</i> (RSA)		AF285017
Sect. <i>Multiflorae</i> (J. Carey) Kük.				
<i>C. vulpinoidea</i> Michx. (1)	U.S.A., Wisconsin	<i>Cochrane 13345</i> (WIS)		AY779180
<i>C. vulpinoidea</i> Michx. (2)	U.S.A., Texas	<i>Roalson 1294</i> (RSA)		AF284968
Sect. <i>Phaestoglochin</i> Dumort.				
<i>C. cephaloidea</i> (Dewey) Dewey	U.S.A., Wisconsin	<i>Hipp & Rothrock 1220</i> (WIS)		AY779080
<i>C. cephalophora</i> Muhl. ex Willd.	U.S.A., Wisconsin	<i>Hipp 528</i> (WIS)		AY779081
<i>C. cf. gravida</i> L. H. Bailey	U.S.A., Wisconsin	<i>Hipp 498</i> (WIS)		AY779083
<i>C. hoodii</i> Boott	U.S.A., California	<i>Hipp & Clifton 705</i> (WIS)		AY779107
<i>C. muehlenbergii</i> Schkuhr ex Willd.	U.S.A., Wisconsin	<i>Hipp 545</i> (WIS)		AY779124
<i>C. occidentalis</i> L. H. Bailey	U.S.A., New Mexico	<i>Hipp et al. 2067</i> (WIS)		AY779128
* <i>C. radiata</i> (Wahlenb.) Small	U.S.A., Wisconsin	<i>Hipp 503</i> (WIS)		AY779149
<i>C. rosea</i> Schkuhr ex Willd.	U.S.A., Wisconsin	<i>Hipp 514</i> (WIS)		AY779153
Sect. <i>Potosinae</i> Mack.				
<i>C. potosina</i> Hemsl.	Mexico, Zacatecas	<i>Villegas & Garcia s.n.</i> (WIS)		AY779142
Sect. <i>Remotae</i> (Asch.) C. B. Clarke				
<i>C. planata</i> Franch. & Sav. (1)	Japan, Tarumizu	<i>Kurosawa 4025</i> (MO)		AY779140
<i>C. planata</i> Franch. & Sav. (2)	Japan, Honshu	<i>Tsugaru & Takahashi 26567</i> (MO)		AY779141
<i>C. remota</i> L.	former U.S.S.R.	<i>Novikov et al. 5863</i> (MO)		AY779150
Sect. <i>Stellulatae</i> Kunth				
<i>C. interior</i> L. H. Bailey	U.S.A., Wisconsin	<i>Thompson 399</i> (WIS)		AY779112

Table 1. Continued.

Carex species	Locality	Voucher	GenBank
Sect. <i>Vulpinae</i> (Heuffel) Christ			
<i>C. stipata</i> Muhl. ex Willd. var. <i>stipata</i>	U.S.A., Wisconsin	Hipp 506 (WIS)	AY779162
Sect. <i>Ovales</i> Kunth			
Alatae group			
<i>C. alata</i> Torr.	U.S.A., Georgia	Rothrock 3922 (MICH)	AY779066
<i>C. albolutescens</i> Schwein.	U.S.A., Ohio	McCormac et al. 6807 (MICH)	AY779067
* <i>C. cumulata</i> (L. H. Bailey) Mack.	U.S.A., Maine	Reznicek 10924 (WIS)	AY779091
<i>C. longii</i> Mack.	Mexico, Umequaro	Zamudio et al. 11237 (MICH)	AY779115
<i>C. ozarkana</i> P. E. Rothrock & Reznicek	U.S.A., Arizona	Hyatt 9357 (MICH)	AY779135
<i>C. silicea</i> Olney	U.S.A., Maine	Reznicek & Reznicek 10915 (WIS)	AY779159
<i>C. vexans</i> F. J. Herm.	U.S.A., Florida	Rothrock 2379 (MICH)	AY779179
Athrostachyae group			
<i>C. athrostachya</i> Olney	U.S.A., California	Hipp et al. 794 (WIS)	AY779070
<i>C. unilateralis</i> Mack.	U.S.A., Oregon	Wilson 5882 (MICH)	AY779177
Cyeroideae group			
* <i>C. bohemica</i> Schreb.	Austria, Zwettl	Wallnofer 13755 (WIS)	AY779073
<i>C. sychnocephala</i> J. Carey (1)	U.S.A., Wisconsin	Hipp s.n. (WIS)	AY779169
<i>C. sychnocephala</i> J. Carey (2)	U.S.A., Wisconsin	Rogers 00-236 (WIS)	AY779168
Festivae group			
<i>C. abrupta</i> Mack.	U.S.A., California	Hipp 799 (WIS)	AY779064
<i>C. bonplandii</i> Kunth	Bolivia, La Paz	Solomon et al. 18926 (MICH)	AY779074
<i>C. ebenea</i> Rydb.	U.S.A., Colorado	Hipp 1683 (WIS)	AY779095
<i>C. gracilior</i> Mack.	U.S.A., California	Hipp 363 (WIS)	AY779102
<i>C. harfordii</i> Mack.	U.S.A., California	Hipp 309 (WIS)	AY779104
<i>C. haydeniana</i> Olney	U.S.A., Utah	Hipp 140.2 (WIS)	AY779105
* <i>C. illota</i> L. H. Bailey	U.S.A., California	Hipp & Clifton 700 (WIS)	AY779110

Phylogeny and Patterns of Convergence in *Carex* Sect. *Ovales* (Cyperaceae)

205

<i>C. integra</i> Mack.	U.S.A., California	Hipp et al. 774 (WIS)	AY779111
* <i>C. macloviana</i> d'Urv.	U.S.A., Wyoming	Hipp 1893 (WIS)	AY779117
<i>C. mariposana</i> L. H. Bailey	U.S.A., California	Hipp & Clifton 644 (WIS)	AY779118
* <i>C. microptera</i> Mack.	U.S.A., Nevada	Cochrane 14110 (WIS)	AY779120
<i>C. cf. microptera</i> Mack. "Pinaleno"	U.S.A., Arizona	Hipp 2138 (WIS)	AY779086
<i>C. cf. microptera</i> Mack.	Mexico	Reznicek 10303 (MICH)	AY779085
<i>C. orizabae</i> Liebm.	Mexico, Ixtapaluca	Rzedowski 36822 (WIS)	AY779130
<i>C. pachystachya</i> Cham. ex Steud.	U.S.A., Utah	Goodrich 21180 (RM)	AY779136
<i>C. roraimensis</i> Steyerl.	Venezuela (Roraima)	Reznicek 11054 (MICH)	AY779152
<i>C. stenoptila</i> F. J. Herm.	U.S.A., Utah	Hipp 1848 (WIS)	AY779161
<i>C. subbracteata</i> Mack.	U.S.A., California	Hipp 448 (WIS)	AY779165
<i>C. teneriformis</i> Mack.	U.S.A., California	Hipp & Clifton 716 (WIS)	AY779172
Festivae or Festucaceae group			
<i>C. multicosata</i> Mack.	U.S.A., California	Hipp & Clifton 714 (WIS)	AY779125
<i>C. preslii</i> Steud.	U.S.A., Montana	Lesica 7874 (MICH)	AY779146
<i>C. subfusca</i> W. Boott	U.S.A., Nevada	Hipp 833 (WIS)	AY779167
Festucaceae group			
<i>C. bebbii</i> (L. H. Bailey) Fernald	U.S.A., Wisconsin	Hipp 516 (WIS)	AY779071
* <i>C. bicknellii</i> Britton var. <i>bicknellii</i>	U.S.A., Wisconsin	Hipp 549 (WIS)	AY779072
* <i>C. brevior</i> (Dewey) Mack. ex Lunell	U.S.A., Texas	Reznicek 10345b (MICH)	AY779075
<i>C. cf. brevior</i>	Mexico	Reznicek 10497 (MICH)	AY779082
"Buffalo River"	U.S.A., Arkansas	Hyatt 10461 (MICH)	AY779077
* <i>C. crawfordii</i> Fernald	U.S.A., Maine	Reznicek & Reznicek 10918 (WIS)	AY779089
<i>C. eGGLESTONII</i> Mack.	U.S.A., Colorado	Hipp 1594 (WIS)	AY779097
<i>C. festucacea</i> Schkuhr ex Willd.	U.S.A., Wisconsin	Hipp et al. 561 (WIS)	AY779098
<i>C. hyalina</i> Boott	U.S.A., Mississippi	Rothrock 2947 (MICH)	AY779109
* <i>C. merritt-fernaldii</i> Mack.	U.S.A., New Hampshire	Rothrock 3475 (MICH)	AY779119
* <i>C. missouriensis</i> P. E. Rothrock & Reznicek	U.S.A., Missouri	Rothrock 3567b (MICH)	AY779121

Table 1. Continued.

Carex species	Locality	Voucher	GenBank
* <i>C. molesta</i> Mack. ex Bright	U.S.A., Missouri	Rothrock 3567.5 (MICH)	AY779122
* <i>C. molestiformis</i> Reznicek & P. E. Rothrock	U.S.A., Oklahoma	Reznicek 9766 (MICH)	AY779123
* <i>C. normalis</i> Mack.	U.S.A., Wisconsin	Rothrock & Hipp 3835 (MICH)	AY779127
<i>C. opaca</i> (F. J. Herm.) P. E. Rothrock & Reznicek	U.S.A., Illinois	Reznicek 10856 (MICH)	AY779129
<i>C. oronensis</i> Fernald	U.S.A., Maine	Reznicek et al. 10931 (WIS)	AY779131
<i>C. reniformis</i> (L. H. Bailey) Small	U.S.A., Arkansas	Hyatt 6996 (WIS)	AY779151
<i>C. scoparia</i> Schkuhr ex. Willd.	U.S.A., Indiana	Rothrock 3633b (MICH)	AY779155
<i>C. scoparia</i> Schkuhr ex. Willd. var. <i>tesselata</i> Fernald & Wiegand	U.S.A., Maine	Reznicek 10923 (WIS)	AY779156
* <i>C. shinersii</i> P. E. Rothrock and Reznicek	U.S.A., Texas	Reznicek 10367 (MICH)	AY779157
<i>C. stramineiformis</i> L. H. Bailey	U.S.A., Nevada	Hipp 847 (WIS)	AY779164
* <i>C. tenera</i> Dewey var. <i>echinodes</i> (Fernald) Wiegand	Canada, Ontario	Reznicek 9509 (MICH)	AY779096
* <i>C. tenera</i> Dewey var. <i>tenera</i>	U.S.A., Ohio	Rothrock 3731 (MICH)	AY779171
<i>C. tetraстachya</i> Scheele	U.S.A., Texas	Reznicek 10411 (MICH)	AY779173
<i>C. tincta</i> (Fernald) Fernald	U.S.A., Maine	Rothrock 3734 (MICH)	AY779174
Fetae group			
* <i>C. feta</i> L. H. Bailey	U.S.A., California	Hipp 457 (WIS)	AY779099
<i>C. hormathodes</i> Fernald	U.S.A., Maine	Reznicek 10929 (WIS)	AY779108
<i>C. straminea</i> Willd. ex Schkuhr	U.S.A., Wisconsin	Hipp et al. 561 (WIS)	AY779163
<i>C. suberecta</i> (Olney) Britton	U.S.A., Wisconsin	Hipp & Zimmerman 598 (WIS)	AY779166
Foeneae group			
<i>C. adusta</i> Boott	U.S.A., Maine	Reznicek 10922 (WIS)	AY779065
<i>C. arapaheensis</i> Clokey	U.S.A., Colorado	Hipp 1659 (WIS)	AY779068
<i>C. argyrantha</i> Tuck. ex Dewey	U.S.A., Maine	Reznicek 10921 (WIS)	AY779069
<i>C. foenea</i> Willd.	U.S.A., Maine	Reznicek 10928 (WIS)	AY779100
<i>C. xerantica</i> L. H. Bailey	Canada, Ontario	Oldham & Bakowsky 17732 (MICH)	AY779182

Phylogeny and Patterns of Convergence in *Carex* Sect. *Ovales* (Cyperaceae)

Fractae group					
* <i>C. fracta</i> Mack.	U.S.A., California	<i>Hipp 635</i> (WIS)			AY779101
Leporinae group					
<i>C. leporinella</i> Mack.	U.S.A., California	<i>Tallent 815</i> (MICH)			AY779114
<i>C. ovalis</i> Gooden.	New Zealand	<i>Ford, K.A. 30/98</i> (MICH)			AY779132
<i>C. ovalis</i> Gooden.	U.S.A., Wisconsin	<i>Judziewicz 6689</i> (WIS)			AY779133
<i>C. ovalis</i> Gooden.	Greece	<i>Strid 24872</i> (RSA)			AF285002
<i>C. ovalis</i> Gooden.	U.S.A., Oregon	<i>Wilson & Kuykendall 7027</i> (WIS)			AY779134
<i>C. phaeocephala</i> Piper	U.S.A., Utah	<i>Hipp 135</i> (WIS)			AY779139
<i>C. praticola</i> Rydb.	Canada, Ontario	<i>Oldham & Bakowsky 21854</i> (MICH)			AY779145
<i>C. taehensis</i> Smiley	U.S.A., California	<i>Hipp 879</i> (WIS)			AY779170
Specificae group					
<i>C. constanceana</i> Stacey	U.S.A., California	<i>Hipp et al. 800</i> (WIS)			AY779088
<i>C. davyi</i> Mack.	U.S.A., California	<i>Hipp 901a</i> (WIS)			AY779093
<i>C. petasata</i> Dewey	U.S.A., Montana	<i>Morse & Jordan 2082</i> (MICH)			AY779138
* <i>C. specifica</i> L. H. Bailey	U.S.A., California	<i>Hipp 861</i> (WIS)			AY779160
* <i>C. wootonii</i> Mack.	U.S.A., New Mexico	<i>Hyatt 8294</i> (MICH)			AY779181
Tribuloideae group					
<i>C. cristatella</i> Britton	U.S.A., Wisconsin	<i>Hipp & Zimmerman 606</i> (WIS)			AY779090
* <i>C. muskingumensis</i> Schwein.	U.S.A., Wisconsin	<i>Hipp & Biggs 2009</i> (WIS)			AY779126
* <i>C. projecta</i> Mack.	U.S.A., Wisconsin	<i>Hipp et al. 1206</i> (WIS)			AY779147
<i>C. tribulooides</i> Wahlenb. var. <i>sangamonensis</i> Clokey	U.S.A., Mississippi	<i>Rothrock 2941</i> (MICH)			AY779175
<i>C. tribulooides</i> Wahlenb. var. <i>tribulooides</i>	U.S.A., Wisconsin	<i>Hipp 185</i> (WIS)			AY779176
Ovales—unallied					
<i>C. cf. lagunensis</i> M. E. Jones	Mexico, Durango	<i>Gonzalez et al. 4482</i> (MICH)			AY779084
<i>C. interjecta</i> Reznicek	Mexico, Morelos	<i>Zika 15398</i> (MICH)			AY779113
<i>C. maackii</i> Maxim.	Japan, Honshu	<i>Kan 8031</i> (RSA)			AY779116

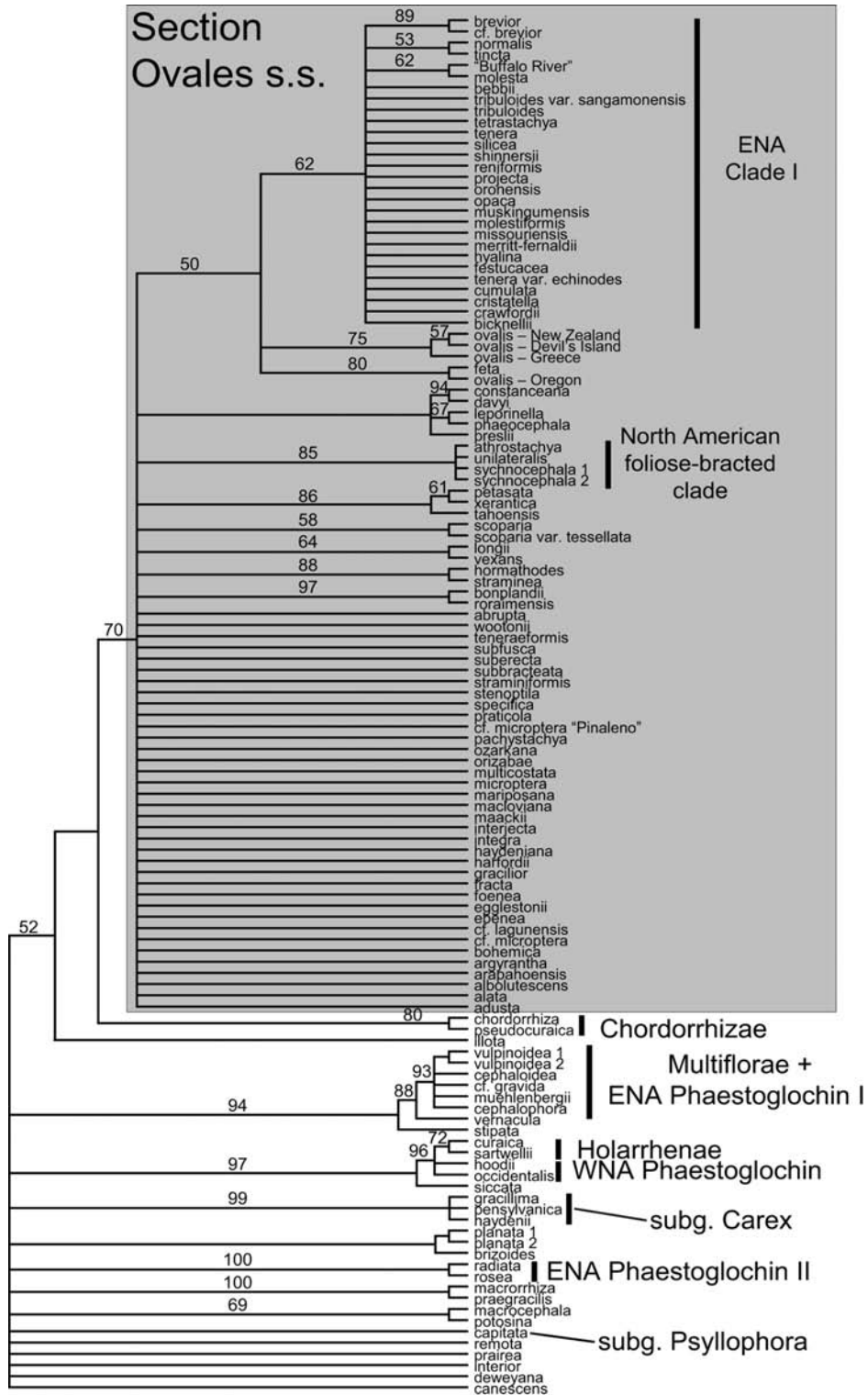


Figure 2. Strict consensus of 90,791 MP trees. Numbers above branches are nonparametric bootstrap values. Tree length (L) = 530 steps, consistency index (CI) = 0.432, retention index (RI) = 0.759.

DISCUSSION

CIRCUMSCRIPTION OF SECTION *OVALES*

The finding that section *Ovales* is monophyletic with the exclusion of *Carex illota* reflects data from more than 90% of the species in the section. Representatives from 15 other sections of subgenus *Vignea* include all likely close relatives, including gynecandrous sections, species with winged perigynia, and species with vegetative culms. Although ITS data fail to reject the monophyly of section *Ovales* with section *Cyperoideae* excluded (WSR), phylogenetic results provide preliminary evidence for submerging *C. sychnocephala* J. Carey and *C. bohemia* Schreb. into section *Ovales*.

The East Asian *Carex maackii* has been included in section *Remotae* (Asch.) C. B. Clarke (as *Planatae* Akiyama) by at least one author (Song-Yun & Yan-Cheng, 1990), but it is generally included in section *Ovales* (Kükenthal, 1909; Reznicek, 1993; Egorova, 1999) based on its possession of winged perigynia (Fig. 1) and vegetative culms. The ITS data place *C. maackii* within section *Ovales* and weakly support its placement as sister to the rest of *Ovales*. A biogeographic hypothesis for the origin of the group is clearly premature. The position of *C. maackii* could reflect either an Old World origin for the section or a long-distance dispersal event followed by a striking lack of species diversification.

POSITION OF *OVALES* WITHIN SUBGENUS *VIGNEA*

ITS data place section *Chordorrhizae* Meinsh. sister to section *Ovales*. Another recent ITS study of subgenus *Vignea* with denser taxon sampling also recovers a clade composed of section *Chordorrhizae* and most of section *Glareosae* G. Don in a position sister to section *Ovales* (Hendrichs et al., 2004). However, these results from ITS alone are not supported by sampling using additional nrDNA and chloroplast DNA (cpDNA) regions (Hipp et al., 2006), leaving the placement of section *Ovales* in doubt. Savile and Calder's (1953) placement of *Ovales* as sister to section *Ammoglochin* is not supported. Egorova's (1999) hypothesis that section *Inversae* Kük. diverges near the base of section *Ovales* has not been evaluated.

CONVERGENCE ON VEGETATIVE CULM PRODUCTION IN SUBGENUS *VIGNEA*

Carex chordorrhiza is a circumboreal species that has traditionally been allied or considered to be conspecific with the Eurasian *C. pseudocuraica* (Hultén, 1962). Both species spread vegetatively via sprouts from the nodes of vegetative culms that behave like stolons (Hultén, 1962; Egorova, 1999). Egorova (1999) viewed this as a convergent character state and recommended splitting section *Chordorrhizae* into sections *Divisae* Christ ex Kük. (*C. chordorrhiza*) and *Holarrhenae* (*C. pseudocuraica*). The ITS data, however, support retaining *C. chordorrhiza* and *C. pseudocuraica* within a single section. This, combined with the fact that section *Holarrhenae* groups with neither section *Chordorrhizae* nor section *Ovales*, implies that there have been two or three origins of vegetative culms in subgenus *Vignea*: one within section *Holarrhenae*, and one either at the base of the clade composed of sections *Chordorrhizae* and *Ovales* (if the ITS resolution for these is correct) or at the base of each of these two sections. Late-season vegetative culms overwinter and act as stolons in three of the *Tribuloideae* and several of the *Alatae* group of section *Ovales* as well as in section *Chordorrhizae* (Eaton, 1959, 1960), and they appear to play a role in competing for light and surviving seasonal inundation in many species in which they do not act as stolons. Although the adaptive value of vegetative culms has not been evaluated using experimental methods, the independent evolution of elongate vegetative culms in several wetland sedge sections (e.g., sections *Carex*, *Chordorrhizae*, and *Holarrhenae*, as well as many species of section *Ovales*) supports the argument that vegetative culms may be adaptive in flooded habitats.

CONVERGENCE AND BIOGEOGRAPHY IN SUBGENUS *VIGNEA* AND SECTION *OVALES*

This study supports recent molecular evidence that phylogeny often correlates better with geography than with traditional taxonomy in *Carex*, both at the species level and below (Roalson & Friar, 2004; Dragon & Barrington, 2008). Monophyly of section *Phaestoglochin*, for example, is strongly rejected in this study ($P < 0.0016$), with taxa from eastern North

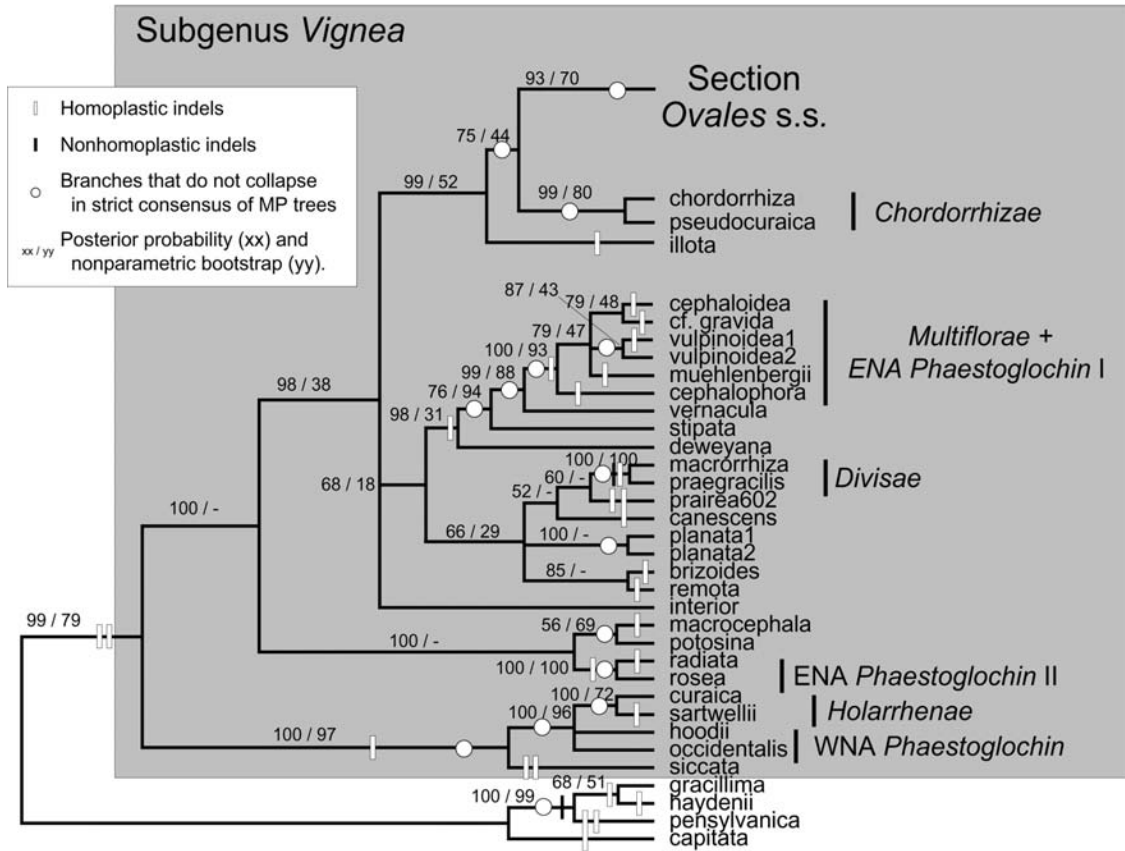


Figure 3. Bayesian majority rule consensus, part I: Subgenus *Vigna*. Numbers above branches are posterior probabilities based on sampling of 7000 trees (from 700,000 MCMC generations).

America forming two clades and western North American species forming a third. Likewise, the Old World species *C. brizoides* of section *Ammoglochin* is more closely related to two other Old World species with winged perigynia—*C. planata* and *C. remota* L.—than it is to *C. siccata*, the New World species of section *Ammoglochin*. This pattern of infrageneric taxa breaking down along geographic lines is of course not confined to *Carex* (cf. Berry et al., 2005) and will probably become more evident with increasingly detailed systematic work in the genus.

A similar pattern is seen within Mackenzie's Festuceae group of section *Ovales*. Species in this group have flat perigynium beaks that are margined to the tip, vegetative culms with leaves clustered at the shoot apex, leaf sheaths that are hyaline on the inner face, and perigynia that are broadest at or below the middle (Rothrock & Reznicek, 2001).

The Festuceae are the most diverse of Mackenzie's species groups (21 to 24 species; Table 1), and they range from the East Coast to the West Coast (Mastrogioiuseppe et al., 2002). The eastern members of the Festuceae group form a single clade in this study, along with the Tribuloideae group and two members of the Alatae group (ENA Clade I; Figs. 2 and 4). In contrast, the species that occur strictly in the west are scattered throughout the largely unresolved western portion of the tree (Fig. 4). This suggests a single origin for the majority of the eastern species in the section and convergence in the western taxa on the complex of morphological characters that Mackenzie used to define this species group.

One of the most striking cases of convergence and biogeographic coherence in section *Ovales* pertains to the relationships of the species traditionally placed in section *Cyperoideae*. The North American member of this group, *Carex sychnocephala*, is

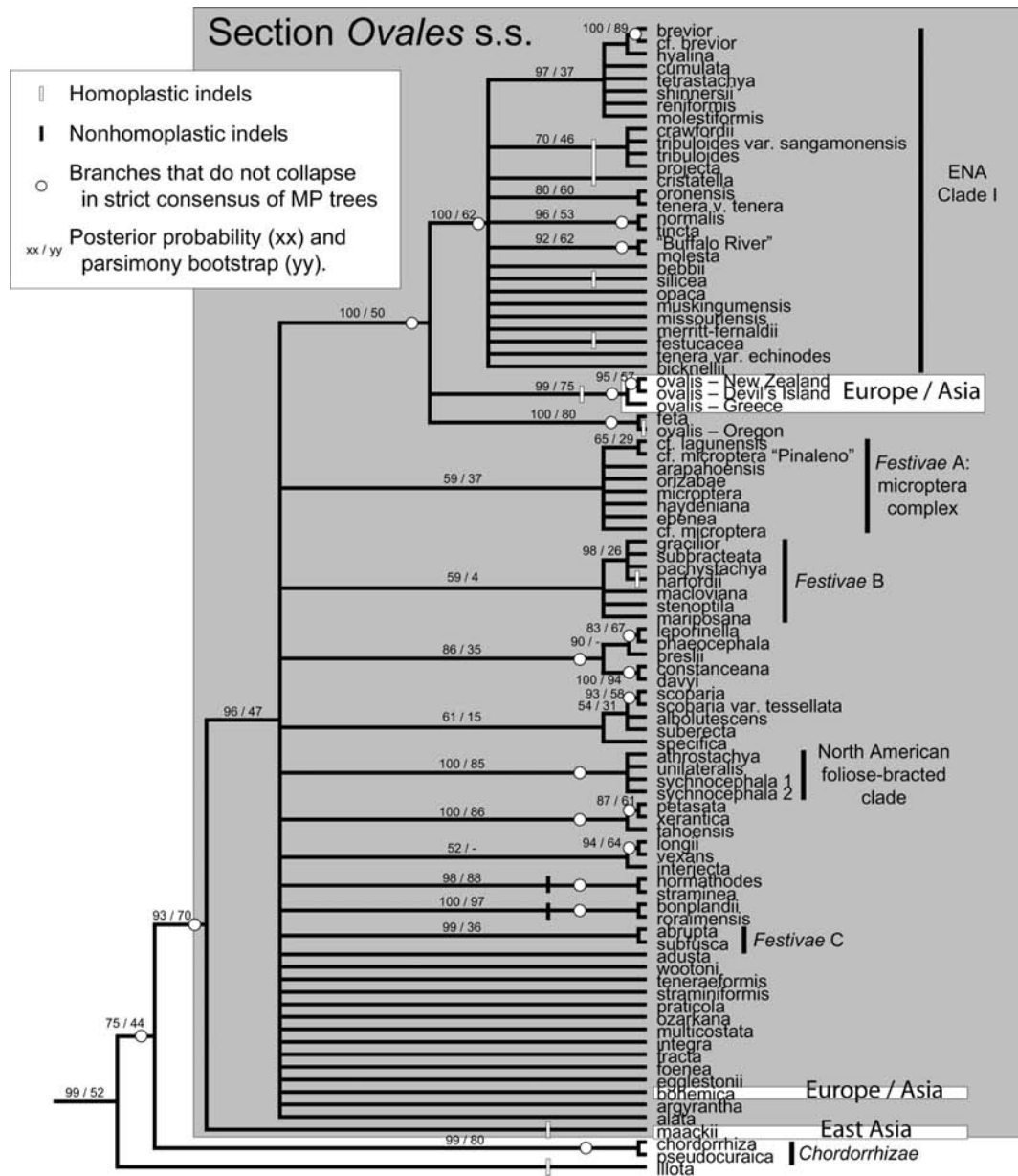


Figure 4. Bayesian majority rule consensus, part II: Section *Ovales*. Numbers above branches are posterior probabilities based on sampling of 7000 trees (from 700,000 MCMC generations).

revealed in this study to be more closely related to *C. athrostachya* Olney and *C. unilateralis* Mack. of Mackenzie's North American *Athrostachyae* group than to its Eurasian counterpart, *C. bohemica* (Fig. 4). This North American foliose-bracted clade of *C. sychnocephala* plus the *Athrostachyae* is marked by three synapomorphies: (1) prominent, foliose bracts

that exceed a (2) capitate inflorescence, with (3) perigynia prominently nerved on the ventral face. However, the similarities in perigynium and bract length between *C. bohemica* and *C. sychnocephala* are far more pronounced than those that define the North American foliose-bracted clade, at least superficially (Fig. 1).

CONCLUSIONS

Section *Ovales* has long been recognized to be a natural group, but convergence in the synapomorphies that define it has not previously been investigated. This study demonstrates that the accuracy of phylogenetic hypotheses below the sectional level in *Carex* based on morphology is dependent on difficult and often subjective decisions about what characters to code and how to code them (Crins, 1990). Work under way within *Ovales* is focused on increasing phylogenetic resolution and developing comparative methods for addressing mechanisms of speciation using highly resolved phylogenies. While, 14 years after Reznicek's (1990) classic study on evolutionary trends in the genus, we are still far from "the end point, a phylogenetic classification of *Carex* to the species level" (Reznicek, 1990: 1430), fine-scale systematic work (Roalson & Friar, 2004; Hipp et al., 2007; Dragon & Barrington, 2008) is finally providing the framework needed to address biogeographic, morphological, and chromosomal patterns of speciation in this huge and ecologically important genus.

ACKNOWLEDGMENTS

The author gratefully acknowledges Anton Reznicek and Paul Rothrock for their generosity and years of work on the taxonomy of *Carex* sect. *Ovales*. Their collections of frozen and silica-dried material permitted nearly exhaustive sampling of the eastern North American taxa in this study. My graduate advisor, Paul Berry, and my wife, Rachel Davis, were a source of advice and good humor throughout this project. I am grateful to Glen Clifton, Theodore Cochrane, Jonathan Coop, Ron Hartman, Kerry Heise, Eric Roalson, Dave Rogers, Julian Starr, Ken Sytsma, David Weixelman, Alan Yen, Elizabeth Zimmerman, and colleagues in the Sytsma and Berry labs for help in field and lab, and to the curators of MICH, MO, RM, RSA, and UC/JEPS for specimen loans. Richard Whitkus, Julian Starr, Julie Dragon, and an anonymous reviewer provided detailed and helpful comments on early drafts of this paper. This research was funded by grants from the Botanical Society of America, American Society of Plant Taxonomists, University of Wisconsin–Madison Department of Botany Davis Fund, University of Wisconsin–Madison Natural History Museums Council, a Lawrence Memorial Award from the Hunt

Institute for Botanical Documentation, and National Science Foundation Dissertation Improvement Grant #0308975 to P. E. Berry and the author.

LITERATURE CITED

- Ball, P. W. & A. A. Reznicek (editors). 2002. *Carex* Linnaeus. Pp. 254–572 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.
- Baum, D. A. & K. J. Sytsma. 1994. A phylogenetic analysis of *Epilobium* (Onagraceae) based on nuclear ribosomal DNA sequences. *Syst. Bot.* 19: 363–388.
- Berry, P. E., A. L. Hipp, K. J. Wurdack, B. Van Ee & R. Riina. 2005. Molecular phylogenetics of the giant genus *Croton* (Euphorbiaceae sensu stricto) using ITS and *trnL-F* DNA sequence data. *Amer. J. Bot.* 92: 1520–1534.
- Buckley, T. R., C. Simon, H. Shimodaira & G. K. Chambers. 2001. Evaluating hypotheses on the origin and evolution of the New Zealand alpine cicadas (Maoricicada) using multiple-comparison tests of tree topology. *Syst. Biol.* 18: 223–234.
- Chater, A. O. 1980. *Carex*. Pp. 290–323 in T. G. Tutin, V. H. Heywood, N. A. Burges, D. M. Moore, S. M. Waters & D. A. Webb (editors), *Flora Europaea*, Vol. 5. Cambridge Univ. Press, Cambridge.
- Crins, W. J. 1990. Phylogenetic considerations below the sectional level in *Carex*. *Canad. J. Bot.* 68: 1433–1440.
- DeBry, R. W. & R. G. Olmstead. 2000. A simulation study of reduced tree-search effort in bootstrap resampling analysis. *Syst. Biol.* 49: 171–179.
- Doyle, J. J. & J. L. Doyle. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissues. *Phytochem. Bull. Bot. Soc. Amer.* 19: 11–15.
- Dragon, J. A. & D. S. Barrington. 2008. East vs. west: Monophyletic clades within the paraphyletic *Carex acuta* complex, section *Phacocystis* (Cyperaceae). Pp. 215–226 in R. F. C. Naczi & B. A. Ford (editors), *Sedges: Uses, Diversity, and Systematics of the Cyperaceae*. Monogr. Syst. Bot. Missouri Bot. Gard. 108.
- Eaton, R. J. 1959. Additional note on vegetative reproduction in *Carex tribuloides* and *C. projecta*. *Rhodora* 61: 294–295.
- . 1960. Vegetative reproduction in *Carex longii* and *C. vexans*. *Rhodora* 62: 338–339.
- Egorova, T. V. 1999. The Sedges (*Carex* L.) of Russia and Adjacent States (Within the Limits of the Former USSR). Missouri Botanical Garden Press, St. Louis.

- Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39: 783–791.
- Gleason, H. A. & A. Cronquist. 1991. *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*, 2nd ed. The New York Botanical Garden, New York.
- Hall, T. A. 1999. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl. Acids. Symp. Ser.* 41: 95–98.
- Hendrichs, M., S. Michalski, D. Begerow, F. Oberwinkler & F. H. Hellwig. 2004. Phylogenetic relationships in *Carex*, subgenus *Vignea* (Cyperaceae), based on ITS sequences. *Pl. Syst. Evol.* 246: 109–125.
- Hermann, F. J. 1970. *Manual of the Carices of the Rocky Mountains and Colorado Basin*. Agricultural Handbook No. 374. U.S. Department of Agriculture, Washington, D.C.
- Hipp, A. L. 1999. A checklist of Carices for prairies, savannas and oak woodlands of southern Wisconsin. *Trans. Wisconsin Acad. Sci.* 86: 77–99.
- , P. E. Rothrock, A. A. Reznicek & J. A. Weber. 2006. Phylogeny and classification of *Carex* section *Ovales* (Cyperaceae). *Int. J. Plant Sci.* 167: 1029–1048.
- , —, — & P. E. Berry. 2007. Changes in chromosome number associated with speciation in sedges: A phylogenetic study in *Carex* section *Ovales* (Cyperaceae) using AFLP data. Pp. 193–203 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.
- Huelsenbeck, J. P. & F. Ronquist. 2001. MrBayes: Bayesian inference of phylogeny. *Bioinformatics* 17: 754–755.
- Hultén, E. 1962. *The Circumpolar Plants. I: Vascular Cryptogams, Conifers, Monocotyledons*. Almqvist and Wiksell, Stockholm.
- Kükenthal, G. 1909. Cyperaceae–Caricoideae. Pp. 1–824 in A. Engler (editor), *Das Pflanzenreich IV*, Vol. 20, heft 38. Wilhelm Engelmann, Leipzig.
- Mackenzie, K. K. 1935. *Carex*: Cariceae. *N. Amer. Fl.* 18: 169–478.
- Maddison, D. R. 1991. The discovery and importance of multiple islands of most parsimonious trees. *Syst. Zool.* 40: 315–328.
- Mastrogriuseppe, J. 2002. *Carex* Linnaeus section *Cyeroideae* G. Don. Pp. 331–332 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.
- , P. E. Rothrock, P. Ball, A. C. Dibble & A. A. Reznicek. 2002. *Carex* Linnaeus section *Ovales* Kunth. Pp. 332–378 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.
- Nylander J. A. A. 2002. MrModeltest v1.1b. Program distributed by the author. Department of Systematic Zoology, Uppsala Univ., Uppsala.
- Raven, P. H. & D. I. Axelrod. 1978. *Origin and Relationships of the California Flora*. Univ. Calif. Publ. Bot. 72. Univ. of California Press, Berkeley.
- Reznicek, A. A. 1990. Evolution in sedges (*Carex*, Cyperaceae). *Canad. J. Bot.* 68: 1409–1432.
- . 1993. A revision of the Mexican members of genus *Carex*, section *Ovales* (Cyperaceae). *Contr. Univ. Michigan Herb.* 19: 97–136.
- & P. M. Catling. 1986. Vegetative shoots in the taxonomy of sedges (*Carex*, Cyperaceae). *Taxon* 35: 495–501.
- & P. E. Rothrock. 1997. *Carex molestiformis* (Cyperaceae), a new species of section *Ovales* from the Ozark Mountain region. *Contr. Univ. Michigan Herb.* 21: 299–308.
- 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.
- & E. A. Friar. 2004. Phylogenetic relationships and biogeographic patterns in North American members of *Carex* section *Acrocystis* (Cyperaceae) using nrDNA ITS and ETS sequence data. *Pl. Syst. Evol.* 243: 175–187.
- Rothrock P. E. & A. A. Reznicek. 2001. The taxonomy of the *Carex bicknellii* group (Cyperaceae) and new species for central North America. *Novon* 11: 205–228.
- Savile, D. B. O. & J. A. Calder. 1953. Phylogeny of *Carex* in the light of parasitism by the smut fungi. *Canad. J. Bot.* 31: 164–174.
- Song-Yun, L. & T. Yan-Cheng. 1990. A conspectus and phytogeography of the genus *Carex* subgenus *Vignea* (P. Beauv.) Kirsch. in China. *Acta Phytotax. Sin.* 28: 237–260.
- Starr, J. R., R. J. Bayer & B. A. Ford. 1999. The phylogenetic position of *Carex* section *Phyllostachys* and its implications for phylogeny and subgeneric circumscription in *Carex* (Cyperaceae). *Amer. J. Bot.* 86: 563–577.
- , S. A. Harris & D. A. Simpson. 2004. Phylogeny of the unispicate taxa in Cyperaceae tribe Cariceae I: Generic relationships and evolutionary scenarios. *Syst. Bot.* 29: 528–544.

- , — & —. 2008. Phylogeny of the unispicate taxa in Cyperaceae tribe Cariceae II: The limits of *Uncinia*. Pp. 227–242 in R. F. C. Naczi & B. A. Ford (editors), *Sedges: Uses, Diversity, and Systematics of the Cyperaceae*. Monogr. Syst. Bot. Missouri Bot. Gard. 108.
- Swofford, D. L. 1998. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods). Vers. 4. Sinauer Associates, Sunderland, Massachusetts.
- Templeton, A. R. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution* 37: 221–244.
- Urbatsch, L. E., B. G. Baldwin & M. J. Donoghue. 2000. Phylogeny of the coneflowers and relatives (Heliantheae: Asteraceae) based on nuclear rDNA internal transcribed spacer (ITS) sequences and chloroplast DNA restriction site data. *Syst. Bot.* 25: 539–565.
- Wheeler, G. A. & G. B. Ownbey. 1984. Annotated list of Minnesota Carices, with phylogeographical and ecological notes. *Rhodora* 86: 151–231.
- White, T. J., T. Birns, S. Lee & J. Taylor. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in M. Innis, D. Gelfand, J. Sninsky & T. White (editors), *PCR Protocols: A Guide to Methods and Applications*. Academic Press, San Diego.
- Whitkus, R. 1988. Systematics and Evolution of the *Carex pachystachya* Complex (Cyperaceae). Ph.D. Dissertation, Ohio State Univ., Columbus.
- & J. G. Packer. 1984. A contribution to the taxonomy of the *Carex macloviana* aggregate (Cyperaceae) in western Canada and Alaska. *Canad. J. Bot.* 61: 1592–1607.
- 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.