

Chapter 9



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

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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, 1999). 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 in 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 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. bohémica*: —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. chordorrhiza*, *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.*

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

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|---|--------------------|---|--|----------|
| 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. curaica</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> Kunth | | | | |
| <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> (Aschers.) 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 |

| Carex species | Locality | Voucher | GenBank |
|---|--------------------|---------------------------------|----------------|
| Sect. <i>Vulpinae</i> Kunth | | | |
| <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 |
| Cyperoideae group | | | |
| * <i>C. bohemica</i> Schreb. | Austria, Zwettl | Wallnofer 13755 (WIS) | AY779073 |
| <i>C. synchnocephala</i> J. Carey (1) | U.S.A., Wisconsin | Hipp s.n. (WIS) | AY779169 |
| <i>C. synchnocephala</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 |

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|---|-----------------------|---------------------------------|----------|
| <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. festucea</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 AY779156 | | U.S.A., Maine | Reznicek 10923 (WIS) |
| * <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> W. 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 |

| | | | | | |
|--|---------------------|---|--|----------|--|
| 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. tahoensis</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 | |

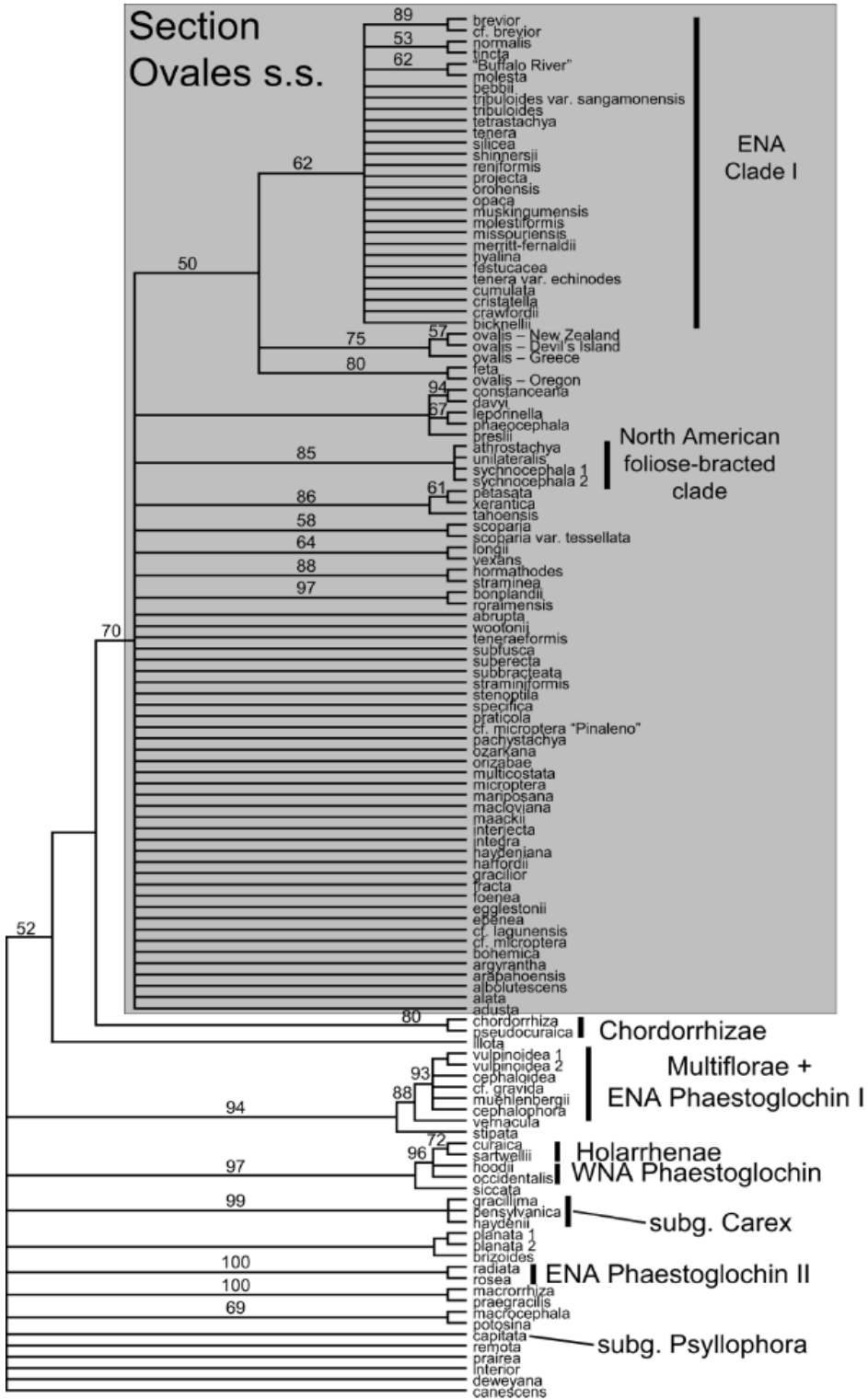


Figure 2. Strict consensus of 90,791 MP trees. Numbers above branches are nonparametric bootstrap values. Tree length (L) = 530 steps, consistency index (CI) = 0.432, retention index (RI) = 0.759.

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. bohemicca* Schreb. into section *Ovales*.

The East Asian *Carex maackii* has been included in section *Remotae* (Aschers.) 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 *Carex 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* (Hulten, 1962). Both species spread vegetatively via sprouts from the nodes of vegetative culms that behave like stolons (Hulten, 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

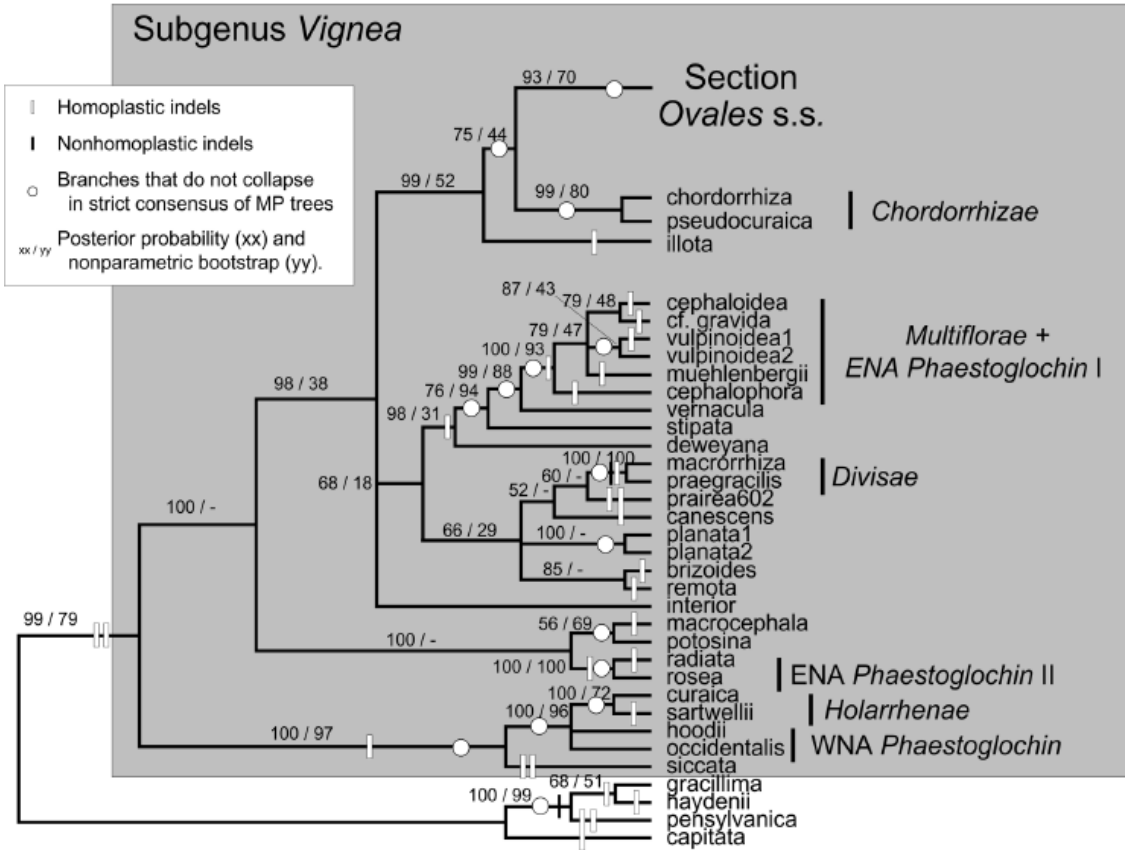


Figure 3. Bayesian majority rule consensus, part I: Subgenus *Vigna*. Numbers above branches are posterior probabilities based on sampling of 7000 trees (from 700,000 MCMC generations).

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 Festucaceae 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 Festucaceae 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 (Mastrogiuseppe et al., 2002). The eastern members of the Festucaceae 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 synchocephala*, is 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. synchocephala* 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. synchocephala* 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.

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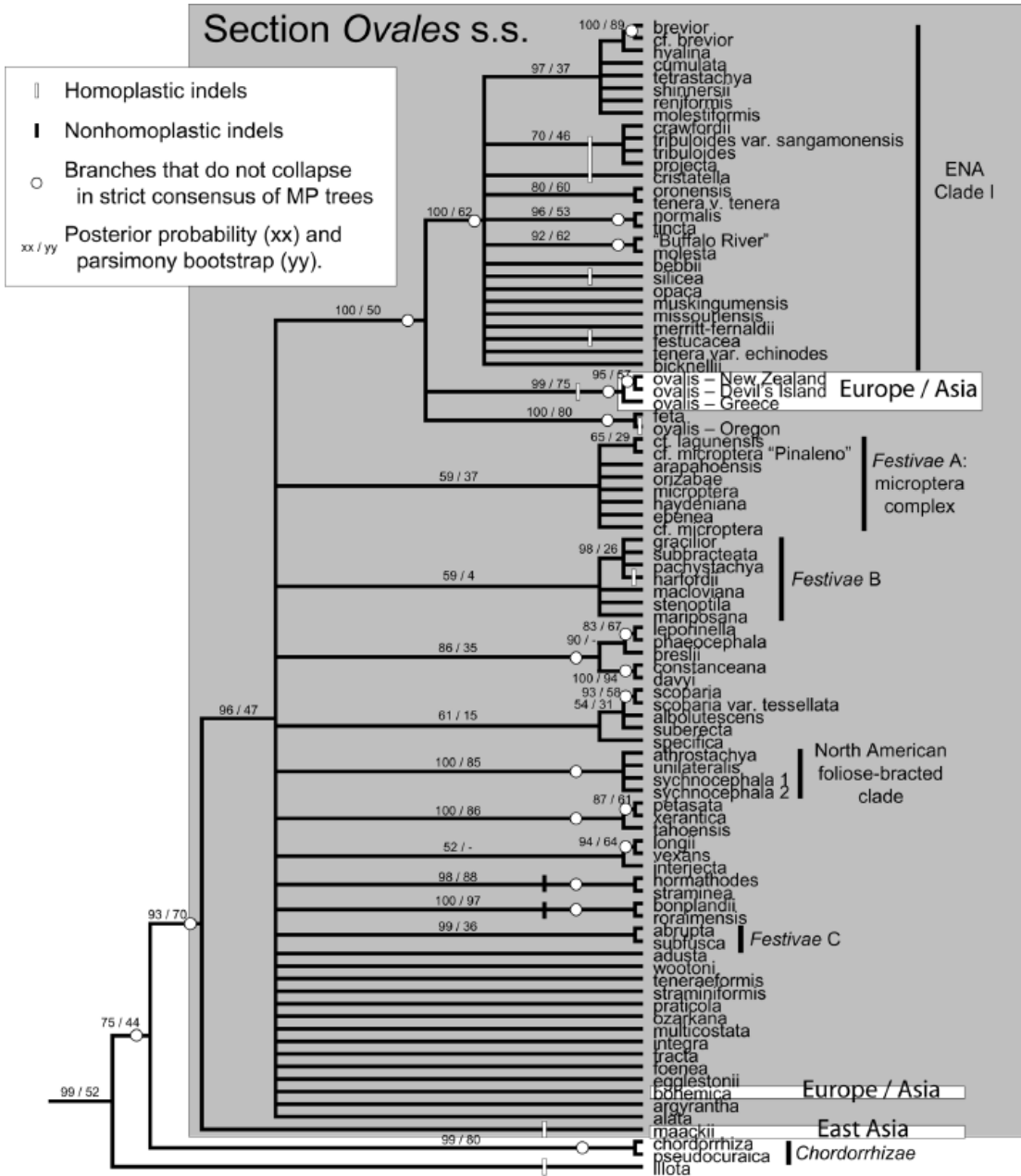


Figure 4. Bayesian majority rule consensus, part II: Section *Ovales*. Numbers above branches are posterior probabilities based on sampling of 7000 trees (from 700,000 MCMC generations).

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