Chapter 12

Phylogeny of the Unispicate Taxa in Cyperaceae Tribe Cariceae II: The Limits of *Uncinia*

Julian R. Starr, Stephen A. Harris, and David A. Simpson

ABSTRACT Debates on the limits and relationships of Cariceae genera and subgenera have historically focused on a small number of unusual "transitional" taxa and on scenarios involving a reduction or proliferation of rachillae (i.e., spikelet secondary axes). The strongest argument for such theories was provided by *Carex microglochin* Wahlenb. and *Uncinia kingii* Boott, a seemingly indisputable link between *Carex* L. and *Uncinia* Pers. In this study we examine the limits of *Uncinia* by focusing on these transitional species and their allies in *Carex* subg. *Psyllophora* (Degl.) Peterm., a reduced unispicate group whose species are largely responsible for blurring generic and *Carex* subgeneric limits. Phylogenies derived from ITS and ETS 1f sequences representing 72 taxa and all five Cariceae genera distinguished four major clades (A, B, C, D), including a predominately unispicate, androgynous clade (A and B) that rejects the classic *U. kingii*/*C. microglochin* transition series (i.e., they are polyphyletic). Nonetheless, analyses strongly support a sister relationship between *Uncinia* s. str. and *U. kingii*. This is an unexpected result, for strong anatomical and morphological evidence would suggest that *U. kingii* is closest to *C. microglochin* and its allies. Moreover, the sister position of *U. kingii* to *Uncinia* s. str. suggests that contrary to previous classifications of *Uncinia* the characters of *Uncinia* sect. *Uncinia* are plesiomorphic. This means that despite section *Uncinia* being largely natural in this analysis, it—like *Uncinia* s.l.—cannot be defined by any known morphological apomorphy. The implications of the analysis for generic and *Carex* subgeneric relationships, including the subgeneric and sectional classification of *Uncinia*, are discussed.

KEY WORDS *Carex microglochin*, Cariceae phylogeny, ETS 1f, generic circumscription, ITS, *Uncinia* classification, *Uncinia kingii*.

The tribe Cariceae Kunth ex Dumort. (ca. 2100 spp.) comprises nearly half of all the species found in the large and taxonomically complex Cyperaceae (Reznicek, 1990). It is a cosmopolitan tribe of herbaceous, predominately anemophilous perennials that occur in diverse habitats ranging from rainforests to tundra. The group is readily marked within the family by the combination of two distinctive features: strictly unisexual flowers and a utricle or perigynium, which is a flask-shaped prophyll that surrounds the naked gynoecium (Blaser, 1944). These uncommon characters clearly discriminate the group, and its circumscription has rarely been debated.

In contrast, the limits and relationships of the tribe's five principal genera (*Carex* L., *Cymophyllus* Mack., *Kobresia* Willd., *Schoenoxiphium* Nees, *Uncinia* Pers.; Reznicek, 1990) are highly controversial (Fig. 1). This is largely due to the numerous taxonomic problems that surround the genus *Carex* (2000 spp.), one of the most widespread and ecologically significant angiosperm genera (Reznicek, 1990). *Carex* exhibits a considerable amount of variation in the structure of its inflorescence (Fig. 2), ranging from the multispicate species in *Carex* subgenera *Carex* p.p., *Vigneastra* (Tuck.) Kük. [= *Indocarex* (Baill.) Kük.], and *Vignea* (P. Beauv. ex T. Lestib.) Peterm. p.p. that may resemble elements in the genera *Schoenoxiphium* or *Kobresia* p.p., to the extremely reduced, unispicate species of *Carex* subg. *Psyllophora* (Degl.) Peterm. [= *Primocarex* Kük.] and *Carex* p.p. that are reminiscent of the genus *Uncinia* or reduced *Kobresia* species. This wide range in the number of flowers and in the structural complexity of the inflorescence has given rise to a long history of tribal classification schemes that are based on evolutionary scenarios involving a small number of "phylogenetic" characters (Kükenthal, 1909; Kreczetovicz, 1936; Nelmes, 1951, 1952; Savile & Calder, 1953), phytogeographical arguments (Kükenthal, 1909; Nelmes, 1951, 1952), and a collection of unusual species that appear to transgress generic limits (e.g., Kükenthal, 1909, 1940; Kreczetovicz, 1936; Ivanova, 1939; Nelmes, 1952).

Historically, the most important characters for generic and subgeneric circumscription have been the gross morphology of the inflorescence (unispicate vs. multispicate), the distribution of the sexes in spikelets (bisexual vs. unisexual), and the degree of fusion of the utricle (open vs. closed to apex) (Fig. 1). These three characters apparently separated the species of *Kobresia* and *Schoenoxiphium* from *Carex* and *Uncinia*, and they further suggested that there was a special relationship between *Uncinia* and *Carex* subg. *Psyllophora* due to the groups' shared solitary spikes, unisexual spikelets, and completely fused utricles. Even though *Uncinia* can be delimited from *Carex* by female spikelets with hooked rachillae (i.e., hooked secondary axes; Figs. 1 and 3), early authors (Tuckerman, 1843; Drejer, 1844; Bentham, 1883; Clarke, 1883) questioned whether these genera were distinct due to the peculiar *C. microglochin* Wahlenb. (section *Leucoglochin* Dumort.), the only *Carex* to possess a consistently exsert rachilla like *Uncinia*. Once viewed as a circumscriptional problem, the discovery of another peculiar species, *U. kingii* Boott [= *C. kingii* (Boott) Reznicek], which has an exsert but only weakly hooked rachilla (Fig. 3), led to the conviction that the rachilla was a character of fundamental significance that demonstrated an indisputable phylogenetic link between *Carex* and *Uncinia* (Reznicek, 1990). This morphological transition series (Fig. 3), which focuses on either rachilla reduction or proliferation, is the source of nearly all controversy regarding *Uncinia* limits and classification, and it represents the most influential and disputed hypothesis used to construct the classic evolutionary scenarios proposed for the Cariceae (e.g., Kükenthal, 1909; Kreczetovicz, 1936; Nelmes, 1952; Savile & Calder, 1953; Hamlin, 1959). In conjunction with other evidence, such as phytogeography (Kükenthal, 1909; Nelmes, 1951, 1952) or smut host-parasite relationships (Savile & Calder, 1953), this hypothesis has been used to suggest an uncinoid origin for many *Carex* subg. *Psyllophora* species (Kreczetovich, 1936; Nelmes, 1952; Hamlin, 1959), as evidence that *Uncinia* had evolved from within *Carex* (Savile & Calder, 1953), that *Carex* itself was derived from *Uncinia* (Kükenthal, 1909), or simply that *Carex* and *Uncinia* should be merged (Koyama, 1961). However, recent studies of the inflorescence (Kukkonen, 1967; Meert & Goetghebeur, 1979) and rachilla (Reznicek, 1990) have suggested that *U. kingii* has more in common with *C. microglochin* than with *Uncinia* s. str. Accordingly, Reznicek (1990: 1419) transferred it to *Carex*, stating that the removal of *U. kingii* made "*Uncinia* a much more uniform and presumably natural genus."

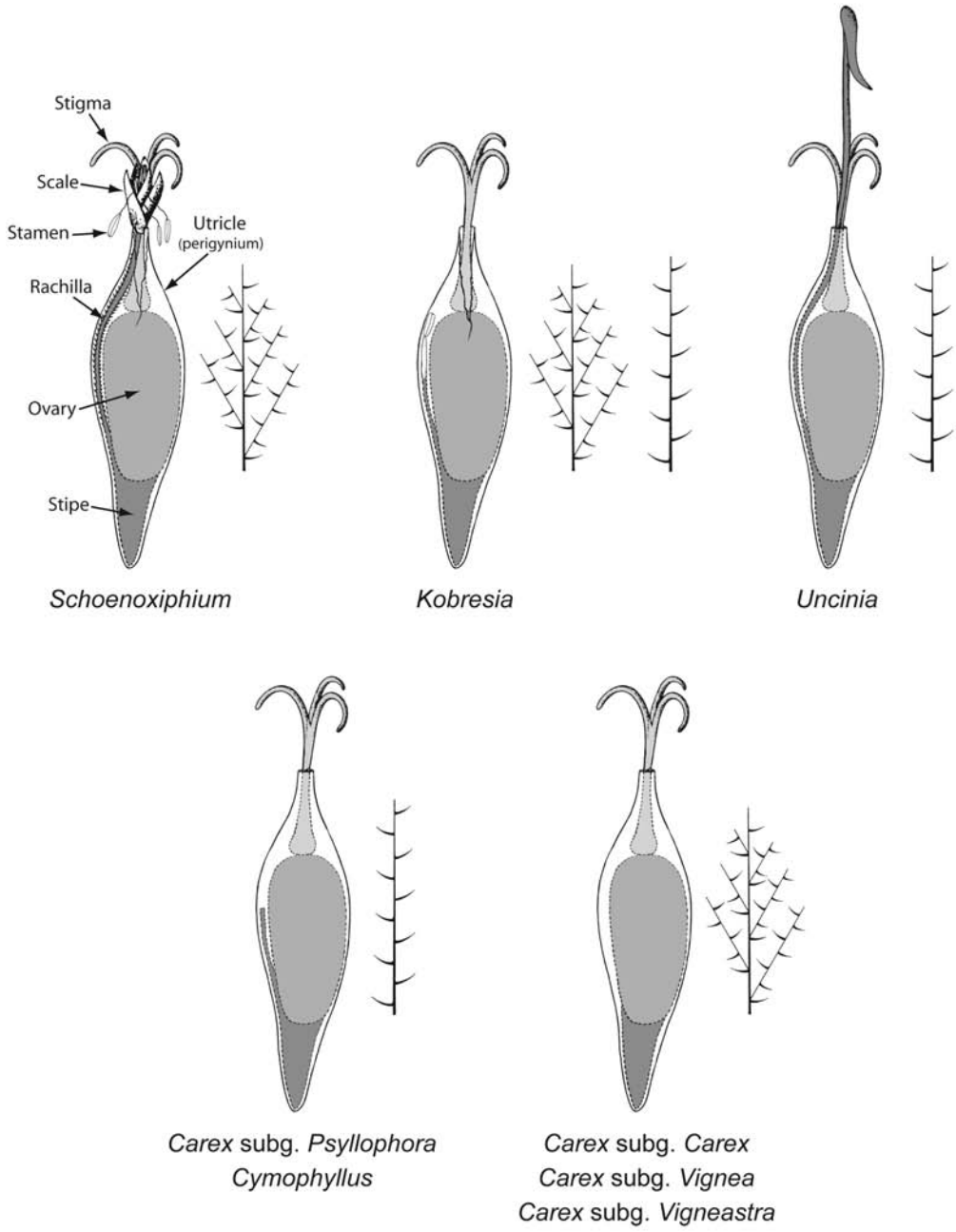

Figure 1. Cariceae generic circumscription. In his monograph of the tribe, Kükenthal (1909) divided genera largely on the basis of female spikelet morphology and the gross structure of the inflorescence. For each genus, typical spikelet morphologies are portrayed next to a stylized representation of their inflorescences (multispicate and/or unispicate). Note that the female spikelets in *Schoenoxiphium* and *Kobresia* have open utricles (i.e., not fused to apex) and rachillae that typically have male flowers at their apex, whereas *Uncinia* and *Carex* have closed utricles and sterile rachillae (i.e., when present). *Schoenoxiphium* can be distinguished from *Kobresia* by flattened rachillae with scabrous or ciliate margins that possess more highly developed male apices, whereas *Uncinia* is separated from *Carex* by hooked rachillae exsert from the utricle (see text and Fig. 3 for more details). *Cymophyllus,* which was segregated from *Carex* (Mackenzie, 1913), can only be separated from *Carex* subg. *Psyllophora* species by vegetative morphology. For a full description of generic features and variability, including problems with circumscription, see Starr et al. (2004). (Figure modified from Kükenthal, 1909; Kern, 1958; Mora Osejo, 1966.)

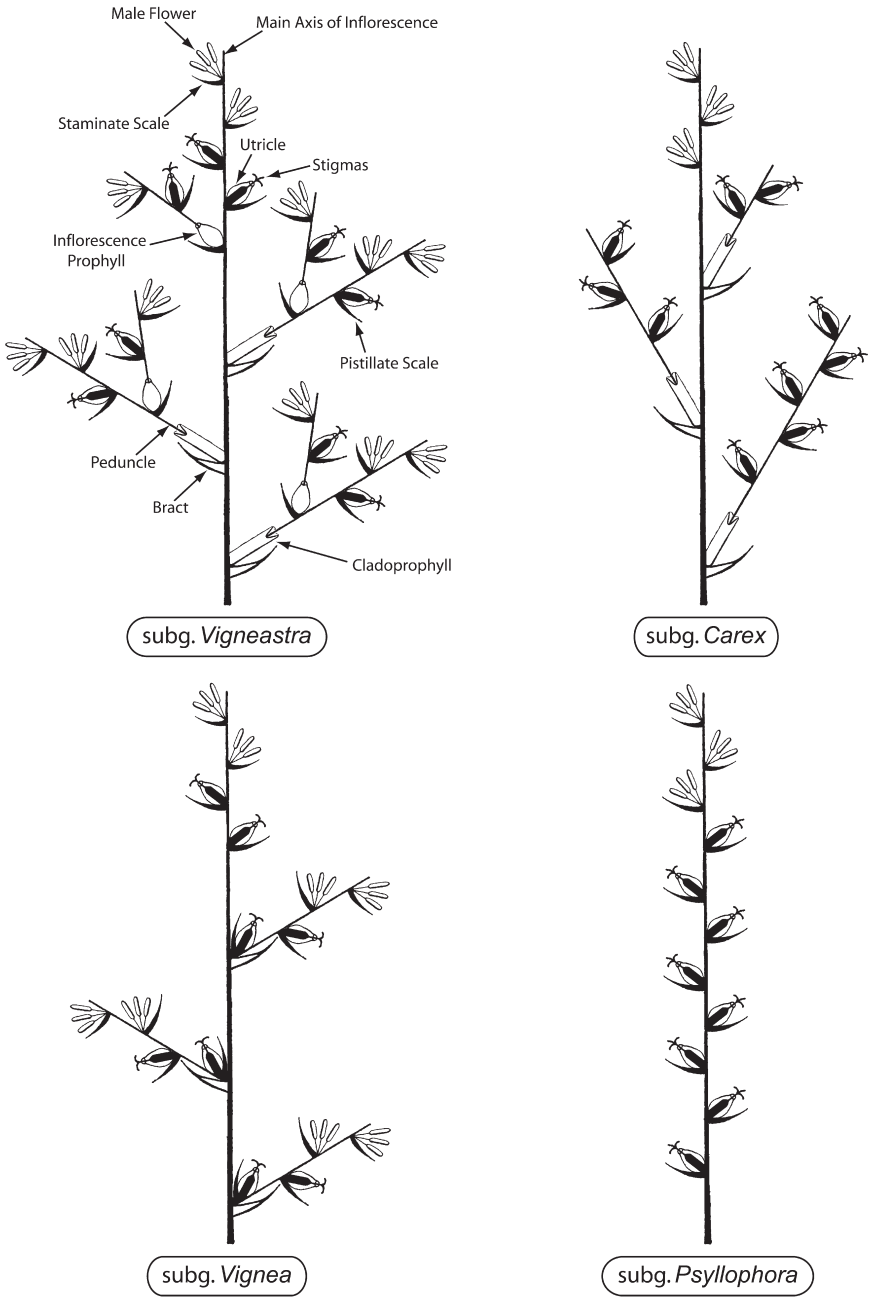

Figure 2. *Carex* subgeneric circumscription. Kükenthal (1909) divided *Carex* into four subgenera on the basis of gross inflorescence structure (unispicate vs. multispicate), the sexuality of spikes (unisexual vs. bisexual), and the presence/absence of peduncles and of tubular (cladoprophylls) or utricle-like prophylls (inflorescence prophylls sensu Reznicek, 1990). Using these characters and others that follow general trends, subgenus *Psyllophora* can be distinguished from other subgenera by a unispicate inflorescence; subgenus *Vignea* by sessile, bisexual spikes (androgynous and gynaecandrous), two stigmas (three exceptions), and the absence of cladoprophylls (four exceptions); subgenus *Vigneastra* by the presence of peduncled, bisexual spikes (androgynous) with cladoprophylls and inflorescence prophylls; and subgenus *Carex* by peduncled, predominately unisexual spikes (lateral females, terminal males) with cladoprophylls. For a full description of *Carex* subgeneric features and variability, including problems with circumscription, see Reznicek (1990) and Starr et al. (2004). (Figure modified from Kern, 1958.)

This is the second of two molecular analyses that focus on the relationships of the unispicate taxa of the Cariceae and their importance to resolving past infratribal classifications and evolutionary scenarios. Our previous study on the relationships of these taxa (Starr et al., 2004) suggested that there was a fundamental split within the unispicate species of the tribe. Dioecious species appeared to be related to multispicate taxa of either *Carex* subgenera *Carex* or *Vignea*, whereas the androgynous species of *Uncinia*, *Kobresia*, *Cymophyllus*, and *Carex* constituted a separate clade that included multispicate species of *Schoenoxiphium* and *Kobresia*. Topologies rejected the common links made between *Schoenoxiphium* and *Carex* subg. *Vigneastra* and the belief that *Schoenoxiphium* and *Kobresia* should be merged, while confirming the monophyly of subgenus *Vignea*, the polyphyly of subgenus *Psyllophora*, and the indistinct nature of subgenera *Carex* and *Vigneastra*. Moreover, this analysis supported the possibility of secondarily derived inflorescence units, and it suggested that cryptic morphological clades might be common in the Cariceae.

This present study concentrates on the outgroup relationships and former infrageneric classifications of *Uncinia*, with particular emphasis on the resolution of the classic transition series presented by the species of *Carex* subg. *Psyllophora* sect. *Leucoglochin* (*C. microglochin*, *C. parva* Nees, *C. pauciflora* Lightf.), *Uncinia kingii* [= *C. kingii*], and the genus *Uncinia* s. str. Despite the importance of these species to resolving the limits of *Uncinia* and numerous evolutionary scenarios, *C. microglochin*, *C. parva*, or *U. kingii* have not been included in previous molecular analyses of the tribe. The purpose of this study is to (1) examine generic and *Carex* subgeneric relationships within the tribe; (2) clarify the outgroup relationships of *Uncinia* for future phylogenetic studies; (3) resolve the historical controversy surrounding rachilla theories and the *Uncinia*/*Carex* sect. *Leucoglochin* transition series; and (4) evaluate former subgeneric and sectional classifications of *Uncinia* in the context of a molecular phylogeny.

Materials and Methods

Choice of Taxa and Outgroup

The taxonomy employed in this study and vouchers for all individuals used in molecular analyses are provided in Appendix 1. As in Starr et al. (2004), taxa were chosen to represent the range of morphological variation within the tribe and its major infratribal groups. Both "typical" exemplars of major historical groups and specific taxa that have played key roles in various evolutionary scenarios were employed in analyses. All 52 taxa included in the molecular phylogeny of the Cariceae by Starr et al. (2004) were used in the present analysis. Sampling included all five of the genera present in the analysis of Starr et al. (2004), and representatives from all four *Carex* subgenera (Kükenthal, 1909), although sampling was limited within the large subgenera *Vignea* (five species of ca. 450 spp.; Reznicek, 1990) and *Carex* (five species of ca. 1400 spp.; Reznicek, 1990). However, extensive sampling within these two subgenera was deemed unnecessary (Starr et al., 2004) because recent molecular studies have confirmed the monophyly of the "core" elements of both groups (Starr et al., 1999, 2004; Yen & Olmstead, 2000; Roalson et al., 2001). Taxonomic and geographic sampling for this prior molecular analysis was the most extensive to date for *Carex* subgenera *Vigneastra* (5/ca. 100 spp., representing Southeast Asia, Africa, and the Americas) and *Psyllophora* (13/ca. 70 spp., representing North America, Asia, Africa, South America, and New Zealand), and for the genera *Uncinia* (2/3 sections; 8/ca. 65 spp., representing South America, Australia, and New Zealand), *Kobresia* (3/4 sections; 7/ca. 50 spp., representing North America, Europe, and the Himalayas), and *Schoenoxiphium* (5/ca. 25 spp. representing the African mainland).

In order to examine the outgroup relationships and former infrageneric classifications of *Uncinia*, taxonomic sampling for this analysis was increased to include six additional species of *Carex* subg. *Psyllophora*, and seven additional species of *Uncinia*, including all previous ITS and ETS 1f sequences published for *Uncinia* (Starr et al., 2003, 2004). Sampling was focused on those members of subgenus *Psyllophora* traditionally linked to *Uncinia* (Kükenthal, 1909; Nelmes, 1952; Hamlin, 1959), especially the species of section *Leucoglochin* (*C. microglochin*, *C. parva*, *C. pauciflora*) and the cryptic *U. kingii*; these "transitional" taxa have provided the strongest historical evidence for evolutionary scenarios in the Cariceae. Owing to morphological variation in the bipolar *C. microglochin* (Kukkonen, 1970; Moore & Chater, 1971), both European and South American

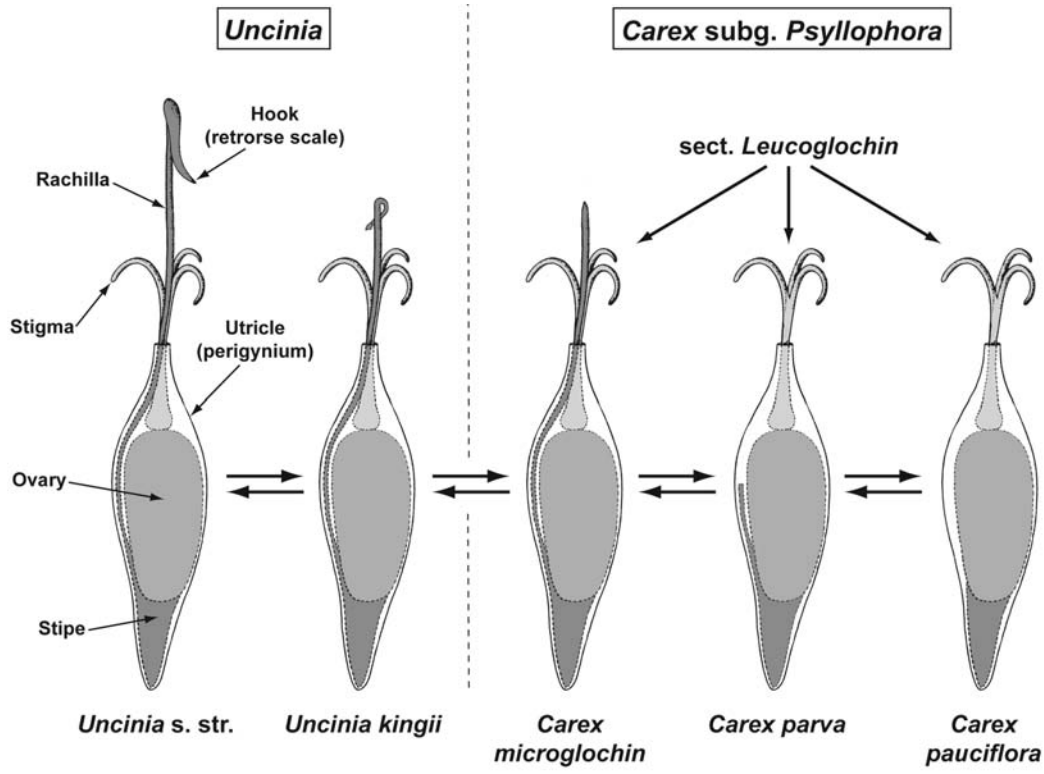

Figure 3. Female spikelets illustrating the historical transition series linking *Uncinia* to *Carex*. Elements of *Uncinia* or *Carex* are derived from each other via the growth or reduction of the rachilla and the gain or loss of hooks. Note that the hook in *U. kingii* is formed by the curvature of the rachilla, whereas in *Uncinia* s. str. it is formed by a retrorse inrolled scale. In *Carex*, the rachilla may be present or absent (e.g., *C. parva* vs. *C. pauciflora*), but it is never hooked. *Carex microglochin* is the only *Carex* where the rachilla is always exsert from the utricle (modified from Mora Osejo, 1966).

individuals were included. Collectively, sampling of subgenus *Psyllophora* in the present study represents approximately one third (i.e., 20 of 60 spp.) of the species recognized by Kükenthal (1909). In *Uncinia*, sampling increases mean that more than one third (24 spp.) of the genus is represented, including the historic representatives of the two subgenera and three sections proposed for the genus, and at least two taxa for each of the nine series described by Hamlin (1958, 1959). Only the monotypic series *Oceanicae* Hamlin (Hamlin, 1963) was not included.

MOLECULAR PROCEDURES, DNA ALIGNMENT, AND SEQUENCE ANALYSIS

DNA isolation, polymerase chain reaction (PCR) amplification, and sequencing of the ITS and ETS 1f regions were performed using the primers and procedures described in Starr et al. (1999, 2003). Leaves used for DNA extractions were only removed from pseudoculms with flowers. Betaine (Sigma # B-0300) was added to all PCR experiments to facilitate amplification (Starr et al., 2003) and to minimize amplicons from nonfunctional paralogues (Buckler et al., 1997). Exon (18S, 5.8S, and 26S nuclear ribosomal DNA [nrDNA]) and spacer (ITS 1, ITS 2, ETS 1f) boundaries were determined as for *Carex* (Starr et al., 1999) and *Uncinia* (Starr et al., 2003). To compare ITS sequences with those used by Starr et al. (2003, 2004) only ITS 1, ITS 2, and five bp at the 5′ end and 17 bp at the 3′ end of the 5.8S gene were used in analyses. ITS and ETS 1f sequences were initially aligned with CLUSTAL X (Thompson et al., 1997) then adjusted manually using parsimony (PAUP* 4.0b10; Swofford, 2002) as an objective cri-

Table 1. Sequence statistics for separate and combined ITS and ETS 1f data sets used in phylogenetic analyses. The 5.8S gene provided only four variable characters (three were parsimony-informative).

	ITS 1 + ITS 2	ETS 1f	nrDNA regions combined
Length range (bp)			
ingroup	425–449	584–600	1013–1045
outgroup included	425–512	528–600	1004–1045
Length mean (bp)			
ingroup	441.84	590.84	1032.7
outgroup included	443.20	589.19	1032.4
Aligned length (bp)			
ingroup	475	643	1118
outgroup included	535	644	1179
GC content range (%)			
ingroup	57.5–75.4	51.5–66.3	57.2–69.5
outgroup included	57.5–75.4	51.5–66.3	57.2–69.5
GC content mean (%)			
ingroup	69.9	59.8	64.1
outgroup included	69.8	58.7	64.0
Sequence divergence (%)			
ingroup	0.0–22.3	0.0–21.6	0.1–19.6
outgroup included	0.0–22.3	0.0–22.3	0.1–20.9
Sequence divergence mean (%)			
ingroup	10.8 ± 3.3	12.2 ± 4.1	11.6 ± 3.6
outgroup included	11.0 ± 3.4	12.6 ± 4.3	11.9 ± 3.7
No. of indels	55	61	116
Potentially informative indels	23	38	61
No. of variable sites	259 (53.1%)	393 (61.0%)	652 (57.6%)
Potentially informative sites	179 (36.7%)	288 (44.7%)	467 (41.3%)
Constant sites	229 (46.9%)	251 (39.0%)	480 (42.4%)
Uninformative sites	80 (16.4%)	105 (16.3%)	185 (16.3%)

terion for selecting among possible alignments (see Starr et al., 2004). The BASEFREQ and SHOWDIST commands in PAUP* were used to calculate uncorrected pairwise distances between individuals as well as sequence lengths and guanine-cytosine (GC) content. These statistics were used to evaluate sequence characteristics and to determine whether sequences might represent paralogues or external contamination.

PHYLOGENETIC ANALYSIS

Heuristic searches in PAUP* 4.0b10 (Swofford, 2002) of a combined ITS, ETS 1f, and insertion/deletion (indel) matrix were conducted using the MULTREES (save all minimal trees) and tree bisection-reconnection (TBR) commands for 5000 replicates of a RANDOM addition of taxa. ITS positions 71–100, 138–141, and 267–279 were excluded from all analyses due to the presence of repeated elements (71–100) or alignment ambiguity (138–141, 267–280). Indels were coded using the "simple" gap coding procedures of Simmons and Ochoterena (2000) as implemented in GapCoder (Young & Healy, 2003). After unusual patterns were discovered in sequence analyses involving *Carex filifolia* Nutt.,

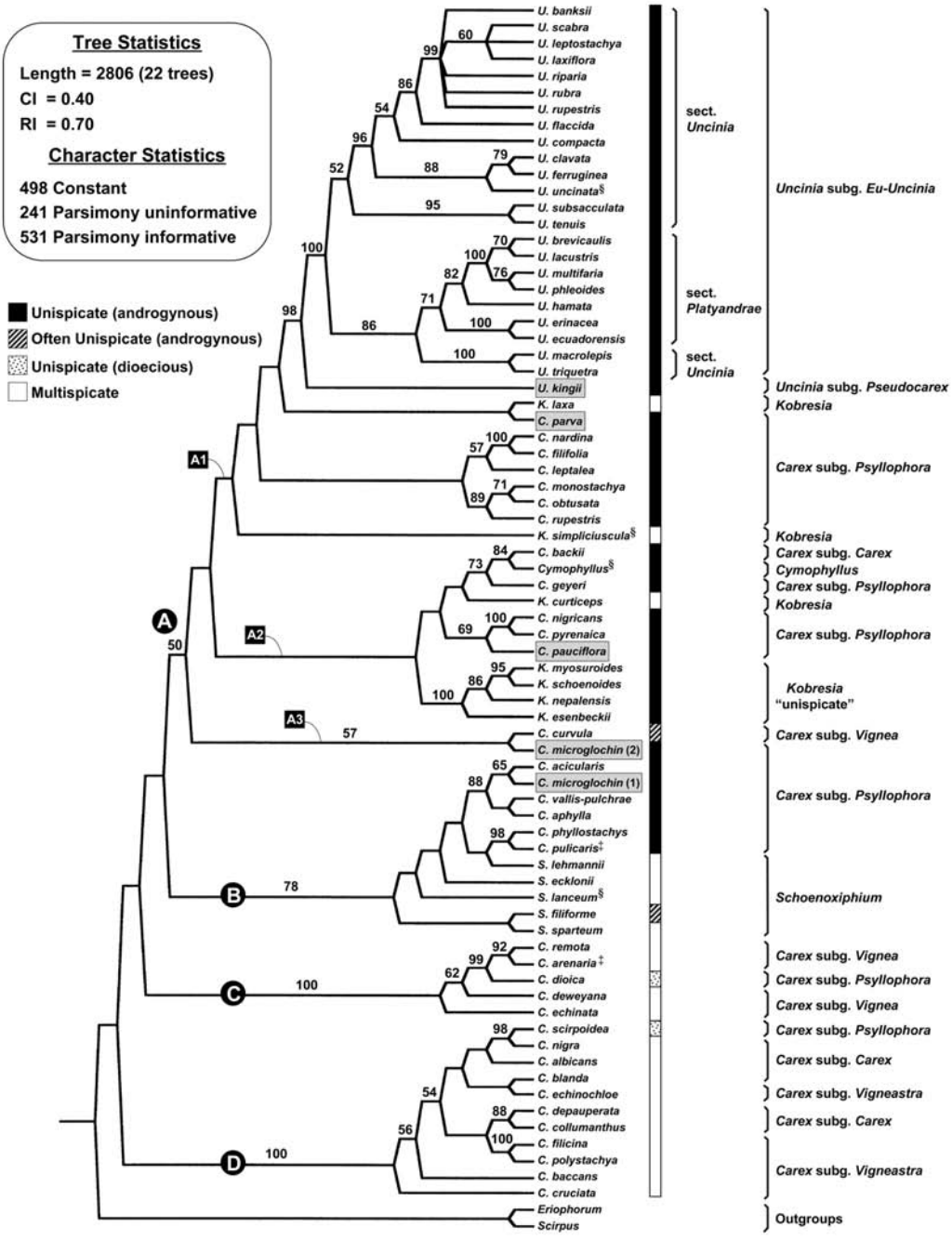

Figure 4. The strict consensus of the 22 most parsimonious trees discovered during heuristic searches. Tree and character statistics are given at the top left. Numbers above branches represent bootstrap values. Major clades described in the text are marked by circles (i.e., A, B, C, D), while minor clades are distinguished by squares (i.e., A1, A2, A3). The type species for Cariceae genera and *Carex* subgenera are marked respectively by (§) and (‡). *Uncinia kingii* and the members of *Carex* subg. *Psyllophora* sect. *Leucoglochin* are highlighted by gray rectangles. The bar to the right of specific epithets summarizes the gross inflorescence morphology of sampled species (the legend is to the left). Numbers in parentheses after epithets correspond to specific vouchers in Appendix 1. Except for *Cymophyllus,* generic names are abbreviated as follows: *S.* = *Schoenoxiphium, K.* = *Kobresia, U.* = *Uncinia, C.* = *Carex.* CI = consistency index; RI = retention index.

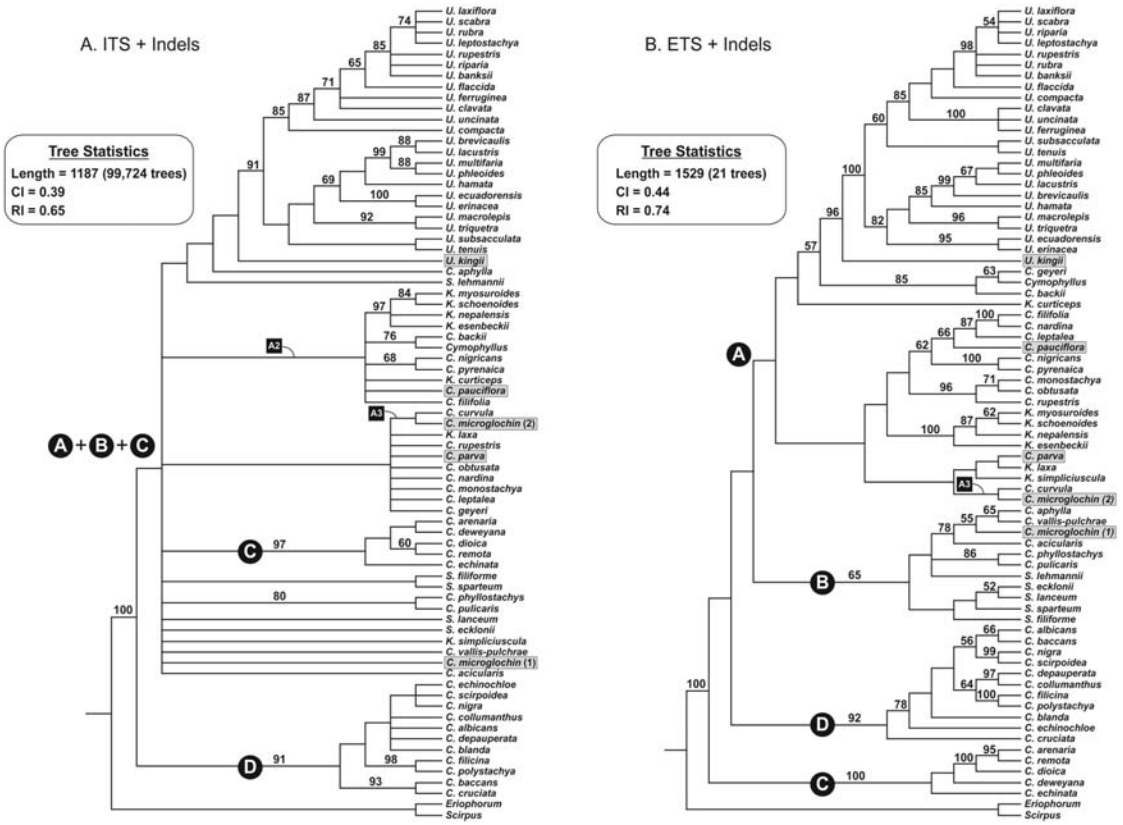

Figure 5. Strict consensus trees for separate ITS and ETS 1f parsimony analyses. — A. ITS plus indels analysis. — B. ETS 1f plus indels analysis. Tree statistics are given at the top left. Numbers above branches represent bootstrap values. Major clades described in the text are marked by circles (i.e., A, B, C, D), while minor clades are distinguished by squares (i.e., A2, A3). *Uncinia kingii* and the members of *Carex* subg. *Psyllophora* sect. *Leucoglochin* are highlighted by gray rectangles. Numbers in parentheses after epithets correspond to specific vouchers in Appendix 1. Except for *Cymophyllus,* generic names are abbreviated as follows: *S.* = *Schoenoxiphium, K.* = *Kobresia, U.* = *Uncinia, C.* = *Carex.*

a search excluding this taxon was also performed to determine whether it had an effect on tree topologies. *Carex filifolia* was included in all subsequent analyses. Separate heuristic searches of ITS and ETS 1f data sets were conducted with and without the inclusion of indels. These searches used TBR branch swapping and a RANDOM addition of taxa for 1000 replicates, with ITS analyses restricted to swapping on only 2000 trees per replicate (NCHUCK = 2000) for time reasons. Clade support was assessed via the bootstrap (BS; Felsenstein, 1985). For all analyses, BS values were derived from 10,000 replicates using a heuristic search strategy, TBR branch swapping, and a SIMPLE stepwise addition of taxa with the MULTREES option "off." DeBry and Olmstead (2000) have shown that this type of search strategy rapidly produces bootstrap proportions that are essentially identical to the values produced by TBR searches with the MULTREES option "on." As in Starr et al. (2004), BS support was categorized as very poor or very weak (< 55%), poor or weak (55%–64%), moderate (65%–74%), good or well (75%–84%), very good or very well (85%–94%), or strong (95%–100%) based on the simulation studies of Hillis and Bull (1993) and Huelsenbeck et al. (1996). Homoplasy levels and character support for trees were assessed by the consistency index (CI; Kluge & Farris, 1969) and retention index (RI; Farris, 1989).

An incongruence length difference (ILD) test (Farris et al., 1994) of the combined ITS and ETS 1f

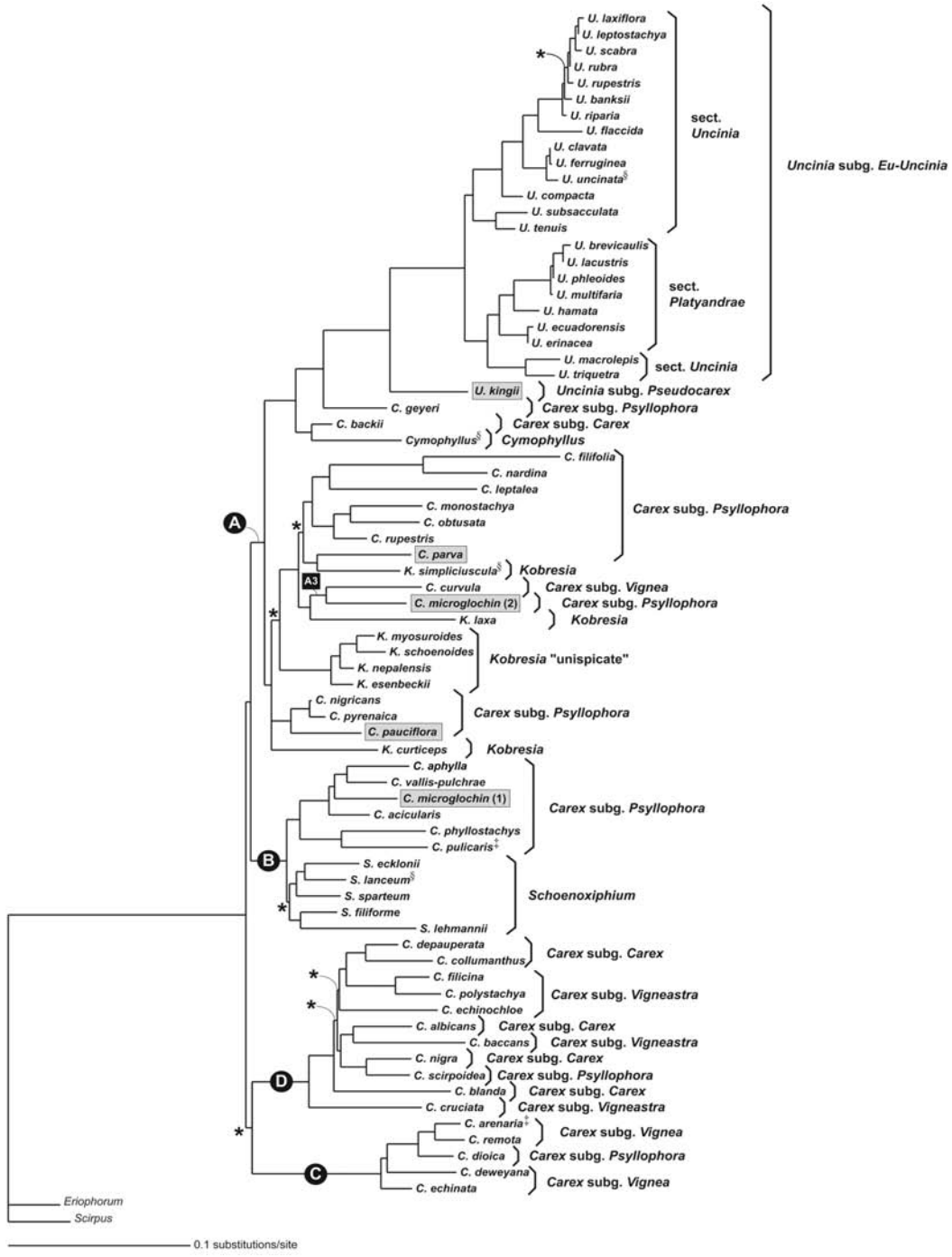

Figure 6. Maximum likelihood tree resulting from heuristic searches of the combined Cariceae ITS and ETS 1f data assuming a GTR + G + I model of sequence evolution. Branches whose confidence intervals do not exclude zero at the $P = 0.05$ level are marked by asterisks. Major clades described in the text are marked by circles (i.e., A, B, C, D), while minor clades are distinguished by squares (i.e., A3). The type species for Cariceae genera and *Carex* subgenera are marked respectively by (§) and (‡). *Uncinia kingii* and the members of *Carex* subg. *Psyllophora* sect. *Leucoglochin* are highlighted by gray rectangles. Except for *Cymophyllus,* generic names are abbreviated as follows: *S. = Schoenoxiphium, K. = Kobresia, U. = Uncinia, C. = Carex.*

data sets (indels included) was also performed in PAUP* using a heuristic search strategy, TBR branch swapping, and a RANDOM addition of taxa (25 replicates per partition, NCHUCK = 100) for 264 random partitions of the data (constant characters were excluded, $\alpha = 0.01$; Cunningham, 1997; Darlu & Lecointre, 2002). Although this test is considered to be the best parsimony-based method for evaluating data set congruence (Cunningham, 1997), the interpretation of the test and its validity have been questioned (e.g., Yoder et al., 2001; Dowton & Austin, 2002). In this study, the test was performed simply to acknowledge the possibility of incongruence between the data sets, even though a "total evidence" approach was taken (Kluge, 1989; Nixon & Carpenter, 1996).

Maximum likelihood (ML) trees were estimated by heuristic searches (TBR, RANDOM addition of taxa, 10 replicates) of the combined ITS/ETS 1f data set (indels excluded) using a general time-reversible (GTR) model that incorporated a correction for rate heterogeneity across sites (i.e., a gamma distribution, G; Yang, 1993) and an estimate of the proportion of invariable characters (I). The GTR + G + I model was chosen by Modeltest 3.06 (Posada & Crandall, 1998), a program that uses likelihood ratio tests and the Akaike information criterion to identify which of 56 nested evolutionary models is optimal for the data. The ZEROLENTEST command in PAUP* ("full" optimization) was used to determine whether branch lengths in the best ML tree were significantly greater than zero.

Owing to low branch support, Shimodaira and Hasegawa (SH; 1999) tests comparing the optimal ML tree with trees where section *Leucoglochin* (with and without *Uncinia kingii*) and a section *Leucoglochin* + *Uncinia* s. str. clade were forced to be monophyletic were used to test the common hypotheses that section *Leucoglochin* is natural and a direct relative of the genus *Uncinia*. The same analyses were performed with constraint trees that included only those individuals of section *Leucoglochin* common to Clade A after unusually high levels of sequence divergence were detected in *Carex microglochin* (see below). One million bootstrap replicates using the re-sampling estimated log-likelihood method (RELL) of Kishino et al. (1990) were used to generate the SH test distribution in PAUP*.

RESULTS

SEQUENCE ANALYSIS

Summary statistics for the 75 taxa used in the combined ITS and ETS 1f Cariceae analysis are given in Table 1. The 5.8S gene was 166 bp long in all taxa sequenced due to a 3 bp insertion that is common to most Cyperaceae.

Pairwise sequence divergence within Cariceae for the combined ITS and ETS 1f data set ranged from 0.0% to 19.6% (*Uncinia triquetra* Kük. × *Carex baccans* Nees). On average, ETS 1f was more variable than ITS, with most pairwise comparisons (75.8%) showing a higher divergence for ETS 1f than for ITS (Table 1). Notable exceptions to this rule were seen in most pairwise comparisons involving *C. filifolia*. This taxon possessed the lowest GC content (58.4%), the second shortest *Carex* sequence (421 bp), the highest average ITS divergence with other Cariceae (18.9% ± 2.3%), and the largest average disparity between pairwise ITS versus ETS 1f divergence (+5.6% ± 3.3%). The disparity between ITS and ETS 1f divergence in comparisons of *C. filifolia* versus *C. nardina* Fr. (ITS = 22.3%, ETS 1f = 0.2%) was particularly noteworthy.

Infraspecific divergence between the two *Carex microglochin* individuals sequenced in this study was high for both the ITS (10.7%) and ETS 1f (9.7%) regions. In the combined data set, Scottish *C. microglochin* was most similar to *C. rupestris* All. (7.2% divergence), whereas Ecuadorian *C. microglochin* was least divergent (4.4% to 5.3%) with three South American carices (*C. acicularis* Boott, *C. aphylla* Kunth, and *C. vallis-pulchrae* Phil.). Ecuadorian *C. microglochin* shared a unique 5.8S mutation (C→T) with *C. acicularis*, *C. aphylla*, and *C. vallis-pulchrae* in a highly conserved portion of the gene (position 130; data not shown). GC contents (ITS, 71.9%–72.9%; ETS 1f, 57.0%–61%) and spacer lengths (ITS, 441–443 bp; ETS 1f, 589–592 bp) for both *C. microglochin* sequences were close to the mean values for ingroup taxa (Table 1). The aligned matrix used for all phylogenetic analyses is available online from TreeBASE (www.treebase.org/treebase/).

PHYLOGENETIC ANALYSES

Aligned sequences for the combined ITS and ETS 1f data set, including small portions of the 5′

and 3′ ends of the 5.8S gene in all Cariceae taxa, resulted in a matrix of 1317 characters (116 indels), of which 47 were excluded from analyses due to repeats or alignment ambiguity. Of the remaining 1270 characters, 498 (39.2%) were constant, 241 (19.0%) were parsimony-uninformative, and 531 (41.8%) were parsimony-informative. No topological differences were detected between parsimony analyses that included and excluded *Carex filifolia*. ILD tests suggested that ITS and ETS 1f data sets were incongruent ($P = < 0.01$).

Heuristic searches under the parsimony criterion for the combined ITS and ETS 1f data set discovered 22 trees, 2806 steps each. The strict consensus of these 22 most parsimonious trees (MPTs) is given in Figure 4. This tree suggests that the tribe consists of four primary clades: (1) a very weakly supported clade (Clade A, 50% BS) composed of species of *Uncinia*, *Kobresia*, *Cymophyllus*, unusual members of *Carex* subgenera *Vignea* (*C. curvula* All.) and *Carex* (*C. backii* Boott), and a majority of the androgynous species of *Carex* subg. *Psyllophora* p.p.; (2) a clade with good support (Clade B, 78% BS), sister to Clade A, that consists of *Schoenoxiphium* species and a smaller group of androgynous species of *Carex* subg. *Psyllophora* p.p.; (3) a strongly supported clade (Clade C, 100% BS), sister to Clades A and B, that consists of "typical" multispicate members of *Carex* subg. *Vignea*, and a single, dioecious species of *Carex* subg. *Psyllophora* (*C. dioica* L.); and lastly, (4) a strongly supported clade (Clade D, 100% BS) comprising "typical" multispicate members of *Carex* subgenera *Carex* and *Vigneastra*, and a single dioecious species of *Carex* subg. *Psyllophora* (*C. scirpoidea* Michx.).

Within Clade A, two very poorly supported clades (A1, A2) and one poorly supported clade (A3) are evident. These three clades each possess one of the three members of section *Leucoglochin* (Fig. 4). The first clade (A1, < 50% BS; Fig. 4), consisting of the genus *Uncinia*, *Carex* subg. *Psyllophora* p.p., and two multispicate members of the genus *Kobresia*, provides strong support for the monophyly of *Uncinia* s.l. (98% BS) and for a sister group relationship between *U. kingii* (i.e., subgenus *Hemihamatae* (Hamlin) Kukkonen) and *Uncinia* s. str. (i.e., subgenus *Eu-Uncinia* Kük. sections *Uncinia* and *Platyandrae* C. B. Clarke). Within *Uncinia* s. str., two major groups are found: (1) a very weak (52% BS) clade of section *Uncinia* species, and (2) a very well-supported (86% BS) clade consisting of a monophyletic section *Platyandrae* (71% BS) sister to section *Uncinia* series *Macrolepidae* Hamlin (100% BS). With the exception of series *Australes* Hamlin (section *Uncinia* clade) and series *Macrolepidae*, *Macrotrichae* Hamlin, and *Trichocarpae* Hamlin (section *Platyandrae*/series *Macrolepidae* clade), trees suggest the series circumscriptions in *Uncinia* are either paraphyletic or polyphyletic. Topologies within Clade A1 also place a very weakly supported clade (< 50% BS) containing the multispicate *K. laxa* Nees and the unispicate *C. parva* (section *Leucoglochin*) as sister to *Uncinia* s.l., while another very weakly supported clade provides very good support for a group comprising elements of *Carex* sections *Obtusatae* (Tuck.) Mack. (*C. obtusata* Lilj.), *Rupestres* (Tuck.) Meinsh. (*C. rupestris*), and *Longespicatae* Kük. (*C. monostachya* A. Rich.), and strong support for a *C. filifolia* + *C. nardina* clade (sections *Filifoliae* (Tuck.) Mack. and *Nardinae* (Tuck.) Mack.). *Kobresia simpliciuscula* (Wahlenb.) Mack., the type of the genus, is found at the base of Clade A1.

The second clade (Clade A2; Fig. 4), consisting of *Kobresia*, the monotypic genus *Cymophyllus*, and several members of *Carex* subg. *Psyllophora*, provides strong support (100% BS) for the monophyly of the unispicate species of *Kobresia* and good support (84% BS) for a sister group relationship between the genus *Cymophyllus* and a unispicate member of *Carex* subg. *Carex* sect. *Phyllostachyae* Tuck. ex Kük. (*C. backii*). Moderate support (69% BS) is also seen for a clade comprising a monophyletic *Carex* sect. *Dornera* Heuff. (*C. nigricans* C. A. Mey. and *C. pyrenaica* Wahlenb.; 100% BS) sister to *C. pauciflora* (section *Leucoglochin*).

The third and last group (Clade A3) is a weak clade (57% BS) consisting of the unusual *Carex curvula* (*Carex* subg. *Vignea* sensu Kükenthal) and European *C. microglochin* (section *Leucoglochin*; Fig. 4).

Relationships within Clade B place a paraphyletic *Schoenoxiphium* at the base of a clade containing mostly androgynous *Carex* subg. *Psyllophora* species (Fig. 4). Only two groups are noteworthy, a clade with very good support (88% BS) consisting of South American members of subgenus *Psyllophora* (sections *Aciculares* (Kük.) G. A. Wheeler, *Leucoglochin*, and *Junciformes* (Boeck.) Kük.) including Ecua-

dorian *C. microglochin*, and a strongly supported clade (98% BS) comprising *C. pulicaris* L. (section *Psyllophora* (Degl.) Koch) and *C. phyllostachys* C. A. Mey. (section *Caryotheca* V. I. Krecz. ex T. V. Egorova).

Clade C is a strongly supported group (100% BS) of predominately multispicate European and North American species of *Carex* subg. *Vignea* (Fig. 4). The nested position of *C. dioica*, a dioecious species of *Carex* subg. *Psyllophora*, is the most noteworthy relationship of the group.

The last group, Clade D, is a strongly supported clade (100% BS) that suggests *Carex* subgenera *Carex* and *Vigneastra* are unnatural, and that *C. scirpoidea*, a dioecious member of *Carex* subg. *Psyllophora*, is a close relative of *Carex* subg. *Carex* species (Fig. 4).

Separate analyses of ITS and ETS 1f data (indels included) respectively produced 99,724 MPTs, 1187 steps long, and 21 MPTs, 1529 steps long. The strict consensus trees for both analyses are given in Figure 5. Notable topological differences between these two trees include the more highly resolved and statistically supported ETS 1f versus ITS analysis, and the positioning of Clade D (ITS analysis) as opposed to Clade C (ETS 1f analysis) as sister to all other Cariceae. Clades A and B were only resolved as monophyletic in ETS 1f analyses, although an A + B clade was seen in ITS analyses that excluded indels (results not shown). All separate ITS and ETS 1f analyses positioned *Uncinia kingii* as sister to *Uncinia* s. str., although ITS support for this relationship was very poor. Clades with good support in either the ITS or ETS 1f analysis were also present in the strict tree for combined analyses. Clade A1 was not resolved in separate analyses.

GTR + G + I model settings used in all ML searches and SH tests are as follows: base frequencies (A = 0.1392, C = 0.3062, G = 0.3399, T = 0.2147), rate matrix ([A–C] = 0.7276, [A–G] = 3.5474, [A–T] = 1.1872, [C–G] = 0.5293, [C–T] = 5.3786, [G–T] = 1.0000), gamma (G) shape parameter = 0.7737, proportion of invariable sites (I) = 0.1498. ML searches of the combined data set produced a single tree with a –ln likelihood (–ln *L*) of 14439.87248 (Fig. 6). This tree recovers the same four major clades (i.e., A, B, C, D) as parsimony analyses, with differences between analyses confined to rearrangements around weak nodes that do not affect general conclusions. Potentially important topological differences in the ML tree, such as a monophyletic *Schoenoxiphium* and a C + D clade, occur at branches that are not significantly different from zero (Fig. 6). SH tests indicate that ML and parsimony trees are not statistically different (Table 2).

SH tests of ML trees that forced section *Leucoglochin* (with and without *Uncinia kingii*) and a section *Leucoglochin* + *U. kingii* + *Uncinia* s. str. clade to be monophyletic were all significantly different from the optimal ML tree when Ecuadorian *Carex microglochin* was included in constrained clades (Table 2). When Ecuadorian *C. microglochin* was excluded from constrained clades, only analyses that forced a section *Leucoglochin* + *U. kingii* clade were found to be significantly different from the optimal ML tree.

DISCUSSION

SEQUENCE ANALYSIS

The size, sequence divergence, and GC contents for the taxa sequenced in this study are comparable to the values seen in previous Cariceae studies that have used the ITS (Roalson et al., 2001; Starr et al., 1999, 2003, 2004) and ETS 1f (Starr et al., 2003, 2004) regions. It is now clear that the three base pair insertion at the 5′ end of the 5.8S gene first discovered by Starr et al. (1999) is a feature common to all Cariceae, but not to all Cyperaceae genera (Roalson & Friar, 2000; Roalson et al., 2001; Starr et al., 2007). Starr et al. (2007) have shown that this insertion is not only useful for delimiting the Cyperaceae, but its pattern of loss and even point mutations within its sequence are useful for defining clades at multiple taxonomic levels. On average, the ETS 1f region is more variable than ITS, which is consistent with the results of most previous angiosperm studies (e.g., Baldwin & Markos, 1998; Bena et al., 1998a, b; Vander Stappen et al., 2003). However, studies within the Cyperaceae have also shown that the ETS 1f region may be as variable or even more conserved than ITS depending on the group studied (Starr et al., 2003; Ford et al., 2006).

In plants, the nrDNA region consists of hundreds to thousands of copies that are tandemly repeated at one or more loci (Baldwin et al., 1995). Variation among these repeats is typically low within species as a consequence of the homogenizing

effects of concerted evolution. This fact is often used to justify minimal sampling within species (typically one individual) since amplicons should be orthologous if speciation is divergent, recombination is absent, and repeat homogenization is complete and maintained over time (Baldwin et al., 1995; Álvarez & Wendel, 2003). Since these assumptions are often violated, the genome of any individual sampled for the nrDNA region may contain paralogues that could confound phylogenetic inference (Hershkovitz et al., 1999; Álvarez & Wendel, 2003). One of the most common sources of nrDNA paralogues within individuals comes from pseudogenes, non-expressed repeats whose relaxed functional constraints are typically revealed by high rates of evolution (Hershkovitz et al., 1999; Álvarez & Wendel, 2003). These nrDNA pseudogenes can sometimes be identified by their large indels, low GC contents, and high sequence divergence, among other features (Buckler & Holtsford, 1996a, b; Buckler et al., 1997). In considering these characteristics, the ITS region of *Carex filifolia* in particular stands out. The consistently high divergence of *C. filifolia* ITS with other taxa, its low GC content, and short length suggest that this sequence may not be under the same selective pressures as a functional ITS region. Moreover, this sequence was not amplified using dimethyl sulfoxide (DMSO) or betaine (Starr et al., 1999). These DNA denaturing or destabilizing cosolvents may be essential PCR additives if functional ITS sequences with high GC contents are to be preferentially amplified over presumably nonfunctional paralogues with low GC contents (Buckler & Holtsford, 1996a; Buckler et al., 1997; Starr et al., 2003; Ford et al., 2006). Further specimens of *C. filifolia* will need to be amplified, cloned, and sequenced to confirm whether the ITS region used in this analysis is a paralogue. The surprisingly low ETS 1f divergence of *C. nardina* × *C. filifolia* does not appear to be the result of contamination as their DNAs were extracted, amplified, and sequenced at least four months apart.

Previous studies that have looked at Cariceae infraspecific variation within the ITS (Starr et al., 1999, 2003; Ford et al., 2006) and ETS 1f (Starr et al., 2003; Ford et al., 2006) regions have generally found levels of sequence divergence to be low (< 1.0%). It is for this reason that the level of divergence detected between Ecuadorian and Scottish samples of *Carex microglochin* is surprising. It is possible that the presence of ITS or ETS 1f paralogues, maybe as a consequence of hybridization, pseudogenes, or other factors (see section "Taxonomy of *Carex microglochin*" below), may account in part for the incongruence detected by the ILD test in this and other Cariceae studies (Roalson et al., 2001; Starr et al., 2004; Ford et al., 2006).

GENERAL RELATIONSHIPS WITHIN THE CARICEAE

Apart from minor branch re-arrangements within Clade A and slight differences in the relationships of *Schoenoxiphium* species at the base of Clade B, the present analysis is entirely consistent with the previous tribal analysis of Starr et al. (2004). Phylogenetic analyses indicate that *Uncinia* is monophyletic and part of a large clade (Clade A) consisting of *Kobresia*, *Cymophyllus*, the unusual *Carex curvula* (subgenus *Vignea*), and unispicate members of *Carex* subgenera *Carex* (section *Phyllostachyae*) and *Psyllophora*. This clade is sister to a clade (Clade B) composed of the genus *Schoenoxiphium* and various members of *Carex* subg. *Psyllophora*. The remaining species fall into two groups, one consisting of "typical" members of *Carex* subg. *Vignea* and a dioecious member of *Carex* subg. *Psyllophora* (*C. dioica*), and the second comprising "typical" members of *Carex* subgenera *Carex* and *Vigneastra*, and a dioecious member of *Carex* subg. *Psyllophora* (*C. scirpoidea*).

Such topologies strongly indicate that the genus *Carex* as presently circumscribed is artificial. Moreover, analyses support proposals to merge *Carex* subgenera *Vigneastra* and *Carex* (e.g., Ohwi, 1936; Koyama, 1962), and they confirm the general consensus that *Carex* subg. *Vignea* is natural (e.g., Nelmes, 1951; Koyama, 1962; Reznicek, 1990), and that subgenus *Psyllophora* is polyphyletic (e.g., Kreczetovicz, 1936; Nelmes, 1952; Smith & Faulkner, 1976). Analyses also reject many long-held hypotheses of homology that would support a monophyletic *Schoenoxiphium* and *Kobresia* (e.g., Nelmes, 1951; Kern, 1974; Smith & Faulkner, 1976), or a phylogenetic link between *Carex* subg. *Vigneastra* and *Schoenoxiphium* (e.g., Kükenthal, 1909; Smith & Faulkner, 1976; Reznicek, 1990). Of direct relevance to this study, analyses continue to support a fundamental split among unispicate

Table 2. Shimodaira-Hasegawa (SH) tests comparing optimal maximum likelihood (1, GTR + G + I) and parsimony (2–3) trees, with trees where section *Leucoglochin*, *Uncinia kingii,* and *Uncinia* s. str. were successively forced to be monophyletic (4, *Leucoglochin* only; 5, *Leucoglochin* + *Uncinia kingii*; 6, *Leucoglochin* + *Uncinia kingii* + *Uncinia* s. str.; trees 7–9 represent the same analyses minus Ecuadorian *Carex microglochin*). Tests are one-tailed and were conducted assuming a GTR + G + I model of sequence evolution. Indel characters were not included in the calculation of tree length. Asterisks (*) next to *P* values indicate significance at the $\alpha = 0.05$ level.

Tree	−ln *L*	−ln *L* Difference	Steps	SH-test *P* value
1 (Optimal ML Tree)	14439.87248	(best)	2638	—
2 (Parsimony–best)	14477.58380	37.71133	2612	0.26
3 (Parsimony–worst)	14483.54808	43.67561	2612	0.22
4 (*Leucoglochin*)	14565.07607	125.20359	2694	< 0.001*
5 (*Leucoglochin* + *U. kingii*)	14610.22162	170.34914	2713	< 0.00001*
6 (*Leucoglochin* + *U. kingii* + *Uncinia*)	14569.85179	129.97932	2686	< 0.0001*
7 (*Leucoglochin–C. microglochin* 1)	14475.04083	35.16836	2662	0.29
8 (*Leucoglochin* + *U. kingii–C. microglochin* 1)	14521.44463	81.57216	2682	0.02*
9 (*Leucoglochin* + *U. kingii* + *Uncinia–C. microglochin* 1)	14485.04641	45.17394	2659	0.16

species where the dioecious members of *Carex* subg. *Psyllophora* are related to multispicate species in either *Carex* subgenera *Carex* or *Vignea*, while the androgynous unispicate members of *Carex* subgenera *Carex* and *Psyllophora*, and the genera *Cymophyllus*, *Kobresia*, and *Uncinia*, are variously placed in a clade that also contains multispicate species of *Schoenoxiphium* and *Kobresia* (Starr et al., 2004). In addition, the firm position of the monotypic genus *Cymophyllus* within Clade A is morphologically consistent with the taxonomic composition of these clades. This supports treatments that regard *Cymophyllus* as a common ally of *Carex* subg. *Psyllophora* species (Kükenthal, 1909).

Despite considerable sampling differences among molecular analyses of the tribe (Yen & Olmstead, 2000; Roalson et al., 2001; Starr et al., 2004), a general consensus among studies appears to be emerging. Even though the arrangement of clades differs from one analysis to the next, three of the four major clades (i.e., Clades A, C, D) described in this analysis are consistent with clades discovered in the chloroplast analysis of Yen and Olmstead (2000) and the combined ITS and *trnT-L-F* analysis of Roalson et al. (2001). Clade B, on the other hand, is novel to this analysis and the analysis of Starr et al. (2004). However, previous analyses have not sampled androgynous *Carex* subg. *Psyllophora* from South America or Europe, or the diversity of taxa sampled within *Schoenoxiphium* for these analyses. Nonetheless, it is interesting to note that the only species of *Schoenoxiphium* sampled in the analysis of Roalson et al. (2001) was sister to taxa representing Clade A.

Regardless of topological congruence among molecular analyses, poor statistical support both within and between the major groups of the Cariceae clearly indicates that assigning clades to the basal node of the tribe is still premature. Moreover, it would be unwise to imply that the conclusions drawn from the present phylogeny will not be affected by future increases in characters or taxa. Nevertheless, the consistency of molecular analyses does represent a considerable step forward for rejecting many historical hypotheses that have defied resolution, and for suggesting future systematic problems that need to be clarified.

OUTGROUPS, RACHILLA THEORIES, AND THE RELATIONSHIPS OF *UNCINIA* AND *CAREX* SECT. *LEUCOGLOCHIN*

The relationships of the unispicate species of *Uncinia* and *Carex* subg. *Psyllophora* have constitut-

ed one of the most difficult and perplexing problems in Cariceae systematics (Reznicek, 1990). The extreme reduction of these two groups has obscured their relationships to the point where even intense studies of tribal inflorescence development have only been able to conclude that they may represent reduced forms of practically any branched inflorescence in the tribe (Smith & Faulkner, 1976; Timonen, 1998). However, the well-developed rachilla of *C. microglochin*, a trait ascribed to other Cariceae genera, combined with the apparently intermediate *U. kingii*, appeared to demonstrate that *Uncinia*, *Carex*, or *Carex* p.p. had evolved from each other via the reduction or proliferation of the rachilla (Kükenthal, 1909; Kreczetovich, 1936; Nelmes, 1952; Savile & Calder, 1953; Hamlin, 1959). Although the evolutionary direction and the specific derivatives of this historic transition series have often been debated, the validity of the transition series itself has only been questioned by Kern (1958) and Reznicek (1990). While Kern (1958) attacked the transition series from a philosophical point of view, Reznicek (1990) recognized that there was compelling evidence from both the study of the inflorescence (Kukkonen, 1967; Meert & Goetghebeur, 1979) and rachilla to suggest that *U. kingii* was more closely related to *C. microglochin* and its allies than it was to *Uncinia* s. str. *Uncinia kingii* had "… nothing in common with *Uncinia* except the superficially similar but independently evolved hook" (Reznicek, 1990: 1419). Moreover, it was "… not a species of remarkable phylogenetic interest … simply a *Carex* very closely related to *C. microglochin* and its allies …" (Reznicek, 1990: 1419).

The present analysis appears to agree with Reznicek (1990) that *Carex* s. str., comprising the multispicate subgenera of the genus, is only distantly related to *Uncinia*, but unlike Reznicek (1990), it also suggests that androgynous species of *Carex* subg. *Psyllophora* are more closely related to *Uncinia*, *Kobresia*, *Schoenoxiphium*, and *Cymophyllus* than they are to *Carex* s. str. Furthermore, this study solidly supports a monophyletic *Uncinia* that includes *U. kingii* [= *C. kingii*], and topologies suggest that section *Leucoglochin* (minus *U. kingii*) is neither natural nor monophyletic with *Uncinia* (but see below; Table 2). These are surprising results since Reznicek's (1990) argument that *U. kingii* was more closely related to *C. microglochin* and its allies than it was to *Uncinia* s. str. is compelling (e.g., Wheeler, 1993–1994), and historically section *Leucoglochin* has commonly been considered as an homogeneous group (e.g., Nelmes, 1952; Reznicek, 1990). Moreover, there appears to be no conspicuous morphological apomorphy that can distinguish *Uncinia* s. str. and *U. kingii* from their sister groups since the hook in *U. kingii* (formed via a curvature of the rachilla axis; Kukkonen, 1967) is not homologous to the hook of *Uncinia* s. str. (formed via a retrorse inrolled scale; Kukkonen, 1967). Such evidence would seem to contradict the validity of the present results; however, the clade within which *Uncinia* is found is highly consistent with previous molecular analyses (see above). Therefore, given the historical inability of authors to determine confidently the relationships of *Carex* subg. *Psyllophora* and *Uncinia* due to their highly reduced inflorescences (e.g., Smith & Faulkner, 1976; Reznicek, 1990), the relationship between *Uncinia* s. str. and *U. kingii* is here interpreted as further evidence that cryptic clades may be common in the Cariceae (Starr et al., 2004). Nonetheless, more data from multiple independent markers are needed to strengthen the current hypothesis and to better assess whether topologies in this and in previous analyses could have been affected by systematic (e.g., natural hybridization, long-branch attraction) and/or random error (sampling artifacts). The very weak support for many groups in Clades A and B, the significant ILD test, and the inability of the data to entirely reject a monophyletic section *Leucoglochin* or section *Leucoglochin* + *Uncinia* clade (i.e., minus Scottish *C. microglochin*) suggest that phylogenetic analyses may have been influenced by some type of error.

If cryptic clades are common in the Cariceae, does this mean that most clades may be impossible to distinguish by morphological synapomorphies? Not necessarily: morphological synapomorphies may be few and groups largely polythetic, but a re-examination of features within the context of phylogeny is likely to reveal new, possibly obscure, homologues. For example, in the case of *Uncinia kingii* and *Uncinia* s. str., the primary morphological structures that form the hook may be analogous, but the bend in the rachilla at the point where the hook begins (cf. figs. 18, 20, and 21 in Reznicek, 1990, and figs. 5 and 6 in Kukkonen, 1967) could be homologous. If the hook formed after this bend pro-

vided *U. kingii* and *Uncinia* s. str. with a key selective advantage such as epizoochorous dispersal (Hamlin, 1959; Mora Osejo, 1966; Starr, pers. obs.), then the considerably more efficient scale versus rachilla mechanism in *Uncinia* s. str. could explain why it is so much more diverse than its sister group. Further anatomical and micromorphological studies of the cells in the bend region of the rachilla may be able to test this hypothesis of homology.

In the history of Cariceae classifications and evolutionary theories, the rachilla has played a central role in indicating the evolutionary position, time, means, and origin of *Carex* subg. *Psyllophora*. Although this analysis rejects Reznicek's (1990) ideas and places *Uncinia kingii*, *Carex* sect. *Leucoglochin* p.p., and many androgynous members of subgenus *Psyllophora* within a single clade, this does not mean that the remaining "rachilla" theories are now credible. It is abundantly clear that the genera in the Cariceae cannot be arranged in a simple evolutionary series as envisioned by Kükenthal (*Schoenoxiphium*→*Kobresia*→*Uncinia*→*Carex* subg. *Psyllophora*→*Carex* s. str.; 1909), and that this analysis does not support the origin of *Carex* subg. *Psyllophora* from within *Uncinia*. Furthermore, despite the fact that this analysis agrees with Kreczetovicz (1936) that subgenus *Psyllophora* is polyphyletic, and that sections *Dioicae* (Tuck.) Pax and *Scirpinae* (Tuck.) Kük. may have their origins from within *Carex* subgenera *Vignea* and *Carex*, the analysis excludes a common origin for *Uncinia* and the androgynous subgenus *Psyllophora* from *Carex* subg. *Vigneastra*, and it rejects the notion that *C. microglochin* or any other *Carex* was derived from within *Uncinia*. This analysis also rejects Savile and Calder's (1953) theory based on smut host-parasite data and their "phylogenetic principles" that those species of *Carex* subg. *Psyllophora* with a rachilla are a natural group, and it strongly excludes any lineage that involves *Uncinia* and *Carex* subg. *Vignea*.

There is, however, some congruence between this analysis and the speculations of Nelmes (1952) and Hamlin (1959). Because Nelmes (1952: 428) believed that the rachilla was "invariably absent" in the "2500 world-wide species" of *Carex* apart from subgenus *Psyllophora*, he thought that the rachilla's presence in subgenus *Psyllophora* species or their near relatives was "grounds alone" (Nelmes, 1952: 429) to suppose that their origins lay within *Uncinia*, *Kobresia*, or *Schoenoxiphium*. Hamlin's (1959) theory was essentially the same except that the "bulk" of subgenus *Psyllophora* and the genera *Kobresia*, *Uncinia*, and *Schoenoxiphium* were not derived from any extant group, but from a hypothetical uncinoid ancestor that retained the rachilla that was lost by the ancestor of *Carex* (i.e., subgenera *Carex*, *Vigneastra*, and *Vignea*). In this analysis, all of the taxa that Nelmes (1952) and Hamlin (1959) believed were derived from *Uncinia*, *Kobresia*, or *Schoenoxiphium* are found in either Clades A or B, and those they believed were derived from *Carex* subgenera *Carex* and *Vignea* are found in either Clades C or D, except the androgynous *C. leptalea* Wahlenb. (Clade A), which Nelmes considered a true *Carex* because it lacks a rachilla.

Nonetheless, it is difficult to give their theories much credibility, particularly in the case of Nelmes (1952: 431) where it is evident that *Uncinia* is not the "chief contributor" to *Carex* subg. *Psyllophora*. Moreover, both theories are based on a false premise; viz., the presumption that rachillae are "invariably absent" (Nelmes, 1952: 428) from subgenera *Carex*, *Vigneastra*, and *Vignea*. In reality, rachillae occur sporadically in all four of the subgenera in *Carex* (Snell, 1936; Svenson, 1972; Smith & Faulkner, 1976; Reznicek, 1990), and according to Snell (1936: 284) "nearly every species of *Carex* shows some remnant of the spikelet axis [i.e., rachilla] within the perigynium [i.e., utricle] at flowering time and even later." The conundrum of the rachilla is even further complicated by teratological specimens. In the case of the unispicate *C. phyllostachys* (section *Caryotheca*) and *C. backii* (section *Phyllostachyae*; Clades A and B), teratological proliferation of the rachilla leads to the production of androgynous spikes from basal utricles, a morphology that basically emulates the vigneastrian condition. It was largely for this reason that Kreczetovicz (1936) considered these taxa as the strongest evidence in favor of his theory that the majority of subgenus *Psyllophora* had evolved from the multispicate subgenus *Vigneastra* by rachilla reduction. As in Starr et al. (2004), the present analysis shows that the basal utricles in these taxa are not homologous to the lateral inflorescence units in subgenus *Vigneastra*. This is not entirely surprising since such teratological growth of lateral inflorescence units is in fact common throughout *Carex* (Smith & Faulkner, 1976;

Reznicek, 1990). It does, however, raise a potential systematic problem; viz., the possibility that teratological growth may become fixed. For example, Reznicek (1990) hypothesized that the androgynous *Vigneastra*-like lateral spikes of *C. baldensis* L. are potentially fixed outgrowths of the rachilla of a unispicate ancestor. This would indicate that the rachilla in one species' utricle may not be homologous to the rachilla in another, which can also be inferred from the conclusions of Smith and Faulkner (1976) and Timonen (1998) that the spikelets of *Kobresia* and *Schoenoxiphium* are not homologous to the spikelets in *Uncinia* and *Carex*. Although a more thorough study of rachilla morphology may yet prove rewarding at some taxonomic level in the Cariceae (Reznicek, 1990), the mere presence of rachillae is not a direct indication of phylogenetic relatedness or primitiveness (Reznicek, 1990; Starr et al., 1999).

THE INFRAGENERIC CLASSIFICATION OF *UNCINIA* AND THE CIRCUMSCRIPTION OF SECTION *UNCINIA*

This analysis is surprisingly consistent with previous infrageneric classifications of *Uncinia*. Clarke (1883) recognized two large sections, *Uncinia* and *Platyandrae*, and a monotypic section for *Carex microglochin* (*Pseudocarex* C. B. Clarke). Later authors, including Clarke (1908), excluded *C. microglochin* from the genus (e.g., Kükenthal, 1909), but they continued to use three principal groups by maintaining Clarke's (1883) sections *Uncinia* and *Platyandrae*, and by treating *U. kingii* as either a monotypic section (Hamlin, 1958) or subgenus (Kükenthal, 1909; Kukkonen, 1967). The present analysis is most consistent with the classification of Kükenthal (1909), who divided *Uncinia* into two subgenera, the first of which was composed of sections *Uncinia* and *Platyandrae* (subgenus *Eu-Uncinia*), while the second contained *U. kingii* (subgenus *Pseudocarex* Kük. nom. illeg. = subgenus *Hemihamatae*). This classification is preferable to that of Hamlin (1958), who recognized three sections (*Uncinia*, *Platyandrae*, and *Hemihamatae*) in that it acknowledges the strong body of evidence (Kukkonen, 1967; Meert & Goetghebeur, 1979; Reznicek, 1990) that *U. kingii* is unique (if treated as an *Uncinia*), while implying a sister group relationship.

The position of *Uncinia kingii* as sister to *Uncinia* s. str. raises, however, a difficult philosophical question as to how section *Uncinia* can be circumscribed from a morphological point of view. Clarke (1883) distinguished the two sections of *Uncinia* s. str. on the basis of whether the filaments were filiform (section *Uncinia*) or dilated (section *Platyandrae*), and on the uneven distribution of two further characters, hispid (all section *Platyandrae* spp.) versus glabrous (most section *Uncinia* spp.) utricles, and persistent (all section *Platyandrae* spp.) versus deciduous (most section *Uncinia* spp.) pistillate scales. *Uncinia kingii* with its filiform filaments, deciduous scales, and glabrous utricles cannot, on the basis of these characters, be separated from section *Uncinia*, and thus it is not surprising that Clarke (1883) placed it in that section and in its segregate section *Patagonicae* C. B. Clarke (Clarke, 1908). If *U. kingii* is in fact sister to *Uncinia* s. str. this would suggest that the characters used to circumscribe section *Uncinia* are plesiomorphic, and that section *Uncinia*, like *Uncinia* s.l., is a cryptic group (but see "Outgroups, rachilla theories, and the relationships of *Uncinia* and *Carex* sect. *Leucoglochin*"). Further support for this contention would appear to come from the position of section *Uncinia* series *Macrolepidae* (hispid utricles, persistent scales) within the section *Platyandrae* + series *Macrolepidae* clade, and by the clear monophyly of section *Platyandrae* (hispid utricles, persistent scales, and dilated filaments) itself. Similar trends in the generic-wide analysis of *Uncinia* by Starr (2001) and in the tribal analysis of Starr et al. (2004) suggest that "cryptic" clades may be common in the Cariceae, and that parallelisms and reversals in even the most important characters used for classification are widespread. This raises the prospect that a phylogenetic classification may be incompatible with the pragmatic need to create groups that can be easily diagnosed by traditional means (i.e., via a dissecting microscope), though a reexamination of morphology within a phylogenetic context may yet reveal previously unrecognized homologies (Starr et al., 2004).

TAXONOMY OF *CAREX MICROGLOCHIN*

In addition to its pivotal importance in the history of Cariceae classifications and phylogenetic theories, *Carex microglochin* is also interesting as one of only a handful of truly bipolar species (Constance et al., 1963; Moore & Chater, 1971). Although morphological (Boott, 1867; Kükenthal, 1909;

Kreczetovich, 1937) and anatomical (Kukkonen, 1970) differences have led authors to treat some South American plants as a separate variety or species, the high levels of infraspecific sequence divergence (10.2%) detected in this analysis and the placement of *C. microglochin* samples in separate clades are unexpected. This is especially true when all previous studies indicate that within species, variability is very low within the Cariceae (Starr et al., 1999, 2003) and angiosperms in general (Baldwin et al., 1995; Hershkovitz et al., 1999). Although the possibility of contamination cannot be entirely ruled out at the point of extraction, the fact that both individuals possessed unique and typical ITS and ETS 1f sequences from Europe and South America suggests that other evolutionary factors, such as hybridization, may be at work.

It is thought that bipolar distributions, like those of *Carex microglochin*, may have resulted during the late Pliocene or Pleistocene when cooler conditions at lower latitudes could have permitted temperate species the opportunity to disperse across tropical latitudes by following the Cordilleran system of North and South America (Constance et al., 1963; Moore & Chater, 1971). It is possible that the extreme differences between Northern and Southern hemisphere samples of *C. microglochin* could be explained by hybridization. Although this hypothesis needs to be confirmed, the exceptional geological and climatic events of the late Pliocene and Pleistocene have been linked to hybridization in several other groups (e.g., *Tellima grandiflora* (Pursh) Douglas, Soltis et al., 1991; *Quercus* L., Schaal et al., 1998; *Arabis* L., Dobeš et al., 2004).

CONCLUSIONS

As in previous Cariceae analyses, this study recovered four major clades in tribe Cariceae, suggesting that a general consensus among analyses is emerging. All studies indicate that *Uncinia* is monophyletic and part of a clade dominated by androgynous unispicate species of *Kobresia*, *Cymophyllus*, and *Carex* subgenera *Carex* and *Psyllophora* that also includes multispicate species of *Kobresia*. This clade is sister to a monophyletic group consisting of *Schoenoxiphium* and androgynous unispicate species of *Carex* subg. *Psyllophora*. The remaining species fall into two clades, one consisting of "typical" members of *Carex* subg. *Vignea* and a dioecious member of *Carex* subg. *Psyllophora* (*C. dioica*), and the second comprising "typical" members of *Carex* subgenera *Carex* and *Vigneastra*, and a dioecious member of *Carex* subg. *Psyllophora* (*C. scirpoidea*), that is sister to the remainder of the tribe.

Trees suggest that *Carex* is paraphyletic with respect to all other Cariceae genera. *Carex* subg. *Vignea* is monophyletic, but analyses suggest that *Carex* subg. *Psyllophora* is polyphyletic, and *Carex* subgenera *Vigneastra* and *Carex* should be merged. Analyses also reject the long-held hypotheses of a monophyletic *Schoenoxiphium* and *Kobresia* and a phylogenetic link between *Carex* subgenera *Vigneastra* and *Schoenoxiphium*. In addition, analyses continue to support a fundamental split among unispicate species. The dioecious members of *Carex* subg. *Psyllophora* are related to multispicate species in either *Carex* subgenera *Carex* or *Vignea*, while the androgynous unispicate members of *Carex* subgenera *Carex* and *Psyllophora* and the genera *Cymophyllus*, *Kobresia*, and *Uncinia* are variously placed in a clade that also contains multispicate species of *Schoenoxiphium* and *Kobresia*. *Cymophyllus* is sister to androgynous unispicate species in *Carex* subg. *Psyllophora*, and it cannot be morphologically separated from them.

Unfortunately, relationships among the major clades in Cariceae remain ambiguous, and statistical support for their monophyly continues to be poor. Although topological congruence would suggest that these clades are real, future increases in taxa and characters are needed to confirm these results.

The present analysis also indicates that *Uncinia* s. str. is sister to *U. kingii* and divided into two clades that roughly correspond to the traditional sections *Uncinia* and *Platyandrae*. This topology is surprisingly consistent with the classification of Kükenthal (1909), who divided *Uncinia* into two subgenera, the first of which was composed of sections *Uncinia* and *Platyandrae* (subgenus *Eu-Uncinia*), while the second contained *U. kingii* (subgenus *Pseudocarex* = subgenus *Hemihamatae*). The position of *U. kingii* as sister to *Uncinia* s. str. is unexpected as the compelling morphological and anatomical argument made by Reznicek (1990) would suggest that *U. kingii* is more closely related to *Carex microglochin* and its allies. The position of *U. kingii* as sister to *Uncinia* s. str. also poses a difficult practical and

philosophical problem as it creates two morphologically cryptic groups: (1) *U. kingii* + *Uncinia* s. str., which cannot be distinguished by any known synapomorphy, and (2) *Uncinia* sect. *Uncinia*, which cannot exclude *U. kingii* since it is circumscribed by plesiomorphic characters. Starr et al. (2004) has also detected such cryptic groups, although a re-examination of morphology within the context of recent phylogenies may reveal previously undetected synapomorphies.

Tree topologies do not support previous phylogenetic scenarios based on the reduction or proliferation of rachillae, although the groups detected in this analysis are most similar to those proposed by Nelmes (1952) and Hamlin (1959). Their evolutionary theories are difficult to accept, however, because they are based on the false premise that rachillae are invariably absent in *Carex* apart from subgenus *Psyllophora*, and the predicted origin of most subgenus *Psyllophora* species from *Uncinia* is unsupported by the data. It is clear that the reduction and/or proliferation of rachillae and spikes may occur in all Cariceae clades, but the mere presence of rachillae gives no indication of relatedness, evolutionary position, or the means by which a group originated.

Despite the seemingly strong morphological evidence that *Carex* sect. *Leucoglochin* is a homogeneous group, the present analysis suggests it is polyphyletic. Nonetheless, more data are needed to confirm this hypothesis as the present data cannot entirely reject a monophyletic section *Leucoglochin* or section *Leucoglochin* + *Uncinia* clade.

Previous authors have suggested that some South American individuals of *Carex microglochin* may constitute a separate variety or species. The Scottish and Ecuadorian samples of *C. microglochin* used in this analysis were placed in separate clades and possessed highly divergent but unique nrDNA spacer sequences. It is suggested that this may be due to hybridization, although further data are needed to confirm this hypothesis.

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APPENDIX 1

Classification and voucher data for Cariceae taxa used in ITS and ETS 1f analyses. Ingroup taxa are arranged in alphabetical order to series, with outgroup taxa placed last. Generic delimitation follows Kükenthal (1909) and Ball et al. (2002). Subgeneric circumscription adheres to Kükenthal (1909), Kukkonen (1967), and Zhang (2001), while sections follow Kükenthal (1909), Wheeler (1989), Egorova (1999), Dai and Liang (2000), Zhang (2001), and Ball and Reznicek (2002). The series of *Uncinia* are circumscribed as in Hamlin (1958, 1959) except for section *Platyandrae* ser. *Trichocarpae*, which includes *U. multifaria* Nees ex Boott (see Starr et al., 2003). Individuals sampled from the same species are numbered (1) and (2). Note that the voucher for *U. riparia* R. Br. could be one of three specimens (i.e., 1a, 1b, 1c), and that ITS and ETS 1f sequences of *U. triquetra* and *U. brevicaulis* Thouars were combined from two separate individuals. The type species for Cariceae genera (Goetghebeur, 1986; Nicolson, 1992) and *Carex* subgenera (Egorova, 1999) included in the analysis are marked respectively by (§) and (‡). GenBank numbers in parentheses represent sequences from Starr et al. (1999, 2003, 2004). Herbarium acronyms follow Holmgren et al. (1990).

Carex L.

subg. *Carex* sect. *Abditispicae* G. A. Wheeler, ***C. collumanthus*** (Steyerm.) L. E. Mora, COLOMBIA: Arauca, Sierra Nevada del Cocuy, *Cleef 8875* (NY) (AY241987, AY241988); sect. *Acrocystis* Dumort., ***C. albicans*** Willd., U.S.A.: Arkansas, Scott Co., *Ford 9440 & Naczi* (WIN) (AF027439, AF027478, AY241986); sect. *Depauperatae* Meinsh., ***C. depauperata*** Curtis ex With., UNITED KINGDOM: England, Surrey, *Rich 01* (OXF) (AY241984, AY241985); sect. *Laxiflorae* (Kunth) Mack., ***C. blanda*** Dewey, CANADA: Ontario, Peterborough Co., *Bakowsky 96-176* (WIN) (AF027445, AF027484, AY241983); sect. *Phacocystis* Dumort., ***C. nigra*** (L.) Reichard, FRANCE: Col du Luitel, *Playford 9807 et al.* (FHO) (AY241989, AY241990); sect. *Phyllostachyae* Tuck. ex Kük., ***C. backii*** Boott, CANADA: Ontario, Niagara R. M., *Ball s.n.* (WIN) (AF027411, AF027453, AY241968).

subg. *Psyllophora* (Degl.) Peterm. (= subg. *Primocarex* Kük.) sect. *Aciculares* (Kük.) G. A. Wheeler, ***C. acicularis*** Boott, NEW ZEALAND: Fiordland, Southland Land District, *Ford 113/98* (FHO) (AY242012, AY242013); ***C. vallis-pulchrae*** Phil., ARGENTINA: Tierra del Fuego, *Laegaard 13290* (AAU) (AY012619, AY012620); sect. *Caryotheca* V. I. Krecz. ex T. V. Egorova, ***C. phyllostachys*** C. A. Mey., TURKEY: Prov. Adana, Bahçe District, *Davis & Hedge* D. 26885 (BM 000059251) (AY242016, AY242017); sect. *Dornera* Heuff., ***C. nigricans*** C. A. Mey., CANA-

DA: British Columbia, Mount Revelstoke Natl. Park, *Ford 9720* (WIN) (AY242042, AY242043); ***C. pyrenaica*** Wahlenb., NEW ZEALAND: Fiordland, Southland Land District, *Ford 104/98* (FHO) AY244528, AY244529; sect. *Filifoliae* (Tuck.) Mack., ***C. filifolia*** Nutt., CANADA: Manitoba, Lauder Sand Hills, *Punter & Punter s.n.* (WIN) (AF027433, AF027473) AY244530; sect. *Firmiculmes* (Kük.) Mack., ***C. geyeri*** Boott, U.S.A.: Montana, Cascade Co., *Starr MT96039* (WIN) (AF027434, AF027474) AY244527; sect. *Junciformes* (Boeck.) Kük., ***C. aphylla*** Kunth, ARGENTINA: Prov. Río Negro, *Laegaard 13496* (AAU) (AY242014, AY242015); sect. *Leptocephalae* L. H. Bailey, ***C. leptalea*** Wahlenb., CANADA: Alberta, 2 km NE of Manly Corner, *Starr 96014 et al.* (WIN) (AY241979, AY241980); sect. *Leucoglochin* Dumort., ***C. microglochin*** Wahlenb., (1) ECUADOR: Prov. Chimborazo, *Molau, Eriksen & Klitgaard 2329* (GB) AY244519, AY244520, (2) UNITED KINGDOM: Scotland, Meall Greigh, *Starr 98017 & Scott* (FHO) AY244517, AY244518; ***C. parva*** Nees, CHINA: Yunnan, Diqing Prefecture, *Aldén et al. s.n., K.E.G. No. 1252* (E) AY244523, AY244524; ***C. pauciflora*** Lightf., FRANCE: Col du Luitel, *Playford 9806 et al.* (FHO) (AY242040, AY242041); sect. *Longespicatae* Kük., ***C. monostachya*** A. Rich., KENYA: *Muasya 1052* (K) (AY241977, AY241978); sect. *Nardinae* (Tuck.) Mack., ***C. nardina*** Fr., U.S.A.: Wyoming, Big Horn Co., *Starr et al. WY96134* (FHO) (AY241973, AY241974); sect. *Obtusatae* (Tuck.) Mack., ***C. obtusata*** Lilj., CANADA: Manitoba, Portage Sand Hills, *Ford 9601 et al.* (WIN) (AY241981, AY241982); sect. *Physoglochin* Dumort., ***C. dioica*** L., UNITED KINGDOM: Scotland, Ben Lawers Visitor's Centre, *Starr 98015 & Scott* (FHO) (AY241999, AY242000); sect. *Psyllophora* (Degl.) Koch, ***C. pulicaris***‡ L., UNITED KINGDOM: England, Yorkshire Dales Natl. Park, *Starr 98001 & Scott* (FHO) (AY242018, AY242019); sect. *Rupestres* (Tuck.) Meinsh., ***C. rupestris*** All., FRANCE: Col du Galibier, *Playford 9801 et al.* (FHO) AY244521, AY244522; sect. *Scirpinae* (Tuck.) Kük., ***C. scirpoidea*** Michx., CANADA: Alberta, Jasper Natl. Park, *Bayer AB-96010 et al.* (WIN) (AF027447, AF027486, AY241991).

subg. *Vignea* (P. Beauv. ex T. Lestib.) Peterm. sect. *Ammoglochin* Dumort., ***C. arenaria***‡ L., UNITED KINGDOM: Scotland, Lunan Bay Sand Dunes, *Starr 98020* & *Scott* (FHO) (AY242003, AY242004); sect. *Curvulae* Tuck. ex Kük., ***C. curvula*** All., FRANCE: Col du Galibier, *Playford 9803 et al.* (FHO) (AY242030, AY242031); sect. *Deweyanae* (Tuck. ex Mack.) Mack., ***C. deweyana*** Schwein., CANADA: Alberta, Edmonton, *Starr* 96007 (WIN) (AF027437, AF027476, AY242007); sect. *Remotae* (Asch.) C. B. Clarke, ***C. remota*** L., UNITED KINGDOM: England, Yorkshire Dales Natl. Park, *Starr 98022 & Scott* (FHO) (AY242001, AY242002); sect. *Stellulatae* (Kunth) Christ, ***C. echinata*** Murray, UNITED KINGDOM: Scotland, Sròn Dha Murchdi, *Starr 98009 & Scott* (FHO) (AY242005, AY242006).

subg. *Vigneastra* (Tuck.) Kük. (= subg. *Indocarex* (Baill.) Kük.) sect. *Baccantes* (T. Koyama) P. C. Li, ***C. baccans*** Nees, TAIWAN: Wu Lai, Taipei, *Yen 078* (WTU) (AF027449, AF027488, AY241994); sect. *Indicae* Tuck., ***C. cruciata*** Wahlenb., MALAYSIA: Mulu Natl. Park, Sarawak, *Yen 075* (WTU) (AF027450, AF027489, AY241995); ***C. echinochloe*** Kunze, KENYA: *Muasya 1051* (K) (AY241992, AY241993); ***C. filicina*** Nees, TAIWAN: Yang Ming Shan Natl. Park, Da Tun Shan, *Yen 0076* (WTU) (AY241996, AY241997); sect. *Polystachyae* Tuck., ***C. polystachya*** Sw., BELIZE: Cayo District, *Jones 11275 & Wipff* (MICH) (AF027448, AF027487, AY241998).

Cymophyllus Mack.

C. fraserianus§ (Ker Gawl.) Kartesz & Gandhi, (1) U.S.A.: Tennessee, Blount Co., along rd. to Cades Cove, *Sharp s.n.* (cultivated at K), *Starr 98024 ex RBG Kew* (FHO) (AY241969, AY241970).

Kobresia Willd.

subg. *Compositae* (C. B. Clarke) Kukkonen, ***K. curticeps*** (C. B. Clarke) Kük., INDIA: Sikkim, East District, *Long & Noltie s.n.*, *E.E.N.S. No. 73* (E) (AY242044, AY242045); ***K. laxa*** Nees, INDIA: Sikkim, North District, *Long & Noltie s.n.*, *E.E.N.S. No. 211* (E) (AY241975, AY241976).

subg. *Kobresia* sect. *Hemicarex* (Benth.) C. B. Clarke, ***K. esenbeckii*** (Kunth) Noltie, INDIA: Sikkim, West District, Bikbari, *Long et al. s.n.*, *E.S.I.K. No. 335* (E) (AY242032, AY242033); ***K. nepalensis*** (Nees) Kük., INDIA: Sikkim, North District, *Long & Noltie, E.E.N.S. No. 291* (E) (AY242034, AY242035); sect. *Kobresia*, ***K. myosuroides*** (Vill.) Fiori, FRANCE: Col du Galibier, *Playford 9804 et al.* (FHO) (AY242036, AY242037); ***K. schoenoides*** (C. A. Mey.) Steud., INDIA: Sikkim, West District, Chhoptha, *E.S.I.K. No. 647* (E) (AY242038, AY242039); ***K. simpliciuscula***§ (Wahlenb.) Mack., CANADA: British Columbia, Yoho Natl. Park, *Ford 9710* (FHO) (AY241971, AY241972).

Schoenoxiphium Nees

S. ecklonii Nees, SOUTH AFRICA: Cape Province, George-Knysna, *Baard 128* (PRE) (AY242024, AY242025); ***S. filiforme*** Kük., SOUTH AFRICA: Eastern Cape, Drakensbergs, *Phillipson 666* (PRE) (AY242020, AY242021); ***S. lanceum***§ (Thunb.) Kük., SOUTH AFRICA: Cape Province, Stellenbosch, *McDonald 829* (PRE) (AY242028, AY242029); ***S. lehmannii*** (Nees) Steud., SOUTH AFRICA: Natal

Province, Ngoye Forest Reserve, *Williams 1007* (PRE) (AY242026, AY242027); ***S. sparteum*** (Wahlenb.) C. B. Clarke, SOUTH AFRICA: Orange Free State, Ladybrand, *De Lange FA 57* (PRE) (AY242022, AY242023).

Uncinia Pers.

subg. *Eu-Uncinia* Kük. sect. *Platyandrae* C. B. Clarke ser. *Hamatae* Hamlin, ***U. hamata*** (Sw.) Urb., ECUADOR: Prov. Pichincha, N face of Pichincha, *Starr 99032* & *Amigo* (FHO) (AY012664, AY012665); ser. *Macrotrichae* Hamlin, ***U. ecuadorensis*** G. A. Wheeler & Goetgh., ECUADOR: Prov. Cotocachi, S face of Nevado Cotacachi, *Starr 99020* & *Amigo* (FHO) (AY012661, AY012662); ***U. erinacea*** (Cav.) Pers., CHILE: Isla Grande de Chiloé, Parque Nacional de Chiloé, *Vann 9804* (FHO) AY244531, AY244532; ser. *Trichocarpae* Hamlin, ***U. brevicaulis*** Thouars, (1) ST. HELENA: Tristan da Cunha, Inaccessible Island, *Christophersen 2473* (BM) AY244533, (2) ST. HELENA: Tristan da Cunha, above Burntwood, *Dickson 25* (AAS) AY244534; ***U. lacustris*** G. A. Wheeler, ECUADOR: Prov. Pichincha, Páramo de Guamani, *Laegaard 51887* (GENT) (AY012673, AY012674); ***U. multifaria*** Nees ex Boott, in Hook. f., CHILE: Isla Grande de Chiloé, P. N. de Chiloé, *Vann 9803* (FHO) (AY012667, AY012668); ***U. phleoides*** (Cav.) Pers., CHILE: Isla Grande de Chiloé, P. N. de Chiloé, *Vann 9801* (FHO) (AY012670, AY012671).

sect. *Uncinia* (= *Stenandrae* C. B. Clarke) ser. *Australes* Hamlin, ***U. clavata*** (Kük.) Hamlin, NEW ZEALAND: Westland Land District, Mt. Wilberg, *Wardle, Buxton & Ford s.n.* (CHR 500096) (AY012646, AY012647); ***U. ferruginea*** Boott, NEW ZEALAND: Wellington Land District, Ruahine Ranges, *Bellingham 786* (CHR) (AY012649, AY012650); ***U. uncinata***§ Kük., NEW ZEALAND: North Island, Auckland Ecological Region, *de Lange s.n.* (AK 226837) (AY242054), AY244543; ser. *Compactae* Hamlin, ***U. compacta*** R. Br., AUSTRALIA: Tasmania, SW Natl. Park, *Croft 10243 & Richardson* (CANB) AY244539, AY244540; ***U. flaccida*** S. T. Blake, AUSTRALIA: Australian Capital Territory, S slope of Mt. Murray, *Gilmour 6604* (CANB) (AY012643, AY012644); ***U. rupestris*** Raoul, NEW ZEALAND: Kokatahi River Catchment, spur W of a major confluence in Blue Duck Creek, *Bellingham 671* (CHR) (AY012640, AY012641); ser. *Graciles* Hamlin, ***U. banksii*** Boott, NEW ZEALAND: North Island, Auckland Ecological Region, *Cameron 7510* (AK) (AY012634, AY012635); ***U. subsacculata*** G. A. Wheeler & Goetgh., ECUADOR: Prov. Pichincha, N face of Pichincha, *Starr 99035 & Amigo* (FHO) (AY012652, AY012653); ***U. tenuis*** Poepp. ex Kunth, ECUADOR: Prov. Imbabura, Cerro Blanco, *Øllgaard 98225* (AAU) (AY012658, AY012659); ser. *Leptostachyae* Hamlin, ***U. leptostachya*** Raoul, NEW ZEALAND: Otago Land District, Otago Peninsula, *Enright s.n.* (CHR 505712) (AY012631, AY012632); ***U. scabra*** Boott, NEW ZEALAND: Wanganui, Waitotara River, *Ogle 2854* (CHR) (AY012625, AY012626); ser. *Macrolepidae* Hamlin, ***U. macrolepis*** Decne., ECUADOR: Prov. Pichincha/Napo, Volcan Antisana, *Starr 99028 & Amigo* (FHO) AY244535, AY244536; ***U. triquetra*** Kük., (1) ARGENTINA: Tierra del Fuego, Cerro Huehuepen, *Laegaard 13233* (AAU) AY244542, (2) CHILE: Laguna el Parrillar, Costa E., *Pisano 3.917* (RNG) AY244541; ser. *Ripariae* Hamlin, ***U. laxiflora*** Petrie, NEW ZEALAND: Wellington Land District, Ruahine Ranges, *Bellingham 789* (CHR) (AY012622, AY012623); ***U. riparia*** R. Br., (1a) AUSTRALIA: Tasmania, Lake St. Clair Natl. Park, *Wilson 8331* (K) AY244537, AY244538, (1b) AUSTRALIA: Tasmania, Pinnacle Mtn., *Hemsley 6652* (K), (1c) AUSTRALIA: Tasmania, 2 km E of Dee Lagoon Dam, *Wilson 6294* (K); ***U. rubra*** Boott, NEW ZEALAND: Cultivated. Provenance—Southland, Garvie Mountains, *Druce APD 1744* (CHR) (AY012628, AY012629).

subg. *Hemihamatae* (Hamlin) Kukkonen (= subg. *Pseudocarex* Kük., nom. illeg.), ***U. kingii*** Boott, CHILE: Isla Hoste, *Pisano 5530* (GH) AY244525, AY244526.

Outgroups

Eriophorum vaginatum L., UNITED KINGDOM: England, *Starr 98007 & Scott* (FHO) (AY242008, AY242009); ***Scirpus polystachyus*** F. Muell., AUSTRALIA: New South Wales, *Wilson s.n.* (MWC 5927) (K) (AY242010, AY242011).