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ORIGINAL RESEARCH

Systematic Rearrangement of Korean *Scirpus* L. s.l. (Cyperaceae) as Inferred from Nuclear ITS and Chloroplast *rbcL* Sequences

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Abstract The genus *Scirpus* L. s.l. (Cyperaceae) has been accepted as a polyphyletic taxon by most plant taxonomists. This genus was separated into different genera by several different authors: *Scirpus* s. str., *Trichophorum* Pers., *Bolboschoenus* (Asch.) Palla, *Schoenoplectus* (Rchb.) Palla, and *Schoenoplectiella* Lye. The heterogeneity of Korean *Scirpus* s.l. has not yet been studied. We examined 17 taxa of Korean *Scirpus* s.l. by morphological characters and phylogenetic analyses based on nuclear ITS and chloroplast *rbcL* sequences. Phylogenetic analyses using maximum parsimony, maximum likelihood, and Bayesian method provided sufficient resolution. The phylogeny revealed the polyphyly of Korean *Scirpus* s.l. with five distinct clades. These clades correspond to *Bolboschoenus*, *Schoenoplectus* s.str., and *Schoenoplectiella*, *Scirpus* s.str., and *Trichophorum*, respectively. These five genera were delimited in terms of the morphology of tuber, bract, and inflorescence. By virtue of our findings, we suggest that the 17 taxa of Korean *Scirpus* s.l. should be placed into five genera as follows: *Bolboschoenus* (two species), *Schoenoplectus* (three species), *Schoenoplectiella* (six species), *Scirpus* s. str. (five species), and *Trichophorum* (one species).

Keywords *Scirpus* · *Bolboschoenus* · *Schoenoplectus* · *Trichophorum* · *Schoenoplectiella* · Cyperaceae · ITS · *rbcL*

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Introduction

The *Scirpus* L. (Cyperaceae) is a cosmopolitan genus consisting of about 160 species (Govaerts et al. 2007), and is used as foods for human or animal, medicines, or ethnobotanical materials (Simpson, 2008). For example, the tubers of *Scirpus maritimus* L. and its allies are food source of wintering birds (Amat 1995). Although this genus has ecological and economic importance, there are insufficient information and taxonomic confusion. Linnaeus (1753) recorded *Scirpus* with 24 species. He described the generic characters of *Scirpus* as having imbricate scales, three stamens and three-fid stigma (Linnaeus 1754). These characteristics are widespread and general in Cyperaceae, thus his broad definition of *Scirpus* caused numerous synonyms in more than 50 genera of Cyperaceae (Beetle 1949). Both Koyama (1958) and Hitchcock and Cronquist (1973) explained *Scirpus* with having spirally imbricate scales, not thickened style base, and sessile achene. For the purpose of this paper, we refer to their circumscription as *Scirpus* s. l. Although other authors suggested a relatively narrow definition of *Scirpus* s.l. (Koyama 1958; Hitchcock and Cronquist 1973), most recent plant taxonomists still considered *Scirpus* s.l. as a polyphyletic group (Koyama 1978; Dahlgren et al. 1985; Bruhl 1995; Goetghebeur 1998; Simpson et al. 2003; Takhtajan 2009). *Scirpus* s.l. has been segregated into several genera such as *Bolboschoenus* (Asch.) Palla, *Schoenoplectus* (Rchb.) Palla, *Scirpus* L. s.str., and *Trichophorum* Pers. *Bolboschoenus* is distinct from other genera in its eligulate leaves, and has several leafy primary bracts and ovoid tubers (Fig. 1a). *Schoenoplectus* has culm-like primary bract (Fig. 1b, c). *Scirpus* s.str. has well developed primary bracts and

Fig. 1 Typical features of Korean *Scirpus* s.l. Habits of **a** *Scirpus fluviatilis* (Torr.) *a* Gray with ovoid tuber; **b** *S. tabernaemontani* C. C. Gmel, with culm-like bract and with pseudo-lateral and branched inflorescence; **c** *S. triangulatus* Roxb., with un-branched inflorescence; **d** *S. radicans* Schkuhr, with leafy bracts and small numerous spikelets; and **e** *S. dioicus* (nom. inval.), with rudimentary bract and single spikelet comprised of only female flowers or male and bisexual flowers at culm terminal. The small box in each figure represents typical feature of each taxon

inflorescence with numerous spikelets (Fig. 1d), while *Trichophorum* has reduced leaf blade and the single spikelet at the culm terminus (Fig. 1e).

Lye (2003) suggested the *Schoenoplectiella* Lye as a new genus. *Schoenoplectiella* should be treated as an independent genus from *Schoenoplectus* (Rchb.) Palla since the old concept of *Schoenoplectus* turned out to still be a polyphyletic taxon based on *rbcL* analysis (Muasya et al. 1998). His establishment of the genus *Schoenoplectiella* was partially compatible with the sections *Supini* and *Actaeogeton*, which are two of the four sections in *Schoenoplectus* (Koyama 1978; Smith and Hayasaka 2001; Smith 2002).

In Korea, *Scirpus* s.l. has been reported by several researchers to be comprised of seven to 21 taxa (Table 1). Komarov (1901), who investigated the flora of Manchuria and the northern part of Korea, reported six species and one variety of *Scirpus*. Throughout his life-time investigation of Korean plants, Nakai (1911) reported *Scirpus* as having ten species and two varieties. The distribution and taxa number of Korean *Scirpus* were more fully addressed by the recent botanists (Chung 1957; Ohwi 1965; Lee 1996, 2003, 2006; Oh and Ham 1998; Oh 2007; Table 1). All of the former researchers had treated Korean *Scirpus* as following the broad concept of the genus, and there were different taxonomic delineations within their studies because of morphologically similar features among relative taxa. For example, Komarov (1901) and Nakai (1911) reported on *Scirpus michelianus* (auct. non L.) which was later transferred to *Cyperus pacificus* (Ohwi) Ohwi. In all of the studies, they did not discriminate between *Scirpus juncoides* Roxb. and *Schoenoplectiella hotarui* Ohwi (Table 1). These kinds of confusions have occurred frequently, as shown in a

Table 1 List of previous reported *Scirpus* L. s.l. from Korea and comparison of the taxonomic treatment among each study

Reported name (Korean name)	Komarov (1901)	Nakai (1911)	Chung (1957)	Ohwi (1965)	Lee (1996)	Oh and Ham (1998)	Lee (2003)	Lee (2006)	Oh (2007)
Scirpus fluviatilis (Torr.) A. Gray (Keun-mae-ja-gi)				○	○	○	○	○	○
S. planiculmis F.Schmidt (Sae-seommae-ja-gi)				○	○	○	○	○	○
S. maritimus L. (Mae-ja-gi)	○	○	○			○		○	○
= *S. affinis* Roth.		○							
S. nipponicus Makino (Mul-go-laeng-i)			○		○	○	○	○	○
S. tabernaemontani C. C. Gmel. (Keun-go-laeng-i)	○		○		○		○	○	○
= *S. tabernaemontani* C.C.Gmel. for. *pictus* (Honda) Ohwi				○					
= *S. lacustris* L. subsp. *creber* (Fern.) T. Koyama						○			
S. triqueter L. (Se-mo-go-laeng-i)		○	○	○	○	○	○	○	○
S. lacustris L.		○							
S. mucronatus L. (Jomsong-i-go-laeng-i)		○	○	○	○		○	○	○
S. triangulatus Roxb. (Song-i-go-laeng-i)				○	○	○	○	○	○
S. hotarui Ohwi (Ol-chaeng-i-gol[a])			○						
= *S. juncoides* Roxb. var. *hotarui* (Ohwi) Ohwi						○		○	
= *S. erectus*, auct. non. Poir.	○	○							
S. juncoides Roxb. (Ol-chaeng-i-gol[a])				○	○		○		○
S. wallichii Nees (Nam-yanggol)				○	○	○	○	○	○
S. lineolatus Franch. & Sav. (Je-ju-ol-chaeng-i-gol)						○			○
S. komarovii Roshev. (Gwangleunggol)				○	○		○		○
= *S. supinus* L. var. *leiocarpus* Komarov		○							
S. juncoides X *wallichii* Tang & Wang ex Oh[a] (Go-seonggol)						○			○
S. wichurai Boeck. (Bang-ul-go-laeng-i)	○						○	○	
= *S. eriophorum* Michx.		○							
var. *asiaticus* (Beetle) T. Koyama					○	○			○
var. *nipponicus* Nakai			○						
S. karuisawensis Makino (Sol-bang-ul-go-laeng-i[a])			○	○	○	○	○	○	○
= *S. fuirenoides* Maximowicz var. *jaluana* Komarov	○	○							
S. mitsukurianus Makino (Sol-bang-ul-gol[a])						○			○
S. sylvaticus L.									○
var. *maximowiczii* Regel (Geom-eun-do-lu-bag-i)				○	○	○	○	○	
S. radicans Schkuhr (Do-lu-bag-i)	○	○		○	○	○	○	○	○
S. fuirenoides Maximowicz (Jomsol-bang-ul-go-laeng-i)		○			○				○
S. maximowiczii C. B. Clarke (Hwangsae-go-laeng-i)				○	○		○		○
S. dioicus, nom. inval. (Dongganggo-laeng-i)								○	
= *S. cespitosus*, auct. non L.							○		
S. hudsonianus (Michx.) Fern. (Ae-gi-hwangsae-pul)				○	○		○	○	○
Cyperus pacificus (Ohwi) Ohwi (Huinbangdongsa-ni)				○	○	○	○	○	
= *C. michelianus* var. *pacificus* Ohwi									○
= *Scirpus michelianus,* auct. non L.	○	○							
No. of recognized taxa (only *Scirpus*)	7	12	8	14	17	16	17	16	21

[a] Confused common name and ambiguous scientific name

recent study on Korean Cyperaceae (Oh 2007). She reported 21 taxa of *Scirpus*, based on morphological and anatomical characteristics (Table 1).

Molecular markers have been used to infer the phylogeny of vascular plants including Cyperaceae (Kress et al. 2005).Various molecular markers have been used in studies for the inference of suprageneric phylogeny in Cyperaceae: *rbcL* (Muasya et al. 1998; Simpson et al. 2007), *rbcL* and *trnL-F* (Muasya et al. 2009), and *ndh*F and 5.8 S nuclear ribosomal DNA (Hirahara et al. 2007). In addition, relationships of subgenus or sections within *Carex* L. were studied using ITS and *trnT-L-F* (Roalson et al. 2001; Hipp 2008). Yano and Hoshino (2005) recently performed a phylogenetic study of Japanese *Schoenoplectus* based on ITS and external transcribed spacer 1 (ETS 1f).

Here, we present a molecular phylogeny of the Korean *Scirpus* s.l. based on the DNA sequence data analyses. The major objective of this study was to examine the polyphyly of Korean *Scirpus* s.l., based on DNA sequences of nuclear internal transcribed spacer (ITS) and chloroplast *rbcL* genes. We also intended to clarify the generic limit of the separated taxa from Korean *Scirpus* s.l. Finally, the taxonomical relationship between *Schoenoplectus* and *Schoenoplectiella* was analyzed.

Materials and Methods

Plant Materials

We collected 17 taxa of *Scirpus* s.l. and three taxa of other genera (*Fimbristylis squarrosa* Vahl, *Eleocharis congesta* D. Don, and *Cladium chinense* Nees) from South Korea in order to undergo the phylogenetic analysis, using ITS and chloroplast *rbcL* DNA sequence data. All voucher specimens were deposited in the herbarium of Ajou University (AJOU). Additionally, sequences of three species for ITS and two species for *rbcL* were taken from GenBank (http://www.ncbi.nlm.nih.gov) were included to determine the phylogeny. Our sampling includes all species of *Scirpus* s.l. in South Korea. The specimen information was described in Appendix 1.

DNA Extraction, Polymerase Chain Reaction (PCR) Amplification, and Sequencing

Total genomic DNA was isolated from fresh tissues or dried specimens, using the modified CTAB method (Chen and Ronald 1999) described by Doyle and Doyle (1987), and quantification and re-suspension of DNA was done as previously described by Kim et al. (2008).

PCR amplification consisted of a 20-ul reaction volume containing 1× *Taq* buffer with 1.5 mM $MgCl_2$, 0.25 mM of each dNTP, 0.5 μM of each primer, 1 U *Taq* DNA polymerase (Solgent), and 100 ng of template DNA. Nuclear ITS regions, including 5.8S gene, were amplified with ITS 1 and ITS 4 primers (White et al. 1990). Genomic DNA (100 ng in 20 μL) was amplified with PTC-200 thermal cycler (MJ Research) programmed for 2 min at 95°C, 30 cycles of 30 s at 94°C (denaturation), 30 s of 55°C (annealing), 1 min at 72°C (extension), and final stage of 8 min at 72°C.

The chloroplast *rbcL* region was amplified using the primers, 1F (Muasya et al. 1998) and 1400R (5′- ATC TAGTTTATCTACCGGATCGA). For sequencing, two internal primers, 636F (Muasya et al. 1998) and 778R (5′-TAAAGCAAGTGTTGGGTTTAAAG), were also used. PCR amplification used the same reaction conditions as ITS, except that the extension time was 2 min.

Amplified products were purified either directly or after separation by in a 1.2% agarose gel in TBE using Gel & PCR Purification System (Solgent) and following manufacture's protocols. Purified products were cycle-sequenced used the Big Dye terminator Ready reaction mix Ver. 3.1 (Applied Biosystems) and run on an ABI Prism 3730XL DNA analyzer (Applied Biosystems). All of the obtained sequences were deposited in GenBank (Appendix 1).

Sequence Alignment and Phylogenetic Analysis

Obtained sequence data were assembled and edited using BioEdit (Hall 1999), and were aligned using ClustalX (Thompson et al. 1997). The aligned sequence was checked and edited manually to minimize software artifacts.

Phylogenetic analyses of ITS and *rbcL* data were performed using maximum parsimony, maximum likelihood, and Bayesian inference of phylogeny. We selected *C. chinense* as the outgroup in all three analytical approaches, based on the result of the phylogenetic relationship of Cyperaceae (Muasya et al. 1998). Parsimony analyses were done with PAUP* version 4.0b10 (Swofford 2002) using the heuristic search option and simple addition sequence and tree-bisection-reconnection branch swapping, ACCTRAN optimization and MULTrees in effect. All gaps were treated as missing data. Tree lengths and tree statistics (consistency index, CI and retention index, RI) were calculated using PAUP*. To assess branch support for the data, maximum parsimony bootstrap analyses (MPBS) were performed using PAUP* heuristic search, with 1,000 replications with the same parameter conditions. For the maximum likelihood analysis and Bayesian inference, MrModeltest 2.3 (Nylander 2004) was used to select substitution models that best fit the dataset under the Akaike Information Criterion (AIC; Posada and Buckley 2004). Maximum likelihood analysis was done using PAUP* with a neighbor-joining tree as a starting tree and the GTR+I+Γ (for ITS) and HKY+I+Γ (for *rbcL*) model selected by MrModeltest 2.3 (Nylander 2004).

Maximum likelihood bootstrap analyses (MLBS) also were done using PAUP* with 1,000 replications with the same parameter. Bayesian inference was conducted using MrBayes v3.1 (Ronquist and Huelsenbeck 2003) with 1×10^6 generations and GTR+I+Γ (for ITS) and HKY+I+Γ (for *rbcL*) model selected by MrModeltest 2.3 (Nylander 2004). Posterior probabilities (PP) were obtained using Markov chain Monte Carlo method (Hastings 1970) and placed on the parsimony strict consensus tree by PAUP*. Four chains were run with temperature of 0.2. Chains were sampled every 100 generations. Trees that preceded the stabilization of the likelihood value (the burn-in) were excluded, and the remaining trees were used to construct a majority rule consensus.

Results

Sequence Data Sets

The length of the ITS sequences varied from 538 bp in *Scirpus triqueter* L. and *Scirpus tabernaemontani* C. C. Gmel to 667 bp in *Scirpus sylvaticus* var. *maximowiczii* Regel. The aligned ITS sequence resulted in 712 characters, with 337 (47.3%) variable sites and 253 (35.5%) parsimony informative sites. Most of the variations were distributed in ITS1 and 2, while 5.8S rRNA gene had 19 variable sites, 12 parsimony informative sites, and three uninformative insertions or deletions. Although there is a significant morphological difference between *S. tabernaemontani* and *S. triqueter*, its ITS sequences were identical. The sequence alignment of the *rbcL* gene resulted in 1,293 characters with no indel. Of these, 101 sites (7.8%) were variable and 62 sites (4.8%) were parsimoniously informative. There were no differences in the *rbcL* sequences among five species: *Scirpus mucronatus* L., *S. triangulatus* Roxb., *S. hotarui*, *Scirpus wallichii* Nees, and *Scirpus lineolatus* Franch. & Sav. Only 1 bp was different between the above-mentioned five species and *S. juncoides*, and also between *S. tabernaemontani* and *S. triqueter* (data not shown).

Phylogenetic Analysis Based on ITS

Parsimony analysis of ITS yielded the 18 most parsimonious trees (Fig. 2a) with the length of 718 steps (CI=0.67, RI=0.80). In maximum likelihood analysis (−*ln* L=4,085.33632) and Bayesian inference, the topologies were congruent with the result of maximum parsimony analysis (not shown).

The *Scirpus* s.l. species divided into five clades (Fig. 2a). The clade I, including *Scirpus fluviatilis* (Torr.) A. Gray and *S. planiculmis* F. Schmidt, is strongly supported by MPBS (100), MLBS (100), and PP (1.00). The level of support for the clade II with comprises *Scirpus nipponicus* Makino, *S. tabernaemontani*, and *S. triqueter* was also high by all analyses (MPBS=100, MLBS=90, and PP=1.00). The clade III included six species, such as *S. mucronatus*, *S. juncoides*, and *S. lineolatus* and was also statistically significantly supported (MPBS and MLBS=100, and PP=1.00). The clade of *E. congesta* and *F. squarrosa* was resolved as a sister of the clade III, albeit support values were low. The clade IV was supported by MPBS=98, MLBS=95 and PP=1.00. The clade V including *S. dioicus* (nom. inval. = *Trichophorum dioicum* J. Jung & H.-K. Choi) and *Scirpus hudsonianus* (Michx.) Fern. is strongly supported by all statistics (MPBS=100, MLBS=99, and PP=1.00) (Fig. 2a). A more inclusive group containing three clades (I–III), *Actinoscirpus grossus*, *E. congesta*, and *F. squarrosa* is clustered significantly (MPBS/MLBS/PP = 87/68/0.93). All of the three statistical indices (MPBS/MLBS/PP = 98/89/1.00) showed that the clade IV is closely related with the clade V (Fig. 2a).

Phylogenetic Analysis Based on *rbcL*

Parsimony analysis of *rbcL* yielded the two most parsimonious trees (length=144, CI=0.74, and RI=0.85). In the maximum likelihood analysis (−*ln* L=2,074.01743) and Bayesian inference, the topologies are congruent with the result of maximum parsimony analysis (not shown). The five clades, their recognition based on ITS (Fig. 2a), are consistently retained in *rbcL* sequence analyses (Fig. 2b). The components of the five clades were consistent with the ITS trees. The position of related taxa (*E. congesta* and *F. squarrosa*) of *Scirpus* was changed, but no significant supports were provided either of data.

The clades I, II, and III are supported significantly by MPBS/MLBS/PP = 100/99/1.00, 95/93/1.00, and 100/100/1.00, respectively. The clade IV is supported well by MPBS=81, while the values of MLBS (64) and PP (0.89) are low. The clade V is supported well by two statistical values (MPBS=86 and PP=1.00) while MLBS (72) is low (Fig. 2b). Most of the statistical indices in *rbcL* sequences analyses significantly supported the five clades, although two clades of Clade IV and V were moderately supported, e.g., MLBS of Clade IV and V (64 and 72, respectively). The larger group, comprising of the clades I–III, has a closer relationship with *E. congesta* and *F. squarrosa* than the other two clades (IV or V; Fig. 2b).

Discussion

Polyphyly of Korean *Scirpus* L. s.l.

Through DNA molecular systematic approaches, we have confirmed that Korean *Scirpus s. l* is a polyphyletic group.

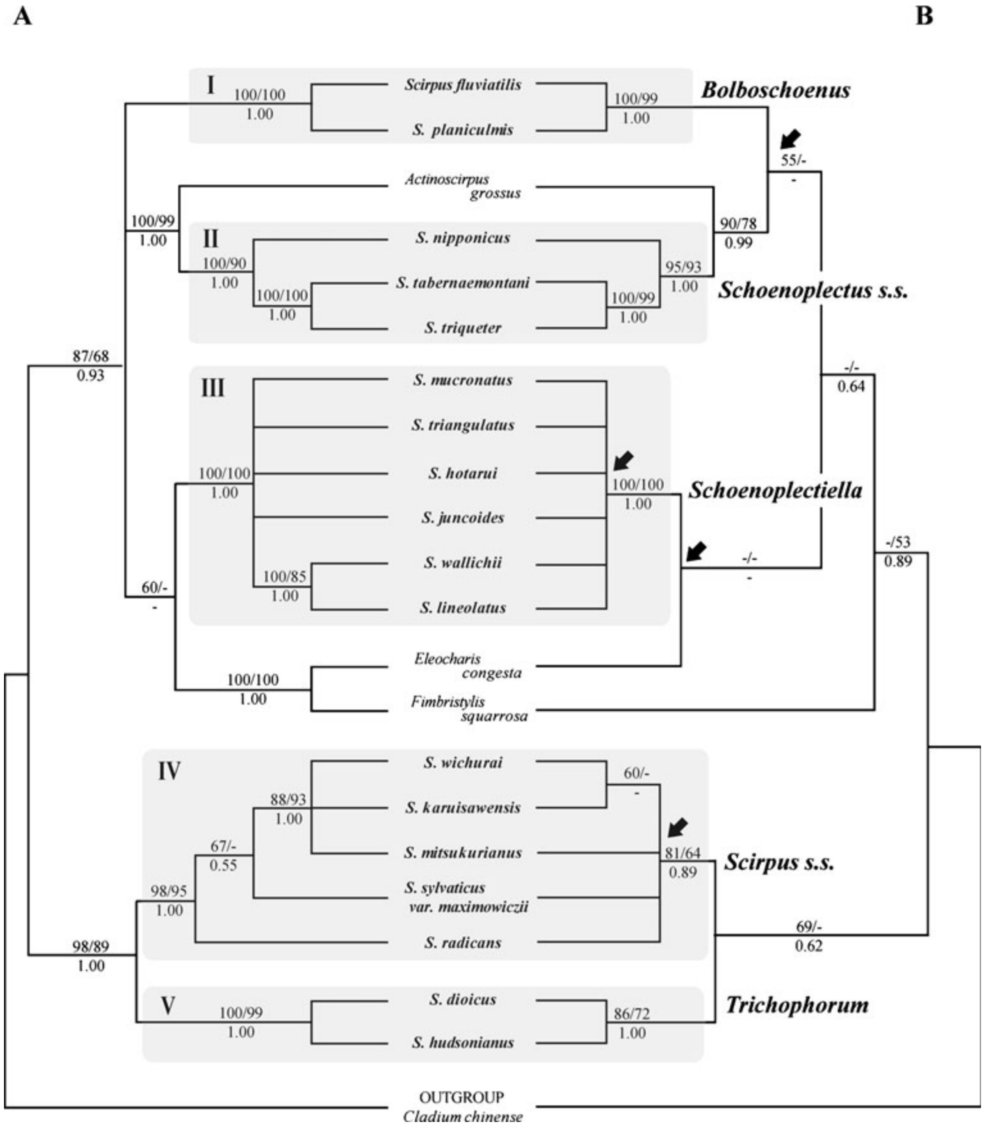


Fig. 2 Strict consensus of most parsimonious trees based on two molecular markers. Using **a** ITS sequence dataset (Length=718 steps, CI=0.67 and RI=0.80) and **b** *rbcL* sequence dataset (Length = 144 steps, CI=0.74 and RI=0.85). The numbers of most parsimonious trees are 18 and 2, respectively. The *numbers above each branch* are bootstrap values (Maximum parsimony/maximum likelihood), and posterior probability values are written below each branch. Support values lower than 50% or 0.5 is indicated by "-". The roman numerals indicate five independent clades, including Korean *Scirpus* s.l. The *arrows* indicate the nodes which differ from tree by ITS sequences in topology. These differences are caused by either low resolution or too remote relationships

The taxa of three clades (I–III) have a closer relationship with *Actinoscirpus*, *Eleocharis*, and *Fimbristylis* rather than to the clades IV or V (Fig. 2). To reconfirm polyphyly of Korean *Scirpus* s.l., we performed an additional analysis using the maximum parsimony method with the *rbcL* sequence of 72 taxa that includes type species of each separated genus, and other related taxa from GenBank (Supplementary Table S1). As the result, we found that the polyphyly of *Scirpus* s.l. is consistent for all molecular analyses and we can suggest the fact that that *Scirpus* s.l. is not monophyletic and should be treated as a complex genus comprised of several independent taxa (Fig. 2, Supplementary Fig. S1). These results are also congruent with those of other approaches, such as the embryo type comparison (Goetghebeur 1986) and the cladistic analysis, using the numerous morphological characteristics (Bruhl 1995), which support the segregation of *Scirpus* s. l. into several genera.

Five Genera Separated From Korean *Scirpus* s.l.

The two molecular markers of ITS and *rbcL* provided sufficient resolution to reveal the monophyly of each clade (Fig. 2a, b). The five clades are independent of each other and congruent with the generic concept by morphological characteristics, clade I to V corresponding respectively to: *Bolboschoenus*, *Schoenoplectus*, *Schoenoplectiella*, *Scirpus* s.str., and *Trichophorum* (Fig. 2b). Members of the five segregated genera partially correspond to those of sections in the previous study for Korean *Scirpus* s.l. (Oh & Ham

1998). They classified 16 taxa in two subgenus with five sections based on morphological and anatomical characteristics (Oh & Ham 1998), *Trichophorum*, one of the sections, is not equivalent genus *Trichophorum* in this study and is just part of genus *Scirpus* s. str. Taxa of genus *Trichophorum* were not examined in their study.

Bolboschoenus is a significantly independent group in the current analyses for both data sets (Fig. 2a, b). Strong (1993) disagree on the separation of this genus from *Schoenoplectus* s.l., based on several intermediate characteristics in morphology. Despite his argument, present analyses and previous molecular phylogenic studies do not support his opinion (Muasya et al. 1998, 2009; Hirahara et al. 2007; Simpson et al. 2007).

Schoenoplectus sensu Palla are placed on two different clades (II and III in Fig. 2). The clade II and III are more closely related *A. grossus* and *E. congesta*, respectively (Fig. 2). The remote relationship between the two clades showed in previous studies is based on the phylogenetic analysis using *rbcL* (Muasya et al. 1998) and ITS and ETS (Yano & Hoshino 2005). The clades II and III include one type of each genus, *Schoenoplectus lacustris* (L.) Palla and *Schoenoplectiella articulata* (L.) Lye, respectively (Supplementary Fig. S1). The distinct characteristics between two clades are either an unbranching or branching inflorescence. The two clades should be treated as independent genera *Schoenoplectus* s.str. (clade II) and *Schoenoplectiella* (clade III).

The species of *Scirpus* s.str. are included in Clade IV and the topology is consistent, although the resolution of both DNA sequences is insufficient to show the phylogenetic relationship among *Scirpus* s.str. species (Fig. 2).

Trichophorum (clade V) has morphology which is distinct from others (Fig. 1 and Table 2). This clade includes *S. hudsonianus* [syn. *Trichophorum alpinum* (L.) Pers., type species of *Trichophorum*] and *Scirpus dioicus* (Table 2 and Fig. 2).

Taxonomical Examination of *Schoenoplectus* and *Schoenoplectiella*

Schoenoplectiella was established as a new genus from *Schoenoplectus* s.l. (Lye 2003). His treatment had some problems, specifically in species organization and the genus description. His concept on the morphological characteristics of *Schoenoplectiella* corresponded only to the section *Supini* of this genus. The genus *Schoenoplectiella* includes section *Supini* and a part of section *Actaeogeton* (such as *S. juncoides* and *S. wallichii*; Table 2). If it is reliable that *S. juncoides* and *S. wallichii* are combined into *Schoenoplectiella*, the section *Actaeogeton* should then be transferred all together, because all species of the section *Actaeogeton* are closely related (as inferred from molecular analyses; Fig. 2). The species of sections *Actaeogeton* and *Supini* belong to the same clade(Supplementary Fig. S1), and share morphological similarities such as un-branched inflorescence. We conclude that five Korean *Scirpus* species of section *Actaeogeton* belong to *Schoenoplectiella* (Table 2).

The distinct characteristics of *Schoenoplectiella* are annual small plants and solitary female flower in the basal leaf sheath (Lye 2003). In contrast, the section *Actaeogeton* plants of *Schoenoplectiella* are often perennial and do not have a solitary female flower, despite Lye's description of this genus. We suggest here, therefore, that the unbranched inflorescence and culm-like primary bract could be the key characteristics of *Schoenoplectiella* (Fig. 1c and Table 2).

Rearrangement of Korean *Scirpus* L. s.l. into Five Separated Genera

The 47 taxa of *Scirpus* s.l. collected in Korea are arranged into five genera by the comparison of morphological characteristics and molecular phylogenetic relationships (Table 2, Fig. 2). In addition, we further treated remaining five Korean species in our analyses, based on morphology and previous molecular data (Yano and Hoshino 2005; Hirahara et al. 2007; Simpson et al. 2007). These species reported the distribution in Korea were not collected by the authors for molecular analyses: *S. maritimus* L., *S. komarovii* Roshev., *S. fuirenoides* Maximowicz, *S. maximowiczii* C. B. Clarke, and *S. hudsonianus* (Table 2).

Bolboschoenus (Asch.) Palla, Syn. Deut. Schweiz. Fl., ed. 3: 2531. 1907. *Scirpus* sect. *Bolboschoenus* Asch., Fl. Brandenburg, 1:753. 1864.; Oh and Ham, Korean J. Pl. Taxon., 28: 231. 1998.

Ascherson (1864) initially mentioned *Bolboschoenus* as a section of *Scirpus* and Palla (1907) treated the section as an independent genus. This genus is clearly identified from *Scirpus* s.l. in terms of several distinct characteristics, such as a large ovoid tuber, eligulate leaves with elongated blade, inflorescence with leafy bracts, and its large spikelet (Fig. 1a, clade I in Fig. 2).

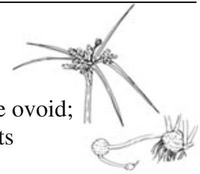
Type of genus: *Bolboschoenus maritimus* (L.) Palla

Species: *B. maritimus* (L.) Palla, *B. fluviatilis* (Torr.) Soják, *B. planiculmis* (F. Schmidt) T.V. Egorova (Table 2).

Korean name: Mae-ja-gi-sog (new suggestion).

Schoenoplectus (Rchb.) Palla, Verh. K.K. Zool.-Bot. Ges. Wien 38: 49. 1888a. *Scirpus* L. subgen. *Schoenoplectus* chb., Icon. Fl. Germ. 8: 40. 1846. *Scirpus* L. subgen.

Table 2 Rearrangement of 17 Korean *Scirpus* L. *s.l.* and morphological characteristics of the separated five genera

Taxonomic treatment		Key character / typical feature
In previous studies	Rearranged name in this study	
Gen. *Scirpus* L. *s.l.* (Go-laeng-i-sog)	**Gen. *Bolboschoenus* (Asch.) Palla (Mae-ja-gi-sog)**	tuber large ovoid; leafy bracts 
Scirpus fluviatilis (Torr.) A. Gray	*B. fluviatilis* (Torr.) Soják	
S. planiculmis F.Schmidt	*B. planiculmis* (F.Schmidt) T.V.Egorova	
S. maritimus L.	*B. maritimus* (L.) Palla*	
	Gen. *Schoenoplectus* (Rchb.) Palla (Keun-go-laeng-i-sog)	culm-like bract; branched inflorescence 
	Sect. *Malacogeton*	
S. nipponicus Makino	*S. nipponicus* (Makino) Soják	
	Sect. *Schoenoplectus*	
S. tabernaemontani C. C. Gmel.	*S. tabernaemontani* (C. C. Gmel) Palla	
S. triqueter L.	*S. triqueter* (L.) Palla	
	Gen. *Schoenoplectiella* Lye (Ol-chaeng-i-gol-sog)	culm-like bract; un-branched inflorescence 
	Sect. *Supini* (none in Korea)	
	Sect. *Actaeogeton*	
S. mucronatus L.	*S. mucronata* (L.) J. Jung & H.-K. Choi	
S. triangulatus Roxb.	*S. triangulata* (Roxb.) J. Jung & H.-K. Choi	
S. hotarui Ohwi	*S. hotarui* (Ohwi) J. Jung & H.-K. Choi	
S. juncoides Roxb.	*S. juncoides* (Roxb.) Lye	
S. wallichii Nees	*S. wallichii* (Nees) Lye	
S. lineolatus Franch. & Sav.	*S. lineolata* (Franch. & Sav.) J. Jung & H.-K. Choi	
S. komarovii Roshev.	*S. komarovii* (Roshev.) J. Jung & H.-K. Choi *	
	Gen. *Scirpus* L. *s.s.* (Go-laeng-i-sog)	leafy bracts; numerous small spikelets 
S. wichurai Boeck.	*S. wichurai* Boeck.	
S. karuisawensis Makino	*S. karuisawensis* Makino	
S. mitsukurianus Makino	*S. mitsukurianus* Makino	
S. sylvaticus L. var. *maximowiczii* Regel	*S. sylvaticus* L. var. *maximowiczii* Regel	
S. radicans Schkuhr	*S. radicans* Schkuhr	
S. fuirenoides Maximowicz	*S. fuirenoides* Maximowicz*	
S. maximowiczii C. B. Clarke	*S. maximowiczii* C. B. Clarke*	
	Gen. *Trichophorum* Pers. (Ae-gi-hwangsae-pul-sog)	scale-like bracts; 1 or few spikelets at culm terminal 
S. dioicus nom. inval.	*T. dioicum* J. Jung & H.-K. Choi	
S. hudsonianus (Michx.) Fern.	*T. alpinum* (L.) Pers.*	

[a] Five species that could not be collected in this study. For the explanation of their rearrangement, see the manuscript

Isolepis, Oh and Ham in Korean J. Pl. Taxon., 28: 232. 1998.

Reichenbach (1846) reported *Scirpus* subgenus *Schoenoplectus*. Palla (1888a) transferred the rank of *Schoenoplectus* from a subgenus to a genus. He combined 17 species to *Schoenoplectus* in the same year (Palla 1888b). The species of this genus share several morphological characteristics, namely ligulate leaves, a culm-like primary bract, and pseudo-lateral branched inflorescence (Fig. 1b, clade II in Fig. 2).

Type of genus: *S. lacustris* (L.) Palla

Species: *S. nipponicus* (Makino) Soják*,* *S. tabernaemontani* (C. C. Gmel.) Palla, *S. triqueter* (L.) Palla (Table 2).

Korean name: Keun-go-laeng-i-sog (new suggestion).

Schoenoplectiella Lye, Lidia 6: 20. 2003. *Scirpus* L. sect. *Actaeogeton*, Oh and Ham in Korean J. Pl. Taxon., 28: 232. 1998.

The species of this genus had been considered as *Schoenoplectus* s. l until Lye (2003) recognized the polyphyly of *Schoenoplectus* s.l. *Schoenoplectiella* differs from *Schoenoplectus* s.str. in its morphology, insofar as having unbranched inflorescence (Fig. 1c, clade III in

Fig. 2). This genus comprises sections *Actaeogeton* and *Supini.* The sections *Actaeogeton* and *Supini* include ca. 23 and 22 species worldwide (Smith 2002). We suggest new combinations for the five Korean species as follows:

> *Schoenoplectiella mucronata* (L.) J. Jung and H. –K. Choi, comb. nov. Basionym: *Scirpus mucronatus* L., Sp. Pl. 50. 1753. *Schoenoplectus mucronatus* (L.) Palla, Bot. Jahrb. Syst. 10:299. 1888b. Type: *Linn. 17.31* (lectotype, LINN)
>
> *Schoenoplectiella triangulata* (Roxb.) J. Jung and H. –K. Choi, comb. nov. Basionym: *Scirpus triangulatus* Roxb., Fl. Ind. 1: 219. 1820. *Schoenoplectus triangulatus* (Roxb.) Soják, Cas. Nár. Mus., Odd. Prír. 141: 62. 1972. Type: BANGLADESH, Chittagong: *Wallich Catalogue No. 3467* (lectotype, designated here, CAL)
>
> *Schoenoplectiella hotarui* (Ohwi) J. Jung and H. –K. Choi, comb. nov. Basionym: *Scirpus hotarui* Ohwi, Repert. Spec. Nov. Regni Veg. 36: 44. 1934. *Schoenoplectus hotarui* (Ohwi) Holub, Folia Geobot. Phytotax. 11: 83. 1976. Type: JAPAN, Honshu: *M. Tagawa 644* (holotype, KYO)
>
> *Schoenoplectiella lineolata* (Franch. & Sav.) J. Jung and H. –K. Choi, comb. nov. Basionym: *Scirpus lineolatus* Franch. & Sav., Enum. Pl. Jap. 2: 545. 1878. *Scheonoplectus lineolatus* (Franch. & Sav.) T. Koyama, Fl. Taiwan 5: 215. 1978. Type: JAPAN, Yokoska: *Savatier 1392* (holotype, P)
>
> *Schoenoplectiella komarovii* (Roshev.) J. Jung and H. –K. Choi, comb. nov. Basionym: *Scirpus komarovii* Roshev., Fl. USSR 3: 579. 1935. *Schoenoplectus komarovii* (Roshev.) Soják, Cas. Nár. Mus., Odd. Prír. 140: 127. 1972. Type: RUSSIA, Amur: Innokent'evka, 21 Jul. 1895, *Komarov s.n.* (LE)

Type of genus: *S. articulata* (L.) Lye

Species: *S. juncoides* (Roxb.) Lye, *S. wallichii* (Nees) Lye, *S. mucronata* (L.) J. Jung and H. –K. Choi, *S. triangulata* (Roxb.) J. Jung and H. –K. Choi, *S. hotarui* (Ohwi) J. Jung and H. –K. Choi, *S. lineolata* (Franch. & Sav.) J. Jung and H. –K. Choi, and *S. komarovii* (Roshev.) J. Jung and H. –K. Choi (Table 2)

Korean name: Ol-chaeng-i-gol-sog (new suggestion).

Scirpus L. Sp. Pl. 47. 1753. *Scirpus* L. sects. *Scirpus* et *Trichophorum*, Oh and Ham, Korean J. Pl. Taxon., 28: 232. 1998.

Instead of a broad concept of *Scirpus*, modern taxonomists (Koyama 1978; Bruhl 1995; Goetghebeur 1998) accepted a strict concept of this genus that is characterized by often tufted, ligulate leaves, several well-developed leafy bracts, and numerous small spikelets with long hypogynous bristles (Fig. 1d, clade IV in Fig. 2). *S. maximowiczii* C. B. Clarke distributed in high land of the north province and it has been considered as a *Scirpus* s.str. However, the taxonomic treatment is not clear because of the intermediate morphology of *Eriophorum* (Koyama 1958).

Type of genus: *S. sylvaticus* L.

Species: *S. wichurai* Boeck., *S. karuisawensis* Makino, *Scirpus mitsukurianus* Makino, *S. sylvaticus* L. var. *maximowiczii* Regel, *S. radicans* Schkuhr, *S. fuirenoides* Maximowicz, *and S. maximowiczii* C. B. Clarke (Table 2).

Korean name: Go-laeng-i-sog.

Trichophorum Pers. Syn. Pl. 1: 69. 1805.

Persoon (1805) reported the *Trichophorum* as an intermediate genus between *Scirpus* s.l. and *Eriophorum* L. He referred to its characteristics as ligulate leaves and reduced blade, inflorescence with single or few spikelets at the culm terminal, and a scale-like primary bract (Persoon 1805; Goetghebeur 1998; Fig. 1e, clade V in Fig. 2). "*Scirpus dioicus"* having these characteristics was reported as a new species in South Korea (Lee 2006), but the name was invalidly published since its holotype was not specified (cf. Art. 37.7, McNeill et al. 2006). Thus, we have suggested a new species *T. dioicum* J. Jung & H. -K. Choi (Jung and Choi, 2010). Moreover, *T. dioicum* consistently revealed being a member of *Trichophorum* clade with *Trichophorum cespitosum*, *T. clitonii*, and *T. rigidum* (Fig. 2 and Supplementary Fig. S1).

Type of genus: *T. alpinum* (L.) Pers.

Species: *T alpinum* (L.) Pers., *T. dioicum* J. Jung & H. -K. Choi (Table 2).

Korean name: Ae-gi-hwangsae-pul-sog (new suggestion).

Based on molecular phylogenetic analyses, we have confirmed that the genus *Scirpus* s.l. from Korea is polyphyletic. The five clades inferred from molecular phylogenetic analysis are congruent with the five genera suggested by embryological (Goetghebeur 1986) and morphological characteristics (Bruhl 1995; Lye 2003; Fig. 1). Seventeen species of Korean *Scirpus* s.l. are arranged into five genera, based on molecular data and the morphological characteristics that follow their corresponding genera (Table 2). The polyphyly of *Schoenoplectus* s.l. is reconfirmed by our study (Fig. 2). It becomes clear that the three genera of *Actinoscirpus*, *Eleocharis*, and *Fimbristylis* should be treated in detail, in order to place their phylogenetic status in *Scirpus* s.l. among Cyperaceae.

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Appendix 1

Analyzed taxa of *Scirpus* L. *s.l.* and related taxa with voucher information

Taxon, locality, voucher (herbarium), GenBank accession number of ITS/*rbc*L

Scirpus S. fluviatilis (Torr.) A. Gray, Korea, Chungcheongbuk-do, Jecheon-si; *Jung 806053* (AJOU), GQ130340/GQ130358; *S. planiculmis* F. Schmidt, Korea, Incheon, Ganghwa-gun; *Jung 806005* (AJOU), GQ130341/GQ130359; *S. nipponicus* Makino [= *Schoenoplectus nipponicus* (Makino) Soják*], Korea, Gangwon-do, Goseong-gun; *Jung 808332* (AJOU), -/GQ130364, Japan, Hokkaido; *Hoshino* et al. *19265* (OKAY), AB206267*/-; *S. tabernaemontani* C. C. Gmel, Korea, Incheon, Ganghwa-gun; *Jung 806016* (AJOU), GQ130349/GQ130365; *S. triqueter* L., Korea, Gyeongsangbuk-do, Yecheon-gun; *Na 80258* (AJOU), GQ130351/GQ130367; *S. mucronatus* L., Korea, Incheon, Ganghwa-gun; *Jung 809002* (AJOU), GQ130348/GQ130363; *S. triangulatus* Roxb., Korea, Chungcheongnam-do, Boryeong-si; *Jung 806034* (AJOU), GQ130350/GQ130366; *S. hotarui* Ohwi, Korea, Chungcheongnam-do, Boryeong-si; *Jung 809003* (AJOU), GQ130345/GQ130360; *S. juncoides* Roxb., Korea, Gyeonggi-do, Suwon-si; *Jung 807020* (AJOU), GQ130346/GQ130361; *S. wallichii* Nees, Korea, Gangwon-do, Hwacheon-gun; *Jung 808320* (AJOU), GQ130352/GQ130368; *S. lineolatus* Franch. & Sav., Korea, Jeollanam-do, Gangjin-gun; *Jung 808041* (AJOU), GQ130347/GQ130362; *S. wichurai* Boeck., Korea, Gangwon-do, Goseong-gun; *Jung 808322* (AJOU), GQ130357/GQ130373; *S. karuisawensis* Makino, Korea, Gyeonggi-do, Ansan-si; *Jung 807017* (AJOU), GQ130353/GQ130369; *S. mitsukurianus* Makino, Korea, Gangwon-do, Hwacheon-gun; *Jung 808304* (AJOU), GQ130354/GQ130370; *S. sylvaticus* var. *maximowiczii* Regel, Korea, Gangwon-do, Pyeongchang-gun; *Jung 806038* (AJOU), GQ130355/GQ130371; *S. radicans* Schkuhr, Korea, Chungcheongnam-do, Boryeong-si; *Jung 806032* (AJOU), GQ130356/GQ130372; *S. dioicus* (nom inval.), Korea, Gangwon-do, Yeongwol-gun; *Jung 804015* (AJOU), FJ797641/FJ797640; *S. hudsonianus* (Michx.) Fern. [= *T. alpinum* (L.) Pers.*], Canada; *Waterway 2002.095, −*/AJ810999*, Japan, Hokkaido; *Sato 13260* (OKAY), AB206270*/-; *A. grossus* (L. f.) Goetgh. & D.A. Simpson*, Malaysia; *Simpson 2660* (K), AB261672*/Y12953*; *Eleocharis, E. congesta* D. Don, Korea, Gyeonggi-do, Icheon-si; *Jung 805083* (AJOU), GQ130343/GQ130375; *Fimbristylis, F. squarrosa* Vahl, Korea, Gyeonggi-do, Ansan-si; *Jung 807041* (AJOU), GQ130344/GQ130376; *Cladium, C. chinense* Nees, Korea, Jeju-do, Seogwipo-si; *Choi 2006* (AJOU), GQ130342/GQ130374

(-) data not available, (*) sequence and used scientific name from GenBank

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