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ORIGINAL RESEARCH

Taxonomic Study of Korean *Scirpus* L. s.l. (Cyperaceae) II: Pattern of Phenotypic Evolution Inferred from Molecular Phylogeny

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Abstract *Scirpus* L. s.l. is well known as one of the polyphyletic groups in Cyperaceae. Recent molecular phylogenetic studies clearly suggested that *Scirpus* s.l. should be separated into several independent genera. In this study, we intend to present the morphological variations and patterns of phenotypic evolution based on molecular phylogeny of Korean *Scirpus* s.l. Five genera, including 21 taxa from Korean *Scirpus* s.l., were examined: three species of *Bolboschoenus*, three species of *Schoenoplectus*, eight species of *Schoenoplectiella* including one hybrid, five species of *Scirpus*, and two species of *Trichophorum.* For morphological analyses, 23 and 48 characters were selected from vegetative and reproductive organs, respectively. Molecular phylogeny was inferred from a nuclear ribosomal internal transcribed spacer, the chloroplast *rbcL* gene, and the chloroplast *trnL-F* region. Distinct characteristics and quantitative variation was presented for identification of the five genera and their species. A pronounced pattern of morphological character change was reduction, although many other character states seem to be homoplastic. We suggest that the reduction of phenotypic characteristics has been expressed in terms of condensation of internodes, reduction of leaf blade, and simplification of inflorescence among five genera of Korean *Scirpus* s.l.

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Introduction

Scirpus L. s.l. (Cyperaceae) comprises approximately 160 species in the world and is an herbaceous aquatic or wetland plant. Delineation of this genus had been variously defined by taxonomists (Linnaeus 1754; Palla 1888; Beetle 1949). One of these delineations that have been commonly used was defined by spirally arranged floral scales, not thickened style base, and sessile achenes (Beetle 1949; Koyama 1958; Hitchcock and Cronquist 1973). Distinct from this broad definition, the independent genera segregated from *Scirpus* s.l. had been suggested by several authors who recognized the heterogeneity of this genus (Persoon 1805; Palla 1888, 1907; Lye 2003). The legitimacy of this segregation is strongly supported by an ample body of evidence, such as, type of embryo, morphological characteristics, and molecular phylogenetic studies (Goetghebeur 1986; Bruhl 1995; Simpson et al. 2007; Muasya et al. 2009; Jung and Choi 2010, 2011).

While the classification of Cyperaceae has undergone considerable changes by molecular phylogenetic studies, utilizing morphological characters as a basis for phylogenetic analysis is relatively rare (Muasya et al. 2009; Naczi 2009). Cyperaceae classifications based on morphological characters are incongruent with recent molecular phylogeny studies using the chloroplasat *rbcL* gene and *trnL-F* region (Bruhl 1995; Goetghebeur 1998; Muasya et al. 2009). In particular, tribe Scirpeae (sensu Bruhl 1995), including *Scirpus* s.l., was placed at several clades in the molecular phylogenetic tree (Muasya et al. 2009).

The interference of phylogeny using morphological data is problematic due to morphological simplicity, uncertainty of polarization, or frequent hybridization in Cyperaceae (Naczi 2009). To interpret the character change, it is useful to optimize the character state inferred from a molecular phylogenetic tree (Muasya et al. 2001; Hipp et al. 2006; Guibert et al. 2009).

Taxa of Korean *Scirpus* s.l. were rearranged into five genera based on morphology and molecular phylogeny, and key characteristics were presented from 21 species of the five genera, respectively: three species of *Bolboschoenus* (Asch.) Palla, three species of *Schoenoplectus* (Rchb.) Palla, eight species of *Schoenoplectiella* Lye including one hybrid, five species of *Scirpus* L. s.str., and two species of *Trichophorum* Pers. (Jung and Choi 2010, 2011). The morphological investigation presented various character states from organs, such as, the underground part, culm, leaf, inflorescence, and floral components (Jung and Choi 2011).

A character change in *Scirpus* s.l. was hypothesized due to reductions in the leaf blade and inflorescence (Koyama 1958). As morphological and molecular phylogenetic analyses of *Scirpus* s.l. lead to disparate classifications, it is necessary to test this hypothesis (Muasya et al. 2009; Jung and Choi 2010).

In this study, the morphological characteristics and quantitative variation are presented from 21 species of Korean *Scirpus* s.l. To reveal the pattern of phenotypic evolution among *Scirpus* s.l., morphological character states are compared with their molecular phylogeny based on a nuclear ribosomal internal transcribed spacer (ITS), chloroplast *rbcL* gene, and chloroplast *trnL-F* region.

Materials and Methods

Plant Materials

This study includes 21 taxa of five genera reported in the previous morphological study of Korean *Scirpus* s.l. (Jung and Choi 2011; Table 1). *Fimbristylis squarrosa* Vahl and *Eleocharis congesta* D. Don were selected as sister groups of *Bolboschoenus* and *Schoenoplectus*, respectively, and *Cladium chinense* Nees was used as an outgroup based on the previous molecular phylogenetic study of Cyperaceae (Muasya et al. 1998, 2009). Four hundred eight specimens were investigated for morphological analyses and were deposited in the herbarium of Ajou University (AJOU). Additionally, specimens of the Sungshin Women's University herbarium (SWU) were used. Plant tissues for molecular analyses were sampled from 24 individuals that represented typical features of each taxon. Information of voucher specimens was shown in Appendix 1.

Table 1 List of taxa for morphological diagnosis and molecular analysis

Taxon	Abbreviation
Scirpus L. s.l. (ingroup)	
Bolboschoenus (Asch.) Palla	
B. fluviatilis (Torr.) Soják (24)	BOFL
B. planiculmis (F. Schmidt) T.V. Egorova (22)	BOPL
B. maritimus (L.) Palla (6)	BOMA
Schoenoplectus (Rchb.) Palla	
S. nipponicus (Makino) Soják (10)	SUNI
S. tabernaemontani (C.C. Gmel.) Palla (20)	SUTA
S. triqueter (L.) Palla (20)	SUTR
Schoenoplectiella Lye	
S. mucronata (L.) J. Jung & H.-K. Choi (17)	SAMU
S. triangulata (Roxb.) J. Jung & H.-K. Choi (20)	SATR
S. hotarui (Ohwi) J. Jung & H.-K. Choi (20)	SAHO
S. juncoides (Roxb.) Lye (30)	SAJU
S. wallichii (Nees) Lye (20)	SAWA
S. lineolata (Franch. & Sav.) J. Jung & H.-K. Choi (22)	SALI
S. komarovii (Roshev.) J. Jung & H.-K. Choi (1)	SAKO
S. x *trapezoidea* (Koidz.) J. Jung & H.-K. Choi (8)	SATZ
Scirpus L. s.str.	
S. wichurai Boeck. (20)	SCWI
S. karuisawensis Makino (20)	SCKA
S. mitsukurianus Makino (20)	SCMI
S. sylvaticus L. var. *maximowiczii* Regel (20)	SCSY
S. radicans Schkuhr (20)	SCRA
Trichophorum Pers.	
T. dioicum J. Jung & H.-K. Choi (20)	TRDI
T. alpinum Pers. (12)	TRAL
Eleocharis R. Br. (sister group)	
E. congesta D. Don (20)	ELCO
Fimbristylis Vahl (sister group)	
F. squarrosa Vahl (8)	FISQ
Cladium P. Browne (outgroup)	
C. chinense Nees (8)	CLCH

Number in parentheses indicates number of inspected specimens. Detailed information of vouchers was described in Appendix 1

Morphological Analysis

Based on the specimens, 71 morphological characters were examined. The character set consisted of 42 quantitative and 29 qualitative characters (Table 2). Twenty-three and 48 characters were selected from vegetative and reproductive organs, respectively (Table 2). The examined characters included the size and features of

Table 2 List of morphological characters and codes of character states for reconstruction of character change

Quantitative characters

Vegetative

1. Plant, height (cm): >80 (0), 30–80 (1), <30(2)
2. Root, diameter (mm): >1.5 (0), <1.5 (1)
3. Stolon, diameter (mm): >6 (0), absent (1), 1.5–6 (2), <1.5(3)
4. Stolon, interval between culms (mm): absent (0), <23 (1), >23 (2)
5. Tuber, length (mm): absent (0), <11 (1), >11 (2)
6. Tuber, width (mm): absent (0), <5.5 (1), >5.5 (2)
7. Culm, height (cm): >56 (0), 25–56 (1), <25 (2)
8. Culm, diameter (mm): >4 (0), 2.3–4 (1), 0.6–2.3 (2), <0.6 (3)
9. Culm internode, length (cm): >1 (0), condensed (1)
10. Leaf blade, length (cm): >51 (0), 18–51 (1), 1.2–18 (2), <1.2 (3)
11. Leaf blade, width (mm): >5.3 (0), 1–5.3 (1), <1 (2)
12. Leaf sheath, length (cm): 5–11 (0), >11 (1), <5 (2)
13. Ratio, culm internode/leaf sheath, in length: 1–2.5 (0), 0.1–1 (1), >2.5 (2), 0 (3)

Reproductive

1. Inflorescence, length (mm): 9.5–81 (0), <9.5 (1), >81 (2)
2. Inflorescence, width (mm): 6.5–60 (0), <6.5 (1), >60 (2)
3. Spikelets number/culm (no.): >100 (0), 2–20 (1), 21–100 (2), 1 (3)
4. Primary bract, length (mm): >112 (0), <112 (1), scale-like bract (2)
5. Primary bract, width (mm): >2.3 (0), 0.8–2.3 (1), <0.8 (2), scale-like bract (3)
6. Branch in inflorescence, length (mm): 16–50 (0), >50 (1), <16 (2), absent (3)
7. Branch in inflorescence, diameter (mm): >0.8 (0), <0.8 (1), absent (2)
8. Spikelet, length (mm): <6 (0), 6–11 (1), >11 (2)
9. Spikelet, width (mm): <3.5 (0), >3.5 (1)
10. Spikelet, ratio of length/width: 1.8–2.7 (0), <1.8 (1), >2.7 (2)
11. Floral scale, length (mm): 2–6 (0), <2 (1), >6 (2)
12. Floral scale, width (mm): 1.65–2.85 (0), <1.65 (1), >2.85 (2)
13. Floral scale, ratio of length/width: 1.7–2.5 (0), <1.7 (1), >2.5 (2)
14. Floral scale, awn length (mm): absent (0), <0.75 (1), >0.75 (2)
15. Perianth bristle, length (mm): <1.86 (0), 1.86–3.5 (1), 3.5–8.8 (2), >8.8 (3)
16. Stamen, length (mm): 2.5–4.7 (0), <2.5 (1), >4.7 (2)
17. Stamen, width (mm): >0.2 (0), <0.2 (1)
18. Anther, length (mm): 1.33–3.8 (0), 0.63–1.33 (1), <0.63 (2), >3.8 (3)
19. Anther, width (mm): <0.36 (0), >0.36 (1)
20. Style, length (mm): 1.1–2.3 (0), >2.3 (1), <1.1 (2)
21. Style, width (mm): >0.15 (0), <0.15 (1)
22. Stigma, length (mm): 2–4 (0), <2 (1), >4 (2)
23. Ratio of style/stigma, in length: 0.8–2 (0), <0.8 (1), >2 (2)
24. Achene, length (including beak, mm): >3.0 (0), 1.7–3.0 (1), <1.7 (2)
25. Achene, width (mm): 1–2.2 (0), <1 (1), >2.2 (2)
26. Achene, ratio of length/width: <1.7 (0), 1.7–2.15 (1), >2.15 (2)
27. Beak of achene, length (mm): >0.27 (0), <0.27 (1)
28. Beak of achene, width (mm): >0.3 (0), 0.145–0.3 (1), <0.145 (2)
29. Beak of achene, ratio of length/width: <2.5 (0), >2.5 (1)

Table 2 (continued)

Quantitative characters

Qualitative characters

Vegetative

1. Shoot, specialized type or habit: long rhizome (0), stolon with tuber (1), short rhizome (2), none and tuft (3)
2. Shoot, propagate type: absent (0), tuber (1), runner (2)
3. Culm, cross sectional outline (near base): circle (0), regular triangle with round apex (1), regular triangle with sharp apex (2), tetragonal, polygonal, or irregular shape (3)
4. Culm, cross sectional outline (middle): circle (0), regular triangle with round apex (1), regular triangle with sharp apex (2), irregular triangle with sharp apex (3), tetragonal, polygonal, or irregular shape (4)
5. Culm, node presence: present (0), condensed at base (1)
6. Culm, surface: rugose (0), smooth (1)
7. Leaf blade, degree of development: well developed (0), reduced (1), mucronate (2)
8. Leaf sheath, shape of membranous region: V type (0), Y type (1), concave-convex (2)
9. Leaf ligule, presence: absent (0), present (1)
10. Leaf ligule, shape: absent (0), acute (1), round-retuse (2), obcordate-V shape(3)

Reproductive

1. Inflorescence, position: terminal and lateral (0), terminal (1), pseudo-lateral (2)
2. Inflorescence, arrangement of spikelets: corymbose and branched (0), fascicled and sessile (1), solitary (2)
3. Bract, primary bract type: leaf-like and spreading (0), culm like (1), scale like (2)
4. Bract, number (only leafy or culm like): two or more (0), one (1), absent (2)
5. Branch in inflorescence, presence: present (0), absent (1)
6. Branch in inflorescence, cross sectional outline: pressed terete (0), half terete (1), polygonal (2), trigonous (3), absent (4)
7. Spikelet, shape: ovate (0), ovate-elliptic (1), elliptic (2), obovate (3)
8. Floral scale, shape: ovate (0), ovate-elliptic (1), elliptic (2), elliptic-obovate, (3), obovate (4)
9. Floral scale, shape of apex: acute (0), apiculate (1), aristate (2), cleft and aristate (3), rounded (4), retuse and mucro (5)
10. Floral scale, presence of projection: absent (0), present (1), rudimentary (2)
11. Floral scale, number of veins: one (0), three (1), absent or not distinct (2)
12. Perianth bristle, number: absent (0), 1–5 (1), 6 (2)
13. Perianth bristle, type: absent (0), curly and smooth (1), straight and barbed (2), strap shaped (3)
14. Stamen, number: two (0), three (1), one (2)
15. Style, shape at base: slightly thickened (0), straight (1), enlarged (2)
16. Stigma, number: 2-fid (0), 3-fid with incomplete one (1), equally 3-fid (2), 4-fid (3)
17. Achene, shape: ovate (0), elliptic (1), elliptic-obovate (2), obovate (3)
18. Achene, cross sectional outline: circle (0), trigonous (1), appressed trigonous (2), bi-convex or plano-convex (3), concave-convex (4), bi-concave (5)
19. Achene, surface: wrinkled (0), smooth (1), rough (2), reticulate (3)

the underground parts, blade and sheath of leaf, bract in inflorescence, spikelet, floral parts, and achene. The morphologies of these organs have been considered as useful identification characteristics of *Scirpus* s.l. taxa (Ohwi 1944; Koyama 1958; Jung and Choi 2011).

Large scale characters (>1 cm) were measured by a ruler (precision=1 mm) or an electronic vernier caliper (precision=0.05 mm; IP66, Mitutoyo) with an input device (IT-012U, Mitutoyo). Characters in small scale (<1 cm) were investigated with magnification (10–40 x) on a stereo microscope (SZ-40, Olympus). Measurement of the small characters were done with images captured by a CCD-camera (Moticam-2300, Motic), using UTHSCSA *ImageTool* ver. 3.0 (University of Texas Health Science Center at San Antonio 2002). Fragile organs (e.g., floral parts) from the dried specimens were observed after rehydration in 0.1 N NaOH for 1 hour, at 60°C (Shobe and Lersten 1967).

DNA Extraction, PCR Amplification, and Sequencing

Total genomic DNA was isolated using the modified CTAB method from fresh tissues or dried specimens (Chen and Ronald 1999).

The nuclear ITS region was amplified using the primers P1 and P4 (White et al. 1990; Table 3). DNA amplifications and sequencing were performed with primers 1F and 1400R for the chloroplast *rbcL* gene and primers c and f for the *trnL-F* region (Taberlet et al. 1991; Muasya et al. 1998; Jung and Choi 2010; Table 3). For sequencing, internal primers used were 636F and 778R for the *rbcL* gene and 647F and 696R for the *trnL-F* region (Muasya et al. 1998; Jung and Choi 2010; Table 3). The PCR amplifications were performed in 20 µl volumes, each containing 100 ng of template DNA, 1 unit of *Taq* DNA polymerase (Solgent), 0.5 µM of each primer, 1 x *Taq* buffer with 1.5 mM $MgCl_2$, and 0.25 mM of each dNTP. Polymerase chain reaction (PCR) thermal cycling conditions (PTC-200, MJ Research) for amplification of ITS were as follows: a 2 min initial denaturation step at 95°C; 30 cycles of 30 s denaturation at 94°C, 30 s annealing at 55°C, and 1 min extension at 72°C; and a final 8 min extension at 72°C. Amplifications of the chloroplast *rbcL* gene and *trnL-F* region were performed using same conditions as the nuclear ITS region but with a longer extension time of 2 min.

Amplified products were purified using Gel & PCR Purification System (Solgent). Purified products were cycle-sequenced using 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 submitted in GenBank (Appendix 1).

Sequence Alignment and Phylogenetic Analysis

Obtained sequence data were assembled and were edited using BioEdit (Hall 1999). Previously published 18 nuclear ITS and 19 chloroplast *rbc*L sequences were included in the analysis (Jung and Choi 2010; Appendix 1). The sequences were aligned using ClustalX (Thompson et al. 1997) and checked manually to minimize software artifacts. Gaps were removed from alignment and added as binary characters according to the simple gap coding method (Simmons and Ochoterena 2000).

Phylogenetic analyses of morphological data and three sequences (ITS, *rbc*L, and *trnL-F*) were performed using maximum parsimony and Bayesian inference. Parsimony analyses were done with PAUP* 4.0b10 (Swofford 2002) using the heuristic search option, simple addition sequence replicates, tree-bisection-reconnection (TBR) branch swapping, ACCTRAN optimization, and MULTrees in effect. Tree lengths and tree statistics (consistency index, CI and retention index, RI) were

Table 3 List of primer sets used in amplification and DNA sequencing for nuclear ITS, chloroplast *rbcL*, and *trnL-F*

Target region/Direction		Primer	Sequence (5′→3′)	Reference
ITS	Forward	P1	GGA AGT AAA AGT CGT AAC AAG G	White et al. 1990
	Reverse	P4	TCC TCC GCT TAT TGA TAT GC	White et al. 1990
rbcL	Forward	1F	TAA AGC AAG TGT TGG GTT TAA AG	Muasya et al. 1998
	Internal forward	636F	GCG TTG GAG AGA TCG TTT CT	Muasya et al. 1998
	Internal reverse	778R	TAT GAT AGG AAC TCC CAA TTC T	Jung and Choi 2010
	Reverse	1400R	ATC TAG TTT ATC TAC CGG ATC GA	Jung and Choi 2010
trnL-F	Forward	c	CGA AAT CGG TAG ACG CTA CG	Taberlet et al. 1991
	Reverse	f	ATT TGA ACT GGT GAC ACG AG	Taberlet et al. 1991
	Internal forward	647F	TGA AAT TTA TAGT AAG AGG AAA ATC	This study
	Internal reverse	696R	ACC CTC ATG ATT TAA AAA ATC G	This study

calculated using PAUP* 4.0b10 (Swofford 2002). To assess branch support for the data, maximum parsimony bootstrap analyses (BS) were performed using PAUP* heuristic search using 1,000 replications with the same parameter conditions.

Substitution models for the Bayesian inference were selected using MrModeltest 2.3 (Nylander 2004) under the Akaike Information Criterion (Posada and Buckley 2004). The selected optimal models were GTR+I+Γ for ITS, HKY+I+Γ for *rbcL*, and HKY+Γ for *trnL-F*. Standard model was used for gap coding data. Bayesian inference was conducted using MrBayes v3.1 (Ronquist and Huelsenbeck 2003) with 1×10^6 generations. Trees were sampled every 100 generations and 25% of sampled trees were removed by burn-in process. Remaining trees were used in construction of a 50% majority rule consensus tree and calculation of posterior probability (PP).

For analysis of combined datasets, an incongruence length difference (ILD) test (Farris et al. 1994) was performed using PAUP* 4.0b10 (Swofford 2002). Phylogenetic analysis of the combined four data (morphology+ ITS+*rbcL*+*trnL-F*) was not performed because the *p* value in an ILD test was 0.001. The combined three molecular data (ITS+*rbcL*+*trnL-F*) was congruent (*p* value=0.443).

Reconstruction of Character State

Ancestral character states were reconstructed using the maximum parsimony method included in Mesquite 2.0 (Maddison and Maddison 2009), with topology of a 50% majority rule consensus tree (ITS+*rbcL*+*trnL-F*) by Bayesian inference. The tree constructed by Bayesian inference had higher resolution than the tree by the maximum parsimony method. The used character state matrix is presented in Appendix 2.

Results

Morphological Characteristics of Korean *Scirpus* s.l.

Results of morphological analyses, with 71 characters from 21 species, are presented in Appendix 2 and Supplementary Table 1. These include characters useful in identifying species or in generic circumscription, such as, the type of underground part, cross section of culm, width and development degree of leaf blade, presence of ligule, type of primary bract and branch of inflorescence, size and number of floral parts, and cross section of achene.

Height of Plant Plants from *Bolboschoenus, Schoenoplectus,* and *Scirpus* s.str. are larger (74–153 cm) than those from *Schoenoplectiella* (16–98 cm). *Trichophorum dioicum* J.Jung & H.-K.Choi (11 cm) and *Trichophorum alpinum* (L.) Pers. (29 cm) are relatively small.

Underground Parts A long stolon appears in *Bolboschoenus, Schoenoplectus, Schoenoplectiella lineolata* (Franch. & Sav.) J. Jung & H.-K. Choi, *Scirpus radicans* Schkuhr, and *Scirpus sylvaticus* L. var. *maximowiczii* Regel. Other species have a short rhizome or tuft. *Bolboschoenus* bears a globular or ovoid tuber, while tubers of *Schoenoplectus nipponicus* (Makino) Soják and *S. lineolata* are irregularly shaped. No tuber is formed in two species of *Scirpus* s.str. (*S. radicans* and *S. sylvaticus* var. *maximowiczii*).

Culm and Leaves A cross section of the culm can be circular, triangular, and polygonal shape, which characterizes a species. The presence or absence of a node on the culm is correlated with leaf blade development and congruent with generic circumscription (except for *S. nipponicus*). *Bolboschoenus* and *Scirpus* s.str. have well-developed leaf blades and culm nodes. The width of the leaf blade is distinctive within *Bolboschoenus* (Fig. 1a) or three species of *Scirpus* s.str. (*Scirpus wichurai* Boeck., *Scirpus karuisawensis* Makino, and *Scirpus mitsukurianus* Makino; Fig. 1b). Nodes of three genera (*Schoenoplectus, Trichophorum,* and *Schoenoplectiella*) are condensed at the base of the culm, and their leaf blades are short or rudimentary (i.e., mucronate sheath). *Schoenoplectus* and *Trichophorum* have short leaf blades, but the leaf blade of *S. nipponicus* elongates to culm length. Leaves of *Schoenoplectiella* are bladeless.

Leaf Ligule The leaf of *Bolboschoenus* is eligulate but ligules are present in the other four genera.

Leaf Sheath Leaf sheaths are distinguished by the shape of the sheath apex: (1) a concave-convex type with a narrow membranous region, (2) a V-shaped type with an obtriangular membranous region, and (3) a Y type with a membranous region elongated to the base of the sheath. The concave-convex type was observed in *S. wichurai* and a part of *Bolboschoenus fluviatilis* (Torr.) Soják individuals. V type shown in *Scirpus* s.str (except *S. wichurai*), *Bolboschoenus,* two species of *Schoenoplectiella* (*Schoenoplectiella triangulata* (Roxb.) J. Jung & H.-K. Choi, *Schoenoplectiella mucronata* (L.) J. Jung & H.-K. Choi), and *Schoenoplectus triqueter* (L.) Palla. In the rest of the species examined, the Y type was observed and the sheath of *S. lineolata* is wholly membranous.

Internode/Leaf Sheath Length Ratio In *Bolboschoenus,* the internodes of *Bolboschoenus maritimus* are shorter than leaf sheath (ratio=0.32±0.11; Fig. 1a). *Bolboschoenus*

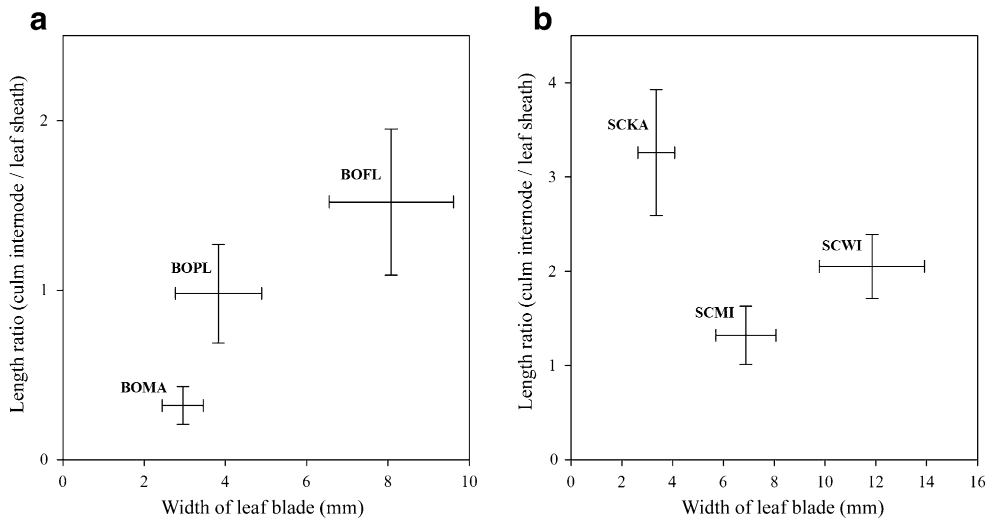

Fig. 1 Examples of discriminated morphological characters in *Scirpus* s.l. Variations in width of leaf blade and culm internode/leaf sheath length ratio do not overlap within *Bolboschoenus* (**a**) and three species of *Scirpus* s.str. (**b**). Abbreviations of taxa correspond to Table 1. *Ends of line* indicate standard deviations

planiculmis (0.98±0.29) has internodes as long as leaf sheath while long internodes were observed in *B. fluviatilis* (1.52±0.43; Fig. 1a). The internodes of *Scirpus* s.str. are longer than leaf sheath and the ratio is distinctive among three species: *S. wichurai,* 2.05±0.34; *S. karuisawensis,* 3.26±0.67; and *S. mitsukurianus,* 1.32±0.31 (Fig. 1b).

Inflorescence Five types of inflorescence were defined by their component characteristics, including: position; number, size, and arrangement of spikelets; presence of a branch; and type of primary bract (Fig. 2). Each inflorescence type corresponded to five genera. Type I (*Schoenoplectus*) is pseudolateral and branched inflorescence, with a culm-like primary bract and several to 100 middle (6–11 mm) spikelets. Type II (*Schoenoplectiella*) is similar to type I but unbranched (i.e., sessile spikelet), with fewer spikelets. Type III (*Scirpus* s.str.) has a leafy primary bract with numerous small (<6 mm) spikelets and terminal or lateral corymbs. Type IV (*Trichophorum*) has a scale-like bract and terminal single spikelet. Type V (*Bolboschoenus*) possesses a leafy primary bract and large (>11 mm) spikelets. Additionally, this type has variations in the number of spikelets from one to several tens, and the presence of branches is varied as individuals in *B. planiculmis* (F. Schmidt) T.V. Egorova.

Floral Scales Floral scale length was categorized as short (<2 mm), middle (2–6 mm), and long (>6 mm). Short scales were observed in three species of *Scirpus* s. str. (*S. wichurai, S. radicans,* and *S. sylvaticus* var. *maximowiczii*) while *Bolboschoenus* has long scales. Middle size scales were observed in the other species examined.

Perianth Bristles Perianth bristles were separated into three types: (1) straight and barbed in *Bolboschoenus, Schoenoplectus, Schoenoplectiella,* and *S. sylvaticus* var. *maximowiczii*; (2) curly and smooth in four species of *Scirpus* s.str. (*S. wichurai, S. karuisawensis, S. mitsukurianus,* and *S. radicans*), and *T. dioicum*; and (3) strap shaped in *T. alpinum*.

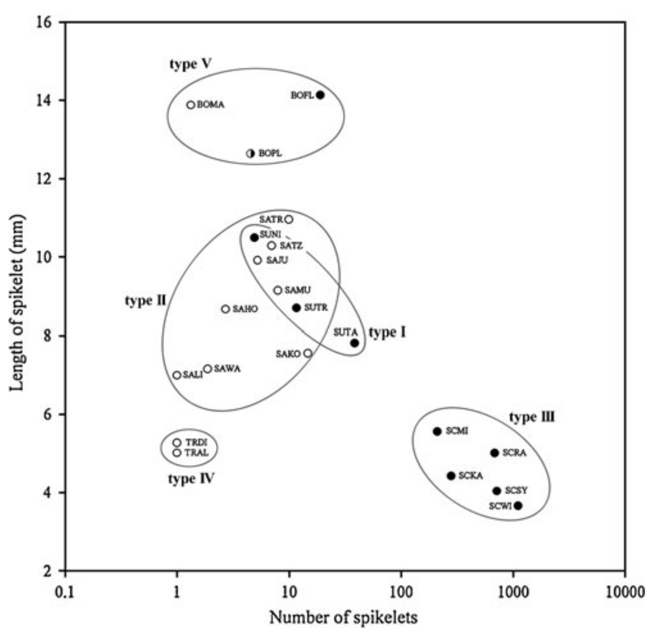

Fig. 2 Five types of inflorescence in *Scirpus* s.l. The five types were distinguished by several characters, such as, number of spikelets, length of spikelet, and presence of branch (Jung and Choi 2010). *Closed and open circles* indicate branched and unbranched inflorescence, respectively. *B. planiculmis* (*BOPL*) has both types. Abbreviations of species correspond to Table 1

Androecium Two stamens are present in three species of *Scirpus* s.str. (*S. wichurai, S. karuisawensis,* and *S. mitsukurianus*) and *S. nipponicus*. Other species have three stamens. The anther of *Bolboschoenus* is long (>3.8 mm) and *Schoenoplectus* and *Scirpus* s.str. have middle (1.33–3.8 mm) and short (0.63–1.33 mm) anthers, respectively. In *Schoenoplectiella* and *Trichophorum*, the length of anther varied in each species. For example, in *Schoenoplectiella*, the anther of *Schoenoplectiella komarovii* (0.47–0.53 mm) is much shorter than other species and a distinct difference was observed between two similar species, *S. mucronata* (0.6–1 mm) and *S. triangulata* (1.6–2.7 mm).

Achene Cross sections of achene were defined as either trigonous or lenticular and then were subdivided by face shape. In *Bolboschoenus*, the achene of *B. fluviatilis* is regular trigonous and its three faces are concave while the achene of *B. maritimus* (L.) Palla is appressed trigonous with plano-convex faces. The achene of *B. planiculmis* is lenticular and bi-concave. The length of achene including the beak is long (>3 mm) in *Bolboschoenus*; intermediate length (1.7–3 mm) in *Schoenoplectus*, *Schoenoplectiella* (except *S. komarovii* (Roshev.) J. Jung & H.-K. Choi), and *T. dioicum*; and small (<1.7 mm) in *Scirpus* s.str., *Schoenoplectiella komarovii,* and *T. alpinum*. The achene surface of *Schoenoplectiella* is more wrinkled or rough compared with the smooth surface of other genera.

Phylogenetic Analysis of Korean *Scirpus* s.l.

Each dataset (morphology, ITS, rbcL, and trnL-F) All 71 morphological characters were variable, and 70 characters were parsimony informative (Table 4). The length of ITS sequences varied from 538 to 658 bp, and aligned sequences were 724 characters long (Table 4). All *rbcL* sequences were 1,293 bp in length, with no insertions or deletions and included 96 variable sites with 61 parsimony informative sites (Table 4). The length of *trnL-F* sequences ranged from 784 to 1,050 bp, and aligned sequences were 1,170 characters long (Table 4). After gap coding, the ITS and *trnL-F* matrix comprised 339 variable sites with 235 parsimony informative sites and 395 variable sites with 206 parsimony informative sites, respectively (Table 4).

The maximum parsimonious tree based on morphology differed from trees using three molecular data (ITS, *rbcL*, and *trnL-F*) in topology (the tree is not shown). In all trees using the three molecular data and the two methods (maximum parsimony, Bayesian inference), the species of five genera always formed five clades, although the position of *E. congesta* and *F. squarrosa* was not fixed (the trees are not shown).

Combined Data Set (ITS+rbcL+trnL-F) The combined dataset was 3,187 characters. The data matrix after gap coding included 830 variable sites with 502 parsimony informative sites (Table 4). A maximum parsimonious 136 tree with 1,277 steps were produced (CI=0.77; RI=0.88; the tree is not shown; Table 4). A strict consensus tree by maximum parsimony method was similar in topology to the majority rule consensus tree by Bayesian inference (Fig. 3).

Five clades corresponded to each genus, and all were strongly supported with PP=1.0 and BS=100 (Fig. 3). The examined species of *Scirpus* s.l. were divided into two major clades. One major clade included three genera (*Bolboschoenus, Schoenoplectus,* and *Schoenoplectiella*) and was supported with PP=1.00 and BS=71 (Fig. 3). *Schoenoplectus* was a sister genus of *Schoenoplectiella* (PP=1.00 and BS=80) within the major clade (Fig. 3). This clade formed a larger clade (PP=1.00 and BS=99) with *Eleocharis* R. Br. and *Fimbristylis* Vahl. Another

Table 4 Descriptive statistics for the datasets analyzed

Characteristic	Morphology	nrITS	*rbcL*	*trnL-F*	nrITS+*rbcL*+*trnL-F*
Number of total characters before alignment	71	538–658	1,293	784–1,050	2,765–3,035
Number of total characters after alignment	71	724	1,293	1,170	3,187
Variable characters after gap coding	71	339	96	395	830
Parsimony informative characters after gap coding	70	235	61	206	502
Length of maximum parsimonious tree	351	550	136	583	1,277
Number of most parsimonious trees	3	8	2	300	136
Consistency index	0.4615	0.7364	0.7426	0.8130	0.7674
Retention index	0.6601	0.872	0.8805	0.8994	0.8792
Selected model for Bayesian inference	Standard	GTR+Γ And standard model for gap coding data	HKY+I+Γ	HKY+Γ	As selected model of each dataset

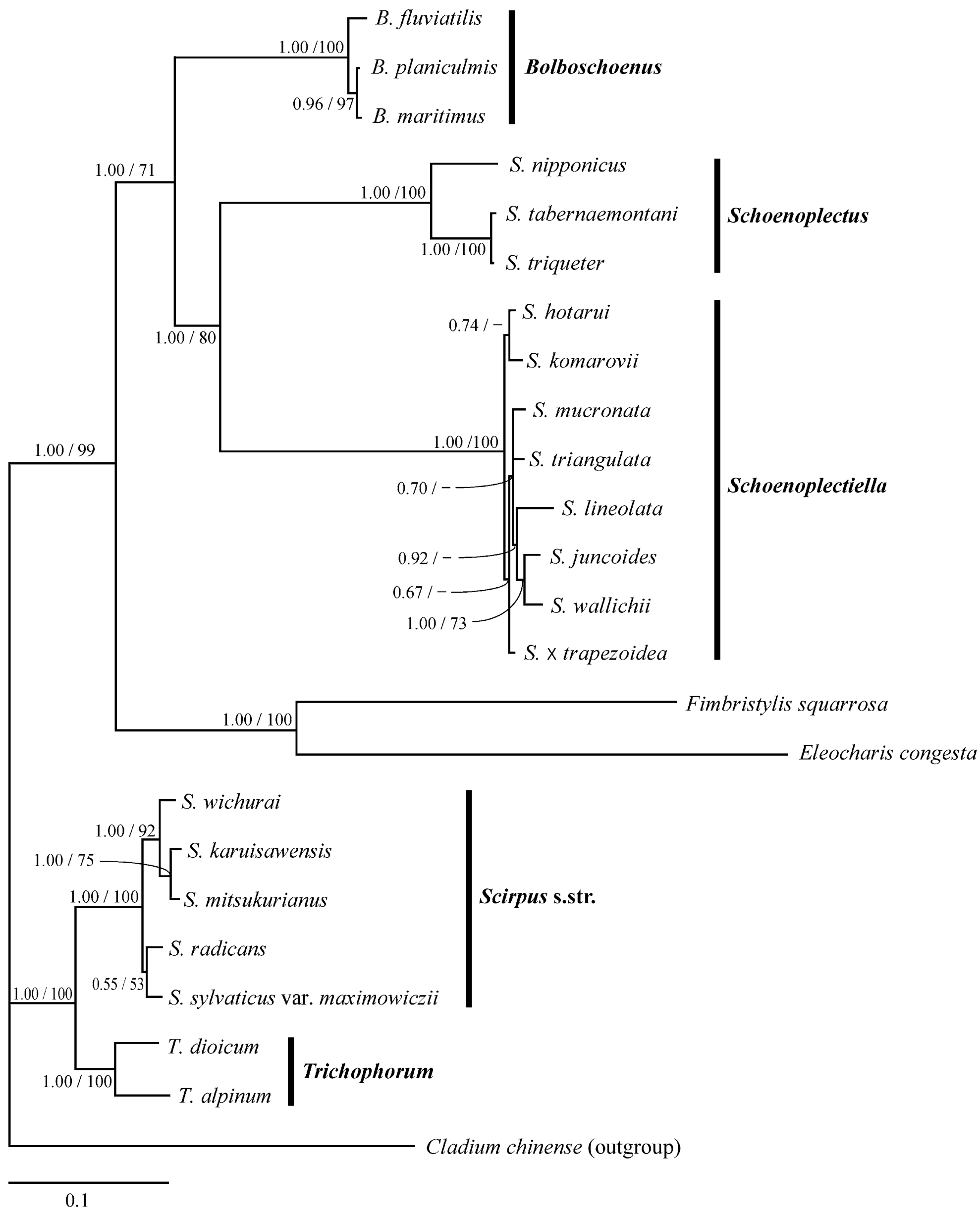

Fig. 3 Bayesian 50% majority rule consensus tree with mean branch lengths based on the combined dataset (nrITS+*rbcL*+*trnL-F*). Posterior probabilities (left, >0.5) in Bayesian inference and bootstrap values (right, >50) in maximum parsimony method are shown on each node respectively. *Scale bar* represents expected changes per site

major clade included two genera (*Scirpus* s.str. and *Trichophorum*) and was supported with BS=100 and PP=1.00 (Fig. 3).

In detail, *B. planiculmis* was a sister species of *B. maritimus* (PP=0.96 and BS=97) within the *Bolboschoenus* clade (Fig. 3). Within the *Schoenoplectus* clade, the relationship of *Schoenoplectus tabernaemontani* (C.C. Gmel.) Palla and *S. triqueter* (PP=1.00 and BS=100) was well supported, and any distinct relationship was not shown in the *Schoenoplectiella* clade, except between *Schoenoplectiella juncoides* and *Schoenoplectiella wallichii* (PP=1.00 and BS=73; Fig. 3). The *Scirpus* s.str. clade was subdivided into *S. karuisawensis*–*S. mitsukurianus*–*S. wichurai* (PP=1.00 and BS=92) and *S. radicans*–*S. sylvaticus* var. *maximowiczii* subclades (PP=0.55 and BS=53; Fig. 3).

Pattern of Morphological Changes

Changes of character state were reconstructed based on the 71 characters examined and phylogeny inferred from three molecular data (ITS+*rbcL*+*trnL-F*; Fig. 4a). Distinct changes of vegetative character state were in the node of culm and leaf blade (Fig. 4b, c). Although the changes

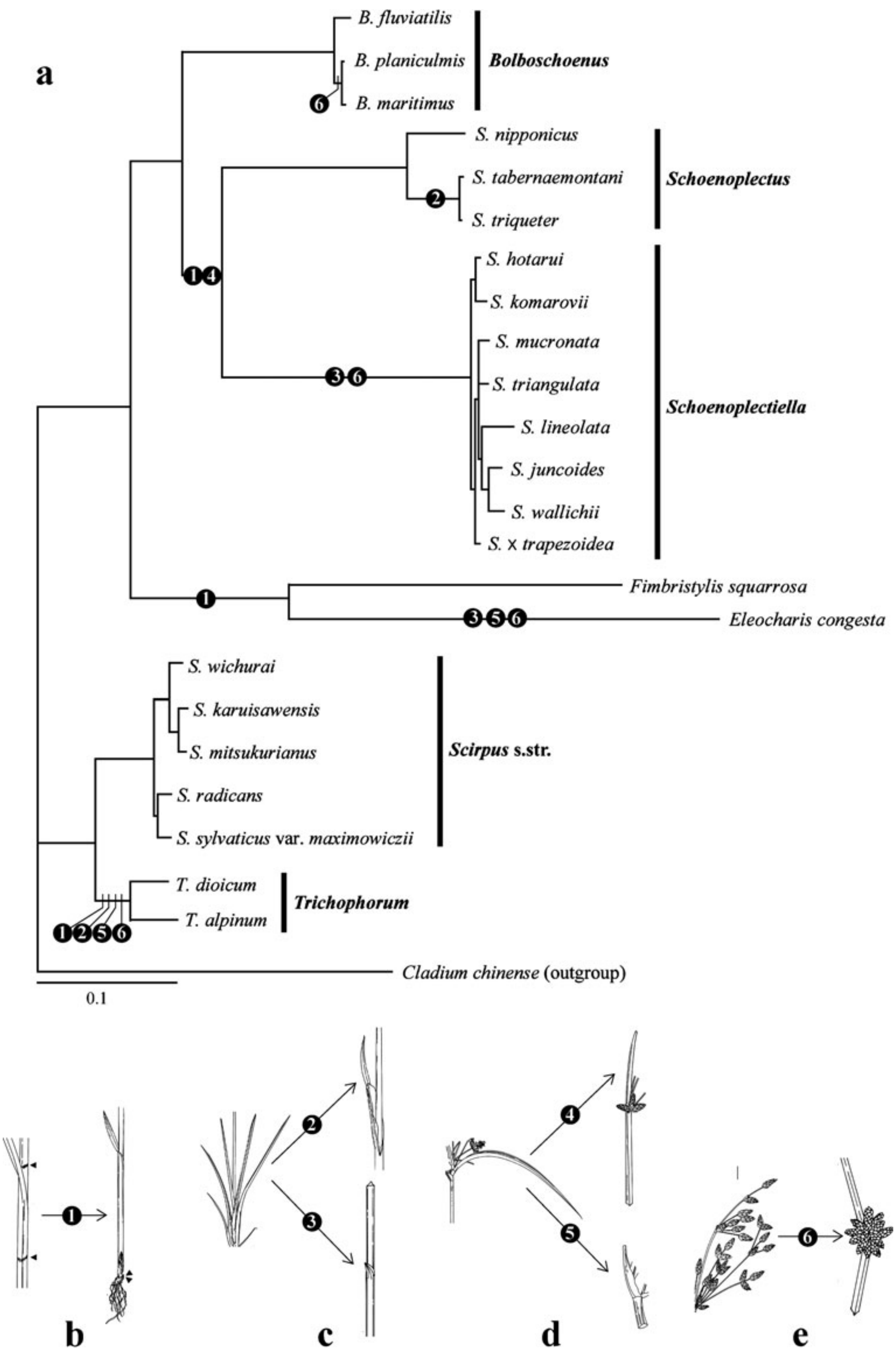

Fig. 4 Reconstruction of four character changes based on molecular phylogeny in *Scirpus* s.l. **a** Represented character changes on molecular phylogenetic tree based on the combined dataset (nrITS+ *rbcL*+*trnL-F*) by Bayesian inference. *Each number* corresponds to a character change in (**b**–**e**). **b** Node of culm (culm with nodes→condensed at base). **c** Development degree of leaf blade (well developed→reduced short/or rudimentary). **d** Type of primary bract in inflorescence (leafy→culm like/or scale like). **e** Presence of branch (branched→unbranched). Small figures used in (**b**–**e**) modified from previous morphological study (Jung and Choi 2011)

comprised multiple events, primitive states were interpreted as culm with node and well-developed leaf blade from culm with nodes to culm without nodes and from long leaf blade to short or rudimentary leaf blade (Fig. 4b, c). In the reproductive characters, the reduction of primary bract and disappearance of the branch in inflorescence are inferred; from leafy bract to culm-like or scale-like primary bract and from branched to unbranched inflorescence (Fig. 4d, e). *Scirpus* s.str. and *Bolboschoenus* have the primitive states in the four characters, but *B. maritimus* and part of *B. planiculmis* have partially derived states in branches of inflorescence (Fig. 4a). *Schoenoplectus* has the derived states of two characters (the node of culm and the primary bract) and partially derived states in the leaf blade (Fig. 4a). *Schoenoplectiella* and *Trichophorum* all have the derived states of the four characters (Fig. 4a).

Discussion

Key Characters of Korean *Scirpus* s.l.

In this study, the five genera of *Scirpus* s.l. were distinguished clearly by several key characters, such as stolon and tuber, nodes of culm, leaf blade, leaf ligule, and type of inflorescence. These characters have been used in circumscription of each genus (Smith 1995; Goetghebeur 1998; Jung and Choi 2010, 2011). In particular, five types of inflorescence were defined by their components (type of primary bract, branch, and size and number of spikelets) and corresponded to five genera, respectively (Fig. 2). Characteristics used to define *Scirpus* s.l., i.e., spirally arranged floral scales, not thickened style base, and sessile achene, are insufficient to define it as a genus because these features are scattered in Cyperaceae. For example, floral scales of many genera (e.g., *Mapania* Aublet, *Rhynchospora* Vahl, and *Fimbristylis*) of Cyperaceae are spirally arranged (Goetghebeur 1998).

The cross section of the culm or achene has been used to identify species within each genus, although such characters are not correlated with generic circumscription (Jung and Choi 2011). It was simple to distinguish *S. tabernaemontani* from *S. triqueter* or *T. alpinum* from *T. dioicum* by the cross section of culm. The cross section of achene was mentioned as a key character by which to identify several *Bolboschoenus* species, which is difficult due to morphological similarity (Browning et al. 1995; Hroudová et al. 2005). Identification was also available in *Schoenoplectiella* by specific cross-section shapes of the achene. In addition, the culm internode/leaf sheath length ratio was shown to be useful in drawing a distinction among species of *Bolboschoenus* or *Scirpus* s. str. in this study (Fig. 1).

Phylogenetic Relationships in Korean *Scirpus* s.l.

The five genera of *Scirpus* s.l. formed independent clades in this phylogenetic analysis (Fig. 3), and it was consistent with previous studies (Muasya et al. 2009; Jung and Choi 2010). The five *Scirpus* s.l. genera were divided into the two major clades (Fig. 3), and it corresponded to the classification of Cyperaceae by Goetghebeur (1986, 1998) rather than by Bruhl (1995). *Scirpus* s.l. along with numerous genera were classified into Scirpeae, a single tribe with broad range, by Bruhl (1995) while the five genera of *Scirpus* s.l. were included in two separated tribes, Furieneae (including *Bolboschoenus, Schoenoplectus,* and *Schoenoplectiella*) and Scirpeae (including *Scirpus* and *Trichophorum*) with narrow range in the classification by Goetghebeur (1986). The two groups in *Scirpus* s.l., Furieneae and Scirpeae, have a closer relationship with tribe Cariceae, including genus *Carex*, and tribe Cypereae, including genus *Cyperus*, respectively, than between themselves (Muasya et al. 2009).

However, intrageneric relationships within tribes Furieneae or Scirpeae including *Scirpus* s.l. were not clear in the molecular phylogentic study (Muasya et al. 2009) based on the two chloroplast sequences (*rbcL* and *trnL-F*). An extensive study to clarify phylogeny of tribes Furieneae and Scirpeae is needed.

Distinct relationships within *Schoenoplectiella* were not confirmed, although many substitutions exist in the sequences (e.g., 40 variable sites between *S. juncoides* (Roxb.) Lye and *S. lineolata* in the three molecular data). Phylogeny of *Schoenoplectiella* will be revealed by a more detailed approach. *Scirpus* s.str. was subdivided into two subclades (Fig. 3). One subclade (*S. wichurai–S. karuisawensis–S. mitsukurianus*) has no stolon and a well-developed basal leaf, while another subclade (*S. radicans–S. sylvaticus* var. *maximowiczii*) has a long stolon and a short basal leaf blade. The two subclades correspond to section *Trichophorum* (this is unrelated to genus *Trichophorum*) with no stolon and section *Scirpus* (=*Nemocharis*) with stolon (Beetle 1944; Koyama 1958).

Pattern of Morphological Evolutionary Changes: Reduction

Reduction was inferred as a major pattern of morphological character change in *Scirpus* s.l. although most character states were derived by multiple events (Fig. 4).

Cladium P. Browne*, Rhynchospora* Vahl, and *Scleria* P.J. Bergius were shown as an outgroup of *Scirpus* s.l. in the recent molecular phylogeny and have culm with nodes, well-developed leaf blades, and paniculate inflorescence with leafy bract (Goetghebeur 1998; Muasya et al. 2009). As the character state of the outgroup was adopted on primitive state, reduced features in *Scirpus* s.l. were considered as derived state. The pattern of reduction was expressed as condensation of nodes at base, reduction of leaf blade, reduction of primary bract, and simplification of inflorescence in *Scirpus* s.l. (Fig. 4). Reduction or simplification was observed in *Scirpus* s.l. and Cyperaceae (Koyama 1958, 1961). The short leaf blade of *Schoenoplectus* was considered as a more primitive type than the bladeless leaf of *Schoenoplectiella*, meaning leaf blade gradually reduced (Koyama 1958). However, this reduction of leaf blade was interpreted as direct changes from well-developed leaf to leaf with short blade or bladeless leaf (Fig. 4c). In the change of inflorescence type, three pathways from paniculate to single spikelet were suggested (Koyama 1958). It could not be a direct comparison because phylogeny of this hypothesis differed from phylogeny in this study. However, multiple pathways and pattern toward reduction was inferred (Fig. 4a, d, e). Paniculate inflorescence was observed in *Scirpus* s.str. and an outgroup in this study, while inflorescence with a single spikelet is shown in several species of four genera (*B. planiculmis, S. lineolata, T. dioicum*, *T. alpinum*, and *Eleocharis*; Appendix 2).

Reduction is well represented in *Schoenoplectus* and *Actinoscirpus* (Ohwi) R.W. Haines & Lye. *Actinoscirpus* is sister group of *Schoenoplectus* and *S. nipponicus* is basal group within this genus (Muasya et al. 2009; Jung and Choi 2010). *Actinoscirpus* has relatively complicated, large organs, such as a long stolon with tuber, well-developed leaf blade, and leafy primary bract compared with *S. nipponicus* with a culm-like primary bract (Ohwi 1944; Goetghebeur and Simpson 1991). Other species of *Schoenoplectus* (e.g., *S. triqueter*) have more reduced features, such as a tuberless stolon and short leaf blade.

This study showed the distinct characteristics of five genera of *Scirpus* s.l., and their species and the pattern of character change based on the phylogeny. A study with more extensive sampling is needed because the five genera and related genera (e.g., *Fuirena* Rottb., *Eleocharis*, *Eriophorum* L., and *Fimbristylis*) are scattered in the several tribes that were weakly supported by molecular phylogeny (Muasya et al. 2009).

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Appendix 1

Specimens used in investigation of morphological characters and molecular analysis. Acronym of herbarium is showed only at the specimens from herbarium of Sungshin Women's University (SWU). The rest specimens were deposited in herbarium of Ajou University (AJOU). Asterisks indicate materials for total genomic DNA extraction. GenBank accession numbers (nrITS/*rbcL*/*trnL-F*) are provided in parenthesis. Previous published sequences of nrITS and *rbcL* are marked in italic (Jung and Choi 2010).

Bolboschoenus fluviatilis KOREA. *Chungcheongbuk-do:* Jecheon-si, 7 May 2008, *J. Jung 805004*; 27 June 2008, *J.Jung 806053** (*GQ130340*/*GQ130358*/JF313190); Boryeong-si, 23 June 2005, *H.-K.Choi s.n.*; 15 June 2008, *J. Jung 806030*, *806035*; Taean-gun, 11 Aug. 2008, *J.Jung 808002*; *Gangwon-do:* Goseong-gun, 15 July 2008, *H.R.Na 80211*; 27 Aug. 2008, *J.Jung 808308*; 4 Sep. 2009, *J.Jung 909119*; Yanggu-gun, 25 June 2009, *J.Jung 906035*; Yangyang-gun, 26 May 2001, *H.-K.Choi s.n.*; *Gyeonggi-do:* Anseong-si, 19 May 2007, *H.-K.Choi s.n.*; Hwaseong-si, 9 July 2004, *H.-K.Choi s.n.*; 12 June 2008, *J.Jung 806027*; Suwon-si, 25 May 2003, *H.R.Na s.n.*; Yeoju-gun, 25 July 2007, *H.R.Na s.n.*; *Gyeongsangnam-do:* Changnyeong-gun, 25 July 2008, *H.R.Na 80300*; 23 July 2009, *H.R.Na 90087*; *Incheon:* Ganghwa-gun, 11 June 2008, *J.Jung 806002*, *806015*; *Jeollabuk-do:* Gimje-si, 28 June 2007, *H.R.Na s.n.*; Jeongeup-si, 27 June 2007, *H.R.Na s.n.*; *Jeollanam-do:* Boseong-gun, 29 May 2008, *H.R.Na 80038*.

Bolboschoenus planiculmis KOREA. *Chungcheongnam-do:* Asan-si, 3 June 2007, *H.R.Na s.n.*; Taean-gun, 26 June 2006, *H.-K.Choi s.n.*; *Gangwon-do:* Gangneung-si, 2 July 2007, *C.Kim s.n.*; Goseong-gun, 3 July 2007, *C.Kim s.n.*; 15 July 2008, *H.R.Na 80191*; Yangyang-gun, 1 July 2006, *H.-K. Choi s.n.*; *Gyeonggi-do:* Ansan-si, 12 June 2008, *J.Jung 806022*; Hwaseong-si, 12 June 2008, *J.Jung 806024*; Siheung-si, 10 July 2004, *H.-K.Choi s.n.*; *Gyeongsangbuk-do:* Gunwi-gun, 24 July 2008, *H.R.Na 80264*; *Gyeongsangnam-do:* Geoje-si, 29 June 2006, *H.-K.Choi s.n.*; Hadong-gun, 27 July 2008, *H.R.Na 807139*; 11 Aug. 2009, *C.Kim & J. Jung 908022, 908035*; *Incheon:* Ganghwa-gun, 11 June 2008, *J.Jung 806005** (*GQ130341*/*GQ130359*/JF313192), *806014*; Ongjin-gun, 12 June 2008, *J.Jung 806025*; *Jeju-do:* Bukjeju-gun, 9 July 2008, *J.Jung 807062*, *807063*; *Jeollanam-do:* Goheung-gun, 29 May 2008, *H.R.Na 80022*; Haenam-gun, 27 June 2006, *H.-K.Choi s.n.*; 28

June 2006, *H.-K.Choi s.n.*; Yeongam-gun, 21 Aug. 2008, *J.Jung 808032*.

Bolboschoenus maritimus KOREA. *Gyeonggi-do:* Paju-si, 26 June 2002, *C.Kim s.n.*; *Incheon:* Ganghwa-gun, 11 June 2008, *J.Jung 806004, 806008** (JF313179/JF313185/JF313191); *Seoul:* Hangang, 30 Oct. 1983, *Y.N.Lee s.n.* (SWU).

Schoenoplectus nipponicus KOREA. *Gangwon-do:* Goseong-gun, 16 Aug. 1996, *S.H.Park s.n.* (SWU); 27 Aug. 2008, *J.Jung 808332** (JF313183/*GQ130364*/JF313209); 5 Sep. 2009, *J.Jung 909127*; Hwacheon-gun, 25 June 2009, *J.Jung 906024*; *Jeju-do:* Bukjeju-gun, 20 Aug. 2007, *Y.R.Lee s.n.*

Schoenoplectus tabernaemontani KOREA. *Chungcheongnam-do:* Taean-gun, 5 June 2008, *H.-K.Choi 806001*; 11 Aug. 2008, *J.Jung 808003, 808005*; *Gangwon-do:* Goseong-gun, 15 July 2008, *H.R.Na 80190, 80206*; Yangyang-gun, 14 July 2008, *H.R.Na 80180*; *Gyeonggi-do:* Yeoju-gun, 26 Apr. 2003, *C.M.Ahn s.n.*; *Gyeongsangbuk-do:* Mungyeong-si, 23 July 2008, *H.R.Na 80245*; *Gyeongsangnam-do:* Haman-gun, 25 July 2008, *H.R.Na 80304*; 9 Oct. 2008, *J.Jung 810011*; *Incheon:* Ganghwa-gun, 11 June 2008, *J. Jung 806013, 806016** (*GQ130349*/*GQ130365*/JF313210); Ongjin-gun, 12 June 2008, *J.Jung 806026*; *Jeju-do:* Bukjeju-gun, 8 July 2008, *J.Jung 807088*; 9 July 2008, *J. Jung 807073, 807079*; *Jeollabuk-do:* Gimje-si, 23 Sep. 2009, *J.Jung 909174*; Gochang-gun, 23 Sep. 2009, *J. Jung & C.Kim 909161, 909171*; Gunsan-si, 21 July 2009, *H.R.Na 90044*; *Ulsan:* Ulju-gun, 29 Aug. 2008, *J.Jung 808337*.

Schoenoplectus triqueter KOREA. *Gangwon-do:* Goseong-gun, 17 Aug. 2001, *C.Kim s.n.*; 27 Aug. 2008, *J.Jung 808316, 808328*; 4 Sep. 2009, *J.Jung* et al. *909113*; Hwacheon-gun, 26 Aug. 2008, *J.Jung 808303*; 6 Sep. 2007, *Y.R.Lee s.n.*; *Gyeongsangbuk-do:* Gunwi-gun, 24 July 2008, *H.R.Na 80265*; Mungyeong-si, 14 Oct. 2004, *H.-K.Choi s.n.*; Uiseong-gun, 24 July 2009, *H.R.Na 90139, 90148*; Yecheon-gun, 24 July 2008, *H.R.Na 80258** (*GQ130351*/*GQ130367*/JF313211); Yeongcheon-si, 16 Sep. 2004, *H.-K.Choi s.n.*; *Gyeongsangnam-do:* Changnyeong-gun, 29 Aug. 2008, *J.Jung 808334*; Hadong-gun, 11 Aug. 2009, *J.Jung 908036*; Miryang-si, 21 Oct. 2004, *H.-K.Choi s.n.*; *Incheon:* Ongjin-gun, 4 Sep. 2008, *J.Jung 809001*; *Jeollabuk-do:* Gochang-gun, 23 Sep. 2009, *J.Jung, C.Kim 909165*; *Ulsan:* Ulju-gun, 29 Aug. 2008, *J.Jung 808338*.

Schoenoplectiella mucronata KOREA. *Gyeongsangnam-do:* Hadong-gun, 11 Aug. 2009, *J.Jung 908034*; *Incheon:* Ganghwa-gun, 4 Sep. 2008, *J.Jung 809002** (*GQ130348*/*GQ130363*/JF313200); 11 July 2007, *H.R.Na s.n.*; *Jeollanam-do:* Gangjin-gun, 22 Aug. 2008, *J.Jung 808035*; Yeongam-gun, 21 Aug. 2008, *J.Jung 808027*, *808028*, *808029*; Yeosu-si, 12 Aug. 2009, *J.Jung 908052*.

Schoenoplectiella triangulata KOREA. *Chungcheongnam-do:* Boryeong-si, 15 June 2008, *J.Jung 806034** (*GQ130350*/*GQ130366*/JF313201); Taean-gun, 11 Aug. 2008, *J.Jung 808001*; *Gangwon-do:* Goseong-gun, 27 Aug. 2008, *J. Jung 808327*; 4 Sep. 2009, *J.Jung* et al. *909114*; 5 Sep. 2009, *J.Jung* et al.*909128*; Hwacheon-gun, 26 Aug. 2008, *J. Jung 808302*; *Gyeongsangbuk-do:* Gunwi-gun, 24 July 2009, *H.R.Na 90135*; Seongju-gun, 23 July 2009, *H.R.Na 90112*; *Gyeongsangnam-do:* Hadong-gun, 11 Aug. 2009, *J. Jung 908040*; *Jeju-do:* Bukjeju-gun, 8 July 2008, *J.Jung 807087*; 9 July 2008, *J.Jung 807074, 807080*; *Jeollanam-do:* Gangjin-gun, 22 Aug. 2008, *J.Jung 808036*; Gokseong-gun, 28 July 2008, *H.R.Na 807142*.

Schoenoplectiella hotarui KOREA. *Chungcheongnam-do:* Boryeong-si, 4 Sep. 2008, *J.Jung 809003** (*GQ130345*/*GQ130360*/JF313196); *Gangwon-do:* Goseong-gun, 26 Aug. 2006, *H.R.Na s.n.*; 27 Aug. 2008, *J.Jung 808329*; 5 Sep. 2009, *J.Jung 909130, 909131*; *Gyeonggi-do:* Ansan-si, 5 Sep. 2008, *J.Jung 809006*; 6 Aug. 2009, *J. Jung 908004, 908006*; *Gyeongsangbuk-do:* Mungyeong-si, 22 Sep. 2009, *J.Jung 909212*; Seongju-gun; *Gyeongsangnam-do:* Hadong-gun, 11 Aug. 2009, *J.Jung 908032*; Hapcheon-gun, 23 July 2009, *H.R.Na 90102*; *Jeju-do:* Bukjeju-gun, 20 Aug. 2007, *H.R.Na s.n.*; *Jeollanam-do:* Gangjin-gun, 22 Aug. 2008, *J.Jung 808038*; 29 Aug. 2006, *H.-K.Choi s.n.*

Schoenoplectiella juncoides KOREA. *Chungcheongbuk-do:* Jincheon-gun, 25 Sep. 2009, *J.Jung* et al. *909153*; *Gangwon-do:* Goseong-gun, 27 Aug. 2008, *J.Jung 808333*; Hwacheon-gun, 25 June 2009, *J.Jung 906025*; 26 Aug. 2008, *J.Jung 808301*; *Gyeonggi-do:* Ansan-si, 9 July 2004, *H.-K.Choi s.n.*; Suwon-si, 1 July 2008, *J.Jung 807020** (*GQ130346*/*GQ130361*/JF313197); 5 Sep. 2008, *J.Jung 809008*; *Gyeongsangbuk-do:* Mungyeong-si, 22 Sep. 2009, *J.Jung 909213*; Yecheon-gun, 24 July 2008, *H.R.Na 80257*; *Jeju-do:* Bukjeju-gun, 7 Aug. 2009, *H.R.Na 908066*; *Jeollabuk-do:* Gimje-si, 23 Sep. 2009, *J.Jung 909163*; Gochang-gun, 23 Sep. 2009, *J.Jung 909172*; Jangsu-gun, 29 July 2008, *H.R.Na 807144*; Jinan-gun, 29 July 2008, *H.R.Na 807145*; 30 Aug. 2005, *H.-K.Choi s.n.*; *Jeollanam-do:* Boseong-gun, 29 Aug. 2005, *H.-K.Choi s.n.*; Gangjin-gun, 22 Aug. 2008, *J.Jung 808034*; 22 Aug. 2008, *J.Jung 808051*; 29 Sep. 2006, *H.-K.Choi s.n.*; Yeongam-gun, 21 Aug. 2008, *J.Jung 808030*; 21 Aug. 2008, *J.Jung 808031*.

Schoenoplectiella wallichii KOREA. *Chungcheongbuk-do:* Okcheon-gun, 20 Aug. 1968, *M.S.Yuk s.n.* (SWU); *Gangwon-do:* Goseong-gun, 23 Aug. 1997, *E.J.Ham & Y.H.Lee s. n.* (SWU); *Gyeonggi-do:* Gwacheon-si, 17 Sep. 1977, *B.Y.Chang s.n.* (SWU); *Jeollabuk-do:* Namwon-si, 7 July 2005, *H.-K.Choi s.n.** (JF313182/JF313188/JF313203).

Schoenoplectiella komarovii KOREA. *Gangwon-do:* Hwacheon-gun, 6 Sep. 2007, *H.R.Na s.n.** (JF313180/JF313186/JF313198).

Schoenoplectiella lineolata KOREA. *Chungcheongbuk-do:* Jecheon-si, 7 July 2009, *J.Jung 907445, 907446*; *Chungcheongnam-do:* Buyeo-gun, 24 Sep. 2009, *J.Jung 909190*; *Gangwon-do:* Chuncheon-si, 26 Aug. 2008, *J.Jung 808310*; Hwacheon-gun, 26 Aug. 2008, *J.Jung 808306, 808321*; *Jeollanam-do:* Gangjin-gun, 22 Aug. 2008, *J.Jung 808041** (*GQ130347*/*GQ130362*/JF313199); 30 Oct. 2008, *J.Jung 810015*; Gwangyang-si, 11 Aug. 2009, *C.Kim & J. Jung 908045*.

Schoenoplectiella x *trapezoidea* KOREA. *Gangwon-do:* Goseong-gun, 27 Aug. 2008, *J.Jung 808330*, *J.Jung 808331** (JF313181/JF313187/JF313202); 5 Sep. 2009, *J. Jung* et al.*909132, J.Jung 909133*.

Scirpus wichurai KOREA. *Chungcheongbuk-do:* Jincheon-gun, 25 Sep. 2009, *J.Jung* et al.*909143*; *Gangwon-do:* Goseong-gun, 14 July 2008, *H.R.Na 80182*; 27 Aug. 2008, *J.Jung 808322** (*GQ130357*/*GQ130373*/JF313208); 27 Aug. 2008, *J.Jung 808325*; 4 Sep. 2009, *J.Jung* et al. *909115*; *Gyeonggi-do:* Ansan-si, 1 July 2008, *J.Jung 807018*; 5 Sep. 2008, *J.Jung 809005*; 6 Aug. 2009, *J.Jung 908002*; Paju-si, 23 Oct. 2007, *H.R.Na s.n.*; Suwon-si, 11 Oct. 2009, *J.Jung 910001*; *Gyeongsangbuk-do:* Mungyeong-si, 22 Sep. 2009, *J. Jung 909193*; *Gyeongsangnam-do:* Hadong-gun, 12 Aug. 2009, *J.Jung 908055*.

Scirpus karuisawensis KOREA. *Chungcheongbuk-do:* Jincheon-gun, 25 Sep. 2009, *J.Jung* et al. *909142*; *Gangwon-do:* Goseong-gun, 27 Aug. 2008, *J.Jung 808324*; 4 Sep. 2009, *J.Jung* et al. *909116*; Yangyang-gun, 5 Sep. 2009, *J.Jung* et al. *909045*; *Gyeonggi-do:* Ansan-si, 1 July 2008, *J.Jung 807017** (*GQ130353*/*GQ130369*/JF313204); 5 Sep. 2008, *J.Jung 809004*; 6 Aug. 2009, *J.Jung 908001*; *Gyeongsangbuk-do:* Mungyeong-si, 22 Sep. 2009, *J.Jung 909194*.

Scirpus mitsukurianus KOREA. *Chungcheongbuk-do:* Taean-gun, 11 Aug. 2008, *J.Jung 808007, 808008*; *Daejeon:* Yuseong-gu, 25 Sep. 2009, *J.Jung* et al.*909148*; *Gangwon-do:* Chuncheon-si, 11 Oct. 2006, *H.R.Na s.n.*; 22 Sep. 2006, *C.Kim s.n.*; 26 Aug. 2008, *J.Jung 808309*; Hwacheon-gun, 26 Aug. 2008, *J.Jung 808304** (*GQ130354*/*GQ130370*/JF313205); *Gyeonggi-do:* Yeoju-gun, 25 July 2007, *H.R.Na s.n.*; 26 Sep. 2003, *C.M.Ahn s.n.*; *Gyeongsangnam-do:* Haman-gun, 9 Oct. 1985, *D.Chung s.n.*; 9 Oct. 2008, *J.Jung 810010*; *Jeollanam-do:* Gokseong-gun, 28 July 2008, *H.R. Na 807143*; 5 Oct. 2005, *H.-K.Choi s.n.*; Jangheung-gun, 28 July 2008, *H.R.Na 807141*; 10 Aug. 2006, *C.Kim s.n.*; *Ulsan:* Ulju-gun, 29 Aug. 2008, *J.Jung 808336*.

Scirpus radicans KOREA. *Chungcheongbuk-do:* Chungju-si, 9 July 1987, *Y.C.Oh* et al. *s.n.* (SWU); 14 Aug. 2002, *C.Kim s.n.*; Yeongdong-gun, 27 May 2005, *H.-K.Choi s.n.*; *Chungcheongnam-do:* Boryeong-si, 25 May 2005, *H.-K.Choi s.n.*; 15 June 2008, *J.Jung 806032** (*GQ130356*/*GQ130372*/JF313206), *806033*; *Gangwon-do:* Hoengseong-gun, 30 July 2009, *J.Jung* et al. *907455*; Hwacheon-gun, 24 June 2009, *J.Jung 906012*; 25 June 2009, *J.Jung 906013*; Pyeongchang-gun, 27 June 2008, *J.Jung 806039, 806040*; 24 June 2009, *J.Jung 906007*; Yanggu-gun, 25 June 2009, *J.Jung 906034*; *Gyeonggi-do:* Yeoju-gun, 29 May 2003, *C.M.Ahn s.n.*; 4 July 2008, *J.Jung 807027*; *Jeollabuk-do:* Namwon-si, 26 May 2005, *H.-K.Choi s.n.*; *Jeollanam-do:* Gokseong-gun, 26 May 2005, *H.-K.Choi s.n.*

Scirpus sylvaticus var. *maximowiczii* KOREA. *Gangwon-do:* Pyeongchang-gun, 27 June 2008, *J.Jung 806038** (*GQ130355*/*GQ130371*/JF313207); 24 June 2009, *J.Jung 906008*; Yanggu-gun, 25 June 2009, *J.Jung 906032*. CHINA. *Jilin: Wonji, 25 July 2007, H.-K.Choi 808016–808019.*

Trichophorum dioicum KOREA. *Gangwon-do:* Donggang, 17 Apr. 2008, *J.Jung 804015** (*FJ797641*/*FJ797640*/JF313213), *804016–80427*; 27 June 2008, *J.Jung 806045, 806046*.

Trichophorum alpinum, CHINA. *Jilin*: Mt. Baekdusan, 9 July 1993, *Y.N.Lee s.n.* (KB), 6 July 2010, *J.Jung 1007071** (JF313184/JF313189/JF313212), *1007072–1007075, 1007089*.

Eleocharis congesta KOREA. *Chungcheongbuk-do:* Jecheon-si, 28 Aug. 2007, *H.R.Na s.n.*; Jincheon-gun, 25 Sep. 2009, *J.Jung* et al. *909150*; Buyeo-gun, 24 Sep. 2009, *J.Jung 909186*; *Gangwon-do:* Goseong-gun, 5 Sep. 2009, *J.Jung* et al. *909125*; Yanggu-gun, 25 June 2009, *J. Jung 906033*; *Gyeonggi-do:* Ansan-si, 23 May 2008, *H.R. Na 80090*; 23 May 2008, *J.Jung 805083** (*GQ130343*/*GQ130375*/JF313194); 1 July 2008, *J.Jung 807015*; *Gyeongsangbuk-do:* Mungyeong-si, 22 Sep. 2009, *J.Jung 909205*; Namhae-gun, 11 Aug. 2009, *C.Kim & J.Jung 908011*; *Jeju-do:* Bukjeju-gun, 8 July 2008, *J.Jung 807075*; 20 Aug. 2007, *H.R.Na s.n.*; 22 Aug. 2007, *H.R. Na s.n.*

Fimbristylis squarrosa KOREA. *Chungcheongnam-do:* Taean-gun, 11 Aug. 2008 *J.Jung 808010*; *Gangwon-do:* Yanggu-gun, 24 Aug. 2010 *J.Jung 1008001*; Yangyang-gun, 17 Aug. 2001 *C.Kim* et al. *s.n.*; 14 Sep. 2001 *C.Kim* et al. *s.n.*; *Gyeonggi-do:* Icheon-si, 4 July 2008, *J.Jung 807041** (*GQ130344*/*GQ130376*/JF313195); *Gyeongsangbuk-do:* Ulju-gun, 5 Oct. 2010 *J.Jung 1010071.*

Cladium chinense KOREA. *Jeju-do:* Seogwipo-si, 14 July 2006, *H.-K.Choi* et al. *s.n.** (*GQ130342*/*GQ130374*/JF313193); 3 Nov. 2010, *J.Jung 1011040.*

Appendix 2

Taxon and coded character state matrix

No.	Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
1	*Bolboschoenus fluviatilis*	0	1	2	2	2	2	2	0	0	1	0	0	0	0	0/2	1	0	0	0	0	2	1	0	2	2	0	2	1	2	0	3	1	1	0	2	0/1
2	*Bolboschoenus planiculmis*	0/1	1	2	2	2	2	0/1	1	0	1	1	0	1	0	0	1	0	1	0	0	2	1	0	2	2	0	2	1	2	0	3	1	1	0	2	0
3	*Bolboschoenus maritimus*	1	1	3	2	1	?	0/1	2	0	1	1	0	1	0	0	1	0	1	3	2	2	1	0	2	2	0	1/2	1	2	0	3	1	1	0	0	2
4	*Schoenoplectus nipponicus*	1	1	2	2	1	1	0/1	1/2	1	0	1	1	3	0	0	1	1	1	2	1	1	1	0	0	0	0	1	2	2	0	0	1	1	0	2	1
5	*Schoenoplectus tabernaemontani*	0	1	0	2	0	0	0	0	1	2	1	1	3	0	0	2	1	1	0	1	1	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1
6	*Schoenoplectus triqueter*	0	1	2	2	0	0	0	1	1	2	1	1	3	0	0	1	1	1	2	1	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	1
7	*Schoenoplectiella mucronata*	1	1	1	0	0	0	0	1	1	3	2	1	3	0	0	1	1	0	3	2	1	1	0	0	2	1	1	1	0	0	1	0	0	0	1	0
8	*Schoenoplectiella triangulata*	0	1	1	0	0	0	0	1	1	3	2	1	3	0	0	1	1	0	3	2	1	1	0	0	2	1	1	1	2	0	0	1	1	0	0	0
9	*Schoenoplectiella hotarui*	1	1	1	0	0	0	1	2	1	3	2	0	3	0	0	1	1	1	3	2	1	1	1	0	2	1	1	1	0	0	1	0	0	0	1	0
10	*Schoenoplectiella juncoides*	1	1	1	0	0	0	1	2	1	3	2	0	3	0	0	1	1	1	3	2	1	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0
11	*Schoenoplectiella wallichii*	2	1	1	0	0	0	2	2	1	3	2	2	3	1	0	1	1	2	3	2	1	0/1	0	0	0	0	1	1	0	1	1	0	0	1	1	0
12	*Schoenoplectiella komarovii*	0	1	1	0	0	0	0	2	1	3	2	1	3	0	0	1	0	1	3	2	1	1	0	0	1	0	1	1	0	1	2	0	2	1	1	1
13	*Schoenoplectiella lineolata*	2	1	3	1	1	1	2	2	1	3	2	2	3	1	1	3	1	2	3	2	1	0	2	0	0	0	1	0/1	0/2	0	0	0/1	1	0	0	0
14	*Schoenoplectiella* x *trapezoidea*	0/1	1	1	0	0	0	0	1	1	3	2	1	3	0	0	1	1	1	3	2	1	1	0	0	2	1	1	1	2	0	0	1	1	0	1	0
15	*Scirpus wichurai*	0	1	1	0	0	0	0	0	0	1	0	0	0	2	2	0	0	0	1	0	0	0	1	1	1	0	0	2	1	1	1	0	2	1	1	1
16	*Scirpus karuisawensis*	0	1	1	0	0	0	0	1	0	0	1	0	2	2	0	0	0	1	0	1	0	0	0/1	0	1	0	0	2	0	1	1	0	2	1	1	0
17	*Scirpus mitsukurianus*	0	1	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	1	2	0	2	0	1	1	0	2	1	1	1
18	*Scirpus radicans*	0	1	?	?	0	0	0	0	0	1	0	0	0	2	2	0	0	0	1	0	0	0	0	1	1	1	0	1/2	1	1	1	0	2	1	1	1
19	*Scirpus sylvaticus* var. *maximowiczii*	0	1	2	?	0	0	0	0	0	1	0	0	0	2	2	0	0	0	1	0	0	0	0	1	1	1	0	0	1	1	1	0	2	1	1	0/1
20	*Trichophorum dioicum*	2	1	1	0	0	0	2	3	1	3	2	2	3	1	1	3	2	3	3	2	0	0	2	0	0	0	1	1/2	2	1	0	1	0/1	0	0	0
21	*Trichophorum alpinum*	2	1	1	0	0	0	1	2/3	1	3	2	2	3	1	1	3	2	3	3	2	0	0	0/1	0	1	2	0	3	2	1	1	0	0	1	0	0
22	*Eleocharis congesta*	2	1	1	0	0	0	2	3	1	3	2	2	3	1	1	3	2	3	3	2	0	0	0	1	1	0	0	0	1	1	2	0	2	1	1	1
23	*Fimbristylis squarrosa*	2	1	1	0	0	0	2	3	1	2	2	2	3	0	0	1	1	2	0	1	0	0	0	1	1	0	1	0	1	1	2	0	2	1	1	0
24	*Cladium chinense*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2 (continued)

No.	Taxons	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71
1	*B. fluviatilis*	0	0	1	0	0	0	1	1	1	2	0	0	0	0/2	0	0	0	0	0	0	0	3	0/2/3	0/2	3	1	0	1/2	2	1	0	2	3	1	1
2	*B. planiculmis*	0	2	0	0	0	0	1	1	1/2	2	0	0	0	0	0	0	1/2	0/1/2	0	0/1	0/1	0/4	0	0	2/3	1	0	1	2	1	0	0	3	5	1
3	*B. maritimus*	0	2	0	0	1	0	1	1	2	2	0	0	0	0	0	0	2	1/2	0	0/1	1	4	0	0	2	1	0	1	2	1	0	0	3	2	1
4	*S. nipponicus*	1	0	1	0	1	0	1	1	2	2	1	1	0	1	1	1	2	0	1	0	0	3	2	1/2	1	1	0	1	2	0	1	0	3	3	1
5	*S. tabernaemontani*	1	0	1	0	1	0	0	0	0	0	1	1	1	1	1	2	2	0	1	1	0	0	0/1	0/4	4/5	1	0	1/2	2	1	0	0	3	3	1
6	*S. triqueter*	1	0	0	0	1	0	0	0	1	2	1	1	1	0	1	2	2	0	1	1	0	0	0	2/4	4/5	1	0	1	2	1	1	0	2/3	3	1
7	*S. mucronata*	1	0	0	1	1	0	2	0	2	2	1	1	2	0	1	2	2	1	1	1	1	4	0	4	1	1	2	1/2	2	1	1	0/2	3	2	0
8	*S. triangulata*	1	0	0	0/1	1	0	2	0	2	3	1	1	2	0	1	2	2	1	1	1	1	4	0	0/1	1	2	2	1/2	2	1	1	2	3	2	0
9	*S. hotarui*	1	0	0	0	1	0	3	0	0	0	1	1	2	1	1	2	2	1	1	1	1	4	0/1	4	1	1	2	2	2	1	1	2	3	2	0
10	*S. juncoides*	1	0	0	1	1	0	2	0	3	4	1	1	2	1	1	2	2	1	1	1	1	4	1	2	1	1	2	2	2	1	1	0/1	3	3	0
11	*S. wallichii*	1	0	0	1	1	0	3	0	0	0	1	1	2	1	1	2	2	1	1	1	1	4	0	0	1	1	2	1/2	2	1	1	0	3	3	0
12	*S. komarovii*	2	1	0	1	2	0	2	0	3	4	1	1	2	1	1	2	2	1	1	1	1	4	0	4	1	1	2	1	2	1	1	0	3	3	2
13	*S. lineolata*	1	0	0	1	1	0	1	1	0	0	1	1	2	1	1	2	2	2	1	1	1	4	0/2	0	1	2	0	0/1/2	2	1	1	0	3	4	2
14	*S.* x *trapezoidea*	1	0	0	0	1	0	2	0	3	4	1	1	2	1	1	2	2	1	1	1	1	4	0	4	1	1	2	2	2	1	1	2	3	2	2
15	*S. wichurai*	2	1	1/2	1	2	0	3	0	1	1	0	1	0	2	1	2	1	0	0	0	0	0	2	0	0/1	0	1	2	1	0	1	2	2	2	1
16	*S. karuisawensis*	2	1	2	0	2	1	3	0	1	1	0	1	0	0	1	3	0	0	0	0	0	0	2	0	0	0	0	2	1	0	1	2	3	2	1
17	*S. mitsukurianus*	2	1	2	0	2	1	3	0	1	1	0	1	0	0	1	3	0	0	0	0	0	0	2	0	0	0	0	2	1	0	1	2	2/3	2	1
18	*S. radicans*	2	1	1/2	1	2	0	0	2	1	1	0	0	0	0	1	3	1	0	0	0	0	0	1	0/1/2	0/4	0	0	2	1	1	0	2	3	2	1
19	*S. sylvaticus* var. *maximowiczii*	2	1	1	1	2	0	0	0	1	1	0	0	0	0	1	2	1	0	0	0	0	1	1	1	0/4	0	1	2	2	1	1	2	2	2	1
20	*T. dioicum*	1	1	2	0	1	0	2	0	3	4	1	0	1	1	1	3	1	2	2	2	1	4	2	0	3/5	1	0	2	1	1	0	2	1	1	1
21	*T. alpinum*	2	1	2	1	1/2	0	2	0	2	2	1	0	1	1	1	2	1	2	2	2	1	4	2	0	0	0	0	2	3	0	0	2	1	3	2
22	*E. congesta*	2	1	2	0	0	0	3	2	3	4	1	0	2	1	0	0	1	2	2	2	1	4	0	3	0	0	2	2	2	2	2	2	3	2	1
23	*F. squarrosa*	2	1	0	1	2	0	3	0	0	4	1	0	0	1	0	0	1	0	0	0	0	2	0/1	0	1/2	1	1	0	0	2	2	0	3	3	3
24	*C. chinense*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0/2/3	0	0	0

Number of characters and code of character states are corresponded to Table 2

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