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Research Article

# Targeted sequencing supports morphology and embryo features in resolving the classification of Cyperaceae tribe Fuireneae s.l.

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**Abstract** Molecular phylogenetic studies based on Sanger sequences have shown that Cyperaceae tribe Fuireneae s.l. is paraphyletic. However, taxonomic sampling in these studies has been poor, topologies have been inconsistent, and support for the backbone of trees has been weak. Moreover, uncertainty still surrounds the morphological limits of *Schoenoplectiella*, a genus of mainly small, amphicarpic annuals that was recently segregated from *Schoenoplectus*. Consequently, despite ample evidence from molecular analyses that Fuireneae s.l. might consist of two to four tribal lineages, no taxonomic changes have yet been made. Here, we use the Angiosperms353 enrichment panel for targeted sequencing to (i) clarify the relationships of Fuireneae s.l. with the related tribes Abildgaardieae, Eleocharideae, and Cypereae; (ii) define the limits of Fuireneae s.s., and (iii) test the monophyly of Fuireneae s.l. genera with emphasis on *Schoenoplectus* and *Schoenoplectiella*. Using more than a third of Fuireneae s.l. diversity, our phylogenomic analyses strongly support six genera and four major Fuireneae s.l. clades that we recognize as tribes: Bolboschoeneae stat.nov., Fuireneae s.s., Schoenoplecteae, and Pseudoschoeneae tr. nov. These results are consistent with morphological, micromorphological (nutlet epidermal cell shape), and embryo differences detected for each tribe. At the generic level, most sub-Saharan African perennials currently treated in *Schoenoplectus* are transferred to *Schoenoplectiella*. Our targeted sequencing results show that these species are nested in *Schoenoplectiella*, and their treatment here is consistent with micromorphological and embryo characters shared by all *Schoenoplectiella* species. Keys to recognized tribes and genera are provided.

**Key words:** Angiosperms353, classification, Cyperaceae, Fuireneae, targeted sequencing, taxon limits, taxonomy.

## 1 Introduction

Since the first molecular phylogenies of sedges (Cyperaceae) over 20 years ago, our knowledge of relationships within the family has improved at an ever-astonishing pace. Initially, these analyses made use of just a few plastid markers (e.g., *rbcL*, *ndhF*, *trnL-F*; Muasya et al., 1998; Yen & Olmstead, 2000) and nuclear markers (e.g., ITS; Starr et al., 1999), but they immediately confirmed the suspicions of many authors on the basis of differences in macro- and micromorphological

features (e.g., Schuyler, 1971; Wilson, 1981; Goetghebeur, 1986; Bruhl, 1995), including embryo types (Van der Veken, 1965; Goetghebeur, 1986), that many generic and tribal circumscriptions within the family did not reflect their evolutionary history. Unfortunately, these early molecular analyses did not have a major impact on family classification due to poor taxonomic sampling or topologies that were either insufficiently resolved or inadequately supported to make lasting taxonomic changes (e.g., Simpson et al., 2003). However, as taxonomic sampling increased and more molecular markers were developed, statistical support for trees improved, and a series of new genera (e.g., *Zameioscirpus* Dhooge & Goetghebeur, Dhooge et al., 2003; *Calliscirpus* C.N.Gilmour, J.R.Starr & Naczi, Gilmour et al., 2013; *Afroscirpoides* García-Madrid & Muasya, García-Madrid et al., 2015) was described. Changes to tribal (Léveillé-Bourret et al., 2018; Léveillé-Bourret & Starr, 2019; Semmouri et al., 2019; Larridon et al., 2021a), generic (Léveillé-Bourret et al., 2020), and subgeneric (Villaverde et al., 2020; Roalson et al., 2021) classifications in the family are now taking place at a rapid pace, owing in part to advances in sequencing technology. However, one major problem has yet to be resolved: the status and classification of tribe Fuireneae Rchb. ex Fenzl.

Fuireneae s.l. is a cosmopolitan tribe consisting of 153 species assigned to six genera: *Bolboschoenus* (Asch.) Palla, *Fuirena* Rottb., *Actinoscirpus* (Ohwi) R.W.Haines & Lye, *Pseudoschoenus* (C.B.Clarke) Oteng-Yeb., *Schoenoplectus* (Rchb.) Palla, and *Schoenoplectiella* Lye (Figs. 1, 2). They are found in tropical to temperate wetlands where they purify water and provide essential food and habitat for wildlife (Fassett, 1957; Smith & Coops, 1991; Kim et al., 2013; Mishra et al., 2015; Naczi et al., 2018), mitigate flooding, and even protect coastal shorelines from erosion (Albert et al., 2013). They are also useful to humans as food, building materials, and medicines (Simpson & Inglis, 2001); however, many are among the world's worst weeds, especially in rice fields (e.g., *Bolboschoenus maritimus* (L.) Palla, *Schoenoplectiella mucronata* (L.) J.Jung & H.K.Choi; Bryson & Carter, 2008).

Like many sedge genera, all six currently placed in Fuireneae are segregates of *Scirpus* L. s.l., a heterogeneous entity now corresponding to c. 50 natural genera and over 250 species (Koyama, 1958; Goetghebeur, 1998). Among the segregates of *Scirpus* s.l., Fuireneae s.l. species are particularly interesting, because they share a series of morphological and embryo features that seem to mark them as a natural group. All Fuireneae s.l. species have terete spikelets with spirally arranged glumes, bisexual flowers with or without perianth parts, and embryos with a distinctive mushroom-like (fungiform) shape. As embryo characters often provide key features for circumscribing sedge tribes and genera (e.g., Léveillé-Bourret & Starr, 2019; Semmouri et al., 2019), Goetghebeur (1998) considered these distinctive embryos of the Bolboschoenus- or Schoenoplectus-type as evidence that Fuireneae s.l. could represent a specialized offshoot within the family. Nevertheless, from the first molecular phylogeny of Cyperaceae (Muasya et al., 1998), it was not only clear that *Scirpus* s.l. consisted of numerous, often distantly related genera, as many had suggested (e.g., Van der Veken, 1965; Schuyler, 1971; Wilson, 1981), but even Fuireneae s.l. could consist of multiple independent lineages.

Molecular studies have since retrieved four distinct lineages within Fuireneae s.l.: (i) a clade comprising species from the subcosmopolitan genus *Bolboschoenus* (15 species; Govaerts et al., 2020); (ii) a clade consisting of the largely American and African, tropical to warm temperate genus *Fuirena* (55 species; Govaerts et al., 2020); (iii) a clade with the monotypic, (sub)tropical, south Asian–Australasian genus *Actinoscirpus* as sister to the cosmopolitan, mainly temperate genus *Schoenoplectus* (27 species, hereafter the Schoenoplectus Clade; Govaerts et al., 2020), and (iv) the monotypic, South African endemic genus *Pseudoschoenus* as sister to the cosmopolitan, mainly tropical genus *Schoenoplectiella* (52 species, hereafter the Schoenoplectiella Clade; Govaerts et al., 2020), which is a segregate of *Schoenoplectus* (Lye, 2003). Among the four larger, widespread genera, *Bolboschoenus* and *Fuirena* are easily defined morphologically and they have always been monophyletic in previous molecular studies (Muasya et al., 2009a; Escudero & Hipp, 2013; Hinchliff & Roalson, 2013; Glon et al., 2017; Semmouri et al., 2019). In contrast, the separation and relationships of *Schoenoplectus* and *Schoenoplectiella* have not been so clear.

As *Scirpus* s.l. was progressively dissolved, the focus for large genera like *Schoenoplectus* was to provide an infrageneric classification that reflected evolutionary relationships while dividing the genus into workable groups (Oteng-Yeboah, 1974a; Raynal, 1976a, 1976b; Smith & Hayasaka, 2001). Authors were basically unanimous that either three or four major taxonomic divisions adopted from *Scirpus* s.l. could be made within *Schoenoplectus*, either at the subgeneric level, as subgenera *Schoenoplectus*, *Malacogeton* (Ohwi) Oteng-Yeboah, and *Actaeogeton* (Reichenb.) Oteng-Yeboah, or at the sectional level, as sections *Schoenoplectus* (=*Scirpus* section *Pterolepis* Pfeiff.), *Malacogeton* (Ohwi) S.G.Smith & Hayasaka, *Actaeogeton* (Reichenb.) J.Raynal, and *Supini* (Cherm.) J.Raynal (Raynal, 1976a; Smith & Hayasaka, 2001; Smith & Hayasaka, 2002). Moreover, it was clear that when treated as sections, taxa could be divided into two distinct groups: (i) sections *Actaeogeton* and *Supini* were typically densely tufted plants with sculptured, black nutlets and entire glume apices, whereas (ii) sections *Schoenoplectus* and *Malacogeton* were rhizomatous plants with smooth, yellow to dark brown nutlets and glumes entire to emarginate (Raynal, 1976b; Smith & Hayasaka, 2001, 2002). Moreover, embryo features supported this division with the embryo scutellum of sections *Actaeogeton* and *Supini* being umbonate or pileate like a mushroom cap versus a turbinate to rhomboid scutellum in sections *Schoenoplectus* and *Malacogeton* (Van der Veken, 1965). When the molecular analysis of Muasya et al. (1998) placed two small, tropical annuals, *S. articulata* (L.) Palla and *S. junceus* (Willd.) J.Raynal, in a clade separate from the type for *Schoenoplectus*, *S. lacustris* (L.) Palla, Lye (2003) decided to segregate 26 species into *Schoenoplectiella*. This new genus was roughly meant to elevate *Schoenoplectus* section *Supini* to generic status, a section defined by Raynal (1976a) to contain the small, tufted annuals of *Schoenoplectus* whose bristles were reduced or

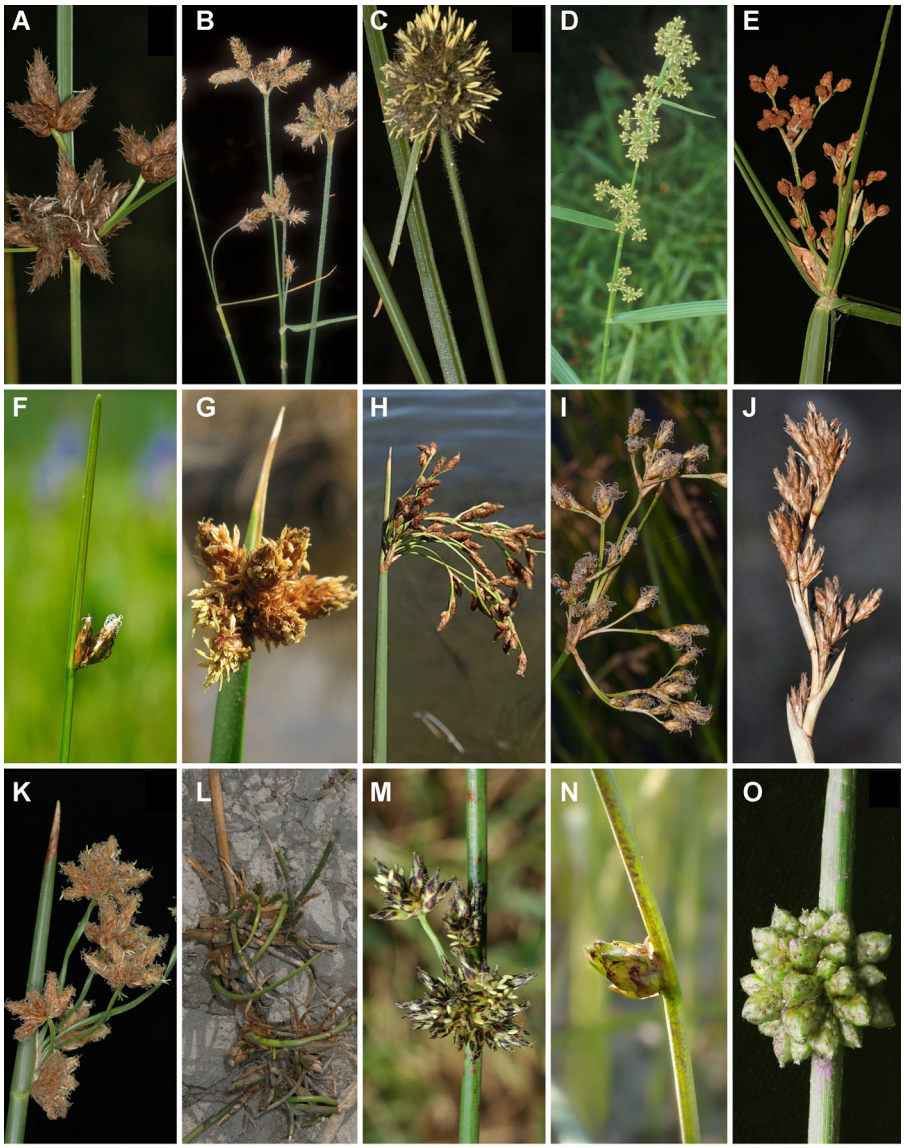


**Fig. 1.** Morphological diversity of Fuireneae s.l. **A**, *Bolboschoenus maritimus* (L.) Palla (Asturias, Spain). **B**, *Fuirena pubescens* (Poir.) Kunth (Ávila, Spain). **C**, *Fuirena hirsuta* (P.J.Bergius) P.L.Forbes (Cape Region, South Africa). **D**, *F. umbellata* Rottb. (Pernambuco, Brazil). **E**, *Actinoscirpus grossus* (L.f.) Goetgh. & D.A.Simpson (Phuket, Thailand). **F**, *Schoenoplectus torreyi* (Olney) Palla (Québec, Canada). **G**, *S. americanus* (Pers.) Volkart (Arizona, USA). **H**, *S. tabernaemontani* (C.C.Gmel.) Palla (Minnesota, USA). **I**, *S. subulatus* (Vahl) Lye (Australia). **J**, *Pseudoschoenus inanis* (Thunb.) Oteng-Yeb. (Cape Region, South Africa). **K**, *Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) J.Raynal (Huelva, Spain). **L**, *S. corymbosus* rooting pseudo-viviparous inflorescence (Huelva, Spain). **M**, *Schoenoplectus confusus* (N.E.Br.) Lye (Trans-Nzoia, Kenya). **N**, *Schoenoplectiella smithii* (A.Gray) Hayas. (Québec, Canada). **O**, *S. senegalensis* (Steud.) Lye (Botswana). Photos **A**–**E** and **J**–**L** by Modesto Luceño. **F** by Jean Marc Vallières. **G** by Julian Starr. **H** by Peter M. Dziuk (reproduced with permission from www.minnesotawildflowers.info). **I** by Russell Barrett; **M** by Marcial Escudero; **N** by Marie-Ève Garon-Labrecque; **O** by Jane Browning.

absent. In addition, the species of section *Supini* also stood out, because beyond sharing other features such as rugulose to highly sculpted nutlets, most displayed amphicarpy, a rare condition in Cyperaceae where pistillate flowers at culm bases develop larger nutlets than the nutlets produced in aerial inflorescences (Raynal, 1976a; Bruhl, 1994). Nonetheless, in a molecular analysis of Korean *Scirpus* s.l., Jung & Choi (2010) expanded the genus to include some species from *Scirpus* section *Actaeogeton*, which does not display amphicarpy, after results suggested they formed a clade with *Schoenoplectiella* species separate from *Schoenoplectus* s.s. (i.e., sections *Schoenoplectus* and *Malacogeton*). Hayasaka (2012) subsequently redefined *Schoenoplectiella* to include all species from sections *Actaeogeton* and *Supini*, which resulted in a genus composed of small, amphicarpic annuals and large, single-fruit-type perennials. Unfortunately, this merger


**Fig. 2.** Ecological diversity of Fuireneae s.l. **A**, *Bolboschoenus maritimus* (L.) Palla (Minnesota, USA). **B**, *Fuirena* sp. (KwaZulu-Natal, South Africa). **C**, *Schoenoplectus torreyi* (Olney) Palla (Minnesota, USA). **D**, *Schoenoplectus americanus* (Pers.) Volkart (Arizona, USA). **E**, *Pseudoschoenus inanis* (Thunb.) Oteng-Yeb. (Cape Region, South Africa). **F**, *Schoenoplectiella smithii* (A.Gray) Hayas. (Québec, Canada). Photos **A** and **C** by Peter M. Dziuk (reproduced with permission from www.minnesotawildflowers.info); **B** and **E** by Modesto Luceño; **D** by Julian Starr; **F** by Étienne Léveillé-Bourret.

meant that all the characters used to separate *Schoenoplectiella* from *Schoenoplectus* were overlapping. Moreover, discontinuous characters could not be found for the separation of *Schoenoplectiella* sections *Actaeogeton* and *Schoenoplectiella* (=*Supini*), even though they were still assumed to be natural groups.

Although our understanding of Fuireneae s.l. has progressed enormously over the past 50 years, and a pattern pointing toward a grade of multiple major clades has emerged, the most recent molecular analyses are equivocal about the way to proceed from a taxonomic point of view. Recent molecular studies of Fuireneae s.l. have retrieved the tribe as a grade of three (Semmouri et al., 2019) or four clades (Muasya et al., 2009a; Escudero & Hipp, 2013; Hinchliff & Roalson, 2013; Glon et al., 2017) branching off after an Abildgaardieae–Eleocharideae Clade and paraphyletic with respect to tribe Cypereae. Depending on the markers used, analyses place either *Bolboschoenus* (Glon et al., 2017; Spalink et al., 2018) or *Fuirena* (Glon et al., 2017) as branching first, and the Schoenoplectiella Clade (Escudero & Hipp, 2013; Shiels et al., 2014) or the Schoenoplectus Clade (Glon et al., 2017; Spalink et al., 2018) as sister to Cypereae or sister to each other (Semmouri et al., 2019). Early molecular analyses have also suggested that *Schoenoplectiella* (Muasya et al., 1998; Simpson et al., 2007) or *Fuirena* (Muasya et al., 2009a) could be sister to tribe Eleocharideae Goetgh. or that *Bolboschoenus* could be sister to tribe Abildgaardieae Lye (Muasya et al., 2009a). These relationships were not entirely implausible, given the early cladistic analyses of sedge morphology by Goetghebeur (1986) and Bruhl (1995),

but support for major clade relationships in molecular analyses was poor and taxonomic sampling was limited. No previous molecular phylogenetic study that has generated novel data has included more than 25 species of Fuireneae s.l., and no study has included more than five plastid markers (*matK*, *ndhF*, *rbcL*, *rps16*, *trnL-F*) and two nuclear markers (ETS-1f, ITS; Semmouri et al., 2019), with the exception of the supermatrix analysis of Hinchliff and Roalson (23 loci; Hinchliff & Roalson, 2013), where the relationships of the major Fuireneae s.l. clades were completely unresolved. Moreover, the limits of *Schoenoplectus* and *Schoenoplectiella* remain unresolved, because molecular studies have often been regional in scope (e.g., Japan, Yano & Hoshino, 2005a; Korea, Jung & Choi, 2010), and even when geographic sampling was wider (e.g. Shiels et al., 2014), a lack of critical species of African *Schoenoplectus* (e.g., *Schoenoplectus rhodesicus* (Podlech) Lye, *S. paludicola* (Kunth) Palla ex J.Raynal; Smith & Hayasaka, 2001; Browning, 2012) or low branch support (Muasya et al., 2009a) has meant that a satisfactory separation for these two genera has yet to be achieved. An overview of the species of *Schoenoplectus* and *Schoenoplectiella*, their distribution range, and inclusion in previous molecular studies is detailed in Table S1.

In this study, we use the Angiosperms353 enrichment panel (Johnson et al., 2019) for targeted sequencing of an in-depth sampling of tribe Fuireneae s.l. (52 species, all genera) and putatively related tribes Eleocharideae, Abildgaardieae, and Cypereae. Additionally, off-target nrDNA sequence data were recovered from the generated raw reads and complemented with ITS sequence data available on GenBank to help resolve the monophyly of *Schoenoplectus* and *Schoenoplectiella*. We include critical tropical African *Schoenoplectus*, and we use embryo morphology and macro- and micromorphological characters to understand Fuireneae s.l. relationships and to circumscribe the natural tribes and genera currently treated within Fuireneae s.l.

## 2 Material and Methods

### 2.1 Taxon sampling for the targeted sequencing study

Sequence data for a total of 99 accessions were analyzed in this study, including an in-depth sampling of (i) tribe Fuireneae s.l., 62 accessions representing 52 species (c. 30%), and (ii) related tribes Abildgaardieae, Eleocharideae and Cypereae (36 species), with *Dulichium arundinaceum* (L.) Britton (tribe Dulichieae W.Schultze-Motel) as the outgroup. Most samples were taken from herbarium specimens; however, some silica gel-dried samples and Kew DNA bank samples are also included (Table S2).

### 2.2 DNA extraction, genomic library preparation, hybridization, and sequencing

Molecular work was carried out at the Sackler Phylogenomics Laboratory, within the Jodrell Laboratory at the Royal Botanic Gardens, Kew (Richmond, Surrey, UK). Genomic DNA was extracted from leaf tissue obtained from herbarium specimens or from samples collected and stored on silica gel using either a standard CTAB approach (Doyle & Doyle, 1987) or a CTAB protocol based on the study of Beck et al. (2012) that was modified for optimal simultaneous extraction of 96–192 samples (i.e., one or two plates) from suboptimal (i.e., herbarium) tissue (see Data Sheet S1 in Larridon et al., 2020). Eighteen accessions were sourced from the Kew DNA Bank (http://dnabank.science.kew.org/) (Table S2). CTAB-extracted samples were purified using an Agencourt AMPure XP Bead Clean-up (Beckman Coulter, Indianapolis, IN, USA). All DNA extracts were quantified using a Quantus™ Fluorometer (Promega Corporation, Madison, WI, USA) and then run on a 1% agarose gel to assess the average fragment size. Samples with very low concentration (not visible on a 1% agarose gel) were assessed on an Agilent Technologies 4200 TapeStation System using Genomic DNA ScreenTape (Santa Clara, CA, USA). DNA extracts with average fragment sizes above 350 bp were sonicated using a Covaris M220 Focused-ultrasonicator™ (Covaris, Woburn, MA, USA), following the manufacturer's protocol, to obtain an average fragment size of 350 bp. Genomic library preparation, quality control, hybridization with the Angiosperms353 probes (Johnson et al., 2019; Arbor Biosciences, Ann Arbor, MI, USA), enrichment, and sequencing were performed following the protocols outlined in the study of Larridon et al. (2020). Raw reads for all accessions are available from the NCBI GenBank Sequence Read Archive (SRA) under Bioproject numbers: PRJNA553989 (http://www.ncbi.nlm.nih.gov/bioproject/PRJNA553989), PRJNA649146 (http://www.ncbi.nlm.nih.gov/bioproject/PRJNA649146), and PRJNA668802 (http://www.ncbi.nlm.nih.gov/bioproject/PRJNA668802) and from the European Nucleotide Archive (ENA) under EMBL Project numbers: PRJEB39590 (https://www.ebi.ac.uk/ena/browser/view/PRJEB39590) and PRJEB41806 (https://www.ebi.ac.uk/ena/browser/view/PRJEB41806).

### 2.3 Read processing and sequence assembly

Bioinformatics settings follow Larridon et al. (2021b). Raw reads were trimmed to remove adapter sequences and portions of low quality with Trimmomatic v.0.39 (Bolger et al., 2014) according to the following settings: LEADING:30 TRAILING:30 SLIDINGWINDOW:4:2:30 MINLEN:36. HybPiper v.1.3.1 (Johnson et al., 2016) was used to process the quality-checked, trimmed reads, with all settings at default, except minimum coverage, which was set to 4x. Paired and unpaired reads from all accessions were mapped to targets with BLASTx (Altschul et al., 1990) using the Angiosperms353 target loci amino acid (AA) sequences (see Data Sheet S3 in Larridon et al., 2020). Mapped reads were subsequently assembled into contigs with SPAdes v.3.13.1 (Bankevich et al., 2012). Exonerate v.2.2 (Slater & Birney, 2005) was then used to align the assembled contigs to their associated target sequence and to remove intronic regions (exons data set). The HybPiper script intronerate was used to generate a supercontigs data set. HybPiper flags potential paralogs when multiple contigs map well to a single reference sequence. As few random paralog warnings were raised, no sequence was excluded.

The consensus sequences for each gene were then used to generate the two nuclear data sets including all accessions (i.e., exons data set and supercontigs data set) for those genes with more than 10 sequences. Contigs were aligned using MAFFT v.7 (Katoh & Standley, 2013) with the "–auto" option. The alignments were trimmed in phyutility (Smith & Dunn, 2008) to remove sites missing in 60% of the samples. The number of potentially parsimony-informative sites was calculated using AMAS (Borowiec, 2016) for each contig alignment, before and after trimming.

**2.4 Phylogenomic analyses of the targeted sequencing data**
Phylogenomic analyses also follow Larridon et al. (2021b). The two data sets (exons and supercontigs) were analyzed using two approaches: a multi-species summary coalescent approach and a concatenated maximum likelihood approach. For the multi-species summary coalescent approach, individual gene trees were constructed using RAxML v.8 (Stamatakis, 2014), applying GTRCAT and 100 bootstrap replicates, followed by a slow ML optimization with the "-f a" option. Branches with support equal to 10 or lower were collapsed using Newick Utilities (Junier & Zdobnov, 2010). Each gene tree set was analyzed in TreeShrink (Mai & Mirarab, 2018) to remove excessively long branches. The resulting trees were used as input to infer species trees in ASTRAL-III v.5.5.11 (Zhang et al., 2018), a summary method that is statistically consistent under the Multiple Species Coalescent (MSC). The option "-t 2" was used to output quartet support values. For the concatenated maximum likelihood approach, gene alignments were first concatenated using AMAS, cleaned by removing the outliers identified by TreeShrink, and analyzed in IQ-TREE 2.1.0 (Minh et al., 2020) with mode set to "MFP+MERGE" and 10000 replicates of ultrafast bootstrap replications (Hoang et al., 2018). Tree images were plotted in R (R Core Team, 2020) using the packages ape (Paradis & Schliep, 2018), ggimage (Yu, 2019a), ggtree (Yu et al., 2017), treeio (Yu, 2019b), and their dependencies.

**2.5 Phylogenetic analyses of nrDNA data**
Off-target nrDNA sequences were recovered from the paired and unpaired trimmed reads of the targeted sequencing data using GetOrganelle (Jin et al., 2018), following the recommended parameters for nrDNA recovery (-R 20 -k 21,45,65,85,105). The two largest sequences were annotated on the basis of two Poaceae complete cistrons (GenBank accession numbers: KT281166 and KY826229), given the absence of complete sequences for Cyperaceae. Using these newly annotated sequences as a query, the regions between 26S and 18S were blasted and those with the complete fragment were kept. A second blast round included the samples with fragmentary recovery, which were then manually curated in Geneious 10.2.6 (https://www.geneious.com). We obtained nrDNA sequence data for 80 of the 99 accessions included in the targeted sequencing study (Table S3). ITS data for a further 58 accessions were obtained from GenBank (Table S3). The retrieved off-target nrDNA sequence data, together with the obtained ITS data, were combined into an alignment in PhyDE 0.9971 (Müller et al., 2010) and aligned using MAFFT on the CIPRES portal (http://www.phylo.org/; Miller et al., 2010), after which the alignment was checked manually following nucleotide homology criteria, as summarized by Morrison et al. (2015). Equally, a reduced sampling alignment of 62 accessions was prepared to answer the key question of this nrDNA study, that is, the monophyly of *Schoenoplectus* and *Schoenoplectiella*. The full sampling alignment of 137 accessions (Data S1) and the reduced sampling alignment of 62 accessions (Data S2) were analyzed on the CIPRES portal using RAxML 8.2.10 (Stamatakis, 2014) with the model set to GTR (gamma).

**2.6 Embryo morphology**
Embryo characteristics are widely acknowledged to be among the most phylogenetically informative features for sedges at the tribal and generic levels (Goetghebeur, 1998; Semmouri et al., 2019). Twenty-nine embryographs representing the six Fuireneae s.l. genera first brought together for the study of Semmouri et al. (2019) were reinvestigated for characters delineating the four Fuireneae s.l. clades (Data S3). These embryographs representatively cover all genera and most infrageneric groupings of the tribe Fuireneae s.l. (except *Schoenoplectus* section *Malacogeton*).

As important differences in size appear to occur among Fuireneae s.l. embryos, all embryographs were measured for length and width at their widest point using ImageJ (Rasband, 1997). To further quantify shape variation, we used geometric morphometrics to test whether the four major clades identified in phylogenetic analyses differed in embryo shape. A total of 17 landmarks and 70 pseudolandmarks representing all shape and size variations found in Fuireneae s.l. embryos were digitized on embryos using tpsDig v2.17 (Rohlf, 2015). Landmark positions are described and illustrated in Fig. S1. Size and shape variables were generated by Generalized Procrustes Analysis using the R v.3.6.3 (R Core Team, 2020) package geomorph (Adams et al., 2020). Differentiation between the four major clades in size+shape was tested by MANOVA and by linear discriminant analysis in the R package MASS (Venables & Ripley, 2002). Finally, the average embryo shape of each clade was computed from group centroids to visually represent salient embryological differences between clades.

**2.7 Micromorphology of nutlet epidermal cells**
The nutlet epidermal cell shape has been shown to be an effective tool for separating genera and infrageneric taxa in Fuireneae s.l. (e.g., Schuyler, 1971; Haines & Lye, 1983; Gordon-Gray, 1995; Hayasaka, 2012; Elkordy et al., 2020). A literature survey of existing data was performed to characterize cell shape in all genera. To clarify the use of terms for the cell shape, the ratio of the length to the width of a representative cell was taken for each taxon when both ends of a cell were clearly visible. The cell shape was characterized as follows: (i) cells <2 times longer than wide were described as isodiametric when roughly round, hexagonal, or quadrate; (ii) cells 2 to 4 times longer than wide were described as oblong when sides were nearly parallel or elliptic when not; (iii) cells >4 to <8 times longer than wide were characterized as elongated, and (iv) cells ≥8 to <21 times longer than wide were described as linear. The morphology of anticlinal cell walls (linear, undulate, sinuous) was described when clearly visible. However, many published images of Fuireneae nutlet epidermal cells do not have the periclinal cell wall removed. This means that the morphology of anticlinal cell walls at their suture with periclinal walls could differ from the morphology observed when the periclinal wall is removed (cf. Figs. 1B, 1D to 1F, 1H in Browning et al., 1996). Consequently, this character was described, but not used in making taxonomic decisions.

Scanning electron microscopy (SEM) of the nutlet epidermal cell shape of *Pseudoschoenus inanis* and *Schoenoplectus scirpoides* (Schrad.) Browning (section *Schoenoplectus*) was also performed, as data were lacking for this

genus and species. Micrographs of fruit epidermal cells were obtained at the Electron Microscope Unit at the University of Cape Town. Nutlets were removed from specimens housed at the Bolus Herbarium (BOL; Thiers, continuously updated), sputter-coated, and images were made using Tescan MIRA3 equipment.

# 3 Results

### 3.1 Quality of the targeted sequencing data

Recovery statistics are available in Table S4 and Fig. S2. The average percentage recovery was 50% (4%–78% range). For the exon data set, the alignment length per gene ranged from 99 to 4341 bp long, with a mean length of 928 bp before trimming, and from 6 to 2320 bp long, with a mean length of 311 bp after trimming (Tables S5A, S6A). For the supercontigs data set, the alignment length per gene ranged from 285 to 27 545 bp long, with a mean length of 6323 bp before trimming, and from 2 to 3269 bp long, with mean length of 488 bp after trimming (Tables S5B, S6B). Therefore, the amount of data retrieved in the supercontigs data set was much larger when comparing the length of the contigs, 166 431 bp vs. 104 349 bp for the exons data set (Table S6), and the total number of parsimony-informative sites (PIS) was also higher (c. 2.2× more PIS) in the supercontigs vs. the exons data set. Nonetheless, before trimming, the relative number of PIS was c. 0.3 PIS/bp for both the exons and supercontigs data sets. However, as a result of the chosen trimming strategy, it was c. 0.4 and 0.5 PIS/bp, respectively, meaning that the contig length is positively correlated with the number of PIS.

### 3.2 Relationships in tribe Fuireneae s.l. as inferred from targeted sequencing data

As the topologies obtained from all analyses were very similar, we only provide a summary of the relationships shown in the tree resulting from the multi-species summary coalescent approach on the supercontigs data set (Fig. 3). The results of the other analyses are presented in Figs. S3–S5. We retrieved a topology showing an Abildgaardieae–Eleocharideae Clade as sister to a Fuireneae s.l. grade, leading to a monophyletic tribe Cypereae. Within the Fuireneae s.l. grade, *Bolboschoenus* is sister to the remaining Fuireneae s.l. grade lineages plus Cypereae, followed by a monophyletic *Fuirena*, the Schoenoplectus Clade, and the Schoenoplectiella Clade. The nodes in the backbone of the phylogeny and for each major clade are well supported with high local posterior probabilities (LPP) and generally high gene tree concordance (Fig. 3).

### 3.3 Relationships in *Fuirena*

Within *Fuirena*, two well-supported clades are visible (Fig. 3): (i) the Pentasticha Clade comprising all species with three-angled stems that roughly corresponds to subg. *Pentasticha* with the addition of some anomalous species with a variable perianth morphology, and (ii) the Fuirena Clade that comprises all species with a relatively stable 3 + 3 perianth placed in subg. *Fuirena*. The Fuirena Clade is subdivided into two well-supported sister subclades: (i) the Umbellata Subclade with the type *F. umbellata* Rottb. and some closely related species with highly compound, corymbiform inflorescences (*F. robusta* Kunth, *F. camptotricha* C.Wright), and (ii) the Squarrosa subclade comprising all other species of subg. *Fuirena* with generally depauperate inflorescences reduced to a single or two to three glomerules of spikelets.

### 3.4 Exploring the monophyly of *Schoenoplectus* and *Schoenoplectiella* using nrDNA

The full sampling alignment included 137 accessions and had a total aligned length of 15 625 characters (Data S1), whereas the reduced sampling alignment included 62 accessions and 12 401 characters (Data S2). The phylogenetic hypothesis obtained for the full sampling alignment is available in Fig. S6. It shows an Abildgaardieae–Eleocharideae Clade as sister to a Fuireneae s.l. grade + Cypereae Clade. Within the Fuireneae s.l. grade, the four major lineages are retrieved as monophyletic: (i) *Bolboschoenus*; (ii) *Fuirena*; (iii) the Schoenoplectus Clade (*Actinoscirpus* + *Schoenoplectus* s.s.), and (iv) the Schoenoplectiella Clade (*Pseudoschoenus* + *Schoenoplectiella* s.l., which includes a group of largely African *Schoenoplectus* species nested in *Schoenoplectiella*). However, nodes in the backbone of the grade are not well supported, resulting in uncertain relationships among these four major clades.

The phylogenetic hypothesis obtained for the reduced sampling alignment is available in Fig. 4. It shows two well-supported clades: (i) the Schoenoplectus Clade (*Actinoscirpus* + *Schoenoplectus* s.s.), and (ii) the Schoenoplectiella Clade (*Pseudoschoenus* + *Schoenoplectiella* s.l.). Within *Schoenoplectus*, sections *Malacogeton* and *Schoenoplectus* are both retrieved as monophyletic. Within *Schoenoplectiella*, section *Schoenoplectiella* is retrieved as paraphyletic with respect to a grade of African *Schoenoplectus* species transferred below to *Schoenoplectiella* (indicated as "new group" in Fig. 4; see Section 5). The crown clade consists of a monophyletic *Schoenoplectiella* section *Actaeogeton*.

Several species in the ITS tree were not monophyletic (*Schoenoplectus triqueter*, *S. mucronata*). However, this was not treated in the Discussion (Section 4), because multiple samples for these species could not be included in our targeted sequencing analysis (ITS taken from Genbank), the bootstrap support for the key branch separating *S. mucronata* samples was low (59%), and two of the three samples of *Schoenoplectus triqueter* were found in the same clade as *S. tabernaemontani*, a species with which it is known to form hybrids (e.g., Smith, 2002).

### 3.5 Embryo morphology

All members of Fuireneae s.l. possess embryos with a more or less mushroom-shaped or top-shaped outline, with leaf primordia in a basal position and a lateral displacement of the root cap (Fig. 5). While rare in the family, fungiform embryos are also typical for tribe Eleocharideae and are sometimes found in some of the largest Abildgaardieae embryos, suggesting that this special morphology is a plesiomorphy for Fuireneae s.l. (Semmouri et al., 2019). Nonetheless, subtle differences can be found among the different clades, and these differences are supported by geometric morphometrics. The MANOVA based on the first three principal components of embryo size + shape (representing 70% of the total variation) found significant

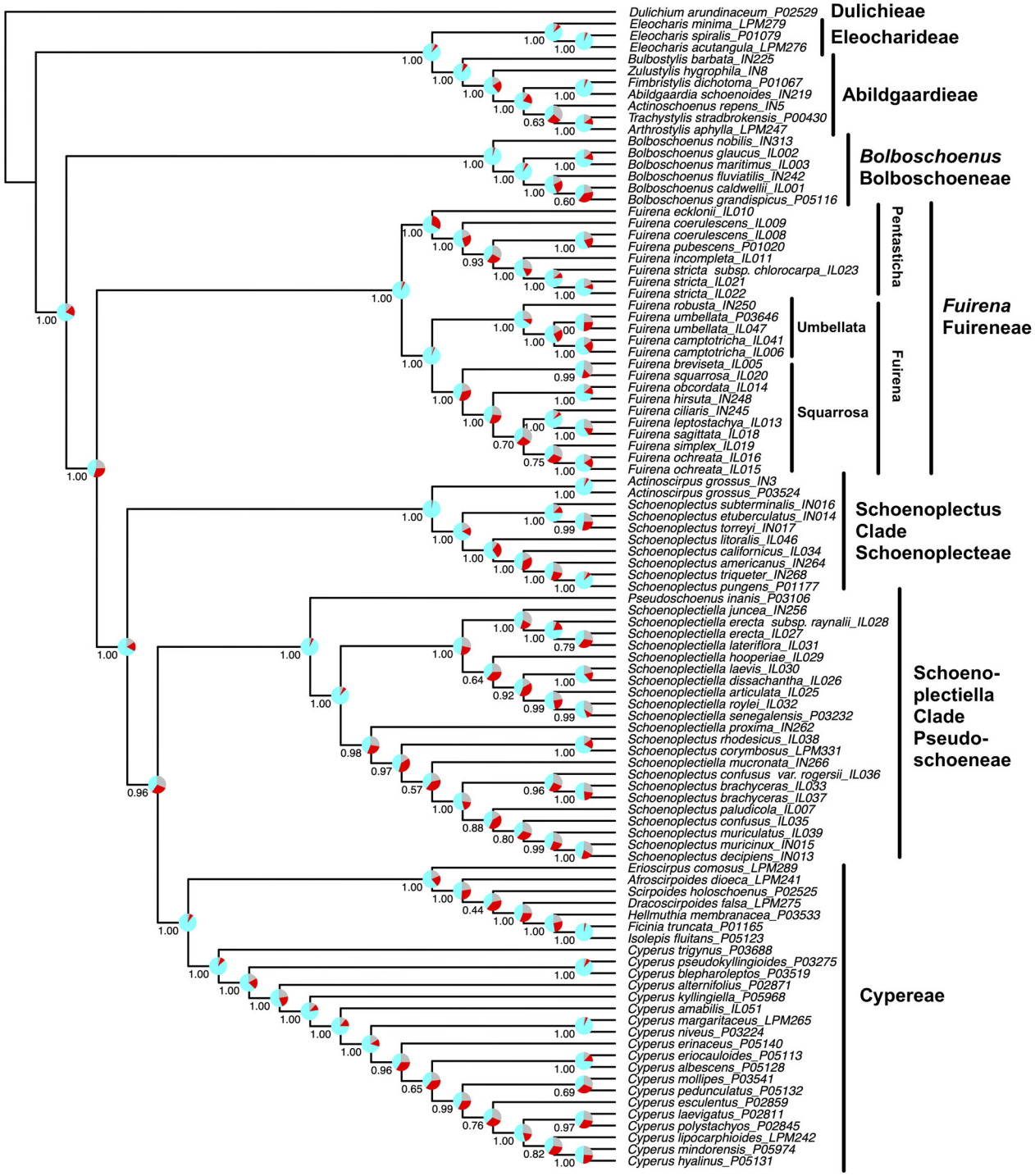


**Fig. 3.** Phylogenetic reconstruction of relationships in tribe Fuireneae s.l. and related tribes based on analysis of the supercontigs data set. Species tree inferred in ASTRAL from RAxML gene trees. Numbers on branches represent local posterior probabilities (LPPs) and pie charts at nodes correspond to quartet support with blue for agreeing genes, red for disagreeing genes, and gray for uninformative genes.

differences between the four clades ($P < 0.0001$), and a linear discriminant analysis on the full size + shape data showed a good separation of the clades and no overlap (Fig. 6).

*Bolboschoenus* has the largest embryos in Fuireneae s.l. (Table 1), with at least two species possessing embryos over a millimeter in length and more than half a millimeter in width. The embryo of *Bolboschoenus* is fungiform, with a broadened, rhomboid scutellum (Figs. 5, 6). The root cap is well differentiated, in a lateral position, and separated from the scutellum by a notch. The first leaf is well developed,

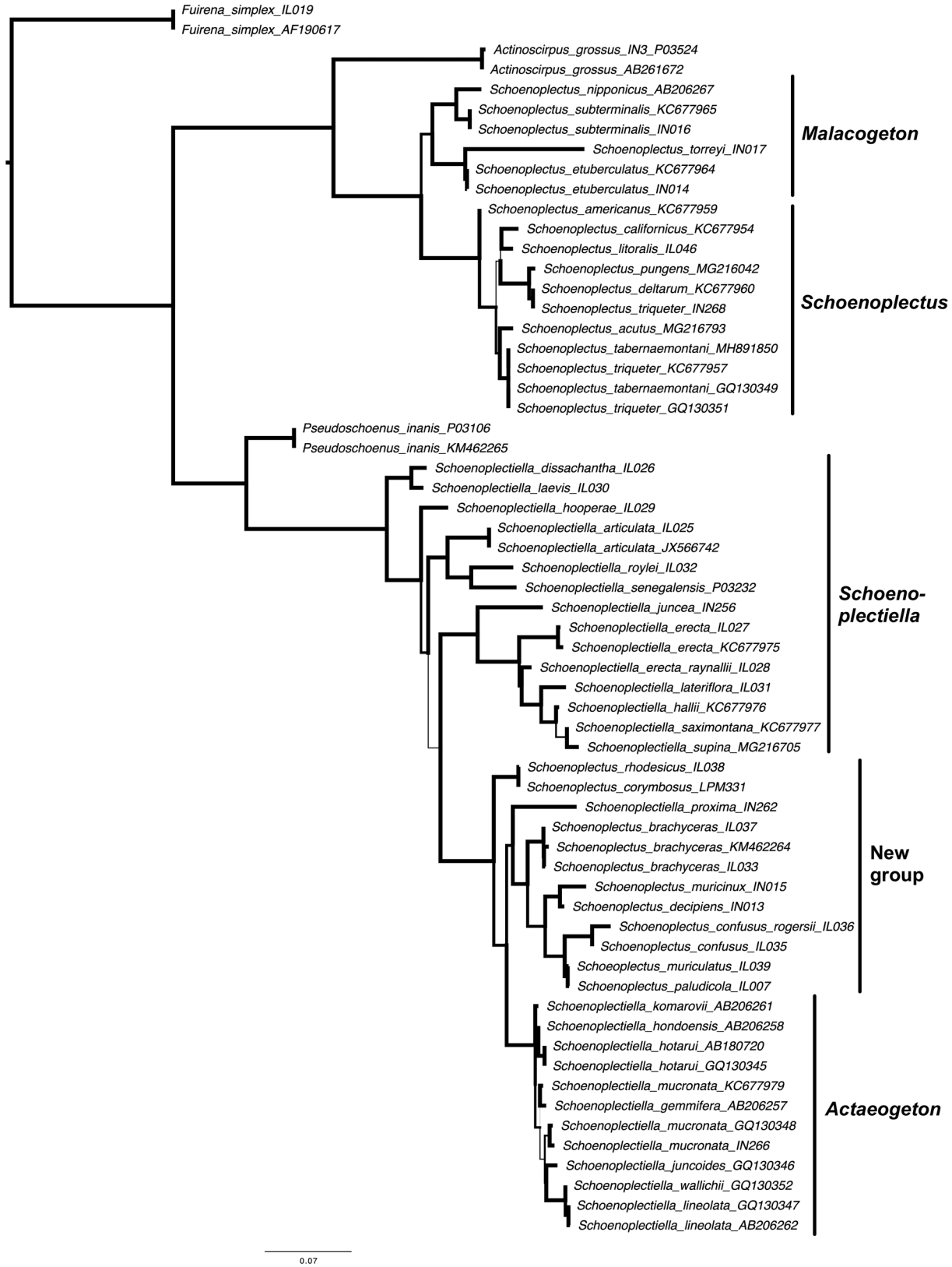


**Fig. 4.** Continued

second and third leaf primordia are present in a basal orientation. The germ pore is slit-like and in a parallel orientation, relative to the first plumular leaf primordium. As stated in Semmouri et al. (2019), these character states correspond most closely to the Bolboschoenus-type embryo, as defined by the typology of Goetghebeur (1986), and variant 1 of the *Scirpus*-type embryo of Van der Veken (1965), as noted by Pignotti (2003).

In length, the embryos of *Fuirena* are the smallest (Table 1), more than three standard deviations smaller in length than the mean of all other Fuireneae s.l. embryos, except *Actinoscirpus* (2.25 standard deviations), and from one to over six standard deviations narrower than other Fuireneae s.l. genera at their widest point. *Fuirena* embryos always displayed length to width ratios below 1.1, a consequence of their roughly turbinate shape, and their horizontally broadened scutellum comprised 40%–60% of the total length of the embryo. In contrast, the embryos of *Actinoscirpus*, *Pseudoschoenus*, *Schoenoplectus*, and *Schoenoplectiella* frequently had length to width ratios above 1.1 (up to 2.0) due to their more elongate fungiform outline and their scutellum comprised only 30%–50% of the total length of the embryo. Moreover, in these genera, the left (or upper) coleoptile lip is strongly outgrown (less so in *Fuirena*) and a second leaf primordium is always present (absent or poorly developed in *Fuirena* species). Given the numerous morphological differences of *Fuirena* embryos noted here, we consider these differences sufficient to recognize the *Fuirena* embryo as a distinct type within the typology scheme of Goetghebeur (1986; i.e., Fuirena-type).

Although *Actinoscirpus*, *Pseudoschoenus*, *Schoenoplectus*, and *Schoenoplectiella* possess very similar embryos (Figs. 5, 6), two groups can be distinguished, which we designate here as *Schoenoplectus*-type I and *Schoenoplectus*-type II given their similarity. Whereas the scutellum in *Actinoscirpus* and *Schoenoplectus* s.s. is turbinate to rhomboid in shape, with straight to convex lower margins, the scutellum of *Pseudoschoenus* and *Schoenoplectiella* is often umbonate, with a distinct knob at the apex, or strongly pileate, with the margins clearly incurved (*Schoenoplectus*-type II). These two groups correspond to the taxonomically significant embryo variants 2 and 3 of the *Scirpus*-type embryo *sensu* Van der Veken (1965) highlighted by Pignotti (2003). Of the nine species of African *Schoenoplectus* nested within our Schoenoplectiella Clade, Van der Veken (1965) includes embryographs for three of these: *Schoenoplectus rhodesicus*, *S. paludicola*, and *S. muricinux*. All three possess strongly pileate, *Schoenoplectus*-type II embryos (Figs. 5, 6), and are more consistent in size with species of *Schoenoplectiella* than *Schoenoplectus* (Table 1). In summary, four groups of embryos are distinguished within Fuireneae s.l. and each corresponds to one of the four major clades retrieved in molecular studies, here recognized as tribes. While no embryo of *Schoenoplectus* section *Malacogeton* has been studied, it seems rather probable that these species also display a *Schoenoplectus*-type I embryo since this is the embryo displayed by both *Actinoscirpus* and *Schoenoplectus* section *Schoenoplectus*.

### 3.6 Nutlet epidermal cell micromorphology

Nutlet epidermal cell shape was isodiametric in all species of *Bolboschoenus* examined (eight species; length to width range 1.00–1.67, mean = 1.22; Tables 2, S7). Anticlinal cell walls for *Bolboschoenus* ranged from straight to undulate.

Cell shape in *Fuirena* was more variable than in *Bolboschoenus* (length to width range 1.01–7.23, mean = 3.42; Tables 2, S7). Among the studied species, three possessed roughly isodiametric cells, whereas four displayed oblong to elongated cells, often in transverse rows. The morphology of anticlinal cell walls in *Fuirena* ranged from straight to undulate.

Most species in the Schoenoplectus Clade (*Schoenoplectus* + *Actinoscirpus*; 12 species examined; Table S7; Fig. 7) displayed isodiametric to oblong or elliptic cells (length to width range 1.05–3.86, mean = 2.15; Table 2), except *S. nipponicus*, the only member of *Schoenoplectus* section *Malacogeton* examined, which possessed elongated cells (length to width 6.32; Tables 2, S7). Within the Schoenoplectus Clade, anticlinal cell walls ranged from straight or slightly undulate in most *Schoenoplectus* section *Schoenoplectus* species, to highly sinuous in *Actinoscirpus* and *Schoenoplectus nipponicus* (section *Malacogeton*).

Cell shape for members of the Schoenoplectiella Clade was nearly uniform (28 species examined; Table S7; Fig. 7). All species possessed linear epidermal cells (length to width range (8.00–)9.22–20.21, mean = 13.87; Table 2) in longitudinal rows, except *Pseudoschoenus inanis*, which displayed isodiametric to oblong cells (length to width range 1.45–3.81, mean = 2.73; Table 2). Anticlinal cell walls in the clade ranged from straight to slightly undulate in almost all species. The linear cells of *Schoenoplectiella* are clearly associated with the wavy, transversely ridged nutlets of annuals from *Schoenoplectiella* section *Schoenoplectiella* (Fig. 7L), but linear cells are also seen in the large perennial species of *Schoenoplectiella* from section *Actaeogeton* regardless of whether the nutlet is sculpted (e.g., *S. mucronata*, *S. juncoides*) or smooth (e.g., *S. lineolata*, *S. wallichii*) (see Table S7). Longitudinally linear epidermal cells were also present in all the African *Schoenoplectus* (8 species) nested within the Schoenoplectiella

**Fig. 4.** Phylogenetic reconstruction of relationships in the Schoenoplectus and Schoenoplectiella Clades based on nrDNA data. The Schoenoplectus Clade comprises the genera *Actinoscirpus* and *Schoenoplectus*, with *Schoenoplectus* divided into two clades, sections *Schoenoplectus* and *Malacogeton*. The Schoenoplectiella Clade consists of the genera *Pseudoschoenus* and *Schoenoplectiella*, with *Schoenoplectiella* section *Schoenoplectiella* paraphyletic with respect to a grade of largely African *Schoenoplectus* species here transferred to *Schoenoplectiella* that is terminated by a monophyletic *Schoenoplectiella* section *Actaeogeton*. The reconstruction is based on an RAxML analysis of the reduced sampling alignment with 62 accessions obtained from nrDNA off-target reads and ITS sequences available from GenBank. Branch thickness represents bootstrap support (values are provided in Fig. S6).

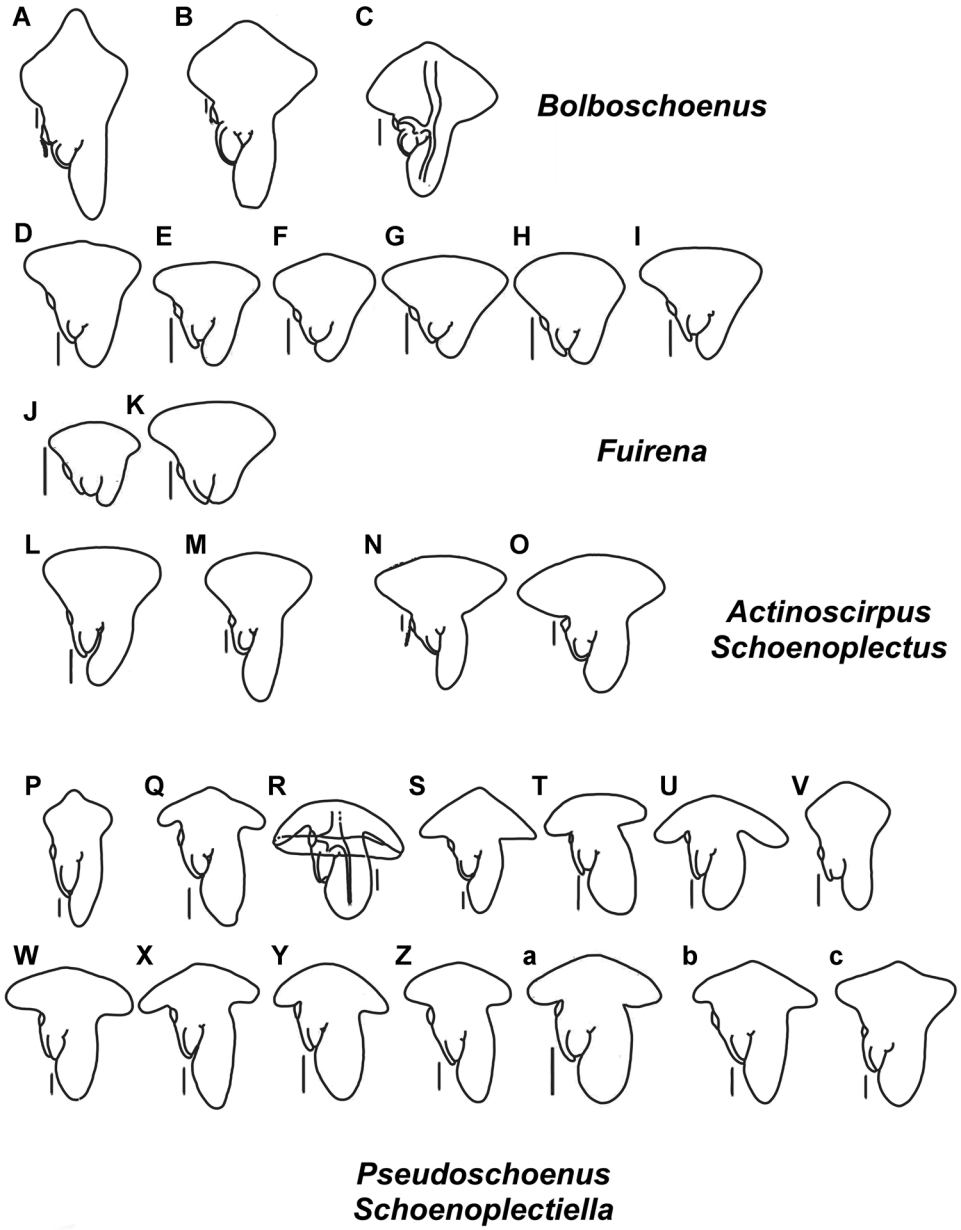


**Fig. 5.** Embryographs of the genera of Fuireneae s.l. *Bolboschoenus*: **A**, *B. fluviatilis* (Torr.) Soják; **B**, *B. maritimus* (L.) Palla; **C**, *B. grandispicus* (Steud.) Lewej. & Lobin; *Fuirena*: **D**, *F. abnormalis* C.B.Clarke; **E**, *F. ciliaris* (L.) Roxb.; **F**, *F. incompleta* Nees; **G**, *F. pachyrrhiza* Ridl.; **H**, *F. scirpoidea* Michx.; **I**, *F. stricta* Steud.; **J**, *F. trilobites* C.B.Clarke; **K**, *F. umbellata* Rottb.; *Actinoscirpus* and *Schoenoplectus*: **L**, *A. grossus* (L.f.) Goetgh. & D.A.Simpson; **M**, *S. californicus* (C.A.Mey.) Soják; **N**, *S. lacustris* (L.) Palla; **O**, *S. litoralis* (Schrad.) Palla; *Pseudoschoenus* and *Schoenoplectiella*: **P**, *P. inanis* (Thunb.) Oteng-Yeb; **Q**, *S. dissachantha* (S.T.Blake) Lye; **R**, *S. juncea* (Willd.) (S); **S**, *S. juncoides* (Roxb.) Lye; **T**, *S. laevis* (S.T.Blake) Lye; **U**, *S. lateriflora* (J.F.Gmel.) Lye; **V**, *S. lineolata* (Franch. & Sav.) J.Jung & H.K.Choi; **W**, *S. mucronata* (L.) J.Jung & H.K.Choi; **X**, *S. praelongata* (Poir.) Lye; **Y**, *S. roylei* (Nees) Lye; **Z**, *S. smithii* (A.Gray) Hayas.; **a**, *S. vohemarensis* (Cherm.) Lye; **b**, *S. paludicola* (Kunth) Palla; **c**, *S. rhodesicus* (Podlech) Lye). Scale bars 100 μm. See Data S3 for the voucher information of the studied embryographs.

Clade (length to width range 15.25–19.56, mean = 16.77; Table 2) for which data was available regardless of whether pericarp surface features were present (*S. muricinux*, *S. muriculatus*, *S. confusus*, Browning, 1991a; Gordon-Gray, 1995; *S. dissachantha*, Hayasaka, 2009) or absent (*S. brachyceras*, *S. corymbosus*, Browning, 1991b; Gordon-Gray, 1995; *S. paludicola*, *S. decipiens*, Browning, 1990; Gordon-Gray, 1995). Two further species of African *Schoenoplectus* not included in our molecular analyses possessed linear epidermal cells in longitudinal rows, *S. pulchellus* (Browning, 1990) and *S. heptangularis* (Jiménez-Mejías & Cabezas, 2009). These species will be treated in *Schoenoplectiella* (see Section 5).

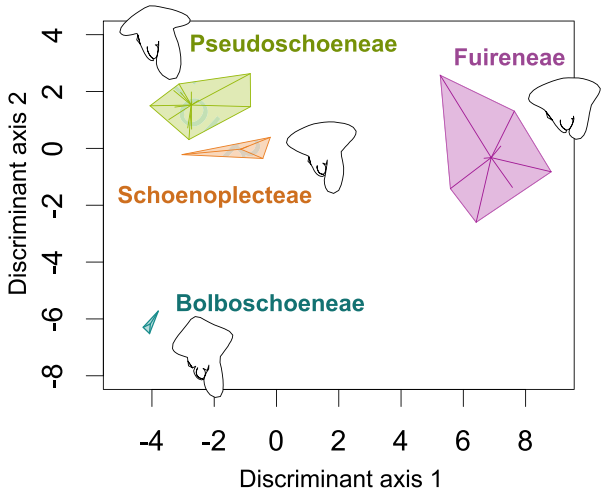


**Fig. 6.** Linear discriminant analysis of embryo size + shape, with each major lineage represented by a convex hull with a distinct color. Embryographs represent the average shape of each major lineage as calculated from group centroids, illustrating the main embryological characters used to delineate the groups.

## 4 Discussion

### 4.1 The Fuireneae s.l. grade consists of six genera and four tribes

As in earlier molecular phylogenetic studies (e.g., Shiels et al., 2014; Spalink et al., 2016; Glon et al., 2017; Semmouri et al., 2019), tribe Abildgaardieae + tribe Eleocharideae form a clade that is sister to the Fuireneae Grade + tribe Cypereae. Our results (Fig. 3) indicate that tribe Fuireneae is a grade of six genera arranged into four major clades that are successive sisters to tribe Cypereae: (i) the genus *Bolboschoenus*; (ii) followed by *Fuirena*; (iii) the Schoenoplectus Clade consisting of *Actinoscirpus* + *Schoenoplectus* s.s., and (iv) the Schoenoplectiella Clade containing *Pseudoschoenus*, *Schoenoplectiella* s.l., and a collection of largely African *Schoenoplectus* species nested in *Schoenoplectiella*. Although all previous molecular analyses have also found Fuireneae s.l. to consist of a grade and have often recovered the same major clades as in our analyses, topological relationships among these major clades have been inconsistent and support for the backbone of trees has been weak. Even in Glon et al. (2017), who used seven markers and obtained the same topology we infer here, the node separating *Bolboschoenus* from *Fuirena*, as well as the node placing the Schoenoplectiella Clade as sister to Cypereae, had very low support in maximum parsimony, maximum likelihood, and Bayesian analyses. Moreover, like all previous analyses that used novel data, the analysis of Glon et al. (2017) included only a fraction of tribal diversity (18 spp. or 12%; others 10–25 spp.). This explains why no taxonomic changes to the circumscription of Fuireneae s.l. have taken place to date, despite ample evidence from previous molecular analyses that the group was not natural.

In our analyses, which include nearly a third of Fuireneae s.l. diversity and numerous generic and infrageneric types (Table S2), statistical support is strong for the backbone of trees and for all four Fuireneae s.l. clades and their six genera. Consequently, we can firmly reject the monophyly of Fuireneae s.l. (Muasya et al., 1998, 2009a; Simpson et al., 2007) or the idea that *Bolboschoenus* cannot be separated from *Schoenoplectus* s.s. (e.g., Lye, 1971a; Haines & Lye, 1983; Tucker, 1987; Strong, 1994). Branch support (in all analyses) and branch lengths (in the concatenated maximum likelihood analyses) clearly indicate that Fuireneae s.l. forms a grade of successive sisters terminating with tribe Cypereae. Moreover, morphology, anatomy, embryo features (Goetghebeur & Simpson, 1991; Tatanov, 2007), and even fungal parasites (Savile, 1972; Léveillé-Bourret et al., 2021) suggest a distant relationship between *Bolboschoenus* and *Schoenoplectus* s.s. Likewise, the genus *Fuirena* is monophyletic and very strongly supported as in previous molecular analyses (e.g., Hinchliff et al., 2010; Spalink et al., 2016; Glon et al., 2017). This is not surprising as many characters, such as terminal racemose or paniculate inflorescences, nodose leafy stems, and peculiar perianth-segments (often unguiculate in form) supported it as an independent genus (Kral, 1978; Haines & Lye, 1983; Goetghebeur, 1998) and potentially a tribe (Haines & Lye, 1983; Tatanov, 2007). Our molecular analyses further support the recognition of the monotypic genera *Actinoscirpus* and *Pseudoschoenus* as each taxon possesses numerous molecular autapomorphies, which is consistent with a series of morphological, anatomical, and embryo features that suggest they represent genera worthy of taxonomic recognition (Oteng-Yeboah, 1974b; Goetghebeur, 1986; Goetghebeur & Simpson, 1991). Their generic status is further supported by the fact they are each sister to strongly supported and morphologically distinct clades that we here recognize as monophyletic genera, *Schoenoplectus* s.s. and *Schoenoplectiella* s.l. Although these genera share numerous overlapping characters that can make identification difficult, we confirm

**Table 1** Size differences among embryos of Fuireneae s.l. genera

| Genus | Species (*n*) | Length, (mean ± SD) | Width (mean ± SD) | Ratio (L:W) |
|---|---|---|---|---|
| *Bolboschoenus* | 3 | 987.4 ± 302.4 | 649.2 ± 188.6 | 1.52 |
| *Fuirena* | 8 | 272.4 ± 60.0 | 288.3 ± 56.4 | 0.94 |
| *Actinoscirpus* | 1 | 407.6 ± n/a | 347.1 ± n/a | 1.17 |
| *Schoenoplectus* s.s. | 3 | 676.2 ± 96.1 | 622.2 ± 145.2 | 1.09 |
| *Pseudoschoenus* | 1 | 716.4 ± n/a | 352.2 ± n/a | 2.03 |
| *Schoenoplectiella* | 10 | 478.5 ± 134.3 | 424.4 ± 149.0 | 1.13 |
| *Schoenoplectus* → *Schoenoplectiella* | 3 | 579.8 ± 70.3 | 483.2 ± 44.0 | 1.20 |

Embryographs were measured for length and width at their widest point using ImageJ. Measurements in μm.

**Table 2** Ratios of fruit epidermal cell length to width

| Genus | Taxa (*n*) | Ratio, range | Ratio, mean ± SD |
|---|---|---|---|
| *Bolboschoenus* | 8 | 1.00–1.67 | 1.22 ± 0.23 |
| *Fuirena* | 7 | 1.01–7.23 | 3.42 ± 2.19 |
| *Actinoscirpus* | 1 | 2.86 | n/a |
| *Schoenoplectus* s.s. | 12 | 1.05–3.86(–6.32) | 2.15 ± 1.35 |
| *Pseudoschoenus* | 1 | 1.45–3.81 | 2.73 ± 1.19 |
| *Schoenoplectiella* | 11 | (8.00–)9.22–20.21 | 13.87 ± 3.66 |
| *Schoenoplectus* → *Schoenoplectiella* | 5 | 15.25–19.56 | 16.77 ± 2.51 |

The largest measurement was always taken as length. More than one cell was measured for *Pseudoschoenus* due to variability.

that each possesses distinct combinations of embryo and micromorphological characters that support their separation. In fact, all four major clades in the Fuireneae s.l. grade can be distinguished by a combination of embryo and micromorphological features, and when this is evaluated within the context of considerable molecular and morphological support, it suggests that each major Fuireneae s.l. clade is best treated as a distinct tribe.

All four major Fuireneae s.l. clades can be distinguished by embryo morphology, a feature acknowledged as being among the most phylogenetically informative characters in sedges at the tribal (e.g., Goetghebeur, 1986; Léveillé-Bourret & Starr, 2019; Semmouri et al., 2019), generic (e.g., Gilmour et al., 2013; Léveillé-Bourret et al., 2015, 2020), or even infrageneric (Larridon et al., 2011) levels. In the case of taxa currently treated in Fuireneae s.l., Van der Veken (1965) recognized three variants of his Schoenoplectus-type embryo that had taxonomic significance (Pignotti, 2003). All three of these variants correspond to natural groups in our analyses, and we here recognize a fourth variant to account for the small embryos of *Fuirena* (on average 135.2 μm shorter and 58.8 μm narrower than *Actinoscirpus*, the next smallest Fuireneae s.l. embryo; Table 1) where a second leaf primordium is either absent or poorly developed and the hypocotyl is only slightly longer than the scutellum. *Bolboschoenus* is unique in having the largest embryos in the tribe (on average 987.4 μm long, 649.2 μm wide; Table 1), and in possessing a plumule where a third primordial leaf develops and a notch is present below the root cap (i.e., variant 1 *sensu* Van der Veken, 1965; Bolboschoenus-type *sensu* Goetghebeur, 1986; Semmouri et al., 2019). Interestingly, the close relationships between the genera *Actinoscirpus* and *Schoenoplectus* s.s. (Schoenoplectus Clade), and between *Pseudoschoenus* and *Schoenoplectiella* s.l. (including tropical, largely African *Schoenoplectus*; the Schoenoplectiella Clade), are also supported by embryo morphology (Fig. 5). Whereas the scutellum in *Actinoscirpus* and *Schoenoplectus* s.s. is turbinate to rhomboid in shape (variant 2 *sensu* Van der Veken, 1965), species in the Schoenoplectiella Clade possess an umbonate or strongly pileate scutellum in the form of a mushroom cap with incurved margins (variant 3 *sensu* Van der Veken, 1965).

In part, these relationships are further supported by the shape of epidermal nutlet cells (Fig. 7). Whereas all species in the Schoenoplectus Clade possess epidermal nutlet cells that are isodiametric to oblong or elliptic, except *Schoenoplectus nipponicus* (elongated), the cells in every species of the Schoenoplectiella Clade are linear, with the exception of *Pseudoschoenus inanis* (isodiametric to oblong). Cell shape thus clearly separates species in the Schoenoplectus Clade from *Schoenoplectiella*, where cells in longitudinal rows can be as much as 20 times longer than wide. In fact, among Fuireneae s.l. species as a whole, only the elongated cells of *Fuirena ciliaris* (7.23 times longer than wide) can even come close to the species of *Schoenoplectiella* with the least linear of cells, *S. articulata* (8.00 times longer than wide), and in this case, there is a clear morphological difference: the elongated cells of *F. ciliaris* are in transverse rows, whereas the linear cells of *S. articulata*—and of *Schoenoplectiella* as a whole—are longitudinally arranged. It is also important to note that although linear epidermal cells are clearly associated with the many small annual members of *Schoenoplectiella* whose nutlets are typically dark at maturity and display distinct, wavy rows of transversely orientated ridges (roughly equivalent to section *Schoenoplectiella*), even smooth nutlets in some large perennial species of *Schoenoplectus* possess these linear cells (Haines & Lye, 1983; Gordon-Gray, 1995). Although Van der Veken (1965) was unaware of this cell shape character, he circumscribed *Scirpus* section *Actaeogeton* (=*Schoenoplectiella* section *Actaeogeton*) to include not only its traditionally large perennials, but also the small annuals of *Scirpus* section *Supini* (=*Schoenoplectiella* section *Schoenoplectiella*) because they all shared strikingly pileate embryos.

Not only can we confirm that all the *Schoenoplectus* species nested within *Schoenoplectiella* s.l. in our analysis possess these distinctively shaped pileate embryos when data is available (i.e., *Schoenoplectus rhodesicus*, *S. paludicola*, *S. muricinux* (C.B.Clarke) J.Raynal), they also possess longitudinally linear epidermal cells regardless of whether the surface is rugose (*S. muricinux*) or smooth (*S. paludicola*) (Gordon-Gray, 1995). The pattern holds even when embryo data is lacking. For the tropical, largely African *Schoenoplectus* species nested in *Schoenoplectiella* s.l. that lack embryo data, but whose epidermal cell shape is known, all species possess longitudinally linear cells regardless of nutlet pericarp texture (smooth in *S. corymbosus* (Roth ex Roem. & Schult.) J.Raynal, *S. brachyceras* (Hochst. ex A.Rich.) Lye, *S. decipiens* (Nees) J.Raynal; vs. rugose in *S. confusus* (N.E.Br.) Lye and *S. muriculatus* (Kük.) Browning; Haines & Lye, 1983; Browning, 1991a, 1991b; Gordon-Gray, 1995). Because embryo and cell shape appear to be such consistently important taxonomic characters, we are confident that *Schoenoplectus* species not included in our

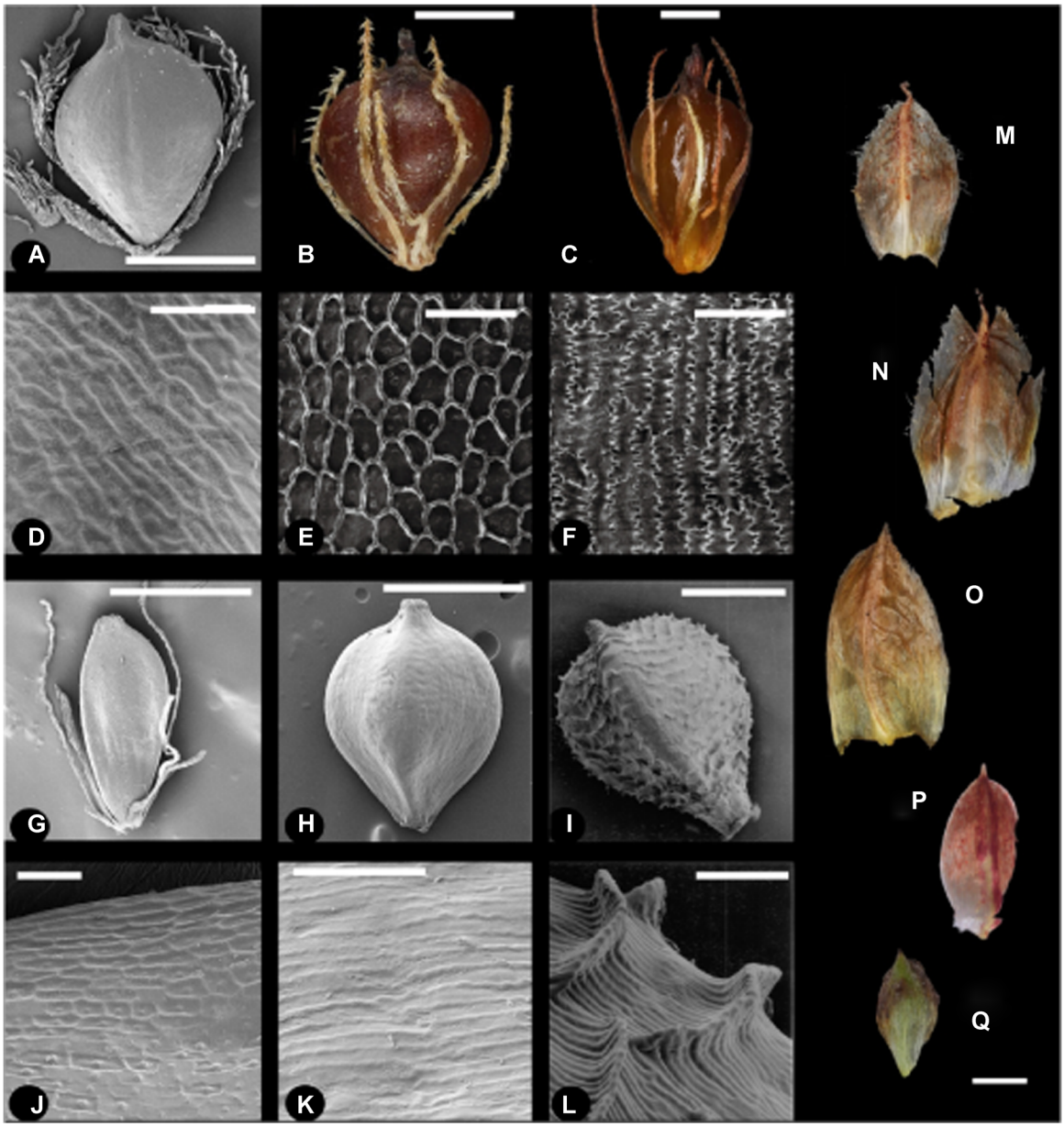


**Fig. 7.** Nutlets and glumes of species of the Schoenoplectus Clade and the Schoenoplectiella Clade. **A**, Scanning electron microscopy (SEM) micrograph of a nutlet, including perianth bristles of *Schoenoplectus scirpoides* (Schrad.) Browning (section *Schoenoplectus*). **B**, light microscopy image of a nutlet, including perianth bristles of *Schoenoplectus acutus* (Muhl. ex Bigelow) Á.Löve & D.Löve (section *Schoenoplectus*). **C**, light microscopy image of a nutlet, including perianth bristles of *Schoenoplectus torreyi* (Olney) Palla (section *Malacogeton*). **D**, SEM micrograph of the nutlet surface of *S. scirpoides*. **E**, SEM micrograph of the nutlet surface of *Schoenoplectus lacustris* (L.) Palla (section *Schoenoplectus*). **F**, SEM micrograph of the nutlet surface of *Schoenoplectus nipponicus* (Makino) Soják (section *Malacogeton*). **G**, SEM micrograph of the nutlet, including perianth bristles and stamen filaments of *Pseudoschoenus inanis* (Thunb.) Oteng-Yeb. (Schoenoplectiella Clade). **H**, SEM micrograph of the nutlet of *Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) J.Raynal (nested in *Schoenoplectiella* s.l.). **I**, SEM micrograph of the nutlet of *Schoenoplectus muricinux* (C.B.Clarke) J.Raynal (nested in *Schoenoplectiella* s.l.). **J**, SEM micrograph of the nutlet surface of *P. inanis*. **K**, SEM micrograph of the nutlet surface of *S. corymbosus*. **L**, SEM micrograph of the nutlet surface of *S. muricinux*. **M**, glume of *S. acutus*. **N**, glume of *Schoenoplectus heterochaetus* (Chase) Soják (section *Schoenoplectus*). **O**, glume of *S. torreyi* (section *Malacogeton*). **P**, glume of *S. corymbosus*. **Q**, glume of *Schoenoplectiella smithii* (A.Gray) Hayas (section *Actaeogeton*). **A**–**C**, **G**–**I**, and **M**–**Q**, scale bar = 1 mm; **D**–**F** and **J**–**L**, scale bar = 50 μm. Samples in **E** and **F** have been treated and the upper periclinal walls removed, displaying the cell lumen with the anticlinal walls entirely exposed. **A**, **G**, **H**, **J**, **K** newly generated for this study by Muthama Muasya; **B**, **C**, **M**–**O**, **Q**, reproduced with permission from www.minnesotawildflowers.info; **D**, **I**, **L** reproduced with permission by Jane Browning (originally published in Gordon-Gray, 1995); **E**, **F** reproduced with permission from Hayasaka (2012); **P** newly generated for this study by P. Jiménez-Mejías.

molecular analyses with one or more of these characters are most likely nested in *Schoenoplectiella* and should be transferred to it. For example, although we did not include *Schoenoplectus heptangularis* Cabezas & Jim.Mejías and *S. pulchellus* (Kunth) J.Raynal in our molecular analyses, these species possess longitudinally linear epidermal nutlet cells. Given this character and the fact that we included species deeply nested in *Schoenoplectiella* to which they are morphologically close (i.e., *S. paludicola* and *S. decipiens* for *S. pulchellus*, Browning, 1990; *S. brachyceras*, *S. corymbosus* and *S. decipiens* for *S. heptangularis*, Jiménez-Mejías & Cabezas, 2009), we are confident these species should be transferred to *Schoenoplectiella*. Likewise, we are confident that two further African species not in our analyses, *Schoenoplectus scirpoides* and *S. subulatus* (Vahl) Lye, should not be transferred to *Schoenoplectiella* because they clearly show a morphological affinity to species in our analyses from *Schoenoplectus* sect. *Schoenoplectus* (e.g., *S. litoralis* (Schrad.) Palla; Browning et al., 1994). In addition, at least one of these species, *S. scirpoides* (Fig. 7D), is known to possess roughly isodiametric to oblong epidermal nutlet cells similar to other species of *Schoenoplectus* like *S. litoralis*, its close relative.

Although the circumscription of the widespread genera *Schoenoplectus* and *Schoenoplectiella* has been difficult, this was largely due to the fact that both taxonomic and molecular studies were often regional in scope. The taxonomic studies of Smith and Hayasaka (e.g., Smith & Hayasaka, 2001, 2002; Hayasaka, 2012) focused on North American and East Asian species; Luceño and Jiménez-Mejías on the Iberian Peninsula (Luceño & Jiménez-Mejías, 2008); Pignotti and Mariotti on Southwestern Europe (Pignotti, 2003; Pignotti & Mariotti, 2004); Wilson on Australia (e.g., Wilson, 1981), and the studies of Haines and Lye (e.g., Lye, 1971b, 2003; Haines & Lye, 1983), Raynal (e.g., Raynal, 1976a, 1976b) and Browning (e.g., Browning, 1990, 2012; Browning et al., 1995) on predominately African material. Molecular studies show a similar pattern with analyses focused on just Korean (Jung & Choi, 2010) or Japanese species (Yano & Hoshino, 2005b), and even in those studies with a broader geographic scope, poor taxonomic sampling, a lack of African material or low branch support (e.g., Muasya et al., 2009a; Shiels et al., 2014; Glon et al., 2017) meant that the patterns discovered in this study were not detected before.

With the transfer of these African *Schoenoplectus* species to *Schoenoplectiella*, we now have six, well-circumscribed genera arranged in a grade of four major Fuireneae s.l. clades. Here, we choose to recognize these four major clades as tribes as each is strongly supported by molecular characters and each can be clearly defined by morphological, micromorphological, and embryo characters (see tribal diagnoses in Section 5).

The alternative strategy of expanding tribe Cypereae to include all four clades or even just the Schoenoplectiella Clade is not adopted because it would mean adding one to three new embryo types to the circumscription of Cypereae, a large and morphologically variable clade of c. 1130 species that is best defined by its Cyperus-type embryo (Muasya et al., 2009b) or the highly similar but uncommon Ficinia-type embryo (Muasya et al., 2009b; Semmouri et al., 2019). Adding any member of Fuireneae s.l. to Cypereae would make it impossible to define Cypereae by any single embryological or morphological character, creating a tribe defined only by molecular synapomorphies. Although the embryo and nutlet epidermal cell shape characters chosen to differentiate Schoenoplecteae from Pseudoschoeneae are subtle, they are stable and permit tribal and generic assignments to be tested independently of molecular data.

The recent recircumscription of tribe Scirpeae also resulted in a small group of genera whose only consistently shared character was their Schoenus- or Fimbristylis-type embryos (Léveillé-Bourret & Starr, 2019). Macromorphological characters are typically highly homoplastic when studied at higher taxonomic levels in sedges (Bruhl, 1995; Simpson, 1995; Muasya et al., 2000), which means the most recalcitrant clades may need to be defined by obscure but consistent features, in addition to characters that may not be shared by all the taxa in a group (i.e., polythetic) (Larridon et al., 2018; Léveillé-Bourret & Starr, 2019; this study).

### 4.2 The classification of *Fuirena* and the role of perianth characters

The unguiculate tepals of *Fuirena* are one of its most striking characteristics (Goetghebeur, 1998), and previous studies and classifications have accordingly put a strong emphasis on patterns of variation in perianth morphology (Vrijdaghs et al., 2004). While most of the c. 55 species of *Fuirena* have such tepaloid perianth parts, a few possess only bristles, show an intergradation between tepals and bristles, or lack any trace of a perianth (Muasya, 1998). These atypical species have sometimes been interpreted as evidence against recognizing *Fuirena* at the generic level (e.g., Koyama, 1958), although most previous authors concluded that the combination of leafy culms, ciliate ligules, paniculiform inflorescences, "bristly" spikelets, and a unique embryo morphology was strong evidence that *Fuirena* was distinct from all other sedge genera (Kral, 1978; Haines & Lye, 1983; Muasya, 1998). There have also been some early controversies about whether the tepals in *Fuirena* represented the ancestral condition for Cyperaceae, inherited from lilioid ancestors (Raynal, 1973), or whether they were derived from bristles (Koyama, 1958), but one commonality in all infrageneric classifications has been to segregate species with tepaloid perianth parts from those without (Clarke, 1901–02, 1908; Chermezon, 1936; Muasya, 1998).

Our molecular phylogenetic results generally uphold the most recent classification of *Fuirena* proposed by Oteng-Yeboah (1974), which was based on a combination of perianth and vegetative features. Subgenus *Pentasticha* was established for species lacking a tepaloid perianth and possessing 3-angled culms, and it was further subdivided into section *Pseudoscirpus* when bristles were present and section *Pseudoisolepis* when the perianth was absent. Species with a tepaloid perianth and 5-angled or terete culms were placed in subgenus *Fuirena* when cauline leaves were bladed and subgenus *Vaginaria* when they were reduced to sheaths. The first major split seen in our phylogenetic analyses of *Fuirena* puts all species with 3-angled culms and various perianth morphologies, roughly equivalent to subgenus *Pentasticha*, in a natural group sister to another clade containing species with 5-angled or terete culms and a perianth of 3 bristles + 3 tepals that correspond to subgenus *Fuirena*.

Within the Pentasticha Clade, we retrieved a mixture of species that either lacked a perianth (*Fuirena pubescens* (Poir.) Kunth; section *Pseudoisolepis*), possessed a variable number of bristles, tepals, or intermediate forms (*F. ecklonii* Nees, *F. coerulescens* Steud.), or displayed a perianth of bristles alone (*F. incompleta* Nees, *F. stricta* Steud.; section *Pseudoscirpus*). The deeply nested position of section *Pseudoscirpus* refutes previous hypotheses positing that a bristles-only perianth could represent a "transitional" form between *Fuirena* and other scirpoid genera (Koyama, 1958). In contrast, our results suggest tepaloid inner perianth parts to be the ancestral condition in *Fuirena*, although character state reconstructions using a greater taxonomic sampling, including often important infraspecific variation (Gordon-Gray, 1995; Muasya, 1998), would be needed to clarify major morphological trends. Moreover, the polyphyly of accessions identified as *F. coerulescens* in our analyses would be consistent with known polymorphisms in perianth and vegetative characters and the existence of morphological "clusters" within this taxon (Forbes, 1997). Molecular studies on *F. coerulescens* and other morphologically variable species might uncover unsuspected diversity within this poorly studied genus.

Morphological patterns are easier to interpret within the Fuirena Clade (subgenus *Fuirena*; Fig. 3), which is subdivided into two sister subclades with clear diagnostic characters. The first subclade comprises the type *F. umbellata* and a few closely related species possessing highly compound, corymbiform inflorescences, and frequently 5-angled culms (Muasya, 1998; Kral, 1978, 2002). The second subclade comprises all other species of subgenus *Fuirena*, with generally reduced inflorescences of 1–3 glomerules of spikelets and terete culms (Gordon-Gray, 1995; Muasya, 1998; Kral, 2002). These two clades could merit taxonomic recognition if further taxonomic sampling and phylogenetic analyses continue to support the morphological pattern seen here.

Although unrepresented in our molecular analyses, the status of subgenus *Vaginaria* is doubtful given the existence of a possible stabilized hybrid (*F. longa* Chapm.) between the type of subgenus *Vaginaria*, *F. scirpoidea* Michx., and *F. breviseta* (Coville) Coville, a member of subgenus *Fuirena* (Kral, 1978, 2002). However, before a formal revision of the infrageneric classification of *Fuirena* can be proposed, future studies will need to expand taxonomic sampling to cover the diversity seen in all its subgenera and to include as many species as possible with anomalous perianths. This is the necessary first step to better understand the morphological patterns of perianth evolution in this most unusual of sedge genera.

### 4.3 The infrageneric classification and delimitation of *Schoenoplectus* and *Schoenoplectiella*

As one of the largest segregates of *Scirpus* with at least 50 species (Goetghebeur, 1998), an early focus for the genus *Schoenoplectus* was to create an infrageneric classification to divide species into manageable groups (e.g., Oteng-Yeboah, 1974a; Raynal, 1976a, 1976b; Smith & Hayasaka, 2001). Authors were basically unanimous in recognizing three or four infrageneric taxa adopted from *Scirpus*, although there was no agreement as to whether these groups should be treated at the subgeneric or sectional level. Whereas Oteng-Yeboah (1974a) divided *Schoenoplectus* into subgenera *Schoenoplectus*, *Actaeogeton*, and *Malacogeton*, Smith & Hayasaka (2001, 2002) treated these taxa as sections in addition to a fourth, section *Supini*, a collection of 24 species largely from Africa and Madagascar that were dominated by amphicarpic annuals. Authors also recognized that these four sections could be divided into two distinct groups. Section *Malacogeton*, a collection of four species from East Asia and eastern North America with long leaves and unique foliar anatomy, appeared to be closely allied with the species of the widespread section *Schoenoplectus* on the basis of embryo morphology (Van der Veken, 1965). Embryo morphology and morphological characters also clearly linked sections *Actaeogeton* and *Supini*, even to the point where some authors felt they should be treated as a single section (e.g., Beetle, 1942; Koyama, 1958; Van der Veken, 1965; Lye, 2003). With the segregation of *Schoenoplectiella* from *Schoenoplectus*, sections *Schoenoplectus* and *Malacogeton* continued as infrageneric taxa within *Schoenoplectus*, whereas the remaining sections were transferred to *Schoenoplectiella* as sections *Actaeogeton* and *Schoenoplectiella* (=*Supini*; Lye, 2003; Hayasaka, 2012).

Within *Schoenoplectus*, our targeted sequencing and nrDNA analyses support the recognition of sections *Schoenoplectus* and *Malacogeton* as both of these sections correspond to strongly supported clades. These results are consistent with previous molecular analyses (Shiels et al., 2014; Glon et al., 2017) and they agree with the morphology and micromorphology of both sections. Whereas section *Malacogeton* possesses glumes with prominent veins, entire or obscurely emarginate apices and tubers often terminating rhizomes, in section *Schoenoplectus*, veins are absent on glumes (except basal glumes), apices are clearly emarginate to deeply bifid in the vast majority of the species, and tubers are absent (Smith & Hayasaka, 2001; Hayasaka, 2012). Moreover, if the elongated epidermal nutlet cells of *Schoenoplectus nipponicus* with their highly sinuous anticlinal walls are shared by all members of section *Malacogeton*, this differs significantly from the mostly isodiametric and hexagonal cells with straight to slightly undulate anticlinal walls seen in section *Schoenoplectus* (e.g., Schuyler, 1971; Hayasaka, 2012; Table S7).

Within *Schoenoplectiella*, our targeted sequencing analyses support two clades as well. One poorly supported clade corresponds almost perfectly to section *Schoenoplectiella*, including the type for the genus, *S. articulata* (Hayasaka, 2003). However, the second strongly supported clade contains a taxonomically confusing collection of species with the type for section *Actaeogeton* (*Schoenoplectiella mucronata* (L.) J.Jung & H.K.Choi) as sister to a clade comprising all the largely African *Schoenoplectus* species we transfer to *Schoenoplectiella* s.l. plus *Schoenoplectiella proxima*. As a small, amphicarpous annual with rugose nutlets, *Schoenoplectiella proxima* clearly belongs in section *Schoenoplectiella sensu* Raynal (1976a) and Hayasaka (2012), but here it is

nested within a clade dominated by large perennials (generally >30 cm, except *S. rhodesicus*) lacking amphicarpy. In addition, several of the African *Schoenoplectus* species in this clade also confuse the current division of *Schoenoplectiella* into two sections. For example, because Smith & Hayasaka (2001) could not assign *Schoenoplectus muriculatus* and *S. paludicola* to any of their four sections, they concluded that a worldwide sectional revision might reveal more, and if all the species in this clade were simply assigned to sect. *Actaeogeton*, the unusual, semi-terrestrial to aquatic *Schoenoplectus rhodesicus* (Browning, 2012) would be the only species in *Actaeogeton* to possess nodose foliated stems (i.e., *Actaeogeton* = stems nodeless, all leaves basal; Smith & Hayasaka, 2001; Hayasaka, 2012). Given that our nrDNA analyses positioned *Actaeogeton* (eight species) within a grade initiated by sect. *Schoenoplectiella* species and that both sections are difficult to separate (e.g., Hayasaka, 2012), one solution to the infrageneric classification of *Schoenoplectiella* would be to avoid sections altogether. However, due to the unusual species noted above and the poor clade support seen in nrDNA analyses, such a solution would be unsatisfactory at this point. The infrageneric classification of *Schoenoplectiella* will only be resolved when a significant increase in taxonomic sampling is accompanied by further molecular and morphological studies.

# 5 Taxonomic Treatment

### 5.1 Key to the tribes of the Fuireneae s.l. grade

1a. Embryo 176–305(–382 μm) long, with scutellum 39%–60% of total embryo length; bracts sheathing, leaf-like, rarely cusp-like; leaves with well-developed blades, hairy at least at the junction of blade and sheath, rarely glabrous when the blade is reduced to a mucronate sheath ..... **Fuireneae s.s.**

1b. Embryo 315–1269 μm long, when <380 μm, scutellum is 28%–32% of total embryo length; bracts sheathless, leaf-like or appearing to be a continuation of the stem; leaves well-developed or reduced to sheaths, glabrous.....2

2a. Lowermost primary bract leaf-like with spikelets 10–40 mm long; embryo with three primordial leaves, notch below the root cap present..... **Bolboschoeneae**

2b. Lowermost primary bract patent to erect, but stem-like, when leaf-like, patent to reflexed with spikelets to 5 mm long; embryo with two primordial leaves, notch below root cap absent.....3

3a. Embryo scutellum turbinate to rhomboid; nutlet epidermal cells isodiametric to oblong or elliptic, 1.0–3.9 times longer than wide, rarely elongated, up to 6.3 times longer than wide (*Schoenoplectus* sect. *Malacogeton*); nutlet surface smooth; basal flowers absent ..... ..... **Schoenoplecteae**

3b. Embryo scutellum umbonate or distinctly pileate; nutlet epidermal cells linear, (8.0–)9.2–20.2 times longer than wide, rarely isodiametric to oblong, 1.5–3.8 times longer than wide (*Pseudoschoenus inanis*); nutlet surface smooth or transversely rugose; basal flowers sometimes present .....**Pseudoschoeneae**

### 5.2 Tribal diagnoses for the members of the Fuireneae s.l. grade

**1. Bolboschoeneae** (Tatanov) J.R.Starr, **stat. nov**.

≡ Schoenoplecteae subtribe Bolboschoeninae Tatanov, in Novosti Sist. Vyssh. Rast. 39: 33 (2007).

**Type:** *Bolboschoenus* (Asch.) Palla

**Diagnosis:** Differs from all other Cyperaceae tribes by this unique combination of characters: Perennials with long rhizomes often forming hard ovoid tubers at tips and nodes. Culms many-noded, 3-sided, thickened at the base. Leaves well-developed, basal and cauline, eligulate with blade often reduced in lower leaves. Inflorescence terminal (in reduced inflorescences, bract may be erect, but clearly leaf-like), sometimes pseudolateral, (compound) anthelate or capitate with 1 to many spikelets. Inflorescence bracts leaf-like, patent, lowermost often suberect. Spikelets with many spirally arranged, deciduous glumes, each subtending a flower. Glumes puberulent, the apex entire to emarginate or deeply 2-fid, awned, or mucronate. Flowers bisexual, perianth present, formed by 3–6 parts, shorter to longer than the nutlet, bristle-like, deciduous with nutlet. Stamens 3. Styles 2 or 3. Style base persistent, barely thickened, if at all. Nutlets obovate, dorsiventrally lenticular or trigonous, surface smooth with epidermal cells more or less isodiametric, 1.0–1.7 times longer than wide. Embryo fungiform with three primordial leaves and a notch below the root cap (Bolboschoenus-type).

**Accepted genus:** *Bolboschoenus* (Asch.) Palla (15 species; temperate to tropical regions worldwide. Fresh to brackish water habitats, saline shores, and marshes along coasts and inland).

**2. Fuireneae** Rchb. ex Fenzl, Gen. Pl.: 116 (1836).

**Type:** *Fuirena* Rottb.

**Diagnosis:** Differs from all other Cyperaceae tribes by this unique combination of characters: Annuals or rhizomatous perennials. Culms many-noded, rarely scapose, 3–5 sided or terete, sometimes thickened at the base. Leaves well-developed, rarely a mucronate sheath, basal and cauline, ligule tubular, membranous, with blade often reduced in lower leaves. Inflorescence terminal, paniculate to capitate with few to many spikelets, rarely pseudolateral. Inflorescence bracts leaf-like, sheathing, lowermost bract sometimes erect, rarely short and scale-like. Spikelets with many spirally or rarely pentastichously arranged, deciduous glumes, each subtending a flower. Glumes often pubescent, the apex entire and mucronate to awned. Flowers bisexual, perianth present, as long or shorter than nutlet, formed by 3 parts, or when 6 in 2 whorls, the inner parts scale-like, the outer parts bristle-like, rarely all parts reduced or absent or only 1 scale developed, deciduous with the nutlet. Stamens 1 to 3. Styles 3. Style base persistent, barely thickened, if at all. Nutlets obovate, triquetrous to trigonous, smooth or variously ornamented with epidermal cells roughly isodiametric or oblong to elongated, often in transverse rows, 1.0–7.2 times longer than wide. Embryo turbinate to weakly fungiform with a horizontally broadened scutellum, first leaf primordium not strongly outgrown, the second leaf primordium either absent or poorly developed (Fuirena-type).

**Accepted genus:** *Fuirena* Rottb. (55 species; tropical and warm temperate regions worldwide, especially in the

Americas and Africa. Open, humid localities, often at low altitude).

**3. Schoenoplecteae** Lye, in Blyttia 29: 147 (1971)
**Type:** *Schoenoplectus* (Reichenb.) Palla.

**Diagnosis:** Differs from all other Cyperaceae tribes by this unique combination of characters: Perennials with long rhizomes sometimes ending in tubers at tips. Culms nodeless, scapose, trigonous to terete, thickened at the base. Leaves usually reduced to a sheath, sometimes developing a ligulate blade, but rarely well-developed. Inflorescence pseudolateral, rarely clearly terminal, anthelate or capitate with (1-)few to many spikelets. Inflorescence bracts often large, erect, stem-like, rarely leaf-like and patent to reflexed (*Actinoscirpus*). Spikelets with many spirally arranged, deciduous glumes, each subtending a flower. Glumes puberulent to glabrous, the margins often ciliate or laciniate distally, apex entire to emarginate or deeply 2-fid, awned or mucronate. Flowers bisexual. Perianth present, formed by (–5–)6 parts, smooth to retrorsely scabrid, bristle-like or sometimes plumose, longer or shorter than nutlet, deciduous with nutlet. Stamens 2 or 3. Styles 2 to 3. Style base not thickened, persistent. Nutlets smooth, obovate, trigonous, or dorsiventrally lenticular, yellow to dark brown when mature. Nutlet epidermal cells isodiametric to oblong or elliptic, rarely elongated, 1.1–3.9(–6.3) times longer than wide. Embryo fungiform, scutellum turbinate to rhomboid in shape, root cap lateral, first (well-developed) and second embryonic leaves basal (Schoenoplectus-type I).

**Accepted genera:** *Actinoscirpus* (Ohwi) R.W.Haines & Lye (1 species; Tropical and subtropical Asia from India east to China and south to Northeast Australia. Common in swampy areas and ditches at low altitudes), *Schoenoplectus* (Rchb.) Palla (16 spp.; predominantly temperate. Common in fresh and brackish wetland habitats, such as in marshes, lakes, and along streams. Often emergent, rarely submerged).

**Key to Schoenoplecteae genera**

1a. Inflorescence terminal; proximal bracts leaf-like, patent to reflexed, forming an involucre at the base of the inflorescence.....***Actinoscirpus***
1b. Inflorescence pseudolateral; proximal bract culm-like, erect, other proximal bracts (if present) scale-like and much reduced.....***Schoenoplectus***

**4. Pseudoschoeneae** J.R.Starr, **tr. nov**.
**Type:** *Pseudoschoenus* (C.B.Clarke) Oteng-Yeb.

**Diagnosis:** Differs from all other Cyperaceae tribes by this unique combination of characters: Annuals or perennials, tufted or with firm, short to creeping rhizomes. Culms nodeless and scapose or 1(–8) noded above the base, trigonous, terete, or rarely 7-sided. Leaves are reduced to a mucronate sheath, rarely with well-developed blades, ligulate, or rarely eligulate (*Pseudoschoenus*). Inflorescence pseudolateral, rarely appearing terminal, anthelate or capitate with one to many spikelets, rarely compound paniculate with a conspicuously sinuous main axis (*Pseudoschoenus*). Inflorescence bracts culm-like, erect, or patent while fruiting, rarely short, rigid, and sheathing, but then appearing as a continuation of the stem. Spikelets with many spirally arranged, deciduous or persistent glumes, each subtending a flower. Glume apex entire to apiculate. Flowers bisexual, rarely polygamo-dioecious. Perianth present or absent, formed by 0–10 parts, smooth or retrorsely scabrid, bristle-like, as long as or longer than the nutlet, deciduous with the nutlet. Stamens 2 or 3, rarely vestigial in female flowers. Basal flowers often present in the axil of leaf sheaths. Styles 2 or 3. Style base undifferentiated, rarely distinct and somewhat thickened, persistent. Nutlets are smooth or transversely rugose to distinctly ridged, obovate, trigonous to planoconvex or biconvex, dark nearing black when mature, sometimes brown. Nutlets from basal flowers (when present) are much larger and bear an elongated lignified style (amphicarpy). Nutlet epidermal cells linear, (8.00–)9.22–20.21 times longer than wide, rarely isodiametric to oblong, 1.45–3.81 times longer than wide (*Pseudoschoenus*). Embryo fungiform, scutellum umbonate or distinctly pileate, root cap lateral, first (well-developed) and second embryonic leaves basal (Schoenoplectus-type II).

**Accepted genera:** *Pseudoschoenus* (C.B.Clarke) Oteng-Yeb. (1 species; Southern Africa, along streams at higher altitudes), *Schoenoplectiella* Lye. (63 species; temperate to tropical regions worldwide. Common in freshwater bogs, lake-edges and along streams, often in seasonally wet habitats or places with large fluctuations in water levels. Terrestrial to emergent, sometimes submerged.)

**Key to Pseudoschoeneae genera**

1a. Inflorescence paniculate or racemose, with a definite sinuous main axis of well-developed internodes .....***Pseudoschoenus***
1b. Inflorescence anthelate or reduced to one or a cluster of sessile spikelets, without a definite main axis due to highly-reduced internodes.....***Schoenoplectiella***

### 5.3 New combinations for species formerly placed in *Schoenoplectus*

A recent study has merged several tropical African *Schoenoplectus* with transversely rugose nutlets under the name *S. muricinux* (Verloove et al., 2018). Although the present study positions several of these taxa within the same monophyletic group (e.g., *S. confusus*, *S. muriculatus*, *S. muricinux*) it also places other broadly accepted taxa, like *S. decipiens* (Browning, 1990; Gordon-Gray, 1995) in the same clade. Moreover, *S. confusus* var. *rogersii*, another taxon in the synonymy of *S. muricinux* (Verloove et al., 2018), is here shown to be sister to *S. brachyceras*, a widely accepted taxon (Browning, 1992; Jiménez-Mejías & Cabezas, 2009) also recognized as close to *S. muricinux* (Verloove et al., 2018), but not placed in its synonymy. Although it is clear that the limits of many of these taxa are not well defined, we re-adopt Browning's (Browning, 1991a) treatment of *S. muricinux* and its allies until molecular, and additional morphological and micromorphological data can be applied to the problem.

***Schoenoplectiella annamica*** (Raymond) J.R.Starr, **comb. nov**.

*Scirpus annamicus* Raymond, Naturaliste Canad. 84: 137 (1957). [basionym]

*Schoenoplectus annamicus* (Raymond) T.Koyama, Brittonia 31: 291 (1979).

**Note:** Koyama (1979) regarded this species as a member of section *Actaeogeton*, similar to the North American *S. hallii*.
**Distribution:** Vietnam

***Schoenoplectiella brachyceras*** (Hochst. ex A.Rich.) J.R.Starr & Jim.Mejías, **comb. nov**.
*Scirpus brachyceras* Hochst. ex A.Rich., Tent. Fl. Abyss. 2: 496 (1850). [basionym]
*Schoenoplectus brachyceras* (Hochst. ex A.Rich.) Lye, Bot. Not. 124: 290 (1971).
**Note:** Often considered conspecific with *S. corymbosus*, previous work has demonstrated it is distinct from *S. corymbosus* (Browning, 1992; Jiménez-Mejías & Cabezas, 2009). Samples of *S. corymbosus* and *S. brachyceras* were not sisters in our analyses.
**Distribution:** Southern Africa north to Ethiopia

***Schoenoplectiella confusa*** (N.E.Br.) J.R.Starr, **comb. nov**.
*Scirpus confusus* N.E.Br., Bull. Misc. Inform. Kew 1921: 300 (1921). [basionym]
*Schoenoplectus confusus* (N.E.Br.) Lye, Bot. Not. 124: 290 (1971).
**Distribution:** Southern Africa north to Ethiopia

***Schoenoplectiella confusa*** subsp. ***natalitia*** (Browning) J.R.Starr, **comb. nov**.
*Schoenoplectus confusus* subsp. *natalitius* Browning, S. African J. Bot. 57: 258 (1991). [basyonym]
**Distribution:** South Africa

***Schoenoplectiella corymbosa*** (Roth ex Roem. & Schult.) J.R.Starr & Jim.Mejías, **comb. nov**.
*Isolepis corymbosa* Roth ex Roem. & Schult., Syst. Veg., ed. 15 bis 2: 110 (1817). [basionym]
*Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) J.Raynal in B.Peyre de Fabregues & J.P.Lebrun, Cat. Pl. Vasc. Niger: 343 (1976).
**Note:** Proliferous inflorescences bearing plantlets at their apex have been observed in this species (Fig. 1L). To date, this characteristic has only been observed in *Schoenoplectiella* species, but never in *Schoenoplectus* s.s. (Hayasaka, 2012).
**Distribution:** Southern Africa north to Spain and east to India

***Schoenoplectiella decipiens*** (Nees) J.R.Starr, **comb. nov**.
*Isolepis decipiens* Nees, Linnaea 10: 157 (1835). [basionym]
*Schoenoplectus decipiens* (Nees) J.Raynal, Adansonia, n.s., 15: 540 (1976).
**Distribution:** Southern Africa to Madagascar

***Schoenoplectiella heptangularis*** (Cabezas & Jim.Mejías) J.R.Starr & Jim.Mejías, **comb. nov**.
*Schoenoplectus heptangularis* Cabezas & Jim.Mejías, Candollea 64: 109 (2009). [basionym]
**Distribution:** Equatorial Guinea

***Schoenoplectiella monocephala*** (J.Q.He) J.R.Starr, **comb. nov**.
*Scirpus monocephalus* J.Q.He, Acta Phytotax. Sin. 37: 291 (1999). [basionym]
*Schoenoplectus monocephalus* (J.Q.He) S.Yun Liang & S.R.Zhang, Novon 20: 170 (2010).
**Distribution:** Eastern China

***Schoenoplectiella muricinux*** (C.B.Clarke) J.R.Starr, **comb. nov**.
*Scirpus muricinux* C.B.Clarke, Bot. Jahrb. Syst. 38: 135 (1906). [basionym]
*Schoenoplectus muricinux* (C.B.Clarke) J.Raynal, Adansonia, n.s., 15: 538 (1976).
**Distribution:** Southern Africa

***Schoenoplectiella muriculata*** (Kük.) J.R.Starr, **comb. nov**.
*Scirpus muriculatus* Kük., Bot. Not. 1934: 75 (1934). [basionym]
*Schoenoplectus muriculatus* (Kük.) Browning, S. African J. Bot. 57: 254 (1991).
**Distribution:** Southern Africa

***Schoenoplectiella paludicola*** (Kunth) J.R.Starr, **comb. nov**.
*Scirpus paludicola* Kunth, Enum. Pl. 2: 163 (1837). [basionym]
*Schoenoplectus paludicola* (Kunth) Palla, Bot. Jahrb. Syst. 10: 299 (1888).
**Distribution:** Southern Africa

***Schoenoplectiella pulchella*** (Kunth) J.R.Starr, **comb. nov.**
*Ficinia pulchella* Kunth, Enum. Pl. 2: 261 (1837). [basionym]
*Scirpus pulchellus* (Kunth) Boeckeler, Linnaea 36: 698 (1870).
*Schoenoplectus pulchellus* (Kunth) J.Raynal, Adansonia, n.s., 15: 542 (1976).
**Distribution:** Southern Africa

***Schoenoplectiella rogersii*** (N.E.Br.) J.R.Starr, **comb. nov**.
*Scirpus rogersii* N.E.Br., Bull. Misc. Inform. Kew 1921: 301 (1921). [basionym]
*Schoenoplectus rogersii* (N.E.Br.) Lye, Bot. Not. 124: 290 (1971).
*Schoenoplectus confusus* var. *rogersii* (N.E.Br.) Lye, Nordic J. Bot. 3: 242 (1983).
**Distribution:** Botswana north to Kenya

***Schoenoplectiella rhodesica*** (Podlech) J.R.Starr, **comb. nov**.
*Scirpus rhodesicus* Podlech, Mitt. Bot. Staatssamml. München 4: 117 (1961).
*Schoenoplectus rhodesicus* (Podlech) Lye, Nordic J. Bot. 3: 242 (1983).
**Distribution:** Zimbabwe north to Tanzania

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## Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.12721/suppinfo:

**Data S1**. Alignment with 127 accessions obtained from nrDNA off-target reads and ITS sequences available from GenBank.

**Data S2**. Reduced sampling alignment of 62 accessions from nrDNA off-target reads and ITS sequences available from GenBank.

**Data S3**. List of all taxa for which embryo data was obtained for this study with their voucher information, literature source, and geographic origin (when known).

**Fig. S1**. Landmark positions on the embryo of *Bolboschoenus maritimus*. Type 1 and 2 landmarks are symbolized by blue points with numbers, and they are placed on (1) root cap lower margin, (2) root cap apex, (3) root cap top margin, (4) junction of scutellum and hypocotyl on the left side (local minimum in curvature), (5) scutellum left side maximum width, (6) scutellum apex, (7) scutellum right side maximum width, (8) junction of scutellum and hypocotyl on the right side (local minimum in curvature), (9) left coleoptile lip base on abaxial face (aligned with landmark #11), (10) left coleoptile lip apex, (11) junction of left coleoptile lip and plumule, (12) plumular leaf 2 apex, (13) plumular leaf 1 base on the adaxial side, (14) plumular leaf 1 apex, (15) junction of plumule and right coleoptile lip, (16) right coleoptile lip apex, and (17) right coleoptile lip base on the abaxial side (aligned with landmark 13). In addition, seven pseudolandmarks are placed at an equal distance along the green curves separating 10 pairs of landmarks: 4–5, 5–6, 6–7, 7–8, 9–10, 10–11, 13–14, 14–15, 15–16, and 16–17. This gives a total of 17 landmarks and 70 pseudolandmarks. The length of the scutellum was also measured, as indicated.

**Fig. S2**. A heatmap of recovery of the Angiosperms353 probes for the accessions included in this study.

**Fig. S3**. Phylogenetic reconstruction of the relationships in tribe Fuireneae s.l. and related tribes based on analysis of the exons data set. Species tree inferred in ASTRAL from RAxML gene trees. Numbers by branches represent local posterior

probabilities (LPPs) and pie charts at nodes correspond to quartet support with blue for agreeing genes, red for disagreeing genes, and gray for uninformative genes.

**Fig. S4**. Phylogenetic reconstruction of the relationships in tribe Fuireneae s.l. and related tribes based on analysis of the exons data set. Concatenated IQ-TREE analysis from RAxML gene trees. Numbers by nodes represent bootstrap support.

**Fig. S5**. Phylogenetic reconstruction of the relationships in tribe Fuireneae s.l. and related tribes based on analysis of the supercontigs data set. Concatenated IQ-TREE analysis from RAxML gene trees. Numbers by nodes represent bootstrap support.

**Fig. S6**. Phylogenetic reconstruction of the relationships in tribe Fuireneae s.l. and related tribes based on a RAxML analysis of the alignment with 137 accessions obtained from nrDNA off-target reads and ITS sequences available from GenBank. Numbers by nodes represent bootstrap support.

**Table S1**. Overview of the species of Schoenoplectus and Schoenoplectiella, their classificationand distribution range (Govaerts et al., 2020). *Available from GenBank, **sequenced for this study, ***sequenced in both.

**Table S2**. Voucher information for the accessions included in the targeted sequencing study.Taxon names are in accordance with Govaerts et al. (2020) and this study. The voucher information includes collector, collector number, herbarium codes according to Thiers (continuously updated), and when available the specimen's herbarium barcode. Origin information refers to whether DNA was extracted from leaf samples taken in the herbarium or stored in silica gel, or whether it originated from the Kew DNA Bank (numbers are provided). Type species for genera and sections are indicated under the column for notes.

**Table S3**. Voucher information for accessions used in the ITS analysis, including GenBank accession numbers for Sanger sequencing data, or laboratory ID numbers (under "Number" column) for data obtained from off-target sequencing reads).

**Table S4**. Percentage recovery of the genes targeted by the Angiosperms353 probes for the accessions included in this study.

**Table S5**. AMAS statistics generated for the exons data set (**A**), and supercontigs data set (**B**).

**Table S6**. AMAS statistics generated for the trimmed exons dataset (**A**), and trimmed supercontigs data set (**B**).

**Table S7**. Overview of nutlet pericarp characters. Note that for references followed by an asterisk "*", species were placed in broad groups for which a single representative illustration was given. Species are not listed from publications where illustrations were not sufficiently resolved to determine nutlet epidermal cell shape.