











Research Article

A new classification of Cyperaceae (Poales) supported by phylogenomic data

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Abstract Cyperaceae (sedges) are the third largest monocot family and are of considerable economic and ecological importance. Sedges represent an ideal model family to study evolutionary biology due to their species richness, global distribution, large discrepancies in lineage diversity, broad range of ecological preferences, and adaptations including multiple origins of C_4 photosynthesis and holocentric chromosomes. Goetghebeur's seminal work on Cyperaceae published in 1998 provided the most recent complete classification at tribal and generic level, based on a morphological study of Cyperaceae inflorescence, spikelet, flower, and embryo characters, plus anatomical and other information. Since then, several family-level molecular phylogenetic studies using Sanger sequence data have been published. Here, more

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than 20 years after the last comprehensive classification of the family, we present the first family-wide phylogenomic study of Cyperaceae based on targeted sequencing using the Angiosperms353 probe kit sampling 311 accessions. In addition, 62 accessions available from GenBank were mined for overlapping reads and included in the phylogenomic analyses. Informed by this backbone phylogeny, a new classification for the family at the tribal, subtribal, and generic levels is proposed. The majority of previously recognized suprageneric groups are supported, and for the first time, we establish support for tribe Cryptangieae as a clade including the genus *Koyamaea*. We provide a taxonomic treatment including identification keys and diagnoses for the 2 subfamilies, 24 tribes, and 10 subtribes, and basic information on the 95 genera. The classification includes five new subtribes in tribe Schoeneae: Anthelepinae, Caustiinae, Gymnoschoeninae, Lepidospermatinae, and Oreobolinae.

Key words: Angiosperms353, classification, Cyperaceae, phylogenomics, Poales, systematics, targeted sequencing, taxonomy.

1 Introduction

Cyperaceae (sedges) are the third largest monocot family (>5600 spp.; Govaerts et al., 2020) and are of considerable economic and ecological importance (Simpson & Inglis, 2001; Spalink et al., 2016a, 2018). Cyperaceae are an ideal model family to study evolutionary biology due to their species richness, global distribution, large discrepancies in lineage diversity (Escudero & Hipp, 2013), broad range of ecological preferences and diverse phenotypes (Naczi & Ford, 2008), multiple origins of C_4 photosynthesis (Besnard et al., 2009), and the presence of holocentric chromosomes (Márquez-Corro et al., 2019, 2021). The family is species-rich in the tropics where it exhibits high generic diversity and a remarkable species richness in the genus *Cyperus* L. with >960 spp. (Govaerts et al., 2020). High diversity in temperate regions is mostly due to the megadiverse genus *Carex* L. with >2000 spp. (Govaerts et al., 2020). The history of the family goes back to the early Cenozoic, as supported by a reliable fossil record dating back to the Paleocene (Smith et al., 2009; Spalink et al., 2016b) and evidence of large genera already established by the end of the Eocene (Jiménez-Mejías et al., 2016a), with a probable origin in South America (Spalink et al., 2016b).

Phenotypic diversity in Cyperaceae is represented among others by a wide range of growth forms, from tiny ephemerals less than 3 cm high such as *Isolepis inconspicua* (Levyns) J.Raynal to climbing herbs that may measure to more than 12 m long such as *Scleria boivinii* Steud. (Fig. 1A), and to the long-lived dwarf-tree-like *Microdracoides squamosa* Hua (Fig. 1B) and the similar looking species of the New Caledonian endemic genus *Chamaedendron* (Kük.) Larridon (Larridon et al., 2018a). It is also ecologically diverse and occurs in a wide variety of habitats ranging from truly aquatic plants in rivers and lakes to annuals and perennials in fire-prone grasslands, forests and high-elevation vegetations (Simpson et al., 2011; e.g., *Carex moorcroftii* Falc. ex Boott has been found up to elevations of 5700 m; Dai et al., 2010), deserts, and coastal sands (Väre & Kukkonen, 2005; Reznicek et al., 2021). There are even species with a tendency for epiphytism (i.e., *Coleochloa domensis* Muasya & D.A.Simpson; Muasya et al., 2010). In some ecosystems, such as wetlands and inselbergs, Cyperaceae are true ecosystem builders providing habitats for many other species (e.g., mats of *Afrotrilepis pilosa* (Boeckeler) J.Raynal; Fig. 1C). In temperate Australia, the genera *Ammothryon* R.L.Barrett, K.L.Wilson &

J.J.Bruhl, *Caustis* R.Br., *Gahnia* J.R.Forst. & G.Forst., *Lepidosperma* Labill., *Netrostylis* R.L.Barrett, J.J.Bruhl & K.L.Wilson, *Schoenus* L., and *Tricostularia* Nees ex Lehm. can be dominant components of the understorey in numerous dryland vegetation communities, with high ecological significance (Barrett, 2013; Barrett et al., 2021a, 2021b). Furthermore, the family exhibits high diversity in reproductive and seed dispersal structures, and use of these morphological characters to define taxon limits has resulted in much of the observed taxonomic complexity of, for example, *Cyperus* (Fig. 1D; Larridon et al., 2011a, 2013) and *Carex* (Global Carex Group, 2015; Jiménez-Mejías et al. 2016b), and the wide range of dispersal vectors known for the family (Goetghebeur, 1998; Larridon et al., 2011b, 2021a), for example, birds in species of *Gahnia* (Fig. 1E), and ants in selected species of *Carex* (Handel, 1976; Vellend et al., 2000) and *Lepidosperma* (Barrett, 2013). Long-distance dispersal has led to unusual disjunct distributions in genera such as *Morelotia* Gaudich. (Barrett et al., 2021c) and *Tetraria* P.Beauv. (Larridon et al., 2018b). Although predominantly wind-pollinated, there are many transitions from wind to insect pollination in Cyperaceae (Fig. 1F; Wragg & Johnson, 2011; Yano et al., 2015; Costa et al., 2018a; Villa-Machío et al., 2020). The sedge family is also physiologically diverse, with species using C_3 , C_4 , or C_3 - C_4 intermediate photosynthesis (Soros & Bruhl, 2000; Bruhl & Wilson, 2007; Besnard et al., 2009). At least six independent origins of C_4 photosynthesis have been recorded in tribe Abildgaardieae and in *Cyperus*, *Eleocharis* R.Br., and *Rhynchospora* Vahl (Bruhl & Wilson, 2007; Besnard et al., 2009; Larridon et al., 2011a, 2021b). Cyperaceae are of worldwide economic significance with about 10% of species used by humans, particularly in the tropics (Simpson & Inglis, 2001). Globally important crop species include *Cyperus esculentus* L. (tiger nuts) as snacks or for the production of “horchata de chufa” (tiger nut milk), and *Eleocharis dulcis* (Burm.f.) Trin. ex Hensch. (water chestnuts) as a popular ingredient in Asian dishes. Several species are notorious weeds (Bryson & Carter, 2008), such as *Cyperus aromaticus* (Ridl.) Mattf. & Kük. (Vitelli et al., 2010; Biosecurity Queensland, 2018), *C. esculentus* (Dodet et al., 2008; Rogers et al., 2008), and *C. rotundus* L. (Goetghebeur, 1998; Rogers et al., 2008; ISSG, 2019). Cyperaceae also have a remarkable and often overlooked importance in human history (e.g., totora or *Schoenoplectus californicus* (C.A.Mey.) Soják, papyrus or *Cyperus papyrus* L.; Banack et al., 2004; Bagnall, 2009) and in human evolution as a food source



Fig. 1. Morphological and ecological diversity of Cyperaceae. **A**, *Scleria boivinii* Steud. **B**, *Microdracoides squamosa* Hua. **C**, *Afrotrilepis pilosa* (Boeckeler) J.Raynal. **D**, *Carex lechleriana* (Steud.) J.R.Starr formerly placed in the segregate genus *Uncinia* Pers. **E**, *Gahnia tristis* Nees. **F**, *Rhynchospora alba* (L.) Vahl. Photos **A** by Javier Galán Díaz; **B** by Charlotte Couch; **C** by Xander van der Burgt; **D** by Modesto Luceño; **E** by Russell Barrett; **F** by Juan Carlos Zamora.

(Sponheimer et al., 2005, 2013; Dominy, 2012; Wynn et al., 2013; Cerling et al., 2013a, 2013b).

Cyperaceae are a well-supported monophyletic family within the monocot order Poales, sister to Juncaceae (Simpson et al., 2007; Muasya et al., 2009a; Givnish et al., 2010; Escudero & Hipp, 2013; Jung & Choi, 2013; Bouchenack-Khelladi et al., 2014; Ruhfel et al., 2014; Spalink et al., 2016b; Semmouri et al., 2019). Goetghebeur's (1998) seminal work on Cyperaceae still provides the most recent complete classification at tribal and generic level, based on a morphological study of Cyperaceae inflorescence, spikelet, flower, and embryo characters, plus anatomical and other information (Goetghebeur, 1986). Since then, a range of molecular phylogenetic studies using Sanger sequence data has been published at the family level (Simpson et al., 2007; Muasya et al., 2009a; Escudero & Hipp, 2013; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Spalink et al., 2016b; Semmouri et al., 2019; Larridon et al., 2021b). Two main clades have been recovered within Cyperaceae, corresponding to subfamilies Mapanioideae and Cyperoideae. Mapanioideae mainly includes broad-leaved tropical forest understory herbs, whereas Cyperoideae is much more diverse in terms of species richness, morphology, and ecology. Other studies have focused on particular tribes or genera, including *Carex* (e.g., Global Carex Group, 2015; Jiménez-Mejías et al., 2016c; Martín-Bravo et al., 2019),

Cyperus (e.g., Larridon et al., 2011a, 2013; Bauters et al., 2014), Abildgaardieae (e.g., Reutemann et al., 2018; Roalson et al., 2019; Muasya et al., 2020), Schoeneae (e.g., Viljoen et al., 2013; Larridon et al., 2018a), or the Scirpo-Caricoid Clade (e.g., Léveillé-Bourret et al., 2014, 2015, 2018a, 2018b; Léveillé-Bourret & Starr, 2019), increasing our understanding of the relationships in Cyperaceae. Despite previous studies, systematic relationships in Cyperaceae at the tribal and generic level are not yet fully resolved because (i) some genera have not yet been sampled and (ii) some relationships are conflicting in different studies.

Molecular phylogenetic studies on Cyperaceae have relied heavily on relatively few loci, such as a selection of plastid markers and the nuclear markers ITS and ETS (e.g., Semmouri et al., 2019). However, phylogeny estimation is more accurate when conducted with tens to hundreds of nuclear loci, because larger numbers of informative characters help to resolve short branches, and historical processes such as deep coalescence can be taken into account (Johnson et al., 2019). Hence, reduced-representation sequencing methods have been developed to sample hundreds of nuclear, orthologous single-copy genes for plant phylogenetic studies (Kadlec et al., 2017; Couvreur et al., 2019; Johnson et al., 2019; Villaverde et al., 2018, 2020), allowing users to yield data sets of a larger scale for phylogenetics without the bioinformatic challenges and

costs associated with whole-genome sequencing. Larridon et al. (2020) provided an overview of earlier high-throughput sequencing studies on Cyperaceae, whereas more recent studies relying on genomic data already show alternative phylogenetic structure in certain sedge groups not previously recovered using Sanger sequencing (Léveillé-Bourret et al., 2018c; Larridon et al., 2020; Starr et al., 2021; Villaverde et al., 2020, 2021).

The aim of this study is to resolve the high-level relationships in Cyperaceae and to test the monophyly of the tribes and genera as currently accepted to generate a new classification from subfamily to generic level. We hypothesize that using genome-scale data and an in-depth sampling will provide significantly more phylogenetic information to resolve the topology of the Cyperaceae Tree of Life. Equally, we postulate that the high-throughput technique-targeted sequencing will enable sequencing historical herbarium specimens with poor DNA quality (Brewer et al., 2019), allowing us to place previously unplaced genera in the family phylogeny for the first time.

2 Material and Methods

2.1 Taxon sampling

A total of 361 accessions of Cyperaceae were sampled, along with 21 accessions representing other families in order Poales as outgroups (Table S1). The sampling includes nearly all currently accepted genera of Cyperaceae (Govaerts et al., 2020). Three monotypic genera were not sampled, and have never been successfully sequenced using Sanger methods: *Nelmesia* Van der Veken and *Trichoschoenus* J.Raynal, which are only known from their type collections, and *Rhynchocladium* T.Koyama. Costa et al. (2021a) recently changed the generic circumscription in tribe Cryptangieae, re-establishing the monotypic genus *Didymian-drum* Gilly, whereas Barrett et al. (2021b) recently described a new monotypic genus *Ammothryon*. These two genera were not sampled. Lab work for samples of three additional monotypic genera, *Blysmopsis* Oteng-Yeb., *Capeobolus* Browning, and *Khaosokia* D.A.Simpson, and the small genus *Blysmus* Panz. ex Schult. did not provide data of sufficient quality. These genera have been previously successfully placed in the Cyperaceae Tree of Life (e.g., Léveillé-Bourret et al., 2014, 2018c; Larridon et al., 2018a; Semmouri et al., 2019). In total, 311 of the 382 accessions were sequenced after enrichment with the Angiosperms353 probes. In addition, 36 accessions enriched with the Angiosperms 1 kit for Anchored Phylogenomics (Léveillé-Bourret et al., 2018c), including *Khaosokia caricoides* D.A.Simpson, were mined for reads overlapping with the data generated using the Angiosperms353 probes, as were 6 accessions enriched with Cyperaceae-specific probes (Villaverde et al., 2020), and 20 transcriptomes available on GenBank (Table S1). Angiosperms353 data for most accessions were newly generated for this study, following the protocol established by Baker et al. (2021). In addition, some data were obtained from recent studies (Larridon et al., 2020, 2021c; Starr et al., 2021; Table S1).

2.2 DNA extraction, library preparation, hybridization, and sequencing

The voucher information and treatment of each sample are provided (Table S1). Molecular work for accessions enriched with

the Angiosperms353 probes was carried out at the Sackler Phylogenomics Laboratory, within the Jodrell Laboratory at Royal Botanic Gardens, Kew (Richmond, Surrey, UK). Genomic DNA was extracted from leaf tissue obtained from herbarium specimens or silica-dried samples, using either a modified CTAB approach (Doyle & Doyle, 1987) or a CTAB protocol, based on Beck et al. (2012), modified for optimal simultaneous extraction of 96 to 192 samples (i.e., one or two plates) from degraded (i.e., herbarium) samples (see Supplementary Data Sheet 1 in Larridon et al., 2020). Lastly, 76 accessions were sourced from the Kew DNA Bank (<http://dnabank.science.kew.org/>) (Table S1). The samples extracted using a CTAB approach were purified using 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 a 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. Dual-indexed libraries for Illumina® sequencing were prepared using the DNA NEBNext® Ultra™ II Library Prep Kit and the NEBNext® Multiplex Oligos for Illumina® (Dual Index Primers Set 1 and 2) from New England BioLabs® (Ipswich, MA, USA) following the manufacturer's instructions but at half the recommended volumes. The quality of the libraries was evaluated on the TapeStation using High Sensitivity D1000 ScreenTape and the libraries were quantified using a Quantus Fluorometer. The final average library size including the adapters was c. 500 bp. Afterward, the samples were pooled and enriched with the Angiosperms353 probes (Johnson et al., 2018) following the manufacturer's instructions (myProbes® Manual v4.01, Arbor Biosciences, Ann Arbor, MI, USA). Final products were again run on the TapeStation to assess quality (i.e., average fragment size) so they could be pooled equimolarly for sequencing. After multiplexing library pools, sequencing was performed on an Illumina® MiSeq instrument (San Diego, CA, USA) with v2 (300 cycles at 2 × 150 bp) or v3 (600 cycles at 2 × 300 bp) chemistry at Royal Botanic Gardens, Kew (Richmond, Surrey, UK), or on an Illumina® HiSeq (San Diego, CA, USA) at either Macrogen (Seoul, South Korea) or GENEWIZ® (Leipzig, Germany), producing 2 × 150 bp long reads. 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>), PRJNA668802 (<http://www.ncbi.nlm.nih.gov/bioproject/PRJNA668802>), and PRJNA669051 (<http://www.ncbi.nlm.nih.gov/bioproject/PRJNA669051>), and from the European Nucleotide Archive (ENA) under EMBL Project number PRJEB35285 (<https://www.ebi.ac.uk/ena/browser/view/PRJEB35285>).

2.3 Read processing, assembly, and phylogenomic analyses

Bioinformatics settings follow Larridon et al. (2021c). Raw reads were trimmed to remove adapter sequences and portions of low quality with Trimmomatic v.0.39 (Bolger et al., 2014) using 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 default settings except for minimum coverage 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 Supplementary Data Sheet 3 in Larridon et al., 2020). Mapped reads were then assembled into contigs with SPAdes v.3.13.1 (Bankevich et al., 2012). Subsequently, exonerate v.2.2 (Slater & Birney, 2005) was used to align the assembled contigs to their associated target sequence and remove intronic regions (exons data set). HybPiper flags potential paralogs when multiple contigs are discovered mapping well to a single reference sequence. As few random paralog warnings were raised, no sequence was excluded.

Phylogenomic analyses were executed in two rounds (following Zuntini et al., 2021) to improve the inference results. In the first round, all exon sequences with at least 50 bp were recovered and then aligned with MAFFT v.7 (Katoh and Standley, 2013) with the “localpair max iterations 1000” option; sites with more than 30% missing data were removed using Phyutility (Smith & O’Meara, 2012), after which IQ-TREE v.2.1.0 (Minh et al., 2020) was run per gene, followed by TreeShrink (Mai & Mirarab, 2018) with threshold set to 0.05. After this, a quality check was performed to see how many times each accession appeared in each gene tree. Finally, ASTRAL-III v.5.5.11 (Zhang et al., 2018) was run after collapsing branches $\leq 10\%$ bootstrap (BS) support using Newick Utilities (Junier & Zdobnov, 2010). This round provided the preliminary result. In the second round, again all sequences with at least 50 bp were recovered, those flagged by TreeShrink were removed, and then aligned with MAFFT, after which we generated summary stats in AMAS (Borowiec, 2016). Short alignments (<100 bp) were removed.

For the coalescent ASTRAL analysis, IQ-TREE was run per gene, after which ASTRAL was executed after collapsing branches $\leq 10\%$ BS support to provide the final result. 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.

For the concatenated IQ-TREE analysis, the individual gene alignments were concatenated in AMAS, and IQ-TREE was run with mode set to “MFP + MERGE” and 10 000 replicates of ultrafast bootstrap replications (Hoang et al., 2018) to generate the final result. We also calculated two measures of genealogical concordance in our data set, the gene concordance factor (gCF) and the site concordance factor (sCF), using the options “-gcf” and “-scf” in IQ-TREE. Trees were plotted in FigTree v.1.4.4 (<https://github.com/rambaut/figtree/releases>).

3 Results

3.1 Capture success and data quality

The success of sequence recovery was variable, with an average of 177 genes per sample (above 25% of target size) and 41% of the total potential target (260 802 bp), as indicated in Johnson et al. (2019). The recovery of samples hybridized with other kits was significantly lower: for

samples hybridized with the Angiosperms I kit for Anchored Phylogenomics, the recovery was 65 genes, on average, above 25% of target length and 17% of total potential length, whereas samples hybridized with Cyperaceae-specific probes yielded, on average, 45 genes and 18% of potential length (Table S2, Fig. S1).

The gene alignments length varied between 123 and 2439 bp (average 623 bp), harboring between 16 and 368 samples (average 236). In total, gene alignments present 196 726 characters, with 30.6% missing data (3.4%–57.6%). The proportion of variable sites and parsimony-informative sites was, respectively, 0.79 and 0.64 (Table S3).

3.2 Phylogenetic relationships

The tree resulting from the coalescent ASTRAL analysis is shown in Fig. 2, and the tree resulting from the concatenated IQ-TREE analysis is shown in Fig. S2. As relationships are very congruent, below we will discuss the relationships as shown in Fig. 2.

Cyperaceae are retrieved as a monophyletic family sister to Juncaceae with strong support (Fig. 2). Within Cyperaceae, 16 main clades are recovered (Fig. 2). Clade 1 represents subfamily Mapanioideae and includes two sister clades representing the tribes Chrysitricheae and Hypolytreae. Clade 2 represents tribe Trilepideae. Clade 3 represents the species-poor tribe Cladieae. Clade 4 is the Bisboeckelereae–Sclerieae Clade, which includes two subclades representing tribe Bisboeckelereae and tribe Sclerieae, respectively. Clade 5 represents the species-poor tribe Carpheae. Clade 6 is formed of the genus *Koyamaea* W.W.Thomas & G.Davidse sister to a clade representing tribe Cryptangieae. Clade 7 represents the diverse and species-rich tribe Schoeneae. Tribe Schoeneae includes a range of well-supported clades; however, the nodes in the backbone of the tribe are not all well supported. Also, its position in the backbone of the family is not well supported (LPP = 0.76). Clade 8 consists of tribe Rhynchosporae. Clade 9 or the Scirpo-Caricoid Clade (SCC Clade) includes a range of species-poor and species-rich lineages: Dulichieae, Khaosokieae, Calliscirpeae, Scirpeae, Trichophoreae, Sumatrosirpeae, and Cariceae. Each tribe is well supported as a monophyletic group as are the backbone nodes. Clade 10 is the Abildgaardieae–Eleocharideae Clade, which falls apart into two sister clades representing the tribes Abildgaardieae and Eleocharideae. Clades 11–14 are often referred to as the Fuireneae s.l. grade, with Clade 11 representing tribe Bolboschoeneae, Clade 12 tribe Fuireneae s.s., Clade 13 tribe Schoenoplecteae, and Clade 14 tribe Pseudoschoeneae. Each tribe is well supported as a monophyletic group and is placed with high support in the backbone of the family. Clades 15 and 16 represent the two main clades of tribe Cypereae, that is, the Ficinia Clade and the Cyperus Clade.

4 Discussion

4.1 Family Cyperaceae

In our results, Cyperaceae are confirmed as a monophyletic family within the monocot order Poales, sister to Juncaceae (Figs. 2, 3). The relationships inferred within Cyperaceae are mostly congruent with those of previous analyses

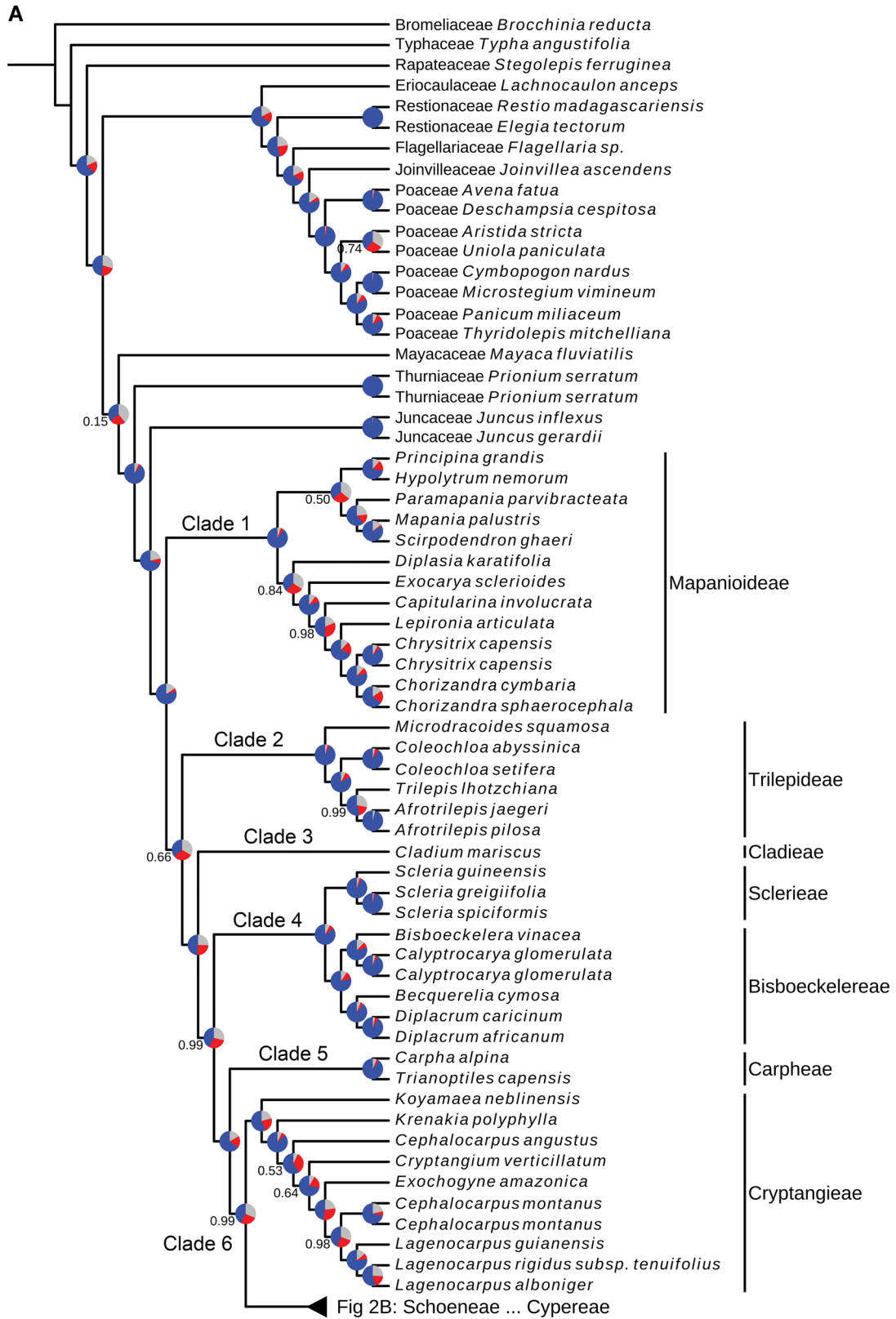


Fig. 2. Continued

(Simpson et al., 2007; Muasya et al., 2009a; Escudero & Hipp, 2013; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Spalink et al., 2016b; Semmouri et al., 2019), with some exceptions. Table S4 provides an overview of the main published classifications of the Cyperaceae and the classification proposed in this study, clearly indicating which changes occurred as more data became available. Table 1 provides an overview of the proposed classification.

Most previous molecular studies, which were largely based on chloroplast sequence data, recognized two subfamilies in Cyperaceae (Muasya et al., 2009a; Escudero & Hipp, 2013; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Spalink et al., 2016b; Semmouri et al., 2019). The targeted sequencing data (Fig. 2) confirm the established topology with subfamily Mapanioideae sister to subfamily Cyperoideae. The main morphological arguments to recognize two subfamilies in Cyperaceae relate to the differences in the morphology of the basic units of the inflorescence. In Cyperoideae, inflorescences are composed of one to many spikelets, each consisting of a rachilla bearing few to many glumes that may or may not subtend a flower (e.g., Goetghebeur, 1998). In contrast, the inflorescence units of Mapanioideae are frequently referred to as spicoids (e.g., Kukkonen, 1984; Simpson, 1992; Simpson et al., 2003; Beentje, 2016 and the preferred term here) or pseudospikelets (e.g., Eiten, 1976; Dai et al., 2010), and comprise 1–13(–100) scales. The homology of these units is still unclear. Many authors consider them to be a much-reduced spikelet (the basic inflorescence unit found in most other Cyperaceae; Dahlgren et al., 1985; Simpson, 1992; Vrijdaghs et al., 2006; Prychid & Bruhl, 2013), whereas others view them as a flower in which the regular trimerous structure of the cyperaceous flower has been disturbed (Goetghebeur, 1986, 1998).

Most previous studies retrieved tribe Trilepideae as sister to all remaining Cyperoideae (Simpson et al., 2007; Muasya et al., 2009a; Escudero & Hipp, 2013; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Spalink et al., 2016b; Semmouri et al., 2019). This relationship is here confirmed (Figs. 2, 3). Otherwise, little congruence can be found concerning the relationships between the early diverging lineages of Cyperoideae in the literature. In Simpson et al. (2007; using only the plastid marker *rbcl*), a Bisboeckelereae–Sclerieae Clade is the second branching clade in Cyperoideae before *Cladium* P.Browne. In Muasya et al. (2009a; using the plastid markers *rbcl* and *trnL-F*), *Cladium* branches off before Bisboeckelereae and Sclerieae that form a polytomy with the remainder of Cyperoideae; in Jung & Choi (2013; using the plastid markers *rbcl* and *trnL-F* plus one nuclear marker ITS),

both clades form a polytomy with the remainder of the Cyperoideae (cf. the Maximum Parsimony results of Semmouri et al., 2019; using five plastid markers and two nuclear markers ETS and ITS). However, in Hinchliff & Roalson (2013; supermatrix approach with scaffold based on two chloroplast markers *ndhF* and *rbcl*), *Cladium* is strongly supported as sister to Schoeneae, with the Bisboeckelereae–Sclerieae Clade retrieved as a separate lineage. In the Maximum Likelihood and Bayesian Inference results of Semmouri et al. (2019), and in the results of Spalink et al. (2016b; using the plastid markers *matK*, *ndhF*, *rbcl*, and *trnL-F*), Cladieae branches off right after Trilepidae, followed by a Bisboeckelereae–Sclerieae Clade sister to the rest of Cyperoideae. In our results (Fig. 2A), after subfamily Mapanioideae (Clade 1), tribe Trilepideae (Clade 2), tribe Cladieae (Clade 3), the Bisboeckelereae–Sclerieae Clade (Clade 4), tribe Carpheae (Clade 5), and tribe Cryptangieae (Clade 6), followed by the rest of subfamily Cyperoideae, branch off subsequently.

The topology of the family (Figs. 2, 3) raises interesting evolutionary and developmental questions in that Clades 1–6 are largely composed of tribes that are characterized by species having unisexual flowers (with the exception of Cladieae and Carpheae), in contrast to the remaining Cyperaceae tribes that are largely characterized by having bisexual flowers (with the exception of the tribes Khaosokieae and Cariceae in the Scirpo–Caricoide Clade). These clades are also characterized by having embryo types that were placed close to the ancestral *Juncus*-type embryo in the semophylysis (evolutionary sequence) of the embryo types according to Goetghebeur (1986; see also fig. 3 of Semmouri et al., 2019). Goetghebeur (1998) placed most of these tribes in two subfamilies: Chrysitricheae and Hypolytreae in subfamily Mapanioideae, and Trilepideae, Bisboeckelereae, Sclerieae, and Cryptangieae in subfamily Sclerioideae. Tribes Carpheae and Cladieae were only recently recognized (Semmouri et al., 2019) and were previously treated as part of tribe Schoeneae (e.g., Goetghebeur, 1998). Simpson et al. (2007) showed that subfamily Sclerioideae was not monophyletic and suggested maintaining only two subfamilies in Cyperaceae, that is, Mapanioideae and Cyperoideae.

4.2 Subfamily Mapanioideae

On the basis of pollen data, Simpson et al. (2003) supported the recognition of the two tribes in subfamily Mapanioideae, that is, Chrysitricheae (Fig. 5D) and Hypolytreae (Fig. 4B). Most Cyperaceae, including tribe Chrysitricheae, have

Fig. 2. Phylogenetic reconstruction of the relationships in Cyperaceae based on analysis of the exons data set. Coalescent ASTRAL analysis. Values by nodes represent local posterior probabilities (LPPs) and pie charts at nodes correspond to quartet support with blue: agreeing genes, red: disagreeing genes, and gray: uninformative genes. **A**, showing Poales outgroups and Cyperaceae Clades 1–6 (Mapanioideae, Trilepideae, Cladieae, the Bisboeckelereae–Scleria Clade, Carpheae, and Cryptangieae). **B**, Clades 7 and 8 (Schoeneae and Rhynchosporaeae). **C**, Clade 9 or the Scirpo–Caricoide Clade (Dulichieae, Khaosokieae, Calliscirpeae, Scirpeae, Trichophoreae, Sumatrosirpeae, and Cariceae). **D**, Clade 10 or the Abildgaardieae–Eleocharideae Clade (Abildgaardieae and Eleocharideae). **E**, Clades 11–14 representing the Fuireneae s.l. Grade (Bolboschoeneae, Fuireneae, Schoenoplecteae, and Pseudoschoeneae). **F**, Clades 15 and 16 or tribe Cyperae (subtribes Ficininae and Cyperinae).

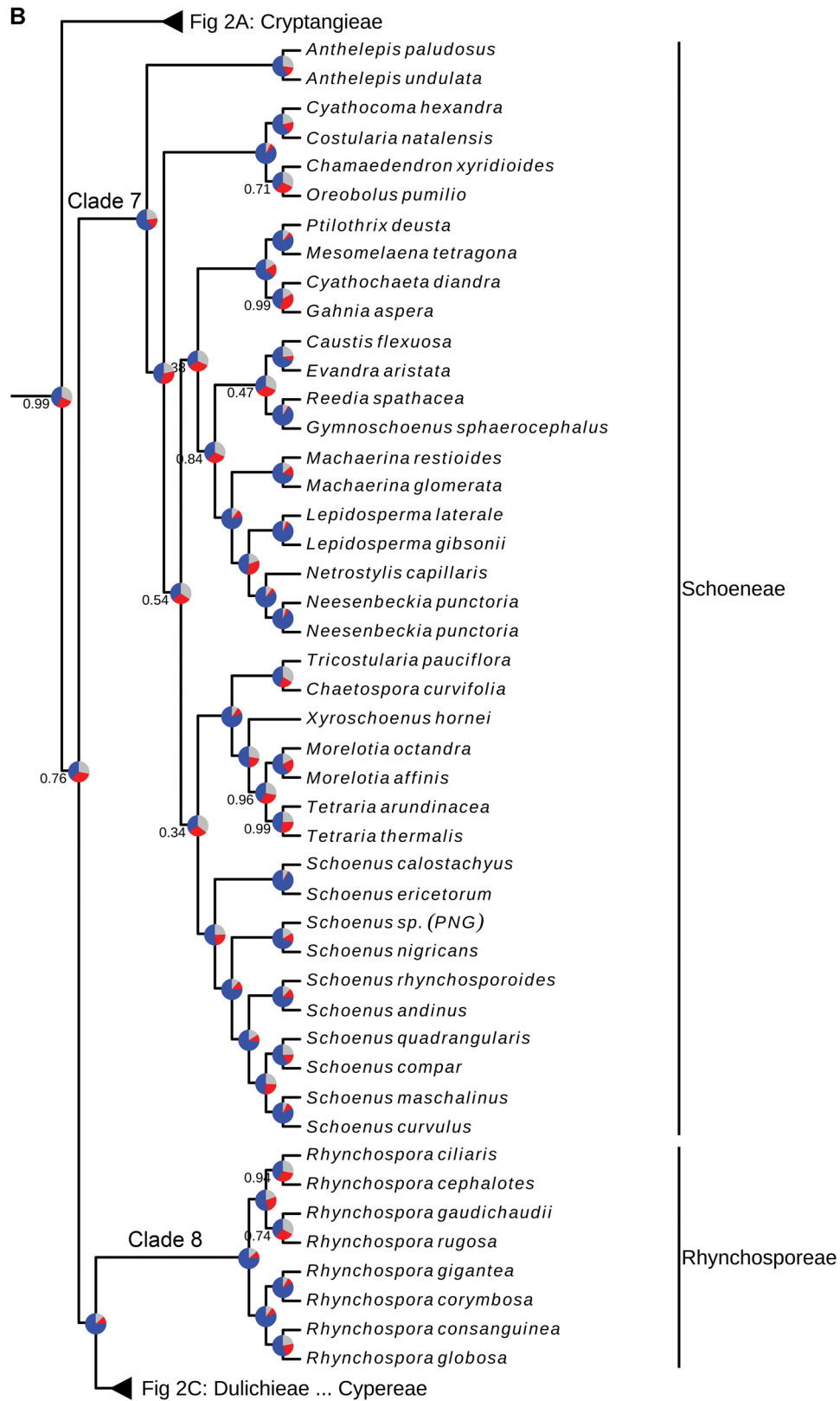


Fig. 2. Continued

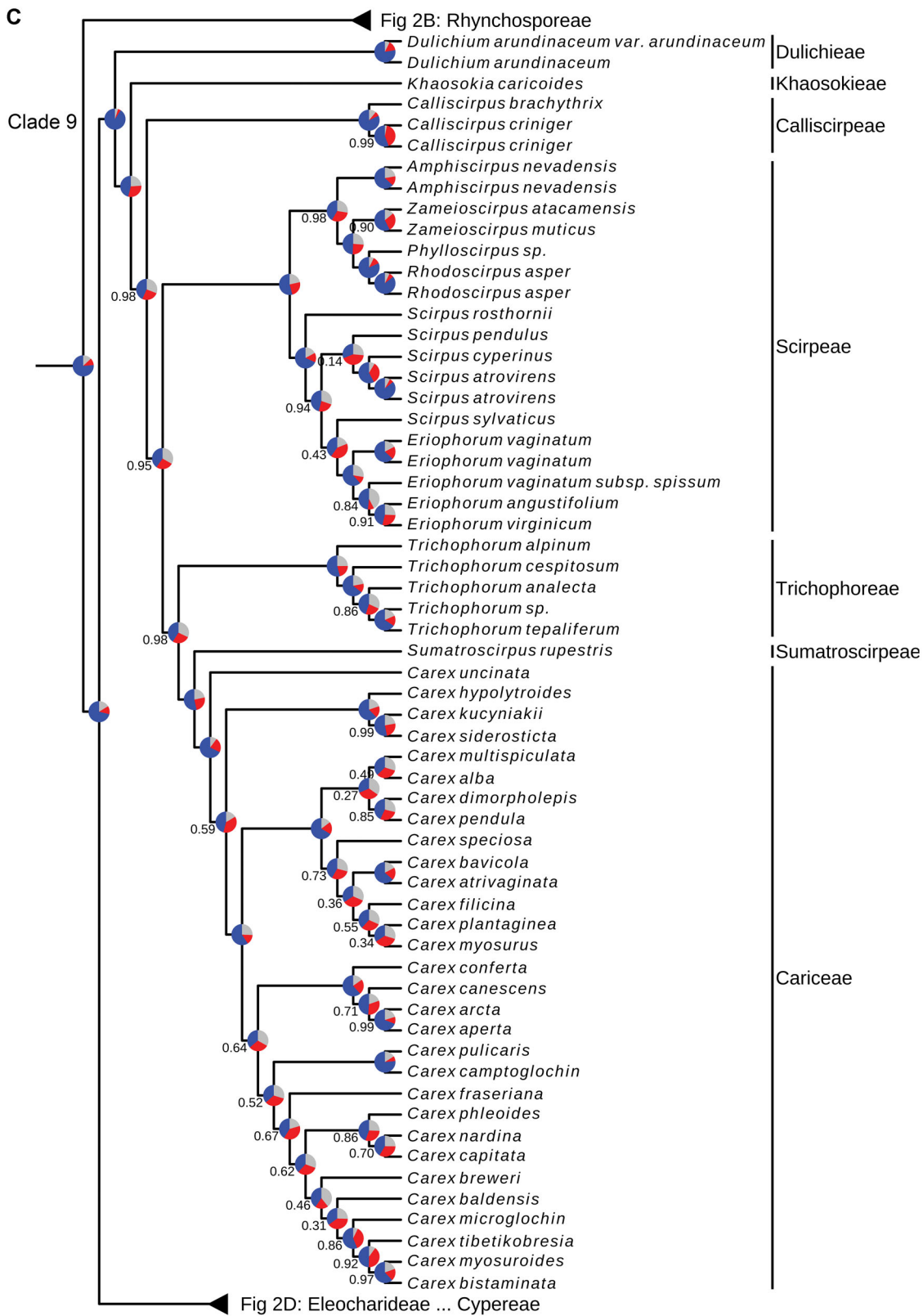


Fig. 2. Continued



Fig. 2. Continued

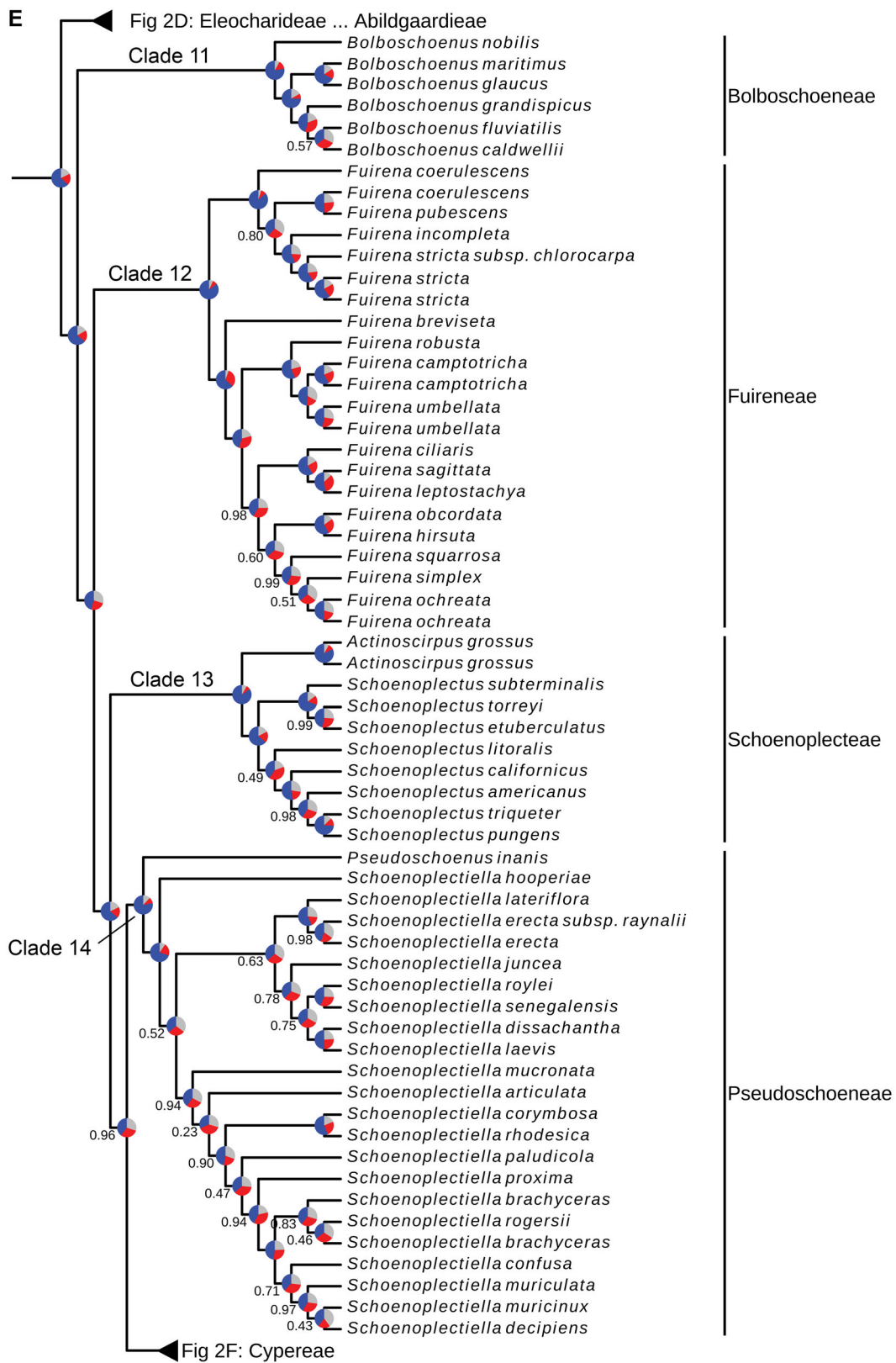


Fig. 2. Continued

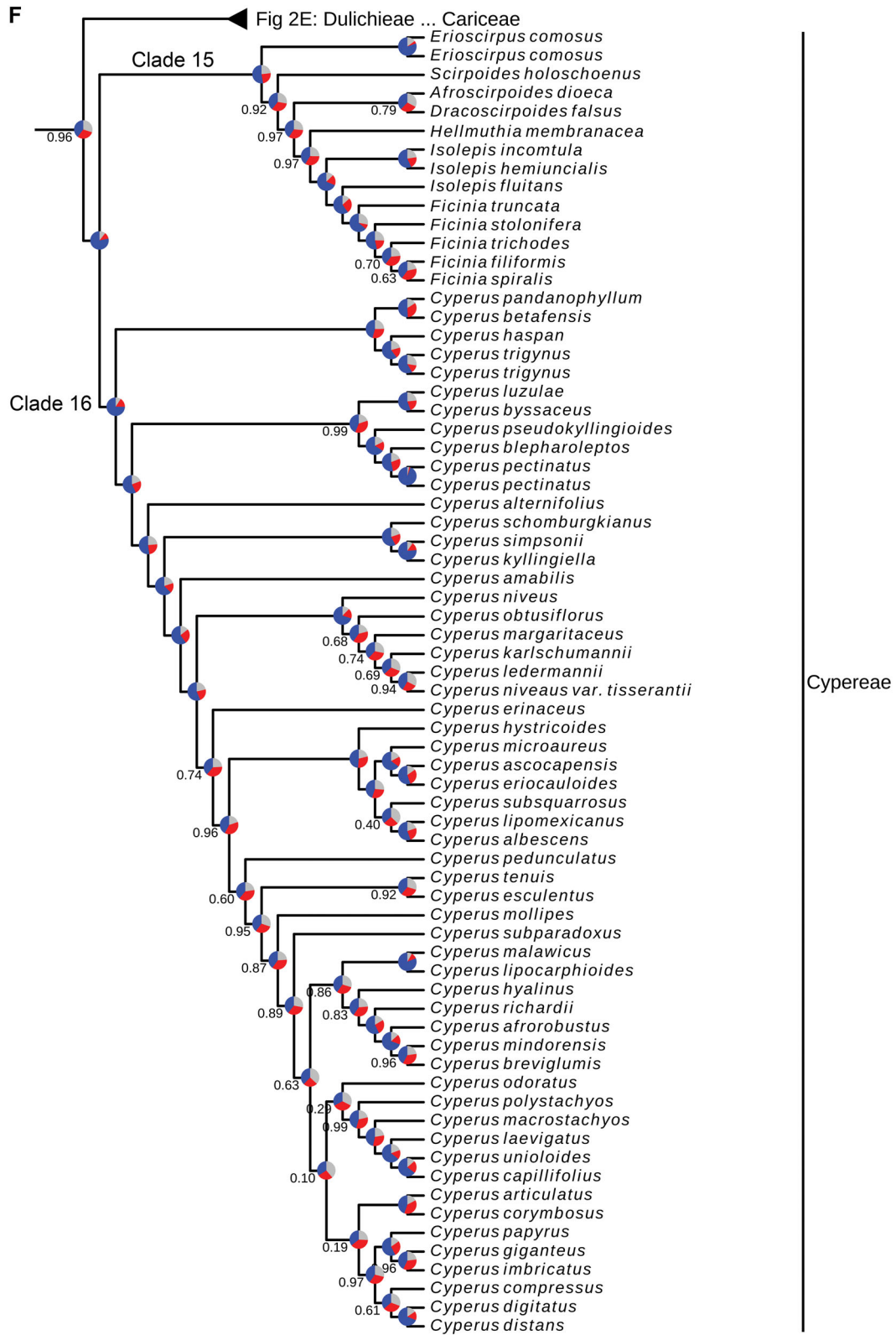


Fig. 2. Continued

thin-walled, pyriform, pseudomonad pollen, whereas Hypolytreae (forest or forest-margin dwellers, where wind pollination is less or not effective) have thick-walled, spheroidal, “Mapania-type” pollen that is coated with lipids, supporting earlier studies, especially Lorougnon (1973), which suggest that Hypolytreae use animal vectors for pollination (Simpson et al., 2003; Nagels et al., 2009). Simpson et al. (2003) indicated that younger, developmental stages of “Mapania-type” pollen were not available for their study and that pollen ontogeny could not be examined. However, Coan et al. (2010) showed that several *Hypolytrum* species have pseudomonads, suggesting that “Mapania-type” pollen in general is pseudomonad.

In most molecular studies, the circumscription of Chrysitricheae and Hypolytreae and the relationships between and within these tribes are not well resolved or have been conflicting (Simpson et al., 2003, 2007; Muasya et al., 2009a; Hinchliff & Roalson, 2013; Semmouri et al., 2019). A case in point is the inconsistent position of *Diplasia karatifolia* Rich. Simpson et al. (2003) and Muasya et al. (2009a) placed *Diplasia* Pers. within tribe Hypolytreae, whereas Semmouri et al. (2019) placed it in a nested position within tribe Chrysitricheae, and its relationship was unresolved in Hinchliff & Roalson (2013). In Spalink et al. (2016b), *Diplasia* was positioned as a separate lineage sister to the often retrieved Hypolytreae–Chrysitricheae Clade. Our results recover the tribes Chrysitricheae and Hypolytreae as monophyletic, with *Diplasia* as sister to the rest of tribe Chrysitricheae with moderate support (LPP = 0.84; Fig. 2A).

A recent molecular phylogenetic study showed that the formerly recognized monotypic genus *Principina* Uittien in nested within *Hypolytrum* (A. Mesterházy et al., unpublished data). In our results, the sample of *Principina* is retrieved as sister to the single included accession of *Hypolytrum*, confirming a close relationship. In Section 5, we follow A. Mesterházy et al. (unpublished data) and relegate *Principina* to synonymy.

4.3 Subfamily Cyperoideae

4.3.1 Tribe Trilepideae

In earlier studies (e.g., Simpson et al., 2007; Muasya et al., 2009a; Hinchliff & Roalson, 2013; Semmouri et al., 2019) and in this study (Figs. 2, 3), tribe Trilepideae (Fig. 5C) is retrieved as the first branching clade sister to the remaining lineages of subfamily Cyperoideae. Trilepideae includes four genera: *Afrotrilepis* (Gilly) J.Raynal, *Coleochloa* Gilly, *Microdracoides* Hua, and *Trilepis* Nees. In our results (Fig. 2A), within Trilepideae, *Microdracoides* appears sister to the other three genera, with *Coleochloa* sister to an *Afrotrilepis*–*Trilepis* Clade. This agrees with morphological argument (see Key to the genera of Trilepideae).

4.3.2 Tribe Cladieae

Tribe Cladieae (Fig. 5B) is monogeneric including only the cosmopolitan genus *Cladium*. Uncertainty remains concerning the relationship between *Cladium* and the monotypic genus *Rhynchocladium* from the Guiana Shield in Guyana and Venezuela. Despite several attempts, *Rhynchocladium* has never been successfully included in a molecular study.

Morphological similarities point at possible relationships between *Rhynchocladium* and *Cladium* (Cladieae), *Rhynchospora* (Rhynchosporae), and *Machaerina* (Schoeneae) (Maguire, 1972; Goetghebeur, 1986). Consequently, *Rhynchocladium* is the only genus here considered as unplaced in the proposed classification.

4.3.3 Bisboeckelereae–Sclerieae Clade

The circumscription of tribe Bisboeckelereae (Fig. 4A) and tribe Sclerieae (Fig. 5A) has not changed since the study of Goetghebeur (1998). *Becquerelia cymosa* Brong. and *Diplacrum africanum* (Benth.) C.B. Clarke have always been retrieved as a clade, ever since the study of Simpson et al. (2007). Muasya et al. (2009a) also included *Calyptrocarya* Nees in their study; however, this resulted in Bisboeckelereae not being monophyletic in their results (but sister to *Scleria* P.J.Bergius and *Becquerelia* Brongn. + *Diplacrum* R.Br.). With a wider species sampling, Hinchliff & Roalson (2013) found a grade of Bisboeckelereae leading to a monophyletic Sclerieae. Only recent studies (Bauters et al., 2016; Spalink et al., 2016b; Semmouri et al., 2019) retrieved a monophyletic Bisboeckelereae sister to the monogeneric Sclerieae. Our results confirm this topology with a monogeneric Sclerieae Clade sister to a Bisboeckelereae Clade (Figs. 2, 3). The latter includes two subclades: (i) *Becquerelia* + *Diplacrum* and (ii) *Bisboeckelera* + *Calyptrocarya* (Fig. 2A), which agrees with morphological arguments (see key to the genera of Bisboeckelereae in Section 5).

4.3.4 Tribe Carpheae

The position of the clade including the genera *Carpha* Banks & Sol. ex R.Br. and *Trianoptiles* Fenzl ex Endl. is variable in the literature. In some studies, *Carpha* is positioned within Schoeneae s.l. clade (Zhang et al., 2004, 2007; Verboom, 2006; Muasya et al., 2009a; Hinchliff & Roalson, 2013), whereas here and in other studies, *Carpha* (+ *Trianoptiles*) is placed outside Schoeneae (Simpson et al., 2007; Jung & Choi, 2013; Viljoen et al., 2013; Larridon et al., 2018a; Semmouri et al., 2019). This clade is also set apart by its unique combination of embryo morphology characters, having an embryo that is more or less rhomboid to top-shaped with a tapered scutellum, with a well-differentiated root cap in a lateral position separated from the coleoptile by a notch. This led Semmouri et al. (2019) to erect a new tribe to accommodate the genera *Carpha* and *Trianoptiles*. We retrieve tribe Carpheae (Fig. 4C) as a separate species-poor clade (Figs. 2, 3).

4.3.5 Tribe Cryptangieae

The relationship between tribe Cryptangieae (Fig. 5G) and the other Cyperaceae tribes varied in different studies (cf. Muasya et al., 2009a; Escudero & Hipp, 2013; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Spalink et al., 2016b; Semmouri et al., 2019). In earlier studies, the diversity of the tribe was represented by only two to three species. On the basis of sequence data of an increased sampling (18 spp.), Costa et al. (2018b) recovered Cryptangieae as monophyletic, supporting its recognition as a tribe in combination with its morphological distinctiveness. However, it remained unclear

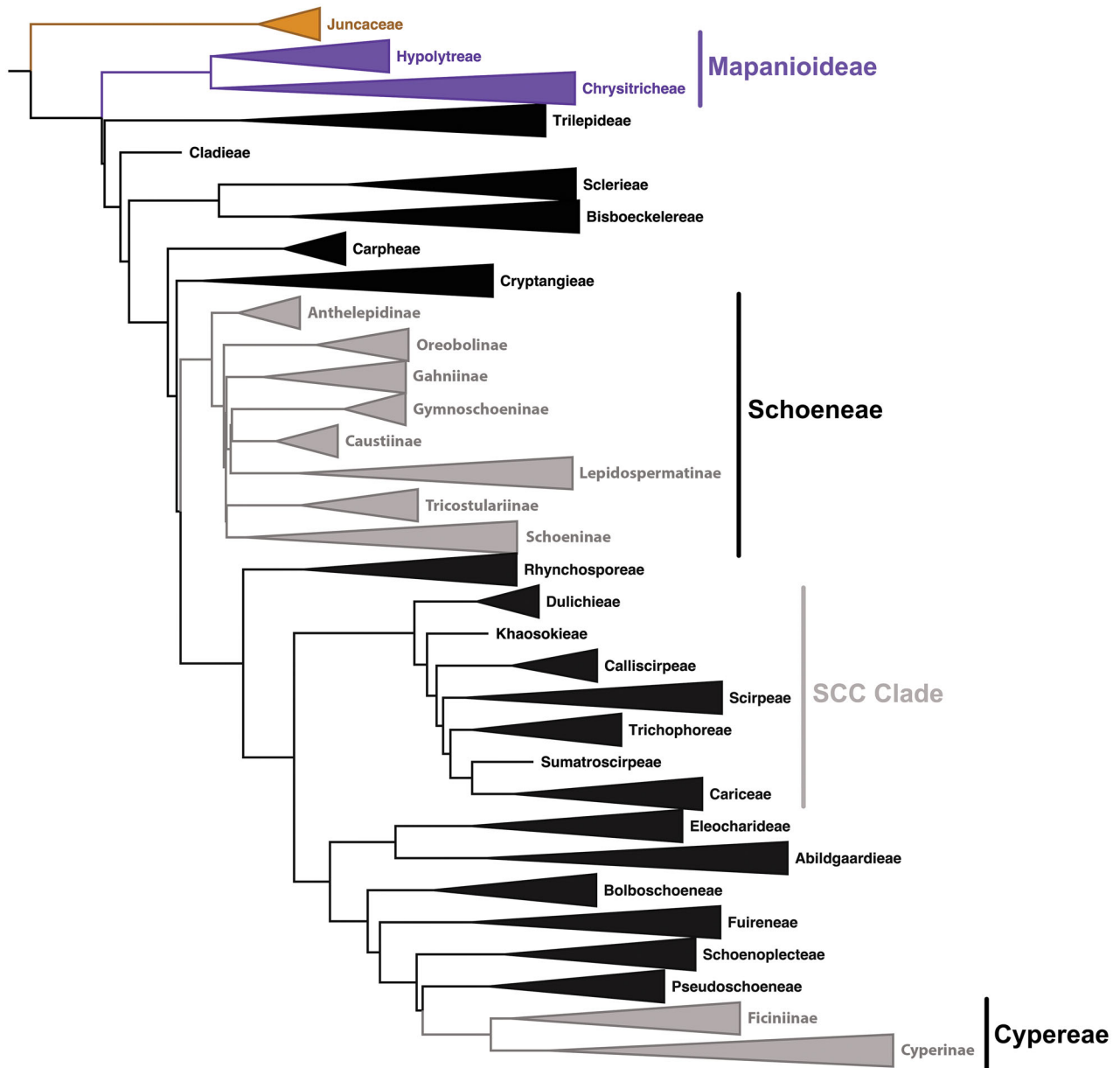


Fig. 3. Summary phylogeny of Cyperaceae at the tribal level showing the topology resulting from the coalescent ASTRAL analysis.

if the tribe is more closely related to tribe Schoeneae, tribe Carpheae, or to a Carpheae–Schoeneae Clade. Also, it did not include sequence data of the genus *Koyamaea*. Our targeted sequencing results show that a clade of *Koyamaea* plus Cryptangieae sensu Costa et al. (2018b) branches after tribe Carpheae and before tribe Schoeneae in the coalescent ASTRAL analysis (Figs. 2, 3); however, in the concatenated IQ-TREE analysis, the positions of Cryptangieae and Schoeneae are inverted (Fig. S2).

Koyamaea neblinensis W.W.Thomas & G.Davidse was described as a new genus and species to science by Thomas & Davidse (1989). Due to its bisexual spikelets, each bearing one pistillate flower and many staminate flowers, presence of well-developed perianth bristles in both kinds of flowers,

spirally arranged glumes, and regular nutlet without a cupule, *Koyamaea* was classified as a new genus of the then recognized subfamily Sclerioideae (Goetghebeur, 1998). As the authors believed that their new genus was not closely related to any other genus, they placed it in its own tribe *Koyamaeae*. Sanger sequence data could not be obtained for this extremely rare species to test its placement in the family and the value of erecting a separate monotypic tribe for it. High-throughput sequencing techniques are better at dealing with fragmented DNA obtained from historical herbarium specimens (e.g., Buerki & Baker, 2015; Hart et al., 2016; Bakker, 2017; Zeng et al., 2018; Brewer et al., 2019). Our targeted sequencing results are the first to place the genus *Koyamaea* in the Cyperaceae Tree of Life. It is here inferred as

Table 1 Proposed classification with number of species per genus and tribe, and number of genera per tribe

Subfamily	Tribe	Subtribe	Genera	Species/ genus	Species/ tribe	General/ tribe
Mapanioideae C.B.Clarke	Hypolytreae Pers.		Hypolytrum Pers.	63		
			Mapania Aubl.	100		
Chrysitricheae Nees			Paramapania Uittien	7		
			Scirpodendron Zipp. & Kurz	2	172	4
			Capitularina J.Kern.	1		
			Chorizandra R.Br.	6		
			Chrysitrix L.	4		
			Diplasia Pers.	1		
			Exocarya Benth.	1		
			Lepironia Pers.	1	14	6
			Afrotrilepis (Gilly) J.Raynal	2		
			Coleochloa Gilly	8		
			Microdracoides Hua	1		
Cladieae Nees			Trilepis Nees	5	16	4
			Cladium P.Browne	3	3	1
			Scleria P.J.Bergius	258	258	1
			Becquerelia Brongn.	6		
			Bisboeckelera Kuntze	4		
			Calyptrocarya Nees	8		
			Diplacrum R.Br.	10	28	4
			Carpha Banks & Sol. ex R.Br.	15		
			Trianoptiles Fenzl ex Endl.	3	18	2
			Cephalocarpus Nees	20		
Carpheae Semmouri & Larridon			Cryptangium Schrad. ex Nees	1		
			Didymiandrum Gilly	1		
			Exochogyne C.B.Clarke	2		
			Koyamaea W.W.Thomas & Davidse	1		
			Krenakia S.M.Costa	10		
			Lagenocarpus Nees	15	50	7
			Anthelepis R.L.Barrett, K.L.Wilson & J.J.Bruhl	4		
			Caustis R.Br.	7		
			Evandra R.Br.	2		
			Cyathochaeta Nees	5		
			Gahnia J.R.Forst. & G.Forst.	41		
			Mesomelaena Nees	5		
	Ptilothrix K.L.Wilson	1				
Schoeneae Dumort.		Anthelepidinae R.L.Barrett				
		Caustiinae R.L.Barrett				
		Gahniinae Pax				

Continued

Table 1 Continued

Subfamily	Tribe	Subtribe	Genera	Species/ genus	Species/ tribe	General/ tribe
		Gymnoschoeninae	Gymnoschoenus Nees	2		
		R.L.Barrett	Reedia F.Muell.	1		
		Lepidospermatinae	Lepidosperma Labill.	80		
		R.L.Barrett				
			Machaerina Vahl	55		
			Neesbeckia Levyns	1		
			Netrostylis R.L.Barrett, J.J.Bruhl & K.L.Wilson	11		
		Oreobolinae R.L.Barrett	Capeobolus Browning	1		
			Chamaedendron (Kük.) Larridon	5		
			Costularia C.B.Clarke	15		
			Gyathocoma Nees	3		
			Oreobolus R.Br.	17		
			Schoenus L.	149		
		Schoeninae Fenzl	Ammothryon R.L.Barrett, K.L.Wilson & J.J.Bruhl	1		
		Tricostulariinae R.L.Barrett	Chaetospora R.Br.	3		
			Morelotia Gaudich.	6		
			Tetraria P.Beauv.	39		
			Tricostularia Nees	11		
			Xyroschoenus Larridon	1	466	25
			Rhynchospora Vahl*	399	399	1
Rhynchosporaeae Nees			Blysmopsis Oteng-Yeb.	1		
Dulichieae W.Schultze-Motel			Blysmus Panz. ex Schult.	3		
			Dulichium Pers.	1	5	3
			Khaosokia D.A.Simpson	1	1	1
			Calliscirpus C.N.Gilmour, J.R.Starr & Naczi	2	2	1
			Amphiscirpus Oteng-Yeb.	1		
			Eriophorum L.	18		
			Phylloscirpus C.B.Clarke	3		
			Rhodoscirpus Léveillé-Bourret, Donadio & J.R.Starr	1		
			Scirpus Toum. ex L.	47		
			Zameloscirpus Dhooge & Goetgh.	3	73	6
Trichophoreae Lévy-Bourret & J.R.Starr			Trichophorum Pers.	19	19	1
Sumatroscirpeae Lévy-Bourret & J.R.Starr			Sumatroscirpus Oteng-Yeb.	4	4	1

Continued

Table 1 Continued

Subfamily	Tribe	Subtribe	Genera	Species/ genus	Species/ tribe	General/ tribe
Cariceae Dumort. Eleocharideae Goetgh. Abildgaardieae Lye			Carex L.	2003	2003	1
			Eleocharis R.Br.*	302	302	1
			Abildgaardia Vahl*	9		
			Actinoschoenus Benth.	2		
			Arthrostylis R.Br.	2		
			Bulbostylis Vahl*	227		
			Fimbristylis Vahl*	320		
			Nelmesia Van der Veken*	1		
			Scleroschoenus K.L.Wilson, J.J.Bruhl & R.L.Barrett	6		
			Trachystylis S.T.Blake	1		
Bolboschoeneae (Tatanov) J.R.Starr Fuireneae Rchb. ex Fenzl Schoenoplectieae Lye			Trichoschoenus J.Raynal	1		
			Zulustylis Muasya	2	571	10
			Bolboschoenus (Asch.) Palla	15	15	1
			Fuirena Rottb.	55	55	1
			Actinoscirpus (Ohwi) R.W.Haines & Lye	1		
			Schoenoplectus (Rchb.) Palla	16	17	2
			Pseudoschoenus (C.B.Clarke) Oteng-Yeb.	1		
			Schoenoplectiella Lye	63	64	2
			Affroscirpoides Garcia-Madr. & Muasya	1		
			Dracoscirpoides Muasya	3		
Cyperaceae Dumort.			Erioscirpus Palla	2		
			Ficinia Schrad.	87		
			Hellmuthia Steud.	1		
			Isolepis R.Br.	69		
			Scirpoides Ség.	4		
			Cyperus L.*	964	1131	8
			Rhynchocladium T.Koyama	1	1	1
			Incertae cedis			
			24 tribes			
			2 subfamilies			
				5687 species		95 genera

The number of species follows Govaerts et al. (2020) except for (i) Cryptangieae that follow Costa SM (pers. comm., 2020); (ii) Schoeneae that follow Barrett RL, Elliott TL, and Larridon I (pers. comm., 2020); (iii) *Rhynchospora* where the number reflects the recent synonymization of *Pleurostachys* Brongn. (Thomas, 2020); (iv) Eriophorum where the number of species follows Novoselova (1994a, 1994b); (v) *Trichophorum* that follows Léveillé-Bourret et al. (2020); (vi) Abildgaardieae that follow Larridon et al. (2021c); (vii) *Schoenoplectus* and *Schoenoplectiella* that follow Starr et al. (2021); (viii) *Ficinia* and *Isolepis* that follow Muasya & Larridon (2021); and (ix) *Cyperus* where the number reflects the recent synonymization of *Androtrichum* (Brongn.) Brongn. (Pereira-Silva et al., 2020). Genera including species using the C₄ photosynthetic pathway are indicated with an asterisk (*).

sister to the genera of Cryptangieae (Fig. 2A). As there are other arguments linking *Koyamaea* to Cryptangieae, that is, morphological (flowers with spiral glumes, bearing perianth and lacking cupule, beaked fruits) and anatomical (thickened pericarp) shared features, we opt to include *Koyamaea* in Cryptangieae.

Generic delimitation in Cryptangieae has fluctuated over the years, either with the number of genera considered in the strict sense, including just one or few species, or lumped into a broader *Lagenocarpus* Nees. Recent molecular studies highlighted the need of an updated generic circumscription (Costa et al. 2018b, 2021a). In the new interpretation, *Cephalocarpus* Nees includes the species formerly placed in *Everardia* Ridley and now encompasses the 20 species of Cryptangieae with an elongate caudex and lateral inflorescences (Costa et al., 2021a, 2021b). In our results, the monophyly of the newly enlarged genus *Cephalocarpus* is supported by the concatenated IQ-TREE analysis (Fig. S2), but not by the coalescent ASTRAL analysis where *Cephalocarpus angustus* (N.E.Brown) S.M.Costa (syn. *Everardia angusta* N.E.Brown) and *Cephalocarpus montanus* (Ridl.) S.M.Costa (syn. *Everardia montana* Ridl.) are not retrieved in a single clade (Fig. 2A). It should be noted that both species were formerly placed in *Everardia*; we did not sequence the type species of *Cephalocarpus* (*Cephalocarpus dracaenula* Nees). *Lagenocarpus* (*sensu* Koyama 2005) species have been split in five genera (Costa et al., 2021a): three of them (*Cryptangium* Schrader ex Nees, *Dydimiandrum* Gilly, and *Exochogyne* C.B.Clarke) with 1–2 species and the others with 10 (*Krenakia* S.M.Costa; Costa et al., 2021a) and 15 species (*Lagenocarpus*). The genera are distinguished mostly by leaf, inflorescence, and fruit characters (Costa et al., 2021a). The results of Costa et al. (2021a) place *Krenakia* as sister to a clade encompassing three subclades: (i) *Didymiandrum* + *Exochogyne*; (ii) *Cryptangium* sister to *Cephalocarpus*; and (iii) *Lagenocarpus* s.s. Our targeted sequencing results show *Koyamaea* sister to a clade encompassing the Cryptangieae *sensu* Costa et al. (2018b, 2021a).

4.3.6 Tribe Schoeneae

Tribe Schoeneae (Figs. 5E, 5F) has been widely recognized, but its exact circumscription has long remained unclear. However, tribe Schoeneae s.s. (excluding Carpheae and Cladieae) has been shown to be monophyletic in recent studies (Viljoen et al., 2013; Spalink et al., 2016b; Larridon et al., 2018a; Semmouri et al., 2019). Goetghebeur (1998) and Simpson et al. (2007) had also placed *Pleurostachys* Brongn. and *Rhynchospora* in Schoeneae s.l., but these genera were moved to a separate tribe Rhynchosporae by Muasya et al. (2009). Our targeted sequencing results (Fig. 2B) confirm a monophyletic tribe Schoeneae *sensu* Semmouri et al. (2019).

Relationships within tribe Schoeneae have not been entirely resolved; however, progress has been made in our understanding of its evolution. Morphologically, tribe Schoeneae is a highly variable group. Previous molecular analyses of the group recovered six main clades: the Caustis Clade, Gahnia Clade, Lepidosperma Clade, Oreobolus Clade, Schoenus Clade, and Tricostularia Clade (Viljoen et al., 2013; Larridon et al., 2018a). In the more deeply sampled phylogenetic study of Semmouri et al. (2019), two additional clades became visible, a clade including the genera *Reedia*

F.Muell. and *Gymnoschoenus* Nees and a separate lineage of *Schoenus paludosus* (R.Br.) Roem. & Schult. Our targeted sequencing results confirm the presence of eight main clades in Schoeneae (Fig. 2B). To facilitate the morphological characterization of the main clades in this morphologically diverse tribe, they are recognized as subtribes in Section 5.

Previous molecular studies remarked on the polyphyly of genera in Schoeneae (Zhang et al., 2004; Muasya et al., 2009a; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Viljoen et al., 2013; Larridon et al., 2018a; Barrett et al., 2019). This mostly concerned the genera *Costularia* C.B.Clarke, *Epischoenus* C.B.Clarke, *Schoenus*, *Tetraria* P.Beauv., and *Tricostularia*, which had species scattered across different clades in tribe Schoeneae, greatly confusing the boundaries of the subtribes recognized here. Recently, efforts have been made to realign the taxonomy of these genera to make them monophyletic.

Anthelepis Clade: In the BI and ML results of Semmouri et al. (2019), *Schoenus paludosus* formed a polytomy with the Gahnia Clade and the Oreobolus Clade, revealing its isolated position from other *Schoenus* species. In fact, *Schoenus paludosus* also differs morphologically from the true *Schoenus* species in having one or sometimes two lower male flowers and an upper bisexual flower at each spikelet, besides a non-zigzag rachilla (as opposed to the usual states for the genus of bisexual flowers and upper internodes of the rachilla elongated and prominently zigzag; Wilson, 1993). *Schoenus paludosus* was recently placed in a new genus *Anthelepis* R.L.Barrett, K.L.Wilson & J.J.Brühl together with the species previously named *Schoenus guillauminii* Kük. and *Tricostularia undulata* (Thwaites) J.Kern (Barrett et al., 2019). The Anthelepis Clade is here strongly supported as sister to the remainder of Schoeneae (Fig. 2B).

Caustis Clade: This clade includes the genera *Caustis* R.Br. and *Evandra* R.Br. (Fig. 2B). The unexpected placement of a lineage previously included in *Tetraria*, that is, *Tetraria borneensis* J.Kern, in the Caustis Clade (Larridon et al., 2018a) is being explored further (Barrett RL & Larridon I, unpublished data). This species could not be sequenced for this study.

Gahnia Clade: The circumscription of the Gahnia Clade, including the genera *Cyathochaeta* Nees, *Gahnia* J.R.Forst. & G.Forst., *Mesomelaena* Nees, and *Ptilothrix* K.L.Wilson (Fig. 2B), remains unchanged, but notably excludes *Morelotia* Gaudich., previously included under *Gahnia*, which is placed in the Tricostularia Clade (e.g., Verboom, 2006; Muasya et al., 2009a; Jung & Choi, 2013; Hinchliff & Roalson, 2013; Viljoen et al., 2013; Larridon et al., 2018a; Semmouri et al., 2019; this study).

Gymnoschoenus–Reedia Clade: This is a small clade of just three morphologically distinctive species placed in the genera *Gymnoschoenus* and *Reedia* (Fig. 2B), each with restricted distributions in southern Australia whose affinities have been much debated.

Lepidosperma Clade: Another lineage previously included in *Tetraria*, that is, the *Tetraria capillaris* (F.Muell.) J.M.Black species complex, native to Australia and New Zealand, was found to be part of the Lepidosperma Clade (Viljoen et al., 2013; Larridon et al., 2018a; Barrett et al., 2019). A recent taxonomic revision of the *Tetraria capillaris* species complex resulted in the publication of

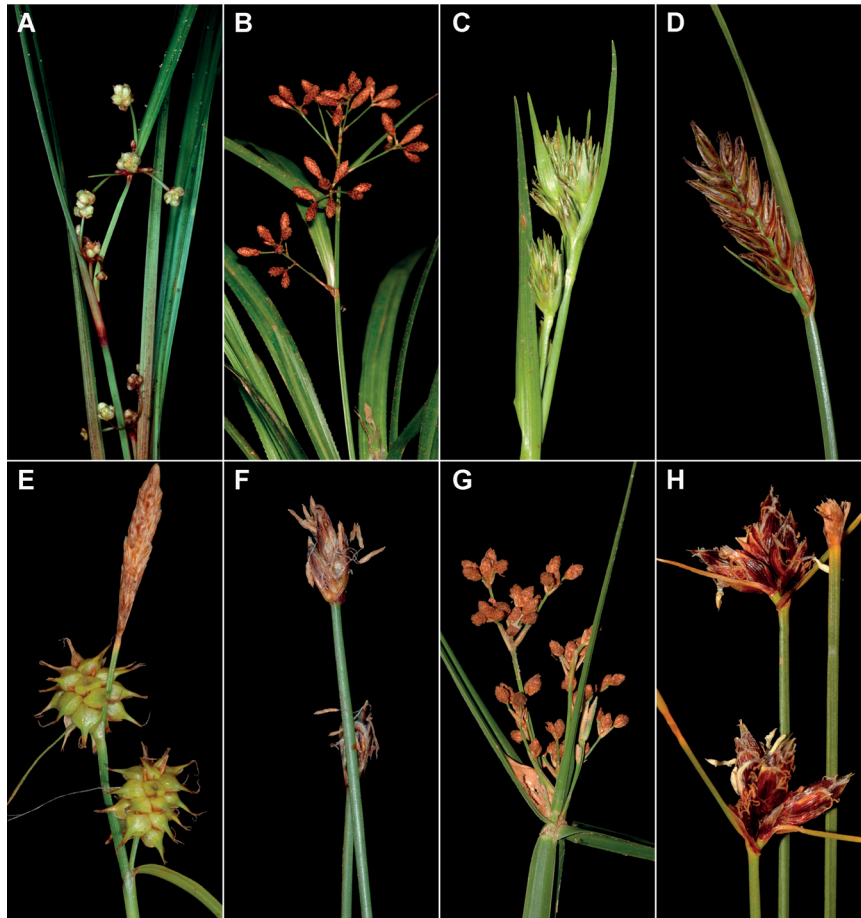


Fig. 4. Morphological diversity of the Cyperaceae tribes. **A**, Hypolytreae, *Mapania floribunda* (Nees ex Steud.) T.Koyama. **B**, Bisboeckelereae, *Calyptracarya poeppigiana* Kunth. **C**, Carpheae, *Carpha capitellata* (Nees) Boeckeler. **D**, Dulichieae, *Blysmus compressus* (L.) Panz. ex Link. **E**, Cariceae, *Carex lepidocarpa* Tausch. **F**, Eleocharideae, *Eleocharis quinqueflora* (Hartmann) O.Schwarz. **G**, Schoenoplecteae, *Actinoscirpus grossus* (L.f.) Goetgh. & D.A.Simpson. **H**, Cyperaeae: Ficiniinae, *Ficinia acuminata* (Nees) Nees. Photos by Modesto Luceño.

a new genus *Netrostylis* (Barrett et al., 2021a). The Lepidosperma Clade appears to have originated in Australia (Viljoen et al., 2013). Previous studies (e.g., Verboom, 2006; Muasya et al., 2009a; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Viljoen et al., 2013; Larridon et al., 2018a; Semmouri et al., 2019) indicated that the clade includes (i) the species-rich genus *Lepidosperma* occurring from China to Australasia; (ii) *Machaerina* Vahl (including *Baumea* Gaudich.), which is widespread from Australia to the Americas; and (iii) the monotypic genus *Neesenbeckia* Levyns endemic from the South African Cape Floristic Region. As retrieved in, for example, Viljoen et al. (2013) and Larridon et al. (2018a), our results confirm that within the Lepidosperma Clade, the genus *Machaerina* is sister to a clade with two subclades: (i) *Lepidosperma* and (ii) *Netrostylis* sister to *Neesenbeckia* (Fig. 2B). The latter sister relationship between *Netrostylis* and *Neesenbeckia* suggests an unusual dispersal event from Australia to southern Africa. Although some taxonomic issues remain in *Machaerina* (Barrett RL, Wilson KL & Bruhl JJ, unpublished data), more work is required in *Lepido-*

sperma, which has c. 200 undescribed species in southern Australia (Barrett & Wilson, 2012, 2013).

Oreobolus Clade: Larridon et al. (2018a) found that *Costularia* s.l. was composed of four distinct evolutionary lineages with two lineages being part of the Oreobolus Clade: (i) a much-reduced genus *Costularia* (Larridon et al., 2019a) and (ii) a small New Caledonian endemic genus *Chamaedendron*. The circumscription of the other genera in this clade (Fig. 2B), that is, *Capeobolus*, *Cyathocoma* Nees, and *Oreobolus* R.Br., remains unchanged.

Schoenus Clade: As some species of *Tetraria* and *Epischoenus* had been shown to be nested within *Schoenus* (Viljoen et al., 2013), Elliott & Muasya (2017) transferred these species to *Schoenus*. The broader circumscription of *Schoenus* is supported by our targeted sequencing results (Fig. 2B), and only a single morphologically variable and geographically widespread genus is recognized in this clade.

Tricostularia Clade: Larridon et al. (2018a) found that the two other distinct evolutionary lineages previously placed in *Costularia* s.l. were part of the Tricostularia Clade: (i) a single-species lineage from the Seychelles *Xyroschoenus hornei*

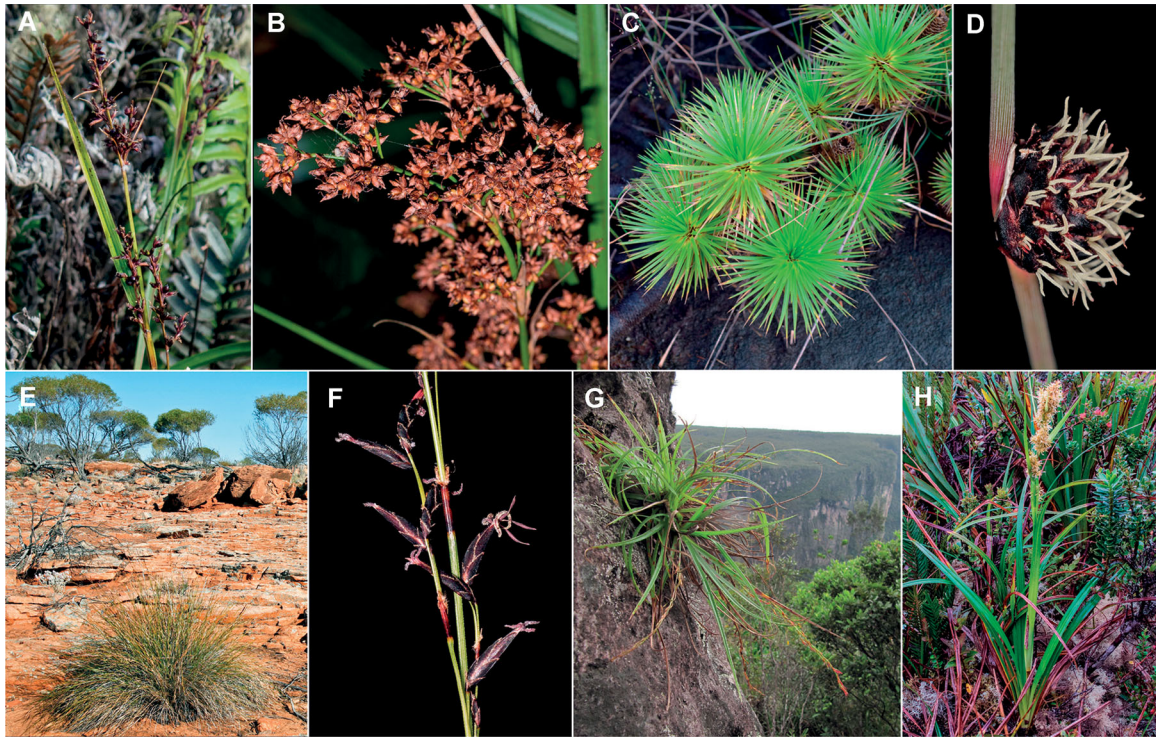


Fig. 5. Morphological diversity of the Cyperaceae tribes. **A**, Sclerieae, *Scleria gaertneri* Raddi. **B**, Cladieae, *Cladium mariscus* subsp. *intermedium* Kük. **C**, Trilepideae, *Microdracoides squamosa* Hua. **D**, Chrysitricheae, *Chorizandra enodis* Nees. **E**, Schoeneae, *Lepidosperma* Labill. sp. **F**, Schoeneae, *Schoenus melanostachys* R.Br. **G**, Cryptangieae, *Cephalocarpus* cf. *maguireanus* (T.Koyama) S.M.Costa. **H**, Rhynchosporeae, *Rhynchospora* Vahl sp. Photos **A**, **B**, and **D–F** by Russell Barrett; **C** by Isabel Larridon; **G** by Suzana Costa.

(C.B.Clarke) Larridon and (ii) the rest of *Costularia* subgenus *Lophoschoenus* that formed a grade including the African “reticulate-sheathed” *Tetraria* species, with a single *Epischoenus* species nested within this clade (i.e., *Epischoenus cernuus* Levyns). As Elliott & Muasya (2017) had already transferred the “non-reticulate sheathed” species of *Tetraria*, including the original type species of *Tetraria*, that is, *T. thuarii* P.Beauv. (= *Schoenus compar* L.), and most of *Epischoenus* into *Schoenus*, Larridon et al. (2017) proposed to conserve the genus *Tetraria* with a new type, *T. thermalis* (L.) C.B.Clarke. The same authors recircumscribed *Tetraria* as including c. 30 “reticulate sheathed” *Tetraria* species, *Epischoenus cernuus*, and most of *Costularia* subgenus *Lophoschoenus* sensu Kükenthal (1939) (Larridon et al., 2018b).

The Tricostularia Clade also includes the Australian species *Tetraria octandra* (Nees) Kük., which Larridon et al. (2018a) suggested should be accepted as *T. octandra* (Nees) C.B.Clarke, as it is not related to *Tetraria*. The taxonomic changes made to *Costularia* s.l. and *Tetraria* by Larridon et al. (2017, 2018a, b) are supported by our targeted sequencing results (Fig. 2B). More recent research has shown that three Australian species until recently placed in *Tetraria*, *T. australiensis* C.B.Clarke, *T. microcarpa* S.T.Blake, and *T. octandra* are closely related to *Morelotia* and *Xyroschoenus* (Barrett et al., 2021b). Therefore, the decision has been taken to expand the circumscription of *Morelotia*, by including the three Australian *Tetraria* species and a Pacific Island species

(originally described as *Machaerina involuta* H.St.John) (Barrett et al., 2021b).

Some *Schoenus* species have been recovered in the Tricostularia Clade, that is, *Schoenus curvifolius* (R.Br.) Roem. & Schult., *S. grandiflorus* (Nees) F.Muell., and *S. turbinatus* (R.Br.) Roem. & Schult. (Viljoen et al., 2013; Larridon et al., 2018a; Barrett et al., 2019; Semmouri et al., 2019). Further research has led to the resurrection and recircumscription of the genus *Chaetospora* R.Br. (Barrett et al., 2019, 2020). *Schoenus grandiflorus* has been recognized as a monotypic genus *Ammothryon* as it is not recovered as sister to any genus in the clade (Barrett et al., 2021b).

Within the Tricostularia Clade, the genus *Tricostularia* itself has been reduced in morphological circumscription with the removal of species now placed in *Anthelepis* (Barrett et al., 2019). In parallel, the number of species was enlarged with the addition of *Lepidosperma aphylla* R.Br. and *L. exsul* C.B.Clarke (Barrett & Wilson, 2012) and ongoing taxonomic revision of species boundaries in southern Western Australia (Barrett, 2012; Barrett et al., 2021b).

4.3.7 Tribe Rhynchosporeae

The topology of the remaining Cyperoideae lineages in our results largely matches previous studies (Simpson et al., 2007; Muasya et al., 2009a; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Spalink et al., 2016b; Costa et al., 2018b; Semmouri et al., 2019), with tribe Rhynchosporeae (Fig. 5H) sister to the Scirpo-Caricoid Clade (SCC Clade) plus the

Abildgaardieae–Eleocharideae–Fuireneae–Cypereae Clade (FAEC Clade) (Fig. 2). Tribe Rhynchosporae is now accepted as monogeneric. The nested position of *Pleurostachys* Brongn. in *Rhynchospora* Vahl has been known for a long time (Thomas et al., 2009; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Semmouri et al., 2019). Moreover, their similar embryo morphology (*Carex*-type embryo; Semmouri et al., 2019) provided an additional argument for the merging of the two taxa. Thomas (2020) recently merged *Pleurostachys* into *Rhynchospora*.

4.3.8 Scirpo-Caricoid Clade

A Scirpo-Caricoid Clade (SCC Clade), referred to as the Scirpeae–Dulichieae–Cariceae Clade (SDC Clade) in some previous studies, was recognized in all recent molecular phylogenetic studies of Cyperaceae as a sister group to the Abildgaardieae–Eleocharideae–Fuireneae–Cypereae Clade (FAEC Clade) (Muasya et al., 2009a; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Spalink et al., 2016b; Léveillé-Bourret et al., 2014, 2015, 2018b, 2018c; Semmouri et al., 2019). The Scirpo-Caricoid Clade contains 41% of all recognized Cyperaceae species (Léveillé-Bourret & Starr, 2019; Govaerts et al., 2020), comprising a curious assemblage of tribes that illustrates the full breadth of inflorescence and floral diversity of Cyperoidae. This includes bisexual, monoecious, and dioecious species with empty proximal glumes or all glumes fertile, spirally or distichously inserted flowers, sterile or fertile prophylls, as well as setiform, tepaliform, or absent perianth (Léveillé-Bourret & Starr, 2019). There are no recognizable synapomorphies for this clade, whose only recognizable characteristic is its center of diversity in cold temperate regions of the Northern Hemisphere (Léveillé-Bourret & Starr, 2019; Martín-Bravo et al., 2019), contrasting with the southern temperate distribution for Schoeneae or mostly tropical diversity of other major Cyperaceae lineages.

The monogeneric tribe Cariceae contains most of the diversity of the clade, with c. 2000 species (Roalson et al., 2021; Villaverde et al., 2020, 2021), and is characterized by a highly derived inflorescence morphology formed of perianthless unisexual flowers, with female flowers strictly associated with the production of secondary branches, and pistils contained within or subtended by the first bract of secondary branches (a prophyll called a perigynium or utricle if closed forming a bottle-like structure; Jiménez-Mejías et al., 2016b). Although relationships within this tribe are not highly supported in the present study, they have been already addressed in Villaverde et al. (2020).

The other 13 genera (c. 88 species) of the Scirpo-Caricoid Clade have all been placed at one point in their history within a broadly circumscribed “tribe Scirpeae,” which was essentially defined by a lack of derived characters. Unsurprisingly, most recent studies suggested paraphyly of Scirpeae when thus circumscribed (Hinchliff & Roalson, 2013; Jung & Choi, 2013; Spalink et al., 2016b). However, an ancient rapid radiation near the crown of the Scirpo-Caricoid Clade made previous phylogenetic analyses extremely difficult, with different analyses supporting different topologies with consistently low support (Hinchliff & Roalson, 2013; Jung & Choi, 2013; Spalink et al., 2016b; Semmouri et al., 2019).

A series of recent studies combining plastid and nuclear ribosomal markers (Gilmour et al., 2013; Léveillé-Bourret et al.,

2014, 2015, 2018a, 2019), genomic data (Léveillé-Bourret et al., 2018c; Villaverde et al., 2020, 2021), and morphological data (Léveillé-Bourret & Starr, 2019) were able to resolve the most recalcitrant backbone branches of the Scirpo-Caricoid phylogeny. Our present results (Fig. 2C) are in agreement with these recent studies and support the taxonomic treatment of the clade as presented in Léveillé-Bourret & Starr (2019).

4.3.8.1 Tribe Dulichieae. As in previous studies, tribe Dulichieae (Fig. 4D), excluding *Sumatrosclirpus* Oteng-Yeb., is strongly supported as monophyletic (e.g., Gilmour et al., 2013; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Léveillé-Bourret et al., 2014, 2015, 2018a, 2018c; Léveillé-Bourret & Starr, 2019; Semmouri et al., 2019). It is easily diagnosed by the presence of distichous spikelets and flowers, scale-like spikelet prophylls subtending flowers, and long narrow beaks on fruits. Two genera have commonly been recognized in Dulichieae, that is, *Blysmus* and *Dulichium* Pers. (Goetghebeur, 1998), but recent studies provide some support for recognizing *Blysmopsis* (Léveillé-Bourret et al., 2014; Semmouri et al., 2019), which was commonly treated as a synonym of *Blysmus* (Goetghebeur, 1998).

4.3.8.2 Tribe Khaosokieae. The monogeneric tribe *Khaosokieae* (Fig. 6B) represents a single recently described genus and species (Simpson et al., 2005) that has proven difficult to place in the suprageneric classification based on morphological arguments due to characters suggesting affinities with several different tribes, that is, unisexual flowers like Cariceae, seven perianth bristles and narrow elongate spikelets suggestive of *Dulichium* (tribe Dulichieae), but spirally inserted flowers and sterile prophylls typical of tribe Scirpeae. All phylogenetic studies have supported its isolated position within the Scirpo-Caricoid Clade, either as sister to all other lineages of the tribe (Muasya et al., 2009a; Jung & Choi, 2013; Semmouri et al., 2019) or as the next diverging lineage after tribe Dulichieae (Simpson et al., 2007; Escudero & Hipp, 2013; Hinchliff & Roalson, 2013; Léveillé-Bourret et al., 2014, 2015, 2018a, 2018c; Spalink et al., 2016b; this study, Fig. 2C).

4.3.8.3 Tribe Calliscirpeae. This monogeneric lineage was recently recognized (Léveillé-Bourret & Starr, 2019) based on species formerly placed in *Scirpus* L. or *Eriophorum* L., but that differ by having antrorsely barbed perianth bristles and a *Carex*-type embryo (Gilmour et al., 2013). All previous studies have consistently supported the isolated position of this lineage in the Scirpo-Caricoid Clade, but its phylogenetic position as sister to a Scirpeae–Trichophoreae–Sumatrosclirpeae–Cariceae Clade has never received strong support (Léveillé-Bourret et al., 2014, 2015, 2018a, 2018c; Semmouri et al., 2019). In our results, tribe Calliscirpeae (Fig. 6A) branches after *Khaosokieae*, sister to the remaining lineages of the Scirpo-Caricoid Clade (Fig. 2C).

4.3.8.4 Tribe Scirpeae. Tribe Scirpeae (Fig. 6C) is a lineage of the Scirpo-Caricoid Clade (e.g., Simpson et al., 2007; Muasya et al., 2009a; Hinchliff & Roalson, 2013; Léveillé-Bourret et al., 2014, 2018a, 2018c; Spalink et al., 2016b; Semmouri et al., 2019). As previously discussed (see Section 4.3.8), tribe Scirpeae sensu Goetghebeur (1998) is not mono-

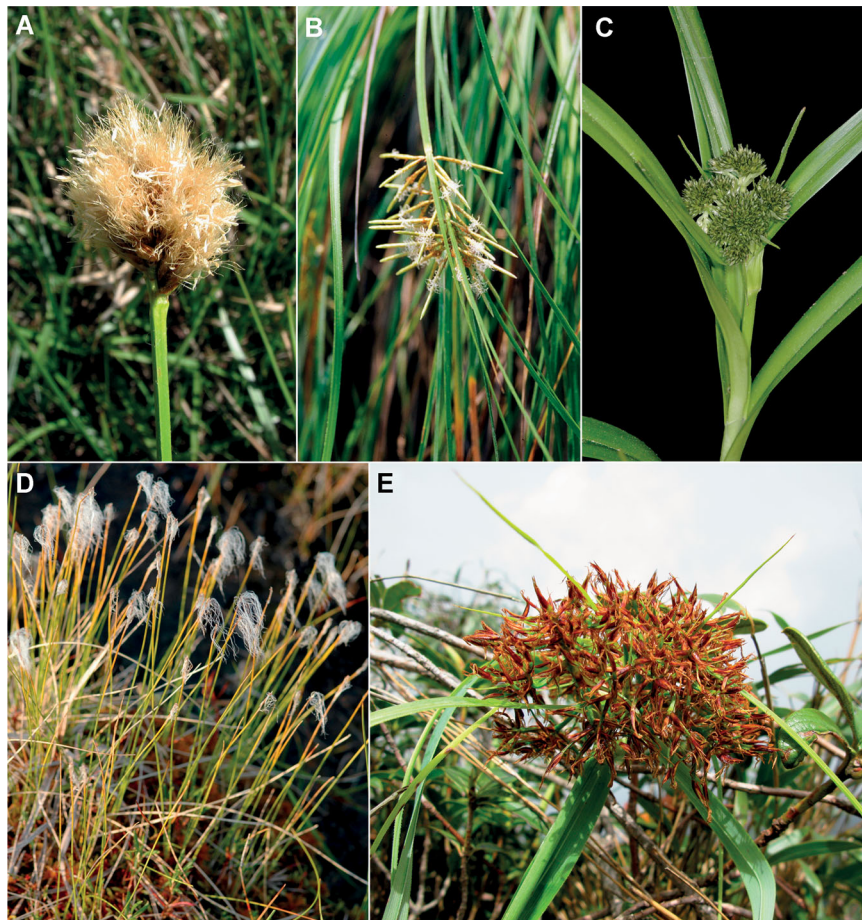


Fig. 6. Morphological diversity of the Cyperaceae tribes. **A**, Calliscirpeae, *Calliscirpus brachythrix* C.N.Gilmour, J.R.Starr & Naczi. **B**, Khaosokieae, *Khaosokia caricoides* D.A.Simpson. **C**, Scirpeae, *Scirpus sylvaticus* L. **D**, Trichophoreae, *Trichophorum alpinum* (L.) Pers. **E**, Sumatrosirpeae, *Sumatrosirpus rupestris* Lév.-Bourret & J.R.Starr. Photos **A** and **E** by Julian Starr; **B** by Rachun Pooma; **C** and **D** by Modesto Luceño.

phyletic and consists of three separate lineages. As a result, Scirpeae was recircumscribed by Léveillé-Bourret & Starr (2019) to include only species possessing a (sub-)lateral germ pore in their embryos, corresponding to Schoenus-type, Fimbristylis-type, or intermediate embryo types. Under this circumscription, Scirpeae is monophyletic. No visible macromorphological character has been found that can unambiguously diagnose this tribe, which means that identification must be done by means of exclusion. Two major subclades are found within this monophyletic Scirpeae (Fig. 2C): (i) a mostly South American group that has been dubbed “Zameioscirpus Clade” is supported in many studies (Dhooge et al., 2003; Muasya et al., 2009a; Léveillé-Bourret et al., 2015), including *Amphiscirpus* Oteng-Yeb., *Phylloscirpus* C.B.Clarke, *Rhodoscirpus* Léveillé-Bourret, Donadío & J.R.Starr, and *Zameioscirpus* Dhooge & Goetgh.; and (ii) a mostly circumboreal “Scirpus Clade,” well supported in our analyses and consistently found in other studies, with the genus *Eriophorum* L. forming a well-supported clade nested within *Scirpus*, thus making *Scirpus* paraphyletic (e.g., Gilmour et al., 2013; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Léveillé-Bourret et al., 2014, 2018a, 2018c).

The circumscription of *Eriophorum* and *Scirpus* is one of the last adjustments needed to achieve a classification of Cyperaceae where all genera are circumscribed as monophyletic entities. Two options for resolving this issue appear viable: (i) *Eriophorum* can be merged with *Scirpus* as proposed by Koyama (1958), or (ii) *Eriophorum* can be maintained by splitting *Scirpus* into a series of new genera. Both of these solutions have drawbacks. If *Eriophorum* is treated within *Scirpus*, the specific epithets for some well-known species such as *Eriophorum gracile* W.D.J.Koch would suddenly be unfamiliar to most in the botanical community (i.e., =*Scirpus ardea* T.Koyama). However, maintaining *Eriophorum* would require splitting *Scirpus* into six to eight genera, each consisting of one to a dozen species. As a taxonomically well-sampled and strongly supported phylogeny for Scirpeae is still lacking, the extent of the taxonomic changes needed to split *Scirpus* remains unclear. Consequently, a decision on merging or splitting should wait until conclusive phylogenetic data are gathered.

4.3.8.5 Tribe Trichophoreae. The recently recognized tribe Trichophoreae (Fig. 6D) contains species that were previously

associated with Scirpeae, but lack the lateral embryo germ pore that now defines tribe Scirpeae s.s. (Léveillé-Bourret et al., 2019). A clade comprising species placed in this tribe has been retrieved within the Scirpo-Caricoid Clade in nearly all phylogenetic studies (Muasya et al., 2009a; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Léveillé-Bourret et al., 2014, 2015, 2018a; Spalink et al., 2016b; Semmouri et al., 2019), with the exception of early analyses based only on *rbcl* (e.g., Muasya et al., 1998; Simpson et al., 2007). However, the phylogenetic placement of Trichophoreae within the Scirpo-Caricoid Clade was settled only recently using a phylogenomic approach (Léveillé-Bourret et al., 2018c). Trichophoreae is monogeneric with the recent inclusion of the formerly recognized genera *Oreobolopsis* T.Koyama & Guagl. and *Cypringlea* M.T.Strong within *Trichophorum* Pers. (Léveillé-Bourret et al., 2020). Under this monophyletic circumscription (Fig. 2C), *Trichophorum* is highly variable in habit, distribution, and ecology, including short unispicate arctic-alpine species, as well as large paniculate subtropical species. Nonetheless, the genus can be distinguished by having only basal leaves usually with mucronate lamina and proximal glumes empty and/or with a longer awn.

4.3.8.6 Tribe Sumatrosirpeae. The genus *Sumatrosirpus* Oteng-Yeb. was formerly placed in Dulichieae (Goetghebeur 1998), but unlike other members of this tribe, it possesses tubular fertile prophylls similar to the perigynia of Cariceae. Léveillé-Bourret et al. (2018a) demonstrated that *Sumatrosirpus* is actually sister to Cariceae and that it corresponds to a morphologically transitional lineage between Cariceae and Scirpeae. This result was confirmed by Semmouri et al. (2019) and is here again confirmed with a completely independent data set (Fig. 2C). We, thus, support its recognition as a monogeneric tribe Sumatrosirpeae (Fig. 6E).

4.3.8.7 Tribe Cariceae. Tribe Cariceae (Fig. 4E) is strongly supported as monophyletic as in previous studies (e.g., Global Carex Group, 2015; Starr et al., 2015; Jiménez-Mejías et al., 2016c; Martín-Bravo et al., 2019; Semmouri et al., 2019; Villaverde et al., 2020). The genus *Carex* has become monophyletic by the inclusion of the formerly recognized segregate genera *Cymophyllus* Mack., *Kobresia* Willd., *Schoenoxiphium* Nees, and *Ucinia* Pers. (Global Carex Group, 2015). This taxonomic decision agrees with our results (Fig. 2C). The previously cited genera were the only ones included in the most recent treatments of the tribe (e.g., Kükenenthal, 1909; Egorova, 1999; Ball & Reznicek, 2002), whose circumscription remains otherwise unaltered. Although the topology within *Carex* largely reflects recent studies focused on *Carex* (e.g., Villaverde et al., 2020), the placement of some species such as *Carex ncinata* L.f. is not well supported, and for a deeper systematic analysis of the genus *Carex*, we refer to those studies. Data of *Carex* species used in this study were generated using three different targeted sequencing probe kits: Angiosperms353 (Johnson et al., 2019), Cyperaceae-specific (Villaverde et al., 2020), and Angiosperms I kit for Anchored Phylogenomics (Léveillé-Bourret et al., 2018c). Lower recovery of the Angiosperms353 genes from data generated with the other probe kits may have contributed to lower resolution within *Carex* in this study.

4.3.9 Abildgaardieae–Eleocharideae–Fuireneae–Cypereae Clade

The Abildgaardieae–Eleocharideae–Fuireneae–Cypereae Clade (FAEC Clade) has long been retrieved in molecular studies of the Cyperaceae family (Simpson et al., 2007; Muasya et al., 1998, 2009a; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Spalink et al., 2016b; Semmouri et al., 2019). The relationships between the lineages have not always been clear; however, most studies recovered an Abildgaardieae–Eleocharideae Clade, a Fuireneae s.l. grade, and a monophyletic tribe Cypereae (e.g., Hinchliff & Roalson, 2013; Jung & Choi, 2013; Spalink et al., 2016b; Semmouri et al., 2019; this study). Within the FAEC Clade, the Fuireneae s.l. grade and tribe Cypereae are characterized by embryos with horizontal germ pores (Léveillé-Bourret & Starr, 2019).

4.3.9.1 Abildgaardieae–Eleocharideae Clade. The monophyly of a clade containing tribe Abildgaardieae and *Eleocharis* R.Br. is well supported in recent phylogenetic studies (Hinchliff & Roalson, 2013; Jung & Choi, 2013; Spalink et al., 2016b; Semmouri et al., 2019; Larridon et al., 2021c), and in this study (Fig. 2D).

Tribe Eleocharideae. Tribe Eleocharideae (Fig. 4F) sensu Goetghebeur (1986) included *Eleocharis* and three monotypic genera (*Chillania* Roiv., *Egleria* L.T.Eiten, and *Websteria* S.H.Wright), whereas Goetghebeur (1998) recognized *Eleocharis*, *Egleria*, and *Websteria*. On the basis of morphological data (e.g., an *Eleocharis*-type embryo) and molecular evidence, these monotypic genera have been combined into *Eleocharis*, resulting in a monogeneric tribe (Roalson & Friar, 2000; Hinchliff et al., 2010; Roalson et al., 2010; Hinchliff & Roalson, 2013; Semmouri et al., 2019). Our results support a monophyletic and monogeneric Eleocharideae (Fig. 2D). However, within the species-rich genus *Eleocharis*, there are significant problems with the infrageneric classification as most of the currently recognized sections and series (González-Elizondo & Peterson, 1997) are not monophyletic (Roalson et al., 2010).

Tribe Abildgaardieae. The monophyly of tribe Abildgaardieae (Fig. 7A) is well supported (Muasya et al., 2009a; Hinchliff & Roalson, 2013; Spalink et al., 2016b; Semmouri et al., 2019; Larridon et al., 2021c; this study, Fig. 2D), as is the monophyly of both clades within this tribe: the *Bulbostylis* Clade and the *Fimbristylis* Clade (Muasya et al., 2009a; Jung & Choi, 2013; Hinchliff & Roalson, 2013; Spalink et al., 2016b; Roalson et al., 2019; Semmouri et al., 2019; Larridon et al., 2021c; this study). Until the inclusion of *Nemum* Desv. in *Bulbostylis* Kunth (Roalson et al., 2018, 2019; Larridon et al., 2019b), *Bulbostylis* was paraphyletic (Simpson et al., 2007; Muasya et al., 2009a; Hinchliff & Roalson, 2013; Spalink et al., 2016b; Reutemann et al., 2018; Semmouri et al., 2019; Larridon et al., 2021c).

The isolated position of *Fimbristylis hygrophila* Gordon-Gray and *F. variegata* Gordon-Gray (Hinchliff & Roalson, 2013; Spalink et al., 2016b; Semmouri et al., 2019; Muasya et al., 2020; Larridon et al., 2021c), sister to the rest of the *Fimbristylis* Clade, recently led to the publication of these species as the new genus *Zulustylis* Muasya (Muasya et al., 2020). The *Fimbristylis* Clade also includes the genera *Actinoschoenus* Benth., *Arthrostylis* R.Br., and *Trachystylis* S.T.Blake (Muasya et al., 2009a; Hinchliff & Roalson, 2013; Spalink et al., 2016b, Semmouri et al., 2019;

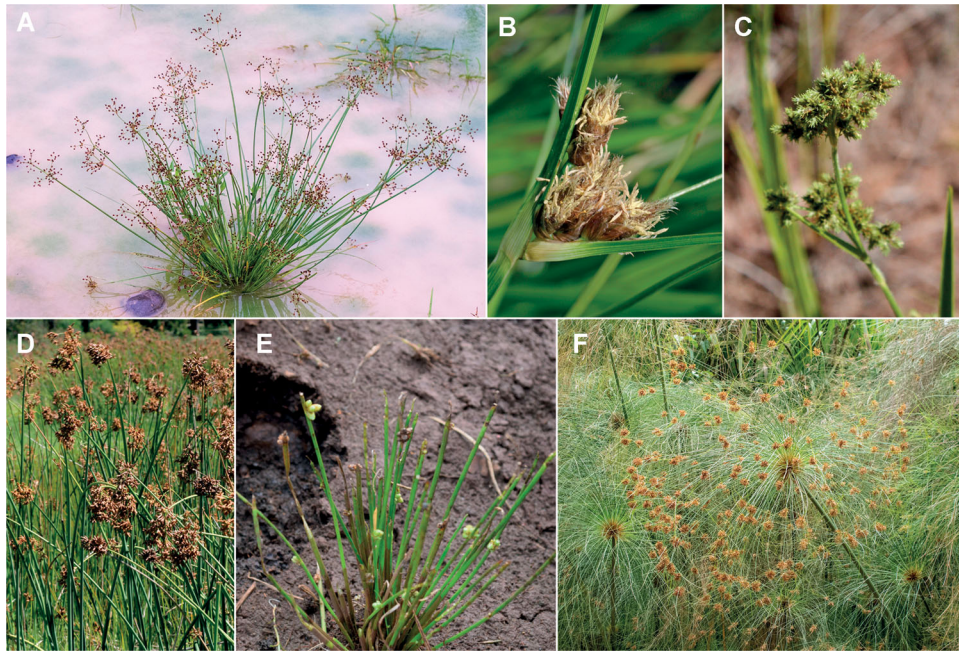


Fig. 7. Morphological diversity of the Cyperaceae tribes. **A**, Abildgaardieae, *Fimbristylis* Vahl sp. **B**, Bolboschoeneae, *Bolboschoenus caldwellii* (V.J.Cook) Soják. **C**, Fuireneae, *Fuirena umbellata* Rottb. **D**, Schoenoplecteae, *Schoenoplectus tabernaemontani* (C.C.Gmel.) Palla. **E**, Pseudoschoeneae, *Schoenoplectiella senegalensis* (Steud.) Lye. **F**, Cypereae: Cyperinae, *Cyperus papyrus* L. Photos **A**, **B**, **D**, and **F** by Russell Barrett; **C** and **E** by Isabel Larridon.

Muasya et al., 2020; Larridon et al., 2021c). These genera had been regarded as constituting the “Arthrostyleidae” (Goetghebeur, 1986; Bruhl, 1995). They were later placed in Schoeneae (Goetghebeur, 1998) and transferred to tribe Abildgaardieae by Muasya et al. (2009a). Larridon et al. (2021c) showed that the “Arthrostyleidae” genera form two clades: (i) a clade of Australian species encompassing *Arthrostylis*, *Trachystylis*, and a new genus *Scleroschoenus* K.L.Wilson, J.J.Bruhl & R.L.Barrett published to place several species recently described in *Actinoschoenus* (Rye et al., 2015); and (ii) a clade of *Actinoschoenus* s.s. These species-poor lineages within the *Fimbristylis* Clade are characterized by (i) the C_3 photosynthetic pathway and (ii) Carex- or Schoenus-type embryos, whereas the remaining lineages use the C_4 photosynthetic pathway and have Abildgaardia-, *Fimbristylis*-, and *Tylocarya*-type embryos (Semmouri et al., 2019; Larridon et al., 2021c). The genus *Abildgaardia* has been treated in a variety of ways, but Larridon et al. (2021c) circumscribe it as a separate genus sister to *Fimbristylis*. Embryo morphology data, in agreement with phylogenetic data, support the recognition of the genus *Abildgaardia*, as the latter differs from *Fimbristylis* by having an Abildgaardia-type embryo (Semmouri et al., 2019). *Crosslandia* W.Fitzg. has been clearly established as being nested within *Fimbristylis* (Hinchliff & Roalson, 2013; Spalink et al., 2016b; Semmouri et al., 2019; Roalson et al., 2019; Larridon et al., 2021c), and a new combination has been published to move it into *Fimbristylis* (Roalson et al., 2019).

4.3.9.2 Fuireneae s.l. grade. Here and in the more recent molecular studies, tribe Fuireneae s.l. (which includes tribes Bolboschoeneae, Fuireneae s.s., Schoenoplecteae, and Pseudoschoeneae sensu Starr et al., 2021) has been retrieved as a grade

toward Cypereae, branching off after the Abildgaardieae–Eleocharideae Clade (Escudero & Hipp, 2013; Hinchliff & Roalson, 2013; Spalink et al., 2016b; Glon et al., 2017; Semmouri et al., 2019; Starr et al., 2021; this study, Fig. 2E). Fuireneae s.l. is not monophyletic, but falls apart into three (Semmouri et al., 2019) or four clades (Muasya et al., 2009a; Escudero & Hipp, 2013; Hinchliff & Roalson, 2013; Glon et al., 2017). Within the Fuireneae grade, a first clade of *Bolboschoenus* (Asch.) Palla branches off first, followed by a clade of *Fuirena* Rottb., with a third clade consisting of a *Schoenoplectiella* Lye and *Pseudoschoenus* (C.B.Clarke) Oteng-Yeb., and a fourth clade of *Schoenoplectus* (Rchb.) Palla and *Actinoscirpus* (Ohwi) R.W.Haines & Lye clade being sister to Cypereae in Glon et al. (2017) and Spalink et al. (2016b). In Escudero & Hipp (2013), the third and fourth clades were inverted in position, whereas in Semmouri et al. (2019), the third and fourth clades form a clade together, sister to Cypereae. Starr et al. (2021) enriched samples of more than a third of Fuireneae s.l. using the Angiosperms353 probes. Their results strongly support the recognition of six genera and four major Fuireneae lineages that they recognize as tribes (Starr et al., 2021), that is, tribe Bolboschoeneae (Fig. 7B), tribe Fuireneae s.s. (Fig. 7C), tribe Schoenoplecteae (Figs. 4G, 7D), and tribe Pseudoschoeneae (Fig. 7E), a conclusion supported by this study. At the generic level, using both Angiosperms353 and nrDNA data sets, Starr et al. (2021) show that most sub-Saharan African perennial species previously treated in *Schoenoplectus* needed to be transferred to *Schoenoplectiella* to make both genera monophyletic.

4.3.9.3 Tribe Cypereae. On the basis of molecular data (Muasya et al., 2002, 2009a), two clades are recognized in tribe Cypereae. Most species of the *Ficinia* Clade (Fig. 4H) are

characterized by spikelets with spirally arranged glumes, whereas most species of the Cyperus Clade (Fig. 2F) usually have spikelets with distichously arranged glumes (Muasya et al., 2009a, 2009b; Larridon et al., 2011a). Although commonly referred to as the Ficinia Clade and Cyperus Clade, subtribal names exist for these groupings that we accept to use in Section 5 (Ficiniinae and Cyperinae; Fig. 3).

In the Ficinia Clade, *Erioscirpus* Palla is the first genus to diverge, before *Scirpoides* Ség. (Fig. 2F). *Erioscirpus* was previously thought to be more allied to *Scirpus* and *Eriophorum*, but molecular studies (Yano et al., 2012; García-Madrid et al., 2015; Muasya & Larridon, 2021) supported its inclusion in the Ficinia Clade. The decision of Reid et al. (2017) to combine *Karinia mexicana* (C.B. Clarke ex Britton) Reznicek & McVaugh into *Scirpoides* Ség. (as *Scirpoides mexicanus* (Reznicek & McVaugh) Goetghebeur ex C.S. Reid and J.R. Carter), based on molecular and morphological evidence, was supported by Semmouri et al. (2019). *Scirpoides mexicanus* was not sampled in this study. Semmouri et al. (2019) strongly supported a sister relationship between *Ficinia* Schrad. and *Isolepis* R.Br. However, several other studies including a larger species sampling have shown that *Isolepis* is paraphyletic and includes *Ficinia* (Muasya et al., 2009b; Muasya & de Lange, 2010; Hinchliff & Roalson, 2013; Spalink et al., 2016b). Recently, Muasya & Larridon (2021) sampled 78% of the Ficinia Clade for a nuclear data set including ETS and ITS and in a chloroplast data set including the genes *matK*, *ndhF*, *rbcL*, and *rps16*, the *trnL* intron, and *trnL-F* spacer with the aim to circumscribe *Ficinia* and *Isolepis* as monophyletic genera. On the basis of the topology obtained with their nuclear data set, Muasya & Larridon (2021) (i) broadened the circumscription of *Ficinia* to include the annual *Isolepis* species characterized by cartilaginous glumes and including all *Isolepis* species retrieved outside the core *Isolepis* clade, and (ii) narrowed the circumscription of *Isolepis* to encompass only those species retrieved as part of the core *Isolepis* clade. Two southern African genera that were recently described, *Afrosirpoides* García-Madr. & Muasya (García-Madrid et al., 2015) and *Dracosirpoides* Muasya (Muasya et al., 2012), form a clade in this study (Fig. 2F). Species segregated into *Dracosirpoides* and *Hellmuthia* are atypical for tribe Cyperaceae, all bearing perianth, and were originally described as part of *Scirpus*. *Hellmuthia* is strongly supported as sister to a clade including *Ficinia* and *Isolepis* (e.g., Simpson et al., 2007; Hinchliff & Roalson, 2013; Jung & Choi, 2013; Semmouri et al., 2019). The scale-like perianth of *Hellmuthia*, interpreted to be analogous to similar structures in Chrysitricheae (subfamily Mapanioideae, here as tribe Hypolytreae s.l.) by Haines & Lye (1976), is now thought to be ontogenetically similar to perianth in other Cyperaceae (Vrijdaghs et al., 2006; Muasya et al., 2009b).

Until recently, the Cyperus Clade included two genera, that is, *Cyperus* L. (962 species; Govaerts et al., 2020) and *Androtrichum* (Brongn.) Brongn. (2 species; Govaerts et al., 2020). Thirteen segregate genera recognized by Goetghebeur (1998), that is, *Courtoisina* Soják, *Kyllingiella* R.W.Haines & Lye, and *Oxycaryum* Nees (C_3 photosynthesis), plus *Alinula* J.Raynal, *Ascolepis* Nees ex Steud., *Ascopholis* C.E.C.Fisch., *Kyllinga* Rottb., *Lipocarpha* R.Br., *Pycrus* P.Beauv., *Queenslandiella* Domin, *Remirea* Aubl.,

Sphaerocyperus Lye, and *Volkiella* Merxm. & Czech (C_4 photosynthesis), had already since been synonymized with *Cyperus* (Larridon et al., 2011a, 2011b, 2013, 2014; Bauters et al., 2014). The small genus *Androtrichum* (C_3 photosynthesis) had not yet been combined into *Cyperus* due to a lack of data (only *rbcL* sequences were available for *Androtrichum*) and conflicting results (Muasya et al., 2009a; Hinchliff & Roalson, 2013; Jung & Choi, 2013). Recently, Pereira-Silva et al. (2020) sank *Androtrichum* into *Cyperus*, based on the results of Semmouri et al. (2019). Our results confirm the placement of the two species previously placed in *Androtrichum*, that is, *Cyperus byssaceus* Pereira-Silva and *C. trigynus* Spreng., among the C_3 lineages of *Cyperus* (Fig. 2F). Previous studies based on a limited set of chloroplast and nuclear ribosomal DNA (nrDNA) markers were able to resolve relationships between species of *Cyperus* using C_3 photosynthesis (Larridon et al., 2011a, 2011b), but not between sections and species using C_4 photosynthesis (Bauters et al., 2014; Larridon et al., 2013, 2014). Owing to the massive size of the genus and the apparent fast radiation of the C_4 Cyperus Clade (Spalink et al., 2016b), a comprehensive and robust phylogeny for *Cyperus* is not easily accomplished. Recently, Larridon et al. (2020) tested the ability of two enrichment probe kits to resolve low-level relationships in the C_4 Cyperus Clade, that is, the universal Angiosperms353 probes (Johnson et al., 2019) and Cyperaceae-specific probes (Villaverde et al., 2020). As in previous studies (e.g., Larridon et al., 2011a, 2013), they found that species of *Cyperus* section *Amabiles*, for example, *Cyperus cuspidatus* Kunth and *C. amabilis* Vahl, are sister to all other taxa in the C_4 Cyperus Clade. Interestingly, after *Cyperus* section *Amabiles*, a clade of white-glumed *Cyperus* species, that is, the *C. margaritaceus*–*C. niveus* complex, was retrieved as sister to the rest of the C_4 *Cyperus* species. Here, a similar topology is obtained (Fig. 2F) based on an analysis of a wider sampling of C_4 *Cyperus* Clade species.

5 Taxonomic Treatment

5.1 Family Cyperaceae

Cyperaceae Juss. Gen. Pl. [Jussieu] 26. 1789, nom. cons.

Type *Cyperus* L.

Description (adapted from POWO, 2020): Perennial or annual herbs, terrestrial, rarely submerged aquatics, or scandent; perennial species rhizomatous, stoloniferous, bulbous, or sub-bulbous; annual species generally caespitose. Some genera have a caudex (e.g., *Microdracoides*). Culms usually trigonous to triquetrous, less often terete, flattened (e.g., *Fimbristylis* spp.), polygonal (e.g., *Fuirena umbellata*, *Schoenoplectiella heptangularis*), or irregular, often with prominent ribs. Leaves basal or basal and cauline, generally tristichous with a closed sheath; blade usually linear, glabrous, scabrous, or hairy, with central midrib prominent, sometimes with an expanded 3-veined blade (*Hypolytrum*, *Mapania*) or elliptic and constricted into a pseudopetiolate base (e.g., *Mapania* spp., *Carex* spp.); ligules present or absent. Inflorescence bracts usually present, leaf-like, bristle-like, or glume-like. Inflorescence simple to compound, lax to condensed, and usually highly branched, paniculate, cor-

ymbose, spicate, or capitate, comprising 1 to many ultimate inflorescence units, very rarely reduced to a single flower (e.g., *Eleocharis confervoides*), the inflorescence units either indeterminate (= spikelets) or, in a few genera, determinate (= spicoids). In subfamily Cyperoideae, spikelets few to many, sometimes reduced to a single spikelet (e.g., *Eleocharis*), terminal or lateral comprising 1-many scales, usually spirally arranged, or sometimes distichous; flowers bisexual, unisexual, or both types present. In subfamily Mapanioideae, spicoids few to many, terminal, with 2–13(–100) membranous scales on a much reduced axis, the lowest 2 scales opposite (sometimes fused), keeled, longer than the flowers within, the whole spicoid subtended and usually hidden by a larger scale-like bract; flowers unisexual and comprising a single naked stamen or pistil. Perianth absent or of 1-many bristles or scales. Stamens 1–3 (up to 6 in *Cyathocoma* and up to 8(–9) in *Morelotia*). Ovary superior, trimerous, or dimerous (extremely rarely tetramerous; e.g., *Carex concinnoides*), locule 1, ovule 1; style short to elongate, base sometimes thickened persistent or not; stigma usually 2–3-branched, rarely 1 (e.g., *Rhynchospora* spp.). Fruit a nutlet, rarely drupe-like (e.g., *Cladium*), sometimes accompanied by a cupule and hypogynium (e.g., *Scleria*).

Includes 24 tribes, 10 subtribes, 95 genera, 5796 species.

Distribution Cosmopolitan

Key to the subfamilies of Cyperaceae

- 1a. Basic inflorescence unit (=spicoid) usually comprising 2, strongly keeled and opposite basal bracts (rarely 1 and unkeeled), with a further (0)–13(–100) scale-like bracts, the bracts subtending 1 stamen, the whole unit with a terminal pistil**Mapanioideae**
- 1b. Basic inflorescence unit (=spikelet) consisting of a rachilla bearing few to many glumes that may or may not subtend a flower (but see *Hellmuthia*)**Cyperoideae**

5.2 Subfamily Mapanioideae

Mapanioideae C.B. Clarke in W.H. Harvey & O.W. Sonder (ed. W.T. Thiselton-Dyer), Fl. Cap. 7: 150. (1897).

Type *Mapania* Aubl.

Diagnosis Characterized by a different morphology of the flowering units compared with Cyperoideae.

Includes 2 tribes, 11 genera, 185 species.

Distribution Mainly tropical and austral temperate.

Key to the tribes of subfamily Mapanioideae

- 1a. Pollen pyriform (except *Diplasia*); predominantly in temperate and subtemperate heathlands and swamps**Chrysitricheae**
- 1b. Pollen spheroidal; predominantly in tropical forests**Hypolytreae**

5.2.1 Tribe Chrysitricheae

Chrysitricheae Nees, Linnaea 10: 144. (1835).

Type *Chrysitrix* L.

Diagnosis Chrysitricheae are robust, rhizomatous, or stoloniferous perennials. The leaves are linear or reduced to basal sheaths. The inflorescence bracts are leaf-like to culm-like and continuous with the culm. The inflorescences are paniculate, anthelate, capitate, or reduced to a single spike. The basic reproductive units comprise spicoids.

The spicoids each have 4–100 (or more) floral bracts and the lowest two bracts are opposite and keeled or, in *Chrysitrix*, spirally arranged. The floral bracts may or may not subtend a single stamen and each spicoid is terminated by a single pistil. The spicoids are subtended and usually hidden by glume-like spicoid bracts and these units are aggregated into spikes that are analogous to spikelets in Cyperoideae genera. The pollen is pyriform, with the exception of *Diplasia* in which it is spheroidal. The style is 2–3-fid and the fruits are 2–3-sided or terete with a hard exocarp.

Accepted genera 6; *Capitularina* J.Kern. (1 sp.), *Chorizandra* R.Br. (6 spp.), *Chrysitrix* L. (4 spp.), *Diplasia* Pers. (1 sp.), *Exocarya* Benth. (1 sp.), and *Lepironia* Pers. (1 sp.). For descriptions and notes on the genera, see Goetghebeur (1998).

Distribution Chrysitricheae mainly have a southern hemisphere (Gondwanan) distribution with the exception of *Diplasia*, which is present in Trinidad and Central and tropical South America. They are found in open swamps or forest.

Key to the genera of tribe Chrysitricheae

- 1a. Spicoid with more than 20 stamens. S Africa (SW Cape), SW Australia**Chrysitrix**
- 1b. Spicoid with less than 20 stamens 2
 - 2a. Leaf blade absent; inflorescence always a single spike... 3
 - 2b. Leaf blade present; inflorescence capitate, anthelate, or rarely a single spike 4
- 3a. Spikes fusiform. Madagascar to Polynesia**Lepironia**
- 3b. Spikes (depressed-) globose. Australia, New Caledonia**Chorizandra**
- 4a. Culm septate; inflorescence capitate or rarely a single spike. New Guinea, Solomon Is.**Capitularina**
- 4b. Culm not septate; inflorescence anthelate..... 5
 - 5a. Culms thick, robust; leaves mostly basal only; primary involucral bracts with coarse teeth; spikes \geq 8 mm long. South America**Diplasia**
 - 5b. Culms thin, slender; leaves basal and cauline; primary involucral bracts without coarse teeth; spikes < 4 mm long. Australia, S New Guinea**Exocarya**

5.2.2 Tribe Hypolytreae

Hypolytreae Nees ex Wight & Arn., Contr. Bot. India: 69 (1834).

Type *Hypolytrum* Pers.

Diagnosis Hypolytreae are rather delicate to very robust (up to 5 m tall), rhizomatous or stoloniferous perennials. The leaves are linear or sometimes with an expanded, linear-oblong to broadly oblong blade and pseudopetiole between the blade and sheath, or rarely reduced to bladeless sheaths. The inflorescence bracts are leaf-like to glume-like. The inflorescences are paniculate, capitate, or reduced to a single spike, rarely anthelate. The basic reproductive units comprise spicoids. The spicoids each have 4–15 floral bracts and the lowest two bracts are opposite and keeled. The lowest two bracts usually subtend a single stamen, whereas the remaining floral bracts may or may not subtend a single stamen and each spicoid is terminated by a single pistil. The spicoids are subtended and usually hidden by glume-like spicoid bracts, and these units are aggregated into spikes that are analogous to spikelets in non-mapiniid genera. The pollen is spheroidal. The style is 2–3-fid and the

fruits are 2–3-sided or terete with a hard, succulent or occasionally berry-like exocarp.

Accepted genera 4; *Hypolytrum* Pers. (63 spp.; including the formerly recognized segregate genus *Principina* Uittien), *Mapania* Aubl. (100 spp.), *Paramapania* Uittien (7 spp.), and *Scirpodendron* Zipp. ex Kurz (2 spp.). For descriptions and notes on the genera, see Simpson (1992), Goetghebeur (1998), and Alves (2015).

Distribution Hypolytreae have a pantropical distribution and occur primarily in forest or forest margins, rarely in savannah.

Key to the genera of tribe Hypolytreae

- 1a. At least some spicoids with more than 8 floral bracts; nutlets corky, with 6–10 deep longitudinal ridges **Scirpodendron**
- 1b. Spicoids with 2–6 floral bracts; nutlets not corky, sometimes with 2–5 shallow ridges or furrows..... 2
- 2a. Floral bracts 2(–3) **Hypolytrum**
- 2b. Floral bracts 4–63
- 3a. Keel of the 2 basal floral bracts coarsely toothed; inflorescence simple anthelate or a single spike. SE Asia, Polynesia **Paramapania**
- 3b. Keel of the 2 basal floral bracts ciliate to entire; inflorescence paniculate, compound anthelate, capitate, or a single spike. Pantropical **Mapania**

5.3 Subfamily Cyperoideae

Cyperoideae Beilschm. in Flora 16 (Bieb. 7): 52, 106. (1833).

Type *Cyperus* L.

Diagnosis Cyperoideae flowering units lack the pair of lateral, opposing and keeled floral bracts found in Mapanioideae.

Includes 22 tribes, 85 genera, 5488 species.

Distribution Cosmopolitan

Key to the tribes of Cyperoideae

- 1a. Flowers all unisexual; pistils 1–2 per female-fertile spikelet..... 2
- 1b. At least some flowers bisexual, rarely all unisexual, but with rudiment of the other sex, or unisexual; pistils >2 in each female-fertile spikelet 7
- 2a. Pistillate flower with hairy perianth scales or bristles 3
- 2b. Pistillate flower without perianth, sometimes with hypogynium 4
- 3a. At least upper glumes distichously arranged; embryo with scutellum transversally widened, *Trilepis*-type **Trilepideae**
- 3b. Glumes all spirally arranged; embryo with scutellum not transversally widened, *Juncus*- or *Carex*-type **Cryptangieae** (in part)
- 4a. Bracts and glumes all spirally arranged; pistil enclosed in sac-like or scale-like prophyll (utricle or perigynium), opposite a larger glumaceous bract, always lateral; fruit without hypogynium; embryo *Carex*- or *Schoenus*-type **Cariceae**
- 4b. Glumes distichous; pistil subtended directly by a single scale-like glume (or in *Bisboeckelereae* enclosed in a sac-like organ or within 2 opposite scales, but then pistil seemingly terminal on axis, and fruit seated on a hypogynium); embryo *Juncus*- or *Fimbristylis*-type 5

- 5a. Fruit not seated on a 3-lobed to disc-like hypogynium; male flower with 2 or more stamens; embryo *Juncus*-type **Cryptangieae** (in part, *Exochogyne*)
- 5b. Fruit seated on a 3-lobed to disc-like hypogynium; male flower with exactly 1 or exactly 3 stamens; embryo *Fimbristylis*-type 6
- 6a. Male flower with 3 stamens; fruit often bony white or pale-colored, extruded and conspicuous at maturity, with one or a few male or empty glumes above **Sclerieae**
- 6b. Male flower with 1 stamen; fruit mostly dark-colored, hidden within glumes or utricle-like structure, seemingly terminal in the spikelet **Bisboeckelereae**
- 7a. Many prophylls containing a flower..... 8
- 7b. All prophylls sterile..... 9
- 8a. Inflorescence spicate or multispicate; spikelet prophyll scarcely differentiated from following glumes; spikelets (pseudo)distichously inserted on rachis; style base linear, forming a long narrow beak on fruit **Dulichieae**
- 8b. Inflorescence corymbiform; spikelet prophyll tubular, distinct from the scale-like glumes; spikelets spirally inserted on rachis; style base enlarged, persistent as a small tubercle on fruit **Sumatrosirpeae**
- 9a. Pistils 1–2 per spikelet, rarely more; glume wings enveloping the flower of the node below; embryo with (sub-)basal root cap 10
- 9b. Pistils >2 per spikelet; glume wings not or scarcely enveloping the flower of the node below; embryo various..... 14
- 10a. Glumes of female-fertile spikelet all deciduous together as a unit, leaving the rachilla intact; perianth absent **Abildgaardieae** p.p. (“*Arthrostylideae*”)
- 10b. Glumes deciduous individually or persistent; perianth often present 11
- 11a. Style 2-fid, fruit flattened, straight; style base enlarged, persistent as a tubercle on fruit **Rhynchosporaeae**
- 11b. Style (2–)3(–9)-fid, fruit trigonous to terete, or rarely style 2-fid (*Cyathochaeta*) but then flattened fruit conspicuously incurved and style base not persistent as a tubercle on fruit 12
- 12a. Anthers grayish or greenish-yellow; embryo with an invagination under outgrown lateral root cap, *Carpachya*-type **Carpheae**
- 12b. Anthers not grayish or greenish-yellow; embryo without invagination under root cap, *Carex*-, *Schoenus*-, or *Helothrix*-type 13
- 13a. Fruit drupe-like, with thick corky beak undifferentiated from fruit body, seated on a broad disc leaving a scar on the fruit; perianth absent; stamens 2(–3); leaves eligulate **Cladieae**
- 13b. Fruit never simultaneously drupe-like and seated on a broad disc leaving scar on fruit; perianth present or absent; stamens usually 3 (rarely 4 in *Morelotia* and *Tettraria*, 6 in *Cyathocoma* and *Reedia*, or even 8–9 in *Morelotia octandra*); leaves ligulate or eligulate **Schoeneae**
- 14a. Flowers unisexual, with 7 antrorsely scabrous perianth bristles; spikelet with 7–9 sterile proximal glumes and >7 upper fertile glumes **Khaosokieae**

- 14b. Flowers bisexual, or if unisexual then never with the above combination of characters15
- 15a. Style base distinct and often thickened or fimbriate, persistent on the fruit or deciduous with the style16
- 15b. Style base neither distinct nor thickened17
- 16a. Leaf blade usually present; inflorescence often corymbose or anthelate, rarely unispicate but then with one involucre bract larger than glumes; perianth absent; embryo not mushroom-shaped, *Abildgaardia*-, *Bulbostylis*-, or *Fimbristylis*-type **Abildgaardieae** (in part)
- 16b. Leaf reduced to a bladeless sheath, or blade sometimes evident as a tiny mucro; inflorescence unispicate, without larger involucre bract; perianth usually present; embryo mushroom-shaped, *Eleocharis*- or *Websteria*-type **Eleocharideae**
- 17a. Embryo with basal or lateral root cap, and perpendicular germ pore18
- 17b. Embryo with a lateral root cap and parallel germ pore20
- 18a. Perianth bristles 6–12, antrorsely scabrous their whole length; ligule and glume ciliate; all glumes fertile **Calliscirpeae**
- 18b. Not this combination of characters19
- 19a. Spikelet with 1–5 sterile proximal glumes, rarely all fertile but then basal glume with longer mucro, 1.5–4 mm wide; perianth parts 0–6; perianth barbs antrorse or divaricate when present; cauline leaves absent; embryo with basal root cap, *Carex*-type **Trichophoreae**
- 19b. Spikelet with all glumes fertile, or rarely with sterile proximal glumes but then basal glume not with longer mucro, 6–15+ mm wide; perianth bristles >10 (*Eriophorum* p.p.); perianth barbs retrorse when present; cauline leaves present or absent; embryo with lateral root cap, *Schoenus*- or *Fimbristylis*-type **Scirpeae**
- 20a. Glumes often distichous; perianth usually absent; usually with bladed leaves all basal; embryo not mushroom-shaped, *Cyperus*-type **Cypereae**
- 20b. Glumes never distichous; perianth usually present; often bladeless, or bladed with leaves basal and cauline; embryo mushroom-shaped, *Bolboschoenus*- or *Schoenoplectus*-type21
- 21a. 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**
- 21b. 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, glabrous22
- 22a. Lowermost primary bract leaf-like with spikelets 10–40 mm long; embryo with three primordial leaves, notch below the root cap present **Bolboschoeneae**
- 22b. 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.....23
- 23a. 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**
- 23b. 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; nutlet surface smooth or transversely rugose; basal flowers sometimes present **Pseudoschoeneae**

5.3.1 Tribe Trilepideae

Trilepideae Goetgh. in Taxon 34: 629. (1985)

Type *Trilepis* Nees

Diagnosis Trilepideae are characterized by a panicle composed of many dense spikes of many tiny spikelets with few distichous glumes, unisexual flowers, a perianth usually formed by 3 fimbriate scales opposite the flat sides of the nutlet, and a *Trilepis*-type embryo (Goetghebeur, 1985; 1998; Semmouri et al., 2019).

Accepted genera 4; *Afrotrilepis* (Gilly) J.Raynal (2 spp.), *Coleochloa* Gilly (8 spp.), *Microdracoides* Hua (1 sp.), and *Trilepis* Nees (5 spp.). For descriptions and notes on the genera, see Goetghebeur (1998).

Distribution West and West Central Africa (*Afrotrilepis*, *Microdracoides*), Tropical and southern Africa and Madagascar (*Coleochloa*), northern South America to Brazil (*Trilepis*). Occurring in tropical areas mostly on inselbergs, growing on shallow soils; one species epiphytic in submontane tropical rain forest.

Key to the genera of Trilepideae (based on Goetghebeur, 1998)

- 1a. Plants dioecious; leaves crowded on top of (branches of) a caudex, blade deciduous, leaving a truncate sheath **Microdracoides**
- 1b. Plants monoecious; leaves different.....2
- 2a. Leaves distichous, with open sheath and deciduous blade; spikes bisexual **Coleochloa**
- 2b. Leaves spirally arranged, sheath closed, blade not deciduous; spikes uni- or bisexual.....3
- 3a. Leaves with ciliate ligule; spikes and spikelets uni- or bisexual **Afrotrilepis**
- 3b. Leaves eligulate; spikes always unisexual **Trilepis**

5.3.2 Tribe Cladieae

Cladieae Nees, *Linnaea* 9: 297. 1834.

Type *Cladium* P.Browne

Diagnosis (Semmouri et al., 2019) Herbs perennial, rhizomatous, and stoloniferous; culms few-noded, hollow; leaves eligulate, following a 1/3 phyllotaxis; inflorescence paniculate, with many spikelets, primary bracts leaflike, sheathing; spikelets with few to many, spirally arranged persistent glumes, lower flower mostly functionally male, upper flowers bisexual with two stamens, bristles absent, nutlet ovoid, with a thick corky beak, surface smooth to wrinkled, embryo small and poorly developed, broadly obovate in outline, with a basal, poorly developed root cap and without a leaf primordium (*Juncus*-type embryo).

Accepted genus *Cladium* P.Browne (3 spp.). For a description and notes on the genus, see Goetghebeur (1998).

Distribution *Cladium* is subcosmopolitan and occurs in swamps and marshes, often in brackish or calcareous habitats.

5.3.3 Tribe Bisboeckelereae

Bisboeckelereae Pax in H.G.A. Engler & K.A.E. Prantl, Nat. Pflanzenfam. Nachtr.: 48. (1897).

Type *Bisboeckelera* Kuntze

Diagnosis Bisboeckelereae are recognized by the (sometimes connate) empty glumes surrounding the apparently terminal female flower, male spikelets with glumes each with a single stamen, and *Carex*-, *Schoenus*-, or *Fimbristylis*-type embryos (Goetghebeur, 1998; Semmouri et al., 2019).

Accepted genera 4; *Becquerelia* Brongn. (6 spp.), *Bisboeckelera* Kuntze (4 spp.), *Calyptrocarya* Nees (8 spp.), and *Diplacrum* R.Br. (10 spp.). For descriptions and notes on the genera, see Goetghebeur (1998).

Distribution Tropical America (*Becquerelia*, *Calyptrocarya*), southern Tropical South America (*Bisboeckelera*), Tropics and subtropics (*Diplacrum*).

Key to the genera of Bisboeckelereae (based on Goetghebeur, 1998)

- 1a. Nutlets smooth or with various ornamentations, not enclosed by a utriculiform glume..... 2
- 1b. Nutlets rather tightly enclosed by either a shortly pubescent or a many-nerved utriculiform glume..... 3
- 2a. Female flower surrounded by only 2 empty glumes; inflorescence capitate, or paniculate with capitate partial inflorescences **Diplacrum**
- 2b. Female flower surrounded by c. 10 empty glumes; inflorescence paniculate with corymbose (rarely capitate contracted) partial inflorescences **Becquerelia**
- 3a. Nutlet compressed ellipsoid or rounded trigonous, enclosed by a pubescent, nerveless glume; female flower surrounded by 3 glumes **Calyptrocarya**
- 3b. Nutlet subtriquetrous, enclosed by a glabrous, many-nerved glume; female flower surrounded by 2 glumes **Bisboeckelera**

5.3.4 Tribe Sclerieae

Sclerieae Wight & Arn., Contr. Bot. India: 71. (1834)

Type *Scleria* P.J.Bergius

Diagnosis Sclerieae have a basically paniculate inflorescence, the spikelets are bisexual or unisexual, flowers unisexual, the nutlet is surrounded at the base by a hypogynium and a cupula (sometimes reduced), and a *Fimbristylis*-type embryo (Goetghebeur, 1998; Semmouri et al., 2019).

Accepted genus *Scleria* P.J.Bergius (258 spp.). For a description and notes on the genus, see Goetghebeur (1998). For infrageneric classification and recent taxonomic treatments, see Bauters et al. (2016, 2018, 2019), Bauters (2018), and Galán Díaz et al. (2019).

Distribution Tropics and subtropics to North America.

5.3.5 Tribe Carpheae

Carpheae Semmouri & Larridon, Bot. Rev. 85: 33 (2019).

Type *Carpha* Banks & Sol. ex R.Br.

Diagnosis (Semmouri et al., 2019) Tribe Carpheae is characterized by the *Carpha*-type embryo, whereas *Carex*- and *Schoenus/Helothrix*-type embryos are prevalent in tribe

Schoeneae. Anthers are typically conspicuously greenish-yellow in this tribe, whereas they are yellow to red-colored in the morphologically similar Schoeneae. Many species of tribe Schoeneae mainly occur in austral temperate dryland habitats that are only seasonally damp (e.g., woodland and heathland), whereas Carpheae occur typically in wetlands and damp areas.

Accepted genera 2; *Carpha* Banks & Sol. ex R.Br. (15 spp.), and *Trianoptiles* Fenzl ex Endl. (3 spp.). For descriptions and notes on the genera, see Goetghebeur (1998).

Distribution Whereas the annual *Trianoptiles* species are endemic to the wetlands of South Africa (SW Cape), perennial *Carpha* occurs in swamps and along stream sides in the southern and central African mountains, Madagascar, Mascarenes, New Guinea, southern Japan, southeastern Australia, New Zealand, and Chile.

Key to the genera of Carpheae (based on Goetghebeur, 1998)

- 1a. Annual plants with frequent amphicarpy; perianth bristles 6, 3 very short, and 3 longer than nutlet **Trianoptiles**
- 1b. Perennial plants without amphicarpy; perianth bristles 6, of subequal length **Carpha**

5.3.6 Tribe Cryptangieae

Cryptangieae Benth. in J. Linn. Soc. London, Bot. 18: 366. (1881).

Type *Cryptangium* Schrad. ex Nees

Diagnosis Cryptangieae are mostly characterized by unisexual spikelets (except for *Koyamaea*, with a more basal single female flower and many male flowers above), spirally arranged glumes (distichously arranged in *Exochogyne*), fruit usually triangular or trigonous in cross-section with three fimbriate perianth scales opposite the flat sides of the nutlet (biconvex and without hypogynous scales in *Exochogyne*), and *Juncus*- or *Carex*-type embryos, although few species have been studied (Goetghebeur, 1998; Semmouri et al., 2019). It seems that all species present a red-pinkish style and stigma, except for some populations in the “campos rupestres” of Chapada Diamantina localities (Bahia, Brazil).

Accepted genera 7; *Cephalocarpus* Nees (20 spp.), *Cryptangium* Schrad. ex Nees (1 spp.), *Didymiandrum* Gilly (1 spp.), *Exochogyne* C.B. Clarke (2 spp.), *Koyamaea* W.W. Thomas & Davidse (1 sp.), *Krenakia* S.M. Costa (10 spp.), and *Lagenocarpus* Nees (15 spp.). For descriptions and notes on the genera, see Costa et al. (2021a).

Distribution Tropical America, in forested (*Koyamaea*, *Didymiandrum*) and open vegetation, mostly at sandy nutrient-poor soils and/or rocky places, from seashores and sandy temporarily wet plains (such as the Amazonian “campinaranas”) to high altitudes (such as the “tepuis” and “campos rupestres”). Also, in some mountains associated with the Andes, but with older and nutrient-poor soils, such as the Cordillera del Condor (Ecuador, Peru).

Key to the genera of Cryptangieae (modified from Costa et al., 2021a)

- 1a. Bisexual spikelets with a basalmost female flower and many male flowers above **Koyamaea**
- 1b. Unisexual spikelets only..... 2
- 2a. Inflorescence spike-like; glumes distichously arranged; nutlet biconvex in cross-section. **Exochogyne**
- 2b. Inflorescence raceme/panicle-like or head-like; glumes spirally arranged; nutlet triangular or trigonous in cross-section..... 3
- 3a. Inflorescence lateral; hypogynous scales with fimbriate margins and glabrous dorsal surface **Cephalocarpus**
- 3b. Inflorescence terminal; hypogynous scales inconspicuous and/or glabrous or with sparsely short-ciliate margins or pubescent at margin and dorsal surface..... 4
- 4a. Male spikelets with (1–)4–5 stamens; nutlet trigonous (trisulcate or inconspicuously ridged) **Lagenocarpus**
- 4b. Male spikelets with 2(–3) stamens; nutlet triangular with sharp ridges..... 5
- 5a. Dioecious herbs; involucre bracts (sterile or fertile) solitary or forming pseudowhorls with elliptic to oblong-elliptic blades. **Didymiandrum**
- 5b. Monoecious herbs; involucre bracts (sterile or fertile) never forming pseudowhorls..... 6
- 6a. Leaf with a developed blade, rarely reduced to sheath; female spikelets with 1(–2) flowers and 3 glumes; nutlet with three conspicuous cavities at the base **Cryptangium**
- 6b. Leaf always reduced to sheath; female spikelets with 1–5 flowers and 3–7 glumes; nutlet cavities absent or inconspicuous. **Krenakia**
- 5a. Glumes distichous..... 6
- 5b. Glumes spirodistichous..... 8
- 6a. Inflorescence compact, dense, with two rigid involucre bracts greatly exceeding the inflorescence (or one bract in *Mesomelaena stygia*) **Gahniinae** (in part)
- 6b. Inflorescence open to dense panicate, sometimes reduced, but not as above..... 7
- 7a. Leaf blades bifacial, well developed (sometimes senescent) **Anthelepidinae**
- 7b. Leaf blades conduplicate, unifacial, or highly reduced **Lepidospermatinae** (in part)
- 8a. Ramets distinctly candelabriform **Lepidospermatinae** (in part)
- 8b. Ramets all produced at a similar level 11
- 9a. Perianth inflated, scale-like, persistent on nutlet **Lepidospermatinae** (in part)
- 9b. Perianth absent or bristle-like, usually not persistent on nutlet **Gahniinae** (in part)
- 10a. Inflorescence enclosed by two greatly enlarged involucre bracts **Gymnoschoeniinae** (in part)
- 10b. Inflorescence not enclosed by two greatly enlarged involucre bracts 10
- 11a. Glumes consistently spirodistichous **Caustiinae**
- 11b. Glumes distichous (a few glumes spirodistichous in *Cyathocoma hexandra* and sometimes in other species) 12
- 12a. Glumes deciduous; plants with leaves well developed **Oreobolinae**
- 12b. Glumes distichous, mostly persistent (deciduous in *Tricostularia*, but then leaf blades usually highly reduced) **Tricostulariinae**

5.3.7 Tribe Schoeneae

Schoeneae Dumort., Fl. Belg. 145 (1827).

Type *Schoenus* L.

Diagnosis Schoeneae are characterized by a (mostly) restricted number of bisexual flowers per spikelet, a \pm well-developed perianth (sometimes absent), spikelets in which the flower(s) are surrounded by the wings of the next glume, and mostly *Carex*- and *Schoenus*-type embryos, although more specialized *Helothrix*-type embryos are also known (Goetghebeur, 1998; Semmouri et al., 2019).

Includes 8 subtribes, 25 genera.

Distribution The tribe has a mostly southern hemisphere distribution, in temperate and subtropical areas, with just a small number of taxa in the northern hemisphere.

Key to the subtribes of Schoeneae

- 1a. Rachilla elongate and flexuose around nutlet(s)..... 2
- 1b. Rachilla straight..... 3
- 2a. Leaves ligulate (usually a prominent tuft of hairs); rhachilla zigzag **Schoeniinae**
- 2b. Leaves eligulate; rhachilla once-elongate **Tricostulariinae** (in part)
- 3a. Leaves ligulate..... 4
- 3b. Leaves eligulate..... 9
- 4a. Inflorescence capitate or subcapitate (lacking spreading bracts that greatly exceed the inflorescence) **Gymnoschoeniinae** (in part)
- 4b. Inflorescence not capitate (may be fan-shaped in *Gahniinae*; *Mesomelaena*, *Ptilothrix*, but then with spreading bracts that greatly exceed the inflorescence)..... 5

5.3.7.1 Subtribe Anthelepidinae

Anthelepidinae R.L.Barrett, **subtr. nov.**

Type *Anthelepis* R.L.Barrett, K.L.Wilson & J.J.Bruhl

Diagnosis Tufted, sometimes rhizomatous, perennial or annual graminoids; leaves mostly basal; culms semi-terete; leaves well developed; ligulate; leaf margins scaberulous or glabrous, flat to channeled; inflorescence terminal, panicle or subracemose; glumes obscurely distichous, usually deciduous; rhachilla non-flexuose, straight; flowers subtended by upper glumes; lower flower(s) functionally male, upper bisexual; upper glumes longer than lower; spikelets ranging from few to many grouped together in spikelet bundles; 3 stamens, stigma 3-fid; nutlets ranging in shape from narrow-ellipsoid to obovoid; perianth bristles (3)6, shorter or longer than the nutlet.

Accepted genus *Anthelepis* R.L.Barrett, K.L.Wilson & J.J.Bruhl (4 spp.). For a description and notes on the genus, see Barrett et al. (2019).

Distribution From Sri Lanka to Hainan, New Caledonia to Australia. Whereas *A. undulatus* is widespread, the other three species are localized.

5.3.7.2 Subtribe Caustiinae

Caustiinae R.L.Barrett, **subtr. nov.**

Type *Caustis* R.Br.

Diagnosis Tufted, sometimes loosely so, distinctly rhizomatous, perennial graminoids; leaves basal and cauline; culms semi-terete, sometimes ribbed or distinctly grooved, or sometimes trigonous; leaves not or well

developed; eligulate; leaf margins ciliate, scaberulous or glabrous, flat to channeled; inflorescence terminal, spike-like or paniculate; glumes spirally arranged or subdistichous, usually persistent; rachilla non-flexuous, straight; flowers subtended by upper glumes; lower flower (when present) usually functionally male, sometimes bisexual, upper flower(s) bisexual or sometimes unisexual; upper glumes longer than lower; spikelets ranging from few to many, solitary on often long peduncles or sometimes grouped together in spikelet bundles; 3–6 or 12–20+ stamens, stigma 3–5- or c. 8-fid; nutlets ranging in shape from cylindrical, ovoid, or obovoid; perianth bristles absent or 2–3(–5), c. as long as the nutlet.

Accepted genera 2; *Caustis* R.Br. (7 spp.) and *Evandra* R.Br. (2 spp.) plus the unplaced species *Tetraria borneensis* J.Kern. For descriptions and notes on the genera, see Goetghebeur (1998).

Distribution Australia (*Caustis* and *Evandra*) and Borneo (*Tetraria borneensis*).

Key to the genera of Caustiinae

- 1a. Glumes subdistichously arranged; stamens 6; style branches 3; perianth present. **Tetraria borneensis**
- 1b. Glumes spirally arranged; stamens 3–6 or 8 or 12–20 or more; style branches 3–8; perianth absent..... 2
- 2a. Stamens 3–6 or 8; style branches 3–8; leaves reduced to a sheath or sometimes with a blade up to 15 cm long. **Caustis**
- 2b. Stamens 12–20 or more; style branches 8; leaves well developed, up to 90 cm long. **Evandra**

5.3.7.3 Subtribe Gahniiinae

Gahniiinae Pax, Bot. Jahrb. Syst. 7: 308 (1886), (as Gahninae)

Type *Gahnia* J.R.Forst. & G.Forst.

Diagnosis Tufted, rhizomatous, sometimes only shortly so, perennial graminoids; leaves mostly basal or cauline on an erect caudex; culms terete or rarely trigonous, sometimes grooved; leaves well developed or reduced; ligulate; leaf margins scaberulous or glabrous, flat to channeled or filiform; inflorescence terminal, paniculate, or compact and obconical to fan-shaped; glumes spirally arranged or distichous, not deciduous; rachilla non-flexuous, straight; flowers subtended by upper glumes; lower flower (when present) functionally male, upper bisexual; upper glumes usually longer than lower, but sometimes shorter; spikelets ranging from few to many grouped together in spikelet bundles; 2–6 stamens, stigma 2–5-fid; nutlets ranging in shape from narrow-ellipsoid to narrow-oblong or obovoid; perianth bristles absent or 3, 4, or 5, shorter or longer than the nutlet.

Accepted genera 4; *Cyathochaeta* Nees (5 spp.), *Gahnia* J.R.Forst. & G.Forst. (41 spp., plus several undescribed), *Mesomelaena* Nees (5 spp.), and *Ptilothrix* K.L.Wilson (1 sp.). For descriptions and notes on the genera, see Wilson (1981, 1993) and Goetghebeur (1998).

Distribution Australia (*Cyathochaeta*, *Mesomelaena*, *Ptilothrix*) and Australasia and the Pacific (*Gahnia*).

Key to the genera of Gahniiinae

- 1a. Inflorescence paniculate, with a single, flexuose bract at the base of the inflorescence..... 2
- 1b. Inflorescence head-like, with two \pm rigid bracts greatly exceeding the spikelets..... 3
- 2a. Stamens usually 2. Style 2-fid. Nut with margins inrolled **Cyathochaeta**
- 2b. Stamens 3–6. Style 2–5-fid. Nut semi-terete to trigonous **Gahnia**
- 3a. Style base persistent, glabrous; nut acutely angled, without an hypogynous disc; hypogynous scales slender, plumose below, antrorsely scabrous above **Ptilothrix**
- 3b. Style base deciduous, shortly pubescent; nut obtusely angled or subterete, seated on a hypogynous disc (except *Mesomelaena graciliceps*); hypogynous scales slender at first, but at maturity, very much broadened below and enclosing the nut, glabrous below, very shortly antrorsely scabrous above **Mesomelaena**

5.3.7.4 Subtribe Gymnoschoeninae

Gymnoschoeninae R.L.Barrett, **subtr. nov.**

Type *Gymnoschoenus* Nees

Diagnosis Tufted, robust, rhizomatous, perennial; leaves basal (*Gymnoschoenus*) or cauline on a thick, erect caudex (*Reedia*; and order followed for characters below); culms terete; leaves well developed; ligulate or eligulate; leaf margins pilose or pungently toothed, thickly to thinly lunate; inflorescence terminal, subglobular or elongate and mostly enclosed by two greatly enlarged inflorescence bracts; glumes distichous or spirally arranged to subdistichous, lower glumes persistent or all deciduous; rachilla non-flexuous, straight; flowers subtended by upper glumes; lower flower functionally male, upper bisexual; upper glumes longer than lower; spikelets many, in spikelet bundles; 3 or 6 stamens, stigma 3-fid; nutlets obovoid to broad-ellipsoid; perianth bristles 0–6, longer than the nutlet.

Accepted genera 2; *Gymnoschoenus* Nees (2 spp.) and *Reedia* F.Muell. (1 sp.). For descriptions and notes on the genera, see Goetghebeur (1998).

Distribution Southern Australia.

Key to the genera of Gymnoschoeninae

- 1a. Plants lacking an erect caudex. Leaves to 1.5–3 mm wide, margins pilose. Inflorescence subglobular. Glumes distichous. Stamens 3 **Gymnoschoenus**
- 1b. Plants with an erect caudex. Leaves to 8 mm wide, margins pungently toothed. Inflorescence elongated and mostly enclosed by two greatly enlarged inflorescence bracts. Glumes spirally arranged. Stamens 6 **Reedia**

5.3.7.5 Subtribe Lepidospermatinae

Lepidospermatinae R.L.Barrett, **subtr. nov.**

Type *Lepidosperma* Labill.

Diagnosis Tufted (rarely cushion-forming in *Lepidosperma*; or rarely semi-scandent in *Machaerina*), rhizomatous, perennial; leaves mostly basal, sometimes cauline (*Machaerina*), or ramets proliferous (in a few *Lepidosperma*); culms highly variable, commonly biconvex, but ranging from flat to terete or quadrangular or occasionally biconvex; leaves well developed or highly reduced (*Neesenbeckia*, *Netrostylis*; some *Lepidosperma*

and *Machaerina*); ligulate or eligulate (*Netrostylis*); leaf margins scaberulous, hispid, ciliate or glabrous, highly variable, commonly biconvex or concavo-convex, but ranging from flat to terete or \pm quadrangular or occasionally biconvex; inflorescence terminal or pseudoaxillary, paniculate, or sometimes appearing spike-like or subracemose (or subcapitate in *Neesenbeckia*); glumes distichous or spirodistichous, usually not deciduous; rachilla non-flexuous, straight; flowers 1–5, subtended by upper glumes; lower flower (s) functionally male, upper 1(2) usually bisexual, sometimes functionally male; upper glumes longer than lower (or 2 middle glumes longest in *Neesenbeckia*); spikelets ranging from few to many grouped together in spikelet bundles; 3 stamens, stigma 3-fid or 6-fid (*Neesenbeckia*), style base conspicuous in *Neesenbeckia* and *Netrostylis*; nutlets ellipsoid to obovoid (sometimes with corky and angular epidermis in *Machaerina*); perianth (3)6 inflated scales (*Lepidosperma*) or absent or bristles 0–6, shorter or longer than the nutlet.

Accepted genera 4; *Lepidosperma* Labill. (80 spp., plus many yet to be described species), *Machaerina* Vahl (55 spp.), *Neesenbeckia* Levyns (1 sp.), and *Netrostylis* R.L.Barrett, J.J.Bruhl & K.L.Wilson (11 spp.). For descriptions and notes on the genera, see Goetghebeur (1998), Barrett & Wilson (2012) for *Lepidosperma*, and Barrett et al. (2021a) concerning *Netrostylis*.

Distribution: Australia, Pacific, and southeast Asia (*Lepidosperma*, *Netrostylis*), Tanzania, West Indian Ocean to Pacific and tropical America (*Machaerina*), South African Cape Province (*Neesenbeckia*).

Key to the genera of Lepidospermatinae

- 1a. Two middle glumes larger than others; perianth of 6 bristles equal to or longer than the nutlet, persistent on the rachilla; stigma 6-fid **Neesenbeckia**
- 1b. Glumes of increasing length from the base, upper glumes the largest; perianth of thickened scales persistent at base of nutlet or bristles 0–5, shorter than the nutlet; stigma (2–)3-fid.....2
- 2a. Perianth of thickened scales persistent at base of nutlet; style base usually cap-like on nutlet (conical to pyramidal only in *Lepidosperma evansianum*, *L. rostratum*) **Lepidosperma**
- 2b. Perianth absent, or consisting of 1–6 flattened scales or bristles; style base persistent, shortly pyramidal or spindle-like.....3
- 3a. New ramets growing out at similar depth to parent ramet; style base shortly pyramidal (continuous with nutlet apex) **Machaerina**
- 3b. New ramets growing out above parent ramet (candelab-riform); style base spindle-shaped (constricted at base) **Netrostylis**

5.3.7.6 Subtribe Oreobolinae

Oreobolinae R.L.Barrett, **subtr. nov.**

Type *Oreobolus* R.Br.

Diagnosis Tufted or cushion-forming, rhizomatous, perennial graminoids; leaves basal or basal and cauline, sometimes cauline on an erect or pseudodendroid caudex; culms terete, elliptical or partially flattened; leaves well developed; eligulate; leaf margins scaberulous or with prickly hairs, flat to thickly lunate; inflorescence terminal, fastigiate paniculate or open paniculate (sometimes a solitary spikelet

or capitate to subcapitate in *Oreobolus*); glumes distichous to spirodistichous, deciduous; rachilla non-flexuous, straight; flowers subtended by upper glumes; lower flower(s) functionally male (rarely bisexual or absent), upper bisexual (rarely functionally male or female); upper glumes longer than lower; spikelets ranging from few to many in spikelet bundles; usually 3 stamens (6 in *Cyathocoma*), stigma 3-fid; nutlets ranging in shape from ellipsoid to ovoid or obloid; perianth bristles 6 (sometimes not all developing), shorter or longer than the nutlet.

Accepted genera 5; *Capeobolus* Browning (1 sp.), *Chamaedendron* (Kük.) Larridon (5 spp.), *Costularia* C.B.Clarke (15 spp.), *Cyathocoma* Nees (3 spp.), and *Oreobolus* R.Br. (17 spp.). For descriptions and notes on the genera, see Goetghebeur (1998), Browning & Gordon-Gray (1999), and Larridon et al. (2018a, 2019).

Distribution South African (*Capeobolus*, *Cyathocoma*), Africa, Madagascar, and West Indian Ocean (*Costularia*), New Caledonia (*Chamaedendron*), Malesia to Australasia and the Hawaiian Islands, and from Costa Rica to the Falkland Islands (*Oreobolus*).

Key to the genera of Oreobolinae

- 1a. Plants short (mostly < 0.25 m); inflorescence cryptic among leaves and sparsely branched; reduced to single or few spikelets.....2
- 1b. Plants taller (mostly > 0.2 m); inflorescence evident with many branches3
- 2a. Leaf blade margins spinulose-serrulate; perianth bristle-like, united at the base by a narrow rim, deciduous with the nutlet **Capeobolus**
- 2b. Leaf blade margins not spinulose-serrulate; perianth narrowly triangular to bristle-like, persistent on the rachilla **Oreobolus**
- 3a. Inflorescence a compact panicle with few to several branches; perianth basally widened and slightly connate; 6 stamens **Cyathocoma**
- 3b. Inflorescence a robust panicle of many branches; perianth bristles feathery; 3 stamens.....4
- 4a. Leaf sheath only slightly wider than leaf blade **Costularia**
- 4b. Leaf sheath generally very broad compared with leaf blade **Chamaedendron**

5.3.7.7 Subtribe Schoeninae

Schoeninae Fenzl in S.F.L. Endlicher, Gen. Pl.: 114 (1836), (as Schoenoideae).

Type *Schoenus* L.

Diagnosis Usually tufted (rarely rhizomatous), perennial or annual graminoids; leaves basal; culms usually terete, but also angular or flattened; leaves sometimes reduced to a sheath but usually well developed; usually ligulate; leaf margins serrate, usually terete, but also flat; inflorescence terminal or sometimes pseudolateral; glumes distichous, deciduous; flowers subtended by upper glumes; lower flowers bisexual upper functionally male; upper glumes longer than lower; spikelets ranging from few (e.g., *S. filiculmis* T.L.Elliott & Muasya) to many grouped together in spikelet bundles; 1–6 stamens, stigma usually 3-fid; nutlets ranging in shape from obovate to rounded trigonous; perianth bristles vary in number from none to many (e.g.,

S. albobaginat T.L.Elliott & Muasya). Perianth bristles can also be rudimentary or longer than the nutlet (e.g., *S. albobaginat*).

Accepted genus *Schoenus* L. (149 spp.; including some species placed in the formerly recognized genus *Epischoenus* C.B.Clarke and some species previously placed in *Tetraria* P.Beauv.). For information on the recircumscription of *Schoenus*, see Musili et al. (2016), Elliott & Muasya (2017, 2018, 2020), Elliott et al. (2019, 2021), and Barrett et al. (2021b).

Distribution Primarily Australasia and South Africa, with a few species in Europe, the Americas, and Caribbean Islands (Kern, 1974; Viljoen et al., 2013).

5.3.7.8 Subtribe *Tricostulariinae*

Tricostulariinae R.L.Barrett, K.L.Wilson & J.J.Bruhl, *Telopea* 24: 74 (2021).

Type *Tricostularia* Nees ex Lehm.

Diagnosis Tufted, rhizomatous, perennial graminoids; leaves basal and commonly cauline, sometimes on an erect caudex (*Ammothryon*, some *Tetraria* and *Xyroschoenus*); culms trigonous or terete; leaves well developed or much reduced; eligulate; leaf margins scaberulous to denticulate, flat to channeled, sometimes V- or M-shaped in section, sometimes involute or revolute; inflorescence terminal, paniculate, sometimes appearing head-like (*Chaetospora*, some *Tricostularia*) or spike-like (some *Tricostularia*); cladophyll present at base of spikelets (except *Ammothryon*), glumes distichous, mostly persistent (deciduous in *Tricostularia*); rachilla mostly non-flexuous, straight (elongate and curved around nutlet in *Morelotia affinis*, *M. gahniiiformis*, *M. octandra*, and *Xyroschoenus*); flowers subtended by upper glumes (except upper glume reduced and infertile in Pacific *Morelotia*); lower flower(s) variously bisexual fertile, functionally male or bisexual sterile, upper bisexual or functionally male (*Morelotia octandra*); upper glumes longer than lower; spikelets ranging from few to many in spikelet bundles; mostly 3 stamens ((3)6 in *Morelotia australiensis*, (4, 6)8(9) in *M. octandra*), stigma mostly 3-fid (3- or 4-fid in some *Tetraria*, 3–5-fid in *Morelotia octandra*); nutlets ranging in shape from ovoid to broad ellipsoid or globose; perianth absent or bristles 2, 6, or 7–8, shorter or longer than the nutlet.

Accepted genera 6; *Ammothryon* R.L.Barrett, K.L.Wilson & J.J.Bruhl (1 sp.), *Chaetospora* R.Br. (3 spp.), *Morelotia* Gaudich. (6 spp.; including the formerly recognized genus *Tetrariopsis* C.B.Clarke), *Tetraria* P.Beauv. (39 spp.; including a species previously placed in the formerly recognized genus *Epischoenus* C.B.Clarke, and some species previously placed in *Costularia* C.B.Clarke s.l.; Larridon et al., 2017, 2018b), *Tricostularia* Nees ex Lehm. (11, plus 4 undescribed species), and *Xyroschoenus* Larridon (1 sp.). For descriptions and notes on the genera, see Goetghebeur (1998); Larridon et al. (2018a): *Chamaedendron* and *Xyroschoenus*; Barrett et al. (2020): *Chaetospora*; Barrett et al. (2021b): all genera in the subtribe.

Distribution Southern Australia (*Tricostularia*), Southern Australia, New Zealand, French Polynesia, Hawaiian Islands (*Morelotia*), New Caledonia to Borneo and New Guinea, South African Cape Floristic Region to tropical Africa (*Tetraria*), the Seychelles (*Xyroschoenus*).

Key to the genera of *Tricostulariinae*

- 1a. Prophyll below spikelet apparently absent; spikelets 12–22 mm long, with 10–14 glumes and 4 bisexual flowers; perianth absent; anthers 7–10 mm long **Ammothryon**
- 1b. Prophyll below spikelet present; spikelets 2.8–25 mm long, with 4–9 glumes and 1–3 bisexual flowers; perianth present or absent; anthers 0.8–6.5 mm long..... 2
- 2a. Culms with 5–10 nodes below the inflorescence; caudex present; inflorescence 10–35 cm wide, branches arcuate; rachilla curved around nutlet; perianth segments (6)7 or 8, 5–6 mm long **Xyroschoenus**
- 2b. Culms with 0–5 nodes below the inflorescence; caudex usually absent (present in some *Tetraria*); inflorescence 0.3–10 cm wide, branches erect to spreading (sometimes arcuate in *Tetraria*); rachilla usually not curved around nutlet (curved in some *Morelotia*); perianth segments 0, 2 or 6, 0–5 mm long..... 3
- 3a. Leaf blades reduced, usually < 1 cm long (rarely up to 7 cm); involucre bracts reduced, bract-like; inflorescence slender or contracted panicle- or head-like, 0.8–9 cm long **Tricostularia**
- 3b. Leaf blades well-formed, 4–100 cm long; involucre bracts leaf-like; inflorescence open, elongate or dense panicle-, head-like, or subglobose, 0.5–1.5 or 5–70 cm long..... 4
- 4a. Culms without nodes; leaf blades 0.3–0.9 mm wide; inflorescence head-like or subglobose, 0.5–1.5 cm long; branchlets compact, hidden **Chaetospora**
- 4b. Culms with 0–5 nodes; leaf blades (0.5–)1–20 mm wide; inflorescence open, elongate, or dense panicle-like, 5–70 cm long; branchlets erect to spreading..... 5
- 5a. Nutlets sessile (shortly stipitate in *Morelotia microcarpa* which differs from *Tetraria* in having a glabrous style base) **Morelotia**
- 5b. Nutlets stipitate. **Tetraria**

5.3.8 Tribe *Rhynchosporae*

Rhynchosporae Nees, *Linnaea* 9: 294 (1834).

Type *Rhynchospora* Vahl

Diagnosis Usually small to medium-sized perennials, rarely annuals, inflorescence very variable; glumes spirally arranged (rarely distichous); anthers (1–2) 3, inconspicuous; style 2-branched; perianth bristles usually 3–6, or absent; nutlet usually lenticular to globose, topped with a persistent style base (tubercle).

Embryo top shaped in frontal view, root cap developed in a (sub)basal position, and first leaf primordium developed in a lateral position (*Carex*-type embryo).

Accepted genus *Rhynchospora* Vahl (399 spp.; including the formerly recognized genus: *Pleurostachys* Brongn.; Thomas, 2020).

Distribution Cosmopolitan.

5.3.9 Tribe *Dulichieae*

Dulichieae W.Schultze-Motel in *Willdenowia* 2: 173. 14 (1959).

Type *Dulichium* Pers.

Diagnosis Flowers bisexual, ligule glabrous, spikelet prophyll fertile and squamiform, spikelets distichous on rachis, glume disposition usually distichous at least on terminal spikelet of main stem, all glumes of spikelet fertile, flowers 3–7 per spikelet, perianth setiform, style base

continuous in texture with fruit, leaving a long narrow beak of variable length on fruit, embryo with basal root cap and lateral plumule (Carex-type).

Accepted genera 3; *Blysmopsis* Oteng-Yeb. (1 sp.), *Blysmus* Panz. ex Schult. (2 spp.), and *Dulichium* (1 sp.). For descriptions and notes on *Blysmus* and *Dulichium*, see Goetghebeur (1998); and on *Blysmopsis*, see http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=104130.

Distribution Temperate northern hemisphere (*Blysmopsis*, *Blysmus*), Canada to U.S.A. (*Dulichium*).

Key to the genera of Dulichieae

- 1a. Spikelets in pedunculate spikes scattered throughout the upper part of the culm, in the axil of normal leaves; perianth of 6–9 (usually 7) bristles **Dulichium**
- 1b. Spikelets in a single terminal spike, rarely with an additional lateral spike; perianth of 0–6 bristles 2
- 2a. Culm 3-angled; leaf blade flat to canaliculate; nutlet c. 2 mm long; perianth bristles as long or longer than fruit, with sharp retrorse barbs, persistent; staminal crest barbed **Blysmus**
- 2b. Culm terete; leaf blade terete to canaliculate; nutlet 3.5–4 mm long; perianth bristles shorter than fruit, with obscure antrorse barbs, deciduous; staminal crest smooth **Blysmopsis**

5.3.10 Tribe Khaosokieae

Khaosokieae Lév.-Bourret & J.R.Starr, Taxon 68: 239 (2019).

Type *Khaosokia* D.A.Simpson

Diagnosis Dioecious, prophylls sterile, proximal glumes of spikelet sterile, flowers ≥ 10 per spikelet, perianth of 7 antrorsely scabrous bristles. Embryo not available.

Accepted genus *Khaosokia* D.A.Simpson (1 sp.). For further notes on the genus, see Simpson et al. (2005).

Distribution Endemic to Thailand.

5.3.11 Tribe Calliscirpeae

Calliscirpeae Lév.-Bourret & J.R.Starr, Taxon 68: 238 (2019).

Type *Calliscirpus* C.N.Gilmour, J.R.Starr & Naczi

Diagnosis Flower bisexual, ligule ciliate, all glumes of spikelet fertile, flowers ≥ 10 per spikelet, perianth of 6–7(–12) long silky antrorsely scabrous bristles forming a cottony mass at maturity, anthers white or yellowish-white, embryo with basal root cap and lateral plumule (Carex-type).

Accepted genus *Calliscirpus* C.N.Gilmour, J.R.Starr & Naczi (2 spp.). For further notes on the genus, see Gilmour et al. (2013).

Distribution West Pacific North America (Oregon to California, U.S.A.).

5.3.12 Tribe Scirpeae

Scirpeae T.Lestib. in B.C.J. Dumortier, Fl. Belg.: 143. (1827).

Note: Validated by a reference to [unranked] Scirpeae T. Lestib., Essai Cyper. 22, 39. 29 (1819).

Type *Scirpus* Tourn. ex L.

Diagnosis Flower bisexual or rarely functionally unisexual with remnant of opposite sex, ligule glabrous or ciliate, prophyll sterile, all glumes of spikelet fertile or rarely 1–12 proximal glumes sterile, flowers (3–)10+ per spikelet, perianth setiform or absent, embryo with lateral

root cap and (sub-)basal plumule (Schoenus-type or Fimbristylis-type).

Accepted genera 6; *Amphiscirpus* Oteng-Yeb. (1 sp.), *Eriophorum* L. (18 spp.), *Phylloscirpus* C.B.Clarke (3 spp.), *Rhodoscirpus* Lév.-Bourret, Donadio & J.R.Starr (1 sp.), *Scirpus* Tourn. ex L. (47 spp.), and *Zameioscirpus* Dhooge & Goetgh. (3 spp.). For descriptions and notes on the genera, see Novoselova (1994a, b), Goetghebeur (1998), Dhooge et al. (2003), and Lév.-Bourret et al. (2015).

Distribution Tropical to subarctic northern hemisphere south to southern South America, and Australia through Malesia.

Key to the genera of Scirpeae

- 1a. Cauline leaves present, node of the distal leaf visible above the sheath of the leaf below 2
- 1b. Cauline leaves absent, leaves all basal with node of the distal leaf hidden in the sheath of the leaf below 4
- 2a. Inflorescence, a white to red cottony mass at maturity due to the exerted flat and silky perianth bristles >10 per flower; 8–50 mm long in fruit **Eriophorum**
- 2b. Inflorescence not appearing as a cottony mass; perianth bristles 0–6, barbed or smooth; spikelets small, 2–15 mm long in fruit 3
- 3a. Ligule, a densely ciliate rim with hairs 0.1–0.4 mm long; glumes red to brown-red with no hint of black, margins ciliate; perianth bristles sharply retrorsely barbed; nutlet gray-brown to brown, with the broadly obovate to suborbicular body (incl. stipe) 1.0–1.3 times as long as wide **Rhodoscirpus**
- 3b. Ligule entire or with scarce teeth or hairs ≤ 0.1 mm long; glumes often black-tinted, often scarcely and minutely toothed, margins rarely short-ciliate; perianth bristles variously antrorsely to retrorsely scabrous or smooth; nutlet often pale yellowish to almost white, rarely brown, the body (incl. stipe) generally >1.5 times as long as wide, rarely almost orbicular **Scirpus**
- 4a. Inflorescence, a dense head of several to many spikelets, rarely unispicate; perianth of retrorsely barbed bristles 5
- 4b. Inflorescence unispicate; perianth absent 6
- 5a. Leaves ligulate; inflorescence pseudolateral; glumes ciliate **Amphiscirpus**
- 5b. Leaves eligulate; inflorescence terminal; glumes entire **Phylloscirpus** (in part)
- 6a. Leaves ligulate **Zameioscirpus**
- 6b. Leaves eligulate **Phylloscirpus** (in part)

5.3.13 Tribe Trichophoreae

Trichophoreae Lév.-Bourret & J.R.Starr, Taxon 68: 239 (2019).

Type *Trichophorum* Pers.

Diagnosis Flower bisexual or rarely functionally unisexual with remnant of opposite sex, ligule glabrous, prophyll sterile, basal (0–)1–9 glumes of spikelet sterile, lowest glume often with conspicuously longer awn than following glumes, flowers 1–10+ per spikelet, perianth setiform, squamiform, or absent, embryo with a basal root cap and lateral plumule (Carex-type).

Accepted genus *Trichophorum* Pers. (19 spp.; including the formerly recognized genera: *Oreobolopsis* T.Koyama & Guagl.

and *Cypringlea* M.T.Strong; Léveillé-Bourret et al., 2020). For notes on the genus, see Léveillé-Bourret et al. (2020).

Distribution Temperate and subtropical northern hemisphere, Andean South America to northwest Argentina.

5.3.14 Tribe Sumatroscirpeae

Sumatroscirpeae Lév.-Bourret & J.R.Starr, Mol. Phyl. Evol. 119: 93–104 (2018).

Type *Sumatroscirpus* Oteng-Yeb.

Diagnosis Flowers bisexual, spikelet prophyll (perigynium) fertile, tubular, spikelets spirally inserted on rachis, glume disposition spiral, sometimes pseudodistichous, all glumes of spikelet fertile, glume wings sometimes partially enveloping the flower of the node below, flowers 7–10+ per spikelet, perianth setiform, style base enlarged, differentiated and persistent on fruit, embryo with basal root cap and lateral plumule (embryo type undetermined).

Accepted genus *Sumatroscirpus* Oteng-Yeb. (4 spp.). For a description and notes on the genus, see Léveillé-Bourret et al. (2017, 2018b).

Distribution Western China to West Sumatra.

5.3.15 Tribe Cariceae

Cariceae Dumort., Fl. Belg.: 145. (1827).

Type *Carex* L.

Diagnosis Cariceae is characterized by unisexual flowers, the female ones being enclosed by a prophyll called a perigynium or if closed forming a bottle-like structure, a utricle (see Jiménez-Mejías et al., 2016b), absence of perianth parts, and a *Carex*-type (very rarely a *Schoenus*-type) embryo.

Accepted genus *Carex* L. (2003 spp.; including the formerly recognized genera: *Cymophyllus* Mack., *Kobresia* Willd., *Schoenoxiphium* Nees, and *Uncinia* Pers.; Global Carex Group, 2015).

Distribution Cosmopolitan, although absent from Antarctica mainland it is the only Cyperaceae group present in a true Antarctic archipelago (South Georgia; Philcox, 1961; Govaerts et al., 2020; see notes in Jiménez-Mejías & Dorr, 2018).

5.3.16 Tribe Eleocharideae

Eleocharideae Goetgh. in Taxon 34: 629. (1985).

Type *Eleocharis* R.Br.

Diagnosis (Goetghebeur, 1998): Eleocharideae is characterized by its reduced vegetative morphology, leaves reduced to a sheath (no blade), unispiculate inflorescence, *Eleocharis*-type embryo, and a helio- and helophilous ecology. Characters shared with its sister tribe Abildgaardieae include a differentiated and thickened style base, and moniliform stigmatic hairs. Characters in common with many Fuireneae include a bristle-like perianth, and an embryo with a broadened cotyledon.

Accepted genus *Eleocharis* R.Br. (c. 302 spp.; including the formerly recognized genera: *Chillania* Roiv., *Egleria* L.T.Eiten, and *Websteria* S.H.Wright; Hinchliff et al., 2010). For a description and notes on the genus, see Goetghebeur (1998) and Hinchliff et al. (2010).

Distribution Cosmopolitan.

5.3.17 Tribe Abildgaardieae

Abildgaardieae Lye in Bot. Not. 126: 328 (1973).

Type *Abildgaardia* Vahl

Diagnosis (Goetghebeur, 1998): Abildgaardieae is characterized by its clearly differentiated style base, which is often thickened and persistent on the nutlet, but it is deciduous in a number of species. Glumes of the spikelet are typically spirally arranged, but distichous glumes are present in some species. Moniliform stigmatic hairs present. Embryos are of the related Abildgaardia-, Bulbostylis-, Carex-, Fimbristylis-, Schoenus- and Tylocarya-type. (Semmour et al., 2019).

Accepted genera 10; *Abildgaardia* Vahl (9 spp.), *Actinoschoenus* Benth. (2 spp.), *Arthrostylis* R.Br. (2 spp.), *Bulbostylis* Kunth (227 spp.; including the formerly recognized segregate genus: *Nemum* Desv.; Roalson et al., 2018, 2019; Larridon et al., 2019b), *Fimbristylis* Vahl (320 spp.), *Nelmesia* Van der Veken (1 sp.), *Scleroschoenus* K.L.Wilson, J.J.Bruhl & R.L.Barrett (6 spp.), *Trachystylis* S.T.Blake (1 sp.), *Trichoschoenus* J.Raynal (1 sp.), and *Zulustylis* Muasya (2 spp.). For descriptions and notes on the genera, see Larridon et al. (2021c).

Distribution Cosmopolitan.

Key to the genera of Abildgaardieae (based on Larridon et al., 2021c)

- 1a. Hypogynous scales 1, adaxial, flat, \pm obovate, bifid at the apex; inflorescence a single terminal spikelet, without obvious involucral bracts. **Nelmesia**
- 1b. Hypogynous scales absent; inflorescence with 1-many spikelets, with or without involucral bracts..... 2
- 2a. Leaf sheath apex with long white hairs; style base mostly enlarged and persistent; style glabrous **Bulbostylis** (in part)
- 2b. Leaf sheath apex without long white hairs, an adaxial ligule of minute hairs present or absent; style base enlarged and mostly deciduous; style fimbriate, hispidulous, rarely glabrous..... 3
- 3a. Fertile flowers per spikelet >2 4
- 3b. Fertile flowers per spikelet 1(–2) 7
- 4a. Glumes long persistent, dark colored; style 2-fid, style base not enlarged; fruit blackish, flattened **Bulbostylis** (*Nemum* in part)
- 4b. Not this combination of characters..... 5
- 5a. Tufted, glabrous perennial; all leaves reduced to their long, spongy sheath; inflorescence of 1–4 spikelets; fruit with a medium to conspicuous stipe; C_3 photosynthesis **Zulustylis**
- 5b. Not this combination of characters; C_4 photosynthesis 6
- 6a. Lowermost involucral bract glume-like, inflorescence of 1–3 spikelets; nutlets 2.0–3.4 mm long (always trigonous, stipitate) **Abildgaardia**
- 6b. Lowermost involucral bract usually not glume-like, inflorescence of 1-many spikelets; nutlets 0.5–1.8 mm (rarely to 2.2 mm) long (many species trigonous some biconvex, stipitate or not) **Fimbristylis**
- 7a. Style 2-fid; leaf blades well developed **Trachystylis**
- 7b. Style 3-fid; leaf blades very poorly developed (<1 cm long) 8
- 8a. Culms strongly flattened, glabrous; glumes spirally arranged; stamens 3+3; stigmas very densely and obviously white-hairy **Arthrostylis**

- 8b. Culms 3–9-ribbed or -angled, hairy or scabridulous; glumes distichously or rarely (sub)spirally arranged; stamens 3; stigmas minutely hispidulous or ciliolate 9
- 9a. Style base persistent, spreading over apex of nutlet; leaves, stem, glumes with many long erect hairs **Trichoschoenus**
- 9b. Style base deciduous with rest of style, slightly enlarged 10
- 10a. Culm intercostal zones differentiated into alternating narrow sections with stomata and small epidermals on the truncate sides (in Transverse Section) and wide astomatal zones with large bulliform-like epidermals, with intercostal zones separated by narrow costal zones; culms 3-angled; nutlet small (<1.6 mm long), not or very shortly stipitate; embryo *Carex*-type **Actinoschoenus**
- 10b. Culm intercostal zones undifferentiated (in Transverse Section); Culms 3–9-angled (always some culms at least 4-angled); nutlet large (>2 mm long), long-stipitate; embryo *Abildgaardia*-type **Scleroschoenus**

5.3.18 Tribe Bolboschoeneae

Bolboschoeneae (Tatanov) J.R.Starr, J. Syst. Evol. 59: 825 (2021).

≡ Schoenoplecteae subtrib. 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. Culms many-noded, 3-sided, thickened at 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), a (compound) corymb-like anthela 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 fruit. Stamens 3. Styles 2 or 3. Style base persistent, barely thickened, if at all. Nutlets obovate, dorsiventrally lenticular, or trigonous. Pericarp with the three highly differentiated layers, exocarp cells often enlarged and hollow, surface smooth, epidermal cells roughly isodiametric. Embryo fungiform with three primordial leaves and a notch below the root cap (*Bolboschoenus*-type).

Accepted genus *Bolboschoenus* (Asch.) Palla (15 spp.).

Distribution Temperate to tropical regions worldwide.

5.3.19 Tribe Fuireneae

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, sometimes thickened at base. Leaves usually well developed, basal and cauline, ligule tubular, membranous, with blade often reduced in lower leaves (rarely all leaf blades reduced).

Inflorescence terminal (in reduced inflorescences, bract may be erect, but clearly leaf-like), paniculate to capitate with few to many spikelets. Inflorescence bracts leaf-like, usually sheathing, lowermost bract sometimes erect. 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 fruit. Stamens 1 to 3. Styles 3. Style base persistent, barely thickened, if at all. Nutlets obovate, triquetrous to trigonous, frequently stipitate, smooth or variously ornamented. 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 spp.).

Distribution Tropical and warm temperate regions worldwide, especially in the Americas and Africa.

5.3.20 Tribe Schoenoplecteae

Schoenoplecteae Lye, in *Blyttia* 29: 147 (1971).

Type *Schoenoplectus* (Rchb.) 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 base. Leaves usually reduced to a sheath, sometimes developing a ligulate blade, but rarely well developed. Inflorescence pseudolateral, rarely clearly terminal, corymb-like anthela 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 lacinate distally, apex entire to emarginate or deeply 2-fid, awned or mucronate. Flowers bisexual. Perianth present, formed by (-)6 parts, smooth to retorsely scabrid, bristle-like or sometimes plumose, longer or shorter than nutlet, deciduous with fruit. 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. Fruit epidermal cells isodiametric to narrowly oblong. Embryo fungiform, scutellum turbinate to rhomboid in shape, root cap lateral, first (well developed) and second embryonic leaves basal (*Schoenoplectus*-type I).

Accepted genera 2; *Actinoscirpus* (Ohwi) R.W.Haines & Lye (1 sp.), and *Schoenoplectus* (Rchb.) Palla (17 spp.). For descriptions and notes on the genera, see Starr et al. (2021).

Distribution Tropical and subtropical Asia from India east to China and south to Northeast Australia (*Actinoscirpus*), predominantly temperate (*Schoenoplectus*).

Key to the genera of Schoenoplecteae (based on Starr et al., 2021)

- 1a. Inflorescence terminal; proximal bracts leaf-like, patent to reflexed, forming an involucre at the base of the inflorescence **Actinoscirpus**

- 1b. Inflorescence pseudolateral; proximal bracts culm-like, erect, other proximal bracts (if present) scale-like and much reduced **Schoenoplectus**

5.3.21 Tribe Pseudoschoeneae

Pseudoschoeneae J.R.Starr, J. Syst. Evol. 59: 826 (2021).

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(–3) noded above the base, trigonous, terete or rarely 7-sided. Leaves reduced to a mucronate sheath, rarely with well-developed blades, ligulate or eligulate. Inflorescence pseudolateral, rarely appearing terminal, a corymb-like anthela 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. Scale apex entire to apiculate. Flowers bisexual, rarely polygamodioecious. 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 fruit. 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 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). Fruit epidermal cells longitudinally elongated in shape. Embryo fungiform, scutellum umbonate or distinctly pileate, root cap lateral, first (well developed) and second embryonic leaves basal (*Schoenoplectus*-type II).

Accepted genera 2; *Pseudoschoenus* (C.B.Clarke) Oteng-Yeb. (1 sp.) and *Schoenoplectiella* Lye (62 spp.). For descriptions and notes on the genera, see Starr et al. (2021).

Distribution Southern Africa (*Pseudoschoenus*), temperate to tropical regions worldwide (*Schoenoplectiella*).

Key to the genera of Pseudoschoeneae (based on Starr et al., 2021)

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

5.3.22 Tribe Cypereae

Cypereae Dumort., Anal. Fam. Pl.: 65. (1829).

Type *Cyperus* L.

Diagnosis Cypereae are characterized by a *Cyperus*-type or the strongly similar *Ficinia*-type embryo (Van der Veken, 1965; Goetghebeur, 1998; Semmouri et al, 2019).

Includes 2 subtribes, 8 genera.

Distribution Cosmopolitan.

Key to the subtribes of Cypereae

- 1a. Glumes usually spirally arranged; anatomy C_3 . If distichously arranged, then 2 or more parallel veins

prominently visible on glume and/or nutlet bearing a distinct gynophore **Ficiniinae**

- 1b. Glumes usually distichously arranged; anatomy C_3 or C_4 . If spirally arranged, then either with elongated anther filaments (formerly *Androtrichum*), usually pale or white head-like inflorescences (e.g., formerly *Kyllingiella* and *Oxycaryum*), or parallel veins not strongly visible on glume and no gynophore **Cyperinae**

Subtribe Ficiniinae. Ficiniinae Fenzl in Endl., Gen. Pl.: 117. (1836).

Type *Ficinia* Schrad.

Diagnosis Annuals or perennials, tufted or with short to creeping rhizomes. Culms nodeless and scapose or noded above the base, trigonous or terete. Leaves reduced to a mucronate sheath or with well-developed blades, ligulate or eligulate. Inflorescence comprising a single terminal spikelet, or pseudolateral, anthelate, or capitate. Spikelets usually terete, flowers bisexual (except in *Afroscirpoides*), perianth absent or varying from scales to cotton-like bristles, nutlet sessile or bearing a gynophore (*Ficinia*). Embryo *Cyperus* or *Ficinia*-type.

Accepted genera 7; *Afroscirpoides* García-Madr. & Muasya (1 sp.), *Dracoscirpoides* Muasya (3 spp.), *Erioscirpus* Palla (2 spp.), *Ficinia* Schrad. (87 spp.), *Hellmuthia* Steud. (1 sp.), *Isolepis* R.Br. (69 spp.), and *Scirpoides* Ség. (4 spp.; including the formerly recognized segregate genus: *Karinia* Reznicek & McVaugh). For descriptions and notes on the genera, see Muasya et al. (2012), Yano et al. (2012), García-Madrid et al. (2015), Reid et al. (2017), and Muasya & Larridon (2021).

Distribution Cosmopolitan.

Key to the genera of Ficiniinae (adapted from García-Madrid et al., 2015)

- 1a. Tufted annual or perennial herbs, without perianth bristles.....2
 1b. Tufted perennial herbs, with perianth bristles.....6
 2a. Annual or perennial herbs. Inflorescence comprising one terminal or < 10 spikelets, if more than 10 spikelet, then nutlets bearing a gynophore3
 2b. Perennial herbs. Inflorescence comprising >10 spikelets, nutlets lacking a gynophore5
 3a. Leaf blades and inflorescence bracts scabrid, nutlets with gynophore **Ficinia**
 3b. Leaf blades and inflorescence bracts smooth, nutlets without gynophore.....4
 4a. Glumes cartilaginous **Ficinia**
 4b. Glumes chartaceous to hyaline **Isolepis**
 5a. Involucral bracts 1–4, culm-like and not spiny. Glumes strongly concave and truncate, with apical mucro **Scirpoides**
 5b. One involucral bract, culm-like and spiny. Glumes not strongly concave and broadly acute, with subapical mucro **Afroscirpoides**
 6a. Anthelate inflorescence (sometimes ± capitate in *Erioscirpus microstachyus*) with few to many sessile spikelets in clusters of (1) 2–3. Long perianth bristles cotton-like **Erioscirpus**
 6b. Capitate inflorescence with sessile spikelets congested into 1 (2) heads. Perianth bristles with barbs or glume-like.....7

- 7a. Leaf blades well developed, with scabrid margins. Perianth bristles 6 (7) with antrorse or retrorse barbs in all flowers **Dracoscirpoides**
- 7b. Leaf blades mostly poorly developed, with smooth margins. Perianth bristles as three glume-like scales in lower flowers **Hellmuthia**

Subtribe Cyperinae. Cyperinae Pax, Bot. Jahrb. Syst. 7: 306. 28 (1886).

Type *Cyperus* L.

Diagnosis Annuals or perennials, tufted or with short to creeping rhizomes. Culms usually nodeless and scapose, trigonous or terete. Leaves reduced to a mucronate sheath or with well-developed blades, eligulate. Inflorescence comprising one to many spikelets, capitate or anthelate. Spikelets usually with distichous glumes, flowers usually bisexual, perianth absent, lacking a gynophore (except *Cyperus lipocarphioides* (Kük.) Lye). Embryo *Cyperus*-type.

Accepted genus *Cyperus* L. (964 spp.; including the formerly recognized segregate genera: *Alinula* J.Raynal, *Androtrichum* (Brongn.) Brongn., *Ascolepis* Nees ex Steud., *Ascopholis* C.E.C.Fisch., *Courtoisina* Soják, *Kyllinga* Rottb., *Kyllingiella* R.W.Haines & Lye, *Lipocarpha* R.Br., *Oxycaryum* Nees, *Pycreus* P.Beauv., *Queenslandiella* Domin, *Remirea* Aubl., *Sphaerocyperus* Lye, and *Volkiella* Merxm. & Czech). For taxonomic changes to the circumscription of *Cyperus*, see Larridon et al. (2011b, 2014), Bauters et al. (2014), Pereira-Silva et al. (2020).

Distribution Cosmopolitan.

5.3.23 Incertae sedis

The monotypic genus *Rhynchocladium* T.Koyama remains unplaced. It is limited in distribution to Guyana and southern Venezuela.

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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.12757/supinfo>:

Table S1. Voucher information for accessions included in the targeted sequencing study.

Table S2. Recovery statistics for the genes targeted by the Angiosperms353 probes for the accessions included in this study.

Table S3. AMAS summary statistics generated for the exons data set. Invariable columns were removed.

Table S4. Overview of the main published classifications of the family Cyperaceae and the classification proposed in this study,

clearly indicating which changes occurred as more data became available. See legend on the right of the table and the included notes.

Fig. S1. Heatmap of recovery of the Angiosperms353 probes for the accessions included in this study.

Fig. S2. Phylogenetic reconstruction of the relationships

in Cyperaceae based on analysis of the exons data set. Concatenated IQ-TREE analysis. Values above branches represent UltraFast Bootstrap support; missing values indicate maximum support. Values below the branches represent gCF/sCF values. Bars on the right indicate subfamilial and tribal classification.