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A linear classification of Cyperaceae

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Summary. This paper provides a linear classification of two subfamilies, 24 tribes, 10 subtribes and 95 genera of the monocot family Cyperaceae (Poales), based on a stable phylogenetic framework resulting from years of morphological, molecular phylogenetic and phylogenomic studies. The family includes c. 5687 species. The most species-rich tribes are the monogeneric tribe Cariceae with c. 2003 species, and tribe Cypereae with c. 1131 species. The highest generic diversity is found in tribe Schoeneae (25 genera), which resulted in the recognition of eight subtribes to facilitate studying this group. The linear classification will help the organisation of Cyperaceae specimens in herbaria according to a systematic order and provides an easy-to-use summary of the current classification of the family.

Key Words. herbaria, phylogenetic hypotheses, systematics, taxonomy.

Introduction

To support curation in herbaria opting to organise their collections in accordance with phylogenetic relationships among genera, and to provide an easy-to-use summary for a variety of audiences, a linear sequence of Cyperaceae is published here. Linear sequences reflect the order of names attached to the tips of a phylogenetic tree, after the branches in the tree have been ordered according to some projection method (Chatrou *et al.* 2018). The methodology for translating tree-like relationships into a linear sequence published by Haston *et al.* (2007) is followed. Linear sequences are available for vascular plants (Wearn *et al.* 2013), lycophytes and ferns (Christenhusz *et al.* 2011a), extant gymnosperms (Christenhusz *et al.* 2011b), angiosperms (Haston *et al.* 2007, 2009), and several plant families including Annonaceae (Chatrou *et al.* 2018) and Fabaceae (Lewis *et al.* 2013).

Following Chatrou *et al.* (2018), the following steps were taken to assemble the phylogenetic tree underpinning the linear sequence, and to translate the tree into the sequence: (1) Largely based on the results of Larridon *et al.* (2021a), a summary tree showing relationships of all genera of Cyperaceae was assembled. Details are given below in the section 'Cyperaceae classification'. (2) Clade size was defined in terms of number of species, with species numbers for all genera based on Larridon *et al.* (2021a). (3) Nodes of the phylogenetic tree were rotated so that clades with fewer species were placed before clades with more species following Haston *et al.* (2007). This clade size criterion was applied to all nodes in the tree, starting from the root node (Fig. 1). As a result, the names along the tips from top to bottom represent the linear sequence.

Cyperaceae classification

A recent paper provided a new classification of Cyperaceae at tribal, subtribal and generic level (Larridon *et al.* 2021a) based on targeted sequencing data obtained with the Angiosperms353 probe kit (Johnson *et al.* 2019) to build a well-supported phylogenetic framework for the family. Only eight genera could not be placed in the phylogenomic study, for five of which (*Ammothryon* R.L.Barrett, K.L.Wilson & J.J.Bruhl, *Blysmopsis* Oteng-Yeb., *Blysmus* Panz. ex Schult., *Capeobolus* Browning, *Didymiandrum* Gilly) their phylogenetic placement is known based on previous Sanger sequencing-based studies (e.g. Larridon *et al.* 2018a; Semmouri *et al.* 2019; Barrett *et al.* 2021a; Costa *et al.* 2021). For *Nelmesia* Van der Veken and *Trichoschoenus* J.Raynal, both monotypic genera only known from a single collection, placement was decided based on (embryo) morphology and biogeography (Larridon *et al.* 2021a, b). *Rhynchocladium* T.Koyama is the only genus that remains unplaced.

Since the Cyperaceae classification of Goetghebeur (1998), the circumscription of several genera has been altered, mostly in tribes Abildgaardieae, Cariceae, Cypereae, Eleocharideae, Schoeneae and Scirpeae, and in the Fuireneae s.l. Grade (tribes Pseudoschoeneae and Schoenoplecteae).

In tribe Abildgaardieae, the circumscription of the genera *Bulbostylis* Kunth and *Fimbristylis* Vahl has changed. Recently, the small mainland African genus

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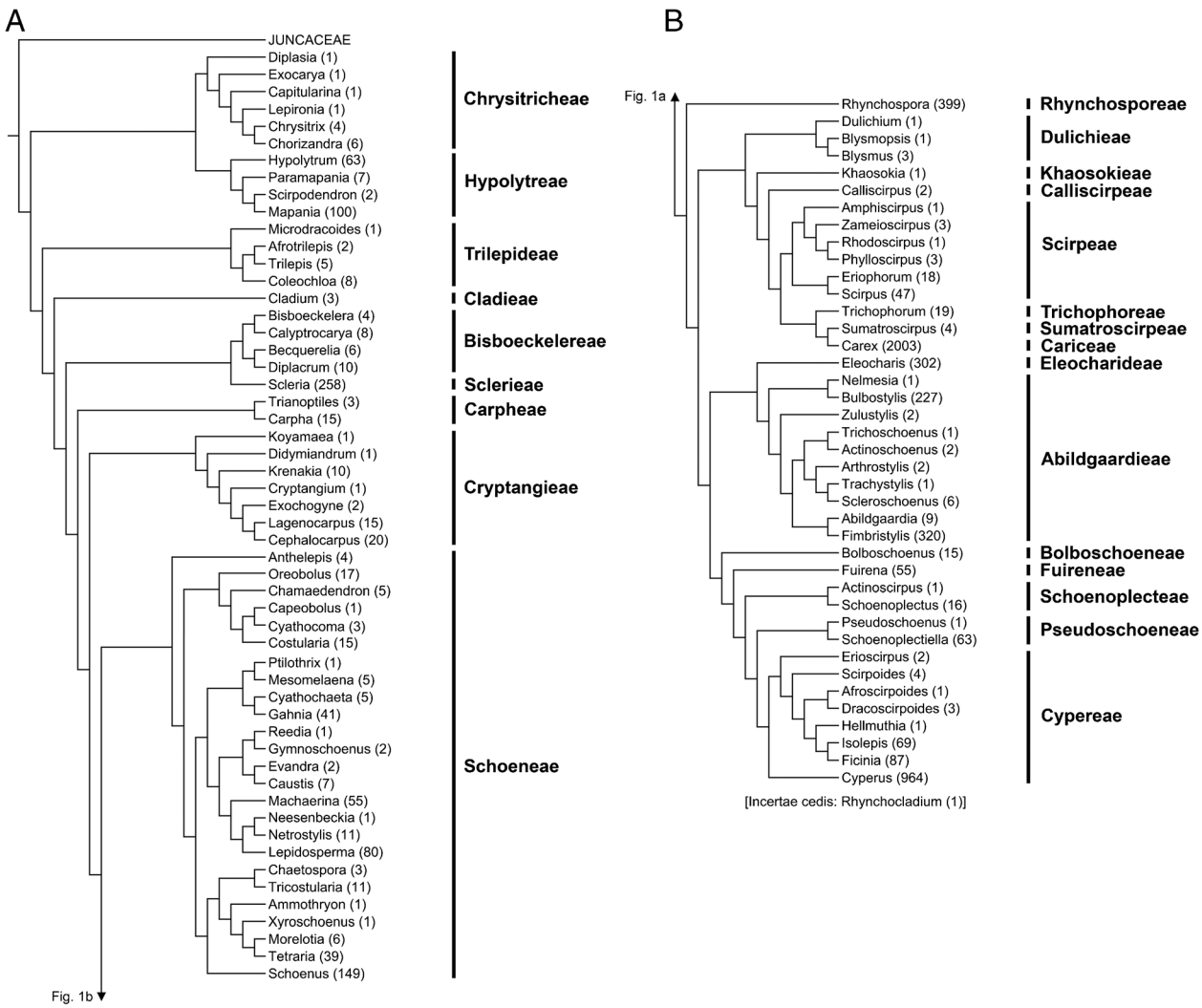

Fig. 1. Summary tree underlying the linear sequence of Cyperaceae genera (A: Chrysitricheae to Schoeneae; B: Rhynchosporeae to Cypereae). Topology based on Larridon *et al.* (2021a), except for the position of *Capeobolus* within Oreobolineae based on Larridon *et al.* (2018a), the approximate position of *Didymiandrum* within Cryptangieae based on Costa *et al.* (2021), the position of *Ammothryon* within Tricostulariinae based on Barrett *et al.* (2021a), and the position of *Blysmopsis* and *Blysmus* in Dulichieae based on Semmouri *et al.* (2019). The approximate positions of *Nelmesia* and *Trichoschoenus* are based on (embryo) morphology data and biogeography (Larridon *et al.* 2021b). The number of species for each genus is indicated. Bars on the right indicate tribal classification

Nemum Desv. was synonymised with *Bulbostylis* (Roalson *et al.* 2019a; Larridon *et al.* 2019), and the Australian monotypic genus *Crosslandia* W.Fitzg. was sunk into *Fimbristylis* (Roalson *et al.* 2019b). Furthermore, a new genus *Zulustylis* Muasya was published for two species previously placed in *Fimbristylis* (Muasya *et al.* 2020). Lastly, a new genus *Scleroschoenus* K.L.Wilson, J.J.Bruhl & R.L.Barrett was published to encompass Australian species previously placed in *Actinoschoenus* Benth., but clearly forming their own lineage related to two other Australian genera, *Arthrostylis* R.Br. and *Trachystylis* S.T.Blake (Larridon *et al.* 2021b).

The Global *Carex* Group (2015) re-circumscribed the megadiverse genus *Carex* (c. 2000 species) as a monophyletic group. To do so, they synonymised the genera *Cymophyllus* Mack., *Kobresia* Willd., *Schoenoxiphium* Nees, and *Uncinia* Pers. with *Carex*.

The biggest taxonomic changes at generic level occurred in tribe Cypereae. After the now monotypic tribe Cariceae, it is the second most species-rich tribe in Cyperaceae with well over 1100 species (Larridon *et al.* 2021a). Before the molecular era, the tribe Cypereae was circumscribed based on embryo morphology; all species included in this tribe have either a *Cyperus* type embryo or similar *Ficinia* type embryo (Goetghebeur 1998; Semmouri *et al.* 2019). Studies have shown that embryos provide some of the best morphological characters to delimit Cyperaceae groups that agree with molecular phylogenetic results (Semmouri *et al.* 2019). Two clades are distinguished

in tribe Cypereae, the Ficinia Clade or subtribe Ficiniinae and the Cyperus Clade or subtribe Cyperinae (Larridon *et al.* 2021a). Ficiniinae species are predominantly characterised by having spikelets with spirally arranged glumes. In contrast, species of the Cyperinae usually have spikelets with distichous or two-ranked glumes. Besides *Cyperus* sensu stricto, 13 segregate genera as circumscribed by the classification of Goetghebeur (1998) belong to Cyperinae (Larridon *et al.* 2021a). Molecular phylogenetic studies revealed that these segregate genera are all nested within *Cyperus* sensu stricto and that several of them do not form natural groups (Larridon *et al.* 2011a, 2013; Bauters *et al.* 2014). As a result, their species were recently transferred to *Cyperus* (Larridon *et al.* 2011b, 2014; Bauters *et al.* 2014; Pereira-Silva *et al.* 2020).

In tribe Eleocharideae, the segregate genera *Chillania* Roiv., *Egleria* L.T.Eiten and *Websteria* S.H.Wright have been sunk into the large and widely distributed wetland genus *Eleocharis* R.Br. (Hinchliff *et al.* 2010).

Recently, efforts have been made to realign the taxonomy of some of the larger tribe Schoeneae genera, i.e. *Costularia* C.B.Clarke, *Epischoenus* C.B.Clarke, *Schoenus* L., *Tetraria* P.Beauv. and *Tricostularia* Nees, to make them monophyletic. This resulted in the description of a range of new genera (*Ammothryon* R.L.Barrett, K.L.Wilson & J.J.Bruhl, *Anthelepis* R.L.Barrett, K.L.Wilson & J.J.Bruhl, *Chamaedendron* Larridon, *Netrostylis* R.L.Barrett, J.J.Bruhl & K.L.Wilson, *Xyroschoenus* (Kük.) Larridon; Barrett *et al.* 2019, 2021a, b; Larridon *et al.* 2018a), recircumscription of existing genera (*Costularia*, *Morelotia* Gaudich., *Schoenus* and *Tetraria*; Elliott & Muasya 2017; Larridon *et al.* 2018b; Barrett *et al.* 2021a), and reinstatement of a previously published genus (*Chaetospora* R.Br.; Barrett *et al.* 2020).

In tribe Scirpeae, the Linnean genus *Scirpus* L. was very heterogenous (Starr *et al.* 2021). Based on molecular phylogenetic and embryo morphology data, a series of new genera were described (e.g. *Zameioscirpus* Dhooge & Goetgh., Dhooge *et al.* 2003; *Dracoscirpoides* Muasya, Muasya *et al.* 2012; *Calliscirpus* C.N.Gilmour, J.R.Starr & Naczi, Gilmour *et al.* 2013; *Afroscirpoides* García-Madr. & Muasya, García-Madrid *et al.* 2015; *Rhodoscirpus* Lév.-Bourret, Donadío & J.R.Starr, Léveillé-Bourret *et al.* 2015).

Further changes at generic level occurred, with recircumscription of some genera including publication of the new genus *Krenakia* S.M.Costa in tribe Cryptangieae (Costa *et al.* 2021), the synonymisation of *Pleurostachys* Brongn. with *Rhynchospora* Vahl in Rhynchosporeae (Thomas 2020), and the synonymisation of *Principina* Uittien with *Hypolytrum* Pers. (Mesterházy *et al.* 2021).

Besides changes to generic limits, tribal limits have also changed with the erection or reinstatement of a number of small or monogeneric tribes representing well-supported lineages that had previously been placed in Schoeneae s.l. (tribes Carpheae and Cladieae; Semmouri *et al.* 2019), Scirpeae s.l. (tribes Calliscirpeae, Khaosokieae, Sumatroscirpeae and Trichophoreae; Léveillé-Bourret *et al.* 2018; Léveillé-Bourret & Starr 2019) and Fuireneae s.l. (Bolboschoeneae, Pseudoschoeneae, Schoenoplecteae; Starr *et al.* 2021). Conversely, the monotypic tribe Koyamaeae was sunk into Cryptangieae (Larridon *et al.* 2021a). The efforts to recircumscribe tribe Fuireneae as a monophyletic group also resulted in a recircumscription of the genera *Schoenoplectus* (Rchb.) Palla and *Schoenoplectiella* Lye (Starr *et al.* 2021). A detailed study of tribe Trichophoreae resulted in lumping *Cypringlea* M.T.Strong and *Oreobolopsis* T.Koyama & Guagl. into *Trichophorum* Pers. (Léveillé-Bourret *et al.* 2020). To summarise, while the previous complete classification at tribal and generic level (Goetghebeur 1998) recognised four subfamilies, 14 tribes and 104 genera, following the current taxonomy (Larridon *et al.* 2021a), two subfamilies, 24 tribes, 10 subtribes and 95 genera are now accepted in Cyperaceae. Currently, c. 5687 species are recognised in the family.

Linear sequence of Cyperaceae

Accepted names are listed in **bold**. Commonly used or recently subsumed synonyms are listed.

CYPERACEAE JUSS.
MAPANIOIDEAE C.B.CLARKE
Chrysitricheae Nees
Diplasia Pers. (1 sp.)
Exocarya Benth. (1 sp.)
Capitularina J.Kern (1 sp.)
Lepironia Pers. (1 sp.)
Chrysitrix L. (4 spp.)
Chorizandra R.Br. (6 spp).

Hypolytreae Nees ex Wight & Arn.
Hypolytrum Pers. (63 spp.)
Principina Uittien
Paramapania Uittien (7 spp.)
Scirpodendron Zipp. ex Kurz (2 spp.).
Mapania Aubl. (100 spp.)

CYPEROIDEAE BEILSCHM.
Trilepideae Goetgh.
Microdracoides Hua (1 sp.)
Afrotrilepis (Gilly) J.Raynal (2 spp.)
Trilepis Nees (5 spp.)
Coleochloa Gilly (8 spp.)

Cladieae Nees
Cladium P.Browne (3 spp.)

Bisboeckelereae Pax
Bisboeckelera Kuntze (4 spp.)
Calyptrocarya Nees (8 spp.)
Becquerelia Brongn. (6 spp.)
Diplacrum R.Br. (10 spp.)

Sclerieae Wight & Arn.
Scleria P.J.Bergius (258 spp.)

Carpheae Semmouri & Larridon
Trianoptiles Fenzl ex Endl. (3 spp.)
Carpha Banks & Sol. ex R.Br. (15 spp.)
Asterochaete Nees

Cryptangieae Benth.
Koyamaea W.W.Thomas & Davidse (1 sp.)
Didymiandrum Gilly (1 sp.)
Krenakia S.M.Costa (10 spp.)
Cryptangium Schrad. ex Nees (1 sp.)
Exochogyne C.B.Clarke (2 spp.)
Lagenocarpus Nees (15 spp.)
Cephalocarpus Nees (20 spp.)
Everardia Ridl.

Schoeneae Dumort.
Anthelepidinae R.L.Barrett,
Anthelepis R.L.Barrett, K.L.Wilson & J.J.Bruhl (4 spp.)

Oreobolinae R.L.Barrett
Oreobolus R.Br. (17 spp.)
Schoenoides Seberg
Chamaedendron Larridon (5 spp.)
Capeobolus Browning (1 sp.)
Cyathocoma Nees (3 spp.)
Costularia C.B.Clarke (15 spp.)

Gahniinae Pax
Ptilothrix K.L.Wilson (1 sp.)
Mesomelaena Nees (5 spp.)
Cyathochaeta Nees (5 spp., plus several undescribed)
Gahnia J.R.Forst. & G.Forst. (41 spp., plus several undescribed)

Gymnoschoeninae R.L.Barrett
Reedia F.Muell. (1 sp.)
Gymnoschoenus Nees (2 spp.)

Caustiinae R.L.Barrett
Evandra R.Br. (2 spp.)
Caustis R.Br. (7 spp.)
unplaced species *Tetraria borneensis* J.Kern

Lepidospermatinae R.L.Barrett
Machaerina Vahl. (55 spp.)
Baumea Gaudich.
Neesenbeckia Levyns (1 sp.)
Netrostylis R.L.Barrett, J.J.Bruhl & K.L.Wilson (11 spp.)
Lepidosperma Labill. (80 spp., plus many yet to be described species)

Tricostulariinae R.L.Barrett
Chaetospora R.Br. (3 spp.)
Tricostularia Nees (11 spp.)
Ammothryon R.L.Barrett, K.L.Wilson & J.J.Bruhl (1 sp.)
Xyroschoenus Larridon (1 sp.)
Morelotia Gaudich. (6 spp.)
Tetrariopsis C.B.Clarke
Tetraria P.Beauv. (39 spp.)

Schoeninae Fenzl
Schoenus L. (149 spp.)

Rhynchosporeae Nees
Rhynchospora Vahl (399 spp.)
Dichromena Michx.
Pleurostachys Brongn.

Dulichieae W.Schultze-Motel
Dulichium Pers. (1 sp.)
Blysmopsis Oteng-Yeb. (1 sp.)
Blysmus Panz. ex Schult. (3 spp.)

Khaosokieae Lév.-Bourret & J.R.Starr
Khaosokia D.A.Simpson (1 sp.)

Calliscirpeae Lév.-Bourret & J.R.Starr
Calliscirpus C.N.Gilmour, J.R.Starr & Naczi (2 spp.)

Scirpeae T.Lestib.
Amphiscirpus Oteng-Yeb. (1 sp.)
Zameioscirpus Dhooge & Goetgh. (3 spp.)
Rhodoscirpus Lév.-Bourret, Donadío & J.R.Starr (1 sp.)
Phylloscirpus C.B.Clarke (3 spp.)
Eriophorum L. (18 spp.)
Scirpus Tourn. ex L. (47 spp.)

Trichophoreae Lév.-Bourret & J.R.Starr
Trichophorum Pers. (19 spp.)
Cypringlea M.T.Strong
Oreobolopsis T.Koyama & Guagl.

Sumatroscirpeae Lév.-Bourret & J.R.Starr
Sumatroscirpus Oteng-Yeb. (4 spp.).

Cariceae Dumort.
Carex L. (2003 spp.)

Cymophyllus Mack.
Kobresia Willd.
Schoenoxiphium Nees
Uncinia Pers.

Eleocharideae Goetgh.
Eleocharis R.Br. (c. 302 spp.)
Chillania Roiv.
Egleria L.T.Eiten
Websteria S.H.Wright

Abildgaardieae Lye
Nelmesia Van der Veken (1 sp.)
Bulbostylis Kunth (227 spp.)
Nemum Desv.
Zulustylis Muasya (2 spp.)
Trichoschoenus J.Raynal (1 sp.)
Actinoschoenus Benth. (2 spp.)
Arthrostylis R.Br. (2 spp.)
Trachystylis S.T.Blake (1 sp.)
Scleroschoenus K.L.Wilson, J.J.Bruhl & R.L.Barrett (6 spp.)
Abildgaardia Vahl (9 spp.)
Fimbristylis Vahl (320 spp.)
Crosslandia W.Fitzg.

Bolboschoeneae (Tatanov) J.R.Starr
Bolboschoenus (Asch.) Palla (15 spp.).

Fuireneae Rchb. ex Fenzl
Fuirena Rottb. (55 spp.)

Schoenoplecteae Lye
Actinoscirpus (Ohwi) R.W.Haines & Lye (1 sp.)
Schoenoplectus (Rchb.) Palla (16 spp.)

Pseudoschoeneae J.R.Starr
Pseudoschoenus (C.B.Clarke) Oteng-Yeb. (1 sp.)
Schoenoplectiella Lye (63 spp.)

Cypereae Dumort.
Ficiniinae Fenzl
Erioscirpus (2 spp.) Palla
Scirpoides Ség. (4 spp.)
Afroscirpoides García-Madr. & Muasya (1 sp.)
Dracoscirpoides Muasya (3 spp.)
Hellmuthia Steud. (1 sp.)
Isolepis R.Br. (69 spp.)
Ficinia Schrad. (87 spp.)
Desmoschoenus Hook.f.

Cyperinae Pax
Cyperus L. (964 spp.)
C_3 Cyperus Grade = subgenus ***Anosporum*** (Nees) C.B.Clarke
Androtrichum (Brongn.) Brongn.
Courtoisina Soják
Kyllingiella R.W.Haines & Lye
Oxycaryum Nees
C_4 Cyperus Clade = subgenus ***Cyperus***
Alinula J.Raynal
Ascolepis Nees ex Steud.
Ascopholis C.E.C.Fisch.
Kyllinga Rottb.
Lipocarpha R.Br.
Mariscus Vahl
Pycreus P.Beauv.
Queenslandiella Domin
Remirea Aubl.
Sphaerocyperus Lye
Torulinium Desv.
Volkiella Merxm. & Czech

Incertae Cedis
Rhynchocladium T.Koyama (1 sp.)

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