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# Phylogeny of Cyperaceae Based on DNA Sequence Data: Current Progress and Future Prospects

**A. Muthama Muasya[1,6,7] · David A. Simpson[2] · G. Anthony Verboom[1] · Paul Goetghebeur[3] · Robert F. C. Naczi[4] · Mark W. Chase[2] · Erik Smets[5,6]**

[1] Botany Department, University of Cape Town, Rondebosch 7701, Cape Town, South Africa
[2] Royal Botanic Gardens, Kew, Richmond Surrey TW9 3AB, UK
[3] Department of Biology, Ghent University, K.L. Ledeganckstraat 35, BE-9000 Ghent, Belgium
[4] Department of Agriculture & Natural Resources, Delaware State University, Dover, DE 19901, USA
[5] National Herbarium of the Netherlands, PO Box 9514, NL-2300 RA Leiden, The Netherlands
[6] Laboratory of Plant Systematics, K.U. Leuven, Kasteelpark Arenberg 31, BE-3001 Leuven, Belgium; e-mail: Smets@nhn.leidenuniv.nl
[7] Author for correspondence; e-mail: Muthama.Muasya@uct.ac.za
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**Abstract** In the last decade, efforts to reconstruct suprageneric phylogeny of the Cyperaceae have intensified. We present an analysis of 262 taxa representing 93 genera in 15 tribes, sequenced for the plastid *rbcL* and *trnL-F* (intron and intergenic spacer). Cyperaceae are monophyletic and resolved into two clades, here recognised as Mapanioideae and Cyperoideae, and the overall topology is similar to results from previous studies. Within Cyperoideae, Trilepideae are sister to rest of taxa whereas Cryptangieae, Bisboeckelerieae and Sclerieae are resolved within Schoeneae. *Cladium* and *Rhynchospora* (and *Pleurostachys*) are resolved into clades sister to the rest of Schoeneae, lending support to the recognition of these taxa in separate tribes. However, we retain these taxa in Schoeneae pending broader sampling of the group. The phylogenetic position of 40 species in 21 genera is presented in this study for the first time, elucidating their position in Abildgaardieae (*Trachystylis*), Cryptangieae (*Didymiandrum*, *Exochogyne*), Cypereae (*Androtrichum*, *Volkiella*), Eleocharideae (*Chillania*), and Schoeneae (*Calyptrocarya*, *Morelotia*). More sampling effort (more taxa and the use of more rapidly evolving markers) is needed to resolve relationships in Fuireneae and Schoeneae.

**Keywords** Suprageneric Classification · Mapanioideae · Cyperioideae · Tribal Circumscriptions · *rbcL* · *trnL-F*

## Introduction

Cyperaceae comprise 109 genera and approximately 5,500 species and have an almost cosmopolitan distribution (Govaerts et al., 2007). About 35% of the genera are monotypic, 26% have two to five species, and there are a seven (6%) genera with

over 200 species, the largest being *Cyperus* (686 species) and *Carex* (1,757 species; Goetghebeur, 1998). The family shows extreme reduction in floral morphology, and the majority of the smaller genera are carved out of the larger ones on the basis on one or few distinguishing features.

Family level phylogenetic studies in the last ten years have used morphological (e.g. Simpson, 1995; Bruhl, 1995; Goetghebeur, 1998), molecular (e.g. Muasya et al., 1998; Simpson et al., in press), and combined morphological and molecular data (Muasya et al., 2000b). The two most recent classifications based on morphological data (including gross morphology, anatomy and embryology) differ in suprageneric groupings of tribes and subfamilies. Bruhl (1995) recognised two subfamilies, Cyperoideae and Caricoideae, whereas Goetghebeur (1998) recognised two additional subfamilies, Sclerioideae and Mapanioideae, both of which were included in Caricoideae by Bruhl (1995). The treatments also differed in tribal circumscription, with Bruhl (1995) recognising 12 tribes and treating Scirpeae broadly to include taxa classified in tribes Dulicheae, Fuireneae, Eleocharideae and Cypereae sensu Goetghebeur (1998).

Molecular DNA sequence data are increasingly used in angiosperm classification. In Cyperaceae, broad suprageneric studies have so far sampled all subfamilies and tribes, but sampling effort is not evenly distributed among all tribes. Family-level studies have been based mainly on *rbcL* sequence data (e.g. Muasya et al., 1998; Simpson et al., 2007), whereas at tribal or subfamilial levels other plastid and nuclear regions have been used. The plastid regions *rps16* intron, *trnL* intron and *trnL-F* intergenic spacer have been used in studies of subfamily Mapanioideae (e.g. Simpson et al., 2003) and a number of studies at tribal and generic level.

This study uses three of the most commonly used plastid regions (the *rbcL* gene, the *trnL* intron, and the *trnL-F* spacer) to reconstruct relationships of the family and presents an overview of the current status of suprageneric phylogenetic studies. The *rbcL* gene has been sequenced for over 60% genera of Cyperaceae (e.g. Simpson et al., 2007) and can be aligned unambiguously, whereas *trnL-F* (both the *trnL* intron and the *trnl-F* intergenic spacer) has been used to a greater extent in generic studies and is more difficult to align at the family level.

## Analysis of *rbcL* and *trnl-F* Data

The analysis includes a total 262 taxa (258 species) of Cyperaceae in 93 genera from the 15 tribes and four subfamilies recognised by Goetghebeur (1998). Sequences from previous studies (Bremer, 2002; Dhooge et al., 2003; Muasya et al., 1998, 2000a, 2000b, 2001, 2002; Simpson et al., 2003, 2007; Verboom, 2006; Zhang et al., 2004) were analysed together with 41 newly sequenced taxa representing 22 genera, nine of which had not been previously sequenced. Total DNA was extracted from vegetative material (leaves or culms) collected in the field or from herbarium specimens (Table 1). DNA extraction, amplification and sequencing were performed according to published procedures (e.g. Muasya et al., 2002); the resulting sequences were aligned manually and are lodged with GenBank (Table 1).

**Table 1** List of Taxa Sampled with vouchers and Genbank Accession Numbers. Classification Following Interpretation of Current Data and Goetghebeur (1998)

| Taxon | Voucher | GenBank accession numbers | |
|---|---|---|---|
| | | *rbcL* | *trnL-F OR intron/spacer* |
| Cyperoideae Suess. | | | |
| Abildgaardieae Lye | | | |
| *Abildgaardia ovata* (Burm. f.) Kral | Kenya: Muasya et al. 684 (EA, K) | Y12985 | AJ295754 |
| *Actinoschoenus repens* Raynal | Zambia: Robinson 3643 (K) | EF178537 | |
| *Arthrostylis aphylla* R. Br. | Australia: Wilson 8249 (NSW) | AY725939 | |
| *Bulbostylis atrosanguinea* (Boeck.) C. B. Clarke | Kenya: Muasya 1037 (EA, K) | Y12992 | |
| *Bulbostylis hispidula* (Vahl) R. W. Haines | Kenya: Muasya 1025 (EA, K) | Y12944 | |
| *Crosslandia setifolia* W. Fitzg. | Australia: Wilson 10147 (K) | EF178538 | EF178592 |
| *Fimbristylis complanata* (Retz.) Link | Kenya: Muasya 1029 (EA, K) | Y13009 | |
| *Fimbristylis dichotoma* (L.) Vahl | Kenya: Muasya 1006 (EA, K) | Y13008 | AJ295755 |
| *Nemum spadiceum* (Lam.) Desv. ex Ham. | WEST AFRICA: Baldwin 9766 (K) | Y12945 | |
| *Trachystylis stradbrokensis* (Domin) Kük. | Australia: Wilson 8175 (K) | EF178539 | EF178591 |
| Bisboeckelereae Pax ex L.T. Eiten | | | |
| *Becquerelia cymosa* Brongn. | Brazil: Thomas et al. 10284 (NY) | Y12948 | |
| *Calyptrocarya bicolor* (H. Pfeiff.) Koyama | RBGKEW DNA 10389 | EF178540 | |
| *Diplacrum africanum* C. B. Clarke | Tanzania: Vollensen 3967 (K) | AY725942 | |
| Cariceae Kunth ex Dumort. | | | |
| *Carex cephalophora* Muhl. ex Willd. | Kress et al. (2005) | DQ006089 | |
| *Carex conferta* A. Rich. | Kenya: Muasya 1055 (K) | Y12999 | |
| *Carex echinochloe* Kunze | Kenya: Muasya 1051 (K) | Y12997 | AF191818 |
| *Carex hostiana* DC. | Chase et al. (1993) | L12672 | |
| *Carex monostachya* A. Rich. | Kenya: Muasya 1052 (K) | Y12998 | |
| *Carex sylvatica* Huds. | Simpson et al. (2003) | | AY344175 |
| *Kobresia simpliciuscula* (Wahlenb.) Mackenzie | Plunkett et al. (1995); Yen et al. (2000) | U49232 | AF164948 |
| *Uncinia nemoralis* K. L. Wilson | Australia: Wilson et al. 9533 (K) | AY725956 | |
| *Schoenoxiphium ecklonii* Nees | S. Africa: Williams 968 (K) | EF178541 | |
| *Schoenoxiphium lehmannii* (Nees) Kunth ex Steud. | Tanzania: J M G 94/94 (K) | EF178542 | |
| *Schoenoxiphium sparteum* (Wahlenb.) C.B.Clarke | Kenya: Muasya 2566 (EA) | EF178543 | |
| Uncertain tribe aff. Cariceae | | | |
| *Khaosokia caricoides* D.A.Simpson, Chayam. & J.Parn. | Thailand: Simpson et al. 1886 (K) | AY725948 | EF178535 |

**Table 1** (continued)

| Taxon | Voucher | GenBank accession numbers | |
|---|---|---|---|
| | | *rbcL* | *trnL-F OR intron/spacer* |
| Cryptangieae Benth. | | | |
| *Didymiandrum stellatum* (Boeck.) Gilly | Venezuela: Liesner 23562 (GENT) | EF178544 | |
| *Exochogyne amazonica* C. B. Clarke | Brazil: Aparecida da Silva 1986 (GENT) | EF178545 | |
| *Lagenocarpus alboniger* (A. St.-Hil.) C. B. Clarke | Brazil: Thomas 11111 (NY) | AY725949 | |
| Cypereae Dumort. | | | |
| *Alinula paradoxa* Goetgh. & Vorster | Tanzania: Faden et al. 96/29 (K) | AJ278290 | AJ295756 |
| *Androtrichum giganteum* (Kunth) H. Pfeiff. | Argentina: Tressens et al. 4292 (K) | EF178546 | |
| *Androtrichum trigynum* (Spreng.) H. Pfeiff. | Argentina: Goetghebeur 4764 (GENT) | EF178547 | |
| *Ascolepis capensis* (Kunth) Ridl. | Kenya: Muasya 1009 (EA, K) | Y13003 | AJ295757 |
| *Ascolepis protea* Welw. | Congo: Fay 2700 (K) | Y13002 | |
| *Courtoisina assimilis* (Steud.) Maquet | Tanzania: Faden et al. 96/119 (K) | AY40590 | AY040595 |
| *Cyperus compressus* L. | Thailand: Muasya 1375 (K) | AF449506 | AF449555/ |
| *Cyperus congestus* Vahl | Australia: Coveny et al. 17492 (K) | AF449507 | AF449556/ AF449568 |
| *Cyperus cuspidatus* Kunth | Thailand: Muasya 1374 (K) | AF449508 | AF449557/ AF449569 |
| *Cyperus cyperoides* (L.) Kuntze | Thailand: Muasya 1277 (K) | AF449509 | AF449558/ AF449570 |
| *Cyperus dichroostachyus* A. Rich. | Kenya: Muasya 976 (EA, K) | Y12965 | /AF449571 |
| *Cyperus endlichii* Kük. | Kenya: Muasya 695 (K) | AF449510 | AF449559/ 449572 |
| *Cyperus involucratus* Rottb. | Madagascar: Kew Acc. 6136603 | Y12967 | AJ295758 |
| *Cyperus kerstenii* Boeck. | Kenya: Muasya 984 (EA, K) | Y13018 | AY040597 |
| *Cyperus laevigatus* L. | Kenya: Muasya 1041 (EA) | Y13017 | AY040596 |
| *Cyperus longus* L. | Europe: Chase 2276 (K) | Y13015 | AY040598 |
| *Cyperus meeboldii* Kük. | Kenya: Muasya 1255 (EA, K) | AF449511 | AF449560/ |
| *Cyperus papyrus* L. | Chad: Hepper 4213 (K) | Y12966 | AJ295759 |
| *Cyperus plateilema* (Steud.) Kük. | Kenya: Muasya 969 (EA, K) | AF449512 | AF449561/ AF449573 |
| *Cyperus pseudovestitus* (C. B. Clarke) Kük. | Kenya: Muasya 1268 (K) | AF449513 | AF449562/ AF449574 |
| *Cyperus pulchellus* R. Br. | Thailand: Muasya 1377 (K) | AY40591 | AY040599 |
| *Cyperus pygmaeus* Rottb. | Kenya: Muasya 1133 (K) | AJ404698 | AJ295760 |
| *Cyperus rigidifolius* Steud. | Kenya: Muasya 1031 (K) | Y13016 | AY040600 |
| *Desmoschoenus spiralis* Hook. f. | New Zealand: Ford 44/94 (NU) | AJ404701 | AJ295753 |
| *Ficinia bergiana* Kunth | S. Africa: Muasya 2337 (BOL) | EF200588 | EF178593 |
| *Ficinia distans* C. B. Clarke | S. Africa: Muasya 2283 (BOL) | EF178548 | EF178594 |
| *Ficinia esterhuyseniae* Muasya | S. Africa: Muasya 2312 (BOL) | EF178549 | EF178590 |
| *Ficinia gracilis* Schrad. | S. Africa: Muasya 2355 | EF178589 | EF178595 |
| *Ficinia gracilis* Schrad. | Tanzania: Faden et al. 96/433 (K) | EF178550 | EF178534 |

**Table 1** (continued)

| Taxon | Voucher | GenBank accession numbers | |
|---|---|---|---|
| | | *rbcL* | *trnL-F OR intron/spacer* |
| *Ficinia gydomontana* T. H. Arnold & K. D. Gordon-Gray | S. Africa: Muasya 2333 (BOL) | EF178551 | EF178596 |
| *Ficinia indica* (Lam.) H. Pfeiff. | S. Africa: Muasya 2318 (BOL) | EF178552 | EF178597 |
| *Ficinia laciniata* (Thunb.) Nees | S. Africa: Muasya 2340 (BOL) | EF178553 | EF178598 |
| *Ficinia nodosa* (Rottb.) Goetgh., Muasya & D. A. Simpson | Australia: Strind 21216 (K) | Y12984 | AJ295793 |
| *Ficinia paradoxa* (Schrad.) Nees | S. Africa: Verboom 534 (BOL) | DQ058354 | DQ058317 |
| *Ficinia pinguior* C. B. Clarke | S. Africa: Muasya 1183 (K) | AJ404703 | AJ295772 |
| *Ficinia polystachya* Levyns | S. Africa: Muasya 2330 (K) | EF178554 | EF178599 |
| *Ficinia ramosissima* Kunth | S. Africa: Muasya 2288 (K) | EF178555 | EF178600 |
| *Ficinia repens* Kunth | S. Africa: Muasya 2347 (K) | EF178556 | EF178601 |
| *Ficinia rigida* Levyns | S. Africa: Muasya 2319 (K) | EF178557 | EF178602 |
| *Ficinia trichodes* (Schrad.) Benth. & Hook. f. | S. Africa: Muasya 2328 (K) | EF178558 | EF178603 |
| *Ficinia tristachya* (Rottb.) Nees | S. Africa: Muasya 1233 (K) | AJ404702 | AJ295771 |
| *Hellmuthia membranacea* (Thunb.) R. W. Haines & Lye | S. Africa: Weerderman et al. 269 (K); Muasya 1145 (K) | Y13000 | AJ295815 |
| *Isolepis aucklandica* Hook. f. | Australia: Wilson et al. 9462 (K) | AJ404704 | AJ295773 |
| *Isolepis bicolor* Carmich. | Tristan Da Cunha: Richardson 105 (K) | AJ404705 | AJ295774 |
| *Isolepis cernua* (Vahl) Roem. & Schult. var. *cernua* | Britain: Muasya 1058 (K) | Y13014 | AJ295775 |
| *Isolepis cernua* var. *meruensis* (Lye) Muasya | Tanzania: Muasya 1061 (K) | AJ404715 | AJ295791 |
| *Isolepis cernua* var. *platycarpa* (S. T. Blake) Muasya | Australia: Coveny et al. 17465 (K) | AJ404716 | AJ295794 |
| *Isolepis cernua* var. *setiformis* (Benth.) Muasya | S. Africa: Muasya 1194 (K) | AJ404725 | AJ295805 |
| *Isolepis costata* A. Rich. | Kenya: Muasya 1049 (EA, K) | Y12981 | AJ295776 |
| *Isolepis crassiuscula* Hook. f. | Australia: Coveny et al. 17478 (K) | AJ404706 | AJ295777 |
| *Isolepis diabolica* (Steud.) Schrad. | S. Africa: Muasya 1163 (K) | AJ404707 | AJ295778 |
| *Isolepis digitata* Nees ex Schrad. | S. Africa: Muasya 1230 (K) | AJ404708 | AJ295779 |
| *Isolepis fluitans* (L.) R. Br. | Kenya: Muasya 1057 (K) | Y12961 | AJ295780 |
| *Isolepis gaudichaudiana* Kunth | Australia: Coveny et al. 17476 (K) | AJ404709 | AJ295781 |
| *Isolepis graminoides* (R. W. Haines & Lye) Lye | Kenya: Muasya 986 (EA, K) | Y12960 | AJ295782 |
| *Isolepis habra* (Edgar) Soják | Australia: Coveny et al. 17477 (NSW) | AJ404710 | AJ295783 |
| *Isolepis hystrix* (Thunb.) Nees | S. Africa: Muasya 1150 (K) | AJ404711 | AJ295785 |
| *Isolepis inundata* R. Br. | Australia: Wilson et al. 9461 (NSW) | AJ404712 | AJ295786 |
| *Isolepis* inyangensis Muasya & Goetgh. | Zimbabwe: Muasya et al. 1125 (K) | AJ297506 | AJ295787 |
| *Isolepis keniaensis* Lye | Kenya: Cabolt plant 'A' (K) | Y12980 | AJ295788 |
| *Isolepis levynsiana* Muasya & D. A. Simpson | S. Africa: Muasya 1151 (K) | AF449514 | AF449563/ AF449575 |
| *Isolepis ludwigii* (Steud.) Kunth | S. Africa: Muasya 1181 (K) | AJ404713 | AJ295789 |

**Table 1** (continued)

| Taxon | Voucher | GenBank accession numbers | |
|---|---|---|---|
| | | *rbcL* | *trnL-F OR intron/spacer* |
| *Isolepis marginata* (Thunb.) A. Dietr. | Australia: Coveny et al. 17452 (K) | AJ404714 | AJ295790 |
| *Isolepis montivaga* (S. T. Blake) K.L.Wilson | Australia: Wilson et al. 9480 (K) | AJ297507 | AJ295792 |
| *Isolepis pellocolea* B. L. Burtt | Lesotho: Gordon-Gray 49694 (NU) | AJ404729 | AJ297514 |
| *Isolepis producta* (C. B. Clarke) K. L. Wilson | Australia: Wilson et al. 9510 (K) | AJ404717 | AJ295795 |
| *Isolepis prolifera* (Rottb.) R. Br. | Australia: Coveny et al. 17487 (K) | AJ404718 | AJ295796 |
| *Isolepis rubicunda* (Nees) Kunth | S. Africa: Muasya 1221 (K) | AJ404719 | AJ295797 |
| *Isolepis sepulcralis* Steud. | Australia: Coveny et al. 17456 (K) | AJ404720 | AJ295798 |
| *Isolepis setacea* (L.) R. Br. | Kenya: Muasya 1059 (K) | Y12962 | AJ295799 |
| *Isolepis striata* (Nees) Kunth | S. Africa: Muasya 1141 (K) | AJ404721 | AJ295801 |
| *Isolepis subtillisima* Boeck. | Australia: Coveny et al. 17474 (K) | AJ297508 | AJ295800 |
| *Isolepis sulcata* (Thouars) Carmich. | Tristan Da Cunha: Richardson 80 (K) | AJ404722 | AJ295802 |
| *Isolepis tenuissima* (Nees) Kunth | S. Africa: Muasya 2369 (K) | AY725947 | |
| *Isolepis varians* Steud. | Chile: Pisano 259 (K) | AJ404723 | AJ295803 |
| *Isolepis venustula* Kunth | S. Africa: Muasya 1189 (K) | AJ404724 | AJ295804 |
| *Isolepis wakefieldiana* (S. T. Blake) K. L. Wilson | Australia: Neish et al. 110 (K) | AJ404726 | AJ295806 |
| *Kyllinga appendiculata* K. Schum. | Kenya: Muasya 1050 (EA, K) | Y13007 | AJ295761 |
| *Kyllinga brevifolia* Rottb. | Australia: Coveny et al. 17459 (K) | AF449515 | AF449564/ AF449576 |
| *Kyllinga bulbosa* P. Beauv. | Kenya: Muasya 1020 (EA, K) | Y12979 | AY040601 |
| *Kyllingiella microcephala* (Steud.) R. W. Haines & Lye | Zimbabwe: Muasya et al. 1118 (K) | AY040592 | AJ295807 |
| *Kyllingiella polyphylla* (A. Rich.) Lye | Tanzania: Wingfield 497 (K) | Y13013 | AJ295515 |
| *Lipocarpha hemisphaerica* (Roth.) Goetgh. | Thailand: Muasya 1217 (K) | AF449516 | AF449565/ AF449577 |
| *Lipocarpha microcephala* (R. Br.) Kunth | Australia: Wilson et al. 3383 (K) | Y12991 | |
| *Lipocarpha nana* (A.Rich.) J. Raynal | Kenya: Muasya 972 (EA, K) | Y12990 | AJ295762 |
| *Oxycaryum cubense* (Poepp. & Kunth) E. Palla | Zambia: Richards 13318 (K) | Y13006 | AY040602 |
| *Pycreus flavescens* (L.) Rchb. | Kenya: Muasya 1022 (EA, K) | Y13005 | AJ295763 |
| *Pycreus mundtii* Nees | Thailand: Muasya 1464 (K) | AF449517 | AF449566/ AF449578 |
| *Pycreus nuerensis* (Boeck.) S. S. Hooper | Tanzania: Muasya 940 (EA, K) | Y13004 | AY040603 |
| *Pycreus sanguinolentus* (Vahl) Nees | Australia: Coveny et al. 17461 (K) | | AF449567/ AF449579 |
| *Queenslandiella hyalina* (Vahl) Ballard | Kenya: Mwachala 296 (EA) | AY725953 | |

**Table 1** (continued)

| Taxon | Voucher | GenBank accession numbers | |
|---|---|---|---|
| | | *rbcL* | *trnL-F OR intron/spacer* |
| *Remirea maritima* Aubl. | Tanzania: Faden et al. 96/48 (K) | AY040593 | AY040604 |
| *Scirpoides burkei* (C. B. Clarke) Goetgh., Muasya & D. A. Simpson | S. Africa: Hargreaves 3361 (K) | Y13001 | AJ295810 |
| *Scirpoides holoschoenus* (L.) Soják | S. Africa: Acocks s.n. (K) | Y12994 | AJ295811 |
| *Scirpoides thunbergii* (Schrad.) Soják | S. Africa: Muasya 1205 (K) | AJ404727 | AJ295812 |
| *Scirpus falsus* C. B. Clarke | S. Africa: Hilliard 13609 (GENT) | EF178559 | |
| *Scirpus ficinioides* Kunth | S. Africa: Hilliard 16095 (GENT) | EF178560 | |
| *Sphaerocyperus erinaceus* (Ridl.) Lye | Tanzania: Faden et al. 96/338 (K) | AJ404699 | AJ295764 |
| *Volkiella disticha* Merxm. & Czech | Namibia: Muller et al. 4245 (K) | EF178561 | |
| Dulicheae Rchb. ex J. Schultze-Motel | | | |
| *Blysmus compressus* Panz. | Afghanistan: Dobson 221 (K) | AJ404700 | AJ295766 |
| *Dulichium arundinaceum* (L.) Britton | USA: Goetghebeur 9914 (GENT); Roalson et al. (2001) | AY725943 | AF285067 |
| Eleocharideae Goetgh. | | | |
| *Chillania pusilla* Roiv. | Chile: Grau 1433 (GENT) | EF178562 | |
| *Eleocharis atropurpurea* (Retz.) Presl | Kenya: Muasya et al. 752 (EA, K) | Y13012 | |
| *Eleocharis gracilis* R.Br. | Australia: Wilson et al. 9462 (K) | EF178563 | |
| *Eleocharis marginulata* Steud. | Kenya: Muasya 1039 (EA, K) | Y13011 | AJ295768 |
| *Eleocharis pauciflora* (Lightf.) Link. | USA: Mastrogiuseppe 7461 (WS) | U49229 | |
| Fuireneae Reichenb. ex Fenzl | | | |
| *Actinoscirpus grossus* (L. f.) Goetgh. & D. A. Simpson | Malaysia: Simpson 2660 (K) | Y12953 | AJ295765 |
| *Bolboschoenus caldwellii* (V. Cook) Soják | Australia: Wilson et al. 9530 (K) | EF178564 | |
| *Bolboschoenus maritimus* (L.) Palla | Botswana: Smith 2452 (K) | Y12996 | AJ295767 |
| *Bolboschoenus nobilis* (Ridl.) Goetgh. & D. A. Simpson | S. Africa: Leistner 144 (K) | Y12995 | |
| *Fuirena abnormalis* C. B. Clarke | Tanzania: Faden et al. 96/118 (K) | EF178565 | |
| *Fuirena ciliaris* (L.) Roxb. | Tanzania: Muasya 951 (EA, K) | Y12971 | |
| *Fuirena coerulescens* Steud. | S. Africa: Muasya 2322 (K) | EF178566 | |
| *Fuirena hirsuta* (Berger) P. L. Forbes | S. Africa: Muasya 2324 (K) | EF178567 | |
| *Fuirena welwitschii* Ridl. | Kenya: Muasya 1024 (EA, K) | Y12993 | EF178605 |
| *Fuirena* sp. | Brazil: Thomas et al. 10404 (NY) | Y12970 | |
| *Isolepis humillima* (Benth.) K. L. Wilson | Australia: Thomas et al. 622 (BRI) | AJ404728 | AJ295784 |
| *Schoenoplectiella articulata* (L.) Lye | Tanzania: Muasya 947 (EA, K) | Y12987 | |
| *Schoenoplectiella juncea* (Willd.) Lye | Kenya: Muasya et al. 775 (K) | Y12952 | |

**Table 1** (continued)

| Taxon | Voucher | GenBank accession numbers | |
|---|---|---|---|
| | | *rbcL* | *trnL-F OR intron/spacer* |
| *Schoenoplectiella senegalensis* (Hochst. ex A. Rich.) Lye | Kenya: Muasya et al. 2440 (EA) | EF178568 | EF178606 |
| *Schoenoplectus confusus* (N. E. Br.) Lye | Kenya: Muasya et al. 2438 (EA) | EF178569 | |
| *Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) J. Raynal | Kenya: Muasya 1004 (EA) | EF178570 | EF178607 |
| *Schoenoplectus lacustris* (L.) Palla | Britain: Muasya 1043 (K) | Y12943 | AJ295809 |
| *Schoenoplectus litoralis* (Schrad.) Palla | Hong Kong: Shaw 883 (K) | EF178571 | |
| *Schoenoplectus mucronatus* (L.) Palla | Thailand: Muasya et al. 1290 (K) | EF178572 | |
| *Scirpus varius* Boeck. ex C.B.Clarke | Botswana: Smith 5376 (NU) | EF178573 | |
| Rhynchosporeae | | | |
| *Pleurostachys* sp. | Brazil: Kallunki et al. 513 (NY) | Y12989 | |
| *Rhynchospora* alba (L.) Vahl | Simpson et al. (2003) | | AY344174 |
| *Rhynchospora brownii* Roem. et Schult. | S. Africa: Verboom 616 (BOL) | DQ058353 | DQ058316 |
| *Rhynchospora fascicularis* (Michx.) Vahl | Plunkett et al. (1995) | U49233 | |
| *Rhynchospora nervosa* (Vahl.) Boeck. | Brazil: Kallunki et al. 512 (NY) | Y12977 | |
| Schoeneae Dumort. | | | |
| *Baumea rubiginosa* (Spreng.) Boeck. | Australia: Wilson et al. 9471 (K) | AY725940 | |
| *Capeobolus brevicaulis* (C. B. Clarke) J. Browning | S. Africa: Verboom 646, BOL | DQ058343 | DQ058303 |
| *Carpha alpina* R. Br. | Wardle et al. (2001); Zhang et al. (2004) | AF307909 | AY230012 |
| *Carpha* sp. | Australia: Wilson et al. 9456 (K) | EF178574 | |
| *Carpha glomerata* (Thunb.) Nees. | S. Africa: Muasya 1176 (K) | AY725941 | |
| *Caustis dioica* R. Br. | Australia: Chase 2225 (K) | Y12976 | |
| *Cladium jamaicensis* Crantz | Brazil: Thomas et al. 10403 (NY) | Y12988 | |
| *Cladium* sp. | Brazil: Mayo 259 (K) | Y12950 | |
| *Cladium mariscus* (L.) R. Br. | Locality unknown: MJC 292 (K) | DQ058338 | DQ058298 |
| *Costularia arundinacea* (Sol. ex Vahl) Kük. | Zhang et al. (2004) | - | AY230036 |
| *Costularia fragilis* (Däniker) Kük. | New Calendonia McKee NSW41617 (K) | EU828589 | |
| *Costularia nervosa* Raynal | Zhang et al. (2004) | - | AY230032 |
| *Costularia pubescens* Raynal | Zhang et al. (2004) | - | AY230037 |
| *Cyathochaeta driandra* (R. Br.) Nees | Zhang et al. (2004) | - | AY230042 |
| *Cyathocoma bachmannii* (Kuk.) C. Archer | S. Africa: Browning 835 (GENT) | EF200590 | EF178604 |
| *Cyathocoma hexandra* (Nees) J. Browning | S. Africa: Verboom 648, BOL) | DQ058344 | DQ058304 |

**Table 1** (continued)

| Taxon | Voucher | GenBank accession numbers | |
|---|---|---|---|
| | | *rbcL* | *trnL-F OR intron/spacer* |
| *Epischoenus quadrangularis* (Boeck.) C. B. Clarke | S. Africa: Verboom 636 (BOL) | DQ058349 | DQ058311 |
| *Evandra aristata* R. Br. | Australia: Wilson et al. 8974 (NSW) | AY725944 | |
| *Gahnia baniensis* Benl. | Malaysia: Simpson 2737 (K) | DQ058342 | DQ058302 |
| *Gahnia deusta* (R. Br.) Benth. | Australia: Alcock 11198 (WS) | U49231 | |
| *Gymnoschoenus sphaerocephalus* (R. Br.) Hook. f. | Australia: Wilson et al. 9463 (K); Zhang et al. (2004) | AY725945 | AY230033 |
| *Lepidosperma tortuosum* F. Muell. | Australia: Coveny et al. 17470 (K); Roalson et al. (2001) | AY725950 | AF285074 |
| *Machaerina mariscoides* (Gaudich.) Kern | Tahiti: Sachet 2636 (GENT) | EF178575 | |
| *Machaerina* sp. | New Guinea: Johns 9195 (K) | DQ058340 | DQ058300 |
| *Mesomelaena pseudostygia* (Kük.) K. L. Wilson | Australia: Chase 2226 (K) | Y12959 | DQ058301 |
| *Mesomelaena tetragona* (R. Br.) Benth. | Australia: Chase 2227 (K) | Y12949 | |
| *Morelotia gahniiformis* Gaudich. | Hawaii: Herbst 1167 (GENT) | EF178576 | |
| *Neesenbeckia punctoria* (Vahl) Levyns | S. Africa: Muasya 1214 (K) | AY725952 | DQ058306 |
| *Oreobolus kukenthalii* Steenis | Malaysia: Simpson 2659 (K) | Y12972 | EF178536 |
| *Oreobolus obtusangulus* Gaudich. | Wardle et al. (2001) | AF307926 | |
| *Oreobolus oligocephalus* W. M. Curtis | Zhang et al., (2004) | - | AY230031 |
| *Oreobolus pectinatus* Hook. f. | Wardle et al. (2001) | AF307927 | |
| *Ptilothrix deusta* (R. Br.) K. L. Wilson | Zhang et al. (2004) | - | AY230041 |
| *Schoenus nigricans* L. | Saudi Arabia: Edmondson 3382 (K) | Y12983 | AJ295814 |
| *Tetraria bolusii* C. B. Clarke | S. Africa: Verboom 606 (BOL) | - | DQ058315 |
| *Tetraria capillaris* (F. Muell.) J. M. Black | Australia: Wilson et al. 9464 (K) | EF178577 | |
| *Tetraria compacta* Levyns | S. Africa: Verboom 614 (BOL) | DQ058351 | DQ058313 |
| *Tetraria compar* (L.) Lestib. | S. Africa: Verboom 549, (BOL) | DQ058350 | DQ058312 |
| *Tetraria crassa* Levyns | S. Africa: Verboom 507 (BOL) | DQ058352 | DQ058314 |
| *Tetraria crinifolia* (Nees) C. B. Clarke | S. Africa: Verboom 638 (BOL) | DQ058348 | DQ058309 |
| *Tetraria microstachys* (Vahl) Pfeiffer | S. Africa: Verboom 640 (BOL) | DQ058347 | DQ058307 |
| *Tetraria thermalis* (L.) C. B. Clarke | S. Africa: Verboom 643 (BOL) | - | DQ058308 |
| *Trianoptiles solitaria* (C. B. Clarke) Levyns | Zhang et al. (2004) | - | AY230028 |
| *Tricostularia pauciflora* (R. Br.) Benth. | Australia: Coveny et al. 17484 (K); Zhang et al. (2004) | AY725954 | AY230038 |
| Scirpeae Kunth ex Dumort. | | | |
| *Amphiscirpus nevadensis* (S. Watson) Oteng-Yeboa | Argentina: Charpin et al. 20575 (GENT) | DQ317926 | DQ317925 |

**Table 1** (continued)

| Taxon | Voucher | GenBank accession numbers | |
|---|---|---|---|
| | | *rbcL* | *trnL-F OR intron/spacer* |
| *Eriophorum angustifolium* Honckney | Simpson et al. (2003) | | AY344177 |
| *Eriophorum vaginatum* L. | Poland: Beyer et al. 2 (K) | Y12951 | AJ295769 |
| *Eriophorum viridicarinatum* (Engl.) Fern. | USA: Boufford 23053 (WS) | U49230 | |
| *Oreobolopsis clementis* (M. E. Jones) Dhooge & Goetgh. | Dhooge (2005) | AJ811011 | Dhooge (2005) |
| *Oreobolopsis inversa* Dhooge & Goetgh. | Ecuador: Laegaard 21492 (GENT) | AJ811009 | DQ317923 |
| *Oreobolopsis tepalifera* T. Koyama & Guagl. | Dhooge et al. (2003) | AJ575932 | AJ576035 |
| *Phylloscirpus acaulis* (Phil.) Goetgh. & D. A. Simpson | Dhooge et al. 2003 | AJ575926 | AJ576029 |
| *Phylloscirpus boliviensis* (Barros) Dhooge & Goetgh. | Ecuador: Laegaard 102805 (GENT) | AJ566081 | AJ566082 |
| *Phylloscirpus deserticola* (Phil.) Dhooge & Goetgh. | Ecuador: Laegaard et al. 21478 (GENT) | AJ704785 | AJ704786 |
| *Scirpus ancistrochaetus* Schuyler | USA: Naczi 7544 (DOV) | EF178578 | |
| *Scirpus atrocinctus* Fernald | USA: Naczi 10456 (DOV) | EF178579 | |
| *Scirpus cyperinus* (L.) Kunth | USA: Naczi (DOV) | EF178580 | |
| *Scirpus expansus* Fernald | USA: Naczi 10050 (DOV) | EF178581 | |
| *Scirpus flaccidifolius* (Fernald) Schuyler | USA: Naczi 9774 (DOV) | EF178582 | |
| *Scirpus georgianus* Harper | USA: Naczi 10458 (DOV) | EF178583 | |
| *Scirpus hattorianus* Makino | USA: Naczi 10369 (DOV) | EF178584 | |
| *Scirpus pendulus* Muhl. | USA: Naczi 10394 (DOV) | EF178585 | |
| *Scirpus polystachyus* F. Muell. | Australia: Pullen 4091 (K) | Y12974 | AJ295813 |
| *Scirpus radicans* Schkuhr | Czechia: Goetghebeur 9882 (GENT) | AJ811012 | Dhooge (2005) |
| *Scirpus sylvaticus* L. | HBUG/86–0541 (GENT) | EF178586 | |
| *Scirpus ternatanus* Reinw. ex Miq. | Hong Kong: Shaw 917 (K) | EF178587 | |
| *Trichophorum alpinum* (L.) Pers. | CANADA: Waterway 2002.95 (GENT) | AJ810999 | DQ317924 |
| *Trichophorum caespitosum* (L.) Hartm. | British Isles: Nelmes 954 (K) | Y12969 | Dhooge (2005) |
| *Trichophorum clintonii* Gray | Canada: Baldwin 4856 (K) | Y12982 | Dhooge (2005) |
| *Trichophorum planifolium* (Spreng.) Palla | USA: Dhooge 24 (GENT) | AJ811001 | Dhooge (2005) |
| *Trichophorum pumilum* (Vahl) Schinz & Thellung | Uncertain locality: Morse & Jordon 2272 (GENT) | AJ811000 | Dhooge (2005) |
| *Trichophorum rigidum* (Steud.) Goetgh., Muasya & D. A. Simpson subsp. *rigidum* | Argentina: Renvoize et al. 5021 (K) | AJ297509 | AJ295808 |
| *Trichophorum rigidum* subsp. *ecuadoriensis* Dhooge & Goetgh. | Ecuador: Laegaard et al. 21574 (GENT) | AJ811008 | Dhooge (2005) |

**Table 1** (continued)

| Taxon | Voucher | GenBank accession numbers | |
|---|---|---|---|
| | | *rbcL* | *trnL-F OR intron/spacer* |
| *Trichophorum subcapitatum* (Thwaites & Hook.) D. A. Simpson | Papua New Guinea: Goetghebeur et al. 6581 (GENT) | AJ811006 | Dhooge (2005) |
| *Zameioscirpus atacamensis* (Phil.) Dhooge & Goetgh. | Bolivia: Ruthsatz & Budde 10328 (Trier) | AJ575929 | AJ576032 |
| *Zameioscirpus gaimardioides* (E. Desv.) Dhooge & Goetgh. | Argentina: Ruthsatz 9212 (gent); Dhooge et al. (2003) | AJ575938 | AJ576031 |
| *Zameioscirpus muticus* Dhooge & Goetgh. | Dhooge et al. (2003) | AJ575927 | AJ576030 |
| Sclerieae Kunth ex Fenzl | | | |
| *Scleria distans* Poir. | Kenya: Muasya 1023 (EA, K) | Y12968 | DQ058299 |
| *Scleria foliosa* A. Rich. | Tanzania: Muasya 939 (EA, K) | Y12986 | |
| *Scleria terrestris* (L.) Fassett | Malaysia: Simpson 2658 (K) | Y12947 | |
| Trilepideae Goetgh. | | | |
| *Coleochloa abyssinica* (A. Rich.) Gilly | Ethiopia: Vollesen 80/2 (K) | Y12975 | |
| *Microdracoides squamosus* Hua | Bonn Acc. 150 | AY725951 | |
| *Trilepis lhotzkiana* Nees | Bonn Acc. s.n. | AY725955 | |
| Mapanioideae C. B. Clarke | | | |
| Chrysitricheae Lestib. ex Fenzl | | | |
| *Capitularia foliata* Uitt. | Indonesia: Johns 8725 (K) | EF178588 | |
| *Capitularina involucrata* (J. V. Suringar) Kern | Simpson et al. (2003) | | AY344168 |
| *Chorizandra cymbaria* R. Br. | Bremer (2002) | AJ419940 | |
| *Chorizandra enodis* Nees | Bremer (2002) | AJ419939 | |
| *Chorizandra sphaerocephala* R. Br. | Simpson et al. (2003) | | AY344170 |
| *Chrysitrix capensis* L. | S. Africa: Muasya 1242 (K) | AJ419938 | AY344171 |
| *Exocarya sclerioides* (F. Muell.) Benth. | Simpson et al. (2003) | | AY344167 |
| *Lepironia articulata* (Retz.) Domin. | Malaysia: Simpson 1236 (K) | Y12957 | AY344169 |
| Hypolytreae Presl ex Fenzl | | | |
| *Diplasia karatifolia* Rich. ex Pers. | Simpson et al. (2003) | | AY344166 |
| *Hypolytrum bullatum* C. B. Clarke | Brazil: Thomas et al. 10318 (NY) | Y12956 | |
| *Hypolytrum nemorum* (Vahl) Spreng. | Malaysia: Simpson 1379 (K) | Y12958 | AJ295816 |
| *Hypolytrum testui* Cherm. | Simpson et al. (2003) | | AY344163 |
| *Mapania cuspidata* (Miq.) Uittien | Brunei: Marsh 4 (K) | Y12955 | AJ295817 |
| *Mapania lorea* Uitt. | Simpson et al. (2003) | | AY344161 |
| *Mapania meditensis* D. A. Simpson | Brunei: Simpson et al. 2515 (K) | Y12954 | AY344160 |
| *Mapania tenuiscapa* C. B. Clarke | Simpson et al. (2003) | | AY344162 |
| *Scirpodendron bogneri* S.S. Hooper | Malaysia: Simpson 2650 (K) | Y12946 | AY344164 |
| *Scirpodendron ghaeri* (Gaertn.) Merrill | Simpson et al. (2003) | | AY344165 |

**Table 1** (continued)

| Taxon | Voucher | GenBank accession numbers | |
|---|---|---|---|
| | | *rbcL* | *trnL-F OR intron/spacer* |
| Outgroups | | | |
| *Juncus effusus* L. | Simpson et al. (2003); Chase et al., 1993 | L12681 | AY344156 |
| *Juncus gerardii* Loisel. | Simpson et al. (2003); Drabbkova et al. (unpublished) | AY216613 | AY344157 |
| *Luzula multiflora* (Retz.) Lej. | Bremer (2002); Simpson et al. (2003) | AJ419945 | AY344158 |
| *Luzula sylvatica* (Huds.) Gaud. | Simpson et al. (2003) | AY216637 | AY344159 |
| *Prionium serratum* Drège | S. Africa: Gettliffe Norris, s.n. (NBG) | U49223 | AY344155 |

Heuristic analyses were carried out using PAUP* (Swofford, 2002). Searches were conducted under Fitch (1971) parsimony, TBR (tree-bissection-reconnection) branch swapping, and random taxon addition (5,000) with the MulTrees option in effect and retaining only ten trees per replicate. Internal support was estimated using 1000 bootstrap replicates (Felsenstein, 1985), with the following search parameters: simple taxon addition, TBR branch-swapping, and MulTrees option in effect with only ten trees held per step.

The aligned matrix has 3,573 characters comprising 1,428 from *rbcL* and 2145 from *trnl-F* (intron and intergenic spacer) region. Some portions of *trnl-F* could not be unambiguously aligned, and 865 characters were excluded from the analysis, leaving 2,708 characters, of which 913 are potentially parsimony informative.

Fifty equally parsimonious trees were recovered of length=5,467 steps, consistency index (CI)=0.45 and retention index (RI)=0.79. The strict con*sensu*s tree (Figs. 1, 2 and 3) is presented and discussed below.

## Subfamily Relationships

Cyperaceae are resolved as monophyletic and sister to Juncaceae, with Mapanioideae sister to all the other Cyperaceae (Fig. 1; tribes and subfamilies sensu Goetghebeur, 1998). Within the last clade, *Coleochloa-Microdracoides* (Trilepideae) form a clade sister to the rest of Cyperaceae. Trilepideae are not sister to *Scleria-Diplacrum* (Sclerieae) as the latter are embedded in the Schoeneae, and therefore the Sclerioideae are not monophyletic. Also Caricoideae are sister to Scirpeae and embedded within Cyperoideae (Fig. 2).

Similar studies in which Mapanioideae are resolved as sister to rest of Cyperaceae have been reported by Bruhl (1995) based on morphological studies and in previous family-level DNA studies (e.g. Muasya et al., 1998, 2000b; Simpson et al., 2007). Mapanioideae have a unique floral morphology compared with the rest of Cyperaceae, with floral units each comprising two to ten or more scales (the lower ones being keeled), two to ten stamens and a single gynoecium. The floral units have been variously interpreted as bisexual flowers in which the arrangement of the

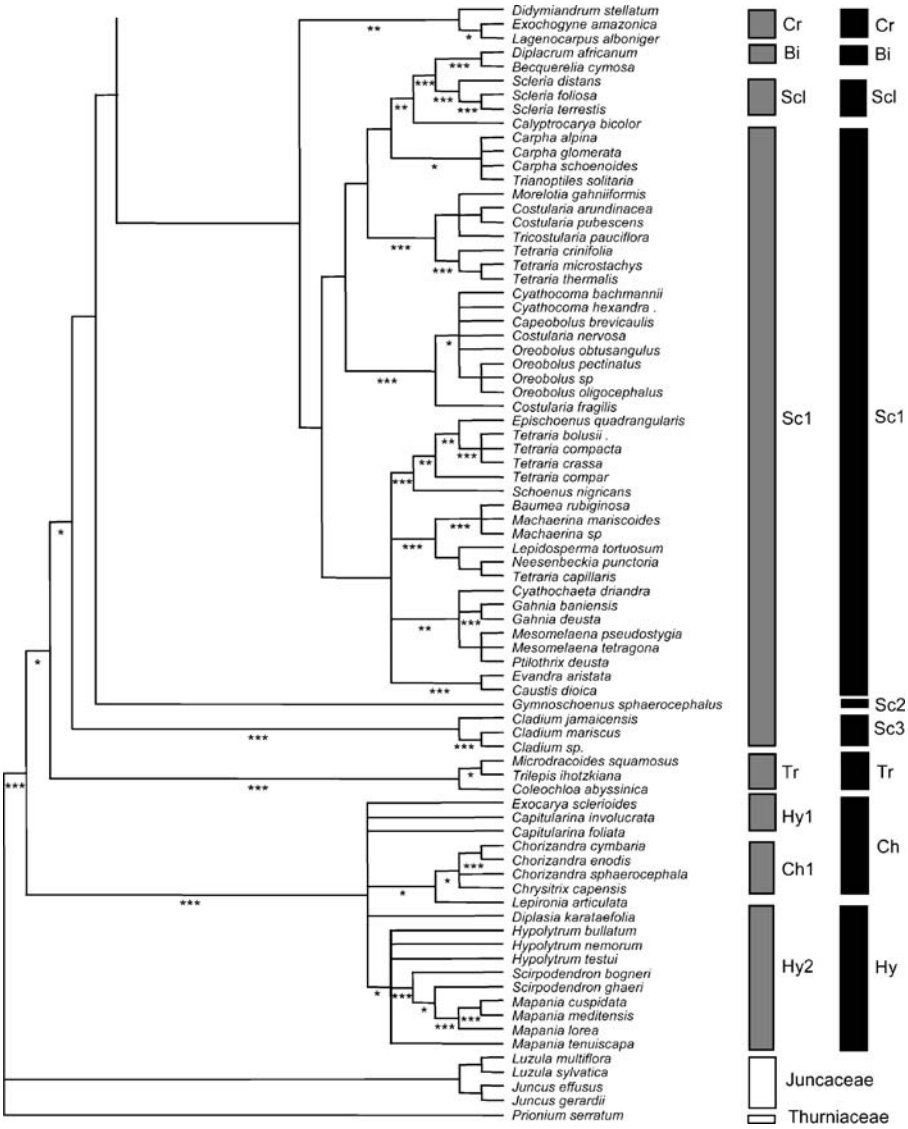
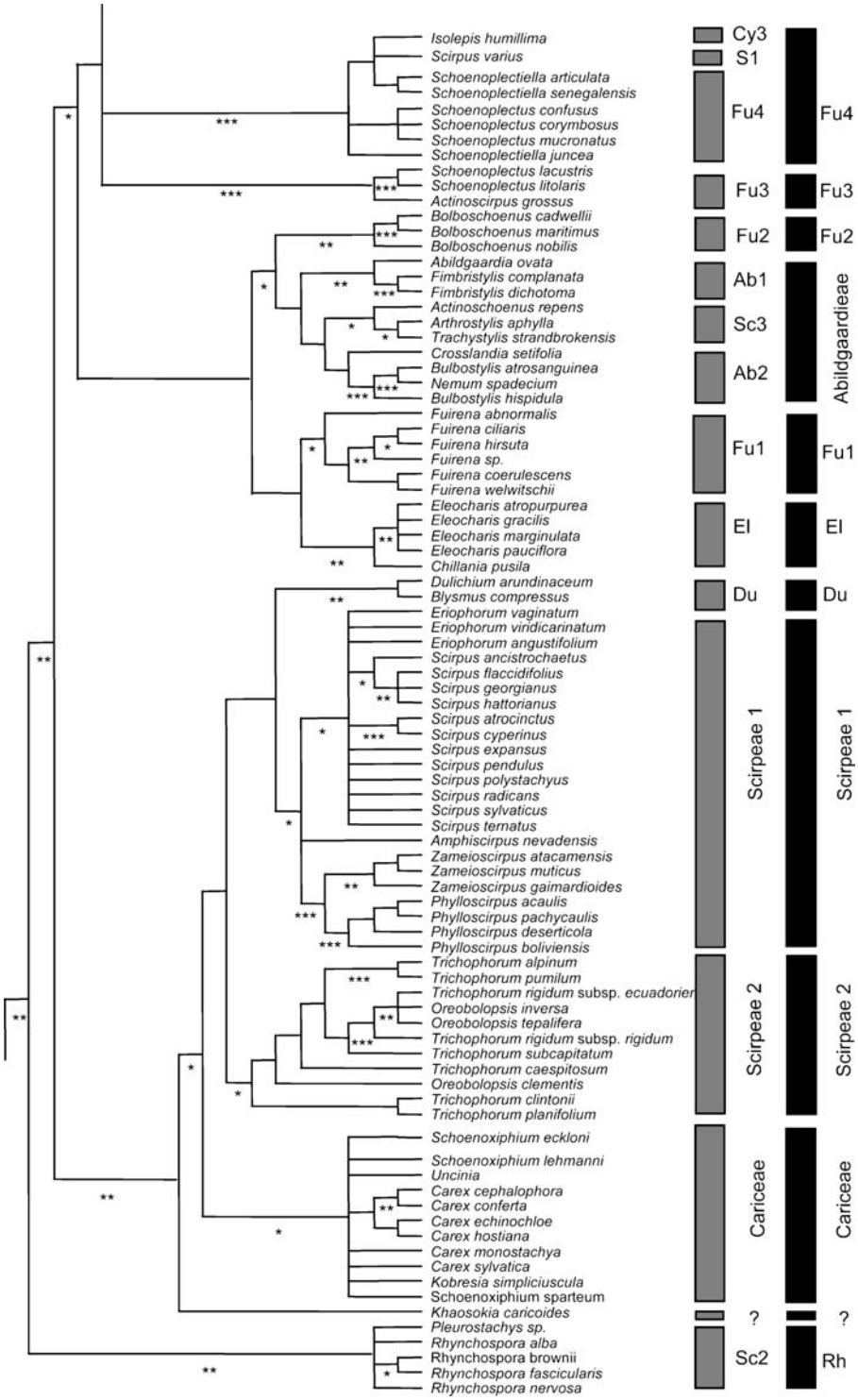



**Fig. 1** Maximum parsimony strict con*sensus* tree of Cyperaceae, showing the outgroup and Cyperaceae tribes Hypolytreae (*Hy*), Chrysitricheae (*Ch*), Trilepideae (*Tr*), Schoeneae (*Sc*), Sclerieae (*Scl*), Bisboeckelereae (*Bi*) and Cryptangieae. Goetghebeur's (1998) classification and the proposed classification are marked by *grey* and *black bars* respectively. Bootstrap support values shown as weak (*=50–74%), moderate (**=75–89%) and strong (***=90–100%)

structures has been disturbed (Goetghebeur, 1998) or as reduced partial inflorescences termed spicoids (Simpson et al., 2003; Richards et al., 2006).

Recognition of Caricoideae and Sclerioideae as subfamilies separate from Cyperoideae (e.g. Goetghebeur, 1998), based on unique morphological characters is not supported by current analysis. Typical Cyperoideae are mostly diagnosed by having at least one (sometimes all) bisexual flower, whereas in Sclerioideae (and


Isolepis humillima
Scirpus varius
Schoenoplectiella articulata
Schoenoplectiella senegalensis
Schoenoplectus confusus
Schoenoplectus corymbosus
Schoenoplectus mucronatus
Schoenoplectiella juncea
Schoenoplectus lacustris
Schoenoplectus litolaris
Actinoscirpus grossus
Bolboschoenus cadwellii
Bolboschoenus maritimus
Bolboschoenus nobilis
Abildgaardia ovata
Fimbristylis complanata
Fimbristylis dichotoma
Actinoschoenus repens
Arthrostylis aphylla
Trachystylis strandbrokensis
Crosslandia setifolia
Bulbostylis atrosanguinea
Nemum spadecium
Bulbostylis hispidula
Fuirena abnormalis
Fuirena ciliaris
Fuirena hirsuta
Fuirena sp.
Fuirena coerulescens
Fuirena welwitschii
Eleocharis atropurpurea
Eleocharis gracilis
Eleocharis marginulata
Eleocharis pauciflora
Chillania pusila
Dulichium arundinaceum
Blysmus compressus
Eriophorum vaginatum
Eriophorum viridicarinatum
Eriophorum angustifolium
Scirpus ancistrochaetus
Scirpus flaccidifolius
Scirpus georgianus
Scirpus hattorianus
Scirpus atrocinctus
Scirpus cyperinus
Scirpus expansus
Scirpus pendulus
Scirpus polystachyus
Scirpus radicans
Scirpus sylvaticus
Scirpus ternatus
Amphiscirpus nevadensis
Zameioscirpus atacamensis
Zameioscirpus muticus
Zameioscirpus gaimardioides
Phylloscirpus acaulis
Phylloscirpus pachycaulis
Phylloscirpus deserticola
Phylloscirpus boliviensis
Trichophorum alpinum
Trichophorum pumilum
Trichophorum rigidum subsp. ecuadorien
Oreobolopsis inversa
Oreobolopsis tepalifera
Trichophorum rigidum subsp. rigidum
Trichophorum subcapitatum
Trichophorum caespitosum
Oreobolopsis clementis
Trichophorum clintonii
Trichophorum planifolium
Schoenoxiphium eckloni
Schoenoxiphium lehmanni
Uncinia
Carex cephalophora
Carex conferta
Carex echinochloe
Carex hostiana
Carex monostachya
Carex sylvatica
Kobresia simpliciuscula
Schoenoxiphium sparteum
Khaosokia caricoides
Pleurostachys sp.
Rhynchospora alba
Rhynchospora brownii
Rhynchospora fascicularis
Rhynchospora nervosa
Cy3
S1
Fu4
Fu3
Fu2
Ab1
Sc3
Ab2
Fu1
El
Du
Scirpeae 1
Scirpeae 2
Cariceae
?
Sc2
Fu4
Fu3
Fu2
Abildgaardieae
Fu1
El
Du
Scirpeae 1
Scirpeae 2
Cariceae
?
Rh

some unusual Cyperoideae) they are all unisexual and in Caricoideae they are all unisexual and enclosed by a utricle. This study and other analyses of DNA data support the recognition of two subfamilies in Cyperaceae, Mapanioideae and Cyperoideae, as proposed by Simpson et al. (2003, 2007).

## Tribes of the Cyperaceae

A number of tribal groups recognised in the recent classification of Cyperaceae by Goetghebeur (1998) are supported by the current study. Within Mapanioideae, some Hypolytreae (*Mapania*, *Hypolytrum* and *Scirpodendron*) and Chrysitricheae (*Lepironia*, *Chrysitrix* and *Chorizandra*) form clades separate from a polytomy comprising other mapanioids (Fig. 1). Although the polytomy observed may be caused by insufficient data for some of the taxa, *Capitularina* and *Exocarya* (both of which traditionally have been placed in Hypolytreae) were resolved together in Chrysitricheae in a combined pollen and DNA data study (Simpson et al., 2003).

The inselberg taxa in Trilepideae (*Coleochloa* to *Microdracoides*; Fig. 1) form a strongly supported clade. This clade is sister to the rest of Cyperoideae and not to other tribes of Sclerioideae (*sensu* Goetghebeur 1998), namely Cryptangieae, Sclerieae and Bisboeckelereae. These other tribes are embedded among Schoeneae (Fig. 1). Notable is the position of *Exochogyne*, a genus unplaced in any tribe of Sclerioideae by Goetghebeur (1998) due to unclear morphological homologies, and which is resolved here among Cryptangieae.

Schoeneae are one of the most heterogeneous tribes in the family, having 29 genera of which *Rhynchospora* is among the largest; over 50% of the genera have fewer than 10 species (Goetghebeur, 1998). This analysis resolves four clades within Schoeneae: (1) *Cladium*, (2) *Gymnoschoenus*, (3) *Caustis* to *Didymiandrum*, and (4) *Rhynchospora* (Figs. 1 and 2). The moderately supported *Rhynchospora* clade has been previously classified in a separate tribe Rhynchosporeae (e.g. Goetghebeur, 1986; Bruhl, 1995) on the basis of, inter alia, distinct style base. Members of the former Sclerioideae (Cryptangieae, Bisboeckelereae and Sclerieae) are resolved among clade (3), an observation reported in previous studies (e.g. Simpson et al., 2007). Schoeneae have an essentially Gondwanan distribution, and several widely distributed genera (e.g. *Costularia*, *Tetraria*; Zhang et al., 2004, Verboom, 2006) are polyphyletic. *Morelotia* is resolved in a clade which includes *Costularia*, *Tricostularia* and reticulate-sheathed *Tetraria* (*Tricostularia* clade in Verboom, 2006), and not together with *Ghania*. A close relationship between *Morelotia* and *Ghania* has been suggested by several authors (e.g. Goetghebeur, 1986), while Bruhl (1995) argued against this relationship after recovering *Morelotia* distant from *Ghania*. The monotypic *Schoenoides* (Seberg, 1988) is embedded in *Oreobolus* here and in other studies (Mandriñán et al., 2004), further supporting the inclusion of *Schoenoides* in *Oreobolus* (e.g. Curtis & Morris, 1994; Govaerts et al., 2007). There

◀ **Fig. 2** Maximum parsimony strict con*sensus* tree of Cyperaceae, showing the Cyperaceae tribes Schoeneae (*Sc*), Cariceae, Scirpeae (*S*), Dulicheae (*Du*), Eleocharideae (*El*), Fuireneae (*Fu*), Abildgaardieae (*Ab*), Arthrostylideae (*Ar*), and Cypereae (*Cy*). Goetghebeur's (1998) classification and the proposed classification are marked by *black grey* and *black* respectively. Bootstrap support values shown as weak (*= 50–74%), moderate (**=75–89%) and strong (***=90–100%)

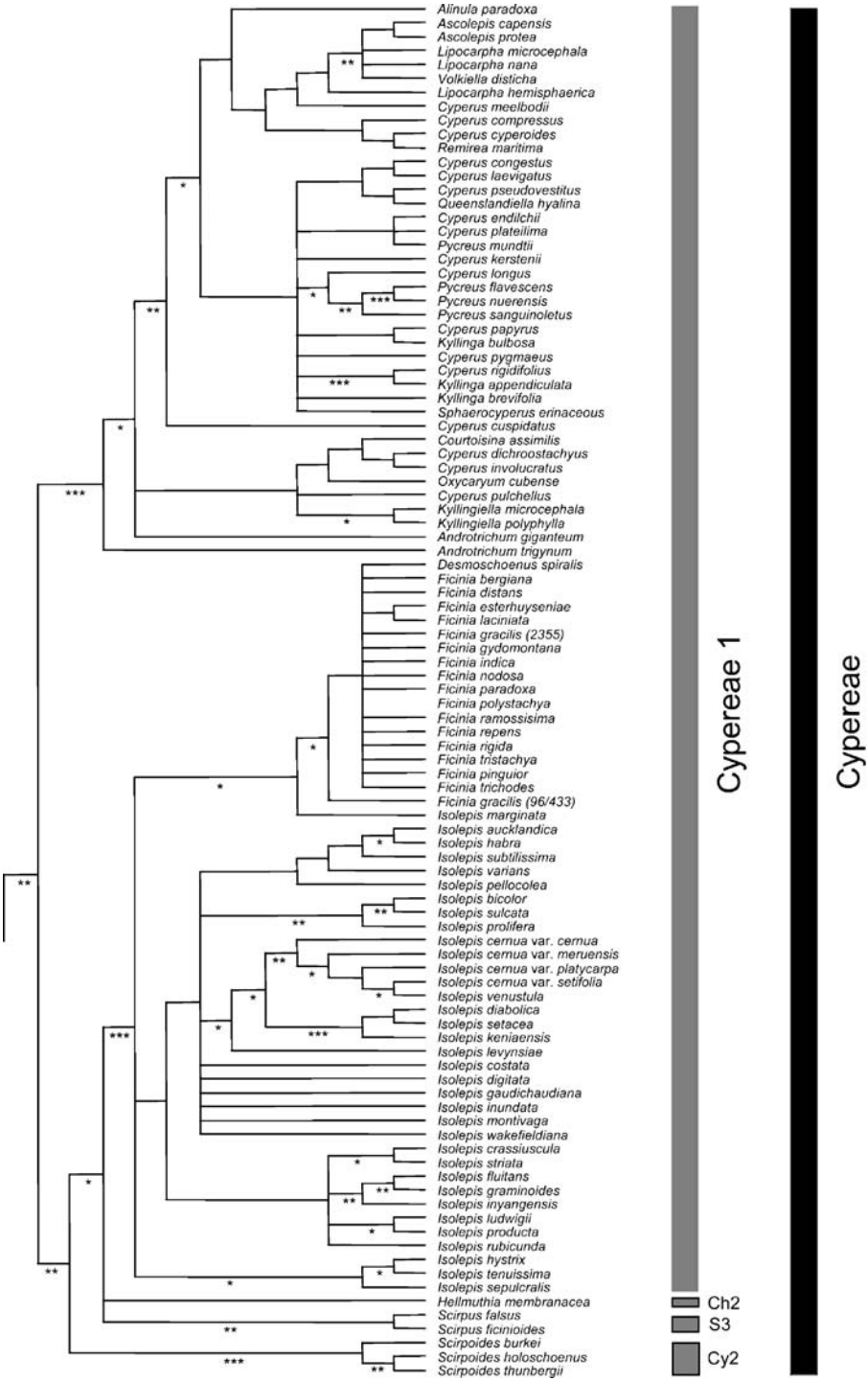

Alinula paradoxa
Ascolepis capensis
Ascolepis protea
Lipocarpha microcephala
Lipocarpha nana
Volkiella disticha
Lipocarpha hemisphaerica
Cyperus meelbodii
Cyperus compressus
Cyperus cyperoides
Remirea maritima
Cyperus congestus
Cyperus laevigatus
Cyperus pseudovestitus
Queenslandiella hyalina
Cyperus endlichii
Cyperus plateilima
Pycreus mundtii
Cyperus kerstenii
Cyperus longus
Pycreus flavescens
Pycreus nuerensis
Pycreus sanguinoletus
Cyperus papyrus
Kyllinga bulbosa
Cyperus pygmaeus
Cyperus rigidifolius
Kyllinga appendiculata
Kyllinga brevifolia
Sphaerocyperus erinaceous
Cyperus cuspidatus
Courtoisina assimilis
Cyperus dichroostachyus
Cyperus involucratus
Oxycaryum cubense
Cyperus pulchellus
Kyllingiella microcephala
Kyllingiella polyphylla
Androtrichum giganteum
Androtrichum trigynum
Desmoschoenus spiralis
Ficinia bergiana
Ficinia distans
Ficinia esterhuyseniae
Ficinia laciniata
Ficinia gracilis (2355)
Ficinia gydomontana
Ficinia indica
Ficinia nodosa
Ficinia paradoxa
Ficinia polystachya
Ficinia ramossisima
Ficinia repens
Ficinia rigida
Ficinia tristachya
Ficinia pinguior
Ficinia trichodes
Ficinia gracilis (96/433)
Isolepis marginata
Isolepis aucklandica
Isolepis habra
Isolepis subtilissima
Isolepis varians
Isolepis pellocolea
Isolepis bicolor
Isolepis sulcata
Isolepis prolifera
Isolepis cernua var. cernua
Isolepis cernua var. meruensis
Isolepis cernua var. platycarpa
Isolepis cernua var. setifolia
Isolepis venustula
Isolepis diabolica
Isolepis setacea
Isolepis keniaensis
Isolepis levynsiae
Isolepis costata
Isolepis digitata
Isolepis gaudichaudiana
Isolepis inundata
Isolepis montivaga
Isolepis wakefieldiana
Isolepis crassiuscula
Isolepis striata
Isolepis fluitans
Isolepis graminoides
Isolepis inyangensis
Isolepis ludwigii
Isolepis producta
Isolepis rubicunda
Isolepis hystrix
Isolepis tenuissima
Isolepis sepulcralis
Hellmuthia membranacea
Scirpus falsus
Scirpus ficinioides
Scirpoides burkei
Scirpoides holoschoenus
Scirpoides thunbergii
Cypereae 1
Cypereae
Ch2
S3
Cy2

**Fig. 3** Maximum parsimony strict con*sensu*s tree of Cyperaceae, showing the Cyperaceae tribes Cypereae (*Cy*), Scirpeae (*S*) and Chrysitricheae (*Ch*). Goetghebeur's (1998) classification and the proposed classification are marked by *grey* and *black bars* respectively. Bootstrap support values shown as weak (*=50–74%), moderate (**=75–89%) and strong (***=90–100%)

have been limited phylogenetic studies in Schoeneae (e.g. Zhang et al., 2004; Verboom, 2006), which lack bootstrap support for the basal nodes, and more data are needed to resolve relationships among the taxa. Further studies of Schoeneae are in progress (Bruhl et al. and Verboom et al., unpublished data).

The moderately supported clade (*Khaosokia* to *Dulichium*) includes members of Cariceae, Scirpeae and Dulicheae (Fig. 2). *Khaosokia* is resolved sister to the rest of the members of this clade, a position suggested by Simpson et al. (2005) from observations of gross morphology and DNA studies. Scirpeae are not monophyletic, as Dulicheae are embedded between Scirpeae I and Scirpeae II. In Scirpeae I, the generic boundaries between *Trichophorum* and *Oreobolopsis* are unclear, and further attention is needed to resolve the polyphyly of *Trichophorum*. Phylogenetic studies involving Andean species of *Scirpus* have recently led to description of a new segregate genus, *Zameioscirpus* (e.g. Dhooge et al., 2003). *Carex* is polyphyletic and includes other genera of Cariceae, a similar pattern has been observed in previous studies (e.g. Yen & Olmstead, 2000; Starr et al., 2004)

Fuireneae are split into four clades (Fig. 2) in our analysis. Fuireneae I (*Fuirena*) is sister to Eleocharideae, Fuireneae II (*Bolboschoenus*) is sister to Abildgaardieae, whereas Fuireneae III (*Schoenoplectus* and *Actinoschoenus*) and Fuireneae IV (*Schoenoplectiella* group) form a polytomy with Cypereae. Relationships among these groups based on DNA data remain unstable (cf. Simpson et al., 2007). *Schoenoplectus* is paraphyletic with several tropical African perennial taxa (e.g. *S. mucronatus*) being resolved together with *Schoenoplectiella*. *Schoenoplectiella*, recently segregated to include annual amphicarpous taxa of *Schoenoplectus* (Lye, 2003), is resolved into a strongly supported clade that includes perennial tropical *Schoenoplectus* species sharing a lateral spikelet morphology. Further studies are in progress (Muasya et al., unpublished data) evaluating relationships in the group.

Abildgaardieae are resolved to include *Arthrostylis aphylla*, *Trachystylis strandbrokensis* and *Actinoschoenus repens* (Fig. 2), taxa which have been previously placed in Schoeneae (Goetghebeur, 1998). *Arthrostylis* and *Actinoschoenus* have been shown to be closer to Abildgaardieae based on plastic and nuclear ribosomal (ITS) data (Ghamkhar et al., 2007). Both *Arthrostylis* and *Trachystylis* are monotypic Australian taxa with bisexual flowers that lack perianth segments, but share gross morphological similarity with Schoeneae (e.g. one- to few-flowered spikelet and wide glume wings enclosing the next flower). On the other hand, *Actinoschoenus repens* is a Zambian endemic, with morphological similarity to both Abildgaardieae and Schoeneae. Although these three taxa had been placed in Schoeneae even with decisive anatomical and embryological data lacking, the DNA data resolve them in Abildgaardieae, and similar results were obtained independently by Ghamkhar et al. (2007). We therefore propose their formal inclusion in this tribe.

Cypereae form a strongly supported clade (Fig. 3) that has received intensive DNA phylogenetic study, both at generic (e.g. Muasya et al., 2001, 2002) and tribal levels (Muasya et al., 2008). Cypereae are characterised by the presence of *Cyperus*-

type embryo and here include *Hellmuthia*, a genus previously considered to belong in Chrysitricheae (e.g. Haines & Lye, 1976; Goetghebeur, 1998; cf. Vrijdaghs et al., 2006, 2008). *Scirpus falsus* and *S. ficinioides*, taxa from the Drakensberg Mountians in South Africa and previously placed in Scirpeae, are resolved here among Cypereae in a clade including *Ficinia*, *Isolepis*, *Hellmuthia* and *Scirpoides*. More studies are in progress to describe a new genus including these taxa (authors, unpublished data).

## Revised Suprageneric Classification of Cyperaceae

Based on the available data, we support the revised classification of Cyperaceae into two subfamilies, Mapanioideae and Cyperoideae (Figs. 1, 2 and 3). We also broadly accept the tribal circumscriptions of Goetghebeur (1998) but with modification to tribes Cypereae (to include *Hellmuthia* and the perianth-bearing Drakensberg *Scirpus*, S. *falsus* and *S. ficinioides*); Abildgaardieae (to include *Arthrostylis*, *Trachystylis* and *Actinoschoenus*); Schoeneae (recognising Rhynchosporeae, *Rhynchospora* and *Pleurostachys*); and Cryptangieae (to include *Didymiandrum* and *Exochogyne*). We refrain from recognising Cladieae (*Cladium*) pending more studies.

## Future Research

Choice of marker and uneven sampling limit the scope for analysing different data sets in combination. The current study and a number of other ongoing studies have focused on more slowly evolving plastid regions, which have less resolution but can be aligned across the family. Among research groups in different institutes, there is need to study the same DNA regions (e.g. *rbcL*, *trnl-F*, *rps16*) for similar taxa to enable different data sets to be aligned in combination.

The intensity of sampling varies among tribes. Although Chrysitricheae, Cypereae, Hypolytreae, Scirpeae and Cariceae are among the better studied tribes, more effort is needed to elucidate phylogenetic relationships within Cryptangineae, Bisboeckelerieae, Fuireneae, Schoeneae, and Sclerieae.

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