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What is a Genus in Cyperae: Phylogeny, Character Homology Assessment and Generic Circumscription in Cyperae

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Abstract Using a DNA-based tree as the framework, the homology of key taxonomic characters in tribe Cyperae (900 species in 19 genera, the largest of which is *Cyperus*) is assessed and revisit the question of generic circumscription. Plastid DNA (*rbcL* gene, *rps16* intron, *trnL* intron and *trnL-F* intergenic spacer) sequence matrix for 50 species in 19 genera of Cyperae is analysed using the maximum parsimony algorithm of PAUP. Two major groups are observed: the *Ficinia* and *Cyperus* clades. The *Ficinia* clade includes taxa with a center of diversity in the Cape Floristic Region of South Africa. These are predominantly perennial herbs (with exception of *Isolepis*, which is predominantly annual) having non-Kranz (C_3) anatomy and spirally arranged glumes. Species of the *Cyperus* clade have a predominately distichous glume arrangement and Kranz anatomy which is either absent (C_3) or present (C_4). *Cyperus* is the core genus in the *Cyperus* clade, in which 13 additional segregate genera are embedded. These segregate genera differ from typical *Cyperus* in one or more of a few gross morphological characters. There are no unambiguous characters separating C_3 and C_4 *Cyperus* species. The circumscription of Cyperae is broadened to include all taxa with a *Cyperus*-type embryo and perianth segments. Three taxa possessing perianth segments, namely *Hellmuthia membranacea*, *Scirpus falsus* and *S. ficinioides*, are supported to be closer to *Cyperus* than to *Scirpus*.

Keywords *Cyperus* Clade · *Ficinia* Clade · Life Forms · Hypogynous Scales · Gynophore · Kranz Anatomy · Inflorescence Morphology · Elongation of Filaments · Dispersal Unit · Nutlet Orientation

Introduction

Taxa included in tribe Cyperaceae are annual or perennial herbs that vary in stature from minute to 5 m tall. Leaves generally have well-developed blades, but are reduced to lobes in some species; there also may be a ligule. Inflorescences are capitate or anthelate. They all have hermaphrodite, trimerous flowers, with each subtended by a papery glume. Glumes are spirally or distichously arranged in the spikelets, apart from some reduced species in which the arrangement is obscure.

Generic classification in tribe Cyperaceae and subfamily Cyperoideae dates back to Linnaeus (1753), who described the genera *Scirpus* and *Cyperus* to include all species of Cyperaceae with bisexual flowers, and distinguished by the spiral versus distichous glume arrangement in *Scirpus* and *Cyperus* respectively. The broad circumscription of *Scirpus*, based on common and widespread characters, resulted in a heterogeneous assemblage which was treated by subsequent workers as one genus (e.g. Boeckeler, 1870; Clarke, 1894, 1898, 1902; Hitchcock et al., 1969) or split into a number of smaller genera (e.g. Brown, 1810; Raynal 1973; Wilson, 1981; Goetghebeur, 1998).

Classification of genera into tribes in Cyperoideae has differed widely among authors, depending on which character(s) were emphasized. Therefore, there is a need to revise generic and tribal circumscriptions and especially incorporate new evidence from morphology and DNA sequence data.

Taxonomic History of Tribe Cyperaceae

Tribal concepts in Cyperoideae have varied over the years. A large number of legitimate tribal names have been published in Cyperoideae, including Cyperaceae, Scirpeae, Fuireneae, Ficiniae, Schoenoplecteae, Abildgaardieae, Lipocarpeae, and Eleocharideae (Goetghebeur, 1985). Cyperaceae and Scirpeae have been the most frequently used tribal names (e.g. Haines & Lye, 1983; Bruhl, 1995; Goetghebeur, 1998). The main difference has traditionally been that Scirpeae have spirally arranged glumes whereas in Cyperaceae glumes are two-ranked (e.g. Lye, 1971). However, this tribal classification has resulted in genera such as *Oxycaryum* and *Isolepis* being classified in Scirpeae even though these genera show closer affinity to *Cyperus*, as pointed out by Raynal (1973).

Embryological data (e.g. Van der Veken, 1965; Haines & Lye, 1971, 1976, 1983; Raynal, 1973, 1977; Wilson, 1981; Goetghebeur, 1996, 1998; Bruhl, 1995) have contributed significantly to generic and tribal circumscription in Cyperoideae. Heterogeneous *Scirpus sensu lato* has embryo types characteristic of *Cyperus*, *Carex*, *Bulbostylis*, *Fimbristylis*, *Schoenus* and *Schoenoplectus*, whereas *Cyperus* has mainly the *Cyperus*-type embryo. Based on the interpretation that several genera could have the same type of embryo but a single genus should have only a single type of embryo, *Scirpus sensu lato* was split into several genera. Currently (Goetghebeur, 1998), tribes in Cyperoideae are classified to include genera sharing a single embryo type. For example, Cyperaceae have the *Cyperus*-type embryo and the similar *Ficinia*-type, whereas Scirpeae *sensu stricto* have only the *Fimbristylis*-type embryo.

Two recent classifications of Cyperoideae, based predominantly on morphological data, have differed in placement of genera in Cypereae. Goetghebeur (1998) classified all taxa characterised by *Cyperus*-type embryo in Cypereae, whereas Bruhl (1995) placed genera having spiral glume arrangement (i.e. *Isolepis*, *Ficinia*, *Desmoschoenus*, *Scirpoides*, *Kyllingiella*, *Oxycaryum*) in Scirpeae. *Hellmuthia*, bearing spirally arranged glumes but having an additional pair of scales in flowers subtended by the most proximal glumes, was placed in Scirpeae by Bruhl (1995) but in Chrysitricheae by Goetghebeur (1998). Bruhl (1995) did not recognise the tribes Eleocharideae and Fuireneae (sensu Goetghebeur, 1998), but included these taxa in Scirpeae.

Phylogeny, Character Homology Assessment and Generic Circumscription

Phylogenetic Relationship Based on Molecular Data

Over the last ten years, molecular systematic data have been used in the classification of ranks above family (e.g. APG, 2003) and in supra-generic classification within Cyperaceae (Muasya et al., 1998, 2000a; Simpson et al., 2007). Studies on Cyperoideae have targeted phylogenetic relationships in Scirpeae (Muasya et al., 2000b, Dhooge et al., 2003) and Abildgaardieae (Ghamkhar et al., 2007), and focussed on genera *Eleocharis* (Roalson & Friar, 2000; Yano et al., 2004), *Isolepis* (Muasya et al., 2001a), *Cyperus* sensu lato (Muasya et al., 2002) and *Schoenoplectus* (Yano & Hoshino, 2005).

Total DNA was extracted from 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., 2001a, 2002), and the resulting sequences aligned manually. We present and discuss here results of a maximum parsimony analysis of representatives of 18 of the 19 genera in Cypereae recognised by us; no material of the monotypic genus *Ascopholis* was available. The DNA data matrix (*rbcL* gene, *rps16* intron, *trnL* intron and *trnL-F* intergenic spacer) comprises 3,721 characters among which 625 are potentially parsimony-informative. The matrix was analysed using the heuristic algorithm in PAUP* (Swofford, 2002), random addition for 10,000 replicates with tree-bisection-reconnection (TBR). Bootstrap analysis was performed for 1,000 replicates under maximum parsimony criterion (random taxon addition, twin replicates, TBR).

The strict consensus tree generated from the maximum parsimony analysis is presented in Fig. 1, with the bootstrap values for the various branches mapped. Cypereae are resolved into the *Cyperus* and *Ficinia* clades. The *Ficinia* clade comprises *Scirpoides*, *Hellmuthia*, *Isolepis*, *Ficinia*, *Desmoschoenus* and two *Scirpus* species (*S. falsus* and *S. ficinioides*). The *Cyperus* clade has *Cyperus sensu stricto* as the core genus, in which the thirteen derived genera (*Alinula*, *Androtrichum*, *Ascolepis*, *Courtoisina*, *Kyllinga*, *Kyllingiella*, *Lipocarpha*, *Oxycaryum*, *Pycreus*, *Queenslandiella*, *Remireia*, *Sphaerocyperus*, and *Volkiella*) are embedded.

Assessment of Morphological Character Homology

Using the DNA phylogenetic framework (Fig. 1), we evaluate the homology of key morphological characters used in classification of the Cypereae. The morphological

Table 1 List of Taxa Sampled with Vouchers and Genbank Accession Numbers

Taxon	Voucher	GenBank accession numbers		
		<i>rbcL</i>	<i>rps16</i>	<i>trnL-F</i> OR <i>intron/spacer</i>
Cyperoideae Suess.				
Abildgaardieae Lye				
<i>Abildgaardia ovata</i> (Burm. f.) Kral	Kenya: Muasya et al. 684 (EA, K)	Y12985		AJ295754
<i>Fimbristylis dichotoma</i> (L.) Vahl	Kenya: Muasya 1006 (EA, K)	Y13008		AJ295755
Cypereae Dumort.				
<i>Alinula lipocarphoides</i> (Kük.) J. Raynal	Kenya: Muasya: 2592 (EA)	–	–	EF178608
<i>Alinula paradoxa</i> Goetgh. & Vorster	Tanzania: Faden et al. 96/29 (K)	AJ278290	–	AJ295756
<i>Androtrichum giganteum</i> (Kunth) H. Pfeiff.	Argentina: Tressens et al. 4292 (K)	EF178546		–
<i>Androtrichum trigynum</i> (Spreng.) H. Pfeiff.	Argentina: Goetghebeur 4764 (GENT)	EF178547		–
<i>Ascolepis capensis</i> (Kunth) Ridl.	Kenya: Muasya 1009 (EA, K)	Y13003	AF449518	AJ295757
<i>Ascolepis protea</i> Welw.	Congo: Fay 2700 (K)	Y13002	–	–
<i>Courtoisina assimilis</i> (Steud.) Maquet	Tanzania: Faden et al. 96/119 (K)	AY40590	AY449519	AY040595
<i>Cyperus compressus</i> L.	Thailand: Muasya 1375 (K)	AF449506	AF449521	AF449555/–
<i>Cyperus cuspidatus</i> Kunth	Thailand: Muasya 1374 (K)	AF449508	AF449523	AF449557/ AF449569
<i>Cyperus involucratus</i> Rottb.	Madagascar: Kew Acc. 6136603	Y12967	AF445920	AJ295758
<i>Cyperus laevigatus</i> L.	Kenya: Muasya 1041 (EA)	Y13017	AF449527	AY040596
<i>Cyperus longus</i> L.	Europe: Chase 2276 (K)	Y13015	AF449528	AY040598
<i>Cyperus papyrus</i> L.	Chad: Hepper 4213 (K)	Y12966	AF449531	AJ295759
<i>Cyperus pulchellus</i> R. Br.	Thailand: Muasya 1377 (K)	AY40591	–	AY040599
<i>Cyperus pygmaeus</i> Rottb.	Kenya: Muasya 1133 (K)	AJ404698	AF449534	AJ295760
<i>Desmoschoenus spiralis</i> Hook. f.	New Zealand: Ford 44/94 (NU)	AJ404701	–	AJ295753
<i>Ficinia bergiana</i> Kunth	S. Africa: Muasya 2337 (BOL)	EF200588	EF078974	EF178593
<i>Ficinia distans</i> C. B. Clarke	S. Africa: Muasya 2283 (BOL)	EF178548		EF178594
<i>Ficinia esterhuyseniae</i> Muasya	S. Africa: Muasya 2312 (BOL)	EF178549	EF078975	EF178590
<i>Ficinia gracilis</i> Schrad.	Tanzania: Faden et al. 96/433 (K)	EF178550		EF178534
<i>Ficinia nodosa</i> (Rottb.) Goetgh., Muasya & D. A. Simpson	Australia: Stind 21216 (K)	Y12984	EF174386	AJ295793
<i>Ficinia rigida</i> Levyns	S. Africa: Muasya 2319 (K)	EF178557	EF174387	EF178602
<i>Ficinia trichodes</i> (Schrad.) Benth. & Hook. f.	S. Africa: Muasya 2328 (K)	EF178558	EF174388	EF178603
<i>Ficinia radiata</i> (L. f.) Kunth	S. Africa: Muasya 2310 (K)	EF200589	EF078976	–
<i>Hellmuthia membranacea</i> (Thunb.) R. W. Haines & Lye	S. Africa: Weerderman et al. 269 (K); Muasya 1145 (K)	Y13000	EF174389	AJ295815
<i>Isolepis cernua</i> (Vahl) Roem. & Schult. var. <i>cernua</i>	BRITAIN: Muasya 1058 (K)	Y13014	AF449538	AJ295775
<i>Isolepis fluitans</i> (L.) R. Br.	Kenya: Muasya 1057 (K)	Y12961	EF174390	AJ295780

Table 1 (continued)

Taxon	Voucher	GenBank accession numbers		
		<i>rbcL</i>	<i>rps16</i>	<i>trnL-F</i> OR <i>intron/spacer</i>
<i>Isolepis hystrix</i> (Thunb.) Nees	S. Africa: Muasya 1150 (K)	AJ404711	-	AJ295785
<i>Isolepis levynsiana</i> Muasya & D. A. Simpson	S. Africa: Muasya 1151 (K)	AF449514	AF449514	AF449563/ AF449575
<i>Isolepis marginata</i> (Thunb.) A. Dietr.	Australia: Coveny et al. 17452 (K)	AJ404714	EF174391	AJ295790
<i>Isolepis setacea</i> (L.) R. Br.	Kenya: Muasya 1059 (K)	Y12962	EF174392	AJ295799
<i>Isolepis tenuissima</i> (Nees) Kunth	S. Africa: Muasya 2369 (K)	AY725947	-	-
<i>Isolepis venustula</i> Kunth	S. Africa: Muasya 1189 (K)	AJ404724	-	AJ295804
<i>Kyllinga appendiculata</i> K. Schum.	Kenya: Muasya 1050 (EA, K)	Y13007	AF449542	AJ295761
<i>Kyllinga brevifolia</i> Rottb.	Australia: Coveny et al. 17459 (K)	AF449515	AF449543	AF449564/ AF449576
<i>Kyllinga bulbosa</i> P. Beauv.	Kenya: Muasya 1020 (EA, K)	Y12979	AF449544	AY040601
<i>Kyllingiella microcephala</i> (Steud.) R. W. Haines & Lye	Zimbabwe: Muasya et al. 1118 (K)	AY040592	AF449540	AJ295807
<i>Kyllingiella polyphylla</i> (A. Rich.) Lye	Tanzania: Wingfield 497 (K)	Y13013	AF449541	AJ295515
<i>Lipocarpha hemisphaerica</i> (Roth.) Goetgh.	Thailand: Muasya 1217 (K)	AF449516	AF449546	AF449565/ AF449577
<i>Lipocarpha nana</i> (A. Rich.) J.Raynal	Kenya: Muasya 972 (EA, K)	Y12990	AF449545	AJ295762
<i>Oxycaryum cubense</i> (Poepp. & Kunth) E.Palla	ZAMBIA: Richards 13318 (K)	Y13006	-	AY040602
<i>Pycreus flavescens</i> (L.) Rchb.	Kenya: Muasya 1022 (EA, K)	Y13005	AF449547	AJ295763
<i>Pycreus nuerensis</i> (Boeck.) S.S.Hooper	Tanzania: Muasya 940 (EA, K)	Y13004	AF449549	AY040603
<i>Queenslandiella hyalina</i> (Vahl) Ballard	Kenya: Mwachala 296 (EA)	AY725953	-	-
<i>Remirea maritima</i> Aubl.	Tanzania: Faden et al. 96/48 (K)	AY040593	AF449550	AY040604
<i>Scirpoides holoschoenus</i> (L.) Soják	S. Africa: Acocks s.n. (K)	Y12994	AY344153	AJ295811
<i>Scirpoides thunbergii</i> (Schrad.) Soják	S. Africa: Muasya 1205 (K)	AJ404727	AF449551	AJ295812
<i>Scirpus falsus</i> C. B. Clarke	S. Africa: Hilliard 13609 (GENT)	EF178559	EF174393	-
<i>Scirpus ficinioides</i> Kunth	S. Africa: Hilliard 16095 (GENT)	EF178560	EF174394	-
<i>Sphaerocyperus erinaceus</i> (Ridl.) Lye	Tanzania: Faden et al. 96/338 (K)	AJ404699	AF449552	AJ295764
<i>Volkiella disticha</i> Merxm. & Czech	Namibia: Muller et al. 4245 (K)	EF178561	-	-
Eleocharideae Goetgh. <i>Eleocharis marginulata</i> Steud.	Kenya: Muasya 1039 (EA, K)	Y13011	-	AJ295768
Fuireneae Reichenb. ex Fenzl <i>Actinoscirpus grossus</i> (L. f.) Goetgh. & D. A. Simpson	Malaysia: Simpson 2660 (K)	Y12953	-	AJ295765

Table 1 (continued)

Taxon	Voucher	GenBank accession numbers		
		<i>rbcL</i>	<i>rps16</i>	<i>trnL-F</i> OR <i>intron/spacer</i>
<i>Bolboschoenus maritimus</i> (L.) Palla	Botswana: Smith 2452 (K)	Y12996	–	AJ295767
<i>Bolboschoenus nobilis</i> (Ridl.) Goetgh. & D. A. Simpson	S. Africa: Leistner 144 (K)	Y12995	–	–
<i>Fuirena</i> sp.	Brazil: Thomas et al. 10404 (NY)	Y12970	–	–
<i>Isolepis humillima</i> (Benth.) K. L. Wilson	Australia: Thomas et al. 622 (BRI)	AJ404728	AF449539	AJ295784
<i>Schoenoplectiella articulata</i> (L.) Lye	Tanzania: Muasya 947 (EA, K)	Y12987	–	–
<i>Schoenoplectus corymbosus</i> (Roth ex Roem. & Schult.) J. Raynal	Kenya: Muasya 1004 (EA)	EF178570	–	EF178607
<i>Schoenoplectus lacustris</i> (L.) Palla	Britain: Muasya 1043 (K)	Y12943	AF449554	AJ295809
<i>Schoenoplectus litoralis</i> (Schrad.) Palla	Hong Kong: Shaw 883 (K)	EF178571	–	–
Scirpeae Kunth ex Dumort.				
<i>Eriophorum vaginatum</i> L.	Poland: Beyer et al. 2 (K)	Y12951	AF449553	AJ295769
<i>Eriophorum viridicarinatum</i> (Engl.) Fern.	USA: Boufford 23053 (WS)	U49230	–	–
<i>Scirpus ancistrochaetus</i> Schuyler	USA: Nacsi 7544 (DOV)	EF178578	EF174395	–
<i>Scirpus sylvaticus</i> L.	HBUG/86–0541 (GENT)	EF178586	EF174396	–
Mapanioideae C. B. Clarke				
Hypolytreae Presl ex Fenzl				
<i>Hypolytrum nemorum</i> (Vahl) Spreng.	Malaysia: Simpson 1379 (K)	Y12958	AY344142	AJ295816
<i>Mapania cuspidata</i> (Miq.) Uittien	Brunei: Marsh 4 (K)	Y12955	DQ058318	AJ295817

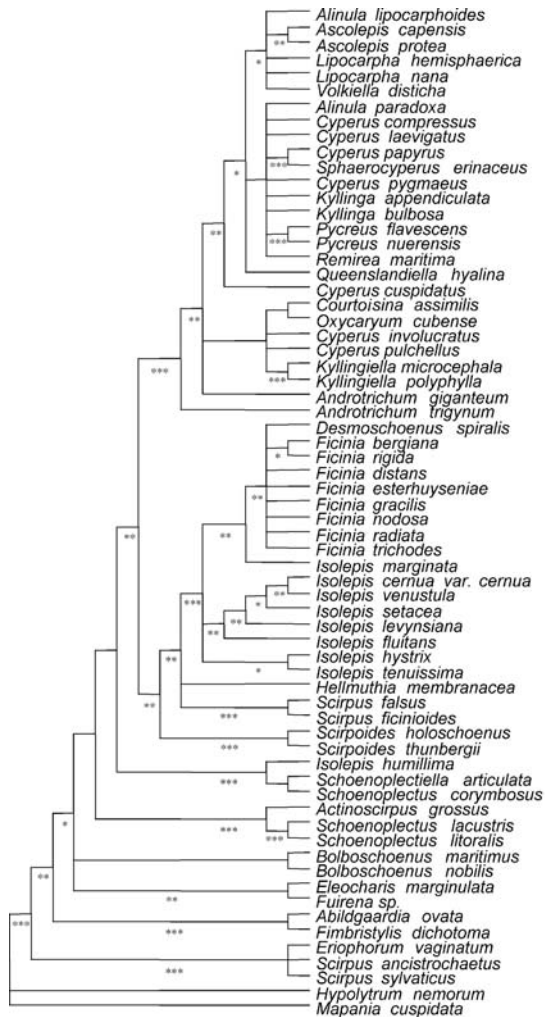
Classification following interpretation of current data and Goetghebeur (1998)

characters are manually plotted on the DNA topology, majority of characters can be unambiguously reconstructed on the phylogeny. *Ascopholis*, a monotypic genus restricted to India (Goetghebeur, 1998), has not been included in this study due to unavailability of material. Generic status of *Ascopholis* is not accepted by all, and it has been suggested to be conspecific to the widespread *Cyperus mollipes* (C. B. Clarke) K. Schum (Govaerts et al., 2007).

Mature Embryo Morphology

Cyperaceae are characterised by the presence of a *Cyperus*-type embryo (Van der Veken, 1965; Haines & Lye, 1971, 1976; Raynal 1973; Wilson, 1981; Goetghebeur, 1985). In the *Ficinia* clade, species of *Ficinia* have a *Ficinia*-type embryo which is similar to *Cyperus*-type, but *Isolepis*, *Hellmuthia* and *Scirpoides* have a typical *Cyperus*-type embryo (Van der Veken, 1965; Haines & Lye, 1971). The embryo type

Fig. 1 Maximum parsimony strict consensus tree of Cyperaceae based on heuristic analysis of plastid DNA sequence data. *Cyperus* and *Ficinia* clades are marked by black and grey bars respectively. Bootstrap support values shown as * for 50–74%, ** for 75–89% and *** for 90–100%



in *Scirpus falsus* and *S. ficinioides* has not been studied, mainly because mature outlets were not available.

Concepts of mature embryo morphological states are subject to individual interpretation of homology, and it may be difficult to distinguish similar embryo types in some cases. For example, *Isolepis humillima*, placed in *Isolepis* due to the presence of spiral glume arrangement, has been interpreted as having an embryo similar to *Scirpoides* (Wilson, 1981). The phylogenetic position of this taxon in molecular analyses is within *Schoenoplectus* subgen. *Actaeogeton*, a group possessing a *Schoenoplectus*-type embryo. The mature embryo in Cyperaceae is less complex when compared to state is the sister tribe Fuireneae (*Schoenoplectus* type), hence our study does not support Juguet's contention (as reported in Raynal, 1973) that the embryogeny of Cyperaceae is very evolved compared to the rest of the family.

Table 2 Summary of Some of the Diagnostic Characters of the Genera in Cyperaceae

Genus (total/ studied species)	Habit	Floret no.	Glume arrangement	Dispersal unit	Nutlet orientation	Photosynthetic type
<i>Alinula</i> (4/2)	Annual	One	Distichous	Nutlet	Dorsiventral	C ₄
<i>Androtrichum</i> (2/2)	Perennial	Many	Distichous	Nutlet & filaments	Dorsiventral	C ₃
<i>Ascolepis</i> (20/2)	Annual/ perennial	One	Distichous	Spikelet/ nutlet	Dorsiventral	C ₄
<i>Ascopholis</i> (1/0)	Perennial	One	Distichous	Spikelet	Dorsiventral	C ₄
<i>Courtoisina</i> (2/1)	Annual	Many	Distichous	Spikelet	Dorsiventral	C ₃
<i>Cyperus</i> (550/7)	Annual/ perennial	1-Many	Distichous/ spiral	Spikelet/ nutlet	Dorsiventral	C ₃ & C ₄
<i>Desmoschoenus</i> (1/1)	Perennial	Many	Spiral	Nutlet	Dorsiventral	C ₃
<i>Ficinia</i> (60/8)	Perennial	Many	Distichous/ spiral	Nutlet	Dorsiventral	C ₃
<i>Hellmuthia</i> (1/1)	Perennial	Many	Spiral	Nutlet	Dorsiventral	C ₃
<i>Isolepis</i> (70/9)	Annual (perennial)	Many	Distichous/ spiral	Nutlet	Dorsiventral	C ₃
<i>Kyllinga</i> (60/2)	Perennial (annual)	Many	Distichous	Spikelet	Lateral	C ₄
<i>Kyllingiella</i> (4/2)	Perennial	Many	Spiral	Nutlet	Dorsiventral	C ₃
<i>Lipocarpha</i> (35/2)	Annual/ perennial	One	Distichous	Spikelet	Dorsiventral	C ₄
<i>Oxycaryum</i> (1/1)	Annual (perennial)	Many	Spiral	Nutlet	Dorsiventral	C ₃
<i>Pycreus</i> (100/2)	Annual/ perennial	Many	Distichous	Nutlet	Lateral	C ₄
<i>Queenslandiella</i> (1/1)	Annual	Many	Distichous	Spikelet	Lateral	C ₄
<i>Remirea</i> (1/1)	Perennial	One	Distichous	Spikelet	Dorsiventral	C ₄
<i>Scirpoides</i> (5/2)	Perennial	Many	Spiral	Nutlet	Dorsiventral	C ₃
<i>Scirpus</i> spp. (3/2; Southern Africa)	Perennial	Many	Spiral	Nutlet	Dorsiventral	?
<i>Sphaerocyperus</i> (1/1)	Perennial	One	Distichous	Spikelet	Dorsiventral	C ₄
<i>Volkia</i> (1/1)	Annual	One	Distichous	Spikelet	Dorsiventral	C ₄

Classification following interpretation of current data and Goetghebeur (1998).

Annual Versus Perennial Life Form

Annual and perennial growth forms are observed among members of tribe Cyperaceae (Haines & Lye, 1983; Goetghebeur, 1998; Table 2). In the *Ficinia* clade, an annual life form has evolved only in *Isolepis* (which also has some perennial species) whereas all other taxa are perennial. In the *Cyperus* clade, an annual life form is exclusively found in *Courtoisina*, *Queenslandiella* and *Alinula*; a predominantly perennial life form is observed in *Oxycaryum*, *Kyllingiella*, *Remirea*, *Sphaerocyperus*, *Kyllinga* and *Ascolepis*); while both annual and perennial life forms are recorded in *Cyperus sensu stricto*, *Pycreus* and *Lipocarpha*.

Glume Arrangement

Spiral glume arrangement is a plesiomorphic state in Cyperoideae (Muasya et al., 2001b). In Cyperaceae (Table 2), the *Ficinia* clade has predominantly a spiral glume

arrangement, except in few species of *Ficinia* (e.g. *F. distans* and *F. angustifolia*) and *Isolepis* (*I. levynsiana* and *I. venustula*). In the *Cyperus* clade, distichous glume arrangement is usual especially in *Androtrichum*, *Cyperus sensu stricto*, *Courtoisina*, *Pycneus*, *Kyllinga*, *Queenslandiella*, *Sphaerocyperus*, *Remirea*, and *Volkiella*. *Oxycaryum*, *Kyllingiella* and *Alinula* have a spiral glume arrangement, while the spikelet is too reduced in *Ascolepis* and *Lipocarpha* for interpretation of glume arrangement (Goetghebeur, 1998). Distichous glume arrangement has evolved more than once in Cyperaceae, occurring in both the *Ficinia* and *Cyperus* clades, and is therefore not unique in *Cyperus sensu stricto*. The unreliability of distichous arrangement as a diagnostic character has been previously shown (e.g. Raynal, 1973), and evident from our study where taxa with the *Cyperus*-like distichous glume arrangement (e.g. *Isolepis levynsiana*) are resolved in the *Ficinia* clade.

Hypogynous Scales

Hypogynous scales, a character considered plesiomorphic in Cyperoidae, are found in Scirpeae, Fuireneae, Eleocharideae, Dulichieae, and Schoeneae but are absent from Abildgaardieae and Cyperaceae (Goetghebeur, 1998). *Scirpus falsus* and *S. ficinioides*, resolved in Cyperaceae in molecular phylogenetic analyses (Fig. 1), have bristle-like perianth segments. Similar perianth segments, some well developed and others rudimentary, have been observed in *Ficinia* material (Muasya et al., unpublished results).

Some florets in *Hellmuthia* have two scales, which have been suggested to be homologous to scales in Mapanioideae (Haines & Lye, 1976; Goetghebeur, 1998). Recent floral ontogenetic studies (Vrijdaghs et al., 2006) have revealed an adaxially situated third scale in some proximal flowers in spikelets of *Hellmuthia*, and these are interpreted to be perianth segments and not glumes of reduced florets as in Mapanioideae. *Hellmuthia* is resolved in the DNA phylogeny among the *Ficinia* clade and closely related to *Scirpus falsus* and *S. ficinioides*.

Gynophores

The gynophore in Cyperaceae, formed by the development of the hypogynous stalk, is characterised by a lobed cup that envelops the basal part of the nutlet (Vrijdaghs et al., 2005). This structure is absent from the rest of Cyperoidae except for *Ficinia*, in which variation is observed in size and shape of the gynophore. However, some *Ficinia* species lack a gynophore, while on the other hand some *Isolepis* species (e.g. *I. marginata*) have a rudimentary gynophore (Clarke, 1898; Levyns, 1950; Muasya et al., 2000c, 2001a). A gynophore is present in *Alinula lipocarphoides*, a taxon previously described in *Ficinia* and later transferred to *Alinula* (Kükenthal, 1936; Raynal, 1977), here resolved in the *Cyperus* clade as sister to *Lipocarpha*.

Kranz Anatomy

As in most angiosperms families, the plesiomorphic photosynthetic system in most of Cyperaceae is C₃ type. Multiple origins of Kranz anatomy are recorded in several lineages including *Rhynchospora*, *Eleocharis*, *Fimbristylis* and *Cyperus* (Raynal,

1973; Estelita, 1993; Goetghebeur, 1998; Soros & Bruhl, 2000; Muasya et al., 2002; Bruhl & Wilson, 2007). Among Cyperaceae, Kranz anatomy has evolved once among *Cyperus* clade and is recorded in Fig. 1 between *Cyperus cuspidatus* to *Alinula lipocarpoides*. Bruhl & Wilson (2007) erroneously reported *Volkiella* to be C₃, while in the supporting references they show isotopic carbon reading (−13.6) which is typical for C₄.

Samples of *Alinula paradoxa* and *Lipocarpha rehmannii*, reported to be C₃ (Stock et al., 2004), might have been based on wrongly identified material, especially since there are four other records as C₄ for *L. rehmannii* (Bruhl and Wilson, 2007), and recent carbon isotope studies have confirmed other samples of these taxa to be C₄ (Muasya, unpublished results).

Inflorescence Morphology

Inflorescence morphology varies greatly in Cyperaceae. The basic inflorescence has spikelets in a panicle (Raynal, 1971), which is often modified into an anthela or contracted into a capitate head, spike or reduced to a single spikelet (Goetghebeur, 1998). In *Cyperus*, C₃ taxa tend to have the spikelets arranged in digitate clusters, which is one of the few morphological characters to distinguish the C₃ and C₄ taxa (which are usually spicately arranged), apart from those species that have the inflorescence reduced to a head (Goetghebeur, 1998). Kükenthal (1935–1936) used this (only partly correctly) to subdivide his subgenus ‘Eu-cyperus’, while Raynal (1973) also noted this (as not being a simple dividing character) particularly in discussing the origins of the ‘Mariscus’ group of species.

Spikelets in a majority of Cyperaceae have many flowers. Several genera (e.g. *Lipocarpha*, *Ascolepis*, *Alinula*) have pseudo-spikelets, in which spikelets are reduced to single flowers (glumes lost) arranged in cones, each single-flower spikelet subtended by a glume-like bract. The resulting cone resembles a spikelet (Haines & Lye, 1983; Goetghebeur & Vorster, 1988) hence the use of the term ‘pseudo-spikelet’.

Elongation of Filaments

Stamen filaments in most members of Cyperoideae are nearly as long as the glumes and inconspicuous after anthesis. *Androtrichum trigynum* and *A. giganteum* have filaments strongly elongating after anthesis, giving the inflorescence a cotton-like look. Such elongation of filaments is not observed in any other species in Cyperoideae.

Dispersal unit

Nutlets (also called achenes by some authors, e.g. Goetghebeur, 1998) in members of Cyperaceae are dispersed singly or together with elongated filaments, one to a few glumes, or parts of the spikelet axis, or even as complete spikelets (Kükenthal, 1935–1936; Raynal, 1973; Haines & Lye, 1983; Goetghebeur, 1998; Table 2). *Courtoisina*, *Queenslandiella*, *Kyllinga*, *Remirea*, *Sphaerocyperus*, *Lipocarpha*, and *Ascolepis* have spikelets dispersing as intact units, whereas all taxa in the *Ficinia*

clade, *Kyllingiella*, *Pycreus*, *Oxycaryum*, and *Remirea* have nutlets dispersed singly. *Cyperus* has nutlets dispersed either singly or as whole spikelets or variants thereof (notably in *Cyperus odoratus*).

Nutlet Orientation

Two kinds of nutlet orientation are observed in Cyperaceae (Table 2). Dorsiventral nutlet orientation is the most common and plesiomorphic state (Kükenthal, 1935–1936; Goetghebeur, 1998; Muasya et al., 2001b). Within Cyperaceae and Cyperaceae, species with distigmatic styles and dorsiventrally compressed nutlets are observed. Only the genera *Kyllinga*, *Pycreus*, and *Queenslandiella* have lateral nutlet orientation with distigmatic styles and laterally compressed nutlets.

Generic Circumscription

Cyperaceae are defined here as including all taxa sharing the *Cyperus*-type of embryo. We expand the tribal circumscription to include characters states such as the occasional presence of floral scales and bristle-like perianth segments, observed in the *Ficinia* clade.

The Ficinia Clade

Taxa in this clade have a predominantly spiral glume arrangement, but note the presence of distichous glume arrangement in *Ficinia* and *Isolepis*. All the genera share ficinioid morphology, e.g. tufted perennials, spiral glume arrangement, and have a center of diversity in the Cape floristic region of South Africa (Goetghebeur, 1998; Archer, 1998; Muasya & Simpson, 2002; Muasya, 2005). The individual genera are diagnosed by a combination of several characters (Table 2), the most notable being the presence of a gynophore and ligule in *Ficinia* (including *Desmoschoenus*), presence of two or three scales in the lower florets in *Hellmuthia*, and perennial growth form and spiral glume arrangement in *Scirpoides*, whereas *Isolepis* includes predominantly annual species with a spiral glume arrangement. Two annual species (*Isolepis leucoloma* and *I. levysiana*) with distichous glumes previously described in *Cyperus* have been transferred to *Isolepis*, based on morphological and molecular data (Archer, 1998; Muasya et al., 2006, 2007).

There is overlap in generic limits between *Isolepis* and *Ficinia* as presently recognised, whereas *Desmoschoenus* is embedded in *Ficinia* (Fig. 1). An annual species with rudimentary gynophore described as *Isolepis* (*I. marginata*) is resolved in DNA analysis as more closely related to *Ficinia*. *Desmoschoenus* and *Sickmannia* (*Ficinia radiata*), taxa with a gynophore but with additional unique features, have been recognised as distinct from *Ficinia*. Phylogenetic results presented here (Fig. 1) show that these taxa are embedded in *Ficinia*, and should be recognized as members of *Ficinia*. *Sickmannia* has already been recognised as *Ficinia* (*F. radiata*) in recent treatments (Goetghebeur, 1998; Archer, 2000), whereas *Desmoschoenus spiralis*, a New Zealand endemic growing in the same coastal habitat as *Ficinia nodosa*, has no name in *Ficinia*. More studies are in progress to resolve relationships in the *Ficinia* clade.

Two of the *Scirpus* species, *S. falsus* and *S. ficinioides* from southern Africa, have the gross morphology of the *Ficinia* clade, including perennial habit, scapose culms, pseudolateral inflorescences, and spiral glumes. Presence of perianth segments has been used to include these taxa in *Scirpus* (e.g. Kunth, 1837; Clarke, 1898; Gordon-Gray, 1995) even though typical *Scirpus* has paniculate inflorescences and noded culms. So far no embryo studies have been done on these taxa, and attempts to locate appropriate material have not been successful as the taxa rarely produce mature nutlets. Phylogenetic studies resolve these taxa as sister to *Hellmuthia* (Fig. 1), a pattern that suggests evolution from a southern African ancestor, unlike *Scirpus*, which is Holarctic. A new genus should be erected to include these two taxa, and more studies are in progress to formalise the recognition of this genus.

The Cyperus Clade

Genera in the *Cyperus* clade are circumscribed by a combination of morphological characters including spikelet morphology, unit of dispersal, and nutlet orientation (Table 2). Although these genera can be grouped into C₃ and C₄ anatomical types, there are few observable gross morphological characters to separate the species of *Cyperus sensu stricto* with the two kinds of anatomy.

Among C₃ genera, *Androtrichum* is diagnosed by the presence of elongated stamen filaments that are persistent and dispersed with the nutlets. However, the two taxa, *A. giganteum* and *A. trigynum*, are not sister (Fig. 1) and their shared character state, presence of elongated filaments, may be a parallel adaptation to dispersal in swampy coastal dunes. *Kyllingiella* and *Oxycaryum*, previously classified in Scirpeae (e.g. Bruhl, 1995), have a spiral glume arrangement unlike C₃ species of *Cyperus sensu stricto*, which have a distichous glume arrangement (Lye, 1971; Haines & Lye, 1978). *Courtoisina* has similar morphology to C₃ species of *Cyperus*, but the whole spikelet is dispersed intact.

The C₄ genera include a number that are monotypic or with few species (i.e. *Queenslandiella*, *Sphaerocyperus*, *Remirea*, *Volkiella*, and *Alinula*), which are separated from the larger genera by a combination of characters. Among the clearly recognizable larger genera are *Kyllinga*, and *Pycneus* (together with monotypic *Queenslandiella*), which have laterally flattened nutlets. *Alinula*, *Volkiella*, *Ascolepis*, and *Lipocarpha* have highly reduced spikelets. The C₄ species of *Cyperus sensu stricto* have spikelets comprising more than one floret and dorsiventrally compressed nutlets.

There are differences in opinion on whether to recognise *Cyperus sensu lato*, in a very broad sense with a number of subgenera (e.g. subgenus *Kyllinga*, and C₃ and C₄ species of *Cyperus sensu stricto* in different subgenera; e.g. Kükenthal, 1935–1936), or in a narrow sense with various segregate genera (with *Cyperus sensu stricto* including C₃ and C₄ species; e.g. Goetghebeur, 1998). Our results show *Cyperus sensu stricto* to be polyphyletic, and merging all the segregate taxa into broadly circumscribed *Cyperus sensu lato* and recognizing various segregates as subgenera would make a monophyletic entity. However, this option is not favored because it would result in a big genus (c. 900 species) and reduce taxonomic clarity. Other partial merging of the taxa into *Cyperus*, recognizing *Oxycaryum*, *Kyllingiella*, *Sphaerocyperus*, *Remirea*, *Lipocarpha*, and *Ascolepis* as distinct, but treating

Courtoisina, *Kyllinga*, *Pycurus*, *Queenslandiella*, and *Alinula* as subgenera of *Cyperus* (e.g. Haines & Lye, 1983; Lye, 1997) is not supported by this study.

We follow Goetghebeur (1998) in recognizing *Cyperus* sensu stricto and recognizing the segregate taxa at generic rank (Table 2) pending more intensive phylogenetic studies to get a full resolution of their relationships.

Future Research

Molecular phylogenetic studies have focused more attention on the *Ficinia* clade (38% sampling) and less on the *Cyperus* clade (5% sampling), yet *Cyperus* clade exhibits wide morphological variation. With more intensive molecular phylogenetic studies and more extensive sampling to include the complete diversity of growth form and morphological types, we expect a better understanding of character homology, which will allow better-informed decisions about generic limits.

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