

Spikelet Structure in Cypereae (Cyperoideae-Cyperaceae)

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Abstract This work provides an analysis of the spikelet structure in Cypereae, and their taxonomic and phylogenetic implications. The main variations in the Cypereae spikelets are seen in: number and phyllotaxis of the glumes, presence/absence of empty glumes, glume morphology, rachilla internode length, prophyll development, flower structure and structure of the dispersal unit. Consistently with the latest molecular phylogenies proposed for Cypereae, our results support the division of this tribe into two groups with spikelet characters more or less typical: the *Cyperus* and the *Ficinia* clades. Within the *Cyperus* clade, the existence of spikelets with convergent characters among the different taxa supports the inclusion of all this clade taxa within one wide genus *Cyperus*, just as the current phylogenetic hypotheses proposed for the group.

Keywords Cyperaceae · Cypereae · Cyperoideae · Spikelet

Introduction

The latest efforts to reconstruct phylogeny within Cyperaceae Juss. support the division of the family into two subfamilies—Mapanioideae and Cyperoideae—and broadly accept the tribal circumscriptions of Goetghebeur (1998) but with modifications in some tribes, among which is Cypereae Dumort. (Simpson et al., 2007; Muasya et al., 2009a). Cypereae is the second most species-rich tribe of Cyperaceae (Larridon et al., 2014), barely outnumbered by Cariceae Dumort. This tribe is currently the target of intense taxonomic and phylogenetic studies (Muasya et al., 2002, 2009b, 2012, 2014; Huygh et al., 2010; Muasya & de Lange, 2010; Larridon et al., 2011a, b, c, 2013, 2014; Reynders et al., 2011; Yano et al., 2012; Bauters et al., 2014). Based on molecular phylogenetic analysis, Cypereae forms a strongly supported clade, and is resolved into two subclades: the “*Cyperus* clade” and the “*Ficinia* clade” (Simpson et al., 2007; Muasya et al., 2009a, b; Larridon et al., 2011b). According to these authors, the *Ficinia* clade comprises *Desmoschoenus* Hook. f., *Ficinia* Schrad., *Hellmuthia* Steud., *Isolepis* R. Br., *Scirpoides* Ség., and *Scirpus falsus* C.B. Clarke and

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S. ficinoides Kunth. *Desmoschoenus* has recently been included in *Ficinia* (Muasya & de Lange, 2010); *Scirpus falsus* and *S. ficinoides* were transferred to the new genus *Dracoscirpoides* Muasya, together with *Dracoscirpoides surculosa* Muasya, Reynders & Goetgh. (Muasya et al., 2012); and an additional genus previously placed in Scirpeae T. Lestib. ex Dumort., *Erioscirpus* Palla, was considered within the *Ficinia* clade based on molecular phylogenetic studies in which *Erioscirpus* is nested in Cyperae (Yano et al., 2012).

The *Cyperus* clade has a paraphyletic *Cyperus* L. s.s. as core genus, in which 13 derived genera (*Alinula* J. Raynal, *Androtrichum* Brongn., *Ascolepis* Nees ex Steud., *Courtoisina* Soják, *Kyllinga* Rottb., *Kyllingiella* R.W. Haines & Lye, *Lipocarpha* R.Br., *Oxycaryum* Nees, *Pycreus* P. Beauv., *Queenslandiella* Domin, *Remireia* Aubl., *Sphaerocyperus* Lye and *Volkiella* Merxm. & Czech) are embedded (Muasya et al., 2009a, b). New combinations within the *Cyperus* clade include the addition of segregate genera to existing or new sections of *Cyperus* (Larridon et al., 2013, 2014), and the recognition of two subgenera into *Cyperus* s.l.: (1) *Cyperus* subgenus *Anosporum* (Nees) C.B. Clarke (paraphyletic, with species using C₃ photosynthesis linked with eucyperoid anatomy, informally termed “C₃ *Cyperus*”) and (2) *Cyperus* subgenus *Cyperus* L. (monophyletic, with species using C₄ photosynthesis linked with clorocyperoid anatomy, “C₄ *Cyperus*”) (Muasya et al., 2002; Larridon et al., 2011b, 2013).

Within Cyperae only the *Cyperus*-type embryo and the similar *Ficinia*-type embryo allow a natural delimitation of the tribe (Goetghebeur, 1998; Van der Veken, 1965). Morphologic characters used in the past to circumscribe Cyperae members, such as presence of spikelets with distichous glumes, and reduced perianthless flowers, are not useful to characterize the modern Cyperae tribe (Larridon et al., 2013).

Reproductive structures in Cyperaceae have been widely used to suggest relationships between taxa, and to propose classifications within the family (Haines & Lye, 1983; Goetghebeur, 1998; Tucker & Grimes, 1999; Guarise et al., 2012). Particularly, inflorescences have proved to be a source of reliable diagnostic traits and indications for phylogenetic pathways in many cases (Guarise et al., 2012, and citations therein); but they have also made evolutionary reconstructions and classifications difficult in other circumstances (Muasya et al., 2009a, b; Larridon et al., 2011b, 2013; Reynders et al., 2012; Yano et al., 2012). Some problems arise when the inflorescence is used in systematic studies of Cyperaceae and they are associated with convergent evolution or with misinterpretation of the inflorescence components (Larridon et al., 2011b, 2013). In compound plant structures as the Cyperaceae inflorescences with complex branching systems, compressed spikelet arrangement and occasionally remnant vestigial structures, comprehensive and comparative morphological analysis are required.

Particularly in Cyperae, the generic circumscriptions being currently established need to incorporate new evidence from morphology, and the reinterpretation of the morphological characters in the context of the current Cyperae (Muasya et al., 2009a; Vrijdaghs et al., 2011; Larridon et al., 2011b, 2013; Reynders et al., 2012; Bauters et al., 2014). Representatives of Cyperae show broad variations in inflorescence and spikelet structures, and this has led to characters related to such structures being widely used to define taxa within the tribe. This review is intended to interpret and characterize morphologic variations observed in the structure of Cyperae spikelets and their taxonomic and phylogenetic implications. For a better characterization of the different taxa, we have used the genus circumscriptions of Goetghebeur (1998),

Muasya et al. (2009a) and Yano et al. (2012), rather than that of Larridon et al. (2013, 2014), in which the segregate genera of *Cyperus* are included in this genus as sections.

The Spikelet Structure in Cyperaceae

In this highly derived tribe within Cyperoideae (Simpson et al., 2007; Muasya et al., 2009a), the spikelets are bisexual, typically monopodial and racemose. The spikelets can be terminal or lateral. Each lateral spikelet emerges from the axillary bud of a bract, bearing a prophyll and a varying number of glumes arranged on an open axis (rachilla); some or all of these glumes develop an axillary flower, so some taxa have empty glumes, while in other taxa each glume carries a flower. A terminal spikelet has neither a bract nor a prophyll (Goetghebeur, 1998; Vrijdaghs et al., 2007). In the Cyperaceae spikelets, there are varying degrees of development of the bract that subtends the spikelet, of the prophyll and of the glume(s) (Figs. 1a–f and 2a–e)

Within this pattern, the Cyperaceae spikelets show variations in (Tables 1 and 2): (A) number and phyllotaxis of the glumes; (B) presence of empty glumes (lack of development of flowers in lower or upper glumes); (C) glume morphology; (D) rachilla internode length; (E) prophyll development; (F) flower structure; (G) structure of the dispersal unit.

Number and Phyllotaxis of the Glumes

The spikelets in Cyperaceae carry only one single glume (Fig. 1c) or few-many glumes (Figs. 1f and 2c). Spikelets with few-many glumes have spiral or distichous phyllotaxis (Fig. 2a) (Goetghebeur, 1998; Muasya et al., 2009b).

Spikelets with few-many glumes and spiral phyllotaxis are typical of *Dracoscirpoides*, *Erioscirpus*, *Ficinia*, *Isolepis*, *Hellmuthia*, *Kyllingiella*, *Oxycaryum* and *Scirpoides* (Fig. 2d). However, few species of *Ficinia* (e.g. *F. distans* C.B. Clarke and *F. angustifolia* (Schrad.) C.B. Clarke) and of *Isolepis* (*I. levynsiana* Muasya & D.A. Simpson and *I. venustula* Kunth) have distichously arranged glumes (Vrijdaghs et al., 2009), and *Scirpoides varius* Browning present the glumes with spiral phyllotaxis but occasionally appearing almost distichous (Browning & Gordon-Gray, 2011). The glumes may change in the course of spikelet development, as in *Dracoscirpoides falsa* (C.B. Clarke) Muasya, where newly formed, distally situated glumes are arranged distichously and more proximally, the glume arrangement is spiral (Vrijdaghs et al., 2010; Muasya et al., 2012).

Spikelets with few-many glumes and distichous phyllotaxis are characteristic of *Androtrichum*, *Courtoisina*, *Cyperus s.s.*, *Kyllinga*, *Pycneus*, *Queenslandiella*, *Remirea* and *Sphaerocyperus* (Fig. 2a). Among these taxa, only some species of *Cyperus s.s.* have spikelets with spiral phyllotaxis (Muasya et al., 2001a, 2014).

Among the spikelets with a single glume, a rachilla remnant may or may not be recognized. Spikelets with rachilla remnant are observed in some species of *Alinula* and *Ascolepis* (Goetghebeur, 1980, 1998). In some species of *Ascolepis* (*A. fimbrillosa* P. Goetghebeur, *A. neglecta* P. Goetghebeur, *A. speciosa* Welw., *A. majestuosa* Duvigneaud & G. Léonard and *A. pinguis* C.B. Clarke), an additional small adaxial

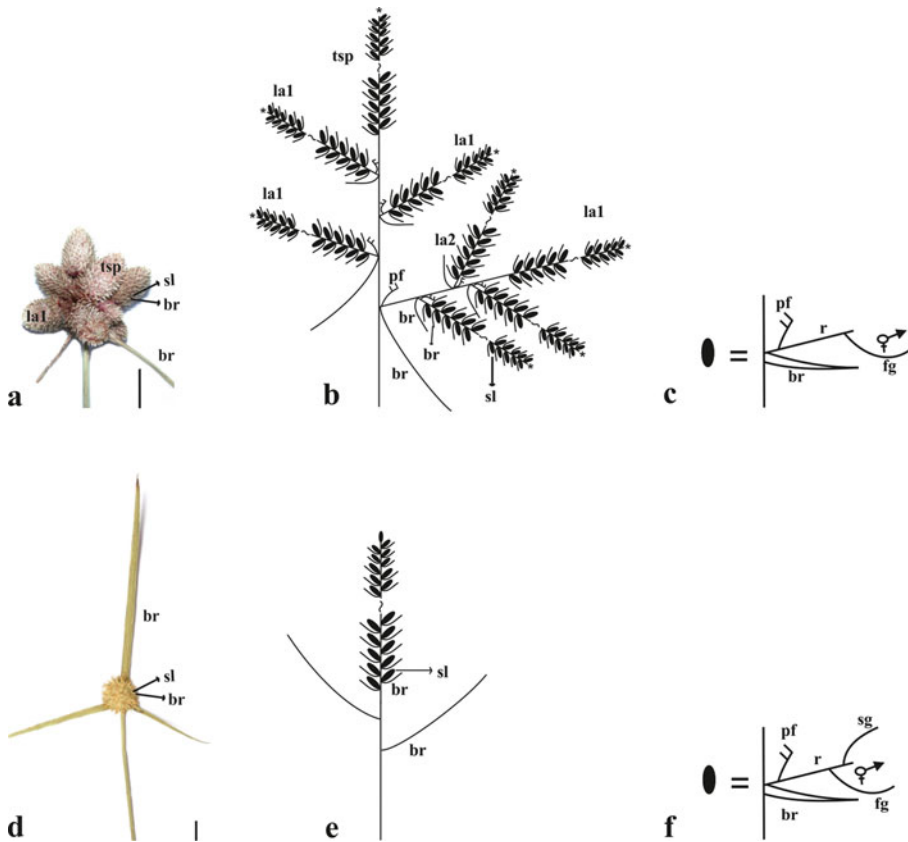


Fig. 1 Photographs of inflorescences, and schematic representations of inflorescences and spikelets in Cypereae. **a–c** *Lipocarpa humboldtiana*; **d–f** *Kyllinga vaginata*. Abbreviations: *br* bract, *fg* fertile glume, *la1* lateral axis of first order, *la2* lateral axis of second order, *pf* prophyll, *r* rachilla, *sg* sterile glume, *sl* spikelet, *tsp* terminal spike. The asterisks in **b** indicate the absence of the terminal spikelet. Bar = 5 mm

scale is observed in the spikelet, which might represent a remnant of the second glume, because the structure of this scale resembles that of the first glume in its thickened top and winged sides (Goetghebeur, 1977; Goetghebeur & Van den Borre, 1989). In *A. capensis* (Kunth) Ridley (Palla, 1905) and *A. protea* Welwitsch (Goetghebeur & Van den Borre, 1989), 2-flowered spikelets have been observed. In *A. brasiliensis* (Kunth) Benth. ex C.B. Clarke, the apical spikelet meristem may only be observed at early developmental stages (see Figs. 4D–F in Reutemann et al., 2014).

Spikelets without rachilla remnant are observed in *Lipocarpa* and *Volkiella*. In *Lipocarpa*, a flower, and only a reduced prophyll and single fertile glume, both hyaline, remain within the subtending bract (Hooper, 1986; Goetghebeur, 1986). The rachilla is detectable only from the peg-like scar left after the achene falls, and the presence of the prophyll (Hooper, 1986). In some species of *Lipocarpa*, either the glume or both the glume and the prophyll can be partly to completely reduced (*L. aristulata* (Coville) G.C. Tucker, *L. drummondii* (Nees) G.C. Tucker, *L. micrantha* (Vahl) G.C. Tucker, *L. occidentalis* (A. Gray) G.C. Tucker) and *L. schomburgkii* (Friedl.) G.C. Tucker (Goetghebeur & Van den Borre, 1989;

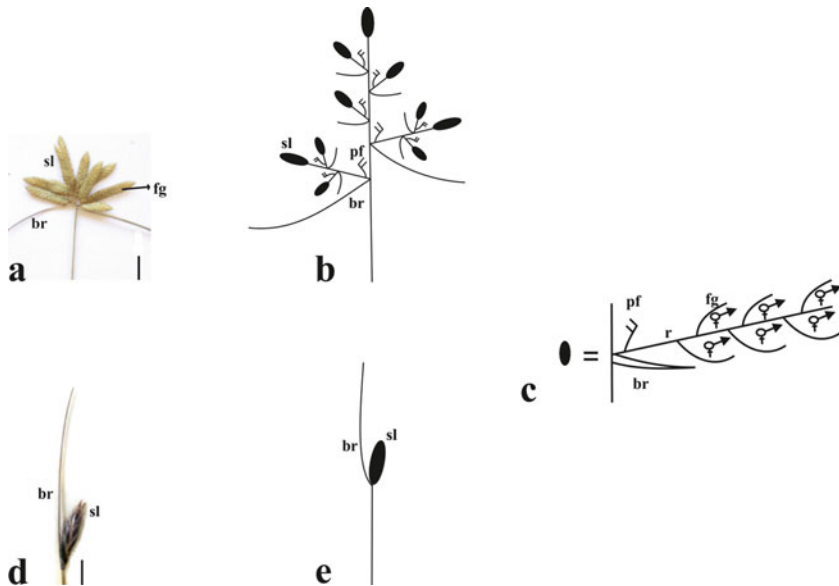


Fig. 2 Photographs of inflorescences, and schematic representations of inflorescences and spikelets in Cyperaceae. **a–c** *Pycurus lanceolatus*; **c–e** *Ficinia* sp. Abbreviations: *br* bract, *fg* fertile glume, *pf* prophyll, *r* rachilla, *sl* spikelet. Bar = 5 mm

Bauters et al., 2014). In *Volkiella*, a flower, and only a prophyll and a very thin transparent glume may be recognized within each glume-like bract (Hooper, 1986; Goetghebeur, 1998).

Presence of Empty Glumes

The presence of spikelets where all glumes subtend a flower is the most widespread condition within Cyperaceae (Figs. 1c and 2c). However, some taxa in this tribe develop spikelets where proximal glumes and/or distal glumes are sterile (Fig. 1f). Spikelets without empty glumes are typical of species of *Alinula*, *Androtrichum*, *Ascolepis*, *Courtoisina*, *Cyperus*, *Dracoscirpoides*, *Kyllingiella*, *Lipocarpha*, *Oxycayum*, *Pycurus*, *Queenlandiella*, *Scirpoides* and *Volkiella*. Spikelets with several empty glumes are typical of *Erioscirpus comosum* (Wall.) Palla (only empty proximal glumes) (eFloras, 2008), and *Remirea* and *Sphaerocyperus* (proximal and distal empty glumes) (Haines & Lye, 1983; Browning & Gordon-Gray, 1993; Goetghebeur, 1998; Larridon et al., 2013).

In the other Cyperaceae genera, the spikelets may have 1-few empty glumes (proximal, distal or both) or bear only fertile glumes, which varies by species and, sometimes, by studied spikelet. In *Ficinia* and *Isolepis*, some species have spikelets with only fertile glumes, whereas other species bear spikelets with 1-few proximal empty glumes. This same variation occurs between different spikelets within the monotypic genus *Hellmuthia*. In *Kyllinga* the spikelet bear 2-few glumes, of which 1-few subtend a flower (Goetghebeur, 1998); the upper glumes are male or sterile, and the lower ones are usually empty (Barros, 1947; Haines & Lye, 1983; Trevisan et al., 2007). *Kyllinga mbitheana* Muasya is the only species of *Kyllinga* with a spikelet bearing up to ten fertile flowers (Muasya et al., 2010).

Table 1 Main spikelet characters in Cyperaceae

	Glumes for spikelet	Glume arrangement	Empty glumes	Glumes with wings	Dispersal unit
<i>Cyperus</i> Clade					
<i>Alinula</i>	1		No	No	Achene
<i>Androrhynchum</i>	Many	Distichous	No	No	Achene with filaments
<i>Ascolepis</i>	1		No	No	Spikelet as intact unit
<i>Courtoisina</i>	2-many	Distichous	No	Yes	Spikelet as intact unit
<i>Cyperus</i> s.s.	Few-many	Distichous/Spiral ^a	No	Yes/No	Achene/Spikelet as intact unit
<i>Kyllinga</i>	2-many	Distichous	Yes, proximal or proximal and distal	Yes/No ^a	Spikelet as intact unit
<i>Kyllingiella</i>	Few-many	Spiral	No	No	Achene
<i>Lipocarpus</i>	0–1		No	No	Spikelet as intact unit
<i>Oxycaryum</i>	Many	Spiral	No	No	Achene
<i>Pycreus</i>	Few-many	Distichous	No	Yes/No ^a	Achene
<i>Queenstandiella</i>	Few-many	Distichous	No	Yes	Spikelet as intact unit
<i>Remirea</i>	3–4	Distichous	Yes, proximal and distal	No	Spikelet as intact unit
<i>Sphaerocyperus</i>	Many	Distichous	Yes, proximal and distal	Yes	Spikelet as intact unit
<i>Volkiella</i>	1		No	No	Spikelet as intact unit
<i>Dracoscirpoides</i>	Many	Spiral/Variable ^b	No	No	Achene
<i>Erioscirpus</i>	Many	Spiral	No/Yes, proximal ^a	No	Achene with perianth hairs
<i>Ficinia</i>	Few-many	Spiral/Distichous ^a	No/Yes, proximal ^a	No	Achene
<i>Hellmuthia</i>	Many	Spiral	No/Yes, proximal ^a	Yes	Achene
<i>Isolepis</i>	Few-many	Spiral/Distichous ^a	No/Yes, proximal ^a	No	Achene
<i>Scirpoides</i>	Many	Spiral/almost Distichous ^a	No	No	Achene

^a Only few species^b In *Dracoscirpoides falsa*

Table 2 Main flower characters in Cyperaceae

Taxon	Perianth	Gynophore	N° stamens	N° stigma branches	Ovary shape and orientation	Style base persistence
<i>Cyperus</i> Clade						
<i>Alimula</i>	Absent	Absent ^b	1–2	3	Trigonous	Persistent
<i>Androtrichum</i>	Absent	Absent	3	3	Trigonous	Persistent
<i>Ascolepis</i>	Absent	Absent	1–5	2–3, 5 ^a	Trigonous/Dimerous-dorsiventrally compressed	Deciduous
<i>Courtoisina</i>	Absent	Absent	3	3	Trigonous	Persistent
<i>Cyperus</i> s.s.	Absent	Absent ^f	1–3	1 ^a , 2–3	Trigonous/Dimerous-dorsiventrally compressed	Persistent/Deciduous
<i>Kyllinga</i>	Absent	Absent	1–3	2	Dimerous-laterally compressed	Persistent
<i>Kyllingiella</i>	Absent	Absent	1–3	3	Trigonous/Dimerous-dorsiventrally compressed ^a	Persistent
<i>Lipocarpha</i>	Absent	Absent	1–3	2–3	Trigonous/Dimerous-dorsiventrally compressed	Persistent/Deciduous
<i>Oxyccaryum</i>	Absent	Absent	3	2	Dimerous-dorsiventrally compressed	Persistent
<i>Pycurus</i>	Absent	Absent ^c	1–3	2	Dimerous-laterally compressed	Deciduous/Persistent ^a
<i>Queenslandiella</i>	Absent	Absent	2	2	Dimerous-laterally compressed	Deciduous
<i>Remirea</i>	Absent	Absent	3	3	Trigonous	Persistent
<i>Sphaerocyperus</i>	Absent	Absent	3	3	Trigonous	Persistent
<i>Volliella</i>	Absent	Absent	2	3	Trigonous	Deciduous
<i>Ficinia</i> Clade						
<i>Dracoscirpoides</i>	Present (bristle-like segments)	Absent	3	3	Trigonous	Deciduous
<i>Erioscirpus</i>	Present (cotton-like segments)	Absent	2	3	Trigonous	Deciduous
<i>Ficinia</i>	Absent/Present (bristle-like segments) ^a	Present/Absent ^d	3	3, 2–1 ^a	Trigonous/Dimerous ^a	Deciduous
<i>Helminthia</i>	Present (scales)	Absent	3	3	Trigonous	Deciduous
<i>Isolepis</i>	Absent	Absent ^f	1–3	2–3	Trigonous/Dimerous-dorsiventrally compressed	Persistent
<i>Scirpoides</i>	Absent	Absent ^f	2–3	3	Trigonous	Persistent

^a Only few species^b Present in *Alimula lipocarphoides*^c Few species have a rudimentary gynophore

Glume Morphology

The most distinctive morphological trait of the glumes is the presence or absence of winged expansions. In many species, the glumes bear hyaline wings. The presence of wings is particularly frequent in spikelets with distichously arranged glumes, where the wings are decurrent with the internode of the rachilla, and partially envelope the lower, opposite flower. Vrijdaghs et al. (2010) state that in most Cyperaceae species with distichously arranged glumes, the basal zone of the wings is fused with the rachilla, and such fusion zone grows as the rachilla rises, causing the wing tips to elongate along the internode and the main part of the glume and the flower primordium in its axil to displace. As a consequence of this phenomenon, a glume originates at a node, and subsequently the main part of it is raised to a higher level, the next node on the rachilla. Hence, the fusion zone of the wings of a glume and rachilla runs along the internode, and the rachilla is usually observed to be winged. Vrijdaghs et al. (2010) propose the term “epicaulescence” to refer to this special kind of recaulescent growth (Weberling, 1992) where a part of the bract primordium is fused with the rachilla itself (and not with a newly formed lateral axis).

In *Cyperus* and *Pycreus*, some species show winged glumes and others do not. In the spikelet with winged glumes of *Cyperus* (*C. capitatus* Poir., *C. laevigatus* L., *C. luzulae* Rottb., *C. odoratus* L.) and *Pycreus* (*P. bipartitus* C.B. Clarke, *P. flavescens* (L.) P. Beauv. ex Rchb., *P. pelophilus* (Ridl.) C.B. Clarke; *P. polystachyos* subsp. *holocericeus* (Rottb.) P. Beauv.; *P. pumilus* (L.) Nees; *P. sanguinolentus* (Vahl) Nees), the wings of one glume partially enveloping the opposite, lower flower, and the basal part of the glume including (part of) the wings are congenitally fused with the rachilla (Vrijdaghs et al., 2011) (Fig. 3a–c). Within *Pycreus*, the epicaulescent metatopic displacement is more pronounced than in species of *Cyperus* or other Cyperoidae, resulting in the typical alcove-like cavities along the rachilla, formed by the growth of this structure, of which the lateral walls consist mainly of the wings of the opposite, higher glume (see Fig. 5 in Vrijdaghs et al., 2011). These authors claim that the congenitally fusion of the glume-rachilla is most obvious in *P. pumilus*, whereas in *P. pelophilus* and *P. flavescens*, a large part of the wings grows free from the rachilla. Barros (1947) mentions *Cyperus* species with wing glume unfused with the rachilla and deciduous (*C. digitatus* Roxb., *C. giganteus* Vahl, *C. pohlii* (Nees) Steud., *C. prolixus* Kunth and *C. rotundus* L.). The glumes of *Cyperus haspan* L. have a small wing, which remains attached to the rachilla once the glume disarticulates; thus the description of this species by Barros (1947) as having a subwinged rachilla.

There are winged glumes also in *Courtoisina* (Larridon et al., 2011b), *Kyllinga* (Haines & Lye, 1983) *Queenlandiella* (Carter & Mears, 2000) and *Sphaerocyperus* (Browning & Gordon-Gray, 1993). In *Hellmuthia* there are wings in the larger glumes only (Vrijdaghs et al., 2006); whereas glumes are wingless in *Alinula*, *Androtrichum*, *Ascolepis*, *Dracoscirpoides*, *Erioscirpus*, *Ficinia*, *Isolepis*, *Kyllingiella*, *Lipocarpa*, *Oxycaryum*, *Remirea*, *Scirpoides*, *Volkiella* and *Kyllinga tanzaniae* (K. Lye) K. Lye (Barros, 1947; Haines & Lye, 1983; Muasya et al., 2012; Yano et al., 2012).

Glumes also vary in terms of size and shape within Cyperaceae. There are glumes ovate, obovate or elliptic, with an obtuse or acute (more rarely emarginated) apex, membranous or coriaceous, thin or thick. Glumes are sometimes strongly scabrid or

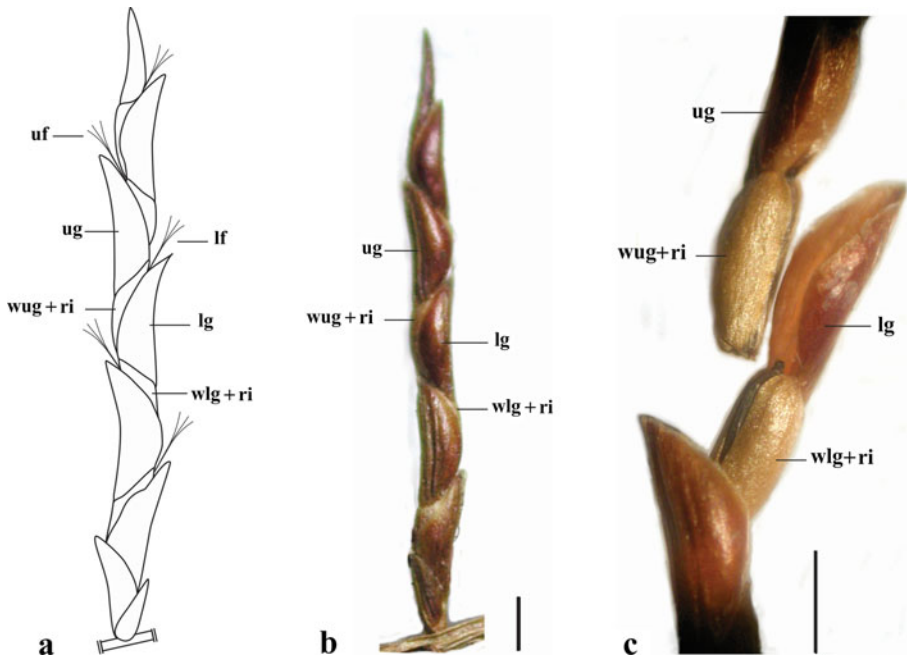


Fig. 3 Winged glumes in *Cyperus odoratus*. **a** schema of a whole spikelet; **b** photograph of a whole spikelet; **c** photograph of a detail of a spikelet. *Abbreviations:* *lf* lower flower, *lg* lower glume, *uf* upper flower, *ug* upper glume, *wlg + ri* wing of the lower glume and rachilla internode, *wug + ri* wing of the upper glume and rachilla internode. Bar = 1 mm

hairy (Haines & Lye, 1983; Goetghebeur, 1998). They may have one edge, or a mucro. The length of the mucro in mucronate glumes usually decreases towards the top of the spikelet (Goetghebeur, 1998). In *Lipocarpha* and *Volkiella*, the spikelets present a hyaline glume. *Oxycaryum* spikelets present the apex of the glumes conspicuously thickened (Goetghebeur, 1998).

In most genera, the glumes are open (not utriculiform), with a higher or lower degree of development. The glumes are rarely utriculiform in *Alinula* and *Ascolepis* (Goetghebeur, 1998).

In many-flowered spikelets, all glumes are usually similar, but in few-flowered spikelets the glume length often increases towards the first flower-bearing glume. In *Remirea*, the spikelets have 3–4 distichous persistent glumes, of which the fertile are large, and the sterile are small, sitting on a finally much enlarged corky rachilla internode (Chermezon, 1922; Goetghebeur, 1998). In *Sphaerocyperus*, the glumes present increased length, and the largest penultimate distal glume subtends a flower (Browning & Gordon-Gray, 1993; Goetghebeur, 1998).

Rachilla Internode Length

The rachilla internodes are usually short in many-flowered spikelets with spirally arranged glumes, and elongated in many-flowered spikelets with distichous glumes. Thus, the rachilla internodes are elongated in *Courtoisina*, *Cyperus s.s.*, *Kyllinga*, *Pycurus* and *Queenslandiella*. In *Remirea* the distal internode are elongated and in

Sphaerocyperus, the rachilla internodes are elongated only in the region of fertile flowers. The internodes elongate somewhat during the fruiting stage or develop into a markedly zigzagging structure as it occurs in some species of *Cyperus* and *Pycurus* (Goetghebeur, 1998).

Prophyll Development

The prophyll develops in most species of Cyperaceae. Single-flowered spikelets of *Ascolepis* lack a prophyll and, therefore, they are even more reduced. This represents an important difference between *Lipocarpa* and *Ascolepis*: in the former, the prophyll is consistently present, while the *Ascolepis* spikelet lacks a prophyll (Goetghebeur, 1977; Hooper, 1986). Development studies have shown that in *Ascolepis brasiliensis* the prophyll initiates early and then stops growing, which means it cannot be observed in the adult spikelet (Reutemann et al., 2014).

Several species in *Cyperus s. l.*, formerly grouped together in *Mariscus*, have spikelets with an adaxial swelling body (pulvinus) at the prophyll base. Swelling of this callus causes divergence of the spikelet from the rachis (Vrijdaghs et al., 2011). This had already been mentioned for *Cyperus tenuis* Sw. by Haines (1967) and Haines and Lye (1983). This pulvinus adjusts the position of both the branch and the bract that subtends it. This kind of pulvinus is also seen in *Pycurus pelophilus* Nees, *P. polystachyos* (Rottb.) P.Beauv., *P. sanguinolentus* (Vahl) Nees, *C. luzulae* (L.) Retz., and species of *Kyllinga* Rottb (Vrijdaghs et al., 2011).

The axillary bud of some spikelet prophylls can develop forming a perfect or pistillate flower. This has been described for *C. entrerianus* Boeck., *C. luzulae* (L.) Retz., *C. virens* Michx. var. *virens* (Guarise & Vegetti, 2007) and *Pycurus macrostachyos* (Lam.) J.Raynal (Cacciolatto et al., 2009). In the three first species the lower glume do not develop a perfect flower. In *P. macrostachyos*, unlike that observed in the mentioned species of *Cyperus*, the lower glume develops a perfect flower.

Flower Structure

The flower of Cyperoidae is tetracyclic with two alternating whorls of three perianth members, one whorl of three stamens opposite the outer perianth parts, and a trimerous gynoecium (Vrijdaghs et al., 2005a, 2009). In Cyperaceae, the main variations at the flower level (Table 2) relate to the presence or absence of perianth parts, the presence or lack of a gynophore, stamen number, stigma branches number, form and orientation of the ovary (and then achene) and style base persistency.

Most Cyperaceae genera have perianthless flowers (Goetghebeur, 1998; Fig. 4c–f). There is no formation of perianth primordium in these taxa (Vrijdaghs, 2006; Vrijdaghs et al., 2009, 2011). In the *Ficinia* clade, *Dracoscirpoides*, *Erioscirpus* and *Hellmuthia* have perianth developed; a few species of *Ficinia* have remnants of a perianth (Vrijdaghs et al., 2006; Muasya et al., 2009a, b; Yano et al., 2012). *Dracoscirpoides* having six to seven bristle-like perianth segments (Muasya et al., 2012), *Hellmuthia* having two well-developed lateral scale-like perianth parts and a third small adaxial scale (Vrijdaghs et al., 2006; Muasya et al., 2009b) (Fig. 4a, b), and *Erioscirpus* presenting 10–30 cotton-like long perianth bristles, white or brownish red, smooth, silky. These perianth bristles in *Erioscirpus* elongate extremely after anthesis, persisting

in the fruits and promoting wind dispersal (Yano et al., 2012). When the perianth develops in *Ficinia*, it resembles a bristle. In *Dracoscirpoides falsa*, the adaxial perianth primordium can split to develop into more than one perianth part (Muasya

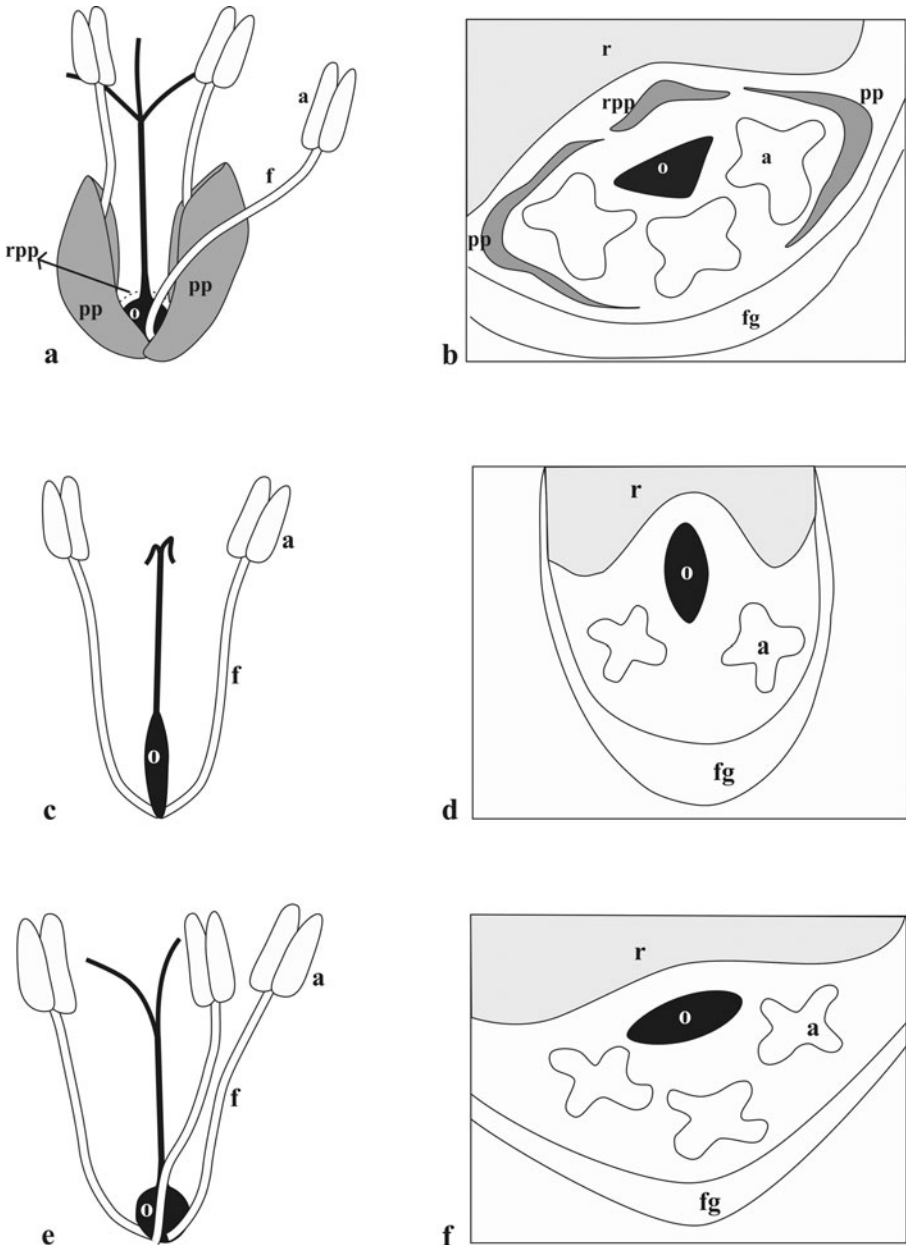


Fig. 4 Flower structure in Cyperaceae. **a** and **b** *Hellmuthia membranacea*; **c** and **d** *Pycreus flavescens*; **e** and **f** *Oxycaryum cubense*. Abbreviations: *a* anther, *f* filament, *fg* fertile glume, *o* ovary, *pp* perianth part, *r* rachilla, *rpp* rudiment of the third adaxial perianth part. **a** modified of Clarke (1909) plus the contributions of Vrijdaghs et al. (2006) that show the existence of a third adaxial perianth part; **b**, modified of (Vrijdaghs et al., 2006)

et al., 2012). A similar phenomenon occurs in *Dulichium* Pers., where up to ten bristles are formed from the usual three inner and three outer perianth part primordia (Vrijdaghs et al., 2005a). In this regard, Yano et al. (2012) consider it is ontogenetically interesting for *Erioscirus* whether the multiple perianths arise from three separate primordia, as in *Dracoscirpoides* (Muasya et al., 2012), or arise from a perigonial primordium, as in *Eriophorum* (Vrijdaghs et al., 2005a). The perianth bristles have diagnostic value at the species classification level. They are densely antrorsely barbed in *Dracoscirpoides falsa*, sparsely retrorsely barbed in *D. ficinioides* (Kunth) Muasya and with scattered antrorse barbs in *D. surculosa* (Muasya et al., 2012).

Within Cyperaceae, the presence of gynophores is typical of the *Ficinia* genus (Arnold & Gordon-Gray, 1982; Goetghebeur, 1986); however, some *Ficinia* species lack a gynophore (e.g. *F. rigida* Levynsh and *F. filiformis* (Lam.) Schrad.) (Muasya et al., 2001b; Muasya & Simpson, 2002). On the other hand gynophores are also observed in *Alinula lipocarphoides* (Kük.) J. Raynal (Haines & Lye, 1983; Muasya et al., 2009b). In some species of *Isolepis*, *Cyperus*, *Pycreus* and *Scirpoides* a rudimentary gynophore appears (Haines & Lye, 1983; Muasya & Simpson, 2002; Muasya et al., 2009b, 2014; Vrijdaghs et al., 2011).

In Cyperaceae, the number of stamens is highly variable, with three as the basic number as in most other Cyperoideae (Fig. 4a, b, e, f). If the number of stamens is two, it is generally abaxial stamen that does not develop (Fig. 4c, d); if the number of stamens is one, it is the abaxial stamen and one of the lateral stamens that do not develop (Vrijdaghs, 2006; Vrijdaghs et al., 2009, 2011). In some species, the number of stamens can also vary within the species, and even within a single plant (*P. pumilus*, Vrijdaghs et al., 2011). These authors considered that the reduction of the abaxial stamen can probably be explained by a limited spatial freedom for the three stamens to develop; additionally, they observed that the reduction of the abaxial stamen occurred independently in different Cyperoideae clades.

The gynoecium in Cyperaceae vary from trigonous with three stigma branches (Fig. 4a, b) to dorsiventrally (Fig. 4e, f) or laterally (Fig. 4c, d) compressed with two stigma branches (Vrijdaghs, 2006; Reynders et al., 2012). The basic gynoecium form in the tribe is trigonous. Some species of *Cyperus* (often classified in a separate taxon *Juncellus* C.B. Clarke), the monotypic genus *Oxycaryum*, and some species of *Ascolepis* and *Lipocarpa* have a dorsiventrally flattened pistil, whereas *Kyllinga*, *Pycreus* and *Queenslandiella* have a laterally compressed gynoecium (Goetghebeur, 1998; Vrijdaghs, 2006; Muasya et al., 2009b; Vrijdaghs et al., 2011). The dorsiventrally flattened gynoecium presents two laterally positioned stigmas; and the laterally compressed one has two dorsiventrally positioned stigmas. Muasya et al. (2009a) suggested that the laterally flattened gynoecia/fruit in *Kyllinga*, *Pycreus* and *Queenslandiella* evolved independently in each of the three genera characterized by it. Dorsiventrally flattened pistils can also be found in diverse genera of the Cyperoideae subfamily such as *Dulichium arundinaceum* (L.) Britton, *Carex* L., *Eleocharis* R. Br., *Fimbristylis* Vahl and *Nemum* Desv. ex Ham. (Goetghebeur, 1998).

Reynders et al. (2012) claim that there is not convinced of the systematic value of flattened pistils for generic delimitation; these authors based this affirmation in the works of Koyama (1961) and Goetghebeur (1986). This is illustrated by some species such as *Cyperus alopecuroides* Rottb. and *Kyllingiella polyphylla* (A.Rich.) Lye, which can have both trimerous and dorsiventrally flattened dimerous pistils within a single

spikelet (Haines & Lye, 1983; Larridon et al., 2011b). In other taxa, the dimerous, dorsiventrally flattened pistil state is constant such as in *Cyperus laevigatus* (Haines & Lye, 1983).

In some African *Cyperus* species (*C. clavinux* C.B. Clarke, *C. lateriticus* Raynal and *C. meeboldii* Kük.), Raynal (1966) observed triangular achenes and a single stigma branch. Goetghebeur (1998) described a significant variation in the stigma branch number and in the stamen number (Table 2) of *Ascolepis*, with some species observed to have up to five stamens and five stigma branches.

In the development studies carried out to date in Cyperaceae (Vrijdaghs, 2006; Vrijdaghs et al., 2005a, b, 2006, 2009, 2010, 2011; Reutemann et al., 2014), it has been determined that the gynoecium is formed from an annular ovary primordium surrounding a central ovule primordium. In this tribe, as it occurs in other Cyperoideae, this annular ovary primordium possibly results from a congenital fusion of three distinct carpel primordia (trigonous ovary) or two carpel primordia (dorsiventrally and laterally compressed ovary). In this regard, Vrijdaghs et al. (2011) consider that, in a strict sense, carpels are not present in cyperoid Cyperaceae since the ovary originates from an annular ovary primordium.

In all genera of Cyperaceae, the style base is not distinct; only in *Androtrichum* it is considered distinct by some authors (Barros, 1947; Goetghebeur, 1998). According to our observations, the style base in *Androtrichum* is very similar to that of the rest of Cyperaceae, and should therefore be treated as not distinct. Within Cyperaceae, the persistence of the style base attached to the fruit is considered a variable character, and there are genera with style base persistent at fruit maturity (*Alinula*, *Androtrichum*, *Courtoisina*, *Isolepis*, *Kyllinga*, *Kyllingiella*, *Oxycaryum*, *Remirea*, *Scirpoides* and *Sphaerocyperus*), genera with style base deciduous (*Ascolepis*, *Dracoscirpoides*, *Erioscirpus*, *Ficinia*, *Hellmuthia*, *Queenslandiella* and *Volkiella*), and genera with style base persistent and deciduous (*Cyperus s.s.*, *Lipocarpha* and *Pycreus*).

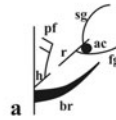
Dispersal Unit

The dispersal unit in the *Ficinia* clade is constant, and is in all cases the fruit singly (Table 1, Fig. 5c). In the *Cyperus* clade the variations in the dispersal unit are associated with the variations in rachilla articulations and spikelet flower number (Table 1). When the spikelets present a reduced number of flowers (1, 2 or 3), the dispersal unit is the spikelet. In these species, disarticulation may (1) occur above the insertion of the prophyll, with the bract, the prophyll and the hipopodium remaining on the rachis (*Alinula*, *Courtoisina*, *Kyllinga*, *Queenslandiella*, *Remirea* and *Sphaerocyperus*) (Fig. 5a) or with the bract also disarticulating (*Volkiella*); or (2) take place below the insertion of the prophyll, with the disarticulation of the prophyll together with the spikelet and also of the bract, with only the reduced hipopodium only remaining on the rachis (*Lipocarpha*) (Larridon et al., 2011b, 2013) (Fig. 5b). The only taxa where the developed prophyll accompanies the achene are *Lipocarpha*. In the case of *Ascolepis*, the bract and the reduced hipopodium persist on the rachis and the reduced spikelet falls, but the prophyll, which starts forming, does not develop to persist in the adult spikelet (Reutemann et al., 2014).

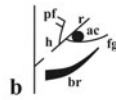
Fig. 5 Structure of the dispersal unit in Cyperaceae. **a** and **b** spikelet with reduced number of flowers, in which the dispersal unit is the spikelet; **c** spikelet with many flowers, in which each achene falls singly (= spikelets without articulate rachilla); **d** spikelet with many flowers, in which the rachilla falls entire (only one articulation present) or **e** spikelet with many flowers, in which the rachilla falls in fragments (several articulations present). *Abbreviations:* *ac* achene, *br* bract, *fg* fertile glume, *h* hipopodium, *pf* prophyll, *r* rachilla, *sg* sterile glume

SPIKELET WITH FEW FLOWERS

Rachilla articulation above prophyll insertion

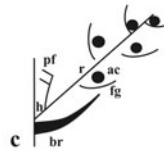


Rachilla articulation below prophyll insertion

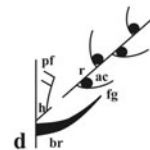
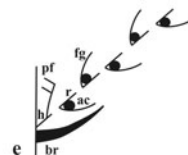


SPIKELET WITH MANY FLOWERS

Not articulated rachilla



Articulated rachilla

With an articulation above prophyll insertion*With articulations along the rachilla*

In many-flowered spikelets, the rachilla may be articulate or not. When the rachilla is not articulate, usually each achene falls singly like its glume, detaching from the base to the spikelet apex (*Cyperus s.s.*, *Cyperus* subg. *Juncellus* (Grisebach) C.B. Clarke, *Kyllingiella*, *Oxycaryum* and *Pycreus*) (Fig. 5c). In some species, the degree of inrolling of the glume margins (as well as the width of the glume wings) determines whether the fruit is clasped by the subtending glume and therefore falls with it (*Cyperus carinatus* R. Br. and *C. cunninghamii* (C.B. Clarke) C.A. Gardner), or whether the mature fruit falls separately from the glume (*Cyperus angustatus* R. Br. and *C. crispulus* K.L. Wilson) (Wilson,

1991). According to Wilson, the fruit may also fall with the glume in species with viscid spikelets: in *C. ixioxarpus* F. Muell., for example, the glume is mostly narrowly winged and the glume margins are not inrolled, but viscid secretions ensure that fruit and glume fall together.

When the rachilla is articulate, it may fall entire (only one articulation present) (Fig. 5d) or in fragments (several articulations present) (Fig. 5e). In the first case, articulation occurs above the prophyll insertion, which determines the spikelet to fall and the bract, the prophyll and the (highly reduced) hipopodium to remain on the rachis (*Cyperus* subgen. *Mariscus*, *Remirea* and *Sphaerocyperus*). In the second case, the articulations occur along the rachilla, generating more than one dispersal unit for each spikelet (*Cyperus* subg. *Torulinium* (Desv. ex Ham.) Kük.). For example, in *Cyperus odoratus* L., the rachilla disarticulates at the level of each glume insertion, and the dispersal unit is then formed by the glume, one rachilla internode and the achene (Barros, 1947; Larridon et al., 2013). Each rachilla internode is fused with the wing of the alternating upper glume; the whole is ovoid depressed on the inside by the pressure of achene, corchy, thick on the back gradually tapering in the wings embracing fruit. According to Barros (1947) *C. odoratus* presents a winged rachilla. But it is the wing of the glume that is fused to rachilla; and then the rachilla is usually observed to be winged (Vrijdaghs et al., 2010, 2011).

The dispersal strategy is directly linked to the dispersal unit structure. Dispersal by wind is probably effective in all species where the achenes are spread while enclosed in the glumes; in *Androtrichum* and *Erioscirpus*, the fruit is surrounded by long bristles, which correspond to elongated stamen filaments or perianth hairs, respectively. Few species have special structural adaptations to dispersal by water, some species of *Cyperus* have achenes which sink in water; the achenes in *Cyperus pectinatus* Vahl and *C. colymbetes* Kotschy & Peyr and *Oxycaryum cubense* (Poepp. & Kunth) Palla are long-floating since they are surrounded by corky tissue. This also applies to *Remirea maritima* Aubl., where corky swollen rachilla internodes remain attached to the achene (Haines & Lye, 1983). These authors recognize that endozooic dispersal is one of the most common ways of dispersal of the achenes.

Pseudospikelet

In the genera with single-flowered spikelets (*Alinula*, *Ascolepis*, *Lipocarpha* and *Volkiella*), the inflorescence consists of only one terminal spikelet-like spike, or presents one terminal and 1-few lateral spikelet-like spikes (Fig. 1a, b). Both terminal and lateral spikes are made up of numerous single-flowered spikelets (Haines & Lye, 1983; Goetghebeur, 1998). The similarity between these spikes and the many-flowered spikelets of Scirpeae has led some authors to refer to them as “pseudospikelets” (Haines & Lye, 1983; Hooper, 1986; Goetghebeur & Van der Borre, 1989). In genera where these pseudospikelets are recognized, the inflorescence performs the spikelet functions (Vrijdaghs et al., 2010). In Cyperoideae, the spikelets tend to take over the flower function, as in the flower-like inflorescences in Asteraceae Bercht. & J. Presl and some Euphorbiaceae Juss. (Vrijdaghs et al., 2010). In many genera of the Cyperaceae, the many-flowered spikelet performs the flower function, but in the highly derived genus of this tribe, the reduction of the spikelet is so advanced that the

inflorescence as a whole takes over the spikelet function (= flower function) (Goetghebeur, 1986; Vrijdaghs, 2006; Vrijdaghs et al., 2010).

Taxonomic and Phylogenetic Considerations of the Cyperae Spikelets

Spikelet structure in the Cyperae tribe is highly variable. Several trends and processes have determined morphological differences and similarities between the genera of this tribe. Different lineages subject to similar trends and processes show parallelism and reversions within Cyperaceae (Reutemann et al., 2012; Muasya et al., 2014).

Many spikelet traits studied in this work seem to have evolved more than once, independently, within Cyperae (Muasya et al., 2009a, b, 2012; Larridon et al., 2011b, 2013; Vrijdaghs et al., 2011; Reynders et al., 2012; Yano et al., 2012). Although there exist many convergent characteristics in cyperoid spikelets, some general traits are worth noting both in the *Cyperus* clade and in the *Ficinia* clade:

- (1) the number of glumes and flowers is highly variable in the *Cyperus* clade (from spikelets with few-many glumes/flowers to single-flowered spikelets), but it is a uniform character in the *Ficinia* clade (all the genera present spikelets with few-many flowers);
- (2) glume phyllotaxis is predominantly spiral in the *Ficinia* clade, except for a few species of *Ficinia* and *Isolepis*, while it is generally distichous in the *Cyperus* clade; only *Alinula*, a few species of *Cyperus* s.s., *Kyllingiella* and *Oxycaryum cubense* present spiral glume arrangement (Vrijdaghs et al., 2009); within the *Cyperus* clade, subclade *Cyperus* C₄ (= subgenera *Cyperus*, Larridon et al., 2013) includes taxa with invariable distichous glume arrangement. In *Cyperus* L. s.l., spikelets are distichously organized, which can be considered as a synapomorphy, though a number of reversals to terete spikelets with spiral glume arrangement are recorded (Muasya et al., 2001a);
- (3) the presence of winged glumes is observed in some genera of the *Cyperus* clade. In the *Ficinia* clade, the development of wings is only reported for the large glumes of *Hellmuthia*;
- (4) the presence of single-flowered spikelets and spikelet-like spikes is only observed within the *Cyperus* C₄ clade. In the phylogeny by Muasya et al. (2009b), if *Alinula paradoxa* (Chern.) Goetgh. & Vorster is excluded; the presence of single-flowered spikelets and spikelet-like spikes might result in a synapomorphy of the clade that groups the *Alinula*, *Ascolepis*, *Lipocarpa* and *Volkiella* genera;
- (5) the development of perianth segments is unique to the *Ficinia* clade and has never been reported for taxa of the *Cyperus* clade. Muasya et al. (2012) considered the presence of perianths to be an ancestral character among the Cyperoideae subfamily and they reported that perianths have been lost independently in multiple lineages, including Abildgaardieae and core Cyperae. These authors consider that the presence of perianths in *Dracoscirpoides*, *Erioscirpus* and *Hellmuthia* is a symplesiomorphy in Cyperae;
- (6) the development of a gynophore is typical of certain species of the *Ficinia* clade (Muasya & Simpson, 2002); in the *Cyperus* clade, the presence of a gynophore

- has only been reported for *Alimula lipocarphoides*. Several species of *Cyperus*, *Pycreus* and *Scirpoides* have a rudimentary gynophore (Vrijdaghs et al., 2011);
- (7) the dispersal unit in the *Ficinia* clade is constant, and is in all cases the fruit singly, but it is variable within the *Cyperus* clade. In the *Cyperus* clade, a significant variation may be observed in terms of the region where articulation occurs, which determines the dispersal unit structure. This topic should be dealt with in development studies encompassing all the observed variations;
 - (8) in the *Cyperus* clade, to a higher degree than in the *Ficinia* clade, there are reduced reproductive structures such as: (a) spikelets with few glumes and, therefore, few flowers; (b) spikelets with empty glumes; (c) perianthless flowers; (d) prophylls, glumes and/or bracts with bare or no development.

Conclusions

Consistently with the latest molecular phylogenies proposed for Cyperaceae, our results support the division of this tribe into two big groups with spikelet characters more or less typical and/or unique: the *Cyperus* and the *Ficinia* clades.

Within the *Cyperus* clade, the existence of spikelets with convergent characters among the different taxa supports the inclusion of all this clade taxa within one wide genus, *Cyperus*, just as the current phylogenetic hypotheses proposed for the group. Nevertheless, we believe deeper morphological studies should be carried out (for example, studies on inflorescence development or flower ultrastructure) on a wide range of species within the *Cyperus* clade. By finding characters to support the different subclades of the *Cyperus* clade, it would not be necessary to recognize a *Cyperus* genus so large and variable that it would be highly complicated to address from a taxonomic perspective.

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