

Spikelet structure and development in Cyperoideae (Cyperaceae): a monopodial general model based on ontogenetic evidence

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- **Background and Aims** In Cyperoideae, one of the two subfamilies in Cyperaceae, unresolved homology questions about spikelets remained. This was particularly the case in taxa with distichously organized spikelets and in Cariceae, a tribe with complex compound inflorescences comprising male (co)florescences and deciduous female single-flowered lateral spikelets. Using ontogenetic techniques, a wide range of taxa were investigated, including some controversial ones, in order to find morphological arguments to understand the nature of the spikelet in Cyperoideae. This paper presents a review of both new ontogenetic data and current knowledge, discussing a cyperoid, general, monopodial spikelet model.
- **Methods** Scanning electron microscopy and light microscopy were used to examine spikelets of 106 species from 33 cyperoid genera.
- **Results** Ontogenetic data presented allow a consistent cyperoid spikelet model to be defined. Scanning and light microscopic images in controversial taxa such as *Schoenus nigricans*, Cariceae and Cypereae are interpreted accordingly.
- **Conclusions** Spikelets in all species studied consist of an indeterminate rachilla, and one to many spirally to distichously arranged glumes, each subtending a flower or empty. Lateral spikelets are subtended by a bract and have a spikelet prophyll. In distichously organized spikelets, combined concaulescence of the flowers and epicaulescence (a newly defined metatopic displacement) of the glumes has caused interpretational controversy in the past. In Cariceae, the male (co)florescences are terminal spikelets. Female single-flowered spikelets are positioned proximally on the rachis. To explain both this and the secondary spikelets in some Cypereae, the existence of an ontogenetic switch determining the development of a primordium into flower, or lateral axis is postulated.

INTRODUCTION

In Cyperaceae, the larger of the two main clades comprises the majority of cyperaceous genera. The smaller clade, sister to the latter, is the mapanioid clade. Whereas previously four subfamilies were considered (Simpson *et al.*, 2007), currently both main clades have been recognized as the only two subfamilies of Cyperaceae, namely Cyperoideae and Mapanioideae (Fig. 1; Muasya *et al.*, 2009). Cyperoid Cyperaceae can easily be distinguished from Mapanioideae by the structure of their flowers, which can be considered as typically monocotyledonous, actinomorphic and pentacyclic (two trimerous whorls of perianth members, a trimerous diplostemonous androecium and a trimerous gynoecium), although reduction tendencies and many modifications occur. A cyperoid flower usually originates in the axil of a subtending bract, called glume (not homologous with glumes in Poaceae), with the glumes and their flowers being organized in spikelets (e.g. Haines and Lye, 1983; Goetghebeur, 1998; Vrijdaghs *et al.*, 2009). In contrast, a typical mapanioid reproductive unit exists comprising an ontogenetic apex with a single, terminal gynoecium, and lateral glume-like scales which may or not be positioned opposite a stamen. In the flowers of most

mapanioid species, 'empty' scales occur in between the terminal gynoecium and the more proximally positioned stamens (Haines and Lye, 1983; Goetghebeur, 1998). Because of this unusual (synapomorphic) organization, floral and spikelet structure remain to be clarified in mapanioid Cyperaceae.

Cyperoid spikelets as units of inflorescence

A cyperoid inflorescence has been described as a compound multiple spike because of the indeterminate nature of the ultimate inflorescence units (Kukkonen, 1994) or as a compound, paniculate inflorescence (Raynal, 1971), essentially a panicle of spikelets (Goetghebeur, 1998), where spikelets functionally replace the individual flowers of a panicle as defined by Weberling (1992). Therefore, the term 'paniculodium' was proposed for a cyperaceous panicle (Kukkonen, 1994; Vegetti, 2003). Usually, each branch of the inflorescence is subtended by a primary or involucre bract, and has an adaxially situated prophyll (between the new branch and its relative main axis or rachis). Modifications and reduction tendencies, including Troll's principle of variable proportions (Troll, 1959), have resulted in a wide range of derived inflorescences

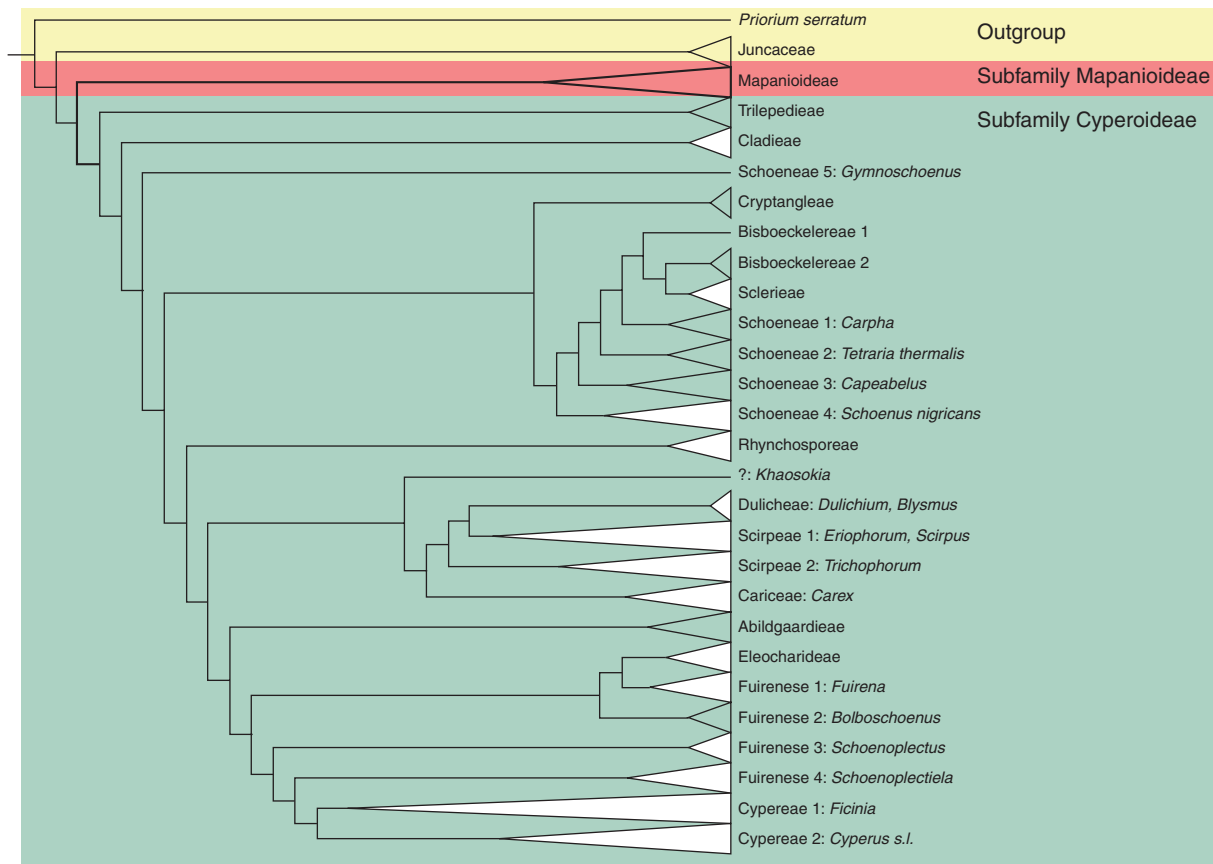


FIG. 1. Simplified cladogram of Cyperaceae, adapted from a strict consensus tree from Muasya *et al.* (2009). The studied species belong to the taxa coloured in white.

in Cyperoideae, varying from indeterminate spikes of spikelets and contracted pseudolateral capitate inflorescences to anthelas of spikelets or, as Kukkonen (1994) correctly called them, ‘anthelodia’ (Figs 2 and 3; Raynal, 1971; Haines and Lye, 1983; Goetghebeur, 1998; Vegetti, 2003; Guarise and Vegetti, 2008). Within the inflorescence, primary branches are subtended by primary or involucral bracts. In several genera, higher order branches are subtended by the prophyll of the relative main axis (Meert and Goetghebeur, 1979; Goetghebeur, 1986).

The structure of a cyperoid spikelet

Cyperoid spikelets are the ultimate branches of the inflorescence, acting both as a morphological and as a functional unit (Fig. 4). Consequently, a spikelet consists of a spikelet axis or rachilla, and few to numerous spirally to distichously arranged glumes, each subtending (or not) a single, bisexual or unisexual flower (Fig. 5; e.g. Eiten, 1976; Kukkonen, 1994; Goetghebeur, 1998). In Cyperoideae, spikelets tend to take over the flower function, as in the flower-like inflorescences in Asteraceae and some Euphorbiaceae. Moreover, taxa such as *Ascolepis*, *Kyllinga*, *Lipocarpha*, *Queenslandiella*, species of *Torulium* (= *Cyperus*), *Carex* and *Uncinia*, and many species belonging to the tribe Cypereae (*sensu* Goetghebeur, 1998) which were formerly classified in a distinct genus

Mariscus, have spikelets that are deciduous as a whole (Nees, 1835, p. 286; Larridon *et al.*, unpubl. res.).

According to Weberling’s typology (1992), the terminal spikelet of the main axis is a florescence and spikelets terminating lateral axes are co-florescences (Vegetti, 2003). The first scale on a lateral spikelet is a typical prophyll: situated adaxially and therefore often referred to as ‘addorsed prophyll’ (e.g. Kukkonen, 1994), usually two-keeled and not subtending a flower, except in Dullicheae and Cariceae *sensu* Goetghebeur (1998), where the prophyll forms a perigynium or utriculus around the female flower. The next glumes subtend (or not) a flower. The internode between the prophyll and the second glume, called an epipodium, is often elongated (e.g. Haines and Lye, 1983; Goetghebeur, 1986). A hypopodium, the internode between the bract subtending the spikelet and the prophyll, is usually absent (Fig. 6). Spikelets laterally positioned on a rachis are each subtended by a bract (Figs 6 and 7).

Many cyperoid species, however, have inflorescences with lateral spikelet clusters, in which several spikelets occur in the axil of a single subtending bract, as in *Cyperus luzulae* (Fig. 8). Guarise and Vegetti (2008) made an elaborate typological study of spikelet clusters in *Cyperus*. Spikelet clusters probably originate from a kind of *dédoublement* from the original primordium in the axil of the subtending bract, resulting in serial axillary buds. In other cases, prophyll branching occurs

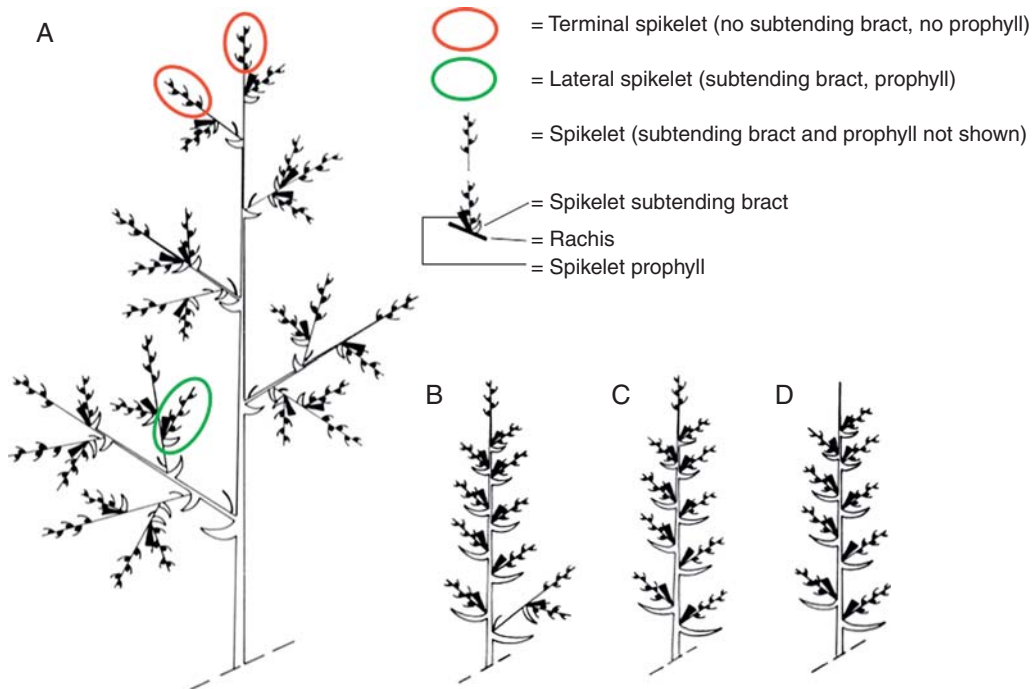


FIG. 2. Schematic representation of a typical cyperoid panicle of spikelets or paniculodium, and some possible modifications of it.



FIG. 3. Photographs illustrating inflorescence variation in Cyperoideae. From upper left- to lower right-hand corner: *Dulichium arundinaceum* (paniculate), *Cyperus haspan* (antherlate), *Rhynchospora latifolia* (capitate), *Eriophorum latifolium* (capitate), *Carex capitata* (compound spike), *Cyperus capitatus* (capitate).



FIG. 4. Photographs of part of the inflorescence in *Cyperus alternifolius* (left) and in *Lipocarpa chinensis* (right), with in each a single spikelet encircled in red. The single-flowered spikelet in *L. chinensis* is so reduced that the inflorescence as a whole takes over the spikelet function.

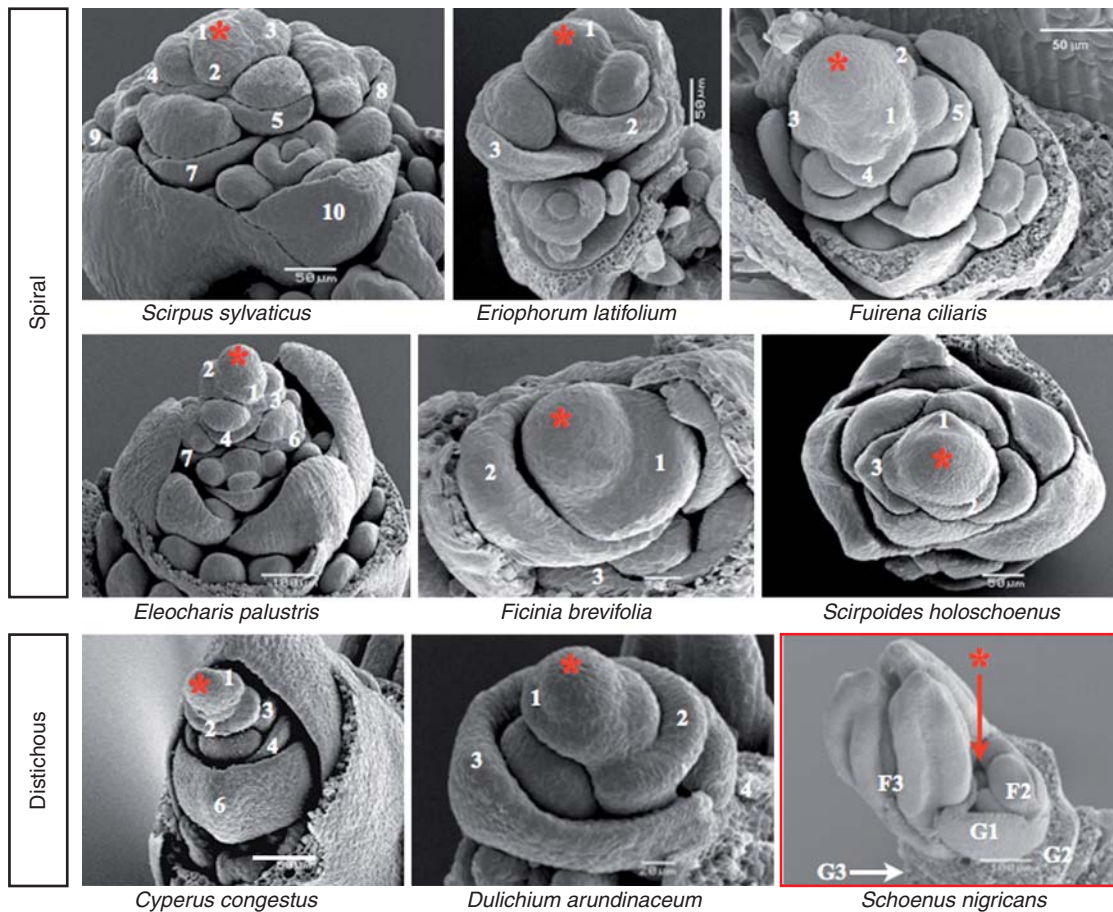


FIG. 5. SEM images of spikelets at early developmental stage in nine different cyperoid species, illustrating spirally and distichously organized spikelets. The two upper rows illustrate spikelets with a spiral arrangement of the glumes, the lower row spikelets with a distichous arrangement of the glumes. Spikelets in *Scirpus sylvaticus*, *Eriophorum latifolium*, *Fuirena ciliaris*, *Eleocharis palustris*, *Ficinia brevifolia* and *Scirpoides holoschoenus* have spirally arranged glumes, whereas spikelets in *Cyperus congestus* and *Dulichium arundinaceum* have distichously arranged glumes. This is also the case in *Schoenus nigricans*, of which only the distal part of the spikelet is shown here, illustrating the metatopic displacement of the distal flower. The numbers (1 = most recently originated) indicate glumes (each with its flower primordium in the axil) at different stages of development. Red frame: shown in more detail in Fig. 14. Abbreviations: F, flower primordium; G, glume; asterisk (*), rachilla apex.

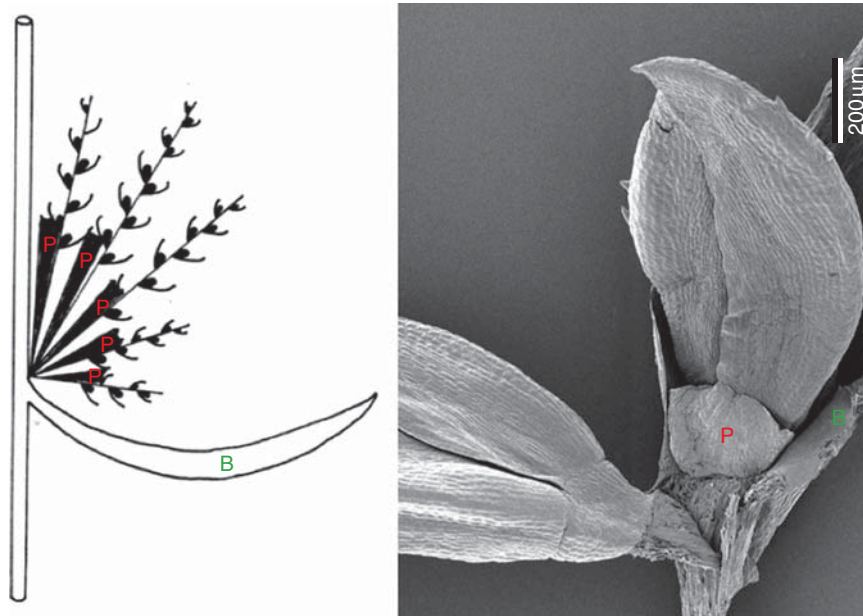


FIG. 8. Schematic presentation and SEM image of a serial spikelet cluster in *Cyperus luzulae*, subtended by a single, common bract. Each spikelet has its own prophyll. Abbreviations: B, bract subtending a serial cluster of spikelets; P, spikelet prophyll.



FIG. 9. Photograph of inflorescences in *Carex capitata*. Each inflorescence is a spike of spikelets, terminated by a florescence consisting of male reproductive units (or a terminal male spikelet), with open rachis. In the proximal part of the rachis, several spirally arranged female spikelets (encircled) occur.

not belong to the spikelet, precisely because in a culm with a terminal spikelet the latter is separated from the bract and prophyll of the culm by the total length of the culm and all branchings in between: ‘...For this reason, the subtending bract and prophyll, and the internode just below and just above the prophyll, are not considered to be part of the

spikelet, even when they are next to it.’ (Eiten, 1976, p. 82). Goetghebeur (1986, 1998) preferred to describe terminal spikelets as spikelets without bract and prophyll and lateral spikelets as subtended by a bract and having a spikelet prophyll.

The current study presents a review of the current knowledge about cyperoid spikelets, and includes some original ontogenetic scanning electron (SEM) and light microscopical (LM) data leading to a general, monopodial cyperoid spikelet model. Because our conclusions are based on over 8 years of observations in a wide range of cyperoid genera (Appendix 1), only a limited, highly illustrative selection of observations is shown here and discussed. The spikelet model allows all types of derived spikelets studied within Cyperoideae to be interpreted in an unambiguous, logical, standardized way.

Because of the large number of species and genera cited and to keep the text readable, an alphabetical list of the species including authorities is provided in Appendix 2.

MATERIAL AND METHODS

Spikelets of 106 species from 33 cyperoid genera (Fig. 1) were examined at early and mature stages (Appendix 1), of which only a representative selection of illustrative examples is presented here (Appendix 1, in bold type). Numbering of glumes and subtended flowers was done from most recently originated (1) to oldest (n), in order to avoid abstract numbers in spikelets with many and/or a variable number of (flower-subtending) glumes. Partial inflorescences were collected in the field or in botanical gardens (Appendix 1) and immediately fixed in FAA (70% ethanol, acetic acid, 40% formaldehyde, 90:5:5). Spikelets were dissected in 70% ethanol under a Wild M3 stereo microscope (Leica Microsystems AG, Wetzlar, Germany) equipped with a cold-light source (Schott KL1500; Schott-Fostec LLC, Auburn, NY, USA).

Scanning electron microscopy

To prepare the material for critical-point drying, it was washed twice with 70% ethanol for 5 min. Next it was placed in a mixture (1:1) of 70% ethanol and DMM (dimethoxymethane) for 5 min. The material was then transferred for 20 min to pure DMM. Critical-point drying was done using liquid CO₂ with a CPD 030 critical-point dryer (BAL-TEC AG, Balzers, Liechtenstein). The dried samples were mounted on aluminium stubs using Leit-C. For SEM observation, the material was coated with gold via an SPI-Module™ Sputter Coater (SPI Supplies, West-Chester, PA, USA). SEM images were obtained with a JEOL JSM-6360 (JEOL Ltd, Tokyo, Japan) at the Laboratory of Plant Systematics (K.U. Leuven), or with a JEOL JSM-5800 LV scanning electron microscope at the National Botanical Garden of Belgium in Meise.

Light microscopy

Spikelets were embedded in LR White Resin (London Resin Company Ltd, London, UK). The material was transferred gradually from pure ethanol to pure LR White (the first step over 1 h, all following steps over 4 h, starting with pure ethanol, followed by pure ethanol/LR White mixtures in decreasing volume proportions of 3:1, 2:1, 1:1, 1:2 and 1:3 and finally pure LR White. Polymerization was performed in an oven at 60 °C over 48 h. In order to remove possible air bubbles within the glumes, the material was treated in a Branson 2210 Auction (Branson Ultrasonics B.V., Soest, The Netherlands) ultrasonic cleaner, during the first two steps. The embedded material was cut at 2.5 µm with a Microm HM360 (Thermo Scientific, Walldorf, Germany) microtome. Staining was done with toluidin blue 0.1%, and subsequently the slices were mounted using Eukitt® (O. Kindler GmbH, Freiburg, Germany). LM images were observed with a Leitz Dialux 20 microscope (Wetzlar, Germany) and digital photographs were made with a PixeLINK (PL-B622CF, Ottawa, Canada) camera.

RESULTS

All cyperoid spikelets studied have an indeterminate axis (rachilla) with few to many glumes, each subtending (or not) a flower. New glumes originate successively immediately below the rachilla apex, as in *Scirpus sylvaticus* (Fig. 10). The glumes are spirally to distichously arranged and this organization may change in the course of spikelet development, as in *Scirpus falsus*, where newly formed, distally situated glumes are arranged distichously and more proximally, the glume arrangement is spiral (Fig. 11). In many species, the glumes become winged in the course of their development. In all distichously organized species studied, wings are present and decurrent, partially enveloping the lower, alternate flower. In the SEM image of *Cyperus laevigatus* (Fig. 12), two successive flowers are visible, an older one to the front coloured red, seen from the lateral–abaxial side, and an alternate, higher positioned, younger, blue-coloured flower to the rear. The wings (also in blue) of the glume subtending the ‘blue’ flower partially envelop the older, ‘red’ flower. The LM

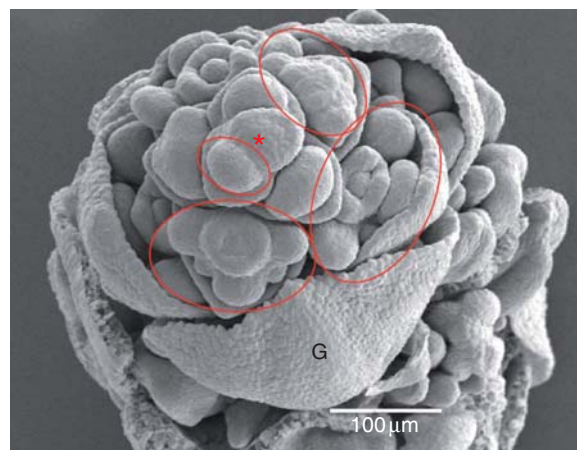


FIG. 10. SEM image of the distal part of a developing spikelet in *Scirpus sylvaticus*. Encircled in red are several glumes, each subtending a flower primordium at different developmental stages. Abbreviations: G, glume; asterisk (*), rachilla apex.

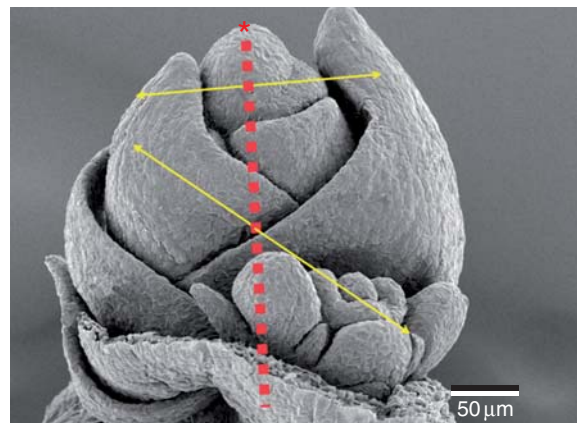


FIG. 11. SEM image of the distal part of a spikelet in *Scirpus falsus*, showing an initially spiral organization, becoming distichous at later (distally situated) stages. The red dotted line indicates the rachilla.

image (Fig. 12) shows a cross-section through a spikelet of *Cyperus laevigatus* at the height of the insertion of the staminal filaments on the flower receptacle of a flower corresponding to the ‘red’ flower in the SEM image, as indicated by a red line on the SEM image. In the LM image, the corresponding flower is encircled. The wings of the flower subtending the glume (coloured in red) are fused with the rachilla (green coloured zone). The fusion zone of wings and rachilla grows with the rising rachilla, as in, for example, *Pycurus pumilus* (Fig. 13), consequently lifting up the main part of the glume. Simultaneously, there is metatopic displacement (see also the first paragraph in the discussion and Fig. 20) of the proximal flower primordium, which was raised by the growth of the rachilla and consequently separated from its subtending glume (indicated by a green double arrow at the right-hand image). The developing proximal flower is partially enclosed by the wings of the subtending glume of the alternate, higher positioned, second flower. In *Pycurus pumilus*, the glume-like prophyll has a swelling body situated between the prophyll/rachilla and the (removed) rachis. Quite early in

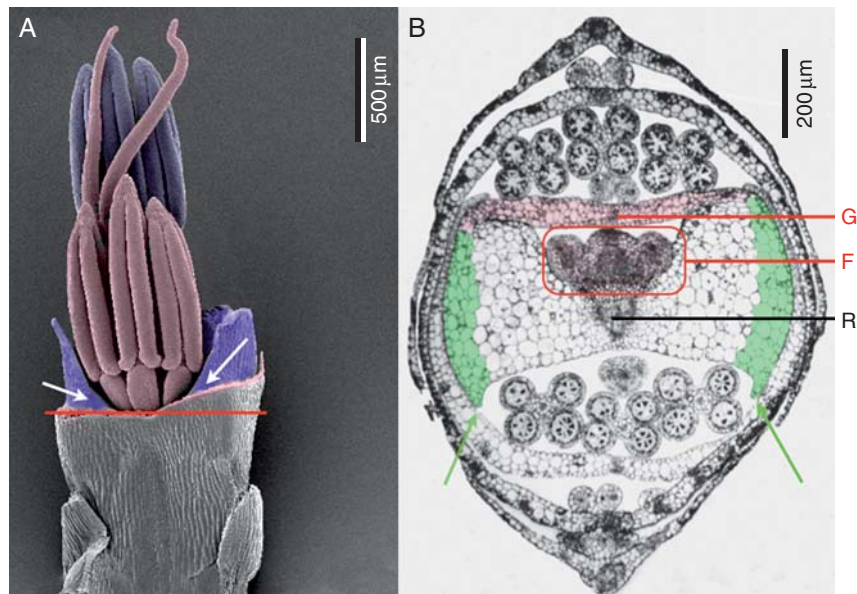


FIG. 12. Spikelet structure in *Cyperus laevigatus*. (A) SEM image of a developing part of a spikelet, with lateral–abaxial view on the flower coloured in red. Of this flower, the three stamens are visible with the two stigma branches protruding above them. This flower is partially enveloped by the glume wings of the alternate, upper flower (coloured in blue). Arrows indicate the wing tips. The red line at the base of the flower indicates the zone represented in the transverse section shown in B, particularly the flower coloured in red. (B) LM image of a transverse section at the base of a flower (encircled in red). The glume of this flower (coloured in red) has wings which are fused with the rachilla (fusion zone coloured in green). The arrows indicate the wing tips at the alternate side. Abbreviations: F, flower; G, glume; RI, rachilla.

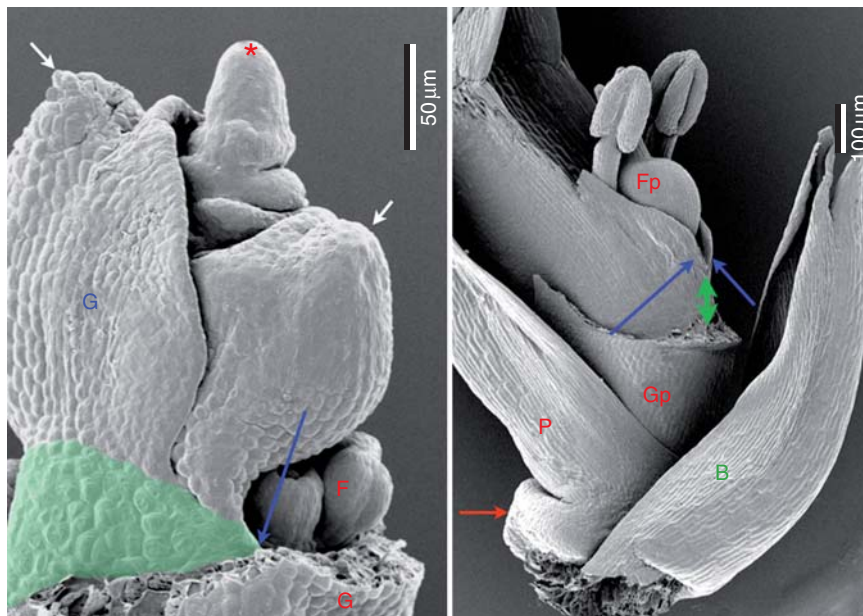


FIG. 13. SEM images of a developing spikelet in *Pycurus pumilus*. The distal part with the rachilla apex is shown at the left; the proximal part with the spikelet subtending bract is shown at the right. Blue arrows indicate the wing tips of an alternate, more distally situated flower, partially enveloping the given flower. White arrows indicate the formation of a mucro, which gives the more mature glumes a cap-like aspect. The red arrow indicates the swelling body at the base of the spikelet prophyll. The double arrow in green shows the metatopic displacement by concaulescent growth of the proximal flower with the rachilla, separating the flower from the proximal glume. Abbreviations: B, spikelet subtending bract; F, flower; Fp, proximal flower; G, glume; Gp, proximal glume; asterisk (*), rachilla apex.

their development, the glumes develop a pointed cap-like mucro (Fig. 13). In *Schoenus nigricans*, the concaulescent displacement of the distalmost positioned flower is so extreme that the distal (empty) glume (Gd) is positioned lower than

the distalmost positioned flower (F1). The glume of this distalmost positioned flower (G1), which is not the distal glume, is positioned alternately and lower than the distal glume (Fig. 14). In this example the rachilla apex is hidden

between the distalmost flower primordium and the distal glume.

In all Cariceae investigated, the male reproduction units together form a (co)florescence or terminal spikelet. Each primordium of a male reproduction unit is formed in the axil of a glume-like scale. These originate successively, immediately below the apex of the indeterminate rachis. Subsequently, this primordium differentiates into three stamen primordia. These develop into filaments and anthers (Fig. 15). Proximally on the rachis, female, single-flowered spikelets are formed with a more or less developed rachilla, depending on the genus or species considered. In most cases, the rachilla

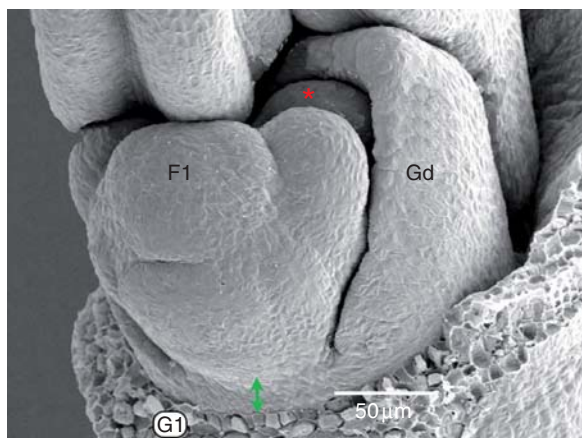


FIG. 14. SEM image of the distal part of a spikelet in *Schoenus nigricans*. The rachilla apex is hidden between the distal glume, which is the most recently formed and (still) empty glume, and the most recently formed flower primordium (F1). This flower primordium is separated from its glume (G1, which is the second youngest glume after the distal one) by concaulescent growth with the rachilla (green double arrow), and partially enveloped by the wings of the distal glume. Abbreviations: F1, most recently formed flower primordium; G1, glume subtending F1; Gd, distal glume; asterisk (*), rachilla apex.

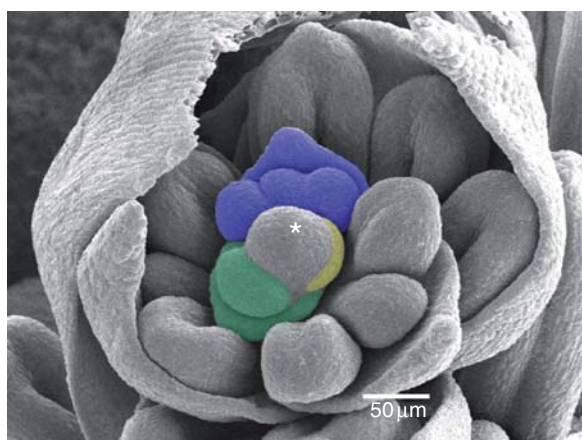


FIG. 15. SEM image of the distal part of a spike of spikelets in *Carex crinitella*, with apical view on the developing terminal male spikelet with several new glume-like bracts, each subtending a male flower primordium at different stages of development (yellow, newly originating bract; green, bract with undifferentiated flower primordium; blue, bract with flower primordium differentiating into three stamen primordia). Abbreviation: asterisk (*), rachis apex.

of a female spikelet grows out radially with respect to the relative main axis. In most *Carex* species, the rachilla remains under-developed, only visible at the abaxial side inside the perigynium (prophyll), below the female flower, at early developmental stages as shown here in *Carex pendula* (Fig. 16). The prophyll of the spikelet in *Carex pendula* is tubular at its base, but forms a two-keeled glume-like structure at the adaxial side (between rachilla and rachis). The developing, single, female flower of the spikelet is subtended by the prophyll (perigynium), and consists of only a dimerous gynoeceum with two, laterally situated, stigma primordia. At this developmental stage, the ovary is still open, showing a single, centrally positioned ovule primordium (Fig. 16). In contrast, in *Uncinia rubra*, the prophyll develops very soon into a closed, tubular utriculus, surrounding both the female flower it subtends and the rachilla. The rachilla grows out and a single glume is formed, which because of its position can be considered to be proximal as well as distal glume. The female spikelets show torsion with respect to the radial plane (determined by the rachis and the bract subtending the spikelet). As a result, the female spikelet appears to be fixed adjacently on the rachis (Fig. 16). The developing female flower in *Uncinia rubra* consists of a trimerous gynoeceum, with the ovary wall surrounding the central ovule primordium, and on the top of the ovary wall two lateral and a single abaxial (with respect to the rachilla) stigma primordia (Fig. 16).

Spikelet reduction has been observed in many other taxa, for example *Lipocarpha*. In *Lipocarpha nana*, an inflorescence at early developmental stage consists of an indeterminate rachis, and many, spirally arranged spikelet primordia, each subtended by a bract. This inflorescence primordium is reminiscent of a developing spikelet in *Fuirena ciliaris*, consisting of an indeterminate rachilla, and many spirally arranged glumes, each subtending a flower primordium (Fig. 17). Spikelet primordia in *Lipocarpha nana* develop into single-flowered spikelets, each with a prophyll and a proximal glume, which subtends the flower primordium (Fig. 18).

DISCUSSION

Spikelets are indeterminate ultimate branches of the inflorescence

In most of the species studied, lateral spikelets obviously consist of an indeterminate rachilla, few to many lateral, distichously to spirally arranged glumes, each subtending (or not) a flower, and a prophyll at the base of the rachilla. All terminal spikelets observed also have an indeterminate axis. In all spikelets studied, older flowers are always situated proximally, whereas new glumes always appear laterally, immediately beneath the rachilla (or axis) apex. Therefore, each previous attempt to interpret spikelets as sympodial structures (e.g. Celakovsky, 1887; Kern, 1962; Richards *et al.*, 2006) seems artificial and requires several auxiliary hypotheses to support the interpretation (Vrijdaghs *et al.*, 2007). However, it is clear that some spikelets are more complex and difficult to interpret. Distichously arranged spikelets with winged glumes in particular have caused interpretational confusion. These spikelets were used as an argument in favour of the sympodial interpretation. Therefore, much attention was given to

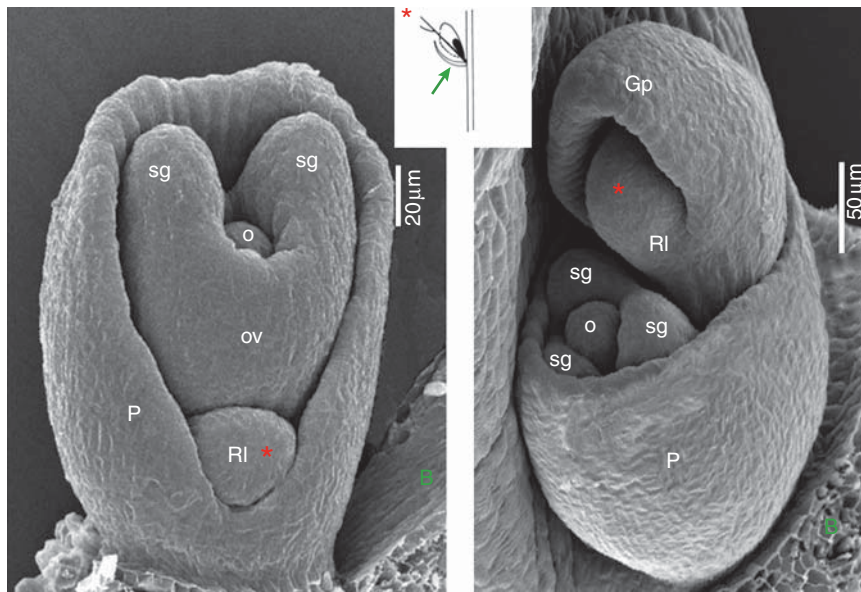


FIG. 16. SEM images of female spikelets in *Carex pendula* (left) and *Uncinia rubra* (right). The view on the female flower in *C. pendula* is adaxial with respect to the rachilla or abaxial if the rachis (not visible) is taken as reference, with the rudimentary rachilla below the female flower. The developing prophyll (perigynium) is situated between rachilla and rachis, at this developmental stage forming two conspicuous keels. The developing female flower consists of a dorsiventrally flattened ovary. The still open ovary wall surrounds the central ovule. On the top of the ovary wall, two laterally situated stigma primordia are visible. The female spikelets in *U. rubra* underwent a torsion with respect to the plane defined by the rachis and the bract subtending the considered spikelet, so that they appear adjacently positioned. The image gives an abaxial (with respect to the rachilla) view of the female flower, subtended by the tubular spikelet prophyll, which forms a nearly closed perigynium. The rachilla in *U. rubra* grows out and a first glume or proximal glume is formed. This glume can also be termed distal glume, as no other glumes are formed. Abbreviations: B, bract subtending a spikelet; Gp, proximal glume; o, ovule; ov, ovary wall; Rl, rachilla; sg, stigma primordium; P, spikelet prophyll; asterisk (*), rachilla apex.

distichously organized spikelets with glumes with large wings, such as the spikelets in many species of the Cypereae tribe (*sensu* Goetghebeur, 1998). Vrijdaghs *et al.* (2007) showed that spikelets in *Schoenus nigricans* have the same *Bauplan* (building plan, blueprint) as the spikelets in most other cyperoid genera. They considered the interpretational confusion in spikelets in *Schoenus nigricans* to be caused by concaulescent metatopic displacement (Weberling, 1992) of flowers. This causes the distal glume to be positioned lower than the last formed flower. The glumes in *Schoenus nigricans* are winged, with the wings partially enveloping the lower alternate flower. This is also the case in most Cypereae species. Figures 12 and 13 show that the bases of the wings are fused with the rachilla. This fusion zone grows with the rising rachilla, elongating the wing tips along the internode and displacing the main part of the glume and the flower primordium in its axil.

In summary, the idiosyncratic structure of distichously organized spikelets is due to two distinct phenomena of metatopic displacement which may be present simultaneously to a greater or lesser degree: (1) concaulescent growth of the flower with the rachilla, which separates it from its subtending glume; and (2) in distichously organized spikelets most of a glume (including the flower primordium in its axil) is displaced by the growth of the fusion zone of the rachilla itself (and not a newly formed lateral axis) and the wings of the glume. As a consequence, 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. At the initial insertion

point of the glume, the wing tips may develop, partially enveloping a previously formed flower, which is at a lower position of the alternate side with respect to the displaced main part of the considered glume (Figs 12, 13 and 19). This kind of metatopic displacement was not defined by Weberling (1992), who distinguished between concaulescence, recaulescence and anaphysis: ‘In recaulescence the axillary bud is shifted for some distance towards the base of the subtending leaf, the insertion of which is displaced on the branch for a smaller or greater distance above its original position, after stretching of the common basal zone of both organs’ (Weberling, 1992, p. 217). Consequently, in recaulescence, the main part of a bract is displaced by growth of the newly formed lateral axis which it subtends, thus transforming the part of the newly formed axis between the insertion point of the bract (where the new axis initially originated) and the displaced main part of the bract into a recaulescent zone. The lateral axis develops further above the displaced main part of the bract, there consisting of a ‘normal’ axis which will be terminated by a flower (Fig. 20). The metatopic displacement of the main part of the glumes in distichous spikelets also differs from Weberling’s definition of anaphysis: ‘We speak of anaphysis if an axillary bud with its subtending bract “is moved up to a position above the bract which follows it genetically” . . .’ (Weberling, 1992, p. 218).

Therefore, we suggest a new term for this kind of ‘recaulescence along the rachilla itself’, *epicaulescence*, as the displacement of the main part of the glume occurs upon the rachilla (Figs 19 and 20). In *Schoenus nigricans*, the concaulescent metatopic displacement of the flower is quite

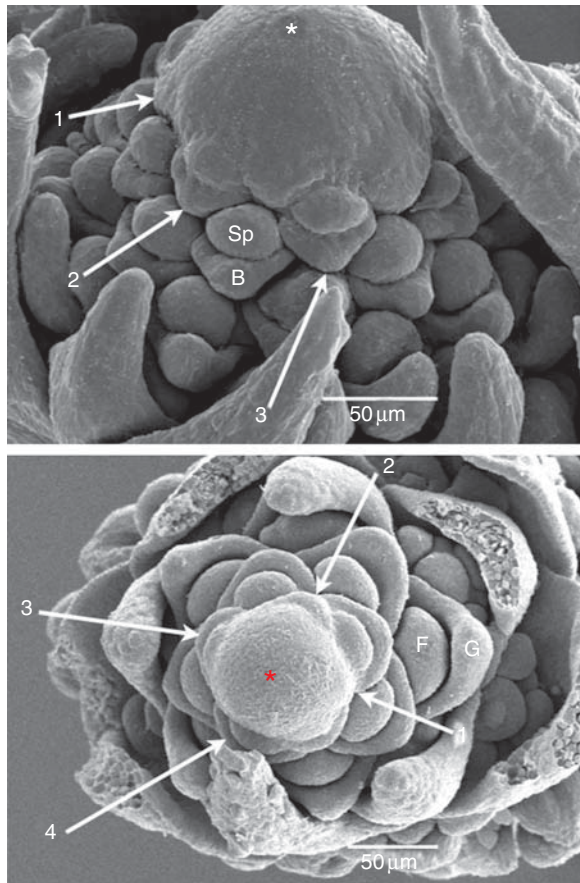


FIG. 17. SEM images of the distal part of a spike of spikelets in *Lipocarpha nana* (top) compared with the distal part of a spikelet in *Fuirena ciliaris* (bottom). Arrows indicate bracts subtending a spikelet, each with a spikelet primordium in its axil for *L. nana*, and glumes, each with a flower primordium for *F. ciliaris*. Numbering from young (1) to more mature. Abbreviations: B, bract; F, flower primordium; G, glume; Sp, spikelet primordium; asterisk (*), rachis/rachilla apex.

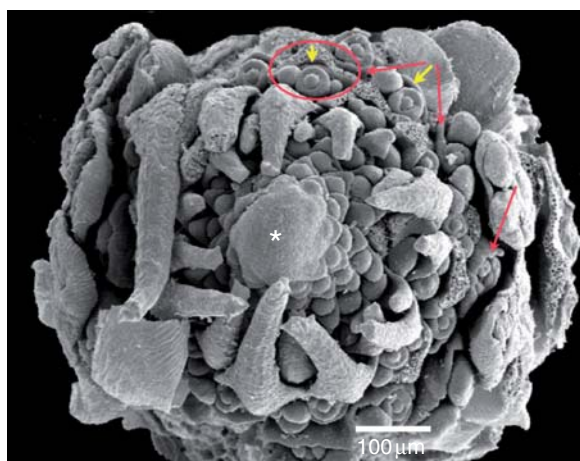


FIG. 18. SEM image; apical view of the distal part of a spike of spikelets in *Lipocarpha nana*. Encircled in red is a developing, single-flowered spikelet. Red arrows indicate spikelet prophylls, yellow arrows glumes subtending a flower. Abbreviation: asterisk (*), rachis apex.

extreme, so it is possible that the next glume originates between the newest flower, which seems to be positioned above the rachilla apex and its subtending glume (Fig. 14). As a consequence, this phenomenon, combined with the epicaulescent growth of the wings of the glumes, gives the impression that the flower is terminating a new lateral axis.

In spikelets of *Cyperus falsus*, the proximal glumes are arranged spirally, whereas the distal ones are arranged distichously. Consequently, distichous arrangement of the glumes occurs at later stages of spikelet development. However, in *Abildgaardia*, the proximal glumes are arranged distichously and the distal ones spirally. In some species, such as *Ficinia fascicularis*, *Machaerina anceps* and *Rhynchospora pubera* (Goetghebeur, 1986), co(florescences) or terminal spikelets have a spiral arrangement of the glumes, whereas the lateral spikelets have a distichous organization. In contrast, in *Blysmus* the terminal spikelets are distichously organized and the lateral ones spirally. This shows that the characters ‘distichous/spiral (and all intermediary phyllotaxies) arrangement of the glumes’ often depend on conditions of growth and spacial environment.

Female spikelets and male (co)florescences/terminal spikelets in Cariceae

In Cariceae, the inflorescence is often a spike of spikelets with the male reproductive units at the distal part, and the female spikelets proximally (Figs 9, 15 and 21). Ontogenetically, this *Bauplan* or building plan raises questions about the concept of the spikelet itself, as Timonen (1998) has already stated. Moreover, as the male reproductive units as well as the female spikelets each originate from a primordium in the axil of a bract, all these primordia are (serially) homologous, taking positional homology as the main criterion (Fig. 21; Remane, 1956; Classen-Bockhoff, 2005). This logically brought Timonen to suppose that the male reproductive units must be highly reduced male spikelets (Timonen, 1993, 1998). However, neither she nor other investigators found indications of a reduction of a hypothetical more developed spikelet with male flowers. In contrast, in the female spikelets, such reduction series exists (e.g. Haines and Lye, 1983; Goetghebeur, 1986). Moreover, ontogenetic investigation of the male reproductive units has until now not revealed remnants of spikelet structures such as a prophyll, rachilla, glumes or non-androecial floral parts (Fig. 15). Therefore, we consider that the male reproduction units are not derived by reduction from a hypothetical ancestral spikelet and that, consequently, further ontogenetic research for remnants of such a reduction is of little value. We consider the male reproductive units to be real male flowers. In analogy with Gould’s (2002) suggestion that floral primordia or phylomes can be considered as ‘empty boxes’ to be filled in by the expression of developmental processes and regulation systems such as the ABC-model of Weigel and Meyerowitz (1994), we postulate that all primordia formed in the axil of successively originating glumes/bracts should be considered as developmentally undetermined, homologous by position to each other and consequently serial homologues. However, due to the open nature of plant development, primordia have a large flexibility to follow one (or possibly several simultaneously expressed) developmental programme(s). The

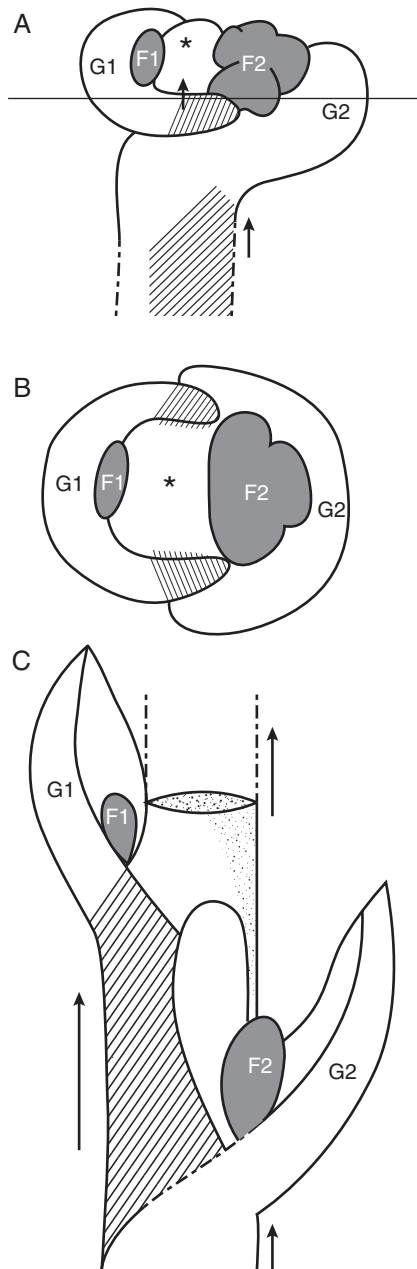


FIG. 19. Schematic outline of the structure of a distichously organized spikelet, based on empirical observation. (A) Lateral view of the distal part of the rachilla. (B) Transverse section as indicated by a line in (A). (C) Lateral view on an internode of a spikelet. Arrows indicate the growth direction of the rachilla. Numbers from young (1) to old (2). In (A), G1 corresponds to the distal glume, subtending the distal flower F1. Shaded zones represent fusion zones between wings of glumes and the rachilla. Because of epicaulescent growth of these zones with the rachilla, the wings of the glumes are elongated along the alternate side of the rachilla. They envelop partially a lower, alternate flower. Abbreviations: F, flower; G, glume; asterisk (*), rachilla apex.

activated developmental programme(s) will eventually determine the ‘special quality’ (Remane, 1956) of the structure that is developed from a given primordium; in other words, its identity. Because of the flexibility of plants to activate different developmental programmes in a given primordium according

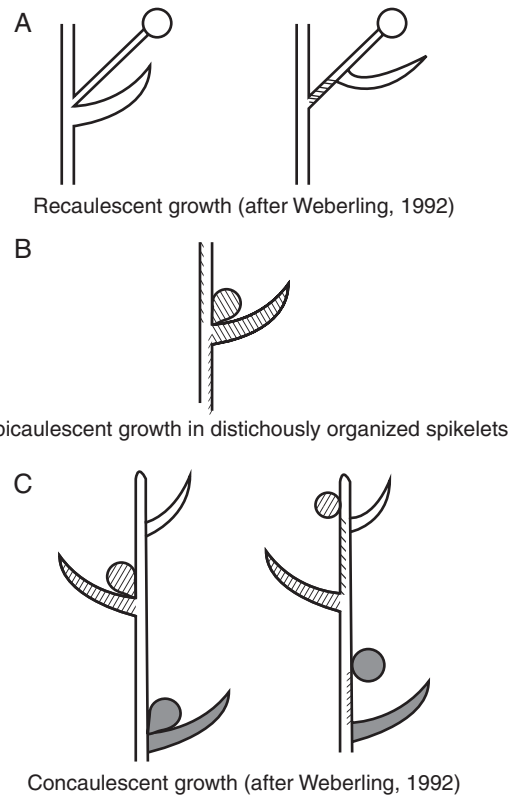


FIG. 20. Schematic theoretical outline of different kinds of metatopic displacement: concaulescence and recaulescence after Weberling (1992); epicaulescence, a newly defined metatopic displacement based on our empirical observations in distichously organized cyperoid spikelets. Concaulescent growth of a flower primordium occurs when it is partially fused with the rachilla apex and lifted up by the growth of the rachilla. Consequently, the flower primordium is separated from its glume. Recalescence occurs when a similar partial fusion of a bract primordium with the axis it subtends causes part of the developing bract to be lifted up by the growth of the lateral axis. Epicaulescence differs from recaulescence in the fusion of a part of the distal bract primordium with the apex of the rachilla. When the rachilla grows, the bract is partially shifted upwards along the rachilla. Both recaulescence and epicaulescence usually cause the axis where the respective phenomenon occurs to be winged.

to circumstances and needs of the moment, we consider that in plants, ‘special quality’ is a secondary, though indispensable, homology criterion, as it depends on the activation of the developmental programme(s) that will eventually give identity to the structure; the only stable morphological homology criterion referring to the ontogenetic origin is ‘position’ (Remane, 1956; Classen-Bockhoff, 2005). This explains that in Cariceae, homologous primordia can develop into structures as different as female spikelets and male flowers. The above-mentioned developmental flexibility of plants also explains why we do not find remnants of spikelet structures in the male flowers, as the switching on or off of developmental programmes (in the case of Cariceae, it concerns the programmes making a given primordium develop into a male flower, or a female spikelet) is not the result of evolution. The fact that in Cariceae this kind of inflorescence apparently is successful only shows that using flexibility in the ‘filling in of empty boxes’ can result in fit plants. Moreover, in Cariceae, the female spikelets are deciduous as a whole. In contrast, the male reproductive units are not,

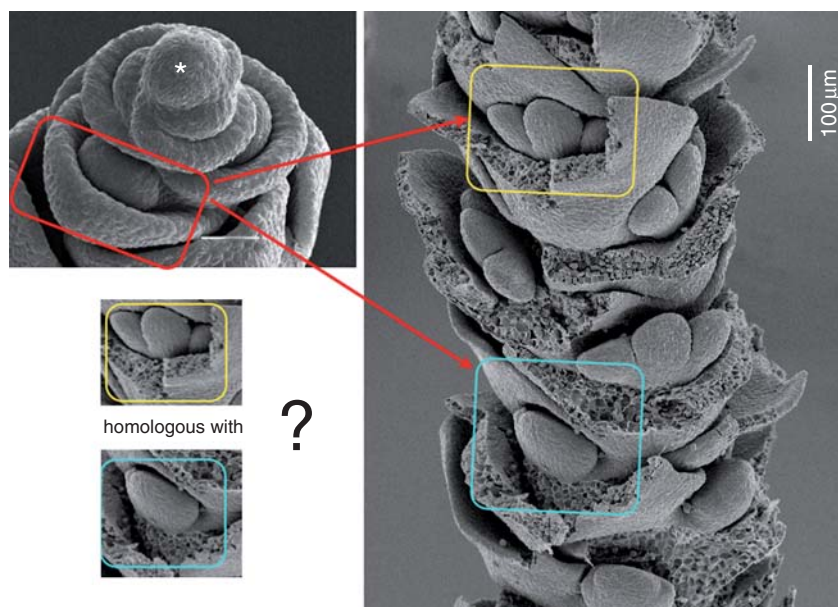


FIG. 21. SEM images of a spike in *Uncinia rubra*, showing the development of a primordium (red frame) into either a male reproduction unit (yellow frame) situated in the florescence, or a female spikelet (blue frame). The latter occurs only at very early stages of spike development, and consequently later female spikelets are always situated proximally in the spike.

and these usually terminate a culm or a lateral axis (with the exception of *Carex* section *Vignea*). Consequently, male (co)florescences are considered to be terminal spikelets, consisting of the axis and glumes subtending male flowers.

Symptoms of an ontogenetic switch 'flower/lateral spikelet'

In several species of the tribe Cyperae *sensu* Goetghebeur (1998), a highly derived tribe within Cyperoideae (Fig. 1), a similar, but inverse phenomenon within spikelets was observed: primordia in the axil of new glumes are supposed to develop into flowers. However, often some of these primordia do not develop into a flower, but into a secondary spikelet (Vrijdaghs *et al.*, 2009). Here, too, all primordia in the axil of a glume are position homologues. And the 'filling in of the empty box' determines the final 'special quality' of the resulting structure, 'flower' or 'secondary spikelet'. One might interpret (as we earlier did) this phenomenon as an indication that spikelets result from a reduction of a compound partial inflorescence, but why then have we not found more transitional forms in all tribes, especially the more basal ones such as Scirpeae (Fig. 1)? The answer is again that there was no such evolution from a compound partial inflorescence to a modern spikelet, but that the occurrence of secondary spikelets follows from the flexibility that plants possess to activate different developmental programmes in a given primordium. Related to the discussion above about the determination of a given primordium is the study of the transition zone in species with terminal spikelets, such as *Cyperus luzulae*. Following Weberling (1992), a terminal spikelet is a florescence (Guarise and Vegetti, 2008), with bracts (glumes) each subtending a flower. These originate in the same way as in lateral spikelets, immediately beneath the apex of the axis (rachis). Developing bracts soon get a primordium in their

axil, which develops into a flower, or at a given moment into a spikelet. Again this concerns position homologues, empty boxes, which will be filled in first as spikelets and later as flowers. Another illustration of this principle is given by the development of species of *Lipocarpha*. There is a striking analogy between the development of an inflorescence (spike of spikelets) of a species such as *Lipocarpha nana* and the development of a spikelet in one such as *Fuirena ciliaris* (Figs 17 and 18). However, each primordium in *L. nana* is determined to develop into a single flower spikelet, whereas similar primordia in *F. ciliaris* develop into flowers (Fig. 18). The results of Smith (1967), showing that phytohormones influence the determination of axillary primordia in *Carex* (whether they develop into male flower, lateral spike of spikelets or female spikelets), also suggest the existence of an ontogenetic switch.

CONCLUSIONS

In all cyperoid species studied, spikelets, the ultimate inflorescence branches, consist of a indeterminate rachilla, and one to many spirally to distichously arranged glumes, each subtending (or not) a flower. Typologically, spikelets are open spikes or racemose ultimate inflorescence branches. In spikelets with distichously arranged glumes, the glumes often have wings. A fusion zone of the wings of a glume and the rachilla grows out with the rising rachilla, displacing metatopically the main part of the glume and the flower primordium in its axil to the next node. This previously undescribed kind of metatopic displacement is termed here 'epicaulescence'. Moreover, in distichously organized spikelets, the flowers tend to grow concaulescently with the rachilla, which separates them from their subtending glume. The combination of both metatopic displacement phenomena results in a zigzagging

rachilla at maturity, which caused interpretational controversy in the past. In several clades, particularly the most derived ones, there is a tendency towards reduction of the spikelets and to transfer the spikelet functions to the inflorescence. In Cyperaceae, primordia in the axil of a glume sometimes develop into a secondary spikelet instead of a flower. This can be explained by a putative ontogenetic switch which determines whether such a primordium will develop into a flower or into a lateral axis (secondary spikelet). In that way, in Cariceae, the initial formation of (later in the development of the proximally positioned spike) female single-flowered spikelets and later the formation of (consequently distally positioned) male flowers, both from positionally homologous primordia, can be understood.

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APPENDIX 1

Species of Cyperaceae studied and voucher data

Species	Collected by	Localization	Date	Voucher number
<i>Alinula lipocarhoides</i>	Muasya	Kenya		AM 2592
<i>Baumea rubiginosa</i>	Hodgon/Bruhl	Western Australia	10/2003	JH 792
<i>Bulbostylis hispidula</i>	Muasya	Kenya		AM 2126
<i>Bulbostylis hispidula</i>	Muasya	Kenya		AM 2466
<i>Carex capitata</i>	Goetghebeur	University of Gent	04/2005	PG 10465
<i>Carex capitata</i>	Goetghebeur	University of Gent	04/2005	PG 10466
<i>Carex cristatella</i>	AV	University of Gent		
<i>Carex elata</i>	AV	Ptk-K.U. Leuven	05/2005	AV 11
<i>Carex pallescens</i>	AV	Ptk-K.U. Leuven	04/2002	AV 07
<i>Carex pendula</i>	Goetghebeur	University of Gent	04/2001	
<i>Carpha</i> sp.	Muasya	South Africa (SA)	12/2006	AM 2907
<i>Cladium mariscus</i>	AV	KDTN-Leuven	04–06/2002	AV 05
<i>Cladium mariscus</i>	AV	KDTN-Leuven	04–06/2002	AV 05
<i>Cladium mariscus</i>	AV	NPMeise	05/2002	AV 06
<i>Coleochloa setifera</i>	Muasya	Kenya		AM 2464
<i>Courtoisina assimilis</i>	Muasya	Kenya		AM 2124
<i>Cyperus capitatus</i>	Goetghebeur	University of Gent, HBUG2003-1782(w)		PG 10744
<i>Cyperus capitatus</i>	Reynders	University of Gent, HBUG2003-1782(w)		
<i>Cyperus congestus</i>	Reynders	University of Gent, HBUG2002-0872		2002-0872
<i>Cyperus denudatus</i>	Muasya	Kenya		AM 2417
<i>Cyperus digitalis</i>	Muasya	Kenya		AM 2162
<i>Cyperus distans</i>	Mwachala	SA	12/2006	Mwachala 694
<i>Cyperus distans</i>	Muasya	Kenya		AM 2121
<i>Cyperus dubius</i>	Muasya	Kenya		AM 2188
<i>Cyperus dubius</i>	Mwachala ea	Kenya		EW 3878
<i>Cyperus eragrostis</i>	I. Larridon	University of Gent, HBUG1986-0588	2008	1986-0588
<i>Cyperus haspan</i>	Muasya	Kenya		AM 2135 (EA)
<i>Cyperus hemisphaericus</i>	Mwachala ea	Kenya		EW 3893
<i>Cyperus involucreatus</i>	I. Larridon	University of Gent, HBUG1900-1130	2008	1900-1130
<i>Cyperus kerstenii</i>	Muasya	Kenya	2005	AM 2534
<i>Cyperus laevigatus</i>	Goetghebeur	University of Gent, HBUG1997-1237	09/2004	PG 10202
<i>Cyperus laevigatus 2002 0878</i>	Reynders	University of Gent, HBUG2002-0878	2006	2002-0878
<i>Cyperus laevigatus</i>	Muasya	Kenya		AM 2610
<i>Cyperus luzulae</i>	AV	University of Gent (S.Am), HBUG1900-3306		19003306
<i>Cyperus pectinatus</i>	Mwachala	Kenya		Mwachala 341
<i>Cyperus podocarpus</i>	A Chevalier	Mali	1910	AC 2472 (BR)
<i>Cyperus prolifer</i>	I. Larridon	University of Gent, HBUG2001-1697	2008	2001-1697
<i>Cyperus natalensis</i>	Muasya	SA	04/2008	AM 3805
<i>Cyperus owanii</i>	I.Larridon	University of Gent, HBUG1985-0260	2008	1985-0260
<i>Cyperus pulchellus</i>	Muasya	Kenya		AM 2131
<i>Cyperus rotundus</i>	Muasya	Kenya		AM 2117
<i>Cyperus rotundus</i>	Muasya	Kenya		AM 2164
<i>Cyperus squamosus</i>	Muasya	Kenya		AM 2122
<i>Scirpus falsus</i>	Muasya	SA	04/2008	AM 3748
<i>Dulichium arundinaceum</i>	Goetghebeur	University of Gent	2003	PG 9914
<i>Eleocharis palustris</i>	AV	KDTN-Leuven	09/04/02	AV07a
<i>Eleocharis palustris</i>	AV	KDTN-Leuven		AV07b
<i>Eriophorum latifolium</i>	Goetghebeur	University of Gent	03/2004	PG 10185
<i>Eriophorum latifolium</i>	AV	KDTN-Leuven		AV 04
<i>Ficinia angustifolia</i>	Muasya	Cape Peninsula, SA	07/11/2002	AM 2202
<i>Ficinia brevifolia</i>	Muasya	Cape Peninsula, SA	07/11/2002	AM 2205 (BOL, EA, K)
<i>Ficinia bulbosa</i>	Muasya	Calendon, SA	15/11/2002	AM 2243
<i>Ficinia capitella</i>	Muasya	Cape Peninsula, SA	07/11/2002	AM 2206 (BOL, EA, K)
<i>Ficinia distans</i>	Muasya	Calendon, SA	21/11/2002	AM 2283
<i>Ficinia dumensis</i>	Muasya	Calendon, SA	15/11/2002	AM 2242
<i>Ficinia gracilis</i>	Muasya	Swellendam, SA	16/11/2002	AM 2248 (BOL, EA, K)
<i>Ficinia gracilis</i>	Muasya	Kenya		AM 2571
<i>Ficinia minutiflora</i>	Esterhuysen	Calendon, SA	1975	33777 (PRE)
<i>Ficinia minutiflora</i>	Muasya	Calendon, SA	17/11/2002	AM 2257 (BOL, EA, K)
<i>Ficinia nigrescens</i>	Muasya	SA	12/2006	AM 2881
<i>Ficinia polystachya</i>	Muasya	Cape Peninsula, SA	30/11/2002	AM 2320
<i>Ficinia radiata</i>	Muasya	Calendon, SA	17/11/2002	AM 2262 (BOL, EA, K)
<i>Ficinia scandia</i>	Muasya	SA	12/2006	AM 2908

Continued

APPENDIX 1 Continued

Species	Collected by	Localization	Date	Voucher number
<i>Ficinia tristachya</i>	Muasya	Calendon, SA	17/11/2002	AM 2255
<i>Ficinia tristachya</i>	Muasya	Calendon, SA	17/11/2002	AM 2256
<i>Ficinia zeyheri</i>	Muasya	Calendon, SA	17/11/2002	AM 2209 (BOL, EA, K)
<i>Fimbristylis complicata</i>	Muasya	Kenya		AM 2147
<i>Fimbristylis dichotoma</i>	Malombe&AMM	Kenya		Malombe 41
<i>Fimbristylis ferruginea</i>	Muasya	Kenya		AM 2127
<i>Fimbristylis pterigosperma</i>	Harwood	Australia, Northern Territories (NT)		RKH 1163
<i>Fimbristylis tetragona</i>	Harwood	Australia, NT		RKH 1128
<i>Fimbristylis xyridis</i>	Harwood	Australia, NT		RKH 1162
<i>Fuirena abnormalis</i>	Muasya	Kenya		AM 2192
<i>Fuirena ciliaris</i>	Harwood	Australia NT		RKH 1173
<i>Fuirena leptostachya</i>	Muasya	Kenya		AM 2136
<i>Fuirena pubescens</i>	Muasya	Kenya		AM 2149
<i>Hellmuthia membranacea</i>	Bytebier	Cape Peninsula, SA	31/07/05	Bytebier 2645
<i>Hellmuthia membranacea</i>	Muasya	Cape Peninsula, SA	07/2005	AM 2792
<i>Isolepis antarctica</i>	Muasya	Swellendam, SA	16/11/2002	AM 2247 (BOL, EA, K)
<i>Isolepis digitata</i>	Muasya	Calendon, SA	17/11/2002	AM 2258
<i>Isolepis fluitans</i>	Muasya	Kenya	2005	AM 2604
<i>Isolepis fluitans</i>	Muasya	Kenya	2005	AM 2541
<i>Isolepis prolifera</i>	Muasya	Calendon, SA	17/11/2002	AM 2265
<i>Isolepis setacea</i>	Muasya	Kenya		AM 2558 (EA)
<i>Isolepis setacea</i>	Muasya	Kenya	2005	AM 2547
<i>Isolepis setacea</i>	Muasya	SA	12/2006	AM 2540
<i>Kobresia myosaroides</i>	Goetghebeur	University of Gent	2004	PG 10009
<i>Kobresia myosaroides</i>	Reynders	University of Gent, HBUG3003-0642	2006	3003-0642
<i>Kyllinga eximia</i>	Muasya	Kenya		AM 2137
<i>Kyllinga apendiculata</i>	Muasya	Kenya (alpine zone)	2005	AM 2563
<i>Kyllinga bulbosa</i>	Reynders	University of Gent	12/2004	
<i>Kyllinga chlorotropis</i>	Muasya	Kenya	2005	AM 2606
<i>Kyllinga comosipes</i>	Musili	Kenya	2005	MM 001
<i>Kyllinga comosipes</i>	Muasya	Kenya		AM 2119
<i>Kyllinga flava</i>	Muasya	Kenya		AM 2125
<i>Kyllinga flava</i>	Musili	Kenya	2005	MM 009
<i>Kyllinga microbulbosa</i>	Muasya	Kenya	2005	AM 2658
<i>Kyllinga microbulbosa</i>	Mwachala	SA	12/2006	Mwachala 799
<i>Kyllinga monocephala</i>	Reynders	University of Gent		MR 19
<i>Kyllinga nemoralis</i>	M. Reynders	University of Gent, HBUG2006-1237	2008	2006-1237
<i>Kyllinga polyphylla</i>	Reynders	Kenya	12/2004	
<i>Kyllinga vaginata</i>	Caris	Berlin, Germany	02/2002	
<i>Kyllingiella polyphylla</i>	Muasya	Kenya		AM 2123
<i>Kyllingiella polyphylla</i>	Muasya	Kenya		AM 2435
<i>Lepidosperma tetraquetrum</i>	Hodgon/Bruhl	Western Australia	03/10/2003	JH 737
<i>Lipocarpha chinensis</i>	Mwachala	SA	12/2006	Mwachala 873
<i>Lipocarpha isolepis</i>	Muasya	Kenya	12/2006	AM 2748
<i>Lipocarpha leymannii</i>	Muasya	Kenya	12/2006	AM 3132
<i>Lipocarpha nana</i>	Muasya	Kenya		AM 2194
<i>Oxycaryum cubense</i>	Mwachala ea	Kenya		Mwachala 340
<i>Pseudoschoenus sp.</i>	Muasya	SA	12/2006	AM 3061
<i>Pycneus bipartitus</i>	Reynders	University of Gent, HBUG2005-0801(s)	11/2004	
<i>Pycneus flavescens</i>	Reynders	University of Gent, HBUG2005-0401	2008	2005-0401
<i>Pycneus pelophylus</i>	Muasya	Kenya		AM 2139
<i>Pycneus pelophilus</i>	Musili	Kenya	2005	MM 029
<i>Pycneus podophylla</i>	Muasya	Kenya	2005	AM 2139
<i>Pycneus polystachyos spp. holosericeus</i>	Reynders	University of Gent, HBUG2006-1258(w)	07/07	2006-1258
<i>Pycneus pumilus</i>	Muasya	Kenya	2005	AM 2134
<i>Pycneus sanguinolentus</i>	Muasya	Kenya		AM 2157
<i>Pycneus sanguinolentus</i>	Reynders	University of Gent, HBUG2006-1753 (w)	07/07	2006-1753
<i>Queenslandiella hyalina</i>	Muasya	Mombasa (Kenya)		AM 2189
<i>Queenslandiella hyalina</i>	Muasya	Mombasa (Kenya)		AM 2190
<i>Rhynchospora DO150138</i>	Harwood	Australia (NT)		RKH 1127
<i>Rhynchospora cephalotes</i>	MS Samain	Surinam	08/2006	MS2006 018
<i>Rhynchospora nervosa</i>	Reynders	Philippines/HBUG2002-0277	11/2007	2002-0277
<i>Schoenoplectus senegalensis</i>	Malombe-Muasya	Kenya		Malombe 40
<i>Schoenoxiphium leymannii</i>	Malombe	Kenya		KG96
<i>Schoenoxiphium sparteum</i>	Muasya	Kenya	2005	AM 2566
<i>Schoenus melanostachys</i>	Bruhl	North-east Australia	2007	J.J. Bruhl 2447 (NE)

Continued

APPENDIX 1 *Continued*

Species	Collected by	Localization	Date	Voucher number
<i>Schoenus nigricans</i>	AV	Ptk-K.U. Leuven	04/2003	AV 01
<i>Scirpoides holoschoenus</i>	AV	KDTN-Leuven		AV 03
<i>Scirpus sylvaticus</i>	AV	Ptk-K.U. Leuven		AV02
<i>Scleria rugosa</i>	Harwood	Australia (NT)		RKH 1134
<i>Uncinia divaricata</i>	Goetghebeur	University of Gent/New Zealand	10/2001	1998-07771-W
<i>Uncinia divaricata</i>	Goetghebeur	University of Gent	10/2001	PG 9728
<i>Uncinia rubra</i>	Goetghebeur	University of Gent	09/2001	PG 9727

Abbreviations: AV, A. Vrijdaghs; KDTN-Leuven, botanical garden of the town of Leuven, Belgium; Ptk-K. U. Leuven, botanical garden of the Institute of Botany of the K. U. Leuven, Belgium; University of Gent, botanical garden of the University of Ghent, Belgium.

APPENDIX 2

Authorities of cyperoid species and genera mentioned in the text.

Abildgaardia Vahl
Ascolepis Nees ex Steudel
Carex L.
Carex cristatella Britton
Carex pendula Moench.
Cyperus L.
Cyperus alternifolius L.
Cyperus capitatus Poir.
Cyperus congestus Vahl
Cyperus haspan L.
Cyperus laevigatus L.
Cyperus luzulae Rottb. ex Willd.
Dulichium L.C. Richard
Dulichium arundinaceum (L.) Britton
Eleocharis palustris (L.) Roem. & Schult.
Eriophorum latifolium Hoppe
Ficinia brevifolia Nees ex Kunth
Ficinia fascicularis Nees
Fuirena ciliaris (L.) Roxb.
Kyllinga Rottb
Lipocarpha R. Brown
Lipocarpha chinensis Osb.
Lipocarpha nana (A.Rich.) Cherm.
Machaerina anceps (Poir.) Bojer
Mariscus Vahl
Pycneus P.Beauv.
Pycneus polystachyos (Rottb.) P.Beauv.
Pycneus pelophilus (Ridl.) C.B.Clarke
Pycneus pumilus (L.) Nees
Pycneus sanguinolentus Nees
Queenslandiella Domin
Rhynchospora latifolia (Baldwin ex Elliott) W.W.Thomas
Rhynchospora pubera Boeckeler
Schoenus nigricans L.
Scirpoides holoschoenus (L.) Soják
Scirpus falsus C.B. Clarke
Scirpus sylvaticus L.
Torulium Desv.(=*Cyperus*)
Uncinia Pers.
Uncinia rubra Colenso ex Boott
